Hydrobiologia (2022) 849:1543–1557
https://doi.org/10.1007/s10750-021-04758-9

PRIMARY RESEARCH PAPER

Gelatinous and soft-bodied zooplankton in the Northeast Pacific Ocean: Phosphorus content and potential resilience to phosphorus limitation

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Received: 6 May 2021 / Revised: 6 November 2021 / Accepted: 8 November 2021 / Published online: 18 November 2021

Abstract Marine ecosystems on continental shelves face multiple challenges due to anthropogenic disturbances, many of which can change the seawater stoichiometry (C:N:P) and consequently elemental ratios of phytoplankton. This change in food quality may not be tolerated by all grazers and predators. Gelatinous and soft-bodied zooplankton (GZ) might be more resilient to such changes. We sampled GZ species in neritic and oceanic waters of the Northeast Pacific off British Columbia, Canada, determined their phosphorus (P) content and elemental ratios (C/P, N/P), and analysed intraspecific variability associated with size and ontogeny. P content was measured for twelve GZ taxa. P % DW (dry weight) decreased with size for the hydrozoan *Aequorea* sp., scyphozoans *Aurelia labiata*, *Cyanea capillata*, and the thaliacean *Salpa aspera*, and differed significantly for two development stages of the salp *S. aspera*. While C/P and N/P were mostly size and stage independent, they were highly variable. C/P values of GZ were generally higher than values of crustacean zooplankton, indicating that GZ represent poor-quality prey for non-GZ

Handling editor: Jörg Dutz

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predators, and that GZ may have a higher resilience towards P-limited (low quality) prey. Changing ocean conditions and nutrient stoichiometry of prey may favour GZ, although large variability in P dynamics among GZ taxa and uncertainty about future ocean stoichiometry changes make generalisations difficult.

Keywords C:N:P value · Ctenophore · Gastropoda · Jellyfish · Salish Sea · Salp · Stoichiometry · Subarctic North Pacific

Introduction

Nutrient stoichiometry, particularly the ratios between carbon (C), nitrogen (N), and phosphorus (P) of marine primary producers are highly variable, with potential repercussions for higher trophic levels (Boersma et al., 2008). Especially the ratio between carbon and phosphorus (C/P) has been used extensively as a descriptor of food quality, particularly in freshwater systems (Sterner et al., 1998), but increasingly also in the marine (coastal) realm, as many areas show increasing P limitation (Peñuelas et al., 2012). Manifold processes are changing the nutrient stoichiometry of ocean waters and are simultaneously at work. For instance, the increase in atmospheric CO_2 leading to ocean acidification impacts coastal organisms (Haigh et al., 2015), and through an increase in C availability can change nutrient stoichiometry of primary producers (Schoo et al., 2013; Cripps et al., 2016). Many coastal areas are experiencing ongoing changes in nutrient concentrations through, for example, eutrophication, as well as declines in P availability resulting from mitigation efforts of industrial countries (Diaz & Rosenberg, 2008; Le Fur et al., 2019). Changes in seawater C and P concentrations are reflected in altered C/P values of phytoplankton (van de Waal et al., 2010). Shifts away from the Redfield ratio (C:N:P = 106:16:1; Redfield, 1934) are known to affect the growth rate of phytoplankton and influence their nutritional quality. Altered elemental ratios of seawater may also favour phytoplankton assemblages with a broader nutrient tolerance (e.g. Shangguan et al., 2017). Evidently, there are a number of changes that warrant a close analysis of effects on consumers.

The effect of P limitation on phytoplankton growth and primary consumers has been studied extensively (Sterner & Elser, 2002). However, knowledge of the effect of P limitation on secondary consumers is limited, especially for gelatinous and soft-bodied zooplankton (GZ; Malzahn et al., 2010; Schoo et al., 2010; Lesniowski et al., 2015; Chen & Li, 2017). Although GZ abundances may be increasing regionally (Richardson et al., 2009; Brotz et al., 2012; Condon et al., 2012; 2013) and have the potential to alter existing food webs (Boero et al., 2008), knowledge gaps still exist with respect to their interactions with other species, contribution to predator diets (Hays et al., 2018), and roles in nutrient cycling (Plum et al., 2020). The GZ include diverse taxonomic and functional groups but with several common traits. These include often transparent tissues/bodies, high water contents facilitating near neutral buoyancy, fast growth, generally large size of adults, and often a lack of hard structures making them fragile and difficult to sample (Madin & Harbison, 2001). Therefore, it is difficult to obtain accurate measurements of their nutrient stoichiometry, and even the predictions of nutrient contents and demands of GZ are not straightforward (Lüskow et al., 2021).

The ‘growth rate hypothesis’ (GRH; Sterner & Elser, 2002) predicts that fast-growing organisms should contain high concentrations of P-rich ribosomes, and thus, have high P contents and low C/P and N/P ratios. Therefore, as GZ generally have high growth rates, we can postulate that they should have relatively high P contents and, thus, low C/P and N/P values. Interestingly, GZ blooms often occur in areas experiencing eutrophication (Richardson et al., 2009; Haraldsson et al., 2012). This not only may indicate bloom-formation dependence on high P (and potentially N) but also reflect a response to shifts in the food web structure (Sommer et al., 2002). Furthermore, behavioural traits may confer an advantage, e.g. GZ taxa are often tactile predators and, therefore, can be more successful in highly turbid waters compared to visually foraging fish species (Richardson et al., 2009; Haraldsson et al., 2012).

Alternatively, the body of many GZ species, and specifically the mesoglea of jellyfish (i.e. cnidarian medusae), consists mainly of ribosome-free and relatively C-rich tissue (glycoproteins and carbohydrates), which may increase the C/P of these animals. Some studies suggest that as a result, GZ may be less susceptible to P limitation (Malzahn et al., 2010; Schoo et al., 2010; Chen & Li, 2017) and may thrive in both low-nutrient and nutrient-limited ecosystems (Parsons & Lalli, 2002). It is also unclear whether GZ taxa with different primary feeding modes (herbivorous versus carnivorous) are similarly resilient to potential P limitation. Hence, the P requirements of GZ are unclear, including their nutrient stoichiometry.

Studying the P demands of GZ is not just of interest from an academic point of view. In general, dominant taxa in an ecosystem determine the availability of major nutrients, because consumers typically excrete those nutrients they take up in excess (Elser et al., 1996; van de Waal et al., 2010; Meunier et al., 2018). Hence, depending on the nutrient demands of GZ, they may either excrete excess N, P, or even C. As a result, GZ are becoming increasingly recognised for their critical roles in biogeochemical cycling, not only because of their impact as predators (e.g. cnidarians and ctenophores), but also via the excretion of dissolved products and fast-sinking faecal pellets (especially from salps; Henschke et al., 2019; Plum et al., 2020). In this latter role, GZ may structure microbial communities (Blanchet et al., 2015) and provide important pathways for the transport of C, N, and P to the seafloor (Guy-Haim et al., 2020). For instance, Plum et al. (2020) showed, using long-term data from the Western Antarctic Peninsula, which changes in key metazoan grazer populations, *Salpa thompsoni* Foxton, 1961 versus *Euphausia superba* Dana, 1850, had measurable effects on the dynamics of dissolved N and P and may affect the phytoplankton composition (Finkel et al., 2010). Therefore, to better represent the functional diversity of GZ in food web and biogeochemical models (e.g. Wright et al., 2021), extending data on their stoichiometry is a crucial step.

One of the caveats of studying stoichiometry is the assumption that what is measured in an organism is a characteristic of that organism and not of the environment. In other words, the organisms need to show homeostasis when it comes to nutrients (Meunier et al., 2014). Unfortunately, there is little information on this for GZ as, out of necessity, these data come from laboratory studies where nutrients can be controlled. Schoo et al. (2010) showed that the C/P value of the ctenophore *Pleurobrachia pileus* (Müller, 1776) was independent of its feeding environment and that the species showed a considerable degree of homeostasis. Furthermore, Malzahn et al. (2010) observed some variability in the C/P values of the limnomedusa *Gonionemus vertens* Agassiz, 1862, but this variability was relatively small. Thus, as indicated by experimental studies (Schoo et al., 2010; Chen & Li, 2017), we assume that GZ maintain some level of homeostasis; hence, measurements of nutrient ratios from field samples can be attributed to species or development stages, rather than to external conditions.

The aims of the present study were (i) to present species-specific P data and elemental ratios (C/P, N/P) for hydro- and scyphomedusae, pelagic gastropods, ctenophores, and salps that may be used as a basis for GZ group-specific parameterisations in biogeochemical models, and (ii) to analyse intraspecific variability of these values related to size and ontogeny, assuming no, or only minor, influence from the external environment (Malzahn et al., 2010; Schoo et al., 2010; Chen & Li, 2017). Previous studies (e.g. Lüskow et al., 2021) have shown that C and N contents per dry weight decrease with size, while elemental ratios (i.e. C/N) are mostly size independent. Based on these findings, we expected GZ taxa to have low weight-specific P content, but high C/P and N/P values compared to crustacean zooplankton, show decreasing weight-specific P content with size, and an independence of C/P and N/P values with size and development stage.

Materials and methods

Study area and specimen collection

In this study, gelatinous and soft-bodied zooplankton (GZ) were defined to include cnidarian (i.e. Hydrozoa, Scyphozoa), ctenophore (i.e. Nuda, Tentaculata), pelagic gastropod, and tunicate (i.e. Doliolida, Pyrosomida, Salpida) species. All GZ samples were collected in the Northeast Pacific Ocean. Between 2014 and 2020, several cruises and land-based collections were carried out in this area (46.36°–54.57° N, 123.07°–147.50° W) between February and October, including the Southern Gulf of Alaska, Queen Charlotte Strait, Queen Charlotte Sound, west coast of Vancouver Island, Strait of Georgia, and Juan de Fuca Strait. GZ specimens were obtained from zooplankton samples collected using various gears (i.e. Bongo net, Multinet, dip net, pelagic trawl) during numerous cruises and shore-based collection events. Removal of guts and gut contents while in the field, especially for smaller specimens, was not feasible and, thus, was not performed, to ensure consistency among samples. Contents of gastrovascular systems and guts may have influenced the phosphorus (P) content data. The decision to accept this potential source of error was in line with earlier studies (Hays et al., 2018). GZ specimens were separated by species and measured individually (umbrella diameter in the case of medusae and total length for ctenophores, salps, and pelagic gastropods). Measurements were taken of maximum extent to the nearest millimetre, and individuals were immediately frozen at − 80 °C until further analysis. For details on the locations and specimen collections, see Lüskow et al. (2021).

Elemental content determination

Before the elemental analysis, all samples (subsamples for large scyphozoans; entire specimens for all other taxa) were freeze dried to constant weight. Individual dry weight (DW) was determined using an analytical balance (Mettler Toledo; 10 µg precision) before homogenisation with pestle and mortar. Between 5 and 20 mg of the dried and homogenised samples were weighed and analysed for their P content as orthophosphate after acidic oxidative hydrolysis with 5% H_2SO_4 at the Biologische Anstalt Helgoland, Germany (Grasshoff et al., 1999). Calibration curves for the appropriate ranges were established and always had a $R^2 = 0.99$. The variation between measurements was typically less than 20%. All analyses were carried out in duplicates. The carbon (C) and nitrogen (N) data were previously reported in Lüskow et al. (2021). C/P and N/P were expressed as molar ratios and were only calculated for specimens with known C, N, and P contents, i.e. elemental ratios were calculated only for specimens with known elemental composition, whereas element contents were not assumed to be equal for all specimens of a species. Size dependencies of C and N, as well as C/N data, are published in a companion study by Lüskow et al. (2021).

Literature research

A literature search in the Web of Science and Google Scholar using the search keywords ‘gelatinous zooplankton’, ‘jellyfish’, ‘ctenophore’, ‘salp’, ‘elemental composition’, and ‘elemental ratio’ was performed. Although most literature was included, some articles (likely early studies) may have been unavailable to the search engines. Seventeen studies reporting species-specific information were found and used, together with results from the present study, in a conceptual comparison among several trophic groups (see below). P % DW, C/P, and N/P were then compared with values from our laboratory analyses and generalised to the taxonomic class level. Elemental ratios were given in the literature either in molar units or by mass. For comparability reasons, elemental ratios given by mass were converted to molar units.

Statistical analyses

Generalised linear models (GLMs) were used to explore significant (α level of 0.05) effects of size (i.e. diameter or length) on P content, C/P, or N/P (Gamma error structure, inverse-link) in the R package ‘lme4’ (Bates et al., 2015). One-way analyses of variance (ANOVA), followed by Tukey-HSD post hoc tests for pairwise comparison were used to investigate differences in P % DW, C/P, and N/P between taxonomic classes or development stages of salps. P % DW, C/P, and N/P data showed heteroscedasticity and the residuals were non-normally distributed (Shapiro–Wilk normality test and Levene’s test for homogeneity of variance). To meet the assumptions of the ANOVA (i.e. normality of data, homoscedasticity of variances, independence of data), data were $\log_{10}$-transformed. We could not assess seasonal differences in any of the variables (collection occurred from February to October) because of the small sample size. All statistical analyses were performed in R (R Core Team, 2021) version 3.6.0.

Results

Phosphorus contents, C/P, and N/P

The specimens ranged in size from 35 to 770 mm (Fig. 1). Phosphorus (P) contents were determined for twelve species from five taxonomic classes (Table 1, Fig. 2). Significant differences between taxonomic classes were evident for some class pairs, but should be considered with caution given the small sample sizes (Table 2). Mean P contents (expressed as per cent of dry weight, DW) encompassed a wide range from 0.02 ± 0.01 P % DW in *Beroe cucumis* Fabricius, 1780 to 0.26 P % DW in *Thetys vagina* Tilesius, 1802.

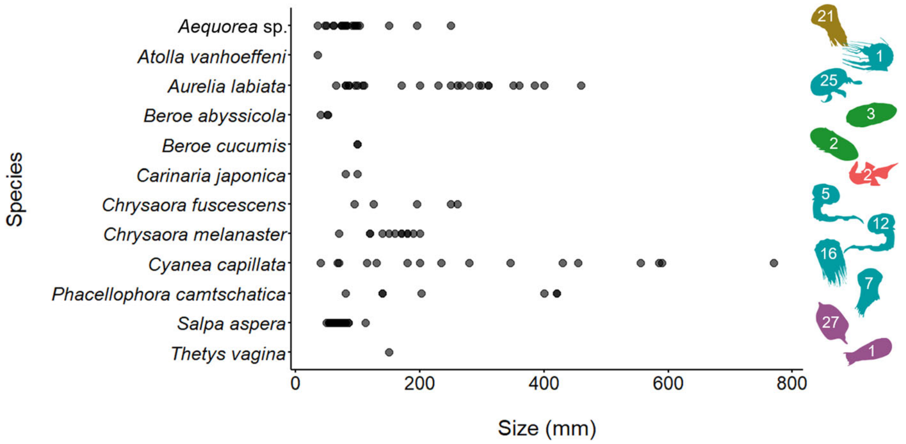

Fig. 1 Size of gelatinous and soft-bodied zooplankton used for phosphorus content determination. Colours of silhouettes refer to taxonomic class affiliation: Dark yellow = Hydrozoa, blue = Scyphozoa, green = Nuda, red = Gastropoda, purple = Thaliacea. The number of samples used in the analysis is indicated in the images of the taxa (total *N* = 122)

Table 1 Phosphorus fractions of dry weight (DW) of twelve gelatinous and soft-bodied zooplankton species (*N* = 122) from five taxonomic classes

Class	Species	*N*	P % DW	*N*	C/P	N/P
Gastropoda	*Carinaria japonica*	2	0.226 ± 0.150	2	217.2 ± 37.6	48.2 ± 11.2
Hydrozoa	*Aequorea* sp.	21	0.072 ± 0.051	18	364.4 ± 381.5	92.9 ± 107.9
Nuda	Class average	5	0.089 ± 0.067	5	414.4 ± 244.0	100.6 ± 56.8
	Beroe abyssicola	3	0.135 ± 0.034	3	252.4 ± 92.0	56.3 ± 20.0
	Beroe cucumis	2	0.020 ± 0.005	2	657.3 ± 156.7	167.0 ± 42.2
Scyphozoa	Class average	66	0.089 ± 0.035	50	208.0 ± 76.8	50.6 ± 20.1
	Atolla vanhoeffeni	1	0.151			
	Aurelia labiata	25	0.088 ± 0.034	18	151.7 ± 48.1	36.6 ± 13.0
	Chrysaora fuscescens	5	0.092 ± 0.019	5	254.7 ± 49.2	58.4 ± 13.5
	Chrysaora melanaster	12	0.073 ± 0.013	7	258.9 ± 84.1	58.4 ± 20.7
	Cyanea capillata	16	0.093 ± 0.048	15	241.5 ± 80.9	60.2 ± 22.2
	Phacellophora camtschatica	7	0.097 ± 0.031	5	200.8 ± 40.0	53.0 ± 12.6
Thaliacea	Class average	28	0.167 ± 0.050	28	236.2 ± 45.5	41.1 ± 8.5
	Salpa aspera	27	0.164 ± 0.047	27	235.4 ± 46.2	41.4 ± 8.5
	Thetys vagina	1	0.261	1	258.4	32.4

N = number of samples. Molar C/P, molar N/P, and mean ± SD are indicated. Carbon and nitrogen data are from Lüskow et al. (2021). The primary feeding mode of thaliaceans is considered herbivorous, whereas all other classes are considered primarily carnivorous

The P contents of gelatinous and soft-bodied zooplankton (GZ) were positively correlated with carbon (C) and nitrogen (N) contents (Fig. 3, Table 3). Large differences in C/P and N/P occurred among species, with *Aurelia labiata* Chamisso & Eysenhardt, 1821 having the lowest (151.7 and 36.6, respectively) and *B. cucumis* having the highest (657.3 and 167.0, respectively) ratios. As a result of the large variation between species, C/P and N/P shown in Table 1 were not significantly different among taxonomic classes (Table 2), except for C/P between Nuda and Scyphozoa (*P* = 0.04) and N/P between Nuda and Thaliacea (*P* = 0.02). All N/P values were clearly above the Redfield ratio (16:1), and hence, all studied taxa were

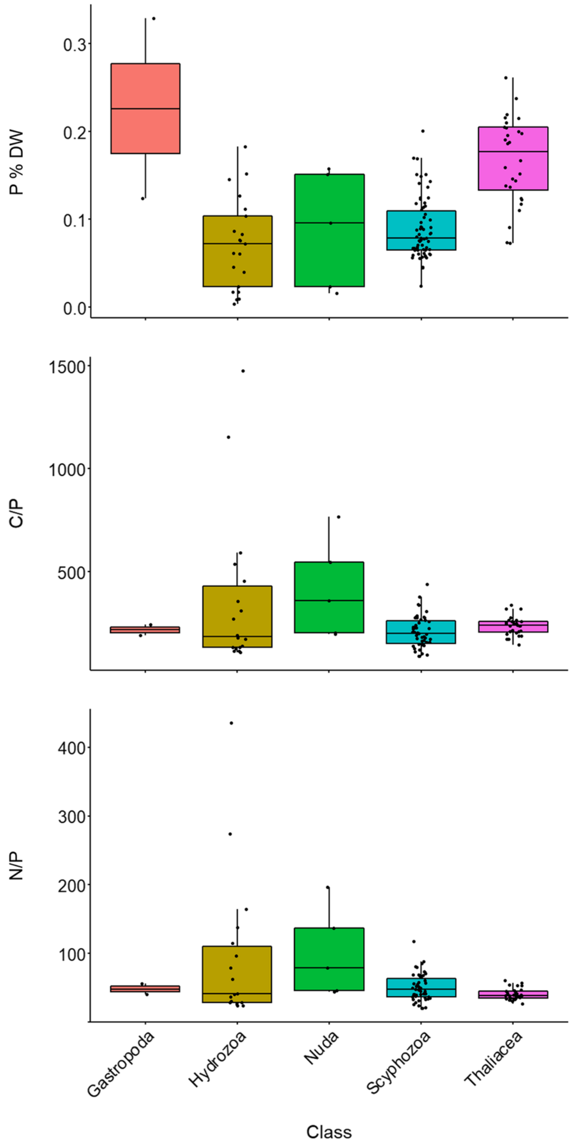

Fig. 2 P % DW (*top panel*), molar C/P (*middle panel*), and molar N/P (*bottom panel*) of gelatinous and soft-bodied zooplankton taxonomic classes. Colours refer to taxonomic class affiliation: Red = Gastropoda ($N = 2$), dark yellow = Hydrozoa ($N = 21$), green = Nuda ($N = 5$), blue = Scyphozoa ($N = 66$), purple = Thaliacea ($N = 28$). For numbers of respective specimens, see Tables 1, 2, and Fig. 1. C and N data originate from Lüskow et al. (2021). Boxes show data between the 25th and the 75th percentiles, with the median represented as a line. The whiskers extend as far as the minimum and maximum values not considered as outliers. An outlier is defined as a value beyond 1.5 × the interquartile range (75th to 25th percentile)

Table 2 Analysis of variance (ANOVA) and Tukey-HSD post hoc test results for $\log_{10}$-transformed P % DW, molar C/P, and molar N/P of gelatinous and soft-bodied zooplankton specimens from several taxonomic classes

P % DW	Gastropoda	Hydrozoa	Nuda	Scyphozoa
Gastropoda				
Hydrozoa	**0.011**			
Nuda	0.113	0.933		
Scyphozoa	0.220	**0.004**	0.796	
Thaliacea	0.981	**< 0.001**	**0.009**	**< 0.001**
C/P	Gastropoda	Hydrozoa	Nuda	Scyphozoa
Gastropoda				
Hydrozoa	0.989			
Nuda	0.673	0.560		
Scyphozoa	0.998	0.233	**0.042**	
Thaliacea	0.999	0.969	0.292	0.487
N/P	Gastropoda	Hydrozoa	Nuda	Scyphozoa
Gastropoda				
Hydrozoa	0.972			
Nuda	0.642	0.644		
Scyphozoa	0.999	0.403	0.096	
Thaliacea	0.991	0.076	**0.023**	0.697

Significant differences ($P < 0.05$) are indicated in bold

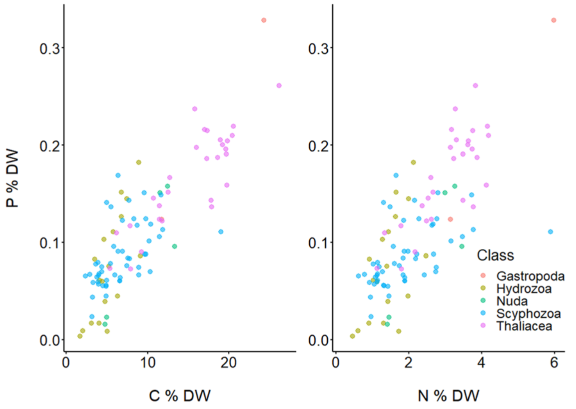

Fig. 3 Relationship between C and P (*left panel*) and N and P (*right panel*) expressed as per cent of dry weight ($N = 103$). Colours refer to taxonomic class affiliation: Red = Gastropoda, dark yellow = Hydrozoa, green = Nuda, blue = Scyphozoa, purple = Thaliacea. For numbers of respective specimens and linear regressions, see Tables 1, 3, and Fig. 1. C and N data originate from Lüskow et al. (2021)

P-poor. Values from the literature and this study are summarised in Table 4 and are generally consistent with each other. Herbivorous GZ (i.e. pelagic thaliaceans) species did not have systematically higher C/P than carnivorous GZ (i.e. cnidarians, ctenophores, pelagic gastropods) species ($F_{1,9} = 0.05$, $P = 0.82$).

Table 3 Phosphorus content (P % DW) of various gelatinous and soft-bodied zooplankton classes as a function of carbon content (C % DW) or nitrogen content (N % DW) following linear functions. N = number of specimens, R^2 = correlation coefficient. All slopes are significant ($P < 0.05$). Data are from Fig. 3

Class	N	Linear regression	R^2
Gastropoda	2	P % DW = 0.013 C % DW	0.99
		P % DW = 0.052 N % DW	0.99
Hydrozoa	18	P % DW = 0.015 C % DW	0.84
		P % DW = 0.053 N % DW	0.77
Nuda	5	P % DW = 0.010 C % DW	0.90
		P % DW = 0.038 N % DW	0.89
Scyphozoa	50	P % DW = 0.012 C % DW	0.86
		P % DW = 0.040 N % DW	0.84
Thaliacea	28	P % DW = 0.011 C % DW	0.97
		P % DW = 0.054 N % DW	0.97

Averaged over all groups, the C/P value for GZ was 208.2 ± 168.7 and the N/P value was 40.1 ± 29.7.

Size and stage dependency of P % DW, C/P, and N/P

Size dependency of these chemical constituents was investigated for *Aequorea* sp. Péron & Lesueur, 1810, *A. labiata*, *Cyanea capillata* (Linnaeus, 1758), and *Salpa aspera* Chamisso, 1819. Unfortunately, sample sizes of other species were too small to test for size effects. The P content (P % DW) decreased significantly with size for *A. labiata*, *C. capillata*, and *S. aspera* ($p \leq 0.03$, $R^2 = 0.23$–0.33), but not for *Aequorea* sp. (Fig. 4A–D; $P = 0.15$, $R^2 = 0.11$). The C/P and N/P values of GZ were not significantly related to size (Fig. 4E–L, $P \geq 0.05$, $R^2 = 0.01$–0.34), except for a significant effect for C/P of *C. capillata* (Fig. 4G; $P = 0.049$, $R^2 = 0.34$).

The P content of a salp species was stage specific as shown for *S. aspera* (Fig. 5). *Salpa aspera* blastozooids (i.e. aggregate stage) had significantly higher P contents than oozooids (i.e. solitary stage; $P = 0.01$), while the C/P and N/P values did not differ significantly between stages ($P \geq 0.17$). Overall, trends depicted in Figs. 4 and 5 showed that differences not only occurred among species, but were also intraspecific.

Discussion

Phosphorus content, elemental ratios, and the 'growth rate hypothesis'

According to the 'growth rate hypothesis' (GRH; Sterner & Elser, 2002), the high growth rates of GZ should correspond with high P contents and low C/P and N/P values. We found that generally our P % DW values fell within published ranges for their respective taxonomic classes and were one order of magnitude lower than crustacean zooplankton (typically 0.05–0.25 for GZ versus 0.8–2.5% DW for crustacean zooplankton; Beers, 1966; Vijverberg & Frank, 1976). This difference is significant, because DWs of GZ, unlike crustaceans, may retain a considerable amount of water (9–23%) and salt due to osmoconformity (Larson, 1986; Hirst & Lucas, 1998). While this may lead to an underestimation of P content in GZ (relative to the DW), even with correction, their relative P content is expected to be substantially lower than non-GZ zooplankton (Beers, 1966; Vijverberg & Frank, 1976). The question of why GZ have low P content and accordingly high C/P and N/P values, combined with high growth rates, contradicting the GRH, remains open but is most likely related to the P-poor and C-rich soft structures, typical for these organisms. Interestingly, Touratier et al. (2003) reported on large differences in C/N values between the body (C/N = 6.2) and the discarded house (C/N = 291.7) of the appendicularian *Oikopleura dioica* Fol, 1872, indicating a strong bias towards C in these structures. Unfortunately, no data on P were reported. Herbivorous GZ (i.e. pelagic thaliaceans) species did not have systematically higher C/P compared to their carnivorous counterparts (i.e. cnidarians, ctenophores, pelagic gastropods). One exception may be the class Nuda, which was the only investigated GZ class with significantly higher C/P and N/P values and very low P % DW compared to Scyphozoa and Thaliacea. While very low P % DW was also recorded for *Beroe* sp. Muller, 1776 (0.090; Table 4) by Ikeda & Mitchell (1982), *B. abyssicola* Mortensen, 1927 (our study) and *B. cucumis* in the coastal temperate Atlantic had P % DW more similar to species in other classes (Curl, 1962). This stoichiometric uncertainty cannot currently be resolved due to small sample sizes and only a few literature values available for this group.

Table 4 Comparison of carbon content, molar C/P, and molar N/P by gelatinous and soft-bodied zooplankton (GZ) species between this study and previously published values

Class	Species	*N*	P % DW	C/P	N/P	References
Gastropoda	*Carinaria japonica*	2	0.226 ± 0.150	217.2 ± 37.6	48.2 ± 11.2	This study
	Clio pyramidata		0.510	184.9	37.0	Ikeda & Mitchell (1982)
	Clione limacina		0.305	222.8	26.1	Curl (1962)
			0.260	397.4	65.5	Ikeda & Mitchell (1982)
	Limacina rangii		0.530	162.3	33.9	Ikeda & Mitchell (1982)
	Limacina spp.		0.580	126.0	15.7	Curl (1962)
Hydrozoa	*Aequorea vitrina*		0.021	961.9	52.7	Curl (1962)
	Aequorea sp.	21	0.072 ± 0.051	364.4 ± 381.5	92.9 ± 107.9	This study
	Craspedacusta sowerbii	12	1.970 ± 0.250	39.0	8.9	Jankowski (2000)
	Gonionemus vertens			220–495	45–95	Malzahn et al. (2010)*
Nuda	*Beroe abyssicola*	3	0.135 ± 0.034	252.4 ± 92.0	56.3 ± 20.0	This study
	Beroe cucumis		0.160		15.2	Curl (1962)
		2	0.020 ± 0.005	657.3 ± 156.7	167.0 ± 42.2	This study
	Beroe sp.		0.090	258.3	56.5	Ikeda & Mitchell (1982)
Scyphozoa	*Atolla vanhoeffeni*	1	0.151			This study
	Aurelia aurita	7	0.001	94.3	22.1	Schneider (1988)
			1.000	70.5	17.3	Emadodin et al. (2020)
	Aurelia labiata	25	0.088 ± 0.034	151.7 ± 48.1	36.6 ± 13.0	This study
	Aurelia sp.		0.040	84.0	19.3	Malej et al. (2009)
			0.300–0.600	50–95	12–23	Chen & Li (2017)*
	Chrysaora fuscescens	5	0.092 ± 0.019	254.7 ± 49.2	58.4 ± 13.5	This study
	Chrysaora melanaster	12	0.073 ± 0.013	258.9 ± 84.1	58.4 ± 20.7	This study
	Cyanea capillata		0.200	149.8	10.0	Curl (1962)
		16	0.093 ± 0.048	241.5 ± 80.9	60.2 ± 22.2	This study
	Nemopilema nomurai		0.140	121.8	26.9	Iguchi et al. (2017)
	Pelagia noctiluca		0.150	155.9	20.7	Curl (1962)
		16	0.240 ± 0.005	99.8 ± 4.9	23.0	Malej et al. (1993)
	Phacellophora camtschatica	7	0.097 ± 0.031	200.8 ± 40.0	53.0 ± 12.6	This study
Tentaculata	*Mnemiopsis leidyi*		0.120	137.8	36.9	Curl (1962)
		30	0.004	109.8		Kremer (1976)
			0.110	83.2	24.1	Borodkin & Korzhikova (1991)
		150	0.400 ± 0.200	107.3 ± 21.9	20.6 ± 4.9	McNamara et al. (2013)
	Pleurobrachia pileus			95–395		Schoo et al. (2010)*
Thaliacea	*Ihlea racovitzai*		0.160	163.1	38.8	Ikeda & Mitchell (1982)
	Pyrosoma sp.		0.140	173.5	5.5	Curl (1962)
	Salpa aspera	27	0.164 ± 0.047	235.4 ± 46.2	41.4 ± 8.5	This study
	Salpa fusiformis		0.235	97.8	9.4	Curl (1962)
		6–7	0.195	108.6	52.9	Le Borgne (1982)
	Salpa maxima	1	0.187			Krishnaswami et al. (1985)
	Salpa thompsoni		0.090	134.9	68.9	Ikeda & Mitchell (1982)
			0.142	106.7	23.3	Iguchi & Ikeda (2004)
	Thalia democratica	4	0.757 ± 0.230			Krishnaswami et al. (1985)

Table 4 continued

Class	Species	*N*	P % DW	C/P	N/P	References
	Thetys vagina	1	0.261	258.3	32.4	This study
Gastropoda			0.402 ± 0.155	218.4 ± 94.7	37.7 ± 17.4	
Hydrozoa			0.688 ± 1.111	430.7 ± 385.3	56.1 ± 35.5	
Nuda			0.101 ± 0.061	389.3 ± 232.1	73.8 ± 65.1	
Scyphozoa			0.258 ± 0.309	150.5 ± 68.9	32.6 ± 18.4	
Tentaculata			0.168 ± 0.159	136.6 ± 63.6	27.2 ± 8.6	
Thaliacea			0.233 ± 0.190	159.8 ± 60.4	34.1 ± 21.3	
GZ			0.280 ± 0.355	208.2 ± 168.7	40.1 ± 29.7	

N = number of samples. Mean ± SD are indicated. * = laboratory study. The primary feeding mode of thaliaceans is considered herbivorous, whereas all other classes are considered primarily carnivorous

Similar to C and N contents and C/N (Lüskow et al., 2021), P % DW changed with specimen size and, in case of *S. aspera*, also with the development stage. Indeed, P % DW decreased with size in *Pelagia noctiluca* (Forsskål, 1775) and *S. thompsoni* oozooids (Malej et al., 1993; Iguchi & Ikeda, 2004), as did values for *Aequorea* sp., *Aurelia labiata*, *Cyanea capillata*, and *S. aspera* examined in our study. The opposite pattern was found, however, by Iguchi et al. (2017) for *Nemopilema nomurai* Kishinouye, 1922. The paucity of published P % DW and elemental ratios does not allow us to conclude whether the size-specific trends reported by Iguchi et al. (2017) were an exception or due to different trends among species. When comparing P % DW of *S. thompsoni* blastozooids and oozooids in the same DW range, no stage specificity was found (Iguchi & Ikeda, 2004).

All N/P values were above the Redfield ratio (16:1), and hence, all studied taxa need to be considered P-poor. Furthermore, all N/P values in our study were higher than those reported for crustacean zooplankton, ranging typically between 13 and 27 (Beers, 1966). Including N/P values derived from the literature (presented in Table 4), 80% of GZ taxa had values greater than the Redfield ratio, indicating that GZ were poor in P relative to their N content. These data suggest that GZ represent poor-quality prey for non-GZ predators.

Filter feeders such as appendicularians, doliolids, pyrosomes, and salps can utilise the entire prey spectrum because of their low P demand, whereas crustacean zooplankton only thrive on low C/P prey (van de Waal et al., 2010). This is a clear advantage for GZ. Pelagic tunicates have no selective filtration or ingestion like raptorial feeders. However, they may selectively digest prey to meet their nutritional demands and let prey of unwanted size or nutritional value pass through the digestive tract (Conley et al., 2018; Dadon-Pilosof et al., 2019). A lower P requirement allows some species (like pelagic tunicates) to survive in low-nutrient (e.g. open ocean) environments with lower maximum growth performance according to the GRH (Sterner & Elser, 2002). However, the opposite is true for many GZs that show high growth rates and high, mostly size-independent, C/P values compared to crustacean zooplankton (e.g. Ikeda, 1984; Masuzawa et al., 1988). This raises the question of whether the GRH is valid for GZ.

Gelatinous and soft-bodied plankton in a conceptual C/P trophic group comparison

Taking into consideration species, size, and stage specificity of C/P values, we can sketch a conceptual comparison among several trophic groups (Fig. 6), with data taken from the present study (Table 1) and the literature (GZ and other taxa). This can be used to understand food quality (C/P stoichiometry) aspects among idealised trophic levels. Usually, trophic transfer efficiency increases with decreasing C/P value, implying a higher likelihood of match between prey elemental stoichiometry and predator demand at

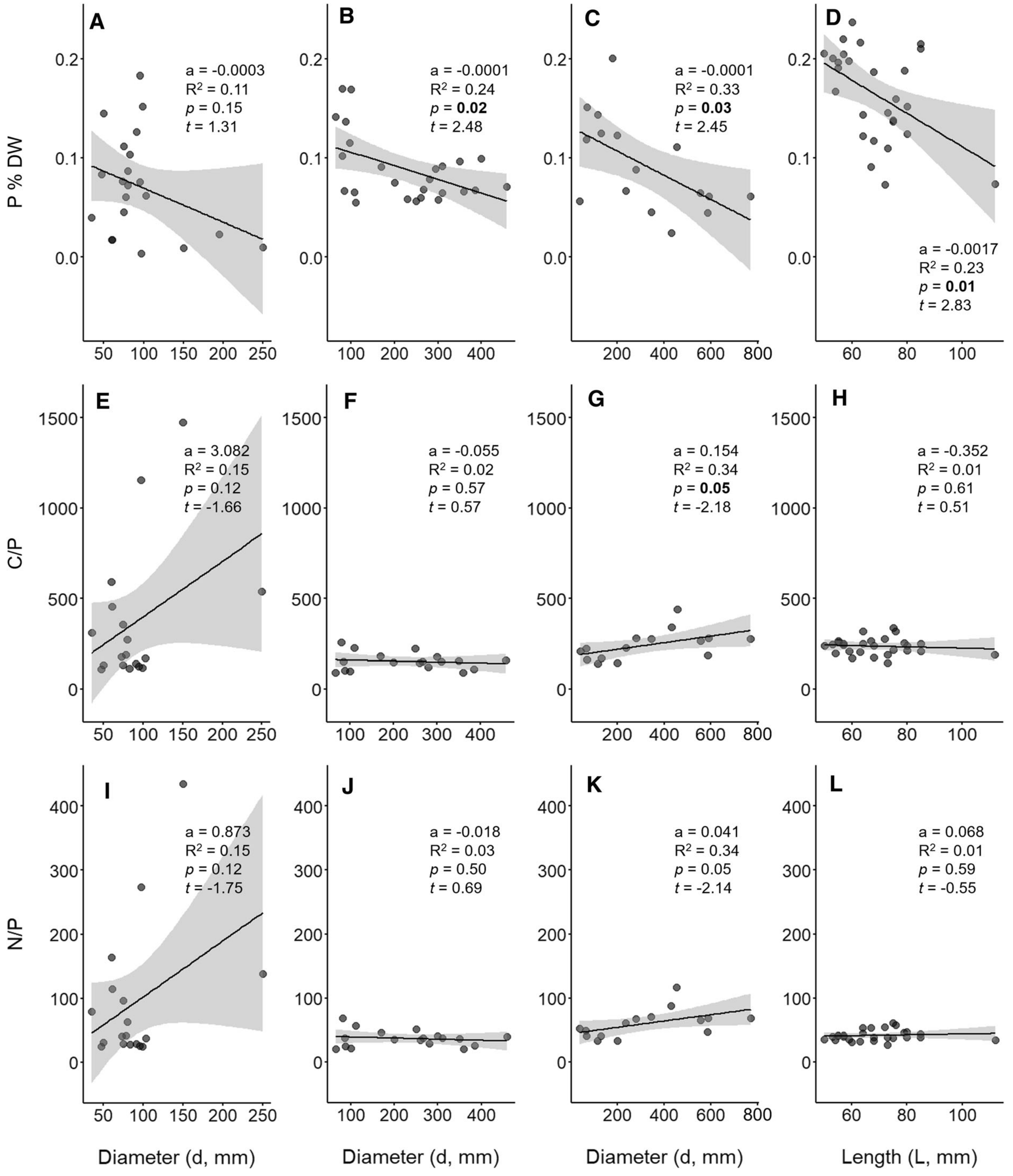

Fig. 4 Relationships of P % DW (*top row*), molar C/P (*middle row*), and molar N/P (*bottom row*) with size (diameter, d, in case of hydro- and scyphomedusae; length, L, in case of salps): **A**, **E**, **I** = *Aequorea* sp., **B**, **F**, **J** = *Aurelia labiata*, **C**, **G**, **K** = *Cyanea capillata*, **D**, **H**, **L** = *Salpa aspera*. a = slope of regression line, R^2 = correlation coefficient, *P*- and *t*-values from GLM based on $\log_{10}$-transformed data are shown. Significant slopes ($P < 0.05$) are indicated in bold. C and N data originate from Lüskow et al. (2021)

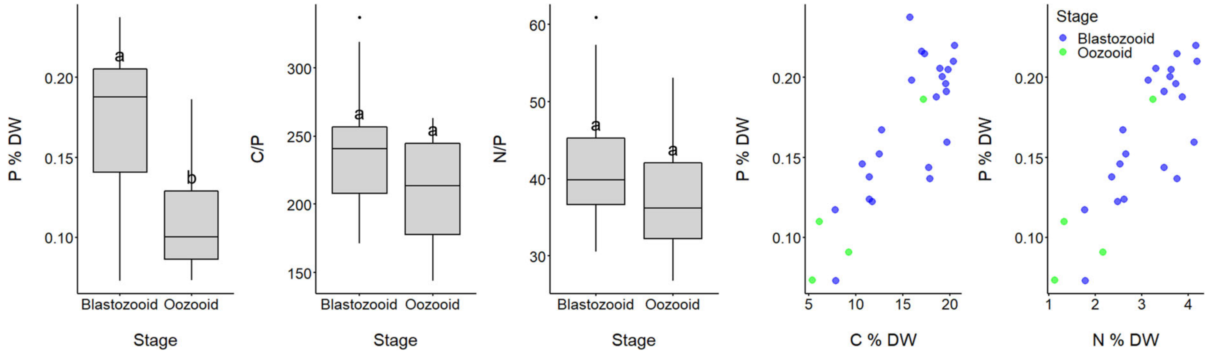

Fig. 5 Stage specificity of P % DW, molar C/P, and molar N/P in *Salpa aspera* (blastozooid, oozooid). Letters indicate significant differences ($P < 0.05$). C and N data are from Lüskow et al. (2021). Boxes show data between the 25th and the 75th percentiles, with the median represented as a line. The whiskers extend as far as the minimum and maximum values not considered as outliers. An outlier is indicated by a dot and defined as a value beyond 1.5 × the interquartile range (75th to 25th percentile)

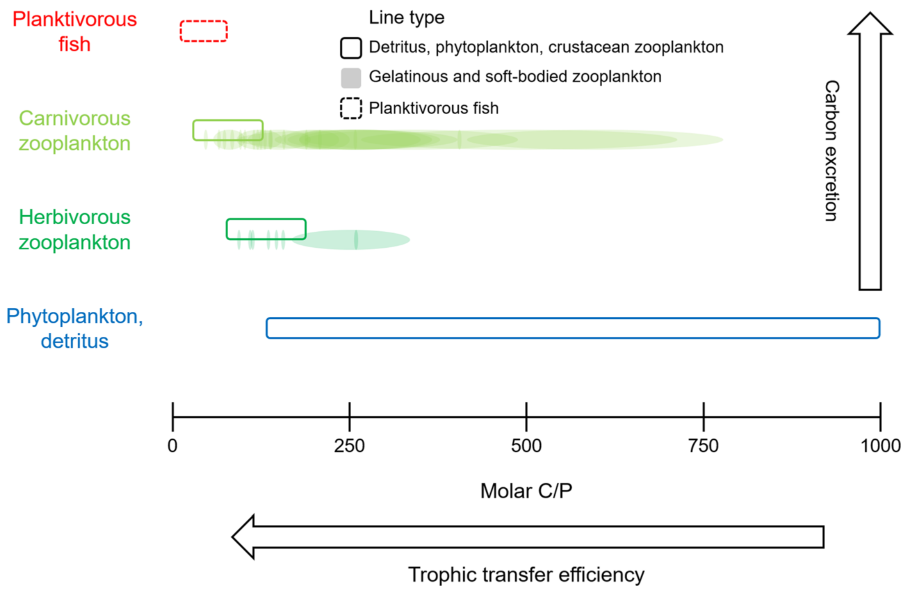

Fig. 6 Conceptual representation of C/P in aquatic ecosystems, inspired by Sterner et al. (1998). Gelatinous and soft-bodied zooplankton (GZ) data originate from Tables 1 and 4, herbivorous crustacean zooplankton data are from Beers (1966) and Vijverberg & Frank (1976), phytoplankton, detritus, carnivorous crustacean zooplankton, and planktivorous fish data are from Sterner et al. (1998). Arrows indicate an increase in trophic transfer efficiency with decreasing C/P value and an increase in carbon excretion with trophic level (represented by primary feeding mode of groups). GZ as well as crustacean zooplankton are shown separately, considering their primary feeding mode. GZ data are shown by ellipses per species (Table 4). Three values (> 950) of Hydrozoa were removed

low C/P values. Further, C excretion increases with trophic level (represented by the primary feeding mode of groups), indicating that carnivorous zooplankton and planktivorous fish need to consume more prey items (and, thus, excrete surplus C; lower C/P) to meet their limiting nutrient needs (e.g. P; Fig. 6). Adding GZ data to the conceptual comparison among several trophic groups show that especially carnivorous GZ are different from previously reported zooplankton taxa.

It may be suggested that a high body C/P indicates a high organismal resilience towards P limitation, whereas low C/P values reflect a high susceptibility to nutrient limitation. Typically, the C/P value decreases from one to the next trophic level (Sterner et al., 1998; van de Waal et al., 2010). For example, phytoplankton have highly variable C/P values among environments, species, and growth conditions, therefore, a wide C/P range, while crustacean zooplankton generally exhibit less variable C/P values and have a narrower C/P range (van de Waal et al., 2010). The diversity of GZ C/P can be compared schematically with C/P values of crustacean zooplankton and pelagic fish, using data from this study and literature sources (Fig. 6). Generally, GZ showed wider ranges of C/P values than crustacean zooplankton and fish, despite considerable overlap between these three groups at the lower end of the C/P range. This is contradictory to the general tendency of lower C/P values, while moving up trophic levels (van de Waal et al., 2010). High GZ taxonomic and functional diversity may explain this. Herbivorous GZ (only salps in this study) tended to have C/P values ranking at the lower end of the C/P value range of their carnivorous counterparts, which may indicate higher nutritional quality. However, the difference in C/P values of both groups was not statistically significant. We need to remember that functional groups (herbivorous versus carnivorous) in this case are also represented by different taxonomic groups (Thaliacea versus all other classes). The tendentially higher nutritional quality of herbivorous GZ is in line with their higher protein and slightly elevated lipid contents compared to carnivorous GZ such as medusae and ctenophores (e.g. Youngbluth et al., 1988; Lucas, 1994; Dubischar et al., 2012). It appears that herbivorous as well as carnivorous GZ have high C/P values in contrast to their crustacean counterparts and potentially are more tolerant to changes in their prey elemental composition. Conversely, crustacean zooplankton and planktivorous fish are more selective (or more efficient in regulating C/P values) and rely more on low-C/P prey to sustain their high protein demands. Hypothetically, if phytoplankton were to have higher C/P values, as may be expected in a warming ocean, crustacean zooplankton and fish may be at a disadvantage, thereby providing an opportunity for an increase of GZ (van de Waal et al., 2010). Unlike crustacean zooplankton, the higher resilience of GZ to nutrient-deficient prey may enable them to endure unfavourable periods and dominate pelagic food webs (e.g. Boero et al., 2008; Plum et al., 2020). Ultimately, increases in GZ with changing ocean conditions will also depend on other factors such as predation and parasitism (e.g. Henschke et al., 2016; Hays et al., 2018). However, this remains a hypothesis, and more nutrient content data are required for confirmation.

Potential implications and future perspectives

Intraguild predation, i.e. consumption of species that share similar feeding and stoichiometric traits, is especially frequent in GZ (Purcell, 1991). This may be due to the nutrient requirements of some GZ taxa. From a stoichiometric perspective, GZ with high C/P values may be more suitable prey for other GZ than for other pelagic organisms. Maybe this is a reason why they are avoided by many predators. However, this needs to be tested experimentally, especially in light of confirming/disproving multiple suggested hypotheses explaining predation on GZ (Thiebot & McInnes, 2020). Manifold feeding interactions among GZ species can be summarised as the ‘jelly web’ (Robison, 2004). These GZ feeding interactions can be diverse, with a recent study in the eastern tropical Atlantic showing that GZ covered most of the isotopic niche space of an entire planktonic food web (Chi et al., 2021). Trophic interactions among GZ species are still poorly understood but likely are more common than currently appreciated, and increasingly more research is dedicated to resolving intraguild GZ predatory interactions and the ‘jelly web’ (Arai & Jacobs, 1980; Choy et al., 2017; Chi et al., 2021). Under changing ocean conditions (warming, water column stratification, change in seawater stoichiometry), these interactions may become more important.

GZ stoichiometric values, and hence their nutrient requirements, are different from crustacean zooplankton, allowing them to co-exist. However, if the conditions for the classical food web, where large calanoid copepods and euphausiids provide a direct link between phytoplankton and fish, deteriorate, e.g. due to a mismatch between the elemental composition of prey and their own demands, conditions may become more suitable for many GZ taxa. Multiple factors such as rising pCO_2, ocean warming, water column stratification, and eutrophication impact the seawater stoichiometry in coastal and open ocean regions such as the Northeast Pacific and are changing. This may affect the shape of food webs and the role of GZ, potentially converting their low P content (and thus demand) into a competitive advantage compared to other metazoans. Decreasing seawater pH as a consequence of increased atmospheric CO_2 may indirectly favour certain GZ species (Chuard et al., 2019) due to altered phyto- and zooplankton compositions and changed nutrient stoichiometry of prey promoting less nutrient-demanding species. However, only a few experimental studies exist on direct effects of ocean acidification (reviewed by Chuard et al., 2019) and stoichiometric changes in prey (Malzahn et al., 2010; Schoo et al., 2010; Lesniowski et al., 2015; Chen & Li, 2017) on GZ fitness. Future studies will help to elucidate nutritional requirements, resilience capability to potential nutrient limitations, and competitive strengths of GZ taxa in globally changing ocean environments.

Acknowledgements We thank Ursula Ecker, Clemens Kozian-Fleck, and Julia Haafke for their help in the laboratory with phosphorus measurements. We also thank three anonymous reviewers for constructive comments made on an earlier version of the manuscript.

Author contributions FL and EAP designed the study. FL, MDG, BPVH, RIP, and EAP performed the field sampling. MB supervised the formal sample analysis. FL analysed the data and drafted the original manuscript. All authors contributed to writing the final manuscript.

Funding FL was supported by a Ph.D. scholarship (International Doctoral Fellowship) from the University of British Columbia. MB acknowledges support from the German Federal Ministry of Education and Research (BMBF), within the BIOWEB project, and the State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein (LLUR).

Data availability Raw data have been deposited in PANGAEA (https://doi.org/10.1594/PANGAEA.933356).

Declarations

Conflict of interest The authors declare they have no conflict of interests.

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