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The development of an indicator of the condition of sublittoral rock communities (Phase 1): biological correlations with environmental and anthropogenic variables

James Asa Strong and Magnus Johnson

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For further information on JNCC's report series please contact:
Joint Nature Conservation Committee
Monkstone House
City Road
Peterborough PE1 1JY
https://jncc.gov.uk/

Communications@jncc.gov.uk

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Summary

This report is capturing the work relating to the Phase 1 development of the sublittoral rock indicator, which took place in 2017.

This analysis seeks to advance the development and testing of a condition indicator (composite of multiple indicator species) for sublittoral rock communities. Threshold Indicator Taxa ANalysis (TITAN) was undertaken in R (TITAN2 package) to facilitate the detection of community change along a gradient of anthropogenic pressure (assumed here to be resuspension from the use of bottom-contacting fishing gear) and the identification of indicator species. The TITAN identifies 'change points' along the resuspension gradient that corresponds to the greatest changes within the community. The analysis then assesses the abundance of each species on either side of the change point. Finally, the analysis estimates the value of each species to be used as an indicator of the communities on either side of the change point, and subsequently of community change.

The TITANs successfully identified indicator species/groups for bedrock, boulder, cobble and high turbidity mixed rock habitats. The species/groups identified included those that increase in abundance along a gradient of anthropogenic resuspension (positive responders) and those that decline with increasing anthropogenic resuspension (negative responders). Validation examined the ability of the suite of indicators associated with each data set to predict whether a group of observations was drawn from above or below the change points identified by the TITAN.

The TITAN is able also to report the threshold at which the majority of the positively responding species increase in abundance along the gradient of anthropogenic resuspension and the threshold at which the majority of the negatively responding species decrease in abundance along the same gradient. This process, therefore, identifies a positive and negative change point. The change points identified by the TITAN indicates that relatively low levels of anthropogenic resuspension caused a community change and that this is especially the case in bedrock habitats. The levels at which species/groups respond positively to anthropogenic resuspension is much higher than the negative change points.

The TITAN results indicated high levels (>80%) of predictive accuracy, for whether sites are above or below the change point (for anthropogenic resuspension), for high turbidity and bedrock habitats, moderate accuracy (>70%) for boulder habitats and low for cobble habitats (>60%) based on the positively and negatively responding species/groups identified.

The indicator species identified by the TITAN analysis were able to predict whether observations were from above or below the change point for anthropogenic resuspension. However, the gradient of anthropogenic resuspension was unable to explain much of the total community variation, i.e. anthropogenic resuspension was not driving much of the change observed within the dataset. Canonical Redundancy Analysis (RDA) of the complete data set states that the explanatory variables included in the analysis only account for 20% of the biological variance. The most important explanatory variables include latitude and longitude (capturing the spatial autocorrelation that exists within the observations), substratum quantity and type, biozone (depth bands) and natural surface turbidity. As such, it is likely that anthropogenic resuspension only explains a very small amount of biological change for all rock substrata. This finding may mean that the method used to represent anthropogenic resuspension was not reflective of the pressure or that the amount of community change/variance from this pressure is very small. It is important to remember the small effect size of the anthropogenic resuspension gradient on biological variance when applying the indicator, i.e. although the indicator can predict community differences above

and below a change point induced by anthropogenic resuspension, this change is relatively insignificant when the total variance is considered.

The inclusion of ecological variables of known ecological relevance, such as depth, temperature, and substratum composition would normally account for a larger proportion of the biological variance. This, therefore, indicates that a large proportion of this variance is associated with the way the data has been collected, structured, and processed rather than being associated with ecological trends that cannot be explained by the included environmental and anthropogenic variables. The unexplained variance might be related to:

1) use of the SACFOR scale for recoding abundance during survey observations;
2) the combined use of species, genus, families and morphological groupings within the community matrices;
3) poor sampling efficiency for small and cryptic species in the video footage when compared with large-bodied or high coverage species that are probably sampled well;
4) use of different contractors to enumerate survey footage;
5) use of semi-quantitative survey methods;
6) being unable to standardise the field of view (and subsequent estimates of abundance) within and between stations and sites;
7) bias and structures introduced into the data through the conversion of the SACFOR scale to logged abundances; and
8) errors introduced due to the scale of the aggregated grids of fishing abrasion layers.

It may not be possible to account for the variance introduced by the points above fully. Should the analysis be repeated, it is recommended that (i) only the species/groups that are known to be sampled with certainty are included, e.g. sponge morphologies, large-bodied species, and high-cover, common species, (ii) a greater proportion of the rare species are removed from the data sets, (iii) more species are aggregated to a higher taxonomic level, and (iv) more of the low quantity rock observations are removed (due to the limited sample size, this analysis only removed observations with less than 10 % rock cover).

Glossary

ANOSIM	Analysis of similarities
CCA	Canonical correspondence analysis
GES	Good Environmental Status
IOP	Inherent Optical Properties
MANOVA	Multivariate analysis of variance
MDS	Multidimensional Scaling
MNCR	Marine Nature Conservation Review
MSFD	Marine Strategy Framework Directive
PCA	Principle Components Analysis
POC	Particulate Organic Matter
RDA	Canonical redundancy analysis
SACFOR(N)	SACFOR(N) scale (Superabundance, Abundance, Common, Frequent, Occasional, Rare, Not present/Absent)
SA	Surface Abrasion
SBA	Sub-surface abrasion
SCI	Site of Conservation Interest
TITAN	Threshold Indicator Taxa Analysis (R package)
VMS	Vessel Monitoring System

Contents

1 Introduction

1.1 Policy context

The Marine Strategy Framework Directive (MSFD) (2008/56/EC) was formally adopted by the European Union in July 2008. It outlines a transparent, legislative framework for an ecosystem-based approach to the management of human activities that supports the sustainable use of marine goods and services. The overarching goal of the Directive is to achieve 'Good Environmental Status' (GES) by 2020 across the marine environment of Europe. GES will ultimately be determined at the level of the marine region or sub-region[1] by a set of qualitative 'descriptors' that are provided in Annex I of the Directive. The Commission Decision (2010/477/EU) provides further guidance on the criteria and indicators for each descriptor for which Member States must develop suitable operational targets and indicators to measure progress for achieving GES.

1.2 Development of indicators

The MSFD required the UK to (i) undertake an initial assessment of its marine waters, (ii) determine the characteristics of GES, and (iii) identify targets and indicators that will contribute to the assessment of GES by 2012. This was submitted to the European Commission (EC) in 2012 as Part One of the UK Marine Strategy (Defra 2012). The Commission Decision (2010/477/EU) was used as a basis for structuring the targets and indicators required. As such, indicators of condition are required for benthic habitats. Indicators for soft substratum habitats are relatively abundant and established. Conversely, there are practically no existing indicators of condition for sublittoral rock habitats. The development of indicators for sublittoral rock has been hampered by the reliance on remote and indirect sampling, such as photography and videography, and the greater focus on sedimentary habitats for the assessment of anthropogenic impacts.

The Joint Nature Conservation Committee (JNCC) wish to develop an indicator of condition for sublittoral rock habitats. Initial work by Haynes *et al.* (2014) assessed the feasibility of an indicator to measure shallow sublittoral rock condition and subsequently proposed four possible methods, namely:

i) Sublittoral species composition and abundance of fragile sponge and anthozoan assemblages.
ii) Morphological diversity of sponge assemblages plus anthozoan species composition and abundance.
iii) Morphological diversity of sponge assemblages plus presence/absence of anthozoan indicator species.
iv) Presence/absence of sponge and anthozoan indicator species.

Haynes *et al.* (2014) also stated that a lack of information about the variation in Porifera and Anthozoa assemblages, caused by natural variation, was hampering our understanding of anthropogenic responses and consequently the development of a condition indicator.

Initial analysis of Solan Bank Reef SCI by Barrio-Frojàn (2016) examined the relationship between biotic patterns and environmental variables and the sensitivity of reduced biotic

[1] The Directive establishes four European Marine Regions (Article 4), based on geographical and environmental criteria. The North East Atlantic Marine Region is divided into four sub-regions, with UK waters lying in two of these (the Greater North Sea and the Celtic Seas).

datasets. This analysis was hindered by (i) the analysis of information from just one site, and (ii) the use of presence/absence information. Understanding natural variability and the detection of anthropogenic signals may only be possible across a larger range of environmental conditions.

This analysis seeks to advance the development and testing of a condition indicator (composite of multiple indicator species) for sublittoral rock communities. The analysis did not limit itself to just 'sponge and anthozoan' but included all of the species encountered during survey work on sublittoral rock. The sponges were represented by morphological classes rather than taxonomic groups due to the difficulties of sponge identification from video footage. All other species were represented according to their taxonomic classification.

Ultimately, if this indicator is to be operationalised, its response must be (i) specific to anthropogenic pressures, (ii) sensitive to changes in pressure, (iii) generate a consistent 'response' between sites, and across the region or sub-region, and over time, and (iv) be simple, pragmatic and cost-effective to use. This analysis has been structured to address these components. Furthermore, to understand the influence of natural variability, this analysis is broader and includes information from eight surveys at seven sites. Biological abundance information has also been maintained within the analysis and therefore better reflects the initial concept for the indicator and actual community changes observed between sites, i.e. this analysis is not based just on analyses using presence/absence information.

1.3 Aims and Objectives

To develop an indicator of condition for sublittoral rock habitats, the individual objectives, listed below, were addressed:

- Collate environmental and anthropogenic information to support the analysis of the biotic dataset.
- Assess community variation between sites, substrata and other environmental zones.
- Understand the influence of abiotic (natural and anthropogenic) factors on community composition.
- Identify indicator species/morphologies that correlate with aspects of habitat condition (indicator development) using spatial regression methods.
- Examine methods for extrapolating the indicator results within the relevant region.

1.4 Rationale for analysis pathway

The objective of the analysis was to identify potential metrics or indicators to assess the condition of sublittoral rock. It was assumed that none of the anthropogenic pressures could change the condition of the physical habitat (i.e. rock substratum could not be lost). Therefore, any changes in condition were assumed to be associated with the biological community. Physical disturbance on the substratum such as boulder and cobble turning may be occurring, but again, this was assumed to be detected through changes in the species present.

Although there are several anthropogenic driven pressures which could cause potential damage to sublittoral rock benthic communities, the most widespread pressure was assumed to be the re-suspension/siltation of sediment from mobile bottom-contact fishing gears. Therefore, this activity was selected for the initial testing analysis of the indicator method. Given the risk of fouling mobile gear, it is unlikely that fishing occurs directly on top of rock habitat, as such, direct, physical abrasion is unlikely to be a significant pressure for rock communities. A notable exception occurs in some areas caused by accidental damage by mobile gears and abrasion from static pots. It is accepted that accidental damage from towed gear does occur, although this activity is fairly rare. The use of pots has anecdotally been found to have a negative impact on fragile epifaunal communities (e.g. *Eunicella* sp.) at Skomer Marine Nature Reserve. In this instance, it is the abrasion of ropes and pots as they scrape past communities on vertical/steep rock faces that cause the most damage. However, most of the sites examined in this analysis do not overlap with significant amounts of potting activity as many are located further north and offshore.

In deep-water areas, and especially below the wave base, fishing activity is typically the most widespread mechanism for the resuspension of sediments (Churchill, 1989). It is also noteworthy that other recent activities, such as drilling for oil/gas, are currently increasing in deeper environments (i.e. not on the continental shelf) and may also represent significant sources of anthropogenic resuspension.

To capture the zone affected by resuspension from mobile fishing, this project combined information from the (i) fishing activity, as swept area ratio, which is derived from fisheries Vessel Monitoring System (VMS), (ii) map of seabed sediment type; and (iii) substratum-specific resuspension coefficients from Churchill (1989). The resulting surface was diffused to represent the dispersal of sediments, generating anthropogenic resuspension from mobile fishing maps (this information was taken as the main pressure gradient across all eight sites).

The objective of the analysis was to find indicators of condition, where condition is taken to be the response of a habitat (and in this case the biological component) to a pressure. As such, the analysis looked for evidence of substantial and significant community change between areas of differing pressure. To ensure that measurable changes in the community area were mainly driven by changes in the pressure gradient, the main dataset was stratified to reduce or eliminate the influence of other local and regional explanatory variables such as depth, rock type, and turbidity. Although the main pressure gradient (anthropogenic resuspension) was not directly sampled, the number and range of sites surveyed provide a representative sample of the pressure typically present in sublittoral rock habitats.

To facilitate the detection of community change along the resuspension gradient and the identification of indicator species, ‘Threshold Indicator Taxa ANalysis’ (TITAN) was undertaken in R (TITAN2 package) using anthropogenic resuspension from mobile bottom fishing gear as the environmental gradient. Existing methods for identifying ecological community thresholds are designed for univariate indicators or multivariate dimension-reduction of community structure. Most are insensitive to responses of individual taxa with low occurrence frequencies or highly variable abundances, properties of the majority of taxa in community data sets (Baker & King 2010). The advantage of using TITAN is that it detects changes in taxa distributions along an environmental gradient (anthropogenic resuspension in this case) over space or time, and assess synchrony among taxa change points as evidence for community thresholds (Baker & King 2010).TITAN was used to assess the abundance of each species on either side of the change point and estimate the value of each species to be used as an indicator of the communities and potential community change in response to the environmental gradient. This was assessed through the calculation of various indices that are explained in Section 3. Additional values were integrated into an overall estimate of ‘indicator quality’, including the commonality of the species abundance, and body size (how easy is it to detect in a photographic still or video segment). The information from TITAN and additional values were then collated and used to select the best indicator species.

1.5 The use of sponge morphology within ecological assessments

Due to their difficult taxonomic identification, sponges are often overlooked or excluded when monitoring hard substrate ecosystems (Bell 2008). Sponges are key components within benthic systems. They support infaunal assemblages, both epi- and endo-bionts (Avila & Ortega-Bastida 2015). The use of morphology diversity as a tool for monitoring sponge diversity has been found to correlate well with species diversity data (Bell 2007; Berman *et al.* 2013). Opinions differ on the exact number of distinct sponge morphologies, but the consensus appears to be 9 to 10 morphology types. However, due to dynamic morphology of sponges (Bell & Barnes 2000; Bell 2007; Avila & Ortega-Bastida 2015), the use of morphological classes need to take into account the environmental factors that can govern sponge morphology and their functional roles in an ecosystem.

Three main factors can affect morphology in sponges:

(i) Depth: Upright and massive sponges often have lower coverage at shallower depths (1 – 20 m) compared with deeper areas, however the coverage of encrusting sponges does not correlate with depth gradients (Ginn *et al*. 2000). Temperature, dissolved oxygen, and salinity often covary with depth, and morphological adaptations can often be attributed to one of these factors. Morphologies within a species have also been demonstrated to be dynamic with regards to depth, although this has been attributed to other factors that coincide with deeper water; less exposure and water velocity and thus increased sedimentation (Bell & Barnes 2000).

(ii) Wave exposure/water flow rate: These are influential factors for sponge morphology in shallower areas. Sponges with a small basal area to volume ratio tend to be absent from high exposure areas, with such areas dominated by encrusting and massive morphologies that typically have increased basal area compared with their height (Bell & Barnes 2000; Bell *et al*. 2002). Sponges are capable of orientating themselves into the direction of a current. Upright sponges often orient themselves perpendicular to the current, whereas encrusting species orient parallel to the current flow in most cases. The strength of this orientation is further modified by the current speed and depth (Ginn *et al*. 2000). Flow speed can also affect the density of upright or branching sponges, speeds greater than 75 cm/s have a detrimental effect on upright morphology types. The less secure, small basal area of upright sponges can lead to dislodgement due to flow/exposure rate when the sponge reaches a specific height (Ginn *et al.* 2000; Bell *et al*. 2002; Bell 2004).

(iii) Sedimentation: The morphology of a sponge and its ability to morphologically adapt to sedimentation can determine its susceptibility to sedimentation. It can suppress sponge growth rates, cause necrosis, impact the ability of sponges to settle onto hard substrates and ultimately result in mortality (Pineda *et al.* 2016). Inclined and vertical surfaces can be advantageous for upright morphologies whereas no preference for a rock type is shown by encrusting sponges (Ginn *et al.* 2000). Cup sponges show a low tolerance, expressed as a high percentage of necrosis, whereas upright sponges are not as susceptible due to their low surface area (Pineda *et al.* 2016). Upright sponges can be found in areas of high sedimentation (typically low energy areas) as their morphology allows them to grow above the sedimentation effects and low surface area prevents clogging of the organism (Bell *et al.* 2002; Pineda *et al.* 2016). Fast initial growth rates of settling sponges also indicate a strategy for growing beyond the influence of sedimentation (Bell 2002).

Sedimentation has been demonstrated to reduce biomass of sponges, predominantly due to energy expenditure for sediments removal, reduced flow rate due to inhalant clogging and reduced feeding capacity (Bell *et al.* 2015; Pineda *et al.* 2016). There are passive and active mechanisms for adapting to sedimentation in sponges. Passive mechanisms include protruding spicule rims and palisades to prevent inhalant clogging, and also the location of the inhalant pores on the underside of the sponge (tubular/ wine glass shape). Active mechanisms include

(i) newly settled sponges being able to crawl away from high sedimentation areas;

(ii) mucous layers that can be shed once loaded with sediment; and

(iii) reversing water flow to force sediment out of the sponge (Bell 2004). Tubular sponge types have shown adaptations for sediment removal, inhalants located on the underside prevent clogging and the oscular position can ensure that the expelled jet forces sediment away from the sponge to prevent settling. This is an energy efficient adaptation as the sponge needs to expel water to feed (Bell 2004). The diameter of the oscula and its orientation can determine the effectiveness of this adaptation.

Overall, there is a lack of consensus about the representativeness of all sponge morphologies for specific environmental conditions. This analysis has made no assumptions about indicator polarity or quality of specific morphologies for reflecting the condition of sublittoral rock. Morphologies here have been included as a more certain method for grouping sponge species together for objective, statistical analysis with TITAN.

2 Methods

2.1 Study sites and data sources

Drop down camera observations from eight site surveys were used (Table 1). These sites represented a cross-section of sublittoral rock habitats (dominated by bedrock, boulder, cobble, and pebble) and included shallow and deep habitats from around the coastline of the UK (Figure 1).

Table 1. Data source and composition for each of the eight site surveys.

Site name	Survey name and year of survey	Useable observations	MSFD Region
Pobie Bank Reef cSAC/SCI	RV Scotia 1013S 2013	345	Greater North Sea
Haig Fras cSAC/SCI “infill”	CEND 10/12, 2012	55	Celtic Seas
Wight-Barfleur Extension rMCZ	CEND 0312 2012	2063	Greater North Sea
Haig Fras SAC	CEND 0915 2015	1824	Celtic Seas
East of Haig Fras MCZ	CEND 0915 2015	939	Celtic Seas
Wyville Thomson Ridge cSAC/SCI	Wyville Thomson Ridge SCI and Faroe-Shetland Sponge Belt Scottish NCMPA Proposal 1512S 2012	373	Celtic Seas
Faroe-Shetland Sponge Belt Scottish NCMPA	Wyville Thomson Ridge SCI and Faroe-Shetland Sponge Belt Scottish NCMPA Proposal 1512S 2012	200	Celtic Seas
Solan Bank Reef cSAC/SCI	Solan Bank 1714S 2014	1053	Celtic Seas

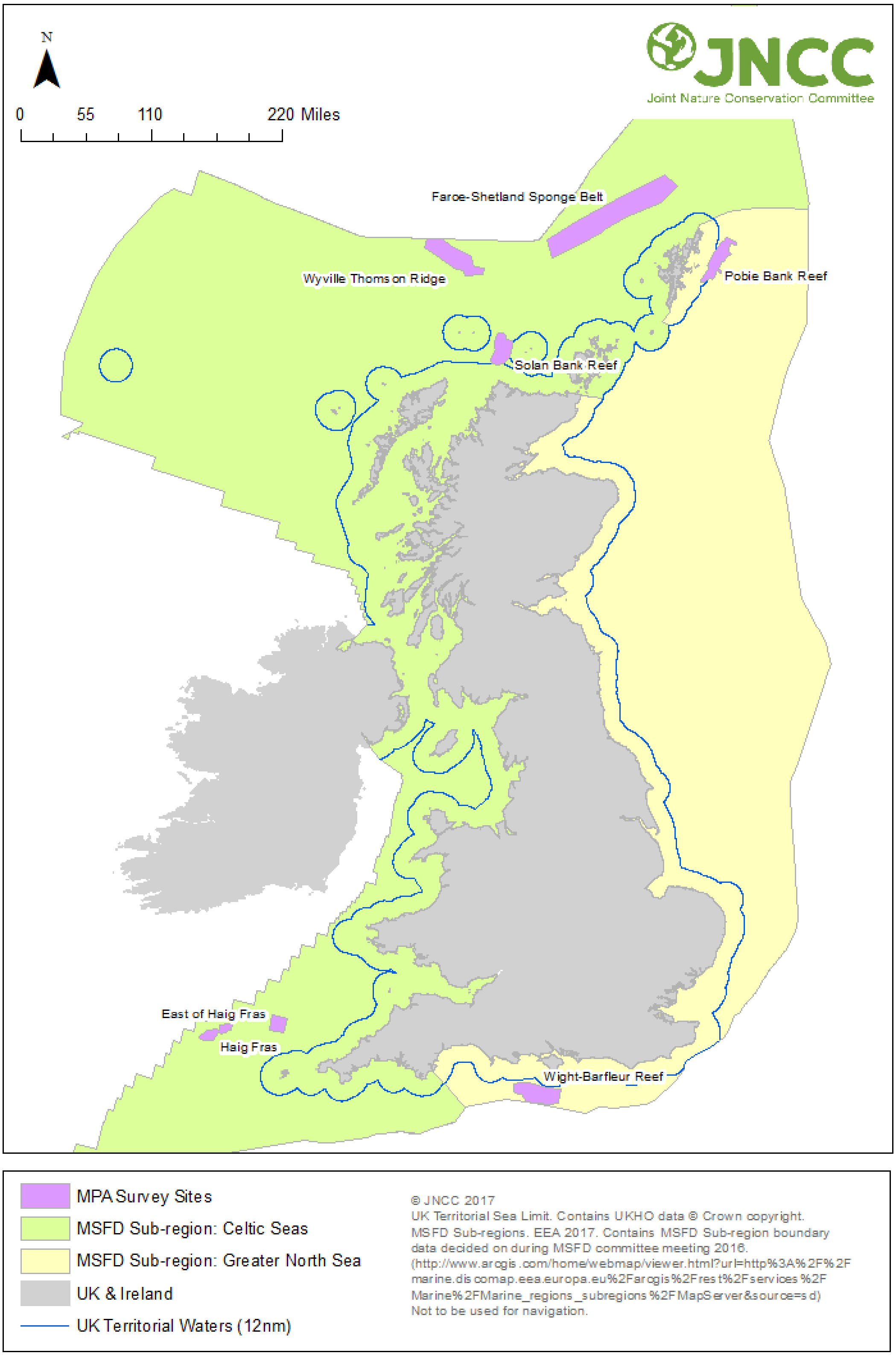

Figure 1. Location of the seven MPA sites used for the development of the indicator of rock condition.

2.2 Data processing

Survey data from the eight site surveys were merged into one ‘species matrix’. All taxa and sponge morphological groups (Berman *et al.* 2013) were included in the merger. Sponges were represented as morphological groups rather than their taxonomic identifier. Where different taxonomic levels and labels had been used for many of the species and groups, taxa were merged into a higher, unifying taxonomic identifiers to improve the consistency between sites for these species. For example records for (i) *Caryophyllia smithii* (ii) *Caryophyllia* sp., and (iii) *Caryophyllia*, were merged into ‘*Caryophyllia*’. Taxonomic entries higher than a family were removed from the matrix, e.g. ‘Porifera’ (when recorded without a morphology). The sponge morphologies ‘globular’ and ‘massive’ were kept separate as they had been recorded individually at each of the eight sites.

Observations were removed from the species matrix if:

1) The observation lacked substratum information (% cover) or a position.
2) The observation was not derived from a drop-down photographic still (i.e. an observation from a video tow).
3) The image quality flags were ‘very poor’ or ‘inadequate.'

Assumptions associated with data processing were made. Photographic stills collected with drop-down cameras tend to have varying fields of view. The size for field of view was provided for one site only. In the absence of this information for all sites, it has been assumed that observations were comparable across all sites. Equally, abundances were typically corrected for the area (field of view), and further correction was not necessary.

2.2.1 The conversion and aggregation of SACFOR

The conversion of semi-quantitative observations to presence/absence removes a substantial amount of information from a data set and makes any analysis of the community composition and structure very limited, if not impossible. As such, the SACFOR scale (see below) used to record the cover or counts of species was converted into a quantitative scale (Table 2).

The Marine Nature Conservation Review (MNCR) cover and density scales adopted from 1990 (SACFOR) provide a unified system for recording the abundance of marine benthic flora and fauna in biological surveys (Table 2). It is now established as one of the main methods of recording marine biological information during intertidal and subtidal surveys. The semi-quantitative scale has proven useful for indirect surveys (observations via video or still photography), large sample sizes where complete enumeration in not practicable, and challenging survey operations such as scuba diving. The main issues to note are: (i) the counts scale increases by a factor of 10 and the cover scale increases by a factor of 2 between classes, (ii) the counts scale is shifted according to body/colony size, and (iii) the cover scale is shifted according to ‘growth form’.

Table 2. The Marine Nature Conservation Review SACFOR scale for the estimation of littoral and sublittoral cover and abundance (1990 onwards). SACFOR classes are: S = Superabundant, A = Abundant, C = Common, F = Frequent, O = Occasional, and R = Rare.

Cover			**Counts**				
	Growth form			**Size of individuals/colonies**			
Percentage cover	**Crust/ meadow**	**Massive/ Turf**	**Density**	**<1cm**	**1-3 cm**	**3-15 cm**	**>15 cm**
>80%	S	-	>10,000 / m^2	S	-	-	-
40-79%	A	S	1000-9999 / m^2	A	S	-	-
20-39%	C	A	100-999 / m^2	C	A	S	-
10-19%	F	C	10-99 / m^2	F	C	A	S
5-9%	O	F	1-9 / m^2	O	F	C	A
1-5% or density	R	O	1-9 / $10m^2$	R	O	F	C
<1% or density	-	R	1-9 / 100 m^2	-	R	O	F
-	-	-	1-9 / 1000 m^2	-	-	R	O
-	-	-	<1 / 1000 m^2	-	-	-	R

2.2.1.1 Conversion of ordinal information into log-transformed quantitative information

The following process was used to convert SACFOR classes into a logged, abundance scale. This process was complicated by the recording of cover and counts, as well as differing body sizes and growth forms (see Box 1). The processing of SACFOR information was as follows:

1) All taxa and morphologies were attributed according to whether they were assessed by the ‘cover’ or ‘counts’ scale.
2) For counts, all taxa and morphologies were attributed with typical body size (SACFOR size classes – Table 2).
3) For those assessed using percentage cover, taxa and morphological groups were allocated to either ‘crust/meadow’ or ‘massive/turf'. This was typically annotated within the survey data or estimated using biological information for each species collated in the MarLIN database[2].
4) For cover, the processing steps were:
    a. All percentage cover classes for ‘massive/turf’ and ‘crust/meadow’ were converted to the mid-range cover values (e.g. 60% for the ‘40-79%’) in Table 3.
    b. Mid-range percentage values were then summed for cover taxa that required merging. This would not be possible using the SACFOR classes (e.g. do two rare encrusting sponges equal an ‘occasional’ class?).
    c. The mid-cover values were then log transformed to base 2 (because the SACFOR ‘cover’ scale doubles between classes).
5) For counts, the processing steps were:
    a. All counts were converted to the abundance value in Table 3. The abundance value is merely an arbitrary, intermediate scale, used during the conversion process. Count and cover scales increase by factors of 10 and 2

[2] http://www.marlin.ac.uk/

respectively (i.e. cover doubles between classes and counts increase by an order of magnitude between classes). To align the resulting log-transformed values for counts and cover (i.e. to avoid over-representation of taxa or morphologies based on which method was used to quantify them), the log-transformed (base 10) abundance values were scaled to the results in the abundance value shown in Table 3.

b. All abundance values were scaled according to body size.
c. Abundance values were summed for counts for taxa that required merging.
d. The abundance values for the counts were logged to base 10 (because the SACFOR scale increases by a factor of 10 between classes for species assessed by their cover).

The 'abundance values' used for the conversion of counts was established following careful alignment of the logged cover (base 2) and logged count (base 10) values. Table 3 shows that after logging, the transformed values for counts and cover fall within the same range of values, and the entire range has a similar mean. This ultimately means that regardless of the unit of measurement (count or cover), the resulting logged values are comparable. The final values from this process were cover and counts observations that are ultimately (i) adjusted to account for body size, (ii) merged with similar taxonomic/morphological entries, (iii) numerically aligned to prevent skew between those measured with counts and those as a cover, and (iv) log transformed.

Table 3. Conversion table for SACFOR to cover and abundance. SACFOR classes are: S = Superabundant, A = Abundant, C = Common, F = Frequent, O = Occasional, and R = Rare.

SACFOR	**Percentage cover (Growth form: crust/ meadow)**	**Mid-range cover value (%)**	**Log (base 2)**	**Counts (Size of individual: 3-15 cm)**	**Abundance value / 0.01 km²**	**Log (base 10)**
S	>80%	90	6.49	100-999 / m²	7,500,000	6.88
A	40-79%	60	5.91	10-99 / m²	750000	5.88
C	20-39%	30	4.91	1-9 / m²	75000	4.88
F	10-19%	15	3.91	1-9 / 10m²	7500	3.88
O	5-9%	7.5	2.91	1-9 / 100 m²	750	2.88
R	1-5% or density	3.5	1.81	1-9 / 1000 m²	75	1.88
Sum			25.93			26.25
Mean			4.32			4.38

2.2.2 The attribution of survey observations with environmental variables

Survey observations were supplied with the following local, environmental attributes:

- Substratum composition (split by bedrock, boulder, cobble, pebble, sand, shell, maerl, mud, artificial surfaces, and biogenic reef).
- Latitude and longitude.
- Depth.
- EUNIS and MNCR classes (not used in the analysis).
- Survey metadata (date, site, station, sample code, surveyor, and visual quality of the observation).

2.2.2.1 Derived environmental variables from the survey observations

Two additional environmental variables were derived from the percentage cover of substratum classes (e.g. ‘bedrock’, ‘cobble’ and ‘sand’) recorded within each image. The first variable attributed the primary source of rock substratum, e.g. bedrock, boulder, cobble or pebble. Due to inconsistencies in the use of the boulder classes between surveys, all boulder size classes were merged into one boulder class. The second captured the total area of sublittoral rock within an observation. However, the proportion of pebbles, cobbles, and boulders that equate to “rock” is dependent on the presence of fragile, robust and encrusting epibiota – see Table 4. The following two sections below describe the calculation of sublittoral rock and its subsequent categorisation into three bands.

The quantity of sublittoral rock

To determine the area of sublittoral rock, all of the species within the matrix were classified as being either ‘fragile’, ‘robust erect’ or ‘other’ using expert judgement and information from the scientific literature. The presence of fragile, robust and ‘other’ species was summarised for each observation. Then, the following rules were followed to calculate the percentage of rock within each observation:

- If ‘fragile’ species/morphologies were present within an observation, the area of bedrock, boulder, cobble, and pebble were summed to calculate the total area of sublittoral rock.
- If ‘fragile’ species were absent, but ‘robust erect’ species were present, the area of bedrock, boulder, and cobble were summed to calculate the total area of sublittoral rock.
- For all other observations, the area of bedrock and boulder were summed to calculate the total area of sublittoral rock.

Table 4. Summary definition of rock and sediment substrata for the purpose of habitat assignment (adapted from Connor 2009 and taken from Parry 2015).

Wentworth category	Boulder (and bedrock)	Cobble	Pebble	Granule	Very coarse sand - Very fine sand	Silt & Clay
Folk category	Gravel				Sand	Mud
Particle size (mm)	>256	64 - 256	4-64	2-4	0.125 - 2	<0.063
Stability ↑ Scour ↓	Can support fragile epibiota	Rock	Rock	Sediment	Sediment	Sediment
	Can support robust erect epibiota	Rock	Sediment	Sediment	Sediment	Sediment
	Can support crusts/shelled epibiota	Sediment	Sediment	Sediment	Sediment	Sediment
	Cannot support epibiota	Sediment	Sediment	Sediment	Sediment	Sediment

Bands of quantity for sublittoral rock

The processing steps above provided a single value for the amount of sublittoral rock present in each observation. To assist in the stratification of the data, the 'quantity of sublittoral rock' was also categorised into one of four classes. These quantity categories were:

- High sublittoral rock quantity included observations with between 71 - 100% rock cover.
- Medium sublittoral rock quantity included observations with between 41 - 70% rock cover.
- Low sublittoral rock quantity included observations with between 11 - 40% rock cover.
- No sublittoral rock included observations with 10% or less rock cover.

Observations classified as having no rock were removed from the main data set and excluded from further analysis.

2.2.2.2 Attribution of survey observations with additional environmental and anthropogenic variables

Additional environmental and anthropogenic variables were sourced for each of the eight site surveys (Table 5). Bathymetry and habitat maps for individual sites were not provided with the survey observations. The regional Astrium bathymetry dataset has been provided by JNCC to provide full coverage depth information for each site. This included variables to capture:

(i) the topography and composition of the rock habitats,
(ii) the environmental conditions at the sites such as temperature, current speed and natural surface turbidity (remotely sensed, total back scatter), and
(iii) anthropogenic pressure (smothering caused by resuspension was assumed to the primary and only significant pressure – the calculation of this variable is provided below).

The ArcMap 'multivalues to points' tool was used to attribute each observation with the remaining environmental variables listed in Table 5. Based on an initial examination of the environmental information, the following processing steps were undertaken:

- The predicted biozone labels were recoded to 1 (shallow) for infralittoral, circalittoral and deep circalittoral and 2 (deep) for the upper slope and upper bathyal.
- Modelled currents from the Atlantic- European North West Shelf- Ocean Physics Reanalysis Model were converted from a northern and easting to a vector (square root (x2 + y2)) and the magnitude used as a predictor variable. This processing combined the two separate tidal components (easting and northing) into one value expressing overall tidal current speed.

Table 5. Information sources used as explanatory variables for the analyses.

Predictor variables	**Continuous or categorical**	**Comment**	**Data source (Local/regional variable)**
Site	Categorical	Abbreviation of survey name generating eight classes	Local survey report
Year	Categorical	Year of observation	Local survey report
Latitude	Continuous	Latitude of observation	Each observation
Longitude	Continuous	Longitude of observation	Each observation
Substratum composition	Continuous	Contribution of bedrock, boulder, cobble, pebble, gravel, shell, maerl, mud and biogenic reef to substratum composition (0-100%)	Local survey data
Rock quantity	Categorical	Classes of sublittoral rock cover (high, medium, low)	Derived from local survey data
Rock type	Categorical	Primary rock type (bedrock, boulder, cobble, pebble)	Derived from local survey data
Depth	Continuous	Depth (m)	Regional model output: Astrium (1 and 6 arcsecond)
Slope	Continuous	Derived from bathymetry (percent rise)	Regional model output: Astrium (1 and 6 arcseconds)
Aspect	Continuous	Derived from bathymetry (360 degrees)	Regional model output: Astrium (1 and 6 arcseconds)
Rugosity	Continuous	Derived from bathymetry (arc-chord ratio)	Regional model output: Astrium (1 and 6 arcseconds)
Curvature	Continuous	Derived from bathymetry[3]	Regional model output: Astrium (1 and 6 arcseconds)
Current speeds	Continuous	Northing and easting surface and seabed velocity ($m\ s^{-1}$) converted to a vector and the magnitude used.	Atlantic - European North West Shelf- Ocean Physics Reanalysis (7 km grid) from Met office (1985-2014) - CMEMS
Mixing	Continuous	Water column mixing	EMODnet Seabed Habitats Portal (accessed 2015) - regional data
Substratum	Categorical	Substratum (modified Folk classes)	EMODnet Geology Portal > IECS in-house production of 1:1m & 1:250k composite[4]
Sea temperature	Continuous	Annual average temperature at the seabed (kelvin)	Atlantic - European North West Shelf - Ocean Physics Analysis and Forecast numerical-model (7 km grid) - CMEMS
Salinity	Continuous	Annual average salinity at the seabed (unitless)	Atlantic - European North West Shelf - Ocean Physics Analysis and Forecast numerical-model (7 km grid) - CMEMS
Depth	Categorical	Salinity zones (oligo, meso, poly and eu-haline)	EMODnet regional seabed habitats portal

[3] http://desktop.arcgis.com/en/arcmap/10.3/manage-data/raster-and-images/curvature-function.htm
[4] 1:1m used to fill shallow coastal strip not covered by the 1:250k surface.

Predictor variables	Continuous or categorical	Comment	Data source (Local/regional variable)
Distance to coast	Continuous	Straight-line distance to coast (km)	IECS
Biozone	Categorical	Biozones from observations and models (various classes – see link[5])	EMODnet Seabed Habitats Portal (accessed Jan 2017) - regional data
Kinetic energy due to waves (Atlantic, Mediterranean)	Categorical	Predicted energy zone (low, moderate and high classes – see link[5])	EMODnet Seabed Habitats Portal (accessed Jan 2017) - regional data
Habitat	Categorical	Predicted ENUIS Level 4 habitats	EMODnet Seabed Habitats portal (accessed Jan 2017) - regional data
Total backscatter at 443 nm	Continuous	Aqua MODIS - whole mission turbidity composite and absorption due to gelbstoff and detrital material at 443 nm (GIOP model at ~4 km resolution)	Ocean Color Web (accessed Jan 2017) - regional data
Particulate Organic Matter	Continuous	POC in mg m^{-3} (~4 km resolution)	Aqua MODIS (total mission composite) - Ocean Color Web (accessed Jan 2017) - regional data
Anthropogenic resuspension for 2009 – 2015	Continuous	Derived from VMS fishing pressure and surface/sub-surface abrasion, substratum, and literature values (Churchill, 1989) (0.05 × 0.05 degree grid c-square format)	JNCC provided the regional VMS data, surficial sediments from EMODnet and resuspension was an in-house production

2.2.2.3 The estimation of anthropogenic resuspension

Anthropogenic resuspension was assumed to be the primary anthropogenic pressure acting upon sublittoral rock communities. To estimate this pressure, surface and sub-surface abrasion (derived from VMS data provided by JNCC) were combined with the classified substratum map of surficial sediments and resuspension coefficients from the scientific literature, to estimate the magnitude of resuspension. This approach scales the likely resuspension according to the type of seabed present, e.g. resuspension from fishing will be greater on mud than on coarse sand. The weighting associated with each substratum type was based on the resuspension rate coefficients in Churchill (1989). These ranged from 0 for rock to 133 for mud. Each substratum class within the substratum layer was attributed with a resuspension coefficient. It should be noted that surface and sub-surface abrasion are calculated in grid of 0.05°. Due to the data limitations of VMS, a homogenous distribution of fishing intensity within is assumed, which will create a degree of error on the spatial distribution of siltation pressures.

The specific steps used to create the anthropogenic resuspension layers are as follows. For each substratum type (Figure 2a), the ArcGIS Raster Calculator was used to multiply the coefficient of resuspension by (i) swept area ratio for surface abrasion and (ii) swept area ratio for subsurface abrasion (Figure 2b). These calculations scaled the surface and sub-surface abrasion by the likelihood of resuspension. Suspended sediments are dispersed by currents; literature values suggest that the radius of dispersal can be up to 200 - 500 m (Durrieu de Madron *et al.* 2005). The ArcGIS Focal Statistics tool was used to average the

[5] http://www.emodnet.eu/seabed-habitats

gridded resuspension values over a radius of 500 m (1000 m diameter) and thereby represent the dispersal of this material. This process was repeated for each year between 2011 to 2015, i.e. producing five annual layers for surface abrasion and five for sub-surface abrasion. This process used information from within the footprint of the protected sites and that surrounding the site contained within a 10 km buffer of the footprint. Examples of the output from the Focal Statistics tool can be found in Figure 2c. The ArcGIS ‘Values to Points’ tool was then used to extract the anthropogenic resuspension from both surface abrasion and subsurface abrasion for each survey observation. Ultimately, each observation was attributed with (i) a resuspension value for the survey year, and (ii) a resuspension value for the year before the survey year, e.g. resuspension for 2013 was used for a 2014 survey. The preceding year of resuspension data was used as the community was expected to respond after the event, i.e. a year later, rather than in the same year as the event.

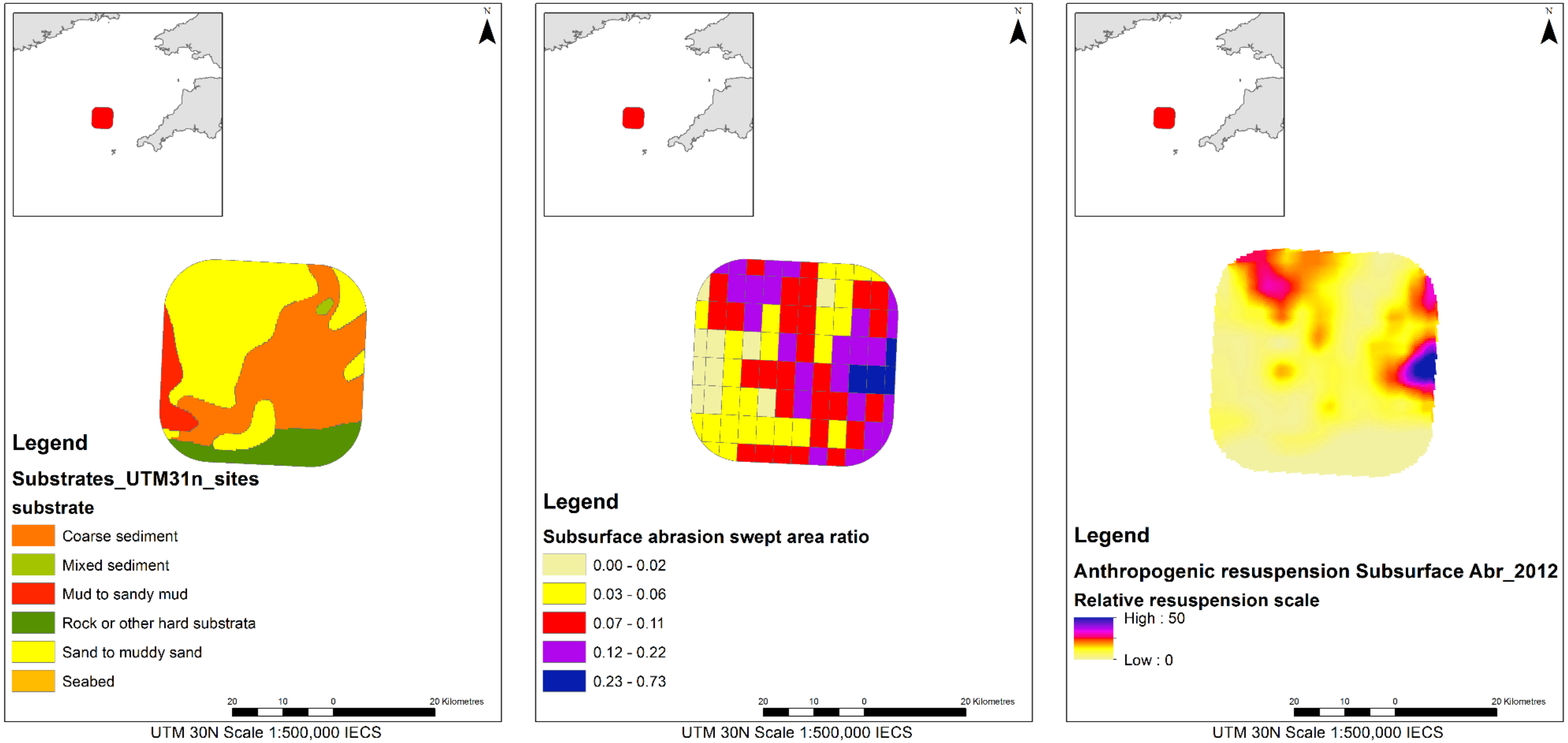

Figure 2a - c. Examples of surficial sediments (Figure 2a - left), swept area ratio for 2012 sub-surface abrasion (Figure 2b - middle), and estimated anthropogenic resuspension for 2012 from sub-surface abrasion (Figure 2c – right), for the East of Haig Fras survey site.

2.3 Data analysis

2.3.1 Removal of very rare species to reduce zero-inflation

An excessive proportion of zeros (‘zero-inflation’) associated with very rare species contributed to over-dispersion within the data set. Taxa with less than 2% commonality (i.e. represented by 137 or fewer observations across the dataset of 6852 observations) were removed to reduce the impact of this zero-inflation (species included and excluded from the analysis are provided in Appendix 1). These very rare taxa (i) significantly contributed to zero-inflation within the species matrix, (ii) were unlikely to be pragmatic indicator species, (iii) were typically observed in fewer than ten observations and therefore exceedingly rare; and (iv) unnecessarily increased the computation time for TITANs. All sponge morphologies were retained regardless of occurrence.

2.3.2 Removal of covarying variables

Covarying environmental variables were identified and removed from the combined species and environmental matrix to meet the statistical assumptions associated with Canonical Redundancy Analysis (RDA). This was performed on the environmental and anthropogenic variables only and not the biological data. A correlation matrix was generated for all environmental variables using R. Correlations between independent variables were considered excessive if the correlation coefficient, r^2, was substantially greater than 0.3. Expert judgement was used to select which variable was excluded from a pair of covarying variables. When possible, the predictor variables considered to be the least certain or have the largest resolution were preferentially excluded.

2.3.2.1 Identification of influential environmental and anthropogenic variables

After the identification and removal of covarying variables, stepwise RDA was used to identify the influential environmental and anthropogenic variables for the biological information (collectively termed explanatory variables). A stepwise modeling approach progressively included more explanatory variables. The threshold for the inclusion of variables was taken as the point at which the Akaike information criterion (a measure of the relative quality of statistical models for a given set of data) stabilised and stopped declining significantly. The influence of individual explanatory variables is highlighted by the F-value (effect size) and *p*-value (significance).

Plots of the RDA output were used to display the environmental variables alongside the biological information. Environmental vector fitting was used to overlay the quantitative environmental on the biological ordination. These analyses helped to visualise the relationships between the biological and environmental information.

2.3.3 Exploratory statistics

Before commencing with the primary analysis, a phase of data exploration investigated:

- Descriptive statistics for sites included:
    - Number of observations and filtered species (i.e. those associated with the highest levels of purity and reliability), and approximate abundance for each site and influential environmental factor (rock quantity, rock type, and biozone)
    - Mean, variance and ranges for the environmental parameters (e.g. temperature, salinity, backscatter and current speed) at each site
- Summary statistics showing the level of anthropogenic resuspension between (i) sites, (ii) rock type (i.e. bedrock, boulder, and cobble), and rock quantity (low, medium and high) species richness. Anthropogenic resuspension was estimated for both surface

abrasion (used as the anthropogenic gradient in the TITAN) and sub-surface abrasion (not used in the TITAN but included in the summary statistics for completeness).

2.3.4 Identification of changes in community condition and the identification of candidate indicator species/groups

Initial investigations of the data suggested that the selection of indicator species would be significantly improved if: (i) the zero value resuspension values (both based on surface and sub-surface abrasion) were removed, (ii) the data set was stratified to partition other important environmental variables (e.g. separate rock types into individual bedrock, boulder and cobble data sets), and (iii) the resuspension was solely based on the surface abrasion. Sub-surface abrasion co-varies with surface abrasion and was therefore not required in the TITANs or included in the RDAs. It is acknowledged that there could be some areas where the sediment disturbed by those parts of the gear, creating sub-surface abrasion, increase the amount of suspended material in the water column. However, this is more of an issue for soft sediments than rock substrata. Consequently, the zero value resuspension observations were removed and only the values based on surface abrasion used in TITAN and data was stratified (Table 6).

2.3.4.1 Stratification of the dataset

The TITAN identifies community change along a specified gradient (anthropogenic resuspension from surface abrasion here). Ideally, other environmental variables that might also induce a change in the community along this gradient should be removed or significantly diminished. Stratification of the main dataset was used to partition out, and thereby reduce, the influence of some environmental variables. Some initial statistical investigations were undertaken to identify the most appropriate approach to stratifying the data – the output of these initial investigations is not provided in the results. Descriptive statistics and PERMANOVA (ADONIS package in R) were used to assess whether resuspension values differed between (i) rock type (bedrock, boulder, and cobble – no observations were dominated by pebble), (ii) rock quantity (high, medium and low), (iii) biozone (reclassified to shelf (1) and deep-water (2)), and (iv) turbidity (backscatter categorised into low (0) and high (1) values based on an absorption threshold of 0.008). All Wight Barfleur observations were in the high backscatter absorption band.

PERMANOVA suggested that the survey observations should be stratified by (i) rock type (bedrock, boulder, or cobble), (ii) rock quantity (low, medium, or high), (iii) turbidity (low or high), and (iv) biozone (shelf or deep-water). The data set was stratified accordingly, and each subset assessed with TITAN. The results from the TITANs were uncertain and associated with high variance. It was apparent that the extensive stratification had reduced the sample size of each subset excessively. The decision was made not to perform certain stratifications. Similarity with the TITAN results suggested that it was more appropriate to merge rock quantity classes rather than rock type classes, i.e. the main data set was split into bedrock, boulder and cobble dataset but not by high, medium and low classes. The high turbidity class was maintained but stratification within this class by rock type and quantity was not performed. There were not enough deep-water observations to perform a TITAN, hence these observations were excluded from the entire analysis.

The final stratification for the main data set, which balanced adequate replication for the TITANs and isolation of influential environmental variables, is shown in Table 6. The four strata used in the main analysis were (i) shallow, low turbidity, bedrock, (ii) shallow, low turbidity, boulder, (iii) shallow, low turbidity, cobble and (iv) shallow, high turbidity (all rock types). For simplicity, these strata will be referred to as ‘bedrock’, ‘boulder’, ‘cobble’ and ‘high turbidity’ respectively.

Table 6. Stratification of the main species matrix for the TITANs. Strata containing fewer than 60 observations were removed from the analysis. Shallow observations were above 200 m depth. Low turbidity observations were below an absorption threshold of 0.008.

	Number of observations				
Full dataset	13852				
Main dataset **(no records with less than 10% rock and 2% commonality)**	6669				
Surface abrasion zero-less dataset	4889				
Stratum	Shallow, low turbidity, bedrock	Shallow, low turbidity, boulder	Shallow, low turbidity, cobble	Shallow, high turbidity (all rock types)	Deep, low turbidity (all rock types)
Observations	1876	540	793	1625	55 (excluded)

2.3.4.2 Threshold Indicator Taxa ANalysis (TITAN)

To facilitate the detection of community change along the resuspension gradient and the identification of indicator species, TITAN was used in R (TITAN2 package). It identifies the optimum value of a continuous variable, anthropogenic resuspension in this case, which partitions the observations above and below the community change point. This is calculated for species that respond positively to anthropogenic resuspension and those that respond negatively (Baker & King 2010). TITAN also uses indicator species scores to integrate occurrence, abundance, and directionality of taxa responses, and thereby assist in the selection of species that are particularly reflective of community changes (specific to the anthropogenic resuspension gradient). Bootstrapping is used to estimate indicator reliability and purity as well as uncertainty around the community change points (Baker & King 2010).

Each stratum was processed in TITAN with the resuspension based on the surface abrasion. This analysis identified the binary partition threshold for species that increase and decrease in abundance along the resuspension gradient. These threshold values were extracted from the output. Each TITAN run also produces output that corresponds to the quality of each species as an indicator for either side of the binary partition. The indicator species output includes:

- 'IndVal' – an index that is 100% when all of the individuals of a species are observed in one partition (on one side of a positive or negative change point).
- Response – a negative or a positive indicator stating whether a species declines or increases in abundance across the resuspension gradient
- Obsiv.prob – the probability of obtaining an equal or larger IndVal score from random data (based on the permutations)
- Purity – proportion of replicates matching observed maxgrp assignment
- Reliability – proportion of replicate obsiv.prob values <= 0.05

The type of analysis conducted by the TITAN package is not influenced by spatial autocorrelation (Baker & King 2010). As such, it was not necessary to test, adjust or compensate for spatial autocorrelation between observations.

2.3.4.3 Extraction of other variables to support the selection of indicator species/morphological groups

To further refine the selection of indicator species, additional indicator indices were derived. These were:

- Typical abundance - scaled between 0 and 1, with values nearer 1 indicating species typically associated with the greatest abundance/cover observed across all candidate species). It is assumed that species/groups that are more abundant are more likely to be recorded in other observations and therefore have a higher practical value as indicator species.
- Body size – scaled between 0 and 1, with values nearer 1 indicating species typically associated with the greatest body size across all candidate species. It is assumed that larger bodied species will be easier to see in video and stills. As such, identity, presence and abundance are likely to be better sampled when compared with smaller and less conspicuous species.

2.3.4.4 Selection of indicator species/morphological groups

The outputs from the TITANs and the additional indicator indices were collated for each species/morphological group within a Microsoft Excel workbook. The selection of the final indicator species was taken as (i) all 'filtered' species and (ii) species with 'indicator quality' values in the top ten. The 'filtered' species have passed the purity (the proportion of change-point response directions (positive or negative) among bootstrap replicates that agree with the observed response at a 95% level of agreement (Baker & King 2010)) and reliability tests (the proportion of bootstrap change points whose IndVal scores consistently results in P-values below one or more at a 95% probability level). The index of indicator quality, developed for this project, has been calculated for each species using the calculation below:

Indicator quality = standardised 'IndVal' + standardised 'Obsiv.prob' + purity + reliability + standardised frequency + body size (small = 0.1, medium = 0.2, large = 0.3)

2.3.4.5 Benchmark abundances for the indicator species/groups

The TITAN identifies the indicator species from each of the four data sets - this information alone is not enough to then apply the indicators to other data sets. One also needs to know the abundance of each indicator that characterises the conditions above and below the change points. As such, the average logged abundance for each indicator species/group, above and below the relevant community change point (positive or negative) was reported for each data set. The logged abundance was also converted back into the SACFOR scale (section 4.2.1 for method) to provide the same information as a relative frequency of the seven classes (including 'absent') above and below the community change points. The average logged abundance and SACFOR profiles above and below the change points have been called the abundance benchmarks.

2.3.4.6 Validation of the indicator species/groups

Validation was performed on the log-transformed (log base 2 for cover and log base 10 for counts) SACFOR datasets (i.e. the data sets used for the RDA and TITANs). A random selection of observations was extracted from observations (i) below), and (ii) above the relevant change point (positive or negative depending on the indicator species). This process was repeated three times using a random selection of 100, 200 and 400 observations drawn from below and above the relevant community change point. Due to a limited number of observations, a random selection of (i) 10, 20 and 30 observations were used for the above positive change point in the boulder and cobble data sets, and (ii) 20, 40 and 60 observations from below the negative change point in the cobble dataset due to only 69 observations being present.

This validation has been designed to operate on a large sample of observations, which is taken to reflect the likely use of the indicator species for a site assessment (i.e. the analysis of the indicator species is applied to a collection of site observations and not to individual observations). The three random selections were averaged to obtain a mean of the logged values. The mean values were then assessed against the ‘benchmark’ logged abundance value for each indicator species for above and below the relevant response type, i.e. a mean value from a random selection was assessed as to whether it was closer to the below change point benchmark or the above change point benchmark. Correctly operating indicator species should have randomised mean values from the below change point that are closer to the ‘below benchmark’ and *vice versa* for the random selection from above the change point. The collective ability of the indicator species to correctly classify the random selections was harvested from 10 iterations of the validation at each of the three random sample sizes. Accuracy here refers to the ability of the indicator species to predict whether an observation is from above or below the relevant change points. Indicators that correctly predicts whether an observation is taken from above or below the relevant change point is scored 1 (0 for incorrect classifications). The average accuracy is the number of correct classifications divided by the total number of indicator species for that data set.

3 Results

3.1 Descriptive statistics for sites

Approximately two-thirds of the total survey observations were described as having an 'adequate' visual quality and one-third were considered 'good' (Table 7). Although Haig Fras and Haig Fras Infill are from the same site, (Haig Fras cSAC/SCI), information from the two surveys have been processed separately as they are from differing years.

Table 7. Survey metadata and sample quality for each of the eight site surveys.

	Survey metadata			Visual quality	
Survey Site	**Survey year**	**Number of samples**	**Number of stations**	**Adequate**	**Good**
East of Haig Fras	2015	1061	132	948	113
Faroe-Shetland Sponge Belt Scottish NCMPA	2012	129	23	129	0
Haig Fras cSAC/SCI	2015	1843	91	1744	99
Haig Fras cSAC/SCI "infill"	2012	70	9	70	0
Pobie Bank Reef cSAC/SCI	2013	275	47	275	0
Solan Bank Reef Site of Community Importance	2014	1016	153	689	327
Wight-Barfleur Extension rMCZ	2013	1924	135	263	1435
Wyville Thomson Ridge SCI	2012	351	25	389	0
Total		6669		67.3%	32.7%

The estimated amount of anthropogenic resuspension and backscatter occurring at each site were summarised (Table 8). The greatest pressure, from estimated anthropogenic resuspension, appears to be occurring at Pobie Bank and East of Haig Fras. Moderate levels of estimated anthropogenic resuspension occur at the main Haig Fras site. Lower levels of estimated anthropogenic resuspension typically occur along the Faroe-Shetland Sponge Belt NCMPA and within the Wight-Barfleur Extension rMCZ. The lowest levels of anthropogenic resuspension were estimated to occur within the Wyville Thomson Ridge SCI and the Solan Bank Reef SCI. The natural levels of backscatter from surface suspended material were consistent between sites except for very high levels observed at the Wight-Barfleur Extension rMCZ. Anthropogenic resuspension from surface abrasion is higher in cobble habitats and lower in bedrock habitats (Table 9). Furthermore, anthropogenic resuspension declines in areas with a high proportion of rock (i.e. 70-100% rock cover).

The Faroe-Shetland Sponge Belt NCMPA and the Wyville Thomson Ridge SCI are both deep-water sites associated with higher current speeds (Table 10). All other sites are located on the continental shelf (Table 10). Across all sites, observations containing medium (40 – 70 %) rock cover were the most common, while those with high quantities of rock (70-100 %) were the least common (Table 9). Observations were more likely to be dominated by either bedrock or cobble, with boulder-dominated observations being less common.

The most frequently observed habitats across all sites, in decreasing order of frequency, were deep circalittoral coarse sediment (A5.15), circalittoral coarse sediment (A5.14), Atlantic and Mediterranean moderate energy circalittoral rock (A4.2), faunal communities on deep low energy circalittoral rock (A4.33), and faunal communities on deep moderate energy circalittoral rock (A4.27) (Table 11).

Table 8. Relative resuspension from anthropogenic sources from surface abrasion and sub-surface abrasion for the year of survey (0) or year before survey (-1) with the absorption from backscatter (Aqua MODIS whole mission turbidity composite and absorption due to gelbstoff and detrital material at 443 nm – GIOP model) for each survey.

Site	Anthropogenic resuspension (relative scale)				
	Calculated using surface abrasion		Calculated using sub-surface abrasion		
	Year 0	Year -1	Year 0	Year -1	Backscatter and backscatter class in brackets
East of Haig Fras	23.16	21.74	3.11	3.54	0.0032 (low)
Faroe-Shetland Sponge Belt Scottish NCMPA	1.62	0.41	0.05	0.02	0.0033 (low)
Haig Fras cSAC/SCI	9.21	8.81	0.28	0.28	0.0032 (low)
Haig Fras cSAC/SCI “infill”	5.18	5.71	0.17	0.19	0.0032 (low)
Pobie Bank Reef cSAC/SCI	21.60	34.5	0.65	0.81	0.0031 (low)
Solan Bank Reef Site of Community Importance	0.00	0.00	0.00	0.00	0.0031 (low)
Wight-Barfleur Extension rMCZ	2.22	2.75	0.09	0.09	0.0126 (high)
Wyville Thomson Ridge SCI	0.00	0.07	0.00	0.00	0.0029 (low)

Table 9. Mean and standard deviation for anthropogenic resuspension from surface abrasion (the year before the survey) by rock type and quantity.

	Mean anthropogenic resuspension (unit-less) for surface abrasion (standard deviation)			
Rock quantity	**Bedrock**	**Boulder**	**Cobble**	**Row totals**
Low	9.91 (±19.30)	6.91 (±20.58)	9.47 (±17.97)	8.78 (±18.86)
Medium	7.49 (±12.84)	9.52 (±15.47)	10.74 (±15.87)	8.99 (±14.57)
High	5.14 (±9.53)	0.93 (±2.68)	0.38 (±0.79)	4.68 (±9.14)
Column totals	6.73 (±12.27)	7.98 (±17.33)	9.92 (±17.15)	8.21 (±15.56)

Table 10. Summary statistics for the physical environment at each survey site.

Site	Observed depth (m) and depth class in brackets	Modelled temperature (degrees Celsius) at seabed	Rugosity from EMODnet bathymetry (arc-chord ratio)	Aspect from EMODnet bathymetry (degrees)	Relative curvature between samples (relative scale)	Currents (magnitude)	Distance from shore (km)
East of Haig Fras	-97 (shallow)	9.50	0.149	137	0.03	0.019	64.30
Faroe-Shetland Sponge Belt Scottish NCMPA	-482 (deep)	10.92	0.010	291	0.10	0.156	106.24
Haig Fras cSAC/SCI	-79 (shallow)	12.11	0.034	177	0.10	0.011	109.07
Haig Fras cSAC/SCI “infill”	-86 (shallow)	12.29	0.000	154	0.05	0.012	103.52
Pobie Bank Reef cSAC/SCI	-92 (shallow)	13.30	0.077	164	-0.70	0.023	31.49
Solan Bank Reef Site of Community Importance	-62 (shallow)	13.10	0.244	199	0.15	0.032	41.63
Wight-Barfleur Extension rMCZ	-57 (shallow)	12.78	0.183	174	1.00	0.017	37.71
Wyville Thomson Ridge SCI	-562 (deep)	12.38	0.019	181	-1.00	0.135	157.42

Table 11. The frequency of observations in different biotope classes (observations attributed using UKSeaMap). Biotope classes are: A3.2 = Atlantic and Mediterranean moderate energy infralittoral rock, A4.11 = Very tide-swept faunal communities on circalittoral rock or A4.13 = Mixed faunal turf communities on circalittoral rock, A4.12 = Sponge communities on deep circalittoral rock, A4.2 = Atlantic and Mediterranean moderate energy circalittoral rock, A4.27 = Faunal communities on deep moderate energy circalittoral rock, A4.31 = Brachiopod and ascidian communities on circalittoral rock, A4.33 = Faunal communities on deep low energy circalittoral rock, A5.13 = Infralittoral coarse sediment, A5.14 = Circalittoral coarse sediment, A5.15 = Deep circalittoral coarse sediment, A5.25 = Circalittoral fine sand or A5.26: Circalittoral muddy sand, A5.27 = Deep circalittoral sand, A5.37 = Deep circalittoral mud, A5.45 = Deep circalittoral mixed sediments, UBCS = Upper bathyal coarse sediment, USCS[6] = Upper slope coarse sediment, USMS = Upper slope mixed sediment, USSMS = Upper slope sand to muddy sand.

Row Labels	A3.2	A4.11 or A4.13	A4.12	A4.2	A4.27	A4.31	A4.33	A5.13	A5.14	A5.15	A5.25 or A5.26	A5.27	A5.37	A5.45	UBCS	USCS	USMS	USSMS
East of Haig Fras										922		139						
Faroe-Shetland Sponge Belt Scottish NCMPA																70	22	37
Haig Fras cSAC/SCI					237	18	612		12	797		37	13	117				
Haig Fras cSAC/SCI “infill”							56			14								
Pobie Bank Reef cSAC/SCI				49	30	40	75			9		63		9				
Solan Bank Reef Site of Community Importance	51			127				198	597	26	10	7						
Wight-Barfleur Extension rMCZ		509	19	612	422				362									
Wyville Thomson Ridge SCI															33	318		
Total	51	509	19	788	689	58	743	198	971	1768	10	246	13	126	33	388	22	37

[6] Please note the upper slope classes no longer exist in the new habitat clarifications.

3.2 Correlation matrix of the environmental and anthropogenic variables

A correlation matrix for the explanatory variables was produced in R (Table 12). Variables were considered covarying if the magnitude of the correlation coefficient was greater than 0.3. Based on this correlation threshold, the following variables were considered to be correlated with other variables and therefore removed from further analysis:

- Distance to shore (correlated with POC, depth, mixing and energy)
- Bottom current magnitude from x and y components (correlated with IOP, POC, slope, depth and mixing)
- Particulate Organic Matter (correlated with backscatter, depth, mixing and energy)
- Seabed slope (correlated with current magnitude, depth and mixing)
- Anthropogenic resuspension (correlated with all other three versions)
- Water column mixing (correlated with distance to shore, POC, backscatter, slope, depth and energy)
- Wave induced energy (correlated with distance to shore, POC and backscatter)

Table 12. Correlation coefficients for the covarying environmental and anthropogenic variables only. Correlation coefficients between -0.3 and 0.3 are not shown as values within this range were not considered to covary. Codes are DTS = distance to shore, Temp = temperature at the seabed, CM = current magnitude, POC = particulate organic carbon, and BS = backscatter. Artificial substrata, biogenic substrata, shell, Maerl and curvature are not shown.

	Latitude	longitude	Bedrock	Boulder	Cobble	Pebble	Gravel	Sand	Mud	DTS	Temp	CM	POC	BS	AR/SA	Rugosity	Aspect	Slope	Depth	Mixing
Longitude	-	1.00																		
Bedrock	-	-0.43	1.00																	
Boulder	-	-	-	1.00																
Cobble	-	0.34	-0.63	-	1.00															
Pebble	-	0.45	-0.50	-	-	1.00														
Gravel	-	-	-0.33	-	-	-	1.00													
Sand	-	-	-0.38	-	-	-	-	1.00												
Mud	-	-0.35	-	-	-	-	-	-	1.00											
DTS	-	-0.76	0.35	-	-0.36	-	-	-	-	1.00										
Temp	-	0.41	-	-	-	-	-	-0.40	-	-	1.00									
CM	0.60	-	-	-	-	-	-	-	-	0.40	-	1.00								
POC	-0.40	-	-	-	0.32	-	-	-	-	-0.46	-	-0.41	1.00							
BS	-0.34	0.71	-0.33	-	0.33	0.37	-	-	-	-0.53	-	-	0.38	1.00						
AR/SA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00					
Rugosity	-	-	-	-	-	-	-	-	-	-0.35	-	-	-	-	-	1.00				
Aspect	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00			
Slope	0.39	-	-	-	-	-	-	-	-	-	-	0.54	-	-	-	-	-	1.00		
Depth	-0.46	-	-	-	-	-	-	-	-	-0.58	-	-0.82	0.45	-	-	-	-	-0.52	1.00	
Mixing	0.39	-	-	-	-	-	-	-	-	0.68	-	0.81	-0.47	-	-	-	-	0.51	-0.97	1.00
Energy	-0.40	0.78	-0.34	-	0.35	0.46	-	-	-	-0.57	0.33	-	0.35	0.89	-	-	-	-	0.31	-0.31

3.3 Canonical Redundancy Analysis (RDA)

3.3.1 Main data set

Overall, the explanatory variables were only able to account for approximately 20 % of the variance within the community data. Examination of the RDA (Figure 3, Table 13 and Table 14) suggest that latitude, longitude, depth/biozone, temperature, backscatter, substratum composition (bedrock, pebble, shell, Maerl, and/or cobble content) and anthropogenic resuspension are the variables that account for the majority of the constrained (explained) variance. It is also possible that some co-correlation is present between latitude and temperature. An analysis of the significance of the explanatory variables listed in Table 14 states that all of the variables are statistically significant (Table 14) but vary greatly in effect size (F value). The F value, and vector, for the anthropogenic resuspension from surface abrasion (year before the survey observation) is relatively small and therefore only explains a small proportion of the constrained variance (Table 14).

Table 13. The summary output from the RDA for the full dataset.

	Variable explained	Proportion explained
Constrained	3.36	0.20
Unconstrained	13.17	0.80
Total	16.53	1.00

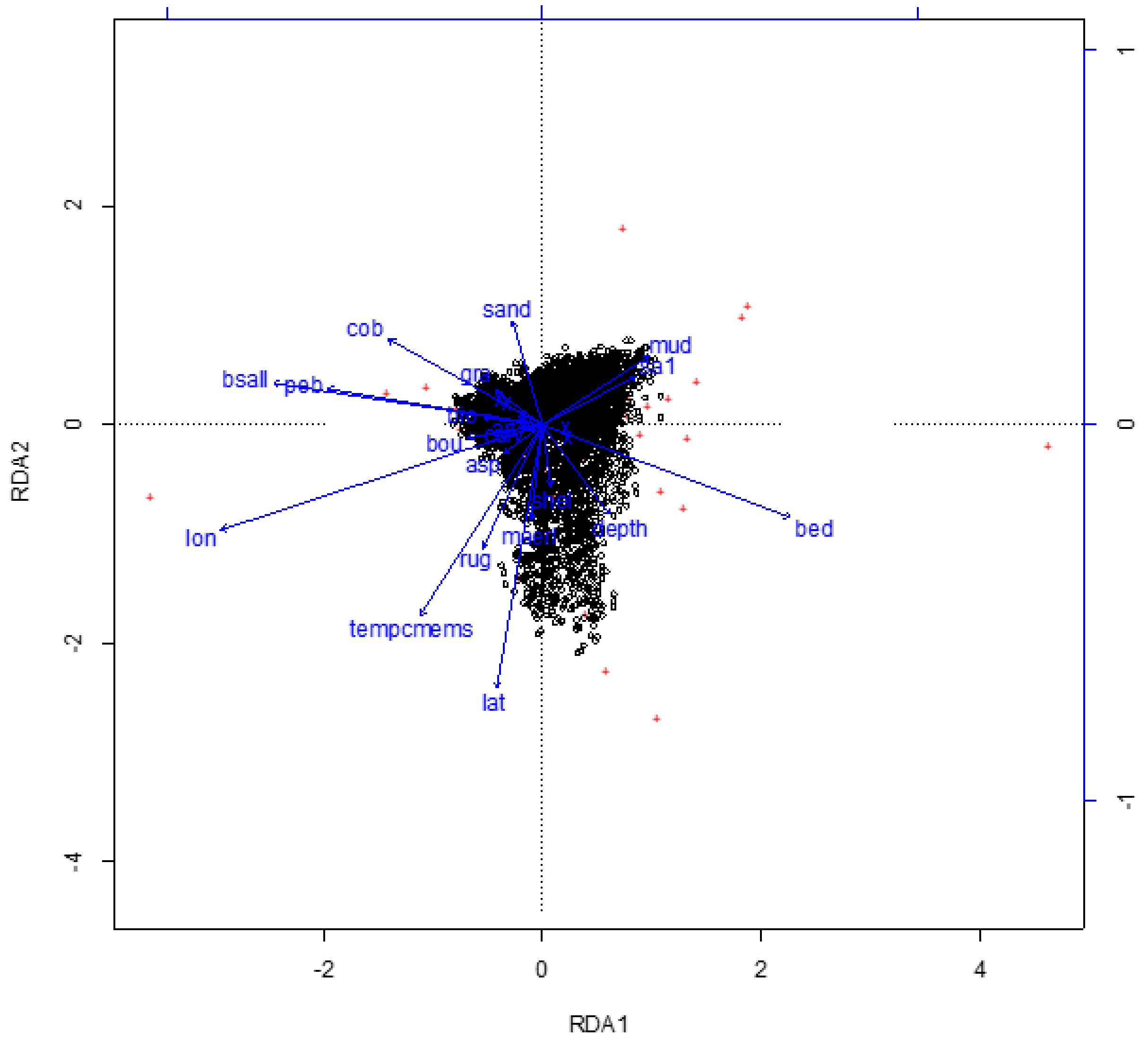

Figure 3. Canonical redundancy analysis plot based on the main data set (all rock types and quantities, all resuspension values for SA1 but only species with an occurrence greater than 2%). Black infilled circles are the observations and the vectors represent the explanatory variables (i.e. environmental and anthropogenic variables). Variable codes are lat = latitude, lon = longitude, bed = bedrock, bou = boulder, cob = cobble, peb = pebble, mae = maerl, bio = biogenic, sa1 = anthropogenic resuspension from surface abrasion (year before the survey observation), gra = gravel, shel = shell, tempcmems = modelled seabed temperature, bsall = particulate backscatter, rug = rugosity, asp = aspect.

Table 14. Canonical redundancy analysis output, for each explanatory variable ('by terms'), for the main data set (all rock types and quantities, all resuspension values for surface abrasion form the year before observations (SA-1) but only species with an occurrence greater than 2%). Excluded variables were removed by the stepwise selection and not included in the final model.

Explanatory variables	Degrees of freedom	Variance	F value	Significance	Ranking
Latitude	1	0.501	249.139	0.001	2
Longitude	1	1.232	612.269	0.001	1
Bedrock	1	0.347	172.450	0.001	3
Boulders	1	0.028	14.092	0.001	15
Cobbles 64 mm to 25 6mm	1	0.046	22.627	0.001	11
Pebbles 4 mm to 64 mm	1	0.074	36.594	0.001	6
Granule 2 mm to 4 mm	1	0.019	9.564	0.001	20
Shell	1	0.077	38.180	0.001	5
Maerl	1	0.068	33.539	0.001	8
Sand	1	0.025	12.299	0.001	17
Mud less than 0.063 mm	1	0.031	15.498	0.001	13
Artificial	1	0.021	10.523	0.001	19
Biogenic Reef	1	0.025	12.568	0.001	16
Rock quantity	2	0.061	15.161	0.001	14
Primary rock type	2	0.027	6.760	0.001	22
Biozone code	2	0.344	85.548	0.001	4
Seabed temperature	1	0.049	24.201	0.001	10
Backscatter	1	0.073	36.485	0.001	7
Anthropogenic resuspension (SA-1)	1	0.056	27.614	0.001	9
Rugosity	1	0.024	11.765	0.001	18
Curvature	Excluded	-	-	-	-
Aspect	1	0.017	8.211	0.001	21
Depth	1	0.045	22.273	0.001	12

3.3.2 Sub-divided data sets

The RDA states that the explanatory variables were only able to account for 18 % of the variance within the bedrock and cobble communities), 16 % for the boulder communities and just 13 % for the high turbidity (all rock classes) communities (Table 15).

For bedrock communities (Figure 4 and Table 16) latitude, longitude, depth, bedrock quantity, aspect, anthropogenic resuspension, and backscatter were the most important variables for explaining the variance (in decreasing order of importance) within the shallow, low turbidity, dataset. For boulder communities (Figure 4 and Table 16.) latitude, cobble quantity, longitude, seabed temperature, pebble quantity, and anthropogenic resuspension were the most important variables for explaining the variance (in decreasing order of importance).

For the shallow, low turbidity, cobble data set (Figure 5 and Table 17) latitude, longitude, depth, cobble content, mud content, pebble content, backscatter and seabed temperature were the top eight most important variables for explaining the variance (in decreasing order of importance). Although significant, the effect size for anthropogenic resuspension (from surface abrasion) was very small – this variable was ranked just 16th for explanatory power.

Finally, for the high turbidity communities (Figure 5 and Table 17) longitude, boulder content, gravel (granule) content, latitude, and pebble content were the top five most important variables for explaining the variance (in decreasing order of importance). Anthropogenic resuspension (from surface abrasion) was ranked in tenth place.

Table 15. The proportion of the community variance explained by the explanatory variables (environmental and anthropogenic variables) for the shallow, low turbidity, bedrock, boulder, cobble, and shallow, high turbidity (all rock types) data sets.

Data set	Variance component	Variance	Proportion of variance
Shallow, low turbidity, bedrock	Total	92.58	1.00
	Explained (constrained)	16.86	0.18
	Unexplained (unconstrained)	75.72	0.82
Shallow, low turbidity, boulder	Total	55.96	1.00
	Explained (constrained)	8.85	0.16
	Unexplained (unconstrained)	47.11	0.84
Shallow, low turbidity, cobble	Total	60.37	1.00
	Explained (constrained)	10.57	0.18
	Unexplained (unconstrained)	49.81	0.82
Shallow, high turbidity (all rock classes)	Total	34.26	1.00
	Explained (constrained)	4.44	0.13
	Unexplained (unconstrained)	29.81	0.87

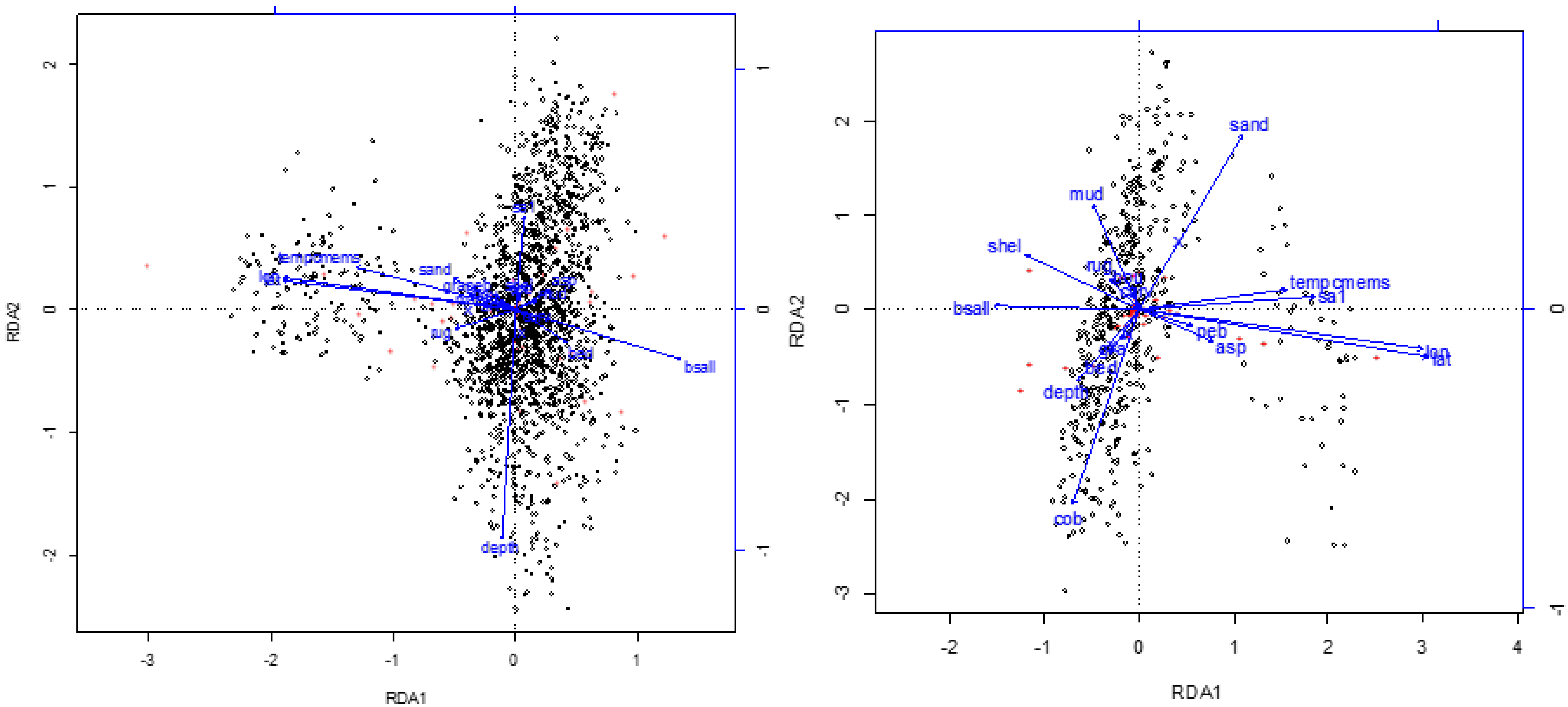

Figure 4. Canonical redundancy analysis plot based on the shallow, low turbidity, bedrock (left) and boulder (right) data set (all rock quantities and all resuspension values above zero for SA1 for both). Black infilled circles are the observations and the vectors represent the explanatory variables (i.e. environmental and anthropogenic variables). Red crosses mark centroids for classes within factor variables (site, rock quantity and rock type). Variable codes are lat = latitude, lon = longitude, bed = bedrock, bou = boulder, cob = cobble, peb = pebble, mae = maerl, bio = biogenic, sa1 = anthropogenic resuspension from surface abrasion (year before the survey observation), gra = gravel, shel = shell, tempcmems = modelled seabed temperature, bsall = particulate backscatter, rug = rugosity, asp = aspect.

Table 16. Canonical redundancy analysis output, for each explanatory variable ('by terms'), for the shallow, low turbidity, bedrock and boulder data set (all rock quantities and all resuspension values above zero for SA1 for both). Excluded ("Excl") variables were removed by the stepwise selection and not included in the final model.

Explanatory variables	Degrees of freedom	Shallow, low turbidity, bedrock				Shallow, low turbidity, boulder			
		Variance	F value	P value	Rank	Variance	F value	P value	Rank
Latitude	1	7.222	219.854	0.001	1	4.635	51.165	0.001	1
Longitude	1	4.213	128.24	0.001	2	0.752	8.301	0.001	3
Bedrock	1	0.737	22.425	0.001	4	Excl			
Boulders	1	0.093	2.83	0.001	17	0.167	1.846	0.015	11
Cobbles	1	0.178	5.426	0.001	11	0.798	8.813	0.001	2
Pebbles	1	0.104	3.176	0.001	16	0.233	2.576	0.003	5
Granule	1	0.072	2.204	0.004	19	Excl			
Shell	1	0.158	4.798	0.001	13	Excl			
Maerl	1	0.309	9.414	0.001	10	Excl			
Sand	1	0.128	3.906	0.001	15	Excl			
Mud	1	0.158	4.823	0.001	12	0.177	1.954	0.013	9
Artificial	1	0.139	4.238	0.001	14	Excl			
Biogenic Reef	1	Excl				Excl			
Rock quantity	2	0.632	9.616	0.001	9	0.382	2.106	0.001	8
Primary rock type	2	Excl				Excl			
Seabed temperature	1	0.356	10.84	0.001	8	Excl			4
Backscatter	1	0.363	11.058	0.001	7	0.42	4.641	0.001	7
Anthropogenic resuspension (SA)	1	0.405	12.319	0.001	6	0.224	2.473	0.004	6
Rugosity	1	0.079	2.397	0.001	18	0.227	2.501	0.002	
Curvature	1	Excl				Excl			

Explanatory variables	Degrees of freedom	Shallow, low turbidity, bedrock				Shallow, low turbidity, boulder			
		Variance	F value	P value	Rank	Variance	F value	P value	Rank
Aspect	1	0.476	14.502	0.001	5	Excl			10
Depth	1	1.016	30.938	0.001	3	0.175	1.927	0.014	1

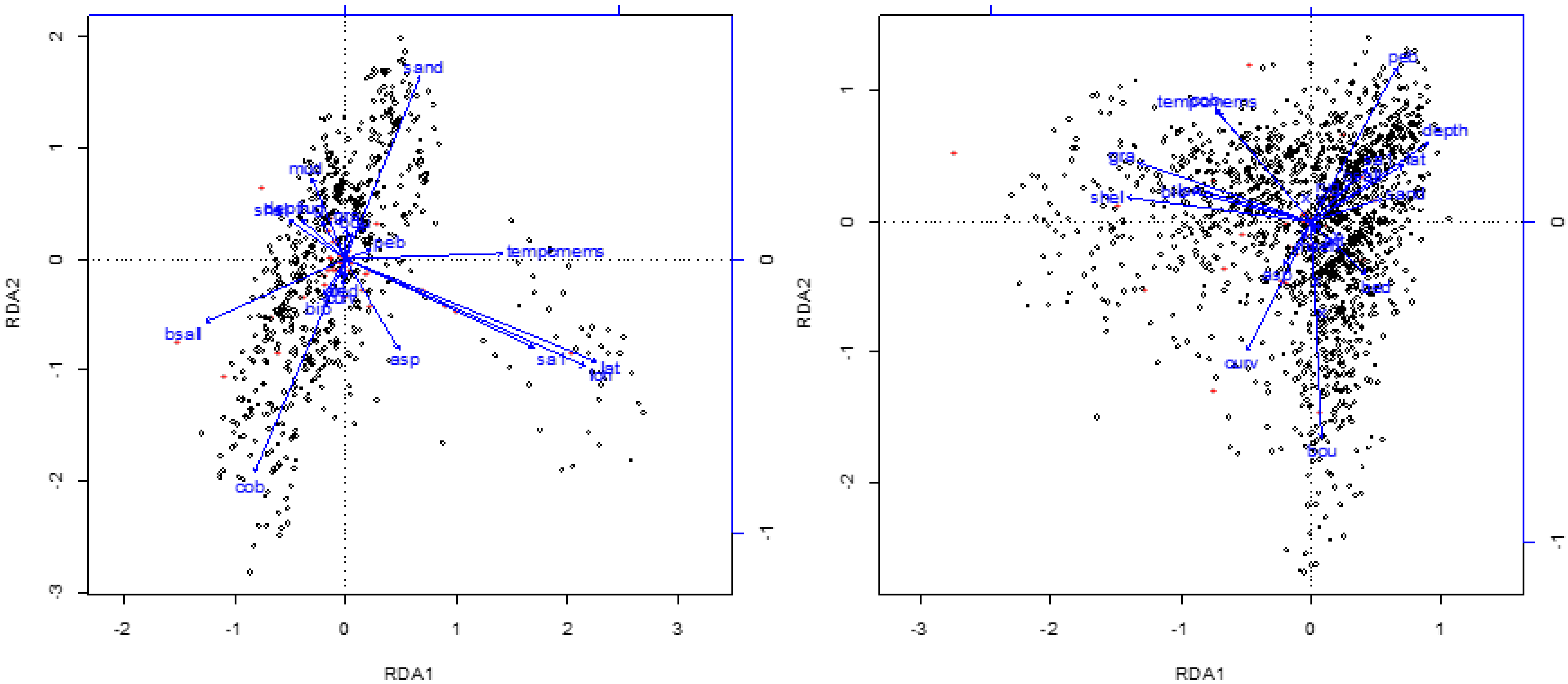

Figure 5. Canonical redundancy analysis plot based on the shallow, low turbidity, cobble (left), and shallow, high turbidity (all rock types) (right) data sets (all rock quantities and all resuspension values above zero for SA1 for both). Black infilled circles are the observations and the vectors represent the explanatory variables (i.e. environmental and anthropogenic variables). Red crosses mark centroids for classes within factor variables (site, rock quantity and rock type). Variable codes are lat = latitude, lon = longitude, bed = bedrock, bou = boulder, cob = cobble, peb = pebble, mae = maerl, bio = biogenic, sa1 = anthropogenic resuspension from surface abrasion (year previous to survey observation), gra = gravel, shel = shell, tempcmems = modelled seabed temperature, bsall = particulate backscatter, rug = rugosity, asp = aspect.

Table 17. Canonical redundancy analysis output, for each explanatory variable ('by terms'), for the shallow, low turbidity, cobble, and shallow, high turbidity (all rock types) data sets (all rock quantities and all resuspension values above zero for SA1 for both). Excluded variables were removed by the stepwise selection and not included in the final model.

Explanatory variables	Degrees of freedom	Shallow, low turbidity cobble				Shallow, high turbidity (all rock classes)			
		Variance	F value	P value	Rank	Variance	F value	P value	Rank
Latitude	1	4.076	85.763	0.001	1	0.411	26.146	0.001	4
Longitude	1	1.514	31.859	0.001	2	0.562	35.777	0.001	1
Bedrock	1	0.221	4.654	0.001	10	0.137	8.713	0.001	13
Boulders	1	Excl				0.505	32.136	0.001	2
Cobbles	1	1.01	21.244	0.001	4	0.245	15.623	0.001	9
Pebbles	1	0.323	6.806	0.001	6	0.379	24.11	0.001	5
Granule	1	0.158	3.333	0.001	12	0.428	27.288	0.001	3
Shell	1	0.156	3.292	0.001	13	0.268	17.043	0.001	7
Maerl	1	0.239	5.023	0.001	9	Excl			
Sand	1	0.138	2.904	0.001	15	0.26	16.569	0.001	8
Mud	1	0.335	7.059	0.001	5	Excl			
Artificial	1	Excl				Excl			
Biogenic Reef	1	Excl				0.283	18	0.001	6
Rock quantity	2	Excl				0.069	2.208	0.001	18
Primary rock type	2	Excl				0.058	1.845	0.007	19
Seabed temperature	1	0.272	5.714	0.001	8	0.159	10.132	0.001	11
Backscatter	1	0.302	6.345	0.001	7	0.125	7.958	0.001	15
Anthropogenic resuspension (SA)	1	0.092	1.94	0.01	16	0.177	11.257	0.001	10
Rugosity	1	0.162	3.404	0.001	11	0.043	2.758	0.002	17
Curvature	1	Excl				0.142	9.069	0.001	12

Explanatory variables	Degrees of freedom	Shallow, low turbidity cobble				Shallow, high turbidity (all rock classes)			
		Variance	F value	P value	Rank	Variance	F value	P value	Rank
Aspect	1	0.138	2.906	0.001	14	0.044	2.812	0.002	16
Depth	1	1.178	24.785	0.001	3	0.127	8.08	0.001	14

3.4 Threshold Indicator Taxa Analysis

The Threshold Indicator Taxa Analysis (TITAN) was undertaken on the four data sets: low turbidity bedrock, boulder and cobble and high turbidity (all rock classes). The positive and negative community 'change points' along the anthropogenic resuspension gradient have been identified by TITAN for each data set (Table 18). It is apparent that negatively responding (declining) species/groups respond at a relatively low level of anthropogenic resuspension when compared with the positively responding species/groups. The change points for the entire species/groups matrix are similar to those generated from just the filtered species. Surprisingly, the high turbidity communities had the lowest change points, i.e. there is a significant change in the composition of positively and negatively responding species/groups at very low levels of anthropogenic resuspension. The validity of this result is discussed in more detail in the Discussion.

Table 18. Community change points along the anthropogenic resuspension gradient (from surface resuspension), for positively and negatively responding species, identified by TITANs for bedrock, boulder, cobble and high turbidity data sets. Descriptive statistics are also included to provide context for the change points.

	Anthropogenic resuspension scale value (unit-less)			
Anthropogenic resuspension gradient	**Low turbidity Bedrock**	**Low turbidity Boulder**	**Low turbidity Cobble**	**High turbidity (all rock classes)**
Minimum gradient value (zeros removed)	0.04	0.04	0.05	0.02
Negative change point based on all negatively responding species	0.43	11.02	2.08	0.08
Positive change point based on all positively responding species	10.55	53.11	70.85	3.25
Negative change point based on 'filtered' negatively responding species	0.47	11.96	9.26	0.09
Positive change point based on 'filtered' positively responding species	10.55	53.11	70.85	3.25
Mean gradient value	9.20	21.42	25.65	3.05
Maximum gradient value	151.50	146.82	158.59	36.29

The detailed TITAN outputs for indicator species that are associated with either side of the change points for each of the four datasets are provided in Appendix 3. The estimated benchmark values for the abundance and SACFOR change points are presented in Appendix 4.

The filtered results from the TITAN analysis of the bedrock dataset identified 14 positively responding species/groups and nine negatively responding species/groups along the anthropogenic resuspension gradient examined (Table 19 and Table 24). Based on the ranking of the indicator quality scores (Table 24), several species/groups not included in the filtered set, due to their low purity and/or reliability scores, were included in the top 10 final indicator list. These included *Alcyonium digitatum, Ophiothrix fragilis*, and *Securiflustra securifrons* as positively responding indicator species and Ophiactidae, Serpulidae, and *Swiftia pallida* as negatively responding species/groups.

The filtered results from the TITAN analysis of the boulder data set only identified four positively responding species/groups and nine negatively responding species/groups along the anthropogenic resuspension gradient examined (Table 19 and Table 25). The top 10 species/groups recommended by the indicator quality score were all included in the filtered set. Examples of high quality positively responding species/groups included Serpulidae, *Swiftia pallida*, and Sertulariidae. Example species/groups with a negative response include encrusting Porifera, arborescent Porifera, *Spirobranchus* spp., and *Stichastrella rosea*.

The filtered results from the TITAN analysis of the cobble data set identified six positively responding species/groups and seven negatively responding species/groups along the anthropogenic resuspension gradient examined (Table 19 and Table 26).The ranked indicator quality score also highlighted *Caryophyllia* spp. as an additional negative responder and Porifera encrusting as a positive responder, both of which were included in the top 10 species/groups recommended by the analysis

The filtered results from the TITAN analysis of the high turbidity data set identified 11 positively responding species/groups and seven negatively responding species/groups along the anthropogenic resuspension gradient examined (Table 19 and Table 27). Nine of the top species/groups for indicator quality overlapped with the filtered indicator species and only Serpulidae was added to the indicator list as a positive responder for high turbidity sublittoral rock on cobble substratum.

It is apparent that many of the same species and groups have been identified as being good indicator species in the four data sets (low turbidity bedrock, boulder and cobble and high turbidity rock). However, the response type often varies between data sets (Table 19). For example, *Caryophyllia* spp. which was identified as a top 10 indicator species for all low turbidity datasets has a positive response on low turbidity bedrock and in high turbidity conditions, but a negative response on low turbidity boulder or cobble. Encrusting sponges have been identified as a positively responding on all but low turbidity bedrock; this was also the only dataset for which it was not identified as a top 10 indicator species. Serpulidae were identified as a top 10 indicator species in all datasets, however the response was positive for all low turbidity rock datasets and negative for high turbidity rock. The final indicator list contains 28 species/groups for low turbidity bedrock habitats, 13 for low turbidity boulder habitats, 14 for low turbidity cobble habitats, and 20 for high turbidity sublittoral rock.

Table 19. Summary of the response of the selected indicator species/groups to anthropogenic resuspension within the four data sets analysed. Full results in Appenxix 3. "P" = positive response, "N" = negative response, "Positive" and "Negative" = 'filtered' indicator taxa response and those with an asterisk (*) were in the top 10 based on indicator quality. Filtered species have passed the purity (the proportion of change-point response directions among bootstrap replicates that agree with the observed response at a 95% level of agreement (Baker and King, 2010)) and reliability (the proportion of bootstrap change points whose IndVal scores consistently results I P-values below one or more at a 95% probability level) tests.

	Response to increases in anthropogenic resuspension from surface abrasion			
Species/group	**Low turbidity Bedrock**	**Low turbidity Boulder**	**Low turbidity Cobble**	**High turbidity (all rock classes)**
Actiniaria	Positive	N	P	Positive*
Alcyonidium spp.	Negative*	P	Negative	N
Alcyonium digitatum	P	P	Negative	P
Antedon bifida	Positive	N	N	N
Asteriidae	Negative	N	Positive*	-
Brachiopoda	Positive*	Negative*	P	-
Calliostoma spp.	Negative	P	N	N
Caryophyllia spp.	Positive*	Negative*	Negative*	Positive
Cirripedia	-	-	-	Positive*
Corallinaceae	Negative	-	-	-
Corynactis spp.	Negative	-	-	P
Crinoidea	Positive	N	P	-
Echinoidea	N	P	Positive*	-
Flustra foliacea	-	-	-	Negative*
Gibbula spp.	-	-	-	Positive*
Henricia spp.	Negative	N	P	N
Munida spp.	Positive	P	P	-
Ophiactidae	N*	P	P	-
Ophiocomina nigra	Positive	N	P	-
Ophiothrix fragilis	P*	N	P	-
Ophiura spp.	Positive*	P	N	-
Ophiura albida	Positive	P	P	-
Ophiuroidea	Positive*	Negative	N	Negative*
Paguroidea	Positive	P	Positive	Positive
Palmiskenea skenei	Positive	N	N	-
Pectinidae	P	P	P	Positive
Pentapora fascialis	-	-	-	Positive
Porania pulvillus	Positive	N	P	-
Porella spp.	P	Negative*	Negative*	-

	Response to increases in anthropogenic resuspension from surface abrasion			
Species/group	**Low turbidity Bedrock**	**Low turbidity Boulder**	**Low turbidity Cobble**	**High turbidity (all rock classes)**
Porifera arborescent	N	Positive*	Positive*	Negative
Porifera columnar	-	-	-	Positive
Porifera encrusting	N	Positive*	Positive*	Positive*
Porifera flabellate	N	Negative	Positive*	-
Porifera globular	Negative	N	P	Negative*
Porifera massive	N	P	P	Negative*
Porifera papillate	Negative*	Negative*	N	Positive
Porifera repent	Positive	N	P	Negative
Porifera tubular	P	-	-	Positive
Rhodophyta	Negative	-	-	-
Sagartiidae	P	-	-	Positive
Securiflustra securifrons	P*	-	-	-
Serpulidae	N*	Negative*	Negative*	P*
Sertulariidae	P	Negative	Negative	-
Spirobranchus spp.	P	Positive*	Positive*	-
Stichastrella rosea	N	Positive*	N	-
Swiftia pallida	N*	Negative*	Negative*	-
Tubulariidae	-	-	-	Negative*

3.5 Validation of the indicator species/groups

The average classification accuracy of the indicator species/groups for each data set is reported for random selections of, when possible, 100, 200 and 400 observations from above and below the relevant change points (Table 20). Due to a limited number of observations, a random selection of (i) 10, 20 and 30 observations were used for the above positive change point in the boulder and cobble data sets, and (ii) 20, 40 and 60 observations from below the negative change point in the cobble dataset due to only 69 observations being present.

The accuracy of the indicators appears to be marginally higher for observations above the positive community change points, compared to negative (for average and generally within datasets). The indicators associated with the high turbidity data set provided the highest accuracy, followed by the bedrock indicators and then the boulder indicators. The indicators from the cobble data set provided the lowest accuracy. The accuracy of the indicators improved with greater sample sizes. The number of observations in the bedrock (n = 1876) and high turbidity (n = 1625) data sets was greater than the boulder (n = 540) and cobble (n = 793) data sets.

Table 20. Average classification accuracy for the suite of indicator species/groups for each data set. The average accuracy has been assessed as randomly selected sample sizes of 100, 200 and 400 observations.

		Average accuracy (%) following ten iterations with the standard deviation in brackets.		
Data set	**Metric**	**100 random observations**	**200 random observations**	**400 random observations**
Low turbidity Bedrock	Accuracy below relevant change point	76.4% (±3.5)	81.4% (±4.1)	82.9% (±3.7)
	Accuracy above relevant change point	79.3% (±6.7)	82.9% (±6.3)	83.9% (±3.5)
Low turbidity Boulder	Accuracy below relevant change point	63.1% (±6.1)	63.8% (±5.2)	61.5% (±5.1)
	Accuracy above relevant change point	79.2% (±6.3)	82.3% (±8.1)	76.2% (±9.2)
Low turbidity Cobble	Accuracy below relevant change point	62.1% (±4.8)	67.1% (±6.9)	65.7% (±5.6)
	Accuracy above relevant change point	70.7% (±4.1)	66.4% (±3.5)	66.4% (±3.5)
High turbidity (all rock classes)	Accuracy below relevant change point	82.1% (±6.7)	85.8% (±7.9)	95.3% (±3.0)
	Accuracy above relevant change point	84.2% (±6.6)	89.5% (±7.0)	91.1% (±3.6)
Average accuracy below relevant change point across all data sets		70.9%	74.6%	76.3%
Average accuracy above relevant change point across all data sets		78.4%	80.3%	79.4%
Average accuracy above and below relevant change point across all data sets		74.6%%	77.4%	77.9%

4 Discussion

4.1 Indicators of community change associated with anthropogenic resuspension

The TITAN successfully identified indicator species/groups from all four data sets. The final list of indicators was collated from both the 'filtered' species and those occurring in the top ten for indicator quality. The species/groups identified included those that increase in abundance along a gradient of anthropogenic resuspension (positive responders) and those that decline with increasing anthropogenic resuspension (negative responders). These lists are the recommended indicator species for sublittoral rock habitats considered (Table 19). The overall accuracy of the indicator will be improved by including as many of the shortlisted (from the filtered and top ten list) species as possible. Furthermore, it is recommended that as many of the species are included when applying the indicator at a specific site, or survey effort at a site, it is unlikely to find or detect all of the species used by the indicator.

Validation examined the ability of the suite of indicators associated with each data set to predict whether a group of observations was drawn from above or below the community change points identified by the TITAN. The results indicated high levels of predictive accuracy (>80%) for high turbidity rock and low turbidity bedrock habitats, moderate accuracy (>70%) for low turbidity boulder habitats and low for low turbidity cobble habitats (>60%). The number of observations was greater for bedrock and high turbidity data sets when compared with boulder and cobble data sets. It is possible that a greater number of observations will have enabled the TITAN to detect more indicator species/groups, i.e. 28 and 19 indicators respectively for low turbidity bedrock and high turbidity datasets compared with 13 and 14 indicators for low turbidity boulder and cobble data sets. This may, in part, indicate why the accuracy varies between data sets and suggests that accuracy can be improved by using more observations in the TITAN.

Several species were consistently selected as suitable indicators, although their response sometimes differed between data sets. *Caryophyllia* spp., Ophiuroidea, *Swiftia pallida* and papillate sponges were typically negative responders. Contrary to this, the MarLIN sensitivity assessment considers *S. pallida*[7] to have an intermediate tolerance to smothering (low confidence) and is tolerant of increases in turbidity (very low confidence). Furthermore, the MarESA approach to sensitivity assessment suggests that the '*Caryophyllia smithii, Swiftia pallida* and *Alcyonium glomeratum* on wave-sheltered circalittoral rock'[8] biotope has a high resistance and resilience to changes in 'suspended solids' and 'smothering and siltation rate changes'. Paguroidea and encrusting sponges were often reported as positive responders in most data sets. Bell *et al*. (2002) and Pineda *et al*. (2016) state that upright sponges are more likely to be found in areas of high sedimentation, which would suggest that encrusting sponges are more likely to have a negative response. However, it might be sporadic and episodic nature of anthropogenic resuspension that modifies this relationship.

The change points identified by the TITAN indicate that relatively low levels of anthropogenic resuspension cause a community change, and that this is especially the case in low turbidity bedrock habitats (Table 18). The levels at which species/groups respond positively to anthropogenic resuspension is much higher than the negative change points. Equally, the positive change points progressively increase from low turbidity bedrock, boulder to cobble data sets, although the high turbidity data set is associated with a low change point. The low change points associated with the high turbidity data set is perhaps surprising, as one might

[7] http://www.marlin.ac.uk/species/detail/1276
[8] http://www.marlin.ac.uk/habitats/detail/1122

have expected that very high levels of anthropogenic resuspension would be required to induce community changes in areas with naturally high turbidity. The properties and interaction between natural and anthropogenic turbidity are worthy of further research and should aid in the interpretation of the indicators identified here.

The validation of the benchmark information (logged abundance, Appendix 4) means that each suite of indicator species/groups can be applied to other sublittoral rock data sets for the assessment of condition, as modified by anthropogenic resuspension. The approach for estimating anthropogenic resuspension (combination of substrata and VMS with resuspension coefficients and diffusion) also provides a potential assessment of the relative intensity of this pressure in other areas. Further validation of the method used to calculate anthropogenic resuspension may allow an 'activity-led' approach for assessing the overlap of sublittoral rock with human pressures.

4.2 The proportion of community variance explained by the indicator

The RDAs state that the explanatory variables included in the analysis only account for 13-20 % of the biological variance (Table 13 and Table 15). The most important explanatory variables include latitude and longitude (capturing the spatial autocorrelation that exists within the observations – a full guide to spatial autocorrelation is provided in Appendix 2), substratum quantity and type, biozone (depth bands) and natural surface turbidity (Table 14,Table 16 and Table 17). Efforts were made to stratify the main data set (Table 6) so that some of the dominance of certain factors was partially removed, e.g. the production of low turbidity bedrock, boulder, and cobble and high turbidity sublittoral rock data sets. An initial investigation stratified the main data set further, by rock quantity, rock type and by turbidity however, the sample size for the resultant data sets was often small and the results of the TITANs variable and uncertain. Further work should examine other stratification structures that might provide more consistent divisions of the main data set.

Given that the explanatory variables only explained a small proportion of the total variance, it is important to place the explanatory power of this indicator into context. The RDAs reported that the commonplace predictor variables (e.g. depth, substratum etc.) were more important in explaining the biological variance than anthropogenic resuspension. As such, it is likely that anthropogenic resuspension only explains a very small amount of biological change. This may mean that the method used to represent anthropogenic resuspension was not reflective of the actual pressure or that the amount of impact from this pressure is actually very small and does not induce much, if any, change within sublittoral rock communities. This point is important to remember when applying the indicator, i.e. although the indicator can predict community differences above and below a change point (induced by anthropogenic resuspension), this change is relatively insignificant when the total variance in considered.

It is assumed that most of the variance that hasn't been captured by the explanatory variables are associated with the way the data has been collected, structured and processed rather than being associated with ecological trends that cannot be explained by the included environmental and anthropogenic variables. The unexplained variance might be related to:

1) the use of the SACFOR scale for recoding abundance during survey observations;
2) the combined use of species, genus, families and morphological groupings within the community matrices;
3) poor sampling efficiency for small and cryptic species in the video footage when compared with large-bodied Anthozoan and big sponges (which are probably sampled fairly well);

4) the use of different contractors to enumerate survey footage;
5) the use of semi-quantitative survey methods, e.g. counts and cover estimates from video or still photography;
6) the possible variations in the survey design, apparatus or conditions experienced (e.g. visibility) between sites;
7) being unable to standardise the field of view (and subsequent estimates of abundance) within and between stations and sites; and
8) bias and structures introduced into the data through the conversion of the SACFOR scale to logged abundances.

It may not be possible to account for the variance introduced by the points above fully. Should the analysis be repeated, it is recommended that:

(i) only the species/groups that are known to be sampled with certainty are included, e.g. sponge morphologies, large-bodied species, and high-cover species;
(ii) a greater proportion of the rare species are removed from the data sets;
(iii) more species are aggregated to a higher taxonomic level;
(iv) greater filtering of observations or sites with different survey designs, apparatus or conditions is undertaken; and
(v) more of the low quantity rock observations are removed (due to the limited sample size, this analysis only removed observations with less than 10 % rock cover).

4.3 Further development of the sublittoral rock indicator

As stated above, repeating the analysis with just the common and conspicuous species or morphological groups is likely to reduce the amount of biological variance that remains unexplained. Furthermore, efforts should be made to validate and ground-truth the anthropogenic resuspension proxies generated from the VMS-derived surface and sub-surface abrasion information. This analysis used the anthropogenic resuspension proxy for the year proceeding the survey observations. Proxies that combine multiple years of information, e.g. 4 to 5 years before the survey observation, might provide a better representation of the long-term pressure. A longer period may better capture the impact of chronic levels of pressure of the benthic community. There is also a significant discrepancy between the spatial scale associated with the biological observations and that of the VMS (gridded at 0.05 degree), and the resulting anthropogenic resuspension information. The coarse spatial resolution of the activity and resulting pressure information results in a generalisation of the impact within sites. This generalisation may weaken the relationship between the response of the biological observations and the predicted level of pressure.

The validation process randomly resampled the existing data used in the TITAN and the selection of indicator species/groups. Ideally, the validation data would be an independent data set obtained by either bootstrapping the TITAN data set or by withholding a small (20 to 30%) proportion of original data, not used in the TITAN, for validation of the indicator. Stratification of the main data set into smaller data sets placed limitations on the number of samples, which meant that withholding a proportion of the observations for validation was not possible.

The relative influence of anthropogenic resuspension on the sublittoral rock communities was small. However, this does not mean that they are not impacted by human activities. This project focused specifically on the possible impact of resuspension from mobile, bottom-contacting fishing gear. Although this is considered the most prevalent human pressure, other anthropogenic pressures may also be modifying the sublittoral rock communities. For example, physical abrasion from accidental contact of fishing gear on rock may be an infrequent but severe impact. Furthermore, there are many anecdotal reports of physical abrasion impacts from pots and pot marker buoys. Much of this activity is likely to be close to shore and in relatively shallow water. Equally, there is no evidence of significant impacts on benthic species and communities on sublittoral bedrock, boulder or cobble reef from potting (Walmsley *et al.* 2015). However, it is accepted that there is a lack of long-term and well-designed studies to specifically address this issue. Further development of this indicator should seek to assess the relative importance of different sources of anthropogenic pressure on sublittoral rock communities.

This project presented a method for the transformation and alignment of SACFOR cover and counts scales. Errors within this process may result in an offset between species assessed using count and cover. As such, the SACFOR conversion needs to be confirmed to ensure it is representing the original data correctly. This process is being currently undertaken by the authors as an independent validation project. Simulated data sets are being used to understand the loss of information when abundances are initially classified according to the SACFOR scale, and the fidelity of information during the conversion process (as used here).

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Appendix 1: Included and excluded species

Table 21. Species and morphological groups included in the main data set.

Abietinaria abietina	*Leptothecatae*	Porifera massive
Actiniaria	*Luidia sarsi*	Porifera globular
Alcyonacea	*Lytocarpia myriophyllum*	Porifera lamellate
Alcyonidium	*Macropodia*	Porifera papillate
Amphiura	*Maja squinado*	Porifera repent
Antedon bifida	Majoidea	Porifera tubular
Antipatharia	*Marthasterias glacialis*	Sabellidae
Aphrodita aculeata	*Mesacmaea mitchellii*	*Sagartia*
Asteriidae	*Metridium dianthus*	Sertulariidae
Brachyura	Nemertea	*Tubularia*
Brisingella coronata	*Neogastropoda*	*Urticina*
Calliactis parasitica	*Ophiopholis aculeata*	*Urticina felina*
Calliostoma	*Ophiura*	*Valvatida*
Caryophyllia	Ophiuroidea	*Vesicularia*
Cellepora pumicosa	*Pentapora foliacea*	
Cerianthidae	Porifera arborescent	
Crinoidea	Porifera boring	
Didemnidae	Porifera columnar	
Ebalia	Porifera cup	
Hydrallmania falcata	Porifera cushion	
Hymedesmiidae	Porifera encrusting	
Inachidae	Porifera erect	
Lanice conchilega	Porifera flabellate	
Leptometra celtica	Porifera lobose	

Table 22. Species and morphological groups excluded from the main data set using the 2% commonality threshold (i.e. very rare species).

Acanthocardia aculeata	*Bathynectes*	*Cerianthus lloydii*
Actiniidae	*Berthella*	Chaetopteridae
Actinostolidae	*Bispira*	Chaetopterus tubes
Adamsia	Bivalvia	*Chlamys*
Aeolidioidea	*Bolocera tuediae*	*Cidaris cidaris*
Aglaophenia	*Botryllus schlosseri*	*Ciona intestinalis*
Aglaopheniidae	Bougainvilliidae	*Cirripedia*
Alcyonium digitatum	*Bowerbankia*	*Cnidaria*
Alcyonium glomeratum	*Brachiopoda*	*Colus*
Amphipoda	Brisingidae	Corallimorphidae
Annelid_Tube_c	Bryozoa	Corallinaceae
Annelida	Buccinidae	*Corymorpha*
Anomura	*Bugula*	*Corynactis*
Antedon	*Bugulidae*	*Crepidula fornicata*
Antedon petasus	*Caberea boryi*	Crisiidae
Antedonidae	*Calveriosoma fenestratum*	*Crossaster papposus*
Anthozoa	*Cancer pagurus*	Crustacea
Ascidia mentula	*Candelabrum*	Cyclostomatida
Ascidia virginea	*Capnea sanguinea*	Decapoda
Ascidiacea	*Capulus*	Demospongiae
Asterias rubens	Caryophylliidae	*Dendrodoa*
Astropecten irregularis	*Cellaria*	*Dendronotus*
Atrina fragilis	Celleporidae	*Diazona violacea*
Balanoidea	*Cereus pedunculatus*	*Diphasia alata*
Ditrupa	Galatheoidea	*Hormathia*
Ditrupa arietina	*Gastropoda*	Hormathiidae
Ditrupa shell	*Gersemia rubiformis*	*Hyalinoecia*
Dysidea fragilis	Geryonidae	*Hydractinia echinata*
Echinidea	*Gibbula*	*Hydrozoa*
Echinocardium	Goniasteridae	*Inachus*
Echinodermata	Goniodorididae	*Janolus cristatus*
Echinoidea	Gorgonacea	*Lafoea dumosa*
Echinus	*Gorgonocephalus*	*Leptasterias muelleri*
Echinus acutus	*Gracilechinus acutus*	*Leuconia*
Echinus esculentus	Grantiidae	Leucosoleniidae
Echiura	*Halcampa*	*Lineus longissimus*
Edwardsiidae	*Halcampoides abyssorum*	*Littorina*

Emarginula rosea	*Halcampoides elongatus*	*Littorinimorpha*
Epizoanthus	Halcampoididae	*Lophelia pertusa*
Eubranchus farrani	*Haleciidae*	*Luidia*
Eucarida	*Heliometra glacialis*	*Luidia ciliaris*
Eudendriidae	Hemiasterellidae	*Madrepora oculata*
Filifera	*Henricia*	*Megalomma vesiculosum*
Fissurellidae	*Hero formosa*	*Mesogastropoda*
Flabellina	Hexacorallia	Microcionidae
Flabellinidae	*Hippasteria phrygiana*	*Molgula*
Flustra foliacea	*Holothuria*	*Munida*
Flustridae	Holothuriidae	Muricidae
Mycalidae	Paguroidea	*Polymastiidae*
Mytiloida	*Pagurus*	*Polynoidae*
Mytilus edulis	*Palinurus elephas*	*Polyplacophora*
Myxillidae	*Palmiskenea skenei*	*Polyzoniae*
Nemertesia	*Parasmittina*	*Pomatoceros triqueter*
Nemertesia antennina	*Parasmittina trispinosa*	*Porania pulvillus*
Nemertesia ramosa	*Parastichopus tremulus*	*Porella*
Neocheilostomatina	*Parazoanthus*	*Porella compressa*
Neoloricata	*Parazoanthus anguicomus*	Porifera
Novocrania	*Paromola cuvieri*	*Portunidae*
Nudibranchia	Patellidae	*Prosobranchia*
Nymphonidae	*Patellogastropoda*	*Prostheceraeus vittatus*
Oceanapia robusta	*Paxillosida*	*Psammechinus miliaris*
Omalosecosa ramulosa	*Peachia*	*Psolus*
Ophiactidae	*Pecten maximus*	*Pycnogonida*
Ophiactis	Pectinidae	*Pyura*
Ophiocomina nigra	Pennatulacea	*Reteporella*
Ophiothrix fragilis	*Pentapora fascialis*	*Rhizocaulus verticillatus*
Ophiura albida	Pholadomyoidea	*Rhodophyta*
Ophiura ophiura	*Pliobothrus*	*Rhodophyta foliose*
Opisthobranchia	Plumularioidea	*Rissoidae*
Osteichthyes	*Polycarpa*	*Sabella*
Oxydromus flexuosus	*Polychaeta*	*Sabellaria spinulosa*
Pachycerianthus multiplicatus	*Polyclinum*	*Sabellida*
Sabellida_Tubes	Terebellidae	
Sagartia elegans	*Thoracica*	
Sagartia troglodytes	*Thuiaria thuja*	

Sagartiidae	*Trivia*
Salmacina	Trochidae
Scaphopoda	Tubulariidae
Scleractinia	*Tunicata*
Scrupocellaria	*Urticina eques*
Securiflustra securifrons	Zoantharia
Serpulidae	
Sertularella	
Sertularia	
Sertularia spp.	
Sipunculidae	
Smittinoidea	
Solasteridae	
Spinulosida	
Spirobranchus	
Spirorbis	
Stichastrella rosea	
Stomphia coccinea	
Suberitidae	
Swiftia pallida	
Syringammina fragillissima	

Appendix 2: Spatial autocorrelation

What is spatial autocorrelation?

Spatial autocorrelation (SAC) is a measure of the correlation of a variable with itself through space. Spatial autocorrelation arises where the values of variables sampled at nearby locations are not independent of each other. This phenomenon gives rise to Tobler's first law of geography: "Everything is related to everything else, but near things are more related than distant things" (Tobler 1970).

Spatial autocorrelation can be positive or negative; put simply, positive SAC occurs when similar values occur near one another, whilst negative SAC occurs when dissimilar values occur near one another (Figure 6).

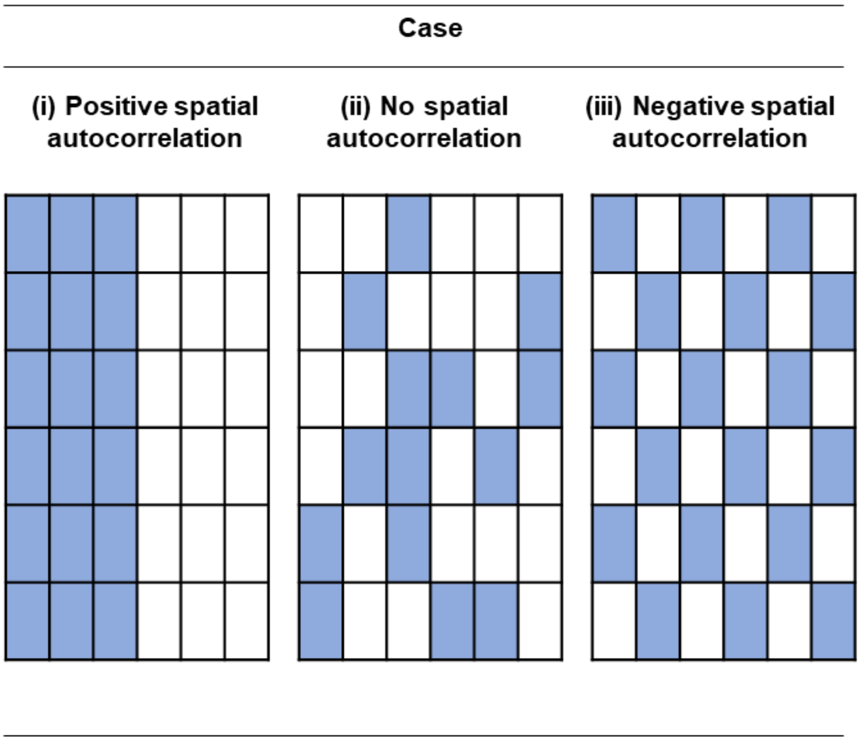

Figure 6. Stylised examples of spatial autocorrelation.

What causes spatial autocorrelation?

Whilst there are many causes of SAC, three factors are particularly common (Legendre & Fortin 1989; Legendre 1993; Legendre & Legendre 1998):

- distance-related biological processes (such as speciation, extinction, dispersal or species interactions) are operating;
- non-linear relationships between environment and species have been erroneously modelled using linear methods; or
- the statistical model fails to account for an important environmental determinant that, in itself, is spatially structured and thus causes spatial structuring in the response.

Note that the second and third of these points may not always be referred to as SAC, but rather as spatial dependency (Legendre *et al.* 2002).

Scale dependence of spatial autocorrelation

The strength of SAC may be influenced by scale or spatial resolution, as illustrated in Figure 7.

High negative SAC is exhibited in Case (i) since each cell has a different value (colour) from its immediate neighbours. Each cell in Case (i) may be subdivided into four smaller cells - i.e. the scale at which the data recorded or reported can be adjusted, increasing the spatial resolution – producing the arrangement as seen in Case (ii).

Assuming homogeneity across the larger cells, the strength of SAC among the black and white cells increases in Case (ii) relative to Case (i), while maintaining the same cell arrangement. This illustrates that SAC varies with the study scale.

Consequently, the potential influence of differing scales should be considered when comparing aspects of SAC between studies, or between datasets within the same study.

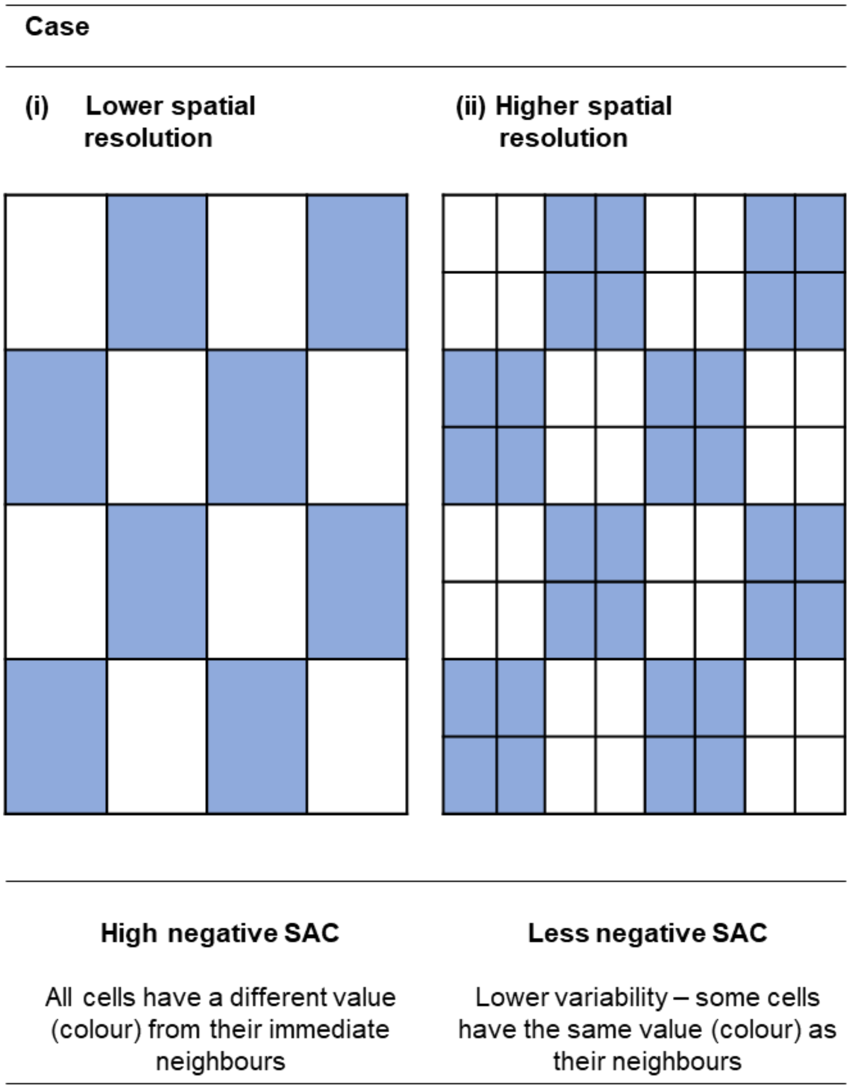

Figure 7. Estimates of spatial autocorrelation may vary with changes in scale (changes in the spatial resolution of data).

Why is spatial autocorrelation important?

Statistical analyses are used to characterise populations based on samples taken from those populations. Both classical and spatial statistics are based on, amongst other factors, the underlying assumption that observations are independent of one another. The prior consideration of SAC is important because, where SAC is in evidence, the assumptions of independence may be violated, and there is a possibility that a bias in the sampling process may be introduced; statistics calculated from a biased sample population will not accurately represent the population that is of interest, with an associated increase in the potential for type I errors to occur (detecting an effect that is not present).

Addressing SAC within a proposed analysis is not impossible and leads to more robust and replicable results. Conversely, where there is no evidence of SAC, analysis using standard statistical approaches is acceptable.

Whilst it may present a challenge to the analysis of spatial data, SAC may also be seen as an opportunity when it provides useful information for inference of process from pattern by, for example, increasing our understanding of contagious biotic processes such as population growth, geographic dispersal, differential mortality or competition dynamics (Griffith & Peres-Neto 2006).

Detecting spatial autocorrelation

Weighting distances

As a spatial phenomenon it is imperative, at the outset of any consideration of SAC, to define what is meant by two observations being ‘close together’, i.e. the relative importance of different distances between observations of a variable x at locations i, j should be determined. This information is usually presented in a weight matrix and define the relationships between locations where measurements of x were made. If data are collected at n locations, then the weight matrix will be $n \times n$, with zeroes on the diagonal.

The weight matrix can be specified in many ways, for example:

- the weight for any two different locations is a constant;
- all observations within a specified distance have a fixed weight;
- k nearest neighbours have a fixed weight, and all others are zero; or
- weight is inversely proportional to the distance between observations (or the distance squared, or the distance up to a specified maximum threshold).

In practice, the selected weight matrix is often row-standardized, i.e. all the weights in a row sum to one, although the actual values in the weight matrix are up to the researcher.

Note that, in addition to the above examples, other weight matrices might be considered appropriate.

Measures of spatial autocorrelation

Moran's I

Moran's I (Moran, 1950) tests for global SAC for continuous data. It is based on cross-products of the deviations from the mean and is calculated for n observations of a variable x at locations i, j, and is calculated as:

$$I = \frac{n}{S_0}\frac{\sum_i \sum_j W_{ij}(x_i - \overline{x})\left(x_j - \overline{x}\right)}{\sum_i (x_i - \overline{x})^2}$$

where $\overline{x}$ is the mean of the x variable, W_{ij} are the elements of the weight matrix, and the normalising factor, S_0, is the sum of the elements of the weight matrix:

$$S_0 = \sum_i \sum_j W_{ij}$$

Moran's I is similar to, but not equivalent with, a correlation coefficient. Values for Moran's I vary from -1 to +1; in the absence of autocorrelation (and regardless of the specified weight matrix) the expected value for Moran's I is $-1/(n-1)$, which tends to zero as the sample size increases. For a row-standardised spatial weight matrix, the normalising factor S_0 equals n (since each row sums to 1), and the statistic simplifies to a ratio of a spatial cross product to a variance. A value for Moran's I larger than $-1/(n-1)$ indicates positive SAC, and a Moran's I less than $-1/(n-1)$ indicates negative SAC (Table 1).

The variance for Moran's I is given by:

$$Var(I) = \frac{\{(n^2 - 3n + 3)S_1 - nS_2 + 3S_0^2\} - k\{n(n-1)S_1 - 2nS_2 + 6S_0^2\}}{(n-1)(n-2)(n-3)S_0^2} - \frac{1}{(n-1)^2}\text{, where:}$$

$$S_1 = \frac{1}{2}\sum \sum_{i \neq j} \left(W_{ij} + W_{ij}\right)^2 = 2S_0 \text{ for symmetric W containing 0s and 1s, and}$$

$$S_2 = \sum_i (W_{i0} + W_{0i})^2 W_{i0}\text{, where } W_{i0} = \sum_j Wij \text{ and } W_{0i} = \sum_j Wji$$

Geary's C

Geary's C (Geary, 1954) is based on the deviations in responses of each observation with one another, and is calculated as:

$$C = \frac{n-1}{2S_0}\frac{\sum_i \sum_j W_{ij}\left(x_i - x_j\right)^2}{\sum_i (x - \overline{x})^2}$$

Values for Geary's C range from 0 (maximal positive autocorrelation) to a positive value for high negative autocorrelation. Values less than 1 indicate positive SAC, whilst in the absence of autocorrelation, its expected value is 1, regardless of the specified weight matrix (Table 1).

The variance for Geary's C is given by:

$$Var(C) = \frac{1}{n(n-2)(n-3)S_0^2\left\{S_0^2[(n^2-3)-k(n-1)^2]+S_1(n-1)[n^2-3n+3-k(n-1)]+\frac{1}{4}S_{2(n-1)[k(n^2-n+2)-(n^2+3n-6)]}\right\}}$$

Where S_0, S_1, and S_2 are the same as for Moran's I (above).

Comparison of Moran's I and Geary's C

Moran's I is a more global measurement and is sensitive to extreme values of x, whereas Geary's C is more sensitive to differences at a more local scale (i.e. in smaller neighbourhoods). Whilst Moran's I and Geary's C generally result in similar conclusions, Moran's I is often preferred as an indicator of SAC as it has been shown to be more powerful than Geary's C.

Table 23. A synopsis of Moran's I and Geary's C.

	Case		
	Positive spatial autocorrelation	No spatial autocorrelation	Negative spatial autocorrelation
Values for Moran's I	I → +1	I ~ 0	I → -1
Values for Geary's C	0 ≤ C < 1	C ~ 1	1 < C < 2

Checking for spatial autocorrelation

Checking for SAC has become a commonplace exercise in geography and ecology; established procedures include:

- plots of Moran's I (also termed Moran's I correlograms);
- Geary's c correlograms; and
- semi-variograms.

In all three cases a measure of similarity (Moran's I, Geary's c) or of variance (variogram) between pairs of observations (x_{ij}) is plotted as a function of the distance between observations (d_{ij}), with distances often grouped into bins.

Moran's I-based correlograms typically show a decrease from some level of SAC to a value of 0 (or below; the expected value of Moran's I in the absence of SAC, $E(I), = 1/(n-1)$, where n = sample size), indicating no SAC at some distance between locations. Variograms depict the opposite, with the variance between pairs of points increasing up to a certain distance, where variance levels off. Variograms are more commonly employed in descriptive geostatistics, while correlograms are the prevalent graphical presentation in ecology (Fortin and Dale, 2005). Values of Moran's I are assessed by a test statistic (the Moran's I standard deviate) which indicates the statistical significance of SAC in (e.g.) model residuals. Additionally, model residuals may be plotted as a map that more explicitly reveals particular patterns of SAC (e.g. anisotropy or non-stationarity of SAC). For further details and formulae see, e.g. Isaaks and Shrivastava (1989) or Fortin and Dale (2005).

Correcting for spatial autocorrelation

Although a variety of methods have been developed to correct for the effects of SAC, only a few are reported in the ecological literature. Available methods fall into three classes and include:

(i) capturing spatial configuration in additional covariates, which can then be included in a generalised linear model (GLM):
  - autocovariate regression;
  - spatial eigenvector mapping (SEVM);

(ii) approaches that fit a variance-covariance matrix based on the non-independence of spatial observations:
- generalised least squares (GLS);
- conditional autoregressive models (CAR);
- simultaneous autoregressive models (SAR);
- generalised linear mixed models (GLMM); and

(iii) splitting the data into smaller clusters before modelling the variance-covariance relationship:
- generalised estimation equations (GEE).

Further details on these approaches are provided in Dormann *et al.* (2007).

Assumptions

The choice of correction method is heavily dependent on the error distribution that is seen in the data. However, all of the methods listed above assume *spatial stationarity*, i.e. SAC and the effects of environmental correlates are constant across the region (there are very few methods to deal with non-stationarity). Stationarity may or may not be a reasonable assumption, depending, among other things, on the spatial extent of the study. If the main cause of SAC is dispersal (for example in research on animal distributions), stationarity is likely to be violated, for example when moving between areas that constrain or restrict movement to differing degrees. One method able to accommodate spatial variation in SAC is a geographically weighted regression, although this method not considered further here because of its limited use for hypothesis testing (coefficient estimates depend on spatial position) and because it was not designed to remove SAC.

Another assumption is that of *isotropic spatial autocorrelation*. This means that the process causing the SAC acts in the same way in all directions. Environmental factors that may cause anisotropic SAC include water currents (e.g. carrying plankton) and directionality in sediment transport (e.g. carrying larvae or plant propagules). Examples of analyses accounting for anisotropy in ecological data are available in the literature, and several of the methods described below can be adapted to such circumstances.

Further options for accommodating spatial autocorrelation in analyses

Finally, there are also methods which correct test statistics for data that display SAC; including a modified t-test (Dutilleul 1993), the CRH-correction for correlations (Clifford *et al.* 1989), randomisation tests such as partial Mantel tests (Legendre & Legendre 1998), or strategies employed by Lennon (2000), Liebhold and Gurevitch (2002) and Segurado *et al.* (2006) which are all useful in enabling the robust assessment of correlation between environmental and response variables.

Appendix 3: Raw TITAN output

The output specifies whether species respond positively or negatively to an increasing gradient of anthropogenic resuspension from surface abrasion in the 'response' column. The filtered responses, shown an as shaded cells in the tables, have passed the purity (the proportion of change-point response directions (positive or negative) among bootstrap replicates that agree with the observed response at a 95% level of agreement (Baker and King, 2010)) and reliability (the proportion of bootstrap change points whose IndVal scores consistently results I P-values below one or more at a 95% probability level).

Table 24. TITAN output for the subset containing low turbidity bedrock observations merged across all rock quantity classes. Cells shaded in green and annotated with an asterisk (*) in the response column are associated with very high levels of purity and reliability (i.e. 'filtered' responses). For indicator quality, values highlighted using † and with blue shaded cells are species with indicator quality values (on a scale of 0 - 3 with higher values corresponding to higher quality indicator properties) ranked in the top 10.

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Abietinaria abietina	80	Negative	5.46	0.74	0.99	1.97
Actiniaria	65	Positive*	4.25	0.99	1.00	2.22
Alcyonidium spp.	519	Negative*	38.26	1.00	1.00	2.49 †
Alcyonium digitatum	24	Positive	1.24	0.51	0.88	1.70
Antedon bifida	300	Positive*	18.79	1.00	1.00	2.35
Asteriidae	307	Negative*	17.47	0.99	1.00	2.33
Brachiopoda	666	Positive*	24.85	0.99	1.00	2.40 †
Calliostoma	151	Negative*	17.04	0.98	0.99	2.20
Caryophyllia spp.	1540	Positive*	49.79	0.99	1.00	2.53 †
Corallinaceae	14	Negative*	1.66	1.00	1.00	2.21
Corynactis spp.	210	Negative*	16.77	1.00	1.00	2.33
Crinoidea	110	Positive*	6.19	0.98	1.00	2.24
Crossaster papposus	17	Positive	1.05	0.81	0.76	1.88
Echinoidea	96	Negative	4.55	0.66	1.00	1.90
Echinus esculentus	229	Negative	16.49	0.91	1.00	2.34

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Galatheoidea	7	Positive	0.71	0.68	0.54	1.42
Henricia spp.	31	Negative*	4.51	0.98	1.00	2.21
Munida spp.	50	Positive*	8.22	0.97	0.98	2.22
Nemertesia spp.	440	Negative	35.72	0.54	1.00	2.01
Ophiactidae	202	Negative	47.83	0.90	1.00	2.44 †
Ophiocomina nigra	169	Positive*	16.62	1.00	1.00	2.33
Ophiothrix fragilis	161	Positive	48.9	0.82	1.00	2.36 †
Ophiura spp.	444	Positive*	20.94	0.98	1.00	2.36 †
Ophiura albida	249	Positive*	15.61	1.00	1.00	2.33
Ophiuroidea	492	Positive*	27.75	1.00	1.00	2.42 †
Paguroidea	301	Positive*	13.73	1.00	1.00	2.31
Palmiskenea skenei	29	Positive*	1.83	0.97	0.99	2.18
Pectinidae	4	Positive	10.95	0.97	0.91	2.16
Polyplacophora	88	Negative	7.44	0.56	0.99	1.71
Porania pulvillus	115	Positive*	5.26	0.95	0.99	2.19
Porella spp.	765	Positive	27.75	0.88	1.00	2.32
Porifera arborescent	299	Negative	16.47	0.93	1.00	2.27
Porifera encrusting	345	Negative	18.03	0.72	1.00	2.07
Porifera erect	34	Positive	2.73	0.59	1.00	1.81
Porifera flabellate	433	Negative	18.47	0.72	1.00	2.07
Porifera globular	75	Negative*	6.45	1.00	1.00	2.25
Porifera lamellate	45	Negative	10.53	0.94	1.00	2.22
Porifera massive	50	Negative	4.09	0.89	1.00	2.22
Porifera papillate	102	Negative*	11.62	1.00	1.00	2.39 †

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Porifera repent	99	Positive*	6.65	1.00	1.00	2.25
Porifera tubular	6	Positive	0.47	0.61	0.30	1.12
Reteporella	57	Negative	7.33	0.62	0.96	1.73
Rhodophyta	98	Negative*	18.39	1.00	1.00	2.34
Sabellida	15	Positive	2.33	1.00	0.96	2.18
Sagartiidae	4	Positive	0.46	0.66	0.60	1.47
Securiflustra securifrons	5	Positive	49.92	1.00	0.99	2.53 †
Serpulidae	1031	Negative	54.25	1.00	1.00	2.64 †
Sertulariidae	154	Positive	9.46	1.00	1.00	2.28
Spirobranchus spp.	142	Positive	74.18	0.58	1.00	2.19
Stichastrella rosea	46	Negative	5.09	0.97	1.00	2.31
Swiftia pallida	146	Negative	8.76	1.00	1.00	2.37 †
Trochidae	228	Negative	10.89	1.00	1.00	2.29
Urticina spp.	7	Positive	0.86	0.96	0.75	1.93

Table 25. TITAN output for the subset containing low turbidity boulder observations merged across all rock quantity classes. Cells shaded in green and annotated with an asterisk (*) in the response column are associated with very high levels of purity and reliability (i.e. filtered' responses). For indicator quality, values highlighted using † and with blue shaded cells are species with indicator quality values (on a scale of 0 - 3 with higher values corresponding to higher quality indicator properties) ranked in the top 10.

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Abietinaria abietina	10	Positive	6.46	0.72	0.62	1.58
Actiniaria	54	Negative	8.6	0.68	0.96	1.90
Alcyonidium spp.	9	Positive	3.33	0.58	0.96	1.77
Alcyonium digitatum	8	Positive	2.2	0.85	0.74	1.90
Antedon bifida	37	Negative	6.79	0.52	0.91	1.68
Asteriidae	123	Negative	19.25	0.93	1.00	2.28
Brachiopoda	144	Negative*	27.03	1.00	1.00	2.40 †
Calliostoma	18	Positive	39.63	0.74	0.92	2.01
Caryophyllia spp.	399	Negative*	66.98	1.00	1.00	2.61 †
Crinoidea	13	Negative	3.57	0.69	0.94	1.86
Echinoidea	16	Positive	12.38	0.88	1.00	2.16
Echinus esculentus	103	Positive	21.55	0.53	0.97	1.95
Galatheoidea	6	Negative	2.72	0.67	0.51	1.40
Henricia spp.	9	Negative	14.98	0.71	0.98	1.99
Munida spp.	85	Positive	13	0.73	0.90	1.93
Nemertesia spp.	103	Positive	20.08	0.45	0.86	1.66
Ophiactidae	11	Positive	6.26	0.75	0.96	1.95
Ophiocomina nigra	8	Negative	3.06	0.84	0.77	1.83
Ophiothrix fragilis	13	Negative	3.88	0.70	0.90	1.83
Ophiura spp.	37	Positive	7.13	0.88	0.94	2.07
Ophiura albida	33	Positive	7.55	0.77	0.99	2.02

Species/group	**Frequency**	**Response**	**Indicator value**	**Purity**	**Reliability**	**Indicator quality**
Ophiuroidea	48	Negative*	11.03	0.99	1.00	2.27
Paguroidea	69	Positive	17.98	0.76	1.00	2.08
Palmiskenea skenei	46	Negative	10.6	0.51	1.00	1.79
Pectinidae	5	Positive	1.37	0.74	0.33	1.29
Polyplacophora	10	Negative	3.28	0.90	0.94	1.97
Porania pulvillus	38	Negative	9.33	0.67	0.99	1.92
Porella spp.	270	Negative*	53.25	1.00	1.00	2.59 †
Porifera arborescent	38	Positive*	57.25	0.99	1.00	2.56 †
Porifera encrusting	58	Positive*	82.35	1.00	1.00	2.72 †
Porifera flabellate	17	Negative*	22.23	0.97	1.00	2.31
Porifera globular	22	Negative	4.4	0.39	0.83	1.46
Porifera lamellate	8	Positive	22.79	0.66	0.99	2.00
Porifera massive	17	Positive	16.22	0.55	0.79	1.74
Porifera papillate	27	Negative*	7.56	0.98	1.00	2.34 †
Porifera repent	8	Negative	4.41	0.90	0.87	2.00
Reteporella	9	Negative	3.51	0.47	0.69	1.29
Sabellida	9	Positive	3.52	0.94	0.90	2.07
Serpulidae	310	Negative*	57.29	0.99	1.00	2.62 †
Sertulariidae	13	Negative*	11.05	1.00	1.00	2.27
Spirobranchus spp.	49	Positive*	72.44	1.00	1.00	2.56 †
Stichastrella rosea	38	Positive*	8.74	0.99	0.99	2.35 †
Swiftia pallida	12	Negative*	13.86	1.00	1.00	2.39 †
Trochidae	20	Negative	8.75	0.83	0.99	2.08
Urticina spp.	7	Positive	12.21	0.99	0.93	2.20

Table 26. TITAN output for the subset containing low turbidity cobble observations merged across all rock quantity classes. Cells shaded in green and annotated with an asterisk (*) in the response column are associated with very high levels of purity and reliability (i.e. filtered' responses). For indicator quality, values highlighted using † and with blue shaded cells are species with indicator quality values (on a scale of 0 - 3 with higher values corresponding to higher quality indicator properties) ranked in the top 10.

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Abietinaria abietina	8	Positive	4.9	0.68	0.90	1.80
Actiniaria	88	Positive	10.95	0.84	0.92	2.03
Alcyonidium spp.	9	Negative*	9.45	0.99	1.00	2.24
Alcyonium digitatum	25	Negative*	3.79	0.97	0.95	2.24
Antedon bifida	22	Negative	2.91	0.78	0.75	1.75
Asteriidae	188	Positive*	17.4	0.99	0.99	2.31 †
Brachiopoda	255	Positive	23.88	0.83	1.00	2.21
Calliostoma	7	Negative	3.13	0.87	0.72	1.71
Caryophyllia spp.	494	Negative	42.66	1.00	1.00	2.42 †
Crinoidea	9	Positive	1.61	0.57	0.65	1.43
Echinoidea	39	Positive*	23.03	1.00	1.00	2.33 †
Echinus esculentus	49	Positive	10.42	0.72	0.99	2.08
Galatheoidea	23	Positive	3.47	0.98	0.92	2.12
Henricia spp.	9	Positive	13.1	0.88	0.99	2.14
Munida spp.	77	Positive	8.72	0.79	0.88	1.93
Nemertesia spp.	153	Negative	14.44	0.85	0.96	2.11
Ophiactidae	18	Positive	7.53	0.67	1.00	1.91
Ophiocomina nigra	24	Positive	3.94	0.76	0.96	1.94
Ophiothrix fragilis	25	Positive	3.77	0.71	0.98	1.92
Ophiura spp.	89	Negative	14.14	0.50	1.00	1.79
Ophiura albida	103	Positive	11.35	0.65	0.93	1.85

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Ophiuroidea	137	Negative	17.43	0.61	0.89	1.82
Paguroidea	154	Positive*	15.64	0.98	0.99	2.28
Palmiskenea skenei	101	Negative	11.7	0.89	1.00	2.18
Pectinidae	14	Positive	2.59	0.92	0.85	1.98
Polyplacophora	30	Positive	3.09	0.63	0.69	1.44
Porania pulvillus	44	Positive	20.87	0.84	0.99	2.15
Porella spp.	219	Negative*	28.09	1.00	1.00	2.38 †
Porifera arborescent	27	Positive*	46.21	1.00	1.00	2.45 †
Porifera encrusting	55	Positive	94.22	1.00	1.00	2.71 †
Porifera flabellate	18	Positive*	37.04	0.97	1.00	2.37 †
Porifera globular	138	Positive	20.75	0.86	1.00	2.19
Porifera lamellate	5	Positive	10.09	0.55	1.00	1.80
Porifera massive	37	Positive	15.06	0.88	0.94	2.20
Porifera papillate	40	Negative*	5.07	0.73	0.98	2.04
Porifera repent	4	Positive	4.35	0.97	0.83	2.02
Reteporella	28	Negative	2.71	0.65	0.76	1.53
Sabellida	8	Positive	2.13	0.55	0.83	1.59
Serpulidae	536	Negative*	70.25	1.00	1.00	2.67 †
Sertulariidae	10	Negative*	13.02	1.00	1.00	2.27
Spirobranchus spp.	40	Positive*	95.65	1.00	1.00	2.62 †
Stichastrella rosea	41	Negative	4.87	0.76	0.89	1.99
Swiftia pallida	12	Negative*	22.64	1.00	1.00	2.43 †
Trochidae	11	Negative	17.76	0.88	0.96	2.14

Table 27. TITAN output for the subset containing high turbidity observations merged across all rock types and quantity classes (i.e. all Wight Barfleur observations). Cells shaded in green and annotated with an asterisk (*) in the response column are associated with very high levels of purity and reliability (i.e. filtered' responses). For indicator quality, values highlighted using † and with blue shaded cells are species with indicator quality values (on a scale of 0 - 3 with higher values corresponding to higher quality indicator properties) ranked in the top 10.

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Actiniaria	144	Positive*	36.78	0.99	1.00	2.59 †
Alcyonidium spp.	34	Negative	2.73	0.95	0.99	2.17
Alcyonium digitatum	157	Positive	8.86	0.85	1.00	2.26
Antedon bifida	6	Negative	0.81	0.94	0.87	2.02
Calliostoma	211	Negative	11.74	0.80	1.00	2.04
Caryophyllia spp.	46	Positive*	4.29	1.00	1.00	2.15
Cirripedia	338	Positive*	47.8	1.00	1.00	2.73 †
Corynactis spp.	168	Positive	9.46	0.85	1.00	2.16
Crossaster papposus	33	Negative	8.23	0.73	0.97	2.09
Flustra foliacea	324	Negative*	20.29	1.00	1.00	2.44 †
Gibbula spp.	154	Positive*	25.23	1.00	1.00	2.48 †
Henricia spp.	69	Negative	4.32	0.69	0.98	1.92
Ophiuroidea	131	Negative*	47.97	1.00	1.00	2.71 †
Paguroidea	83	Positive*	9.1	0.97	0.99	2.27
Pectinidae	213	Positive*	17.02	1.00	1.00	2.40
Pentapora fascialis	179	Positive*	10.32	1.00	1.00	2.32
Polyplacophora	10	Negative	1.18	0.91	0.78	1.80
Porifera arborescent	249	Negative*	19.27	1.00	1.00	2.42
Porifera columnar	127	Positive*	13.28	1.00	1.00	2.35
Porifera encrusting	1345	Positive*	47.32	1.00	1.00	2.80 †
Porifera erect	14	Negative	3.75	0.93	1.00	2.17

Species/group	Frequency	Response	Indicator value	Purity	Reliability	Indicator quality
Porifera globular	514	Negative*	32.91	1.00	1.00	2.58 †
Porifera lamellate	7	Negative	2.04	0.96	0.90	2.08
Porifera massive	217	Negative*	13.22	1.00	1.00	2.45 †
Porifera papillate	90	Positive*	8.17	1.00	1.00	2.39
Porifera repent	6	Negative*	3.03	1.00	0.99	2.22
Porifera tubular	37	Positive*	7.05	1.00	1.00	2.28
Sabellaria spinulosa	549	Positive	29.54	0.65	1.00	2.20
Sagartiidae	260	Positive	17.64	1.00	1.00	2.41
Serpulidae	901	Positive	38.1	0.85	1.00	2.52 †
Trochidae	4	Negative	1.62	0.97	0.84	2.03
Tubulariidae	345	Negative*	20.71	0.98	1.00	2.43 †
Urticina spp.	165	Positive	15.83	0.48	1.00	1.86

Appendix 4: Benchmark abundance and SACFOR for indicator species and morphological groups

Table 28. The 'benchmark' logged abundance for the low turbidity bedrock observations below and above the positive or negative community change point for each indicator species along with the minimum, mean and maximum logged abundance.

		Logged abundance				
Species/group	**Response**	**Minimum (all observations)**	**Mean below change point**	**Mean (all observations)**	**Mean above change point**	**Maximum (all observations)**
Actiniaria	Positive	0.00	0.13	0.17	0.28	4.88
Alcyonidium spp.	Negative	0.00	0.91	0.77	0.70	3.88
Antedon bifida	Positive	0.00	0.60	0.79	1.28	5.88
Asteriidae	Negative	0.00	1.28	0.92	0.73	5.88
Brachiopoda	Positive	0.00	1.41	1.44	1.55	5.88
Calliostoma	Negative	0.00	0.46	0.39	0.35	5.88
Caryophyllia spp.	Positive	0.00	3.67	3.83	4.25	6.88
Corallinaceae	Negative	0.00	0.01	0.03	0.04	5.93
Corynactis spp.	Negative	0.00	1.13	0.60	0.33	5.93
Crinoidea	Positive	0.00	0.25	0.28	0.38	4.88
Henricia spp.	Negative	0.00	0.16	0.08	0.04	5.88
Munida spp.	Positive	0.00	0.11	0.13	0.18	4.88
Ophiactidae	Negative	0.00	0.67	0.54	0.48	5.88
Ophiocomina nigra	Positive	0.00	0.32	0.44	0.78	5.88
Ophiothrix fragilis	Positive	0.00	0.48	0.46	0.40	6.88
Ophiura spp.	Positive	0.00	1.05	1.18	1.53	5.88
Ophiura albida	Positive	0.00	0.49	0.65	1.07	4.88
Ophiuroidea	Positive	0.00	1.08	1.28	1.81	5.88

		Logged abundance				
Species/group	**Response**	**Minimum (all observations)**	**Mean below change point**	**Mean (all observations)**	**Mean above change point**	**Maximum (all observations)**
Paguroidea	Positive	0.00	0.68	0.77	1.03	4.88
*Palmiskenea ske*nei	Positive	0.00	0.01	0.01	0.01	0.93
Porania pulvillus	Positive	0.00	0.30	0.30	0.30	4.88
Porifera globular	Negative	0.00	0.39	0.20	0.10	5.18
Porifera papillate	Negative	0.00	0.26	0.13	0.07	4.95
Porifera repent	Positive	0.00	0.04	0.04	0.03	0.93
Rhodophyta	Negative	0.00	0.53	0.18	0.00	5.93
Securiflustra securifrons	Positive	0.00	0.00	0.01	0.02	3.09
Serpulidae	Negative	0.00	2.68	2.31	2.12	4.95
Swiftia pallida	Negative	0.00	0.55	0.38	0.29	5.88

Table 29. The 'benchmark' logged abundance for the low turbidity boulder observations below and above the positive or negative community change point for each indicator species along with the minimum, mean and maximum logged abundance.

		Logged abundance				
Species/group	**Response**	**Minimum (all observations)**	**Mean below change point**	**Mean (all observations)**	**Mean above change point**	**Maximum (all observations)**
Brachiopoda	Negative	0.00	1.68	1.08	0.96	4.95
Caryophyllia spp.	Negative	0.00	3.04	3.07	3.07	5.88
Ophiuroidea	Negative	0.00	0.25	0.44	0.48	5.88
Porella spp.	Negative	0.00	1.69	1.67	1.68	4.00
Porifera arborescent	Positive	0.00	0.18	0.34	3.09	4.88
Porifera encrusting	Positive	0.00	0.15	0.27	2.31	3.09
Porifera flabellate	Negative	0.00	0.56	0.15	0.06	5.88
Porifera papillate	Negative	0.00	0.02	0.12	0.15	4.95
Serpulidae	Negative	0.00	2.47	2.33	2.31	5.88
Sertulariidae	Negative	0.00	0.55	0.11	0.01	4.88
Spirobranchus spp.	Positive	0.00	0.26	0.51	4.76	5.88
Stichastrella rosea	Positive	0.00	0.35	0.34	0.13	4.88
Swiftia pallida	Negative	0.00	0.54	0.11	0.01	4.88

Table 30. The 'benchmark' logged abundance for the low turbidity cobble observations below and above the positive or negative community change point for each indicator species along with the minimum, mean and maximum logged abundance.

		Logged abundance				
Species/group	**Response**	**Minimum (all observations)**	**Mean below change point**	**Mean (all observations)**	**Mean above change point**	**Maximum (all observations)**
Alcyonidium spp.	Negative	0.00	0.29	0.03	0.01	2.88
Alcyonium digitatum	Negative	0.00	0.00	0.05	0.06	2.88
Asteriidae	Positive	0.00	1.41	1.38	0.76	5.88
Caryophyllia spp.	Negative	0.00	2.63	2.63	2.63	6.88
Echinoidea	Positive	0.00	0.19	0.24	1.37	4.88
Paguroidea	Positive	0.00	0.95	0.95	0.76	4.88
Porella spp.	Negative	0.00	1.24	0.86	0.82	4.00
Porifera arborescent	Positive	0.00	0.06	0.17	2.59	4.88
Porifera encrusting	Positive	0.00	0.08	0.17	2.43	3.09
Porifera flabellate	Positive	0.00	0.04	0.11	1.83	4.88
Serpulidae	Negative	0.00	2.20	2.76	2.82	4.95
Sertulariidae	Negative	0.00	0.57	0.05	0.00	4.88
Spirobranchus spp.	Positive	0.00	0.07	0.27	5.13	5.88
Swiftia pallida	Negative	0.00	0.85	0.07	0.00	4.88

Table 31. The ‘benchmark’ logged abundance for the high-turbidity (across all rock classes) observations below and above the positive or negative community change point for each indicator species along with the minimum, mean and maximum logged abundance.

		Logged abundance				
Species/group	**Response**	**Minimum (all observations)**	**Mean below change point**	**Mean (all observations)**	**Mean above change point**	**Maximum (all observations)**
Actiniaria	Positive	0.00	0.23	0.28	0.44	0.49
Caryophyllia spp.	Positive	0.00	0.08	0.07	0.06	0.03
Cirripedia	Positive	0.00	0.34	0.57	1.34	0.39
Flustra foliacea	Negative	0.00	0.89	0.70	0.64	0.89
Gibbula spp.	Positive	0.00	0.15	0.27	0.68	0.11
Ophiuroidea	Negative	0.00	0.50	0.46	0.45	0.50
Paguroidea	Positive	0.00	0.13	0.16	0.26	0.13
Pectinidae	Positive	0.00	0.32	0.45	0.89	0.27
Pentapora fascialis	Positive	0.00	0.10	0.11	0.16	0.06
Porifera arborescent	Negative	0.00	0.67	0.45	0.39	0.67
Porifera columnar	Positive	0.00	0.19	0.33	0.84	0.07
Porifera encrusting	Positive	0.00	2.90	3.02	3.41	2.61
Porifera globular	Negative	0.00	1.35	1.04	0.95	1.35
Porifera massive	Negative	0.00	0.51	0.46	0.45	0.51
Porifera papillate	Positive	0.00	0.11	0.18	0.40	0.03
Porifera repent	Negative	0.00	0.01	0.00	0.00	0.01
Porifera tubular	Positive	0.00	0.05	0.07	0.13	0.00
Sagartiidae	Positive	0.00	0.38	0.48	0.81	0.35
Serpulidae	Positive	0.00	1.56	1.66	2.03	1.70
Tubulariidae	Negative	0.00	0.93	0.76	0.71	0.93

Table 32. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted negatively responding low turbidity bedrock indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence / absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Alcyonidium spp.	Below	0.68	0.32	-	-	-	-	0.29	0.3
	Above	0.75	0.25	-	-	-	-	0.23	0.3
Asteriidae	Below	0.77	0.23	-	0.18	0.5	-	-	-
	Above	0.87	0.13	-	0.1	0.3	-	-	-
Calliostoma	Below	0.9	0.1	-	-	-	0.8	0.2	-
	Above	0.93	0.07	-	-	-	0.7	-	-
Corallinaceae	Below	1	0	-	-	-	-	-	-
	Above	0.99	0.01	-	-	-	-	-	-
Corynactis spp.	Below	0.8	0.2	-	0.14	0.4	0.2	-	-
	Above	0.93	0.07	-	0.2	0.4	0.1	-	-
Henricia spp.	Below	0.97	0.03	-	-	0.3	-	-	-
	Above	0.99	0.01	-	-	0.1	-	-	-
Ophiactidae	Below	0.87	0.13	-	0.2	0.11	-	-	-
	Above	0.9	0.1	-	0.2	0.8	-	-	-
Porifera globular	Below	0.92	0.08	-	-	0.8	-	-	-
	Above	0.98	0.02	-	-	0.2	-	-	-
Porifera papillate	Below	0.89	0.11	-	-	-	0.1	0.11	-
	Above	0.98	0.02	-	-	-	0.1	0.2	-
Rhodophyta	Below	0.85	0.15	-	0.1	0.3	0.2	0.4	0.6
	Above	1	0	-	-	-	-	-	-

Species/group	Change point partition	Presence / absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Serpulidae	Below	0.38	0.62	-	-	0.19	0.44	-	-
	Above	0.49	0.51	-	-	0.9	0.43	-	-
Swiftia pallida	Below	0.89	0.11	-	0.11	-	-	-	-
	Above	0.94	0.06	-	0.6	-	-	-	-

Table 33. Benchmark profile of SACFOR classes for observations below / above the change point (CP) for all shortlisted positively responding low turbidity bedrock indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	CP partition	Presence / absence on either side of the CP		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Actiniaria	Below	0.97	0.03	-	-	0.3	-	-	-
	Above	0.94	0.06	-	-	0.6	-	-	-
Antedon bifida	Below	0.88	0.12	-	0.1	0.11	-	-	-
	Above	0.74	0.26	-	0.1	0.26	-	-	-
Brachiopoda	Below	0.66	0.34	-	-	0.7	0.27	-	-
	Above	0.62	0.38	-	-	0.6	0.32	-	-
Caryophyllia spp.	Below	0.22	0.78	-	-	0.7	0.42	0.3	-
	Above	0.8	0.2	-	-	0.8	0.47	0.38	-
Crinoidea	Below	0.95	0.05	-	-	0.5	-	-	-
	Above	0.92	0.08	-	-	0.8	-	-	-
Munida spp.	Below	0.98	0.02	-	-	0.2	-	-	-
	Above	0.96	0.04	-	-	0.4	-	-	-
Ophiocomina nigra	Below	0.94	0.06	-	0.1	0.6	-	-	-
	Above	0.84	0.16	-	-	0.16	-	-	-
Ophiothrix fragilis	Below	0.91	0.09	-	0.5	0.4	-	-	-
	Above	0.92	0.08	-	0.2	0.5	-	-	-
Ophiura spp.	Below	0.79	0.21	-	0.3	0.18	-	-	-
	Above	0.69	0.31	-	0.3	0.29	-	-	-
Ophiura albida	Below	0.9	0.1	-	-	0.1	-	-	-
	Above	0.78	0.22	-	-	0.22	-	-	-
Ophiuroidea	Below	0.78	0.22	-	-	0.22	-	-	-

Species/group	CP partition	Presence / absence on either side of the CP		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
	Above	0.63	0.37	-	0.2	0.36	-	-	-
Paguroidea	Below	0.86	0.14	-	-	0.14	-	-	-
	Above	0.79	0.21	-	-	0.21	-	-	-
Porania pulvillus	Below	0.94	0.06	-	-	0.6	-	-	-
	Above	0.94	0.06	-	-	0.6	-	-	-

Table 34. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted negatively responding low turbidity boulder indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence/absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Brachiopoda	Below	0.62	0.38	-	-	0.1	0.29	-	-
	Above	0.73	0.27	-	-	0.03	0.25	-	-
Caryophyllia spp.	Below	0.31	0.69	-	-	0.02	0.22	0.46	-
	Above	0.23	0.77	-	-	-	0.11	0.66	-
Ophiuroidea	Below	0.95	0.05	-	-	0.05	-	-	-
	Above	0.91	0.09	-	-	0.09	-	-	-
Porella spp.	Below	0.51	0.49	-	-	-	0.1	0.38	0.01
	Above	0.48	0.52	-	-	-	0.17	0.34	0.02
Porifera flabellate	Below	0.89	0.11	-	0.01	0.1	-	-	-
	Above	0.97	0.03	-	-	0.02	-	-	-
Porifera papillate	Below	0.99	0.01	-	-	-	-	0.01	-
	Above	0.95	0.05	-	-	-	0.01	0.04	-
Serpulidae	Below	0.43	0.57	-	0.01	0.09	0.47	-	-
	Above	0.4	0.6	-	-	0.03	0.57	-	-
Sertulariidae	Below	0.89	0.11	-	-	0.11	-	-	-
	Above	0.97	0.03	-	-	0.02	-	-	-
Swiftia pallida	Below	0.9	0.1	-	0.1	0.01	-	-	-
	Above	0.98	0.02	-	0.02	-	-	-	-

Table 35. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted positively responding low turbidity boulder indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence/absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Porifera arborescent	Below	0.96	0.04	-	-	0.04	-	-	-
	Above	0.42	0.58	-	-	0.71	-	-	-
Porifera encrusting	Below	0.93	0.07	-	-	-	-	0.02	0.05
	Above	0.17	0.83	-	-	-	-	0.38	0.54
Spirobranchus spp.	Below	0.95	0.05	-	-	0.04	0.01	-	-
	Above	0.17	0.83	-	-	0.58	0.42	-	-
Stichastrella rosea	Below	0.93	0.07	-	0.07	-	-	-	-
	Above	0.96	0.04	-	-	0.04	-	-	-

Table 36. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted negatively responding low turbidity cobble indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence/absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Alcyonidium spp.	Below	0.91	0.09	-	-	-	-	0.09	-
	Above	1	0	-	-	-	-	-	-
Alcyonium digitatum	Below	1	0	-	-	-	-	-	-
	Above	0.97	0.03	-	-	-	-	0.03	0.01
Caryophyllia spp.	Below	0.36	0.64	-	-	0.01	0.12	0.49	-
	Above	0.38	0.62	-	-	-	0.14	0.48	-
Porella spp.	Below	0.65	0.35	-	-	-	0.07	0.29	-
	Above	0.73	0.27	-	-	-	0.02	0.22	0.03
Serpulidae	Below	0.48	0.52	-	-	0.06	0.46	-	-
	Above	0.31	0.69	-	-	0.06	0.63	-	-
Sertulariidae	Below	0.88	0.12	-	-	0.12	-	-	-
	Above	1	0	-	-	-	-	-	-
Swiftia pallida	Below	0.83	0.17	-	0.17	-	-	-	-
	Above	1	0	-	-	-	-	-	-

Table 37. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted positively responding low turbidity cobble indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence/absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Asteriidae	Below	0.76	0.24	-	0.23	0.01	-	-	-
	Above	0.81	0.19	-	-	0.19	-	-	-
Echinoidea	Below	0.96	0.04	-	-	0.04	-	-	-
	Above	0.67	0.33	-	-	0.3	-	-	-
Paguroidea	Below	0.8	0.2	-	-	0.2	-	-	-
	Above	0.85	0.15	-	-	0.19	-	-	-
Porifera arborescent	Below	0.98	0.02	-	-	0.01	-	-	-
	Above	0.44	0.56	-	-	0.63	-	-	-
Porifera encrusting	Below	0.96	0.04	-	-	-	-	0.01	0.02
	Above	0	1	-	-	-	-	0.11	0.89
Porifera flabellate	Below	0.99	0.01	-	-	0.01	-	-	-
	Above	0.67	0.33	-	-	0.41	-	-	-
Spirobranchus spp.	Below	0.98	0.02	-	-	0.01	0.01	-	-
	Above	0.04	0.96	-	-	0.41	0.63	-	-

Table 38. Benchmark profile of SACFOR classes for observations below and above the change point for all shortlisted negatively responding high turbidity (all rock classes) indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	Change point partition	Presence/absence on either side of the change point		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Flustra foliacea	Below	0.73	0.27	-	0.04	0.04	0.03	0.1	0.05
	Above	0.82	0.18	-	0.02	0.04	0.04	0.06	0.02
Ophiuroidea	Below	0.92	0.08	0.06	0.01	-	-	0.01	-
	Above	0.92	0.08	0.03	0.01	0.01	0.02	0.01	-
Porifera arborescent	Below	0.78	0.22	-	-	0.02	0.04	0.07	0.1
	Above	0.87	0.13	-	-	0.01	0.01	0.06	0.04
Porifera globular	Below	0.58	0.42	-	0.02	0.02	0.07	0.15	0.17
	Above	0.72	0.28	-	-	0.04	0.08	0.09	0.06
Porifera massive	Below	0.82	0.18	0.01	0.01	0.03	0.03	0.07	0.04
	Above	0.88	0.12	0.02	0.03	0.02	0.02	0.02	0.01
Tubulariidae	Below	0.77	0.23	-	0.04	0.05	0.02	0.05	0.07
	Above	0.79	0.21	-	0.01	0.03	0.04	0.07	0.06

Table 39. Benchmark profile of SACFOR classes for observations below / above the change point (CP) for all positively responding high turbidity (all classes) indicators. SACFOR classes are super-abundant (S), abundant (A), common (C), frequent (F), occasional (O), and rare (R).

Species/group	CP partition	Presence/absence on either side of the CP		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
Actiniaria	Below	0.93	0.07	-	-	0.01	0.01	0.01	0.03
	Above	0.87	0.13	0.01	-	0.02	0.04	0.03	0.04
Caryophyllia spp.	Below	0.97	0.03	-	-	-	-	-	0.03
	Above	0.99	0.01	-	-	-	-	0.01	0.01
Cirripedia	Below	0.86	0.14	-	-	0.01	0.02	0.02	0.09
	Above	0.54	0.46	-	0.01	0.09	0.06	0.09	0.22
Gibbula spp.	Below	0.93	0.07	-	-	-	-	0.01	0.05
	Above	0.81	0.19	-	-	-	0.16	0.01	0.03
Paguroidea	Below	0.95	0.05	-	-	-	-	0.03	0.01
	Above	0.93	0.07	-	-	0.03	0.01	0.03	-
Pectinidae	Below	0.9	0.1	-	-	0.01	0.03	0.05	0.01
	Above	0.76	0.24	-	0.01	0.04	0.11	0.07	0.01
Pentapora fascialis	Below	0.97	0.03	-	-	-	-	-	0.03
	Below	0.94	0.06	-	-	-	-	-	0.06
Porifera columnar	Above	0.95	0.05	-	0.01	0.01	0.01	0.01	0.01
	Below	0.84	0.16	0.01	0.05	0.07	0.03	0.01	-
Porifera encrusting	Above	0.18	0.82	-	0.01	0.1	0.38	0.18	0.14
	Below	0.14	0.86	-	0.04	0.26	0.31	0.15	0.11
Porifera papillate	Above	0.96	0.04	-	-	-	0.01	0.02	-
	Below	0.9	0.1	-	0.02	0.05	0.04	-	-
Porifera tubular	Above	0.98	0.02	-	-	-	-	0.01	0.01

Species/group	CP partition	Presence/absence on either side of the CP		Profile of SACFOR classes below filtered change point					
		Absence	Presence	S	A	C	F	O	R
	Below	0.95	0.05	-	-	-	0.01	0.01	0.03
Sagartiidae	Above	0.86	0.14	-	-	0.01	0.02	0.05	0.05
	Below	0.76	0.24	-	-	-	0.13	0.08	0.03
Serpulidae	Above	0.48	0.52	-	-	0.01	0.05	0.47	-
	Below	0.33	0.67	-	-	0.02	0.05	0.6	-