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Marine long-term biodiversity assessment suggests loss of rare species in the Skagerrak and Kattegat region

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Abstract Studies of cumulative and long-term effects of human activities in the ocean are essential for developing realistic conservation targets. Here, we report the results of a recent national marine biodiversity inventory along the Swedish West coast between 2004 and 2009. The expedition revisited many historical localities that have been sampled with the same methods in the early twentieth century. We generated comparable datasets from our own investigation and the historical data to compare species richness, abundance, and geographic distribution of diversity. Our analysis indicates that the benthic ecosystems in the region have lost a large part of its original species richness over the last seven decades. We find evidence that especially rare species have disappeared. This process has caused a more homogenized community structure in the region and diminished historical biodiversity hotspots. We argue that the contemporary lack of rare species in the benthic ecosystems of the Kattegat and Skagerrak offers less opportunity to respond to environmental perturbations in the future and suggest improving the poor representation of rare species in the region. The study shows the value of biodiversity inventories as well as natural history collections in investigations of accumulated effects of anthropogenic activities and for re-establishing species-rich, productive, and resilient ecosystems.

Keywords Benthic · Marine conservation · Shifting baselines · Biodiversity inventory · North East Atlantic

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Introduction

Marine habitats experience rapid declines in biodiversity worldwide (Jackson et al. 2001; Halpern et al. 2008), a process that creates urgent demand for a better understanding of the long-term effects of such severe alterations in ecosystem diversity (Rockström et al. 2009; Lotze 2010). Over the past decades, the impacts of major anthropogenic pressures on coastal and benthic marine biodiversity have been studied intensely. Here, especially field assessments investigated the negative effects arising from bottom trawling (Jennings and Kaiser 1998; Kaiser et al. 2006; Tillin et al. 2006; Worm et al. 2006; Olsgard et al. 2008), coastal nutrient loading (Rosenberg and Nilsson 2005; Quijon et al. 2008), and climate change (Norderhaug et al. 2015). However, since many of these drivers act on the ecosystems simultaneously and over long periods of time (Lotze et al. 2006; Halpern et al. 2008), it is difficult to infer cumulative impacts from such assessments (Moksnes et al. 2008; Robinson and Frid 2008). Furthermore, in many experimental field studies, the impacts are already a

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part of the control (Pauly 1995), and hence it is not possible to rely on contemporary and experimental investigations alone when examining long-term changes in marine ecosystems.

Historical studies can offer valuable insight in ecosystem-wide responses to the overall sum of human pressures that act in concert and over long periods of time. For such investigations the benthos around the region of the North Sea is especially well suited. Compared to most coastal regions of the world, this area has a long history of biological recording with quantitative surveys dating back to the late nineteenth and early twentieth century (Petersen 1918; Robinson and Frid 2008; Narayanaswamy et al. 2010). Based on this information, a large number of historical comparisons have already been carried out. For example, long-term investigations of fish, plankton, and benthos in the Western English channel found indications for regime shifts during the last century caused by fishing pressures (Southward et al. 2005). Other studies investigated the Southern and central parts of the North Sea and found similar evidence for long-term changes in benthic community structure attributed to fishing (Pennington et al. 1998; Rumohr and Kujawski 2000; Bradshaw et al. 2002; Robinson and Frid 2008) and nutrient loading (Schroeder 2005; Schumacher et al. 2014). Likewise, a series of historical studies from the eastern parts of the North Sea documented remarkable long-term changes in benthic communities attributed to trawling pressure and eutrophication (Rosenberg and Möller 1979; Pearson et al. 1985; Rosenberg et al. 1987; Göransson 2002). Such assessments allow valuable insight into long-term transformation of ecosystems and may help to identify important biodiversity trends in a region, a feature highly relevant for future conservation policies (Pereira et al. 2013).

During the early twentieth century, an expedition led by L.A. Jägerskiöld inventoried the benthic diversity of the Kattegat and Skagerrak region (Jägerskiöld 1971). We were able to revisit many of these historical locations during a recent national marine biodiversity inventory program, and we used this opportunity to test the validity of historical data for understanding the long-term trends in biodiversity in this region. Our expedition re-sampled a large number of historical locations with similar equipment and methods, and we subsequently generated comparable datasets from both expeditions to analyse ecosystem-wide changes in species diversity over a period of more than 70 years.

Materials and methods

Data collection

The historical inventory was carried out in the Swedish, Danish, and Norwegian Economic Zone by L.A. Jägerskiöld in 1921–1938 (Jägerskiöld 1971). Overall, 440 benthic localities were visited in the Kattegat and Skagerrak, from shallow to deep water, and typically between spring and autumn (Fig. 1a), generating a dataset with 33,661 species observations. Usually, several samples were taken per locality by combining various dredges and trawls (Tables 1 and 2). Organisms that were obviously picked up in the water column were discarded. All living marine invertebrate species larger than 1 mm were collected, identified, preserved, and stored (fixed in formaldehyde, ethanol, or formol, and later transferred to ethanol). Subsequently, all specimens were vouchered, catalogued, reexamined by experts if necessary, and finally stored at the Gothenburg Natural History Museum, Sweden.

Our recent inventory revisited the historical locations between 2004 and 2009 (Fig. 1a). Here, altogether 504 localities were sampled during spring and autumn, generating a dataset with 17,249 species observation records. The equipment used was of the same type and with similar dimensions and mesh size as applied in the historical inventory (Tables 1 and 2). The same criteria for collection and identification were applied as in the historical inventory, while all material was stored in ethanol at the Gothenburg Natural History Museum, Sweden.

We prepared and submitted all original data from our own inventories as well as from the museum collections (Fig. 1a) including overall 50,910 species records to the Swedish Environmental and Climate Data Repository (www.ecds.se) under the identifier 01d148f8-f87c-47e3-adfc-c10619f6e9a1 (metadata) and http://webdav.swestore.se/snic/ecds/prod/BenthicInventories/ (data file).

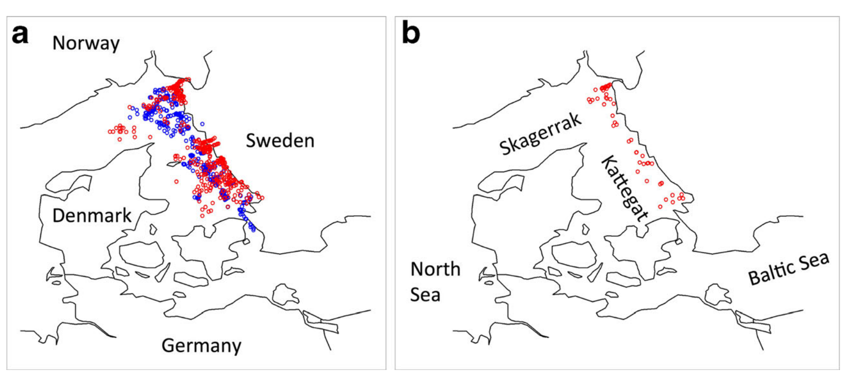


Fig. 1 Overview of analysed datasets. (**a**) Localities in the historical (*red*) and recent (*blue*) inventories; (**b**) Selected localities in the refined dataset used for statistical analysis

Table 1 Specifications of the sampling gear used in the historical and recent inventory

Inventory	Equipment code	Equipment type and dimension	Catchment area (m^2)
Historical	Agas-100	Agassiz trawl 100 × 50 cm	0.500
Historical	Agas-75	Small Agassiz 75 × 40 cm	0.300
Historical	Ring-100	Large ring dredge 100 cm (diameter)	0.790
Historical	Ring-58	Small ring dredge 58 cm (diameter)	0.265
Historical	Tri-60	Triangular dredge 60 cm	0.156
Historical	Rect-75	Rectangular dredge 75 × 20 cm	0.150
Recent	Agas-80	Agassiz trawl 80 × 50 cm	0.400
Recent	Ring-70	Ring dredge 70 cm (diameter)	0.385
Recent	Rock-80	Rock dredge 80 × 20 cm	0.160
Recent	Rock-40	Rock dredge scraper 40 × 20 cm	0.080
Recent	War-60	Warén sledge 60 × 15 cm	0.090

Data cleaning, refinement, and taxonomic name resolution

We employed a semi-automated workflow developed by Mathew et al. (2014) to generate comparable datasets from the metadata of both inventory programs. The workflow provides a user interface for preparation of taxonomically accurate species lists and observational records and can be executed online (https://portal.biovel.eu/workflows/641). All locations were assigned to the following habitat categories: soft bottom (sand, mud), hard bottom (rocks, boulders, stones), or shell gravel. We then structured species occurrences and sample locations according to habitat, geographical reference, sampling gear, and depth profile. Revisited and comparable samples were defined as locations with similar geographical reference up to the first decimal of both latitude and longitude. Locations also had to have overlapping or adjacent depth profiles, while all locations above the halocline (app. 15 m) were excluded because the research vessels could not adequately sample such shallow habitats. Based on these criteria we selected a group of 54 revisited and comparable localities in the Swedish Exclusive Economic Zone (Fig. 1b, Table 2).

Sample effort was calculated as overall haul volume from the dimensions of the individual sample equipment and the haul length at each location (Tables 1 and 2). For the historical samples, this information was derived from the original log-books of the Jägerskiöld inventory available at the Gothenburg Natural History Museum, Sweden.

Species observations from selected localities were cleaned and refined in the following order. We only included taxa unambiguously identified by taxonomic experts in both inventories, but excluded endoparasites. Spelling errors and variations in species names were identified and corrected with the taxonomic ‘cluster’ function of the workflow (Mathew et al. 2014). A few ambiguous entries such as missing species epithet (only listed as *sp.*), records with genus names only, or entries with ‘cf’ references were either resolved or excluded. All species names were transformed to the accepted name provided by the web services of Catalogue of Life (Roskov et al. 2014) and World Register of Marine Species (WoRMS) to eliminate all synonymies in the dataset (Mathew et al. 2014). Multiple records of the same species in a location were removed, leaving only presence information for further analysis in the data set. The resulting dataset (shown in Fig. 1b, available as supplementary online material File S1) was then used for the statistical analysis.

Statistical analysis

The variation between the samples was explored to identify and correct for any potential sampling bias in the historical and recent inventories. Variables included in the analysis were species richness, sampling effort, habitat, geographic location, depth, and season. First, we plotted the frequency distribution of mismatches in sampling effort, average sampling depth, sampling date, and substrate type for all revisited localities (Fig. 2). Second, we performed multidimensional scaling of all samples to visualize the similarity in species composition among and between localities of the two inventories (Fig. 3). Finally, we log transformed species richness and sampling effort (as advised by a preliminary Box–Cox analysis) and evaluated the variables using a generalized additive model (GAM) with bi-dimensional smothers, taking the dis-homogeneity in the sampling effort into account (Zuur et al. 2009). Altogether, 703 models (160 of which included a biodiversity hotspot variable defined after exploratory analysis) were tested to compare the effect of the different variables on the variance in the data set (Fig. S1, Table S1–S3).

Species richness (number of species) was calculated as a function of sample effort (haul volume). In addition, we applied a classical rarefaction analysis, re-sampling the observations and the localities to assess significance and the species richness abundance-based coverage estimator (ACE) for each inventory. We used a non-parametric species richness

Table 2 Overview of selected localities and sample properties in the refined dataset. Column legend: **1**, locality station code; **2**, geographic coordinates; **3**, minimum–maximum depth (in m); **4**, date; **5**, habitat type (S, soft bottom; H, hard bottom; G, shell gravel); **6**, sample equipment (with haul length in m), see Table 1 for specifications of individual sample volume; **7**, sample effort as overall haul volume per location (in m^3); **8**, species richness (no. of species); **9**, relative species richness (no. of species/100 m^3 haul volume); **10**, distance between localities (in m)

Historical inventory										Recent inventory								
1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9
JS342	56.9143 11.9063	26–26	7/13/32	S	Agas-100 (160), Ring-58 (160)	122.4	147	120.1	538	***KA26***	56.9104 11.9112	25–28	5/23/07	S	Rock-80 (240)	38.4	16	41.7
JS409	56.6150 12.4594	26–26	7/15/32	S	Agas-100 (160), Ring-58 (160)	122.4	72	58.8	1655	***KA40***	56.6016 12.4715	26–28	5/24/07	S	Rock-80 (200), Ring-70 (82)	63.6	8	12.6
JS421	56.3658 12.1937	30–30	6/30/33	S	Agas-100 (160), Ring-100 (160), Tri-60 (2 × 160)	256.2	117	45.7	134	***KA48***	56.3644 12.1919	32–33	5/25/07	S	Rock-80 (330), War-60 (280)	78	31	39.7
JS419	56.4670 12.4604	27–27	6/21/33	S, G	Agas-100 (160), Ring-100 (160), Ring-58 (160)	248.8	76	30.5	0	***KA53***	56.4670 12.4604	28–29	5/29/07	S	Rock-80 (130), War-60 (260)	44.2	21	47.5
JS416	56.5491 12.6056	23–23	7/16/32	S, G	Rect-75 (2 × 160), Ring-58 (2 × 160)	132.8	77	58.0	510	***KA54***	56.5501 12.5985	22–23	5/29/07	S	Rock-80 (280), War-60 (425)	83.05	32	38.5
JS415	56.5438 12.6830	20–20	6/16/33	S, G	Agas-100 (160), Tri-60 (160)	104.9	67	63.9	180	***KA55***	56.5423 12.6838	20–21	5/29/07	S	Rock-80 (280)	44.8	22	49.1
JS411	56.6249 12.6523	19–19	6/15/33	S	Agas-100 (160), Ring-58 (160), Rect-75 (2 × 160)	146.4	92	62.8	149	***KA57***	56.6245 12.6501	19–22	5/30/07	S	Rock-80 (280, 390)	107.2	20	18.7
JS410	56.5235 12.3143	30–30	6/22/33	S	Tri-60 (3 × 160)	74.7	79	105.8	570	***KA58***	56.5200 12.3204	31–34	5/30/07	S	Rock-80 (280)	44.8	25	55.8
JS298	57.2918 12.0118	27–27	6/26/29	S	Agas-100 (160)	80	59	73.8	1919	***KA67***	57.2790 12.0327	26–29	5/31/07	S	War-60 (445)	40.05	20	49.9
JS296	57.3027 11.9320	42–42	7/08/32	H	Tri-60 (2 × 160), Ring-58 (4 × 160)	219.4	117	53.3	98	***KA68***	57.3022 11.9330	21–49	5/31/07	S, H	Rock-80 (225), War-60 (260)	59.4	27	45.5
JS297	57.2954 11.9170	31–31	6/15/28	S	Tri-60 (160)	24.9	44	176.7	2713	***KA69***	57.3103 11.8830	29–45	5/31/07	S	Agas-80 (240)	96	32	33.3
JS299	57.2846 11.8347	55–55	5/24/29	S	Tri-60 (3 × 160)	74.7	61	81.7	467	***KA70***	57.2874 11.8402	39–57	5/31/07	S, H	Rock-80 (465)	74.4	16	21.5
JS258	57.3154 11.7517	63–67	5/30/29	S, H	Tri-60 (2 × 160)	49.8	39	78.3	313	***KA71***	57.3153 11.7470	63–75	5/31/07	S	Rock-80 (350)	56	8	14.3
JS245	57.4593 11.8090	26–26	5/30/29	S, H	Tri-60 (160)	24.9	47	188.8	124	***KA72***	57.4587 11.8074	25–39	5/31/07	S, H	Rock-80 (220)	35.2	31	88.1
JS243	57.5356 11.6803	37–37	7/21/22	S	Tri-60 (160)	24.9	39	156.6	524	***KA73***	57.5349 11.6718	33–39	5/31/07	S	War-60 (315)	28.35	15	52.9
JS165	57.7725 11.5143	30–35	8/11/21	H	Tri-60 (150)	23.4	30	128.2	302	***KA76***	57.7726 11.5193	28–39	6/01/07	H	Rock-80 (240)	38.4	22	57.3
JS162	57.8020 11.5643	18–21	8/11/21	S, G	Rect-75 (370), Tri-60 (370)	113.1	47	41.6	321	***KA77***	57.7995 11.5667	18–23	6/01/07	S	Rock-80 (500)	80	13	16.3
JS158	58.1806 11.2154	52–52	3/07/33	S	Tri-60 (160)	24.9	8	32.1	3370	***SK66***	58.2042 11.1816	63–64	8/20/07	S	Ring-70 (240)	92.4	6	6.5
JS159	58.1357 11.2529	50–50	3/07/33	S, H	Tri-60 (160)	24.9	35	140.6	309	***SK67***	58.1345 11.2574	46–51	8/20/07	S, H	Agas-80 (365)	146	19	13.0
JS156	58.5700 10.9817	60–60	3/07/33		Rect-75 (160)	24	27	112.5	424	***SK71***	58.5670 10.9853	36–61	8/21/07	S, H	Rock-80 (330, 350), Ring-70 (205)	187.72	40	21.3
JS155	58.5864 11.1914	48–48	7/03/35	S	Agas-100 (2 × 160), Tri-60 (3 × 160)	234.7	51	21.7	252	***SK73***	58.5887 11.1911	27–52	8/21/07	S	Rock-80 (350)	56	8	14.3
JS122	58.6945 10.8377	50–85	7/11/34	S, H	Rect-75 (2 × 120)	36	35	97.2	208	***SK75***	58.6934 10.8401	42–75	8/22/07	H	Rock-80 (2 × 240)	76.8	34	44.3
JS142	58.6949 11.0412	150–195	6/22/35	S, H	Rect-75 (4 × 125), Tri-60 (4 × 125)	152.9	58	37.9	388	***SK81***	58.6929 11.0368	45–203	8/22/07	S, H	Rock-80 (540, 480)	163.2	16	9.8
JS104	58.7881 11.0307	37–43	6/20/35	S, H	Tri-60 (3 × 165), Agas-75 (2 × 165)	176.13	16	9.1	702	***SK84***	58.7883 11.0427	24–45	8/23/07	H	Rock-80 (85, 205)	46.4	26	56.0
JS69	58.8864 10.7962	50–69	8/02/26	S, H	Tri-60 (2 × 150)	46.74	39	83.4	1588	***SK86***	58.8812 10.8194	54–69	8/23/07	S, H	Rock-80 (135)	21.6	28	129.6
JS55	58.9098 10.9307	26–37	7/19/34	S, H	Tri-60 (3 × 100)	46.74	44	94.1	6126	***SK89***	58.9453 11.0123	12–52	8/23/07	S, H	Rock-80 (280)	44.8	31	69.2
JS44	58.9264 10.9450	30–45	7/13/34	S, H	Tri-60 (2 × 150)	70.11	102	145.5	95	***SK90***	58.9270 10.9459	23–36	8/23/07	S	Rock-80 (100)	16	19	118.8
JS46	58.9207 10.9551	36–36	7/13/34	S, H	Tri-60 (160)	24.9	78	313.3	43	***SK91***	58.9210 10.9549	28–37	8/23/07	S	Rock-80 (180)	28.8	15	52.1
JS41	58.9309 10.9865	25–35	7/21/25	S	Agas-100 (160), Tri-60 (160)	104.9	48	45.8	154	***SK92***	58.9310 10.9837	18–34	8/23/07	H	Rock-80 (350)	56	24	42.9
JS38	58.9481 11.0194	30–50	7/20/25	S	Tri-60 (160)	24.9	99	397.6	332	***SK93***	58.9478 11.0138	31–58	8/24/07	S, H	Rock-80 (260, 280)	86.4	21	24.3
JS53	58.9126 11.0365	50–80	7/29/27	S	Agas-100 (4 × 160)	320	99	30.9	4192	***SK94***	58.9512 11.0188	13–47	8/24/07	S	Rock-80 (280)	44.8	18	40.2
JS33	58.9554 11.0219	30–80	7/14/34	S	Agas-100 (160), Tri-60 (2 × 240)	154.78	111	71.7	169	***SK95***	58.9565 11.0200	26–79	8/24/07	S	Rock-80 (295)	47.2	24	50.8
JS31	58.9583 11.0219	20–50	7/30/26	S, H	Rect-75 (4 × 160)	96	114	118.8	431	***SK96***	58.9615 11.0266	14–49	8/24/07	S	Rock-80 (260)	41.6	25	60.1
JS32	58.9605 11.0540	200–200	7/22/25	S	Agas-100 (3 × 160)	240	38	15.8	257	***SK97***	58.9585 11.0523	215–226	8/24/07	S	Agas-80 (700)	280	17	6.1
JS30	58.9605 11.0717	40–60	8/07/26	S, H	Rect-75 (2 × 160)	48	69	143.8	97	***SK99***	58.9598 11.0725	25–60	8/24/07	S, H	Rock-80 (225)	36	22	61.1
JS25	58.9864 11.0857	93–93	7/10/34	S, H	Agas-100 (160), Ring-58 (160), Tri-60 (160)	147.3	67	45.5	197	***SK100***	58.9860 11.0825	77–125	8/24/07	S, H	Rock-80 (130, 260)	62.4	21	33.7
JS23	58.9972 11.1094	30–100	7/29/25	S, H	Agas-100 (200)	100	46	46.0	162	***SK101***	58.9984 11.1109	18–106	8/24/07	S	Rock-80 (130)	20.8	13	62.5
JS26	58.9806 11.0830	100–100	8/19/27	S	Agas-100 (160)	80	14	17.5	1126	***SK102***	58.9714 11.0750	11–74	8/24/07	S	Rock-80 (110, 205)	50.4	40	79.4

Table 2 (continued)

Historical inventory										Recent inventory								
1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9
JS43	58.9231 10.9834	15–30	8/01/27	S, H	Agas-100 (400), Tri-60 (400), Rect-75 (400)	322.3	143	44.4	470	***SK103***	58.9265 10.9882	16–30	8/24/07	S, H	Rock-80 (350)	56	23	41.1
JS48	58.9210 10.9907	25–25	6/28/34	S	Agas-100 (160), Ring-58 (160)	122.4	108	88.2	58	***SK104***	58.9215 10.9910	19–25	8/27/07	S, H	Rock-80 (295)	47.2	22	46.6
JS47	58.9323 10.9821	26–26	6/29/34	S	Ring-58 (160)	42.4	41	96.7	1184	***SK105***	58.9217 10.9836	19–32	8/27/07	S, H	Rock-80 (315, 295)	97.6	18	18.4
JS66	58.8712 10.9603	25–30	08/06/27	S, H	Agas-100 (100), Tri-60 (3 × 100)	96.74	127	131.3	70	***SK106***	58.8706 10.9599	14–34	8/27/07	S, H	Rock-80 (2 × 225, 240)	110.4	30	27.2
JS129	58.6613 10.7273	90–90	7/11/34	S	Agas-100 (160), Ring-58 (160), Tri-60 (2 × 160)	172.2	32	18.6	1630	***SK109***	58.6567 10.7011	89–97	8/28/07	S	Rock-80 (225, 280)	80.8	7	8.7
JS128	58.6736 10.6542	100–100	7/05/34	S, H	Tri-60 (160)	24.9	11	44.2	158	***SK110***	58.6725 10.6530	100–104	8/28/07	S	Rock-80 (2 × 240)	76.8	7	9.1
JS130	58.6278 10.6833	126–133	7/10/35	S, H	Ring-58 (160), Tri-60 (160)	67.3	29	43.1	22	***SK111***	58.6277 10.6833	101–133	8/28/07	S, H	Rock-80 (2 × 205)	65.6	37	56.4
JS157	58.3258 11.1674	55–55	3/07/33	S	Tri-60 (160)	24.9	11	44.2	137	***SK132***	58.3260 11.1651	40–60	8/31/07	S, H	Rock-80 (365, 260)	100	27	27.0
JS160	58.1095 11.1815	76–76	3/06/33	S, H	Tri-60 (160), Rect-75 (160)	48.9	34	69.5	585	***SK137***	58.1075 11.1728	80–86	6/09/08	S, H	War-60 (340)	30.6	16	52.3
JS140	58.7132 11.0225	68–68	7/17/35	S, H	Tri-60 (2 × 160)	49.8	44	88.4	494	***SK175***	58.7096 11.0273	43–73	6/15/08	H	Agas-80 (390), Rock-40 (395)	187.6	15	8.0
JS148	58.6809 11.1160	47–47	6/19/35	H	Tri-60 (4 × 160)	99.6	31	31.1	17	***SK177***	58.6809 11.1157	36–54	6/16/08	S, H	Rock-80 (255, 220, 330)	322	22	6.8
JS244	57.5317 11.6731	6–15	9/02/22	H	Tri-60 (160)	24.9	12	48.2	232	***KA122***	57.5327 11.6764	16–24	8/21/09	G	Rock-40 (315)	25.2	7	27.8
JS311	57.1175 11.7045	27–27	8/07/30	H	Tri-60 (160)	24.9	93	373.5	787	***FL23***	57.1237 11.6987	22–24	6/17/05	H, G	Rock-80 (280)	112	22	19.6
JS360	56.8701 12.2223	19–19	7/15/31	H	Agas-100 (160), Rect-75 (3 × 160)	152	53	34.9	120	***MB20***	56.8708 12.2207	19–19	9/08/05	H, G	Rock-80 (280)	112	8	7.1
JS361	56.8652 12.2244	27–27	7/16/31	S, H	Agas-100 (2 × 160), Rect-75 (2 × 160)	208	65	31.3	254	***MB18***	56.8637 12.2213	25–28	9/08/05	S	Ring-70 (280)	107.8	29	26.9
JS362	56.8498 12.1901	54–54	7/18/31	S	Agas-100 (160), Ring-58 (160)	122.4	40	32.7	111	***MB15***	56.8502 12.1885	45–55	9/07/05	S	War-60 (650)	58.5	14	23.9

estimator (ACE-1) as advised in Gotelli and Colwell (2011) to obtain a quantitative estimate of species richness for repeated incidence data. Analyses were implemented with R scripts (Wang 2011; R Core Team 2013).

Species abundance was calculated as the relative frequency of occurrence for individual species in the selected 54 locations. We defined abundance thresholds at 10% of the total number of locations for rare species and at 50% for common species. This allowed us to classify all species into four abundances classes: absent (0%), rare (0% – <10%), intermediate (10–50%), and common (>50%).

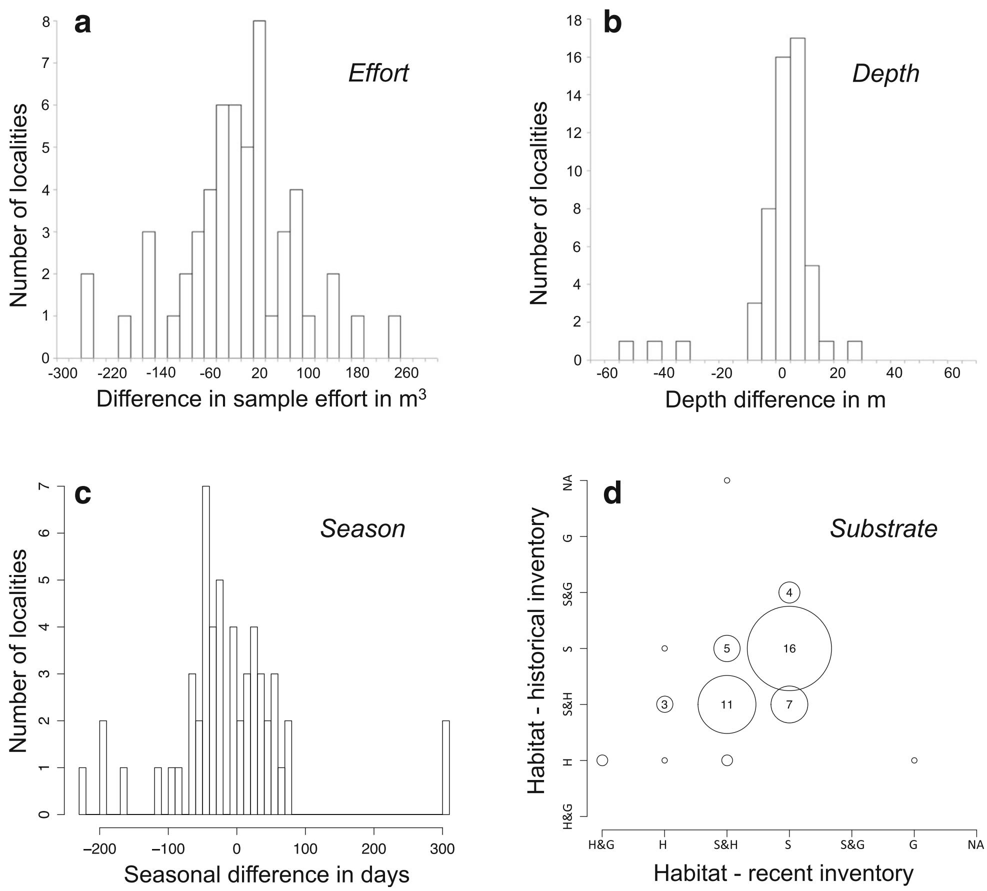
Geographical structure was assessed by comparing the marginal values of the Akaike information criterion weight (wAIC) across 543 generalized additive models resulting from the different parameterisations of the geographical information, including spatial smothers (Table S1). Subsequently, the geographical structure was modelled with groupings of historical hotspots for a total of 160 models (Table S2). Historical hotspots were defined as the locations with the highest species richness in the historical data set, and included 16 localities with an average richness of 103 species/100 m^3 haul volume. The analysis was done with R scripts (Wood 2006; Rhodes et al. 2009; R Core Team 2013).

Results

Exploration of variance

Variation in sample effort was considerable (Figs. 2a, 4b, Table 2), both within and between inventories (historical/recent effort minimum = 23/16 m^3, maximum = 322/322 m^3, average = 104/78 m^3, standard deviation = 80/60 m^3). Most of the revisited localities had a mismatch in sampling effort between 20 and 100 m^3 (Fig. 2a). Depth profiles only had substantial variation within each inventory, but not between inventories (historical/recent depth minimum = 11/19 m, maximum = 200/220 m, average = 51/47 m, standard deviation = 36/35 m). Most of the revisited localities showed mismatches in depth of ±15 m (Fig. 2b). The seasonal variation within and between inventories was confined to the summer months. Historical locations were sampled mostly between June and August, while most of the recent localities were sampled either in May or in August, resulting in a seasonal mismatch between the revisited localities of up to 3 months (Fig. 2c). The variation in the substrate between historical and recent localities was very small. Most localities consisted of either soft bottom or mixed soft and hard bottoms at both times of sampling (Figs. 2d and 3). Overall, there was no bias in the data sets that indicates systematic over- or under-sampling of a certain habitat, season, depth, effort, or sample gear in one of the two inventories (Figs. 2 and 3) and localities are comparable with regard to these variables. The variation in sampling effort, however, needs to be included when comparing species richness.

Fig. 2 Variation in sampling conditions between historical and recent localities. Diagrams show the frequency distribution of mismatches in (**a**) sampling effort, (**b**) average sampling depth, and (**c**) sampling date. Diagram (**d**) shows mismatches in substrate type, where the size of circles corresponds to the number of revisited localities that change from one substrate to another. S, soft bottom; H, hard bottom; G, shell gravel; NA, information missing



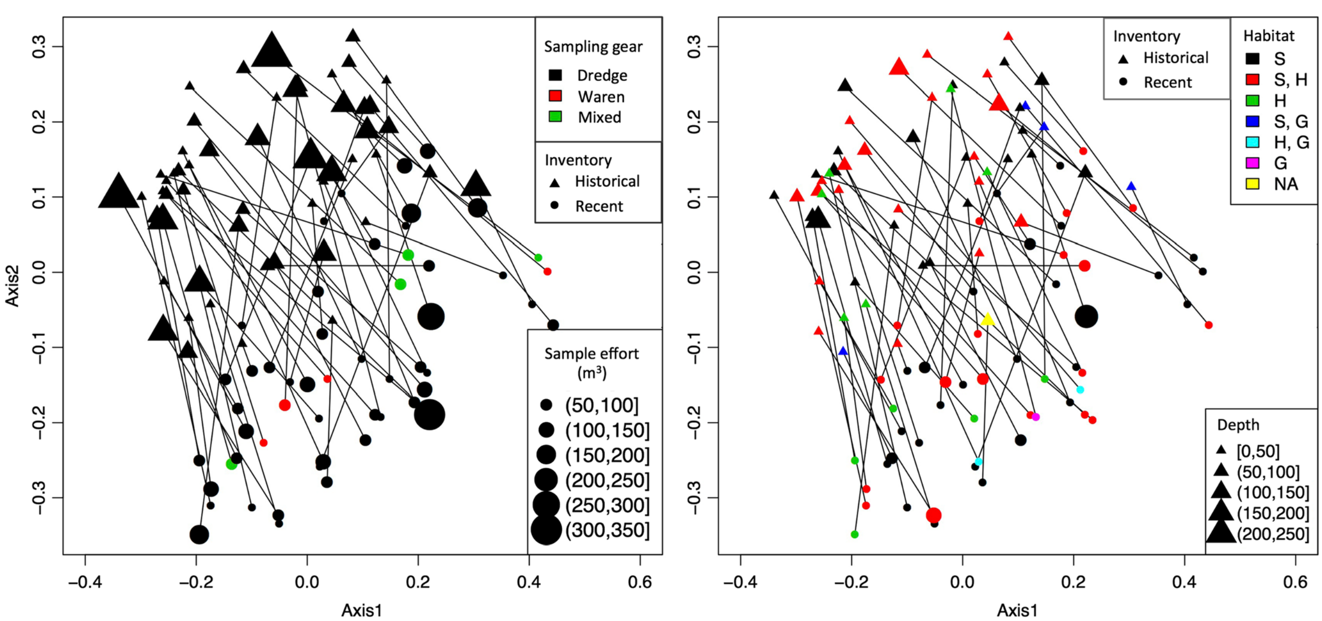


Fig. 3 Multidimensional scaling of the 108 sampling events (54 locations visited in the recent and historical inventory) using the Jaccard distance matrix. The same graph is shown twice to illustrate the covariates of the sampling events. Revisited localities are connected by a *solid line*. Habitat: S, soft bottom; H, hard bottom; G, shell gravel, and combinations thereof. Sampling gear: dredge (Agazziz trawls and dredges), Waren (Warén sledge), and mixed (combinations of the previous types) refer to the sample equipment in Table 1. Depth (average depth)

The GAM approach attributed the variance to the habitat, biodiversity hotspots, sampling effort, and depth. Apart from depth, all variables had a different influence between the historical and recent inventory (Fig. S1, Table S3). In the historical inventory, 16.2% of the variance in species richness was assigned to sampling effort (significant at $P = 0.00277$), while in the recent inventory, there was no relationship between species richness and sampling effort ($P = 0.95$). This indicates that the sampling in the historical inventory was still unsaturated (Fig. 4b, Table S3).

Species richness

The refined dataset included, overall, 648 species (4412 species records) across 54 revisited locations in the investigated region (Table 2). The historical partition included 607 species (3282 species records), while the recent partition included 254 species (1130 species records). Overall, 32.8% of the species were recovered across both inventories, while 60.8% occurred exclusively in the historical dataset, and 6.3% occurred only in the recent dataset.

The rarefaction curve indicated a halfway reduction of recent compared to historical species richness (Fig. 4a), which was confirmed by the ACE-1 estimator (Chao and Lee 1992) showing that the overall estimated species richness in the recent data set decreased to 47.2% of the historical values (Fig. 5). On average, historical localities recovered 88.2 species/100 m^3 haul volume, while recent localities recovered only 38.6 species/100 m^3 haul volume (Table 2). Also, the relations between species richness and sample effort were different between the historical and recent data set. Increasing effort resulted in higher species richness in historical samples, but this was not the case in recent samples (Fig. 4b).

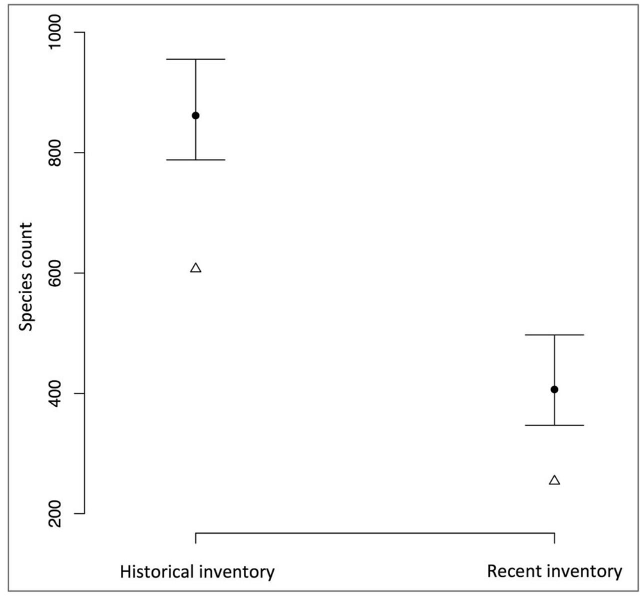


Fig. 5 Diagram showing observed (*triangles*) and estimated (*dots*) values calculated by the ACE-1 estimator of species richness. Upper and lower bounds are indicated by the *whiskers*

Abundance trends

The comparison of abundances between the historical and recent data sets showed a predominating negative trend (Fig. 6, Table 3). Overall, 74.7% of the investigated species

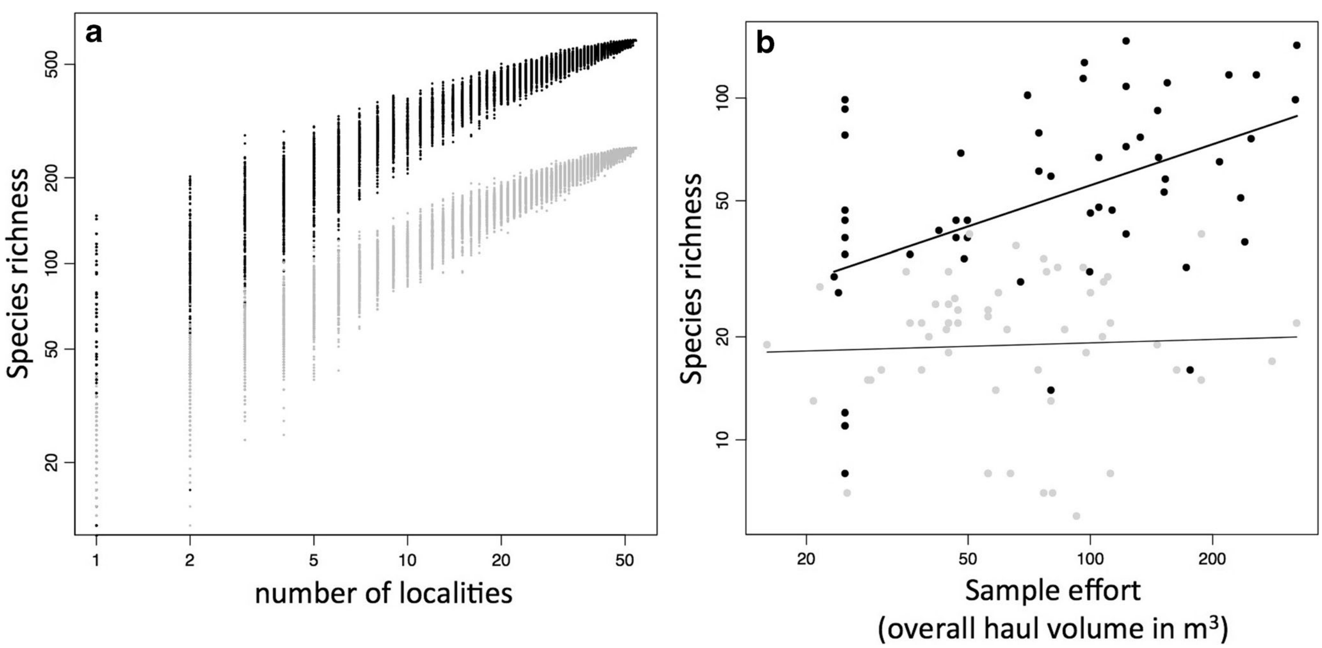


Fig. 4 Species richness in historical and recent inventories. Diagram (**a**) shows the rarefaction curve for overall species richness as a function of number of localities for the historical (*black*) and recent (*grey*) data set, using a logarithmic scale. The graph is based on 100 permutations for sampling size plotted. Diagram (**b**) shows species richness (number of species) over sampling effort (overall haul volume) at individual locations. Historical samples are shown with *black circles* and a *bold trend line*. Recent samples are shown with *grey circles* and a *regular trend line*

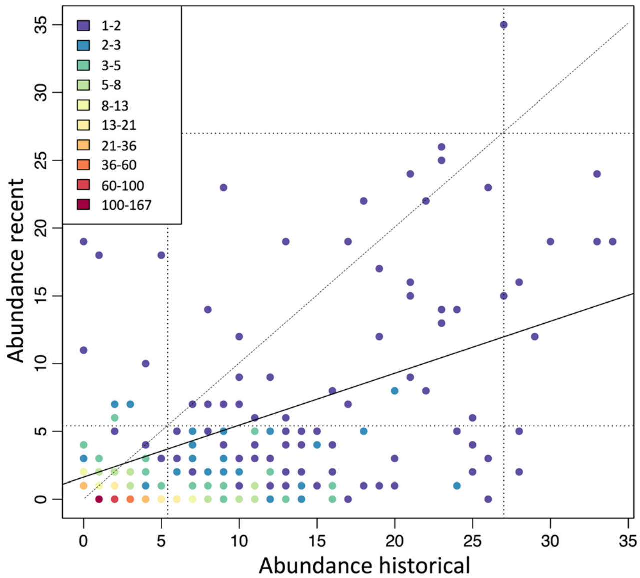


Fig. 6 Temporal changes in species abundance. The diagram shows a plot of abundance for 648 species in the historical (x-axis) and recent (y-axis) inventory. Abundance is measured as relative frequency of occurrence in the 54 locations. *Colours* indicate how many species have the same given pairs of counts (see legend within figure). The *solid line* is the trend line, while *dotted lines* indicate selected thresholds for rare species (10%) and for common species (50%). The *dotted diagonal line* indicates equal abundances across both inventories

showed decreasing abundances, changing either from rare to absent, intermediate to absent, intermediate to rare, common to rare, or common to intermediate. In contrast, only 7.8% of the species showed increasing abundances, changing from absent to rare, absent to intermediate, and rare to intermediate. Finally, 17.5% of the species remained in their historical abundance classes.

Among the species with strongest positive abundance trends, we found corals (*Caryophyllia smithii*, *Kophobelemnon stelliferum*, *Alcyonium digitatum*), bivalves (*Nucula nitidosa N. nucleus, Mysia undata, Abra alba, Pecten maximus, Thracia convexa, Pododesmus patelliformis, Modiolarca subpicta*), and one polychaete (*Nephtys kersivalensis)*. These species are typically small- to medium-sized suspension or deposit feeders, living on top or within the sediment (epifauna, infauna). Among the species with the strongest negative abundance trends, we found especially polychaetes (*Pectinaria auricoma*, *Goniada maculata*, *Aphrodita aculeata, Pista cristata, Owenia fusiformis*), but also one echinoderm (*Psammechinus miliaris*), a crustacean (*Verruca stroemia*), and a mollusc (*Buccinum undatum*). These species are typically small- to medium-sized predators, scavengers or suspension feeders, living on top or within the sediment (epifauna, infauna).

Geographic distribution of diversity

The analysis of the historical samples across 160 GAM models with a biodiversity hotspot predictor rendered three areas with high biodiversity (n = 16) in the historical data set (Fig. 7). The northernmost area (n = 7) lies in the centre of a national marine sanctuary (Gonzalez-Mirelis et al. 2014), while the others are located on the shallow water banks (n = 3) and in the coastal zones (n = 6) between Denmark and Sweden. By grouping all 16 species rich localities together, we obtained a 95% confidence set with 6 models, while the best model included 54% of the weight of the selected models (Table S2). The geographical structure is well described by the

Table 3 Changes in species abundances as indicated by the number (and percentage) of species classified in different abundances classes in the two surveys. Grey cells indicate species without changes in abundance trends. Species with increasing abundances are above the grey cells, while species with decreasing abundances are below

	Recent			
Historical	Absent	Rare	Intermediate	Common
Absent	0	39 (6.0%)	2 (0.3%)	0
Rare	336 (51.9%)	77 (11.9%)	10 (1.5%)	0
Intermediate	58 (9.0%)	83 (12.8%)	33 (5.1%)	0
Common	0	2 (0.3%)	7 (1.1%)	1 (0.1%)

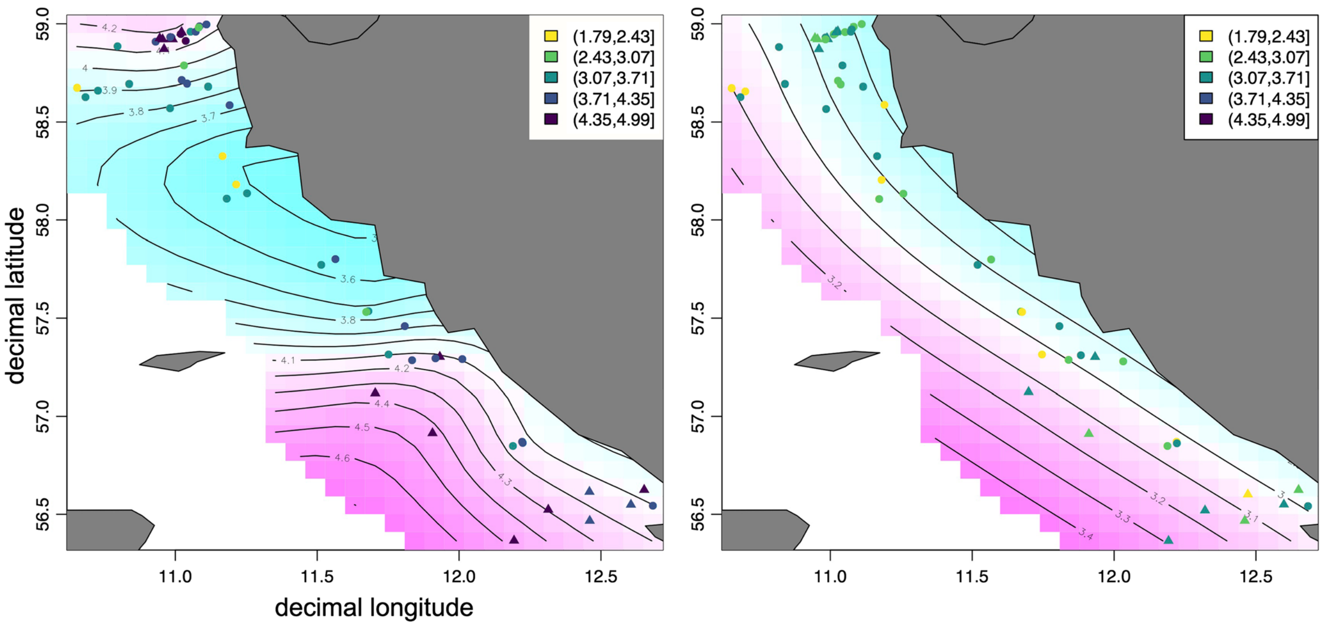


Fig. 7 Geographical distribution of species richness. Alpha diversity is mapped in the investigated area after smoothing with a generalized additive model for (**a**) the historical and (**b**) the recent dataset. *Lines* connect values indicating the log of the species richness, after correction for the non-geographic parameters and smoothing, while *colours* range from *blue-green* (low values) to *purple* (high values). Historical hotspots are indicted with *triangles*, while all other localities are indicated with *circles*. Results are shown without a confidence interval. Colour of localities indicates the log of the relative species richness (see legend within figure)

hotspot-grouping variable (96% of wAIC). This hotspot structure was strong in historical samples (79.7% of variance of fitted values) but has faded in the recent samples (9.2% of variance of fitted values), indicating that hotspots are less pronounced and species richness is more evenly distributed in the recent data set.

Discussion

Sampling bias and working with inconsistent data sets

Our study investigated the changes in richness, abundance, and geographic distribution of benthic species in the Kattegat and Skagerrak region based on the recordings made by two large biodiversity inventories. Although both inventories had a very similar design, the data generated by these investigations retained considerable heterogeneity. By using a carefully filtered subset of 54 revisited localities sampled with similar methods during the summer season, we could remove a large part of the heterogeneity. However, some variance in depth, season substrate, and constitution of the sample gear remained and may influence the observed patterns. However, we found no evidence of systematic bias in any of these variables across both inventories. Additional factors that may have influenced the historical changes observed in this study may be the coarse partitioning of the localities into three habitat types (hard bottom, soft bottom, and shell gravel), or the estimation of sample effort from the equipment's catchment area and the overall haul length. Also, the overall sampling period, which was longer for the historical data set (1921–35) than for the recent one (2004–09) may have captured more of the temporal species turnover and hence contributed to the higher levels of alpha diversity observed in the historical data. In conclusion, our results cannot entirely be assigned to the long-term changes in the region, and may to some extent be caused by the deviations between the sampling routines that we could not control. In this context, our objective was not to remove all sampling bias from the data, but attempt to find a trade-off between the degree of harmonization of the data sets and the conclusions that can be drawn from the analysis.

Historical trends

Our results indicate a reduction of species richness in the investigated region, which can be explained to some extent by the extirpation of rare species. The comparison of species abundances in the historical and recent inventory suggests that more than 50% of the recorded species change status from rare to absent. This trend seems to have contributed to a more homogenized community structure across the investigated region and may have diminished former biodiversity hotspots. Although the longer sampling period of the historical inventory may have increased the overall capture of rare species, it does not influence the species richness at the level of individual localities. Our results show that historical localities not only have a higher yield of species for a given sampling effort, but also a tendency to obtain more species with higher sampling effort. This is not the case in recent localities, where higher sampling effort does not yield more species. One of the explanations for these differences may be the absence of rare species in the recent localities.

A comparison with similar historical accounts shows that substantial regime shifts over longer time periods are known for the region (Rosenberg and Möller 1979; Robinson and Frid 2008). Our results show a 32% overlap in species assemblages between the historical and recent inventory, a figure that is very similar to estimates obtained by Pearson et al. (1985) and Rosenberg et al. (1987) over a similar period. However, in contrast to previous long-term studies, which report the species turnover as a balance between species recruitment and extirpation, our study also indicates a severe loss of alpha diversity in addition to the regime shift.

Potential causes and consequences of species reduction

A deeper analysis of ecological responses due to changes in the species composition is limited by the lack of consistent trait information for the majority of the species included in this study. However, some responses to prevalent pressures in the region may be discussed using representative species. Anthropogenic drivers that influence benthic diversity in the North Sea are typically associated with pollution, overfishing, habitat destruction, invasive species, and climate change (Lotze et al. 2006; Doney and Schimel 2007; Halpern et al. 2008). The reduction of alpha diversity observed in our study is likely to be related to a combination of these factors, but we have little indication of any specific causes for the observed loss in species richness. However, depletion of ecological niches through continuous physical disturbance (e.g. seabed trawling) is a well-documented process in the region, which is known to remove rare and specialist species from the ecosystem (Jennings and Kaiser 1998; Kaiser et al. 2006; Clavel et al. 2011). In addition, we observed that fragile infauna such as burrowing and tube-dwelling polychaetes were among the species with the strongest signals of decline, which may also be a response to continuous trawling activities. In contrast, more robust in- and epifauna like molluscs and corals seemed to have increased over time, and this pattern may be indicative for a better resistance of such species to physical disturbance. However, the observed changes in community composition are likely to be caused by a combination of several factors. Many of the species that have become more dominant are suspension and deposit feeders, organisms that benefit from the elevated nutrient levels in the region (Graneli and Sundback 1985; Posey et al. 1999; Karlson et al. 2002), while other important drivers of the observed changes in community composition may also include constantly rising sea temperatures and associated changes in water quality that can affect individual species differently (Hiddink et al. 2015). In conclusion, our study only includes two distant sampling periods, while specific environmental data associated with potential drivers of change were not available for analysis. Future inventories and monitoring programs should therefore emphasize the collection or linkage to environmental information to allow a deeper understanding of the impact of specific drivers on biodiversity decline.

The reduction of rare species indicated in our study may have implications on the resilience of the benthic ecosystems in the region. Specialist decline is known to cause functional homogenisation, which effects ecosystem functioning and productivity in the long-term and may ultimately lead to deterioration of important ecosystem services (Clavel et al. 2011; Cardinale et al. 2012). An increasing amount of studies shows that undisturbed marine ecosystems possess a broader functional reservoir allowing them to react better to environmental perturbations compared to exploited systems (Stachowicz et al. 2007; Rasher et al. 2013). Therefore, the constitution of rare species in the ecosystem should be better monitored in marine conservation programs. Appropriate indicators for biodiversity already exist as a part of national and international legislation (Borja 2006) and should be used to actively improve the representation of rare species in benthic assemblages. This intention could be realized by introducing new assessment methods into biodiversity monitoring programs, which enable a better accounting for rare species (Bourlat et al. 2013).

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Compliance with ethical standards This study complies with ethical standards, according to the rules and guidelines of thejournal.

Conflict of interest The authors declare that they have no conflict of interest.

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