



Original Article

Biodiversity baseline for large marine ecosystems: an example from the Barents Sea

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Biodiversity is an increasingly important issue for the management of marine ecosystems. However, the proliferation of biodiversity indices and difficulties associated with their interpretation have resulted in a lack of clearly defined framework for quantifying biodiversity and biodiversity changes in marine ecosystems for assessment purpose. Recent theoretical and numerical developments in biodiversity statistics have established clear algebraic relationships between most of the diversity measures commonly used, and have highlighted those that most directly relates to the concept of biological diversity, terming them “true” diversity measures. In this study, we implement the calculation of these “true” diversity measures at the scale of a large-marine ecosystem, the Barents Sea. We applied hierarchical partitioning of biodiversity to an extensive dataset encompassing 10 years of trawl-surveys for both pelagic and demersal fish community. We quantify biodiversity and biodiversity changes for these two communities across the whole continental shelf of the Barents Sea at various spatial and temporal scales, explicitly identifying areas where fish communities are stable and variable. The method is used to disentangle areas where community composition is subject to random fluctuations from areas where the fish community is drifting over time. We discuss how our results can serve as a spatio-temporal biodiversity baseline against which new biodiversity estimates, derived from sea surveys, can be evaluated.

Keywords: Barents Sea, baseline, biodiversity, fish community, hierarchical partitioning.

Introduction

As evidence accumulates that biodiversity contributes to ecosystem resilience and to the maintenance of ecosystem functions and services (Hooper, 2005; Balvanera *et al.*, 2006; Cardinale *et al.*, 2012), the topic of biodiversity becomes of increasing concern in the management of marine systems (Greenstreet, 2008; Rice and Garcia, 2011). Still, there is some reluctance in using directly biodiversity measures as indicators of ecosystem state and traditional metrics such as age or size structure of target species or groups are often preferred (Rochet and Trenkel, 2003; Greenstreet, 2008). For example, Link (2005) reviews and suggests a set of indicators for the state of marine systems, together with warning thresholds. Among the 15 indicators recommended, 10 are related to biomass or biomass ratios of groups of species; 3 are related to demography; 1 is specifically designed for corals; and only 1, species richness, is

explicitly related to biodiversity, although this is in its most restrictive form, as species richness ignores variations in species abundances. There is a necessity for the development and application of more informative biodiversity indices to follow the state of marine ecosystems.

Biodiversity is often disdained in the assessment and management of marine systems today for it is sometimes perceived as a vague concept, hard to measure unambiguously and to link to manageable pressures (Rice, 2000; Mayden, 2002; Rochet and Trenkel, 2003; Greenstreet, 2008). Indeed, as biodiversity indices summarize changes across many species, they can be difficult to link to one single driver. This is all the more true that diversity indices have proliferated in the second half of the twentieth century (reviewed in Magurran, 2004), casting doubt and confusion among practitioners about how to measure diversity. As a result, some studies have

recommended the joint use of as many indices as possible, to ensure the capture of all aspects of diversity (e.g. Rice, 2000). In the absence of clear framework for measuring diversity, this recommendation appears justified, but the trade-off is an increasing risk of confusion and misinterpretation of the multiple indices used. Greenstreet (2008) points out that many biodiversity measures often poorly match some of the criteria that define a good state indicator for marine systems. According to ICES (International Council for the Exploration of the Sea), such indicator should be sensitive to a manageable human activity, tightly coupled in time to that activity, easily and accurately measured with low error rate, and should be responsive primarily to a human activity, with low responsiveness to other causes of change. Studies attempting to link biodiversity changes to fishing pressure led to contrasting results depending on the way sampling effort was accounted for (Greenstreet and Hall, 1996; Piet and Jennings, 2005; Greenstreet and Rogers, 2006; Greenstreet and Piet, 2008).

Should the above limitations justify that biodiversity indices be systematically disregarded when looking for ecosystem indicators? Studies on the link between biodiversity and ecosystem functioning highlight many desirable properties of diverse ecosystems from a management perspective, suggesting that even if challenging, the use of quantitative measure of biodiversity should be part of the array of ecological indicators of the state of marine ecosystems. The empirical evidence accumulated so far (reviewed in Stachowitz *et al.*, 2007) showed that high biodiversity tends to decrease variability in community properties and to favour resistance to and recovery from disturbance or invasion. Biodiversity also affect foodweb mechanisms, as diverse assemblages tend to be more resistant to top-down controls, use their own resources more completely, and increase consumer fitness. The links between biodiversity and the resilience of ecosystems, together with calls to implement resilience-based management for marine ecosystems (Levin and Lubchenco, 2008), support the idea that if not today, numerical measures of biodiversity may be an important part of the management of marine ecosystems tomorrow.

One important challenge is to set-up reference levels and management targets in terms of biodiversity measures. As clear driver-response relationships are not available, alternatives must be sought, such as the use of spatio-temporal baseline (Nielsen *et al.*, 2007; Borja *et al.*, 2012; Samhuri *et al.*, 2012), meaning that the reference corresponds to what has been observed in a selected area for a given period. With such an approach, future changes are interpreted against past changes, and although there is no clear driver-indicator link, it is possible to quantify how much biodiversity has been gained, lost, or in which way it has been modified compared with the baseline. Such baseline can be established for marine ecosystems that have been appropriately sampled for decades. This can constitute the first step of the use of biodiversity indices within a management framework. A biodiversity baseline should quantify the amount of biodiversity in marine ecosystems as well as the amount of biodiversity change they have been undergoing during the selected period. It could be used as a reference to characterize the evolution of the state of ecosystems, to detect and quantify gradual changes away from their previous state, or pinpoint catastrophic regime shifts. To do so, the baseline needs to be constructed using a clear and robust statistical framework. In the present study, we show how to extract such a spatio-temporal biodiversity baseline for the Barents Sea, using a 10-year monitoring dataset on the demersal and pelagic fish communities.

Methods

Biodiversity measures for marine ecosystems: a statistical challenge

Biodiversity measures and especially species richness are sensitive to sampling effort and sample aggregation. Classical marine biodiversity samples such as trawl hauls are small sampling units compared with the habitat they sample and, as a result, species composition and abundance in a single haul may be highly variable. Sensitivity to sampling effort, along with difficulty to distinguish between change in species richness and change in evenness, and confounding effects of changes in α - and β -diversity, are common problems encountered when using biodiversity indices in an assessment or management context (Rice, 2003; Rochet and Trenkel, 2003; Greenstreet and Piet, 2008). To solve these issues, methods based on rarefaction and extrapolation can be used to obtain a robust estimate of diversity. Models can be fitted to empirically constructed species area relationships examining how species richness increases as the number of samples accumulate. Previously, these models were mostly restricted to species richness estimates (Gotelli and Colwell, 2001; Chao and Jost, 2012). They have recently been extended to more general diversity measures (Chao *et al.*, 2014), for cases where the abundance of each species in the sample is expressed in number of individuals.

However, most of these biodiversity statistics are based on sampling models for counts (either number of individuals or incidences), and assumptions underlying the use and parameterization of rarefaction and extrapolation models are no exceptions (Chao *et al.*, 2014 and references therein). This makes them difficult to transpose to diversity measures based on continuous abundance measures, such as biomass or coverage. In many at-sea surveys of fish community based on trawl hauls however, biomass can be seen as the primary abundance currency for several reasons. First, it is much easier to sort and weight the catch than to sort and number it, especially when many small fish have been caught. Second, number-based biodiversity measures are largely influenced by recruitment variability which tends to be high in marine systems (Rice, 2003). In the specific case of the Barents Sea, Certain *et al.* (2014) demonstrated that spatial patterns of biomass-based fish biodiversity measures were better explained by environmental variables than their number-based counterpart, making biomass-based diversity measures more informative of the potential changes the fish community is likely to undergo. This result suggested that in the Barents Sea, energy allocation between species might contribute more to the shaping of biodiversity than stochastic demographic processes controlling the numbers of individuals (Morlon *et al.*, 2009; Henderson and Magurran, 2010; Magurran and Henderson, 2012). Because a single fish species can encompass many size classes, total biomass per species is a better proxy for the size of the niche and the amount of energy captured by that species than number of individuals. Finally, many other proposed indicator for marine systems are based on biomass or biomass ratios of specific fish groups. For these reasons, it seems reasonable to favour the use of biomass data over numbers when assessing fish biodiversity in the Barents Sea. However, the choice of biomass prevents the use of the whole suite of rarefaction and extrapolation tools (Chao *et al.*, 2014).

A unified framework to measure diversity

In recent years, unification of biodiversity measurements has been the focus of specific research (Jost, 2006, 2007; Tuomisto,

2010a, b, c; Chao *et al.*, 2014). This has resulted in a framework for measuring biodiversity that integrates many of the previously developed indices and places them in a context where they can easily be related to each other through some algebraic transformation, thereby reducing the confusion that arose from the use of multiple biodiversity indices and improving inter-comparability between studies. This framework is based on the seminal papers of Whittaker (1972), who noted that the total species diversity observed in a landscape could be partitioned in conceptually different components, and Hill (1973), who proposed a general mathematical formulation of diversity indices. The use of Hill's numbers is motivated by their advantageous numerical property. First, they have an explicit measurement unit. Second, they present a "doubling property", meaning that when two species assemblages with exact same Hill diversity are mixed in equal proportions, the diversity of the resulting assemblage is doubled. Third, they can easily be modified to incorporate a phylogenetic or a functional component (Chao *et al.*, 2010; Leinster and Cobbold, 2012; Chiu and Chao, 2014). Fourth, they allow for the hierarchical partitioning of diversity into a suite of "intra" and "inter" components, termed, respectively, α - and β -diversity. By explicitly measuring α - and β -diversity, it is possible to detect and quantify changes in species composition through time and across sites, therefore solving the issue that diversity index is not sensitive to change in species composition, which is a problem when the focus is on α -diversity only.

Hill's diversity refers to a dataset with as many rows as biodiversity samples and as many columns as categories used to sort the biological material. These categories can be of many types, the only requirement being that they are clearly defined and remain unchanged in the whole set of diversity samples considered (Tuomisto, 2010a). For taxonomic diversity, these categories are taxonomic units (i.e. species, genus, class, etc.). The allocation of individuals to categories can be made in various abundance units, e.g. numbers, biomasses, and area of coverage. The simplest way to measure biodiversity from an abundance dataset is to use "true" diversity measures, termed as such by Jost (2007) because they have the most direct connection to the mathematical concept of diversity (Tuomisto, 2010c).

In a dataset consisting of j in $1 \dots N$ samples where individuals are divided into i in $1 \dots S$ categories, the diversity can be partitioned into α -diversity, the diversity of categories represented within a sample, and β -diversity, the diversity of sample types. For "true" diversity indices, multiplicative partitioning ensures that the α - and β -components are independent and have different measurement units, which eases comparison of α - and β -diversity across regions or through time (Jost, 2007; Tuomisto, 2011). Following Tuomisto (2010a), "true" α -diversity is noted ${}^qD_\alpha$ and is calculated as a weighted average of relative abundances of species:

$${}^qD_\alpha = \frac{1}{q\bar{p}_{ij}}, \quad \text{with } q\bar{p}_{ij} = \sqrt[q-1]{\sum_{j=1}^N w_j \sum_{i=1}^S p_{ij}^q}. \quad (1)$$

Here, p_{ij} is the proportional abundance of the i th species in the j th sample, and w_j the proportional abundance of the j th sample relatively to the entire dataset. Total diversity in the dataset, ${}^qD_\gamma$, is calculated as:

$${}^qD_\gamma = \frac{1}{q\bar{p}_i}, \quad \text{with } q\bar{p}_i = \sqrt[q-1]{\sum_{i=1}^S p_i^q}. \quad (2)$$

Here, p_i is the proportional abundance of the i th species in the whole dataset. From there, "true" β -diversity ${}^qD_\beta$ is obtained by ${}^qD_\gamma/{}^qD_\alpha$ (Tuomisto, 2010a). The above equations partition diversity as follows: the α -component provides a diversity measure at the sample level, the γ -component provides a diversity measure at the dataset level, and the β -component scales the diversity measure from the sample to the dataset level. Considering further levels result in the addition of level-specific β components. For example, when one intermediate level is added between the lowest (sample) and the highest (whole dataset), the partitioning of diversity leads to:

$${}^qD_\gamma = {}^qD_\alpha \times {}^qD_{\beta 1} \times {}^qD_{\beta 2}. \quad (3)$$

Here, α -diversity at the sample level is ${}^qD_\alpha$, while α -diversity at the intermediate level is ${}^qD_\alpha \times {}^qD_{\beta 1}$. In practice, level-specific ${}^qD_\alpha$ are computed from Equation (1) by aggregating the diversity samples at the level under focus, ${}^qD_\gamma$ is computed from Equation (2), and the level-specific ${}^qD_\beta$ are deduced therefore (see Tuomisto, 2010a, for further details).

The measurement unit of ${}^qD_\gamma$ is the effective species number, i.e. the number of equally abundant virtual species that would provide the same diversity measure as the one observed in the whole dataset. The measurement unit of sample diversity, ${}^qD_\alpha$, is the effective number of species per compositional unit in the dataset. The measurement unit of ${}^qD_\beta$ is the effective number of compositional units, i.e. the number of virtual sampling unit that has the same species diversity (i.e. effective number of species) as the real sampling units do on average, but does not share any effective species with any of the other effective compositional units. Conceptually, effective sampling units are to samples what effective species numbers are to species.

In Equations (1) and (2), the parameter q controls the influence of abundant over rare species on the diversity metric. As q increases, the diversity measure becomes more sensitive to the abundant species and less sensitive to the rare ones (Hill, 1973). The parameter q can vary in the interval $[0, +\infty[$. When q equals 0, "true" diversity equals species richness. When q tends towards 1, "true" diversity equates the exponential of the Shannon index. When q equals 2, "true" diversity equals the reciprocal of the Simpson index. When q tends towards $+\infty$, "true" diversity tends towards the reciprocal of the relative abundance of the most abundant species. A common practice is to measure diversity along a range of q values. This is called a diversity profile and it highlights how the diversity measure changes when the relative influence of rare and abundant species is gradually reversed (Hill, 1973). Slopes of diversity profiles reflect unevenness in species abundance distribution: the steeper the profile, the larger the differences in the frequencies between the abundant and rare species. In this study, we restrict the analyses to q in the interval $[0, 4]$. The upper limit, 4, is chosen because diversity profiles tend to be very stable beyond this point (Hill, 1973; Chao *et al.*, 2014).

The dataset: pelagic and demersal trawl hauls in the Barents Sea

The fish community of the Barents Sea (Figure 1a) has been sampled annually in August–September during the joint Norwegian–Russian ecosystem survey since 2004 (Michalsen *et al.*, 2013). Five research vessels have been simultaneously deployed to cover the 1.5 million km² of this large marine ecosystem. On board, multiple observations and sampling methodologies are operated to record data on hydrography, primary and secondary production, fish and

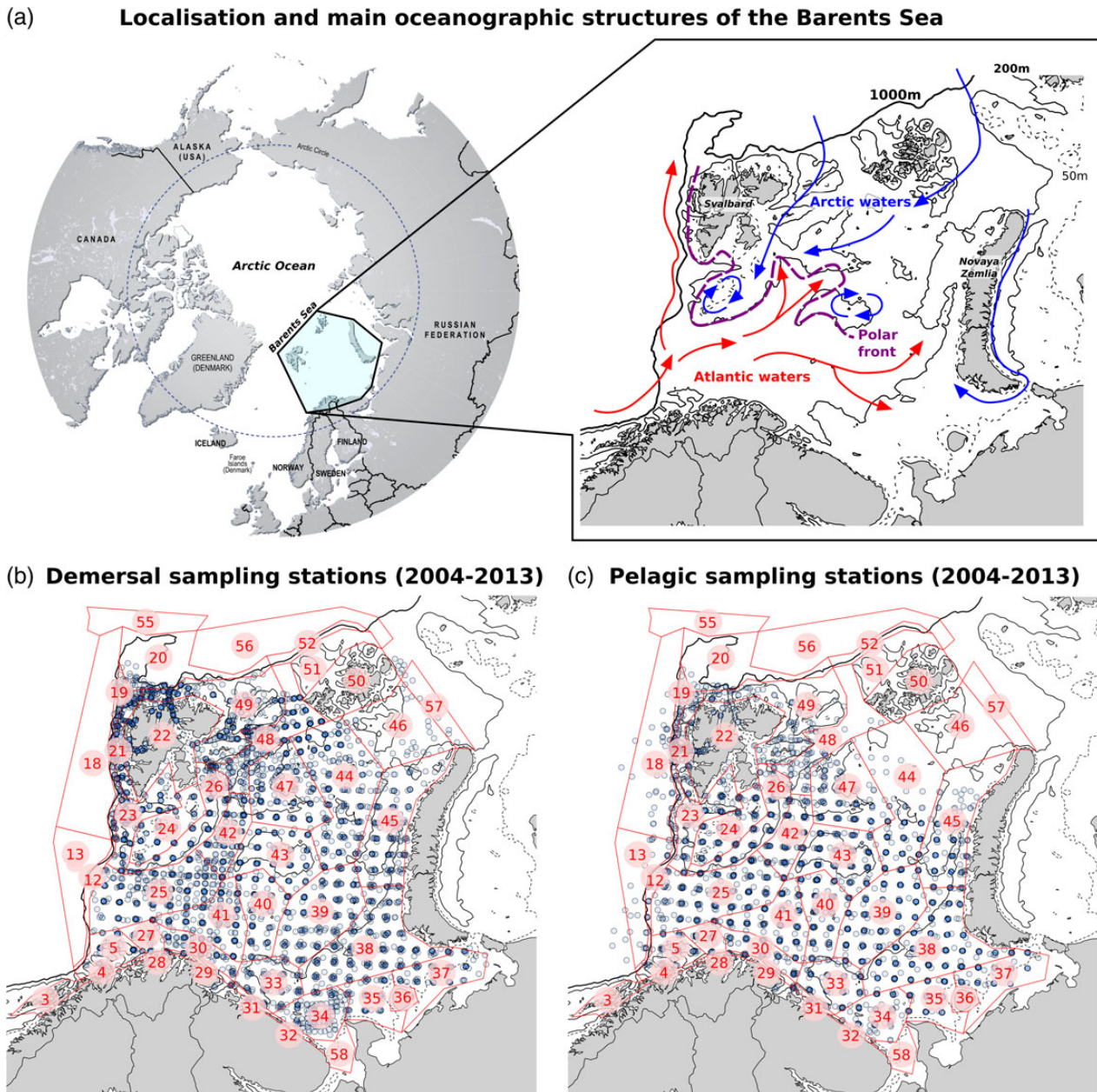


Figure 1. (a) Geographical location of the Barents Sea and main bathymetric and oceanographic structures, (b) location of demersal sample trawl between 2004 and 2013, (c) location of pelagic sample trawl between 2004 and 2013, superimposed sample trawls are identified with darker colours. Red polygons and numbers represent ecological subregions in the Barents Sea.

benthos communities, and top predators (Michalsen *et al.*, 2013). Among these, pelagic and bottom trawl hauls are conducted over a regular sampling scheme comprising ~400 demersal and ~300 pelagic trawl stations each year (Figure 1b and c). Variations in the sampling grid have occurred over the years to adjust to various constraints. Sample is collected following a standardized protocol (i.e. standardized gear, trawling depth, and time, see Wienerroither *et al.*, 2011, pp. 14–15 for details) that ensures homogeneity of sampling effort between trawls of the same type (i.e. demersal or pelagic). On board, all species caught in a trawl haul are identified, weighted, and counted. With a few exceptions, fishes are taxonomically identified down to the species level. Between 2004 and 2013, 4229 bottom trawl hauls and 3039 pelagic trawl hauls were conducted in the Barents

Sea, providing biomass information on 86 and 76 fish taxa, respectively (see list in Supplementary Appendix S1). These two datasets are the basis for the present assessment of the fish biodiversity in the Barents Sea. As sampling effort has been carefully standardized, each trawl can be considered equally representative. Therefore, species biomasses per trawl have been standardized per total trawl biomass before analysis, so that each trawl receives the same weight w_j in Equation (1).

Hierarchical partitioning of diversity: defining partitioning levels

Any diversity assessment based on hierarchical partitioning relies on the choice of levels across which diversity is partitioned. Some levels

naturally stem from the sampling design; in the present case, these are the individual trawl hauls (sampling units), the whole Barents Sea (global level), and the individual surveys (years). Other levels can be build-up, for example, based on previous knowledge on the structure of the landscape and environmental condition and can thereby constitute another level of partitioning that is spatially explicit. The Barents Sea environment is clearly marked by strong spatial heterogeneities organized around important landscape features such as the Polar Front separating Atlantic and Arctic waters, a contrasted bathymetry, the location of the ice edge or changes in current strength and direction (Sakshaug *et al.*, 2009; Jakobsen and Ozhigin, 2011). Here, we used a geographical discretization of the Barents Sea into polygons (Figure 1b and c) that represent major mesoscale spatial units, i.e. environmentally homogeneous entities in terms of oceanography, climatic conditions, and bottom structure. They constitute the geographical units of the numerical end-to-end model Atlantis currently under development for the Barents and Norwegian Seas (Jähkel, 2013, <http://www.imr.no/temasider/modeller/atlantis/nb-no>). Spatial partitioning based on these polygons can further allow for direct comparisons of the biodiversity assessments with outputs from the Atlantis model, thus facilitating the joint formulation of management recommendation based on these two approaches in the future. It is also an indirect way to investigate how mesoscale environmental heterogeneities control changes in fish community in the Barents Sea.

Controlling for sampling heterogeneities: bootstrap subsamples

Spatial partitioning is based on geographical polygons of different shapes and size. As a result, the number of trawl samples can vary between polygons, which constitutes a possible source of bias in estimating β -diversity (Tuomisto, 2010b). To account for this bias, we used the following non-parametric subsampling bootstrap procedure: 1000 bootstrap subsamples were taken by randomly selecting 5 trawl haul per polygon and year, without replacement, for the pelagic and demersal datasets. Polygons in which the total number of trawl haul in a given year was < 10 were rejected in the process. The diversity analysis was conducted on the bootstrapped subsamples to extract the median and confidence intervals for the diversity profiles measured. To check the extent to which the effect of sampling intensity remained in our diversity estimates, an additional analysis of remaining effect was conducted using generalized additive models.

Diversity analysis of demersal and pelagic trawl in the Barents Sea

The diversity analysis was conducted on the following hierarchical levels: samples, polygons, years, and total. The sample level corresponds to the most local measures of diversity; the polygon level corresponds to mesoscale entities in the Barents Sea; the year level captures diversity variations in time, and the total level corresponds to the whole dataset over the 10 years. Our results are presented in a succession of three analyses, namely (i) global hierarchical partitioning, (ii) partial hierarchical partitioning at the polygon level, and (iii) year-to-year β -diversity at the polygon level.

Global hierarchical partitioning of diversity

This analysis corresponds to the simplest application of the diversity assessment framework described above. Five types of diversity profiles were computed with q ranging from 0 to 4: α_{trawl} , $\beta_{\text{trawl|poly|year}}$, $\beta_{\text{poly|year}}$, β_{year} , and γ . The α_{trawl} profile measures the average

diversity of a single sample trawl taken in the Barents Sea. The $\beta_{\text{trawl|poly|year}}$ profile represents the diversity of trawl samples in a polygon during 1 year. It is a measure of how sample trawls taken in the same polygon and the same year differs in terms of species composition and abundances. As the analysis is carried out by randomly selecting five trawl samples per polygons and per year, $\beta_{\text{trawl|poly|year}}$ ranges between 1 (all trawl samples have the same species composition and abundance) and 5 (all trawl samples have a completely different species composition). Similarly, $\beta_{\text{poly|year}}$ represents the diversity between polygons in one year and ranges from 1 (all polygons share the same species composition and abundance) to the number of polygon sampled (19 for the demersal dataset, 15 for the pelagic dataset). Finally, β_{year} measures the diversity between years in the dataset and ranges between 1 (all years are equals) and 10 (all years are completely different). The γ profile is the product of the four first profiles and corresponds to total diversity. Both β_{year} and γ are integrated at the scale of the entire Barents Sea. By plotting these diversity profiles for demersal and pelagic datasets, we quantified how fish diversity in the Barents Sea is successively partitioned across the sample (trawl), regional (polygon), and temporal (year) levels.

Partial hierarchical partitioning at the polygon level

In this analysis, α_{trawl} , $\beta_{\text{trawl|year}}$, β_{year} , and γ -diversity were measured independently for each polygon. This diversity partitioning is termed “partial” as the polygon level was intentionally set aside to visualize spatial patterns. This analysis provides a spatial representation of α - and β -diversity, and is used to map spatial patterns of diversity together with temporal patterns of changes in diversity in the Barents Sea. Four set of maps were produced along the diversity profile, corresponding to $q = 0, 0.5, 1, \text{ and } 2$.

Temporal variability: separating random variation from community drift

β_{year} quantifies changes in diversity between years, and can be interpreted as the variability of the community during the 10 years of sampling. However, a single β_{year} value computed for the 10 years of data does not indicate whether this variability results from random changes in species composition or abundances or if the community composition has gradually changed over time. In the former case, the expected variability between 2 years is independent from the amount of time separating these 2 years. In the latter, dissimilarity in community composition between 2 years is expected to be greater when the duration between 2 years of observation is high. For convenience, we will refer to the former patterns as “random variation”, and to the latter pattern as “community drift”.

To discriminate between drift and random variations, we used new β_{year} values, thereafter denoted $\beta_{2\text{years}}$, measured by taking any pair of years. We denote the temporal distance separating these 2 years as “lag time”. Drift in community composition is expected to increase $\beta_{2\text{years}}$ with lag-time, while random year-to-year variations are not. For each bootstrap subsample, we tested this pattern at the polygon level using regression on dissimilarity matrices (Goslee and Urban, 2007). The slope of this regression can be interpreted as the “drifting” coefficient as it measures the rate at which the community drift through time. From these regressions, we also computed the expected mean variation in diversity between two consecutive years as the expected value of $\beta_{2\text{years}}$ at lag-time “1”, which can be interpreted as a “random variation” parameter.

Results

Global hierarchical partitioning

Diversity profiles from the global hierarchical partitioning analysis (Figure 2) reveal rather steep α - and γ -diversity profiles for both the demersal and the pelagic fish community, as expected from communities strongly dominated by a few abundant species. The importance of the scaling from the α to the γ profile reveals the contribution of the various β -diversities in both communities. At $q = 0$, α - and γ -diversity equals 10 and 70 for the demersal community, i.e. a scaling factor of 7, while for the pelagic community, α - and γ -diversity equals 5 and 55, i.e. a scaling factor of 11. Comparatively, β -diversity is almost twice higher in the pelagic dataset than in the demersal dataset. In both, the relative contribution of the hierarchical levels to the β -diversity is similar. The highest diversity profile is $\beta_{\text{poly|year}}$ which ranges from 2.3 at $q = 0$ to 2 at $q = 4$ for the demersal community, and 2.5 at $q = 0$ to 2 at $q = 4$ for the pelagic community. This indicates that the observed regional differences in terms of species composition and abundance across polygons are of the same level as if the Barents Sea was composed of two or three regions with completely different communities. When compared with the 19 (15) polygons considered for the demersal (pelagic) community, this result suggests a rather strong overlap in terms of biodiversity between polygons. In both demersal and pelagic communities, the $\beta_{\text{trawl|poly|year}}$ profile ranges from 2 at $q = 0$ to 1.5 at $q = 4$. These numbers, even if lower than $\beta_{\text{poly|year}}$, actually suggest a large variability at the trawl sample level when compared to their maximum value (which is 5). This means that, at $q = 0$, the biodiversity observed in five trawl samples taken the same year in the same polygons equates the diversity that one would get with two virtual trawl samples composed of completely different species. Finally, the β_{year} profile obtained for both communities is very close to 1 for large q values, indicating that over the 10 years and at the scale of the whole Barents Sea, no changes in dominance regime have occurred. At $q = 0$ however, the β_{year} profile for the pelagic community is close to 2, indicating that the observed pelagic species richness observed during these 10 years equates what one would have observed with two virtual years composed of completely different species. Knowing that these numbers are interpreted at the scale of the entire Barents Sea, this indicates that rather strong changes in terms of pelagic species richness have occurred during the period of study. Given the relative similarities in $\beta_{\text{trawl|poly|year}}$ and $\beta_{\text{poly|year}}$ profile between the demersal and pelagic dataset, it is clear that the higher β -diversity observed for the pelagic dataset is mostly attributable to this temporal effect, i.e. year-to-year variations in the composition of the pelagic community are greater than for the demersal community.

Partial hierarchical partitioning: demersal community

Spatial patterns of biodiversity and biodiversity changes can be visualized by leaving polygons out of the hierarchical partitioning. For the demersal community (Figure 3), these spatial patterns can be fairly well marked, and also depend on the order q of the biodiversity measure, with distinct differences between $q = 0$ (species richness) and $q > 0$ (when species abundance also matters). Patterns of α_{trawl} at $q = 0$ show a clear longitudinal gradient, with eastern areas presenting lower values. However, at $q > 0$, the number of high diversity areas reduces progressively, and only the central part of the Barents Sea still displays high α_{trawl} values at $q = 2$. Concerning β -diversity, $\beta_{\text{trawl|year}}$ at $q = 0$ is high in the northwestern and southeastern part of the Barents

Sea, but as q increases, only the northwestern part still presents high values. More interestingly, patterns of β_{year} diversity display a contrasted picture at $q = 0$ and $q > 0$. At $q = 0$, temporal variability is high in the southeastern Barents Sea, while at $q > 0$, the northwestern and northeastern areas become the most variables. Across the 10 years of the study, patterns of γ -diversity primarily reflect α_{trawl} , but with larger value around Svalbard attributable to $\beta_{\text{trawl|year}}$ and β_{year} patterns. The diversity values displayed on these maps together with confidence intervals are provided in Supplementary Appendix S2.

Partial hierarchical partitioning: pelagic community

For the pelagic fish community, spatial patterns of diversity (Figure 4) are not as contrasted between $q = 0$ and $q > 0$ as they are for the demersal. High α_{trawl} diversity is observable around Svalbard at $q = 0$, as well as for the southwestern polygons at $q > 0$. $\beta_{\text{trawl|year}}$ displays very similar patterns than for the demersal community, with highest value in Northwestern and Southeastern areas. However, temporal variability patterns are still well contrasted between $q = 0$ and $q > 0$. At $q = 0$, high β_{year} patterns are widespread in the west-central part of the Barents Sea, but restricted to the Northwestern areas around Svalbard when $q > 0$. Over the 10 years, γ -diversity patterns of the pelagic fish community display high values around Svalbard, at both $q = 0$ and $q > 0$. The diversity values displayed on these maps together with confidence intervals are provided in Supplementary Appendix S2.

Temporal variability: separating random variation from community drift

Figure 5 displays spatial patterns of the community drift coefficient and random variation parameters issued from the regression on dissimilarity matrices of $\beta_{2\text{years}}$ against lag time (see Supplementary Appendix S3 for the corresponding numerical values and graphical plots). Three major features of community temporal variability are observed on these maps. First, spatial patterns of drift coefficients differ from spatial patterns of random fluctuations. Second, clear differences between patterns at $q = 0$ and $q > 0$ are observed, suggesting that our perception of community temporal variability depends on whether species richness or dominance regime are emphasized. Third, drift coefficients tend to be higher when dominance is emphasized (as q increases), suggesting that community drift in the Barents Sea mostly concerns changes in dominance regime rather than changes in species composition. This pattern is even more striking when looking at the regressions plots presented in Supplementary Appendix S3.

More specifically for the demersal dataset, community drift is negligible at $q = 0$ with most drift coefficients being inferior to 0.01. However at $q = 2$, they increase up to 0.07 in the two Northeastern polygons. A drifting coefficient of 0.07 indicates that the time required to reach a complete reconfiguration of the community ($\beta_{2\text{years}} = 2$) is around 15 years (see Supplementary Appendix S3). As this is obtained for a diversity measure that emphasizes dominance regime ($q = 2$), this should be interpreted as the expected time by which previously dominant species will be replaced by new ones in these areas. In addition from community drift in the Northeastern Barents Sea, larger random fluctuations in temporal variability can be noted in the Southeastern polygons at $q = 0$ and in the surroundings of Svalbard area when $q > 0$. For the pelagic dataset, higher drifting coefficients at $q = 0$ are largely distributed in the Eastern half of the Barents Sea, a result consistent with the high β_{year} values noted in the global hierarchical

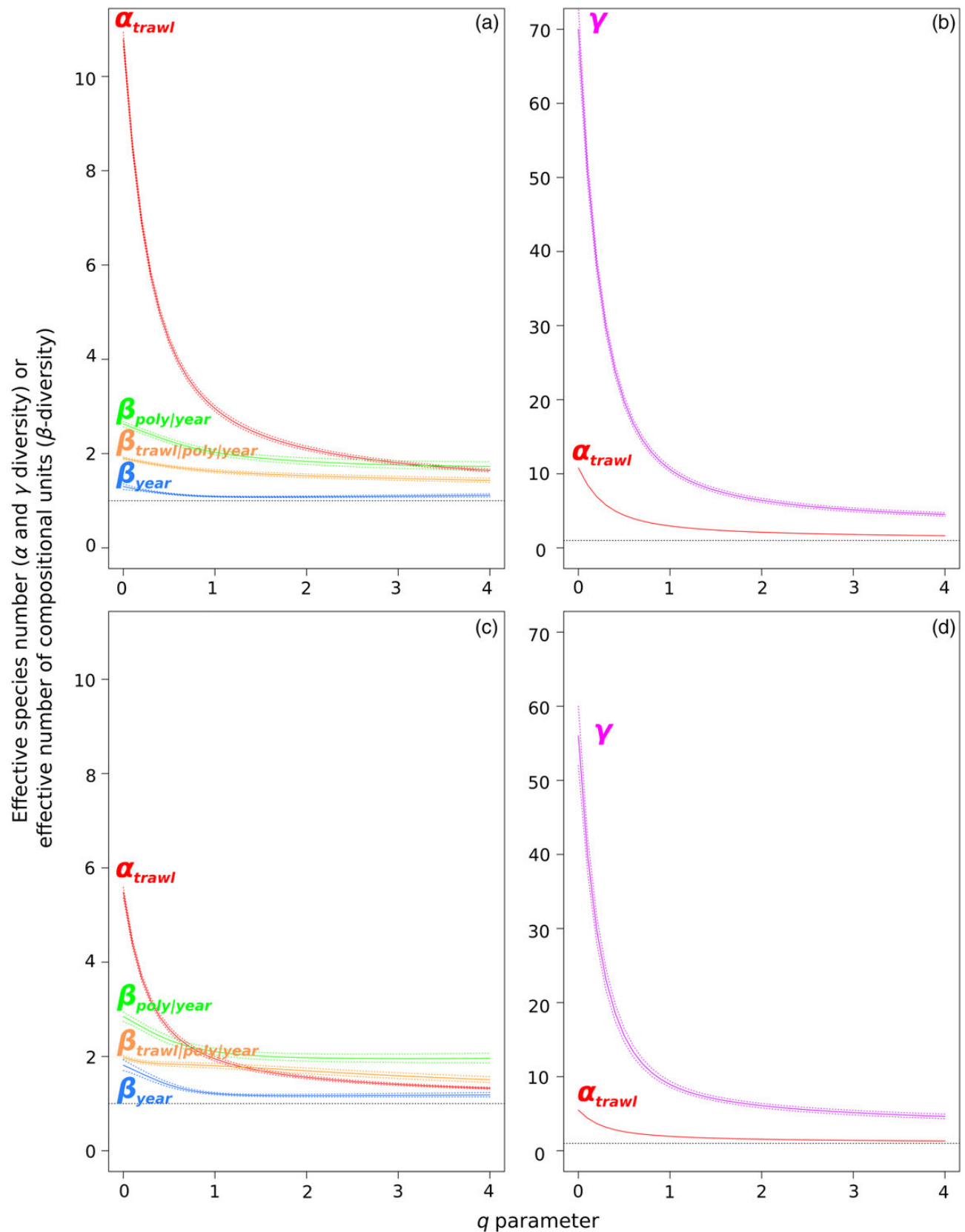


Figure 2. Global hierarchical partitioning for the demersal (upper panels) and pelagic (lower panels) datasets. The γ -diversity profile is the product of the four other profiles. Dotted lines around the profiles show 95% confidence intervals. α_{trawl} denotes diversity in a sample trawl; $\beta_{trawl/poly/year}$ denotes diversity of trawl samples in the same polygon in the same year, $\beta_{poly/year}$ denotes diversity of polygons in the same year, β_{year} denotes diversity of years, and γ is the diversity profile of the whole dataset across the 10 years of the study. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

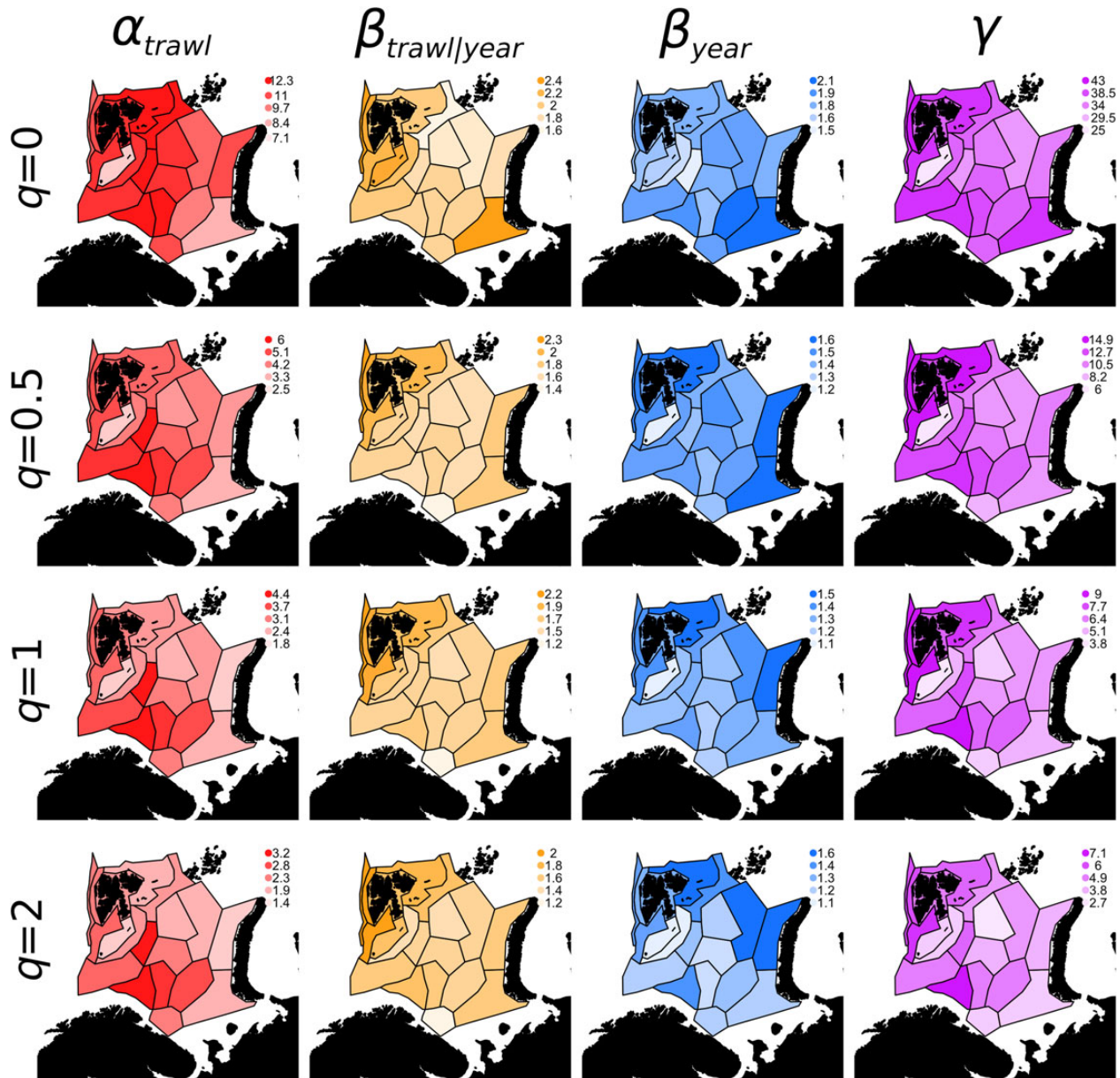


Figure 3. Result of the partial hierarchical partitioning of biodiversity for the demersal dataset. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

partitioning. As q increases, higher drifting coefficients are progressively restricted to the northernmost polygons. Patterns of random variations are similar across q values and again emphasize Svalbard surroundings as a more randomly variable area.

Detailed results at the species level

The objective of this study was not to detail the species-specific patterns underlying changes in biodiversity. However, the present biodiversity assessment reveals a number of patterns that the interested reader may wish to further investigate. We provide in Supplementary Appendix S4 additional figures that summarize changes in biodiversity at the species level for specific subregions. Three examples are provided. The first one focuses on demersal and pelagic species composition and abundances in the Northeastern Barents Sea, where a strong community drift has been observed. The second one focuses on Svalbard

surroundings, as these present high levels of random fluctuations. Finally, the last example focuses on polygons in the central Barents Sea, for which our biodiversity assessments did not reveal strong temporal changes. These examples show how such a biodiversity assessment can help to quickly identify important patterns at the species level.

Effect of sampling heterogeneity on diversity measures

Usually, no significant relationships could be found between diversity measures and the number of samples available per polygons (Supplementary Appendix S5). This illustrates that the bootstrap-subsampling approach has been efficient in dealing with this bias. One exception is a relationship found for β_{year} for the demersal community. But this relationship is observed neither in the pelagic dataset nor in $\beta_{poly/year}$, which makes it difficult to attribute

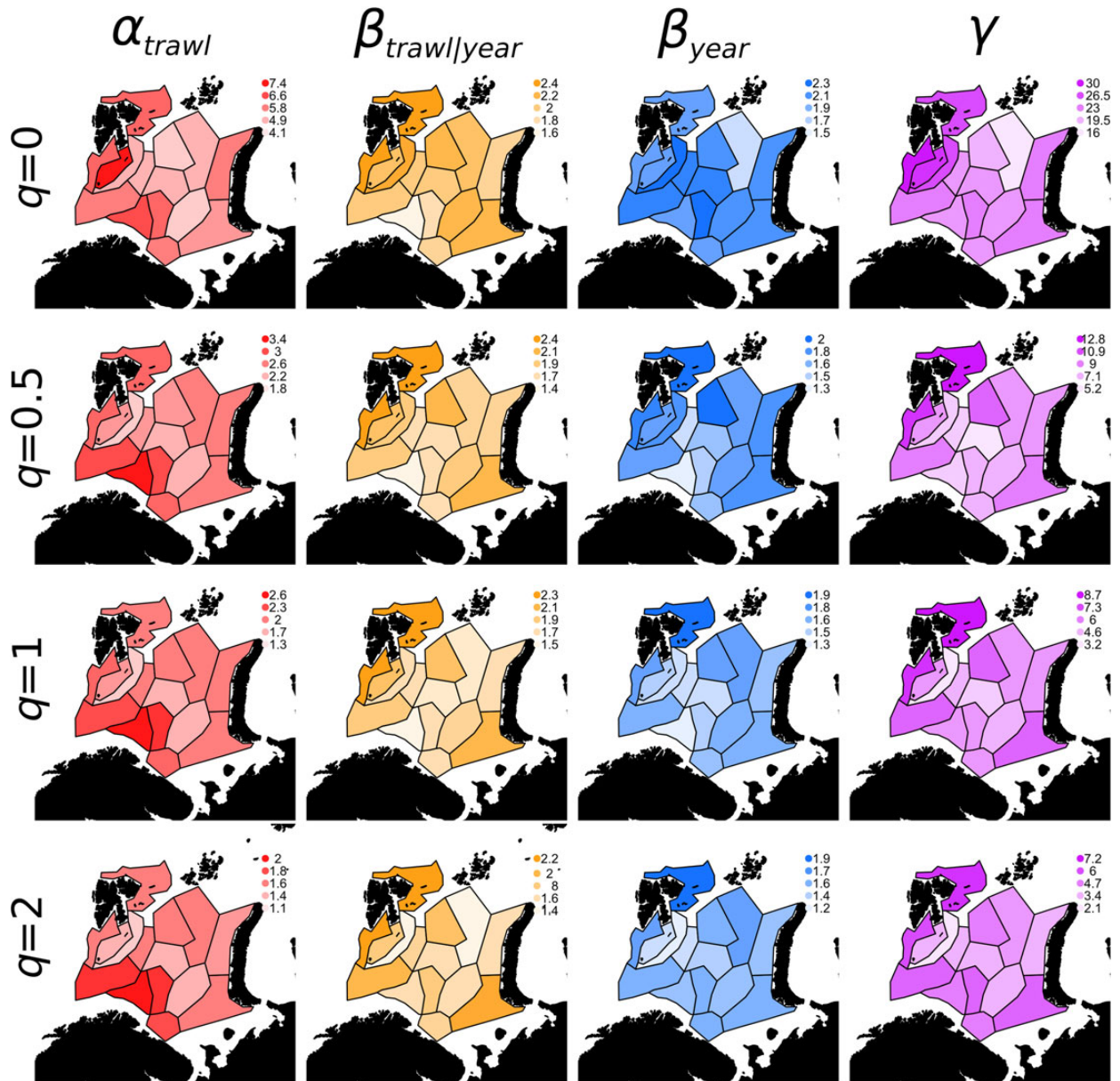


Figure 4. Result of the partial hierarchical partitioning of biodiversity for the pelagic dataset. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

it to a sampling bias. Therefore, we do not think that it represents a strong concern for the validity of the present study.

Discussion

What do we learn from and how to use the biodiversity baseline

The present analysis complements previous studies of the biodiversity of the Barents Sea fish community that solely focused on either α - or γ -diversity. Johannesen *et al.* (2012a) proposed a cluster-based description of the demersal fish community and quantified species richness at large scale (γ -diversity at $q = 0$). Certain *et al.* (2014) developed predictive models for fish α_{trawl} -diversity, highlighting contrasting responses of different demersal fish guilds and pointing to the best combination of methodological choices for prediction. Finally, Wiedmann *et al.* (2014a, b) described the functional

diversity in the Barents Sea, using an approach restricted to α -diversity and presence/absence data (α_{trawl} at $q = 0$). These studies have provided useful descriptions and understanding of diversity patterns in the Barents Sea, but as they select only one aspect of biodiversity (e.g. either α or γ) or one point along the profile (most often $q = 0$), they only catch small pieces of the whole picture, which can be difficult to compare with each other. They were furthermore restricted to the demersal community. Our approach that presents the analysis along the whole diversity profile and account for the partitioning of biodiversity in space and time (β -diversity) provides a much more integrated picture, and is able to reveal and quantify many interesting patterns that have not been clearly described prior to this study.

For example, the almost systematic differences between α - and β -diversity patterns at $q = 0$ and $q > 0$ show that conclusions on

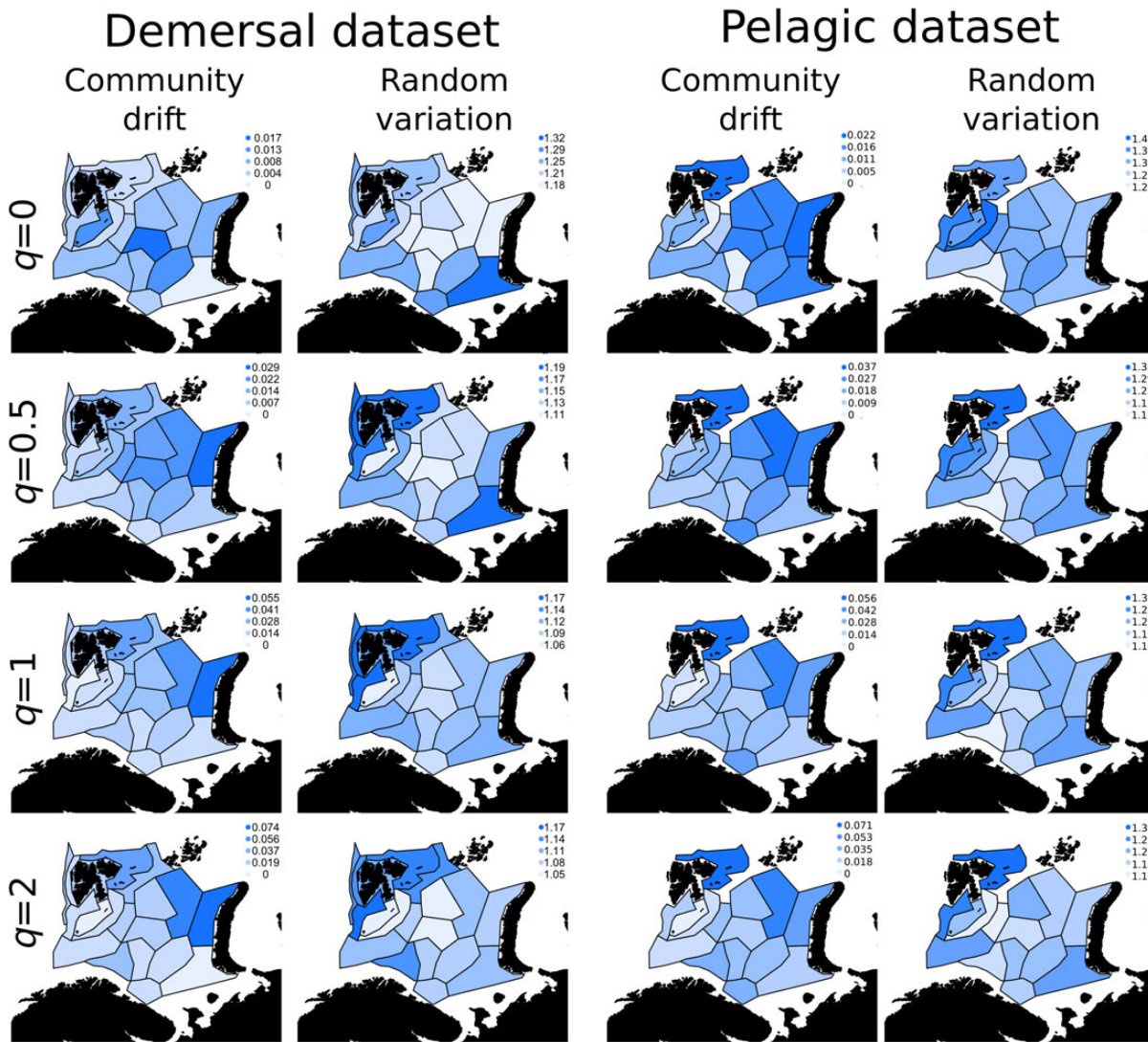


Figure 5. Community drift coefficient and random variation parameter for the demersal and pelagic dataset, obtained through the regressions on dissimilarity matrices of $\beta_{2\text{years}}$ against lag time. Community drift is the slope of the regression, while random variation is the expected value of $\beta_{2\text{years}}$ at lag time 1. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

biodiversity cannot be drawn from only focusing on one point on the profile. Such practice is risky, as one has a large chance of missing important patterns only occurring at one or the other end of the diversity profile. Explicitly quantifying β -diversity in space and time leads to measures of biodiversity changes. Such measures are crucially important to setting a biodiversity baseline, as they tell how much change is to be expected between two particular areas, or within a given period.

Between 2004 and 2013, temporal changes in biodiversity were not strong when the Barents Sea was considered as a whole. But at the scale of subareas, strong discrepancies in α - and β -diversity were observed and quantified. Our results show that some areas experienced changes in species composition (Eastern Barents Sea, pelagic dataset) and changes in dominance regime (Northeast Barents Sea, pelagic and demersal datasets). We identified areas such as Svalbard surroundings where strong random fluctuations are to be expected, both at small spatial scale (reflected by β_{polyyear}) and through time (reflected by β_{year}). All these features had previously not been explicitly

described or quantified. The strong change in pelagic and demersal dominance regime we noted in the Northeastern Barents Sea, where previously dominant polar cod is being replaced by Atlantic cod and capelin (see Supplementary Appendix S4), together with the assumed key role of these species in the ecosystem functioning (Hop and Gjøsaeter, 2013) suggests that a major ecosystem reconfiguration is going on in this area, which may trigger cascading effects and ecological surprises.

The Barents Sea ecosystem is expected to experience further substantial changes soon, as a consequence of increased anthropogenic activity such as oil extraction (Olsen *et al.*, 2007) or modification of the ocean climate (Slagstad *et al.*, 2011). The method presented in this paper allows highlighting and disentangling between many possible patterns in biodiversity change. The loss of species will be associated with a decrease in α -diversity with low q order, while increased dominance of a few species will be associated with a decrease in α -diversity with high q order. These will be perceived either at the trawl, polygon, or whole Barents Sea level, depending

on the scale at which the change in biodiversity occurs. Increased local heterogeneity, for example, triggered by increased fragmentation of the benthic habitats, would be revealed by increases in β -diversity at the trawl level, while local homogenization of the communities would lead to decreasing β -diversity at the trawl level. Changes in species spatial distribution within the Barents Sea would lead to changes in β -diversity at the polygon level. Should the fish community experience greater temporal variability, this would be reflected in an increase in β -diversity at the year level. If these changes are significant enough to affect the biodiversity at the scale of the Barents Sea, with species entering in or disappearing from the area, these would be apparent in measures of γ -diversity. Since we provide quantitative measures of α - and β -biodiversity at different spatial and temporal scales, together with measures of uncertainty, it will be possible to quantitatively test if future measures of biodiversity in the Barents Sea depart from what has been observed between 2004 and 2013.

Methodological aspects

The diversity measures presented in this study are conditional to specific sampling and analytical protocols and as such, they cannot be compared directly with biodiversity estimates from other areas, where sampling or analytical protocols are different. Correction for sampling heterogeneity is a critical step that will need to be replicated in future analyses. In the present case, since methods using rarefaction and extrapolation do not apply to biomass data, an alternative bootstrapping method was used. This makes the current approach more general, and a similar bootstrap subsampling procedure can be used when analysing new sets of data.

The choice of the number of polygons, their sizes and shapes are subjective, but the use of polygons as a nested spatial level for biodiversity assessment is a practical approach to standardization of spatial analyses across datasets and a pragmatic advance towards spatially resolved integrated assessments. Some criticism may be voiced, such as the polygon shape not being perfectly adapted to the sampling design, but there is likely no set of polygons which can satisfy simultaneously the analytical constraints of several datasets and modelling approaches. The advantage of the current design is that it integrates the main oceanographic features of the Barents Sea and therefore allows for similar biodiversity assessments in the Barents Sea for a wide range of taxa, including zooplankton (Søreide *et al.*, 2003; Dalpadado *et al.*, 2008), benthos (Carroll *et al.*, 2008; Cochrane *et al.*, 2009; Jørgensen *et al.*, 2015), or top-predators communities (Fauchald *et al.*, 2002). This is even simplified since the monitoring of all these compartments is now integrated within the Barents Sea ecosystem survey (Michalsen *et al.*, 2013).

The importance of measuring β -diversity

There is now evidence that β -diversity is the diversity level at which climate change effects are mostly expressed. The loss of α -diversity, though widespread, is not a systematic trend in ecological communities. Rather, communities appear undergoing massive turnover in the species that constitute them (β -diversity), resulting in the global emergence of communities with novel species configurations (Dornelas *et al.*, 2014). Measures of β -diversity capture these effects, as shown here for the Northeast Barents Sea. It is also possible to separate changes in biological communities that follow random patterns from those who are subjected to temporal drift. Disentangling drift from random variability is a key question, which needs to be resolved before observed changes in biodiversity can be used to trigger management actions or new monitoring programmes. In the present analysis,

we estimate the expected time for a complete reconfiguration of the community (by using the fitted regression between $\beta_{2\text{years}}$ and lag time to compute the expected time for which $\beta_{2\text{years}}$ reaches 2). In most polygons, this community turnover time is of several decades (Supplementary Appendix S3), suggesting slow drift rates and great community stability, a finding somewhat contrasting with the common idea that the Barents Sea is a highly variable system (Link *et al.*, 2009). Nevertheless, this high level of stability is not true for all polygons as drift in community composition is ongoing for demersal and pelagic species in the northern polygons, where the community turnover time comprises between 10 and 25 years (Supplementary Appendix S3). These time intervals are computed under the assumption of a linear increase, but they may be shorter if changes prove to be non-linear and accelerating. Most changes observed in these areas are due to increasing abundance of species of commercial interest, and decreasing abundance of Arctic species with little or no commercial values. If these modifications are sustained in the coming years, fishing pressure will most probably increase therefore in these areas.

Link with other assessment framework

The present biodiversity assessment constitutes the first biodiversity baseline for the Barents Sea. Whether future changes in biodiversity happen as slow continuous drifts or rapid and abrupt changes, it will be possible to quantify such changes against this baseline. In addition, spatial patterns of biodiversity level, of temporal variability, and of drift provide an extended context within which species-specific assessment models can be interpreted. Biodiversity values can have a consultative role in marine spatial planning (Olsen *et al.*, 2007; Douvère, 2008), e.g. when prioritize areas of low diversity for the establishment of wind-farms or oil-extraction platforms. Most current integrated ecosystem assessments are based on multivariate analyses conducted on time-series aggregated at large spatial scales (e.g. Choi *et al.*, 2005; Kenny *et al.*, 2009; Johannesen *et al.*, 2012b) and therefore miss or underestimate regional changes observed at the polygon level. The current work provides this spatially explicit description for biodiversity. Finally, the present biodiversity assessment can serve to derive indicators or ecosystem state in support to management, if biodiversity has been recognized as a priority target by management institutions (Levin *et al.*, 2009).

Conclusion

In the present study, we quantified biodiversity patterns in space and time in the Barents Sea over a 10-year period. This constitutes a biodiversity baseline against which future changes in biodiversity can be compared. We demonstrate how a single framework, associated with a suitable definition of spatial and temporal levels, can be used to quantify biodiversity and biodiversity changes across a set of nested spatio-temporal levels. We also show how this framework can be used to distinguish random changes in community structure from temporal drifts. The proposed methodology is general and can be applied to biodiversity assessment for other foodweb compartments in the Barents Sea, as well as in other large marine ecosystems.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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