

**TROPHIC ECOLOGY OF THE INVASIVE FRESHWATER JELLYFISH
CRASPEDACUSTA SOWERBII, REVEALED THROUGH STABLE ISOTOPE
ANALYSIS**

by

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ABSTRACT

The freshwater jellyfish *Craspedacusta sowerbii* is considered invasive in Canada. *C. sowerbii* medusae sporadically form high-density blooms, during which they may exert significant pressure on their prey and competitors, with cascading effects for the entire ecosystem. However, the diet of *C. sowerbii* and its interactions with native zooplanktivores can be difficult to determine due to limitations associated with previously employed methods. This project uses stable isotope analysis, a powerful technique that can determine diet and reconstruct food webs. We measured carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of *C. sowerbii*, its potential prey and competitors from an oligotrophic lake in BC, with the goal of characterizing niche overlap and diet. We found that small (125-250 μm) zooplankton and particulate organic matter were major components of *C. sowerbii* medusae diet. Diet showed little temporal variation throughout the summer and did not vary with medusae size. There was differentiation between the isotopic niches of *C. sowerbii* and competitors, *G. aculeatus* and *Chaoborus*. Taken together, these results indicate that *Chaoborus* may be impacted by *C. sowerbii* through direct predation and competition for small zooplankton prey, while *G. aculeatus* represents a possible predator of *C. sowerbii*. These findings contribute to our understanding of *C. sowerbii* ecosystem impacts and can inform ecosystem management strategies.

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I would also like to acknowledge that this research was conducted on the traditional, ancestral, and unceded territories of the Coast Salish Peoples. Specifically, our study site (Hotel Lake) is located near the traditional settlement of kalpilin (Pender Harbour) and is part of the swiya (lands) of the shíshálh. These lands continue to be integral to the Shíshálh way of life. The University of British Columbia is located on the traditional territory of the Musqueam, who have been stewards of this land for generations. I am grateful for the opportunity to study and learn on their lands.

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INTRODUCTION

1.1. Overview of the literature

Vulnerability of lakes to non-native species

Freshwater ecosystems are experiencing greater declines in biodiversity relative to marine and terrestrial systems (Reid et al., 2019). Lakes may experience these declines due to their exposure to anthropogenic impacts such as climate change, shoreline development, and pollution (Havel et al., 2015; Reid et al., 2019). These disturbances make lakes more vulnerable to invasive species by destabilizing the existing native ecosystem and increasing opportunities for non-native species to be introduced (Havel et al., 2015). Invasive non-native species such as Zebra mussels, Alewife fish, and Japanese stiltgrass have had well-documented impacts on predator-prey interactions, water quality, and fisheries in Canadian lakes (Lower et al., 2024), demonstrating the wide-ranging implications of freshwater ecosystem vulnerability.

The terminology used to describe invasive species can be variable, preventing clear communication between researchers, policymakers, and the public. In this project, the definitions described in Soto et al. (2024) are employed. Non-native species are introduced through anthropogenic processes to an area in which they do not have an evolutionary history. Invasive species are a subcategory of non-native species, made distinct by continuing to spread beyond their point of introduction. These categorizations are based on the stage of the invasion process, and do not provide information about

the extent of environmental damage caused. The use of precise terminology is critical for the clear communication of research on invasive species.

Functional traits of non-native species

The Peach Blossom Jellyfish, *Craspedacusta sowerbii*, is a species of freshwater hydrozoan jellyfish (Marchessaux et al., 2021). While they likely originated in the Yangtze River Delta in China, non-native populations of *C. sowerbii* are now found on all continents but Antarctica (Dumont, 1994). *C. sowerbii* has a variety of lifecycle traits that likely contribute to its success in spreading and establishing in such a wide range. Like all hydrozoan jellyfish, *C. sowerbii* has two primary life stages: the microscopic benthic polyp and the larger pelagic medusa (Winata et al., 2024). However, unlike their marine relatives, freshwater jellyfish must be able to disperse between separate bodies of water. To that end, *C. sowerbii* polyps can asexually produce podocysts, a drought-resistant lifecycle stage thought to be the primary form of dispersal (Dumont, 1994). It has been proposed that migratory birds, aquaria trade, and soldier movement could be possible vectors of introduction (Dumont, 1994; Luskow et al., 2024; Marchessaux et al., 2021). Once introduced, these strategies allow *C. sowerbii* to spread to nearby lakes as an invasive non-native species.

Once introduced to a new environment, asexual reproduction likely contributes to the success of *C. sowerbii* in establishing populations (Luskow et al., 2024). Newly introduced podocysts form polyps, and the polyps divide asexually to produce more polyps (Winata et al., 2024). The second lifecycle stage is initiated when polyps bud off medusae, a process thought to be triggered by high water temperatures (Minchin et al.,

2016). These pelagic medusae range in diameter from 1 to 26 mm and can appear in high-density blooms during the summer months. In their native range, male and female medusae undergo sexual reproduction, producing planula larvae which settle and become polyps (Dumont, 1994). However, non-native *C. sowerbii* are not thought to complete their sexual lifecycle, as populations of medusae are observed to be unisexual, either all male or all female depending on the location (Lüskow et al., 2021). Clonal polyp reproduction continues despite the lack of sex, allowing for the successful establishment of non-native *C. sowerbii* populations.

Diet of C. sowerbii

Given the vulnerability of lake ecosystems to non-native species and the life history traits making *C. sowerbii* so effective at establishing in non-native environments, it is critical to understand the ecosystem impacts of non-native *C. sowerbii* populations. The ecosystem impacts of invasion are varied but can be predicted based on the trophic position of the invasive species. For example, non-native filter feeders are associated with declines in zooplankton and phytoplankton biomass and increases in macrophyte abundances, while predatory invasive species often cause declines in zooplankton and benthic invertebrates but increase phytoplankton biomass (Gallardo et al., 2016). By understanding the trophic interactions of *C. sowerbii*, their ecosystem impacts can be predicted and mitigated.

Previous research suggests that *C. sowerbii* medusae are zooplankton predators. In lab-based predation trials, *C. sowerbii* medusae consistently consume zooplankton prey with sizes ranging from 500 to 2000 μm (Dodson & Cooper, 1983;

Smith & Alexander, 2008; Spadinger & Maier, 1999). However, attempts to estimate the selectivity of *C. sowerbii* towards specific sizes of zooplankton have yielded conflicting results. Dodson and Cooper (1983) found a preference for the large (1500 μm) cladoceran *Daphnia*, while Spadinger and Maier (1999) reported a preference for smaller zooplankton (100-500 μm) such as rotifers and nauplii. It is also unclear the extent to which these findings reflect the feeding behavior of medusae in a natural zooplankton assemblage. Medusae prey selectivity is also impacted by encounter rates with prey, which is not accounted for in these experiments. While zooplankton are likely a component of *C. sowerbii* medusae diet, the relative contributions of various fractions remain unclear.

Gut content analysis allows for the examination of *C. sowerbii in-situ* feeding behaviour. Spadinger and Maier (1999) examined the gut contents of freshly caught medusae. By comparing the natural abundance of prey to their abundance in medusae guts, the authors suggested that *C. sowerbii* selectively feeds on copepods and nauplii. They also noted that zooplankton between 400 and 1200 μm were selected for, sizing that coincides with the spacing between larger tentacles on the medusae bells. These results led them to propose that tentacle spacing may determine selectivity towards various sizes of zooplankton. However, gut content analysis can be highly variable as it reflects diet on a short (hourly) time scale and can be biased by the variable digestion time of prey items. Although *C. sowerbii* medusae clearly feeds on zooplankton, the contributions of more rapidly digested prey remain unquantified.

Monitoring the responses of natural zooplankton communities to *C. sowerbii* predation can provide valuable information about their long-term diet. In a mesocosm experiment, Jankowski et al. (2005) found that the presence of *C. sowerbii* medusae decreased the abundance of *Bosmina*, copepods, and nauplii. Meanwhile, Schachtl et al. (2026) showed that higher concentrations of medusae in mesocosms were associated with overall declines in crustacean zooplankton biomass and increases in chlorophyll concentration, but the impacts on specific zooplankton groups varied between lakes. Lake monitoring shows similar trends. A three-year time series in a eutrophic German lake showed that years with high *C. sowerbii* abundance had particularly low copepod biomass (Jankowski et al., 2005). Similarly, monitoring in an oligotrophic Canadian lake revealed that copepod abundances were lower in years with high *C. sowerbii* density (Dana Halay, unpublished). Taken together, these results suggest that copepods may be particularly impacted by *C. sowerbii* predation. However, it is not clear if the vulnerability of copepods is a result of selective predation on adults or juveniles, or a consequence of longer generation times preventing rapid population recovery relative to cladocerans. Overall, copepods or their juvenile stages likely contribute in some part to *C. sowerbii* medusae long-term diet.

Competitive interactions

By feeding primarily on zooplankton, *C. sowerbii* medusae may exhibit competitive interactions with native zooplanktivores. The larval form of the Phantom Midge, *Chaoborus*, is common in lakes around the world. *Chaoborus* is a gape-limited raptorial predator that migrates to the surface at night to feed selectively on zooplankton

smaller than 500 μm (Campbell, 1991). Gießler et al. (2023) found isotopic niche overlap between *C. sowerbii* medusae and *Chaoborus* larvae in a eutrophic water body, indicating competition for similar food resources. The Three Spine Stickleback, *Gasterosteus aculeatus*, is a common small fish with a generalist diet that includes zooplankton (Campbell, 1991). While Gießler et al. (2023) demonstrated isotopic niche overlap between juvenile Roach (*Rutilus rutilus*, another fish species) and *C. sowerbii*, the relationship between *G. aculeatus* and *C. sowerbii* remains unknown. Understanding the overlap in the niches of *C. sowerbii* medusae and potential competitors is critical to predicting which species may be negatively impacted by competitive interactions.

Stable isotope analysis

Predation experiments, gut content analysis, and zooplankton community monitoring are all techniques with limitations that can prevent them from capturing the long-term *in-situ* diet of *C. sowerbii* medusae. Alternatively, stable isotope analysis (SIA) offers another approach. SIA uses the ratios of naturally occurring isotopes, often carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), to understand energy flow in ecosystems. Foundational to SIA is the assumption that the isotope ratios of a predator reflect the isotope ratios of its prey (Nielsen et al., 2018). When an organism is eaten, some of that food is incorporated into biomass while the rest is respired or excreted. Heavier isotopes such as ^{15}N and ^{13}C are preferentially retained, causing a phenomenon known as trophic enrichment (Nielsen et al., 2018). Trophic enrichment is the trend of heavy isotopes being concentrated higher up food chains, and the trophic discrimination factor

(TDF) represents how much isotope ratios increase per each trophic level. Typically, the TDF is 3.4‰ for $\delta^{15}\text{N}$ and 1‰ for $\delta^{13}\text{C}$, although there is variation depending on the tissue type and trophic level of the organism in question (Stephens et al., 2023). This pattern of trophic enrichment allows for the reconstruction of food webs based on isotope ratios in tissue.

Specific analytical methods using SIA have recently been deployed to study food web modifications by invasive species (McCue et al., 2020). By comparing the isotopic niches of invaders and their native counterparts, researchers can explore potential overlaps in resource utilization and can assess competitive or predator-prey interactions (McCue et al., 2020). Given the isotopic ratios of potential prey items, mixing models can be used to estimate the potential contributions of various prey sources to the long-term diet of an invasive predator (Parnell et al., 2013; Stock et al., 2018). Using these methods, SIA has the potential to provide valuable insights into the trophic interactions of *C. sowerbii* medusae in aquatic ecosystems.

1.1. Research objectives

This project applies stable isotope analysis to data collected from an oligotrophic lake in British Columbia, with the aim of addressing the following research objectives.

1. What are the temporal diet dynamics of *C. sowerbii* medusae, and how do they change with jellyfish size?
2. What are the interactions between *C. sowerbii* medusae and native zooplankton predators *Chaoborus* and *G. aculeatus*?

METHODS

2.1 Sample collection and processing

Study location

Samples were collected from Hotel Lake (49°38'23.4"N, 124°02'44.3"W) on the Sunshine Coast of British Columbia on June 25th, July 21st, and August 13th of 2025. Hotel Lake is an oligotrophic lake that is 10.6 m deep, with a surface area of 0.252 km². The average chlorophyll-a concentration in the surface waters during the summer was 1.3 µg/L, and the average phosphate concentration was 0.09 µM.

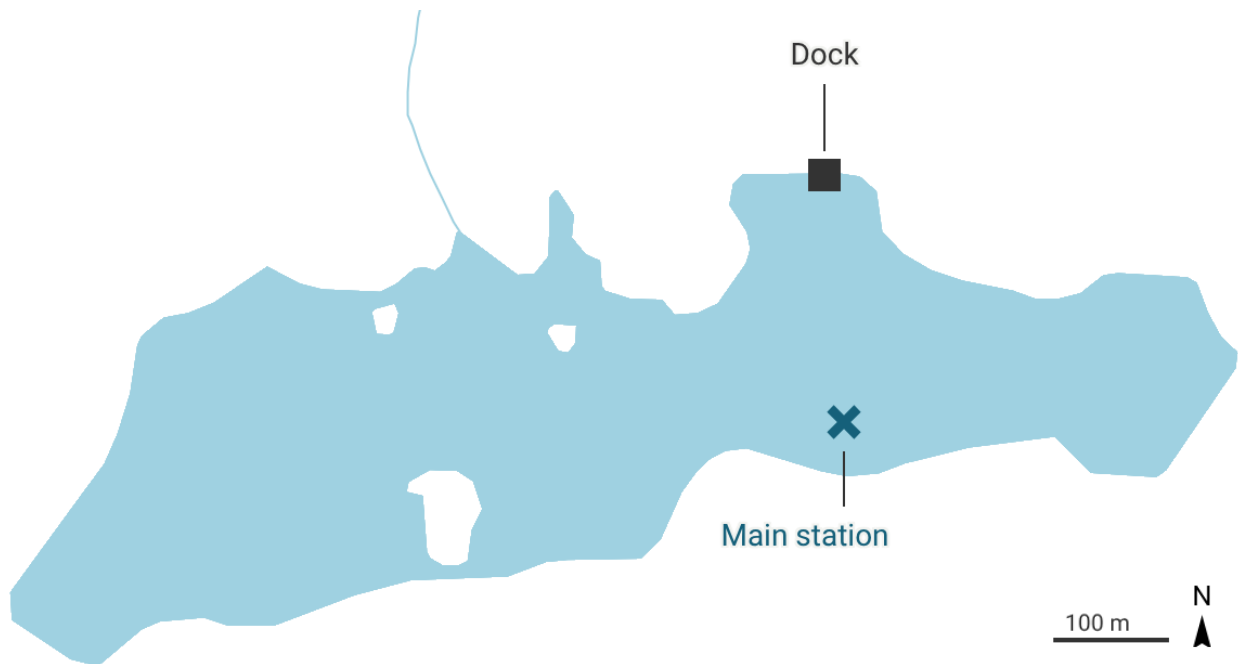


Figure 1. Map of Hotel Lake. Zooplankton samples were collected from the main station. Surface tows occurred between the main station and the dock. Medusae were collected opportunistically throughout the entire lake, as abundances were low. Littoral samples, shoreline plants, aquatic plants, periphyton, and lily pad leaves were collected near the dock. This figure was created using Datawrapper.

Sample collection

Zooplankton samples were day/night pairs, where each sample consisted of 2 vertical tows using a 30 cm diameter circular net with 150 μm mesh size to a depth of 8 m at the main station shown in **Figure 1**. For each timepoint, 2 samples each were in the afternoon and after sunset. One of each day/night samples was fixed in formalin, while the other was size fractionated using stacked sieves with mesh sizes of 125, 250, 500, 1000, 2000 μm . Each size fraction was vacuum filtered onto GF/F filters and frozen. To sample particulate organic matter (POM), surface water was collected from the main station during the day in opaque bottles, which were rinsed 3 times with surface water. The water was filtered through a 125 μm sieve to remove zooplankton, then collected on a 0.7 μm pore size GF/F filter and frozen. In August, samples of material from the littoral zone, shoreline plant leaves, pondweed, periphyton growing on a submerged log, and lily pad leaves were collected and frozen.

At night, horizontal surface tows from the main station to the dock (see **Figure 1**) were collected using a 30 cm diameter circular net with 150 μm mesh size. Under a dissecting microscope, instars of *Chaoborus* were sorted into large (instars 3 and 4, head capsule length over 500 μm) and small (instars 1 and 2, head capsule length smaller than 500 μm). The 1000-2000 and 2000+ zooplankton size fractions collected at night were composed almost entirely of *Chaoborus*. Sticklebacks were caught from shallow water near a dock, using hand nets. The maximum total length was measured and fish with a total length less than 26 mm were considered small, while fish 26 cm and greater were considered large. Medusae were caught using hand nets in deep

water. Their bell diameters were measured and medusae were categorized as large if their bell diameter was 15 mm or greater. Not enough medusae were found on the sampling day, so additional organisms were collected over the following week. All samples were stored at -20 °C until processing for stable isotopes began.

Table 1. Sample collection information

Sample	Collection time	Collection dates	Size categories
Zooplankton	Day	June, July, August	150-250, 250-500, 500-1000
Zooplankton	Night	June, July, August	150-250, 250-500, 500-1000
Particulate organic matter	Day	June, July, August	1.2-125 μm
<i>Chaoborus</i>	Night	June, July, August	NA
<i>C. sowerbii</i> medusae	Day	July and August (not present in June)	9-14 mm (small), 15-22 mm (large)
<i>G. aculeatus</i>	Day	June, July, August	17-24 mm (small), 25-53 mm (large)
Littoral material	Day	August	NA
Shoreline plant leaves	Day	August	NA
Pondweed (aquatic plant)	Day	August	NA
Lily pad leaves	Day	August	NA
Benthic periphyton	Day	August	NA

Sample preparation for stable isotope analysis

The medusae were placed whole in uncapped Eppendorf tubes. Fish were thawed, the head and fins were removed from the body, and the stomach was preserved in ethanol for stomach content analysis. The remaining body was placed in

an uncapped Eppendorf tube for drying. Zooplankton samples on GF/C filters were dried in open plastic petri dishes. Samples from the littoral zone, shoreline plant leaves, pondweed, periphyton, and lily pad leaf were placed in uncapped Eppendorf tubes for drying. The medusae were dried in a Thermo ModulyoD freeze dryer for 48 hours, while all other sample types were placed in a Fisher Scientific Isotemp drying oven for 48 hours at 50 °C.

After drying, samples were homogenized using a mortar and pestle that was cleaned with ethanol between samples. For the zooplankton, fish and medusae, 0.8 ± 0.15 mg of sample were weighed using a Sartorius microbalance and was encapsulated in Elemental Microanalysis 8 x 5 mm tin-pressed capsules. For the POM samples, the top layer of the filter was peeled off and encapsulated in 12 x 6 tin-pressed capsules from Elemental Microanalysis. POM samples weighed approximately 10 mg each, which included the POM itself and the remaining layer of the GF/C filter. For the littoral zone, shoreline plant leaves, pondweed, periphyton, and lily pad leaf samples, 3.5 ± 0.25 mg was encapsulated in 12 x 6 mm Tin pressed capsules from Elemental Microanalysis.

Due to the small size of many organisms sampled, it was occasionally necessary to pool individuals to obtain sufficient weight for isotope analysis. The zooplankton and *Chaoborus* samples were pooled (i.e. each sample was composed of many individuals), and 3 subsamples were encapsulated per sample. Each individual fish was homogenized separately, so each replicate represents an individual organism. Individual medusae were pooled and 2 subsamples were taken for each pooled sample

(unlike the zooplankton and *Chaoborus*, there were multiple distinct pools of individuals per timepoint and size category). Replicates of POM, littoral zone, shoreline plant leaves, aquatic plant leaves, periphyton, and lily pad leaf samples were homogenized separately.

Determination of stable isotope ratios

Samples were run on the EA-IRMS at the Pacific Center for Isotopic and Geochemical Research at the University of British Columbia. Proteinaceous samples (fish, zooplankton, medusae) were run with 0.5 mg caffeine, 0.8 mg marine collagen protein, 0.8 mg bovine collagen protein, and 0.8 mg fish gelatin standards between every 10 samples. All other samples were run with 0.5 mg caffeine, 3.0 mg spinach, 3.0 mg sorghum, and 3.5 mg casein standards between every 10 samples. The measured ratio of heavy to light isotopes in a sample (R_{sample}) was converted to delta notation with units permille (‰) according to $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{VPDB}} - 1) \times 1000$ and $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{atmospheric dinitrogen}} - 1) \times 1000$. The average standard deviation of the standards was 0.17 ‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

ZooScan and EcoTaxa workflow

Zooplankton samples were filtered out of formalin using a 64 μm sieve and split using a Motoda box splitter until a subsample of 1000-1500 individuals was obtained. Samples were scanned on a Hydroptic ZooScan according to the protocol outlined in the user manual with a minimum particle pixel size of 0.3 mm (Gorsky et al., 2010). The Zooprocess software split each scan into an image containing a single organism, referred to as a vignette. The vignettes were uploaded to the website EcoTaxa in the

project Hotel Lake (project ID 21224). All automatic classifications were manually validated. For cladocerans, organisms were identified as either *Bosminidae*, *Ceriodaphnia*, *Chydoridae*, *Daphnia*, *Diaphanosoma*, and *Holopediidae*. Copepods were identified as either nauplii, *Cyclopoida* or *Diaptomus*. Larger organisms such as *Chaoboridae*, *Chironomidae*, and *Hydrachna* were also identified. Non-living particles were categorized as detritus, bubbles, or fibers and were excluded from subsequent analyses.

Major axis length was calculated using **Equation 1**, and was used to sort organisms to size fractions corresponding to the size fractions of the stable isotope zooplankton samples.

Eq. 1 $major\ axis\ (\mu m) = major\ axis\ (pixels) \times process\ particle\ pixel\ size\ \left(\frac{mm}{pixel}\right) \times 10^3$

Fish stomach content analysis

The fish stomachs were removed from ethanol and soaked in water for 30 minutes to rehydrate in a glass petri dish. Stomachs were cut open and the contents were sorted under a dissecting scope into the following categories: terrestrial arthropod, benthic invertebrate, zooplankton, *Chaoborus*, or *Chironomid*, or unknown. The percent that each group contributed to the total stomach content volume was estimated visually, such that the total of all the groups was 100%.

2.2. Statistical analysis

All analyses were conducted in R, version 5.4.2. Isotopic niche overlap was calculated using the package SIBER (Jackson et al., 2011). Mixing models were run

using the package MixSIAR (Stock et al., 2018). Models for the Bayesian isotopic niche area in SIBER were run with 500,000 iterations, 100,000 burn-ins, 10 thins and 5 chains and uninformative priors. The MixSIAR mixing models used *C. sowerbii* as the mixture, with sampling month (July or August) and medusa size (large or small) as random non-nested factors. Run length was set to “normal”. The day and night zooplankton samples were pooled for the zooplankton mixing model sources. The trophic discrimination factor for *C. sowerbii* was set to 2.09 ± 0.52 for $\delta^{15}\text{N}$, and 1.19 ± 0.37 for $\delta^{13}\text{C}$ (Schaub et al., 2021). Model sensitivity analyses were conducted by running the mixing models with doubled and halved trophic discrimination factors.

RESULTS

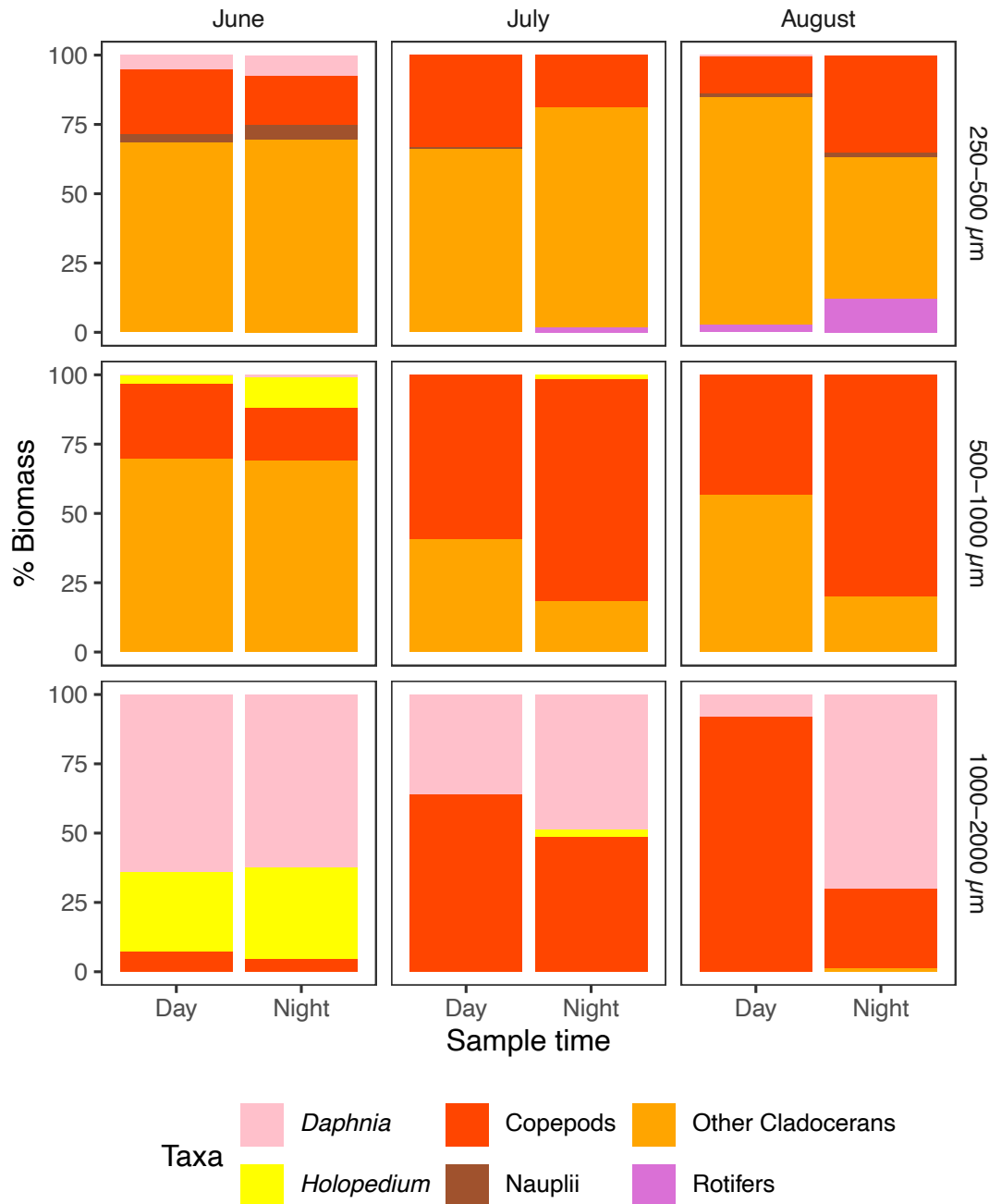


Figure 2. Zooplankton size fraction taxonomic composition. Calanoid and cyclopoid copepods were combined, other cladocerans include *Bosmina*, *Ceriodaphnia*, and *Diaphanosoma*. Organisms were sorted into size fractions based on their major axis length (μm). The minimum particle size was 0.3 mm, so no organisms less than 300 μm were detected by the ZooScan.

The 125-250 μm size fraction was not visible on the ZooScan, but based on microscopy was primarily composed of rotifers, nauplii, and microzooplankton with some small cladocerans also present. As shown in **Figure 2**, the 250-500 μm size fraction was dominated by small cladocerans (*Bosmina* and *Ceriodaphnia*), while the 500-1000 μm size fraction was composed of small cladocerans (*Bosmina*, *Ceriodaphnia*, *Diaphanosoma*) and calanoid copepods. The 1000-2000 μm size fraction was composed of *Daphnia* and large calanoid copepods. The contribution of copepods relative to cladocerans increased throughout the summer in the 500-1000 μm and 1000-2000 μm size fractions, while the composition of the 250-500 μm size fraction remained constant.

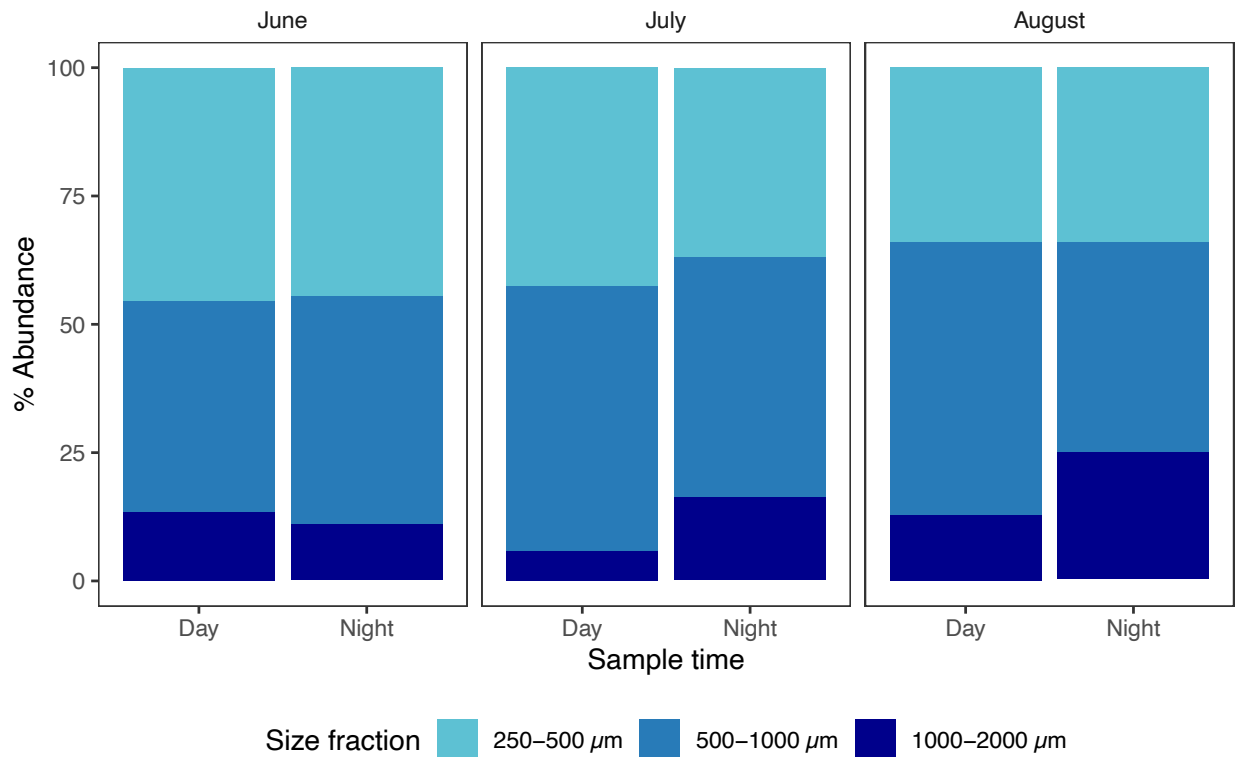


Figure 3: Relative abundances of zooplankton size fractions. Organisms were sorted into size fractions based on their major axis length (μm). The minimum particle size was 0.3 mm, so no organisms less than 300 μm were detected by the ZooScan.

The relative abundances of the 250-500 μm , 500-1000 μm , and 1000-2000 μm size fractions throughout the summer are shown in **Figure 3**. In all samples, smaller size fractions were more abundant than larger size fractions.

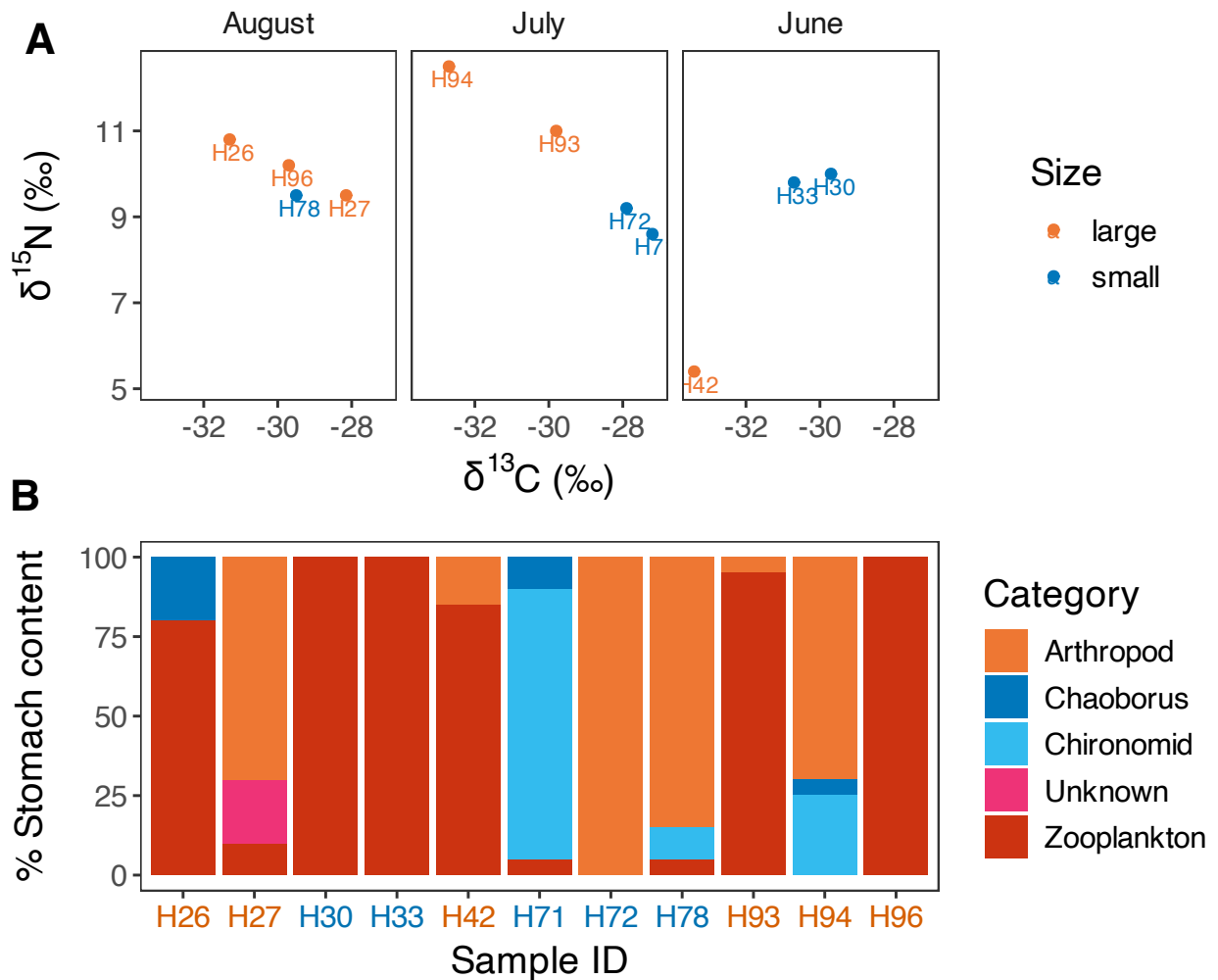


Figure 4. Paired stomach content and isotopic ratios of *G. aculeatus*. Only fish for which both isotopic and stomach content analysis were successful were included in this figure. **A.** shows the isotope biplots of *G. aculeatus*, split by sampling month with colour indicating size (fish with total length less than 26 mm were considered small). **B.** shows the stomach contents of each fish, estimated visually as percent volume.

Paired analysis in **Figure 4** shows the percent volume of prey categories found in the stomachs of *G. aculeatus*, along with the isotope ratios of each individual. Linear regressions found no significant ($p < 0.05$) relationships between the percent volume and isotope ratio for all combinations of prey category and isotope.

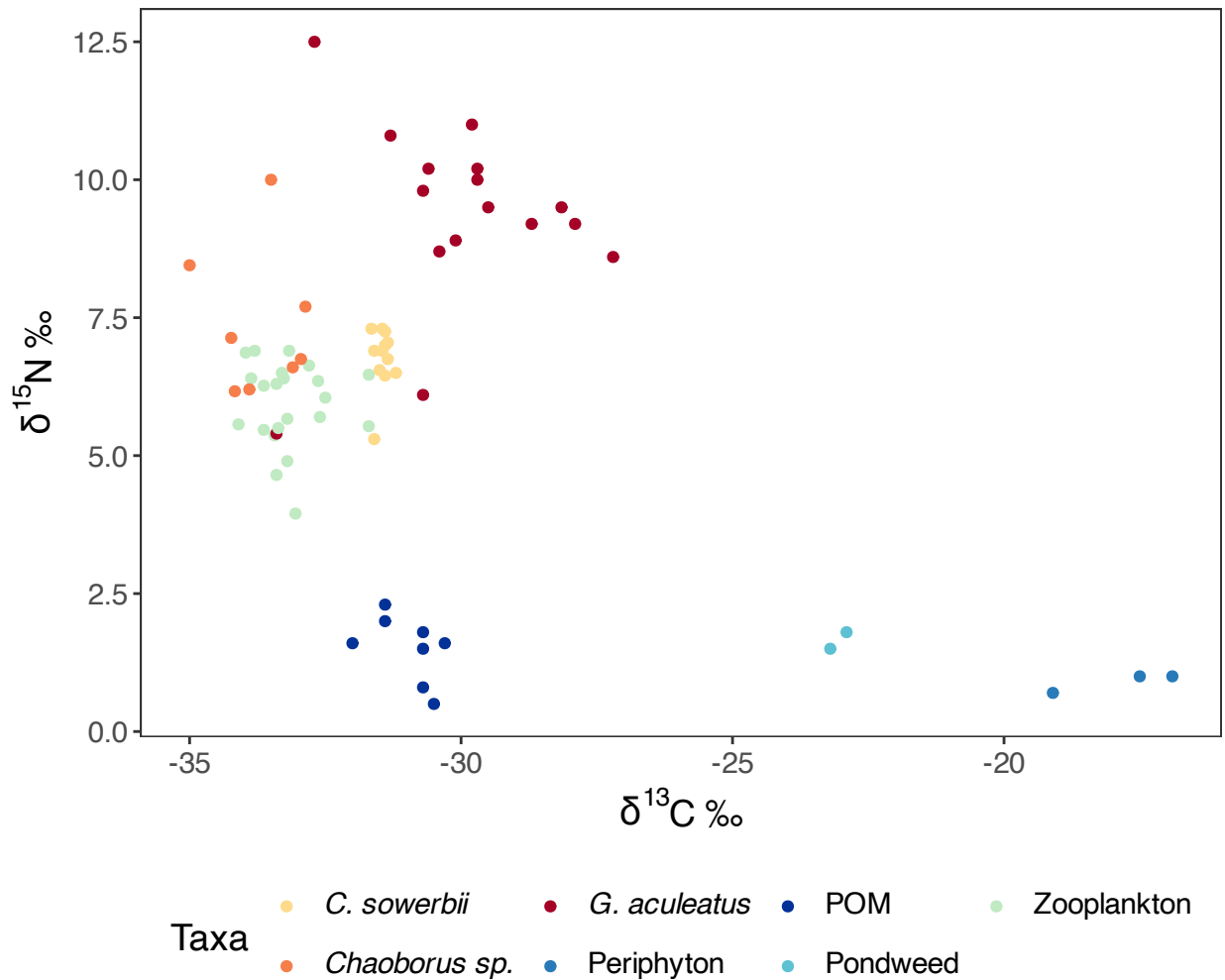


Figure 5. Isotope ratios of organisms in the Hotel Lake food web. Samples from June, July, and August are all included. Size fractions of zooplankton, medusae, and fish are grouped together.

The isotope data for all months combined is plotted in **Figure 5** to demonstrate fractionation between sources. Periphyton, pondweed and POM, all primary producers,

show low $\delta^{15}\text{N}$ values, but are differentiated by their $\delta^{13}\text{C}$ values. *Chaoborus*, *C. sowerbii*, and the zooplankton have higher $\delta^{15}\text{N}$ values but a smaller range of $\delta^{13}\text{C}$ values. *G. aculeatus* has the highest $\delta^{15}\text{N}$ enrichment and a broader range of $\delta^{13}\text{C}$ values.

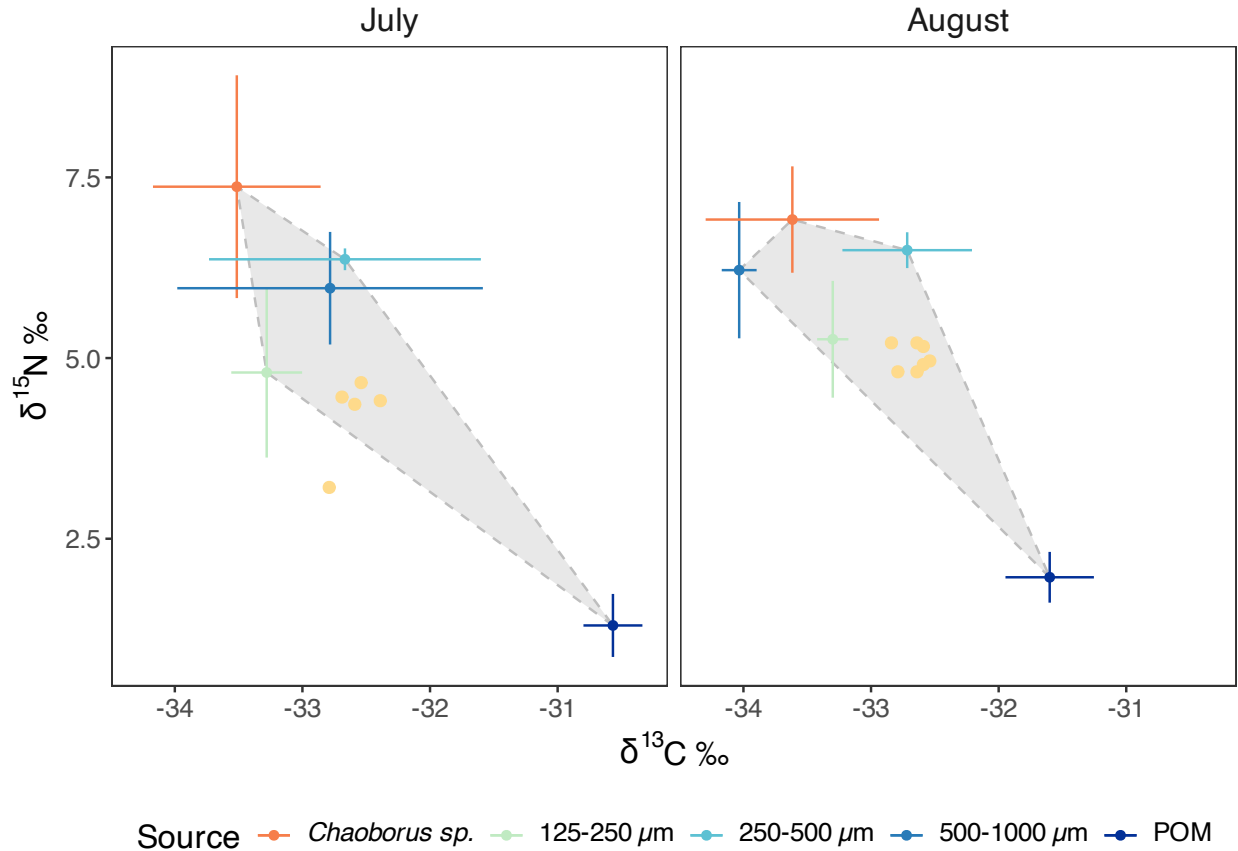


Figure 6. Mixing model inputs. The sources are plotted as the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with the standard deviation as the error bars. Each *C. sowerbii* medusa datapoint is the average of three triplicates, with the trophic discrimination factors subtracted ($\Delta\delta^{15}\text{N} = 2.09$, $\Delta\delta^{13}\text{C} = 1.19$). The convex hull of the sources is shown in grey.

The mixing model used zooplankton in the 125-250 μm , 250-500 μm , and 500-1000 μm size fractions, *Chaoborus* and POM as potential sources. The mean and

standard deviation of each source is shown in **Figure 6**. The medusae, with their TDF subtracted, fall within the convex hull of the sources.

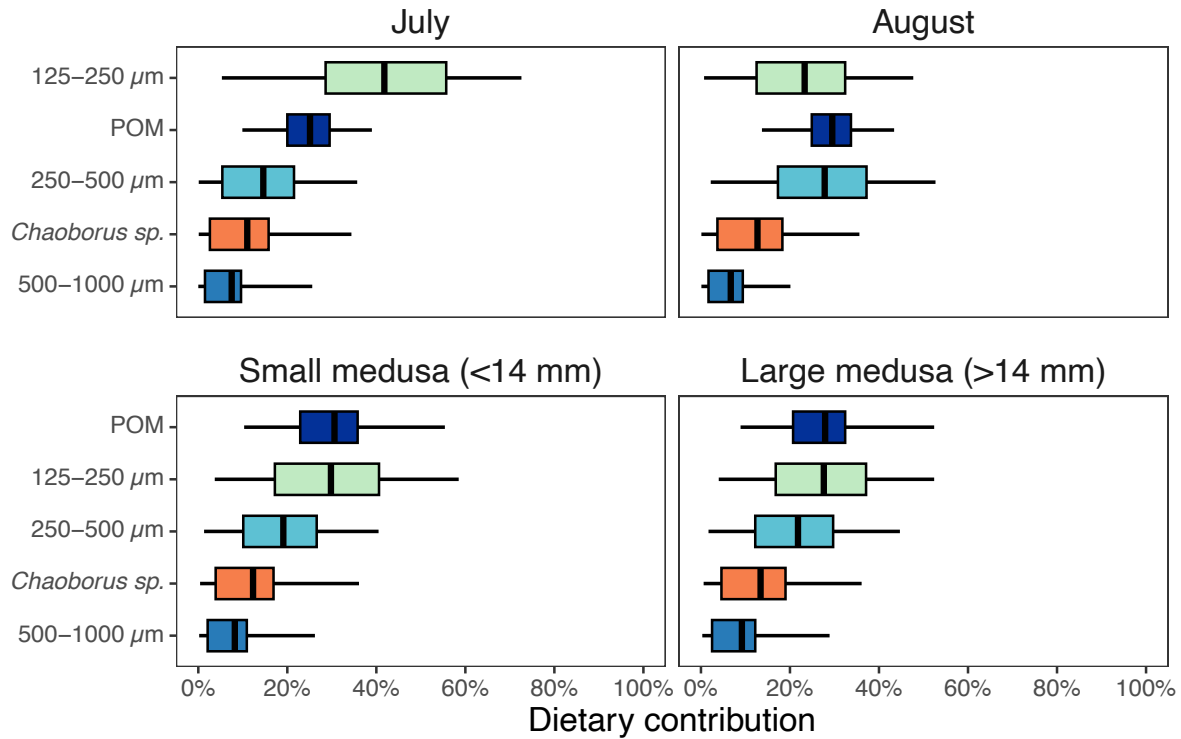


Figure 7. Contributions of potential prey to the diet of *C. sowerbii*. The vertical bar shows the mean percent contribution, while the box encompasses the 50% credible interval and the bars show the 95% credible interval.

According to mixing model outputs in **Figure 7**, the diet of *C. sowerbii* medusae was composed primarily of zooplankton in the 125-250 μm and 250-500 μm size fractions and POM. Between July and August, the mean contributions of the 125-500 μm zooplankton decreased from 41.8% to 23.3%, while the contribution of the 250-500 μm size fraction increased from 14.6% to 27.8%. The mean contribution of POM, 500-100 μm , and *Chaoborus* remained relatively constant between July and August. Medusae size had no impact on diet composition.

Table 2. Mean and standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for zooplankton predators by month.

	Mean $\delta^{15}\text{N}$	Standard deviation $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	Standard deviation $\delta^{13}\text{C}$	N
June					
<i>Chaoborus</i>	7.32	1.59	-34.4	0.78	2
<i>G. aculeatus</i>	7.82	2.41	-31.1	1.59	4
July					
<i>C. sowerbii</i>	6.20	0.60	-31.40	0.17	5
<i>Chaoborus</i>	7.85	2.08	-33.5	0.64	3
<i>G. aculeatus</i>	10.0	1.66	-29.5	2.15	5
August					
<i>C. sowerbii</i>	7.06	0.21	-31.50	0.11	7
<i>Chaoborus</i>	6.83	0.275	-33.4	0.70	3
<i>G. aculeatus</i>	9.73	0.711	-29.8	1.10	7

As described in **Table 2**, the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *G. aculeatus* and *Chaoborus* remained constant between July and August. For *C. sowerbii*, the mean $\delta^{13}\text{C}$ remained constant at -31.4 ± 0.17 in July and -31.5 ± 0.11 in August while the mean $\delta^{15}\text{N}$ increased from 6.20 ± 0.6 in July to 7.06 ± 0.21 in August. There were no significant differences between the mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of small and large medusae (supplementary, **Table A1**).

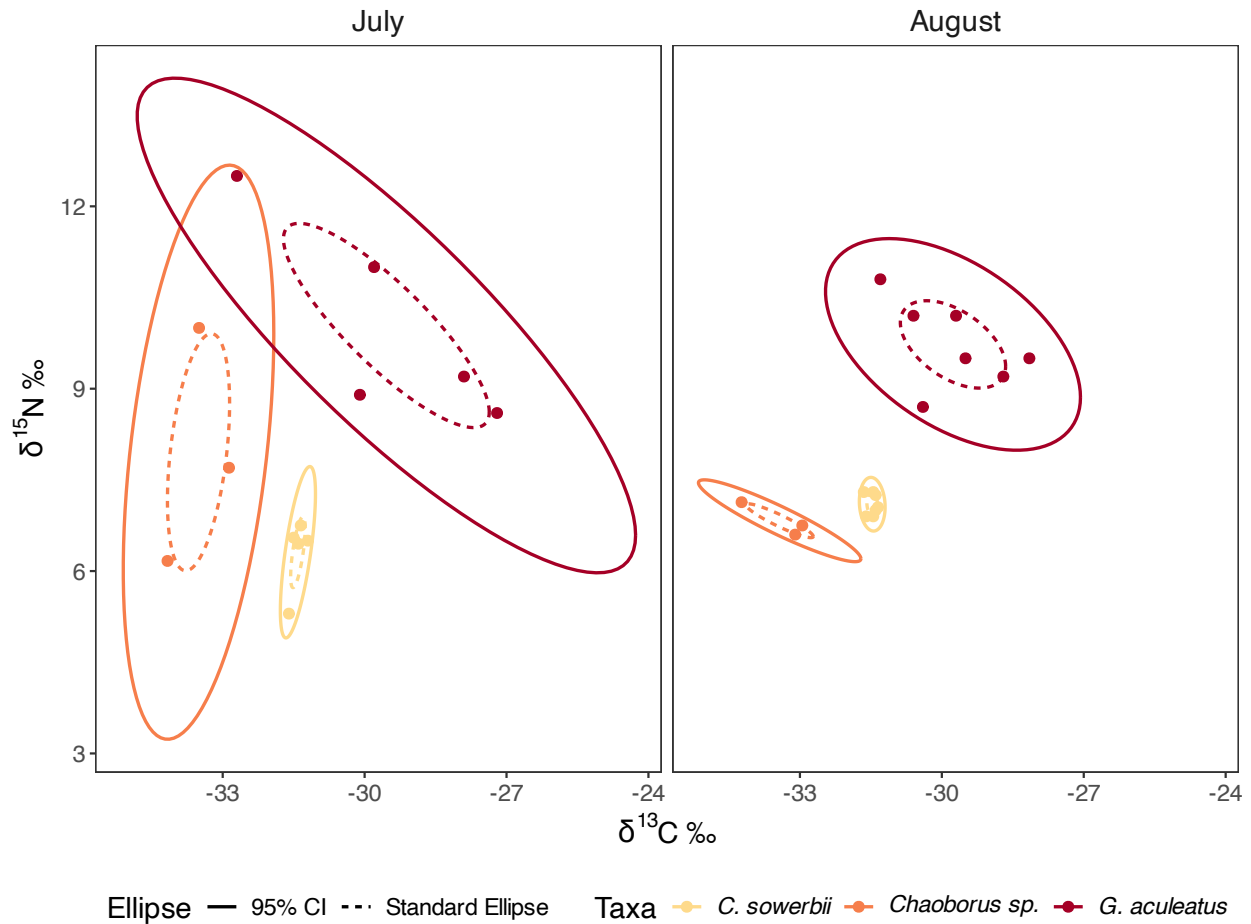


Figure 8. Isotopic niches of zooplankton predators in Hotel Lake.

The points shown are the average of the triplicates for each sample. The dashed lines are the Standard Ellipse, corrected for small sample size (SEA.c). The solid lines are the 95% confidence intervals of the bivariate means.

Isotopic niche was represented as the standard ellipse (containing 40% of the data) and the 95% confidence interval of the bivariate mean in **Figure 8**. There was no overlap between the isotopic niches of *C. sowerbii* and either *G. aculeatus* or *Chaoborus*. In July, the 95% confidence interval of the bivariate mean of *Chaoborus* and *G. aculeatus* overlapped. Similarly, analysis of the percent overlap of the Bayesian Standard Ellipses showed no overlap between the isotopic niches of *C. sowerbii*, *G. aculeatus*, and *Chaoborus*, as described in **Table 3**.

Table 3. Percent overlap of the Bayesian Standard Ellipse Area. This table needs to be read horizontally, where the percent of *C. sowerbii*'s niche (row) that overlaps with *Chaoborus* (column) is different from the percent of *Chaoborus*' niche (row) that overlaps with *C. sowerbii* (column). The mode of the posterior distribution is reported in brackets as the 95% credible interval.

July			
	<i>C. sowerbii</i>	<i>Chaoborus</i> sp.	<i>G. aculeatus</i>
<i>C. sowerbii</i>	-----	0 (0 - 89.283)	0 (0 - 10.427)
<i>Chaoborus</i> sp.	0 (0 - 1.474)	-----	0 (0 - 13.545)
<i>G. aculeatus</i>	0 (0 - 0.187)	0 (0 - 10.990)	-----
August			
<i>C. sowerbii</i>	-----	0 (0 - 8.541)	0 (0 - 9.818e-18)
<i>Chaoborus</i> sp.	0 (0 - 0.445)	-----	0 (0 - 1.124e-16)
<i>G. aculeatus</i>	0 (0 - 6.559e-17)	0 (0 - 5.973e-17)	-----

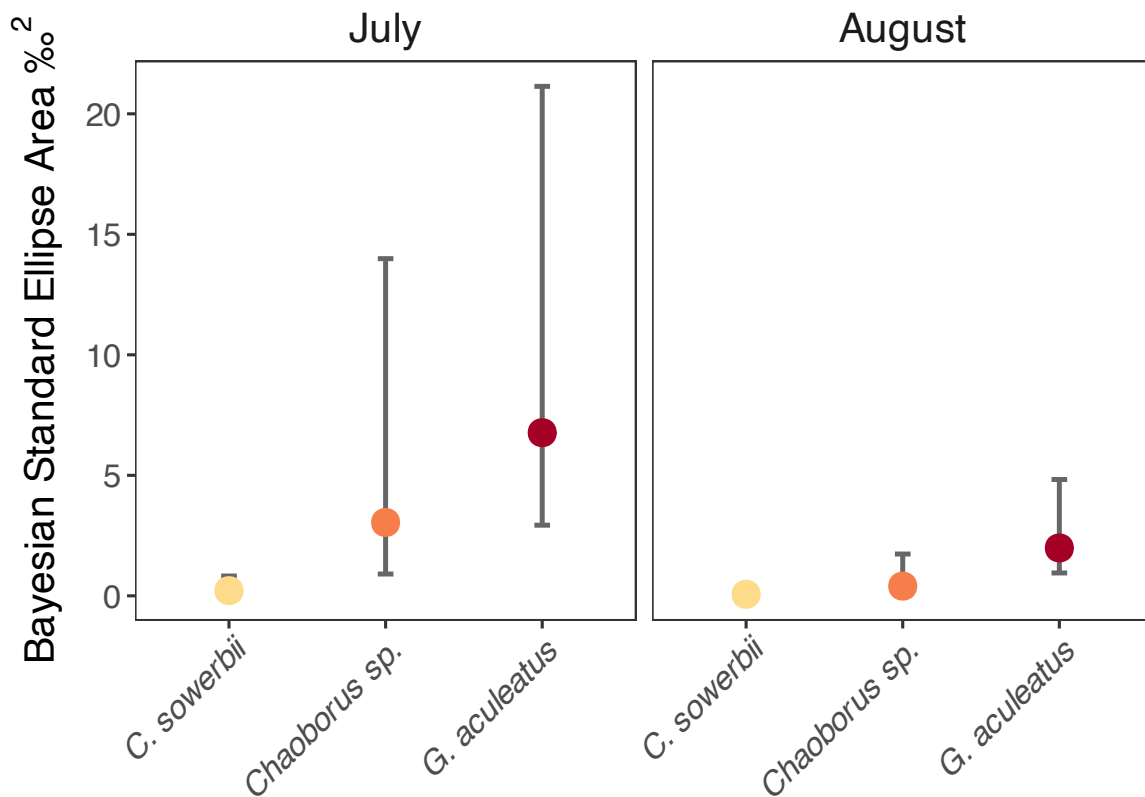


Figure 9. Bayesian standard ellipse area of zooplankton predators. The points show the mode, while the error bars show the Bayesian 95% credible interval.

The isotopic niche area of *C. sowerbii* was remarkably small when compared with *G. aculeatus* and *Chaoborus* in **Figure 9**. The mode of the Bayesian Standard Ellipse area (‰²) for *C. sowerbii* was 0.216 in July and 0.063 in August. *Chaoborus* had a mode isotopic niche area of 3.045 in July and 0.403 in August, while *G. aculeatus* had 6.77 in July and 1.987 in August.

DISCUSSION

4.1. *C. sowerbii* medusae diet

The mixing model results suggest that POM and the 125-250 μm zooplankton size fraction are primary components of *C. sowerbii* medusae diet. The 125-250 μm size fraction, primarily composed of rotifers, nauplii, and microzooplankton, was estimated to contribute to over 25% of *C. sowerbii* diet. These results align with Smith and Alexander (2008), who found that *C. sowerbii* preferentially fed on smaller zooplankton such as rotifers and nauplii. The other major food source identified by the mixing model was particulate organic matter (POM), which was also estimated to contribute to approximately 25% of diet. In this study, POM was the 0.7-125 μm size fraction filtered from surface water, which likely consisted of microzooplankton, phytoplankton, and detritus (**Figure 10**). Despite the wide variety of organic matter contributing to POM, the 95% credible intervals for this source were the narrowest and critically, did not include 0%. This indicates that POM is very likely a part of *C. sowerbii* diet and that there is high confidence in our estimate of the mean contribution. Thus, the role of POM in the diet of *C. sowerbii* is perhaps the most robust conclusion from the mixing model.

Zooplankton in the 500-1000 μm size fraction showed only minor contributions to *C. sowerbii* diet, suggesting that they may only occasionally be consumed. The low, ~8%, contribution of this size fraction is highly notable in the context of previous research. The 500-1000 μm size fraction was primarily composed of *Daphnia* and large calanoid copepods, which are often considered to be the primary prey of *C. sowerbii* (Boothroyd et al., 2002; Spadinger & Maier, 1999). Similarly, previous studies report

that high medusae abundances are often associated with declines in populations of large crustacean zooplankton, which were abundant in our 500-1000 μm size fraction (Jankowski et al., 2005; Schachtl et al., 2026). However, our results suggest this decline may not be due to direct predation. Rather, the medusae could be killing but not consuming large zooplankton, as observed in predation experiments by Spadinger and Maier (1999). Or, as our results support, the declines in populations of large crustacean zooplankton could be caused by strong predation on juvenile stages such as nauplii, which were abundant in our 125-250 μm size fraction. These findings suggest that *C. sowerbii* medusae may limit recruitment of mature crustacean zooplankton populations by feeding on juvenile cladocerans and nauplii.

The mixing model results suggest that *Chaoborus* larvae may experience predation from *C. sowerbii* medusae. *Chaoborus* was estimated to contribute to ~12% of diet, a result supported by the findings of Spadinger and Maier (1999), who noted that *Chaoborus* larvae were present in gut contents of 15 out of 120 medusae. *Chaoborus* has 4 larval stages (instars), which vary in their size, diet, and behaviour (Fedorenko, 1975). To investigate if *Chaoborus* instars were differentially impacted by *C. sowerbii* predation, *Chaoborus* larvae were divided into early (instars 1 and 2) and late (instars 3 and 4) during sample collection. Unfortunately, insufficient sample size and sample mass meant that early and late instars could not be distinguished isotopically. However, behavioural differences between early and late instars may inform the extent to which they experience *C. sowerbii* predation. *Chaoborus* larvae exhibit a well-studied diel vertical migration (DVM), spending the daytime at depth to avoid fish predation and

rising to the surface at night to feed (Dawidowicz et al., 1990). However, early instars of *Chaoborus* do not perform DVM (Lagergren et al., 2008). At the same time, *C. sowerbii* medusae exhibit positive phototaxis, descending in the water column at night and occupying surface waters during the day (Lüskow et al., 2025). This difference in DVM could prevent spatial overlap between *C. sowerbii* and late, but not early instars of *Chaoborus*. Thus, these early instars are most likely to experience *C. sowerbii* predation given their smaller size and spatial overlap with *C. sowerbii*.

Our results inform the validity of proposed mechanisms for size-selective predation by investigating impact of medusae size on diet composition. In 1999, Spadinger and Maier suggested that tentacle spacing may determine which sizes of prey medusae selectively consume. Based on the relationship between the number of tentacles and the bell diameter characterised by Boothroyd et al. (2002) and assuming a constant tentacle width, we would expect that larger medusae have fewer tentacles per unit length of bell circumference. Thus, larger medusae would feed on larger zooplankton, because smaller zooplankton would pass through the gaps between tentacles. However, I did not observe that larger medusae were consuming a greater proportion of the larger size fractions of zooplankton. More broadly, medusae size had no impact on the diet composition estimated by the mixing model. I also found no significant differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between large and small jellyfish. Thus, my results do not support the hypothesis that differences in tentacle spacing govern size selective predation in *C. sowerbii* medusae.

The diet of *C. sowerbii* remained relatively constant between July and August. The primary shift was that in August, the percent contribution of the 125-250 μm size fraction decreased while the contribution of the 250-500 μm size fraction increased. An increasing mean medusae size is likely not the explanation for this change in diet, as the jellyfish sampled in this study had the same average size in July and August. Additionally, the mixing model found that medusae size had no impact on diet. So more likely, changes in the zooplankton community composition are responsible for the shift in the relative contributions of the 125-250 μm and 250-500 μm size fractions. Unfortunately, as the ZooScan only detected particles larger than 300 μm , we are unable to confirm if the relative abundance of the 125-250 μm size fraction decreased in August.

Overall, these results suggest that the prey selectivity of *C. sowerbii* medusae may be controlled primarily by prey abundances. Models of planktonic predation describe prey selectivity as a function of encounter rate and capture efficiency (Gerritsen & Strickler, 1977). In the case of *C. sowerbii* medusae, the encounter rate is controlled by the relative abundances of various prey and their position in the water column relative to *C. sowerbii*. As discussed above, differences in the vertical migration patterns of late *Chaoborus* instars and *C. sowerbii* may lower their encounter rate, ultimately limiting predation. The 500-1000 μm size fraction may be similarly affected, as the relative abundance of this size fraction declined during the day. Contrastingly, the relative abundances of the smaller zooplankton size fractions either increase or remain constant during the day. Thus, the encounter rate between *C. sowerbii* and smaller

zooplankton is likely higher, which may explain why they make up a greater component of diet. If *C. sowerbii* diet were governed by encounter rates, we would expect prey to be consumed in proportion to their abundance in the water column, a pattern which was indeed observed by Yan et al. (2025). However, differences in capture efficiency (the success rate of medusae in actually consuming the prey they encounter) can also impact prey selectivity. While this study does not directly examine the capture efficiency associated with specific prey, it does suggest that capture efficiencies do not vary with medusae size. As discussed above, diet composition was constant between large and small medusae, which suggests that selectivity, and thus capture efficiency, also remain constant. Additional evidence can be found in the analysis of *C. sowerbii* isotopic niche area. A predator population with similar encounter rates and constant capture efficiencies would have homogenous diets between individuals, which would lead to a small population isotopic niche area (Vander Zanden et al., 2010). In our results, we observed that the isotopic niche area of *C. sowerbii* was remarkably small compared to *Chaoborus* and *G. aculeatus*, suggesting that capture efficiency must be constant across medusae sizes. These findings support the hypothesis that *C. sowerbii* medusae diet is determined by prey encounter rates.

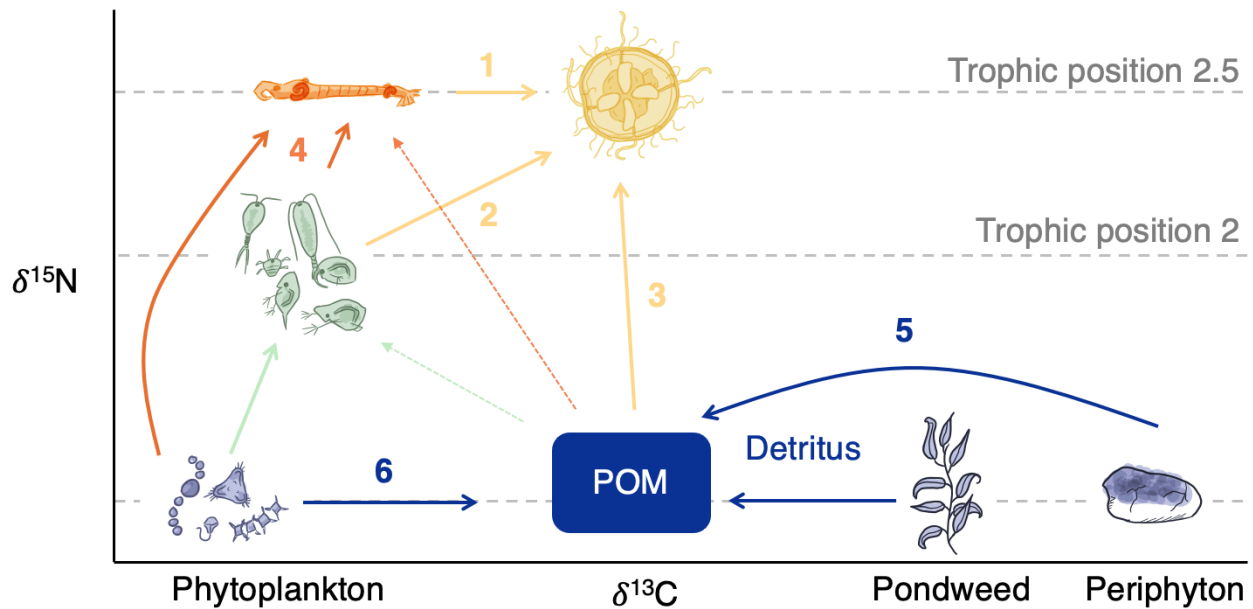


Figure 10. Conceptual model of the Hotel Lake Food web. Solid arrows indicate energy flow. (1) *C. sowerbii* feeding on early *Chaoborus* instars. (2) *C. sowerbii* feeding on 125-250 & 250-500 μm zooplankton (3) *C. sowerbii* feeding on POM. (4 & 5) POM composed of phytoplankton, microzooplankton, and detritus from benthic production. (6) *Chaoborus* feeding on zooplankton and phytoplankton. Dashed arrows indicate potential energy flow. This figure was based on data presented in **Figure 5**.

4.2. Interactions between *C. sowerbii* and native zooplanktivores

Competition between *G. aculeatus* and *C. sowerbii* medusae appears to be minimal given their isotopic niche differentiation. *G. aculeatus* had approximately 2‰ greater $\delta^{13}\text{C}$ and 3‰ greater $\delta^{15}\text{N}$ than *C. sowerbii*. This indicates that they are a trophic level above *C. sowerbii* (see appendix, **Figure A3**) and utilize a different combination of carbon pools. *G. aculeatus* was also characterized by a broader isotopic niche area than *C. sowerbii*, indicative of a flexible generalist diet. This interpretation of the isotopic data is supported by the results of *G. aculeatus* stomach content analysis. The stomachs occasionally contained *Chaoborus* larvae, which indicates that *G. aculeatus* indeed occupies a trophic level above *C. sowerbii* and *Chaoborus*. A wide

variety of prey were found, representing input from benthic (benthic invertebrate larvae and *Chironomid* larvae), terrestrial (terrestrial arthropods) and pelagic (zooplankton and *Chaoborus* larvae) carbon pools. The stomach contents also varied greatly between individual fish, reflecting a generalist population with a broad niche. Isotope and stomach content data confirm each other, suggesting that competition between *C. sowerbii* medusae and *G. aculeatus* is unlikely.

However, based on the relative trophic positions of *G. aculeatus* and *C. sowerbii*, predation by *G. aculeatus* remains a possibility. As discussed above, the high $\delta^{15}\text{N}$ of *G. aculeatus* suggests these fish occupy trophic position above *C. sowerbii* medusae. However, none of the fish stomachs analyzed in either Dodson and Cooper (1983) or in our study contained medusae. Due to the fragility of medusae, it is possible that the absence of *C. sowerbii* in *G. aculeatus* stomachs is due to a rapid digestion time. Nevertheless, our findings using stable isotopes suggest that the relationship between *G. aculeatus* and *C. sowerbii* medusae may be predatory.

Competitive relationships between *C. sowerbii* and *Chaoborus* are complex but may be impacted by ecosystem productivity. We found no overlap between the isotopic niches of *C. sowerbii* and *Chaoborus*, a result often interpreted as a lack of competition. Notably, the only other study of *C. sowerbii* using stable isotopes reported significant overlap between the isotopic niches of *C. sowerbii* medusae and *Chaoborus* instars, indicative of competition (Gießler et al., 2023). This apparent contradiction is likely a consequence of differences in ecosystem productivity, as Hotel Lake (from this project) is an oligotrophic lake while Lake Alsdorf (from Gießler et al., 2023) is a eutrophic pond.

Lake trophic state has clear impacts on *Chaoborus* diet, but the impacts of *C. sowerbii* are unknown. In highly productive eutrophic systems, *Chaoborus* exhibits pure zooplanktivory, but transitions to omnivory and then herbivory in less productive systems (France, 2012). Indeed, the trophic position of *Chaoborus* in Hotel Lake is 2.5, indicating substantial omnivory (supplementary **Figure A3**). Similarly, **Figure 3** demonstrates that *Chaoborus* has a similar $\delta^{13}\text{C}$ to zooplankton but is slightly enriched in $\delta^{15}\text{N}$, which indicates that they may be eating largely the same prey as other zooplankton while supplementing their diet with small zooplankton (omnivory). Meanwhile, *C. sowerbii* medusae in Hotel Lake show equal $\delta^{15}\text{N}$ to *Chaoborus*, indicating that they too exhibit omnivory. This suggests that niche differentiation between *Chaoborus* and *C. sowerbii* cannot be explained by variable degrees of omnivory.

The utilization of more varied carbon pools appears to be critical in differentiating the isotopic niche of *C. sowerbii* from *Chaoborus* in oligotrophic systems. As mentioned above, *Chaoborus* feeds on zooplankton and phytoplankton, only consuming carbon from the pelagic pool. In our study, mixing model results suggested that *C. sowerbii* fed predominantly on small zooplankton and, critically, POM. It is important to note that POM is a mixture of microzooplankton, phytoplankton and detritus, such as stirred up periphyton or organic material from the numerous aquatic plants in Hotel Lake. A conceptual model of these relationships is shown in **Figure 10**. As such, the isotope ratios of POM are a mixture of the low $\delta^{13}\text{C}$ pelagic signal from phytoplankton and the high $\delta^{13}\text{C}$ benthic carbon signals of aquatic plant material and periphyton. The

consumption of $\delta^{13}\text{C}$ -enriched POM appears critical in differentiating the isotopic niches of *C. sowerbii* and *Chaoborus* and suggests that *C. sowerbii* medusae may play a role in the detrital food web, as well as being a zooplankton predator.

Changes to the composition of POM may be a mechanism controlling the isotopic niche of *C. sowerbii* medusae in oligotrophic and eutrophic systems. In oligotrophic systems, POM is primarily composed of non-living organic matter while in eutrophic systems, POM is dominated by living phytoplankton (Gu, 2009). In eutrophic lakes, *C. sowerbii* likely feeds on zooplankton and phytoplankton, since POM is dominated by phytoplankton. This would lead to isotopic niche overlap between *Chaoborus* and *C. sowerbii* medusae due to similar trophic positions and shared utilization of purely pelagic carbon. However, in oligotrophic systems like Hotel Lake, POM is dominated by non-living particles. That means *C. sowerbii* medusae would feed less on phytoplankton and more non-living particles such as $\delta^{13}\text{C}$ -enriched detritus, which would lead to differentiation between the isotopic niches of *C. sowerbii* and *Chaoborus*. This relationship can also be interpreted ecologically. The high zooplankton and phytoplankton biomass in eutrophic systems means that *C. sowerbii* and *Chaoborus* can share the same niche without competing or limiting each other. However, in oligotrophic systems the lower abundances of zooplankton and phytoplankton leads to competition between *C. sowerbii* and *Chaoborus*. In order for them to coexist in a resource-limited system, niche differentiation is required.

Stable isotope analysis is a powerful tool for characterizing long-term *in-situ* diet; however, it must be interpreted with caution. First, an isotopic niche is not the same as

an ecological niche, so the lack of overlap in isotopic niche does not necessarily indicate of a lack of competition. Second, trophic enrichment varies widely between taxa. There are no experimentally derived trophic discrimination factors (TDFs) for *C. sowerbii*, in fact, there are very few for all jellyfish. This necessitates the assumption that the trophic discrimination factor derived for marine jellyfish also applies to freshwater jellyfish. To understand the sensitivity of the mixing model to trophic discrimination factors, we ran the model with doubled and halved TDFs, the results of which are shown in the appendix **Figures A5** and **A7**. In both cases, the adjusted TDFs meant that the medusae isotopic ratios plotted outside the convex hull of the possible sources (shown in appendix **Figures A4** and **A6**). This means that there is no possible combination of the sources that yields the isotopic ratios of the medusae, resulting in non-sensical model outputs. Not only do the estimated diet contributions change with TDF but the system no longer meets the assumptions to be an interpretable mixing model, thus showing high sensitivity to TDF. Third, the isotopic turnover rates for *C. sowerbii* are unknown, making it unclear the extent to which the medusae still reflect the isotopic ratios of their polyp stage. In the marine jellyfish *Aurelia aurita*, turnover rates have been broadly estimated as 14.5 ± 12.5 days for $\delta^{13}\text{C}$ and 35.6 ± 48.4 days for $\delta^{15}\text{N}$ (Schaub et al., 2021). Thus, it is likely that this phenomenon would impact smaller medusae more strongly, since they are younger. Future work should derive species-specific trophic discrimination factors and isotopic turnover rates for *C. sowerbii* to improve confidence in the findings of subsequent isotopic analyses.

4.3. Ecosystem impacts

Invasive populations of *C. sowerbii* medusae have already been shown to have wide-ranging ecosystem impacts. *C. sowerbii* has been implicated in altered nutrient cycling by transporting phosphate to the surface through its vertical migration (Schachtl et al., 2023). Our results suggest that other impacts may also be possible. Through their consumption of POM, *C. sowerbii* medusae may impact carbon cycling by consuming particles which otherwise would have sunk below the surface layer. Medusae also demonstrate top-down control, causing trophic cascades by feeding on zooplankton and releasing phytoplankton from grazing pressure (Jankowski et al., 2005; Schachtl et al., 2026). Our findings support this, as we determined that juvenile zooplankton may be a major food source. However, the trophic cascades are complicated by our findings that *C. sowerbii* may feed on *Chaoborus*, which could release predation pressure on zooplankton. Another question critical to understanding ecosystem impacts of *C. sowerbii* is that of their predators. Our results show that isotopically, it is plausible that *G. aculeatus* could feed on *C. sowerbii* medusae, but this relationship has never been observed. Without predators, *C. sowerbii* medusae would sink in “jelly falls”, potentially leading to hypoxia in deep waters (Lüskow et al., 2024). To prevent these impacts, freshwater ecosystem management should aim to limit medusae abundances. Our results suggest that lake trophic state may play a key role in moderating the relationship between *C. sowerbii* and *Chaoborus*. Thus, conservation practices should focus on preventing the eutrophication of oligotrophic lakes, which could allow for the competition between *Chaoborus* and *C. sowerbii* to continue to limit medusae populations.

CONCLUSION

C. sowerbii is an invasive non-native species of freshwater jellyfish with the potential to disrupt lake ecosystems. Understanding the trophic ecology of *C. sowerbii* medusae is critical for predicting and mitigating its ecosystem impacts. Stable isotope analysis revealed that *C. sowerbii* medusae diet was primarily composed of small zooplankton (125-250 μm) and particulate organic matter, which included detritus from benthic production and microzooplankton. Diet composition did not vary with medusae size and remained relatively constant throughout the summer. *C. sowerbii* medusae prey selectivity may be governed by encounter rates, resulting in a highly homogenous diet between individuals and a narrow isotopic niche. We found no isotopic niche overlap between *C. sowerbii* medusae and *G. aculeatus*, and at this point, we cannot rule out that *G. aculeatus* may feed on *C. sowerbii* based on their trophic positions. Despite *Chaoborus* and *C. sowerbii* both consuming small zooplankton prey, we observed isotopic niche differentiation between them. This may be due to *C. sowerbii* feeding on $\delta^{13}\text{C}$ -enriched benthic carbon in the POM of oligotrophic systems. As the range of *C. sowerbii* continues to expand, ecosystem management should focus on preventing eutrophication as it may limit medusae abundance, mitigating their ecosystem impacts.

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APPENDIX

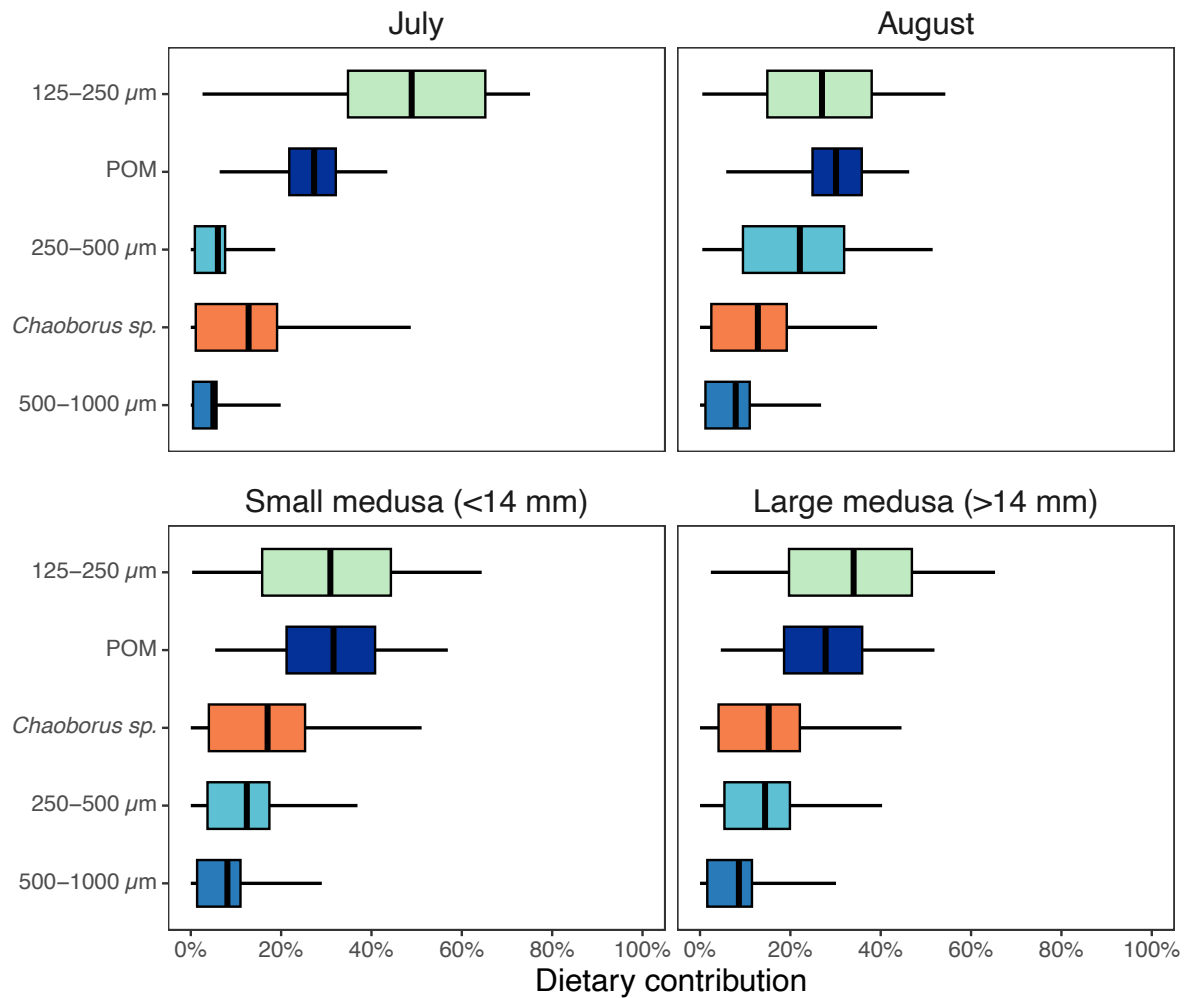


Figure A1. Contributions of potential prey to the diet of *C. sowerbii* using only daytime zooplankton samples. The vertical bar shows the mean percent contribution, while the box encompasses the 50% credible interval and the bars show the 95% credible interval.

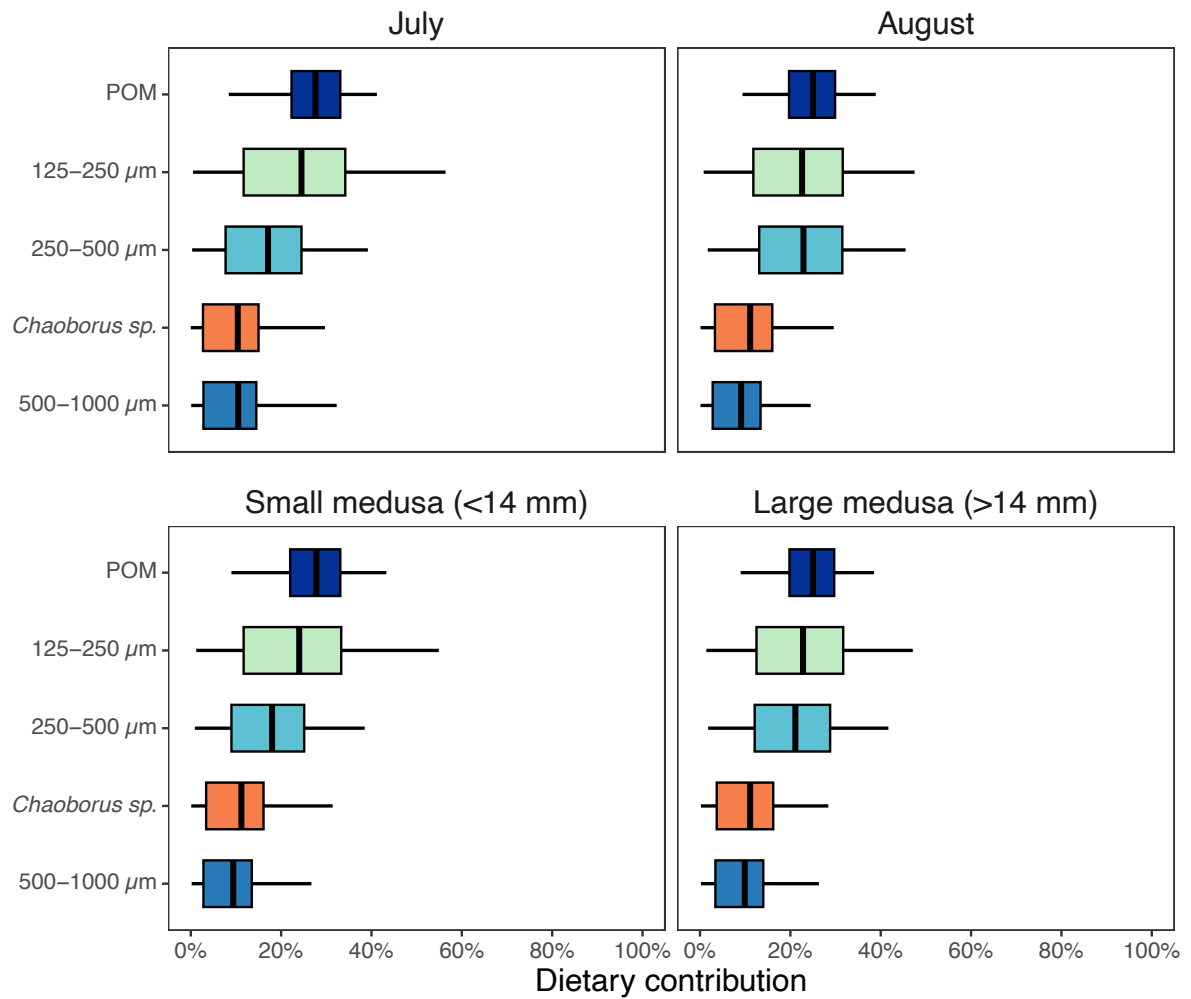


Figure A2. Contributions of potential prey to the diet of *C. sowerbii* using only nighttime zooplankton samples. The vertical bar shows the mean percent contribution, while the box encompasses the 50% credible interval and the bars show the 95% credible interval.

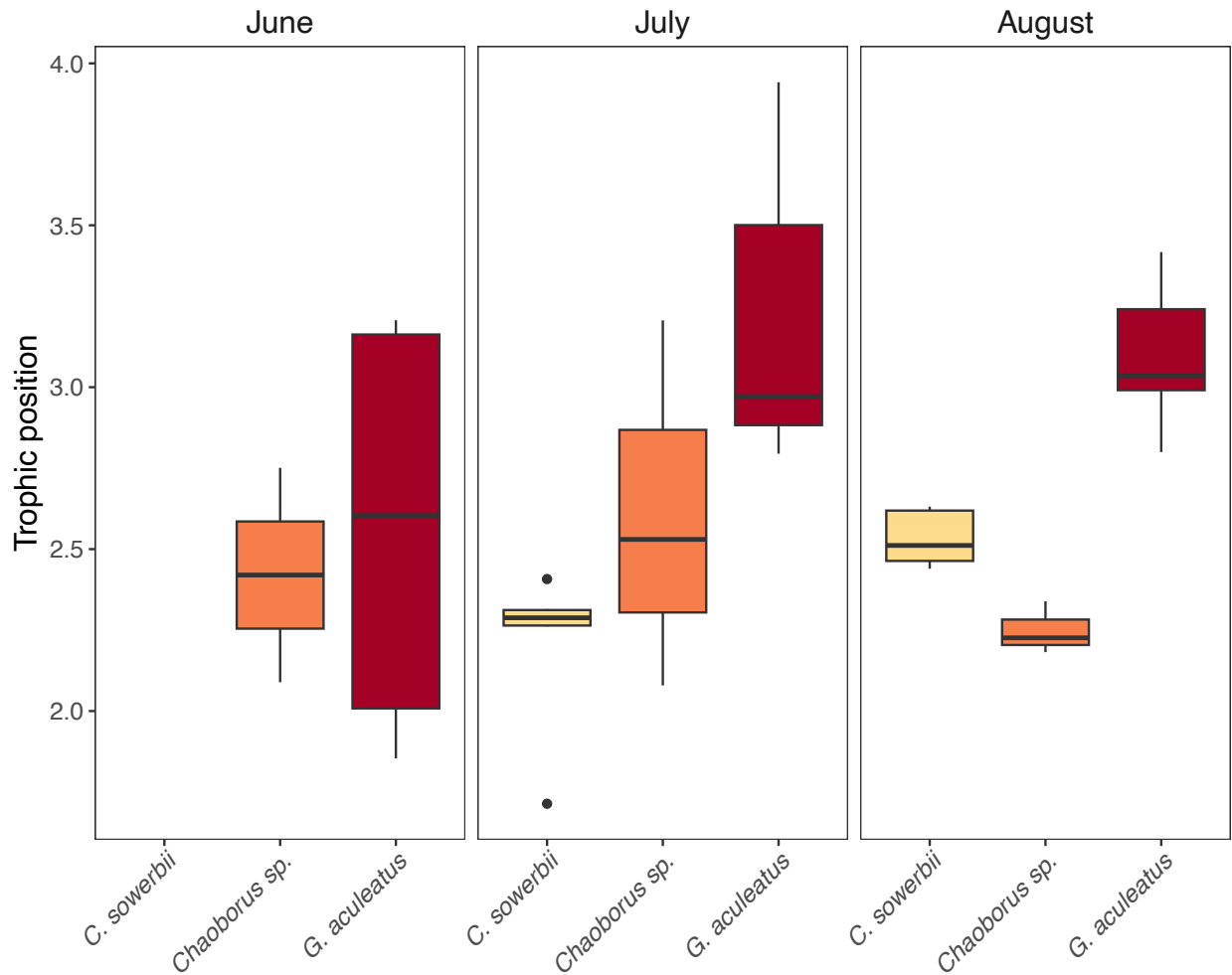


Figure A3. Trophic level of zooplankton predators. Trophic level was calculated as the difference between the predators and the mean zooplankton nitrogen enrichment for that month, divided by the trophic discrimination factor (3.4 for *G. aculeatus* and *Chaoborus*, 2.09 for *C. sowerbii*), plus 2.

Table A1. Test statistics of t-test comparing of carbon and nitrogen enrichment of large and small medusae

	t	df	p-value
$\delta^{15}\text{N}$	1.208	3.5493	0.3013
$\delta^{13}\text{C}$	-0.74542	4.2529	0.4951

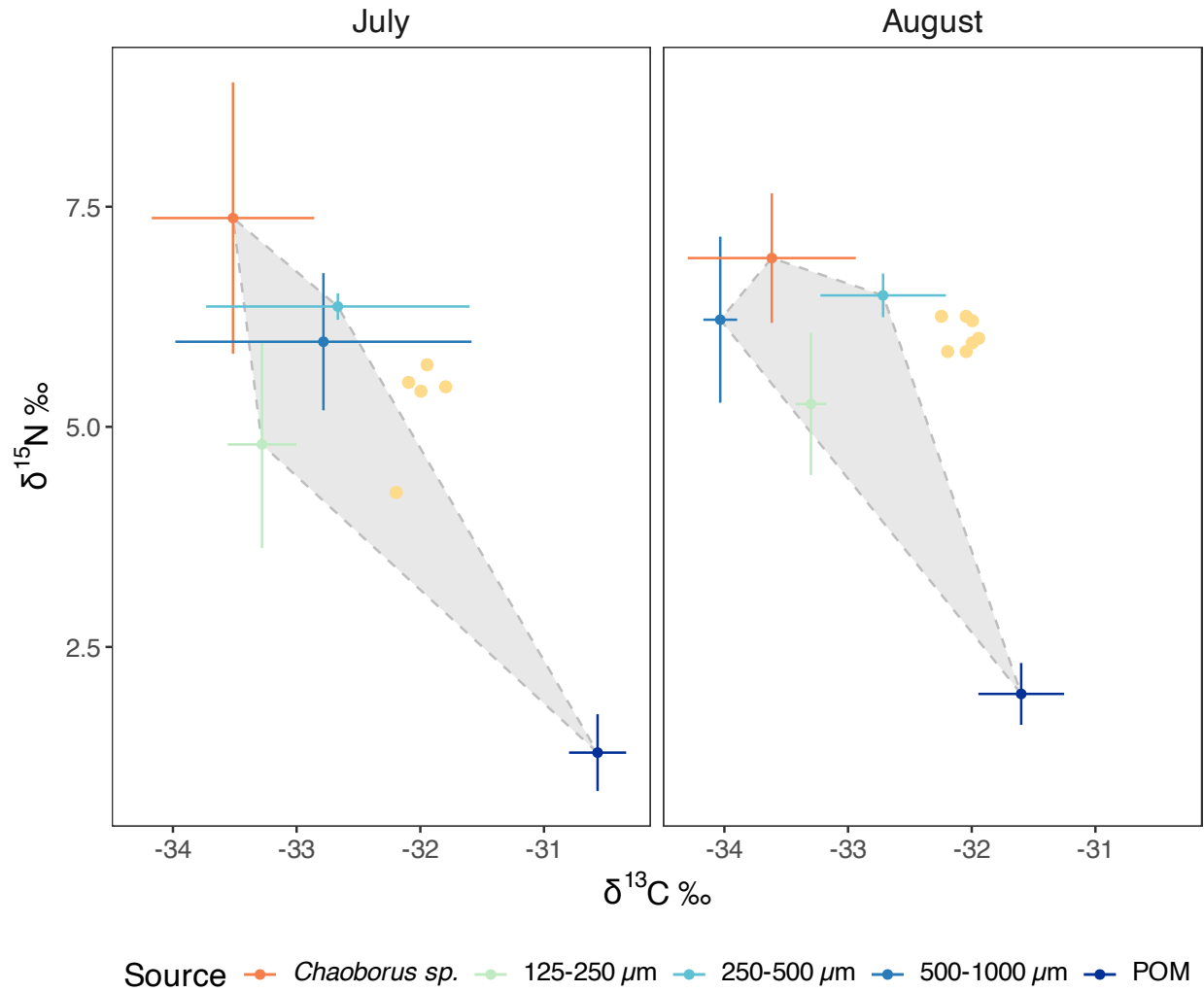


Figure A4. Sensitivity analysis mixing model inputs with low TDFs. The sources are plotted as the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with the standard deviation as the error bars. Each *C. sowerbii* medusa datapoint is the average of three triplicates, with the half of the trophic discrimination factors subtracted ($\Delta\delta^{15}\text{N} = 1.045$, $\Delta\delta^{13}\text{C} = 2.38$). The convex hull of the sources is shown in grey.

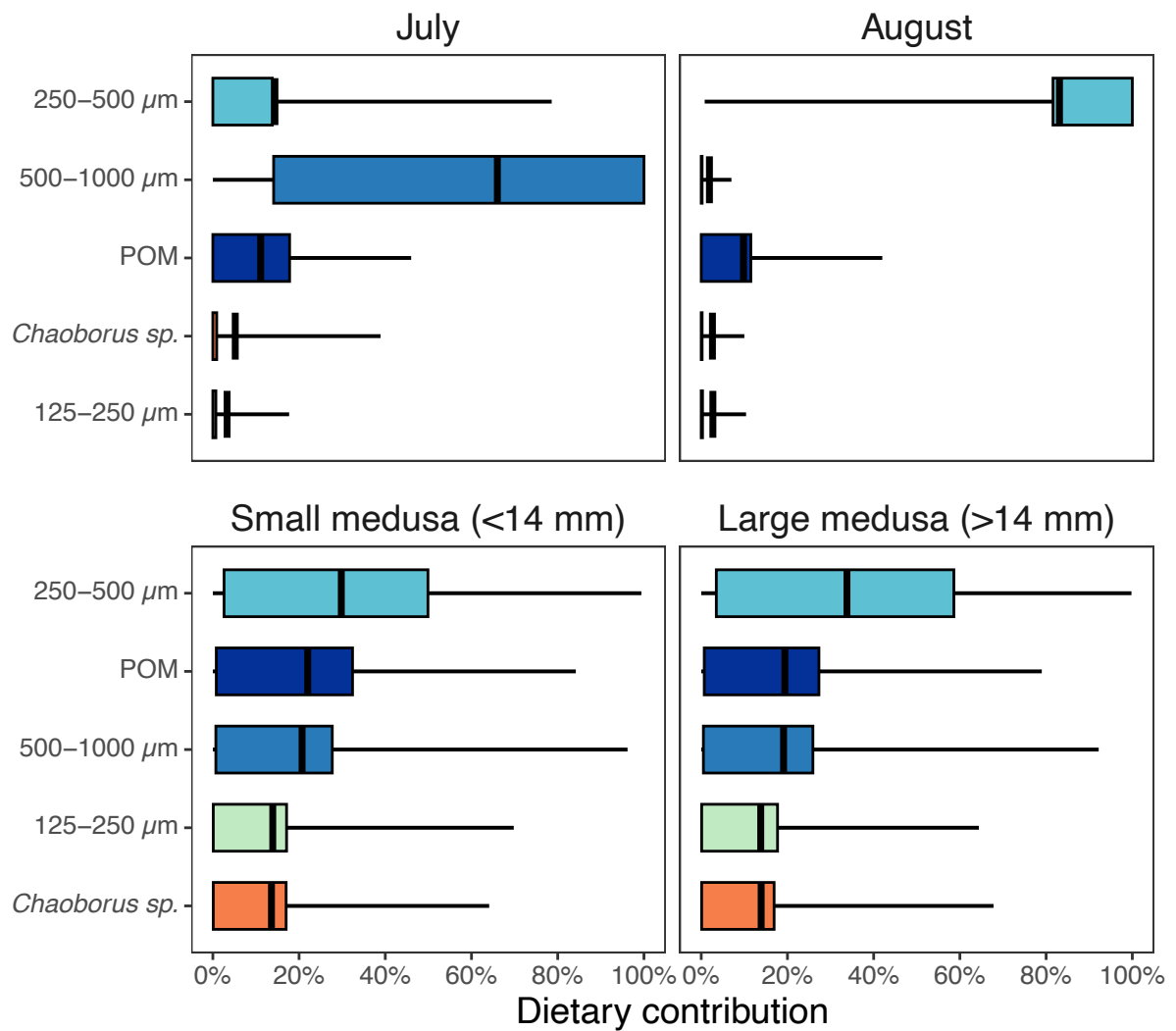


Figure A5: Mixing model sensitivity analysis with low trophic discrimination factors. TDF was halved such that $\Delta\delta^{15}\text{N} = 1.045$, $\Delta\delta^{13}\text{C} = 0.595$. The vertical bar shows the mean percent contribution, while the box encompasses the 50% credible interval and the bars show the 95% credible interval.

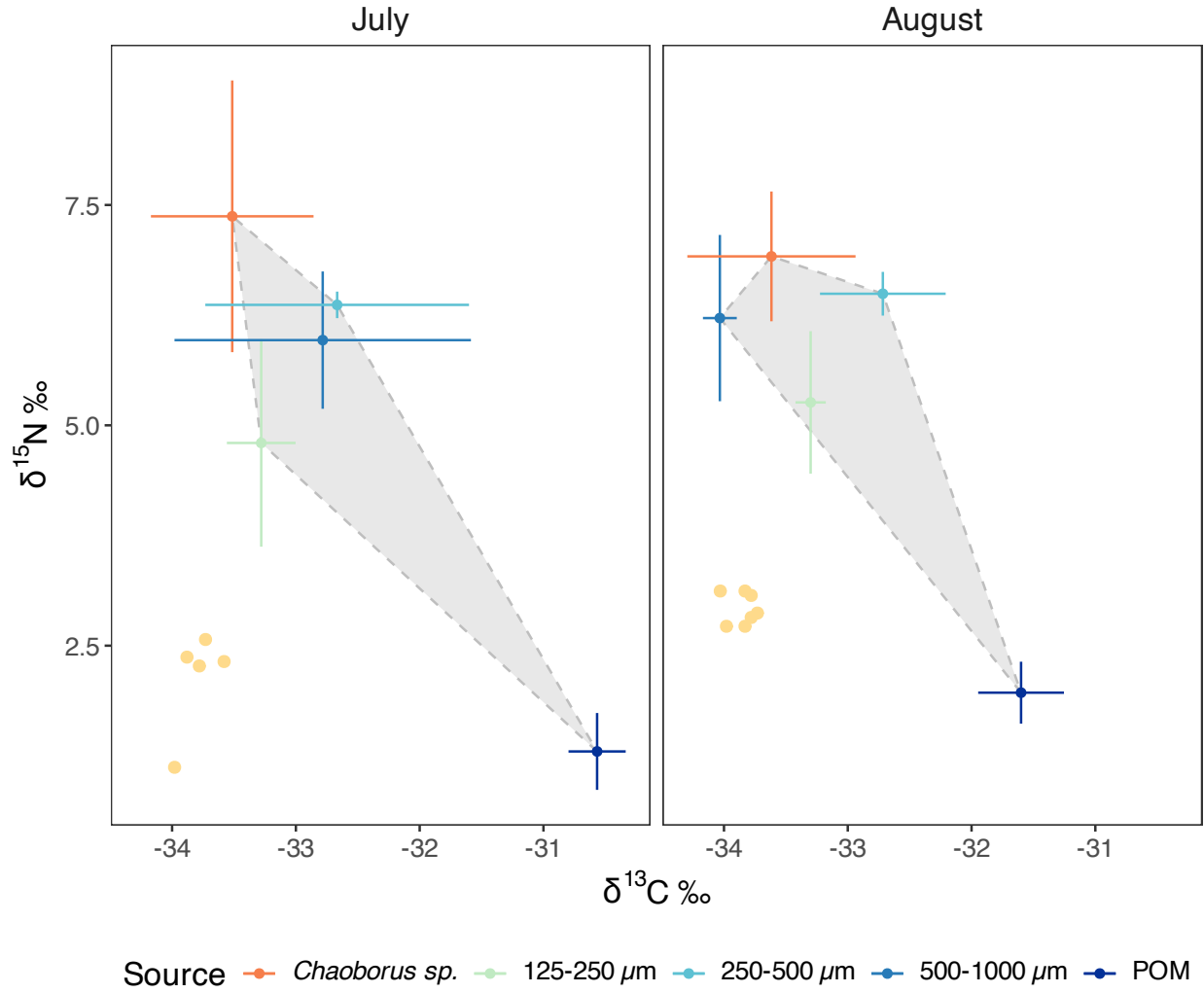


Figure A6. Sensitivity analysis mixing model inputs with high TDFs. The sources are plotted as the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with the standard deviation as the error bars. Each *C. sowerbii* medusa datapoint is the average of three triplicates, with the half of the trophic discrimination factors subtracted ($\Delta\delta^{15}\text{N} = 4.18$, $\Delta\delta^{13}\text{C} = 2.38$). The convex hull of the sources is shown in grey.

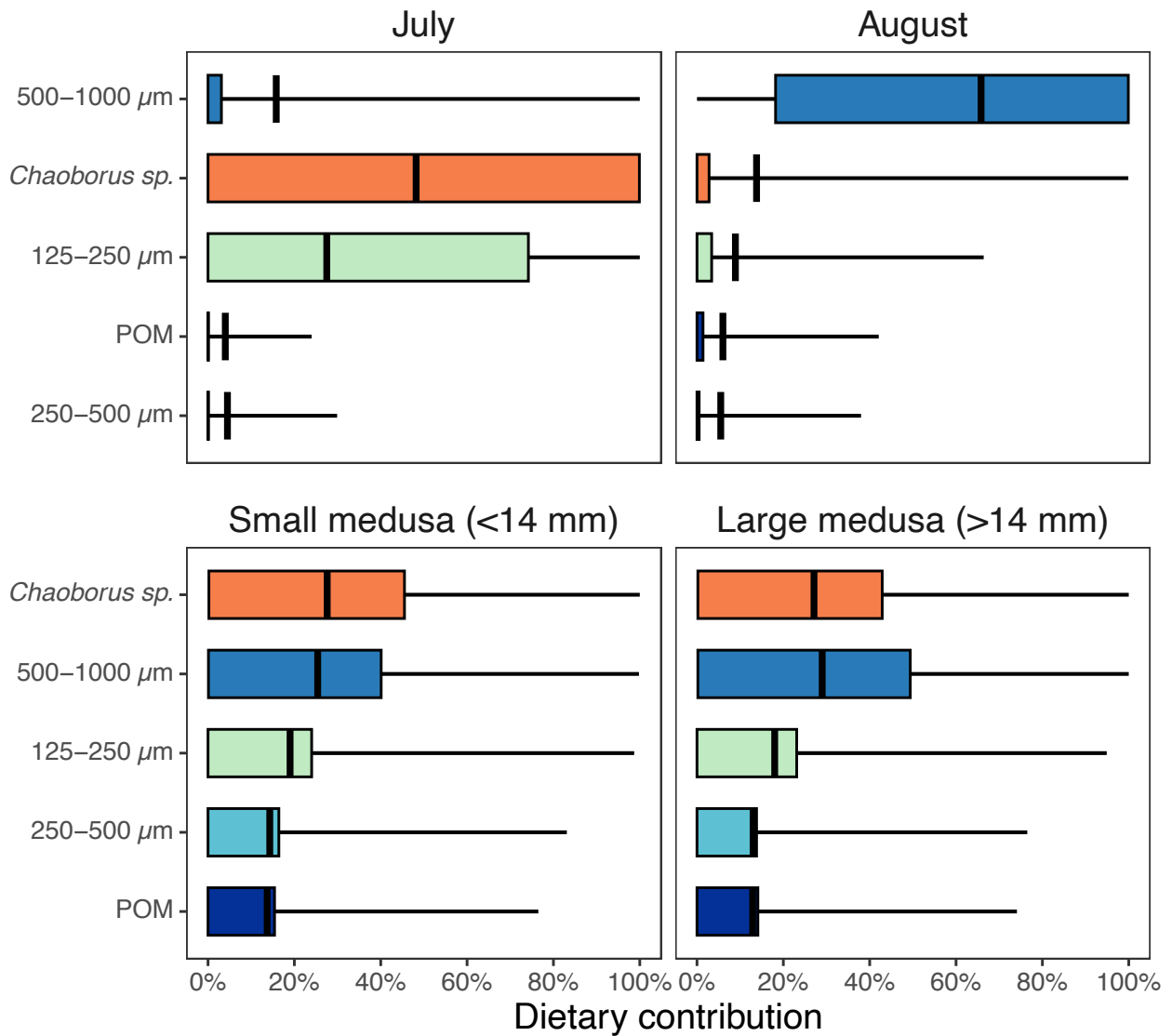


Figure A7: Mixing model sensitivity analysis with high trophic discrimination factors. TDF was doubled such that $\Delta\delta^{15}\text{N} = 4.18$, $\Delta\delta^{13}\text{C} = 2.38$. The vertical bar shows the mean percent contribution, while the box encompasses the 50% credible interval and the bars show the 95% credible interval.