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Biomass and trait biogeography of cephalopods on the European and North American continental shelves

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Abstract

Aim: We evaluate whether the biomass and trait biogeography of cephalopods follow the distribution expected by metabolic theory for ectotherms with rapid growth and high metabolic rate.

Location: Continental shelves of the North Atlantic and Northeast Pacific oceans; global marine ecoregions.

Time Period: 1968–2020.

Major Taxa Studied: Cephalopods and fishes (Chondrichthyes and Osteichthyes).

Methods: We map the biomass of cephalopods and their traits across marine shelves using scientific bottom trawl survey data from the North Atlantic and Northeast Pacific. We further map global fisheries catch. We apply statistical methods to evaluate how temperature, zooplankton productivity and depth drive these patterns.

Results: Cephalopods represent a small fraction (1%) of the combined fish and cephalopod biomass on continental shelves. However, their distribution displays a high regional heterogeneity, with some areas being virtually absent of cephalopods and other areas accounting for up to 24% of total biomass. Higher temperatures and zooplankton productivity are associated with increased cephalopod biomass and proportional biomass relative to fish. The largest cephalopods are found in the Northeast Pacific. Growth rates are highest in warmer waters with fastest growth rates found in lower latitudes of the North Atlantic. Cephalopods constitute 5% of the combined fish and cephalopod global fisheries catch. This proportion varies across regions. Higher temperature and zooplankton productivity are associated with increased cephalopod catch relative to fish.

Main Conclusions: Temperature and productivity shape the large-scale biogeography of cephalopods and their traits on marine shelves. The relations with temperature suggest that future warming could lead to a proliferation of fast-growing cephalopods in cold and temperate systems, with implications for ecosystem dynamics and fisheries. Despite a relatively low observed biomass, cephalopods hold substantial potential to change ecosystem structure and functioning given their high energy lifestyle.

KEYWORDS

asymptotic size, fishery catch, growth, lifespan, metabolic rate, trawl survey

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1 | INTRODUCTION

Ectotherm species exhibiting rapid growth and high metabolic rates have high energy demands (Clarke, 2017). Fast growth and high metabolic rates are typically associated with shorter lifespans and early reproduction, that is, 'live fast, die young' strategy (Metcalfe & Monaghan, 2003). Rapid growth tends to be prevalent in regions characterized by high prey productivity and temperatures. This is because, if energy requirements are met, warm temperatures can provide an advantage to species with high metabolic rates. For example, fast-living marine fish are found to be more dominant in warmer waters (Pecuchet et al., 2017). Rapid growth is also observed in variable environments where a fast lifestyle allows opportunistic species to respond to environmental fluctuations (Pauly & Lam, 2023; Winemiller & Rose, 1992). These macro-ecological patterns highlight the importance of fast lifestyles in explaining the biogeography of species and communities in food webs.

So far, most studies on marine food webs have ignored the role of cephalopods (squid, cuttlefish and octopus) in structuring these food webs (de la Chesnais et al., 2019). Cephalopods are widespread in global oceans, where they are important as fishery resources and in transferring energy through the food web (Hunsicker et al., 2010). As prey, they represent an important fraction in the food composition of some predatory fish (i.e. tuna, billfish, sharks and rays), sea birds (i.e. gulls, albatrosses, penguins and shearwaters), marine mammals (i.e. toothed whales and pinnipeds) and other cephalopods (Boyle & Rodhouse, 2005). As predators, they can have a disproportional effect on their prey and competitors because their fast growth requires them to feed voraciously (Boyle & Rodhouse, 2005; Wells & Clarke, 1996). Thus, understanding the drivers for where and why cephalopods thrive is important to understand the dynamics of the entire ecosystem, even if they make up a smaller proportion than fish in the total community biomass (FAO, 2022; Hunsicker et al., 2010).

Cephalopods have an extraordinary capacity to expand their range in altered ecosystems thanks to a set of traits that facilitate rapid adaptation in changing environments (Burford et al., 2022; Chasco et al., 2022; Oesterwind et al., 2022; Zeidberg & Robison, 2007). They are opportunistic species that on average grow approximately five times faster than the average fish, they mature and reproduce at an early age of 1 or 2 years, and they die after reproducing, resulting in a short life cycle and high turnover rate (Boyle & Rodhouse, 2005; Denéchère et al., 2023; O'Dor & Webber, 1986). According to the 'live fast, die young' theory, we can hypothesize that (1) cephalopod biomass is relatively low compared to fish due to a higher turnover rate, (2) cephalopod biomass increases with productivity due to a high resource demand and (3) cephalopod biomass (relative to fish) and growth rates increase with water temperature because warm water favours the active metabolism that cephalopods rely on. These hypotheses have been partially tested. Most information of cephalopod biomass and trait distributions originates from fishery landings (reviewed in Arkhipkin et al., 2015; Sauer et al., 2019), local monitoring programs (e.g. Geraci et al., 2021; Tsikliras, 2021) and other exceptional stock assessments (Arkhipkin et al., 2021). These

studies provide valuable information on the biology, diversity and stock biomass of cephalopods at various scales. However, the information provided by these studies is local, scattered and has not been synthesized into a general understanding of the macroecological patterns and drivers of cephalopods on marine shelves.

Our objective is to evaluate these three hypotheses by investigating the broad-scale biogeography and trait distribution of cephalopods on continental shelves. We use multidecade bottom trawl survey data in continental shelves of Northeast and Northwest Atlantic and Northeast Pacific to examine the spatial patterns of cephalopod biomass and three biological traits—body size, lifespan and growth rate. We complement this analysis with data of global fisheries landings. The focus of this study is to obtain a 'snapshot' of the spatial distribution of cephalopods in recent decades ignoring interannual fluctuations. This approach provides a complementary perspective to previous studies (Arkhipkin et al., 2015; Doubleday et al., 2016; Mildenerger et al., 2021; Sauer et al., 2019) and enables to examine how cephalopod's lifestyle shapes the biogeography of upper trophic level species and communities in marine food webs.

2 | MATERIALS AND METHODS

We map cephalopod biomass and traits across well-studied shelf areas and relate these patterns to key environmental variables. We then evaluate the degree to which these patterns match observed fisheries landings at a global scale. First, we conduct an analysis on survey data of Northeast Pacific and North Atlantic shelves. Absolute cephalopod biomass and its relative proportion to fish biomass are evaluated in relation to water temperature, zooplankton productivity and bottom depth with statistical methods. Then, we evaluate how asymptotic body size, lifespan and somatic growth rate are affected by the same explanatory variables. Finally, we repeat our analysis using fisheries landings data to evaluate how the proportion of cephalopods relative to fish is affected by the same environmental variables at a global scale.

2.1 | Data acquisition and processing

To calculate biomass per unit area of cephalopod and fish, we use trawl survey data from public repositories downloaded in 2021 and standardize their biomass to kg km⁻² to correct for different sampling design (see appendix S1 in van Denderen et al., 2023). We only use surveys that sample the community with otter trawls and select all trawls conducted at a bottom depth <400 m in surveys that recorded cephalopods (Table 1), excluding surveys with no cephalopods records, for example, the Baltic Sea, Gulf of St. Lawrence and Bering Sea. We process the survey data using modified scripts from earlier works (Maureaud et al., 2019; Pinsky et al., 2013; van Denderen et al., 2023). For the data from Northeast Pacific and Northwest Atlantic, we used the provided weight per species per trawl. However, most data of Northeast Atlantic are instead

TABLE 1 Data obtained from trawl surveys and fisheries estimates.

Region	Years	No. trawls	No. grid cells	No. ecoregions
Northeast Pacific	1968–2020	32,170	196	6
Northwest Atlantic	1977–2019	61,600	192	7
Northeast Atlantic	1967–2019	50,697	529	6
Global	1999–2019	–	–	164

reported as count and length measurements of the sampled individuals. Thus, we calculate the species-specific trawl biomass applying length–weight relationships from the literature (Froese & Pauly, 2018 for fish) (Jereb et al., 2005, 2015; Jereb & Roper, 2005; Palomares & Pauly, 2022 for cephalopods). For missing information at the species level, we infer the length–weight relationship based on an average value of higher taxonomic groupings (genus/family/order). Some surveys in European waters contain species-specific measurements of both biomass per trawls and individual length. Comparing both these measurements, we find that weights calculated from length measurements are 1% and 3% (median) lighter than weights measured directly for fish and cephalopods, respectively. This effect is small and estimating weight from length-based observations is therefore suitable. We calculate the swept area of each trawl using the net wingspread and tow speed and duration to standardize trawl biomass to kg km^{-2} (van Denderen et al., 2023).

Trawl nets only capture a portion of the existing fish and cephalopods in the path of the trawl. Thus, caught biomass values must be corrected with a catchability coefficient to obtain more accurate estimates of real biomass (Walker et al., 2017). Catchability is taxon-specific and depends on body shape, behaviour, habitat preferences and typical position in the water column. To evaluate how sensitive biomass estimates are to catchability corrections, we apply three types of catchability corrections for cephalopods (see Supplementary Methods SM1). In the Results section, we report biomass estimates of the non-corrected data and after correcting all cephalopods with a catchability coefficient = 0.3, as estimated by Link et al. (2008). Other results from this sensitivity analysis can be found in the Supplementary Material SM1.

We evaluate three key cephalopod traits: asymptotic weight W_{∞} (g), lifespan $\mathcal{T}$ (months) and growth coefficient A ($\text{g}^{-1/3} \text{yr}^{-1}$). We use the growth coefficient A instead of the von Bertalanffy coefficient K because K measures maturation rate rather than somatic growth rate. In this way, we avoid the correlation between K and asymptotic weight (Charnov, 2010). Information about the asymptotic weight and lifespan are obtained from the literature (Jereb et al., 2005, 2015; Jereb & Roper, 2005; Palomares & Pauly, 2022). For missing information at the species level, we infer their traits based on higher taxonomic groupings (genus/family/order). Growth coefficient A is estimated from lifespan and asymptotic weight, which is possible since cephalopods are typically semelparous species that grow continuously until they die after reproducing. We thus assume that growth in body weight W of juveniles scales as

$$\frac{dW}{dt} = A \cdot W^{2/3}, \quad (1)$$

and they reach their asymptotic weight W_{∞} at age $\mathcal{T}$. We can use this information to calculate the growth coefficient A for each species as

$$A \approx (3/\mathcal{T}) W_{\infty}^{1/3} \quad (2)$$

Glazier (2005), Andersen (2019, eq. 3.25).

We relate the traits and biomass distribution to sea temperature in the top 100m of the water column $Temp$ ($^{\circ}\text{C}$), zooplankton productivity $ZProd$ ($\text{gm}^{-2} \text{y}^{-1}$) and bottom depth $Depth$ (m). We selected these parameters because studies typically link the abundance of cephalopods to one or several of these environmental conditions (e.g. Kooij et al., 2016; Mildenerberger et al., 2021). For temperature and zooplankton productivity, we use outputs from the Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT) ecosystem model. COBALT is based on climatology of the global earth system model (ESM2.6) under greenhouse gas concentrations of 1990 and has a correlation coefficient for annual average sea temperature with temperature data from the World Ocean Atlas of 0.997 (Stock et al., 2017). The zooplankton productivity used from COBALT describes the productivity that is not consumed by other zooplankton and is therefore available for higher trophic levels like fish and cephalopods. As bottom depth, we use the mean depth of the trawls in each cell.

In the regional analysis, we split the sampled areas in hexagonal grid cells of 6200 km^2 each and pool the information of all trawls within each cell. Then, we calculate the mean biomass (kg km^{-2}) of fish and cephalopods, and mean biomass proportion of cephalopods relative to both fish and cephalopods. We further calculate cephalopod mean asymptotic weight, lifespan and growth coefficient A , weighted geometrically by the species biomass in each trawl:

$$e^{\sum \text{species biomass} \cdot \log(\text{species trait}) / \sum \text{species biomass}} \quad (3)$$

Following the regional analysis, we evaluate how the same environmental variables affect the proportion of cephalopod catch across marine ecoregions globally. For this, we use fisheries catch estimates of marine ecoregions (Table 1) and calculate the proportion of cephalopods to total (cephalopod + fish) catch. Fisheries data were downloaded from the *Sea Around Us* data set (Pauly et al., 2020) in November 2022 for the period of 1999–2019, whereas all explanatory variables (including depth) were obtained from Stock et al. (2017) and averaged per marine ecosystem. We include all marine ecoregions ($n = 164$; Spalding et al., 2007) that overlap with areas defined as large marine ecosystems (Sherman et al., 1990). *Sea Around Us* database lacks the taxonomic resolution required to evaluate cephalopod traits (Pauly et al., 2020). Furthermore, because marine ecoregions differ in size, the analysis of total catch per unit area would carry inherent artefacts. Thus, we restrict our analysis to evaluate only how environmental variables affect the proportion of cephalopod catch relative to cephalopod and fish catch.

2.2 | Data analysis

2.2.1 | Survey data

We apply generalized additive mixed models (GAMMs) and random forest analysis to evaluate how environmental conditions affect the biomass and traits distribution of cephalopods. We generate a GAMM model for each response variable (cephalopod biomass, fish biomass, cephalopod biomass proportion, log10 (asymptotic weight), lifespan or growth parameter A), and all GAMM models follow the same structure,

$$\text{Response}_{i, \text{Region}} \sim \beta_0 + s_1(\text{Temp}_{i, \text{Region}}) + s_2(\text{Depth}_{i, \text{Region}}) + s_3(\text{ZProd}_{i, \text{Region}}) + \gamma_{\text{Region}} + \varepsilon_{i, \text{Region}} \quad (\text{Model 1})$$

where *Response* is each of the response variables. The subindex *i* stands for each hexagonal cell, γ_{Region} is a categorical random effect that discriminates the intercept of Northeast Pacific, Northwest Atlantic and Northeast Atlantic, and ε is the model residual. All smoothing parameters are indicated with *s* and are restricted to three knots to prevent over-fitting the model (Wood, 2017). Based on the nature of the data, we use negative-binomial distribution for cephalopod and fish biomass, beta distribution for cephalopod biomass proportion and normal distribution for the cephalopod traits (we confirm the appropriateness of these distributions after inspection of model residuals, and zero values of cephalopod proportion are reset to near-zero values to satisfy the beta distribution). To identify the explanatory variables that affect each response variable, we use the Akaike information criteria (AIC) and evaluate the model smooth plots (i.e. visual depiction of the underlying pattern in the data; [Supplementary Material SM1](#)) (Zuur et al., 2009).

Spatial variables (latitude and longitude) are strongly correlated with other explanatory variables and we therefore exclude them from the GAMM models (see [Supplementary Material SM2](#)). Latitude is particularly correlated with water temperature (−0.88) and we use the terms latitude and temperature interchangeably in the results and discussion sections. To evaluate the sensitivity of our models to spatial variables, we replicate all GAMM models including spatial autocorrelation structures and compare the results with the models that lack spatial autocorrelation ([Supplementary Material SM2](#)). As expected, the effects of explanatory variables on response variables are weaker when spatial autocorrelation is included, but the overall shape and direction of the effect remains the same ([Figure S5](#)).

We evaluate the performance of each model using 100 training and validation data sets. Each training data set contains two-thirds of the original data (randomly selected), and the remaining one-third of the data are used to validate model predictions. For each of these 100 iterations, we evaluate the fit of the model predictions to the validation data by calculating the adjusted variance explained (Adj. R^2) and the mean squared errors (MSE). We therefore obtain 100 values of R^2 and MSE for each model that we summarize (mean ± SD) in [Table S2](#).

To complement the analysis with a different statistical approach, we replicate all GAMM models with random forest regressions (Breiman, 2001), which are computed as

$$\text{Response}_i \sim \text{Temp}_i + \text{Depth}_i + \text{ZProd}_i + \text{Coast}_i \quad (\text{Model 2})$$

where all terms are defined above. Each regression forest contains 1000 tree iterations, and two variables are sampled at each decision split. No model selection is applied in this case. We evaluate the performance of each RF model following the same training and validation protocol described above for the GAMM models. We inform in advance that both analytical approaches yield similar relationships between the explanatory and response variables. For simplicity, we only focus on GAMM outputs in the Results section below. Further comparisons and results from the random forest regressions can be found in the [Supplementary Material SM3](#).

2.2.2 | Fisheries data

We model the proportion of cephalopod catch *CephProp* across 164 marine ecoregions as a function of temperature, depth and zooplankton productivity as.

$$\text{CephProp}_j \sim \beta_0 + s_1(\text{Temp}_j) + s_2(\text{Depth}_j) + s_3(\text{ZProd}_j) + \varepsilon_j, \quad (\text{Model 3})$$

where *j* is each ecoregion and the other terms are defined above. We apply a beta distribution and conduct sequential model selection with AIC and evaluating smooth plots ([Supplementary Material SM4](#)).

To complement the analysis with a different statistical approach, we replicate the analysis applying a random forest regression:

$$\text{CephProp}_j \sim \text{Temp}_j + \text{Depth}_j + \text{ZProd}_j. \quad (\text{Model 4})$$

Results of the random forests and its comparison to the GAM analysis are found in the [Supplementary Material SM5](#). Diagnostics of the model performance are found in the [Supplementary Table S2](#), [Figures S9](#) and [S10](#).

3 | RESULTS

3.1 | Spatial patterns in biomass

The average biomass of cephalopods across all surveyed areas is considerably lower (raw data = 47 kg km^{−2}; catchability-corrected estimates = 157 kg km^{−2}) than that of fish (raw data = 7168 kg km^{−2}; catchability-corrected estimates = 52,198 kg km^{−2}), accounting for a low proportion (raw data = 1.3%; catchability-corrected = 0.8%) of the total fish and cephalopod biomass combined. The spatial distribution of cephalopod biomass is heterogeneous in all three regions ([Figure 1a–d](#)).

In the Northeast Atlantic and Northeast Pacific shelves, higher cephalopod biomasses are found in lower latitudes ([Figure 1a,b](#)), particularly near the continental slopes of the Celtic Sea (raw data = 844 kg km^{−2}; catchability-corrected = 2812 kg km^{−2}) and

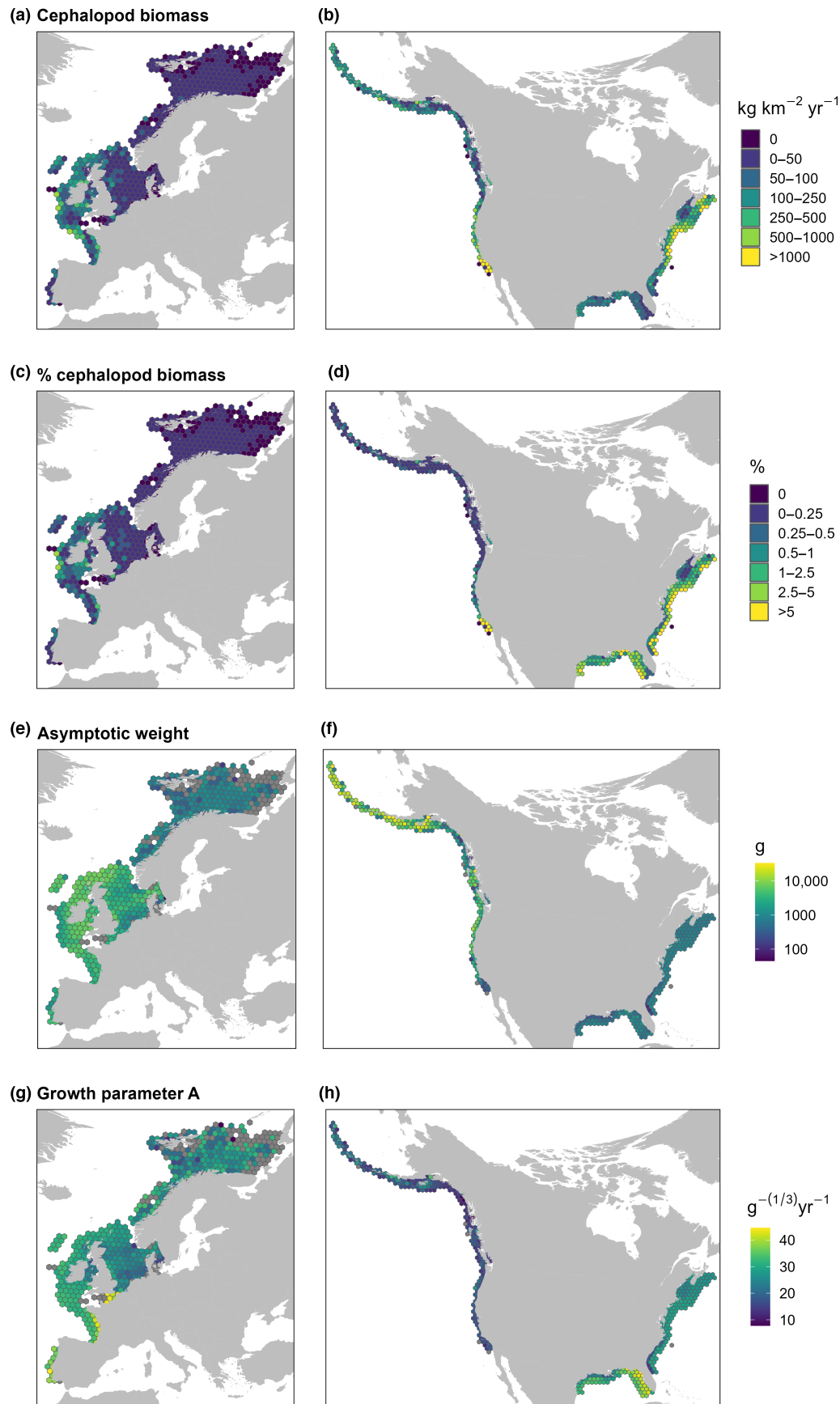


FIGURE 1 Distribution of observed cephalopod biomass and traits in waters of Europe and North America after catchability correction. (a,b) Cephalopod biomass (kg km⁻²). (c,d) Proportion of cephalopod biomass (%). (e,f) Asymptotic weight (g). (g,h) Growth parameter A (g^{-1/3} yr⁻¹). All trait values are averages weighted by the biomass of the species found in each grid cell. Grey cells in panels e–h are cells without cephalopods.

southern California (raw data = 1736 kg km^{-2} ; catchability-corrected = 5787 kg km^{-2}), whereas lowest cephalopod biomass is observed in the Barents Sea (not considering the Baltic Sea). These patterns align with the proportion of cephalopod biomass (Figure 1c,d), which show the greatest proportion of cephalopod biomass near the slope area of the Celtic Sea (raw data = 27%; catchability-corrected = 12%) and Southern California (raw data = 36%; catchability-corrected = 24%), while the Norwegian and Barents Seas have values close to zero (Figure 1c). In the Northwest Atlantic shelf, the highest biomasses of cephalopods are near the slope areas off (Figure 1b,d), with the highest absolute values observed off Nova Scotia (raw data = 736 kg km^{-2} ; catchability-corrected = 2453 kg km^{-2}), and the highest proportion observed near the slope from the northern Florida peninsula to Nova Scotia (up to 28% [raw data]; 21% [catchability-corrected]).

Temperature has a positive effect on cephalopod biomass, and a negative effect on fish biomass (orange line in Figure 2a,c), resulting in an exponential increase in the proportion of cephalopod biomass with temperature (Figure 1e). The biomass of both taxa increases with zooplankton productivity (up to $200 \text{ g m}^{-2} \text{ yr}^{-2}$ for cephalopods), but the range of change is about two orders of magnitude greater for cephalopods than for fish (Figure 2b,d). Thus, the proportion of cephalopod biomass also increases with productivity up to $200 \text{ g m}^{-2} \text{ yr}^{-2}$ and levels off at greater values (Figure 2f). Depth has a weaker effect than temperature and productivity on cephalopod biomass, which increases with depth up to 200 m (Figure S1). Cephalopod biomass is more strongly affected by zooplankton productivity (it ranges two orders of magnitude) than by water temperature or depth (one order of magnitude). Contrastingly, fish biomass is more strongly affected by temperature (one order of magnitude) than by zooplankton productivity or depth (same order of magnitude). All three environmental variables affect the proportion of cephalopods with similar strength (temperature = 0.5%–2.5%, zooplankton productivity = 0.4%–1.2%, depth = 0.3%–1.1%).

3.2 | Spatial patterns in biological traits

The largest cephalopods are found in the Northeast Pacific, particularly at higher latitudes where asymptotic weights reach up to 33 kg (weighted mean per grid cell; Figure 1f). Cephalopods follow the opposite pattern in the Northeast Atlantic, with smaller sizes at higher latitudes (i.e. 140 g in the Barents Sea; Figure 1e) and larger sizes around Ireland and the British Islands (up to 3.8 kg). Asymptotic weight is more homogeneously distributed in the Northwest Atlantic shelf, with a median of 715 g. Growth in the Atlantic shelves tends to be faster at lower latitudes. In the Northeast Atlantic, growth is fastest in coastal areas of the Iberian Peninsula, Bay of Biscay and the English Channel (up to $44.5 \text{ g}^{-1/3} \text{ yr}^{-1}$; Figure 1g). In the Northwest Atlantic shelf (Figure 1h), growth is faster south off the Floridian peninsula (up to $44.6 \text{ g}^{-1/3} \text{ yr}^{-1}$). Cephalopods in the Northeast Pacific tend to

grow slower than in the Atlantic (max = $34.6 \text{ g}^{-1/3} \text{ yr}^{-1}$), with no strong latitudinal trend.

Despite regional differences, temperature has an overall negative effect on cephalopod size and lifespan, and a positive effect on growth rate (Figure 2g,i,k). The overall effect of zooplankton productivity on cephalopod traits is not clear, as there are big regional differences (Figure 2h,j,l). Overall, zooplankton productivity has a stronger effect on asymptotic weight (it ranges by 10-fold) and lifespan (it ranges by threefold) than temperature (asymptotic weight ranges by twofold and lifespan by 50%). However, growth is more heavily affected by water temperature (it ranges by 50%) than by zooplankton productivity (it ranges by 20%). Depth has a weak effect on all three traits.

3.3 | Global catch

On average, cephalopods represent 5% of total fish and cephalopod catch in the period of 1999–2019. This is about five times higher than the biomass fraction observed in the survey data. The highest cephalopod proportions are found in the Falkland (Malvinas) Islands Ecoregion (73%), Northern California (55%), Uruguay–Buenos Aires shelf (43%) and North Patagonia Gulf (29%) (Figure 3), all of which are areas with upwelling or boundary currents. The relation between proportion of cephalopod catch and temperature and zooplankton productivity (orange lines in Figure 4) is similar to that of the survey data analysis (Figure 2e,f). It increases up to 7.5% at 20°C and $225 \text{ g m}^{-2} \text{ yr}^{-1}$ and decreases at greater temperature (weakly) and at greater zooplankton productivity. Average ecoregion depth has no effect, likely because average depth of each ecoregion (>1000 m in most cases) does not reflect the range of depths where cephalopods are mostly targeted by fisheries (Figure S7b).

4 | DISCUSSION

Combining extensive survey data from three major marine regions, we have performed the largest fisheries-independent analysis evaluating patterns of biomass and traits distribution of cephalopods. As expected from their fast lifestyle, cephalopods make up an overall small fraction of the combined cephalopod and fish biomass on shelf areas. Temperature has a positive effect on cephalopod biomass and growth, and prey productivity has a positive effect on biomass. These effects confirm our initial three hypotheses that cephalopod biomass is low compared to fish, their proportion increase with temperature and productivity and their growth rate increases with temperature. The same patterns are observed in the fisheries catch, yet the proportion of cephalopod catch is five times larger than the proportion of cephalopod biomass on shelves. Our results uncover strong regional differences in biomass and traits distribution, that do not consistently follow latitudinal trends nor a gradient in temperature or productivity.

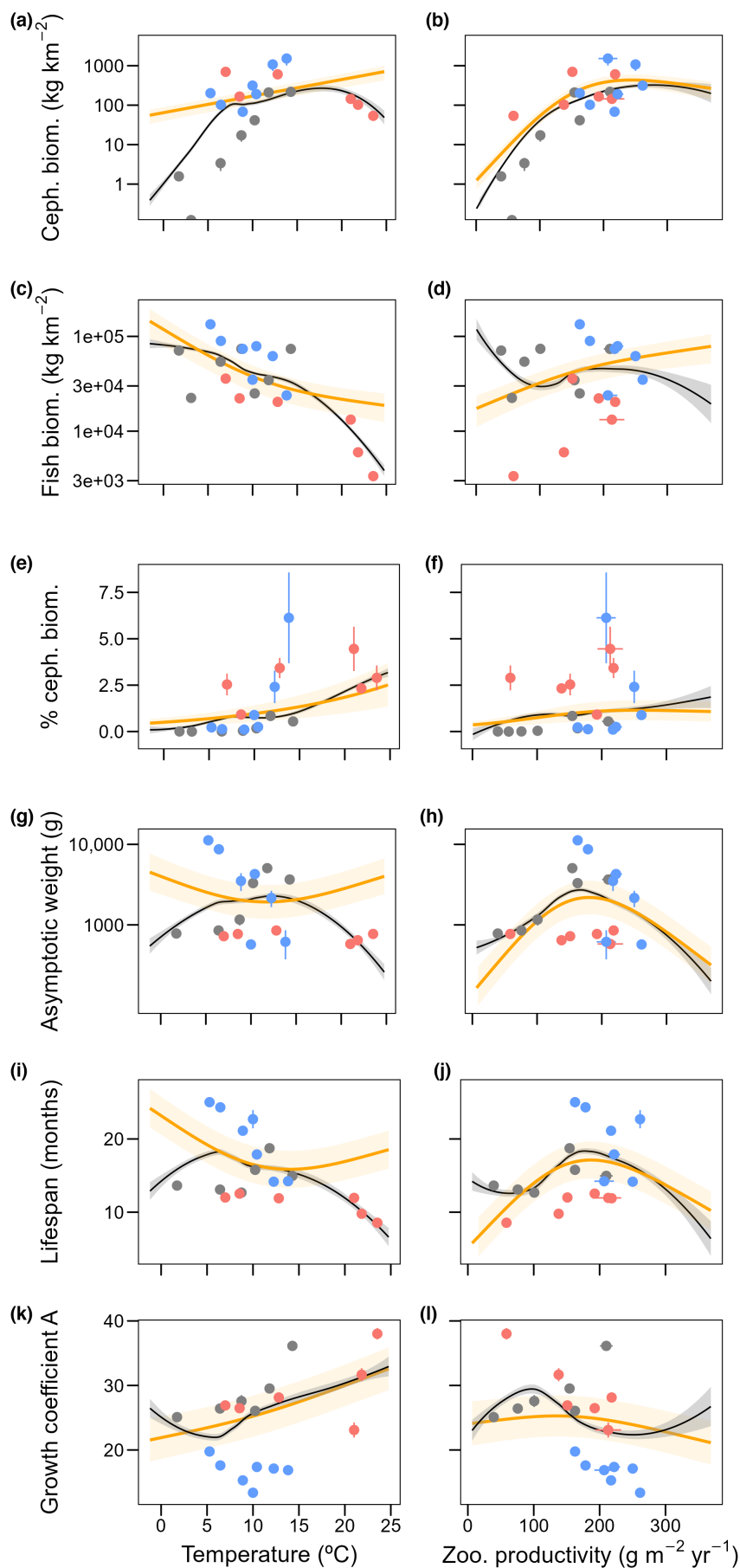


FIGURE 2 Effect of water temperature and zooplankton productivity on cephalopod and fish biomass, and on three key cephalopod traits across shelves of Northeast and Northwest Atlantic and Northeast Pacific. Orange lines are partial effects of each predictor obtained from a GAMM with $n = 917$; black lines are predictions of the same model using observed variables; orange and black shading are the respective standard errors. Models are fit at the grid cell level, whereas coloured dots are observed values averaged by marine ecoregion (with respective standard error bars) where grey = Northeast Atlantic waters, red = Northwest Atlantic coast and blue = Northeast Pacific.

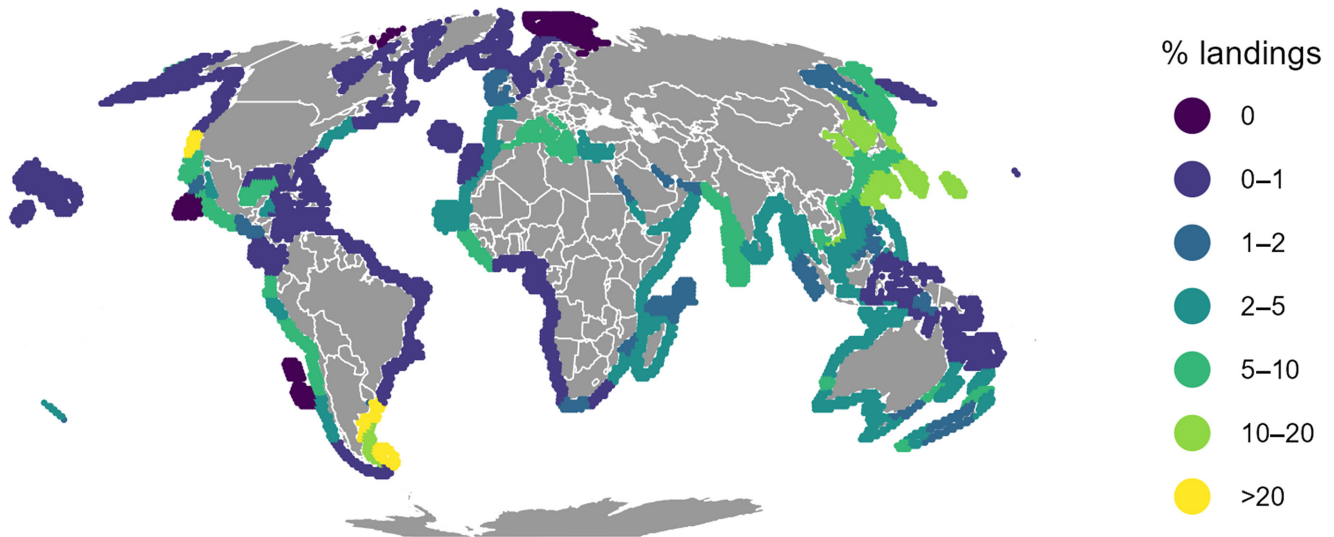


FIGURE 3 Global map of the proportion (%) of cephalopod catch using fisheries data of 164 marine ecoregions from 1999 to 2019. Values are truncated at 20% for visual purposes.

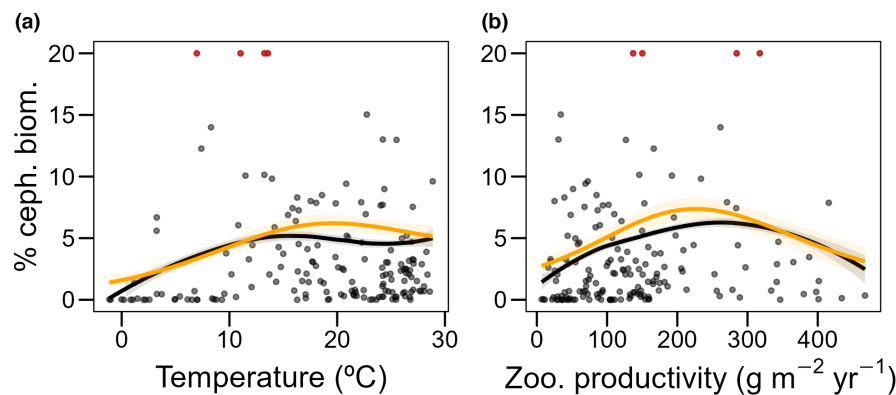


FIGURE 4 Effect of water temperature and zooplankton productivity on cephalopod catch proportion of 164 marine ecoregions (dots). Orange lines are partial effects of each predictor obtained from a GAM; black lines are predictions of the same model using observed variables; orange and black shading are the respective standard errors. The y-axis is truncated at 20% for visual purposes. Red dots are marine ecoregions where cephalopod catch proportion >20%; the patterns are consistent after repeating the analysis excluding these ecoregions.

4.1 | Biomass

Our findings are consistent with previous studies that cephalopods generally account for a small fraction of the total biomass (Arkhipkin et al., 2015; Doubleday et al., 2016; FAO, 2022; Kooij et al., 2016; Mildenerberger et al., 2021; Seto et al., 2023). However, the distribution of their absolute and relative biomass is uneven, with some areas being virtually absent and other areas accounting for up to 24% of total biomass. Previous work has shown that cephalopods tend to be more abundant in slope areas and in upwelling/boundary currents (Moustahfid et al., 2021). Although our survey data analysis is truncated at 400m depth, the results are consistent with the literature, as they show that cephalopods are most abundant near slope areas of the California upwelling system, followed by the slope areas along the Gulf stream and the Celtic Sea. Notably, the four areas with greatest cephalopod catch

on a global scale are also located in upwelling/boundary currents (yellow areas in Figure 3).

Temperature has a positive relation with cephalopod biomass in the Northeast Atlantic and Northeast Pacific. Such an increase of biomass with temperature is somewhat counterintuitive as temperature increases the turnover rate of individuals and communities and thus reduces standing biomass (Brown et al., 2004). This discrepancy may be due to cephalopods performing better than fish and gaining competitive advantage in warmer waters because warmer waters provide favourable conditions for their rapid growth, active metabolism and overall life cycle (Boyle & Rodhouse, 2005). Our results support this hypothesis as the proportion of cephalopods relative to fish also increases with temperature. This link is not as clear for the northwest Atlantic. This area is dominated by the northern shortfin squid *Illex icebrosus*, a migratory species whose regional

abundance is heavily influenced by oceanographic variability caused by the interplay of the Gulf Stream, mesoscale eddies, the shelf break Jet and other shelf-slope exchange processes (Salois et al., 2023).

In our study, productivity has a positive effect on both cephalopod and fish abundance at values $<200 \text{ gm}^{-2} \text{ yr}^{-1}$. This effect is stronger for cephalopods than for fish, confirming that the biogeography of cephalopods is more constrained by food availability than that of fish due to their greater metabolic rate (Boyle & Rodhouse, 2005; Wells & Clarke, 1996). The relative biomass of cephalopod no longer increases at productivities $>200 \text{ gm}^{-2} \text{ yr}^{-1}$, highlighting that other processes also affect cephalopod biomass.

Cephalopod fisheries contribute a small fraction of total catch in the world, but their average market value is higher than that of fishes, and their importance as a fisheries resource has grown over the past decades (Hunsicker et al., 2010). While our analysis reveals that the proportion of global cephalopod catch is five times higher than the proportion of cephalopod biomass on shelves, temperature and zooplankton productivity have a similar effect in both cases, giving a degree of confidence to the analysis. Both trawl survey data and fisheries catch are sensitive to biases, and this may affect the average proportion of cephalopods observed in these data. We therefore verified the results with 38 Ecopath with Ecosim (EwE) models obtained from EcoBase (Colléter et al., 2013; Supplementary Table S1). The average biomass proportion of cephalopods in the EwE models is 7.5%, which is in line with both the survey and fisheries catch data (given that no EwE models were selected where cephalopods are absent).

4.2 | Traits

Like other ectotherms, cephalopods tend to grow faster in warmer waters, and we find that the growth parameter A increases by a ratio of 1.2 each 10°C (Q_{10} is 1.2). Such a growth increase is less than expected from metabolic predictions (Brown et al., 2004) but in line with average growth increases with temperature in teleost fish (van Denderen et al., 2020). This pattern is not observed on the Northeast Pacific shelf, where growth is relatively constant across different temperatures. This constant growth is driven by a high abundance of large species like the giant Pacific octopus *Enteroctopus dofleini* (Jereb et al., 2005). These species also live longer than smaller species, thus yielding a relatively constant growth parameter A (Equation 2) across different temperatures in this region.

The overall effect of temperature and productivity on asymptotic weight is unclear, as it differs among regions reflecting different characteristics of each system and traits plasticity of cephalopods. For instance, the high productivity of the California current system, the warmer water along Gulf Stream and wide continental shelf in European Waters are regional characteristics that may feature specific trait distributions among cephalopods in each studied region (Burford et al., 2022; Frawley et al., 2019; Hoving et al., 2013; Jereb et al., 2015).

The large deviations in some regions between predicted and observed biomass and traits as a function of the explanatory variables highlight that they are influenced by other conditions. For example, cephalopods are sensitive to oxygen limitation (Seibel, 2016) and changes in the food web structure (Denéchère et al., 2023; Zeidberg & Robison, 2007). Thus, some of the model deviations may be driven by variability in these other conditions. Furthermore, groups like the Ommastrephidae and Loliginidae often become extraordinary abundant in upwelling systems and boundary currents (Moustahfid et al., 2021; Suca et al., 2022), generating outliers that do not necessarily follow the generic trends in Figures 2 and 4. Still, the models have revealed significant relationships with temperature and secondary productivity, and deviance explained by the regional statistical models ranged from 44% for asymptotic weight to 64% for lifespan.

Although abundance of cephalopods is low relative to fish, their impact on ecosystem processes can be disproportionately large. The results of this study suggest that an increase in water temperature in cold-temperate regions could lead to an increase of cephalopod biomass proportion, particularly that of fast-growing species. Similarly, an increase in zooplankton productivity in low-moderate productivity systems can also boost cephalopod biomass. The fast lifestyle of cephalopods could lead to a disproportionately large increase in resources consumption in these regions (Burford et al., 2022), as they are expected to metabolize around five times more resources than fish to sustain their rapid growth (Andersen, 2019, chapter 9; Denéchère et al., 2023). Through competitive and trophic interactions with fish, this increase may lead to changes in the ecosystem structure, reduce landings of fish and increase the relevance of cephalopods as a fisheries resource.

Understanding the drivers of cephalopod biomass and traits distribution is key to better understand their ecological niche and validate food web models that predict how the biogeography and ecosystem functions of cephalopod will be affected by fisheries and climate change (de la Chesnais et al., 2019; Denéchère et al., 2023; Moustahfid et al., 2021; Schickele et al., 2021). This study confirms the general predictions from ecological theory that a fast lifestyle is associated with high temperatures and productivity.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data and R code are available on Dryad: <https://doi.org/10.5061/dryad.9cnp5hqqb>.

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