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ORIGINAL PAPER

Diet, prey selection, and individual feeding rates of the jellyfish *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae)

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Abstract

Large scyphomedusae can deplete zooplankton communities when occurring in high densities and the assessment of their trophic impacts relies on basic information of the species' feeding habits. We quantified in situ gut contents of the South American jellyfish *Lychnorhiza lucerna* Haeckel, 1880 and described the procedures to determine the diet, prey-selectivity patterns, and feeding rates of this species. Specimens were collected between 2008 and 2011 from surface waters along the southeastern coast of Brazil (23°–25°S, 45°–48°W), where they were immediately preserved simultaneously with plankton samples near aggregations of medusae. Most prey items (~ 70%) were extracted from the central cruciform stomach by rinsing, although ~ 16% remained in the gastric cavity even after several rinses. Non-digestive body regions (oral arms and umbrellar canals) accounted for a small proportion of the prey found (< 10%). Calanoid copepods were the most abundant (53%) prey, followed by cyclopoid (15.1%) and poecilostomatoid (11.4%) copepods and bivalve veligers (~ 7%). The dietary composition was mostly similar to the proportional abundances in the surrounding mesozooplankton. As medusa size increased, the proportion of calanoids increased, but dietary diversity decreased. The ingestion rates quantified did not supply the species minimum carbon requirements as estimated from oxygen consumption rates; therefore, nutritional resources (e.g., dissolved and particulate organic matter) in addition to mesozooplankton must be considered in further studies. We estimated that from 110 to 102,871 copepods were ingested daily by medusae (5–30 cm diameter), which indicates the species have one of the highest feeding rates among scyphomedusae. Therefore, the aggregations of *L. lucerna* along the southwestern Atlantic coast must be better studied to understand what are the predatory impacts and the role of this species in local production process.

Introduction

Large scyphomedusae are voracious predators and can deplete plankton communities when they occur in high abundances (Möller 1984; Purcell 1985; Purcell 2009). Problems caused by blooms of some populations have increased the demand for knowledge of their feeding biology and trophic impacts on ecosystems (Purcell 2009; Gibbons and Richardson 2013). The wide variety of pelagic cnidarians display different prey-capture mechanisms and foraging strategies (Costello et al. 2008) that result in considerable dietary diversity (Purcell 1997). This diversity has been demonstrated by studies employing different approaches such as gut-content analysis (Larson 1991; Matsakis and Conover 1991; Zeman et al. 2016) and stable-isotope analysis (Nagata et al. 2015; Fleming et al. 2015). While there is a comparatively robust body of knowledge regarding the feeding habits of a few, better-studied taxa (e.g., *Aurelia* and *Chrysaora* spp.), medusae of Rhizostomeae remain the least-known

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group among large scyphomedusae [but see Larson (1991), Álvarez-Tello et al. (2016)].

Nutritional strategies of rhizostome medusae are diverse, ranging from a diet of different mesozooplankton taxa in azooxanthellate species (Fancett 1988; Larson 1991; Pitt et al. 2008) to zooplanktivory, along with autotrophy in zooxanthellate species (Smith 1936; García and Durbin 1993). From a functional perspective, the unique morphology of the complex oral arms of rhizostome medusae impedes the ingestion of large prey. Whereas, in most scyphomedusae groups (coronates and semaeostomes), the mouth consists of a large central aperture; in rhizostome medusae, the oral arms bear numerous small mouths with narrow apertures (< 3 mm in diameter) along their oral arms (Uchida 1926; Lee et al. 2008; Nagata et al. 2016). Thus, while semaeostome medusae can feed on both small and large prey (e.g., copepods, ctenophores, and large medusae), rhizostome jellyfish have a complex feeding apparatus adapted to feed only on micro- and mesozooplankton (Larson 1991).

In the tropical and subtropical southwestern Atlantic, *Lychnorhiza lucerna* Haeckel, 1880 is the most common and abundant rhizostome species (Morandini et al. 2005; Schiariti et al. 2008; Oliveira et al. 2016). Along the southern Brazilian and northern Argentinean coast (32–35°S), large aggregations of *L. lucerna* occur during austral summer (Schiariti et al. 2008; Nagata pers obs), whereas, in the South Brazil Bight (23−28°S), these medusae occur throughout the year, with seasonal patterns differing by region (Morandini 2003; Nogueira Júnior et al. 2010; Nogueira Júnior and Haddad 2017). Episodes of dominance of *L. lucerna* in coastal waters (e.g., Colombo et al. 2003) can interfere with local fisheries (Schiariti et al. 2008; Nagata et al. 2009), but the potential predatory impact of these aggregations is unknown. Although details of the species' filter-feeding mechanisms and predator–prey interactions were described recently (Nagata et al. 2016), what this predator captures in nature remain uncertain. This information is essential for understanding what sources sustain these populations and whether their predatory impact may compromise energy transfer to higher trophic levels.

A broader view of the ecological roles of jellyfish as consumers depends on information generated through multiple approaches, and the traditional gut-content analyses continue to be useful. This low-cost approach can be applied with minimum laboratory facilities and provides highly precise taxonomic identification of recently ingested prey, as well as estimates of prey selectivity and consumption rates. Since the pioneer work of Lebour (1922), numerous studies have used gut-content analyses to elucidate the feeding biology of large scyphomedusae (Larson 1991; Purcell 1997; Zeman et al. 2016). Nevertheless, unlike for cephalopods or fish (e.g., Hyslop 1980), methods for gut-content analysis of large medusae still need to be standardized (Gibbons and Richardson 2013). It has been demonstrated that sampling jellyfish by means of trawling or plankton nets results in cod-end feeding and loss of gut contents (Purcell 2003; Barz and Hirche 2005); nevertheless, many studies still have used such methods for capturing these fragile predators for gut-content analysis (Online Resource 1). Gibbons and Richardson (2013) showed that of ten studies of jellyfish gut contents, where individuals were collected with a solid sampler (e.g., jar and bucket), only 40% reported the size of the mesh used to retain the gut contents. Efforts toward standardization and improvement of sampling/quantification protocols are essential to improve the quality of data in jellyfish research (Gibbons and Richardson 2013).

Because *L. lucerna* is the most abundant scyphomedusan species in the southwestern Atlantic, our study quantified gut contents to: (1) evaluate whether different procedures of gut-content extraction and quantification alter estimates of feeding rates in medusae of Rhizostomeae; (2) describe the species' diet and prey-selectivity patterns; (3) quantify the species' feeding rates and evaluate whether total ingestion support the metabolic demand of the medusae. We tested the hypothesis that as the strength of bell pulsations scales with body size (Nagata et al. 2016), increasingly faster feeding currents would enable predators to capture more-rapidly escaping prey (Costello and Colin 1994; D'Ambra et al. 2001). If so, the capture of rapidly escaping prey (e.g., calanoid copepods and brachyuran zoeae) would increase in larger medusae. Another consequence of the stronger and faster swimming of rhizostome medusae than those of other groups (D'Ambra et al. 2001; Nagata et al. 2016) may be a higher metabolic demand (Purcell et al. 2010) and, consequently, higher feeding rates. We compared feeding rates of *L. lucerna* with those of other scyphomedusan species and evaluate whether this parameter changes with size and prey density.

Methods

Study area

Over the shallow shelf (< 15-m isobath) of the South Brazil Bight (Fig. 1), the coastal water mass predominates. This water mass results from the combination of land-drainage and shelf waters and is characterized by thermohaline features determined by the local climate and seasons (Castro et al. 2006). Especially in the central part of the South Brazil Bight, the coastal area off the Paranaguá and Cananéia estuaries (Fig. 1a, b) receives outflows of nutrient- and plankton-rich continental water. The São Sebastião Channel is a curved channel 25 km long between São Sebastião Island and the mainland (Fig. 1c).

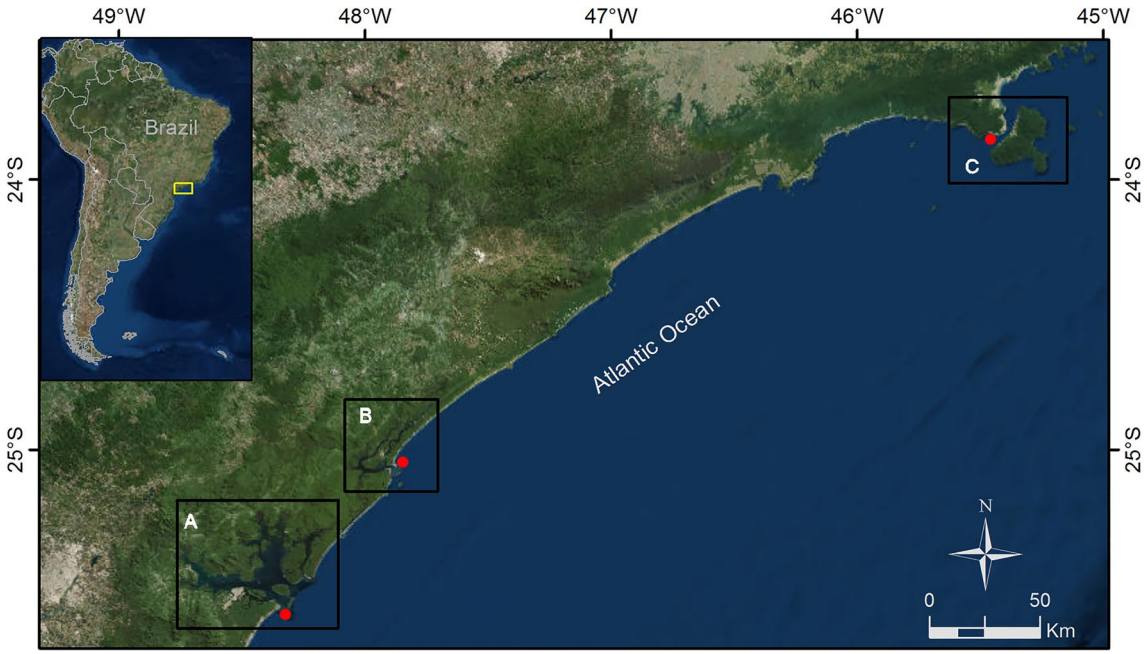

Fig. 1 Map of South America showing sampling sites along the South Brazil Bight. Paranaguá Estuary (A), Cananéia Estuary (B), and São Sebastião Channel (C). Source: ArcGIZ Desktop 8.1

This channel is dominated by coastal waters with meso-oligotrophic features, but, during the austral spring and summer, a flow of high-salinity (> 36) and low-temperature (< 18 °C), nutrient-rich South Atlantic Coastal Water can be detected in the deepest layers (Gianesella et al. 1999). These three coastal areas have higher chlorophyll-*a* concentrations along the central part of the South Brazil Bight (Gaeta and Brandini 2006), zooplankton densities, and fish spawning activity (Lopes et al. 2006). Despite the medusa *L. lucerna* is seasonally found in high densities in these regions, there are a few information of environmental variables associated with occurrences of this species (but see Nogueira Júnior and Haddad 2017).

Sampling

A minimum of 6 medusae were collected at each sampling site, of a total of 40, from small boats in daytime between 2008 and 2011. Seawater temperature ranged from 18.8 to 21.5 °C (Table 1). Medusae were carefully collected from surface waters using buckets or a dip net (1-mm mesh size). Bell diameter between opposite rhopalia was measured to the nearest 1 mm. Specimens were immediately preserved in 4% formaldehyde in filtered (45 µm) sea water, packed in individual plastic bags, and stored in buckets. The composition of co-occurring zooplankton was estimated by collecting plankton samples ($N = 3-4$) near aggregations of medusae in short (~ 2 min) subsurface horizontal tows with a 50-cm mouth diameter, 200-µm mesh plankton net. Samples were preserved in 4% formaldehyde solution in seawater.

Table 1 Sampling sites, dates, water temperatures, numbers of *Lychnorhiza lucerna* medusae collected, bell diameter (cm), method of quantification, and numbers of plankton samples collected from the South Brazil Bight

Local	Date	Water temperature (°C)	Medusae sampled	Size range (cm)	Extracted gut contents	Total body dissection	Field plankton samples
Paranaguá	25 Jun 2008	18.8	8	12–26	8	0	3
Cananéia	08 Jun 2011	21	13	9–24.5	9	4	3
	20 Jun 2011	20	7	20–30	5	2	4
	26 Aug 2011	20.4	6	5–22	5	1	3
São Sebastião	27 Jul 2011	21.5	6	7.5–24.5	6	0	4
Total			40	5–30	33	7	17

The volume of water filtered in each tow was estimated with a Hydro-Bios flowmeter secured in the mouth of the net. Several hundred organisms were counted from subsamples (6.25–25%) taken with a Motoda splitter and mean densities per sampling site were used for prey selection estimates.

Medusa dissection and quantification of total ingestion (*G*)

In medusae of Rhizostomeae, prey are captured on the surface of the oral arms and transported to the oral-arm canals through many millimeter-wide pores termed mouthlets. From the oral-arm canals, prey are transported to the oral disc and to the cruciform stomach (Fig. 2b, c) where digestion occurs and, subsequently, to the umbrellar canals (Fig. 2e). Further details of prey-capture and transport

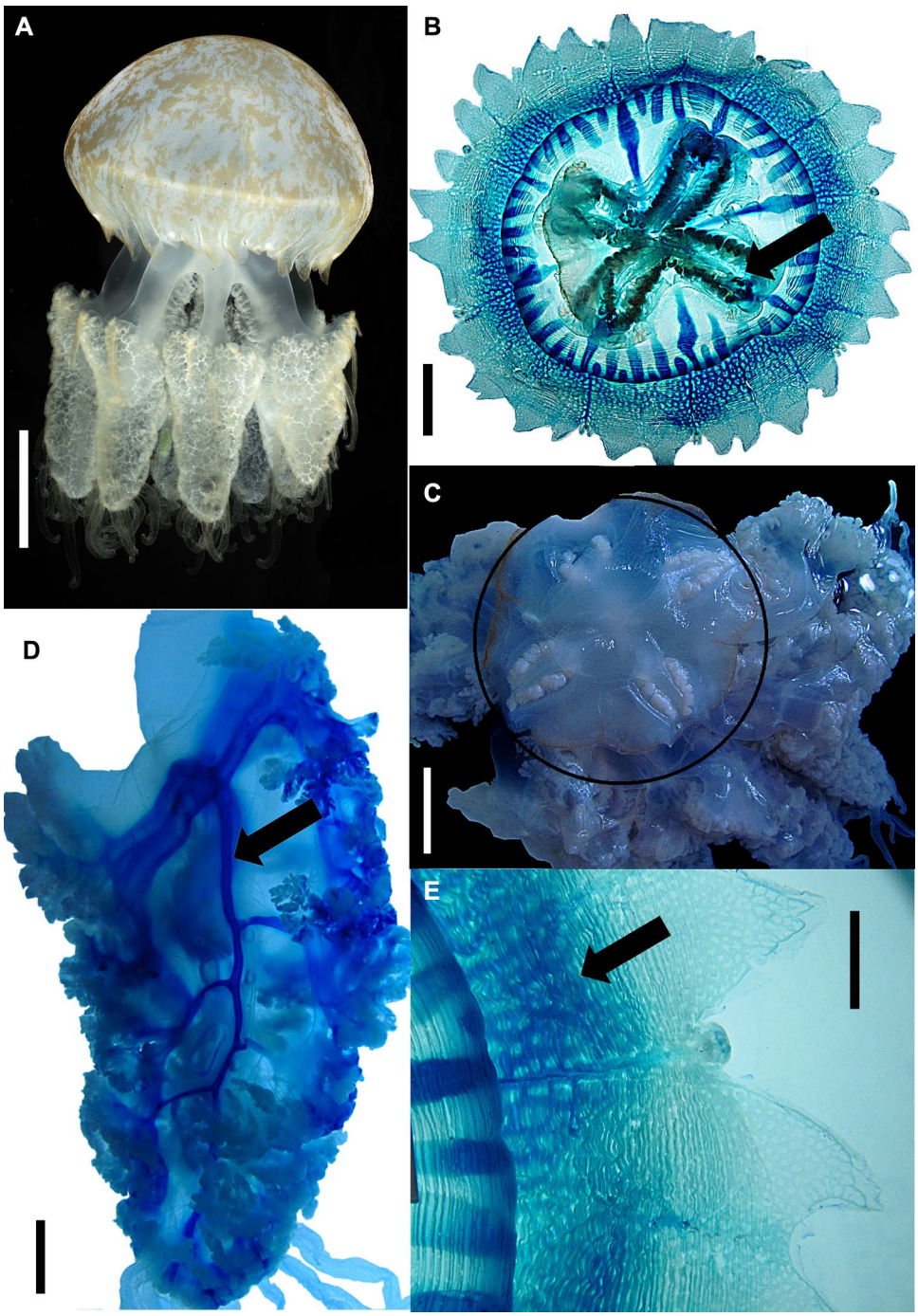

Fig. 2 *Lychnorhiza lucerna,* adult medusa in side view, scale bar 3 cm, image from AE Migotto (**a**). Subumbrellar view of umbrella (oral arms removed). Note umbrellar canals injected with methylene blue. Arrow indicating the cruciform stomach, from which gut contents were extracted by rinsing, scale bar 5 cm (**b**). Oral arms inserted in the oral disc (circle), scale bar 3 cm (**c**). Oral arm with oral canals stained, arrow indicating the central canal, scale bar 1 cm (**d**). Detail of umbrellar margin, with blue stain, arrow indicating umbrellar canals, scale bar 1 cm (**e**)

processes in rhizostome medusae are available in Lee et al. (2008) and Nagata et al. (2016).

To quantify the possible loss of captured prey during storage, the formaldehyde solution around some of the preserved animals ($n = 7$) was filtered. The plastic storage bags were washed over a 45-µm sieve. Prey items were quantified in all body regions of seven specimens: oral arms, oral disc, cruciform central stomach, and umbrellar canals (Fig. 2a–e). Prey were identified to the lowest possible taxonomic level with the aid of a stereomicroscope. For these seven individuals, total ingestion (G) was considered as the total number of prey items counted in all these body regions.

For dissection, the oral arms and oral disc were removed by cutting the four pillars of the oral disc (Fig. 2). Methylene blue was injected into the umbrellar and oral-arm canals to facilitate dissection (Fig. 2b, d). To quantify prey in the oral arms, the external surfaces and then the internal canals were examined. The oral disc of rhizostomes is a thick structure that connects the four pairs of oral arms to the bell by four pillars inserted at the tips of the cruciform stomach (Fig. 2c). The four large canals of the oral disc and the complex canal system of the umbrella were dissected and the prey were counted with the aid of the stereomicroscope.

In the bell, the cruciform stomach was excised from the subumbrellar side by cutting around the edges (Fig. 2b). The layer removed and the cavities of the cruciform stomach were rinsed and the contents were retained in a 45-µm sieve. The contents were kept in 50-mL plastic tubes for decanting. The cruciform stomachs were repeatedly rinsed (four to eight times) until no prey could be found in the 45-µm sieve. After 1 h of decantation, the supernatant in the tubes was discarded and the remaining 10% with the prey was stored in 4% formaldehyde solution. This sample was termed "extracted gut contents" and the prey items in the contents were counted in a Bogorov chamber with the aid of a stereomicroscope. After prey extraction, the pleated walls of cruciform stomach and the layer removed were examined with the aid of a stereomicroscope to quantify the number of prey that remained attached to the gastric cirri even after consecutive rinses. This sample was termed the residuals of the pleated walls. For the remaining animals ($n = 33$), only the prey extracted from the gut contents were quantified and the total ingestion (G) was estimated assuming that the extract from the gut content represented a constant proportion of G, as follows in the results.

Diet composition, prey selectivity, and ontogenetic changes in feeding parameters

Parameters of dietary diversity from the extracted from gut contents of 40 individuals were calculated as the number of prey taxa, the proportions of dominant prey groups (calanoid copepods, non-calanoid copepods, non-copepod crustaceans, and non-crustaceans) and as the Shannon-Weaver diversity index (H'). Prey selectivity was estimated by the index "C" of Pearre (1982), which is commonly used in the studies of jellyfish (e.g., Purcell 1989). The significance of "C" was tested by a x^2 analysis of a 2×2 contingency table constructed with prey densities in situ (org. m^{-3}) and their abundance in the extracted from the gut contents. Values of "C" range from – 1 to 1, reflecting the magnitude of this prey selection, with 0 equaling no significant selection. Prey selectivity was evaluated only for taxa quantitatively sampled by our plankton net, thus excluding prey items < 200 µm (e.g., copepod nauplii and bivalve veligers).

To evaluate whether changes in medusa body size were related to changes in diet parameters (e.g., prey composition and prey-selectivity patterns), these last were used as dependent variables against wet weight (g) in simple and multiple linear-regression analyses. Bell diameter was transformed to wet weight (WW, g) by applying equations described for *L. lucerna* by Nogueira Júnior and Haddad (2006) as: $WW = 0.1266\ (Bd)^{2.9514}$, where Bd bell diameter (cm). The dependent variables used in regression analyses included: (1) total ingestion, (2) number of taxa in the diet, (3) proportions of dominant prey groups; (4) Shannon-Weaver diversity index; (5) "C" selectivity index. Prior to all regression analyses, the assumptions of normality and homoscedasticity were tested, and when necessary, data were $\log_{10}$-transformed.

Copepod daily ration (DR)

Parameters of ingestion rates (copepod daily ration and daily carbon ration) were calculated from the estimations of total ingestion (G). The daily ration (copepods eaten medusa^{-1} day^{-1}) was estimated as: $DR = G_{cop} \times 24\ h \times DT^{-1}$, where G_{cop} total number of copepods ingested and DTdigestion time (h). Copepod digestion times estimated by Larson (1991) for *Stomolophus meleagris* were applied here. However, because digestion times are strongly temperature-dependent, these values were adjusted to the temperatures at our sampling sites. The temperature effect on a physiological rate, such as the digestion times, can be expressed as the coefficient Q_{10} (Martinussen and Båmstedt 2001), and we utilized a $Q_i = 2.08$, calculated by Purcell (2009) for the effect of temperature on the digestion times of three scyphozoan species. Therefore, the temperature-adjusted digestion rates (Dr_2) (inverse of digestion times, 1/DT) were estimated as: $Dr_2 = Dr_1 \times Q_{10}^{\frac{(T_2 - T_1)}{10^\circ}}$, where Dr_1 are the digestion rates from Larson (1991) and T_2 and T_1 are, respectively, the temperatures at our sampling sites and the temperatures recorded by Larson (1991). All digestion times calculated by Larson (1991) and the temperature-adjusted values used here were included in Online Resource 2.

Multiple linear regression analyses were performed to explore possible relationships between DR as the dependent variable, and wet weight (g) and prey density (copepods m^{-3}) as predictors. To compare *L. lucerna* DR with those of other scyphomedusae, we plotted the linear regression described by Purcell (2009) along with our data. Because the variation in DR of *L. lucerna* was not explained by the variation in copepod field density, we applied the mean copepod field density of this study as a fixed value (3863 copepods m^{-3}) to equations described by Purcell (2009).

Daily carbon ration (DCR)

We calculated the DCR as mg of carbon ingested medusa^{-1} day^{-1}, including prey items that represented < 99% of their diet. The carbon content of each prey item is listed in Online Resource 2. These carbon-content values were applied to the specific daily ration and temperature-adjusted digestion times were used to estimate DCR. Statistical analyses were performed using R (R Development Core Team 2011) and plots were constructed in Sigma-Plot (Systat Software, Inc.).

Results

Allocation of prey items in the body regions

To establish the percentage of total ingestion that each body part contributed, we quantified prey items in all body regions in seven individuals. Prey items counted from the extracted from the gut content equaled a mean of 69.8% (SE = ± 5.9) of total ingestion (Fig. 3). The number of prey found in the formaldehyde solution around seven animals was low (mean 2.5% ± 2.3) compared to the total prey ingested. Small proportions of prey were found on the oral arms, on the oral disc, and least in the umbrellar canals (Fig. 3). Most prey (> 90%) were counted in digestive body regions, the extract from the contents of the gut and, to a lesser extent, from a visual inspection of the pleated walls of cruciform stomach and of the oral disc, which are both covered with gastric cirri (Fig. 3). Although most prey were found in the digestive body regions, the proportions of major prey groups were similar among the five body regions for calanoid copepods (Kruskal–Wallis $\chi^2 = 2.73$, $df = 4$, $p = 0.60$), non-calanoid crustaceans (Kruskal–Wallis, $\chi^2 = 0.98$, $df = 4$, $p = 0.91$), and other prey (Kruskal–Wallis, $\chi^2 = 2.92$, $df = 4$, $p = 0.57$). Because each body region contained similar proportions of these prey groups, for the 33 individuals of which only the extract from the gut content (EGC) was quantified, the total ingestion (G) was assumed to be: $G = (\text{EGC } 69.8^{-1}) \times 100$.

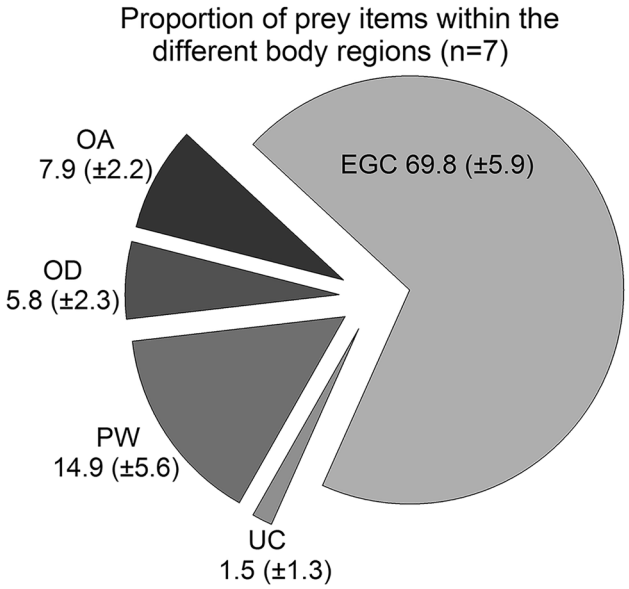

Fig. 3 Proportion of prey items (% ± SE) in the cavities of *Lychnorhiza lucerna* ($n = 7$). *EGC* extracted gut contents from central stomach, *OA* oral arms, *OD* oral disc, *PW* pleated walls of central stomach, *UC* umbrellar canals

Diet composition, prey selectivity, and ontogenetic changes in feeding parameters

We quantified the gut contents of 40 medusae, ranging from 5 to 30 cm in bell diameter (WW = 14–2897 g). A total of 69,049 prey items belonging to 43 taxa were found (Table 2). The predominant items were calanoid copepods (53.7%), particularly of the genera *Temora, Acartia,* and *Paracalanus*, together with cyclopoid (15.1%) and poecilostomatoid (11.4%) copepods, bivalve veligers (8.4%), and diatoms (4.3%) constituted > 90% of items found. All copepod prey items totaled > 80% of prey found. Some prey items were in an advanced state of digestion, allowing identification only to major taxonomic group, such as calanoids or harpacticoid copepods, which represented ~ 17% of quantified prey items (Table 2). For some highly digested copepods (e.g., *Temora turbinata* and *Acartia* spp.), identification to genus or species was often possible, because of their characteristic body shape.

The total ingestion ranged from 17 to 12,138 prey items medusa^{-1}. Regression analysis demonstrated that G was significantly related to medusae wet weight (Fig. 4a). The number of taxa per medusa ranged from 7 to 31, but was not significantly related to medusae wet weight (Fig. 4b). Although the proportions of non-calanoid copepods (mean ± SE = 22.57% ± 12.89) and non-copepod crustaceans (12.74% ± 12.94) were not significantly linearly related to medusae wet weight, the proportion of calanoid copepods increased with increasing medusae wet

Table 2 Composition and mean abundance (% ± standard deviation) of prey items found in *Lychnorhiza lucerna* from the South Brazil Bight

Prey item	Mean relative abundance of prey item per sampling occasion ± (SD)					Total relative abundance	Frequency of occurrence
	Paranaguá	Cananéia I	Cananéia II	Cananéia III	São Sebastião		
Calanoida						53.7	100
Temora turbinata	29.4 (10.1)	11.5 (8.5)	6.9 (8)	20.6 (11.6)	14.8 (8)	16.3 (9.7)	95
Paracalanus spp.	25.2 (15.4)	8.11 (4.7)	2.5 (2.1)	19.8 (8.9)	13.5 (8.6)	12.7 (12.6)	95
Acartia tonsa	13.4 (16.4)	5.3 (5.4)	3 (3.8)	2.7 (3.3)	6 (7)	7.1 (9)	97.5
Pseudodiaptomus acutus	0	0.04 (0.1)	1.7 (3.5)	0	3.2 (5.6)	3.7 (7.5)	40
Acartia lilljeborgii	0.6 (1.2)	1.2 (1.9)	0.4 (0.5)	0.04 (0.1)	7.9 (14.6)	0.4 (6)	47.5
Temora stylifera	0.15 (0.3)	0.02 (0.07)	0.2 (0.6)	0	0	0.02 (0.3)	10
Copepodites	1.1 (1.6)	4.5 (5.9)	27.4 (22.2)	3.4 (3.1)	4.5 (2)	6.8 (13.2)	82.5
Nauplii	0.04 (0.1)	2.5 (5.8)	6 (11.3)	1.4 (3.3)	0	0.4 (6)	42.5
Small calanoids (< 0.4 mm)	0.4 (0.6)	3.6 (2.7)	4.4 (2.8)	10.3 (4)	11.6 (9.4)	5.4 (5.7)	85
Medium calanoids (< 0.4–1 mm)	0.3 (0.4)	4.1 (2.1)	1.3 (1.7)	4.4 (4)	6.3 (5.2)	3.7 (3.4)	75
Large calanoids (> 1 mm)	0.1 (0.1)	0.6 (1)	0.2 (0.3)	0.1 (0.2)	1.7 (3.3)	0.4 (1.4)	52.5
Cyclopoida						15.1	95
Oithona spp.	9.2 (6.2)	5.1 (7.1)	8.9 (6.5)	27.1 (7.8)	12.1 (8.9)	15.07 (10)	95
Poecilostomatoida						11.4	97.5
Oncaea spp.	2.9 (3.5)	17.5 (14.6)	4.5 (6.3)	0.2 (0.4)	1.5 (1.6)	10.5 (11.2)	82.5
Corycaeus spp.	0.7 (0.9)	1.1 (2.2)	0.4 (0.9)	0.2 (0.2)	0.2 (0.3)	0.4 (0.2)	55
Poecilostomatoida sp. 1	0.98	0.07 (0.2)	0.02 (0.06)	0	0.01 (0.04)	0.3 (0.9)	12.5
Harpacticoida						0.6	72.5
Euterpina acutifrons	1.1 (0.4)	0.3 (0.4)	0.7 (0.9)	0.4 (0.4)	0.5 (0.8)	0.5 (0.6)	70
Microsetella sp.	0	0.07 (1)	0	0.01 (0.02)	0	0.04 (0.4)	15
Harpacticoida sp. 1	0	0.15 (0.4)	0.07 (0.2)	0	0.01 (0.04)	0.06 (0.2)	12.5
Bivalve veliger	10.1 (9.1)	13 (8.6)	8.6 (7.8)	6.3 (7)	5.4 (7.6)	8.4 (0.8)	92.5
Diatoms	0.01 (0.01)	11.1 (14.2)	8 (6.8)	0.3 (0.5)	3.9 (3.9)	4.3 (9.7)	60
Tintinnidae	0	6.5 (11.8)	5 (4.5)	0	0	1.7 (7.6)	40
Unidentified eggs	0.3 (0.4)	1.7 (3.2)	0.3 (0.6)	0	0.5 (1.2)	1.5 (0.9)	32.5
Oikopleura dioica	0.6 (0.4)	3 (5)	3 (4)	0.1 (0.2)	0.01 (0.02)	0.9 (3.5)	72.5
Gastropod veliger	0.2 (0.4)	1.3 (1.2)	1.5 (2.5)	0.2 (0.2)	0.4 (0.7)	0.6 (0.2)	65
Penilia avirostris	0.9 (0.8)	0.1 (0.2)	0.4 (0.9)	2.1 (1.8)	0.1 (0.2)	0.6 (1)	52.5
Brachyuran zoeae	1 (0.6)	0.04 (0.1)	0.4 (0.7)	0.01 (0.02)	0.01 (0.04)	0.2 (0.5)	40
Parasagitta friderici	0.5 (0.5)	0.04 (0.07)	0.6 (1.7)	0.02 (0.04)	1.6 (2.5)	0.2 (1.2)	40
Ostracoda	0	0.6 (1.5)	0.4 (0.6)	0.02 (0.05)	3.1 (4.4)	0.1 (2)	27.5
Fish eggs	0.04 (0.08)	0.7 (2.1)	0.31 (0.6)	0	0	0.1 (1.2)	17.5
Podon sp.	0.01 (0.02)	0.02 (0.06)	1.1 (2.9)	0	0	0.1 (1.2)	10
Polychaete larvae	0.2 (0.4)	0.08 (0.1)	0.3 (0.5)	0	0.07 (0.2)	0.1 (0.3)	32.5
Gammaridae	0.02 (0.04)	0.02 (0.07)	0.3 (0.9)	0	0	0.05 (0.4)	12.5
Cyphonauta larvae	0	0.07 (0.1)	0	0	0	0.05 (0.07)	10
Bivalve veliger	0.1 (0.2)	0.02 (0.06)	0	0	0.5 (0.9)	0.04 (0.4)	29.6
Hyperiidae	0	0.01 (0.03)	1 (1.9)	0	0	0.04 (0.8)	10
Ceratium spp.	0	0.06 (0.2)	0	0.01 (0.04)	0	0.03 (0.1)	10
Decapoda	0.1 (0.2)	0	0	0	0	0.02 (0.2)	20
Liriope tetraphylla	0.1 (0.1)	0	0	0	0.01 (0.04)	0.01 (0.05)	10
Isopoda	0	0.01 (0.03)	0	0	0.07 (0.2)	0.01 (0.07)	5
Polychaeta	0.06 (0.1)	0	0	0	0	0.01 (0.06)	5
Fish larvae	0.02 (0.04)	0	0	0	0	0.003 (0.02)	5
Siphonophora	0.02 (0.05)	0	0	0	0.07 (0.17)	0.003 (0.07)	5

Table 2 (continued)

Prey item	Mean relative abundance of prey item per sampling occasion ± (SD)					Total relative abundance	Frequency of occurrence
	Paranaguá	Cananéia I	Cananéia II	Cananéia III	São Sebastião		
Mysida	0.01 (0.04)	0	0	0	0	0.001 (0.02)	2.5
Prey Number for each date	12349	24496	5931	23795	2478	69049	

Proportions were calculated by sampling occasion, and grouped in overall values of total relative abundance and frequency of occurrence

weight, whereas the proportion of non-crustacean prey decreased with increasing medusae wet weight (Fig. 5a). Shannon-Weaver diversity Index (H') of the *L. lucerna* diet decreased with increasing medusa wet weight (Fig. 5b).

The proportions of the ten most abundant prey items from the environment samples were generally similar to the proportions found in gut contents, although a few consistent patterns were observed. Some taxa found in the field were absent from the gut contents, such as echinoderm larvae, the

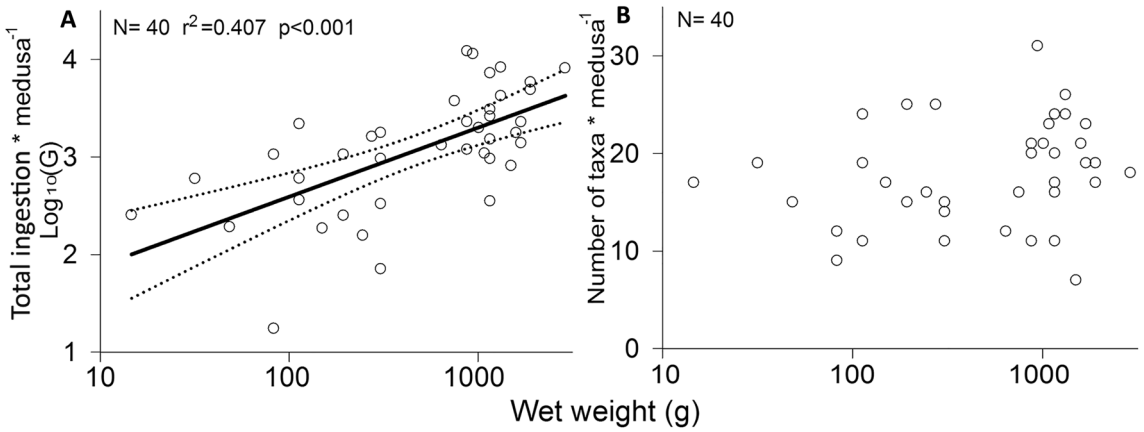

Fig. 4 Number of prey items from medusae of *Lychnorhiza lucerna* ($Log_{10}G$) according to medusa size as wet weight (in log_{10} scale). Linear regression (solid line) and 95% confidence interval (dashed lines) The regression line shown is (±95% confidence limits in parentheses) $Log_{10}(G) = 1.18\ (\pm 0.38) + 0.71\ (\pm 0.13) \times Log_{10}WW(g)$ (**a**). The number of taxa found in medusae of *L. lucerna* was not significantly related to medusa wet weight (**b**)

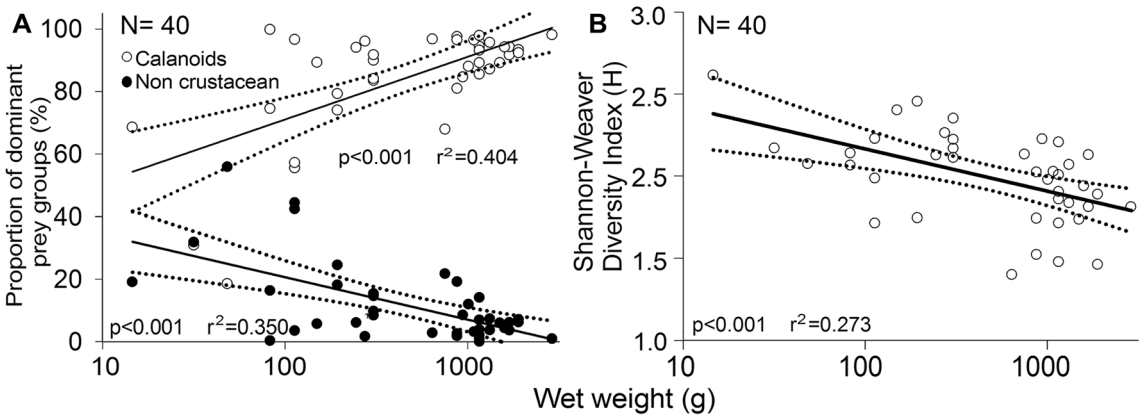

Fig. 5 Proportions of prey groups (calanoid copepods and non-crustacean prey) with significant relationships with *Lychnorhiza lucerna* medusa wet weight (g). Regression lines shown are (±95% confidence limits in parentheses): %Calanoids = 30.91 (±10.80) + 20.07 (±3.96) × Log_{10}WW (g), %Non-crustaceans = 47.83 (±8.18)–13.58 (±3.00) × Log_{10}WW (g) (**a**). The Shannon's H' decreased with medusa wet weight (**b**). The regression line shown is (±95% confidence limits in parentheses): Shannon's $H' = 2.68\ (\pm 0.19) – 0.26\ (0.07) \times Log_{10}WW$ (g)

sergestoid shrimp *Belzebub faxoni,* the copepods *Eucalanus* sp. and *Labidocera* sp., and sipunculid larvae. Curiously, some taxa found in the medusae were absent in the field, such as the copepods *Temora stylifera* and *Microsetella* sp., isopods, and hyperiids. The proportions of calanoid copepods (*Acartia* spp., *Temora turbinata*, and *Paracalanus* spp.) were sometimes higher in the gut contents and other times in the field (Fig. 6). The cladoceran *Penilia avirostris,* the chaetognath *Parasagitta friderici*, and the copepods *Euterpina acutifrons* and *Pseudodiaptomus acutus*, when relatively abundant in the field, were found in lower proportions in the gut contents (Fig. 6). Bivalve veligers, copepodites, and copepods of the genera *Oithona, Oncaea*, and *Corycaeus,* when relatively abundant in gut contents, were present in lower proportions in the field (Fig. 6).

Prey-selectivity values (Pearre's "*C*") for the copepods *Temora turbinata, Acartia* spp., *Paracalanus* spp., *Pseudodiaptomus acutus,* and *Euterpina acutifrons* (Fig. 7a–e) ranged from –0.3 to 0.3. For these copepod species, patterns of prey selectivity were constant over the range of medusa body sizes. For *T. turbinata*, most values were on the positive side, indicating positive selectivity, whereas, for *P. acutus,* most values indicated negative selectivity (Fig. 7a, d). For *Parasagitta friderici, Oikopleura dioica, Penilia avirostris,* and brachyuran zoeae, "*C*" values tended to decrease with increases in medusa wet weight (Fig. 7f–i; Online Resource 3).

Daily ration (DR)

The DR of *L. lucerna* ranged from 110 to 102,871 copepods ingested medusa^{-1} day^{-1}. Significant relationships were found between DR and medusa wet weight ($\log_{10}$ transformed), whereas prey density (as $\log_{10}$ total copepod density) were not significantly related to DR (Table 3). Parameters of linear regression of *L. lucerna's* DR along with of the other four scyphozoan species in the Fig. 8 are listed in Table 3.

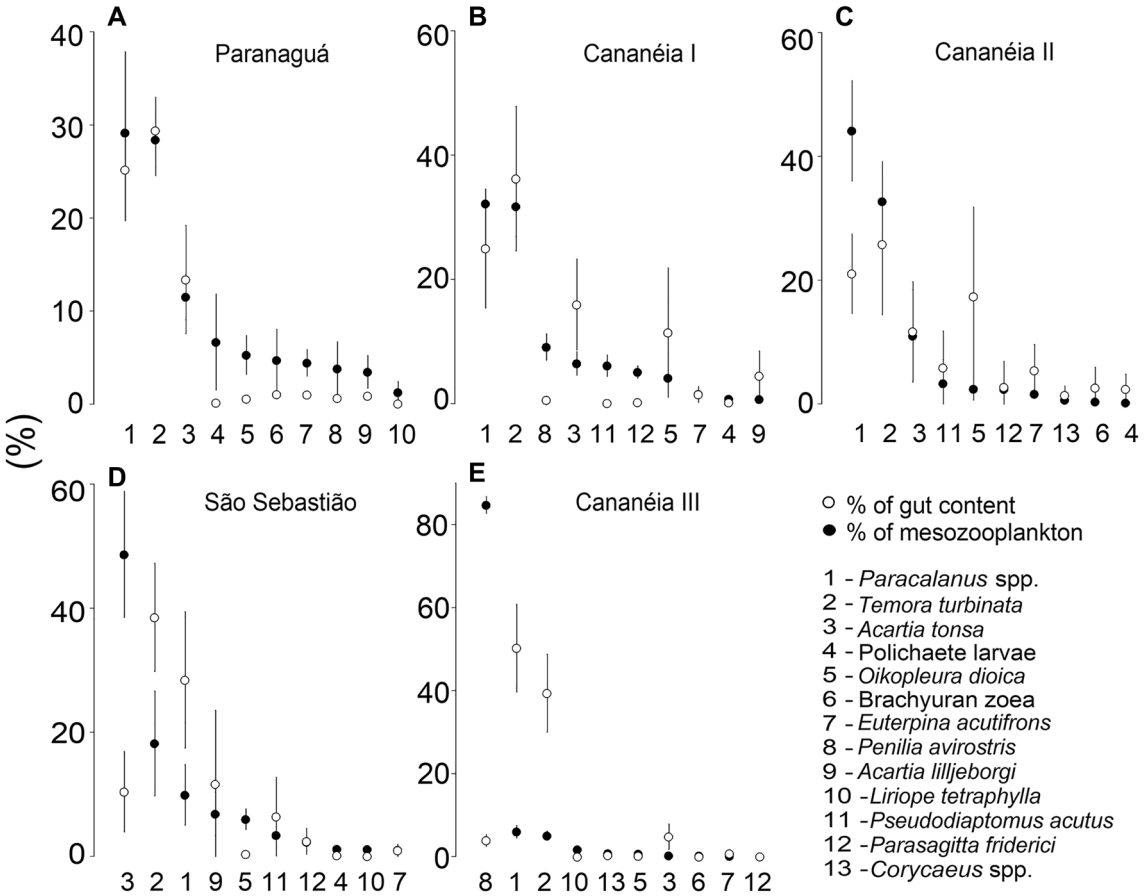

Fig. 6 Composition of mesozooplankton in surrounding water and in the guts of *Lychnorhiza lucerna.* Graphs show mean ± standard error of the ten most abundant prey items, in decreasing order of abundance in mesozooplankton samples from each location. Numbers of gut-content samples/mesozooplankton samples are: 8/3 for Paranaguá, 14/3 for Cananéia I, 6/4 for São Sebastião, 6/3 for Cananéia II, and 6/4 for Cananéia III. The numbers of gut-content and plankton samples per sampling site are listed in Table 1

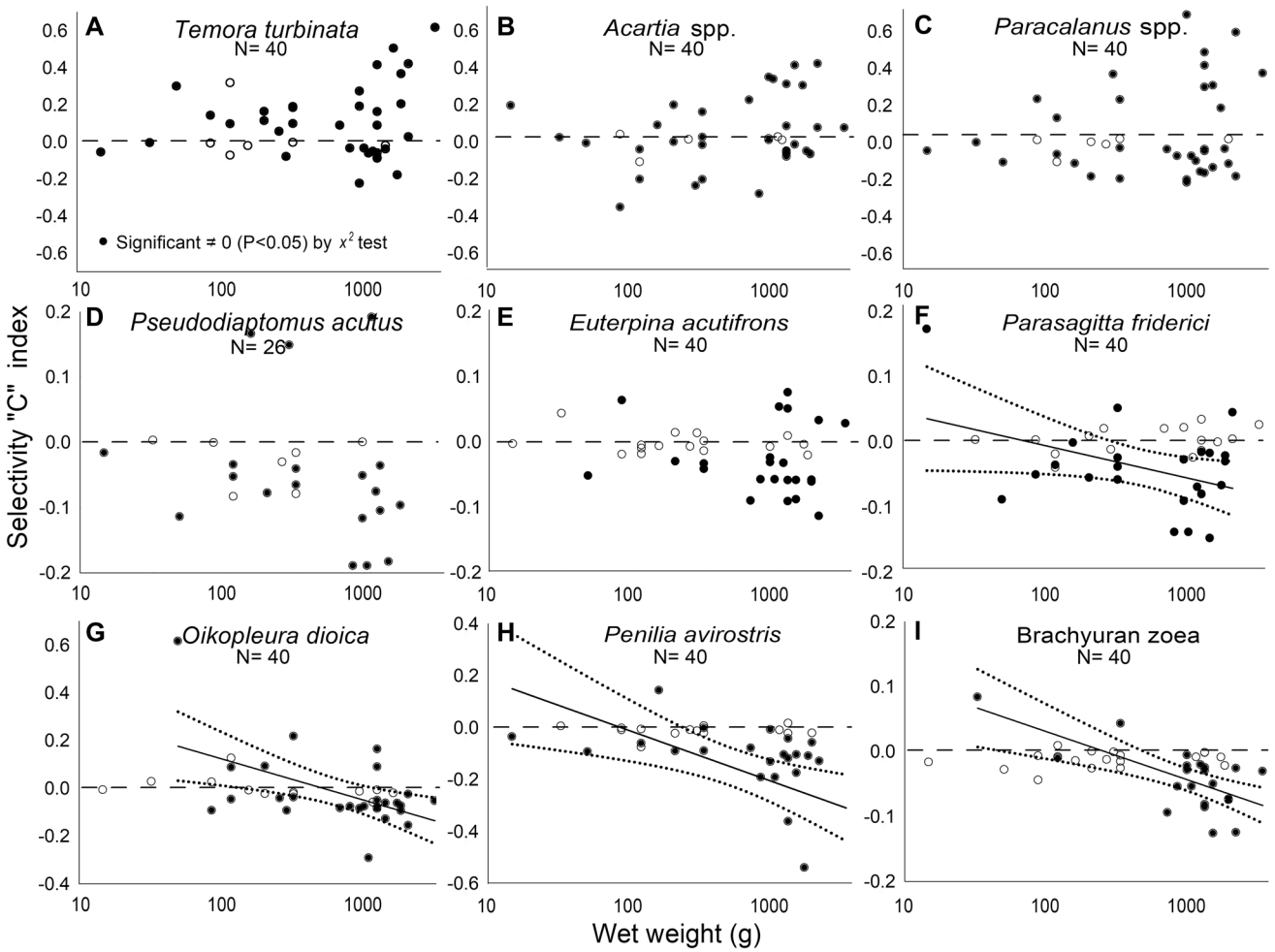

Fig. 7 Selectivity index "*C*" of Pearre (Pearre Jr. 1982) for mesozooplankton prey in different sizes of *Lychnorhiza lucerna* medusae. The dashed straight line is a reference for selectivity "*C*" = 0. Positive or negative values indicate selectivity at a rate above or below environmental concentration. Solid dots are significant values of "*C*" ($p < 0.05$) by x^2, and open circles are non-significant values. The solid straight lines indicate linear regressions, and the dotted lines show the 95% confidence intervals of the estimated models. The data for the regression lines are listed in Online Resource 3

Daily carbon ration (DCR)

Total DCR ranged from 0.48 to 175.77 mg C medusa^{-1} day^{-1} (Fig. 9). Calanoid copepods were the main prey items, with a mean contribution of 63.41% of the total DCR. The proportions of calanoid copepods to total DCR increased with medusa size (Fig. 9). The mean contributions of remaining prey of DCR were lower: non-calanoid copepods 11.15%, non-copepod crustaceans 4.18%, and non-crustaceans 2.08%. Parameters of linear regressions of DCR and wet weight for total ingestion and for the ingestion of prey groups are presented in Online Resource 4.

Discussion

Medusa dissection and quantification of total ingestion (*G*)

Our sampling protocol resulted in negligible loss of prey during the storage period, since a few prey items were present in the water surrounding the animals. The lack of a large central mouth in *L. lucerna* and other rhizostome medusae minimizes the loss of prey during storage. Quantification of prey in all body regions demonstrated that the time-consuming dissection of non-digestive regions, including the oral

Table 3 Parameters of multiple linear-regression analyses for *Aurelia* spp., *Cyanea capillata,* and *Chrysaora chesapeakei,* taken from Purcell (2009), and *Lychnorhiza lucerna* from this study

Species (number examined) and location	Wet weight (g) range, *t* and *P*	Prey density (number m^{-3}) range, *t* and *P*	Temperature (T in ºC), *t* and *P*	Daily Ration *DR* (copepods eaten day^{-1}) rate range	Multiple R^2, F, *P* and SE	Predictive equation
Lychnorhiza lucerna (40) South Brazil Bight[a]	14–2897 $t = 4.721$ $P < 0.001$	2795–5704 $t = 0.610$ $P = 0.546$	18.8–21.5 $t = 0.072$ $P = 0.943$	191–166,288	$r^2 = 0.474$ $F_{2, 37} = 34.26$ $P < 0.001$ SE 0.484	$Log_{10}DR = 0.807*Log_{10}WW + 1.935$
Aurelia coerulea (68) Inland Sea of Japan[b]	48–1440 $t = 8.451$ $P < 0.001$	830–13,990 $t = 3.288$ $P = 0.014$	16.2–24.8 $t = 0.626$ $P = 0.950$	312–96,576	$R^2 = 0.705$ $F_{3, 64} = 77.703$ $P < 0.001$ SE 0.283	$Log_{10}FR = 1.189*Log_{10}WW + 0.346*Log_{10}PD - 0.314$
Aurelia sp.*6* (144) Palau[c]	3–1139 $t = 22.674$ $P < 0.001$	2556–74,222 $t = 2.825$ $P = 0.005$	31 No data	34–28,631	$R^2 = 0.787$ $F_{2, 141} = 260.97$ $P < 0.001$ SE 0.285	$Log_{10}FR = 0.802*Log_{10}WW - 0.153*Log_{10}PD + 2.11$
Chrysaora Chesapeakei (386) Chesapeake Bay, USA[d]	0.007–146 $t = 12.052$ $P < 0.001$	400–232,218 $t = 8.757$ $P < 0.001$	22.9–29.1 $t = 5.076$ $P < 0.001$	1–17,011	$R^2 = 0.455$ $F_{4, 381} = 106.55$ $P < 0.001$ SE 0.359	$Log_{10}DR = 0.367*Log_{10}WW + 0.258*Log_{10}PD + 1.447$
Cyanea capillata (156) Alaska, USA[e]	1.4–1642 $t = 5.702$ $P < 0.001$	203–10,211 $t = 6.255$ $P < 0.001$	14 No data	12–5148	$R^2 = 0.284$ $F_{2,152} = 30.4$ $P < 0.001$ SE 0.475	$Log_{10}DR = 0.389*Log_{10}WW + 0.670*Log_{10}PD - 0.512$

The analyses assessed the relationships between wet weight (WW), prey density (PD), and daily ration (DR) as number of copepods eaten day^{-1}. Original data were taken from: [a]this study, [b]Uye and Shimauchi (2005), [c]Dawson and Martin (2001), [d]Purcell (1992), [e]Purcell (2003)

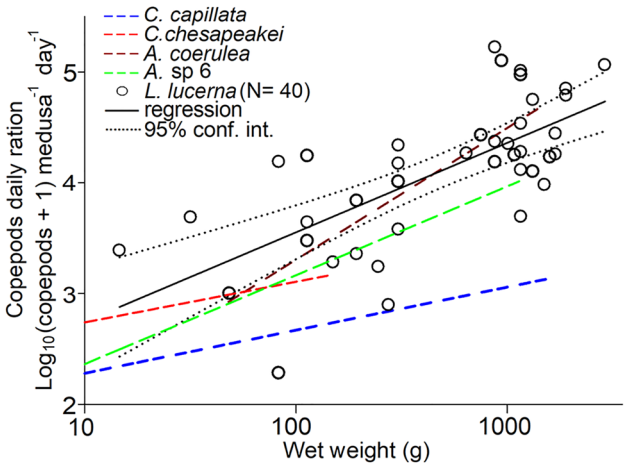

Fig. 8 Copepod daily ration (DR, log_{10} copepods +1 eaten day^{-1}) of scyphomedusae from field gut contents vs. medusa wet weight. For *Aurelia coerulea*, *A.* sp. 6, *Cyanea capillata*, and *Chrysaora chesapeakei,* equations described by Purcell (2009) (see Table 3) were plotted using the mean prey density (3863 copepods m^{-3}) found in the present study. Empty circles are individuals of *Lychnorhiza lucerna* ($N = 40$). The solid black line is the linear regression for *L. lucerna,* and the dashed black line is the 95% confidence-interval prediction error

arms and umbrellar canals that contained < 10% of total prey ingested, could be avoided. The small number of prey in the umbrellar canals is a possible consequence of the complete digestion of prey in the central stomach. The small number of prey in the oral arms illustrates the rapid transport toward the cruciform stomach, which, for *L. lucerna* (5–15 cm), required only 5–10 min (RMN, pers obs).

Because ~ 90% of prey items were found in digestive cavities (e.g., pleated walls, oral disc), analyses of these samples are necessary for the estimations of total ingestion. Although storage of large-bodied jellyfish can be a problem for space-limited laboratories, extraction of gut contents of animals in situ is not advisable for two reasons. First, handling of the medusae triggers mucus release (e.g., Larson 1991; Graham et al. 2003), which agglutinates prey into opaque balls of mucus and makes prey quantification much more laborious. Mucus is not usually found on oral arms of *L. lucerna* in the field, nor in other species (e.g., Larson 1991). By preventing clumping of prey, subsampling of gut-content samples is suitable, since a biased distribution is avoided (van Guelpen et al. 1982). Second, the gastric cirri of the cruciform stomach firmly attach to the prey and inefficient rinsing of the gastric cavity can lead to underestimation of total ingestion. In addition to the extraction, it is necessary to retain prey items with a sieve of appropriate mesh size, or directly analyze the body cavities without rinses. In this study, microzooplankton, such as heterotrophic ciliates and flagellates, that can represent an important fraction gut contents and nutritional sources of some semaeostome and rhizostome medusae (Stoecker et al. 1987; Hays et al. 2011), proved to

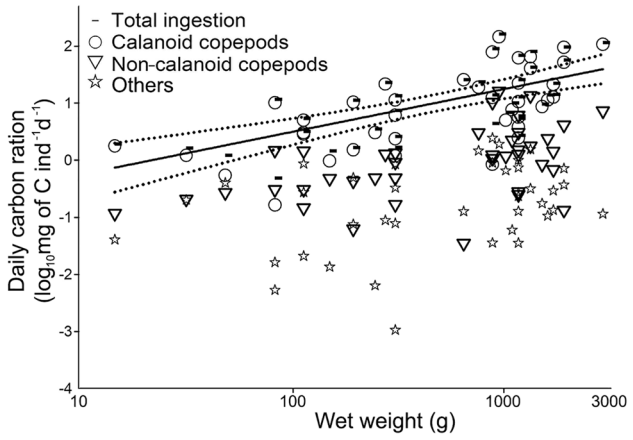

Fig. 9 Daily carbon ration (mg C ind.$^{-1}$ day^{-1}) in relation to *Lychnorhiza lucerna* medusa wet weight (g) for total prey ingested and for groups of prey (calanoid copepods, non-calanoid copepods, non-copepod crustaceans, and non-crustaceans). Values were calculated applying temperature-corrected digestion times, over species-specific carbon-content values for prey items. The linear regression and 95% confidence intervals were calculated for medusa wet weight as a predictor of total ingestion. Parameters of linear regression are provided in Online Resource 4

be unimportant. Mesozooplankton were the major prey of *L. lucerna*; however, it is still necessary to investigate the role of microzooplankton in the species' diet by other methods that better quantify microzooplankton.

Prey quantification methods are often poorly described and vary among studies of large medusae. For example, 12% of studies did not mention how prey was extracted from animals, 29% extracted the prey in situ, and 59% preserved the animals and dissected them under a stereomicroscope (Online Resource 1). Adequate collection is critical to obtain reliable gut-content data for delicate and fragile jellyfish. Careful collection methods should be applied, such as sampling in surface waters using dip nets or buckets (Larson 1991; Purcell 2018), or by scuba diving (e.g., Riascos et al. 2014). Because collections performed with nets are subject to loss of gut contents (Barz and Hirche 2005) and cod-end feeding (Matsakis and Conover 1991), data obtained using these methods are only of qualitative significance.

Studies over large spatial and temporal scales require larger numbers of samples. Because large-bodied rhizostome medusae ingest thousands of small prey individuals, gut content-based studies are extremely time-consuming and impracticable for large species such as *Nemopilema nomurai*. The tedium of this method can be mitigated by analyzing the extracted from the gut contents, applying protocols of zooplankton subsampling (van Guelpen et al. 1982). Subsampling allows the analyses of larger numbers of samples, which, in turn, could provide a broader view of the trophic impacts of jellyfish populations.

Diet composition, prey selectivity, and ontogenetic changes in feeding parameters

In general, the feeding habits of rhizostome species are largely unknown, with the dietary composition being quantified for only 5 (Table 4) of 89 known species in this group (Jarms and Morandini in press). Those studies indicated that mesozooplankton is the major food source (Fancett 1988; Larson 1991), although the percentages of prey items differ widely among species (Table 4). Predation on fish eggs and larvae is common in Rhizostomeae medusae when these prey are available (Graham et al. 2003; Padilla-Serrato et al. 2013; Álvarez-Tello et al. 2016). In *L. lucerna*, fish eggs and larvae were found in lower proportions, probably because these items were rare in the environment. Among rhizostome medusae, *L. lucerna* ingested mostly copepods (81%), followed by *P. haeckeli* (33%), *P. punctata* (23%), and other

Table 4 Percentage (%) of prey items of the gut contents of rhizostome medusae; (−) indicates significant negative selectivity and (+) indicates significant positive selectivity for this prey item

	Mollusk veligers	Diatoms	Tintinnids	Fish eggs	Cladocerans	Cirriped larvae	Copepods	Decapod larvae	Other
Lychnorhiza lucerna[a]	9	4.3	1.7	0.1	0.6 (−)	0	80.8	0.4	3
Stomolophus meleagris[b]	71.2 (+)	0	9.3	< 1	< 1	< 1	7.3 (−)	1	< 1
Stomolophus meleagris[c]	26.4	0	0	65.3	0.1	4.1	1.5	2	3
Stomolophus meleagris[d]	29.9	< 0.1	0.1	49.8	< 0.1	5.7	8.3	1.6	4.6
Cotylorhiza tuberculata[e]	6	85	5	0	0	0	3	0	0
Rhizostoma pulmo[e]	3	65	30	0	0	0	1	0	0
Phylorhiza punctata[f]	35	0	23	15	0	0	23	0	4
Pseudorhiza haeckeli[g]	0	0	0	40.8 (+)	4 (−)	1	34.8 (+*)	4.9	15

*The authors found positive selectivity for calanoid and harpacticoid copepods and negative selectivity for cyclopoid copepods

[a]This study, [b]Larson (1991), [c]Padilla-Serrato et al. (2013), [d]Álvarez-Tello et al. (2016), [e]Pérez-Ruzafa et al. (2002), [f]Graham et al. (2003) and [g]Fancett (1988)

species with < 10% (Table 4). *L. lucerna* ingested calanoid copepods in similar proportions to their availability, whereas *P. haeckeli* showed positive selection (Fancett 1988), and *S. meleagris* showed negative selection (Larson 1991; Álvarez-Tello et al. 2016). Other rhizostomes, like *C. tuberculata* and *R. pulmo,* feed mainly on non-evasive prey such as mollusk veligers, diatoms, tintinnids, and fish eggs, a pattern that is well established for *S. meleagris* (Table 4). This dietary diversity among rhizostome species may be a consequence of the high morphological diversity of the mouth arm structure, which, in turn, may be associated with different feeding mechanisms.

It is uncertain whether the early morphological development leads to a change in the species' feeding habits. The feeding habits of recently released *L. lucerna* ephyrae and young medusae (< 3 cm) remain unknown, except for laboratory observations of the ingestion of other scyphozoan ephyrae (Carrizo et al. 2016) and food items provided in culture (*Artemia* nauplii, rotifers, and macerated clam gonad). Although the individuals analyzed here (> 4 cm bell diameter) already possessed the adult morphology and feeding mechanisms, the composition of their diet shifted from more general to one dominated by copepods, which constituted > 90% of the prey items and carbon source of larger animals. This explains the ontogenetic increase in the trophic level of *L. lucerna* revealed by stable-isotope analyses (Nagata et al. 2015). Patterns of ontogenetic changes in diet differ among scyphomedusae. While *L. lucerna* decreased the diversity of its diet during growth, other jellyfish, such as *Aurelia* sp., *Chrysaora plocamia*, and *S. meleagris* increased their dietary diversity, which may indicate different feeding strategies during the course of development (Graham and Kroutil 2001; Riascos et al. 2014; Álvarez-Tello et al. 2016). A comparison of these patterns should be analyzed with care, due to the lack of complementary evidences to the gut-content data and due to the existence of data for a few other scyphozoan species.

Increasing negative selection with the increase in body size was found for different types of prey, such as larvaceans, crab zoeae, and cladocerans (Figs. 7f–i). Negative selectivity for *Penilia avirostris* was clear; even when this cladoceran represented a high percentage of the zooplankton in the field (~ 80%), captures were low (~ 2% of prey items). Apparent negative selectivity for other prey should be evaluated with caution, because these were only in low abundance (or occasionally absent) in the field. Carr and Pitt (2008) suggested that the negative selectivity for crab zoeae by the rhizostome *Catostylus mosaicus* might be attributable to a possible ability of the zoeae to detect chemical signals in the water and avoid medusa predators. Post-encounter factors should also be evaluated further. It is unclear whether contact with several types of plankton items, such as diatoms, elicits a retention reaction in some cnidarians (Stoecker et al. 1987; Nagata et al. 2016). A possible selective discharge of nematocysts could explain the failure to capture certain types of prey (Purcell 1997).

During growth, the velocity of the feeding currents produced by bell pulsation increases, which presumably enables the medusa to capture more-evasive prey (e.g., calanoid copepods) (Costello and Colin 1994; Sullivan et al. 1994). Although the velocity of the feeding currents of larger scyphomedusae (> 20 cm bell diameter) has never been measured experimentally, smaller (< 10 cm) rhizostome medusae such as *P. punctata, Cassiopea* sp., and *L. lucerna* produce feeding currents between 8–15 cm s^{-1} (D'Ambra et al. 2001; Nagata et al. 2016). The calanoid copepods (*Temora, Paracalanus* and *Acartia*) co-occurring with *L. lucerna* reach velocities between 30 and 60 cm s^{-1} during their escape jumps (Buskey et al. 2002; Nagata et al. 2016). Although this suggests that these copepods could successfully escape from medusa predators (Costello and Colin 1994), even smaller *L. lucerna* ingest this kind of prey in similar proportions to their presence in the environment. The capture of rapidly moving copepods by medusae that produce slow feeding currents was demonstrated for *Aurelia* sp. and for *Chrysaora chesapeakei* (Sullivan et al. 1994; Ford et al. 1997). This can be explained, because even if escape speeds and accelerations were adequate to avoid certain predators, animals with limited detection abilities would be susceptible to predation (Fields and Yen 1997; Nagata et al. 2016). Thus, multiple features such as prey-detection abilities, reaction time, and handling efficiency should be considered to further evaluate predator–prey interactions.

Daily ration (DR)

The daily ration of copepods captured by *L. lucerna* was a function of body size, but was not significantly related to prey density [but see Purcell (2009)], probably because this parameter differed only slightly among sampling sites. When comparing daily ration among scyphomedusae, *Lychnorhiza lucerna* and *Aurelia coerulea* (from the Inland Sea of Japan) had the highest DR (Fig. 8). DR of *A. coerulea* exceeded the *L. lucerna* DR at larger medusa sizes (Fig. 8). *Aurelia* sp. 6 (from Palau) and *Chrysaora chesapeakei* (from the Chesapeake Bay, USA) had comparatively lower DR, but still higher DRs than *Cyanea capillata* (from Alaska, USA) (Fig. 8). DR of *L. lucerna* can be applied to investigate the species' predatory impact (PI) through the inclusion of data on predator and prey densities, as: PI=DR (D_{Pred} $D_{Prey}{}^{-1}$) × 100, where PI represents the percentage of prey standing stock consumed by the medusa population day^{-1}, D_{Pred}= predator density (org. m^{-3}), and D_{Prey}=copepod density (copepods m^{-3}) (Purcell 2003; Barz and Hirche 2005). Unfortunately, densities of *L. lucerna* have not been measured along the Brazilian coast. Nevertheless, Colombo et al.

(2003) estimated a density of 14 medusae 100 m^{-3} of *L. lucerna* (3–31 cm bell diameter, mode: 11 cm), by means of acoustic methods and net sampling, at the mouth of the Río de la Plata estuary. Zooplankton densities were not calculated along with predator densities by Colombo et al. (2003), but if we assume the copepod densities found by Viñas et al. (2002) at the same place (ranging from 2364 to 4233 copepods m^{-3}), that *L. lucerna* population would consume 6–12% of copepod standing stock day^{-1}. These predatory impacts represent a population of relatively small medusae (~ 150 g WW), and thus, the predatory impacts of larger medusae (> 1500 g), which occur annually along the coasts of Brazil and northern Argentina (Schiariti et al. 2008; Nagata et al. 2009), potentially would exert much higher predation pressure on the plankton population. The individual feeding rates calculated here are useful first assessments of the species' predatory impact and would serve as a more-realistic model for other rhizostome medusae [but see Larson (1991), García and Durbin (1993)]. The higher individual feeding rates of *L lucerna* than of other scyphomedusae highlight the potential of this species as a key consumer in southwestern Atlantic coastal environments, during its yearly periods of high abundances.

Daily carbon ration (DCR)

Rhizostome medusae have higher metabolic demands than semaeostome medusae on a wet-weight basis, but similar demands on a carbon-content basis (Purcell et al. 2010). DR of *L. lucerna* was similar to *Aurelia coerulea* medusae, but higher than *C. chesapeakei* and *C. capilatta* (Fig. 8). Assuming a conversion factor for carbon % of wet weight (C %WW) of 0.466 (as the mean of *Phyllorhiza punctata* = 0.46, *Nemopilema nomurai* = 0.6, and *Rhizostoma pulmo* = 0.34, from Purcell et al. 2010), the carbon content of *L. lucerna* individuals was estimated to range from 0.06 to 13.5 g. *L. lucerna* feeding rates as DCR (0.48–175.77 mg C day^{-1}) represented on average 1.23% (min−max ± SD: 0.09−9.32 ± 1.77) of the animal's body carbon content. The minimum carbon requirement on the basis of an animal's carbon content, calculated applying respiration rates and a respiratory quotient of 0.8 (Ishii and Tanaka 2006; Purcell et al. 2010), demonstrated that animals within this size range would require between 5.7 and 818.4 mg C day^{-1}. Thus, our DCR estimate explains, on average, only 17.32% (1.35−112.04 ± 22.37%) of the animals' minimum carbon requirement. Lower feeding rates than minimum carbon requirements were also found for *S. meleagris,* in a similar approach (Larson 1991). In this study, other potential carbon sources could not be quantified, such as dissolved and particulate organic matter (e.g., Skikne et al. 2009) and microzooplankton. Microzooplankton, such as dinoflagellates and ciliates, which could be observed under our analytical conditions, were unimportant prey items. Studies of the genetic diversity of gut contents (e.g., King et al. 2008) would potentially reveal presently unknown prey items. In addition, approaches such as stable-isotope and fatty-acid analyses can also show the contribution of non-quantifiable food sources by means of gut-content analysis.

Gut content-based studies reveal only snapshots of a species' trophic ecology. Because plankton communities may change as consequence of advection, population dynamics and behavior (e.g., diel vertical migration), the diet of jellyfish is subject to changes in food availability and distribution. Further studies should include nocturnal sampling, since there is evidence of the importance of emergent/vertically migrating zooplankton as food sources for the rhizostome medusa *Catostylus mosaicus* (Pitt et al. 2008). An estimate of the trophic role of *L. lucerna,* based on ^{13}C and ^{15}N isotope signatures, showed that this medusa species shares its trophic position with other zooplanktivorous species (Nagata et al. 2015), which supports the conclusion that mesozooplankton is, indeed, the species' main food source.

We compiled values of digestion times of other medusae of Rhizostomeae from the literature, although a specific digestion times for *L. lucerna* would provide more-reliable feeding-rate estimates. These digestion times were calculated for smaller sized medusae (*Stomolophus meleagris*) and the large specimens analyzed here may have faster digestion times. Moreover, ongoing experiments of digestion rates of *L. lucerna* have estimated digestion times of 3–4 h, for calanoid copepods, at similar temperatures to this study (Lisboa, pers. comm.). This evidence gives support to the feeding rates here estimated and reinforces that the use of temperature-adjusted digestion times of other scyphozoan species can be a useful approach when specific data are unavailable. Further studies should refine our DR and DCR models, through the inclusion of specific digestion times, which in turn should include sources of variation caused by prey type, amount of prey, and predator's size (e.g., Martinussen and Båmstedt 2001).

Conclusion

Lychnorhiza lucerna is a generalist predator with a diet mostly reflecting prey availability. Nevertheless, larger sized medusae consumed larger proportions of calanoid copepods. Even young medusae with comparatively slower marginal flow velocities (~ 10 cm s^{-1}) captured rapidly escaping copepods, which demonstrated that escape velocity alone cannot unsatisfactorily explain prey-selectivity patterns. *L. lucerna* feeding rates were comparable to those of *Aurelia coerulea* and higher than other semaeostome medusae. Our estimates of the daily carbon ration for *L. lucerna* were insufficient for the animal´s minimum carbon requirements, suggesting

that other, non-quantified food items may be necessary nutritional sources of this medusa. Even so, the daily ration expressed as copepods ingested medusa^{-1} day^{-1} demonstrated that aggregations of *L. lucerna* may exert substantial trophic impacts, but the lack of in situ data on medusae and prey densities hinders a broad comprehension of the species' predatory impact in coastal waters of South America.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. The funding agencies had no role in the goals, the design, analytical approach, or in any step of the preparation of this study.

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