Habitat modelling limitations – Puck Bay, Baltic Sea – a case study*

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Abstract

The Natura 2000 sites and the Coastal Landscape Park in a shallow marine bay in the southern Baltic have been studied in detail for the distribution of benthic macroorganisms, species assemblages and seabed habitats. The relatively small Inner Puck Bay (104.8 km^2) is one of the most thoroughly investigated marine areas in the Baltic: research has been carried out there continuously for over 50 years. Six physical parameters regarded as critically important for the marine benthos (depth, minimal temperature, maximum salinity, light, wave intensity and sediment type) were summarized on a GIS map showing unified patches of seabed and the near-bottom water conditions. The occurrence of uniform seabed forms is weakly correlated with the distributions of individual species or multi-species assemblages. This is partly explained by the characteristics of the local macrofauna, which is dominated by highly tolerant, eurytopic species with opportunistic strategies. The history and timing of the assemblage formation also explains this weak correlation. The distribution of assemblages formed by long-living, structural species (*Zostera marina* and other higher plants) shows the history of recovery following earlier disturbances. In the study area, these communities are still in the stage of recovery and recolonization, and their present distribution does not as yet match the distribution of the physical environmental conditions favourable to them. Our results show up the limitations of distribution modelling in coastal waters, where the history of anthropogenic disturbances can distort the picture of the present-day environmental control of biota distributions.

1. Introduction

The Baltic Sea displays a specific gradient in species richness and functional diversity that falls away with diminishing salinity from W to NE (Bonsdorff & 1999, Bonsdorff 2006). The Polish Exclusive Economic Zone (Polish EEZ) is situated in the centre of the above gradient, and the inner part of Puck Bay is regarded as the most diverse and biologically valuable part of the Polish Marine Areas (PMA, Węsławski et al. 2009). Puck Bay is protected as a Natura 2000 site under both the birds and habitats directives; it is also a designated Baltic Sea Protected Area (BSAP), and its inner waters are part of the Coastal Landscape Park. Puck Bay is considered a key site for a number of species that are not present along the open sea coast. The area has also been subjected to strong anthropogenic pressure (pollution and nutrification) with well-documented losses of habitats and species, particularly among the macrophytobenthos (Pliński & Florczyk 1984). Documentation of marine habitats, their changes and monitoring are among the national obligations of Natura 2000 site management. At the moment, however, there are no management and protection plans in place for the marine Natura 2000 areas. Since biological sampling and analyses are expensive and time-consuming, there is a great demand for modelling and other indirect environmental assessment methods. These include the use of ecological quality or integrity indicator species (Anderson & Thompson 2004, Borja et al. 2008). They not only support the evaluation of achievements against certain criteria, most often a defined set of predetermined standards or management goals (Pomeroy et al. 2004), but also communicate knowledge to managers and decision makers (e.g. Diedrich et al. 2010, Douvere & Ehler 2011). These functions make indicator selection a process that is political, social and value-based rather than purely scientific (McCool & Stankey 2004). Species distribution or habitat modelling is crucial for marine resources management and conservation initiatives. Species distribution models can predict distributions across landscapes (e.g. Reiss et al. 2011), habitat preference modelling can nominate areas that are important for species conservation (e.g. Cañadas et al. 2005), multilayered ecosystem models can determine ecological carrying capacity for aquaculture development (e.g. Ferreira et al. 2008), and various modelling approaches can simulate cumulative impacts (e.g. Nobre et al. 2010) and produce maps of the expected status of marine ecosystems (e.g. Parravicini et al. 2012). The basic approach to species distribution modelling is the selection of physical variables that are optimal or preferred by a species or a species assemblage (Yen et al. 2004). The basic variables are salinity, temperature, sediment type and depth. With a better coverage of measurements, the number of variables can be raised, so long as the additional variables are correlated with known species/assemblage distributions. The aim of this study was to assess the level of correlation between the occurrence of habitat-forming species and seabed environment typology. The basic hypothesis was that proper recognition of key physical characteristics of the sea bed would yield a pattern explaining the occurrence/distribution of benthic organisms and assemblages.

2. Material and methods

The following environmental variables were used to describe the benthic fauna habitat:

- DEPTH – depth;
- TMIN – annual minimum near-bottom temperature (cold season);
- TMAX – annual maximum near-bottom temperature (warm season);
- SMIN – annual minimum near-bottom salinity;
- SMAX – annual maximum near-bottom salinity;
- PAR – photosynthetic active radiation reaching the seabed;
- WAVE – annual maximum orbital velocity near the bottom (wind waves);
- SEDIMENT – sediments classified according to EUNIS recommendations (Table 1).

The information at the 500 m spatial resolution grid was extracted from underlying thematic maps.

In order to reveal the hidden pattern of observations, data mining techniques were applied (Table 2). A classical non-hierarchical k-medoid technique of clustering (Partitioning Around Medoids – PAM algorithm) was applied to a range of input data scenarios (cluster package in R; Maechler et al. 2005). The first approach assumed the use of various combinations of the eight variables, which were initially standardized. Further analysis included also exp(TMAX) and log(PAR). The second approach was to reduce the number of variables by finding the most important principal components. The results showed that three principal

Table 1. Sediment reclassification scheme

Sediment class	Sediment class description according to EUNIS
1	51 gravel and coarse sands
2	52 medium sands 53 fine sands 54 fine sands with mud admixture 55 fine-grained marine sand 8 medium-grained marine sand 19 marine clay
3	55 fine-grained aleurite – silt/clay 56 coarse-grained aleurite – mud 57 coarse-grained aleurite with gyttia 58 peat with sand and mud admixture

Table 2. Pearson's correlation matrix of environmental variables. Correlations greater than the absolute 0.5 are shown in parentheses

DEPTH	TMIN	TMAX	SMIN	SMAX	PAR	WAVE	SEDIMENT	exp(TMAX)	log(PAR)	
DEPTH	1.000									
TMIN	−0.338	1.000								
TMAX	−0.465	(0.719)	1.000							
SMIN	−0.041	0.208	−0.169	1.000						
SMAX	−0.216	(0.681)	0.395	(0.609)	1.000					
PAR	(−0.777)	0.267	0.267	0.182	0.254	1.000				
WAVE	−0.451	−0.307	−0.221	0.009	−0.145	0.422	1.000			
SEDIMENT	−0.461	−0.002	0.054	0.199	0.171	0.445	0.419	1.000		
exp(TMAX)	−0.473	(0.711)	(0.937)	−0.053	(0.531)	0.283	−0.171	0.142	1.000	
log(PAR)	(−0.799)	0.353	0.451	0.006	0.216	(0.702)	0.347	0.317	0.432	1.000

components with eigenvalues of more than one explained 80.9% of the total variability. DEPTH, exp(TMAX), log(PAR) and TMIN made a large contribution to PC1, WAVE to PC2 and SMIN to PC3 (Tables 3 and 4).

The clustering procedure was run for different numbers of clusters (from 2 to 25) and every set of variables in order to identify the number of clusters for which the highest reference measure – the average silhouette coefficient – would be obtained (Figure 1).

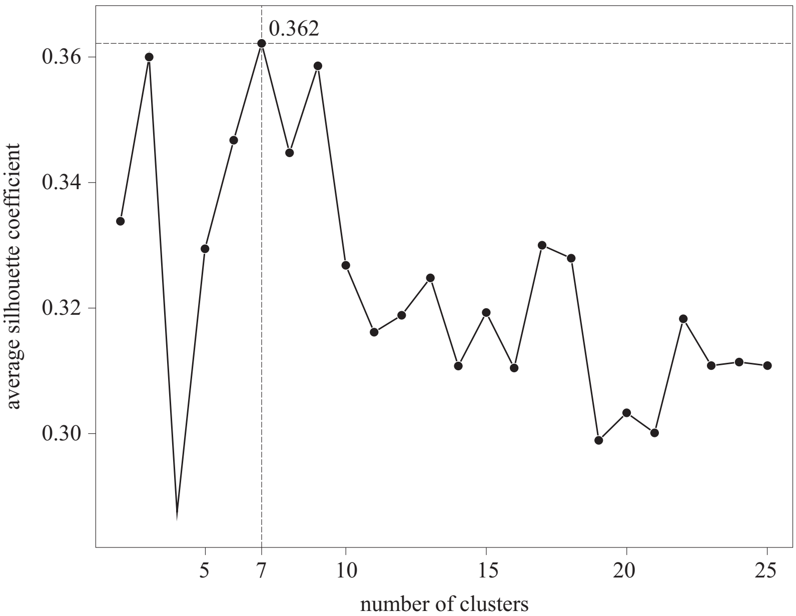

Figure 1. Average silhouette coefficients plotted against the number of clusters (PCA results taken as input to the PAM algorithm)

In most cases analysed, the suggested number of clusters was 3, 7, 9 and 10. The optimal solution of 7 was chosen as the best descriptor of near-bottom conditions in the study area on the basis of the following criteria: a relatively high average silhouette coefficient, the spatial distribution of the groups, and the scale of the analysis performed. Nevertheless, the clustering structure of the observations was rather fragile (silhouette coefficient ranging from 0.25 to 0.50; Kaufman & Rousseeuw 1990), and the mapped clusters presented well-defined unified patches (Figure 2).

The last step was to create a continuous surface of cluster presence by applying Indicator Kriging. The method uses the transformed binary (0 and 1) variables indicating each class membership (de Smith et al. 2007).

Table 3. Principal components from the correlation matrix of environmental variables

	Eigenvalues of the correlation matrix							
	1	2	3	4	5	6	7	8
	1.764	1.425	1.155	0.7804	0.6171	0.465	0.4419	0.3527
	Percentage of the total variance explained							
	1	2	3	4	5	6	7	8
	38.8931	25.3687	16.6677	7.61305	4.76076	2.70113	2.44101	1.55461
	Component loadings							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
DEPTH	0.44265	−0.34062	0.13752	−0.15591	0.17128	−0.11722	0.60413	−0.48659
TMIN	−0.41909	−0.37306	−0.15398	0.04076	0.07955	−0.75202	−0.20146	−0.21764
SMIN	−0.17983	−0.18317	0.73641	0.27831	−0.22039	0.21525	−0.27090	−0.38219
SMAX	−0.39835	−0.35035	0.32970	0.02045	0.29911	0.08037	0.42191	0.57924
WAVE	−0.09224	0.58293	0.19661	0.22979	0.70820	−0.14087	0.02527	−0.19544
SEDIMENT	−0.25572	0.35719	0.32015	−0.78400	−0.21466	−0.17717	0.09895	−0.05102
exp(TMAX)	−0.43188	−0.20066	−0.34907	−0.28963	0.30783	0.56244	−0.08176	−0.38691
log(PAR)	−0.42069	0.28435	−0.20826	0.38055	−0.42886	0.01890	0.57090	−0.20923

Table 4. Summary statistics for the clusters. Codes used for the cluster description: −− the lowest average value of the variable; − low average value of the variable; + high average value of the variable; ++ the highest average value of the variable

Cluster	Average depth [m]	Area [km^2]	SEDIMENT*	DEPTH	PAR	WAVE	TMAX	TMIN	SMAX	SMIN
1	1.243	2.8	3	−−	−	++	+		−	
2	2.036	36.6	2	−	−		+	++	+	++
3	2.434	10.5	2	−	−−	+	−	−	−	−−
4	3.277	28.2	2		+		++	+		
5	4.466	23.1	1	+	++	−			−−	−
6	5.944	6.6	2	+	+	+	−−	−−		
7	6.709	6.4	1	++		−−			++	+

*prevailing sediment type.

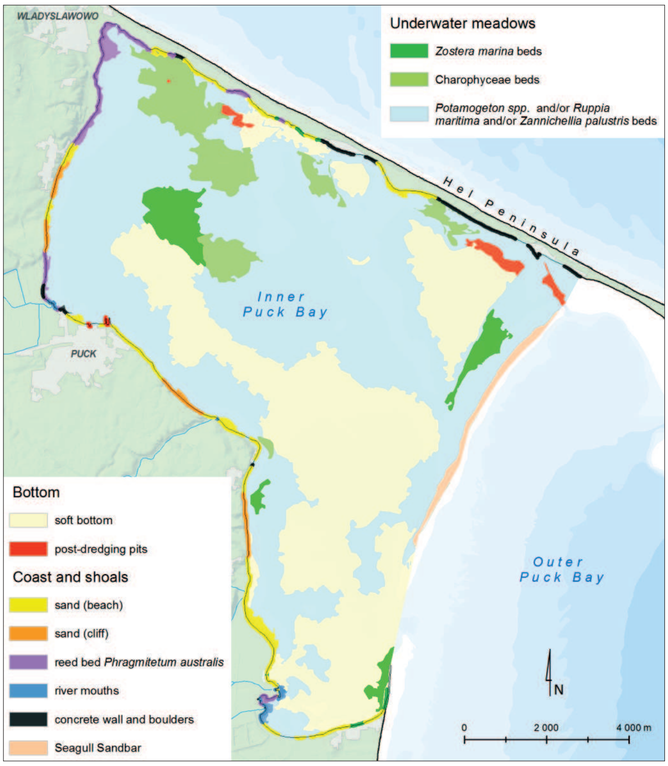

Figure 2. Distribution of macrophyte assemblages – situation in 2007, inner Puck Bay; map taken from the *Atlas of Polish marine area bottom habitats* . . . (Gic-Grusza et al. (eds.) 2009)

All the field data were collected during the Habitat Mapping project, 2007–2009, funded by the EEA Financial Mechanism (http://www.pom-habitaty.eu/). Sampling was performed between June and September at over 60 sampling stations, distributed as evenly as possible to form a grid over the whole study area. The basic gear used was a 15 × 15 cm Reineck sampler. The vegetated bottom was sampled with the use of a scuba diver operated DAK quantitative frame with a net of 30 × 30 cm area. Salinity and temperature were measured by mini CTD profiling during the sampling season. To take account of the seasonal temperature and salinity signals, all seasonal measurements were taken at two nearby stations on either side of the Bay (Hel and Gdynia). Maps of the physical parameters, habitats and macrozoobenthos abundance for the research area were published in the Atlas of Polish marine area bottom habitats (Gic-Grusza et al. (eds.) 2009, freely available at http://www.iopan.gda.pl/hm/atlas/Atlas_all.pdf).

3. Results

Long-living sessile species and key perennial assemblages are listed in Table 5 and their occurrence is illustrated on Figure 2. The basic pattern consists of isolated patches of *Zostera marina*, a large area covered with other vascular plants (*Ruppia*, *Potamogeton* and *Zanichella*) and bare sands. The typology of the seabed conditions is shown on Figure 2, where the Bay is divided into a NE part (shallower and sandy) and a SW part (deeper

Table 5. Statistical correlations between the occurrence of perennial sessile species and uniform seabed types. Sixth cluster omitted owing to different area coverage (numbers according to Figure 3)

Species or assemblage/ seabed unit	1	2	3	4	5	7	Total area [km^2]	Percentage of Inner Puck Bay
Zostera marina beds	0	0.23	0.11	**0.61**	0.05	0	3.2	3%
Ruppia/Potamogeton/ Zanichella	0.04	0.46	0.05	0.28	0.16	0.02	55.5	53%
Charophycae	0.02	**0.80**	0	0.18	0	0.01	6.2	6%
Mytilus trossulus	0.03	0.22	0.10	0.28	0.32	0.04	36.5	35%
Mya arenaria	0.03	0.31	0.14	0.18	0.25	0.10	49.4	47%
Macoma baltica	0.01	0.27	0.1	0.34	0.22	0.06	74.0	71%
Cerastoderma glaucum	0.03	0.33	0.08	0.28	0.23	0.06	102.3	98%
Total area [km^2]	2.8	36.6	10.5	28.2	23.1	6.4		
Percentage of Inner Puck Bay	3%	35%	10%	27%	22%	6%		

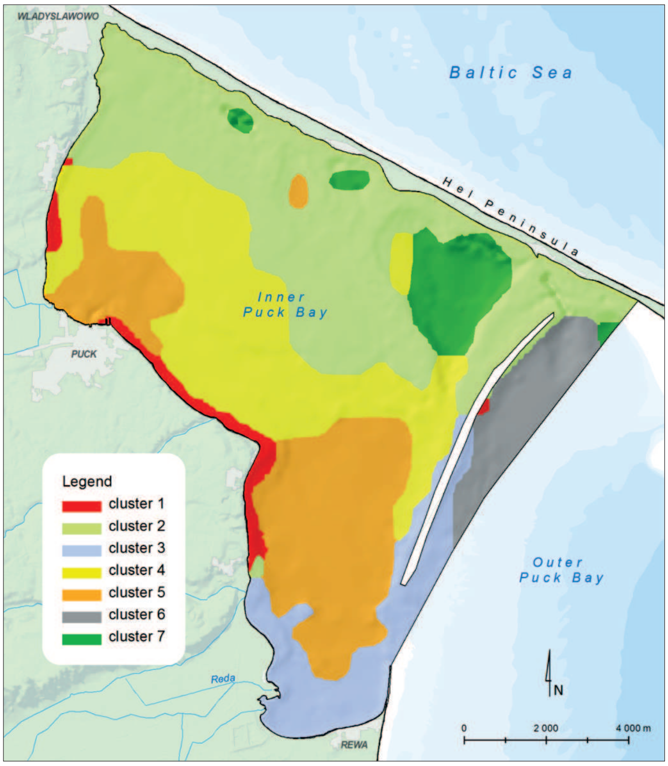

Figure 3. Uniform patches of seabed in Inner Puck Bay (for uniformity criteria, see the methods)

with more diverse sediment). The nearshore areas and three post-extraction pits are distinctive. The statistical relation between the biological entities (species and assemblages) and the physical factors is very weak (Table 5).

4. Discussion

The common understanding of the function of Marine Protected Areas (MPA) is that species protection is a secondary goal, and conservation of seascapes and habitats is much more important (Olenin & Ducrotoy 2008). MPA protection often focuses on habitat formation – large biogenic structures like shell beds or vascular plant meadows. Habitat-forming species are scarce in the Polish part of the Baltic Sea, however. Small biogenic reefs may be formed from mixed beds of *Mytilus trossulus* (a hybrid of *Mytilus edulis trossulus*) and *Balanus improvisus*, usually on hard or mixed substrata, randomly dispersed throughout the area, with a few offshore patches of stony bottom (Gic-Grusza et al. (eds.) 2009). Otherwise there are only a handful of vascular plants (genera *Zostera*,

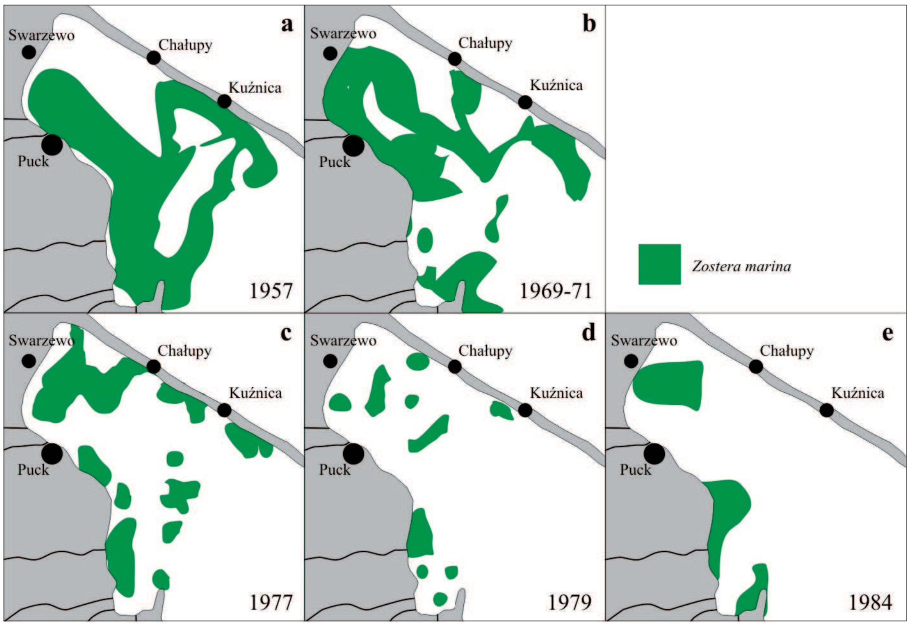

Figure 4. History of *Zostera marina* coverage changes in Puck Bay based on literature sources (http://water.iopan.gda.pl/projects/Zostera/history.html)

Potamogeton, *Ruppia*, *Myriophyllum*) and a few species of large, erect algae (*Chara* spp.), Warzocha (1995). Other habitat-forming species (*Fucus vesiculosus*) disappeared from the Polish EEZ in the late 1970s (Pliński & Florczyk 1984). Local species of bryozoans and hydroids are small and not numerous (Grzelak & Kukliński 2010), so their role in habitat formation is of no importance.

The history of the occurrence of vascular plants in Puck Bay has been relatively well-documented since the early 1950s (Ciszewski et al. 1962; see Figure 4). This date is usually given as a temporal reference point for the natural conditions before eutrophication became a serious problem (HELCOM 2009a,b). The former distribution of *Zostera* beds in the Puck Bay area (Figure 4) covers not only its present-day distribution but also the areas of clusters 4 and 5 (Figure 3). Today, the area of cluster 5 is covered by organically enriched fine sands and muddy sands, where anoxic conditions can strongly affect the benthos (Pearson & Rosenberg 1978, Hyland et al. 2005).

Fragmentation is the principal threat to habitats and populations (changes in dispersal, isolation of subpopulations, restricted gene flow) in terrestrial nature conservation (Zschokke et al. 2000). This is not regarded as a danger to marine populations because of the easy dispersal of larvae and propagules in water (Heip et al. 2009). The size of an algal patch neither influences species richness nor the abundance of associated macrofauna (Roberts & Poore 2005). With regard to crustaceans, colonization was faster in small isolated patches than in large, contiguous patches (Roberts & Poore 2005). Modelling of the effects of entire habitat loss in Puck Bay (one out of three) shows a species loss of only 10% (Włodarska-Kowalczuk et al. 2010). This is the effect of the extremely low diversity of the Baltic ecosystem, together with the predominance of eurytopic species that effectively occur in almost all available habitats.

Previous disturbances to the seabed of the Bay of Puck were serious and differentiated, beginning with the physical destruction of the seabed to organic contamination (Table 6). Most of these stressors were reduced or ceased altogether with the adoption of the market economy and new environmental protection standards. Sediment removal tends to have long-lasting effects, as demonstrated by the natural and man-made pits in the Bay: more than 10 years following the disturbance the local fauna was still very different from that of the undisturbed area (Szymelfenig et al. 2006).

The detrimental changes to the seagrass and plant cover of the Puck Bay seabed that followed eutrophication (Pliński & Florczyk 1984) led to greater patchiness and fragmentation of the system than had existed before. At the same time, the numbers of species and general benthic

Table 6. Summary of stressors that over time may have had a direct impact on the distribution of benthic life-forms in Puck Bay (based on Pliński & Florczyk (1984), Osowiecki (2000), Węsławski et al. (2009)

Stressor	Time of occurrence	Effect on sea bed ecosystem
Dredging for red and brown algae	1960–1965	Physical destruction of the sea bed and perennial algae vegetation, increased suspensions, biomass removal
Larger discharges of communal sewage	1960–1989	Local eutrophication, bacterial contamination, local anoxia
Sand extraction	1975–1990	Physical destruction of the sea bed, greater turbidity
Coastal protection (to combat shoreline erosion)	1975–2000	Physical destruction of coastal habitats, removal of reeds, construction of stone walls
Camp-site expansion	2000–2010	Removal of reeds, disturbance to sediments because of intensified motorboat traffic
Intensification of agriculture	1975–1990	Increased eutrophication, growth of filamentous algae

biomass increased (Osowiecki 2000). This effect is probably due to greater habitat fragmentation and the arrival of new, alien species. Since 1975 two gammarid species have disappeared from the area and at least six new amphipod species have been recorded (Jażdżewski et al. 2004, Dobrzycka-Krahel & Rzemykowska 2010), not to mention two species of shrimps, three polychaetes, one mysid, a crab, a fish, a bivalve and a snail (see the review in the 'Alien species in Poland' data base at http://www.iop.krakow.pl/ias/default.aspx).

Habitat modelling methods are an important tool in marine and coastal management. Despite some limitations, these methods are invaluable when data is scarce or missing. Modelled spatial distribution maps of marine habitats and human pressures help to identify the most efficient management solutions and minimize the risk of unpredicted impacts (e.g. Halpern et al. 2009, Stelzenmüller et al. 2012). However, ecosystems that are subject to strong anthropogenic pressure cannot be managed without knowledge of how human activities influenced ecosystems in the past. Therefore, ecosystem-based management in such areas requires not only good quality habitat maps and broad environmental information, but also knowledge of the history of disturbance to and recovery of benthic communities (Forst 2009). A proper historical perspective not only supports the definition of ecosystem baselines, but also helps to understand how an ecosystem may react in the future in response to implemented management measures (Forst 2009, Borja et al. 2012). Management options that do not consider past changes in ecosystems tend to advocate unrealistic indicators, produce erroneous interpretations of results, and are misaligned to stunted temporal scales (Forst 2009). Finally, they are likely to consider such a system as more stable and pristine than it is in reality (Hughes et al. 2005). Only when a temporal scale, and consequently lag-effects, are fully recognized in any management system, can such a system achieve long-term sustainability and social-ecological resilience. However, social and institutional coherence must follow spatial and temporal scales in order to avoid scale mismatches and to fully address the challenges in marine resources management.

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