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Kleptopredation: a mechanism to facilitate planktivory in a benthic mollusc

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Predation occurs when an organism completely or partially consumes its prey. Partial consumption is typical of herbivores but is also common in some marine microbenthic carnivores that feed on colonial organisms. Associations between nudibranch molluscs and

colonial hydroids have long been assumed to be simple predator-prey relationships. Here we show that while the aeolid nudibranch *Cratena peregrina* does prey directly on the hydranths of *Eudendrium racemosum*, it is stimulated to feed when hydranths have captured and are handling prey, thus ingesting recently captured plankton along with the hydroid polyp such that plankton form at least half of the nudibranch diet. The nudibranch is thus largely planktivorous, facilitated by use of the hydroid for prey capture. At the scale of the colony this combines predation with kleptoparasitism, a type of competition that involves the theft of already-procured items, with predation to form a feeding mode that does not fit into existing classifications, which we term kleptopredation. This strategy of subsidised predation helps explain how obligate-feeding nudibranchs obtain sufficient energy for reproduction from an ephemeral food source.

1. Introduction

The understanding of trophic strategies and the resultant linkages among species are critical to any description of community dynamics and energy flow [1]. Ecological specialisation is ubiquitous in the animal kingdom [2], and particularly well-examined in the area of insect-plant relationships in terrestrial ecosystems [3, 4], but believed to be less common in the marine realm [5]. Many marine herbivores and predators are generalists, but recent literature reveals increasing numbers of marine taxa with distinct habitat and/or dietary specialisation [6] comparable to terrestrial insect-plant associations [7, 8]. Opisthobranch molluscs are one marine taxon that commonly exhibits specialist behaviour, including both herbivorous and carnivorous species that feed either on particular species of algae, sponges, or colonial cnidarians [7, 9]. The association between nudibranchs and cnidarian colonies has hitherto been regarded as a simple predator-prey relationship, albeit one where the cnidarian host may provide both shelter and food supply, as well as defensive capability in some cases [10]. Where

host species are seasonally abundant, the temporal window within which predators must exploit resources and successfully reproduce is limited. Local extirpation of ephemeral hosts, which nudibranchs are capable of doing in part or entirely [7, 9, 11, 12], may risk the local reproductive capacity of the predator. Abundances of hosts such as the Mediterranean hydrozoan *Eudendrium racemosum* vary seasonally [11, 13-15] and are exploited by summer increases in the density of the aeolid nudibranchs, such as *Flabellina affinis* and *Cratena peregrina* [11]. Here, we investigate the feeding ecology of *C. peregrina* to establish mechanisms by which the nudibranch balances energy intake with preservation of its habitat.

2. Methods

(a) Sample collection and preparation

Nudibranchs, hydroids, and plankton samples were collected from Scopello, northwestern Sicily, Italy (38.073°N, 12.823°E) for all analyses. Individual *C. peregrina* and colonies of *E. racemosum* were hand collected as required by scuba diving or snorkelling at 2-5 m depth. Nudibranchs and hydroid colonies were transported to the laboratory and maintained in 60 L aquaria for behavioural experiments.

(b) Behavioural assays

The behavioural response of *C. peregrina* to feeding stimuli was tested using a simple choice experiment, where the nudibranch was presented with starved hydroid colonies, hydroids that were fed with *Artemia salina* nauplii, nauplii alone, or a blank control. Nudibranch attack rates on fed or unfed polyps and prey handling times were measured using behavioural assays of 10 min duration (see electronic supplementary material for details).

(c) Stable isotope analysis

Stable isotopes of C and N were analysed for *C. peregrina*, *E. racemosum*, two size classes of plankton, and suspended particulate organic material, and the relative importance of potential dietary sources for *C. peregrina* assessed using a series of stable isotope mixing models (see electronic supplementary material for details).

3. Results

In the simple choice experiment, a null response from random movement would result in expected frequencies of five for each of the possible outcomes. Nudibranchs moved to the fed hydroids in 14 of the 25 trials (electronic supplementary material, figure S1), which differed significantly from random ($\chi^2 = 22.0$, $p < 0.01$). To determine if this response was a stimulatory cue that manifested as increased feeding rate, we measured the rate of consumption by *C. peregrina* of *E. racemosum* hydranths that were starved or fed, and under varying levels of nudibranch hunger. The time taken for consumption of a single hydranth when fed was approximately twice that taken to consume an empty hydranth, and this was consistent regardless of the hunger level of the nudibranch (figure 1a, table 1a). We therefore excluded handling time from the attack rate calculations. Nudibranch attack rate on hydranths increased with the degree of nudibranch hunger, and they consistently consumed approximately double the number of fed hydranths compared to unfed hydranths (figure 1b, table 1b).

The mean value of isotopic enrichment of *C. peregrina* relative to *E. racemosum* was $<1\text{‰}$ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (figure 2), indicating that the hydroid is not the sole prey of the nudibranch. A simple predator-prey relationship would result in predator $\delta^{15}\text{N}$ values 2.5-3.5 ‰ higher than the prey [16, 17]. We hypothesise that this discrepancy comes about because the hydroid provides a relatively low percentage of the total prey ingested by volume. Similarly, although micro-zooplankton (64-200 μm) are of an appropriate size for consumption by *E. racemosum*

[18], the difference in $\delta^{15}\text{N}$ was only ca. 1.1‰ (figure 2). This latter result is probably due to the non-selective nature of feeding in *E. racemosum*, which while considered to be primarily carnivorous [11, 19] is known to be capable of ingesting and assimilating diatoms [20].

Posterior probabilities from Bayesian stable isotope mixing models estimated that small zooplankton contribute a greater or equivalent proportion of *C. peregrina*'s diet than *E. racemosum* (electronic supplementary material, figure S2a-c). Only the model run specifying a low nitrogen trophic discrimination value of 1.9‰ resulted in micro-zooplankton forming a lower proportion of the diet, with a mean of 23% (Fig. S2d).

4. Discussion

Our results indicate that the diet of the nudibranch *C. peregrina* is formed largely of small (<200 μm) plankton captured by its host hydroid. The stimulus of a fed hydroid colony resulted in elevated feeding rates in nudibranchs. This response might be adaptive if prey capture by hydroids is sporadic and the nudibranch seeks to profit energetically by consuming occupied polyps. It is unknown what cues stimulate the nudibranch's response to prey capture by hydranths. Species-specific substances released from different hydroids are known to be responsible for selective chemotactic behaviour of nudibranch molluscs [21]. While it is possible that olfactory cues play a part, in our preference experiment the nudibranchs distinguished between *A. salina* nauplii that were swimming freely and those captured by the hydroid. In the hydrozoan *Halocordyle disticha*, nematocyst discharge and polyp killing ability is reduced by heavy feeding upon *Artemia* nauplii, due to accumulation of discharged nematocyst venom constituents (polypeptides and enzymatic proteins) [22]. These molecules may play a role in stimulating chemoreceptors in the nudibranch's rhinophores. Also, if the

hydroid itself does not release olfactory stimulants, it is possible that the *C. peregrina* feeding response is activated by diet cues derived from captured *Artemia* nauplii.

The strong behavioural response of the nudibranch to fed hydroid colonies in the prey choice experiment suggests that nudibranchs will, by preference, consume hydranths that have captured and are handling prey. This supports the explanation that *C. peregrina* is an opportunistic predator that utilises the hydroid as a means of obtaining prey from the water column, and ingestion of the hydranth provides just a fraction of the diet by volume.

A feeding hydranth, having just captured or engulfed fresh prey, would constitute a more rewarding prey type - in terms of increased energy content - for the nudibranch. Its "selective" behaviour would represent an adaptive mechanism governing resource acquisition and consumption towards optimization of survival and reproductive success. If energy values for *Tubularia* polyps [23] are an appropriate proxy for Mediterranean hydroids such as *Eudendrium spp.*, consumption of feeding hydranths provides an important nutritional subsidy [24], satiating the nudibranch with consumption of fewer hydranths and perhaps extending the life of the hydroid colony.

Our ability to understand food webs and produce useful predictive models of ecosystems in the face of environmental change is impeded by a lack of understanding of the nature and strength of trophic linkages [25]. Food stealing from *Eudendrium spp.* by caprellids has been described as kleptocommensalism [26] because no damage is incurred by the hydroid, although this is a condition of kleptoparasitism [27]. This previously unknown case of kleptopredation combines both kleptoparasitic competition and direct predation. This may be widespread among other invertebrate specialists, altering our understanding of the functional roles of suspension feeders [28], and cautions against over-simplistic interpretation of predator-prey interactions.

Ethics. This work was conducted in accordance with the EU Directive 2010/63 and Italian DL 2014/26, and was approved by the University of Portsmouth Animal Welfare and Ethical Review Body, approval 917A.

Data accessibility. Datasets supporting this article have been uploaded as part of the electronic supplementary material.

Author contributions. FB and TJW conceived the study, and designed the experiments with LM and TVF. Experiments were performed by KTLB, CR., LM, TVF, SP and RARM, and TJW analysed the data. TJW & FB wrote the paper with input from all other authors. All authors approve the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We have no competing interests

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Table 1. a) Analysis of variance testing the effects of whether hydroids were Fed with brine shrimp, and hunger level (Time since capture) of nudibranchs, on the time taken for *Cratena peregrina* to consume hydroid polyps (data plotted in Fig 1a); and b) Analysis of variance testing the effects of whether hydroids were Fed with brine shrimp, and hunger level (Time since capture) of nudibranchs, on the attack rate on hydroid polyps by *Cratena peregrina* (data plotted in Fig 1b).

a)

Source	df	SS	MS	F	p
Fed	1	2233.4	2233.4	4.79	0.04
Time	2	172.2	86.1	0.18	0.83
Time x Fed	2	186.8	93.4	0.20	0.82
Residual	19	8862.8	466.4		
Total	24				

b)

Source	df	SS	MS	F	p
Fed	1	3.78	3.78	6.41	0.02
Time	2	5.31	2.65	4.50	0.02
Time x Fed	2	0.005	0.003	0.004	0.99
Residual	24	14.15	0.59		
Total	30				

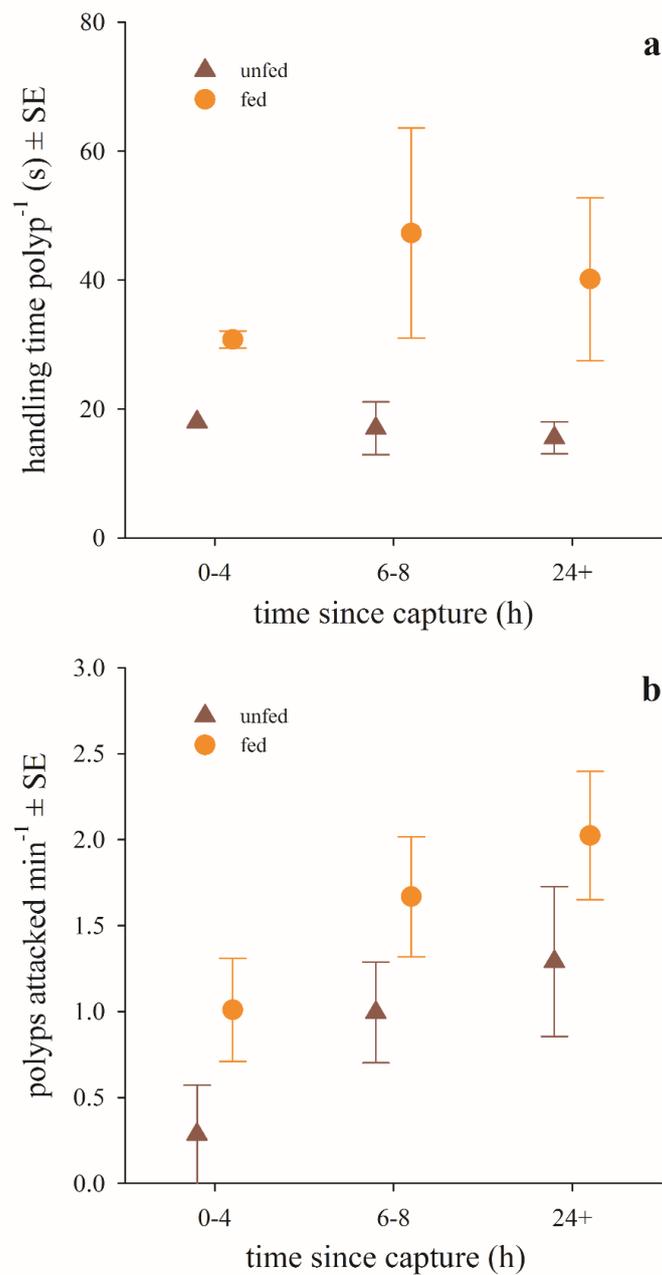


Figure 1. Feeding rate responses of *Cratena peregrina* at varying rates of starvation on *Eudendrium racemosum* colonies that are either fed with brine shrimp (*Artemia sp.*) or not fed. **a**, mean time to consume a hydranth, **b**, attack rate, taking into account variation in handling time.

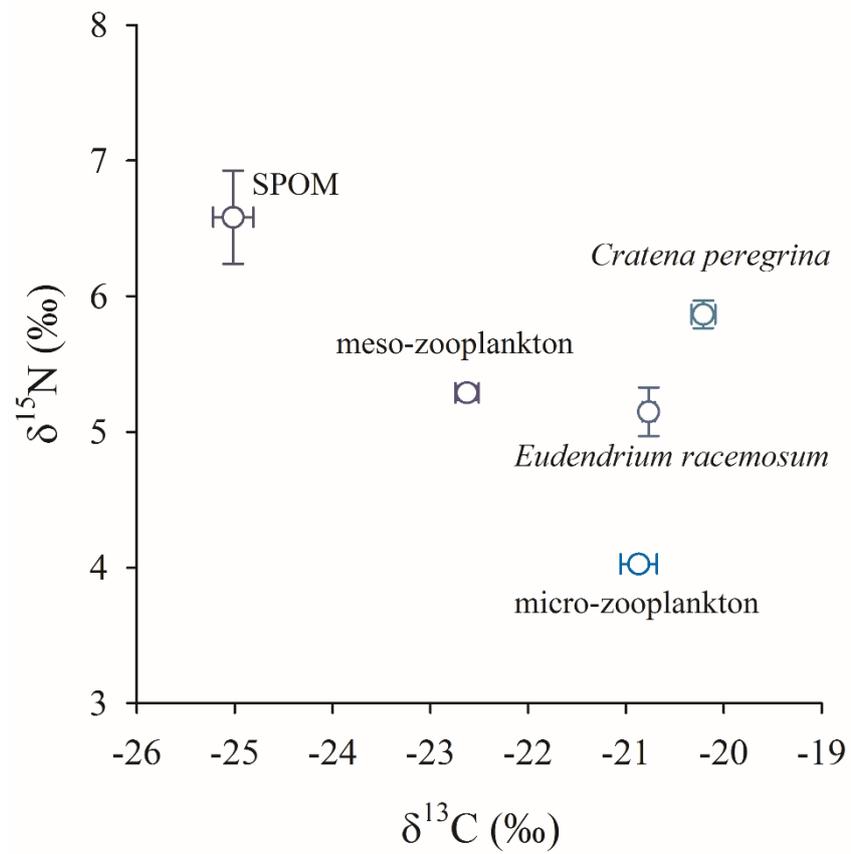


Figure 2. Biplot of the mean (\pm standard error) isotope values for *Cratena peregrina* and its putative prey. SPOM = suspended particulate organic material.

Kleptotrophy: a mechanism to facilitate planktivory in a benthic mollusc

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Behavioural assays

Behavioural responses to stimuli were assessed by a simple choice experiment, where four fine (200 μm) mesh plastic bags were placed equidistantly around a 260 mm diameter petri dish filled with filtered seawater, containing respectively a starved (>12 hr) colony of *E. racemosum*, brine shrimp (*Artemia salina*) nauplii, and a *E. racemosum* colony fed with *Artemia*. The fourth bag was left empty as a control. Hydroid colonies were fed by pipetting *Artemia* to a branch of hydroid colony contained in a 6 cm petri dish with seawater. Capture of *Artemia* was observed using a stereo microscope, and feeding stopped when >90% of the hydranths had captured at least one brine shrimp. A single nudibranch (mean wet weight = 0.096 ± 0.055 g, range 0.021-0.250 g) was placed in the centre of the petri dish and observed for 10 min. There were five possible outcomes: the nudibranch would make no choice, or move to one of the four mesh bags. A choice was recorded where the nudibranch climbed onto a bag, or touched a bag with its rhinophores. The experiment was repeated 25 times. A fresh nudibranch and hydroid colonies were used with clean equipment for each replicate, and the position of the four treatments was randomised for each run.

We assessed nudibranch responses to the presence of hydroid prey using a series of behavioural assays. Nudibranch feeding rates on hydroid colonies that were either starved (>12 hr) or fed with *Artemia* (as for the Simple Choice experiment) were measured as the consumption rate of individual hydranths over a 20 min observation period. We preferred to use *Artemia* nauplii rather than wild-caught zooplankton both because the latter are difficult to maintain alive, and to avoid the introduction of other confounding factors to the experiment (i.e. species composition and size of copepod and possibly chemical cues coming from damaged individuals).

Since the feeding rate of nudibranchs was likely to be affected by their degree of hunger, we divided nudibranchs into three treatments: unstarved (< 4 hr from capture), 6-8 hr from capture, and starved > 24 hr. The two treatments were incorporated into a two-way factorial design with five replicates per cell. Nudibranchs were observed using a dissecting microscope and each of three activity categories (moving, resting, and prey handling) was timed (s). Handling was the time spent consuming a single hydranth (Supplementary Video), and differences in handling time between fed and unfed hydroids by nudibranchs at three starvation levels were tested with two-way Analysis of Variance (ANOVA). Since the time required to ingest fed hydranths was approximately double that of unfed hydranths (see Results), analysis of attack rates among treatments excluded handling time from the denominator when calculating attacks per unit time. Differences in attack rates by nudibranchs were tested using the same two-way ANOVA model.

Stable isotope analysis

Specimens collected for stable isotope analysis were euthanized by freezing at -20°C . Plankton samples for stable isotope analysis were collected in two size class by towing a $200\ \mu\text{m}$ mesh net and a $64\ \mu\text{m}$ mesh net, respectively, to collect meso-zooplankton and micro-zooplankton. Five tows of 30 min at 1.5 kt were made for each mesh size. After collection, meso-plankton samples were sieved through a $500\ \mu\text{m}$ mesh and a $200\ \mu\text{m}$ mesh, and micro-plankton sieved through a $200\ \mu\text{m}$ mesh and a $64\ \mu\text{m}$ mesh. Carbonates were removed from plankton samples by acidification using 0.1 M HCl and washing with distilled water. All samples were dried for more than one week in a 60°C oven. Hydroid samples were composed solely of hydranths that were dissected after drying and combined into a 1 mg sample. *Cratena peregrina* samples were excised from the ventral surface of the foot to avoid possible bias introduced by the sequestration of hydranth nematocysts in the skin or cerata [1].

Samples were analysed using a Delta V mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) coupled with a Costech ECS 4010 Elemental Analyser (Milan, Italy). Samples were run with three laboratory standards (gelatine, glycine and alanine) with known isotope values. Replicate measurements on internal laboratory standards indicated analytical errors of 0.3 ‰ for $\delta^{15}\text{N}$ and 0.06 ‰ for $\delta^{13}\text{C}$ (estimated as the standard deviation of three different sized replicates of ground tryptophan). All stable isotope values were reported as parts per thousand (‰) and expressed in delta notation from international standards (Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$): $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Source proportions of nudibranch diet were estimated using a Bayesian mixing model in the R package SIAR [2, 3], incorporating concentration-dependence using measured concentrations of C and N [4]. Since the diet-tissue discrimination factors among trophic levels are unknown, for the plankton-*Eudendrium* relationship we used the common baseline values of $\Delta\text{N} = 3.4\ \text{‰} \pm 1.1$ (sd) and $\Delta\text{C} = 1.0\ \text{‰} \pm 0.63$ [5], but ran the model with a variety of values for ΔN (1.9 - 3.4 ± 1.1 in steps of 0.5) between *Cratena* and its prey, since higher trophic levels may have relatively low ΔN depending on dietary composition and inverse relationships with dietary $\delta^{15}\text{N}$ [5, 6]. No prior probabilities were specified in the models, so all potential sources were assumed to be consumed with equal probability.

Figure S2 presents probability distributions of the relative importance of dietary components under different model runs where we vary the trophic enrichment factor to determine the effects of this unknown quantity on our interpretation. This is an important component of mixing model analysis that is mostly ignored [7], but mixing models are very sensitive to variation in these discrimination factors [8]. Commonly a value of 3.4‰ for changes in $\delta^{15}\text{N}$ with trophic level (i.e. $\Delta^{15}\text{N}$) is used and accepted as an adequate proxy in the absence of detailed long-term diet-switching experiments that can provide empirical estimates of isotopic enrichment between predator and prey. In reality, there is considerable variation in $\Delta^{15}\text{N}$ among taxa [6] as well as a significant inverse relationship between $\Delta^{15}\text{N}$ and dietary $\delta^{15}\text{N}$ [6, 9, 10]. This latter finding suggests that $\Delta^{15}\text{N}$ tends to diminish with increasing trophic level [5]. At the lower end

of the food web, as in this study, $\Delta^{15}\text{N}$ is unlikely to take values below 2.5‰. Our models therefore show that, at expected values of $\Delta^{15}\text{N}$, plankton provide more than half of the total diet of *Cratena peregrina*, and plankton becomes a relatively unimportant dietary component only when $\Delta^{15}\text{N}$ is assumed to be smaller than usually found at low trophic levels [5, 6]. We also note that the standard deviations assumed for $\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$ are deliberately large relative to the modelled values to reflect uncertainty as to the specific trophic enrichment values.

Supplementary References

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Supplementary Video

Cratena_feeding.mov

Video file of *Cratena peregrina* feeding on *Eudendrium racemosum*, showing how the nudibranch engulfs and removes entire hydranths.

Supplementary Figures

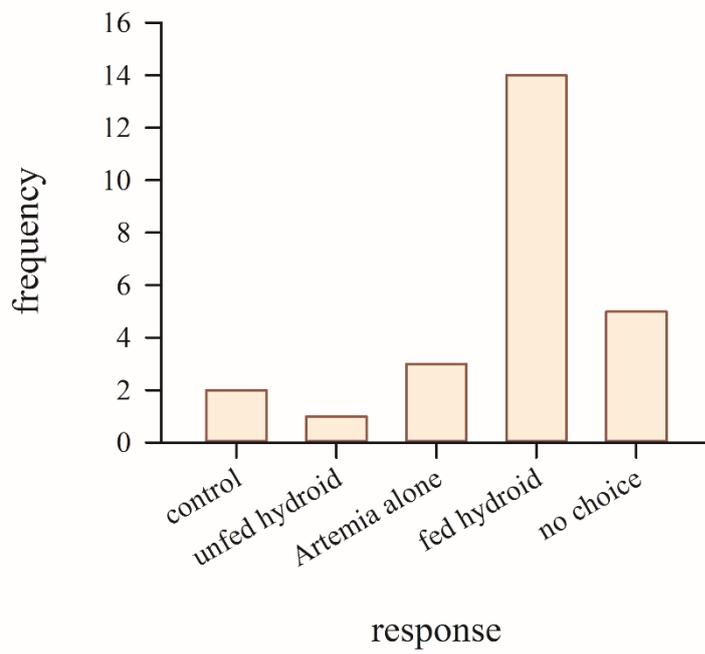


Figure S1. Behavioural response frequencies of *Cratena peregrina* to alternative prey choices in a simple choice experiment (n = 25 trials).

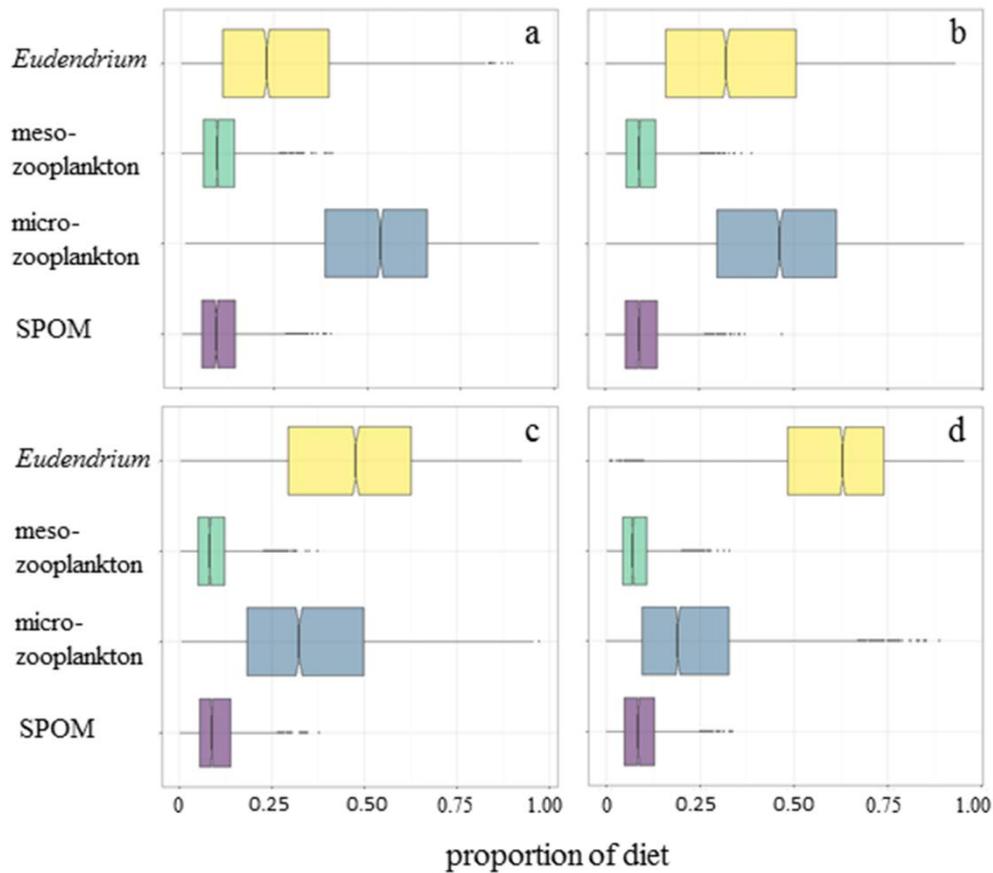


Figure S2. Dietary proportions of *Cratena peregrina* estimated from a Bayesian stable isotope mixing model. Box plots represent the medians with 25% and 75% credible intervals. Whiskers represent 2.5% and 97.5% credibility intervals. Proportions estimated using trophic enrichment factors of (A) $\Delta N = 3.4\text{‰} \pm 1.0$ and $\Delta C = 1.0\text{‰} \pm 0.63$ (sd) for all prey types, and altering ΔN of *Eudendrium racemosum* to (B) $2.9\text{‰} \pm 1.0$, (C) $2.4\text{‰} \pm 1.0$, and (D) $1.9\text{‰} \pm 1.0$.