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Fisheries disrupt marine nutrient cycles through biomass extraction

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Fisheries' effects on marine life have been widely acknowledged for decades, but only recently have we considered their impact on marine nutrient cycles. Through the removal of marine biomass, fisheries represent a unique and historically novel pathway for nutrients to be extracted from the sea. Here, we examined the magnitude of carbon, nitrogen, and phosphorus extraction by industrial fisheries through large spatiotemporal scales and broad ecological contexts. Between 1960 and 2018, industrial fisheries removed approximately 431 million tonnes of carbon, 110 million tonnes of nitrogen, and 23 million tonnes of phosphorus. Nutrient extractions occurred most intensely in highly productive regions within Exclusive Economic Zones. Additionally, >53% of all nutrient extractions occurred through the removal of mid-level trophic groups and pelagic species. Our findings indicate that fisheries can remove substantial amounts of nutrients each year and warrant further studies that consider the ecosystem-level impacts of nutrient reductions.

Commercial fisheries have contributed to an estimated two-thirds reduction in target species biomass over the past century[1–3]. This considerable decline, coupled with changes in the structure of marine biological communities, has intensified questions on how fisheries influence ecosystem processes and functions[4–7]. Recognizing that ocean productivity heavily relies on efficient nutrient recycling[8,9], a key concern is how the annual removal of millions of tonnes of marine species by fisheries influences marine nutrient cycling[10–14]. Notably, some studies suggest that the biogeochemical impacts of fisheries could be comparable to those from anthropogenic climate change[2]. To further our understanding in this area of concern, our study analyzed the temporal, spatial, and ecological patterns of carbon (C), nitrogen (N), and phosphorus (P) loss associated with the extraction of ~4 billion tonnes of marine biomass between 1960 and 2018. The selective nature of fisheries, which is driven by the targeting of specific sizes and species, shapes the patterns, and magnitude of nutrient removals. By examining nutrient removals through an ecological lens, our study shows that the selective nature of fisheries likely influences how, where, and to what extent fisheries impact marine nutrient cycling.

Earlier estimates have suggested that industrial fisheries annually remove millions of tonnes of C, N, and P from the ocean via the removal of marine species[12–15] (Table 1). While these figures provide an initial sense of the impact fisheries removals have on these nutrients, they fail to contextualize these losses in a way that aligns with our understanding of the selective nature of fisheries and the diversity of processes that control nutrient cycling in different marine habitats. It is crucial to consider that the species targeted by fisheries vary in their elemental composition and span a wide range of trophic and functional groups[16,17]; thus, variations in the magnitude of their removal will yield differing ecological consequences for nutrient cycling. Additionally, the selection of target species is shaped by both natural variability in species distributions and evolving socio-political factors that control fishing practices and consumer demand[18,19], adding layers of spatial and temporal complexity to how and where fisheries might affect marine nutrient cycling[15]. This multifaceted perspective, which takes into consideration the ecological context of targeted species and spatiotemporal variability in fisheries, is essential for a comprehensive understanding of how this industry influences the delicate balance of marine nutrient dynamics.

Here, we quantified the extent of industrial fishery-based C, N, and P extractions across time (1960–2018) and space. Additionally, we characterized nutrient extraction through different ecological contexts by assessing nutrient loss via fisheries catches across trophic and functional groups. To do so, we compiled a dataset of the body compositions of three key nutrients—C, N, and P—from 330 fishery-targeted species representing 126 families. This approach allowed us to capture the orders of magnitude variation in bodily nutrient compositions of different fishery-targeted organisms; an important consideration overlooked in previous studies[12,13,15], but an essential one for estimating spatiotemporal trends and understanding the

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Table 1 | Comparison of nutrient extraction estimates for carbon (C), nitrogen (N), and phosphorus (P) from this study and previous studies

Study	Reference number	Nutrient	Study context	Study estimate
This study	NA	C	Mean annual extractions between 1960-2014	7.3 Mt yr^{-1}
Mariani et al.[13]	13	C	Total extractions through large pelagic fish between 1950 and 2014	37.5 Mt
Martin et al.[24]	24	C	Mean extraction for the year 2018	9.3 Mt yr^{-1}
This study	NA	N	Mean annual extractions between 1960-2014	1.9 Mt yr^{-1}
Maranger et al.[12]	12	N	Mean annual extractions in large marine ecosystems between 1960−1969	0.9 Mt yr^{-1}
Maranger et al.[12]	12	N	Mean extraction in LMEs for the year 2000	2.3 Mt yr^{-1}
Allgeier et al.[11]	11	N	Mean annual extractions in the 2010s	2.1 Mt yr^{-1}
Le Mézo et al.[15]	15	N	Mean extractions at the time of peak global catch (1990s).	5.4 Mt yr^{-1}
This study	NA	P	Mean annual extractions between 1960 and 2014	0.4 Mt yr^{-1}
Huang et al.[14a]	14	P	Mean extraction for the year 2016	1.1 Mt yr^{-1}
Le Mézo et al.[15]	15	P	Mean extractions at the time of peak global catch (1990s).	1.2 Mt yr^{-1}

[a] The estimate generated by this reference included extractions produced by aquaculture and inland fisheries which we did not consider in our study.

Table 2 | Total nutrient extractions from industrial fisheries across different time periods

Nutrient	1960–1964	1993–1997	2014–2018	1960–2018
Carbon	17.792 (17.214–18.472)	45.457 (44.637–46.183)	39.449 (39.002–39.924)	431.158 (428.866–433.478)
Nitrogen	4.492 (4.365–4.606)	11.720 (11.566–11.856)	10.025 (9.942–10.125)	110.293 (109.957–110.711)
Phosphorus	0.947 (0.861–1.047)	2.447 (2.330–2.601)	2.060 (2.013–2.129)	22.818 (22.514–23.110)

Nutrient extraction data is shown in million tonnes (Mt) with 95% confidence intervals shown in parentheses.

potential consequences of nutrient loss. Our final nutrient composition dataset was combined with spatially explicit catch data from the Sea Around Us database[20] for the fisheries record between 1960 and 2018, and for three distinct periods: the 1960s (earliest globally reported fisheries data), 1990s (peak global catch), and 2010s (contemporary fishing effort). Furthermore, we compared our taxa-specific estimates with estimates produced by single, uniform values for C, N, and P reported in the literature[13,15]. Finally, we calculated the molar ratios of the nutrient extractions (hereafter "extraction molar ratios") to examine trends in the relative extractions of the three nutrients.

Results

Nutrient extraction across time

Between 1960 and 2018, industrial fisheries extracted 431.2 ± 1.1 million tonnes (Mt) of C, 110.3 ± 0.2 Mt of N, and 22.8 ± 0.2 Mt of P (Table 2). Nutrient extractions followed similar trends across the 59-year temporal range and, as expected, aligned with trends in industrial catches (Fig. 1a–d). Between the 1960s (lowest recorded fishing effort in the study period) and the 1990s (peak fisheries catch), nutrients removed by industrial fisheries more than doubled. Following peak catch in the 1990s, nutrient extractions decreased by ~13% into the 2010s, leveling off at an average extraction of 7.9 ± 0.1 Mt of C yr^{-1}, 2.0 ± 0.02 Mt of N yr^{-1}, and 0.4 ± 0.01 Mt of P yr^{-1}. Extraction molar ratios of C:N, C:P, and N:P did not show a notable trend, although small variations occurred over time (Fig. 1e–g). However, using uniform nutrient composition values (12.5% C[13], 2.8% N[15], and 0.6% P[15]) masked these small annual variations in extraction molar ratios and consistently overestimated C:N and C:P compared to taxa-specific estimates (Fig. 1e, f). Furthermore, uniform values resulted in annual overestimates of C extractions by 0.3–1.6 million tonnes, equating to a ~15% overestimate per year (Supplementary Fig. 1a).

Spatiotemporal trends in nutrient extractions

To analyze spatiotemporal patterns, we estimated nutrient extractions for 283 Exclusive Economic Zones (EEZs) and 18 high seas regions for a total of 301 marine regions (see the "Methods" section). Between 1960 and 2018, total nutrient extractions varied widely across regions, with the highest levels found in the Cambodian EEZ (76,066 ± 389 kg km^{-2} of C, 20,724 ± 64 kg km^{-2} of N, and 4937 ± 54 kg km^{-2} of P; Fig. 2). The effect of using uniform C, N, and P values for estimates of nutrient extractions varied spatially. For C and N, uniform values overestimated extractions within EEZs and high latitudes, while underestimating extractions in the high seas (Fig. 2a, b). In contrast, uniform values generally overestimated P extractions in the high seas, high latitude EEZs, and several EEZs in Oceania, but underestimated P extractions from the Caribbean, West Africa, and the Mediterranean (Fig. 2c).

Although we observed only minor changes in extraction molar ratios over time, their spatial distributions varied substantially (Fig. 3, Supplementary Figs. 2–4). In most coastal systems, the extraction ratios of N and P relative to C were higher than expected compared to those calculated using uniform composition values (C:N ~ 5.2, C:P ~ 53.8). Conversely, more C was extracted relative to P in the high seas around Oceania and the Antarctic than predicted by uniform values. Compared to N extraction, more P was extracted than expected in many Antarctic seas, coastal areas along Africa, parts of Europe, the Pacific Northwest of the USA, and the Caribbean. Lastly, we found that high-seas fisheries extracted more N relative to P than predicted by using uniform values.

In the 1960s, nutrient extractions were most intense in European EEZs, particularly in northern Europe, as well as the Peruvian EEZ and the east coast of the United States. For this early period, regions that were among the top 10% for extractions removed upwards of 728 kg km^{-2} of C, 156 kg km^{-2} of N, and 38 kg km^{-2} of P. By the 1990s, 213 regions, covering ~78% of the global ocean area, saw an increase in nutrient extractions (Fig. 4) with many regions (n = 151, 67% of global ocean area) more than doubling their extraction rates. Notably, many Indo-Pacific EEZs experienced increased

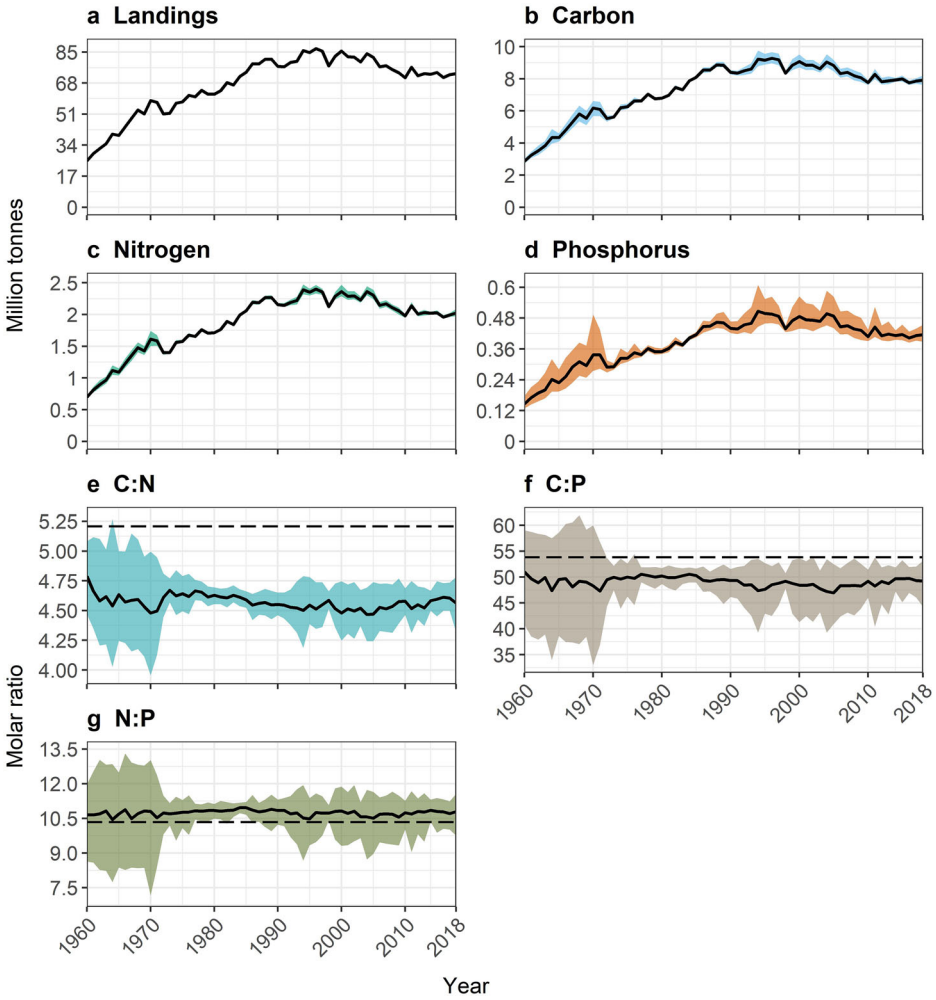

Fig. 1 | Annual nutrient extraction by industrial fisheries between 1960 and 2018. Temporal trends of **a** landings, **b** carbon, **c** nitrogen, and **d** phosphorus extractions and extraction molar ratios **e** C:N (carbon:nitrogen), **f** C:P (carbon:phosphorus), and **g** N:P (nitrogen:phosphorus). Nutrient extraction estimates and extraction molar ratios were calculated as the mean of 100 generated estimates per year, with shaded areas representing the 95% confidence intervals. In the extraction molar ratio plots, dashed lines represent the expected uniform extraction molar ratios based on the following literature-derived uniform nutrient composition values: 12.5% for carbon[13], 2.8% for nitrogen[15], and 0.6% for phosphorus[15].

nutrient extractions by >20× their rates in the 1960s. Moreover, the 1990s saw fisheries extend their operations into the high seas and Antarctic regions, including areas previously untouched by industrial fishing. Contrary to the global trend of rising nutrient extractions throughout the 1990s, the northwestern Atlantic, parts of the Caribbean and Mediterranean, and many islands around the tropical Pacific experienced notable declines.

Following peak catch rates in the 1990s, 160 regions (~31% of the global ocean area) experienced a mean decline of 50% in nutrient extractions by the 2010s (Fig. 4). Conversely, 131 regions (~62% of the global ocean area) exhibited varying levels of increased extractions, ranging from minimal changes to increases of >200% into the 2010s. Tropical/subtropical regions, especially in the Pacific, experienced considerable increases in nutrient extractions. Furthermore, the ongoing expansion of industrial fisheries into the high seas between the 1990s and 2010s caused an average increase of 73% in nutrient extractions across most of these regions.

Nutrient extractions per trophic group

The Sea Around Us estimates trophic levels for targeted organisms, enabling us to classify exploited species into five trophic groups (Fig. 5a) and examine nutrient extraction trends for each group (see the "Methods" section). We found that ~62% of nutrient extractions occurred through the fishing of mesopredators (e.g., herrings and mackerels), followed by high-level predators (e.g., tunas and billfishes; 20% of the total), then low-level consumers (e.g., omnivores/herbivores; 17%; Fig. 5b). In general, nutrient extractions peaked in the 1990s for most trophic groups, followed by a decline in the 2010s (Fig. 5c–e). However, the magnitude of nutrient extractions from each trophic group varied across time periods.

Mesopredators (trophic levels 2.8–4) accounted for the largest nutrient extractions among all trophic groups (Fig. 5b). In total, industrial fisheries extracted 267.7 ± 0.3 Mt of C, 67.0 ± 0.06 Mt of N, and 14.6 ± 0.03 Mt of P through mesopredators (Supplementary Tables 1–3). Across all three time periods, mesopredator removal consistently contributed to the highest extractions across trophic groups (Fig. 5c–e). Extractions through mesopredators followed a similar trend to total nutrient extraction, increasing nearly threefold between the 1960s and 1990s, followed by a ~15% decline in the 2010s. When results from taxa-specific concentrations were compared to extraction estimates using uniform C, N, and P values, we found that uniform values overestimated extractions via mesopredators by ~15% for C, ~3% for N, and marginally for P (Fig. 5f).

Fishing of high-level predators (trophic levels 4-5) accounted for the second largest nutrient extractions between 1960 and 2018 (Fig. 5b). Industrial fisheries extracted 88.9 ± 0.09 Mt of C, 23.3 ± 0.01 Mt of N, and 4.2 ± 0.009 Mt of P through high-level predators. By the 1990s, nutrient extractions through high-level predators had increased by 2.5 times their amounts in the 1960s (Fig. 5c–e). However, during the 1990s, nutrient extraction through high-level predators was nearly equivalent to lower-level species, with each group accounting for less than one-quarter of the total nutrient extractions for that period. Moreover, high-level predators were the only trophic group that saw an increase in nutrient extractions in the 2010s, increasing their contribution to total nutrient extraction to 25% (10.0 ± 0.03 Mt of C, 2.6 ± 0.005 Mt of N, 0.5 ± 0.003 Mt of P; Fig. 5c–e). Compared to taxa-specific estimates, uniform C, N, and P values overestimated extractions from high-level predators by ~10% for C and ~12%

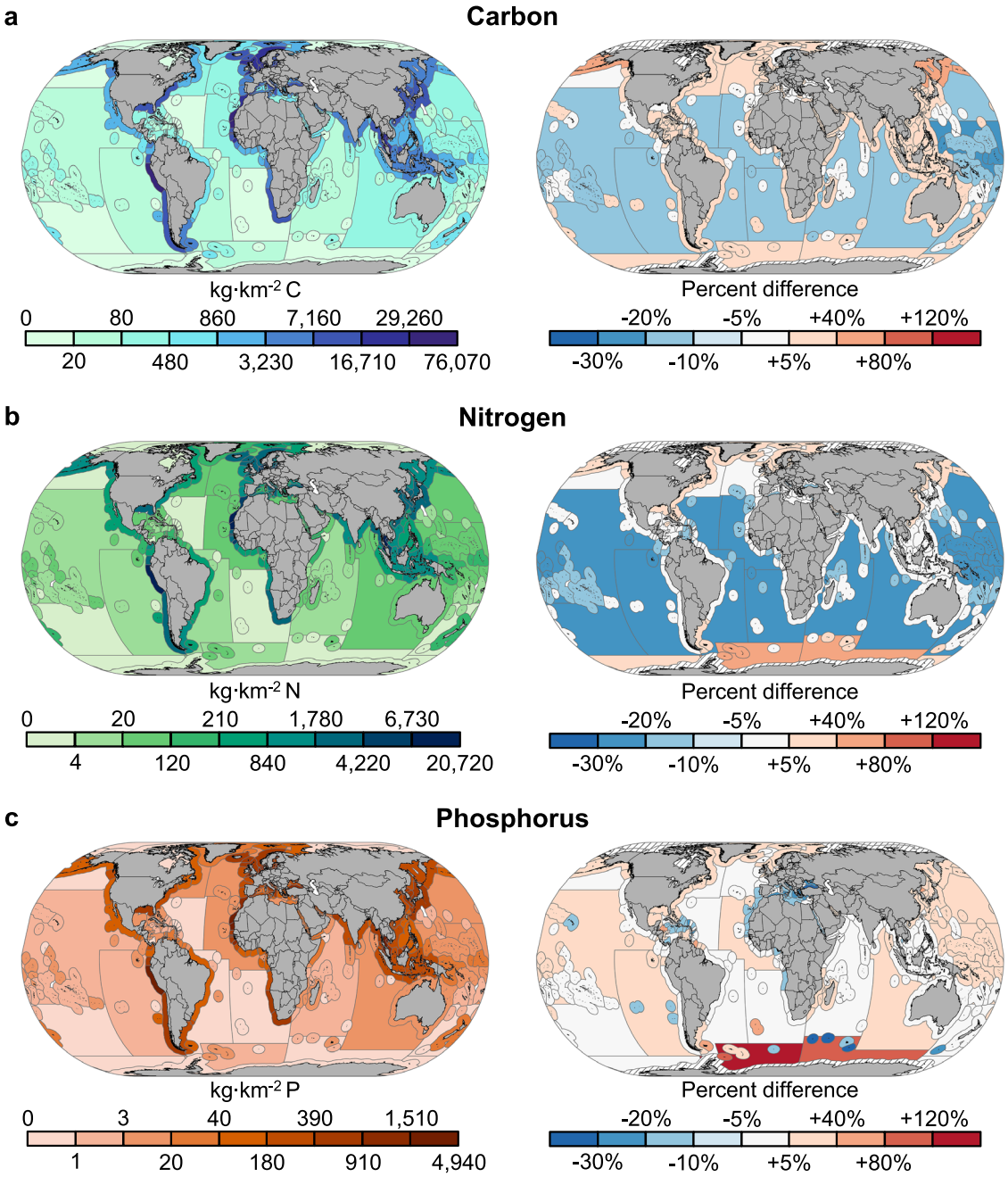

Fig. 2 | Spatial distribution of total nutrient extractions between 1960 and 2018 across Exclusive Economic Zones and high seas regions. The left panels show total nutrient extraction in kilograms per square kilometer (kg km^{-2}) for **a** carbon, **b** nitrogen, and **c** phosphorus. Color scale breaks correspond to the 10th, 30th, 50th, 60th, 70th, 80th, 90th, and 95th percentiles of each nutrient's extraction per square kilometer. Estimates were calculated as the mean of 100 generated values for each spatial region. The right panels display the percent differences in estimates when using uniform nutrient composition values versus taxa-specific models for **a** carbon, **b** nitrogen, and **c** phosphorus. Red (positive) percentages indicate that using uniform values leads to an overestimate, while blue (negative) percentages indicate an underestimate. Uniform nutrient composition values were defined based on literature values as follows: 12.5% for carbon[13], 2.8% for nitrogen[15], and 0.6% for phosphorus[15]. Exclusive Economic Zones and high seas shapefiles provided by the Sea Around Us. Country shapefiles obtained from ESRI.

for P (Fig. 5f). Conversely, uniform values underestimated N extractions from high-level predators by 6%.

Low-level consumers (trophic levels 2–2.8), which included omnivores (e.g., sardines) and herbivores (e.g., parrotfish), accounted for most of the remaining nutrient extractions between 1960 and 2018 (Fig. 5b). Through these low-level consumers, industrial fisheries extracted a total of 74.4 ± 1.1 Mt of C, 19.9 ± 0.2 Mt of N, 4.0 ± 0.2 Mt of P. Nutrient extractions through low-level consumers composed a larger portion of the extractions in the 1960s, accounting for ~28% of all extractions (4.6 ± 0.3 Mt of C, 1.3 ± 0.07 Mt of N, 0.3 ± 0.05 Mt of P) (Fig. 5c–e). By the 1990s, the contribution of low-level consumers to total nutrient extractions fell to ~21% (9.2 ± 0.4 Mt of C, 2.5 ± 0.07 Mt of N, 0.5 ± 0.07 Mt of P). In the 2010s, nutrient extractions from low-level consumers (6.2 ± 0.2 Mt of C, 1.5 ± 0.04 Mt of N, 0.3 ± 0.03 Mt of P) declined faster than total extractions, decreasing by ~38% after the 1990s (Fig. 5c–e). The largest difference between taxa-specific concentrations and uniform values was observed in C extraction estimates from low-level consumers, where uniform values overestimated C extractions by ~22%. For N extractions, there was a

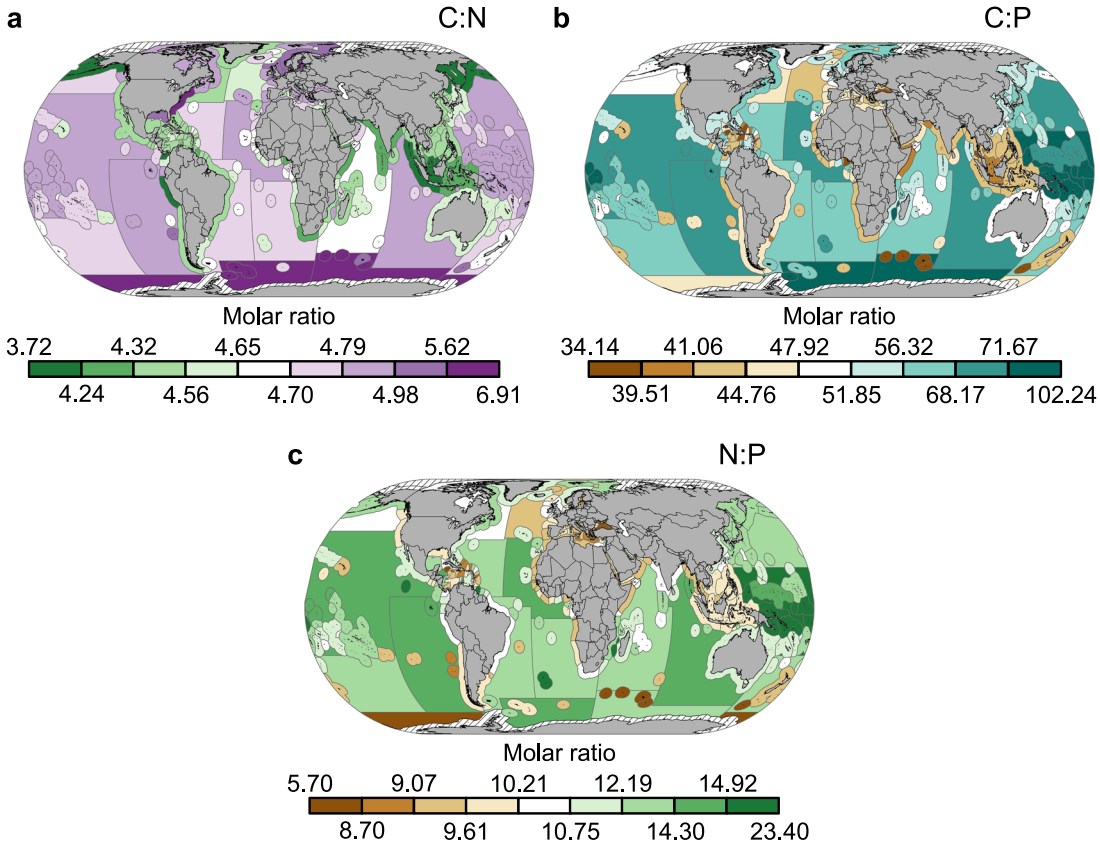

Fig. 3 | Mean extraction molar ratios (i.e., the molar ratios of extracted nutrients) in Exclusive Economic Zones and high seas regions from 1960 to 2018. Estimates of **a** carbon:nitrogen (C:N), **b** carbon:phosphorus (C:P), and **c** nitrogen:phosphorus (N:P) extraction ratios were calculated as the mean of 100 generated estimates for each spatial region. Color scale breaks correspond to the 5th, 10th, 30th, 45th, 55th, 70th, 90th, and 95th percentiles of each nutrient ratio across Exclusive Economic Zones and high seas regions. Hatched areas indicate regions where no nutrient extractions occurred. Exclusive Economic Zones and high seas shapefiles provided by the Sea Around Us. Country shapefiles obtained from ESRI.

minimal overestimation of ~2%, while uniform *P* values overestimated extractions by ~10% (Fig. 5f).

Nutrient extractions across trophic groups also varied spatially. Extractions from most continental EEZs and the northernmost high seas were mainly composed of nutrients from mesopredators (Fig. 6a). In contrast, nutrient extractions from the high seas and the EEZs of tropical and subtropical Pacific islands were dominated by extractions from high-level predators (Fig. 6b). Finally, lower trophic levels dominated nutrient extractions in the Gulf of Mexico, Peru's EEZ, and the waters around Antarctica (Fig. 6c).

Nutrient extractions per functional group

We used the Sea Around Us functional group categorizations to analyze temporal trends in nutrient extraction per functional group (see the "Methods" section). Most nutrient extractions occurred by exploiting three functional groups (15 groups total): pelagics, demersals, and benthopelagics. Together, these three functional groups accounted for ~86% of the total C, N, and P removals by fisheries, although the contribution of different functional groups to extractions varied spatially (Fig. 6d–g). The three major functional groups followed similar temporal trends, with a few exceptions (Fig. 7a–c). When comparing extraction estimates produced from taxa-specific values versus those from uniform values, we found that using uniform values led to both overestimations and underestimations depending on the nutrient and functional group. Specifically, uniform values overestimated C extractions for the top seven functional groups, but underestimated N extractions for pelagics and P extractions for demersals and reef fish (Fig. 7d). Furthermore, invertebrate functional groups (e.g., cephalopods and shrimps) all demonstrated high levels of overestimation across nutrients, especially for P, where we found that uniform values would have overestimated extractions by ~74–182%.

The removal of pelagic species accounted for the largest proportion of nutrient extractions across the 59-year fishing record and dominated extractions from the high seas and many tropical/subtropical EEZs (Fig. 6d). Overall, industrial fisheries extracted a total of 229.2 ± 1.1 Mt of C, 57.8 ± 0.2 Mt of N, and 11.9 ± 0.2 Mt of P through the removal of pelagic species, which accounted for over 50% of all nutrient extractions. Similar to total extractions, nutrient extractions from the removal of pelagic species were lowest in the 1960s before extractions more than doubled in the 1990s (Fig. 7a–c). Proportionally, the contribution of pelagic species to total nutrient extractions was similar between the 1960s and 1990s, representing ~58% and ~54%, respectively. Small- and medium-sized pelagic species (e.g., sardines and scads, respectively) accounted for the majority (~88%) of nutrient extractions within the pelagic group, contributing similarly to the three periods. However, small-sized pelagics had a slightly higher share of nutrient extractions during the 1960s (4.7 ± 0.4 Mt for C, 1.4 ± 0.07 Mt for N, and 0.3 ± 0.05 Mt for P) when compared to medium-sized species (4.7 ± 0.03 Mt for C, 1.0 ± 0.006 Mt for N, and 0.2 ± 0.004 Mt for P; Supplementary Tables 4–6). Although small- and medium-sized pelagic species contributed similarly in the 1990s and 2010s, the overall contribution of pelagic species to nutrient extractions decreased by 8.5% between the two periods. Large-sized species (e.g., tunas and billfishes) consistently contributed the least to nutrient extractions among pelagics. However, unlike the declining trend observed for the smaller pelagic groups, nutrient extractions through large pelagic species increased by ~40% between the 1990s and 2010s.

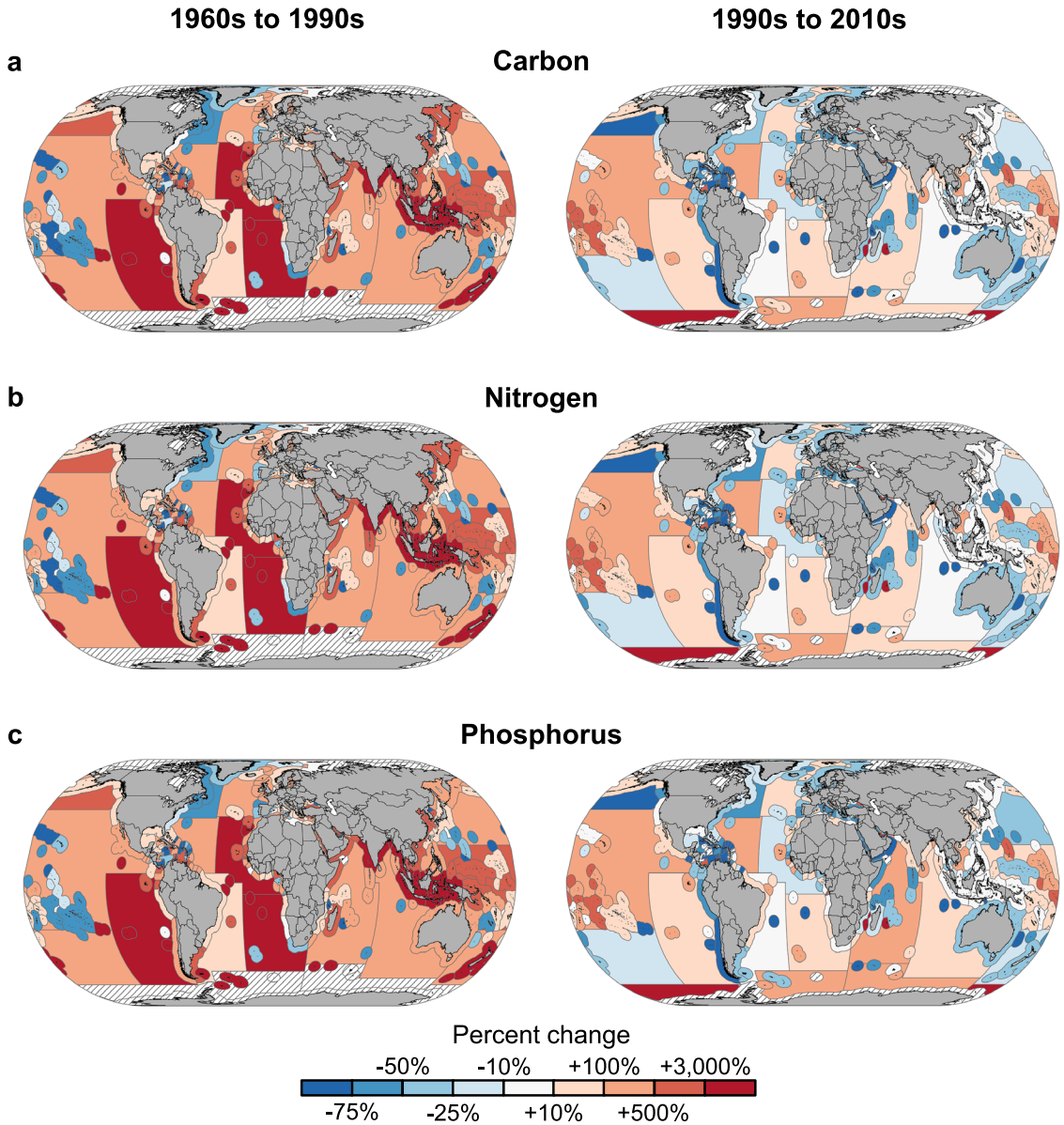

Fig. 4 | Spatiotemporal changes in fisheries-mediated nutrient extractions. Percent change in nutrient extraction per square kilometer for Exclusive Economic Zones and high seas between the 1960s and 1990s (left panels) and between the 1990s and 2010s (right panels) for **a** carbon, **b** nitrogen, and **c** phosphorus. Hatched areas indicate regions where no nutrient extractions occurred in the preceding period. Exclusive Economic Zones and high seas shapefiles provided by the Sea Around Us. Country shapefiles obtained from ESRI.

Demersal species (e.g., haddocks) accounted for the next largest proportion of nutrient extractions (Fig. 7a–c) and played an important role in extractions from EEZs around northern Africa and many Pacific regions (Fig. 6e). Between 1960 and 2018, industrial fisheries extracted 80.0 ± 0.2 Mt of C, 20.7 ± 0.03 Mt of N, and 5.1 ± 0.02 Mt of P by removing demersal species. Unlike pelagic species, nutrient extraction through demersal species was highest in the 2010s, totaling 8.4 ± 0.07 Mt of C, 2.2 ± 0.01 Mt of N, and 0.5 ± 0.006 Mt of P (Fig. 7a–c).

Finally, benthopelagic species accounted for the third largest nutrient extractions (Fig. 7a–c) and contributed to a sizable proportion of extractions from high latitudes (Fig. 6f). In total, industrial fisheries extracted 59.9 ± 0.2 Mt of C, 16.7 ± 0.03 Mt of N, and 3.3 ± 0.02 Mt of P through benthopelagic species. During the 1960s, large-sized species (e.g., Atlantic cod) contributed to the largest proportion of nutrient extractions from benthopelagic species (~62–71%; Supplementary Tables 4–6). However, by the 1990s, ~64% of nutrient extractions from benthopelagic species came from removing medium-sized species (e.g., Alaskan pollock). Nutrient extractions via the removal of benthopelagic species decreased between the 1990s and 2010s, although this decrease was not as strong as that observed for pelagic species.

Discussion

Before the rise of industrial fishing, the transfer of nutrients from the ocean to land was largely limited to specific, localized events like storm-driven seaweed deposits, the upstream journeys of anadromous organisms, and the deposition of feces by seabirds and pinnipeds at rookeries[21,22]. However, industrial fishing has created a substantial new pathway for the large-scale loss of nutrients from the ocean. For example, seabirds and anadromous fish were estimated to transfer ~0.15 Mt yr^{-1} of P inland during the Pleistocene[21]. At their peak, fisheries extracted ~3 times as much P yr^{-1} compared to Pleistocene seabirds and anadromous fish, highlighting the scale of nutrient removal by modern-day fisheries compared to previous natural processes.

Overall, global industrial fisheries removed ~431 Mt of C, ~110 Mt of N, and ~23 Mt of P between 1960 and 2018, with the largest extractions

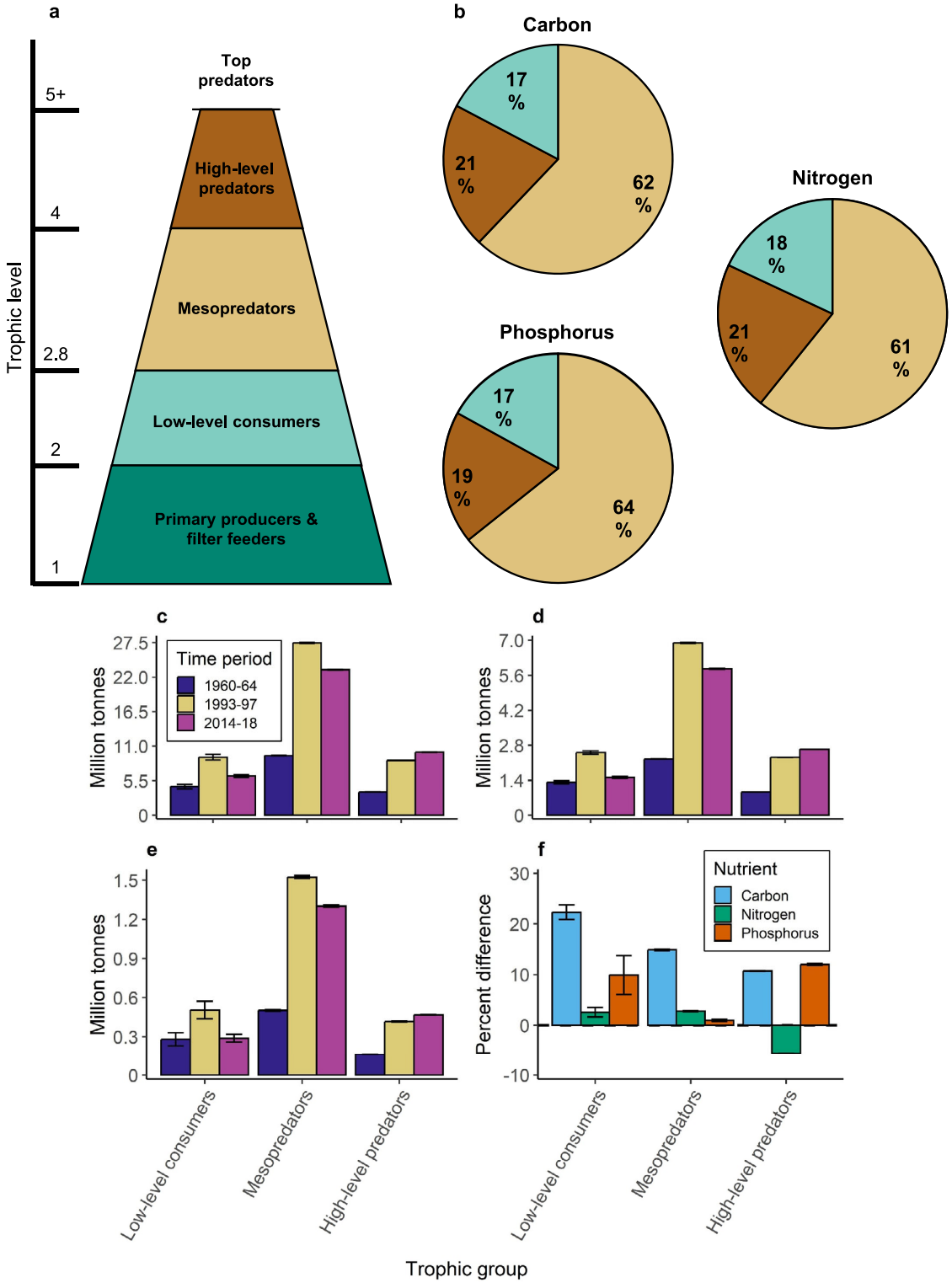

Fig. 5 | Total nutrient extractions by trophic group across time periods. **a** Generalized marine trophic pyramid, adapted from FishBase[64]. **b** Proportion of total carbon, nitrogen, and phosphorus extracted from each trophic group between 1960 and 2018. Total extractions (±1 standard deviation) of **c** carbon, **d** nitrogen, and **e** phosphorus from industrial fisheries for each trophic group for the 1960s, 1990s, and 2010s. Estimates were calculated as the mean of 100 generated values per trophic group, with error bars representing one standard deviation. **f** Percent differences in estimates when using uniform nutrient composition values versus taxa-specific models for carbon, nitrogen, and phosphorus. Positive percentages indicate that using uniform values leads to an overestimate, while negative percentages indicate an underestimate. Uniform nutrient composition values were defined based on literature values as follows: 12.5% for carbon[13], 2.8% for nitrogen[15], and 0.6% for phosphorus[15]. Trophic levels below 2 (primary producers and filter feeders) and above 5 (top predators) accounted for <0.1% of the total catch and are therefore not included in the bar graphs.

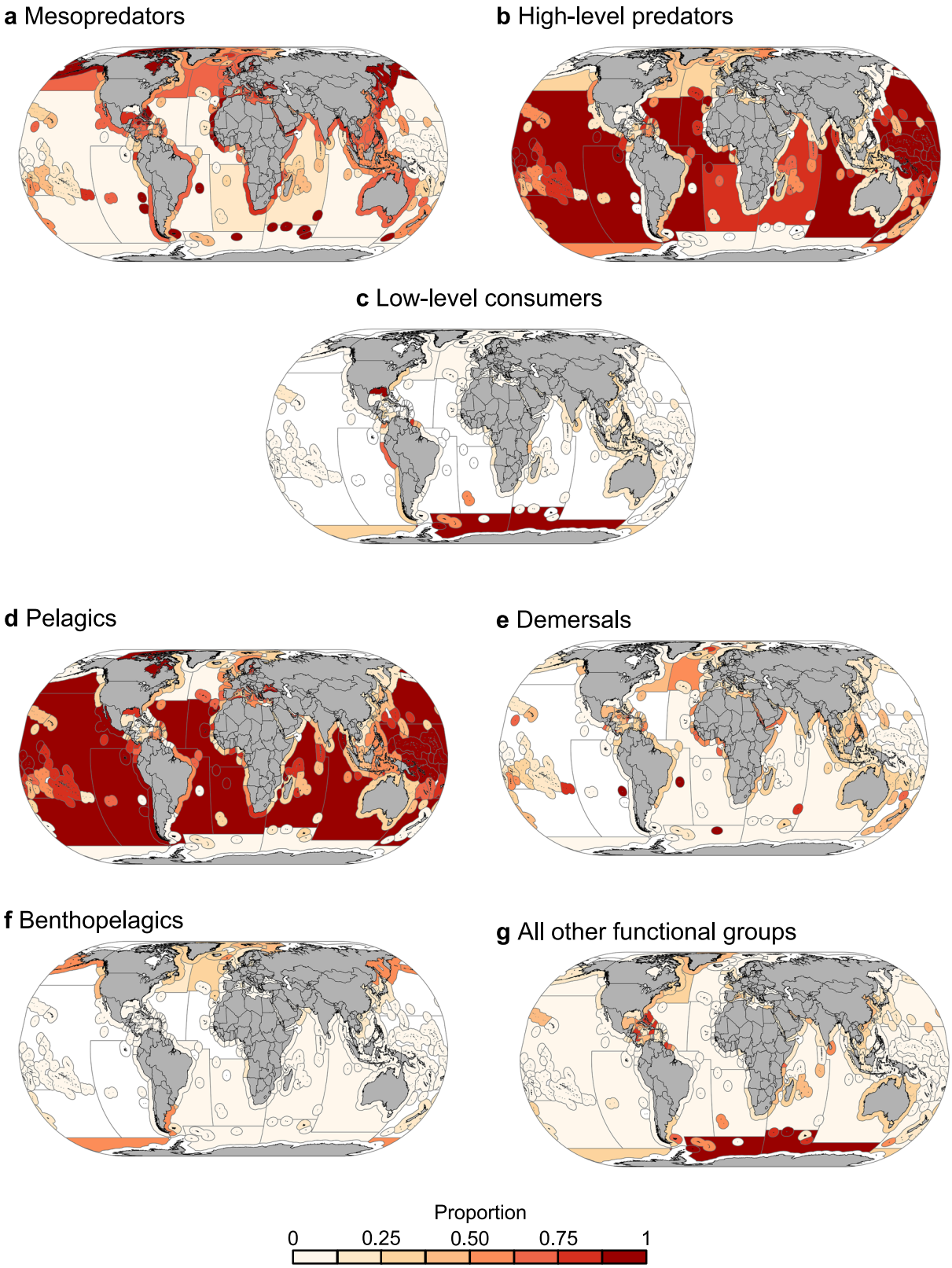

Fig. 6 | Proportion of total carbon extracted from trophic and functional groups across different Exclusive Economic Zones and high seas regions. Panels represent extractions by trophic groups **a** mesopredators, **b** high-level predators, **c** low-level consumers, as well as functional groups: **d** pelagics, **e** demersals, **f** benthopelagics, and **g** all other functional groups. Exclusive Economic Zones and high seas shapefiles provided by the Sea Around Us. Country shapefiles obtained from ESRI.

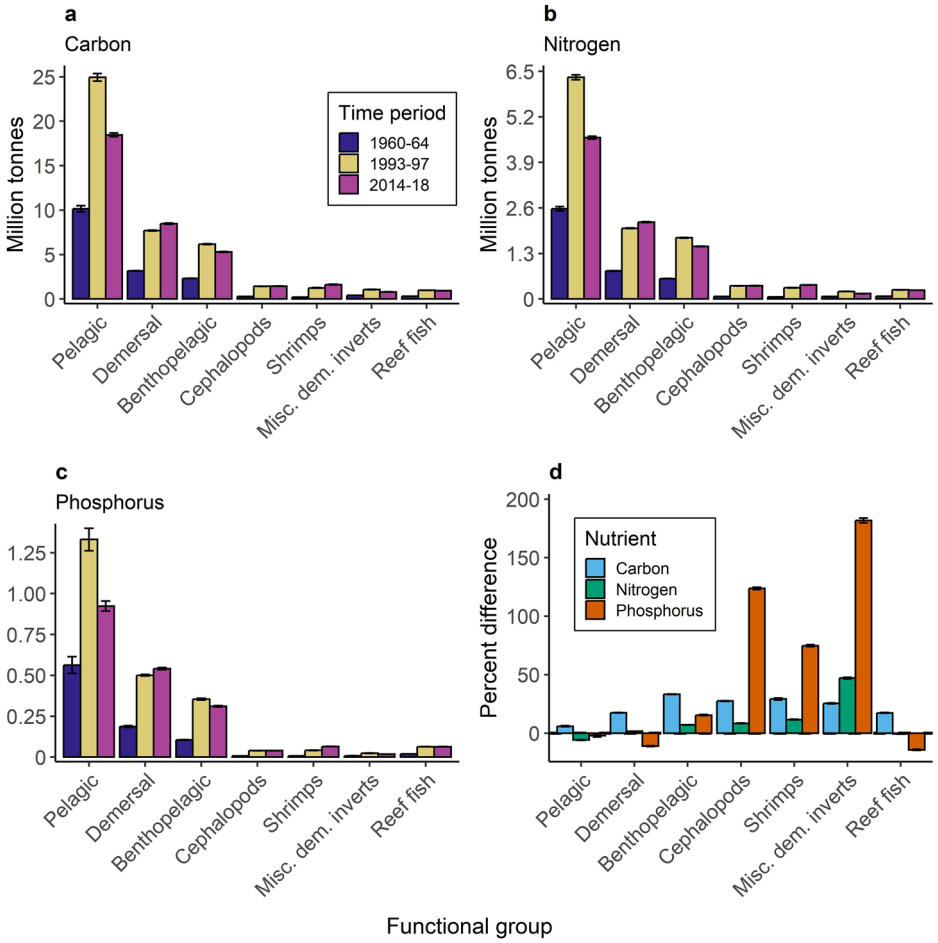

Fig. 7 | Nutrient extractions by functional group across time periods. Total extractions (±1 standard deviation) of **a** carbon, **b** nitrogen, and **c** phosphorus from industrial fisheries for each functional group during the 1960s, 1990s, and 2010s. Estimates were calculated as the means of a distribution of 100 generated estimates for each functional group, with error bars representing 1 standard deviation. **d** Percent differences in estimates when using uniform nutrient composition values versus taxa-specific models for carbon, nitrogen, and phosphorus. Positive percentages indicate that using uniform values leads to an overestimate, while negative percentages indicate an underestimate. Uniform nutrient composition values were defined based on literature values as follows: 12.5% for carbon[13], 2.8% for nitrogen[15], and 0.6% for phosphorus[15]. Functional groups that made up less than 2% of the total catch are not shown.

occurring along the coasts. Extraction molar ratios (i.e., the molar ratio of C, N, and P extractions) remained fairly consistent over time. However, spatial differences in extraction molar ratios reveal how the selective targeting of species, which vary in their body composition of C, N, and P relative to biomass, influence geographic patterns in nutrient extractions.

Our global estimates of annual and total removals of C, N, and P via fisheries generally agree with previous studies, though they differ considerably from others[11,12,14,23] (Table 1). These differences mainly arise from each study's distinct assumptions and methodologies. For instance, our estimates for N and P are ~50% less than those from Le Mézo et al.[15], but that study acknowledged that its models might overestimate extractions by up to 50%, which likely explains the discrepancy. Despite the variation in the nutrient composition of exploited species, the consistency of our results with earlier studies suggests that global estimates of nutrient removals by fisheries are fairly robust across different methodologies. This is unsurprising, as the aggregate data reflect that only a few dominant species, mainly finfish, have driven global fisheries catches since the 1960s. However, including detailed taxa-specific nutrient data in our study provides a more quantitatively accurate and ecologically relevant view of nutrient extraction by industrial fisheries, particularly across space. Our unique approach reveals that the selective nature of fishing influences the relative extractions of C, N, and P, highlighting the previously unrecognized, dynamic effect of fisheries on biomass-stored nutrients. Thus, our approach not only quantifies the magnitude of fisheries extractions but also their potential for ecological consequences, providing insights beyond the basic patterns visible from the biomass data alone.

Differences in the spatial and temporal patterns of fisheries-mediated nutrient extractions are driven by various factors shaping the demand for wild-caught fish. Events such as political changes (e.g., Brexit)[24], health advisories (e.g., heavy metal warnings on tuna)[25], advancements in technology, the establishment of no-take reserves[26], changes to legislation regulating fisheries management[27], and changes in fish populations (e.g., the decline of the Atlantic cod)[28], have led to intricate changes in the types, locations, timings, and quantities of species that are targeted. Despite the complexity of these influencing factors, there is a noticeable preference for targeting predatory species, especially mesopredators. Mesopredators, such as herring, were consistently responsible for at least 60% of total nutrient extractions between 1960 and 2018.

We found that, on average, targeted predatory species store higher proportions of C, N, and P than other trophic groups, which suggests a potentially greater reduction of biomass-stored nutrients through the removal of predatory species. However, we observed varied nutrient concentrations within this group, leading to spatial differences in the molar ratios of nutrient extractions. Catches of mesopredators were concentrated primarily along continental shelves and overlapped with regions showing lower C:P, N:P, and, to a lesser extent, C:N extraction molar ratios. These lower ratios suggest that, per unit of biomass, mesopredators store relatively greater amounts of limiting nutrients (N & P) than other trophic groups. Therefore, disproportionately removing mesopredators may diminish the ecosystem's pool of nutrient-rich biomass and reduce the availability of nutrient-rich prey for higher-level predators.

High-level predators are doubly at risk from fisheries, as they not only compete with fisheries for prey but have also increasingly become direct targets of the fishing industry. Extractions from high-level predators rose by ~15% between the 1990s and the 2010s, opposite the trend observed for the other trophic groups. While reducing the number of high-level predators could theoretically help rebalance ecosystems where mid-level mesopredators have been heavily fished, our results highlight a spatial mismatch

between these groups. Most high-level predator extractions occur in the high seas, whereas mesopredator extractions are concentrated within EEZs. However, some high-level predators are transient and feed in shallower nearshore environments. In these cases, increased targeting of transient predators may help mitigate the cascading effects caused by exploiting mid-tier trophic levels in previous decades.

Catches in high seas regions are dominated by tunas and billfishes, which we estimate store ~50% more C than other high-level predators (e.g., cods and haddocks; Supplementary Data 2) and play a key role in deep-sea nutrient fluxes. As these larger pelagic organisms tend to have fewer natural predators, their sinking carcasses provide critical pulses of nutrients to the seafloor. This process is important for C sequestration in the ocean because bodies that sink below 1000 m contribute to long-term C storage in deep-sea environments[13]. Since most biomass caught by fisheries is either consumed or disposed of in landfills, removing predators from the ocean means their biomass will be remineralized to CO_2[13]. Thus, when converting the amount of extracted C to CO_2 equivalents, we estimate that fisheries-mediated C extractions produce approximately 29 Mt of CO_2 annually. Of this total, about a quarter comes from extracting high-level predators, particularly on the high seas.

Much like the variations observed within trophic groups, we observed variations in extraction molar ratios within functional groups. Notably, small-sized pelagic species, which comprised ~21% of the total catch, displayed notable spatial differences in extraction molar ratios driven by differences in nutrient compositions. For example, anchoveta (*Engraulis ringens*) have higher N compositions relative to C and drove the low C:N extraction molar ratios of 4.0–4.5 along western South America. Conversely, Atlantic herring (*Clupea harengus*) have relatively lower N compositions to C, resulting in the observed C:N ratios of ~5.3 in the northeast Atlantic. Thus, even when targeting functionally similar species, the selective nature of fisheries can have highly varied impacts on biomass-based nutrient storage worldwide.

The impacts of removing targeted species extend beyond the loss of biomass-stored nutrients. Exploiting mid-tier trophic level species—and depleting this nutrient-rich biomass—can substantially disrupt nutrient flow to higher trophic levels, ultimately altering the structure of marine food webs. In less-fished parts of the ocean, biomass distribution often forms an hourglass shape[29]. These top-heavy systems are attributed to high-level predators consuming a broad range of prey sizes[30]. This diversity in diet allows for a surprisingly large accumulation of biomass in higher-level predators, which is supported not only by the trophic level directly beneath them but also by prey from lower levels. However, intense fishing pressure that disproportionately removes biomass and nutrients from mid-trophic levels threatens the balance of such ecosystems. If high-level predators, including marine mammals, which are no longer exploited, compensate for the depletion of mid-level prey by switching to even lower-level organisms (e.g., small sardines), it could result in a trophic cascade. On the other hand, if these predators cannot compensate for the loss of mid-level prey, as might be the case in areas like the eastern United States where mesopredators (e.g., Atlantic menhaden)[31] are heavily targeted, there could be a top-down collapse of the food web.

The size-selective aspect of fisheries and their impact on nutrient supply should also not be ignored. The size structure of targeted species had decreased due to various factors, including those unrelated to fishing (e.g., warmer water temperatures)[32–36]. These changes likely affect nutrient storage, retention, and supply rates because fish size is positively linked with longevity, metabolism, and excretion rates[11,37,38]. For example, Allgeier et al.[39] found that fish size structure and the average maximum size per species predicted nutrient supply and storage in coral reefs, mangroves, and seagrasses. Specifically, that study observed that ecosystems with larger fish had higher supplies of N and P and greater storage of C, N, and P[39]. Therefore, ecosystems where larger individuals are disproportionately targeted are likely to experience greater reductions in fish-stored nutrients.

Moreover, the unique ecological roles of fish across trophic and functional groups remain crucial[11,40]. For instance, removing high-level predators can also have far-reaching and complex effects on ecosystems[41,42]. For example, a past study found that N and P excretion rates from gray snapper at unfished sites in the Bahamas were 456% and 541% higher, respectively than at fished sites[43]. Consequently, the strength of N and P co-limitation on primary production was weaker at unfished sites compared to fished ones. Another study found that predators disproportionately supply P to marine systems relative to their biomass[39]. Additionally, pelagic, demersal, and benthopelagic species, which account for ~87% of all extractions, contribute to nutrient fluxes across the water column and ecosystems. Small pelagic species, which make up about 20% of C extractions, are also estimated to contribute 12–16% to deep-sea C sequestration via their fecal pellets and deadfall[40,44]. Certain benthopelagic species, such as anadromous salmon, are essential for transferring nutrients from marine to inland ecosystems during spawning migrations upriver[45–47]. Yet between 1960 and 2018, the removal of salmon before they could reach their spawning rivers led to the loss of 2.74 Mt C, 0.6 Mt N, and 0.1 Mt P, likely reducing stream and lake primary productivity[45,48]. Therefore, the effects of disproportionate fishing pressure across ecological groups may exacerbate nutrient limitation, limiting primary and secondary productivity.

However, past studies have suggested that human activities add more C, N, and P to the ocean than what is lost through industrial fishing, potentially mitigating fisheries' impacts on nutrient availability[12,14,15,49]. Yet this view oversimplifies the ocean's nutrient cycles. Most of the ocean's yearly productivity predominantly depends on effectively recycling nutrients within its waters. Only about 10−20% of the ocean's net primary production is fueled by nutrients from the atmosphere, rivers, and upwelling[50,51]. For instance, of the 21 Mt of P annually transported to the ocean from rivers, only 10% is accessible to marine organisms[52]. The rest of the P quickly sinks, bound to soil particles, and becomes buried in the seafloor. Therefore, the amount of biologically active P added to the ocean from rivers might only be ~2 Mt yr^{-1}, indicating that the organic P directly removed by fisheries could roughly account for 20% of this input.

Furthermore, anthropogenic activities have also accelerated N inputs substantially faster than P, increasing the N:P ratio of global inputs from 19:1 in the 1980s to 30:1 in 2020[53]. This shift in N:P ratios can intensify P limitation in aquatic systems, which then influences the structure of aquatic communities[54]. Fisheries may contribute to this P limitation by extracting organisms rich in P relative to N and C, especially in EEZs, where mean extraction molar ratios were ~51 and ~10 for C:P and N:P, respectively. Additionally, extraction molar ratios are lower than the global average stoichiometric ratios for phytoplankton and seawater (C:P = 106 and N:P = 16). Consequently, the removal of marine nutrients and the disturbance of the natural nutrient cycling processes performed by fish[2] could influence spatial and temporal patterns of nutrient limitation in the ocean. The opposing effects of anthropogenic nutrient additions from rivers and the atmosphere versus nutrient removals by fisheries create a complex and uncertain picture of their overall impact on ocean systems and nutrient cycling[55]. Therefore, robust studies considering the combined effects of nutrient additions and removals are urgently needed at local and regional scales.

The global scale of our study limits our ability to thoroughly assess the extent to which fishery-based nutrient extractions influence nutrient dynamics at the ecosystem scale. This limitation arises from several factors: only ~67% of the Sea Around Us catch data is reported at the species level, there is insufficient data on the nutrient composition of several species and how it varies across regions and age classes, and there are uncertainties associated with the global catch data. Local and regional studies that more accurately capture nutrient variations in targeted organisms, the role of fisheries species in ecosystem nutrient dynamics, and variations in fisheries catch will enhance our understanding of how fisheries impact ecosystem-level nutrient dynamics[10,56].

Fishery-based nutrient extractions represent another way humans are increasingly altering nutrient flows within and between ecosystems[57–59]. This study highlights temporal and spatial patterns in the ecological characteristics of targeted species that drive fisheries-mediated nutrient extractions from the ocean. These spatiotemporal changes likely affect how and to what extent

fisheries impact nutrient dynamics in marine ecosystems. Thus, although general patterns in global estimates of nutrients extracted by fisheries from 1960 to 2018 using biomass-based estimates are relatively reliable, the specific effects of these extractions—and ongoing losses—on ecosystem structure and function are context-dependent and require further studies[11]. Moreover, understanding how fisheries influence ecosystem processes, especially resilience and recovery, through nutrient supply and storage will provide important insights to inform fisheries policy and strengthen support for ecosystem-based fisheries management[60]. As fisheries policy and management aims to rebuild depleted stocks and ensure sustainable fisheries for the future[26,61,62], supporting the restoration of essential nutrient pathways could simultaneously improve ecosystem health and stability.

Methods

Industrial catch data

We used the Sea Around Us (www.seaaroundus.org) reconstructed catch data for the period between 1960 and 2018[20]. The Sea Around Us database is based on fisheries landings data reported to the United Nations' Food and Agriculture Organization (FAO) and is complemented with catch data from various fisheries neglected by national governments, notably subsistence and recreational fisheries, as well as discards from industrial fisheries, to provide an estimate of global marine fisheries catches[63]. The Sea Around Us categorizes catch data by fishing sector (industrial, artisanal, subsistence, recreational), fishing country, catch type (landings or discards), reporting status (reported or unreported), functional group, and commercial group. While estimates of unreported catches carry a degree of uncertainty, so do reported data which are also based on estimates and/or varied sampling methods[63]. Therefore, we included both reported and unreported data in our analyses to better capture trends in fisheries landings over time. However, to minimize uncertainties in the taxonomic resolution of the estimated landings, we excluded data from 1950 to 1959 because these data are largely extrapolated from reports from the 1960s and, therefore, have greater taxonomic uncertainty[20]. Furthermore, we chose to focus solely on industrial fisheries (~74% of total landings) as these have been better documented than small-scale and subsistence fisheries[63].

To quantify nutrient extractions across different ecological contexts, we used the Sea Around Us database to assign functional and trophic groups to all organisms in our dataset. The Sea Around Us defines functional groups based on a species' habitat preferences, feeding habits, and maximum size, including benthopelagic and demersal groups. While benthopelagics can be considered a subset of demersal species, the Sea Around Us defines benthopelagic species to be those that inhabit and feed across the water column, and demersal species as those that inhabit the bottom and feed on benthic organisms. Additionally, the Sea Around Us subdivides some functional groups into size-based categories (e.g., small-, medium-, and large-sized pelagic species; see Supplementary Tables 4–6). To facilitate comparisons among groups in our analyses (e.g., pelagics vs. demersals), we aggregated estimates across the size-based categories and reported results of these combined functional groups ($n = 15$) and the full list of groups ($n = 30$; Supplementary Tables 4–6). Trophic levels of exploited species, which are estimated from diet composition data in FishBase[64] and SeaLifeBase[65], were categorized into trophic groups, which include primary producers/filter feeders (TL < 2), low-level consumers (TL ≧ 2 and <2.8), mesopredators (TL ≧ 2.8 and <4), high-level predators (TL ≧ 4 and <5), and top predators (TL ≧ 5).

To illustrate spatial patterns in nutrient extractions, we quantified extractions within the geopolitical boundaries of EEZs (based on definitions by the Flanders Marine Institute[66]) and high seas regions (based on the United Nations Convention on the Law of the Sea). The latter's definition states that the high seas are all areas of the ocean that are beyond the limits of EEZs and national jurisdictions.

Nutrient composition database

We assembled an extensive dataset on the bodily C, N, and P compositions for 330 species of fishery-targeted organisms. We gathered nutrient composition data from published studies, reports, and nutrient datasets containing C, N, or P bodily compositions for wild-caught or aquaculture-raised organisms (Supplementary Data 1). We collected bodily C, N, or P data for any species and higher-level taxonomic grouping (e.g., family) with industrial fisheries catches in the Sea Around Us database. Additionally, we collected data for species that do not have catches reported in the Sea Around Us database but belonged to taxonomic groups (up to the level of order) caught by industrial fisheries. The inclusion of these additional species helped to supplement the nutrient composition data of targeted taxonomic groups with limited or no information on bodily nutrient compositions.

To ensure a consistent and high-quality dataset, we adhered to the following rules to search for data and compile our dataset. (1) Since species may display ontogenetic differences in nutrient composition[67,68], we did not collect bodily nutrient composition data reported from larvae, fry, or fingerlings. However, we did collect data from juveniles when only data from juvenile specimens were available for a given taxon (accounted for 15 observations). (2) In some cases, studies presented their data as the average of multiple categorical or experimental groupings, while others provided data for each individual grouping. To maintain consistency in our dataset, we calculated the arithmetic mean body nutrient composition when data were not already averaged, or when categorical/experimental groupings were present in the original source. (3) Since catch data were reported as wet-weight biomass (also known as fresh- or live-weight biomass), we converted all nutrient composition data reported on a dry-weight basis to a wet-weight basis using the following equations:

$$K_W = K_D * \left(1 - \frac{M}{100}\right) \quad (1)$$

$$K_D = K_W / \left(1 - \frac{M}{100}\right) \quad (2)$$

where K_W represents nutrient composition in grams per 100 g on a wet-weight basis and K_D represents nutrient composition in grams per 100 g on a dry-weight basis as reported in the original source (Supplementary Data 1). M represents the moisture composition in grams per 100 g on a wet-weight basis as reported in the original source. (4) We included only studies that analyzed whole-body C, N, or P composition; studies that reported nutrient data for only one body part or organ (e.g., muscle) were not included.

Our full dataset comprised a total of 777 observations across all three nutrients representing 330 species and 29 functional groups. In total, those 330 species accounted for ~50% of the industrial landings between 1960 and 2018. Across the 777 observations, bodily wet-weight compositions ranged from 0.02−22.4% C, 0.01–4.6% N, and 0.004–2.0% P.

Predictive models for nutrient composition

We estimated missing C, N, and P composition data for organisms by developing linear mixed-effects models that predicted the C:N, C:P, and N:P ratios of industrial fishery-targeted organisms. For organisms and taxonomic groups with at least one reported nutrient, we used these modeled nutrient ratios to derive missing nutrient compositions. Prior research has shown linear mixed-effects models to be an effective method for predicting bodily stoichiometric relationships in fish based on bodily nutrient compositions and taxonomic groupings[56]. To test if a single reported nutrient could adequately predict nutrient ratios, we ran linear mixed-effects models with bodily nutrient composition and a vertebrate/invertebrate (V/I) classification as the fixed effects and taxonomic grouping as the random effect. Additionally, we included an interaction term between the bodily nutrient composition and V/I classification to account for different stoichiometric relationships among vertebrates and invertebrates. For each nutrient ratio, the starting fixed structure was:

$$R_P = \beta_0 + \beta_1 K + \beta_2 V.I. + \beta_3 (K * V.I.) + \varepsilon \quad (3)$$

where R_P is the predicted nutrient ratio, K is the observed bodily nutrient composition, and VI represents the binary V/I classification. We developed competing models for each nutrient ratio with the same starting fixed structure but different random structures. We tested models that included taxonomic grouping as a random effect on the intercept alone, as well as on both the intercept and the slope of parameter K (β_1). Additionally, we included nested taxonomic groupings (e.g., genus nested within the family) as possible random effect structures when generating the competing models. Each model set was assessed using the Akaike Information Criterion (AIC). After identifying the optimal random effect structure, we compared different fixed effect structures to determine if the V/I classification and interaction term were significant and should remain in our models. Lastly, we checked that all assumptions for mixed-effects models were met.

After assessing all competing models, we designated a single model structure for all nutrient ratio predictions because, when random effects were accounted for, this single model structure was able to explain at least 75% of the variation in nutrient ratios across all model sets (Supplementary Table 7). The model structure had the same fixed structure as the starting fixed structure described above with a genus nested within the family random effect structure on the intercept and slope of parameter K (β_1).

For each observation with at least one reported nutrient and an associated random effect for the corresponding taxonomic group, we used the linear mixed effects model to generate a distribution of 10,000 nutrient ratios incorporating parameter uncertainty, random effects, and residual error. We then calculated the mean and standard deviation of the unobserved nutrient ratios from these distributions. In cases where observations had data for at least one nutrient, but no random effects estimated for the corresponding taxonomic group, we sampled 10,000 random effect values from a multivariate normal distribution with mean 0 and a variance–covariance matrix based on the model's estimated random effects. We then predicted nutrient ratios as stated above, using each of the 10,000 sampled random effects values to incorporate uncertainty in nutrient composition estimates for taxa with incomplete nutrient data.

We then estimated missing C, N, and P compositions for organisms based on their observed nutrient compositional data and the predicted nutrient ratios for each observation. We first generated a normal distribution of 10,000 predicted nutrient ratios from the mean and standard deviations estimated above to account for the uncertainty in our nutrient ratio predictions. Then, we calculated 10,000 values for each missing nutrient composition value based on the observed nutrient compositional data and the 10,000 predicted nutrient ratios generated by the normal distribution. Finally, we calculated the arithmetic mean and standard deviation of the 10,000 predicted values for use in subsequent analyses.

Nutrient compositions for higher-level groups and data-sparse species

Approximately 68% of the industrial landings across the 59-year fisheries record were reported to the species level, and a substantial portion was reported at the genus level or above. To estimate nutrient extractions from catch data reported for these higher-level taxonomic groups, we aggregated our empirical and predicted nutrient data at the species level to generate C, N, and P compositions at the genus level, and then up to each subsequent taxonomic level (Supplementary Data 2). For each higher-level taxonomic group, we calculated the mean and standard deviation of nutrient composition values based on the corresponding species in our nutrient database. To reduce the influence of over-represented species in our calculations, we calculated the mean and standard deviations of nutrient composition values for each species represented in our dataset. To account for compounding uncertainty among our observed and predicted values, we calculated the compounded standard deviation for nutrient compositions as:

$$S_C = \sqrt{\frac{\sum_{i=1}^{n} S_i^2 + (K_i - K_M)^2}{n}} \quad (4)$$

where S_C is the compounded standard deviation for the species, $S^2{}_i$ is the variance of the nutrient composition for observation i, and K_i is the nutrient composition (proportion of mass composed of either C, N, or P) for observation i. K_M is the mean nutrient composition (proportion of mass composed of either C, N, or P) for the species and n is the total number of nutrient composition values for that species. After calculating the means and standard deviations at the species level, we calculated the means and standard deviations of nutrient compositions for all taxonomic levels from genus to phylum from the observed and estimated values for each taxonomic group's corresponding species. Once again, we calculated a compounded standard deviation for each taxonomic group to account for the uncertainty across each taxonomic group's mean nutrient composition values.

Even after the above calculations were made, several taxa still lacked nutrient composition estimates. For these taxa, we assigned the mean nutrient compositions and standard deviations from the next lowest taxonomic level available. For example, if a species had no nutrient composition data available, but a mean and standard deviation of nutrient composition were available for its genus, we assigned the genus-level values to the data-deficient species. This process ensured that all species and taxonomic groups with reported industrial fisheries catches were assigned a C, N, and P composition (Supplementary Data 2).

Estimating nutrient extraction

To convert the total catch by industrial fisheries to total nutrient extraction, we used the following equation:

$$E = \sum_{i=1}^{n} L_i * K_i \quad (5)$$

where E is the annual nutrient extraction (tonnes yr^{-1} of C, N, or P), L_i is the total landed amount (tonnes yr^{-1}) for species/group i, and K is the corresponding whole-body nutrient composition (proportion of mass composed of either C, N, or P) for species/group i.

Total catches (tonnes yr^{-1}) for each species and taxonomic group caught in an EEZ or high seas region between 1960 and 2018 resulted in a catch database of over 6.7 million entries. For each entry's species/taxonomic group, we randomly sampled 100 composition values for each nutrient from a normal distribution characterized by each species/taxonomic group's mean nutrient compositions and standard deviations. These 100 random composition values were then multiplied by the total landed amount, as defined in the equation above, to generate 100 estimates of nutrient extraction for each entry in the catch database. From these 100 estimates of nutrient extractions, we took the mean as the estimated C, N, and P extraction values for each of the 6.7 million entries in the database. We also calculated the standard deviations and 95% confidence intervals from the distribution of 100 estimates generated for each of the entries.

To provide a comparison between our estimates and those produced by previous studies, we generated estimates of nutrient extractions using uniform nutrient compositions reported in other studies. Specifically, we used the following values from the literature: 12.5% C[13], 2.8% N[15], and 0.6% P[15]. Substituting these values for K_i in Eq. (5), we calculated the following uniform estimates:

$$\text{Carbon} : E = \sum_{i=1}^{n} L_i * 0.125 \quad (6)$$

$$\text{Nitrogen} : E = \sum_{i=1}^{n} L_i * 0.028 \quad (7)$$

$$\text{Phosphorus} : E = \sum_{i=1}^{n} L_i * 0.006 \quad (8)$$

where E is the annual nutrient extraction (tonnes yr^{-1} of C, N, or P) and L_i is the total landed amount (tonnes yr^{-1}) for species/group i. We then

calculated both the absolute and percent difference between these uniform estimates and our species-specific estimates to assess how the use of uniform values might over- or underestimate nutrient extractions across time, space, and ecological groups.

Additionally, we calculated the molar ratios of the extracted nutrients (i.e., extraction molar ratios) from the estimates generated above. Specifically, we took the distribution of 100 estimates produced for each nutrient and calculated the ratios as follows:

$$R_E = \left(\frac{K_a}{K_b}\right) * \left(\frac{m_b}{m_a}\right) \quad (9)$$

where R_E is the estimated nutrient molar ratio, K_a and K_b are each the estimated extracted amount of C, N, or P, and m_a and m_b are the molar masses of K_a and K_b, respectively. This equation was applied to each pair of the 100 extracted estimates between two nutrients to generate distributions of 100 molar ratios of C:N, C:P, and N:P for each year, region, and ecological group. We then took the mean of each distribution to be the estimated extracted nutrient ratio. Additionally, we calculated the standard deviations and 95% confidence intervals from the distribution of 100 estimates generated for each of the entries.

Mapping nutrient extraction

We calculated nutrient extraction for all 283 modern-day EEZs and 18 high-seas regions. To account for the different sizes across geographical regions, we standardized total nutrient extraction within each region to a kg km^{-2} basis. Additionally, we subset nutrient extraction for three time periods: 1960–1964, 1993–1997, and 2014–2018, and then calculated the differences between these periods to look at spatiotemporal trends in nutrient extractions. These time periods represent the earliest recorded 5-year period within the catch database (1960–1964), peak catches (1993−1997), and contemporary fishing effort (2014–2018). For simplicity, we referred to these time periods as the 1960s, 1990s, and the 2010s. It is important to note that we mapped nutrient extraction to modern-day geographical boundaries, which we used for geographical reference alone. These boundaries are the same for all maps and do not necessarily represent historic boundaries for any of the three time periods.

Uncertainties and limitations

Prior research has demonstrated that functional/trophic group categorizations were unable to account for variations in bodily nutrient compositions among marine organisms[11]. Instead, Allgeier et al.[56] demonstrated that taxonomic identity best explained variations in bodily nutrient content, with representative data at the family level required to accurately estimate nutrient compositions. For our study, we aggregated nutrient compositions from 126 fisheries-targeted families, which represented ~80% of the total landings. However, the representation of the three nutrients in the dataset varied. Nitrogen and P data were widely available at the family level, accounting for ~80% and ~74% of the landings, respectively. Conversely, C data was limited to only 80 species from seven families, which only represented 3% of all landings. Because most of the C data was reported on a dry-weight basis, it was mainly used to generate the nutrient ratio linear mixed-effects models. Specifically, this meant that C compositions predicted by our models were taxonomically limited in scope and increased uncertainties in our C composition estimates. Furthermore, when estimating C extraction, most C compositions also had to be inferred from taxonomic group averages. This lack of bodily C data signals a strong research gap in understanding variation in bodily C content across marine organisms. Nevertheless, correlations between single elements still provide a suitable avenue for predicting missing nutrient compositions such as C[56].

The Sea Around Us catch database inherently has multiple uncertainties and limitations that could have propagated our nutrient extraction estimates. Approximately two-thirds of the Sea Around Us catch data was reported at the species level. This limitation constrained the application of species-specific nutrient compositions, potentially reducing our ability to detect some spatiotemporal patterns in nutrient extraction estimates. However, nutrient compositions are well constrained at the family level[56]. Therefore, estimates derived from catch data at the family level, which made up ~84% of the total biomass caught, are more robust to uncertainties.

The Sea Around Us also reports uncertainty scores in the catch data which are subjectively assigned based on procedures adapted by Zeller et al.[69] from Mastrandrea et al.[70], which provides approximate confidence intervals. The uncertainty scores were defined as follows: 1 (±50% of the catch value), 2 (±30%), 3 (±20), and 4 (±10). We tested the impact of catch uncertainties on our estimates by integrating the score-based uncertainties into our nutrient extraction estimates. For catch values lacking an uncertainty score, we assigned the median score value of 3. Using the uncertainty scores, we calculated a standard deviation for each catch value. For example, if a catch value was 50 tonnes and had an uncertainty score of 2 (±30%), then the resulting standard deviation would be 15 tonnes. We ran 100 iterations of Eq. (5) per entry, randomly sampling both nutrient composition values and catch values. For the catch value, we randomly sampled from a normal distribution determined by the catch value and its calculated standard deviation. From each set of 100 estimates, we derived the estimated C, N, and P extracted from the mean and derived standard deviations and 95% confidence intervals.

To examine the effects of catch uncertainty on our extraction estimates, we compared nutrient extraction estimates that integrated catch value uncertainties with those that did not. We found no meaningful difference between the two estimates, and the inclusion of catch uncertainty did not add further variation (Supplementary Tables 7–9). These results reflect the independent sampling of the catch and nutrient composition values, along with the stabilizing effect of the central limit theorem, which likely explains why incorporating catch uncertainties did not substantially affect our estimates. Given these observations and the subjective nature of the uncertainty scores, we elected to quantify our estimates without integrating fisheries uncertainties in the main text but reported them in Supplementary Tables 8−10.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data sources of bodily nutrient compositions used for this study are listed in Supplementary Data 1. The nutrient compositions derived from our analyses and used to estimate nutrient extractions have been provided in Supplementary Data 2. The catch data for industrial fisheries were provided by the Sea Around Us database (www.seaaroundus.org). Data on nutrient extraction estimates, including the distribution of nutrient extraction estimates for the entire catch database, can be found on Figshare: https://doi.org/10.6084/m9.figshare.28500593.

Code availability

The code used to generate our mixed-effects models, estimate nutrient compositions, estimate nutrient extractions, estimate extraction molar ratios, and produce our figures was written in R 4.3.1. This code has been made publicly available through the following GitHub repository: https://github.com/FishyAdrian/Fishing_Out_Nutrients.

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Author contributions

A.A.G.O. led the collection, preparation, and analysis of nutrient data and extraction estimates; wrote the first draft of the manuscript; and contributed substantially to manuscript preparation. T.E.W. and E.H. contributed substantially to data analyses. M.L.D.P. and D.P. contributed to the Sea Around Us reconstructed catch data (1960–2018). T.B.A. conceived the study and contributed substantially to data analysis and manuscript preparation. All authors contributed to manuscript revisions.

Competing interests

The authors declare no competing interests.

Additional information

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