Global patterns of planktonic diversity are mainly determined by the dispersal of propagules with ocean currents. However, the role that abundance and body size play in determining spatial patterns of diversity remains unclear. Here we analyse spatial community structure - β-diversity - for several planktonic and nektonic organisms from prokaryotes to small mesopelagic fishes collected during the Malaspina 2010 Expedition. β-diversity was compared to surface ocean transit times derived from a global circulation model, revealing a significant negative relationship that is stronger than environmental differences. Estimated dispersal scales for different groups show a negative correlation with body size, where less abundant large-bodied communities have significantly shorter dispersal scales and larger species spatial turnover rates than more abundant small-bodied plankton. Our results confirm that the dispersal scale of planktonic and micro-nektonic organisms is determined by local abundance, which scales with body size, ultimately setting global spatial patterns of diversity.
The oceans represent the largest continuous environment on Earth. Over long timescales, all marine ecosystems are connected to each other by ocean currents. However, biological connectivity, or the exchange of individuals across geographically separated subpopulations, is not uniform as there exist barriers to dispersal. Such barriers include not only land masses, but also persistent frontal features at a range of spatial scales, sharp environmental gradients, and other oceanographic features. Further, dispersal along ocean currents and the effect of these 'physical barriers' varies across taxa. In particular, as seen in terrestrial examples, differences in body size and abundance amongst taxa are hypothesized to play a major role in determining both the distributional patterns and the scale of dispersal for marine planktonic species. In order to understand how marine biodiversity is maintained locally and structured spatially, it is therefore necessary to investigate the relationship between planktonic dispersal, body size, and local abundance.

The shift in species composition among locations, or β-diversity, is strongly influenced by environmental heterogeneity and seascapes, such as differences in temperature or geographic distance. The scale-dependence of β-diversity can be described as a 'distance-decay' rate, measured as the slope of a linear relationship between the logarithm of community similarity and the logarithm of geographic distance among pairs of sites. In both oceanic and terrestrial ecological communities, distance-decay patterns are set by three major mechanisms: (1) local niche-based processes, which are summarized by the statement that, below 1-mm body size, “everything is everywhere, but the environment selects”; (2) the effects of dispersal limitation, as hypothesized by the neutral theory of biodiversity; and (3) the spatial configuration of the seascapes, which can also dictate the rate at which organisms disperse among sites. It is a major challenge to elucidate which of these mechanisms is dominant for any given ecological community, since differences in key environmental characteristics are often strongly correlated with geographic distance. Indeed, while distance-decay patterns have been observed for specific taxa in terrestrial e.g., rainforest trees, freshwater (e.g., aquatic beetles; fish and macroinvertebrates), and marine communities (e.g., coral reefs; marine bacteria and prokaryotes; and macrobenthos and plankton), few studies have identified a robust distance-decay pattern across taxa or across key physiological traits, such as body size.

Body size is the dominant physiological factor determining individual metabolic rates and, according to the metabolic theory of ecology, it also controls numerous ecological processes. For example, smaller organisms have higher metabolic rates, faster growth rates, shorter generation times, and higher energy needs relative to larger organisms. Small organisms are generally more abundant, in terms of population density, than larger organisms. This means that smaller organisms are expected to have lower local extinction rates and, therefore, reduced demographic stochasticity and ecological drift compared to larger organisms. Importantly, among smaller, mostly passively dispersed taxa, body size is expected to be inversely correlated with the spatial scale of dispersal. In fact, dispersal limitation has been hypothesized to increase with body size in planktonic communities. In the oceans, therefore, smaller planktonic organisms, which are relatively more abundant, are expected to disperse farther with oceanic currents, leading to shallower distance-decay slopes than those of larger planktonic organisms.

Here we have quantified empirically derived distance-decay slopes and measured dispersal scales for a number of planktonic and micro-nektonic organisms, spanning a wide range of body sizes and abundances, from prokaryotes to small mesopelagic fishes. With these analyses, we have tested the hypothesized size-dependence of community dispersal scales and resulting spatial patterns of regional connectivity. To do so, we first explored the importance of surface ocean transit times, derived from previous Lagrangian particle simulations, in explaining spatial patterns of β-diversity for each biological group, accounting for the relative contribution of environmental filtering. Since β-diversity is controlled by surface ocean transit time, we then used the distance-decay slopes of each biological group to infer the community dispersal scale as a proxy of distribution range (sensu biogeography). These analyses are based on samples of pelagic communities collected across the subtropical and tropical ocean during the Malaspina 2010 Circumnavigation Expedition. Our results show that the species composition of plankton and micro-nekton communities in tropical and subtropical open ocean is in large part determined by oceanic currents. Given this finding, we also explored the dispersal scale of each biological group and found a negative relationship between dispersal scale and body size: less abundant large-bodied plankton and micro-nekton communities in near-surface epipelagic waters show significantly shorter dispersal scales and larger spatial species-turnover rates compared to more abundant small-bodied plankton.

Results

Community assembly contributors. We find that the relative influence of surface ocean transit times and differences in environmental factors on plankton and micro-nekton community structure vary among groups (Mantel tests Table 1, Supplementary Fig. 1). For example, planktonic community β-diversity is significantly correlated with surface ocean transit times in all groups, explaining on average 22% of the variance (Table 1). Correlations with environmental distances are only significant for Cercozoa and myctophids, explaining 6–8% of the variance. In these two groups, the correlation between β-diversity and surface ocean transit times remains significant after controlling for environmental factors (Table 1). We also find low-shared covariation between environmental distance and surface ocean transit times, indicative of the low-spatial autocorrelation in oceanic factors. In fact, the correlation between the surface ocean transit times and the environmental distance among the all pair sites is rather weak (Mantel \( r = 0.09 \), Supplementary Table 1). A large fraction of the β-diversity variance remains unexplained by the selected explanatory factors (multiple regression on distance matrices, Table 1). This finding reflects the complexity of interacting mechanisms controlling spatial community assembly in the oceans. In addition, we find no relationship between the relative contribution of environmental drivers and body size (non-parametric bootstrap, \( p \)-value > 0.05, Supplementary Table 2).

Community dispersal scales and spatial turnover. The significant negative relationship observed between oceanic transit times and β-diversity for planktonic and micro-nektonic organisms, more so than environmental distance, let us estimate community dispersal scales and spatial species turnover rates. The former is determined by means of the halving-time, that is, the oceanic transit time at which species similarity halves; the latter comes from the slope of the distance-decay relationship for each group (Methods section; Fig. 1 and Table 2). In addition to the Mantel tests, the distance-decay slopes and the community similarity halving-times reinforce the result that community similarity decreases with the logarithm of surface ocean transit times (Fig. 1, Supplementary Fig. 2). For example, prokaryotes...
3.5 × 10−160 m 133 0.21** 0.04 — — 0.21** — — 0.12*

Mesozooplankton 0–200 m 36 0.40** Not available — Not available 0.40** — —

Gelatinous zooplankton 61 0.11** 0.04 — — 0.11** — —

Macrozooplankton 65 0.23** 0.05 — — 0.27** — —

Myctophids 95 0.32** 0.08** 0.20** 0.32** 0.30** 0.04 0.20** 0.32**

| Biological groups | Mantel correlation | | | | Mantel partial correlation | | | |
| --- | --- | --- | --- | | | | --- | --- | |
| | N pairs | Ocean transit time | Environmental distance | | Ocean transit time partialling out environmental distance | | Ocean transit time + environmental distance | | |
| Prokaryotes | 120 | 0.28** | 0.02 | | — | 0.29** | | |
| Small heterotrophic flagellates | 112 | 0.30** | 0.04 | | — | 0.31** | | |
| Green algae | 112 | 0.27** | 0.04 | | — | 0.28** | | |
| Fungi | 89 | 0.13** | 0.02 | | — | 0.13** | | |
| Microbial eukaryotes ALL | 112 | 0.24** | 0.005 | | — | 0.24** | | |
| Parasites | 112 | 0.23** | 0.002 | | — | 0.23** | | |
| Cercozoa | 107 | 0.10** | 0.06 | | 0.07** | 0.12** | | |
| Large flagellates | 112 | 0.19** | 0.08 | | — | 0.22** | | |
| Coccolithophores 0-160 m | 133 | 0.28** | 0.01 | | — | 0.28** | | |
| Diatoms 0-160 m | 133 | 0.21** | 0.02 | | — | 0.22** | | |
| Diatoms surface | 93 | 0.17** | 0.04 | | — | 0.18** | | |
| Dinoflagellates 0-160 m | 133 | 0.21** | 0.004 | | — | 0.21** | | |
| Dinoflagellates surface | 112 | 0.11** | 0.04 | | — | 0.12* | | |
| Mesozooplankton 0–200 m | 36 | 0.40** | Not available | | — | Not available | | |
| Gelatinous zooplankton | 61 | 0.11** | 0.04 | | — | 0.11** | | |
| Macrozooplankton | 65 | 0.23** | 0.05 | | — | 0.27** | | |
| Myctophids | 95 | 0.32** | 0.08** | | 0.20** | 0.32** | | |

Mantel correlations and Multiple Regression on distance Matrices (MRM) between β-diversity (i.e., community variation in space), environmental distance, and pair-site ocean transit times; and Mantel partial correlations after controlling for the effects of environmental distance, in statistically significant cases. N pairs: number of pair-sites considered at each group. The statistical significance of comparisons is assessed using Mantel and partial Mantel tests based on Pearson’s product moment correlation using 9999 permutations.

*p-value ≤0.05, **p-value ≤0.01

and microbial eukaryotes exhibit very long halving-times: 5094 and 866 years, respectively. In contrast, gelatinous zooplankton (15.5 years), myctophids (1 year) and macrozooplankton (2 years) show the shortest halving-times (Table 2). Likewise, the time-decay slopes are highest for large-sized groups, such as myctophids (−0.0807), macrozooplankton (−0.0657), and gelatinous zooplankton (−0.0336) (Fig. 1a, Table 2). Myctophids and macrozooplankton show very high initial similarity between neighboring stations, denoting a high-spatial dependence in community structure compared to smaller organisms (Fig. 1a, Table 2). In contrast, the shallow time-decay slopes and long halving-times of prokaryotes and microbial eukaryotes indicate globally mixed distributions for these groups (Fig. 1a, b). These groups of small organisms show the highest local abundance values (prokaryotes = 3.30 × 1011 ± 4.10 × 1010 ind. m−3; microbial eukaryotes = 1.72 × 109 ± 1.49 × 108 ind. m−3), 8–10 orders of magnitude more abundant than larger organisms (macrozooplankton = 1.79 × 107 ± 2.5 × 106 ind. m−3; myctophids = 3.5 × 103 ± 1.9 × 102 ind. m−3) (Table 3). The hypothesized size-dependence of dispersal in planktonic and micro-nektonic organisms is supported by a significant negative log-log relationship between the organism size and halving-time and time-decay slope (Fig. 2, Table 4). As expected, we also find a strong significant negative correlation between the organism’s body size and its local abundance (r² = 0.93; p-value <0.001) (Fig. 3c), as well as a significant positive log-log relationship between the local abundance and halving-time and time-decay slope (Fig. 3a, b, Table 4).
groups, such as surface dinoflagellates, community similarity is never less than half of the initial similarity, even for stations located far apart. As such, the halving-time is a relative indicator, or proxy, of community dispersal scale, and should not be interpreted as an absolute value of the transit time that operates among the sub-communities. Therefore, communities of small organisms (body size < 2 mm) and high-local abundance are likely to have a panmictic worldwide distribution. On the other hand, larger-sized organisms exhibit stronger spatial patterning and need only a few decades of surface ocean transit time, ~20 years at most, to halve their initial similarity. This means that for these large-sized organisms, species will be similar at geographically proximate locations, and dissimilar between distant locations. These results highlight that patterns of β-diversity in open-ocean in planktonic and micro-nektonic organisms are size-dependent. In order to explain the underlying process of this empirical finding, we have identified a significant positive relationship between the local abundance and the community dispersal scales. This was expected since local abundance scales negatively with body size, as confirmed in our data. Moreover, generation time also scales negatively with body size. Locally abundant species are exposed to lower local extinction rates and hence, reduced demographic stochasticity and ecological drift. Therefore, we suggest that large population
In contrast, larger planktonic organisms generally have longer generation times and smaller population densities, and are therefore more sensitive to local extinctions and ecological drift, resulting in stronger spatial structure. In addition, lower sinking rates and relatively weak spatial structure of these organisms explains little of the observed spatial variation in community structure in both plankton and micro-nekton groups. This evidence of dispersal limitation for myctophids is likely a result of their migration patterns being mostly vertical (rather than horizontal), as they move daily between the mesopelagic and epipelagic zones. In contrast, numerous marine megafauna, such as large pelagic fish and marine mammals, actively move horizontally, either to forage for food or to complete long-distance migration. Indeed, previous research has demonstrated a positive relationship between dispersal distance and body size for such megafauna. For myctophids, horizontal movement occurs predominantly as larvae, with passive transport by ocean currents in epipelagic waters. The observed similarity in dispersal patterns of myctophids and macrozooplankton may thus arise from the same processes: passive horizontal dispersion of

densities and short generation times of micro-planktonic organisms are the mechanisms explaining the larger geographic range and relatively weak spatial structure of these organisms. In contrast, larger planktonic organisms generally have longer generation times and smaller population densities, and are therefore more sensitive to local extinctions and ecological drift, resulting in stronger spatial structure. In addition, lower sinking losses and longer survival times of resting stages of small passively dispersed plankton (from prokaryotes to phytoplankton) allow their populations to travel greater distances than large-sized plankton.

In our study, the environment, through environmental species sorting, explains little of the observed spatial variation in community structure in both plankton and micro-nekton groups. There are multiple plausible explanations for this finding. First, the Malaspina sampling was restricted to tropical and subtropical regions and took place in summertime, when horizontal environmental gradients are typically low at surface. As a result, it is difficult to capture assemblage variations due to climate. Second, the presence-absence indices that we used are less sensitive compared to relative abundances. We anticipate that the latter indice would potentially identify a stronger relationship in both small and large-sized plankton and micro-nekton with environmental gradients. Other potential reasons might stem from the other environmental variables not measured in our study, and the exclusion of biotic variables, which might play a role driving spatial distribution, particularly in large planktonic taxa. Finally, marine microbial communities are mainly dispersed by advection and diffusion. These, together with their relatively high niche plasticity compared to the plasticity of larger-bodied taxa, results in microbes showing broad spatial distributions. However, our results do not identify low niche plasticity in large-bodied taxa, and we observe no significant relationship between organism body size and environmental variability. This is in line with a recent meta-analysis by Soininen, that concluded that body size and environmental species sorting are not significantly related in a data set spanning a range in body size of up to 12 orders of magnitude. This apparent contradiction in thinking and evidence highlights the need for further research on the strength of environmental species sorting among organisms of different size.

In addition to passively dispersed planktonic organisms, we also analysed connectivity in myctophid fish communities (micro-nekton), which are active swimmers. The myctophid group showed short dispersal scales and a steep distance-decay slope comparable with those of other large-bodied passive dispersers (i.e., gelatinous zooplankton and macrozooplankton). This evidence of dispersal limitation for myctophids is likely a result of their migration patterns being mostly vertical (rather than horizontal), as they move daily between the mesopelagic and epipelagic zones. In contrast, numerous marine megafauna, such as large pelagic fish and marine mammals, actively move horizontally, either to forage for food or to complete long-distance migration. Indeed, previous research has demonstrated a positive relationship between dispersal distance and body size for such megafauna. For myctophids, horizontal movement occurs predominantly as larvae, with passive transport by ocean currents in epipelagic waters. The observed similarity in dispersal patterns of myctophids and macrozooplankton may thus arise from the same processes: passive horizontal dispersion of

| Biological groups | Logarithmic decay between species similarity and surface ocean transit time | Size range (mm) | Size mean (mm) | Sampling depth (m) | Habitat |
|-------------------|-------------------------------|-----------------|----------------|-------------------|--------|
|                   | Slope (c) | $S_0$ | HT (years) |                  |        |
| Prokaryotes       | -0.0232** | 0.52 | 5094  | 0.0003-0.001 | 0.0005 | 0 | E |
| Small heterotrophic flagellates | -0.0231** | 0.34 | 56  | 0.0008-0.003 | 0.002 | 0 | E |
| Green algae       | -0.0222** | 0.24 | 5  | 0.0008-0.003 | 0.0025 | 0 | E |
| Fungi             | -0.0194** | 0.16 | 3  | 0.0008-0.003 | 0.003 | 0 | E |
| Microbial eukaryotes all | -0.0102** | 0.22 | 866 | 0.0008-0.003 | 0.002 | 0 | E |
| Parasites         | -0.0100** | 0.22 | 802 | 0.0008-0.003 | 0.004 | 0 | E |
| Cercozoa          | -0.0121** | 0.12 | 12.5 | 0.0008-0.003 | 0.005 | 0 | E |
| Large flagellates | -0.0181** | 0.39 | 1215 | 0.0008-0.003 | 0.006 | 0 | E |
| Coccolithophores 0-160 m | -0.0341** | 0.52 | 198 | 0.002-0.5 | 0.0142 | 0-160 | E |
| Diatoms 0-160 m   | -0.0275** | 0.27 | 158 | 0.002-0.4 | 0.033 | 0-160 | E |
| Diatoms surface   | -0.0206** | 0.17 | 1 | 0.002-0.4 | 0.033 | 0 | E |
| Dinoflagellates 0-160 m | -0.0156** | 0.35 | 7325 | 0.002-0.5 | 0.043 | 0-160 | E |
| Dinoflagellates surface | -0.0046** | 0.19 | 14,931,726 | 0.008-0.003 | 0.043 | 0 | E |
| Mesozooplankton 0-200 m | -0.0135** | 0.16 | 18 | 0.3-5 | 2.65 | 0-200 | E |
| Gelatinous zooplankton | -0.0336** | 0.38 | 15.5 | >5 | 5 | 0 | N |
| Macrozooplankton  | -0.0657** | 0.55 | 2 | 4-15 | 5.41 | 0 | N |
| Myctophids        | -0.0807** | 0.47 | 1 | 20-110 | 35 | 0 | M&N |

| Mean biological groups | Abundance ± SD (ind. m⁻³) |
|------------------------|---------------------------|
| Prokaryotes            | $3.30 \times 10^{11} \pm 4.10 \times 10^{10}$ |
| Microbial eukaryotes all | $1.72 \times 10^{9} \pm 1.49 \times 10^{9}$ |
| Coccolithophores 0-160 m | $8.08 \times 10^{6} \pm 7.60 \times 10^{6}$ |
| Diatoms 0-160 m | $7.16 \times 10^{6} \pm 1.30 \times 10^{6}$ |
| Dinoflagellates 0-160 m | $2.80 \times 10^{6} \pm 1.80 \times 10^{6}$ |
| Mesozooplankton surface | $6.00 \times 10^{3} \pm 1.09 \times 10^{4}$ |
| Gelatinous zooplankton | $0.04235 \pm 1.49 \times 10^{9}$ |
| Macrozooplankton | $0.179 \pm 0.251$ |
| Myctophids             | $0.0035 \pm 0.0193$ |

Mean abundance and standard deviation (ind. m⁻³) of main biological groups (microbial eukaryotes subgroup abundance is not determined).
larvae, with movement as juvenile and adults mainly devoted to diel vertical behavior. It is worth noting that contradictory results have been found in a study by Jenkins et al., whose findings suggested that body size controls the dispersal of active dispersers, but not of passive dispersers like planktonic organisms. However, this study did not characterize the full range of body sizes that we have studied, and therefore is limited in its scope. Our data support the existing understanding that β-diversity in the pelagic domain increases with body size in small and mainly passive organisms but decreases in actively mobile larger taxa (pelagic fishes, cetaceans), because high-dispersal capacity reduces compositional differences between sites. Furthermore, given that the community dispersal scale defined here is a good proxy for the geographic range of a particular community, it seems that the local abundance of the species from an ecological guild relates positively to their geographic range in plankton, similar to many other groups from marine and terrestrial domains, including both passively and actively dispersing species.

The spatial distribution of community similarity, identified using hierarchical clustering, revealed distinct size-dependent spatial patterns. In particular, we identified large-scale frontal zones as areas of low β-diversity in the case of mesozooplankton and especially myctophid fishes. These frontal zones act as barriers separating subtropical gyres and are typically areas of relatively high-primary production. Limited dispersal between distinct pelagic provinces has been shown to play a major role in plankton population differentiation, and in the creation of strong genetic breaks and enhanced diversity in bridging regions. Another interesting conclusion drawn from these network maps is that modeling results of global ocean transit times indicate that the Atlantic Ocean is less connected than are the Pacific and Indian Oceans. This is mirrored in the spatial clustering of...
Methods

key determinants of global patterns of biodiversity in marine more abundant micro-plankton groups. Together, these results scales and higher species spatial turnover rates when compared to migrating mesopelagic myctophid shes (Supplementary Table 3). In this paper, we focus on the northern and southern hemisphere. Samples included pelagic communities (~0.0003 – 0.001 mm) and small microbial eukaryotes (~0.0008 – 0.003 mm), large microbial eukaryotes (i.e., phytoplankton (~0.002 – 0.5 mm), surface mesozooplankton (~0.2 – 3 mm) and epipelagic mesozooplankton (~0.3 – 5 mm), macrozooplankton (~4 – 15 mm), gelatinous zooplankton (>5 mm), and myctophid fishes (20–110 mm) (Supplementary Table 3). In this paper, we focus on the neuston, epipelagic, and neuston-migrating mesopelagic communities. Neuston planktonic organisms found in our data, particularly in myctophids and macrozooplankton, where a set of unique clusters are only seen in the Atlantic Ocean (orange-color stations), and another set of unique clusters (pink and dark-orange stations) only in the Pacific and Indian Oceans.

In summary, we have shown that planktonic and micro-
nektonic β-diversity declines logarithmically with surface ocean transit times, and that dispersal limitation is a more powerful determinant of community structure than is niche segregation in transient communities include mesozooplankton (epipelagic), phytoplankton divided as diatoms, coccolithophores and dinoflagellates, and prokaryotes and small microbial eukaryotes living in the first 200 m of the water column. Mesopelagic communities include myctophid fishes found in the neuston layers during their nightly migration (Supplementary Table 3). At each sampling location, ~12 L of seawater was used to determine the composition of microbial communities (marine prokaryotes and small microbial eukaryotes). Water samples were pre-filtered through a 200 μm mesh to remove large plankton, followed by sequential filtration, involving filtering the sample through a 20-μm Nylon mesh followed by a 3 μm pore-size polycarbonate filter (Poretics), and finally through a 0.2 mm polycarbonate filter (Poretics) using a peristaltic pump (MasterFlex 7535-89 with cartridges Easy Load II 77200-62, Cole-Parmer Instrument Company) to collect the prokaryotes and small eukaryotes (size fraction: 0.0003 – 0.001 mm). The filters were then flash-frozen in liquid N2 and stored at ~80°C until DNA extraction. Water samples for nano- and micro-
autotrophic plankton (for simplicity, hereafter ‘phytoplankton’) determination were taken from surface waters (3 m) using a 30 L Niskin bottle, and from the depth receiving 20% of the light (PAR) incident just below the surface, and the depth of the chlorophyll maximum, using a Rosette sampler system fitted with 24, 10 L Niskin bottles and a SeaBird CTD sensor. The water was introduced in glass bottles that were hermetically capped after fixation with hexamine-buffered formaldehyde solution (4% final formalin concentration) (<9). Gelatinous zooplankton, macrozooplankton, surface mesozooplankton and myctophid fish were sampled using a neuston sampler (80 cm wide, 30 cm high) fitted with a 200 μm mesh size, towed at 2–3 knots during 10–15 min at a depth of 15 cm and a distance of 5 m from the starboard side of the hull (<5). Deeper mesozooplankton communities (0–200 m) were sampled with a multi-net (300–5000 μm mesh size).

Species identification. Traditional taxonomy approaches were used to identify species of phytoplankton (<9), gelatinous zooplankton (<9), surface mesozooplankton, and juvenile and adult stages of myctophids (<9) (Supplementary Table 3). For phytoplankton examination, 100 ml aliquots of sample were settled in composite

### Table 4

| Main biological groups (n = 9) | Confidence interval | p-value | RMSE | Adjusted $\beta^2$ | Equation | Statistic | Parametric model | Bootstrap |
|-------------------------------|--------------------|--------|------|----------------|----------|-----------|----------------|----------|
| Ln (HT) vs Ln (size)          |                    |        |      |                |          |           |                |          |
| p-value                       | 0.001              |        | 1.542| 0.767          | $y = 9.093 - 0.724x$ |           |                | (-1.067, -0.715) |
| Ln (time-decay slope) vs Ln (size) | Linear regression equation | 0.050 | 0.020 | 0.363 | $y = -0.042 - 0.004x$ |           |                | (-1.180, -0.236) |
| Ln (HT) vs Ln (abundance)    |                    |        |      |                |          |           |                |          |
| p-value                       | 0.001              |        | 1.547| 0.766          | $y = 7.892 + 0.248x$ |           |                | (0.727, 1.057) |
| Ln (time-decay slope) vs Ln (abundance) |                | 0.222 | 0.018 | 0.487 | $y = -0.051 + 0.001x$ |           |                | (<0.001) |

### All biological groups (n = 16)

| Ln (HT) vs Ln (size)          |                    |        |      |                |          |           |                |          |
| p-value                       | 0.230              |        | 4.199| 0.037          | $y = 9.223 - 0.406x$ |           |                | (>0.709, 0.100) |
| Ln (time-decay slope) vs Ln (size) |                | 0.005 | 0.016 | 0.406 | $y = -0.040 - 0.004x$ |           |                | (>0.252) |

Evaluation of the log-log relationship between (i) group size vs halving-time (HT) and time-decay slope, and between (ii) local abundance vs halving-time and time-decay slope in main- and all biological groups. The table shows parametric models (all observations included) and non-parametric bootstrap cross-validations (95% confidence interval).

Ln: Napierian logarithm. RMSE: root mean square error.

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samples and observed under an inverted microscope, following the Utermöhl method. At least two transects of the chamber bottom were examined under high magnification (×312) to count the smaller cells, and the whole chamber bottom was scanned at ×125 to enumerate the larger, less frequent forms. Large phytoplankton (dinoflagellates, diatoms and coccolithophores) were identified using inverted microscopy to species level when possible. However, some taxa could only be identified to genus (e.g., Thalassiosira spp.) or to more general categories like ‘Small dinoflagellates’ or ‘Small coccolithophores’. Gelatinous zooplankton were identified combining morphological taxonomical approaches and high-resolution photography (Supplementary Table 3). The use of molecular approaches in gelatinous zooplankton has many gaps, and the most common markers used in techniques, such as DNA barcoding like COI or ITS are often not useful in resolving all gelatinous phyla. We confirmed some morphological identifications using mainly DNA barcode with COI as molecular marker. However, in groups like Ctenophora or in thaliaceans the identification approach was based solely on morphology because the molecular markers were not valid to differentiate between species. Myctophids and surface mesozooplankton were identified using morphometric and morphological parameters. Metabarcoding was used to identify macrozooplankton, epipelagic mesozooplankton (0–200 m), and microbial communities (prokaryotes and microbial eukaryotes) (Supplementary Table 3). Specifically, DNA from macrozooplankton (crustacean, mollusks, and insects) was extracted as in Marco-Herrero et al. Target mitochondrial DNA from the 16S rRNA and COI genes was amplified with polymerase chain reaction (PCR). Primers 1472 (5’-AGATATTGCGGGCTCAAAAC-3’) and 162 (5’-GCTGCTTATTCAAAAACAT-3’) were used to amplify 540 bp (base pair) of 16S, while primers COH6 (5’-TADACTTCGAGGRTGDCACAAAYCA-3’) and CO16b (5’-ACAATGACAAAGATATYGG-3’) allowed amplification of 670 bp of COI. The PCR products were sent to external laboratories to be purified and then bidirectionally sequenced (Sanger). Sequences were edited using the Chromas software version 2.0 (http://technelysium.com.au/wp/chromas/). With the final DNA sequences obtained, a BLAST search was executed on the NCBI webpage (https://www.ncbi.nlm.nih.gov/) to get the sequence that matched best. Macrozooplankton specimens were identified at species level when sequences fit 100%. Assignations to generic or familial level were made with a 90–99% divergence, depending on taxa and genes analysed. For lower % of divergence Operational Taxonomic Units (OTUs) were kept without taxonomical adscription. DNA from mesozooplankton (0–200 m) samples was extracted following Corell and Rodriguez-Ezpeleta. The V4 of the 16S rRNA gene was amplified using the #1/2RC primer pair following the ‘16S Metagenomic Sequence Library Preparation’ protocol (illumina, California, USA). Amplicons were purified using the AMPure XP beads, quantified using Quanti-IT dsDNA HS assay kit with a Qubit 2.0 Fluorometer (Life Technologies, California, USA) and pooled for high throughput sequencing in the Illumina MiSeq platform (Illumina, California, USA). After demultiplexing based on index, reads were trimmed at 200 bp (as overall Phred quality scores decreased after this position) and processed following the mothur MiSeq SOP. Briefly, sequences with ambiguous bases, chimeras, and global singletons were removed, and OTUs were created by merging reads at 97% similarity. Prokaryotic diversity was assessed by amplicon sequencing of the V4–V5 regions of the 16S rRNA gene in the Illumina MiSeq platform (iTags) using paired-end reads (2 × 250 bp) and primers 515F-Y (5’-
GTG/CAGCGCGGCTA-3’) and 926 R (5′-CCGYCAATTYMTT-TRAGTTT-3′) targeting both Archaea and Bacteria63. Small microbial eukaryotic diversity was assessed by amplicon sequencing of the V4 region of the 18S rRNA gene with the Illumina MiSeq platform using paired-end reads (2 × 250 bp) and the universal eukaryotic primers TAReukFWD1 (5′-CCAGCASCYGCGGTAATTCC-3′) and TAReukREV3 (5′-ACTTTCGTTCTTGATYRA-3′)64. For both groups, sequence data processing was performed using an UPARSE65 based workflow implemented in a local cluster [Marbits platform, ICM] (Logares66). Briefly, raw reads were corrected using BayesHammer67 following Schirmer et al.68. Corrected paired-end reads were subsequently merged with PEAR69; sequences longer than

Fig. 4 Spatial community patterns. Hierarchical clustering based on the Jaccard similarity index for, a diatoms 0–160 m, b mesozooplankton 0–200 m, and c myctophids. Each color represents a different hierarchical cluster. The size of stations indicates the number of connections (i.e., species/OTUs similarity between sites), that is, larger sized circles share more species (or OTUs) within all stations, compared to small sized circles. Some stations have been aggregated based on proximity for clarity.
200 bp were quality-checked (maximum expected errors 0.5) and de-replicated using USEARCH\textsuperscript{85}. OTU were delineated at 97% similarity using UPARSE V8.1.175665. To obtain OTU abundances, reads were mapped back to OTUs at 97% similarity using an exhaustive search (-maxaccepts 20 -maxrejects 10).

### Table 5: Environmental variables used and model selection for explaining species similarity

| Main biological groups | Environmental variables | BIOENV variable selection |
|------------------------|-------------------------|--------------------------|
| Prokaryotes            | T, S, O2, Conduct, Fluo, PARi, SPARi, Turb, Beam-att-1m, O2volt, Z\textsubscript{max} | O2, Turb, Beam-att-1m, Z\textsubscript{max} |
| Microbial eukaryotes ALL | T, S, O2, Chl-a, Conduct, O2volt, Fluo, PARi, SPARi, Turb, Beam-att-1m | Turb, Z\textsubscript{max}, O2 |
| Coccolithophores 0-160 m | T, S, O2, Chl-a, Conduct, O2volt, Fluo, PARi, SPARi, Turb, Beam-att-1m | SPARi |
| Dinoflagellates 0-160 m | Not available | Not available |
| Diatoms 0-160 m        | SST (remotely sensed), SST, S, Chl-a, W, Z | S, Turb, S |
| Mesozooplankton 0-200 m | T, S, O2, O2volt, Fluo, PARi, SPARi, Turb, Beam-att-1m | T\textsubscript{A00} |
| Gelatinous zooplankton | T, S, O2, O2volt, Fluo, PARi, SPARi, Turb, Beam-att-1m | |
| Macrozooplankton       | T, S, O2, O2volt, Fluo, PARi, SPARi, Turb, Beam-att-1m | |
| Myctophids             | T, S, O2, T\textsubscript{A00}, T\textsubscript{200}, T\textsubscript{400}, D\textsubscript{agg}, O2\textsubscript{min}, Fluo, Z\textsubscript{surf} | |

Environmental variables and best BIOENV model selection for each of the different plankton groups. SST sea surface temperature (°C), S, salinity, O2 oxygen (ml/l), O2\textsubscript{vol} oxygen voltage (volts), O2\textsubscript{vol} oxygen minimum concentration (ml/l), Conduct conductivity (S/m), Fluo fluorescence (volts), PAR\textsubscript{max} maximum photosynthetic active radiation (µE/cm²/s), SPARi surface photosynthetic active radiation (µE/cm²/s), Beam-att-1m beam attenuation coefficient at 1 m depth (m⁻¹), Z\textsubscript{surf} maximum depth of sampling (m), Chl-a chlorophyll-a (µg/L), W wind (m/s), Z\textsubscript{surf} depth of station (m), T\textsubscript{A00} temperature at 400 m (°C), T\textsubscript{200} temperature at 200°C (°C), S\textsubscript{agg} salinity at 400 m, S\textsubscript{agg} salinity at 200 m.

Correlations between community similarity and descriptors. Mantel correlations\textsuperscript{21} were estimated for species dissimilarity and surface ocean transit times, and environmental distances. Partial Mantel tests were also used to determine the relative contribution of surface ocean transit times and environmental distance in accounting for community similarity. All Mantel tests were performed using the vegan package in R\textsuperscript{78}. Further, Multiple Regressions on Distance Matrices (MRM) were used to apportion the variability in species composition among the different predictor factors. The Mantel tests should be restricted to questions that concern dissimilarity matrices, and not 'raw data' tables of spatial coordinates, from which one can compute dissimilarity matrices\textsuperscript{79}. In our study, the surface ocean transit times among sites are not vectors of raw data tables from which a dissimilarity matrix can be calculated; therefore, Mantel tests are suitable for our purpose.

Halving-time and time-decay slope. When β-diversity correlated significantly with oceanic transit time, after partilling out by environmental factors, we
The halving-time metric, which is a time-decay-based proxy for the scale of dispersal\cite{16}, is calculated as the time at which community similarity decreases by a factor of two under the assumption of exponential decay.

Spatial patterns of β-diversity. Network graphs were used to explore spatial patterns of community similarity among all pairs sites, using the igraph package\cite{89} in R. Specifically, sampling stations were grouped according to their species composition (based on Jaccard distances), using hierarchical clustering. In addition, the Analysis of Similarities (ANOSIM), performed using the vegan package\cite{78} in R, permits us to obtain a significant number of clusters for the biological group. Subsequently, network graphs were drawn with nodes (sampling stations) proportional to the similarity between sites and color-coded to represent cluster membership. In other words, the size of stations indicates the number of connections—that is, larger-sized circles share more species (or OTUs) within all stations, compared to small-sized circles, and the color represents a given hierarchical cluster. A minimum similarity threshold was imposed allowing all nodes to have a given connectivity degree.

Code availability. All code was written in the R programming language, which is open source and freely available. Enquiries about the code used here can be directed to the corresponding author, E.V.

Data availability. The presence/absence data of species and OTUs that support the findings of this study are publicly available in the Pangaea open repository (https://www.pangaea.de/) with the https://doi.org/10.1594/PANGAEA.874689 DOI identifier.

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Author contributions

E.V. and G.C. conceived and designed the research. E.V., G.C., J.R.W., C.M.D., and X.I., wrote the main text of the manuscript. E.V., G.C., and L.C. analysed the data and E.V., G.C., X.I., J.R.W., and C.M.D., interpreted the results. J.R.W. and B.J. run the simulation to obtain oceanographic data of the Global Circulation Model. J.M.G., G.S., and S.G.A. provided prokaryotes data; R.M., R.L., C.R.G., and M.C.P. provided microbial eukaryotes data; M.E. and S.A. provided phytoplankton data; M.P.O. provided small mesopelagic fish data; N.R.-E. and J.C. provided epipelagic mesozooplankton data; J.L.A. and A.M.-R. provided gelatinous zooplankton data; J.G.-G. and J.A.C provided macrozooplankton and surface mesozooplankton data; E.F.-N. provided hydrographic data; A.C. and E.M. took part in the sampling and data processing. All authors discussed the results and commented on the manuscript.

Additional information

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