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Predation patterns and prey quality of medusae in a semi-enclosed marine lake: implications for food web energy transfer in coastal marine ecosystems

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Veliko Jezero (Mljet, Croatia) is a nearly enclosed karstic depression filled with salt-water, where jellyfish and prey exchange with the Adriatic Sea is negligible, making this small ecosystem ideal for the controlled study of medusae in food webs. Based on the analysis of their gut contents, medusae appeared to ingest less carbon than expected on the basis of their carbon content. To accurately define carbon ingestion by medusae, we determined the diet of *Aurelia* sp. 5 (Dawson and Jacobs, 2001) (Scyphozoa: Semaestomeae) from Veliko Jezero by combining gut content and stable isotope analyses. During daytime, gut contents identified a mix of small copepods as the dominant prey (62%). In contrast, feeding models based on stable isotope values of medusae and their potential prey analyzed using Stable Isotope Analysis in R indicated appendicularians could have made the greatest contribution to *Aurelia* sp. 5 diet (14–78%), followed by calanoid copepods (0–50%) and fish larvae (0–43%). Because appendicularians and fish larvae are abundant with medusae at night near the bottom of the “lake” and contain more carbon than small copepods, we suggest diel movements of *Aurelia* sp. 5 and carbon content of prey determine the carbon assimilated by medusae, with night-time prey making a

greater contribution to medusa diet than daytime prey. These data suggest medusae assimilate more carbon than previously estimated and suggest that jellyfish play an important role mediating carbon transfer in coastal food webs.

KEYWORDS: gut content; stable isotope; SIAR; daily ration; *Aurelia* sp.; jellyfish

INTRODUCTION

The role of carnivorous gelatinous zooplankton in food web energy transfer is not well defined in ecosystem models (Pauly *et al.*, 2009). Jellyfish predation may result in the top-down control of zooplankton communities (reviewed in Purcell, 1997) and depletion of zooplankton standing stocks (Matsakis and Conover, 1991; Behrends and Schneider, 1995; Møller and Riisgård, 2007). Although jellyfish are occasionally preyed upon by fish and other vertebrates (Utne-Palm *et al.*, 2010; Cardona *et al.*, 2012), the low dietary quality of organisms with high water content suggests that jellyfish reduce energy flow from lower to higher trophic levels in comparison with planktivorous fish (Ruzicka *et al.*, 2012).

A basic step to determine carbon transfer via jellyfish within the food web is the assessment of carbon ingested. Dietary composition of jellyfish has been determined in several ecosystems (reviewed in Purcell, 1997). However, when prey ingested have been converted into carbon, medusae appeared to ingest a small fraction of carbon per day, suggesting that medusae were food limited (Båmstedt, 1990; Olesen *et al.*, 1994; Lucas *et al.*, 1997; Suchman *et al.*, 2008). These estimates of daily carbon ingestion by medusae have been calculated based on analysis of daytime gut contents alone, potentially under-evaluating differences in predation patterns between daytime and night-time (Pitt *et al.*, 2008). Underestimating the contribution of nocturnal zooplankton may explain the discrepancy between the carbon content of medusae and the carbon ingested calculated on the basis of daytime gut contents (Pitt *et al.*, 2008).

Quantification of carbon transfer in food webs involving jellyfish is complicated by contrasting dietary compositions of medusae obtained using different methods. Gut content analyses typically suggest that medusae feed largely on mesozooplankton (reviewed in Purcell, 1997) and microzooplankton (Stoecker *et al.*, 1987; Matsakis and Conover, 1991; Sullivan *et al.*, 1994; Malej *et al.*, 2007). Conversely, fatty acid composition of *Aurelia aurita* (Linnaeus, 1789) in Seto Inland Sea (Japan) indicated potential for feeding on detritus (Fukuda and Naganuma, 2001), and stable isotopes of *Catostylus mosaicus* (Quoy and Gaimard, 1894) from Smiths Lake (Australia) identified large, demersal zooplankton as the main food source of medusae (Pitt *et al.*, 2008). It is not

clear if these feeding patterns are due to location or to species-specific differences in diet. Alternatively, the relative contribution of detritus and large zooplankton to the diet of medusae may be underestimated when using gut content alone.

Gut contents provide a relatively short-term dietary assessment, due to rapid digestion rates of medusae (Martinussen and Båmstedt, 1999) and some soft-bodied prey types (Purcell *et al.*, 1991). Additionally, this method takes into account foods that are ingested, but may not necessarily reflect assimilated foods (Arai, 1997). Stable isotopes allow for a time-integrated definition of diet and reflect foods actually assimilated (Pitt *et al.*, 2008; Frost *et al.*, 2012). A suitable method to accurately identify potential prey and calculate dietary compositions using stable isotopes is Stable Isotope Analysis in R (SIAR), a recently developed package in R using Bayesian mixing models that considers species-specific fractionation values, which can reduce the error in trophic assessments due to generalized fractionation values (Parnell *et al.*, 2010). Given the inconsistent and sometimes conflicting assessments of jellyfish diet in the past, SIAR is likely to be useful to refine diet analyses and define the contribution of jellyfish to local food webs.

Veliko Jezero is a nearly enclosed marine “lake” on Mljet Island (Croatia), where the exchange of medusae and zooplankton with the outside Adriatic Sea is negligible. To determine whether medusae ingested less carbon than their carbon content, we defined the contribution of detritus and different zooplankton taxa to the diet of *Aurelia* sp. 5 (Dawson and Jacobs, 2001) using a combination of gut content and stable isotope analyses. We identified prey in guts of medusae and calculated their contribution to the carbon ingested daily by medusae. To define longer-term assimilated diet, we determined and compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of medusae and their potential prey. Two models of diet composition were computed using SIAR.

METHOD

Study site

Veliko Jezero (“Big Lake”, 42°46.0'N, 17°21.1'E to 42°46.7'N, 17°22.6'E) in Mljet National Park (Croatia) is a karstic depression (maximum depth 46 m) filled with

saltwater (Benović *et al.*, 2000). The hydrographic and ecological characteristics of the “lake” are described in detail in previous studies (Benović *et al.*, 2000; Malej *et al.*, 2007; Alvarez Colombo *et al.*, 2009; Graham *et al.*, 2009). Veliko Jezero is connected to the Adriatic Sea by a shallow channel, but exchange of water is reduced and migration of organisms negligible (Benović *et al.*, 2000). During spring, water temperature is about 20°C above the thermocline (10–20 m depth), decreasing to 10°C at depth >20 m. Salinity averages 37.0 ± 0.5 . Zooplankton abundance and diversity are low, with a distribution regulated by the seasonal thermocline (Benović *et al.*, 2000; Malej *et al.*, 2007).

Sample collection

Sampling was conducted from 15 to 23 May 2009. Medusae and their potential prey were collected from the basin in Veliko Jezero (maximum depth 30 m) inhabited by a resident population of *Aurelia* sp. 5 earlier described in Malej *et al.* (Malej *et al.*, 2007) and Graham *et al.* (Graham *et al.*, 2009). A total of 45 *Aurelia* sp. 5 was collected in the thermocline during daytime by SCUBA divers and measured for bell diameter (as the distance between two opposite rhopalia, ± 0.1 cm) on the boat. For gut content analysis, 30 medusae were preserved in a buffered 4% formaldehyde solution. For determination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, 15 *Aurelia* were stored in acid-washed plastic jars on ice.

Potential prey of medusae were collected at 3, 12 and 25 m depths, representing points above, within and below the thermocline to account for potential differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with depth, given the stratification of the water column. To isolate detritus, water was collected using a 5-L Niskin bottle deployed at each depth, filtered on the boat using a 64- μm sieve and stored in acid-washed bottles. Zooplankton were collected using a 0.54 m diameter, 53- μm mesh Nansen net with a closing system towed horizontally at each depth. Samples were stored in acid-washed plastic jars. All samples were kept on ice during transport to the field laboratory.

Sample processing

For gut content analysis, preserved *Aurelia* sp. 5 were dissected in the laboratory and gut contents were identified to the lowest possible taxonomic level using a dissecting microscope. For stable isotope analysis, freshly caught medusae were rinsed with ultrapure water to remove any zooplankton or detritus from the outside of the jellyfish and dried at 60°C.

Water was filtered under vacuum on pre-ashed (4 h at 500°C) Whatman GF/F glass fiber filters (2.5-cm

diameter, 0.2- μm pore size) to concentrate sufficient detritus for stable isotope analysis. Potential zooplankton prey were isolated by sieving samples through nested meshes to obtain three size classes: 53–200 μm (microzooplankton), 200–500 μm and 500–2000 μm (large zooplankton). A mix of cyclopoid copepods, copepod nauplii and copepodites (hereafter referred to as “mixed small copepods”) was sorted out under a dissecting microscope from the 200–500- μm fraction. Large zooplankton were identified as calanoid copepods, appendicularians and fish larvae. Each taxon was analyzed separately. All samples were rinsed with ultrapure water, dried at 60°C and homogenized using a mortar and pestle.

Determination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Stable isotope composition was determined from 30.0 ± 3.0 mg of whole medusae ($n = 15$) and 1.0 ± 0.2 mg of potential prey ($n = 30$) sent to the Stable Isotope Facility for Environmental Research (SIRFER) at the University of Utah (USA). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined using an isotope ratio mass spectrometer (Finnigan Delta Plus; Bremen, Germany) coupled with an elemental analyzer (model 1110; Carlo Erba, Milan, Italy) through an open split interface (CONFLO III; Finnigan, Bremen, Germany). Final $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were expressed as ‰ relative to international standards: Pee Dee Belemnite for C and air for N. The long-term standard deviations were 0.13‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{15}\text{N}$.

We corrected $\delta^{13}\text{C}$ values of samples with C:N > 3.5 to normalize the effect of individual and species-specific lipid content on $\delta^{13}\text{C}$ (Post *et al.*, 2007; Logan *et al.*, 2008). Protocols to calculate the corrections are described in D'Ambra (D'Ambra, 2012). The equations applied were:

$$\Delta\delta^{13}\text{C} = -9.43 + 2.69 * \text{C:N}_{\text{bulk}}$$

for medusae and

$$\Delta\delta^{13}\text{C} = -2.45 + 0.62 * \text{C:N}_{\text{bulk}}$$

for zooplankton.

Data analysis

We defined the dietary composition of *Aurelia* sp. 5 in Veliko Jezero based on gut content analysis by averaging the percentage of prey in the guts of *Aurelia* sp. 5 across the 30 medusae analyzed in this study. Using the carbon content of each prey category (Table I; Martinussen and Båmstedt, 1995), we computed the carbon daily ingested by medusae. The total number of prey found in each gut was corrected

for a digestion time of 2 ± 1 h (Purcell, 2009), assuming medusae fed continuously throughout the day (Martinussen and Bámstedt, 1995; Suchman *et al.*, 2008). To calculate carbon daily ration, we converted medusa bell diameter to dry mass (Larson, 1985), and then to carbon, according to the carbon content of medusae determined at SIRFER ($0.9 \pm 0.3\%$ of medusa dry mass). The carbon daily ingested was divided by the carbon content of each medusa. To determine the relationship between carbon daily ration and bell diameter, we \log_{10} -transformed mean carbon daily rations and calculated Pearson’s correlation coefficient. Errors were propagated throughout calculations according to Taylor (Taylor, 1996).

Because $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of potential prey were not normally distributed with depth using Bartlett’s tests, we applied Kruskal–Wallis tests to identify potential variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of prey with depth accounting for small sample size ($n = 6$). To define the diet of *Aurelia* sp. 5 based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of medusae and their potential prey, we computed two feeding models using the package SIAR (version 4.1) downloaded with R (version 2.13.1) from the Comprehensive Archive Network site (CRAN, <http://cran.r-project.org/>). Feeding models were based on prey composition inferred either from gut contents alone (model 1) or from all feasible prey (model 2). The proportional diet composition of medusae was estimated using the fractionation values ($\Delta^{13}\text{C} = 4.2 \pm 0.3\text{‰}$; $\Delta^{15}\text{N} = 0.3 \pm 0.1\text{‰}$) determined in laboratory experiments for *Aurelia* sp. (D’Ambra, 2012). Tests were considered significant at $P < 0.05$.

RESULTS

Gut content analysis

The mean bell diameter of the 30 *Aurelia* sp. 5 collected in this study was 8.4 ± 2.6 cm. The mean number of prey found in their guts was 17 ± 9 prey per medusa.

Table I: Fraction of total prey in the gut, carbon content per prey, and fraction of total carbon daily ingested (mean \pm SD) of Aurelia sp. 5 in Veliko Jezero (Croatia)

Prey	Fraction total prey (% of total prey day ⁻¹)	C content ($\mu\text{g prey}^{-1}$)	Fraction total C ingested (% of total C ingested day ⁻¹)
Mixed small copepods	62 ± 29	1.0	42 ± 32
Calanoid copepods	33 ± 30	5.0	57 ± 32
Copepod nauplii	4 ± 7	0.2	1 ± 1
Appendicularians	1 ± 5	1.9	1 ± 2
Fish larvae	–	1.9–5.6	–

Carbon content per prey from Martinussen and Bámstedt (Martinussen and Bámstedt, 1995).

Gut contents from *Aurelia* sp. 5 collected in the sub-thermocline during the day were dominated by mixed small copepods, followed by calanoid copepods, copepod nauplii and appendicularians (Table I). When converted into carbon, mixed small copepods provided a lower percentage of carbon per day than the less abundant calanoid copepods due to their different carbon contents (Table I). Carbon daily rations computed from gut content analysis averaged $6.9 \pm 2.6\%$, indicating that medusae ingested less carbon per day than their own content. \log_{10} -transformed carbon daily rations decreased with increasing bell diameter ($r^2 = -0.73$, $P < 0.001$; Fig. 1).

Stable isotope analysis

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of potential prey did not vary significantly with depth (Table II). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of microzooplankton and mixed small copepods were not different when compared using a *t*-test ($t = 2.45$, $df = 7$, $P = 0.06$ for $\delta^{13}\text{C}$; $t = -1.92$, $df = 7$, $P = 0.09$ for $\delta^{15}\text{N}$) and were pooled. Detritus had the most depleted $\delta^{13}\text{C}$ ($-25.0 \pm 0.4\text{‰}$) and $\delta^{15}\text{N}$ ($2.1 \pm 0.7\text{‰}$) values, while medusa tissues showed the most enriched $\delta^{13}\text{C}$ ($-20.5 \pm 0.3\text{‰}$) and $\delta^{15}\text{N}$ ($7.2 \pm 0.4\text{‰}$) values (Fig. 2). The isotope signatures of mixed small copepods ($\delta^{13}\text{C} = -21.5 \pm 0.7\text{‰}$; $\delta^{15}\text{N} = 5.0 \pm 0.5\text{‰}$) and calanoid copepods ($\delta^{13}\text{C} = -23.1 \pm 0.6\text{‰}$; $\delta^{15}\text{N} = 6.4 \pm 0.2\text{‰}$) were intermediate between detritus and medusae (Fig. 2). Appendicularians and fish larvae had $\delta^{15}\text{N}$ values similar to medusae (7.7 ± 0.6 and $7.4 \pm 0.1\text{‰}$), but were depleted in $\delta^{13}\text{C}$ (-22.2 ± 0.3 and $-21.3 \pm 0.1\text{‰}$) (Fig. 2). Given the potential for a shift in trophic position with increasing bell diameter of medusae (Fleming *et al.*,

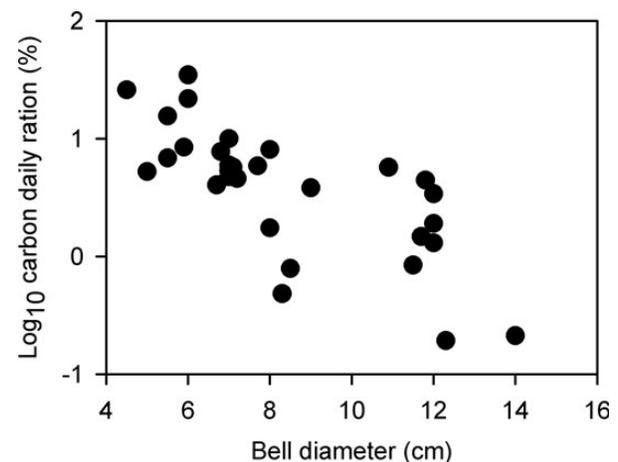


Fig. 1. \log_{10} -transformed daily carbon ration (%) compared to the bell diameter (cm) of *Aurelia* sp. 5 in Veliko Jezero, Croatia ($n = 30$; $r^2 = -0.73$; $P < 0.001$).

Table II: Kruskal–Wallis tests comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the potential prey of *Aurelia* sp. 5 in Veliko Jezero (Croatia) within three different depths (3, 12 and 25 m)

Prey	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	H-value	P-value	H-value	P-value
Detritus	2.26	0.32	2.57	0.28
Microzooplankton	4.57	0.10	3.53	0.17
Mixed small copepods	1.54	0.46	2.28	0.32
Calanoid copepods	3.71	0.16	4.33	0.12
Appendicularians	4.57	0.10	4.57	0.10

For all comparisons $n = 6$, $df = 2$.

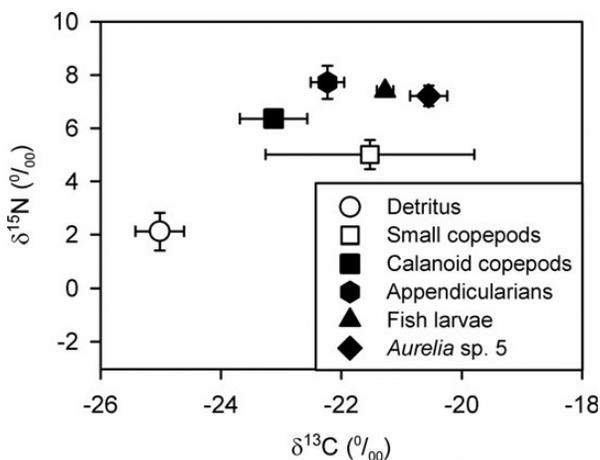


Fig. 2. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm SD) of *Aurelia* sp. 5 and their potential prey (not corrected for trophic enrichment) in Veliko Jezero (Croatia), collected from 15 to 23 May 2009.

2011), we calculated Pearson's correlation coefficient between $\delta^{15}\text{N}$ and bell diameter. Because the correlation was not significant ($r = -0.008$; $P = 0.98$), we pooled $\delta^{15}\text{N}$ of medusae for analysis in SIAR.

Model outputs were similar. Appendicularians made the highest contribution to the assimilated diet of medusae in each model (33–78% in model 1, Fig. 3A; 14–66% in model 2, Fig. 3B), followed by calanoid copepods (3–59%, Fig. 3A; 0–50%, Fig. 3B). When fish larvae were included in the model, their contribution was similar to the range of calanoid copepods (0–43%; model 2; Fig. 3B). Models indicated relatively little contribution (<20%) of detritus and mixed small copepods to the diet of *Aurelia* sp. 5 (Fig. 3).

DISCUSSION

Closed and semi-enclosed ecosystems (lakes, bays, fjords, lagoons) are suitable locations to define jellyfish dietary

composition and evaluate their contribution to food web dynamics because immigration and emigration terms are negligible (Schneider and Behrends, 1994; Lucas *et al.*, 1997; Malej *et al.*, 2007; Lo and Chen, 2008). *Aurelia* sp. 5 are the most abundant gelatinous zooplankton in Veliko Jezero (Benović *et al.*, 2000). Medusae are observed throughout the year in the lake but none is found in the adjacent Adriatic Sea waters (Benović *et al.*, 2000). Gut content analysis and *in situ* feeding experiments previously conducted in Veliko Jezero indicate that medusae feed predominantly on small copepods (Malej *et al.*, 2007; Turk *et al.*, 2008). Fish predation on *Aurelia* sp. 5 has been observed *in situ*, but not quantified (Alvarez Colombo *et al.*, 2009; Graham *et al.*, 2009). This ecosystem, therefore, is ideal to define the diet of *Aurelia* sp. 5 and evaluate energy flow in the food web.

We found that diet composition based on analysis of gut contents was different from SIAR models. Gut contents indicated mixed small copepods were the most abundant prey of medusae (Table I), in agreement with previous gut content analyses in Veliko Jezero (Malej *et al.*, 2007). In contrast to gut contents, SIAR feeding models suggested that appendicularians, fish larvae and calanoid copepods could make the greatest contributions to the diet of *Aurelia* sp. 5 (Fig. 3). Because fractionation values applied to interpret the trophic shift from predators to their potential prey impact SIAR outputs (Parnell *et al.*, 2010), we opted to use fractionation values recently determined in the laboratory for *Aurelia* sp. (D'Ambra, 2012) to accurately define dietary composition of *Aurelia* sp. 5 in Veliko Jezero. Although we used fractionation values different from generic values applied in stable isotope analysis (<1‰ for carbon and 3–4‰ for nitrogen; McCutchan *et al.*, 2003; Vanderklift and Ponsard, 2003), our choice relied on the similarity between fractionation values determined in the laboratory and field observations of isotope values of jellyfish and their potential prey in the North Sea (Frost *et al.*, 2012) and the northern Gulf of Mexico (D'Ambra, 2012). Therefore, to resolve the discrepancy between diet compositions, we suggest vertical movements of medusae between the surface and the deep layer of the “lake” and carbon content of prey are key to interpreting our results.

Different diet definitions between daytime gut contents and SIAR models may reflect distinct feeding patterns between daytime and night-time due to vertical movement of medusae to the bottom of the “lake” at night. *Aurelia* sp. 5 swarm in the sub-thermocline during the day and descend to the deepest layer at night (Malej *et al.*, 2007; Alvarez Colombo *et al.*, 2009). Their zooplankton prey are distributed with depth: mixed small copepods are dominant above and within the thermocline (Benović *et al.*, 2000), while appendicularian biomass peaks at

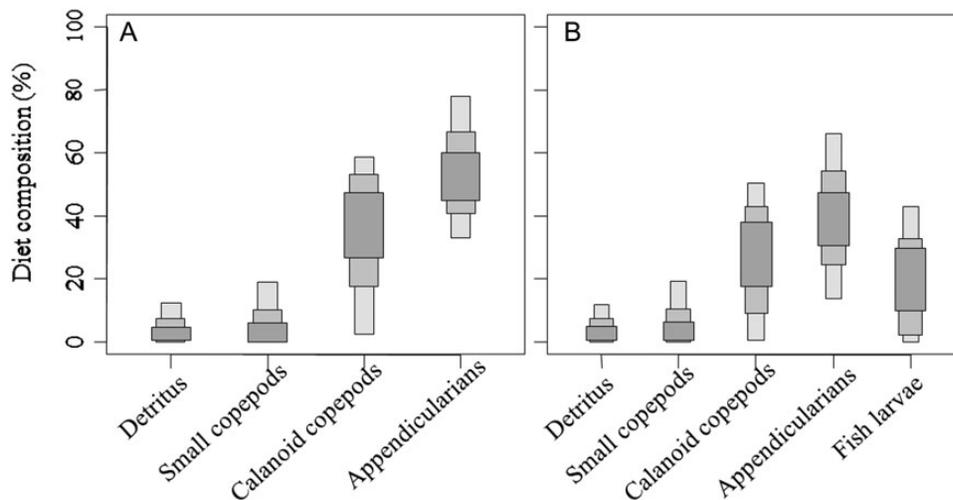


Fig. 3. Percentage dietary composition of *Aurelia* sp. 5 in Veliko Jezero (Croatia) according to two models based on (A) gut contents (model 1) and (B) interpretation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of medusae and their potential prey (model 2). Gray scale (light to dark) indicates 95, 75 and 25% confidence intervals.

depth >20 m (D. Lučić, Dubrovnik, personal communication). Fish larvae co-occur with medusae in deep waters at night (G. Alvarez Colombo, M. Acha, H. Mianzan, Mar del Plata, personal communication). Therefore, medusae could feed on small copepods during daytime in the water column and prey on appendicularians and fish larvae near the bottom of the “lake” at night. Analysis of gut contents was conducted only during daytime in this and previous studies (Malej *et al.*, 2007). Given scyphozoan digestion rates 1–3 h (Martinussen and Båmstedt, 1999; Suchman *et al.*, 2008), daytime gut contents alone are insufficient to detect night-time feeding patterns (Pitt *et al.*, 2008).

The interpretation of the discrepancy between daytime gut contents and SIAR models as an indication of diel feeding patterns of medusae is supported by carbon content of prey. Mixed small copepods had the lowest carbon content of all prey found in the guts of *Aurelia* sp. 5. This explains why, although numerically dominant in gut contents of medusae, they represented a minor contribution to the carbon budget and assimilated diet of medusae. Calanoid copepods had five times the carbon content of mixed small copepods, which provide the greater contribution to the carbon budget and assimilated diet, although calanoid copepods were numerically less abundant than mixed small copepods. Appendicularians and fish larvae contained more carbon per prey than mixed small copepods, which may explain their contribution to the assimilated diet either when only prey found in the guts were considered (model 1, Fig. 3A) or when all feasible prey were included in the analysis (model 2, Fig. 3B). Because night-time feeding rates of medusae are unknown, the

estimation of carbon provided by appendicularians and fish larvae to the carbon daily ingested by medusae (Table I) is likely undervalued.

Underestimating the contribution of the carbon provided by night-time prey to the diet of medusae may explain why *Aurelia* sp. 5 in Veliko Jezero appeared to ingest less carbon than expected based on their baseline carbon content (Fig. 1). Daily rations similar to this study were calculated in Raunefjorden, Norway (Martinussen and Båmstedt, 1995), Tokyo Bay, Japan (Ishii and Tanaka, 2001), and the Northern California Current (Suchman *et al.*, 2008). Assuming no other losses in carbon, respiration alone requires three to eight times the carbon content of *Aurelia* spp. per day, depending on medusa size and environmental conditions (Larson, 1987). These energetic costs explain the high daily rations (up to 600%) determined in experimental work, when medusae were exposed to non-limiting prey concentrations (Båmstedt, 1990). This mismatch between field and experimental determinations has been explained as food limitation in natural populations (Båmstedt, 1990; Olesen *et al.*, 1994; Lucas *et al.*, 1997; Suchman *et al.*, 2008), while our results suggest that differences in feeding between day and night may have been left undefined using daytime gut contents alone.

Our results highlight the importance of carbon content of prey in the diet of *Aurelia* sp. 5 in Veliko Jezero. Medusae feed on small copepods in surface waters during daytime, but their main carbon source may come from prey captured in deeper waters at night that contained more carbon than daytime prey. Daily carbon rations of *Chrysaora quinquecirrha* (Desor, 1848) in the

Northern California Current increased when eggs and larval stages of euphausiids, which contained more carbon than other prey of medusae, were found in the gut contents (Suchman *et al.*, 2008). Although carbon budgets were not determined, large, emergent zooplankton, which provided the greatest contribution to the diet of *Catostylus mosaicus*, were likely enriched in carbon compared with daytime copepods (Pitt *et al.*, 2008). The similarity of results among ecosystems and species suggests that carbon richness of prey may not be a location or species-specific pattern, but a metabolic requirement previously underestimated.

Although the details of the mechanism are not fully resolved, evidence for feeding on discrete pools of carbon supports the assertion that jellyfish may be more important in mediating energy transfer within local food webs than previously recognized. *Aurelia* spp. may reduce carbon transfer to higher trophic levels due to the limited predation on medusae (Graham *et al.*, 2009), a mechanism described for the North California Current food web (Ruzicka *et al.*, 2012). Medusae, however, may be an underestimated food source for fish that feed on them, particularly in closed systems like Veliko Jezero. The bogue *Boops boops* (Linnaeus, 1758) were observed to feed on *Aurelia* sp. 5 in Veliko Jezero, but predation rates have not been determined (Graham *et al.*, 2009). Regardless of the mechanism regulating energy transfer in the Veliko Jezero food web, *Aurelia* sp. 5 play a key role in determining the carbon available to higher trophic levels. Defining the role of jellyfish in this simple, nearly enclosed ecosystem may help understanding the functioning of complex coastal food webs.

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