

1 **Assessing the conservation status of marine habitats: thoughts from a**
2 **sandflat on the Isles of Scilly**

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Abstract

Statutory monitoring of the fauna of the ‘mudflats and sandflats not covered by seawater at low tide’ biotope complex on St Martin’s Flats, a part of the Isles of Scilly Complex Special Area of Conservation, was undertaken in 2000, 2004 and 2009. The targets set by Natural England for “characteristic biotopes” were that “composite species, abundance and diversity should not deviate significantly from an established baseline, subject to natural change”. The three specified biotopes could not be distinguished, and instead three assemblages were subjectively defined based on sediment surface features. There were statistically significant natural changes in diversity and species composition between years, especially in the association initially characterized by the razor-clam *Ensis*, and possible reasons for this are discussed. It is suggested that setting fixed local limits on natural variability is almost always impractical. Two possible approaches to distinguishing between natural and anthropogenic changes are suggested; a change in ecological condition as indicated by AMBI scores, and a significant change in average taxonomic distinctness (Δ^+) compared with expectation. The determination of species biomasses as well as abundances might also open more possibilities for assessment. The practice of setting objectives for a marine SAC feature that include the range and number of biotopes cannot be supported, in view the difficulty in ascribing assemblages to recognised biotopes. A more realistic definition of species assemblages might best be gained from examination of the species that *consistently* make a substantial contribution to the Bray Curtis similarity among samples collected from specific sites.

Key words: Marine benthos, biotope definition, diversity, species composition, natural variability, AMBI scores, taxonomic distinctness

1. Introduction

The global Convention on Biological Diversity (CBD) held in Rio de Janeiro in 1992 (Secretariat of the Convention on Biological Diversity 2000) called for the creation and enforcement of national strategies and action plans “to conserve, protect and enhance biological diversity”. The European Union Directive 92/43/EEC (Habitats Directive) and the Oslo and Paris Convention (OSPAR Commission 2008) have each encouraged national commitments to marine biodiversity conservation. Although loss of biodiversity is regarded as the main marine conservation issue (Ray & McCormick-Ray, 2014), the practical implementation of such legislation has unfortunately sidestepped this issue, and biodiversity *per se* has not been an explicit conservation attribute. The Habitats Directive requires the maintenance or restoration of natural habitats and species of European interest at “*favourable conservation status*”, with a network of Special Areas of Conservation (SACs) being one of the main means of achieving this. Given that the framework within which marine conservation is monitored and managed, and the associated language, may not be familiar to scientists in the broader ecological community it is worth giving a brief explanation.

Each SAC is designated because it is considered to contain examples of habitats listed in Annexe 1 of the directive, or is essential for the maintenance of a population of a species listed in Annexe 2. Within the UK these are collectively referred to as ‘*interest features*’ (Davies et al. 2001). Examples of features in the Isles of Scilly Complex SAC are sandbanks and mudflats. For each feature at least one *conservation objective* is formulated. This is a statement of what is to be achieved in terms of managing the feature. Features may be broken down into *sub-features*. For each feature or sub-feature certain *attributes* are defined, which are the measurable aspects of the feature which are to be monitored. For each attribute certain *measures* are chosen which are considered to be indicative of the overall health of the feature, and for each measure *target conditions* are set. The purpose of monitoring in this framework, therefore, is to determine those measures and see if they are consistent with the target conditions. If they are, the conservation objectives are being met and the feature may be considered to be in favourable status. A monitoring strategy for a feature must measure at least one attribute, such as its extent, biotic composition, biological structure and physical structure (Davies et al., 2001). Central to the delivery of marine conservation in the UK is the *biotope*. The idea is that suites of species commonly co-occur in locations with similar environmental conditions. The collective term biotope encompasses both of these biotic and abiotic elements. Attributes usually refer to the diversity, extent, distribution and species composition of “biotopes”, and considerable effort has gone into defining and describing a hierarchical habitat classification for UK marine waters (Connor et al. 2004) to underpin their use in marine management. This classification has 6 levels, and is compatible with the European Nature Information System EUNIS (<http://eunis.eea.europa.eu/about.jsp>). Biotopes sit at level 5 (and sub-biotopes at level 6). Each is then nested within increasing levels, namely biotope complexes (Level 4), habitat complexes (Level 3), broad habitat types (Level 5) and ultimately marine or terrestrial environments (Level 1). Described categories in each level have associated codes. For example, the biotope “Polychaetes, including *Paraonis fulgens*, in littoral fine sand” has a EUNIS code A2.2311. A2 indicates the broad habitat type, littoral sediment,

A2.2 the habitat complex, littoral sand and muddy sand, A2.231 the biotope complex, polychaetes in littoral fine sand, and finally the full code A2.231 indicates the particular biotope within that complex. Within the UK similar categories are used, but with different codes. Thus the code for this biotope is LS.LSa.FiSa.Po.Pful. In this paper we describe a programme to monitor the conservation status of intertidal sediments in the Isles of Scilly Complex SAC and recent results. We focus on issues that arise through the application of the framework described above, and suggest possible solutions to perceived problems.

2. St Martin's Flats monitoring

2.1 Methods

2.1.1. The monitoring framework to be addressed

Two Annex I habitats for which the Isles of Scilly Complex SAC has been designated are "sandbanks which are slightly covered by seawater all the time" and "mudflats and sandflats not covered by seawater at low tide". The conservation objective set by Natural England is, "subject to natural change" to "maintain the mudflats and sandflats not covered by seawater at low tide in favourable condition". There are no intertidal mudflats on Scilly, and the biotopes comprising the intertidal sand habitat specified by Natural England (2000) are:

IMS.EcorEns: Urchin *Echinocardium cordatum* and razor shell *Ensis* spp. in lower shore fine sands and muddy sands;

CGS.Ven: Purple heart urchin *Spatangus purpureus* and bivalve community in lower-shore sands; and

LGS.Lan: Sand mason worm *Lanice conchilega* in tidal-scoured lower-shore sands

The attribute to be measured is the "species composition of characteristic biotopes", the measure is "presence, abundance and diversity of composite species from a range of sites, measured once per reporting cycle" and the target that "composite species, abundance and diversity should not deviate significantly from an established baseline, subject to natural change".

2.1.2. Field sampling and sample analysis

Monitoring of the fauna of three biotopes that fall within the 'intertidal mud and sandflats' feature began in August 2000. The three biotopes specified by Natural England (see above) could not be distinguished, since the characterizing species of each were frequently found together at a single site. Instead, three biotopes were defined subjectively during an initial visual survey, based largely on physical and biogenic sediment surface features. These were:

1) "*Arenicola*" Biotope: Fine sand with blackening close to the surface. Abundant *Arenicola* holes and casts on sediment surface;

2) "*Ensis*" Biotope: Smoother, more waterlogged sand with evidence of live *Ensis* plus large numbers of empty *Ensis* shells on sediment surface; and

3). "*Lanice/Echinocardium*" Biotope: Ripple-marked sand with sparse *Lanice* tubes (fans apparently rather degraded) and *Echinocardium* burrow openings present.

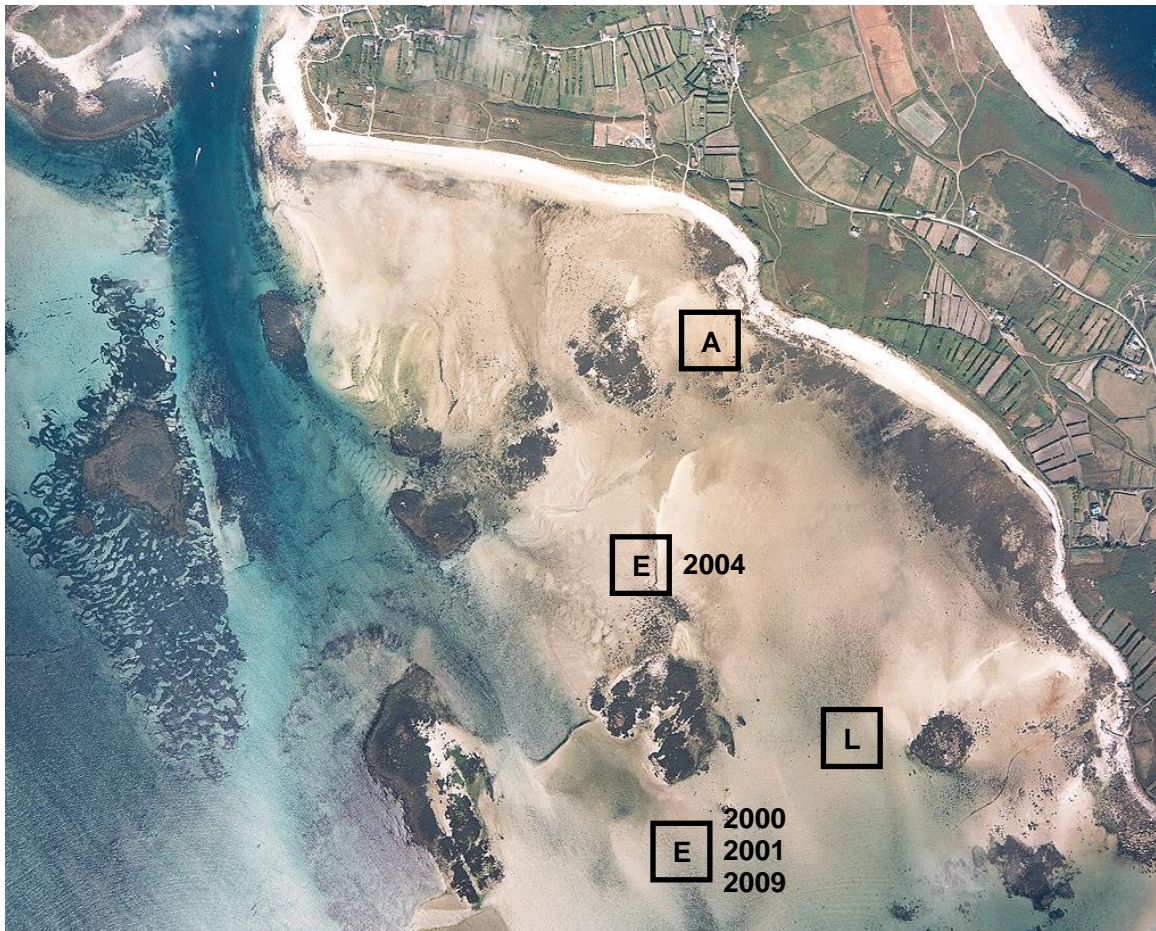


Fig. 1 Aerial photograph of the St Martin's sedimentary shore indicating the areas sampled for each of the 3 biotopes: L = *Lanice/Echinocardium*, E = *Ensis* and A = *Arenicola* (Web colour, print B/W)

10 replicate core samples, haphazardly distributed, were collected within a 20 m radius of a central point: *Arenicola* 49°57'58.6"N 6°17'35.3"W; *Ensis* 49°57'33.78"N 6°17'34.1"W; *Lanice/Echinocardium* 49°57'40.0"N 6°17'17.0"W (Fig. 1). For each sample, a 0.1 m² stainless steel square corer was pushed into the sediment to a depth of 30 cm. Sediment within the core was then removed and gently sieved (puddled) over a 1mm mesh. The residue on the sieve was elutriated by resuspending the sediment in a bucket of seawater that had been pre-filtered through a 0.5 mm sieve, and decanted onto a 1mm-mesh sieve. After 3 elutriations, the residue remaining in the bucket was carefully hand-sorted and all organisms extracted and added to the elutriate. The sample was preserved in 10% formalin.

In the laboratory, samples were washed free of formalin on a 0.5 mm mesh sieve and the animals picked out under a binocular microscope. Individuals were identified to the lowest practical taxonomic level using the most recent peer approved keys and literature available. On St Martin's flats four species of the amphipod genus *Urothoe* were recorded, but the positive identification of these species requires dissection and can be very time-consuming, since several hundred specimens are present in the samples. There is also some uncertainty regarding specific identification between different sample analysts. Identification to genus level is less of a problem (dissection is not necessary) so this group of species was been identified to genus level only. Species nomenclature follows Howson & Picton (1997).

The survey was repeated in October 2004. The initial intention was to sample exactly the same sites as were sampled in 2000. However, the original "*Ensis*" site sampled in 2000 was situated at Extreme Low Water of Spring Tides and was not uncovered by the tide during that visit, despite this being the period of the lowest predicted tides for the latter part of 2004. Accordingly an alternative site was selected (Fig. 1) which appeared to have similar surface features to the original site, and five trial samples were collected here for comparison. Additionally, four samples had been collected at the original "*Ensis*" location in April 2001 using identical methodology but for a different study (Warwick et al., 2006), and these samples are also used in the analysis of change. Most recently, the survey was repeated in September 2009, when spring tides were sufficiently low that the original "*Ensis*" site sampled in 2000 was exposed and could be resampled.

2.1.3. Data analysis

To address the measure "presence, abundance and diversity of composite species" univariate measures of community structure and diversity [number of species (S), number of individuals (N) and Simpson's evenness index ($1-\lambda'$)] were calculated for each sample. Diversity profiles were visualised by plotting *k*-dominance curves, and species accumulation plots were constructed based on the means of up to 999 permutations of the sample ordering. Multivariate data analyses followed the methods described by Clarke 1993 and Clarke & Warwick, 2001 using the PRIMER (Plymouth Routines In Multivariate Ecological Research) v.6 software package (Clarke & Gorley, 2006), and using the Bray-Curtis similarity measure on square root transformed species abundance data.

In addition, two other types of univariate measures were determined, and applied to the time-series of data. AMBI (AZTI's Marine Biotic Index) was designed to analyse the response of macrobenthic assemblages in European coastal waters to changes in environmental quality (Borja et al., 2000, 2003). The species are classified into five ecological groups depending on their sensitivity to environmental stress, and the index is based on the relative abundances of individuals in each group. The index has become one of the mainstays for the assessment of ecological status under the European Water Framework Directive, and it was therefore considered appropriate to assess the ecological status of the St Martin's Flats assemblages on these terms.

A group of biodiversity measures that are independent of species richness and sampling effort, yet responsive to anthropogenic disturbance, considers the taxonomic relatedness of species in the assemblage (Warwick & Clarke, 2001). It is well known that in impacted

assemblages of organisms the taxonomic spread of species is reduced, and in extreme cases they may be sibling species belonging to the same genus, or at least very closely related. Unimpacted assemblages, on the other hand, have a wider taxonomic spread and the species belong to many different genera, families, orders, classes and phyla. The measures used here are the average path length or taxonomic distance, traced through a taxonomic classification, between every pair of individuals (Δ), between every pair of individuals conditional on them being in different genera (Δ^*) and between every pair of species (Δ^+). A further measure (Δ^+) indicates the variability in the path lengths between species. The measures are independent of sample size or sampling effort, and are little affected by small variations in habitat type (Leonard et al., 2006). They can be used for data consisting simply of species lists and arising from unknown or uncontrolled sampling effort, which usually renders it impossible to read anything into the relative size of these lists. For Δ^+ there are permutation tests for the significance of departure from expectation under specific null hypothesis conditions.

2.2. Results

2.2.1. Faunal diversity

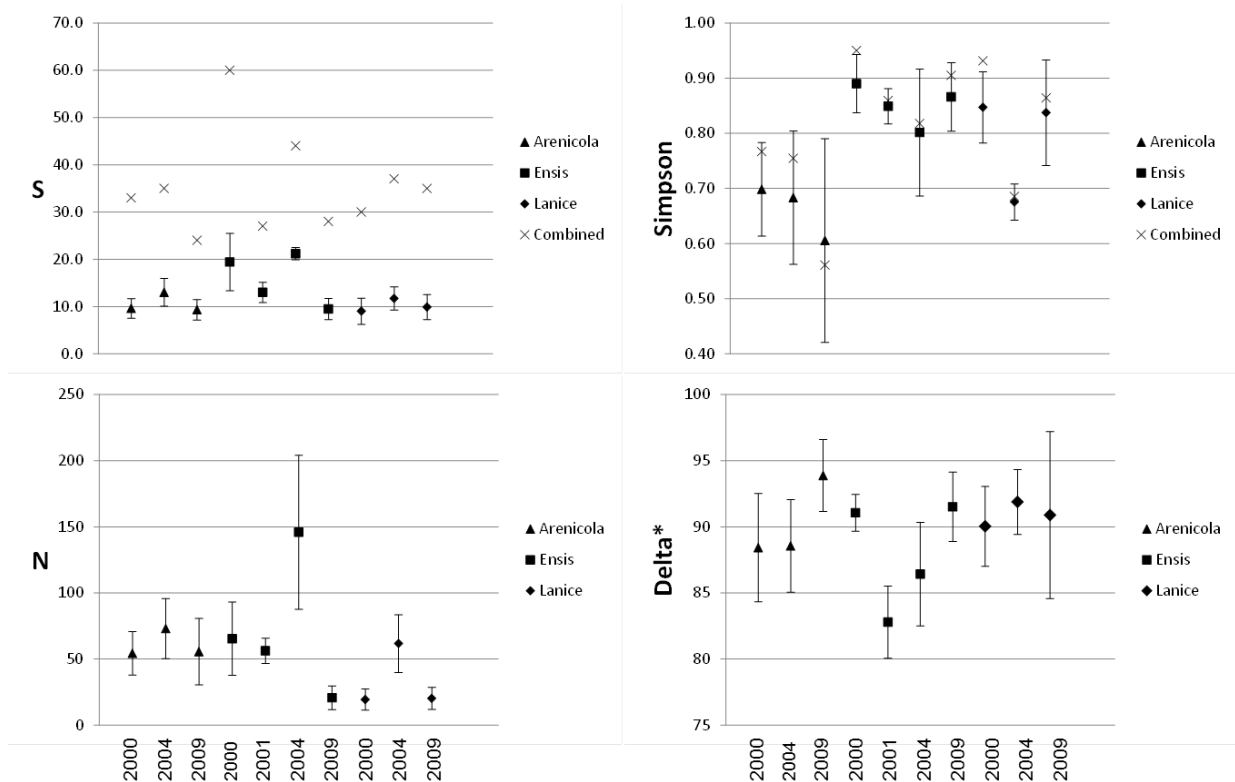


Fig. 2. Univariate measures (S, number of species; N, number of individuals; Simpson, Simpson's evenness $1-\lambda'$ and; Delta*, taxonomic distinctness) from each biotope in each survey calculated from individual samples (mean \pm s.d.). Values calculated from pooled samples are shown where these could differ markedly in behaviour from average values from replicates.

Values of a range of univariate measures (Figure 2) do not indicate consistent patterns within or among biotopes. Within-sample species richness is fairly consistent among samples from the *Arenicola* and *Lanice/Echinocardium* biotopes from different years, while richness in the *Ensis* biotope is more variable. Total richness, however, varies markedly across years in all biotopes. Abundance is highly variable across years in the *Ensis* and *Lanice/Echinocardium* biotopes, and less so in the *Arenicola* biotope. Within-sample evenness varies markedly across years in the *Lanice/Echinocardium* biotope, and less so in the others, while within-year variability is highest in the *Arenicola* biotope. Evenness calculated from combined samples from each survey tends to exacerbate among-year variability. Delta* shows clear changes among years in the *Ensis* biotope, less clear changes in the *Arenicola* biotope and little difference among years in the *Lanice/Echinocardium* biotope.

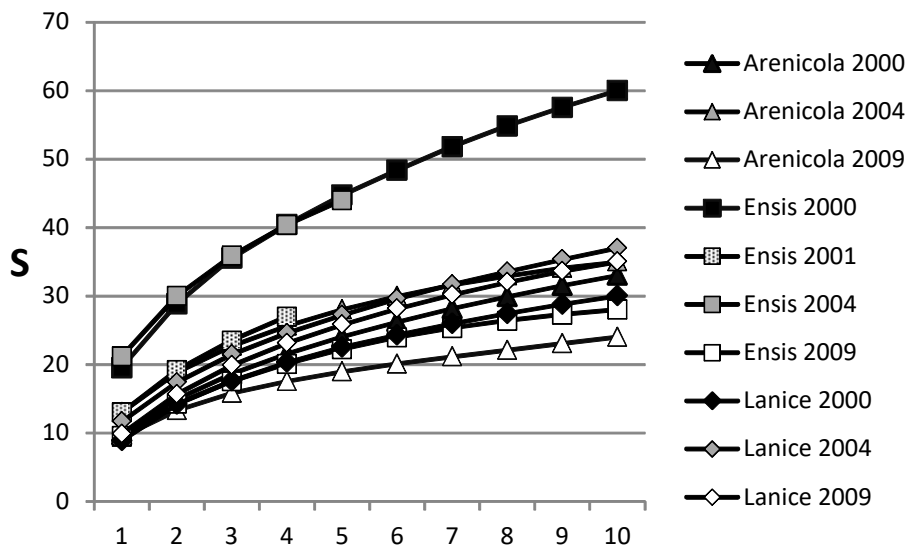


Fig. 3. Species accumulation curves calculated from 1000 random permutations of replicate data from each biotope in each survey.

In view of the difference in sampling effort among years in the *Ensis* biotope, perhaps a better way of comparing richness is by examining species accumulation curves (Fig. 3). These plots allow sample sets with different numbers of replicates to be directly compared. They clearly separate two higher diversity sample sets, *Ensis* 2000 and *Ensis* 2004, and one lower, *Arenicola* 2009, from the remainder. Another graphical/distributional method, *k*-dominance curves (Fig. 4), indicate that diversity in combined samples from each survey was highest in the *Ensis* biotope in 2000, while differences among other combinations of biotope and year are less clear.

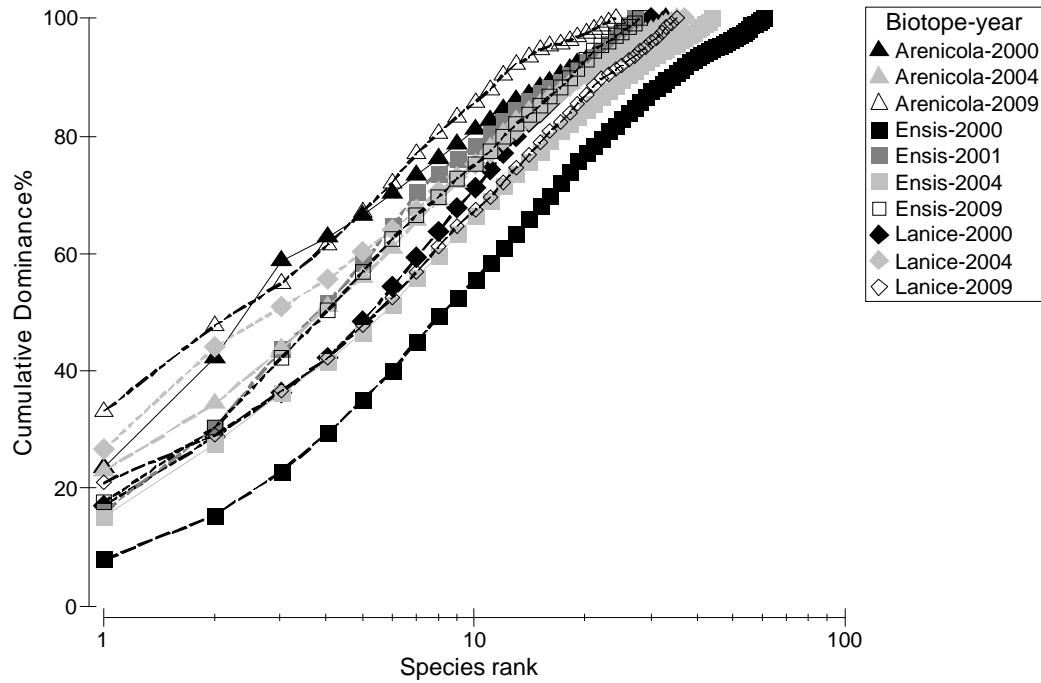


Fig. 4. *k*-dominance plots calculated from pooled data from each biotope in each survey.

2.2.2. Community composition

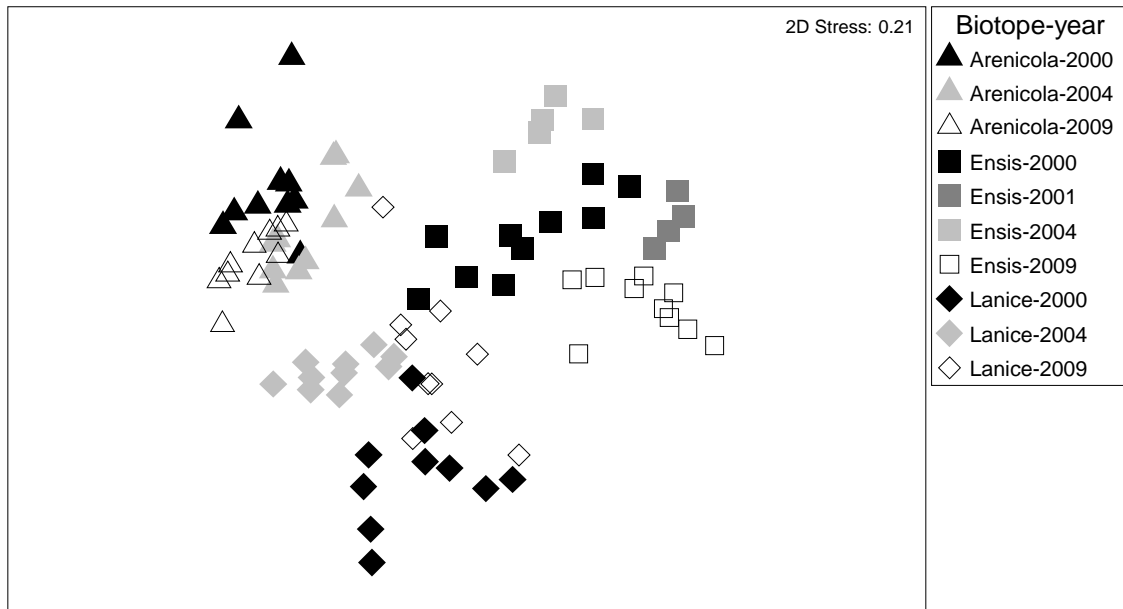


Fig. 5. MDS ordination of similarities among all samples, calculated using the Bray-Curtis coefficient on square-root transformed abundances.

Moving beyond analyses focusing on abundance and diversity, changes in species composition may be visualised using multivariate methods. An MDS ordination (Fig. 5) based on similarities among all samples clearly shows that the assemblages within each biotope remain distinct across years. The plot also indicates, however, that there are clear differences in species composition between different years within biotopes. Two-way SIMPER (Similarity Percentages) analysis was used to determine the species responsible for the similarity in the species composition among replicates from each biotope across all years, based on the root transformed species abundance data and the Bray Curtis similarity measure (Tables 1-3). In general, changes in species composition between years resulted from rather subtle changes in the relative abundances of a large number of species, rather than dramatic changes in abundance of a few dominants. A notable exception to this was the complete disappearance in 2009 of the distinctive cumacean *Apseudes latreilli* from the “Ensis” biotope, in which it had been very abundant in earlier years.

Table 1 Percentage species contributions to the average similarity (46.96) among replicates across all years in the “*Lanice/Echinocardium*” biotope, ranked in order of importance, with a cut-off at 90%

<i>Species</i>	<i>Av. Abund</i>	<i>Av. Sim</i>	<i>Contrib%</i>	<i>Cum. %</i>
<i>Urothoe</i> spp.	3.23	15.97	34.01	34.01
<i>Ophelia rathkei</i>	1.72	6.43	13.69	47.71
<i>Travisia forbesii</i>	1.07	5.03	10.71	58.41
<i>Echinocyamus pusillus</i>	0.80	3.04	6.47	64.88
<i>Perioculodes longimanus</i>	0.77	2.76	5.88	70.76
<i>Echinocardium cordatum</i>	0.53	2.10	4.47	75.23
<i>Angulus tenuis</i>	0.51	1.58	3.37	78.60
<i>Amphioxus lanceolatus</i>	0.38	1.36	2.90	81.50
<i>Tellimya ferruginosa</i>	0.30	0.91	1.95	83.44
<i>Leptosynapta inhaerens</i>	0.23	0.82	1.75	85.19
Spionidae indet	0.32	0.81	1.71	86.91
<i>Dosinia exoleta</i>	0.35	0.80	1.70	88.61
<i>Nephtys caeca</i>	0.33	0.78	1.67	90.28

Table 2 Percentage species contributions to the average similarity (49.92) among replicates across all years in the “*Ensis*” biotope, ranked in order of importance, with a cut-off at 90%

<i>Species</i>	<i>Av. Abund</i>	<i>Av. Sim</i>	<i>Contrib%</i>	<i>Cum. %</i>
<i>Dosinia exoleta</i>	1.93	8.40	16.84	16.84
<i>Ehlersia cornuta</i>	2.03	5.55	11.12	27.96
<i>Glycera lapidum</i> complex	1.30	5.22	10.46	38.42
<i>Notomastus latericeus</i>	1.83	3.97	7.95	46.38
<i>Apseudes latreillii</i>	1.87	3.31	6.64	53.01
<i>Aonides oxycephala</i>	1.68	2.94	5.90	58.91
<i>Urothoe</i> spp.	1.28	2.80	5.61	64.52
<i>Echinocardium cordatum</i>	0.53	2.26	4.53	69.05
<i>Echinocyamus pusillus</i>	0.99	1.94	3.89	72.93
<i>Leptosynapta inhaerens</i>	0.62	1.52	3.05	75.98

<i>Amphioxus lanceolatus</i>	0.76	1.49	2.99	78.97
<i>Moerella pygmaea</i>	0.69	1.37	2.75	81.72
<i>Lutraria lutraria</i>	0.29	0.84	1.69	83.41
<i>Perioculodes longimanus</i>	0.54	0.83	1.66	85.06
<i>Iphinoe trispinosa</i>	0.67	0.79	1.58	86.64
<i>Ensis arcuatus</i>	0.41	0.70	1.40	88.04
<i>Gari depressa</i>	0.42	0.69	1.39	89.43
<i>Mediomastus fragilis</i>	0.48	0.47	0.95	90.38

Table 3 Percentage species contributions to the average similarity (56.19) among replicates across all years in the “*Arenicola*” biotope, ranked in order of importance, with a cut-off at 90%

Species	Av. Abund	Av. Sim	Contrib%	Cum. %
<i>Urothoe</i> spp.	4.90	18.71	33.30	33.30
<i>Scoloplos armiger</i>	3.21	13.76	24.49	57.79
<i>Malacoceros fuliginosus</i>	1.01	4.13	7.34	65.13
<i>Nephtys hombergii</i>	0.76	2.92	5.20	70.33
<i>Notomastus latericeus</i>	1.13	2.82	5.01	75.35
<i>Euclymene oerstedii</i>	0.71	1.53	2.73	78.07
<i>Arenicola marina</i>	0.68	1.28	2.29	80.36
<i>Spio filicornis</i>	0.57	1.16	2.06	82.42
<i>Pygospio elegans</i>	0.47	1.05	1.87	84.29
<i>Sphaeroma serratum</i>	0.41	1.00	1.77	86.06
<i>Crangon crangon</i>	0.47	0.98	1.74	87.80
<i>Angulus tenuis</i>	0.41	0.83	1.47	89.27
<i>Perioculodes longimanus</i>	0.40	0.69	1.23	90.50

An alternative multivariate approach is to ask whether there is any evidence for differences in average (or total) species composition among surveys. An MDS based on pooled samples from each survey (Fig. 6) indicates consistency in composition within biotopes as surveys are grouped together, with a similarity >30. The contours in Fig. 6 show samples that cluster together at given levels of similarity within a corresponding cluster analysis. A corresponding Similarity Profiles (Simprof) test shows no evidence for multivariate structure within the clusters grouped at 30% similarity.

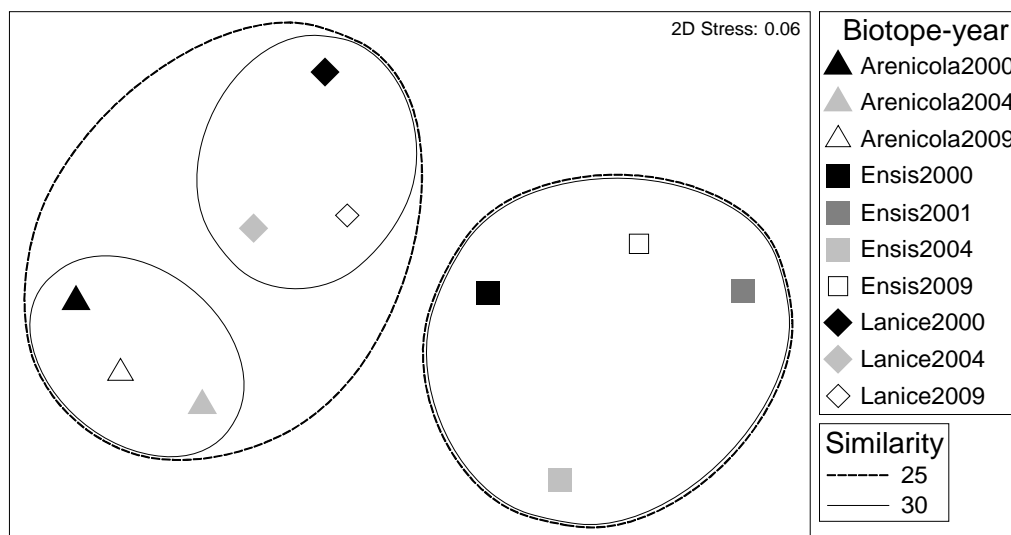


Fig. 6. MDS of similarities among averaged data from each biotope in each survey, derived from Bray-Curtis similarities and square-root transformed abundances.

2.2.3. Statistical significance

Differences in variability and sampling effort present problems in the context of applying standard statistical methods, such as analysis of variance, to determine whether differences in univariate measures among biotopes and across years are in some sense significant. There is an alternative robust non-parametric testing framework available, which is to calculate differences in a measure among samples and to analyse the resulting distance matrix using ANOSIM. ANOSIM can also be used to test for differences in k -dominance curves among groups of samples, by calculating distances between curves, and also in its more familiar application to analyse for differences in multivariate community structure using a resemblance matrix. Here we use the Bray-Curtis resemblances among samples calculated from square-root transformed abundances. A summary of results (Table 4) clearly shows that most methods, univariate, graphical/distributional and multivariate, indicate statistically significant differences among all combinations of biotopes and years. Simprof, an alternative approach which tests for multivariate structure without recourse to an a priori defined group structure, does not detect any difference in community structure between the pooled samples from the *Lanice* and *Arenicola* biotopes, but does between samples from the *Ensis* biotope and the others. In other words, samples grouped together at a similarity of >25 in Fig. 6 form 2 distinct groups within which there is no statistical support for further subdivision.

Table 4 Summary of 1-way Anosim tests for differences between biotopes and surveys. Entries indicate tests with $p < 0.05$, inferring differences. Response variables are indicated as: S, number of species; N, number of individuals; E, Simpson's evenness index; D, taxonomic distinctness Δ^* ; k, k -dominance curves; B, Bray-Curtis similarities calculated using root-transformed abundances.

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Arenicola 2004	S, k, B	...							
Arenicola 2009	E, D, k, B	S, D, B	...						
Ensis 2000	S, E, D, k, B	S, E, D, k, B	S, E, D, k, B	...					
Ensis 2001	S, E, k, B	D, B	S, D, k, B	D, B	...				
Ensis 2004	S, N, E, k, B	S, N, k, B	S, N, D, k, B	N, D, B	S, N, k, B	...			
Ensis 2009	N, E, D, k, B	S, N, E, k, B	N, E, k, B	S, N, k, B	S, N, D, B	S, N, D, k, B	...		
Lanice 2000	S, N, E, k, B	S, N, E, k, B	N, E, D, k, B	S, N, k, B	N, D, B	S, N, D, k, B	B	...	
Lanice 2004	S, E, D, k, B	E, B	E, k, B	S, E, k, B	E, D, k, B	S, N, E, D, k, B	N, E, k, B	N, E, k, B	...
Lanice 2009	N, E, k, B	N, E, k, B	N, E, k, B	S, N, D, k, B	N, D, B	S, N, k, B	B	B	N, E, k, B
	Arenicola 2000	Arenicola 2004	Arenicola 2009	Ensis 2000	Ensis 2001	Ensis 2004	Ensis 2009	Lanice 2000	Lanice 2004

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2.2.4. Alternative approaches

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In the context of the monitoring framework under discussion, the relevant target is that “composite species, abundance and diversity should not deviate significantly from an established baseline, subject to natural change”. The issue with all of the methods discussed so far is that comparisons are relative. A measure in one biotope in one year can only be compared to the same measure calculated from comparable survey data in another biotope and/or another year. Rather than comparing surveys among years, an alternative approach is to apply measures that have, in some sense, expected values reflecting differences in environmental quality. AMBI is a measure of the average pollution tolerance of an assemblage based on the observed pollution tolerances of species within the assemblage. A low score indicates that most individuals belong to species known to be intolerant of pollution, while a high score indicates that most individuals belong to species highly tolerant of pollution. Based on survey data from a large number of sites in the NE Atlantic numerical limits for AMBI have been selected to indicate differences in ecological status, so ecological status may be assigned based on single samples. Based on average values from the replicate data (Fig. 7), the majority of surveys indicate undisturbed assemblages, dominated by individuals from species which are considered to be intolerant of pollution. The *Arenicola* biotope in 2000 and 2004 and the *Ensis* biotope in 2001 and 2004 fall into the slightly disturbed category, indicating the presence of individuals from species which have some pollution tolerance. All surveys, however, indicate that the environment is in good status or better. While there is a potential for values calculated from pooled data to show slightly different patterns, for these data differences in AMBI calculated directly from pooled data and averages from replicates were small (<0.1 units) and in no case altered the conclusions to be drawn.

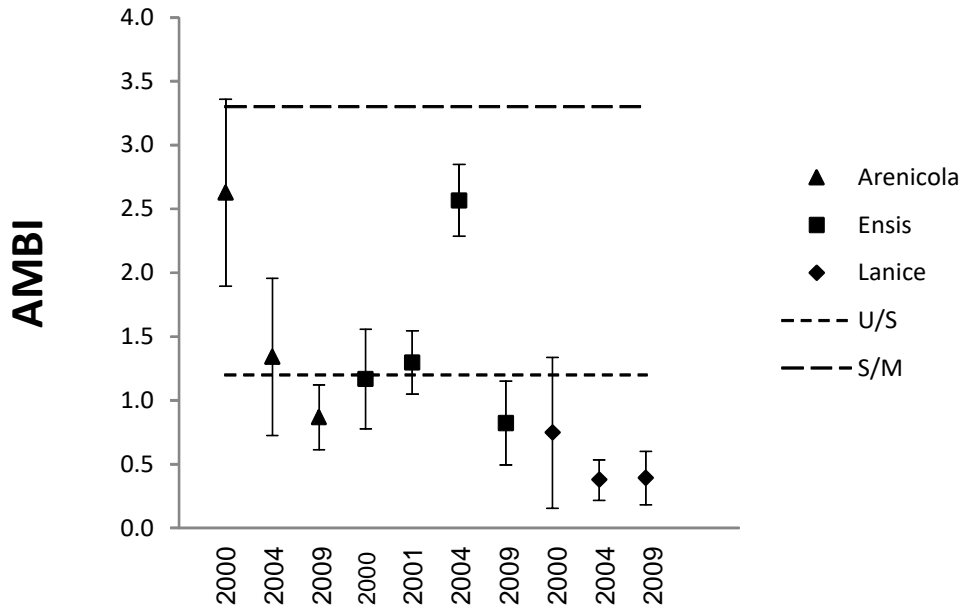


Fig. 7. Values for AMBI (mean \pm 1 s.d.) from samples in each biotope in each survey. Lower values indicate better ecological state, with U/S indicating the ‘undisturbed/slightly disturbed’ boundary and S/M the ‘slightly/moderately disturbed’ boundary. Values from pooled samples track mean values very closely, so they are not shown.

A different approach is to look at the average relatedness of species in assemblages, using Δ^+ . A combination of observation and theory suggests that under unimpacted conditions the species observed at a particular time or place will be a random subset of the species that may occur there, while under the influence of environmental stress the species observed will tend to become more closely related to each other. Using a list of all species recorded in all surveys to date as the master list, results (Fig. 8) indicate that most samples fall within expectation. In other words, there is no evidence that species are more closely related to each other than expected. This is true of both individual samples and of pooled samples from each survey.

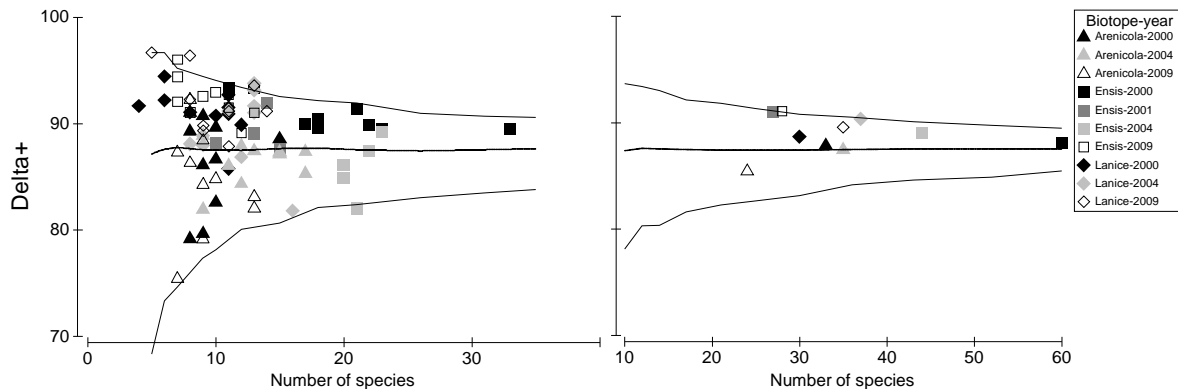


Fig. 8. Funnel plots indicating how observed values of taxonomic distinctness calculated from species lists (Δ^+) plotted against the number of species in each list, relate to values

corresponding to species being picked at random from the complete list of species collected from St Martin's Flats. Lines indicate the expected mean Δ^+ and 95% of observations are expected to lie between the upper and lower bounds. Individual replicate samples on left, pooled samples on right.

2.3. Discussion

2.3.1. Faunal changes over time

A subjective impression of the surface features of the three sites suggested that in the "Lanice/Echiocardium" biotope there were fewer feeding fans of the sand-mason worm *Lanice* in 2009 than in previous years and in the "Ensis" biotope there were fewer dead razor shells on the sediment surface and less evidence of the presence of live specimens (i.e. squirting water when disturbed).

Detailed analysis shows that, although the species composition of each biotope has changed significantly, the biotopes have retained their integrity between 2000 and 2009. Each biotope in 2009 was closer in composition to that same biotope in 2000 and 2004 than to any other biotope. Diversity profiles (particularly in terms of species accumulation plots) were unchanged for the "Lanice/Echinocardium" and "Arenicola" biotopes, but for the "Ensis" biotope diversity was much lower in 2009 than in 2000, the only other strictly comparable year in terms of sampling location and number of replicates. There were also larger changes in the species composition of the "Ensis" biotope between years than in the other two biotopes (Figs 5 & 6). This biotope is a more physically dynamic habitat than the other two, as evidenced by the coarseness of the sediment, and is therefore more likely to be subject to short term fluctuations in species composition and diversity. Small short-lived species are likely to fluctuate in abundance from year to year, as exemplified by the disappearance of the cumacean *Apseudes latreilli* from this biotope. Some large species that can live for many years may have regular recruitment in each year and establish temporally stable populations, while others may have exceptionally successful recruitment in some years but recruitment failures in others. An example of the former is the clam *Dosinia exoleta*, which was represented in the 2009 samples by about 10 year-classes of various strength (Fig. 9). On the other hand another large bivalve, the razor shell *Ensis arcuata*, large specimens of which had initially been used to define this biotope, had virtually disappeared in 2009, while very large and conspicuous specimens of the bivalve *Lutraria lutraria* were present (Fig. 10). This species was absent in the 2000 samples and the specimens all appeared to be of the same age (~8 years) with no younger individuals present, suggesting settlement soon after 2000 but with no subsequent recruitment.

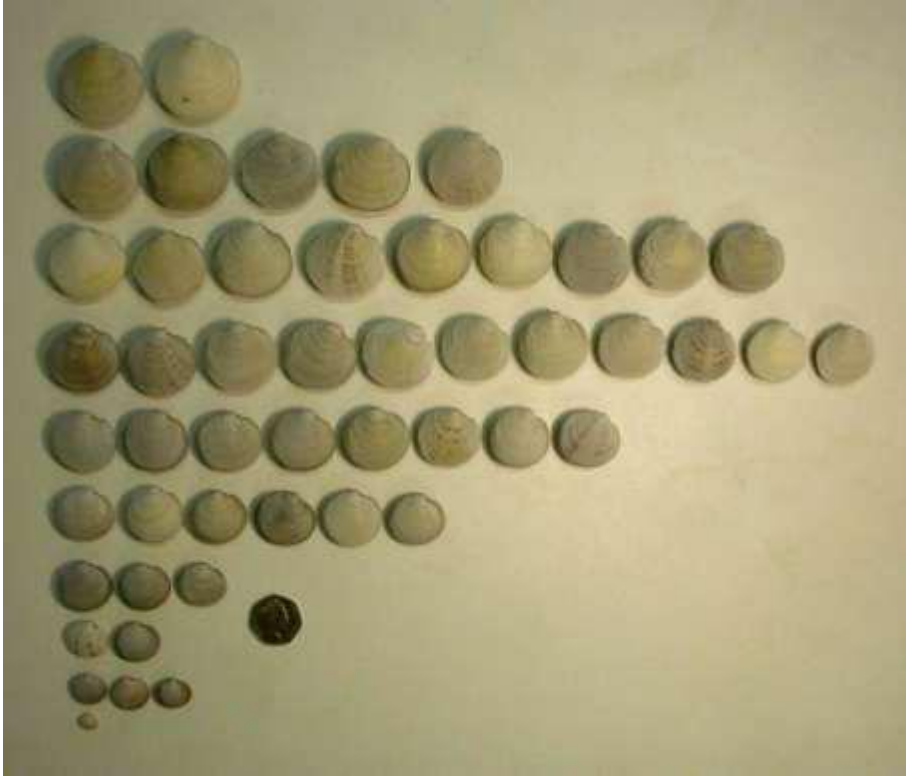


Fig. 9. Specimens of the clam *Dosinia exoleta* from the “*Ensis*” biotope in 2009, arranged in year classes and indicating successful recruitment each year. (Web colour, print B/W)



Fig. 10. Specimens of the clam *Lutraria lutraria* from the “*Ensis*” biotope in 2009, indicating a single year-class with no recruitment in recent years. (Web colour, print B/W)

2.3.2. Biotope identification

To recap, within the monitoring framework which aims to underpin marine conservation in the UK, a number of steps need to be taken to assess whether conservation objectives are being achieved. Characteristic biotopes must be identified, and within them composite species, abundance and diversity should not deviate significantly from an established baseline, subject to natural change.

It is immediately apparent that the classification system erected for marine biotopes in the UK does not include the biotopes present on St Martin’s flats. The point of interest is, then, whether it should, or could. It is not our goal, here, to critique the hierarchy in its entirety, or to discuss its general utility in its current form. We do, however, question some of the assertions on which it is based. The idea that, given identical environmental conditions (and sufficient time), an identical association of species should develop, underpinned much of the development of community ecology in the first half of the 20th century, building on the work of Francis Clements. In what is still, probably, the most insightful review of marine benthic ecology, Thorson (1957) implicitly considers the consequences of such a view of community development on classification schemes for marine benthic communities. Although from the 1950s onwards a strict Clementsian view of ecological development has generally been replaced by a Gleasonian view of ecology, in which individual species’ responses underpin apparent associations and a stochastic element is important, Thorson’s (1957) views are still highly relevant. Among these is that the “level bottom lacks the numerous “microlandscapes” (exposed or protected rocks, associations of different plants, holes, crevices etc.), each with a special microclimate, so characteristic of epifaunal environments”. It is worth noting that the

biotope classification was initially devised using, primarily, data gathered on the shore and using SCUBA with a focus on epifaunal environments. Thorson's view is that soft-bottom habitats are primarily driven by hydro-physical factors operating over large areas, which determine sediment composition, food supply and larval settlement, so while it may be possible to split epifaunal environments into "micro-units", a "similar splitting of level-bottom communities should be avoided" and "it seems reasonable, therefore, to divide the animal communities in accordance with these large natural bottom units". None of the apparent biotopes on St Martin's Flats corresponds exactly with any of those currently classified by the JNCC (Connor et al., 2004). This is either because these sedimentary habitats are unlike any of those surveyed to construct the classification, or because the classification itself is too discriminating, as Thorson's (1957) work would suggest. In fact, it is likely that both factors have an influence. Matches can be found with levels 2 and 3 of the biotope classification which relate to the physical characters of the habitat, but at level 4 and higher the faunistic composition begins to comprise part of the definition and no exact matches can be found. An online supplementary table lists potential candidates from the National Biodiversity Network database for level 2 Littoral sediment (LS) and Sublittoral sediment (SS) habitats previously recorded from Scilly. The latter were considered because, as noted by early naturalists (Carus 1850), there are many species that occur intertidally on Scilly that are only found in deeper water elsewhere in Britain. Many species characterizing level 5 habitats (biotopes) that belong to the level 2 Sublittoral sediment habitat in the JNCC classification were found intertidally in the surveys of St Martin's Flats. Holme (1961) listed a number of bivalve molluscs from other locations on Scilly that fall into this category, as do the crinoid *Antedon bifida*, the conspicuous orange seven-armed starfish *Luidia ciliaris* and the cephalochordate *Branchiostoma lanceolatum* (the latter being frequent on St Martin's Flats). Harvey (1969) makes a number of suggestions as to the causes of this phenomenon. The relative scarcity of near zero temperatures may permit animals to come up into the littoral, as may the negligible lowering of salinity compared to other places where lower salinities might deter some species, especially echinoderms, from littoral life. The phenomenon is not confined to the macrobenthos. Hummon and Warwick (1990) found several meiobenthic interstitial gastrotrich species in sandy beaches of Scilly that elsewhere only occurred sublittorally. They suggested that an additional possible explanation for this was the angularity of the sand grains derived from granite, which were tightly packed and restricted drainage from the beach at low tide, resulting in an interstitial environment no different from the sublittoral. It is clear from the online supplementary table that a large number (nearly half) of the 97 records from Scilly provide an uncertain match with a previously recognised biotope, in which cases attempts to ascribe them to such biotopes seems inappropriate. Furthermore, only 65 of these were identified as biotopes (level 5), of which 35 were uncertain matches, the remainder being identified either at level 4 (biotope complexes, 21 records) or level 3 (habitat complexes, 7 records). Nevertheless, at least two or three recognisable associations of species are present on St Martin's Flats, and more extensive mapping might reveal more. If these were to be formalised for the purposes of inclusion in a wider classification the biotope names initially ascribed to two of these associations for the purposes of this study, "*Lanice/Echinocardium*" and "*Ensis*", should not be retained since *Lanice* and *Ensis* are

no longer features of them, or at least have been shown to be inconsistent indicators. A more realistic definition of these assemblages could be gained from examination of the species that *consistently* make a substantial contribution to the Bray Curtis similarity among samples collected from each location (Tables 1-3). Candidate species that *typify* that assemblage should be found at a consistent abundance throughout, so the standard deviation of their contribution is low, and the ratio of Similarity/SD is high. For the “*Ensis*” biotope there is a clear candidate for the characterising species: the clam *Dosinia exoleta* makes the greatest contribution to the similarity among replicates and is the most consistent, with the highest Similarity/SD ratio (Table 2). It is also large and easily recognisable (Fig. 9). For the “*Arenicola*” biotope (Table 3) the greatest contribution to the similarity among samples is made by *Urothoe* spp., but these amphipods also make the greatest contribution to the “*Lanice/Echinocardium*” biotope. The next most important contribution is made by the polychaete *Scoloplos armiger*, which is unique to this assemblage and is also the most consistent, and it is also appropriate to retain the lugworm *Arenicola marina* as an assemblage-defining species in view of its large size and the consistently clear indications of its presence from surface features (casts and burrows). Thus this could be designated the “*Arenicola/Scoloplos*” assemblage. The original “*Lanice/Echinocardium*” biotope is the most problematic, since many of the species that contribute to the similarity among samples are also found at the other two sites. However, two opheliid polychaetes *Ophelia rathkei* and *Travisia forbesii* make the second and third highest contributions to inter-sample similarity (Table 1) and are unique to this assemblage, so this could be termed the “*Echinocardium/Opheliid polychaetes*” assemblage. The term “assemblage” rather than “biotope” is used here for the purposes of this study, rather than adding to the plethora of named biotopes that already exist and which are constantly being added to with each new area investigated. Of course, an alternative view could be that despite differences between different areas of the Flat these do not represent separate biotopes, but variation between different places driven by differences in tidal height and exposure. An objective method, such as Simprof, reinforces this idea, providing statistical support only for separating the *Ensis* biotope, from the extreme lower shore, from the other two (Fig. 6).

2.3.3. Favourable condition

The targets for the benthic fauna are that composite species, abundance and diversity “should not deviate significantly from an established baseline, subject to natural change”. The obvious problems here are defining the baselines, distinguishing between natural and anthropogenic change and determining how much change constitutes significant deviation. The question also arises as to whether significance is a biological, social or statistical construct.

Multivariate analyses have shown that, for each of the three study areas, there have been statistically significant changes in species composition between years. There is no reason to suppose that these changes are not natural, and with a naturally fluctuating baseline it is not easy to determine what degree of change is acceptable and how this could be measured. Similarly, a reduction in species diversity in 2009 for the “*Ensis*” biotope, compared with earlier years, is difficult to assess unless the range of natural variation to be expected in such a habitat is known, and sampling on only three occasions

cannot establish this. The ecological condition determined by the AMBI score is based on a global comparison with other areas. All three biotopes were in the “undisturbed” category in 2009, and future change into a category worse than has been found any of the earlier surveys could, in future, be taken as an unfavourable condition needing further investigation.

Taxonomic distinctness measures of biodiversity are, unlike species richness measures, relatively insensitive to small natural changes in habitat but are sensitive to anthropogenic disturbance (Leonard et al., 2006). For taxonomic distinctness indices based on simple species lists (presence or absence of species) there is a potential framework within which these measures can be tested for departure from expectation (see Warwick & Clarke, 2001). This envisages a master list or inventory of species encompassing the appropriate region/biogeographic area, from which the species found at one locality can be thought of as drawn. For example, Fig. 8 uses the complete faunal list for St Martin’s Flats in all biotopes and years. The species complement at any particular biotope and year can be compared with the master list, to ask whether the observed subset of species is representative of the biodiversity expressed in the full species inventory. Clearly, such a comparison is impossible for species richness since the list at one location is automatically shorter than the master list. However, the key point here is that average taxonomic distinctness (Δ^+) of a randomly selected sublist does not differ, in mean value, from AvTD for the master list, and reductions from this level can be interpreted as loss of biodiversity. Furthermore, there is a natural testing framework for how large a decrease (or increase) from expectation needs to be, in order to be deemed statistically significant. For an observed set of m species at one location, sublists of size m are drawn at random from the master inventory, and their AvTD values computed. From, say, 999 such simulated sublists, a histogram can be constructed of the expected range of Δ^+ values, for sublists of that size, against which the true Δ^+ for that locality can be compared. If the observed Δ^+ falls outside the central 95% of the simulated Δ^+ values, it is considered to have departed significantly from expectation. The construction of these 95% probability intervals can be repeated for a range of sublist sizes ($m = 10, 15, 20, \dots$) and the resulting upper and lower limits plotted on a graph of Δ^+ against m . When these limit points are connected across the range of m values, the effect is to produce a funnel plot (such as seen in Fig. 8). The real Δ^+ values for a range of observational studies are now added to this plot, allowing simultaneous comparison to be made of distinctness values with each other and with the expected limits. For the St Martin’s flats biotopes, measured values of Δ^+ all fall within the 95% confidence limits of the simulated null distribution based on random samples from the master list (Fig. 8), suggesting that biodiversity in these terms does not depart from expectation. If biotopes fall outside these 95% confidence limits in future, an unfavourable condition would be indicated.

2.3.4. Temporal variability

In the specific case of St Martin’s Flats we have addressed the question of the extent of natural variation that should be accounted for when setting conservation objectives. In a much wider study, to be reported elsewhere, we searched for raw data relevant to features which could be the target of marine conservation objectives from anywhere on the continental shelf of the North-East Atlantic. None had the combination of spatio-

temporal coverage and relevance required for them to be used to set, quantitatively, levels of natural variation which could be built into robust and defensible conservation objectives. This should not be a surprise. Gray and Elliott (2009) identify three general patterns of temporal variability in marine benthic systems. Some species tend to maintain population numbers relatively constant through time and may be said to be persistent; many organisms undergo repeatable cycles, which may be annual or longer term with periods from 6-7 to >30 years; there may be changes in response to longer-term processes which may or not be cyclical such as variation in the NAO. These patterns may be regarded as stable as changes are to some extent predictable, but may only be understood if we have monitoring data at the appropriate temporal and spatial scales. Populations change with variable recruitment (and the processes underlying that variability): some species recruit regularly, such as *Dosinia exoleta* in the St Martin's Flats example, while others have highly successful pulses of recruitment followed by long periods with no recruitment at all, such as *Lutraria lutraria* in the St Martin's Flats example. Whether the latter may be considered stable or not depends on the repeatability of the cycles and the scale at which variation is considered. Gray and Elliott (2009) state that insufficient information is available on this, and go on to say "In fact, so little data is available on long-term cycles and variations in recruitment that the patterns described above may in time prove not to be typical at all. Understanding recruitment variability and the factors causing that variability is one of the central problems in understanding long-term fluctuations in benthic communities." It should also be noted that not only species and populations exhibit variation on many temporal scales. Assemblages also do, and most assemblages are in some form of dynamic equilibrium. Thus repeat surveys of the same place might detect very similar communities, but as in the St Martin's Flats example, they will not be identical. They might detect very different communities which form parts of a natural successional cycle (e.g. mussels, barnacles or algae, on rocky shores). In terms of setting objectives, consideration needs to be made of the degree of change that might be considered trivial, as opposed the degree if change that might be of concern. In such a framework, however, percent change is unlikely to be an applicable measure. The question then is: how to take account of natural variation within conservation objectives without having a clearly defensible method for setting numerical limits? The simplest is to phrase objectives in a way that acknowledges that variation occurs, while allowing expert judgement to play a role in determining the cause and consequences of that variation. Conservation objectives consider two main components of features: extent and status (or quality). While it may be difficult to do in practice, determining changes in the extent of a feature presents little intellectual challenge unless the feature is poorly defined. Setting of objectives relating to conservation status, however, is more challenging in a quantitative context. The nature, direction, degree and interpretation of changes depend, critically, on how status is defined and determined. For example, Warwick et al. (2002) demonstrated that different measures of diversity, applied to the same dataset, led to very different interpretations of change in the community under consideration. Measures of abundance and species richness, the types of measures describing amounts and therefore amenable to incorporation in a numerical framework based on percent change, were uninformative and varied considerably. Other measures showed a clear step-change in community structure which could be interpreted as positive (improvement) or negative (decline) depending on the underlying conceptual model

being applied. A classic example is the failure of the monitoring of Norwegian oil platforms to detect change, when using simple numerical treatments of monitoring data (Gray et al. 1990). Application of alternative numerical methods to the same data showed that conservation objectives (no change beyond 500m from the rigs) were not being complied with, and led to major changes in the industry and the way in which monitoring was carried out. It seems sensible, therefore, to focus numerical ranges and limits for conservation objectives on aspects of features that may be described in appropriate terms. An objective of the form “diversity of species should not decline by more than 10%” is unlikely to be useful, unless there is a clear expectation that such a decline may occur and may be informative. A further consideration is that of statistical power. Setting a conservation objective with numerical bounds implies that changes may be detected accurately. Several benthic studies (e.g. Rogers et al. 2006) have shown that the degree of sampling effort required for the detection of small (<10%) changes is prohibitive (100s to 1000s of samples being required) and only if changes in the order of 50-75% are to be detected with any degree of certainty does the required sampling effort begin to be practical. On the other hand, an objective of the form “good conservation status must be maintained” leaves the door open for sensible data collection, analysis and interpretation.

3. Conclusions

Anthropogenic threats to marine biodiversity are many and varied, and operate on spatial and temporal scales ranging from local short-term pollution incidents or coastal developments to regional long-term effects of fishing activities, eutrophication, climate change or the effects of introduced species. Because most traditional biodiversity indices based on species richness are strongly affected by natural environmental variability, distinguishing between natural and anthropogenic changes is generally recognised as the most difficult challenge facing biodiversity monitoring. ICES (2002) has observed the inappropriateness of the ‘pristine state’ as a default reference point against which the biodiversity of potentially impacted sites can be evaluated. Nevertheless, there is a requirement to assess “good ecological condition / favourable condition” for designated sites. We suggest above that setting limits on natural variability is almost always impractical, or at least requires subjective judgement which is often indefensible. Disentangling the drivers of biodiversity change adequately has required experiments in which environmental variables can be manipulated individually in a controlled way; generally impractical for routine monitoring programmes and of dubious relevance to the real world. The advantage of taxonomic distinctness is that variability in biodiversity due to natural environmental factors generally falls within a predictable range (Leonard et al. 2006) , based on the expectation of random selection from a regional species pool. This expectation then becomes the baseline against which biodiversity change is determined, instead of relying on historical time-series data. Anthropogenic influences modify this pattern, such that biodiversity falls below the predicted range. The taxonomic distinctness index is easy to measure (relying on simple species lists rather than quantitative data) and it has been shown to be appropriate as an indicator of the effects on biodiversity of anthropogenic events over a range of spatial and temporal scales (Leonard et al. 2006). It

also explicitly addresses issues of conservation, protection and enhancement of biological diversity advocated by the global Convention on Biological Diversity.

Another alternative to setting limits of natural variability based on time-series data at a particular site is to examine the spatial variability in habitat quality over the geographical range that that habitat occupies. Many data exist, but they are difficult to use in quantitative comparisons. With the taxonomic distinctness index the concept of spatial reference sites is replaced by the concept of a “reference condition”, i.e. the null hypothesis that the species present are structured as if they are a random selection from the regional species pool. This could enable the establishment of a reference condition in a region that was entirely impacted to some degree, and where no appropriate reference sites are available. Thus, the desired “favourable condition” for an interest feature in an SAC might not necessarily be the condition it was in at the time it was designated. The application of AMBI (AZTI’s Marine Biotic Index) is a means of comparing the ecological status of an assemblage of species based on their sensitivity to pollution and disturbance at a wide range of reference sites, and the AMBI score is an additional means of assessing favourable condition irrespective of temporal variability in community composition and diversity.

Generally faunistic surveys only determine species abundances, which limits the number of techniques available for assessing ecological condition. Some consideration might also be given to the determination of species biomasses as well as abundances (simple blotted wet-weights would suffice). This would open more opportunities for the assessment of anthropogenic disturbance, for example the abundance / biomass comparison (ABC) method or the phylum level meta-analysis (see Clarke & Warwick 2001). In the ABC method, separate *k*-dominance curves for species abundance and species biomass act as internal controls against each other, providing a snapshot of ecological condition that obviates the need for reference samples in space or time (Warwick 1986; Warwick et al. 1987; Warwick and Clarke 1994). The phylum level meta-analysis compares the proportional ‘production’ of higher taxa (based on a combination of abundance and biomass) at a location with a training data set comprising a range of pollution/disturbance scenarios (Warwick and Clarke 1993; Savage et al. 2001; Somerfield et al. 2006).

The UK’s approach to setting a conservation objective for a marine SAC feature includes as an attribute “range of biotopes” and as a target “number of biotopes should not deviate from baseline” (Figure 1-1 in Davies et al 2001). In view of the difficulty in ascribing the assemblages on St Martin’s Flats to recognised biotopes in the JNCC or EUNIS level 5 classifications, this seems to be an impractical aspect of the approach. We would recommend a more robust approach to defining species assemblage composition, tailored to specific sites (as we have done above for St Martin’s Flats), rather than forcing these assemblages to conform with previously recognised biotopes, or creating new ones. Such habitat classifications are obviously acceptable up to level 3 (habitat complexes such as littoral sand) that utilise only physical characters, but not at level 4 and above where faunistic composition become part of the habitat definition.

Davies (1990) described the area as follows: “St Martin’s Flats is the largest continuous area of sand in the Isles of Scilly. Tidal currents vary over the area resulting in different degrees of sediment sorting which in turn leads to different infaunal communities. Small populations of amphioxus, *Branchiostoma lanceolatum* are occasionally present. Large populations of the sand mason *Lanice conchilega* extend from mid to low tide level. Rich

infaunal communities were characterised by heart urchins and bivalve molluscs, including the uncommon species *Lutraria lutraria*. Nichols and Harris (1982) recommend that these sediment shores be considered for statutory protection in view of their high habitat diversity and associated species richness.” Statutory protection was put in place, and as a result the Flats have been regularly monitored, showing that Davies’ description is as good now as it was then. The question that needs to be considered, then, is whether the use of a biotope classification has helped in any way in this process or, indeed, has it hindered?

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5. References

- Borja A, Franco J, Perez V (2000) A marine biotic index to establish the ecological quality of soft bottom benthos within European estuarine and coastal environments. *Mar Pol Bull* 40:1100-1114
- Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. *Mar Pol Bull* 46:835-845
- Carus JV (1850) A general view of the zoological features of the sea round the Scilly Islands. In: North IW A week in the Isles of Scilly. London, Longman & Co, pp 161-181
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Clarke KR, Gorley RN (2006) PRIMER v6: User Manual / Tutorial. PRIMER-E, Plymouth
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. 2nd Edition. Plymouth Marine Laboratory, Plymouth

- Connor DW, Allen JH, Golding N, Howell KL, Lieberknecht LM, Northen KO, Reker JB (2004) The marine habitat classification for Britain and Ireland Version 04.05. JNCC, Peterborough. (internet version) jncc.defra.gov.uk/MarineHabitatClassification
- Davies, J. (1990) Benthic marine ecosystems of Great Britain: a review of current knowledge. Western Channel and the Bristol Channel and approaches (MNCR coastal sectors 8 and 9). Nature Conservancy Council. CSD Report, No. 1173. (Marine Nature conservation review report MNCR/OR/009).
- Davies J, Baxter J, Bradley M, Connor D, Khan J, Murray E, Sanderson W, Turnbull C, Vincent M (2001) Marine Monitoring Handbook. Joint Nature Conservation Committee, Peterborough
- Gray JS, Clarke KR, Warwick RM, Hobbs G (1990). Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. *Mar Ecol Progr Ser* 66:285-299
- Gray JS, Elliott M (2009) Ecology of marine sediments: from science to management. 2nd ed. Oxford University Press, Oxford
- Harvey, LA (1969) The marine flora and fauna of the Isles of Scilly. The islands and their ecology. *J nat Hist* 3:3-18
- Holme NA (1961) The bottom fauna of the English Channel. *J mar biol Ass UK* 41:397-461
- Howson CM, Picton BE (1997) The species directory of the marine fauna and flora of the British Isles and surrounding seas. Ulster Museum Publication No. 276. Ulster Museum and the Marine Conservation Society, Belfast and Ross-on-Wye
- Hummon WD, Warwick RM (1990) The marine flora and fauna of the Isles of Scilly - Gastrotricha. *J nat Hist* 24:519-525
- ICES (2002) Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES CM 2002/ACE:03. International Council for the Exploration of the Sea, Copenhagen
- Leonard DRP, Clarke KR, Somerfield PJ, Warwick RM (2006) The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. *J env Manag* 78:52-62
- Natural England (2000) Isles of Scilly Complex European Marine Site. English Nature's advice given under Regulation 33(2) of the Conservation (Natural Habitats &c.) Regulations 1994. http://www.ukmpas.org/pdf/Sitebasedreports/Isles_of_Scilly_complex_33.pdf
- Nichols D., Harris, T. (1982) A survey of the low tide flats of the Isles of Scilly. (Contractors: Department of Biological Sciences, University of Exeter). Nature Conservancy Council. CSD Report, No. 413.
- OSPAR Commission (2008) Case Reports for the OSPAR List of threatened and/or declining species and habitats. OSPAR Commission, London.
- Ray GC, McCormick-Ray J (2014) Marine conservation: science, policy and management. Wiley, Oxford.
- Rogers SD, Somerfield PJ, Schratzberger M, Warwick R M, Maxwell T, Ellis J (2008) Sampling strategies to evaluate the status of offshore soft-sediment assemblages. *Mar Pol Bull* 56:880-894

- 837 Savage C, Field JG, Warwick RM (2001) Comparative meta-analysis of the impact of
838 offshore marine mining on macrobenthic communities versus organic pollution
839 studies. *Mar Ecol Prog Ser* 221:265-275
- 840 Secretariat of the Convention on Biological Diversity (2000) Sustaining life on Earth:
841 how the Convention on Biological Diversity promotes nature and human well-being.
842 Secretariat of the Convention on Biological Diversity, Montreal
- 843 Somerfield PJ, Atkins M, Bolam SG, Clarke KR, Garnacho E, Rees HL, Smith R,
844 Warwick RM (2006) Relative impacts at sites of dredged-material relocation in the
845 coastal environment: a phylum-level meta-analysis approach. *Mar Biol* 148, 1231-
846 1240
- 847 Thorson G (1957) Bottom communities (sublittoral or shallow shelf). *Mem Amer Geol*
848 *Soc* 67 (1): 267-293
- 849 Warwick RM (1986) A new method for detecting pollution effects on marine
850 macrobenthic communities. *Mar Biol* 92:557-562
- 851 Warwick RM, Clarke KR (1993) Comparing the severity of disturbance: a meta-analysis
852 of marine macrobenthic community data. *Mar Ecol Prog Ser* 92:221-231
- 853 Warwick RM, Clarke KR (1994) Relearning the ABC: taxonomic changes and
854 abundance/biomass relationships in disturbed benthic communities. *Mar Biol*
855 118:739-744
- 856 Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on
857 relatedness of species. *Oceanogr mar Biol an Rev* 39: 207-231
- 858 Warwick RM, Pearson TH, Ruswahyuni (1987) Detection of pollution effects on marine
859 macrobenthos: further evaluation of the species abundance/biomass method. *Mar*
860 *Biol* 95:193-200
- 861 Warwick RM, Ashman CM, Brown AR, Clarke KR, Dowell B, Hart B, Lewis RE,
862 Shillabeer N, Somerfield PJ, Tapp J F (2002) Inter-annual changes in the biodiversity
863 and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK,
864 associated with local and regional environmental events. *Mar Ecol Progr Ser* 234:1-
865 13
- 866 Warwick RM, Dashfield SL, Somerfield PJ (2006) The integral structure of a benthic
867 infaunal assemblage. *J exp mar Biol Ecol* 330:12-18
- 868