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How do plankton species coexist in an apparently unstructured environment?

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Abstract

In a paper entitled the paradox of plankton, Hutchinson asked “*how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials*”. Particularly relevant for phytoplankton, this paradox was based on two implicit, and perhaps naive, postulates, i.e. (i) that all plankton species have similar requirements and (ii) that the marine environment is relatively homogeneous in space and time. A number of hypotheses, based on purely theoretical or experimental studies, have been proposed to solve this conundrum, ranging from spatio-temporal environmental heterogeneity to biotic chaotic variability. Here, we characterize the ecological niche of 117 plankton species belonging to three different taxonomic groups and show that all species have a niche sufficiently distinct to ensure coexistence in a structured marine environment. We also provide evidence that pelagic habitats are, unsurprisingly, more diverse in space and time than Hutchinson imagined, the marine environment being neither unstructured nor stable in space and time. We therefore conclude that the niche theory, and its corollary the principle of competitive exclusion, apply as much for the plankton as for other forms of life, be they terrestrial or marine.

1. Introduction

Marine plankton is composed of both uni- and multicellular organisms covering a wide range of size, from less than 0.2 μm (virioplankton) to a few meters (e.g. the giant jellyfish *Nemopilema nomurai*)[1]. They are at the basis of the food web and play a key role in carbon dioxide regulation, influencing the composition of the Earth's atmosphere [1–4]. The great diversity they exhibit has fascinated marine biologists for a long time [5–7] and it is now apparent that there is even more diversity than originally realised [8,9]. The mechanisms sustaining the plankton biodiversity remain debated, however, because it is assumed that plankton species coexist in an apparently homogeneous environment with few niches (*sensu* Hutchinson realised niche i.e. the set of environmental conditions modulated by biotic interactions, enabling a species to grow and reproduce [10]) thought to be available [11,12].

Although it has been suggested that plankton species may share niches and coexist [13], many theoretical and laboratory studies have tried to resolve the “paradox of the plankton”[11] and have shown that the number of coexisting plankton species at equilibrium in a community cannot exceed the number of limiting resources [14–17]. Consequently, coexistence of a large number of species on a small number of limiting resources is only possible when other mechanisms are involved such as (i) temporal heterogeneity (i.e. a continuously changing pelagic environment due to the seasonal changes in hydro-meteorological forcing) and its influence on the structure of the water column [11,18–20], (ii) spatial heterogeneity in the relative resource supply rate [21]), (iii) spatial subdivision [22], (iv) chaotic variations in species abundance induced by competition [23] or (v) difference in the array of resources limiting species growth [17,24]. The tenet that underlies the paradox of the plankton —that the plankton environment is unstructured and so different plankton share the same niche, and therefore the question of whether niche separation might promote plankton coexistence— has received little attention, however.

In this article, we examine how niche separation can enable plankton coexistence. Niche separation, which is often estimated by the degree of overlapping (i.e. the opposite of niche separation)[25], results from the principle of competitive exclusion [26,27]. By allowing a better exploitation of the available resources, this mechanism has been shown to enable terrestrial plant species coexistence [28,29]. Here, we examine the two postulates on which the paradox of the plankton is based, i.e. (i) do plankton species share niches and (ii) is the oceanic environment unstructured. To do so, we estimate the degree of niche overlapping of 117 plankton species belonging to three taxonomic groups (diatoms, dinoflagellates and calanoid copepods). We show that species' niches of the three taxonomic groups are well separated and that the environment is much more structured in space and time than Hutchinson envisioned [11]. We conclude that these two mechanisms jointly ensure plankton species coexistence.

2. Materials and Methods

(a) Biological data

Plankton abundance data came from the Continuous Plankton Recorder (CPR) survey (Supplementary Text S1)[30]. It is a long-term plankton monitoring programme using a high-speed plankton recorder sampling at a depth of ~7-10m. Started in 1931, the CPR programme has since sampled plankton on a monthly basis in the North Atlantic Ocean and its adjacent seas [31,32]. We used the data collected between 1998 and 2018 in the North Atlantic Ocean and its adjacent seas [33]. This time period was chosen because it corresponds to the period covered by the environmental datasets we used (see Sections b and c). Species that were found in less than 100 CPR samples were removed from the analysis so that the total number of species used was 117; this reflected abundance data for 71 phytoplankton (i.e. 45 diatoms and 26 dinoflagellates) and 46 calanoid copepod taxa.

(b) Environmental data

We used a set of nine different environmental variables to characterise the niches of the 117 species. The chosen variables were: bathymetry (in m), nitrate, phosphate and silicate concentrations (mmol.m^{-3}), Mixed Layer Depth (MLD, m), temperature ($^{\circ}\text{C}$), Photosynthetically Active Radiations (PAR, $\text{E.m}^{-2}.\text{day}^{-1}$), salinity (no unit) and chlorophyll-a concentration (mg.m^{-3}). Detail descriptions and references for each dataset are provided in Supplementary Text S2.

(c) Data pre-processing

We used the environmental data collected between 1998 and 2018 to work on a common time period with respect to all datasets. All data were subsequently arranged on a grid covering the North Atlantic Ocean (100°W - 10°E and 35°N - 65°N). By means of nearest-neighbour interpolation [34], we attributed to each CPR sample a value for each of the nine chosen environmental variables at a depth of 8 m (except for bathymetry), a value included in the range of sampling depth of the CPR instrument [30,31]. All the samples with a missing value along a single dimension were discarded prior to the analyses. We therefore used a total of 90,527 CPR samples.

(d) Niche separation

To characterise and compare the multidimensional niches of the 117 planktonic species, we used the recently proposed “species chromatogram” method [35,36]; this technique uses a chromatogram to display the multidimensional niche of a species in a two-dimensional space. To do so, p-standardised environmental gradients (one per environmental variable, e.g. temperature or nutrients), representing the p-niche environmental dimensions, are defined between 0 (the lowest value taken by an environmental variable) and 1 (the highest). Each gradient is divided into α equidistant categories (here $\alpha=50$ for all chromatograms). For each category along each dimension (i.e. gradient), the mean species abundance is estimated by averaging the values of the k% of the CPR samples (associated to that category by means of the nearest-neighbour interpolation, see the previous section) with the highest abundance values (here $k=5\%$), if at least m samples are present in that category (here $m=20$ CPR samples). The mean abundances along each dimension are then standardised between 0 and 1, and smoothed by means of a second-order simple moving average to alleviate the noise associated with the CPR data. Finally, the niche is displayed as an array of coloured cells, which is called a species chromatogram (Supplementary Figure S1-12)[36].

As each environmental gradient is globally standardised between 0 and 1, the niches of different species can be compared and a degree of niche overlapping (called index D) can be estimated among species [36]. This index is estimated by considering the categories with an abundance greater than or equal to a threshold T along each dimension, with $0 < T \leq 1$. They are then used to calculate the niche hypervolume, the shape of the niche being assimilated to a hyperrectangle. D is finally assessed for each pair of species by calculating the ratio of the hypervolume of the niche common to the two species on the total volume filled by the two species. The method is fully described in Kléparski & Beaugrand [36].

Here, D was estimated for each pair of plankton species and for each combination of 1 to p-environmental dimensions (i.e. 1 to p-dimensions considered simultaneously) and five thresholds T: 0, 0.1, 0.25, 0.5 and 0.75. For phytoplankton (i.e. diatoms and dinoflagellates), we chose eight environmental dimensions ($p=8$): bathymetry, nitrate, phosphate and silicate concentrations, MLD, temperature, PAR and salinity (Figure 1 and Supplementary Figure S1-8). For copepods, we used six dimensions ($p=6$): bathymetry, MLD, temperature, PAR, salinity and chlorophyll-a concentration (Figure 1 and Supplementary Figure S9-12). D was calculated among species belonging to the same taxonomic group, i.e. among diatoms (45 species), dinoflagellates (26 species), phytoplankton (45 diatoms + 26 dinoflagellates = 71 species) or calanoid copepods (46 species).

All species chromatograms on which index D is based are displayed in Supplementary Figures S1-12. We have synthesized the information of all species chromatograms by means of a community chromatogram [35,36]. To do so, species' abundance was first replaced by 1 when its standardised abundance was higher than or equal to 0.5 in a category [35](see Figure 1a-d). Then, we estimated the number of co-occurring species in each category of the chromatogram and we converted it into percentage. Therefore, a community chromatogram displays the percentage of co-occurring species in each environmental category.

(e) Habitat diversity

Habitat diversity of the pelagic environment was estimated with respect to each environmental variable (but bathymetry that is constant) by means of the Shannon entropy [37]. In other words, we quantified the diversity of values that is taken by an environmental variable for each day or in each geographical cell. To do so, eight environmental matrices (121 latitudes x 441 longitudes x 24 depth levels (except for MLD) x 7670 days) were used and standardised between 0 (i.e. the lowest value of an environmental variable at the scale of the North Atlantic) and 1 (i.e. the highest). The environmental values taken by each matrix were then divided into 50 categories and the habitat diversity $H(S)$ (expressed in bit) was calculated as follows:

$$H(S) = -\sum_{i=1}^{50} S_i \times \log_2(S_i) \quad (1)$$

With S_i the probability that the value of the i^{th} category was observed, i.e. its relative frequency. The estimate of the Shannon entropy was performed in two ways for each year between 1998 and 2018: (i) at a daily scale using all geographical cells and depth levels between 0 and 20 m and (ii) at a spatial scale using all the days and depth levels between 0 and 20m. The resulting annual cycles were then averaged (1998-2018).

3. Results

(a) Niche separation

Species chromatograms are all displayed in Supplementary Figure S1-12. Their examination revealed that each species has a unique chromatogram and therefore a specific niche, although many overlaps were observed along all niche dimensions. The species chromatograms were summarised by taxonomic group under the form of a community chromatogram, where species abundance was

replaced by the percentage of co-occurring species in an environmental category (Figure 1a-d). At this organisational level, niche separation occurred between diatoms and dinoflagellates along five niche dimensions (bathymetry, silicate, temperature, PAR and salinity; Figure 1b-c). Similarly, a clear niche separation can be seen between phytoplankton and copepods with respect to salinity, although the two groups have overlapping chromatograms for bathymetry, temperature and PAR (Figure 1a and d). Hence, each group seems to have distinct environmental requirements, although niche overlaps are the rule.

The calculation of the degree of niche overlapping (i.e. Index D) confirmed that species niches were rapidly separated when the number of environmental dimensions of the niche rose (Figure 1e-h). Niche overlapping diminished rapidly below 30% for the four taxonomic groups (Figure 1e-h). We therefore investigated whether T (i.e. the threshold of abundance between 0 and 1) influenced our perception of niche separation. When T increased from 0 to 0.75, overlapping rapidly reached a value below 20% and even close to 0% when T becomes higher than 0.25. Consequently, the niches of the four groups were almost totally separated towards the optimal part of their niche (i.e. the part of the niche where a species has its highest abundance [38,39]), although some overlapping was still observed in the suboptimal parts (i.e. the parts where a species has low abundance, i.e. when $T < 0.25$) (Figure 1e-h), as might be the expected outcome of competition and natural selection [40].

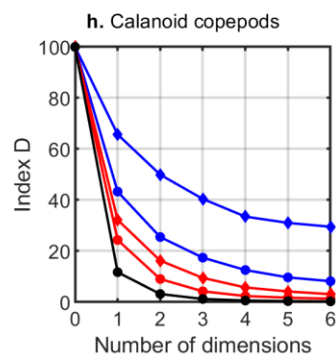
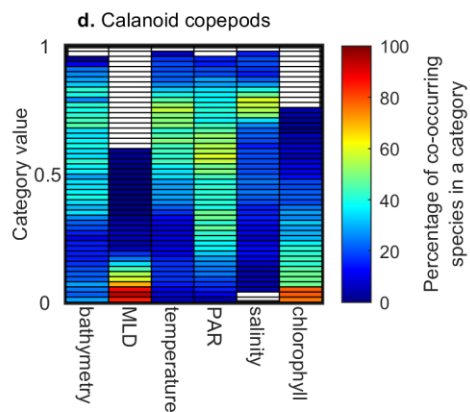
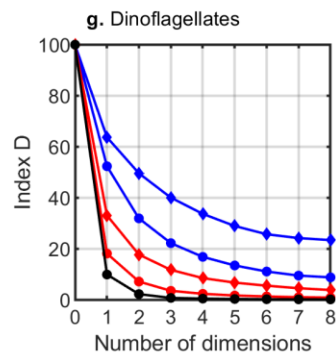
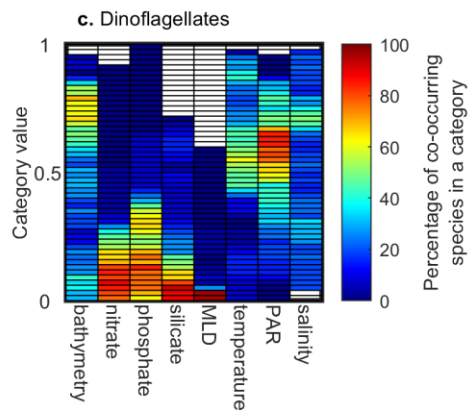
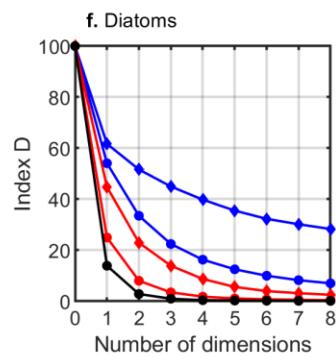
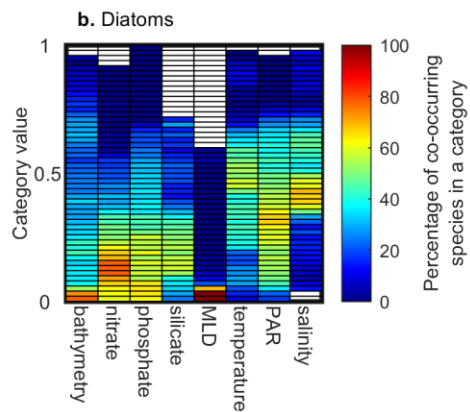
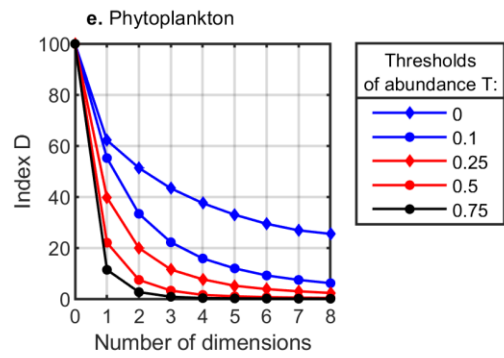
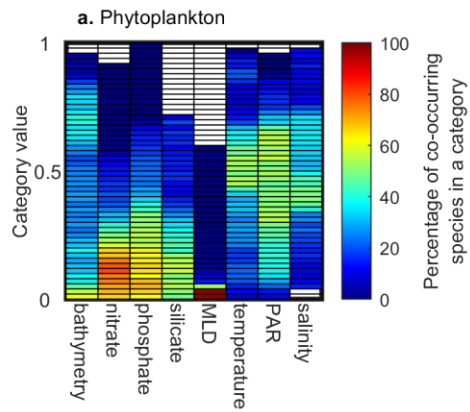


Figure 1. Community chromatograms and changes in the degree of niche overlapping for four groups of plankton. Community chromatogram of (a) phytoplankton, (b) diatoms, (c) dinoflagellates and (d) calanoid copepods. In a-d each column represents an environmental dimension. The Y axis corresponds to the 50 environmental categories standardised between 0 and 1, i.e. it represents all the values taken by an environmental variable from the lowest (bottom category) to the highest (top category). Colours denote the percentage of co-occurring species in each category. High co-occurrence values are in red and low values in blue. Categories where no CPR samples are available are shown in white. Panels e-f represent the changes in the degree of niche overlapping for (e) phytoplankton, (f) diatoms, (g) dinoflagellates and (h) calanoid copepods. Niche overlapping has been estimated by means of a species chromatogram (i.e. index D, M&M section). Overlapping was assessed by considering simultaneously an increasing number of environmental dimensions, from 1 to 8 for phytoplankton, diatoms and dinoflagellates, and from 1 to 6 for calanoid copepods. Overlapping among species was based on five thresholds of abundance $T=0$ (blue lines with diamond), 0.1 (blue lines with dot), 0.25 (red lines with diamond), 0.5 (red lines with dot) and 0.75 (black lines with dot).

(b) Habitat diversity

We quantified habitat diversity in the North Atlantic Ocean by means of the Shannon entropy. The analysis was performed in two ways. First, based on different depth levels (0-20 m) for all geographical cells of the North Atlantic, we found two different daily patterns in habitat diversity: the first pattern revealed higher diversity with respect to nutrients, MLD and chlorophyll-a in Spring (plots in Figure 2a, b, e, f and h) and the second pattern revealed high diversity in Summer for temperature, salinity and PAR (plots in Figure 2c, d and g). Second, based on depth levels (0-20m) and days, we identified spatial patterns in habitat diversity. High diversity was found in the northern parts of the North Atlantic Ocean for nutrients, MLD and chlorophyll-a (maps in Figure 2 a, b, e, f and h) whereas high habitat diversity was found along continental shelves and in the southern part of the North Atlantic Ocean for temperature and salinity (maps in Figure 2c-d). PAR showed high habitat diversity everywhere in the North Atlantic (Figure 2g). Our results therefore confirm that not only the environment is diverse in space and time but that it is also highly impermanent at the same scales (Figure 2).

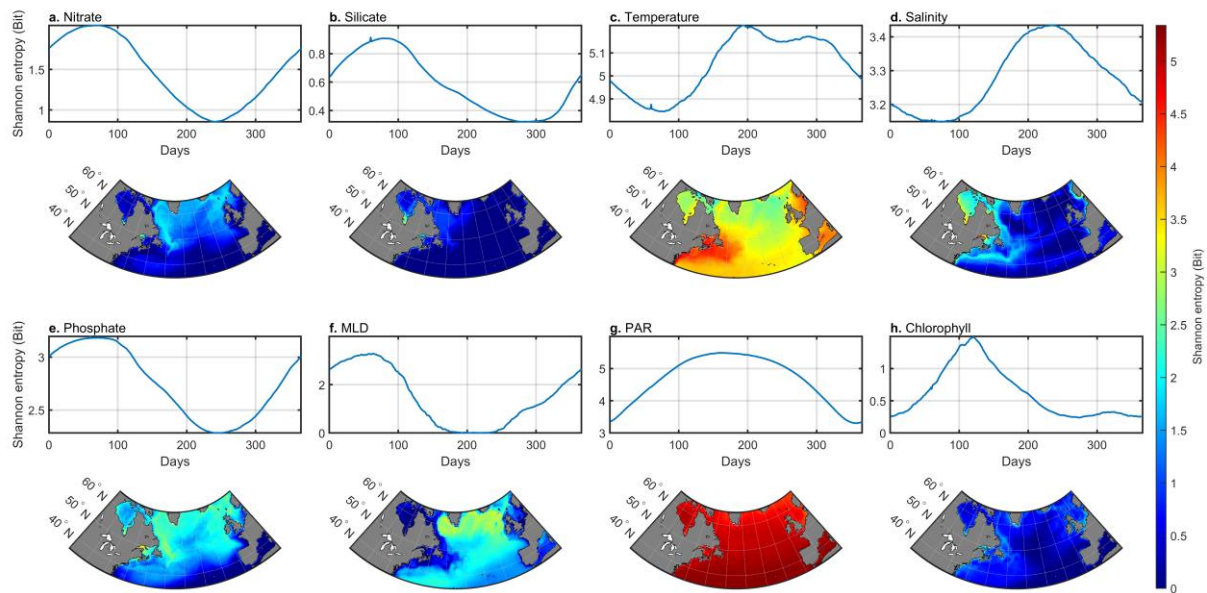


Figure 2. Habitat diversity in the North Atlantic Ocean. Habitat diversity for (a) nitrate, (b) silicate, (c) temperature, (d) salinity, (e) phosphate, (f) MLD, (g) PAR and (h) chlorophyll-a. Changes in temporal diversity are shown by the plots and changes in spatial diversity by the maps below the plots. Habitat diversity was assessed by means of the Shannon entropy estimated on the annual changes of each environmental variable (see M&M section). High values of Shannon entropy (red colour in the maps) mean that habitats diversity is high and low values (blue colour in the maps) that habitat diversity is small.

4. Discussion

It is known that diatoms and dinoflagellates have distinct environmental requirements [41]. Here, our results are going farther and show that the niches of both phyto and zooplankton species rapidly separate when the number of niche dimensions rises (Figure 1). They also demonstrate that the pelagic environment is not only diverse but also impermanent in space and time (Figure 2), a result that has been shown by many studies since the original paper of Hutchinson [42–44]. Therefore, the two implicit postulates on which the Hutchinson’s paradox was based are incorrect. High niche differentiation leads species to have a unique combination of environmental conditions (i.e. a unique niche) where their performances in terms of growth and reproduction are optimal [28]. Therefore, each species covers a part of the multidimensional environmental space and the segregation along various environmental niche dimensions enables them to coexist in space and time, a mechanism that has been suggested to enable terrestrial plant coexistence [28,29]. Furthermore, we have shown that niche separation can occur along a single unique dimension in a multivariable space. For example, two phytoplankton species may still coexist if they share the same niche for a nutrient but utilise a different

light wavelengths [45]. In other words, to simply resolve the plankton paradox we just need to fully understand marine environmental heterogeneity as it applies to the plankton.

Because of the duality between the niche space and the real physical space (i.e. Hutchinson's duality [46]), niche separation (Figure 1) can be related with the diversity of habitats we have observed (Figure 2). Environmental variability is an important mechanism known to promote species coexistence because of a mechanism known as the "storage effect" [47,48]. This mechanism has three requirements: (i) the species of a given community have to develop strategies to survive during unfavourable environmental conditions, (ii) these species have distinct responses to environmental variability (i.e. distinct niches) and (iii) this variability affects competition, meaning that the niche-environment interaction modulates competition (i.e. a species is more resistant to competition when its environment is more in adequation with its niche and inversely)[49,50].

Expectedly, niche separation is maximal at the optimal part of a species' niche (Figure 1e-h). Therefore, this separation alleviates competition and prevents competitive exclusion. Niche separation takes place through evolution via an alteration in life history strategies. Plankton have developed various strategies, like the development of pigments, cysts, spores, resting eggs or lipidic bags, that enable them to survive during adverse environmental conditions [51–55]. Some strategies (e.g. diatom morphological traits) even explain phenology and annual plankton succession [56,57]. Our study therefore shows that the niche theory, and its corollary the principle of competitive exclusion, applies for the plankton as for other groups, be they terrestrial or marine.

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389 **Data availability**

390

391 All the data used in this article are already freely available (see the M&M section and Supplementary
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393

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399

400 **Conflict of interest**

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402 The authors declare no conflict of interest.