



# Trophic flows to mesozooplankton support the conventional paradigm of pelagic food web structure in ocean ecosystems

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## Abstract

The current conventional paradigm of ocean food web structure inserts one full level or more of microzooplankton heterotrophic consumption, a substantial energy drop, between phytoplankton and mesozooplankton. Using a dataset with contemporaneous measurements of primary production (PP), size-fractionated mesozooplankton biomass, and micro- and mesozooplankton grazing rates from 10 tropical to temperate ocean ecosystems, we examined whether the structural inefficiencies in this paradigm allow sufficient energy transfer to support active metabolism and growth of observed zooplankton standing stocks. Zooplankton carbon requirements (ZCR) were determined from allometric equations that account for ecosystem differences in temperature and size structure. ZCRs were relatively low (~30% of PP or less) for both oligotrophic systems and bloom biomass accumulation in eutrophic coastal waters. Higher relative ZCRs (>30% PP) were associated with elevated mesozooplankton grazing scenarios (bloom declines, abundant salps), advective subsidies, and open-ocean upwelling systems. Microzooplankton generally dominated as grazers of PP but were equal or secondary to direct herbivory as nutritional support for mesozooplankton in five of eight regional studies. All systems were able to satisfy ZCR within the conventional food-web interpretation, but balanced open-ocean upwelling systems required the most efficient alignments of contributions from microzooplankton grazing, direct herbivory, and carnivory to do so.

**Keywords:** production; grazing; zooplankton biomass; carbon demand; trophic structure; food-web efficiency

## Introduction

Over the decades since the microbial loop hypothesis (Azam et al. 1983) transformed understanding of marine food web relationships, microzooplankton (the taxonomically diverse assemblage of <200-μm consumers, functionally dominated by protists but also including small metazooplankton) have emerged as the dominant grazers of primary production (PP) globally and a major transfer link to higher trophic levels (Sherr and Sherr 2002, Calbet and Landry 2004, Landry and Calbet 2004). The current conventional paradigm of food web structure reflects this understanding by inserting a full trophic level or more of microzooplankton heterotrophic consumption, a significant energy drop, between phytoplankton and mesozooplankton (Steinberg and Landry 2017). Nonetheless, the major pathways of matter and energy flow through complex ocean food webs remain enigmatic and open to different points of view, especially regarding their effects on overall trophic transfer efficiency to mesozooplankton. One alternate perspective is that widespread mixotrophy among protistan consumers could substantially improve energy transfer through the lower food web by combining the functions of photo- and phagotrophy into a single trophic level (Flynn et al. 2019; Ward and Follows, 2016). In another, food web structures of the oligotrophic open ocean are proposed to operate at high efficiencies similar to eutrophic systems because gelatinous suspension feeders in oligotrophic systems can short-

circuit microbial trophic steps by preying directly on bacteria-sized primary producers (Everett et al. 2022).

In the present analysis, we use a dataset from 10 ocean studies to address two questions that relate to these different views of food-web structure. Can the conventional, relatively inefficient, interpretation of structure provide sufficient carbon (C) flow to support actively metabolizing and growing mesozooplankton in the oceans (i.e. are more efficient paradigms required to understand how zooplankton can thrive)? Is there evidence of significant efficiency variability among and within ocean regions that can be explained by trophic process studies?

To answer these questions, we first estimate the carbon requirements needed to support active metabolism and growth of mesozooplankton using allometric equations that normalize for ecosystem differences in temperature and biomass size structure. Relative efficiencies are inferred by comparing the C requirement estimates to contemporary measurements of PP. For eight of the regions, C-based estimates of trophic flows are also available from experimental studies of micro- and mesozooplankton grazing and secondary production constraints on carnivory, allowing measured rate comparisons to the calculated C needs for active zooplankton. Our results suggest relative inefficiencies on both the eutrophic and oligotrophic ends of the productivity spectrum, with open-ocean upwelling systems needing the most efficient alignments of contributions

from all nutritional sources to satisfy zooplankton C demand. Microzooplankton remain the dominant grazers of PP in this analysis but are not always the main source of nutritional support for mesozooplankton.

## Materials and methods

### PP and mesozooplankton biomass

The present analysis utilizes data products from 10 studies of tropical-to-temperate habitats of the Atlantic, Pacific, and Indian Oceans (Fig. 1, Table 1). The Bermuda Atlantic Time Series (BATS) and Hawaii Ocean Time-series (HOT) programs are large datasets of PP and mesozooplankton biomass from major subtropical biomes. In addition to the same core measurements of PP and zooplankton biomass, eight experimental studies provide contemporary estimates of micro- and mesozooplankton grazing rates from 173 individual stations or days of multi-day experiments (Table 1). The former are represented by the Arabian Sea (AS; 7 fixed stations for 4 monsoon seasons), Equatorial Biocomplexity (EB; N-S and E-W station transects on each of 2 cruises), and 110°E Revisited studies (110E; 20 transect stations sampled on successive days from 39.5 to 11.4°S). The remaining five studies (E-Flux Cyclone Opal—OPAL; California Current Ecosystem—CCE; Costa Rica Dome—CRD; BLOOFINZ-Gulf of Mexico—GOM; SalpPOOP—SP) were conducted as Lagrangian experiments, with *in situ* incubations done on a free-floating array during multiple days of repeated sampling and experiments of the marked water parcels (e.g. Landry et al. 2009).

Most PP estimates are net  $^{14}\text{C}$  bicarbonate uptake rates from 24-h *in situ* incubations at 6–8 depths, which are presented as integrated rates ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) for the euphotic zone. EB and 110E experiments, however, were done in seawater-cooled light-calibrated deck incubators (Balch et al. 2011, Landry et al. 2022b), and OPAL and 110E studies substitute C-based estimates of phytoplankton growth from 24-h dilution experiments for  $^{14}\text{C}$  uptake rates (Landry et al. 2008a, 2022b).

Mesozooplankton were collected with oblique net tows in the upper 200 m (0.7–1.0 m<sup>2</sup> mouth area nets, 200- $\mu\text{m}$  Nitex mesh) and size-fractionated with nested Nitex screens to produce biomass estimates for five size classes (0.2–0.5, 0.5–1, 1–2, 2–5, and >5 mm) for mid-day (D) and mid-night (N), except for AS samples, which were only collected during nighttime and combine 2–5 and >5 m fractions. C biomass estimates were determined by elemental analysis of dry weight subsamples, or in the case of CCE, CRD, EB, OPAL, and SP studies estimated from size-fractionated dry weights (DW) assuming a mean C:DW ratio of 0.34 (Landry et al. 2001).

### Zooplankton carbon requirements

Estimates of zooplankton carbon requirement (ZCR) were calculated from size-fractionated C biomass and environmental temperature assuming that ingestion rates were sufficient to support active metabolism and growth of the mean upper-ocean biomass plus the additional needs of diel migrants that reside in deeper waters during daytime. The general equation for such calculations is:

$$\text{ZCR} = \sum_{i=1}^5 A_i \times (M_i + G_i) / \text{AE}$$

where  $i$  = size classes 1–5,  $A_i$  is abundance in size class ( $\text{ind m}^{-2}$ ),  $M_i$  and  $G_i$  are average carbon-based estimates

of metabolism ( $M_i$ ) and growth ( $G_i$ ) rates ( $\mu\text{g C ind}^{-1} \text{ d}^{-1}$ ) within size classes, and AE is food absorption efficiency (= 0.7; Steinberg and Landry 2017). ZCR components for the portion of the community that resides in the upper 200 m over the full day (the average of daytime and nighttime biomass) and the portion that migrates out of the upper layer during the daytime period (nighttime—daytime biomass) were computed separately and added together to get total ZCR.

For calculations pertaining to upper 200-m zooplankton, we used depth-integrated mean temperatures for the euphotic zone and mean carbon estimates for individual zooplankton (2.45, 7.46, 41.5, 147, and 3060  $\mu\text{g C ind}^{-1}$  for the 0.2–0.5 mm to > 5-mm size fractions, respectively) determined from measured size-fractionated abundances and carbon biomass from 144 net tows from HOT (Landry et al. 2001). For diel migrants, we assumed 0.5-day residence at mean 300–500 m temperatures and used mean individual weights of 3.16, 25, 64.4, 216, and 5500  $\mu\text{g C ind}^{-1}$  determined for the 0.2–0.5 mm to > 5-mm size fractions of the migratory portion of the community. For both upper ocean and migratory zooplankton, areal abundances ( $A_i$ ,  $\text{ind m}^{-2}$ ) were calculated by dividing the C biomass in each size fraction by the mean C weight of individuals in the fraction. Where we could not determine the migratory contribution to ZCR (the AS study), we used the nighttime zooplankton standing stock as an overestimate of feeding requirement at euphotic-zone temperature for the full day.

Metabolic rates were computed as 1.3 times the C equivalents of zooplankton respiration rates from the empirical equation of Ikeda (1985):

$$\ln R_o (\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}) = 0.8354 \times \ln C_i (\text{mg C ind}^{-1}) + 0.0601 \times T (^\circ\text{C}) + 0.5254$$

where  $C_i$  is the average carbon content of individuals in size-fraction  $i$  and  $T$  is the temperature experienced by mean euphotic zone residents or daytime migrants. Hourly rates were multiplied by 24 h for mean euphotic zone residents and by 12 h for the daytime migrants. Both were converted to C equivalent rates by multiplying times  $RQ \times 12/22.4$ , where  $RQ$  is the respiratory quotient of 0.97 (Hernández-León and Ikeda 2005), 12 is the molecular weight of C, and 22.4 is the molar volume of an ideal gas at standard temperature and pressure. The 1.3 multiplication factor accounts for zooplankton excretory loss of dissolved organic C, which occurs in addition to respiration (Steinberg et al. 2000).

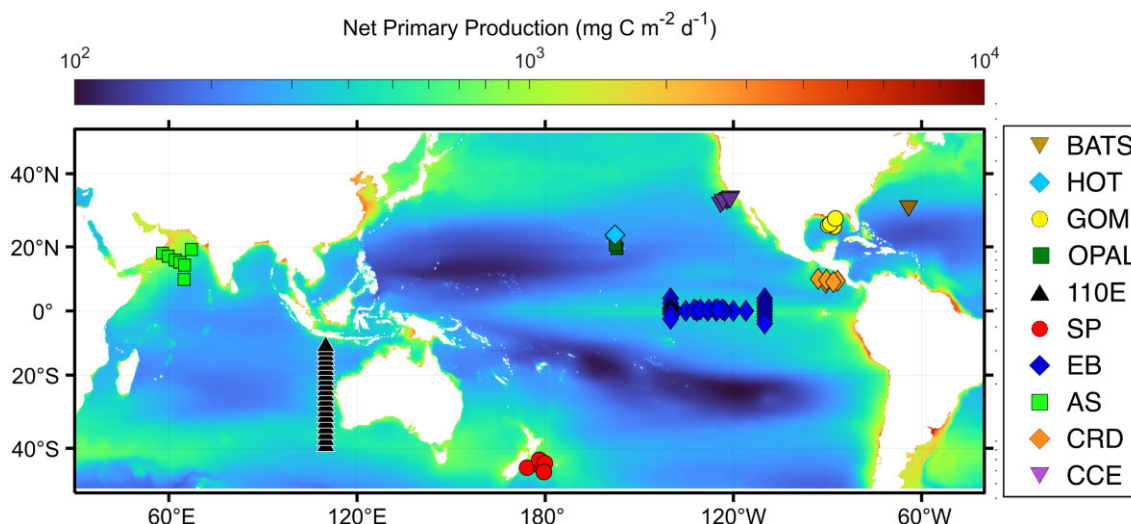
Growth rate estimates were similarly computed from the allometric equation of Hirst and Shearer (1997):

$$\log_{10}(\text{d}^{-1}) = -0.2962 \times \log_{10} C_i (\mu\text{g C ind}^{-1}) + 0.0246 \times T (^\circ\text{C}) - 1.1355$$

For each size class, we first determined the daily instantaneous rate of growth ( $\text{d}^{-1}$ ) for individuals of mean size-class C content and used that to compute daily incremental C growth ( $G_i$ ,  $\mu\text{g C ind}^{-1} \text{ d}^{-1}$ ) for the ZCR equation.

For the special case where salps were abundant (3 of 5 multi-day experiments) in the SP study, we used the equation of Iguchi and Ikeda (2004) for *Salpa thompsoni* at 1.3°C:

$$\log_{10} R_o (\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}) = -2.433 + 2.386 \log_{10} \text{BL (body length, mm)}$$



**Figure 1.** Locations of study sites. Background is distribution of annual Net Primary Production (NPP) based on VGPM satellite products from <http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst.php>.

**Table 1.** Experimentally determined estimates of the percentage of protistan microzooplankton in the diets of mesozooplankton from field-based studies conducted in various ocean habitats.

Study/Region	Cruises	Years	Exps	Study descriptions
Bermuda Atlantic Time Series (BATS), subtropical Atlantic	268	1994–2020	–	Madin et al. 2001
Hawaii Ocean Time-series (HOT), subtropical Pacific	257	1994–2020	–	Landry et al. 2001
US JGOFS Arabian Sea (AS), 4 monsoon seasons	4	1995	30	Smith et al. 1998, Landry 2009
Equatorial Biocomplexity (EB), equatorial Pacific	2	2004, 2005	33	Nelson and Landry 2011
Cyclone OPAL (OPAL), E-Flux, subtropical Pacific	1	2005	9	Benitez-Nelson et al. 2007
California Current Ecosystem (CCE), CCE-LTER	2	2006, 2007	25	Landry et al. 2009
Costa Rica Dome (CRD), CRD FLUZE	1	2010	19	Landry et al. 2016a
Gulf of Mexico (GOM), BLOOFINZ-GoM	2	2017, 2018	17	Gerard et al. 2022, Landry et al. 2022a
SalpPOOP (SP), Chatham Rise, Southwest Pacific	1	2018	21	Décima et al. 2023
110°E Revisited (110E), IIOE-2, Eastern Indian Ocean	1	2019	19	Landry et al. 2022b

Exps = number of independent process experiments conducted for the integrated euphotic zone.

and  $Q_{10} = 2.0$  to calculate respiration rates of individual salps collected in each tow. The C equivalent rates of respiration were multiplied by 4.3 ( $= 3/0.7$ ) to estimate the feeding requirements to satisfy total metabolism, growth, and egestion.

### Micro- and mesozooplankton grazing

Grazing rate estimates for micro- and mesozooplankton were taken largely as described in the original studies. Rate estimates for microzooplankton were mainly from two-treatment dilution experiments in which seawater samples from 6 to 8 depths were incubated for 24 h *in situ* on free-drifting arrays (OPAL, CCE, CRD, GOM, SP) or in light-calibrated shipboard incubators (EB, 110E). These were generally coordinated with PP experiments, which experienced the same incubation conditions. Grazing rates determined from the differences in net changes in Chl *a* in the dilution treatments were converted to C equivalents based on estimates of phytoplankton C from microscopy and flow cytometry and then integrated for the euphotic zone (Landry et al. 2008a, 2011, 2016b, 2022a, b). For SP, C: Chl *a* estimates came from the ratios of  $^{14}\text{C}$ -based C-synthesis versus dilution-based Chl *a* synthesis. For all experiments, C-based estimates of microzooplankton grazing rates were assumed to produce microzoo-

plankton C biomass for mesozooplankton consumption with a gross growth efficiency (GGE) of 30%, the mean GGE of protistan consumers (Straile 1997).

Rate estimates for mesozooplankton herbivory were mainly from applications of the gut fluorescence technique in which size-fractionated subsamples from the net tows were analyzed for phaeopigment as an index of ingested Chl *a* and multiplied times a gut turnover rate to get % of water column Chl *a* consumed per day (Décima et al. 2011, 2016, Landry and Swalethorp 2022). For the SP study, the additional component of salp grazing estimates by gut fluorescence were done for individual solitary or aggregate specimens in the net tows and summed for the total population. Grazing estimates determined as Chl *a* ingestion rates were converted to C equivalents using C:Chl *a* ratios from phytoplankton C analyses (Landry et al. 2008b, Décima and Landry 2011, 2016b, 2020, 2022a, b).

Methods for the AS study are the main departures from the above. Microzooplankton grazing rates for the AS were from full, multi-treatment dilution experiments incubated for 2–3 depth strata in shipboard incubators (Landry et al. 1998, Caron and Dennett 1999) and thus differed from *in situ* conditions of the PP incubations, which were also conducted at



more depths (Barber et al. 2001). Phytoplankton C estimates for each AS station are from Garrison et al. (2000). Additionally, AS mesozooplankton grazing estimates were only done for two of the four seasonal cruises and using a short-term  $^{14}\text{C}$  *in situ* incubation method analogous to  $^{14}\text{C}$  PP (Roman and Rublee 1981). Despite these methodological differences, zooplankton grazing and production estimates for the AS have been shown to fit a simple food web model in which productivity and losses are balanced on average and constrained by measured carbon flows through phytoplankton and bacteria (Landry 2009).

### Data groupings

In order to highlight the main similarities and differences among and between regional studies, we grouped and averaged the data in various ways. BATS and HOT were each divided into quartiles of the lowest to highest measured rates of PP and averaged for those groups. AS station data were grouped by the four cruises/monsoon seasons (Smith et al. 1998, Landry 2009). EB data were grouped for the two transects of stations (N-S and E-W) sampled on each of the two cruises (Nelson and Landry 2011). OPAL was partitioned by experiments conducted at stations IN and OUT (controls) of the eddy diatom bloom (Décima and Landry 2020), and 110E was divided into 4 equal groups by latitude, reflecting the range in habitats and monotonically increasing environmental temperatures sampled (Landry et al. 2022b). The remaining studies (CCE, CRD, GOM, SP) were each conducted as separate multi-day Lagrangian experiments (cycles) and averaged for those groups. Rate results in figures are available as mean values  $\pm$  SEM (standard error of mean) in Supplementary Table S1 and as individual experimental results from eight regional studies in Supplementary Table S2.

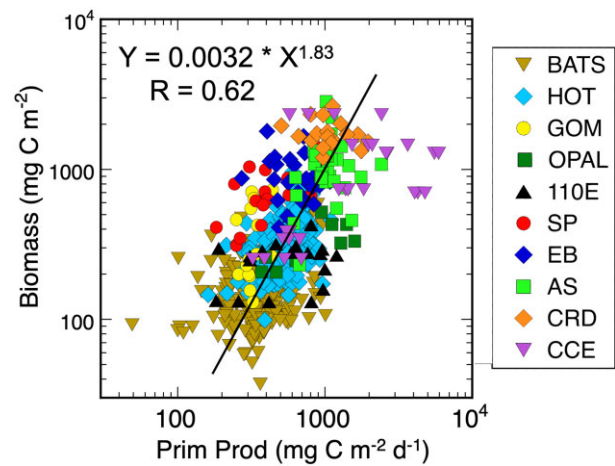
## Results

### Mesozooplankton biomass relationship to PP

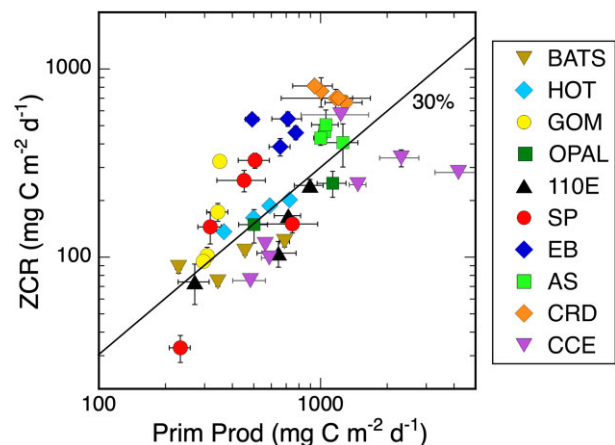
Paired contemporary estimates of mesozooplankton biomass and PP show a strong positive relationship (Fig. 2). Both biomass and production are lower for subtropical oligotrophic regions (BATS, HOT, GOM, 110E) and notably higher for the regions associated with open-ocean or coastal upwelling (EB, AS, CRD, CCE). The  $>1.0$  slope (95% confidence limits = 1.67, 2.02) of the relationship intuitively suggests that richer systems have higher overall efficiency of trophic transfer, resulting in larger zooplankton standing stocks supported by a given level of productivity. This needs to be interpreted with caution, however, as the relationship does not account for inter-regional differences in environmental temperature and zooplankton size structure, which could substantially alter the magnitude of biomass supported by any given combination of productivity and transfer efficiency. This is the rationale for normalizing the ingestion requirements to support standing stocks in the different regions using temperature and allometric size scaling in the ZCR calculations.

### ZCR trends with PP

After accounting for temperature and size effects on zooplankton feeding needs, group-averaged values of ZCR retain similar features to the full biomass dataset, such as relative positioning of the regional studies with respect to system productivity (Fig. 3). Group averaging does help, how-



**Figure 2.** Relationship between individual estimates of mesozooplankton carbon biomass ( $\text{mg C m}^{-2}$ ) and contemporary rate of PP ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) in 10 ocean system studies: Bermuda Ocean Time Series (BATS); Hawaii Ocean Time-Series (HOT); Gulf of Mexico (GOM); Hawaii mesoscale eddy (OPAL); 110°E Indian Ocean (110°E); SalpPOOP (SP); Equatorial Biocomplexity (EB); Arabian Sea (AS); Costa Rica Dome (CRD); and California Current Ecosystem (CCE). Fitted line is Model 2 (Reduced Major Axis);  $P = 9.7 \times 10^{-74}$ .



**Figure 3.** Relationship between mean estimates of carbon requirement to support mesozooplankton biomass (ZCR) and contemporary rates of PP ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) in 10 ocean system. Abbreviations for regions/studies as in Fig. 2. Uncertainties are  $\pm$  standard errors of mean values.

ever, to better visualize and explain variability among regions and experiments within regions. For this, we highlight the line  $\text{ZCR} = 30\% \text{ PP}$ , which represents the amount of mesozooplankton nutrition that could be explained if 100% of PP was consumed by microzooplankton and passed to mesozooplankton with 30% efficiency (Straile 1997). Balanced steady-state systems at or under the  $\text{ZCR} = 30\% \text{ PP}$  line can be readily explained by the conventional food-web paradigm of at least one trophic level of transfer through heterotrophic microzooplankton. Systems above the  $\text{ZCR} = 30\% \text{ PP}$  line require a more efficient transfer of PP to meet ZCR (i.e. some direct mesozooplankton herbivory) or involve unbalanced growth and loss processes, as described further below.

The ZCR estimates for BATS and HOT are well described by the 30% line, as are many of the sites with strong sub-

tropical or oligotrophic influences, such as 110E, OPAL, two of the four GOM experiments, and two of the five SP experiments. Most of the CCE experiments also reside below the 30% line, but for different reasons. The three CCE experiments with relatively low productivity ( $<700 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) were conducted offshore in low-nutrient waters adjacent to the North Pacific Subtropical Gyre, and thus have some similarities to HOT. However, CCE temperatures are cooler, and there is a net offshore advection from the richer coastal waters that subsidizes the offshore food web and export there (Kelly et al. 2018). The three CCE experiments at high PP but below the 30% line sampled a coastal upwelling bloom when phytoplankton biomass was strongly accumulating (therefore, unbalanced) and not being efficiently consumed by the combination of micro- and mesozooplankton (Landry et al. 2009).

Experiments that appear significantly above the 30% line include the three studies of open-ocean upwelling systems (AS, EB, and CRD) as well as specific experiments from the GOM, CCE, and SP studies (Fig. 3). For GOM, the main departures are unbalanced experiments that received strong lateral subsidies of organic material from the rich continental margin (Kelly et al. 2021, Landry and Swalethorp 2022). For CCE, the main departure is the documented (unbalanced) decline phase of a 2007 coastal upwelling bloom, in which phytoplankton biomass was decreasing sharply due to mesozooplankton overgrazing (Landry et al. 2009). The three SP experiments above the  $\text{ZCR} = 30\%$  PP line are waters sampled during salp blooms with documented high direct grazing pressure by salps on the phytoplankton community (Décima et al. 2023).

### Microzooplankton grazing

For all experiments combined, microzooplankton consumed an average of  $67.0\% \pm 3.5\%$  of euphotic-zone integrated values of PP, consistent with previous estimates from global compilations of dilution results (Calbet and Landry 2004, Schmoker et al. 2013, Steinberg and Landry 2017). Mean estimates of microzooplankton grazing for most individual experiments were generally high ( $>60\%$  of PP) and sometimes around 100% (Fig. 4a). The main exceptions were from CCE and one SP experiment with high salp abundance, for which microzooplankton grazing accounted for the utilization of only 10%–20% of PP (Fig. 4a).

Assuming a trophic transfer loss of 70% ( $\text{GGE} = 0.3$ ) for converting microzooplankton grazing to microzooplankton C production, mesozooplankton consumption of microzooplankton production could satisfy an average of  $56.3\% \pm 3.9\%$  of the ZCR determined for all experiments (Fig. 4b). However, the estimates exhibit a wide range of variability among and within regions (Supplementary Table S1). Higher estimates are observed for 110E, the SP experiments without salps, and most of the GOM experiments. Lower estimates are from CCE upwelling blooms, the CRD region, the SP experiment with high salp abundance, and the GOM experiment with lateral shelf supplement.

### Mesozooplankton grazing

For all experiments combined, mesozooplankton grazing accounted for mean utilization of  $23.1\% \pm 2.0\%$  of PP, which is similar to the 23% global estimate (Steinberg and Landry 2017) that derives from the data compilation of Calbet (2001). As expected from general food-web size relationships,

mesozooplankton grazing estimates are typically low for experiments conducted in oligotrophic waters (GOM, 110E, AS intermonsoon, SP without salps, OPAL controls, CCE offshore) (Fig. 5a, Supplementary Table S1). Higher estimates of direct mesozooplankton herbivory come from the EB and CRD open-ocean upwelling regions and are also seen in SP experiments with salps as well as the decline phases of CCE upwelling blooms and the OPAL diatom bloom.

Because mesozooplankton herbivory applies directly to satisfying energy requirements with no trophic transfer loss, the average contribution to ZCR for the full dataset,  $53.4\% \pm 3.4\%$ , is substantially higher than, more than double, the mean percentage of PP consumed. Most regional experimental estimates fall in the range of satisfying 30%–60% of ZCR (Fig. 5b). Mesozooplankton grazing estimates for the GOM are uniquely low in this regional comparison. On the high end, direct herbivory can account for  $\sim 100\%$  of ZCR in several of the experimental scenarios: SP salp studies, the OPAL diatom bloom, and CCE upwelling blooms (Supplementary Table S1).

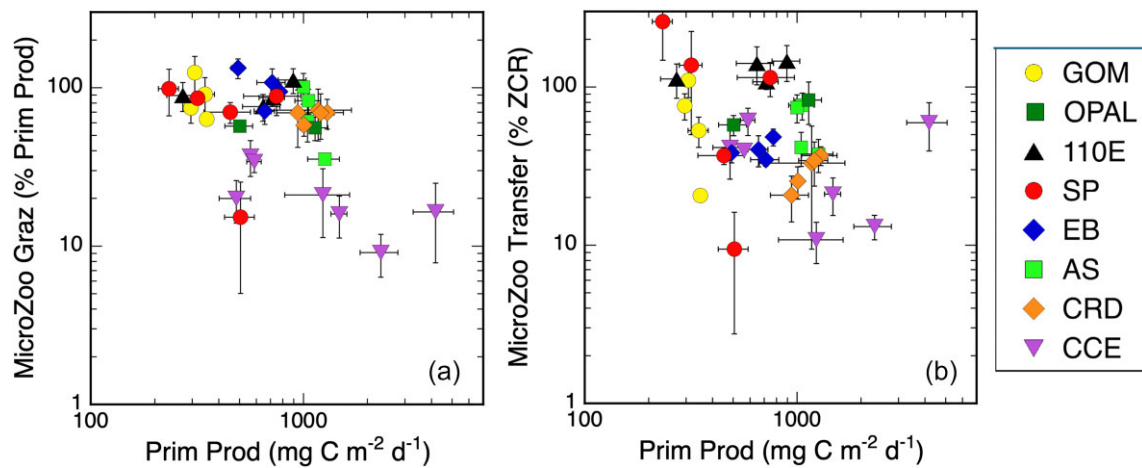
### Combined grazing contributions to ZCR

Combined grazing and transfers from micro- and mesozooplankton grazing substantially meet or exceed ZCR estimates for four of the eight experimental studies (110E, SP, OPAL, CCE) (Fig. 6, Supplementary Table S1). AS grazing estimates fall short (89% of ZCR) but are missing mesozooplankton grazing measurements for the SW monsoon cruise (Supplementary Table S1), when diatom biomass was highest (Garrison et al. 2000) and the highest direct grazing contribution to ZCR would be expected. GOM grazing estimates explain 75% of ZCR, but mainly because they include one experiment with a strong coastal margin subsidy (GOM Cycle 5 in Supplementary Table S1). The remaining GOM experiments satisfy ZCR ( $92\% \pm 13\%$ ) within experimental uncertainty. Combined grazing estimates for EB and CRD account for  $84\% \pm 5\%$  and  $72\% \pm 8\%$  of ZCR, respectively.

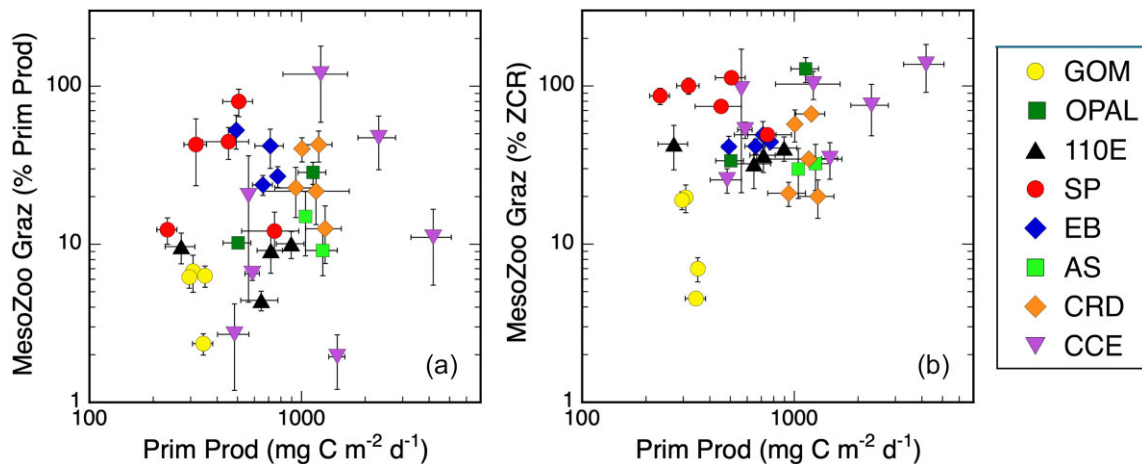
Overall, the relative contributions of microzooplankton transfer to ZCR tend to be higher for waters with subtropical affinities or low-nutrient non-bloom conditions, like 110E, GOM, and some individual AS stations. For OPAL, feeding on microzooplankton exceeds the direct phytoplankton contribution to ZCR by a factor of 1.7 for control station experiments in typical subtropical waters, but the ratio falls to 0.6 in the mesoscale eddy stations enriched by the diatom bloom (Fig. 6, Supplementary Table S1). For SP experiments, the microzooplankton contribution to ZCR exceeds direct herbivory by a factor of 2.4 without salps (Cycles 3 and 5, Supplementary Table S1), but the ratio averages 0.4 for the experiments involving salp blooms (Cycles 1, 2, and 4, Supplementary Table S1). These within-system variabilities are masked in the regional averages.

### Discussion

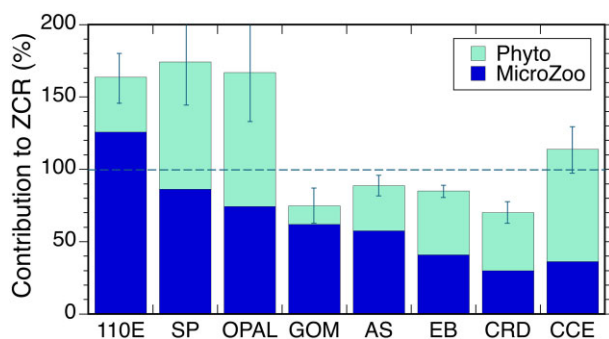
For eight regional studies, the relative magnitudes of micro- and mesozooplankton grazing on phytoplankton production are shown to vary substantially between and within ecosystems due to environmental circumstances and especially bloom dynamics (Figs 4a and 5a). Nonetheless, for all cases, combined grazing comes close to satisfying the C ingestion



**Figure 4.** Experimentally determined rates of microzooplankton grazing in 8 ocean regions presented as (a) % of PP and (b) % contribution to ZCR assuming 30% transfer efficiency. Abbreviations for regions/studies as in Fig. 2. Uncertainties are  $\pm$  standard errors of mean values.



**Figure 5.** Estimates of mesozooplankton direct grazing on phytoplankton in 8 ocean regions presented as (a) % of PP and (b) % contribution to ZCR. Abbreviations for regions/studies as in Fig. 2. Uncertainties are  $\pm$  standard errors of mean values.



**Figure 6.** Average contributions to ZCR by microzooplankton production transfer (MicroZoo) and mesozooplankton direct grazing on phytoplankton (Phyto) in 8 ocean regions. Abbreviations for regions/studies as in Fig. 2. Uncertainties are  $\pm$  standard errors of mean values.

requirements for actively metabolizing and growing mesozooplankton communities, accounting for 100% of ZCR, on average (Figs 4b and 5b) and no less than 72% of ZCR for individual studies (Fig. 6). In the subsections below, we further consider the underlying assumptions, methodological caveats, and data qualities of our approach, the likely magnitudes

of other flux contributions to ZCR, and, lastly, the implications for conventional understanding of food web structure in pelagic marine systems.

### Assumptions, measurement caveats, and data qualities

The central assumption of our analysis is that zooplankton assemblages of even oligotrophic open-ocean ecosystems can achieve the relatively high rates of active metabolism and growth defined by empirically determined relationships based on temperature and body size (Ikeda 1985, Hirst and Shearer 1997). Similar assumptions have been applied, implicitly or explicitly, in a broad array of zooplankton studies: to compute active flux contributions to carbon export by migratory zooplankton (Al-Mutairi and Landry, 2001; Stukel et al. 2013); to evaluate diet adequacy for meeting minimum respiratory requirements (Zhang et al. 1995, Calbet et al. 2009), to determine epipelagic community production and carbon budgets (Roman et al. 2000, 2002); to quantify carbon demand in the mesopelagic environment (Steinberg et al. 2008); and to parametrize marine ecosystem models (Townsend et al. 1994, Stock and Dunne 2010). In the present analysis, we used the



assumption to set levels of presumptive feeding requirements (ZCR) that are entirely independent from the measured feeding rates to which they would be compared. ZCR calculations were additionally liberal in accounting for DOC excretion (1.3X Ikeda 1985 respiration rates), the ingestion needs of diel migrants, and in using euphotic-zone temperatures, rather than the lower mean net-tow temperatures, for rate estimates. We assumed, in effect, that zooplankton were heavily concentrated in the euphotic zone rather than evenly distributed over deeper depths of net tows, which elevates ZCR to higher mean temperature. These ingestion assumptions produce mesozooplankton biomass with mean GGE of  $24.4\% \pm 0.2\%$ , similar to the 26% average for copepods (Straile 1997).

The grazing rate estimates for regional studies come mainly from similarly conducted measurements by the dilution and gut fluorescence techniques for micro- and mesozooplankton, respectively. Dilution nonlinearities can lead to underestimates of microzooplankton grazing when phytoplankton concentrations are high and saturating, or overestimates when grazer growth rates are disproportionately depressed in the diluted treatments (Gallegos 1989, Dolan and McKeon 2005). Gut fluorescence can overestimate mesozooplankton grazing if detrital particles with significant phaeopigment concentration contaminate samples, or underestimate grazing if the chlorophyll-to-phaeopigment transition is not conserved in the digestion process (Conover et al. 1986). Significant discrepancies of these types were not noted, however, in the original studies.

To the contrary, the original studies emphasized the many ways in which micro- and mesozooplankton grazing estimates supported one another or explained independently observed ecological properties. For EB, the combined grazing of micro- and mesozooplankton balanced phytoplankton growth with insignificant residual, allowing for the partitioning of all major phytoplankton groups between production and loss processes (Landry et al. 2011), and they were also consistent with independent assessments of biogenic silica cycling by the diatom component (Krause et al. 2010). Inverse modeling of EB production and grazing measurements further illustrated how the experimentally measured food web fluxes fully supported active metabolism and growth of mesozooplankton in the equatorial Pacific, as well as independently measured estimates of  $^{18}\text{O}$  gross to net productivity ratio, DOC fluxes to bacterial production, and C export (Landry et al. 2020). Similarly, measured rates were consistent with general steady-state balances of production and grazing in CRD and GOM studies, other than the one GOM experiment with a lateral shelf subsidy (Landry et al. 2016; Landry and Swalethorp 2022) and with seasonal or regional process balances in the AS and 110E studies (Landry 2009, Landry et al. 2022b). For CCE upwelling experiments conducted as Lagrangian experiments with repeated daily samplings of marked water parcels, dilution estimates of phytoplankton growth and the combined measured grazing rates of micro- and mesozooplankton accounted for 91% of the variability of independently measured Chl *a* net growth in the ambient environment, including large swings in biomass accumulation and overgrazing decline (Landry et al. 2009). Thus, despite the relative simplicity and caveats of the grazing methods, their application together in designed system-level studies appears to have captured the main production and loss dynamics of the regions investigated.

## Contributions of other trophic processes to ZCR

In addition to mesozooplankton herbivory and production transfer from microzooplankton grazing on phytoplankton, other trophic processes such as bacterivory, detritivory, and carnivory could make meaningful contributions to satisfying ZCR. For bacterivory, for example, there is ample evidence that mesozooplankton consumers, like appendicularians, can feed directly on prey as small as heterotrophic bacteria and effectively short circuit the microbial loop (Gorsky and Fenaux 1998, Scheinberg et al. 2005), and even large particle-feeding crustaceans should be able to utilize some bacterial production associated with aggregates. Here, however, we seek to reconcile trophic fluxes to mesozooplankton without considering unmeasured processes (direct mesozooplankton grazing on bacteria, mixotrophy) that might substantially enhance the upward transfer efficiency of bacterial production. Taking the most conservative view of the microbial loop grazing chain (Azam et al. 1983), half of bacterial production of typically 10%–15% of PP is lost to viral mortality (Anderson and Ducklow 2001), leaving only ~2% of PP to pass to mesozooplankton after one intermediate level of protistan consumer and < 1% of PP after two transfers. Given that ZCR estimates average about half of PP, bacterivory transfer to mesozooplankton with our conservative assumptions would satisfy < 4% of ZCR.

In the inverse analysis of food web C flows based on EB experimental results and steady-state assumptions, detritus was estimated to account for 15% of mesozooplankton ingestion in the equatorial Pacific (Landry et al. 2020). While detritus utilization of this magnitude could be realistic for open-ocean ecosystems given abundant evidence for zooplankton feeding on aggregates (Lampitt et al. 1993, Dilling et al. 1998, Möller et al. 2012) and the rapid decline of particle fluxes (fecal pellets and aggregates) with depth in most systems, we also take a conservative view to assessing detritivory contribution to ZCR. Quantitative estimates of detrital contributions to zooplankton nutrition are not only difficult to make and compare among study regions with different ecological conditions (Cawley et al. 2021), they are also not entirely distinct from gut fluorescence estimates of herbivory, which must certainly include some pigments from aggregate and pellet feeding as well as contaminants. To avoid double counting of nutritional contributions to ZCR, we therefore assumed that detritivory fell within the methodological uncertainties of the gut fluorescence method.

Carnivory is, however, a valid and distinct additional source to zooplankton nutrition. Obligate carnivores, including chaetognaths, pelagic cnidarians, and predatory crustaceans, typically increase in relative contribution to zooplankton biomass in oligotrophic open-ocean compared to richer coastal regions (McGinty et al. 2018; Brandão et al. 2021), and many other taxa derive at least part of their nutrition from opportunistic omnivorous feeding on small metazoans (Landry 1981, Ohman 1984). In the GOM experiments, for example, carnivorous taxa (mainly chaetognaths, Luciferidae shrimp, and Euchaetidae copepods) comprised 70% of the biomass of > 1-mm net-collected zooplankton, consistent with a >0.5 trophic level increase between 0.2–0.5 and 2–5 mm size fractions based on  $\delta^{15}\text{N}$  enrichment (Landry and Swalethorp 2022). In the equatorial Pacific, carnivorous taxa accounted for 45% of total zooplankton biomass other than copepods, which were not partitioned

by feeding type (Le Borgne *et al.* 2003). For the present analysis, the maximum trophic flux to planktivorous carnivores is set by the mesozooplankton production calculation based on Hirst and Shearer (1997), which averages 24.4% of ZCR (excluding SP salps). Such flux is presumed to be consumed mostly within the zooplankton assemblages of open-ocean regions, whereas a larger portion of zooplankton production in richer coastal systems must go to supporting the increased biomass of planktivorous fish in those regions (Koslow 1981, Kelly *et al.* 2019).

### Implications for food web structure

When carnivory is considered in addition to phytoplankton grazing, all regions are able to satisfy the nutritional requirements for active zooplankton within the conventional understanding of food web structure. For the AS and EB studies, 100% of ZCR is met if planktonic carnivores utilize half or two-thirds of estimated zooplankton production, respectively. The CRD is more difficult to reconcile, possibly because the pronounced temperature gradient (15°C difference between surface waters and 100 m) and shallow O<sub>2</sub> minimum zone there can lead to substantially different metabolism and growth rate estimates depending on how zooplankton distribute and behave with respect to those gradients. Nonetheless, if planktonic carnivores consume all of the estimated CRD zooplankton production, ZCR is satisfied (96% ± 8%) within experimental uncertainty. Among the different regions, it is notable that open-ocean upwelling regions (CRD, EB, AS) are the most challenging for measured feeding rates to satisfy ZCR, while other systems often show trophic fluxes in excess of ZCR, even without considering carnivory. We interpret these differences in terms of inter-regional trends in food-web efficiency, but the explanations vary for CCE coastal waters on the high end of the productivity scale versus oligotrophic open-ocean regions on the low end.

For CCE upwelling experiments, relatively low efficiency in converting PP to zooplankton biomass is due at least in part to production-grazing imbalances, with the majority of our experiments capturing periods of rapid biomass accumulation of ungrazed phytoplankton (Landry *et al.* 2009). It might also be the case that zooplankton metabolism and production in these richer waters can exceed the rate estimates from Ikeda (1985) and Hirst and Shearer (1997) equations, which are based on data averages, not maximum potential. Thus, actual carbon requirements in excess of calculated ZCR, allowing higher-than-average growth somatic growth or fecundity rates on the Hirst and Shearer (1997) scale, could contribute to the impression of relatively low efficiency.

For oligotrophic regions (110°E, OPAL, GOM, SP without salps), trophic flux estimates that are substantially in excess of ZCR more likely reflect structural inefficiencies as might be caused by additional transfer steps. For example, we note that HOT values are close to the ZCR = 30% PP line in Fig. 3 and are consistent with trophic structure inferences for the subtropical Pacific based on Compound Specific Isotopic Analyses of Amino Acids (CSIA-AA), which indicate one intermediate trophic step, on average, between PP and particle-feeding copepods (Hannides *et al.* 2009, Landry and Décima 2017). This does not mean, however, that the food web structure has only one intermediate step, but rather that the sum of direct mesozooplankton herbivory and food-web pathways with one, two, or more intermediate steps has an average of one step. Similarly, for the oligotrophic regions where total

grazing exceeds ZCR, the grazing transfer estimates for microzooplankton are likely partially dissipated (therefore less efficient) by going through two intermediate transfers instead of one.

The current analysis is weighted toward warm, nutrient-poor, open-ocean ecosystems where protistan mixotrophic strategy should be most important and its efficiencies most apparent in trophic flows (Flynn *et al.* 2019, Ward and Follows 2016, Edwards 2019). Had the results shown a large discrepancy between the conventional interpretation of experimentally measured rates and the requirements to support mesozooplankton biomass, a more efficient mixotrophy paradigm could reasonably have been invoked to explain the difference. Support of the conventional paradigm does not, however, diminish the widespread occurrence of mixotrophic potential among protistan groups and its strategic importance for nutrient acquisition and nutritional flexibility. Nonetheless, there is broad variability in how individual taxa align on the spectrum of traditional autotrophic to heterotrophic roles and considerable uncertainty in how that manifests in aggregate for mixed natural assemblages (Caron 2016). One explanation for our results could be that the dilution method for estimating phytoplankton growth and microzooplankton grazing rates already accounts for C fluxes through mixotrophs and are, therefore, included in conventional food-web interpretations. In contrast, however, a laboratory-designed dilution experiment showed negligible or negative grazing rates for mixotrophs when measured in terms of Chl<sub>a</sub>, leading to the conclusion that mixotroph grazing contributions were not included in Chl<sub>a</sub>-based rates (Ferreira *et al.* 2021). By logical extension, if that conclusion is considered for the studies analyzed here, the very good results with Chl<sub>a</sub>-based rate measurements and their consistency with other independently determined ecosystem properties would suggest that ZCR can be explained by obligate photo- and heterotrophs alone. This would seem to undermine rather than support the importance of mixotrophy argument. We advance that conundrum (is mixotroph grazing included or not in Chl<sub>a</sub>-based dilution rates?) as a challenge for future studies.

Lastly, the present results offer a different perspective to a recent suggestion, based on the similarities of mean biomass spectra in eutrophic coastal and oligotrophic open-ocean regions, that pelagic systems self-organize into food webs of similar efficiency (Everett *et al.* 2022). From the discussion above, a eutrophic coastal system (CCE) and several oligotrophic subtropical systems have different inefficiencies that give comparable biomass structures on average. However, when the requirements to support zooplankton stocks are compared on a normalized basis that considers environmental temperature and size structure, the main contrast is not between the extremes of coastal eutrophy and open-ocean oligotrophy, but between the latter and mesotrophic regions with open-ocean upwelling (AS, EB, and CRD), which are both balanced with respect to the coupling of production and grazing processes compared to the more dynamic coastal regions. Systems that lie well above the ZCR = 30% PP line in Fig. 3 need to be more efficient, by definition, in moving PP to zooplankton than those at or below the line, but the explanations can differ. For the anomalous GOM example, the higher ZCR:PP ratio is explained by advective subsidy from the adjacent coastal margin (Kelly *et al.* 2021). For the SP examples, salp grazing accounts for efficiency differences among the five experiments (Décima *et al.* 2023). For the more productive open-ocean regions (EB,





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