Renato Mitsuo Nagata

Bases morfo-funcionais da alimentação e o papel trófico
de *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae)

São Paulo
2015

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de *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae)**

Morphofunctional bases of feeding and the trophic role
of *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae)

Tese apresentada ao Instituto de
Biociências da Universidade de São Paulo,
para a obtenção de Título de Doutor em
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Orientador: Dr. André Carrara Morandini

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Epígrafe

The poet's eye, in a fine frenzy rolling,
Doth glance from heaven to earth, from earth to heaven;
And as imagination bodies forth
The forms of things unknown, the poet's pen
Turns them to shapes, and gives to airy nothing
A local habitation and a name

William Shakespeare,
A Midsummer Night's Dream, Act V, Scene 1

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INTRODUÇÃO GERAL

Cifomedusas: sua importância para o ecossistema e para o homem

O subfilo Medusozoa (Cnidaria) é caracterizado pela presença do estágio de medusa no ciclo de vida e reúne as classes Staurozoa (~50 spp.), Scyphozoa (~200 spp.), Cubozoa (~36 spp.) e Hydrozoa (~ 3500 spp.) (Petersen, 1979; Daly *et al.*, 2007). São caracterizados pela simetria radial e representam geralmente o estágio sexuado e vágil do ciclo de vida. Medusas de Scyphozoa, as águas-vivas, são exclusivamente marinhas e se destacam pelo grande tamanho de algumas espécies (Russell 1970; Mianzan & Cornelius 1999). As cifomedusas, exceto algumas espécies de Coronatae, são conspícuas, medindo geralmente >5 cm e algumas espécies até >2 m de diâmetro (Cornelius, 1997; Arai, 1997; Mianzan & Cornelius, 1999, Kawahara *et al.*, 2006).

Uma característica da biologia de algumas cifomedusas são os fenômenos de “*blooms*”, quando há um rápido aumento do número de indivíduos que leva a densidades altíssimas (Graham *et al.*, 2001; Boero *et al.*, 2008; Hamner & Dawson, 2009; Miranda *et al.*, 2012). *Blooms* são uma característica natural da biologia populacional das espécies, estando relacionados a fenologia e a ciclos sazonais (Russell, 1970; Boero *et al.*, 2008) ou interanuais (Goy, 1989; Brodeur *et al.*, 2008; Quiñones *et al.*, 2012). Porém, em algumas partes do mundo os *blooms* têm aumentado em magnitude e frequência (Brodeur *et al.*, 1999; Mills, 2001; Lynam *et al.*, 2006; Kawahara *et al.*, 2006) e têm sido relacionados a alterações no ambiente marinho (eutrofização, introdução de espécies, mudanças climáticas e sobrepesca) que favoreceriam a proliferação destes animais (Parsons & Lalli, 2002; Richardson *et al.*, 2009; Purcell, 2012). Não existe ainda um consenso sobre as causas dos *blooms* e se há uma tendência de aumento, uma vez que monitoramentos sistemáticos de longa duração são esparsos ou inexistentes para a maioria das regiões (Condon *et al.*, 2012; Brotz *et al.*, 2012; Gibbons & Richardson, 2013). De qualquer forma, esses fenômenos são deletérios para economias costeiras, impactando atividades como o turismo, pesca e produção de energia (Kawahara *et al.*, 2006; Purcell *et al.*, 2007; Nagata *et al.*, 2009). Além de afetarem drasticamente o ecossistema via controle predatório sobre outras populações (Behrends & Schneider, 1995) e via uma cascata de consequências desencadeadas por alterações nas assembleias planctônicas (Pitt *et al.*, 2007; Brodeur *et al.*, 2008b).

Cifomedusas são consideradas elementos prejudiciais às atividades recreativas e econômicas em zonas costeiras (revisado em Purcell *et al.*, 2007), no entanto podem proporcionar benefícios econômicos, particularmente as medusas da ordem Rhizostomeae. Esses animais são tradicionalmente consumidos como uma iguaria em países do leste asiático, onde pescarias industriais e artesanais são milenares e encontram-se em expansão (Kitamura & Omori 2010). A pesca industrial de medusas têm aflorado ao redor do mundo, em países não consumidores, como no Golfo do México (EUA e México) explorando *Stomolophus meleagris* L. Agassiz, 1862 e sendo atualmente o maior recurso pesqueiro do Texas, na Austrália (*Catostylus mosaicus* (Quoy & Gaimard, 1824)) e Turquia (*Rhizostoma pulmo* (Macri, 1778)) (Doyle *et al.*, 2014). Além disso, o colágeno extraído de medusas Rhizostomeae é um forte candidato a substituição do colágeno extraído de bovinos em aplicações biomédicas e diversas pesquisas tem avaliado suas propriedades e aplicações (Addad *et al.*, 2011), inclusive com um projeto financiado no Brasil (FAPESP 2013/50267-3). Por fim, outra atividade econômica em expansão é o cultivo ornamental de águas-vivas para fins recreativos, ou mesmo em aquários marinhos de visitação pública como o Enoshima Aquarium e o Kamo Aquarium no Japão e Monterey Bay Aquarium, no Estados Unidos, que possuem exposições permanentes de águas-vivas (Doyle *et al.*, 2014).

Recentes estudos têm demonstrado a grande importância de cifomedusas na prestação de serviços ecológicos, como por exemplo, ao compor a dieta de 124 espécies de peixes (Arai, 2005; Pauly *et al.*, 2009) e de outros vertebrados como tartarugas marinhas (Houghton *et al.*, 2006). Seus volumosos corpos com estruturas como braços orais e pórticos genitais, oferecem micro ambientes onde vivem peixes juvenis (Ohtsuka *et al.*, 2009), caranguejos (Nogueira Jr. & Haddad, 2005), tremátodes (Morandini *et al.*, 2005; Nogueira Jr *et al.*, 2014) e camarões (Martinelli Fº *et al.*, 2008). Esses simbioses buscam proteção contra predadores, parasitam as medusas, ingerem suas presas e outros simbioses (Ohtsuka *et al.*, 2009). Mais recentemente, especulou-se que organismos simbioses e predadores de gelatinosos, poderiam estar aumentando juntamente com o aumento de populações de gelatinosos (Utne-Palm *et al.*, 2010). Em vista da importância ecológica e sócio-econômica desses organismos maiores esforços são necessários para a compreensão de aspectos básicos de sua biologia. O que esses animais comem? Quanto comem? Com quais outros consumidores eles competem? Tais informações podem revelar detalhes que auxiliem no entendimento do sucesso

ecológico desses organismos e ao mesmo tempo melhorar nossa compreensão sobre os fenômenos de *blooms* e suas consequências para o ecossistema.

O papel de cifomedusas como consumidores nos ecossistemas pelágicos

Impactos tróficos de hidromedusas pequenas (<1cm) geralmente são pouco relevantes sobre a comunidade planctônica (mas veja Yilmaz *et al.*, 2014), porém diversos estudos demonstraram que cifomedusas podem consumir uma grande parcela do zooplâncton disponível (Hays *et al.*, 1990; Garcia & Durbin, 1993; Purcell *et al.*, 1994; Mills, 1995; Purcell, 1997; Hansson *et al.*, 2005). Em ocasiões de grande densidade populacional cifomedusas como *Aurelia* spp. e *Chrysaora melanaster* podem diariamente consumir de 20 a 60% do zooplâncton disponível (Matsakis & Conover, 1991; Behrends & Schneider, 1995; Brodeur *et al.*, 2002; Uye & Shimauchi, 2005). Apesar da importância de cifomedusas como consumidores, poucas espécies tiveram suas dietas estudadas. As espécies se alimentam aleatoriamente de acordo com a disponibilidade de presas no ambiente? Ou possuem especializações mecânicas e funcionais que determinam hábitos alimentares específicos? Acessar a dieta desses organismos é primordial para a compreensão de seu impacto predatório e as consequências para a trofodinâmica dos ecossistemas pelágicos (Feigenbaum & Kelly, 1984; Pérez-Rufaza *et al.*, 2002; Pitt *et al.*, 2008). Tais consequências incluem, por exemplo, prejuízos econômicos para a indústria pesqueira devido ao impacto predatório (Möller, 1980; Behrends & Schneider, 1995; Purcell, 1991; Purcell & Arai, 2001) ou pela competição por alimento (Purcell & Studervant, 2001) entre cifomedusas e ovos e lavas de peixes.

Estudos de conteúdos estomacais têm descrito a dieta de espécies de Scyphozoa desde o trabalho pioneiro de Lebour (1922; 1923). A Tabela 1 reúne dados de 38 artigos que quantificaram a composição da dieta de cifomedusas em porcentagens numéricas ou de massa desde 1961. Trabalhos que trazem apenas dados qualitativos não foram incluídos (*e.g.* Kikinger, 1992; Sørnes *et al.*, 2008). Para trabalhos mais antigos Alvarino (1985) reuniu os dados disponíveis em tabelas semelhantes. Das cerca de 200 espécies de Scyphozoa, apenas 19 (<10%) tiveram sua dieta quantificada. Medusas de Coronatae são as menos estudadas, com apenas um trabalho, seguidas por medusas de Rhizostomeae, 6 trabalhos (5 espécies). Medusas de Semaestomeae são de longe as mais estudadas com 31 trabalhos (13 espécies), dos quais pouco mais da metade se

refere a *Aurelia* spp. (ou “*Aurelia aurita*”). A grande maioria desses estudos se concentra no hemisfério norte (principalmente no oceano Atlântico), em regiões temperadas, enquanto apenas 3 trabalhos foram realizados em regiões tropicais (Flynn & Gibbons, 2007; Lo & Chen, 2008; Kanagaraj *et al.*, 2011).

Uma vez que os tempos de digestão dos itens planctônicos são desconhecidos para a maioria das espécies, esses dados são apenas de caráter qualitativo (Martinussen & Båmstedt, 1995; 1999; 2001), no entanto, algumas generalizações podem ser feitas. Cifomedusas são estritamente carnívoras exceto por *Cotylorhiza tuberculata* e *Rhizostoma pulmo* em que diatomáceas representam grande proporções da dieta (62 e 85%) (Peréz-Ruzafa *et al.*, 2002). Crustáceos são as principais presas, representando em média 58% da dieta. Entre esses, os copépodes são os itens mais importantes, consumidos por todas as espécies, ocorrendo em 87% dos estudos, com abundância média de 37%. Outros crustáceos (*e.g.* larvas de decápodes, ostrácodes e eufausiáceos) são o segundo item em frequência de ocorrência (52%) e abundância média (15%) na dieta, seguidos por ovos e larvas de peixes (40% de frequência de ocorrência e 8% de abundância média). Mesmo espécies mais bem estudadas como *Aurelia* spp. e *Cyanea capillata* apresentam grande variação nas dietas entre os diferentes trabalhos, o que provavelmente se explica pela variabilidade da composição do plâncton. Apesar de cifomedusas serem frequentemente consideradas consumidores generalistas (*e.g.* Mills, 1995), comparações entre a dieta e a composição do plâncton co-ocorrente indicam que algumas espécies se alimentam seletivamente dos itens disponíveis (*e.g.* Larson, 1991; Purcell, 1997; Barz & Hirche, 2005). Mesmo assim, frequentemente estudos de modelagem ecossistêmica ainda simplificam o papel trófico de cifomedusas, agrupando diferentes espécies em uma única categoria de consumidores pelágicos (Pauly *et al.*, 2009; Condon *et al.*, 2012).

Bases morfológicas e funcionais da alimentação de cifomedusas

Ainda não é possível prever os hábitos alimentares da grande maioria das espécies de cifomedusas com base no conhecimento sobre seus mecanismos alimentares. Entender como as estruturas corporais operam para encontrar, capturar e ingerir as presas e quais suas limitações funcionais é de grande relevância para a compreensão dos hábitos de vida e do papel ecológico desses organismos. Estudos sobre os mecanismos alimentares são restritos a poucas espécies de Scyphozoa

(Sandrini & Avian, 1989; Costello & Colin, 1995; Ford *et al.*, 1997; D'Ambra *et al.*, 2001; Sötje *et al.*, 2007) e estão longe de contemplar a diversidade morfológica do grupo. Compreender a mecânica funcional da alimentação pode aumentar o conhecimento sobre as consequências tróficas dos *blooms* e também revelar mecanismos que geram vantagens a esses predadores em detrimento a outros consumidores (*e.g.* Eiane *et al.*, 1999; Acuña *et al.*, 2011; Pitt *et al.*, 2013), e assim melhor se compreender fatores chave do seu sucesso ecológico e evolutivo.

Medusas estão entre os primeiros metazoários a desenvolver natação propelida pela força muscular (Costello *et al.*, 2008). Os mais antigos fósseis são do período Cambriano médio, de exemplares de atuais grupos de cifomedusas (Rhizostomeae e Semaestomeae) (Willighby & Robison, 1979; Hagadorn *et al.*, 2002; Cartwright *et al.*, 2007; Young & Hagadorn, 2010), mas veja Wade (1994) para uma proposta distinta. Cifomedusas dispõem de um repertório celular limitado e organização tecidual simples, no entanto possuem considerável diversidade morfológica e funcional (Gladfelter, 1973; Arai, 1997; Costello *et al.*, 2008). Ao longo de mais de 500 milhões de anos houve grande variação abiótica e faunística no ambiente pelágico como o surgimento de grupos hoje dominantes em vários ecossistemas (*e.g.* diatomáceas, copépodes e peixes) (Rigby & Milsom, 2000; Bradford-Grieve, 2002). A permanência das cifomedusas e a conservação de seu plano corporal ao longo desse período, com as severas transições ambientais, evidencia a versatilidade morfológica e o sucesso desses consumidores (Richardson *et al.*, 2009). Essa diversidade, na forma de estruturas de captura de presas, como tentáculos, apêndices e braços orais, pode estar associada a captura de diferentes itens alimentares (Madin, 1988; Purcell, 1990; Sötje *et al.*, 2007). Da mesma forma, características funcionais como modos de forrageio, desempenhos natatórios, mecanismos de encontro com presas e de filtração (Gerritsen & Strickler, 1977; Costello & Colin 1995; Umland *et al.*, 2014) são determinantes para a diversificação trófica (Costello *et al.*, 2008) e devem ser melhor compreendidos.

Em cifomedusas, as pulsações da umbrela que proporcionam o impulso locomotor, também transportam fluidos (e presas) contra as estruturas de captura de alimento, onde as mesmas são retidas através de um mecanismo filtrador (Larson, 1978; 1991; Costello, 1992; Costello & Colin, 1995; Dabiri *et al.*, 2005). Devido ao acoplamento entre os sistemas locomotor e alimentar, através das pulsações umbrelares, diferenças na performance natatória (*e.g.* velocidade, frequência de pulsação) poderiam afetar mecanismos alimentares? Mudanças ontogenéticas nessas

performances também poderiam afetar mecanismos alimentares e o papel ecológico das espécies? Costello & Colin (1994) propuseram que a força (*i.e.* velocidade) dos vórtices gerados pelas pulsações umbrelares devem ser comparados a velocidades máximas das possíveis presas zooplantônicas, para se avaliar a probabilidade de sucesso na captura das mesmas. Medusas de Rhizostomeae (~90 spp.), que representam cerca de 60% da diversidade de Scyphozoa (Kramp, 1961; Mianzan & Cornelius, 1999; Daly *et al.*, 2007), são as nadadoras mais robustas desse grupo (Costello & Colin, 1995; D'Ambra *et al.*, 2001). Por essa razão, D'Ambra *et al.*, (2001) sugeriram que medusas de Rhizostomeae poderiam capturar presas mais rápidas e evasivas como copépodes calanóides. No entanto, trabalhos que analisaram o conteúdo estomacal de medusas desse grupo demonstraram tanto padrões de seletividade alimentar positiva (Fancett, 1988), quanto negativa (Larson, 1991) para esses copépodes.

Medusas de Semaestomeae ingerem presas tão grandes quanto seu próprio tamanho (*e.g.* outros gelatinosos) por meio de sua ampla abertura bucal na subumbrela (Mills, 1995; Purcell, 1997). Já medusa de Rhizostomeae possuem inúmeras aberturas bucais milimétricas ao longo dos braços e estariam estruturalmente limitadas a ingestão de pequenos itens mesozooplântônicos (Russell, 1970; Larson, 1991; Lee *et al.*, 2008). Pouco se sabe sobre o exato modo de filtração dos braços orais dessas espécies, exceto por trabalhos que demonstram a passagem dos fluxos ao redor dos animais em uma escala macroscópica (*e.g.* Costello & Colin 1995; D'Ambra *et al.*, 2001; Santhanakrishnan *et al.*, 2012).

Compreender esse modo filtração, pode revelar um importante mecanismo estruturador de ecossistemas pelágicos tropicais e subtropicais, uma vez que muitas espécies são conspicuas e provavelmente exercem um papel predatório importante sobre outras populações planctônicas. Ainda, algumas espécies de Rhizostomeae são responsáveis pelos mais intensos (e danosos) *blooms* reportados recentemente (Dawson & Hamner, 2009; Brotz *et al.*, 2012) como os de *Nemopilema nomurai* no Japão (Kawahara *et al.*, 2006), *Crambionella orsini* (Vanhöffen, 1888) no Golfo de Omã (Daryanabard & Dawson, 2008), *Phyllorhiza punctata* von Lendenfeld, 1884, no Golfo do México (Graham *et al.*, 2003) e *Rhopilema nomadica* Galil, Spanier, & Ferguson, 1990, no Leste do Mediterrâneo (Lotan *et al.*, 1994). Porém, quase nada se conhece sobre sua ecologia alimentar (Purcell, 2009).

Figura 1 - Medusa *Lychnorhiza lucerna* de distintos padrões de coloração (A e D). Medusa adulta em águas superficiais no estuário de Cananéia, SP (B). Pólipo de *L. lucerna* (E). Éfira de *L. lucerna* (F). Picos populacionais de *L. lucerna* representam um empecilho para pescadores no litoral de São Paulo (C) e no Paraná (G). Pictures D Álvaro E. Migotto. Pictures E and F, André C. Morandini. Escalas A = 2 cm; B = 5 cm; D = 1 cm; E = 0.1 cm; F = 0.2 cm.

No Brasil, a medusa Rhizostomeae *Lychnorhiza lucerna* Haeckel, 1880 (Fig. 1) é provavelmente a cifomedusa mais abundante e durante seus picos populacionais, pode dominar a biomassa capturada por redes de arrastos (Branco & Verani, 2006; Nagata *et al.*, 2008). As agregações dessa espécie chegam a representar um entrave físico a realização dessa atividade no sul do Brasil (Nagata *et al.*, 2009) e no norte da Argentina (Schiariti *et al.*, 2008). Apesar do ciclo de vida de *L. lucerna* ter sido recentemente descrito (Schiariti *et al.*, 2008) e de alguns avanços na compreensão de sua biologia reprodutiva (Schiariti *et al.*, 2012; 2014) e em suas associações simbióticas (Nogueira Jr & Haddad, 2005; Moyano *et al.*, 2012; Nogueira Jr *et al.*, 2014) nada se sabe sobre aspectos alimentares, implicações de seus *blooms* sobre o ecossistema e seu papel ecológico.

Tabela 1- Principais itens alimentares de cifomedusas, que tiveram sua dieta quantificadas em valores numéricos ou de massa em 38 artigos (1961–2014). Quando disponíveis, dados de número de indivíduos analisados, número de estômagos vazios, diâmetro umbrelar médio, mínimo e máximo.

Espécie	Copépodes	Cladóceros	Outros crustáceos	Ovos e larvas de peixes	Véligers	Medusas e ctenóforos	Larváceos	Quetognatos	Rotíferos	Ciliados	Diatomáceas/fito plâncton	Outros	Fonte
Coronatae													
<i>Periphylla peryphylla</i> (N=39, 15 vazios)	100	0	0	0	0	0	0	0	0	0	0	0	Fosså, 1992
Semaeostomeae													
<i>Aurelia</i> sp. (N=40, 28–160 mm)	45	3	2	0	11	0	5	2	0	32	0	0	Mironov, 1967
<i>Aurelia</i> sp. (N=379, 80–260 mm)	32	4	7	0	56	0	0	0	0	0	0	0	Kerstan, 1977
<i>Aurelia</i> sp. (N=961, 11–20 mm)	56	13	0	30	0	0	0	0	0	0	0	0	Möller, 1980
<i>Aurelia</i> sp. (N=1200, 36–50 mm)		63		34	0	0	0	0	0	0	0	0	Möller, 1980
<i>Aurelia</i> sp. (N=20)	77	0	0	0	22	0	0	0	0	0	0	0	Hamner <i>et al.</i> , 1982
<i>Aurelia</i> sp. (N=189, 85 vazios, 10–150 mm)	48	0	0	0	0	34	0	0	0	0	6	12	Matsakis & Conover, 1991
<i>Aurelia</i> sp. (N=55, 28–34 mm)	100	0	0	0	0	0	0	0	0	0	0	0	Olesen <i>et al.</i> , 1994
<i>Aurelia</i> sp. (N=17, 2.5 mm)	0	0	0	0	0	0	0	0	93	7	0	0	Olesen <i>et al.</i> , 1994
<i>Aurelia</i> sp. (N=360, 6–12 mm)	8	0	0	0	0	4	0	0	88	0	0	0	Sullivan <i>et al.</i> , 1997
<i>Aurelia</i> sp.	42	4	0	3	35	0	0	0	0	0	0	16	Mutlu 2001
<i>Aurelia</i> sp. (N=71)	44	1	31	4	0	0	7	0	7	2	0	3	Uye & Shimauchi 2005
<i>Aurelia</i> sp. (N=50, 126 mm, dip net)	7	84	0	0	9	0	0	0	0	0	0	0	Barz & Hirche, 2005
<i>Aurelia</i> sp. (N=81, 103 mm, BIOMOC)	22	77	0	0	1	0	0	0	0	0	0	0	Barz & Hirche, 2005
<i>Aurelia</i> sp. (N=42)	72	0	8	0	17	0	2	0	0	0	0	0	Malej <i>et al.</i> , 2007
<i>Aurelia</i> sp. (N=143, 70–280 mm)	90	0	4	2	3	0	<1	0	0	0	0	1	Lo & Chen, 2008
<i>Aurelia</i> sp. 5 (N=30, 84 mm)	99	0	0	0	0	0	1	0	0	0	0	0	D'Ambra <i>et al.</i> , 2013
<i>Aurelia labiata</i> (N=13, 215 mm)	77	0	19	0	0	3	0	0	0	0	0	1	Radchenko, 2013
<i>Aurelia labiata</i> (N=8, 262 mm)	60	0	16	0	18	0	5	0	0	0	0	<1	Purcell 2003
<i>Aurelia labiata</i> (N=34, 106 mm)	10	12	4	0	69	0	1	0	0	0	0	4	Purcell 2003
<i>Aurelia labiata</i> (N=30, 74 mm)	49	5	2	0	34	0	4	0	0	0	0	5	Purcell 2003
<i>Aurelia labiata</i> (N=8, 236 mm)	6	0	68	0	0	24	0	0	0	0	0	2	Suchman <i>et al.</i> , 2008
<i>Aurelia limbata</i> (N=331, 20 vazios, 200–450 mm)	9	0	63	10	0	13	0	3	0	0	0	2	Gorbatenko <i>et al.</i> , 2009
<i>Aurelia limbata</i> (N=5)	0	0	100	0	0	0	0	0	0	0	0	0	Zavolokin <i>et al.</i> , 2008
<i>Chrysaora hysoscella</i> (N=48, 150–380 mm)	25	44	19	0	0	0	0	5	0	<1	0	6	Flynn & Gibbons, 2007

Tabela 1- Continuação.

Espécie	Copépodes	Cladóceros	Outros crustáceos	Ovos e larvas de peixes	Véligeres	Medusas e ctenóforos	Larvários	Quetognatos	Rotíferos	Ciliados	Diatomáceas/fito plâncton	Outros	Fonte
<i>Chrysaora</i> cf. <i>caliparea</i> (N=23, 147 mm)	77	0	0	9	9	2	0	0	0	0	0	3	Kanagaraj <i>et al.</i> , 2011
<i>Chrysaora melanaster</i> (N=188, 305 mm)	58	0	39	0	0	0	0	0	0	0	0	3	Radchenko, 2013
<i>Chrysaora melanaster</i> (N=18, 2 vazios, 110–400 mm, Data=1999)	16	0	64	9	0	11	0	0	0	0	0	0	Brodeur <i>et al.</i> , 2002
<i>Chrysaora melanaster</i> (N=29, 1 vazios, 120–310 mm, Data=1997)	14	0	40	24	0	21	1	0	0	0	0	0	Brodeur <i>et al.</i> , 2002
<i>Chrysaora melanaster</i> (N=77 2 vazios, 453:200–750 mm)	26	0	54	4	0	4	0	12	0	0	0	<1	Gorbatenko <i>et al.</i> , 2013
<i>Chrysaora melanaster</i> (N=6)	0	0	20	42	0	0	0	0	0	0	0	38	Zavolokin <i>et al.</i> , 2008
<i>Chrysaora quinquecirrha</i> (N=150, >18 mm)	55	0	0	0	0	0	0	0	0	0	0	45	Purcell, 1992
<i>Chrysaora quinquecirrha</i> (N=240, >18mm)	71	0	0	0	0	0	0	0	0	0	0	29	Purcell, 1992
<i>Chrysaora quinquecirrha</i> (N=80, >31 mm)	72	0	0	22	0	0	0	0	0	0	0	0	Purcell <i>et al.</i> , 1994
<i>Chrysaora quinquecirrha</i> (N=31, 15 vazios, 4 mm)	25	0	0	2	1	0	0	0	22	48	0	0	Olesen <i>et al.</i> , 1996
<i>Chrysaora quinquecirrha</i> (<6 mm)	0	0	0	0	0	0	0	0	23	61	0	0	Haven & Morales-Almo, in Purcell 1992
<i>Chrysaora quinquecirrha</i> (N=12, 1 vazio, 256:70–420 mm)	79	0	3	1	0	0	0	17	0	0	0	0	Gorbatenko <i>et al.</i> , 2013
<i>Chrysaora plocamia</i> (N=68, 70–470 mm)	50	0	1	39	6	0	0	0	0	0	0	3	Riascos <i>et al.</i> , 2014
<i>Cyanea capillata</i> (N=103, 72 vazios, 40–700 mm)	0	0	0	44	0	56	0	0	0	0	0	0	Plotnikova, 1961
<i>Cyanea capillata</i>	11	29	0	14	0	9	31	0	0	0	0	0	Fancett, 1988
<i>Cyanea capillata</i> (N=44, 68mm)	8	5	0	0	0	0	83	0	0	0	0	4	Purcell & Sturdevant, 2001
<i>Cyanea capillata</i> (N=57, 81 mm)	16	15	5	0	20	0	43	0	0	0	0	<1	Purcell 2003
<i>Cyanea capillata</i> (N=30, 74 mm)	42	4	2	0	8	0	41	0	0	0	0	1	Purcell 2003
<i>Cyanea capillata</i> (N=120, 10 vazios, 284:190–460 mm)	36	0	31	7	0	22		4	0	0	0	0	Gorbatenko <i>et al.</i> , 2013

Tabela 1 - Continuação

Espécie	Copépodes	Cladóceros	Outros crustáceos	Ovos e larvas de peixes	Vélígers	Medusas e ctenóforos	Larváceos	Quetognatos	Rotíferos	Ciliados	Diatomáceas/fito plâncton	Outros	Fonte
<i>Cyanea capillata</i> (N=8)	8	0	85	0	0	0	0	0	0	0	0	7	Zavolokin <i>et al.</i> , 2008
<i>Drymonema dalmatinum</i> (N=13, 5 vazios)	0	0	0	0	0	100	0	0	0	0	0	0	Larson, 1987 A
<i>Pelagia noctiluca</i> (n=51, 19 vazios)	29	0	14	0	0	14	0	14	0	0	0	0	Giorgi <i>et al.</i> , 1991
<i>Pelagia noctiluca</i> (n=38, 9 vazios)	44	7	39	3	0	0	0	2	0	0	0	0	Giorgi <i>et al.</i> , 1991
<i>Pelagia noctiluca</i> (N=5680, 5226 vazios, 4–12 mm)	52	3	9	14	4	4	3	5	0	0	0	0	Sabatés <i>et al.</i> , 2010
<i>Pelagia noctiluca</i> (N=138; 29–120 mm)	90	4	0	2	0	0	0	0	0	0	0	4	Rosa <i>et al.</i> , 2013
<i>Phacellophora camtschatica</i>	7	0	0	27	0	24	27	0	0	0	0	15	Purcell, 1990
<i>Phacellophora camtschatica</i> (N=119, 235 mm)	57	0	40	2	0	0	0	0	0	0	0	<1	Radchenko 2013
<i>Phacellophora camtschatica</i> (N=11, 153mm)	5	17	0	0	1	66	0	0	0	0	0	10	Suchman <i>et al.</i> , 2008
<i>Phacellophora camtschatica</i> (N=2)	0	0	100	0	0	0	0	0	0	0	0	0	Zavolokin <i>et al.</i> , 2008
Rhizostomeae													
<i>Cotilorhiza tuberculata</i>	3	0	0	0	6	0	0	0	0	5	85	0	Perez-Rusafa <i>et al.</i> , 2002
<i>Phyllorhiza punctata</i> (N=15)	23	0	0	15	35	0	0	0	0	23	0	4	Graham <i>et al.</i> , 2003
<i>Pseudorhiza haeckeli</i>	33	4	5	41	0	0	8	0	0	0	0	0	Fancett, 1988
<i>Rhizostoma pulmo</i>	1	0	0	0	2	0	0	0	0	35	62	0	Perez-Rusafa <i>et al.</i> , 2002
<i>Stomolophus meleagris</i> (N=165, 21–83 mm)	16	<1	<1	0	71	0	3	0	0	9	0	0	Larson, 1991
<i>Stomolophus meleagris</i> (N=51, 41–140 mm)	1	<1	5	65	26	0	0	0	0	0	0	3	Padillha–Cerrato <i>et al.</i> , 2013

OBJETIVOS

O objetivo geral desta tese é compreender o papel ecológico predatório de *Lychnorhiza lucerna* (Rhizostomeae). Para tanto conduziu-se uma abordagem morfo-funcional, empregando técnicas videográficas para a descrição da mecânica de natação e de captura de presas, combinada com estudos de ecologia trófica que aplicaram a análise de conteúdos estomacais e a análise de isótopos estáveis para a compreensão de seu papel predatório e sua posição trófica no ecossistema. As seguintes questões norteiam a realização desta tese:

1 – Quais as bases morfológicas e biomecânicas da alimentação de *L. lucerna*? Como esse mecanismo se desenvolve em éfiras da espécie?

A filtração de partículas pelos braços orais de medusas Rhizostomeae a partir de correntes alimentares geradas pela natação é um processo pouco conhecido para o grupo. A biomecânica da natação e de captura do alimento foram descritas a partir de técnicas videográficas utilizando câmeras de alta frequência de captura de imagens. Propriedades cinemáticas desses fluxos e a interação dos vórtices com os braços orais que retêm as presas, podem ser determinantes para a captura de presas. Essas propriedades foram quantificadas ao longo do desenvolvimento, desde éfiras até indivíduos com o plano corporal adulto (<7 cm). Os processos de captura de presas também foram descritos através dessas técnicas.

2 – Qual é a dieta e os potenciais impactos predatórios de *L. lucerna*?

Devido sua natação robusta e produção de fortes correntes alimentares, acredita-se que esses organismos (medusas Rhizostomeae) possam capturar presas de maior capacidade escape. Por outro lado, o tamanho das bocas milimétricas dos braços orais restringiria o tamanho das presas ingeridas. O seu padrão de natação robusto também deve ser energeticamente dispendioso, o que demanda maiores taxas de consumo, e maiores impactos predatórios. A relevância dessas considerações em populações naturais é desconhecida. Conteúdos estomacais de medusas e as densidades das potenciais presas nos mesmos locais foram quantificados para se conhecer as taxas alimentares, seletividade alimentar e melhor se conhecer o potencial impacto predatório da espécie.

3 – Qual a posição trófica dos organismos gelatinosos, relativa a outros consumidores em um ecossistema relativamente preservado?

Algumas populações de organismos gelatinosos têm aumentado nos últimos anos. Uma possível substituição de peixes por gelatinosos estaria ocorrendo em alguns ambientes marinhos. No entanto, as relações tróficas entre esses organismos, são pouco conhecidas em ambientes conservados. O estudo trófico com a análise de isótopos estáveis descreveu a estrutura trófica de um sistema estuarino relativamente preservado, as principais fontes de carbono para os consumidores e variações sazonais nos padrões isotópicos. Foram avaliadas as posições tróficas de possíveis consumidores chave (peixes, gelatinosos e outros invertebrados), a amplitude de seus nichos isotópicos e suas sobreposições. Essa descrição pretendeu fornecer uma visão geral sobre os papéis tróficos, as interações e o grau de redundância funcional entre espécies, conhecimentos fundamentais para a compreensão de dinâmicas compensatórias devido a remoção ou a proliferação de consumidores chave dos ecossistemas.

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**CAPÍTULO 1: IMPLICATIONS OF ANIMAL-
FLUID INTERACTIONS TO THE FEEDING
BEHAVIOR OF *LYCHNORHIZA LUCERNA*
(SCYPHOZOA, RHIZOSTOMEAE)**

IMPLICATIONS OF ANIMAL-FLUID INTERACTIONS TO THE FEEDING BEHAVIOR OF *LYCHNORHIZA LUCERNA* (SCYPHOZOA, RHIZOSTOMEAE)

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ABSTRACT

Young stages of Scyphozoa (ephyrae) have a conserved body plan, contrasting to the highly specialized adult morphology. Ephyral growth results in changes in fluid dynamics, which affect propulsive and feeding strategies. We applied high-speed videography, digital particle image velocimetry (DPIV) and dye visualization techniques to characterize mechanisms of swimming and feeding of the Rhizostomeae species *Lychnorhiza lucerna* at distinct developmental stages. The early ontogeny involves alterations in bell and oral arms enabling effective swimming and feeding in a changing fluid environment. For example, the ephyral lips with a single mouth opening evolve into a complex filtering structure, resulting in multiple millimetric mouths, which in turn are flanked by finger-like projections, armed with terminal nematocysts clusters. In ephyrae, the viscous environment of lower Reynolds number ($Re < 100$) imposes constraints to feeding mechanisms based on fluid transport. In contrast, adult medusa fluid flows are dominated by inertial forces generated by bell pulsations that transport fluids and prey toward the oral arms. Oral arms retain prey captured by sieving and sticking mechanisms. The distal elongation of oral arms occurs at the same extent that the dissipation of feeding currents takes longer, maximizing contact with increasingly stronger vortices. The strength of vortices, relative to prey escape abilities, determines the likelihood of capture success. Despite rhizostome medusae have stronger bell pulsations and swimming patterns than other scyphomedusae, maximum velocities of feeding currents of *L. lucerna* are 3–5 times smaller than prey escape responses of fast calanoid copepods, which suggest inability to capture these prey items. However, captures of these copepods were observed which suggests that other factors, may govern this predator prey interaction (*e.g.* prey detection ability). Further effort such as gut content studies, experiments with predators and prey, should be addressed to better characterize this interaction, which have important evolutionary and ecological implications.

Keywords: *feeding behavior, foraging mode, filter-feeding, jellyfish, gelatinous zooplankton.*

INTRODUCTION

Large medusae of the class Scyphozoa occur in almost all marine environments, playing an important role of consumers in pelagic trophic webs. Many scyphozoan species have the capacity to quickly increase the number of individuals through asexual reproduction, generating extremely high densities (Boero *et al.* 2008; Hammer & Dawson 2009; Schiariti *et al.* 2014). During these episodes of high abundance, also known as blooms, species with high feeding rates may exert an important predatory pressure over other planktonic populations (Olesen 1995), limiting the growth of many species by competition and predation (Behrends & Schneider 1995). The consequences of the predatory impact of large medusae on marine trophodynamics depend on how effectively medusae capture prey. Most scyphomedusae have some degree of prey selectivity, consuming different types of prey at variable feeding rates (Fancett 1988; Larson 1991; Purcell 1992). Patterns of prey selectivity depend on both the functional morphology of structures of prey capture (*e.g.* tentacles, oral arms) and on the foraging mode (Madin 1988; Colin *et al.* 2006).

Many hydromedusae and siphonophores feed as ambush predators, which remain stationary most of the time, waiting for the collision of prey with their expanded capture surfaces (*e.g.* marginal tentacles). In contrast, scyphomedusae, along with other oblate medusae, are cruising predators which swim constantly. These medusae swim using periodic bell pulsations and the wake they produce during swimming also operates to capture planktonic prey (Larson 1991; Costello & Colin 1995). The bell pulsation cycle is divided in a contraction phase that produces a starting vortex and an expansion phase that produces a stopping vortex (Dabiri *et al.* 2005). These vortices rotate in opposite directions and interact to form a vortex superstructure that generates forward thrust and also directs the surrounding fluids downstream. This flux promotes

encounter of prey with a predator's feeding structures – the tentacles and the oral arms (Costello & Colin 1994; Dabiri *et al.* 2005).

Scyphomedusae, in general, pulse constantly, but some characteristics of swimming kinematics change remarkably among species. Some species pulse at low frequencies, such as *Chrysaora quinquecirrha* (Desor, 1848) and *Cyanea capillata* (Linnaeus, 1758) (0.8 and 0.5 Hz), whereas others, particularly medusae of the order Rhizostomeae, swim at higher frequencies (~3 Hz), such as *Stomolophus meleagris* Agassiz, 1862 and *Phyllorhiza punctata* von Lendenfeld, 1884 (Costello & Colin 1994; Costello & Colin 1995; Ford *et al.* 1997; D'Ambra *et al.* 2001). In addition, bell pulsations of rhizostome medusae are stronger than other scyphomedusae, when comparing animals of similar body size (D'Ambra *et al.* 2001). Such differences on swimming behavior can affect: (i) feeding performance, since the volume of cleared water depends on the volume of entrained water by vortex of bell pulsations (Acuña *et al.* 2011; Katija *et al.* 2011); and (ii) prey selectivity, since the strength on feeding currents may affect the types of prey entrained (Costello & Colin 1994).

The utilization of swimming to pump water through feeding structures to capture prey is a widespread mechanism among scyphomedusae (Costello *et al.* 2008). Nevertheless, the mode of prey retention varies due to the diversity of body architectures and prey capture structures (tentacles, oral arms, bell margin) that trail in that wake behind scyphomedusan bell. All of these structures are armed with clusters of nematocysts, which discharge and penetrate or entangle prey, before the prey are transported to the mouth opening. Not merely the shape, but also the position of prey capture structures varies widely among scyphomedusae groups. While most species position tentacles towards the oral side of the bell, some coronates swim with their tentacles advanced, in an aboral position (Raskoff 2002). Species of Pelagiidae have

fewer long and widely spaced tentacles, species of Ulmaridae have thin and closed spaced tentacles, and species of Rhizostomeae lack marginal tentacles, capturing prey only by means of their highly specialized oral arms. These morphological variations determine prey capture mechanisms (Madin 1988; Colin *et al.* 2006) and have evolutionary and ecological implications (Costello *et al.* 2008).

Rhizostomeae is the most diverse group of scyphomedusae with ~60% (~90 spp.) of described scyphozoan species (Daly *et al.* 2007). Such species are conspicuous components of the ecosystems and are found mainly from tropical and subtropical regions (Russell 1970). Despite their ecological (Purcell 2008) and economical (Kitamura & Omori 2010) importance, medusae of the Rhizostomeae are among the least known organisms of the gelatinous zooplankton. One of the most remarkable features of these medusae are their highly modified feeding structures relative to the primitive medusa body plan. Besides lacking marginal tentacles, Rhizostomeae have eight relatively rigid elongated and branched oral arms (Russell, 1970; Mianzan & Cornelius 1999). Each oral arm has a system of canals that branches into many small canals, which in turn open to the outside by millimeter mouth openings (Larson 1991; Lee *et al.* 2009). The margins of the oral arms are highly folded and hold numerous small capitate finger-like structures with clusters of nematocysts on the tip, called *digitata* (Russell 1970, Fig. 1). Both the diameter of the small canals on oral arms and the size of the small mouths limit the ingestion of larger prey in Rhizostomeae (Larson, 1991).

Figure 1. The structure of the oral arm of *Lychnrohiza lucerna*. An oral arm with the internal wing on the left and two external wings on the right scale bar = 5 mm **A**. The canal system of an oral arm **B**. The highly bifurcated margin of the oral arm, covered with small *digitata*, forming the sieve structure, scale bar = 2 mm **C**. The structure of the small mouths *M*, terminal appendages *A*, the small pore of the canal inlet *P*, the *digitata* were suppressed, **D**. Illustrations: Silvia de Almeida Gonsales.

Whereas the structure and organization of *digitata* as a filtration apparatus are apparently conserved among Rhizostomeae medusae (Uchida 1925; Sugiura 1966; Kawahara *et al.* 2006; Holst *et al.* 2007; Costello *et al.* unpublished data), at a larger size scale, the morphology of bell, oral arms, and their relative spatial arrangement are highly diverse (Russell 1970). Some aspects of swimming and feeding mechanisms have been described for several species (Costello & Colin 1994; D'Ambra *et al.* 2001; Santhanakrishnan *et al.* 2012) but the exact mode of filtration, as well as the development of this feeding mechanisms through the animal ontogeny are still unknown in the group.

In South and Southeast Brazil, *Lychnorhiza lucerna* Haeckel, 1880 is the most abundant rhizostome medusa, occurring all year with spring population increases (Morandini 2003; Nogueira Jr. 2006). During its blooms, the species composes up to 95% of the biomass caught by shrimp trawlers (Nagata *et al.* 2008). These blooms represent a nuisance to shrimp trawlers in Brazil (Nagata *et al.* 2009) and northern Argentina (Schiariti *et al.* 2008). Information on the trophic role of this conspicuous component of South Atlantic Subtropical coastal areas is still lacking. This study aims to describe mechanisms of swimming and feeding, which will be used to better understand the potential ecological role of *L. lucerna*. The scientific goals are: *i*- to quantify the swimming kinematics of *L. lucerna*; *ii*- to analyze the fluid motions around swimming medusae and the interaction of wake vortex rings with feeding structures; *iii*- to quantify the utility of wake vortices as a feeding for *L. lucerna*; *iv*- To analyze how parameters of swimming and bell kinematics, and animal-fluid interaction change throughout development; and *v*- to describe the process of prey capture by *L. lucerna*.

MATERIAL AND METHODS

Sampling and cultivation of medusae

We collected medusae of *L. lucerna* in surface waters of Cananéia Estuary, Southeast Brazil, near Bom Abrigo Island in March and April 2013. Aggregations were located on surface waters around the estuary plume. Animals were collected with hand nets, and packed in plastic bags with local seawater. Medusae ranged in bell diameter (distance from opposite rhopalia) from 3–7 cm. After sampling, animals were transported to CEBIMar in São Sebastião, São Paulo state. Animals were kept inside containers of 5m³, with running water at ambient temperatures (20-24°C), and fed daily with natural plankton collected with a 200 µm net (see appendix 1 for sampling site, collection and cultures of medusae). Ephyrae and young medusae (0.5–2 cm bell diameter) were reared in laboratory from polyps kindly provided by Dr Agustin Schiariti (INIDEP), from the region of Clamercó, NE coast of Argentina. We maintained polyps following protocols of Jarms *et al.* (2002) (in the dark, fed weekly, at constant temperature of 22° C and salinity of 20). Ephyrae were reared in *planktonkreisels* similar to those described by Raskoff *et al.* (2003) and fed daily with *Artemia* sp. nauplii. Although the largest size classes (2–7 cm) were not yet reproductive, we are referring to them as adults because their exterior morphology was similar to larger reproductive individuals.

Video Recordings

We placed animals within rectangular aquariums with dimensions of 30 x 40 x 10 cm (width x height x depth) containing filtered (3 µm) seawater. Video vessels were greater than 10 body-lengths wide to avoid wall effects on fluid interactions. We used three imaging set-ups for our analyses: i- laser sheet illumination for swimming and

bell kinematic analyses and for the digital particle image velocimetry (DPIV) quantitation of the velocity fields surrounding the animal (see appendix 2); ii- side illuminated fluorescein dye visualization of flow, for a qualitative description of the interaction between the vortex ring and the inner structures of oral arms; and iii- high magnification collimated light illumination for predator-prey interactions and prey capture visualization.

The laser sheet was generated using a 680-nm wavelength laser and white light, for fluorescein dye and collimated light techniques, using light emitting diodes (LEDs). We used 50 and 100 mm macro lens connected by extension tubes of 12, 20 and 36 mm. Videos were recorded at 1000 frames s⁻¹ using a high-speed digital video camera (FASTCAN 1024 PCI; Photron), placed perpendicular to the laser sheet. Videos for DPIV were recorded with filtered seawater, seeded with hollow glass spheres (10 µm). A laser sheet illuminated a two-dimensional plane of fluid and data were collected when the center of the medusa bell was bisected by the laser plane, following Colin *et al.* (2013). Medusae were left swimming from the bottom to the top of the vessel for at least 3-5 cycles of bell pulsation and the video sequences of a few seconds were recorded (see appendix 3). For the fluorescein dye technique, a syringe was used to add the dye near the umbrella margin of swimming medusae. The formation of start vortex ring and its motion towards the inside structures of the oral arms were recorded. For prey capture videos, we added natural plankton collected with a 200 µm net.

Data Analyses

Bell and swimming kinematics were analyzed using Image-J software (NIH). All measurements were taken at intervals (*t*) of 0.01 s for ephyrae and young medusae, and of 0.02 s for larger animals. In addition to the image sequences of *L. lucerna*, sequences of other scyphomedusae (*Aurelia* sp. and *Chrysaora quinquecirrha*) were

also analyzed for a comparative approach. Alterations in bell shape were measured by the fineness ratio, f , according to (Costello & Colin 1994) as:

$$f=H/D,$$

where H = bell height, and D = bell diameter.

The contraction angle (c) of the bell margin was measured by the difference between the angle of bell margin relative to the animal's axis of symmetry at the maximum relaxation phase (θ), and at the maximum contraction phase (θ'), as:

$$c=\theta - \theta'.$$

The scheme of the measurements is presented at Fig. 2.

Figure 2 – Measurements of bell kinematics. The dotted line is the outline of the bell at the maximum relaxation phase, and the solid line, the outline at the maximum contraction. The dark grey line is the bell angle θ' at the maximum contraction and the light grey dotted line, the bell angle θ at the maximum relaxation. Bell height = H , bell diameter = D at maximum contraction.

Distance traveled, m , was measured from sequential changes in position of the anterior most point of the exumbrellar surface over t intervals. The final and initial position on axes X and Y of the screen were measured using Image-J software, and the displacement was calculated by applying the Pythagorean theorem:

$$m = \sqrt{(X_f - X_i)^2 + (Y_f - Y_i)^2},$$

where X_f and Y_f are the final and X_i and Y_i the initial position at each axes. Medusa swimming velocity u for a time interval (t) was calculated as:

$$u = m/t$$

Mean swimming velocity u_m was calculated as mean u during three successive complete bell contraction cycles.

Reynolds number (Re) was calculated as:

$$Re = d * u / \nu,$$

where u is the medusa velocity and ν is the kinematic viscosity of seawater ($\nu = 1.05 \times 10^{-6} \text{m}^2 \text{s}^{-1}$ at 20°C).

For measurements of flow velocities with digital particle image velocimetry (DPIV), we used the software package (DaVis, Lavis) that analyzes sequential video frames using a cross-correlation algorithm. Image pairs were analyzed with shifting overlapping interrogation windows of decreasing size (64X64 pixels then 32X32 pixels). This analysis generates velocity vector fields around the swimming medusae (Colin et al. 2013). We measured the maximum velocities of feeding currents u_f along the full cycle of bell relaxation and contraction by DPIV.

In order to evaluate possible ontogenetic changes on swimming and bell kinematics, as well as on the strength of feeding currents, we applied linear regression analysis with body size (as bell diameter) as independent variable, and as dependent variables: Reynold numbers of surrounding fluids (Re), maximum contraction angle c , bell fineness f , maximum velocity of feeding currents u_f , mean and maximum swimming velocity u_m and u_{max} .

Oblate cruising medusae are highly dependent on locally generated flow current to capture prey (Costello & Collin 1994; 1995; Dabiri *et al.* 2005). Other rhizostome species like *Cassiopea* sp. transports fluid from outside, towards surfaces of prey capture during both contraction and relaxation of bell (Santhanakrishnan *et al.* 2012). To achieve a better visualization on how directed flow interacts with oral arms, we calculated fluid velocities in a transect along the prey capture surface on oral arms.

In order to generate a capture map of oral arms, we quantified prey captures along the surface of oral arms of medusae ($n=5$). Animals were incubated in a container with seawater and *Artemia* spp. nauplii for 2 minutes. After incubation, individuals were carefully removed and preserved in a 4% formaldehyde solution in seawater. We quantified the number of nauplii in four oral arms (of a total of 8 oral arms) of each individual under stereomicroscope. The oral arm surface comprises three wings (two external and one internal), each wing was subdivided into regions (5 for the external and 6 for the internal wing) according to the distance from the bell (Fig. 12). In order to estimate prey capture per unit of area (cm^3), we estimated the oral arm surface area as the surface of a truncated cone as:

$$S_{ob} = \pi(r_1 + r_2) \sqrt{h^2 + (r_1 - r_2)^2},$$

Where r_1 = large radius, r_2 = small radius, and h = section height, according to Fig 12.

RESULTS

Swimming kinematics among large scyphomedusae

Bell pulsation cycle was divided into two phases, (i) the contraction phase, when circular muscles contract, reducing subumbrellar volume and expelling fluid, which produces the thrust. During this phase, bell fineness ratio f increases and peaks of this parameter coincide with maximum bell contraction (Fig. 3, A–C); and (ii) the expansion or recovery phase, when circular muscles relax and bell diameter increases, decreasing f (Fig. 3, A–C), while the medusa slows down (Fig. 3, J–L). The medusa *Lychnorhiza lucerna* swam at higher pulsations frequencies (>2 Hz) than common semaeostome species such as *Aurelia* sp. and *Chrysaora quinquecirrha* (~ 1 and ~ 0.5 Hz respectively) (Fig. 3, B–C). The peak Reynolds number (Re) of fluids surrounding medusae occurs at the beginning of contraction, when animals reach maximum velocities. For *L. lucerna* and *C. quinquecirrha* peak Re reached ~ 1000 , while for *Aurelia* sp. peak were ~ 300 , which represents a dominance of viscous forces during swimming cycle, while for the former, inertial forces dominate fluid environment (Fig. 3, D–F). Cumulative distance covered by *L. lucerna* (~ 47 mm) was about twice the distance of *C. quinquecirrha* (~ 24 mm) and three times the distance of *Aurelia* sp. (~ 14 mm) (Fig. 3, G–H). Maximum velocities of *L. lucerna* and *C. quinquecirrha* were similar (5.3 and 5.2 cm*s⁻¹) and two times higher than those of *Aurelia* sp. (2.2 cm*s⁻¹) (Fig. 3 J–L). Velocity peak (Fig. 3 J–L) occur just before maximum bell contraction (Fig. 3 A–C).

Figure 3 Swimming kinematics of scyphomedusae *Lychnorhiza lucerna*, *Aurelia* sp. and *Chrysaora quinquecirrha*. Fineness ratio f illustrates changes on bell shape throughout the swim cycle **A-C**; Reynolds number Re is an indicative of relative dominant forces (viscous vs. inertial) on fluid environment of medusae **D-F**; Cumulative distance covered represents the forward thrust throughout swimming cycle **G-I**; Instant velocities u represents the thrust generated by bell pulsation, with its peak just before maximum bell contraction **J-L**.

Ontogenetic transitions on bell and swimming kinematics

We examined bell kinematics during full swimming cycle of ephyrae and adult shaped medusae (bell diameter >2 cm). Observations of the bell outline revealed measurable differences between contraction and relaxation phases of both ephyrae and adult animals (Fig. 4). A larger portion of the ephyrae umbrella moves during both contraction and expansion (Fig. 4, A and B). In ephyrae, the expansion of the bell led to a partial inversion of the umbrella (Fig. 4 B). In adult-shaped animals only the distal portion, close to the bell margin moves, whereas the region representing ~50% close to the bell apex stays almost immobile (Fig. 4, C and D). The contraction of bell in ephyrae is 2x faster than the relaxation, and 4x faster than the bell contraction of adult-shaped animals (Fig. 4).

Figure 4 – Outlines of half of the bell of *Lychnorhiza lucerna* at equal time intervals (1–8) during bell contraction (A) and relaxation (B) in ephyrae, (scale = 1 mm), and contraction (C) and relaxation (D) in adult-shaped animal (scale = 10 mm).

To evaluate how bell kinematic changes along the transition from ephyra to adult stages, we measured fineness ratio and bell contraction angle in a range of animal sizes (6–70 mm; N=17). For smaller animals, the average fineness ratio (f) was lower ($f = 0.2$ – 0.5) and bell fineness increased considerably during development. After 20 mm of bell diameter, animals had a typical adult bell shape ($f = 0.5$ – 0.8) (Fig. 4). The bell contraction angle (c) also changed during development, which is probably related to changes on f . In ephyrae, movements of contraction and expansion of bell margin were wider ($c=48$ – 78 degrees), whereas in adult shaped animals, this movement was much more restrict ($c=28$ to 35 degree) (Fig. 5).

Figure 5 – Bell kinematics of *Lychnorhiza lucerna* (N=17). Changes in bell shape were quantified by Fineness ratio f (where f = bell height / diameter) and Bell contraction angle c (where c = bell angle at max. expansion – bell angle at max contraction), along the range of bell diameter (mm).

Ontogenetic changes of swimming (u_m , u_{max}) and of feeding current velocities u_f

Similar to other scyphomedusae, *L. lucerna* undergoes a Reynolds numbers (Re) transition in its fluid environment during growth from ephyrae to adult stages. In ephyrae <15 mm of bell diameter ($\log_{10}bd < 1.17$), maximum Re were <325 ($\log_{10}Re < 2.5$) and mean Re were <100 ($\log_{10}Re < 2$) and predominantly near 50 ($\log_{10}Re \sim 1.7$) (Fig. 6). For fluid flowss in the range of Re $1 < Re < 100$, where the

swimming predominantly occurred, both viscous and inertial forces are highly important. In contrast, the fluid environment of larger medusae, >25 mm of bell diameter ($\log_{10}bd < 1.4$), was characterized by higher mean and maximum Reynolds numbers, $Re > 300$ and > 800 respectively ($\log_{10}Re < 2.5$ and 2.9). In this range the fluid environment is dominated by inertial forces (Fig. 6).

Figure 6 – Relationship between body size, as Log₁₀ of bell diameter (mm) and Log₁₀ of mean and maximum Reynolds Number Re in *Lychnorhiza lucerna*.

In order to understand the effect of body size on swimming performance and on the strength of feeding currents, we quantified the mean (u_m) and maximum (u_{max}) swimming velocities and maximum velocities of feeding currents (u_f) produced by bell pulsations for a range of medusan sizes. Body size explained a great proportion of the variation in swimming velocities with u_{max} increasing as bell diameter increased ($F_{1,16}=39.30$; $r^2=0.72$; $p<0.0001$). Maximum velocities of feeding currents u_f also increased linearly as bell diameter increased ($F_{1,16}=84.40$; $r^2=0.84$; $p<0.0001$), but the slope of u_f linear regression was 1.29, while the slope of u_{max} was 0.59 (Fig. 7). Peak fluid velocities, u_f , in small medusae (bell diameter <20 mm) were a slightly lower than

peak swimming velocities, u_{max} . However, in larger medusae, u_f became increasingly greater than u_{max} . Unlike u_f and u_{max} , mean swimming velocities u_m increased with size but plateaued after a 20 mm bell diameter (Fig. 7).

Figure 7 – Relationships between bell diameter of *Lychnorhiza lucerna* (n=17) and maximum velocity of feeding currents (u_f), maximum swimming velocity (u_{max}), and mean swimming velocity (u_m).

Mechanism of fluid entrainment and fluid velocities surrounding the medusae

Analysis of the digital image particle velocimetry (DPIV) revealed the formation of starting and stopping vortices during contraction and relaxation phases, respectively. Fig. 8 shows fluid velocities at different intervals during pulsation cycle; and also shows the medusa at maximum contraction phase, on top at $T=0$, just before the starting of bell expansion. The expansion of the bell was followed by the entrainment of fluids surrounding the exumbrella, and below the bell margin towards the subumbrella ($T= 50\%$). With the maximum bell expansion ($T= 100\%$), fluid entrainment decreased. After maximum bell expansion, the bell margin contracted (Fig. 8, bottom). Between $T=0$ and $T=50\%$ (Fig. 8, bottom), fluids surrounding exumbrella circulated which formed into the starting vortex. Usually, maximum fluid velocities ($u_f=10\text{ cm*s}^{-1}$) were found near bell margin at $T\approx 50\%$ contraction. From $T=0$ to $T=50\%$, the center of the starting vortex was near the bell margin, later moving away

from bell, towards oral arms. After the maximum contraction of bell, the water displacement kept adding energy to the rotation of vortex.

Figure 8– Image sequence of the digital particle image velocimetry (DPIV) technique demonstrating the velocity of fluids ($\text{cm}\cdot\text{s}^{-1}$) surrounding a swimming medusa of *Lychnorhiza lucerna*. Figures on top show the expansion phase, when stopping vortex is formed just below bell margin, and surrounding fluids refill subumbrellar space. Figures on bottom demonstrate the contraction phase, when the starting vortex is formed and the highest velocities are shown at 50% of the period of bell contraction. The white vectors indicate velocities greater than $8 \text{ cm}\cdot\text{s}^{-1}$ ($\sim 9 \text{ cm}\cdot\text{s}^{-1}$). Scale bar = 1 cm.

Fluid transport and oral arms positioning

The manner in which the vortices interact with oral arms may determine how and where prey are captured. Velocities of fluid motion produced by bell pulsations can be decomposed into axial velocities, of a vertical (Y) component, that represents the thrust component, and a horizontal (X) component that represents the fluid transport towards oral arms, or the feeding component (Dabiri et al. 2005). Fig. 9 shows the X

axial velocity ($\text{cm}\cdot\text{s}^{-1}$), relative to the positioning of surfaces of prey capture on oral arms, at different periods during full bell pulsation cycle. Fluid transport from exumbrella towards inside the bell are represented as negative values, whereas transport from inside the bell to outside are positive values (Fig. 9).

Bell contractions in ephyrae produce the highest axial X velocities immediately below bell margin, at 25 and 50 % of the period of total contraction. However, in ephyrae, viscous forces of fluid environment are dominant relative to inertial forces and the velocities are quickly dissipated between 75 and 100% of contraction period. As a consequence of this rapid dissipation, fluid velocities at the surface of prey capture are nearly zero, or slightly positive. During bell expansion, fluids are also transported towards the animal's central axis, but at slower velocities than during contraction. Similarly to bell contraction, fluid transport was also dissipated before reaching prey capture surfaces during bell expansion (Fig. 9). Thus, both bell contraction and expansion are less effective at producing fluid transport towards prey capture surfaces in ephyrae.

Figure 9 – Axial (X) instant velocities during both bell contraction and expansion of an ephyra of *Lychnorhiza lucerna*. Velocities were measured along a transection from the bell margin to the end of oral arm. Each curve represents the velocities taken at time intervals between the start (0) and the end (100%) of both movements.

In adult-shaped animals (>26 mm), similar to the ephyrae, the transport of fluids surrounding the exumbrella towards animal's symmetry axis occurs during both bell contraction and expansion (Fig. 10). After contraction starts, peak velocities were found

between 50 and 100 % of total contraction time. The fluid transport during both contraction and expansion were found in a region of oral arms without prey-capture structures (*digitata* surrounding small mouths), just below bell margin and above the beginning of the surface of prey capture (SPC) (Fig. 10).

In contrast to ephyrae, for adults the starting vortex moves away from bell and continues to transport fluids towards SPC. During both phases, it is possible to see a smaller velocity peak at the end of oral arms of adults. This peak, with nearly half the velocity of the peak just below bell margin, represents the movements of fluids generated during the previous bell pulsation cycle, propagated away from the bell and still transporting the surrounding fluids towards the oral arms (Fig. 10). Thus, because of the higher pulsation frequency of *L. lucerna* and the slower dissipation of vortices, the oral arms receives simultaneously fluids transported by two subsequent bell pulsations.

Figure 10 - Axial (X) velocities during both bell contraction and expansion of an adult-shaped medusae of *Lychnorhiza lucerna* of 26 mm bell diameter. Velocities were measured along a transection from the umbrellar margin to the end of oral arm. Each curve represent the velocities taken at time intervals between the start (0) and the end (100%) of both movements.

Fluid transport inside oral arm structure and the filtration process

One limitation of DPIV technique is the inability to visualize fluid movements between oral arms structures. The fluorescein dye technique was applied in order to visualize filtration process by oral arms. As the medusae expands its bell, fluid is transported just below bell margin to refill subumbrellar cavity (Fig. 11, $T=0$ s). During bell contraction starting vortex is formed and its core rotates outside the oral arms, while the border of vortex ring entrains the oral arm towards animal's symmetry axis (Fig. 11, $T=0.28$ s). During the next bell expansion and formation of its associated stopping vortex on subumbrellar surface, the previous starting vortex rotates along oral arm (Fig. 11, $T=0.56$ s). As the next contraction starts, the fluid previously transported to the inner region of oral arms loses its vorticity, and only diffuses through the end of oral arm (Fig. 11, $T=0.84$ s). The oral arms surface operates as a filtration area as fluid transported to inside oral arms diffuses to outside. The passage of prey through oral arms surface probably triggers nematocyst release by clusters located on the tip of *digitata* and on several parts of inner oral arm structure.

Figure 11 – Sequence of vortex formation by two pulsations cycles and interaction of vortex with oral arms of *Lychnorhiza lucerna*, and a scheme of the sieving mechanism of an oral arm. At 0 and 0.56 s bell is expanding and 0 s shows fluorescein dye been entrained within subumbrellar cavity, below bell margin. Frames at 0.28 and 0.84 s show bell contraction phase and formation of starting vortex, near the beginning of the surfaces of prey capture on oral arms. The frame at 0.84 s shows the fluid diffusing at the tip of the oral arm. Illustration: Silvia de Almeida Gonsales

Prey capture maps

We counted 5893 *Artemia* sp. nauplii captured on oral arms of 5 medusae. In the comparison of prey captures (as percentage) between three wings of oral arms, captures were significantly different (ANOVA, $F_{2,12}= 5.59$, $p<0.05$, Fig. 12) with higher captures along the external wing 2 (EW2) in relation to the internal wing (IW) (Tukey's Test $p<0.05$). At the internal wing there was no significant differences between the regions (1–6) of the oral arm (ANOVA, $p>0.05$), while for EW1 (ANOVA, $F_{4,20}= 8.07$, $p<0.001$, Fig. 12) and EW2 (ANOVA, $F_{4,20}=10.73$, $p<0.001$), significant differences were found, with the most distal region “6” with lower captures than regions “3” and “4”, for the EW1 and with region “6” with lower captures than any other region for EW 2 (Tukey's Test $p<0.05$). When the percentage of captures were normalized by the area of the surface of capture, no significant differences were found between the three wings (ANOVA, $p>0.05$). For both three wings distal regions (5 and 6) had higher captures per unit of area than proximal region “1” (Fig. 12).

Figure 12– Map of prey captures along three distinct wings (one internal and two external), which were subsequently divided in regions (1-6 for the internal wing or 2-5 for the external wings) in relation to the distance from the bell.

Mechanisms of prey escape or capture

In order to describe modes of prey capture, we added live net-collected zooplankton around swimming *L. lucerna* medusae. Video sequences revealed prey reactions to feeding currents produced by medusae pulsations and several prey capture events. Bell pulsations produce vortices that transported fluid surrounding the exumbrella towards surfaces of prey capture characterized by nematocyst clusters on oral arms. Prey items in the fluid that were entrained by bell pulsations sometimes reacted to this transport by exhibiting fast escaping jumps (Fig. 13).

Figure 13 – Scheme of escaping response performed by the copepod *Temora turbinata*, after the encounter with the predator *Lychnorhiza lucerna*. At the time of the encounter, the copepod is upside down and predators bell is fully expanded (opaque bell). The beginning of bell contraction triggers an immediate escape response from the copepod. The copepod performed several escaping jumps, and its position along 4 time intervals of 15-ms is shown as opaque figures and the final position in a solid figure. Scale bar = 2 mm.

If prey did not exhibit escape responses or if the kinematic properties of feeding currents overwhelmed the of escape jumps, prey were transported down the bell margin toward oral arms. Depending on the location where prey were transported, they

interacted with predator's oral arms in different ways. When prey were transported to the outside the oral arm surface, they were vulnerable to the fluid transport by the starting vortex as it is propagated downwards and pulled fluids toward oral arm surface (Figs. 8 and 10). Figure 14 shows the capture of a copepod *Temora turbinata*, which was transported to outside the oral arm. The copepod approached the oral arm at $T=0.000$ s and starts a escaping jump at $T=0.012$ s (Fig. 14). Nevertheless the narrow angle of this jump, relative to the oral arm surface, plus the fluid transport by the starting vortex, transported the copepod towards oral arms surface at $T=0.024$ and $T=0.036$ s where the *digitata* discharge nematocysts that sticks to the prey and stay immobilized up to the end of this sequence (Fig. 14).

Figure 14 – Image sequence of the capture of a copepod *Temora turbinata* by the medusa *Lychnorhiza lucerna*. The copepod detects the predator's oral arm at time $T = 0.000$ s and starts a escaping jump ($T=0.012$ – 0.024 s). Nevertheless the escaping jump is performed in an angle that result in capture by the predator (0.036 s).

Another mode of prey capture involves transport to inside oral arms and a sieving mechanism. Fig. 15 shows a copepod that was transported through the upper part of oral arms, just below the bell margin, where there is not a surface of prey capture

(Fig. 10). Prey passed freely inside the oral arms. Afterwards, as fluid diffused throughout oral arm surface to outside, some prey items then contacted the *digitata*, and were retained in a sieving process (Fig. 11). Figure 14 shows a copepod of *Temora turbinata* at the inner region of oral arm ($T=0.000$ s) trying to emerge at the oral arm surface by a gap between the *digitata*. Nevertheless, at $T=0.016$ s, the copepod touched some *digitata*, and was immediately captured. The copepod exhibited an escape jump ($T= 0.032$ s), but it was captured by another region with *digitata* ($T= 0.048$, Fig. 15).

Figure 15 – Image sequence of the capture of a copepod *Temora turbinata* by the medusa *Lychnorhiza lucerna*. The copepod is transported by the feeding currents to the inside region of oral arms, where it is at time $T= 0.000$ s. The copepod tries to emerge at the oral arm surface (towards the reader) but touches the *digitata* of the oral arms surface ($T=0.016$ s). After that, the copepod tries to exhibit another escape jump (0.032 s) and is captured again ($T= 0.048$ s).

The contact of prey with nematocyst clusters on the tips of *digitata* may trigger nematocyst discharge that entangles or perforates prey. After the contact of prey with *digitata* in the oral arms, the latter immediately starts a contraction movement, bringing the attached prey toward the mouth opening. When captured, some copepods are

instantly immobilized, while others struggle to escape by exhibiting jumping behaviors, but *digitata* adhere strongly to prey. On the other hand, several sequences revealed the absence of capture reaction by the *digitata*, especially in the case of contact with diatoms of the genus *Coscinodiscus* (Fig. 16). Figure 16 shows a detail of the oral arm of *L. lucerna*, with a diatom colliding with *digitata*, which do not react. At $T= 0.128$ s, a copepod of *Temora turbinata* is transported toward the same region where the diatom was and is immediately captured by a fast reaction of the *digitata* (Fig. 16). In a next step of our project, we will quantify contacts of several types of prey with the predator *L. lucerna*, in order to better understand this possible factor of prey selectivity, at the level of response of nematocysts to the contact of different types of prey.

Figure 16 – Image sequence of the contact of a diatom *Coscinodiscus* sp. (red circle) with the *digitata* of *Lychnorhiza lucerna* oral arms and the absence of capture reaction by the predator. At time $T=0.128$ s, a copepod *Temora turbinata* is transported by feeding currents towards the same region of the diatom, and is immediately captured by the medusae, while the diatom is released.

DISCUSSION

Swimming kinematics among scyphomedusae

Despite the phylogenetic constraints on general morphology of scyphomedusae (Costello *et al.* 2008), some variation on morpho-functional traits may be observed relative to swimming kinematics. Larger scyphomedusae share some morphological and functional features such as the relatively flattened bell (bell fineness <1) and the constant bell pulsations transporting fluids toward surfaces of prey capture (Ford *et al.* 1997; Costello *et al.* 2008). Nevertheless, patterns of swimming kinematics vary between the groups. When comparing individuals between 2 and 4 cm of bell diameter among the group of Semeostomeae medusae, *Chrysaora quinquecirrha* (Desor, 1848) and *Cyanea capillata* (Linnaeus, 1758) swim at lower bell contraction frequencies (0.8 and 0.5 Hz) while the Rhizostomeae, *Lychnorhiza lucerna*, *Stomolophus meleagris* Agassiz, 1862 and *Phyllorhiza punctata* von Lendenfeld, 1884 swim at higher frequencies (2-3 Hz) and reach maximum velocities between 5 and 7 $\text{cm}\cdot\text{s}^{-1}$ (Costello & Colin 1995; Ford *et al.* 1997; D'Ambra *et al.* 2001).

Higher bell pulsation frequencies of rhizostome medusae are in part due to the fast recovery of the bell after contraction. When comparing time of bell contraction vs. expansion, both phases are faster in *L. lucerna* (0.26 vs. 0.30 s) than for *C. quinquecirrha* (0.36 vs. 0.40 s) or for *Aurelia* sp. (0.28 vs. 0.44). The bells of rhizostome medusae expand faster probably because of mechanical properties of its mesoglea compared to other groups of scyphomedusae. The mesoglea is formed by collagen fibers with elastic properties, and stores elastic potential energy of the bell contraction. Thus, the mesoglea is responsible for the bell recovering, in an antagonistic action to the circular subumbrellar musculature (Muskatine & Lenhoff 1974; Shaposhnikova *et al.* 2005). Rhizostomeae medusae (*Cotylorhiza tuberculata* and

Rhizostoma pulmo) have up to six times more collagen than scyphostome medusae (*Aurelia* sp. and *Pelagia noctiluca*) (Addad *et al.* 2011). The remarkable hardness of rhizostome medusae bell allows higher swimming, and potentially feeding performance, since the volume of cleared water depends on the volume of entrained water by bell contractions (Acuña *et al.* 2011; Katija *et al.* 2011). Whereas some scyphostome medusae enhance prey encounter rates by developing long capture structures, such as in *C. capillata* which bears tentacles up to 10 m long (Russell, 1970), rhizostome medusae have high frequency swimming patterns which allow larger volume of fluids filtered and also higher encounter rates with prey.

Ontogenetic transitions on bell and swimming kinematics

While adult scyphomedusae can reach up to 2 m of bell diameter in some species, ephyrae (juvenile scyphomedusae) measure only a few millimeters. The increase in body size of scyphomedusae occurs parallel to the transition from a fluid environment where viscous and inertial forces are equally important ($Re < 100$), to an environment where inertial forces become increasingly dominant in adults (Higgins *et al.* 2008). Morphological and functional changes that follow transition in scale and in fluid environment enable organisms to operate (*e.g.* propulsion and feeding) efficiently throughout development. This morphogenesis in early development of scyphomedusae is adapted to a cost-effective allocation of tissue growth in order to effectively perform swimming (Feitl *et al.* 2009, Narowth *et al.* 2010) and feeding (Higgins *et al.* 2008), while animal's face the necessities of a shifting fluid environment.

L. lucerna changes the typical ephyra bell morphology in early development. After 2 cm bell diameter (Fig. 7) the bell transitions from a very oblate ephyral bell (fineness ratio $f=0.2-0.4$) to a more prolate bell ($f=0.5-0.8$). This transition meets the demand for a more hydrodynamic body shape in an inertial dominated fluid

environment and results in change in the pulsation mode. In ephyrae, bell pulsations have much longer stroke lengths, the bell become inverted at maximum expansion and a great proportion of the bell bends, resulting in higher contraction angles whereas in adults little more than the tip of bell margin bends (Figs 4 and 5). This is because in ephyrae, the mode of propulsion is a drag-based paddling, which is a common alternative in organisms living in low Re (Higghins *et al.* 2008, Feitl *et al.* 2009). In this mode, the forward thrust is directly related to the projected surface area (*i.e.* ephyra lappet), velocity and stroke length (Blough *et al.* 2009). In an environment dominated by viscous forces, forward thrust immediately ceases after the power stroke, thus the wider contraction angle of bell maximize the amplitude of the stroke and enables higher amount of thrust produced.

Ontogenetic changes of swimming (u_m , u_{max}) and of feeding current velocities u_f

Another consequence of body size increase is an ontogenetic scaling on the force of swimming (u_m and u_{max}) and of feeding currents (u_f). For small lower Re ephyrae (bell diameter <20 mm), the medusa's velocity was greater than the maximum fluid velocity ($u_{max} > u_f$). In contrast, adults bell pulsations moved the fluid faster than maximum medusae speeds ($u_f > u_{max}$). Adult medusae (bd >20mm) accelerated fluids by generating a pair of adjacent opposite rotating vortices (stopping vortex at bell expansion and of starting vortex during bell contraction. This greatly accelerated fluid contributes to increased swimming thrust and enables a low-cost mode of propulsion (Dabiri *et al.* 2005). Nevertheless, our observation that $u_f > u_{max}$ in a fluid regime dominated by inertial forces, indicates that not all acceleration observed on fluids, after bell pulsation, translate into swimming movement for the animal.

Maximum u_f values were found at the interface of these adjacent vortices. It is not clear how the interaction of two opposite-sign vortices affect local fluid dynamics,

and which are the consequences for fluid transport to prey capture structures. Dabiri *et al.* (2005) argued that at the interface of these vortices total momentum of each wake vortex is increased, which probably had generated the maximum velocities of feeding currents found here, around 50% of bell contraction time and near bell margin (Fig. 8).

Fluid transport and oral arms positioning

In the viscous dominated stages ($Re < 100$) momentum transfer of flow is minimal and bell pulsations of *L. lucerna* ephyrae produce weaker fluid transport toward surfaces of prey capture (Fig. 9). The utility of bell pulsations as a particle transfer mechanism in ephyrae is thus very limited, since vortices of bell pulsations quickly dissipate after leaving bell margin (Hamlet *et al.* 2011). As medusae grow, dissipation of vortices takes longer and vortices become increasingly important to fluids transport toward oral arms. Higgins *et al.* (2008) demonstrated that the elongation of oral arms and tentacles in *C. capillata* occurs at the same extent that the dissipation of feeding currents takes longer in a transition to inertial dominated environment. These authors also questioned how universal is the coincidence between hydrodynamic and morphological development among scyphomedusae. In *L. lucerna* the oral arms also undergoes a distal elongation as a transition to the adult body plan takes place. Longer trailing structures enable a better utilization of fluid transport, while the bell of adults is pulsating to produce a pair of vortices structures, the vortices produced by the previous pulsation cycle are still pulling fluids toward the tip of oral arms (Fig. 10). It appears that scyphomedusae invest in tissue production of longer prey capture structures only after more powerful flows are produced by larger animals, which consistently transport prey further from the bell margin.

Interaction of vortex with oral arms and the filtration process

The oral arms of Rhizostomeae have a very complex three-dimensional arrangement, which operates as a filtration structure. The original ephyra lip is laterally folded and ramified into a structure that resembles the head of a cauliflower in adults (Russell 1970). This highly complex edge has many millimetric mouth apertures, flanked by small finger-like processes called *digitata*, which terminate in a nematocyst cluster (Fig.1 and 11). Between these structures there are many gaps of rounded or hexagonal shape whereby the fluid entrained pass through, while larger particles may be retained in a sieving process. The fluid entrained into oral arms diffuses to outside losing speed and vorticity, probably because the boundary layers surrounding the gaps may overlap to the extent that flow in between these structures is highly reduced. Nevertheless, ciliary currents on external oral arm surface may enhance outward flow motion, similar to the feeding mechanism of *Aurelia* sp. (Southward, 1955). In addition to this sieving process, the center of the vortex moves downwards turning and continuously transporting prey to outside surface of oral arm. When prey touches oral arms, the *digitata* release nematocysts that capture prey in a sticking mechanism.

Although the production of feeding currents via bell pulsations is widely used among large medusae (Colin & Costello 1995), the shape and positioning of feeding structures in relation to swimming vortices are variable. These traits can result in distinct modes of prey capture and prey selectivity. In medusae with marginal tentacles, like the scyphozoan *Aurelia* sp. and the hydrozoan *Aequorea victoria*, tentacles lie in the center of the starting vortex (Dabiri *et al.* 2005; Lipinski & Mohseni 2009). However, Rhizostomeae lack marginal tentacles and have a great diversity of bell morphologies and oral arms shapes, which generate distinct modes of interactions between vortices of bell pulsation and oral arms (Fig. 17). In *L. lucerna*, the edge of the

wake vortices contact the oral arms entraining fluids thorough and the center of vortex moves freely downwards transporting the surrounding fluids towards the oral arms. This is very different from the medusa *Cassiopea* sp., which has a flatter bell and oral arms furthest from the animal's symmetry axis, the entire vortex (not only its vicinity) translates through the oral arms (Hamlet *et al.* 2011; Santhanakrishman *et al.* 2012).

Figure 17. An overview of the diversity of body plans among Rhizostomeae medusae; the schemes are representing members of different genera. *Cassiopea* (A); *Cephea* and *Netrostoma* (B); *Stomolophus* and *Eupilema* (C); *Rhopilema* (D); *Acromitus* (E); *Phyllorhiza* (F); *Thysanostoma* (G); *Lobonema* (H); *Crambionella* (I).

The position of the millimeter scale mouthlets also changes among species of Rhizostomeae. In *L. lucerna* mouths are restricted to the three oral wings, on the oral

arms, whereas in *Stomolophus meleagris* (as well as in some species of the Suborder Daktylophorae, formerly known as the superfamily Scapulatae), mouths are also present on scapulets (a second area of the mouth arms which also contains mouth openings) inside subumbrella (Russell 1970). The scapulets capture prey during expansion phase, while fluid entrainment refills subumbrellar cavity (Larson 1991; Costello & Colin 1995). Although *L. lucerna* lacks scapulets, prey captures during bell expansion may occur since fluid transport toward oral arms occurs during both bell expansion and contraction, likewise in *P. punctata*, which also lacks scapulets (D'Ambra *et al.* 2001).

Our inability to visualize the fluid motion inside structures of oral arms limits our DPIV analysis. Nevertheless, use of the fluorescein dye technique allowed the visualization of fluid passing through the filtering structure of oral arms (Fig. 11). During bell expansion, fluid surrounding exumbrella is transported to inside oral arms. At the beginning of bell contraction, the edge of the starting vortex is entrained to inside oral arms losing its vorticity, whereas the center of starting vortex keeps turning while moves away from the bell (Fig. 11). The way in which water is driven across the oral arms explained differences on the amount of prey captures between regions of oral arms. The internal wing receives only fluids entrained below bell margin in the region without prey capture structures (Fig. 10). Yet the external wings had higher proportions of prey capture since they receive both the flux entrained within oral arms (similar to the internal wing) sieving prey items, but also continuously receive the fluids pulled by the vortices moving away from the bell margin, sticking prey items from outside (Fig. 14).

The unique morphology of filtration apparatus at the scale of the *digitata* in Rhizostomeae seems to be very conserved among species (Uchida 1926; Sugiura 1966; Russell 1970; Holst *et al.* 2007), possibly demonstrating selective advantages and

constraints imposed by the fluid regime, to operate efficiently. A deeper evaluation of morphological and functional properties of this structure must be carried out over a wide set of Rhizostomeae species, which dominates tropical and subtropical pelagic areas, in order to understand ecological success of species in the species in this group.

Mechanisms of prey escape or capture

Through the transport of fluids towards structures of prey capture, animals increase the rate of predator–prey encounter. Several mechanical, physiological and environmental parameters may govern this type of predator–prey interaction. In relation to prey, features such as prey perception to chemical (Carr & Pitt 2007) or hydrodynamic stimuli (Fields & Yen 1997; Buskey *et al.* 2002), prey escape force (Viitsalo *et al.* 1998) and prey size (Suchman & Sullivan 2000) may affect the likelihood of prey to be captured. In relation to predators, the velocity of feeding currents (Costello and Colin 1994), the capacity of predator to stay undetectable to its prey (Colin *et al.* 2010), the volume of entrained water (Acuña *et al.* 2011), the reaction of retention structures to prey encounter (Jaspers *et al.* 2011) and the retention efficiency (Riisgård 1988) are among the main parameters governing prey capture success. In addition, features of surrounding fluids may affect predators–prey interactions, such as: (i) higher levels of turbulence, which erode feeding currents produced by predators (Sutherland *et al.* 2014); (ii) low levels of dissolved oxygen, which decrease prey escape ability (Decker *et al.* 2004) and feeding performance of predators (Shoji *et al.* 2005); (iii) low levels of visibility, which decrease effectiveness of visual foraging (Eine *et al.* 1999).

Costello and Colin (1994) proposed a model for mechanisms of prey capture for medusae, which relies on the comparison between velocity of feeding currents of bell pulsations and prey escape speed. Since rhizostome medusae are robust swimmers they

probably would be able to capture more evasive prey than other scyphozoan groups (D'Ambra *et al.* 2001). The maximum velocities of feeding currents u_f found here ($\sim 10 \text{ cm} \cdot \text{s}^{-1}$) (Figs 6 and 18) were lower than the escape response of calanoid copepods, which are usually between 30 and 50 $\text{cm} \cdot \text{s}^{-1}$ (Burdick *et al.* 2007; Buskey *et al.* 2011). Data about diet and prey selectivity for other rhizostome species are scarce and not conclusive regarding a possible trend of positive selection for fastest escaping prey (Fancett 1988; Larson 1991). Despite values of u_f would suggest success in escape of copepods, gut content data of *L. lucerna* demonstrate that these medusae are capturing highly evasive calanoid copepods (*Acartia* spp., *Paracalanus* spp. and *Temora turbinata*) at the same proportions as field availability (Nagata *in prep*). Thus, would be possible that medusae capture prey even if prey escaping response reaches higher velocities than predators feeding current?

Figure 18 – Images of the digital particle image velocimetry (DPIV) technique demonstrating the velocity of fluids ($\text{cm} \cdot \text{s}^{-1}$) surrounding a swimming medusa. On left, at $T=0$, is the contraction phase and at $T= 0.160 \text{ s}$ the expansion phase. During contraction starting vortex (red area) is formed and velocity of up to 10 cm s^{-1} are found driving fluids toward oral arms. During bell expansion, stopping vortex (blue area) is formed near bell margin while stopping vortex moves downwards and continues to pull fluids toward oral arms.

A preliminary evaluation suggested that both successful escaping jumps and prey retention occurs with evasive calanoid copepods (Figs 13–16). Copepod escaping jumps are usually short-term (up to 30 ms) responses and copepods reach distances smaller than 20 mm (Buskey *et al.* 2002; Burdick *et al.* 2007). Yet, the vortices produced by *L. lucerna* affect an area up to half of bell diameter and transport surrounding fluids toward oral arms for longer periods (up to 500 ms). Thus, in order to avoid the entrainment, the copepod must exhibit more than one escape jump and with the direction opposite to the flow velocity. The reorientation of the copepod before the escaping jump not always occurs to an opposite direction in relation to disturb source (Buskey *et al.* 2002), which explains “mistakes” of reorientation leading to jumps towards oral arms (Fig. 14). Several other factors such as the position of the copepod at the moment of fluid transport and the reaction timing may determine the likelihood of a prey successfully escape predation (Peng & Dabiri 2009; Buskey *et al.* 2011). Further efforts should be addressed in order to quantify features of this predator-prey interaction such as: (i) distance from predators where preys trigger the escaping response; (ii) the intensity of hydrodynamic signal that triggers this response; (iii) kinematic properties of escaping jumps among prey species.

CONCLUSIONS

Swimming behavior of *L. lucerna*, which characterizes Rhizostomeae medusae, is much more robust in relation to other scyphozoan groups. A collagen-rich mesoglea in Rhizostomeae enables faster recovering of bell and higher frequency of bell pulsations. The ontogeny of *L. lucerna* medusae involves substantive alterations on bell and oral arms morphology as well as in its functional mechanisms, which meets the demands of a changing fluid environment. In ephyrae, the viscous environment of lower Reynolds number ($Re < 100$) imposes constraints to the feeding mechanisms based on

fluid transport by vortices. Whereas in adults as inertial forces become dominant, vortices produced by bell pulsations become increasingly important to fluids transport toward oral arms. *L. lucerna*, as well as other scyphomedusae, maximizes the contact with these vortices by developing long trailing structures (oral arms) at the same extent that the dissipation of feeding currents takes longer. A combination of DPIV and fluorescein dye visualization technique demonstrates the interaction of vortices with the complex structure of oral arms where prey capture occurs. Prey capture events demonstrated that a simple comparison between speeds of feeding currents vs prey escape response is insufficient to predict the likelihood of capture success. Many other factors may govern this interaction such as, prey detection ability, prey reorientation for elicit jumps, selective discharge of nematocysts. Further research effort is needed to better characterize details of pre and post encounter between medusae and their prey, which have important ecological implications, helping to improve our understanding about their roles in the pelagic ecosystems.

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Appendix 1 – Sampling points off Cananéia Estuary (A). The estuary plume (B), where organic material (C) and medusae (D) accumulates on surface waters. Collection of a *Lychnorhiza lucerna* medusa with hand net (E). Medusae maintained inside containers at CEBIMar-USP (F). Medusa fed with *Artemia* sp. nauplii, scale bar = 1 cm.

Appendix 2 – Scheme of a digital particle image velocimetry system. Camera FASTCAN 1024 PCI A. Vessels where animals were recorded B. 530-nm wavelength laser sheet C.

**CAPÍTULO 2: DIET, PREY SELECTIVITY AND
FEEDING RATES OF THE RHIZOSTOME
SCYPHOMEDUSA *LYCHNORHIZA LUCERNA* IN
SOUTHWESTERN ATLANTIC COAST**

DIET, PREY SELECTIVITY AND FEEDING RATES OF THE RHIZOSTOME SCYPHOMEDUSA *LYCHNORHIZA LUCERNA* IN SOUTHWESTERN ATLANTIC COAST

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Despite the ecological importance of Rhizostomeae medusae and discussions about increases in some populations, the group is one of the least known among gelatinous zooplankton. This study quantifies *in situ* gut content of the South American species *Lychnorhiza lucerna* in order to: (i) evaluate procedures of extraction and quantification of gut content (ii) describe the species diet, (iii) describe prey selectivity patterns, and (iv) quantify feeding rates in order to evaluate the specie's potential trophic impacts. Specimens were collected in surface waters along the southeast coast of Brazil, immediately preserved, along with plankton samples near medusae aggregations. Most prey items (~70%), were extracted by rinses on the cruciform stomach, ~16% remained attached to gastric cirri after rinses, non-stomach body regions (oral arms and umbrellar canals) accounted for a small proportion of prey found (<10%). A total of 43 taxa were identified in gut contents, with calanoid copepods of the genera *Acartia*, *Temora*, and *Paracalanus* as the main (53%) components, followed by copepods of Cyclopoida (15.1%) and Poecylostomatoida (11.4%), bivalve veligers (~7%), and diatoms (4.3%). *L. lucerna* is a generalist zooplanktivore with diet composition mostly similar to the environment availability. Nevertheless, proportion of calanoid copepods increases with medusa size, whereas diversity of diet decreases. The ability of *L. lucerna* to capture fast and sensitive calanoid copepods of larger sizes increases as the medusae grow, because of ontogenetic scaling in the feeding current strength. Feeding rates of *L. lucerna* ranged from 110 to 102871 copepods ingested day⁻¹. We estimated that an aggregation of *L. lucerna* reported in north Argentina coast could consume from 6 to 12% of copepods standing stock day⁻¹, which indicates that this species play a major trophic role in Southwestern Atlantic coastal waters.

Key words: gelatinous zooplankton, predation, jellyfish, feeding biology, scyphomedusae.

INTRODUCTION

Scyphomedusae are known as voracious predators of plankton, because of their higher feeding rates (Mills 1995, Purcell 1997, Purcell & Arai 2001). When they occur in high densities, planktonic communities can be completely depleted, potentially compromising the recruitment of fish species of commercial value (Möller 1984, Behrends & Schneider 1995). Since blooms of some jellyfish populations become problematic, there has been an increasingly demand for knowledge about their feeding biology and their trophic role (Purcell 2009, Gibbons & Richardson 2013).

Studies on feeding ecology (and other biological aspects) of scyphomedusae are concentrated in a few better-studied taxa such as *Aurelia* and *Chrysaora* spp., whereas medusae of Rhizostomeae (~ 90 spp., 60 % of Scyphozoa) (Daly *et al.*, 2007) remain as one of the least known groups of gelatinous zooplankton (Purcell 2009). Rhizostome medusae occur mainly in tropical and subtropical coastal areas (Kramp 1970, Russell 1970), where intense blooms of some populations affect negatively coastal activities such as fisheries, tourism and energy production (reviewed in Purcell *et al.* 2007). On the other hand, these medusae are traditionally consumed as food in many countries of Asia, and fisheries targeting these medusae are now expanding throughout other non-consumer countries (Doyle *et al.* 2014). Despite the ecological and economic importance of rhizostome medusae, the lack of biological information still limits the understanding of their trophic role, as well as the ecological consequences of their blooms.

Along tropical and subtropical Southwestern Atlantic, *Lychnorhiza lucerna* Haeckel, 1880 is the dominant rhizostome species (Morandini *et al.* 2005, Schiariti *et al.* 2008). While in north Argentinean coast (35°S) the presence of this species is

restricted to the warmer months (December–May), in South and Southeast coast of Brazil (22°–32°S), the species occur throughout the year, without a common seasonal pattern of population increments between distinct regions (Morandini 2003, Nogueira Jr. 2006, Nogueira Jr. et al. 2010, Schoeder et al. 2014, Morandini unpublished data). Aggregations of *L. lucerna* represent a nuisance to fishermen because they reduce total captures and catch quality, damage nets and traps and even prevent operations such as shrimp trawling (Schiariti et al. 2008, Nagata et al. 2009). Despite this species is occasionally dominant in pelagic environment of South Atlantic (Colombo et al. 2003, Nagata et al. 2009), its trophic role and potential predatory impacts are completely unknown due to lack of basic data on its feeding biology

Nutritional strategies are diverse among rhizostome medusae, ranging from a diet over distinct mesozooplankton items in azooxanthellate species (Fancett 1988, Larson 1991, Peach & Pitt 2005, Pitt et al. 2008) to the ingestion of micro and mesozooplankton, along with autotrophy in zooxanthellate species (Smith 1936, Muscatine & Marian 1982, Kikinger 1992, García & Durbin 1993). Since most medusae are selective feeders (Purcell 1997) and knowledge about feeding habits of rhizostome medusae are limited, generalizations may lead to conceptual mistakes. Concerning rhizostomes a few morphological and behavioral traits are indicative of their diet, but are still far from determine their feeding habits.

The morphology of the feeding apparatus of rhizostome medusae imposes a limitation to the ingestion of large prey. The four mouth lips of rhizostome ephyrae develop into eight filtering oral arms in adults, with thousands of small mouths with narrow apertures (<3 mm of diameter) (Huxley 1849, Uchida 1925, Sugiura 1966, Russell 1970, Lee et al. 2008). Thus, while semaeostome and coronate medusae can ingest both small and large prey (*e.g.* large bodied jellyfish and fish) rhizostome

medusae are structurally limited to a prey size fraction of mesozooplankton (Larson 1991).

In scyphomedusae, the bell pulsations that propel the animals also operates to prey transport and increase predator–prey encounter rates (Costello 1992, Costello & Colin 1994). During the pulsations, fluids are accelerated forming a complex wake-vortex structure that transport prey through oral arms and tentacles (Costello 1992, Costello & Colin 1995, Dabiri et al. 2005). Costello & Colin (1994) proposed that the likelihood of success on prey capture may be determined by a comparison between maximum velocity of feeding vortex and the maximum velocity of swimming of prey during escaping responses. Thus, swimming prey items faster than marginal flux of bell pulsation would be able to detect threshold shear and trigger evasive jumps, and avoid capture (Costello & Colin 1994). Since rhizostome medusae are stronger swimmers and produce faster vortex than other scyphomedusae, they would be able to capture more evasive prey (*e.g.* large calanoid copepods) (Costello & Colin 1995, D’Ambra et al. 2001; Nagata *et al.*, non-published data). Nevertheless, prey selectivity of the two studied rhizostomeae medusae for fast prey (calanoids) were non-conclusive, one being positive (Fancett 1988), and the other negative (Larson 1991), and thus additional studies are still necessary to check if there is a general pattern for the group.

A considerable number of studies, mainly since ~1970, has applied gut content quantifications in order to answer questions about feeding ecology of scyphomedusae. Nevertheless, unlike for cephalopods and fishes, protocols of extraction and quantification of prey are still to be standardized for medusae (Hyslop 1980, Gibbons & Richardson 2013). This study quantifies gut content of *Lychnorhiza lucerna* in order to: (i) evaluate procedures of extraction and quantification of gut content applied to Rhizostomeae, (ii) describe its diet, (iii) evaluate patterns of prey selectivity, and (iv)

quantify feeding rates. We hypothesized that as the strength of bell pulsations scales with size (D'Ambra et al. 2001) increasingly faster feeding currents enables predators to capture faster escaping prey. If so, the capture of fast prey such as calanoid copepods, relative to field availability, would increase as medusae grow. Dietary shifts as a consequence of growth was described for a few scyphozoan species such as *Aurelia* sp. (Sullivan et al. 1994, Graham & Kroutil 2001), but was never tested among rhizostome medusae. Another possible consequence of the strongest swimming pattern of rhizostomes than sennaeostomes is a probably higher metabolic demand (Purcell 2009), which would be demonstrated by possible higher feeding rates, than species of other groups. We compared feeding rates of *L. lucerna* with other scyphomedusae, and we evaluate whether this parameter changes with size, temperature and field prey density. Other specific questions addressed in this study include: *i*- What are the consequences of distinct sampling protocols to gut content-based estimates of feeding rates? *ii*- Does copepod size in diet, relative to field population, changes along medusae size range? *iii*- Does our estimates of total ingestion are enough to support animal's metabolic demands?

MATERIAL AND METHODS

Samplings

Samplings were carried out in three locations of South Brazilian Bight: Cananéia Estuary; Paranaguá Estuary; and São Sebastião channel, aboard small boats (Fig. 1). At each sampling site a minimum of 6 animals and a total of 40 animals were collected. For complete dataset description (sampling sites, dates, number of animals, sizes and analytical approach) see Tab. 1. Individuals were carefully collected in surface waters using buckets or a dip net of 1 mm mesh size. Bell diameter between opposite rhopalia were measured using a plastic ruler (mm scale); specimens were immediately preserved in 4% formaldehyde solution in filtered (45µm) sea water, and individually packed into plastic bags and stored inside buckets. The composition of co-occurring zooplankton was estimated in order to evaluate prey selectivity. Plankton samples (N = 3–4) were collected from the surface water near medusae aggregations, in short horizontal tows performed by hand, with a 50 cm mouth diameter, 200µm mesh plankton net. The volume of filtered water was measured with a Hydrobios flowmeter.

Figure 1 – Sampling sites along South Brazilian Bight. Paranaguá Estuary (A), Cananéia Estuary (B), and São Sebastião channel (C).

Table 1 – Sampling sites, dates, number of medusae collected, size range (cm), method of quantification and number of plankton samples collected.

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

Total dissection: proportion of prey within body regions

Prey items were quantified within all animal's body regions (see Fig. 2B, C) of seven animals, in order to evaluate the amount of bias resulted from quantification of prey from isolate body regions, or by onboard extraction of prey. Body regions were classified as: oral arms (*OA*), oral disc (*OD*), cruciform stomach (*CS*), and umbrellar canals (*UC*), according to the terminology of Russell (1970) and Mianzan & Cornelius (1999). Prey items were identified to the lowest taxonomic level under stereomicroscope. Total ingestion (*G*) was considered as the total prey items counted in all these body regions.

In order to quantify a possible loss of prey during the storage, we filtered the formaldehyde solution around the preserved animal ($n = 7$), washed the storage plastic bags and the content were retained using a 45 μ m sieve. First, the oral arms and the oral disc were removed from the umbrella, by cutting the four pillars (Fig. 2C). In the bell, the *CS* was dissected from the subumbrellar side by cutting around the edges. The layer removed from the *CS* is formed by pleated walls covered by gastric cirri, where the digestion occurs (Mianzan & Cornelius 1999). This layer, as well as the cavity of the *CS*, was rinsed with jets of tap water, over a flat container, the content retained in a 45 μ m sieve, and stored in 50 ml plastic tubes for settling. The processes of rinsing, filtering and storing the gut content from *CS* were repeated until no prey items could

be found, examining the sieve under the stereomicroscope. After 1h of settlement, the supernatant of the 50 ml tubes were discarded and the remaining were concentrated and stored in 4% formaldehyde. This sample was called “extracted gut content” (*EGC*) and were counted in a Bogorov chamber under a stereomicroscope.

The removed layer from *CS* were scanned under stereomicroscope to count prey items that remained attached to the gastric cirri after the rinses, and this sample was named residual of the “pleated walls” (*PW*). The *OA* were detached from *OD* and stored apart. To enhance the visualization of internal canals of the *OA*, we injected methylene blue using a syringe (Fig. 2D). The quantification of prey in *OA* was carried out under stereomicroscope firstly scanning the surface of *OA*, and later dissecting the canals. The *OD* of *L. lucerna* is a thick structure that connects the 4 pairs of *OA* to the umbrella by means of four large pillars inserted on the subumbrellar surface (Fig. 2C). Internally to the *OD*, four large canals transport the food from *OA* to the *CS*. Gastric cirri cover these canals, which makes the *OD*, the first digestive region of the animal’s body. These canals were dissected under stereomicroscope and prey counted within gastric cirri. In the umbrella, the complex canal system (*e.g.* ring, centripetal, radial canals) were also stained with methylene blue and dissected under the stereomicroscope, from the subumbrellar side. For the remaining 33 animals, only samples of the *EGC* were quantified.

Figure 2. *Lychnorhiza lucerna*, adult medusa, scale bar 3 cm, picture of Dr. Alvaro E. Migotto (A). Subumbrellar view of detached umbrella. Note umbrellar canals (UC) stained with methylene blue. Arrows indicate central part of cruciform stomach (CS) and edges with pleated walls (PW), from which extracted gut content (EGC) was obtained, scale bar 5 cm (B). Oral arms inserted in the oral disc (OD), scale bar 3 cm (C). Oral arm (OA) with oral canals stained, arrow indicating the central canal, scale bar 1 cm (D). Detail of umbrellar margin, with stained umbrellar canals, scale bar 1 cm (E).

In the seven animals that all body regions were analyzed, the *EGC* represented 69.79% (± 5.86) of the total number of prey found in all body parts (*G*). We assumed that proportion, to estimate the total ingestion (*G*) of the remaining 33 animals, which only *EGC* was quantified as: $G = EGC * 69.79^{-1} * 100$. See also Results section for details.

Diet composition, prey selectivity and ontogenetic changes on feeding parameters

We calculated the diversity of *L. lucerna* diet as number of prey taxa per medusae and with the Shannon's diversity index (H') of the *EGC*. Prey selectivity was estimated by the index "C" of Pearre (1982) which is commonly used in studies of gelatinous zooplankton (Purcell 1991, Purcell & Surtevant 2001, Graham & Kroutil 2001). This index evaluates the predator's preference or avoidance for a determined prey item, considering its availability in the field. The significance of the selectivity is calculated by an χ^2 analysis of a two x two contingency table elaborated with densities of a prey item in the field and its abundance in the *EGC*. We applied temperature-corrected digestion time. The value of "C" ranges from -1 to 1 reflecting the magnitude of this prey selection. Prey selectivity was evaluated only for taxa sampled quantitatively by our plankton net, excluding prey items <200 μ m, such as small copepods and mollusk larvae, which were probably undersampled.

In order to test whether changes in medusae body size are related to changes on diet parameter (*e.g.* prey composition, prey selectivity index "C", and prey size), these last were used as dependent variables against wet weight (g) in simple and multiple linear regressions analyses. Bell diameter was transformed into wet weight (g) applying regression equations described for *L. lucerna* by Nogueira Jr. & Haddad (2006) as: $ww = 0.1266 \cdot (Bd)^{2.9514}$, where Bd = bell diameter (cm). The dependent variables used in linear regressions analysis included: *i*- proportions of the major categories of prey (calanoid copepods, non-calanoid copepods, non-copepod crustaceans, and non-crustaceans); *ii*- Number of taxa in the diet and Shannon's diversity index; *iii*- Number of prey ingested (G) and daily carbon ration DCR (see below); *iv*- "C" selectivity index; and *v*- Prey Size Ratio, PSR (see below). Before all regression analyses, the

assumptions of normality and homogeneity of variances were tested and when necessary, data were log₁₀-transformed.

We calculated the *PSR*, through the comparison of prossome length (*PL*) of the most abundant calanoid copepod prey (*Temora turbinata*, *Paracalanus* spp. and *Acartia* spp.) in the plankton samples with the *PL* of the same prey items in the gut contents (*EGC*) of 25 medusae as: $PSR = PL_{field} / PL_{gut\ content}$, where PL_{field} = mean *PL* (mm) of each copepod in plankton samples and $PL_{gut\ content}$ = mean *PL* of each copepod in *EGC*. For each copepod species, we measured the *PL* of 30 individuals per species, per plankton sample, and of 10–30 individuals of each species per medusae. If $PSR \approx 1$, prey size in field is $\approx$ to prey size in gut contents. Deviations from $PSR \approx 1$ were interpreted as size-based prey selectivity. Statistical analyses were performed using the software “R” (R Development Core Team 2011) and plots were elaborated in Sigma-Plot (Systat Software Inc).

Daily Ration (*DR*)

The daily ration of *L. lucerna* (as copepods eaten*medusae⁻¹*day⁻¹) was estimated according to Larson (1991) for each medusa as: $DR = G_{cop} * 24h * DT^{-1}$, where G_{cop} = total copepods ingested, and DT = digestion times. Because of the scarcity of studies on the feeding biology of rhizostome medusae, few data on digestion times are available, except for Fancett (1988) and Larson (1991). Possible sources of variations on digestion times due to medusae size, prey number, temperature (Martinussen & Båmstedt 1999, Purcell 2009) are still to be evaluated in species of this group. Nevertheless, we used DT estimated by Larson (1991) for *Stomolophus meleagris* (Tab. 2) on copepods adjusted by temperature, assuming the value of $Q_{10} = 2.08$ calculate by Purcell (2009), with published data of *Aurelia* spp.

Multiple linear regressions analyses were performed to explore relationships between *DR* as dependent variable, and *Ww* (g), Temperature (°C), and Prey density (copepods m⁻³) as predictors. In order to compare our feeding rates estimations with those calculated for other scyphomedusae, we added 1 to all *DR* (log-transformed), following Purcell (2003, 2009).

Daily Carbon Ration (*DCR*)

We also calculated the *DCR* as mg of carbon ingested*medusa⁻¹day⁻¹, considering the most abundant prey, which represented <99% relative abundance (see Tab. 4). Carbon content values of each prey item are described in Tab. 2. These carbon content values were applied to specific daily ration, and temperature-adjusted digestion times in order to estimate total daily carbon ration.

Table 2 – Values of carbon ($\mu\text{gC}\cdot\text{ind}^{-1}$) of taxa representing >99% of prey found in the gut content of *L. lucerna*, and respective digestion times. For calanoid copepods conversion equations were used to transform values of prossome length (*PL*) in carbon content (Ara 2001). For the other taxa, fixed values of carbon were used. The digestion times calculated for the Rhizostomeae medusae *Stomolophus meleagris* from Gulf of Mexico (Larson 1991) were applied for most taxa. For *Penilia avirostris** we used *DT* calculated for *Pleurobrachia bachei* (Hirota 1974); for brachyuran zoea** we used *DT* of *P. bachei* calculated for euphausiid larvae (Larson 1987); and for chaetognats*** we used *DT* of *Sagitta enflata*, calculated for *Sagitta friderici* (Martinussen & Båmstedt, 2001). All values of *DT* were adjusted for temperature.

Species	Carbon Content ($\mu\text{gC}\cdot\text{ind}^{-1}$)	Digestion Times (h)	Source for Carbon Content
<i>Acartia tonsa</i>	$C=(9.622*10^{-9}Pl^{2.931})*0.4422$	1.5	Ara (2001)
<i>Acartia lilljeborgi</i>	$C=(6.177*10^{-9}Pl^{3.029})*0.4533$	1.5	Ara (2001)
Gastropod veliger	0.2	1.5	Martinussen & Båmstedt (1995)
<i>Oncaea</i> spp.	0.3832	1.5	Satapoomin (1999)
Bivalve veliger	0.2	4	Martinussen & Båmstedt (1995)
Copepod nauplii	0.017	1.5	Sabatini & Kiørboe (1994)
<i>Paracalanus</i> spp.	$C=(6.829*10^{-11}Pl^{3.671})*0.4626$	1.5	Ara (2001)
<i>Penilia avirostris</i> *	1.2	1.83	Uye (1982)
<i>Euterpina acutifrons</i>	0.01	2	Ara (2001)
<i>Pseudodiaptomus acutus</i>	$C=(1.306*10^{-9}Pl^{3.361})*0.4611$	1.5	Ara (2001)
<i>Temora tubinata</i>	$C=(1.471*10^{-8}Pl^{3.064})*0.4457$	1.5	Ara (2001)
Tintinids	0.055	1.5	Loret <i>et al.</i> (2000)
<i>Oikopleura dioica</i>	1.04	1.5	Paffenhöfer (1976)
<i>Oithona</i> sp.	0.2	1.5	Ara (2001)
Small (<0.4mm)	0.4	1.5	Ara (2001)
calanoids			
Medium (0.4-1mm)	3.2	1.5	Ara (2001)
calanoids			
Large (>1mm)	10	1.5	Ara (2001)
calanoids			
Copepodits	1	1.5	Ara (2001)
Brachyuran Zoea**	184.4	3.4	Uye (1982)
<i>Corycaeus</i> spp.	2	1.5	Uye (1982)
<i>Sagitta friderici</i> ***	43.38	0.67	Stuart & Verheye (1991)

RESULTS

Total dissection: Proportion of prey within body regions

The number of prey found in the formaldehyde solution around seven animals was low (mean $2.51\% \pm 2.28$) compared to the total number of prey ingested (*G*). The loss of prey during fixation and storage time can occur, but is not a general problem of the present method. A small proportion of prey was found in oral arms (*OA*) and in the oral disc (*OD*), and the smallest within the umbrellar canals (*UC*) (Fig. 3). On the other

hand, higher proportions were extracted from the gastric cavity (*EGC*), and at a lesser extent, from the pleated walls (*PW*) (Fig 3). Most (>90%) of prey were found within digestive body regions which are covered by gastric cirri (*OD*, *PW* and *EGC*).

Figure 3 - Proportion of prey items (% $\pm$ standard deviation) inside the cavities of *Lychnorhiza lucerna* (n = 7). **EGC** = Extracted gut content; **OA** = Oral arms; **OD** = Oral disc; **PW** = Pleated walls; **UC** = Umbrellar chanals.

Diet composition, prey selectivity and ontogenetic changes on feeding parameters

We quantified gut content (*EGC*) of 40 medusae, ranging from 5 to 30cm of bell diameter (14 to 2,897g of wet weight). A total of 65,177 prey items belonging to 43 taxa were found (Tab. 3). The dominant items were calanoid copepods (53.7%), particularly of the genera *Temora*, *Acartia* and *Paracalanus*. Calanoids, together with Cyclopoid (15.1%) and poecylostomatoid (11.4%) copepods, bivalve veligers (8.4%) and diatoms (4.3%) represented >90% of prey items. Copepod prey items pooled together represented more than 80% of quantified prey. The complete list of prey taxa, the mean relative abundances in each sampling site and date are presented in Tab. 3.

Table 3 – Composition, mean abundance (% $\pm$ standard deviation) of prey items in guts of *Lychnorhiza lucerna* from the South Brazilian Bight. Proportions were calculated per sampling date, and grouped in global values of total relative abundance and frequency of occurrence.

Prey item	Mean relative abundance of prey item per sampling location $\pm$ (SD)					Total relative abundance	Frequency of occurrence
	Paranaguá 25/06/2008	Cananéia I 08/06/2011	Cananéia II 20/06/2011	Cananéia III 26/08/2011	S. Sebastião 27/07/2011		
Calanoid copepods						53.7	100
<i>Temora turbinata</i>	29.4(10.1)	11.5(8.5)	6.9(8)	20.6 (11.6)	14.8(8)	16.3(9.7)	95
<i>Paracalanus</i> 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
<i>Acartia tonsa</i>	13.4(16.4)	5.3(5.4)	3(3.8)	2.7(3.3)	6(7)	7.1(9)	97.5
<i>Pseudodiaptomus acutus</i>	0	0.04(0.1)	1.7(3.5)	0	3.2(5.6)	3.7(7.5)	40
<i>Acartia lilljeborgi</i>	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
<i>Temora stylifera</i>	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
Cyclopoid copepods						15.1	95
<i>Oithona</i> 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
Poecylostomatoid copepods						11.4	97.5
<i>Oncaea</i> 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
<i>Corycaeus</i> 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
Poecylostomatoida sp. 1	0.98	0.07(0.2)	0.02(0.06)	0	0.01(0.04)	0.3(0.9)	12.5
Harpacticoid copepods						0.6	72.5
<i>Euterpina acutifrons</i>	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
<i>Microsetella norvegica</i>	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
Tintinids	0	6.5(11.8)	5(4.5)	0	0	1.7(7.6)	40
non identified eggs	0.3(0.4)	1.7(3.2)	0.3(0.6)	0	0.5(1.2)	1.5(0.9)	32.5
<i>Oikopleura dioica</i>	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
<i>Penilia avirostris</i>	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 zoea	1(0.6)	0.04(0.1)	0.4(0.7)	0.01(0.02)	0.01(0.04)	0.2(0.5)	40
<i>Sagitta friderici</i>	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
<i>Podon</i> 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
Gammarids	0.02(0.04)	0.02(0.07)	0.3(0.9)	0	0	0.05(0.4)	12.5
Cifonauta 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
Hiperiids	0	0.01(0.03)	1(1.9)	0	0	0.04(0.8)	10
<i>Ceratum</i> spp.	0	0.06(0.2)	0	0.01(0.04)	0	0.03(0.1)	10
Decapodid	0.1(0.2)	0	0	0	0	0.02(0.2)	20
<i>Liriope tetraphylla</i>	0.1(0.1)	0	0	0	0.01(0.04)	0.01(0.05)	10
Isopods	0	0.01(0.03)	0	0	0.07(0.2)	0.01(0.07)	5
Polychaets	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
Siphonophores	0.02(0.05)	0	0	0	0.07(0.17)	0.003(0.07)	5
Mysids	0.01(0.04)	0	0	0	0	0.001(0.02)	2.5

The total ingestion (G) ranged from 17 to 12,138 prey items. Regression analysis demonstrated that G was significantly related to medusae wet weight (Fig. 4A). The number of taxa found per medusae, ranged from 7 to 31 but was not significantly related to medusae wet weight (Fig. 4B).

Figure 4 – Number of prey items in medusae of *Lychnorhiza lucerna* ($\text{Log}_{10}G$) along medusae size as wet weight (in log_{10} scale). Wet weight ranged from 14 to 2,897g. G was estimated from extracted gut content counts, applying the proportion of 69.8% (see above). Linear regression (solid line) and 95% of confidence interval (dashed lines) (A). Number of taxa found in medusae of *L. lucerna* was not significantly related to medusa wet weight (B).

The proportions of the four major prey categories (calanoid copepods, non-calanoid copepods, non-copepod crustaceans, non-crustaceans) were compared to medusae wet weight through linear regressions. The proportions of non-calanoid copepods (mean $\pm$ standard deviation: 22.57 ± 12.89), non-copepod crustaceans (12.74 ± 12.94) were not significantly related to medusae wet weight. Instead, the proportion of calanoid copepods were positively related to medusae wet weight ($P < 0.001$), while the proportion of non-crustacean prey were negatively related to medusae wet weight ($P < 0.001$, Fig. 5A). The Shannon's Diversity Index (H') of *L. lucerna* diet (EGC) decreased with increase in medusae size (Fig. 5B), which is a possible consequence of the increasing proportion of a low number of calanoid copepod taxa, and a decreasing proportion of highly diverse non-crustacean with increase in medusa size.

Figure 5 – Proportion of prey groups with significant relationships with *Lychnorhiza lucerna* wet weight (g). While calanoid copepods in the diet increased with medusae wet weight, the proportion of non-crustacean prey decreased with increased medusae wet weight (**A**). The Shannon’s diversity index H' decreased with medusa size (**B**).

In general, diet composition was similar to the environmental availability, nevertheless, some zooplankton taxa found in the field were absent in the guts of *L. lucerna*, such as: echinoderm larvae, *Lucifer faxoni*, *Eucalanus* sp., *Labdocera* sp., sipunculid larvae. Instead, some prey items found in the guts were absent in the field samples, such as: *Temora stylifera*, *Microsetella norvegica*, isopods and hyperids.

The comparison of the percentages of the 10 most abundant prey items in mesozooplankton samples of each location, with the percentages in the guts demonstrated few consistent patterns of differences. Proportions of the main prey items (calanoid copepods: *Acartia* spp., *Temora turbinata*, and *Paracalanus*) were sometimes higher in gut content and sometimes in the field (Fig. 6). The cladoceran *Penilia avirostris*, the chaetognath *Sagitta friderici*, and the copepods *Euterpina acutifrons* and *Pseudodiaptomus acutus* when relatively abundant in the field were not found in high proportions in the guts (Fig. 6). Bivalve veligers, copepodites and copepods of genera *Oithona*, *Oncaea* and *Corycaeus*, when relatively abundant in gut content were not

found in high proportions in the field (Fig. 6). Nevertheless, the densities of these last items were probably underestimated by our plankton net.

Figure 6 - Composition of mesozooplankton, in ambient water, and in the guts of *L. lucerna*. Graphs show mean $\pm$ standard error of the 10 most abundant prey, in decreasing order of abundance in mesozooplankton samples from each location. Number of gut content samples/mesozooplankton samples are: 8/3 for Paranaguá, 14/3 for Cananéia I, 6/4 for São Sebastião, 6/3 Cananéia II, and 6/4 in Cananéia III.

In order to evaluate possible patterns of prey selectivity, we calculated Pearre's "C" selectivity index (Pearre 1982) for mesoplanktonic prey, which were quantitatively sampled by our plankton net. In order to evaluate whether patterns of prey selectivity are related to changes on medusae size, we applied linear regressions between "C" and medusae wet weight. For the copepods *Temora turbinata*, *Acartia* spp., *Paracalanus* spp., *Pseudodiaptomus acutus*, and *Euterpina acutifrons* (Figs 7 A–E), patterns of prey selectivity were similar among medusae sizes with most of "C" values ranging from -0.3 to 0.3. The values for these copepod species were equally distributed along the negative and positive sides of the bi-plots without a clear pattern of selectivity, except

for *P. acutus*, in which most values indicated negative selectivity. Instead, for *Sagitta friderici*, *Oikopleura dioica*, *Penilia avirostris*, and brachyuran zoea, “C” values tended to decrease with the increase in medusae wet weight (Figs 7 F–I; Tab 4).

Figure 7 – Selectivity “C” index of Pearre (Pearre 1982) for mesozooplanktonic prey along medusae sizes. The dashed straight line is a reference for selectivity 0. Positive or negative values indicate selectivity at a rate above or below environment concentration. Solid dots are significant values of “C” ($p < 0.05$) by χ^2 , whereas hollow dots are non-significant values. The solid straight lines indicate linear regressions and the dotted lines, the 95% confidence intervals of the estimated model.

Table 4– Linear regression equations tested to use the wet weight (g) of medusae as a predictive of selectivity “C” index of Pearre.

Taxa	P	“C” index variation	r^2 e F	Equation
<i>Penilia avirostris</i>	$p < 0.005$	-0.83 – 0.1	$r^2 = 0.217$ F=8.866	“C”=0.096-0.056*Log ₁₀ WW
<i>Euterpina acutifrons</i>	$p = 0.05$	-0.09 – 0.04	$r^2 = 0.092$ F=3.8528	“C”=0.067-0.031*Log ₁₀ WW
Crab Zoea	$p < 0.001$	-0.11 – 0.07	$r^2 = 0.349$ F=20.357	“C”=0.134-0.059*Log ₁₀ WW
<i>Oikopleura dioica</i>	$p = 0.006$	-0.14 – 0.24	$r^2 = 0.189$ F= 8.594	“C”=0.228-0.090*Log ₁₀ WW
<i>Sagitta friderici</i>	$p = 0.049$	-0.16 – 0.06	$r^2 = 0.097$ F= 4.100	“C”=0.041-0.028*Log ₁₀ WW

In order to test whether possible patterns of prey selectivity are related to prey size (as copepod prossome length) we compared the size of the main copepod species in the gut content, with the size in the field, along the medusae sizes (as wet weight). For *Temora turbinata*, most of prey size ratio (PSR) values were above 1, which means that prey in gut content were larger than prey found in field (Fig. 8A). This pattern were constant along different medusae sizes. For *Acartia* spp. and *Paracalanus* spp. we found a pattern of increasing prey size ratio along with the increase medusae sizes, which means that *L. lucerna* tends to increase the size of prey captured in relation to field mean sizes, along its growth (Figs 8B–C).

Figure 8 – Prey size ratio (PSR) of the main calanoid copepods, estimated by a comparison of mean prey size in gut content samples of *Lychonorhiza lucerna*, and in the field. If $PSR \approx 1$ size of copepods in guts are $\approx$ as in field, if $PSR < 1$, prey size in guts $>$ field and if $PSR >$, prey size in guts $<$ field.

Daily ration (DR)

DR of *L. lucerna* ranged from 110 to 102871 copepods ingested day⁻¹. We found significant relationships between (DR) and medusae size (log₁₀ medusae wet weight), whereas water temperature and prey density (as log₁₀ total copepod density) were not significant related to (DR) (Tab. 2). In order to compare copepods daily ration between different scyphomedusae species, we plotted multiple linear regression equations of Purcell (2009) with our data in (DR) vs. medusae wet weight (g) bi-plots. Since variation on DR was not explained by variation on copepod field density, we applied mean copepod field density of this study as a fixed value (3863 org*m⁻³) to equations of Purcell (2009).

Figure 9 - Copepods daily ration (DR, log₁₀ copepods +1 eaten day⁻¹) of scyphomedusae from field gut contents vs. medusae wet weight. For *Aurelia aurita* I, *A. aurita* II, *Cyanea capillata*, *Chrysaora quinquecirrha*, equations described by Purcell (2009) (see Tab. 5) were plotted using fixed mean prey density (3863 copepods.m⁻³) found in this 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, the 95% confidence intervals prediction error.

Lychnorhiza lucerna and *Aurelia aurita* I (from the Inland Sea of Japan) had the highest copepod daily ration *DR* of the five species studied (see Purcell 2009). *A. aurita* I overcomes *L. lucerna* at larger sizes (Fig. 9). *Aurelia aurita* II (from Palau) and *Chrysaora quinquecirrha* (from Chesapeake Bay, USA) have comparatively lower *DR*, but still higher values than *Cyanea capillata* (from Alaska, USA) (Fig. 9).

Parameters of all multiple linear regressions used are in Tab. 5.

Table 5 – Parameters of multiple linear regressions analyses for *Aurelia* spp., *Cyanea capillata*, *Chrysaora quinquecirrha*, calculated by Purcell 2009, and *Lychnorhiza lucerna* from this study. The analyses evaluated the relationships between wet weight, prey density, temperature, and daily ration as number of copepods eaten day⁻¹.

Species (number examined) and location	Wet Weight (g) Range, <i>t</i> and <i>P</i>	Prey density (number m ⁻³) Range, <i>t</i> and <i>P</i>	Temperature (T in °C), <i>t</i> and <i>P</i>	Daily Ration <i>DR</i> (copepods eaten day ⁻¹) Rate Range	Multiple <i>R</i> ² , <i>F</i> , <i>P</i> and SE	Predictive equation
<i>Lychnorhiza lucerna</i> (40) South Brazilian Bight	14–2897 <i>t</i> = 4.721 <i>P</i> < 0.001	2,795–5,704 <i>t</i> = 0.610 <i>P</i> = 0.546	18.8–21.5 <i>t</i> = 0.072 <i>P</i> = 0.943	191–166,28 8	<i>r</i> ² = 0.474 <i>F</i> _{2, 37} = 34.26 <i>P</i> < 0.001 SE 0.484	Log ₁₀ <i>DR</i> = 0.8071*Log ₁₀ <i>WW</i> + 1.935
<i>Aurelia aurita</i> I (68) Inland Sea of Japan	48–1,440 <i>t</i> = 8.451 <i>P</i> < 0.001	830–13,990 <i>t</i> = 3.288 <i>P</i> = 0.014	16.2–24.8 <i>t</i> = 0.626 <i>P</i> = 0.950	312–96,576	<i>R</i> ² = 0.705 <i>F</i> _{3, 64} = 77.703 <i>P</i> < 0.001 SE 0.283	Log ₁₀ <i>FR</i> = 1.189*Log ₁₀ <i>WW</i> + 0.346*Log ₁₀ <i>PD</i> – 0.314
<i>Aurelia aurita</i> II (144) Palau	3–1,139 <i>t</i> = 22.674 <i>P</i> < 0.001	2,556–74,222 <i>t</i> = 2.825 <i>P</i> = 0.005	31 No data	34–28,631	<i>R</i> ² = 0.787 <i>F</i> _{2, 141} = 260.97 <i>P</i> < 0.001 SE 0.285	Log ₁₀ <i>FR</i> = 0.802*Log ₁₀ <i>WW</i> – 0.153*Log ₁₀ <i>PD</i> + 2.11
<i>Chrysaora quinquecirrha</i> (386) Chesapeake Bay, USA	0.007–146 <i>t</i> = 12.052 <i>P</i> < 0.001	400–232,218 <i>t</i> = 8.757 <i>P</i> < 0.001	22.9–29.1 <i>t</i> = 5.076 <i>P</i> < 0.001	1–17,011	<i>R</i> ² = 0.455 <i>F</i> _{4, 381} = 106.55 <i>P</i> < 0.001 SE 0.359	Log ₁₀ <i>DR</i> = 0.367*Log ₁₀ <i>WW</i> + 0.258*Log ₁₀ <i>PD</i> + 1.447
<i>Cyanea capillata</i> (156) Alaska, USA	1.4–1,642 <i>t</i> = 5.702 <i>P</i> < 0.001	203–10,211 <i>t</i> = 6.255 <i>P</i> < 0.001	14 No data	12–5,148	<i>R</i> ² = 0.284 <i>F</i> _{2, 152} = 30.41 <i>P</i> < 0.001 SE 0.475	Log ₁₀ <i>DR</i> = 0.389*Log ₁₀ <i>WW</i> + 0.670*Log ₁₀ <i>PD</i> – 0.512

Daily Carbon Ration (*DCR*)

We calculated *DCR* applying carbon specific values (Tab. 2) over total prey ingestion (*G*), with specific temperature-adjusted digestion times (Tab. 2). Values of total *DCR* ranged from 0.48 to 175.77 mgC ind⁻¹*day⁻¹. Calanoid copepods represented the main prey items with a mean contribution of 63.41% of total *DCR*. The proportions of calanoid copepods to total *DCR* increased with medusae size (Fig.

10). The contribution of remaining prey were fairly lower, with non-calanoid copepods with a mean contribution of 11.15%, followed by non-copepod crustaceans with 4.18%, and non-crustaceans with 2.08% of *DCR*. We calculated linear regressions from values of $\log_{10}DCR$, and $\log_{10}$ Wet weight (g) for total prey ingestion and for groups of prey items (Tab. 6).

Figure 10 – Carbon Daily Ratio ($\text{mg C} \cdot \text{ind}^{-1} \cdot \text{day}^{-1}$) in relation to medusae wet weight (g) for total prey ingested and groups of prey (Calanoid copepods, Non-calanoid copepods, Non-copepod crustaceans and Non-crustaceans). Medusae wet weight ranged from 48 to 2,875 g. Values were calculated applying temperature corrected digestion times, over species-specific carbon content values of prey items. The linear regression and 95% confidence intervals were calculated for medusae wet weight as predictive of total ingestion *DCR* and parameters of linear regression are in Tab. 6.

Table 6– Parameters of linear regression analysis between $\log_{10}$ Wet Weight (g) and daily carbon ration *DCR* (as $\text{mg C ind}^{-1} \cdot \text{day}^{-1}$) calculated for total prey ingested and groups of prey: calanoid copepods, non-calanoid copepods, non-copepod crustaceans, and non-crustacean prey. Medusae wet weight ranged from 48 to 2,875 g.

Group of prey items	t and P	DCR variation (g C*ind ⁻¹ *day ⁻¹)	r ² e F	Equation
Total Carbon Daily Ration	t=4.648 P<0.0001	0.486–175.768	r ² = 0.362 F=21.600	$\log_{10}DCR = 0.637 * \log_{10}WW - 0.570$
Calanoid copepods DCR	t= -1.96 P=0.05	0.164–144.178	r ² = 0.426 F=28.264	$\log_{10}DCR_{cal} = 0.805 * \log_{10}WW - 1.251$
Non-calanoid copepods DCR	t= 3.651 P<0.0008	0.035–16.188	r ² = 0.260 F=13.336	$\log_{10}(DCR_{Ncal}) = 0.510 * \log_{10}WW - 1.584$
Non-copepod crustaceans DCR	t= 1.992 P= 0.054	0.003–35.227	r ² = 0.095 F= 3.967	$\log_{10}(DCR_{Ncop}) = 0.569 * \log_{10}WW - 1.674$
Non-crustacean DCR	t = 1.753 P=0.087	0.021– 20.653	r ² = 0.080 F= 3.076	$\log_{10}(DCR_{Ncrs}) = 0.401 * \log_{10}WW - 1.246$

DISCUSSION

Total dissection: Proportion of prey within body regions

Despite the disadvantage of gut content methodology concerning the exhausting quantification effort, it is still a unique tool for ecological studies of scyphomedusae. Traditional sampling protocols (handling, preservation and storage of the whole animal) do not resulted in loss of prey during storage period, probably because *L. lucerna*, as other rhizostome medusae, lacks a large central mouth. The quantification of prey within all body regions demonstrated that a time-consuming dissection of non-digestive regions, like oral arms (OA) and umbrellar canals (UC) could be avoided since it accounted for only <10% of total prey ingested (G). The small number of prey inside umbrellar canals is a consequence of complete digestion prey. The small number of prey in oral arms indicates fast transport kinetics towards central gastric cavity. For *Aurelia* sp. the transport of copepods ranged from 10-50 minutes (Southward 1955), while for *L. lucerna*, the transport of *Artemia* nauplii to the cruciform cavity takes between 5 and 10 minutes (pers. obs.).

Since ~90% of prey items were counted within digestive cavities (pleated walls *PW*, oral disc *OD*, and extracted gut content *EGC*), analyses of these samples are advisable for estimations of total ingestion. Furthermore, a vigorous washing of *PW* is recommended, since even after several rinses, still 14% of prey counted remained attached to the gastric cirri of *PW*. Despite the storage of large bodied jellyfish can be a problem for space-limited laboratories, onboard extraction of gut content is not advisable for two reasons: *i*- the handling of the medusae triggers mucous release (*e.g.* Larson 1991; Graham *et al.* 2003), which agglutinates prey into opaque balls and makes counting process much more laborious. Mucus is not usually found on oral arms of medusae in the field (Larson 1991; pers. obs.). By preventing clumping of prey, subsampling of gut content become suitable since biased distribution is avoided (Van Guelpen 1982); and *ii*- an inefficient rinse of gastric cavities leads to underestimation of prey ingestion. Besides the extraction, it is necessary to retain prey items with a sieve of appropriated mesh size. In our case, prey on oral arms and oral disc were directly analyzed without rinses and microzooplankton (tintinnids, dinoflagelates) was unimportant. Thus, since mesozooplankton were the major prey of *L. lucerna*, quantification through conventional gut content methods are adequate (Purcell 2009).

Methods of extraction of prey are poorly described and body regions analyzed vary among many studies (see appendix 1 for a comparison of extraction and analytical methods). Adequate collection are critical in order to obtain reliable *in situ* gut content samples of fragile jellyfish. Collections made with nets are subject to biases of loss of gut content (Barz & Hirsch 2005, Purcell 2003) and cod-end feeding, due to the concentrating effects (Larson 1987, Matsakis & Conover 1991). Careful collection methods should be applied, such as samplings in surface waters by using dip nets or buckets (Larson 1991) or by scuba-diving (Raskoff *et al* 2003, Hansson 2006).

Studies over large spatial and temporal scales often require higher number of samples. Since large bodied rhizostome medusae ingest thousands of small prey, gut content-based studies are extremely time-consuming and impracticable for species like *Nemopilema nomurai*. Nevertheless, the tedium of this method may be overcome by sub-sampling of *EGC* by the application of standard protocols of plankton samples (e.g. Van Guelpen *et al.* 1982), which should be considered in further studies.

Diet composition, prey selectivity and ontogenetic changes on feeding parameters

In general, the diet of rhizostome species is widely unknown. A few qualitative observations and quantitative studies (e.g. Smith 1936, Fancett 1988, Larson 1991) indicated mesozooplankton as the major food source. Even zooxanthellate species, such as *Cassiopea* spp. and *Cotylorhiza tuberculata* capture and ingest planktonic prey (Smith 1936, Garcia & Durbin 1993, Kikinger 1992). The proportion of prey items is highly variable among species in which the diet was quantitatively described (Tab. 8). Predation over fish eggs and larvae, which is common in scyphomedusae (Purcell 1997, Graham *et al.* 2003, Padilha-Serrato *et al.* 2013), was negligible in *L. lucerna*, probably because these items were rare in our field samples. Among other rhizostomes, *L. lucerna* had the highest proportion of copepods (80.8%) in the diet, followed by *P. haeckeli* (32.8%), *P. punctata* (23%) and other species with <10% (Tab. 7). *L. lucerna* ingest large calanoid copepods at similar feeding rates as field availability (Figs 7 A–C), whereas *P. haeckeli* had positive selection (Fancett 1988) and *S. meleagris*, negative selection (Larson 1991). Other rhizostomes feed mainly over non-evasive prey such as mollusk veligers, diatoms, tintinids and fish eggs, a pattern that was found twice for *Stomolophus meleagris* (Tab. 7). Despite the higher proportion of mollusk veligers in the diet than in the field for some species (*L. lucerna*, *S. meleagris* and *P. punctata*) its

nutritional importance is questionable. Purcell *et al.* (1991) found that bivalve veligers were ingested but not digested by *Chrysaora quinquecirrha*, since they were egested alive. Thereby, accumulation in the guts would explain this pattern.

Table 7 — Proportion (%) of prey items of the gut content of Rhizostomeae medusae; (-) indicates negative selectivity and (+) indicates positive selectivity for this prey item. ¹ this study, ²Larson (1991), ³Padilla-Serrato *et al.*, (2013), ⁴Pérez-Ruzafa *et al.*, (2002), ⁵Graham *et al.*, (2003) e ⁶Fancett (1988) *the authors found positive selectivity for calanoid and harpacticoid copepods and negative selectivity for cyclopoid copepods.

	Mollusk veligers	Diatoms	Tinti- nids	Fish eggs	Clado- cerans	Cypris larvae	Cope- pods	Decapod lavvae	Other
<i>L. lucerna</i> ¹	9	4.3	1.7	0.1	0.6(-)	0	80.8	0.4	3
<i>S. meleagris</i> ²	71.2(+)	0	9.3	<1	<1	<1	7.3(-)	1	<1
<i>S. meleagris</i> ³	26.4	0	0	65.3	0.1	4.1	1.5	2	3
<i>C. tuberculata</i> ⁴	6	85	5	0	0	0	3	0	0
<i>R. pulmo</i> ⁴	3	65	30	0	0	0	1	0	0
<i>P. punctata</i> ⁵	35	0	23	15	0	0	23	0	4
<i>P. haeckeli</i> ⁶	0	0	0	40.8 (+)	4(-)	1	34.8 (+*)	4.9	15

L. lucerna shift the composition of diet from a more generalist, in smaller sizes, decreasing the diet diversity, while the proportion of copepods increases, which represent >90% of prey items and of carbon source in larger animals. It is opposite to the diet shift of other gelatinous species, such as *Aurelia* sp., *Chrysaora plocamia* and *Mnemiopsis leidyi*, in which the diversity of prey increases as animals grow (Graham & Kroutil 2001, Rapoza *et al.* 2006, Riascos *et al.* 2014). While Sullivan *et al.* (1994) found an ontogenetic increase in copepod proportion during metamorphosis from ephyra to the adult body plan (<1–3 cm), individuals here analyzed (> 4 cm of bell diameter) already had developed the adult body plan. This means that *L. lucerna* changes its diet even after metamorphosis, but pre-metamorphosis feeding habits remain unknown for this species due to absence of ephyrae in field samples.

Increasing negative selection, with the increase in body size were found for distinct prey, such as larvaceans, crab zoea and cladocerans (Figs 7F–I). Few empirical observations help to explain these patterns. For the cladoceran *Penilia avirostris*, negative selectivity was clear, since even when proportion of the cladoceran in field was high (~80%), captures by medusae were low (~2% of prey items). For other preys with a possible negative selectivity pattern, this should be evaluated with caution,

because of their low abundance (or absence) in the samples. Negative selectivity for crab zoeae was also found for other rhizostome *Catostylus mosaicus* (Carr & Pitt 2008). This pattern was explained by the authors due to a possible ability of zoeae in detecting chemical signals in the water, and thus avoiding predators (Cohen & Forward 2003, Carr & Pitt 2008). Pre- and post-encounter factors should be further evaluated in order to understand mechanisms of prey selectivity. It is not known, for instance, whether the contact with all types of plankton trigger nematocyst discharge in medusae. The hypothesis of selective discharge in nematocysts could help to explain absence of capture reaction to certain prey types (Hanson & Kiørboe 2006) and prey selectivity patterns (Peach & Pitt 2005) but is still to be tested in the group.

A consequence of body size increase is the scaling in the strength of feeding currents, which presumably enables the capture of more evasive prey (*e.g.* calanoid copepods) (Costello & Colin 1994, Sullivan *et al.* 1994). The velocity of feeding currents of larger scyphomedusae (>20 cm of bell diameter) were never experimentally measured, but small (<10 cm) Rhizostomeae medusae like *P. punctata*, *Cassiopea* sp. and *L. lucerna* produce feeding currents between 8–15 cm s⁻¹ (D' Ambra *et al.* 2001, Santhanakrishnan *et al.* 2012, pers. obs.). The higher speeds of copepods of the genera *Temora*, *Paracalanus*, and *Acartia* during escaping jumps are 30–60 cm s⁻¹ (Buskey *et al.* 2002, Waggett & Buskey 2006). Though such a comparison suggests an inability of small medusae to capture these copepods (Costello & Colin 1994). Nevertheless, even smaller *L. lucerna* ingest these copepods at similar feeding rates as field availability, which indicates that this model is insufficient to explain this predator-prey interaction. The capture of fast escaping copepods by medusae that produces slower feeding currents was demonstrated for *Chyrsaora quinquecirrha* and *Aurelia* sp. (Purcell 1992, Ford *et al.* 1997, Suchman & Sullivan 1998, 2000). Fields & Yen (1997) suggested that

even if escape speeds and accelerations were adequate to escape from certain predators, animals with limited detection abilities would be susceptible to predation. Thus, other features of predator and prey should be evaluated along with the kinetic performance.

A combination of morphological, behavioral and physiological features of predator and prey affect the likelihood of capture and determine predator's selectivity and trophic niche (Fields & Yen 1997, Viitasalo *et al.* 1998). The main calanoid copepods in the diet of *L. lucerna* – *Temora*, *Acartia* and *Paracalanus* – have distinct patterns of size selectivity (Figs 8A–C), which may be explained by their distinct abilities to detect shear threshold by approaching predators. *T. turbinata* is the poorest escaper among these species, whereas *Acartia* is able to detect deformation rates (s^{-1}) up to five times lower than the first one (Buskey *et al.* 2002, Waggett & Buskey 2006, Colin *et al.* 2010). *L. lucerna* captures larger-size *T. turbinata* than average size in the field, probably due to a combination of higher likelihood of capture of larger copepods than smaller ones (Suchman & Sullivan 1998, 2000) and the weak detection ability of this species (Colin *et al.* 2010).

Smaller sized *L. lucerna* tends to capture *Acartia* and *Paracalanus* copepods of smaller size than field populations. Nevertheless, as medusae grow, they become able to capture these copepods at similar, or larger sizes, relative to field populations (Figs 8B–C). We suggest that only smaller copepods are vulnerable to predation by smaller sized medusae, because their reduced detection and swimming abilities, relative to their larger sized counterparts (Greene & Landry 1988, Fields & Yen 1997). Thereby, the ontogenetic scaling on feeding currents of *L. lucerna* enhances its capacity of transporting and capturing the fast-escaping adult copepods of these two species.

Feeding rates and daily carbon ration

Feeding rates expressed as copepods ingested day⁻¹ (*DR*) are a useful parameter because these are the main prey of most scyphomedusae (Purcell 1997, 2009) and represented in average 84% of prey items and 74% of carbon ingested by *L. lucerna*. *DR* of *L. lucerna* were function of body size (as wet weight), but were not significantly related to prey density (e.g. Uye & Shimauchi 2005, Purcell 2009), nor temperature, probably because these variables changed slightly among sampling sites. *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 medusae population day⁻¹, D_{Pred} = predator density (org. m⁻³), and D_{Prey} = copepod density (org. m⁻³) (e.g. Brodeur *et al.*, 2002; Purcell, 2003; Barz & Hirche, 2005; Uye & Shimauchi, 2005). Unfortunately, estimates of predator densities were still not quantified for *L. lucerna* along 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, at the month off Río de la Plata estuary. Zooplankton densities were not calculated along with predators densities by Colombo *et al.*, (2003), but if we assume copepod densities found by Della-Viña *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 *PI* represent a population of relatively small medusae (~11 cm bell diameter), thus the *PI* of larger medusae (>25 cm), which are yearly found along Brazil and North Argentina coasts (Nogueira Jr. 2006; Schiariti *et al.*, 2008; Nagata *et al.* 2009) would potentially have higher *PI*. These estimates are valuable as a first assessment of the species predatory impact and can be used as a more realistic model for other rhizostome medusae (but see Larson 1991; Garcia & Durbin,

1993). It also highlights to the potential of this species as a key consumer, based on high individual feeding rates and occasional dominance in coastal areas (Colombo *et al.*, 2003; Schiaritti *et al.*, 2008; Nagata *et al.*, 2009).

Rhizostome medusae have higher metabolic demands on wet weight basis, than semaeostome medusae, but similar demands on carbon content basis (Purcell *et al.* 2010). Feeding rates of *L. lucerna* as copepods ingested day⁻¹ were similar to medusae of *Aurelia*, but slightly higher than *C. quinquecirrha* and *C. capillata* (Purcell 2009). By applying a biometric conversion factor of carbon % of wet weight of C%WW=0.466, as an average of rhizostome medusae (*Phyllorhiza punctata*=0.46, *Nemopilema nomurai*=0.6, and *Rhizostoma pulmo*=0.34) (Purcell *et al.* 2010), *L. lucerna* carbon content ranged from 0.06 to 13.5 g. *L. lucerna* feeding rates as DCR (0.48 to 175.77 mgC day⁻¹) represented on average 1.23 % (min–max ± SD: 0.09–9.32 ± 1.77) of animal's body carbon content. The minimum carbon requirement MCR on animal's carbon content basis, calculated applying respiration rates and respiratory quotient of 0.8 (Ishi & Tanaka 2006, Purcell *et al.* 2010), demonstrated that animals within this size range would require between 5.7–818.4 mgC day⁻¹. Thus, our DCR estimate explains on average only 17.32% (1.35–112.04 ± 22.37) of animals MCR. Lower feeding rates than MCR, were also found for *S. meleagris*, in a similar approach (Larson, 1991). In this study, other potential carbon sources could not be quantified in this study, such as dissolved and particulate organic matter (*e.g.* Skikne *et al.* 2009), and microzooplankton. However, microzooplankton such as dinoflagellates and ciliates, which could be visualized under our analytical conditions were not important prey items. The genetic diversity of gut content could be further evaluated in order to verify non-quantifiable prey items (*e.g.* King *et al.* 2008). Another potential source of errors are the digestion times *DT* compiled from the literature. These *DT* were

calculated for distinct species, over smaller sized medusae, although prey/predator specific *DT* should be applied (Martinussen & Båmstedt 1999). Our *DCR* are thus conservative, since large sized animals have faster digestion rates, which would result in higher feeding rates estimates. Thus, further studies should refine our *DR* and *DCR* models, through the inclusion of parameters, such as specific digestion times, which in turn include sources of variation caused by prey type, amount of prey and predator's size.

CONCLUSION

A broader view of the ecological role of jellyfish as consumers depend on the support of biological information based on distinct approaches, of which traditional gut content methods are still unique and a useful tool. There is no other method of trophic studies that gives a complete picture of feeding biology. Gut content analysis allows a high taxonomic precision of ingested prey, with low analytical costs, and good representation of recent ingestion, which are not possible by applying stable isotopes or fatty acid analyses. The distribution of prey within distinct body regions of *L. lucerna* demonstrated that digestive cavities (*OD*, *PW* and *EGC*) should be sampled. Careful manipulation of medusae and immediate preservation avoid mucous production and clumping of prey, which allow a sub-sampling of extracted gut content, overcoming the tedium of this method. *L. lucerna* is a generalist predator with a diet mostly similar to prey availability, nevertheless, a specialization for calanoid copepods were found with increasing medusae size. Capture of fast-escaping copepods occurs even for medusae with smaller flow velocities ($\sim 10\text{cm s}^{-1}$), than copepod's escaping velocities ($30\text{--}60\text{cm s}^{-1}$), which demonstrate that comparison of kinetic performance is insufficient to explain prey selectivity patters. Patterns of prey-size selectivity were distinct between calanoid copepod species. Such patterns were explained by distinct prey detection and

swimming abilities, and also by the ontogenetic scaling on the strength of feeding currents by this medusae. *L. lucerna* feeding rates were comparable to those of *Aurelia*, but higher than other semaeostome medusae. Our estimates of carbon daily ration of *L. lucerna* did not explain animal's minimum carbon requirements, which suggests that other non-quantified food items can comprise nutritional sources of this medusa. Other carbon sources than mesozooplankton should be considered for this species. Even so, daily ration as copepods ingested medusa⁻¹ day⁻¹ demonstrated that aggregations of *L. lucerna* may exert substantial trophic impacts, but the lack of data on medusae and prey field densities still limits a broad comprehension of the species' predatory impact.

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Appendix 1 – Comparison of methods and estimates of ingestion in gut content based studies. Ingestion rates are calculated as total ingestion G , daily ration DR , or daily carbon ration DCR . Linear regression equations usually apply wet weight WW , or bell diameter D , as independent variable for prediction of ingestion rates.

Species/ Local	Bell diameter (cm)	Method of extraction of prey	Total prey ingested (G)*medusa ⁻¹	Linear regressions of feeding rates (G , DR ou DCR)	Reference
Rhizostomeae					
<i>C. mosaicus</i>	20 - 25	OA	9920	No data	Peach & Pitt 2005
Australia					
<i>L. lucerna</i> Brazil	7.5 - 26	Total dissection, EGC	17–12137	G = Tab. 5 DR = Tab. 6 DCR = Tab. 7	Present study
<i>P. haeckeli</i> Australia	10-15.5	EGC	476 - 2645	Not estimated	Fancett 1988
<i>P. punctata</i> , Australia	22 – 27	OA	5509	Not estimated	Peach & Pitt 2005
<i>S. meleagris</i> Gulf of Mexico, USA	1.5 - 10	Total dissection	400 – 9300	$G=148(WW)^{-0.45}$ $DCR=4.01 + WW*0.12$	Larson 1991
<i>S. meleagris</i> Gulf of Mexico, Mexico	4–14	EGC	0–210	Not estimated	Padilla-Serrato <i>et al.</i> 2013
Semaeostomeae					
<i>Aurelia</i> sp. Gulf of Mexico, USA	5 – 35	ECG	28 – 1550	$G= 10^{(0.17 + 0.076*D)}$	Graham & Kroutil 2001
<i>Aurelia</i> sp. Tokyo Bay, Japan	5-26	ECG	166 – 2013	Not estimated	Ishi & Tanaka 2001
<i>Aurelia</i> sp. Palau	3 – 29	ECG	No data	$\text{Log}_{10}DCR = \text{Log}[0.954 - 0.026D]$	Dawson & Martin 2001
<i>Aurelia</i> sp. Japan	48 – 1260 (g)	ECG	0 - 8289	Not estimated	Uye & Shimauchi 2005
<i>A. labiata</i> Alaska, USA	No data	Total dissection	No data	$\text{Log}_{10}G= 1.83\text{Log}_{10}D + 0.62\text{Log}_{10}PD - 4.14$	Purcell 2003
<i>Chrysaora</i> cf. <i>caliparea</i> . India	5.8 – 19.7	EGC + PW	72	Not estimated	Kanagaraj <i>et al.</i> 2011
<i>Chrysaora plocamia</i> , Chile	7–47	EGC	No data	$\text{Log}_{10}G=0.8765+0.0192D$	Riascos <i>et al.</i> 2014
<i>C. capillata</i> Alaska, USA	No data	Total dissection	No data	$\text{Log}_{10}G = 3.32\text{Log}_{10}D + 0.14\text{Log}_{10}PD - 5.39$	Purcell 2003

**CAPÍTULO 3: FOOD WEB
CHARACTERIZATION BASED ON $\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$
REVEALS ISOTOPIC NICHE PARTITIONING
BETWEEN FISH AND JELLYFISH IN A
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FOOD WEB CHARACTERIZATION BASED ON $\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$ REVEALS ISOTOPIC NICHE PARTITIONING BETWEEN FISH AND JELLYFISH IN A RELATIVELY PRISTINE ECOSYSTEM

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ABSTRACT

Human-induced stresses on the marine environment seem to favor some jellyfish species to the detriment of other competitors such as planktivorous fishes. In pristine ecosystems, trophic relationships among these consumers are poorly understood. We determined stable carbon and nitrogen isotope signatures of representative consumers in the relatively pristine ecosystem of the Cananéia Estuary, Brazil, in order to understand the food web structure. We described isotopic niche breadth, position, and overlaps between fish and jellyfish (including comb jelly) species. Most of the $\delta^{13}\text{C}$ values suggest that phytoplankton is the major carbon source especially for pelagic consumers. Sessile benthic invertebrates had enriched $\delta^{13}\text{C}$ values, suggesting a contribution of microphytobenthic algae. Seasonal variation of values was significant only for ^{13}C , with different patterns for pelagic and benthic organisms. Isotopic niche breadth of some jellyfishes was wider than those of fish species of the same trophic group, possibly as a consequence of their broad diets. Isotopic niche overlaps of fish and jellyfish species were related to: (1) trophic diversity, since planktivorous species occupied more distinct niches than macroinvertebrate/fish feeders; and (2) life stages, since isotopic niche partitioning pattern can change during species ontogeny. Replacement of declining populations of fish by jellyfish competitors probably depends on the pool of other compensatory species, as well as on reproductive, growth, and feeding performance of other consumers. Description of isotopic niches provides a general picture of trophic roles, interactions and the degree of functional redundancy among species, allowing an evaluation of possible directions of community shifts resulting from the removal or proliferation of keystone consumers.

KEY WORDS: *Gelatinous zooplankton · Trophic position · Forage fish · Dietary overlap · Stable isotopes*

INTRODUCTION

Although some controversies exist concerning changes in the number and extension of jellyfish blooms (Condon et al. 2012, Gibbons & Richardson 2013), historical data from some parts of the world show that jellyfish populations are increasing (Brotz et al. 2012, Purcell 2012). Factors whereby jellyfish may increase have been widely discussed, and it has been speculated that human-induced stresses to the marine environment (eutrophication, species introduction, climate change, overfishing) seem to favor the proliferation of gelatinous zooplankton species (Purcell 2012). Trophic interactions may account for these increases, since evidence suggests that the depletion of fish stocks has shifted some ecosystems from planktivorous fish- to jellyfish-dominated, such as in the northern Benguela Current (Richardson et al. 2009).

Because many jellyfish feed on fish eggs and larvae, top-down control is a possible explanation to the inverse relationship between these populations, as first stated by Möller (1980). The predation impact of jellyfish species can be high, with some species like *Chrysaora melanaste*, in the Bering Sea and *Aurelia* sp. in Japan consuming one-third 33% d⁻¹ and 26% d⁻¹, respectively, of standing stock zooplankton (Brodeur et al. 2002, Uye & Shimauchi 2005). Jellyfish species have diverse feeding habits, yet their ecological roles are often oversimplified (Condon et al. 2012). Species occupy a variety of trophic levels, feeding on micro- and mesozooplankton, epibenthic invertebrates, other jellyfish, and fish (Purcell 1997), and potentially use the same resources as many other consumers (such as crustaceans and fishes). Trophic overlap between planktivorous jellyfish and fish populations was demonstrated in studies applying stomach-content methods (Purcell & Grover 1990, Purcell & Sturdevant 2001) and stable-isotope analyses (Brodeur et al. 2002, Brodeur et al. 2008, Shoji et al.

2009). Richardson et al. (2009) argued that in ecosystems dominated by fish, jellyfish populations are kept in check through predation and competition. Nevertheless, jellyfish may overtake fish competitors when overfishing opens a vacant niche for the former, but also under some conditions such as: low oxygen concentrations, when feeding performance of fish decreases (Shoji et al. 2005); and low visibility, when visual foraging of fish is hampered (Eiane et al. 1999).

In order to understand the ecosystem's response to the removal of a consumer, it is important to examine the trophic position of several keystone species, which probably will fill that vacated trophic niche. Stable Isotope Analysis (SIA) has been used over the past ~25 yr to describe food web structures of different ecosystems, leading to huge advances in this field (Layman et al. 2012). SIA data integrate spatial and temporal information and provide long-term evidence of trophic relationships that cannot be gleaned from "snapshot" dietary analysis (Layman et al. 2012). Although stomach-content analyses provide valuable insights into feeding relationships, they have analytical limitations, since they require many samples and do not always reflect the assimilated food. Studies with SIA can evaluate the trophic structure of many coastal ecosystems, by investigating issues such as the primary sources of organic matter, as well as the energy pathways through a large number of consumers (Sherwood & Rose 2005, Layman et al. 2012). The position of consumers in the isotopic space (δ -space) also illustrates some aspects of the actual ecological niche, such as habitat and resources used, in the concept of the 'isotopic niche' (Newsome et al. 2007). The isotopic values of a given group of community members can be analyzed to quantify aspects of their trophic ecology, such as species niche breadth and niche overlaps (Newsome et al. 2007, Jackson et al. 2011, Newsome et al. 2012).

The productive waters of estuaries are used by different fish species (including coastal and oceanic populations) to feed and as nurseries (Potter et al. 2001). Because larvae and juveniles of most fish species are zooplanktivorous, regardless of what they eat in adulthood (Bond 1996), it is reasonable to suggest that the trophic niche of juveniles of many fish species overlaps with that of zooplanktivorous jellyfish. The South Brazilian Bight (SBB) (23° to 28° S) is a transitional region of mixed climate and faunal components with warm-temperate characteristics (Heileman & Gasalla 2008). The coast of the central SBB receives outflows from large adjacent estuarine systems (Cananéia and Paranaguá) and harbors high zooplankton biomasses and ichthyoplankton densities (Lopes et al. 2006). A relatively high diversity of large jellyfishes (10 species of Cubozoa and Scyphozoa) (Morandini et al. 2005) with distinct trophic roles is present. A historical baseline of field population abundances and seasonality is lacking for jellyfish (but see Nogueira et al. 2010), although a few studies have mentioned episodes of high biomasses in nearby areas (Moreira 1961, Mianzan & Guerrero 2000, Graça-Lopes et al. 2002, Nagata et al. 2009). Because of the good conservation status of the Cananéia Lagoon Estuarine System (CLES) area (MMA 2007), an analysis of its food web structure represents a unique opportunity to understand the trophic role of jellyfish at lower levels of anthropogenic stresses that are presumed to favor their proliferation.

This study, thus, aims to provide a general picture of the food web structure of the CLES based on ^{13}C and ^{15}N isotope signatures of species of mesozooplankton, gelatinous zooplankton, demersal macrofauna, and nekton. We analyzed isotope data in order to answer the following questions: (1) Knowing that the main sources of organic matter in the CLES, phytoplankton, mangrove litterfall, and microphytobenthos (Schaeffer-Novelli et al. 1990), have distinct $\delta^{13}\text{C}$ values, what is

their respective contribution to the consumers of this ecosystem? (2) How much do isotopic signatures vary during an annual cycle? (3) Based on recently developed Bayesian statistical tools for SIA, do jellyfish and other consumers (mainly fish) occupy similar isotopic niches in this ecosystem? For this last question, we compared isotope data of known dominant pelagic species (jellyfish and fish consumers) to assess isotopic niche breadth, seasonal variability, and possible overlaps. Note that in this article we use the term jellyfish synonymously with the term gelatinous zooplankton, i.e. we include ctenophores as well as cnidarians.

MATERIALS AND METHODS

Study site

The Cananéia Lagoon Estuarine System (CLES) is located in the state of Sao Paulo, Brazil, in a wide coastal plain surrounded by mountains of the Serra do Mar. The CLES is a mangrove-bordered estuary with an area of 100 km² of which 52 km² are covered by mangroves (Schaeffer-Novelli et al. 1990). Terrestrial organic matter comes from the Ribeira River valley and from several small creeks. Primary production in estuary waters is phytoplankton-based with values ranging from 0.10 to 0.80 g C m⁻² d⁻¹ (Tundisi et al. 1973), but probably also influenced by the export of materials from mangrove forest (Knoppers & Kjerfve 1999). The contribution of the C₄ saltmarsh cordgrass *Spartina alterniflora* to the estuary total production is lower because of its limited distribution (Schaeffer-Novelli et al. 1990). Another important source of primary production is the microphytobenthos, based on high values of chlorophyll *a* (870 µg cm⁻²) found in the sediments (Schaeffer-Novelli et al. 1990). Mesozooplankton densities are high year-round, with summer increases (Ara 2004). Copepods account for ~84.8% (annual mean = 3.33×10^4 org m⁻³) of the mesozooplankton organisms

(Ara 2004). The fish fauna in CLES is represented by 68 species, with Carangidae (10 species), Ariidae (7), and Engraulidae (7) the best-represented families (Tundisi & Matsumura-Tundisi 2001). Artisanal fisheries within the estuary target many fish species such as mullet *Mugil platanus*, snook *Centropomus* spp., and whitemouth croaker *Micropogonias furnieri*; and invertebrates such as the mangrove crab *Ucides cordatus*, oysters *Crassostrea brasiliana*, and mussels *Mytella falcata* (Mendonça & Katsuragawa 2001). The CLES is part of the Cananéia, Iguape, and Paranaguá Lagoon Estuarine System, which is surrounded by the largest continuous remnant of Brazil's Atlantic rainforest (MMA 2007). The area has been proclaimed a Biosphere Reserve Biodiversity Hotspot and a Natural World Patrimony Site for scientific knowledge and the conservation of human values and traditional knowledge (UNESCO 1999).

Fig. 1. Study site with sampling station (X) at the mouth of the Cananéia Lagoon Estuarine System (CLES)

Sampling and processing

Sampling was carried out from a small boat in April (autumn), July (winter), October (spring) 2011, and January (summer) 2012, in the Cananéia Sea, between the islands of Ilha Comprida and Ilha do Cardoso), at the mouth of the estuary (Fig. 1) during high tide. We sampled at the mouth of the estuary because we expected to find here a more diverse assemblage of gelatinous species and co-occurring fish species than further up the estuary system, since few large jellyfish species are found in upper estuaries of the SBB (except for *Chrysaora lactea* and *Mnemiopsis leidyi*) (Morandini 2003, Nogueira et al. 2010). Mesozooplankton was collected with a plankton net (200 μm mesh size), and larger organisms with a bottom trawl net (1 cm mesh size). Plankton samples were split into 2 parts: one, with all organisms, was immediately frozen (-10°C) after collection; the other was screened in the laboratory for sorting (~ 1 mg per species/taxonomic group) and then frozen. For fish species, 2 to 3 g of muscle tissue was removed from between the dorsal and caudal fins and stored in plastic tubes and frozen (-10°C), and the total length (nearest cm) was measured for each specimen. For macroinvertebrates, we discarded the guts and collected samples from different tissues depending on the group: leg muscle of crabs, caudal muscle of shrimp, peduncle core of sea pansies *Renilla reniformis*, gonads of echinoderms, tentacle core of squids *Lolliguncula brevis*, whole colony of bryozoans, and pieces of the umbrella for jellyfishes or of the ectoderm of the lobes of comb jellies *Mnemiopsis tinoi*, and then frozen (10°C). Samples were dried to constant weight in a drying oven at 50°C (96 h for gelatinous zooplankton and 48 h for other animals) and ground to a fine powder using a mortar and pestle. Mesozooplankton samples were split again into 2 parts: one was used to estimate $\delta^{15}\text{N}$ and was not acidified, and the other was used to estimate $\delta^{13}\text{C}$ and was soaked in 1 N HCl for 3 h in order to remove carbonates and exoskeletons,

and the samples then re-dried. Between 0.5 and 2 mg of each powdered sample was stored in tin capsules. The isotope ratios were determined at the Laboratory of Isotope Ecology (Universidade de São Paulo, Brazil). Each sample was oxidized in an elemental analyzer coupled with a mass spectrophotometer, and with the resulting CO₂ and N₂, the ratio of ¹⁵N and ¹³C was measured. The values were expressed in delta notation (‰), defined as parts per thousand, and the change in relation to international reference materials as the formula: $\delta^{13}\text{C}$ (or $\delta^{15}\text{N}$) = 1000 × [($R_{\text{sample}} - R_{\text{reference}}$) / $R_{\text{reference}}$], where $R = ^{13}\text{C}/^{12}\text{C}$ (or $^{15}\text{N}/^{14}\text{N}$). The reference materials were Pee Dee Belemnite (PDB) for ¹³C and atmospheric nitrogen for ¹⁵N. The samples (10%) were analyzed in duplicate; the standard mean error was 0.11‰ for $\delta^{13}\text{C}$ and 0.12‰ for $\delta^{15}\text{N}$ (n = 45).

Trophic level estimation

Several studies have demonstrated that enrichment factors can vary for $\delta^{15}\text{N}$, depending on the species, diet, and other factors (see Discussion). However, these factors could not be controlled in our study. In order to provide a broad overview of the trophic structure of CLES, we estimated the trophic level of the organisms relative to the calanoid copepod *Parvocalanus crassirostris*, which we assumed occupy to trophic level (TL) 2 (primary consumer), according to a previous study (Eskinazi-Sant'Anna 2000). We then calculated the relative trophic level of consumers, following Post (2002):

$$\text{TL} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{P. \text{ crassirostris}}) / \Delta \quad (1)$$

where λ is the trophic position of *P. crassirostris* (TL: 2, primary consumer); $\delta^{15}\text{N}_{\text{consumer}}$ is the value of each consumer, which is measured directly; and Δ is the enrichment in $\delta^{15}\text{N}$ per trophic level. We assumed a constant enrichment factor (Δ) of 3.4‰, according to Minagawa & Wada (1984).

Distinctive isotopic values of the main primary producers allow an evaluation of the main carbon sources for consumers. It was not possible to directly determine the stable isotope signatures of pelagic phytoplankton and microphytobenthos, and thus models to quantify relative contribution of primary sources (Layman et al. 2012) were not employed. We used $\delta^{13}\text{C}$ values of particulate organic matter (POM) (-19.40‰), measured at the same site, from Barcellos et al. (2009), as an indication of phytoplankton. For microphytobenthos, we used the value of -13‰ , since benthic algae have enriched $\delta^{13}\text{C}$ values (6‰ on average), in relation to phytoplankton (France 1995). Values of mangrove leaves measured here were depleted (-27.86‰) in relation to phytoplankton and microphytobenthos (see Table S1 in the Supplement at www.int-res.com/articles/suppl/mXXXpXXX_supp.pdf for average stable isotope values by taxon). Relative position of consumers and resources on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots were evaluated in order to make general inferences on carbon sources for consumers.

We classified the species into trophic guilds (primary producers, zooplankton, gelatinous zooplankton, sessile benthic invertebrates, vagile benthic invertebrates, benthic fish, demersal fish, benthopelagic fish, cephalopods, and cetaceans) according to taxonomy and habitat (following Sherwood & Rose 2005). To identify general patterns of isotopic values of species, a cluster analysis was performed. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of species were used to apply a hierarchical cluster analysis, with group average linking over a matrix of Euclidean distances between species. This approach created a cluster that gathers groups of species with similar patterns of isotopic values. We identified the main clusters at <2.5 times the Euclidean metric distance (EMD); species not clustered within these groups at <7 EMD (*Alcyonacea* spp., *Penilia avirostris* and *Rhizophora mangle*) were excluded from the analysis. Mean isotopic values of species in each cluster were grouped and plotted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots.

This grouping aimed to provide an overview of consumers groups with similar isotopic values in this ecosystem for general exploratory purposes, such as comparison with the previous classification of trophic guilds.

MANOVA was also used to test seasonal differences in the isotopic signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for taxa present during the 4 seasons. When significant ($p < 0.05$) differences were found, ANOVA was used to separately test interspecific differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Normal distribution (Shapiro-Wilk's W test) and homogeneity of variances (Bartlett test) were tested before these analyses. Deviations from the normal distribution or homogeneous variances were corrected by log-transforming the data (absolute values were used for $\delta^{13}\text{C}$), otherwise Kruskal-Wallis tests were used if necessary.

The position of a certain species in these $\delta^{13}\text{C}/\delta^{15}\text{N}$ biplots reflects the isotopic niche (δ -space), which can be considered a representation of its ecological niche (Newsome et al. 2007). In order to evaluate the total trophic-niche breadth, we applied quantitative metrics using a Bayesian approach (Jackson et al. 2011). We calculated the Standard Ellipse Area, corrected for small sample sizes (SEAc), from individual measurements, which are bivariate equivalents to standard deviations in a univariate analysis (Jackson et al. 2011). To evaluate possible niche overlap between jellyfish and other consumers of the same trophic group (classified by cluster analysis), we estimated the trophic-niche overlap as the percent of overlapping SEAc between these species, applying step size = 5 (Parnell et al. 2008). These analyses were performed using the Stable Isotope Analysis in the R (SIAR) package (Parnell et al. 2008) for the R statistical computing package (R Development Core Team 2011).

RESULTS

We analyzed the isotope values of 62 taxa collected seasonally (see Table S2 in the Supplement). The signatures (mean $\pm$ standard deviation) of the most important taxa of each trophic guild are shown in Fig. 2. For the carbon isotope, the largest variation was found for the primary producers, ranging from -27.87‰ in mangrove leaves to -13‰ for macroalgae.

Among mesozooplankton, $\delta^{13}\text{C}$ ranged over 11 δ units, with wider variation in values (as indicated by the SD) for the pooled taxa (e.g. brachyuran zoeae, fish eggs) and *Penilia avirostris* than those that were separated at species level (Fig. 2). Among benthic invertebrates, values ranged over 10.88 δ units, with more enriched values for sessile benthic invertebrates (mean: -11.85‰) (Fig. 2). Among gelatinous zooplankton and fish, variation of $\delta^{13}\text{C}$ was narrower: values ranged over 5.84 δ and 7.79 δ units. On one hand, most ($\sim 70\%$) $\delta^{13}\text{C}$ data for pelagic groups (mesozooplankton, gelatinous and pelagic fish) varied from -21 to -17‰ (Fig. 2), which suggests a major contribution by phytoplankton to organic production. On the other hand, depleted $\delta^{13}\text{C}$ values, indicating a mangrove contribution, were detected in just a few samples of brachyuran zoeae ($\delta^{13}\text{C}$: -24 to -27‰).

For the nitrogen isotope, the highest $\delta^{15}\text{N}$ variation was observed among mesozooplankton (~ 13 δ units). Of the 4 trophic levels, most mesozooplankton taxa and vagile and sessile benthic invertebrates were below TL 3. Most gelatinous zooplankton, cephalopods, and fish taxa were placed between TL 3 and 4. The tucuxi dolphin *Sotalia guianensis* had the most enriched $\delta^{15}\text{N}$, and was the sole occupant of TL 4 (TL: 4.3) (Fig. 2).

Fig. 2. Isotope signatures (mean $\pm$ SD) for the most representative taxa of the Cananéia Lagoon Estuarine System. Data presented for each trophic guild, trophic-level estimates, and feeding habits (symbols) according to the literature

Cluster analysis

The cluster analysis identified distinct groups of consumers using carbon and nitrogen isotopic signatures (Fig. 3), with some similarities to the trophic guilds (Fig. 2). The cetacean *S. guianensis* is the only species of branch A. Sessile benthic invertebrates, which were characterized by enriched $\delta^{13}\text{C}$, were grouped into clusters F (species occupying a higher TL) and G (species in a lower TL and also Microphytobenthos) (Fig. 3).

Fig. 3. Hierarchical cluster analysis (group-average method and Euclidean distances) of consumers from the Cananéia Lagoon Estuarine System, Brazil. Based on mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Capital letters indicate the main clusters at 2.5 Euclidean metric distance and symbols indicate the classification by trophic guilds from Fig. 2

Mesozooplankton species were grouped into clusters E and D. Cluster E occupied the lowest TL among all consumers and grouped herbivorous zooplankton and phytoplankton. Cluster D grouped omnivorous and carnivorous zooplankton, and the ctenophore *Mnemiopsis leidyi*. Cluster C grouped conspicuous benthic (*Xiphopenaeus kroyeri* and *Callinectes danae*) and planktonic (*Lucifer faxoni*) decapods. These species occupied lower trophic levels and were enriched in $\delta^{13}\text{C}$ in relation to other large crustaceans (Fig. 2).

Gelatinous zooplankton species (except *Mnemiopsis leidyi*) were grouped with fish species in the large cluster B, which also grouped some consumers in a higher TL (Fig. 3). Cluster B was subdivided into clusters B1, B2, B3, and B4. Gelatinous species occupied distinct positions in B, with at least one species in each subgroup of B. Cluster B1 grouped benthic invertebrate feeders and piscivore species, such as the limnomedusa *Olindias sambaquiensis*, the catfish *Cathropsis spixii*, and the squid *Lolliguncula brevis*. Cluster B2 grouped planktivorous species, such as the scyphomedusae *Chrysaora lactea* and *L. lucerna*, and the fish *Chloroscombrus chrysurus*, as well as benthic invertebrate feeders such as the catfish *Genidens genidens* and the lined sole *Achirus lineatus*. Cluster B3 grouped fish and invertebrates of benthic and demersal habits, except for *Mola mola* and *Chaetodipterus faber* which are pelagic fish. Cluster B4 grouped the hydromedusa *Rhacostoma atlanticum* and the fish *Anchoa* spp., which are pelagic species in the highest TL among fish and invertebrate consumers (Fig. 2).

Trophic groups from Cananéia Estuarine system

Mean isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of species in each cluster were plotted along with the main primary sources of carbon at the mouth of CLES to provide a general picture of the food web structure (Fig. 4). The main primary producers were separated by ~ 6 δ units of ^{13}C . Consumers occurred near values of phytoplankton and microphytobenthos. Similarities to mangrove samples were absent. Sessile benthic invertebrates of lower and higher trophic levels clearly rely on benthic carbon of microphytobenthos (Fig. 4). Herbivorous and carnivorous zooplankton, as well as planktivorous-benthic feeders, piscivorous-macroinvertebrate feeders, and cetaceans were aligned with phytoplankton carbon (Fig. 4). Some groups lying between phytoplankton and microphytobenthos such as decapods occupying a lower trophic level, benthic-demersal consumers, and pelagic consumers of a higher trophic level possibly receive contributions from both carbon sources (Fig. 4).

Fig. 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean $\pm$ SD) and trophic-level estimates of trophic groups of consumers from the Cananéia Lagoon Estuarine System, Brazil. The groups (letters in parentheses) were defined by a hierarchical cluster analysis (see Fig. 3)

Seasonal variation

We observed seasonal differences (MANOVA, $F = 20.861$, $p < 0.001$) in the isotope values of pooled samples of pelagic organisms that occurred in all seasons (*Acartia lilljeborgi*, *Mnemiopsis leidyi*, *Lychnorhiza lucerna*, *Stellifer rastriifer*, *Chloroscombrus chrysurus*) and total mesozooplankton. In the univariate analysis, only $\delta^{13}\text{C}$ differed among seasons (ANOVA, $F = 16.13$, $p < 0.001$), with the most depleted values in the spring (Tukey Test, $p < 0.001$). In tests for $\delta^{13}\text{C}$ of each species, *S. rastriifer* had no seasonal differences, while *A. lilljeborgi* (ANOVA, $F = 7.25$, $p = 0.003$, Tukey Test, $p < 0.05$), total mesozooplankton (Kruskal-Wallis, $H = 17.25$, $p < 0.001$), and *M. leidyi* (ANOVA, $F = 5.12$, $p < 0.01$, Tukey Test, $p < 0.05$) had more depleted $\delta^{13}\text{C}$ in spring, and *L. lucerna* (ANOVA, $F = 38.24$, $p < 0.001$, Tukey Test, $p < 0.05$) and *C. chrysurus* (ANOVA, $F = 12.60$, $p < 0.001$; Tukey Test, $p < 0.05$) had enriched values in autumn (Fig. 5). Among the benthic organisms, *Callinectes danae* (ANOVA, $F = 3.36$, $p = 0.047$) and *Xiphopenaeus kroyeri* (ANOVA, $F = 12.82$, $p < 0.001$, Tukey Test, $p = 0.051$) showed enriched $\delta^{13}\text{C}$ in spring (Fig. 5).

Fig. 5. Seasonal variation of $\delta^{13}\text{C}$ in pelagic and benthic organisms. * = $p < 0.05$

Isotopic niche of jellyfish and potential competitors

The isotopic location of jellyfish species differed substantially. The macroinvertebrate/fish feeder *Olindias sambaquiensis* (see trophic categories in Fig. 2) occupied an upper area of the biplot, whereas planktivorous jellyfishes *Mnemiopsis leidyi*, *Lychnorhiza lucerna*, and *Chrysaora lactea* dominated an intermediate-lower area (Fig. 6A,B). The SEAc of *O. sambaquiensis* and *C. lactea* was wider than most all other consumers in their trophic groups (Table 1, Fig. 6). The SEAc of *O. sambaquiensis* did not overlap with *L. lucerna* and *M. leidyi*, and had a minimal overlap with *C. lactea* comprising 2.5% of its SEAc (Table 1, Fig. 6A,B). The SEAc of

zooplanktivorous jellyfish had a high degree overlap. *C. lactea* had overlaps of 61.3 and 46.9% of its SEAc with *L. lucerna* and *M. leidy*, respectively. The overlaps between *L. lucerna* and *M. leidy* were relatively low, representing 26.1 and 31% of their SEAc's (Table 1, Fig. 6A,B). Table S2 presents detailed population metrics of the species mentioned in Fig. 6.

Fig. 6. (A) Biplots of isotope values of jellyfish species, and (B) their isotopic niche (as size-corrected Standard Ellipse Area, SEAc) from the Cananéia Lagoon Estuarine System. Isotope values of jellyfish were plotted along with (C–F) other consumers of the same trophic group, according to the cluster analysis

The trophic-niche overlap was high among animals of the same cluster (see Fig. 4), which possibly reflects similarities of their feeding habits. The SEAc of the jellyfish *O. sambaquiensis* overlapped with 100% of *Pellona harroweri* SEAc and with most of *S. rastrifer* (63%), *L. brevis* (78.3%), and ‘other consumers of cluster B1’ (73.2%) SEAc’s (Fig. 6C,D). Species of cluster B2 occupied an intermediate-lower area of the biplot (Fig. 6E,F), which possibly reflects feeding habits on lower trophic levels. The SEAc of the lined sole *A. lineatus* did not overlap with *G. genidens*, but all other pairs of species of B2 had overlaps among themselves (Table 1). The SEAc of *A. lineatus* had the lowest overlap with other species (11% on average), while the SEAc of the scyphomedusa *L. lucerna* had the highest overlap (48.5% on average) with other species.

The upper part of the SEAc of *L. brevis*, *S. rastrifer*, ‘other consumers of Cluster B1’, *Genidens genidens*, and *Chloroscombrus chrysurus* overlapped with the jellyfish *O. sambaquiensis*, whereas the lower part overlapped with the zooplanktivorous jellyfishes *C. lactea* and *L. lucerna* (Table 1). In order to evaluate if this pattern is a consequence of ontogenetic shifts of niche occupancy, we evaluated a possible relationship between body size and $\delta^{15}\text{N}$. For most species, a significant relationship was absent (see Fig. S1 in the Supplement). Nevertheless, body size explained a considerable amount of variation in $\delta^{15}\text{N}$, with increasing $\delta^{15}\text{N}$ as body size increased for *L. lucerna* ($F_{1,29} = 10.22$, $p < 0.01$, $r^2 = 0.28$), *A. lineatus* ($F_{1,11} = 5.87$, $p < 0.05$, $r^2 = 37$), *C. chrysurus* ($F_{1,15} = 39.24$, $p < 0.001$, $r^2 = 0.74$), *Spherooides* spp. ($F_{1,9} = 6.70$, $p < 0.05$, $r^2 = 0.46$), and ‘other consumers of cluster B1’ ($F_{1,7} = 5.47$, $p < 0.05$, $r^2 = 0.47$). This pattern demonstrates that some species explore distinct trophic levels and exhibit a pattern of trophic niche overlap dependent on the life cycle stage.

Table 1. Trophic-niche width as the sample size-corrected Standard Ellipse Area (SEAc) as δ units² of the main jellyfish species (in bold) and their potential competitors, and the overlap of their SEAc between pairs of species, as δ units²

	SEAc (δ units ²)	Cluster	Overlap on SEAc (δ units ²)										
			<i>O s</i>	<i>S r</i>	<i>L b</i>	Ot B1	<i>P h</i>	<i>L l</i>	<i>C l</i>	<i>C c</i>	<i>G g</i>	<i>A l</i>	<i>P p</i>
<i>Olindias sambaquiensis</i>(n=7)	5.07	B1											
<i>Stellifer rastrifer</i> (n = 24)	1.61	B1	1.01										
<i>Lolliguncula brevis</i> (n = 10)	2.20	B1	1.72	0.95									
Other B1 (<i>Paralanchurus</i> + <i>Cathorops</i>) (n = 8)	3.39	B1	2.48	1.31	1.63								
<i>Pellona harroweri</i> (n = 4)	0.23	B1	0.23	0.16	0.19	0.23							
<i>Lycnorhiza lucerna</i> (n = 30)	2.46	B2	0.00	0.00	0.09	0.40	0.00						
<i>Chrysaora lactea</i> (n = 17)	3.08	B2	0.13	0.00	0.22	0.67	0.00	1.89					
<i>Chlroscombrus chrysurus</i> (n = 16)	2.16	B2	0.59	0.52	0.95	1.27	0.11	1.22	1.40				
<i>Genidens genidens</i> (n = 10)	2.68	B2	1.49	0.87	1.30	2.01	0.20	0.82	1.24	1.25			
<i>Achirus lineatus</i> (n = 12)	3.45	B2	0.00	0.00	0.00	0.00	0.00	0.87	0.46	0.21	0.00		
<i>Peisos petrunkevitchi</i> (n = 6)	1.68	B2	0.00	0.00	0.28	0.00	0.00	1.17	0.92	0.90	0.41	0.39	
<i>Mnemiopsis leidyi</i> (n = 22)	2.07	D	0.00	0.00	0.00	0.03	0.00	0.64	1.44	0.18	0.56	0.00	0.14

DISCUSSION

Isotopic signatures of primary producers were similar to others found in subtropical regions (Bouillon et al. 2002). The designation of the value of -19.40‰ (from Barcellos et al. 2009) for phytoplankton $\delta^{13}\text{C}$ is indirectly supported by the $\delta^{13}\text{C}$ of the herbivore copepod *Parvocalanus crasirostris* (-19.18‰), and within the range expected for phytoplankton from tropical regions (from -22 to -18‰) (Peterson & Fry 1987). Since the carbon fixed by the main primary producers of the region (marine phytoplankton, microphytobenthos, and C_3 plants) have distinct $\delta^{13}\text{C}$ values, the carbon source for this ecosystem could be distinguished; $\delta^{13}\text{C}$ data of pelagic groups suggest

major contribution by phytoplankton to organic production. Despite the high production of mangrove litterfall ($9.02 \text{ t ha}^{-1} \text{ yr}^{-1}$) in CLES (Tundisi & Matsumura-Tundisi 2001), its importance to the total organic production at the mouth of the estuary must be minimal as well as in other similar mangrove-bordered systems (Heithaus et al. 2011). Nevertheless, it is important to mention that our samplings were spatially limited and probably do not represent inner regions of CLES. The contribution of mangrove litter should be higher in the upper estuary and near creeks, whereas in the mouth of the estuary, phytoplankton is considered more important.

Values of $\delta^{13}\text{C}$ discriminated the benthic vs. pelagic pathway of matter transfer and showed consumers with intermediate values possibly receiving contributions from both sources (Fig. 4). Enriched values of $\delta^{13}\text{C}$ among benthic consumers, especially sessile animals, are common in coastal ecosystems (Sherwood & Rose 2005, Newsome et al. 2007). An explanation for these values relies on microphytobenthos production, which have enriched $\delta^{13}\text{C}$ values (6‰ on average) in relation to phytoplankton (France 1995). Decapods occupying a lower trophic level had intermediate $\delta^{13}\text{C}$ values between phytoplankton and microphytobenthos (Fig. 4). Due to the high abundance of these decapods (Graça-Lopes et al. 2000), they represent an important link coupling pelagic and benthic primary production to higher trophic levels, such as benthic-demersal consumers (Fig. 4).

The seasonal variation of isotopic signatures of pelagic taxa (Fig. 5) showed some similarities, with enriched values of $\delta^{13}\text{C}$ in autumn and depleted values in spring. These changes may be caused by shifts in the balance of carbon contributions from the major primary producers during the seasonal cycle. Pulses in production of the main primary producers may shift the mean values of consumers. Concerning phytoplankton and mangrove litterfall, in Cananéia Estuary, individual studies have recorded

increased production rates in spring and summer; however, seasonal data for microphytobenthos are lacking (Schaeffer-Novelli et al. 1990).

Trophic niches of fish and jellyfish and ecological implications of trophic overlaps

Planktivorous jellyfish species (*Mnemiopsis leidyi*, *Chrysaora lactea*, and *Lychnorhiza lucerna*) had low isotopic niche overlap with the hydromedusa *Olindias sambaquiensis*. *O. sambaquiensis* occupied a high trophic level, which is compatible with its known diet, since the species can feed on larger prey, such as large decapods and fishes, close to its own size (<10 cm), and also on copepods (Zamponi & Mianzan 1985). The planktivorous jellyfishes *M. leidyi* and *L. lucerna* had low isotopic niche partitioning, as a consequence of their distinct prey selectivity patterns. The ctenophore *M. leidyi* feeds on a variable diet ranging from microzooplankton and slowly swimming zooplankton to calanoid copepods (Granhag et al. 2011); whereas, the scyphomedusa *L. lucerna* like other rhizostome medusae probably feeds on micro- and mesozooplankton (Larson 1991), and on large and emergent zooplankton (Pitt et al. 2008). The trophic diversity found here illustrates the importance of a more precise characterization of the ecological role of jellyfish species, which are often pooled into a single trophic category in ecosystem models (Condon et al. 2012).

The jellyfish species *O. sambaquiensis* and *C. lactea* had wider isotopic niches (as SEAc area) than most fish species of their trophic groups, possibly as a consequence of their broad diets. Species of the genus *Chrysaora* consume a wide range of prey, including other gelatinous species (Purcell 1997), fish eggs and larvae, and holoplanktonic crustacean zooplankton (Riascos et al. 2014). Larger trophic niche areas may be evidence of the versatility of feeding habits of these species, from copepods to

fish in the case *O. sambaquiensis* (Zamponi & Mianzan 1985). This feature provides potential advantages to jellyfish over narrow-niched fish species, especially when changes in the trophic structure of pelagic environments switch the biomass dominance to lower trophic levels (Richardson et al. 2009).

Similar to many other estuaries, most fish species were found at young and juvenile stages (e.g. Potter et al. 2001), when they are zooplanktivores and/or benthic invertebrate feeders, which explains why they occupy relatively low trophic levels. Some exceptions to these feeding habits can be noted for the gelatinous zooplankton feeders *Chaetodipterus faber* and *Mola mola*, which showed trophic levels lower than expected, i.e. lower than the zooplanktivore *Anchoa* sp. (Fig. 2). One reason may be that both *C. faber* and *M. mola* possibly feed on prey other than gelatinous zooplankton (e.g. Syväranta et al. 2012). The high TL of the zooplanktivore *Anchoa* sp. is surprising since the species eats mainly calanoid copepods (Din & Gunter 1986). Another reason could be an erroneous trophic classification of *Anchoa* sp. , as well as *P. harroweri*, as zooplanktivorous fish as both can also feed on benthic crustaceans and fish (Höfling et al. 2000).

Overlaps of isotopic niches of fish and jellyfish were related to life stage, since the pattern of overlap can change with the animal's growth. Ontogenetic shifts in trophic level were absent for jellyfishes except for *L. lucerna*. Nevertheless, several fish species increased their trophic level with body size. The increase of TL of the fish *Chloroscombrus chrysurus*, resulting in changes in trophic-niche partitioning, must be a pattern of many other fish species. At young stages (<5 cm of body length), the fish feeds on mesozooplankton, mainly copepods (Silva & Lopes 2009), as well as filter-feeding jellyfish. For the medusae *L. lucerna* and *C. lactea*, and the fish *C. chrysurus*, the highest overlap (winter and summer) coincided with the smallest sizes of the fish

(Fig. 7). Thereafter, at larger sizes (>5 cm), the fish starts to feed on other prey items, such as epibenthic crustaceans and other fish (Silva & Lopes 2009). This explains the rise in its trophic level when large-sized individuals of *C. chrysurus* had overlaps with invertebrate/fish-feeders such as the hydromedusa *O. sambaquiensis* and the fishes *Stellifer rastrifer* and *G. genidens* (Fig. 6, Table 1).

Fig. 7. $\delta^{15}\text{N}$ vs. size as body length for *Chloroscombrus chrysurus* and as bell diameter for *Lychnorhiza lucerna*. Fish specimens >5 cm body length (inside the ellipse) occupied a higher trophic level and were not observed in association with the medusa

Another possible explanation for the overlap of the isotopic niches of *C. chrysurus* and *L. lucerna* is a symbiosis between them. Up to 5 cm, small individuals of the fish species are commonly found as symbionts of scyphomedusae (Tolley 1987). The ecological importance of symbiosis involving large medusae is scarcely understood, and regarding fish, it is usually classified as phoresy, with the symbionts merely transported by the host (Ohtsuka et al. 2009), possibly gaining some protection against predators (Purcell & Arai 2001). Nevertheless, an alternative explanation, based on the similarities of the trophic niches of *L. lucerna* and young *C. chrysurus*, is that the fish symbionts, besides gaining some protection, steal prey captured by the medusa (Purcell & Arai 2001, Lynam & Brierley 2007). As the fish grows, larger individuals

(>5 cm) leave the protection of the host jellyfish and start to exploit new habitats (Tolley 1987). Unlike *C. chrysurus*, the medusa *L. lucerna* showed a slight increase in its trophic level during its growth (Fig. 7, Table S3). Similar to other rhizostome medusae, *L. lucerna* has a mouth measured in millimeters, which limits the size of ingested prey (Larson 1991). Therefore, even larger medusae (>25 cm in bell diameter) may feed on mesozooplankton items only a few millimeters long (<2 mm).

The isotopic niche overlap of planktivorous and predatory fish and jellyfish species highlight the ecological significance of possible resource partitioning among these populations. The diet of jellyfish can be similar to co-occurring pelagic fish species (Purcell & Sturdevant 2001, Brodeur et al. 2008), but few studies have demonstrated competition between these consumers (but see Purcell & Grover 1990). Despite the significant advance in understanding possible triggers of jellyfish outbreaks (Condon et al. 2012, Purcell 2012), the reasons why they do not bloom are scarcely understood. It has been suggested that competition for planktonic food and predation (on polyps, ephyrae, and medusae) by fishes may prevent proliferations of jellyfishes (Richardson et al. 2009). In the CLES, a great number of potential predators of gelatinous animals are found, ranging from sessile invertebrate feeders, sea turtles, some specialized jellyfish feeders (e.g. *Mola mola*, stromateoid fishes), amphipods, and other jellyfish (e.g. *Beroe* spp. and *C. lactea*). In addition, a great number of potential competitors, such as the examples shown here (Fig. 6), along with many other species not sampled may use the same planktonic resources as jellyfish. Given the key ecological role of competitors and predators of jellyfish, identifying trophic relationships among these consumers is urgently needed to understand the importance of biological interactions keeping gelatinous populations ‘in check’ in pristine ecosystems.

Our SIA-based trophic niche characterization identified potential competitors allowing a further examination on the possible consequences of environmental changes, such as the decline of keystone consumers. When a dominant species is removed, the community can respond through compensatory increases in other species (Frank et al. 2007). It has been demonstrated that overexploited planktivorous fish populations (e.g. anchovy, sardine, or herring) were replaced by filter-feeding jellyfish, in highly productive areas such as in the northern Benguela Current, Sea of Japan, and the Bering Sea (Purcell 2012). Richardson et al. (2009) proposed that jellyfish increase after the collapse of an overexploited planktivorous fish, if an alternate fast responding planktivorous species is absent and unable to replace that collapsed fish stock. Subtropical marine regions harbor higher fish species richness than colder regions (Macpherson 2002), and thus have a potentially larger set of species capable of replacing a lost keystone consumer (Frank et al. 2007). In addition, the jellyfish species sampled here (*C. lactea*, *L. lucerna*, *M. leidyi*, and *R. atlanticum*) are taxonomically and functionally similar to the blooming species in other areas, providing significant chances to replace a declining consumer. Since species-rich food webs contained a larger pool of compensatory species (Gonzalez & Loreau 2009), possible responses to species removal or decline may be less predictable. Thus, it is necessary to evaluate other biological features of key members, like reproductive, growth, and feeding performance in order to understand an ecosystem's response to stresses like overfishing.

Conclusions based solely on isotope data must be carefully interpreted, especially when using only isotope data as input to analytical models (Layman et al. 2012). It is essential to understand the species' natural history in order to reach well-founded interpretations of trophic relationships (Layman et al. 2012). Because of the

different factors that generate variation in isotope values, our data provide only indirect evidence of the actual trophic structure of CLES and of the isotopic niches of the species studied. Some pre-analytical factors can affect $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. For jellyfish, processing methods still need to be standardized (Fleming et al. 2011). The widespread preservation method of freezing can increase $\delta^{15}\text{N}$ values of jellyfish (Fleming et al. 2011), whereas for fish, octopus, and kelp samples, no effect of freezing was found (Kaehler & Pakhomov 2001).

Tissues rich in lipids are depleted in $\delta^{13}\text{C}$ values relative to those rich in proteins (DeNiro & Epstein 1977). Trophic interpretations based on $\delta^{13}\text{C}$ may, therefore, be biased by lipid effects (e.g. Wada et al. 1987). In contrast to temperate and higher latitude environments, tropical and subtropical zooplankton is characterized by low lipid contents, and does not accumulate lipid reserves seasonally (Hagen & Auel 2001). Lipids were not chemically extracted from our samples, and the $\delta^{13}\text{C}$ values were not mathematically corrected. The carbon-to-nitrogen (C:N) ratio is a proxy of lipid content, indicating the need to apply lipid extraction or correction to $\delta^{13}\text{C}$ values, if C:N > 3.5 (Post et al. 2007). The lipid bias in our study should be minimal, as the majority of our samples were low-lipid muscle tissues (except for some benthic invertebrates). In our dataset, all fish and medusae samples were <3.5. Most C:N values of the ctenophore *M. leidyi* were >3.5 with $\delta^{13}\text{C}$ estimated error up to 5%, using the correction described by Post et al. (2007). For mesozooplankton, 30% of samples (n = 68) were >3.5 and <5, with estimated error between 0.5 and 15% (mean: 4%). Among benthic invertebrates, 31% of samples (n = 23) were >3.5 and <8.6, with estimated error between 0.5 and 51% (mean: 16%).

Estimates of trophic level from ^{15}N require a good knowledge of the variation of baseline values and trophic fractionation factors ($\Delta^{15}\text{N}$). We used the globally

accepted value of $\delta^{15}\text{N}$: 3.4‰ in coastal studies (Minagawa & Wada 1984). Trophic Enrichment Factors (TEF) for C and N need to be experimentally studied in different taxonomic groups. Recent reviews demonstrated that for ^{15}N this factor may vary (from 2 to 4.5‰) among groups of organisms, and could be related to the consumer's nutritional status, diet quality, size, age, dietary ontogeny, and the biochemical form of nitrogen excretion (Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001, Vanderklift & Ponsard 2003). $\delta^{15}\text{N}$ of the planktivorous jellyfishes *L. lucerna* (mean: 10.31), *C. lactea* (10.64), and *M. leidyi* (10.66) were from 1.95 to 2.29‰ higher than total mesozooplankton (8.37), which is probably the main food source for these predators. For jellyfishes, the only experimental study to determine TEF showed much higher values for C (~4‰) in *Aurelia* sp., compared to other animals (~1‰) (Post 2002) and lower than typical for N (<1‰) in *Aurelia* sp. compared to other animals (2–4‰) (D'Ambra et al. 2014).

Because of the wide variation in $\delta^{13}\text{C}$ values of the main primary producers, phytoplankton carbon is probably the main source for most consumers, especially for pelagic groups (zooplankton, jellyfish, fish, and cephalopod). For some benthic species (especially sessile invertebrates), the enriched $\delta^{13}\text{C}$ suggests a contribution of microphytobenthic carbon. Depleted $\delta^{13}\text{C}$, which may characterize terrestrial carbon from mangrove litterfall, was uncommon. Connectivity between primary (zooplankton) and secondary consumers (planktivorous fish and jellyfish) is suggested by their patterns of seasonal variation of ^{13}C . Jellyfish species had high trophic diversity, and their feeding habits (planktivorous, benthic invertebrate feeders) were distinguished in isotopic space. Isotopic niche of jellyfish were often broader than fish at the same trophic category, possibly as a consequence of their broad diets. This study demonstrates an overlap of isotopic niche between jellyfish and fish with similar

feeding habits (Figs. 2 & 6), which can change along a species' life history (Fig. 7). Description of isotopic niches provides a general picture of trophic roles, interactions, and the degree of functional redundancy among species, allowing an evaluation of possible directions of community shifts resulting from the removal or proliferation of keystone consumers. Further laboratory and field studies are needed to understand the mechanisms regulating jellyfish outbreaks, and to evaluate the consequences of possible environmental changes to the pelagic community of relatively pristine ecosystems.

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Food web characterization based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ reveals isotopic niche partitioning between fish and jellyfish in a relatively pristine ecosystem

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Table S1. Mean isotopic values of ^{15}N and ^{13}C (standard deviation in brackets), and Carbon:Nitrogen ratios of primary producers, mesozooplankton, gelatinous zooplankton and nekton species collected along the 4 seasons, from April 2012 to January 2013, at Cananéia Lagoon Estuarine System. - means no measurement.

Primary producers	n	AUTUMN			n	WINTER			n	SPRING			n	SUMMER		
		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N
Phytoplankton*						3.81	-20.18	-	-	-	-	-	-	-	-	-
Microphytobenthos*						3.81	-14.18									
<i>Rhizophora mangle</i>	-	-	-	-	3	4.61(0.09)	-27.86(0.46)	27.52								-
<i>Spartina alterniflora</i>	-	-	-	-	3	4.01(0.49)	-13.23(0.20)	17.60	-	-	-	-	-	-	-	-
<i>Enteromorpha</i> sp.	-	-	-	-	1	8.33	-13.06	9.34	-	-	-	-	-	-	-	-
Zooplankton																
Mollusca:																
Bivalve veliger	1	5.97	-19.88	3.64	-	-	-	-	-	-	-	-	-	-	-	-
Gastropod veliger	-	-	-	-	-	-	-	-	1	7.00	-15.08	4.45	-	-	-	-
Decapoda:																
Brachyura Zoeae	3	5.77(2.94)	-22.41(4.90)	4.75	2	7.63(0.19)	-19.08(0.29)	3.65	3	4.43(1.07)	-20.1(1.02)	3.74	3	6.95(1.25)	-18.52(6.79)	4.29
<i>Lucifer faxoni</i>	2	8.26(1.14)	-16.79(0.28)	4.43	1	9.40	-19.49	4.43		-	-	-	1	6.67	-18.36	4.74
Dendrobranchiata:																
<i>Peisos petrunkevitchi</i>	3	10.19(0.39)	-17.38(0.21)	3.46	-	-	-	-	6	9.99(1.03)	-17.94(0.49)	3.12	-	-	-	-
Mysidacea sp.	-	-	-	-	2	6.87(0.68)	-17.86(0.43)	3.29	-	-	-	-	1	6.74	-17.89	3.88
Cladocera:																
<i>Penilia avirostris</i>	-	-	-	-	-	-	-	-	3	8.50(0.48)	-21.60(1.68)	3.27	1	7.97	-19.00	3.53
Polichaeta: Polichaete larvae	-	-	-	-	1	10.47	-17.50	2.73	-	-	-	-	-	-	-	-
Chaetognatha:																
<i>Sagitta friderici</i>	1	9.81	-19.16	3.74	2	10.23(0.17)	-19.88(0.06)	3.26	-	-	-	-	-	-	-	-
Copepoda:																
<i>Acartia lilljeborgi</i>	4	8.64(0.29)	-18.32(0.46)	3.52	3	9.14(0.43)	-18.56(0.22)	3.14	5	8.50(0.60)	-19.86(0.86)	3.11	5	8.50(0.60)	-19.86(0.86)	3.60
<i>Corycaeus</i> sp.	1	11.16	-19.42	4.36	-	-	-	-	2	9.88(0.88)	-20.87(0.77)	3.02	-	-	-	-
<i>Parvocalanus crassirostris</i>	-	-	-	-	-	-	-	-	-	-	-	-	3	7.21(0.48)	-19.18(0.60)	3.81
<i>Euterpina acutifrons</i>	-	-	-	-	-	-	-	-	1	7.21	-17.11	3.17	-	-	-	-

<i>Temora turbinata</i>	1	7.33	-18.78	4.15	2	8.90(0.11)	-18.71(0.51)	4.15	9	8.76(0.74)	-18.90(0.48)	3.45	5	8.25(0.30)	-19.03(0.41)	3.88
Vertebrata: Fish eggs	-	-	-	-	1	9.90	-19.07	3.90	3	13.02(2.02)	-19.46(0.69)	4.20	1	10.70	-16.58	3.94
Thaliacea:	-	-	-	-	-	-	-	-	2	11.90(1.89)	-29.58(1.49)	3.16	-	-	-	-
<i>Thalia democratica</i>	-	-	-	-	-	-	-	-	2	11.90(1.89)	-29.58(1.49)	3.16	-	-	-	-
Total mesozooplankton	7	8.63(0.90)	-17.73(0.13)	3.72	5	7.33(1.52)	-17.39(0.33)	4.49	6	8.30(1.98)	-20.43(1.02)	4.43	6	8.23(0.74)	-19.60(0.75)	4.05
Gelatinous zooplankton																
Cnidaria: <i>Chiropsalmus quadrumanus</i>	-	-	-	-	2	10.72(0.37)	-15.98(0.70)	3.10	-	-	-	-	-	-	-	-
<i>Chrysaora lactea</i>	2	10.79(1.38)	-17.86(1.03)	3.24	1	11.23	-17.73	2.91	7	10.60(0.91)	-19.55(1.18)	2.87	7	10.55(0.42)	-17.38(0.57)	2.62
<i>Lychnorhiza lucerna</i>	7	10.34(0.90)	-17.11(0.72)	3.34	5	11.01(0.26)	-17.55(1.48)	2.54	12	10.43(0.70)	-18.70(0.88)	2.61	6	9.91(0.40)	-17.62(0.81)	2.54
<i>Olindias sambaquiensis</i>	-	-	-	-	-	-	-	-	6	12.28(1.07)	-17.72(1.45)	2.97	1	11.95	-16.24	1.62
<i>Rhacostoma atlanticum</i>	-	-	-	-	2	12.71(0.08)	-15.88(1.01)	1.55	-	-	-	-	-	-	-	-
Ctenophora:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mnemiopsis leidyi</i>	6	10.01(0.97)	-18.64(0.46)	4.00	4	11.06(0.26)	-18.93(0.41)	3.95	6	11.38(0.63)	-19.62(0.63)	3.70	6	10.01(0.97)	-18.64(0.46)	2.86
Benthos																
Brachyura:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Arenaeus cribrarius</i>	2	9.77(0.24)	-16.69(0.80)	3.24	3	8.54(0.33)	-15.75(0.56)	3.81	-	-	-	-	-	-	-	-
<i>Callinectes danae</i>	3	9.87(1.28)	-17.86(1.14)	3.10	3	8.68(0.66)	-17.74(1.92)	2.97	5	9.55(2.38)	-14.97(6.65)	2.96	10	8.11(0.71)	-16.46(1.73)	2.91
Caridea: <i>Caridea</i> sp.	-	-	-	-	3	11.94(0.40)	-15.72(0.46)	2.96	3	9.32(1.09)	-18.20(0.27)	3.17	-	-	-	-
Dendrobranchiata:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xiphopenaeus kroyeri</i>	4	8.83(0.66)	-17.29(0.92)	3.08	3	9.32(0.24)	-15.98(1.27)	2.78	5	9.08(2.67)	-12.70(0.37)	2.87	10	8.11(0.71)	-16.46(1.73)	2.93
Octocorallia:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Renilla reniformis</i>	-	-	-	-	3	8.50(0.60)	-11.28(2.73)	6.89	2	8.50(0.19)	-12.23(0.35)	6.49	2	9.89(0.48)	-9.36(1.22)	7.88
<i>Alcyonacea</i> sp.	-	-	-	-	1	9.60	-14.91	5.43	-	-	-	-	-	-	-	-
Bryozoa: <i>Bryozoa</i> sp.	-	-	-	-	2	7.51(0.24)	-8.60(0.55)	4.52	5	7.83(1.05)	-15.95(1.09)	4.47	-	-	-	-
Asteroidea:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Luidia senegalensis</i>	-	-	-	-	3	10.67(0.72)	-9.53(0.24)	4.15	-	-	-	-	1	10.06	-9.60	6.45
Holothuroidea:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Holothuria grisea</i>	-	-	-	-	-	-	-	-	2	6.72(0.25)	-12.62(0.19)	3.05	-	-	-	-
Nekton																
Mollusca:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lolliguncula brevis</i>	3	11.94(0.38)	-18.12(2.51)	3.98	3	12.33(1.52)	-17.74(1.31)	3.45	4	11.57(0.64)	-17.65(0.52)	3.25	-	-	-	-
Elasmobranchii:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhinobatos</i> sp.	1	11.45	-15.57	2.97	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei:	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Achirus lineatus</i>	-	-	-	-	5	9.39(1.64)	-16.88(2.14)	2.97	4	10.62(0.24)	-15.27(0.92)	2.85	3	9.93(0.29)	-17.87(1.02)	2.91
<i>Anchoa</i> sp.	-	-	-	-	3	12.85(0.18)	-15.72(0.11)	3.65	-	-	-	-	-	-	-	-
<i>Cathorops spixii</i>	-	-	-	-	3	12.02(1.46)	-17.12(1.53)	3.05	-	-	-	-	-	-	-	-
<i>Cyclichthys spinosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	9.61(0.19)	-15.04(1.43)	2.67
<i>Chaetodipterus faber</i>	-	-	-	-	-	-	-	-	-	-	-	-	3	11.53(0.54)	-17.24(0.05)	2.97
<i>Chloroscombrus chrysurus</i>	3	11.94(0.69)	-16.59(0.36)	3.27	5	9.98(0.47)	-18.04(0.06)	2.60	5	11.25(0.38)	-18.20(0.45)	2.77	3	9.95(0.24)	-17.84(0.74)	2.99
<i>Dactylopterus volitans</i>	3	-	-	-	1	10.01	-16.93	3.03	3	10.27(0.22)	-16.54(0.92)	2.90	-	-	-	-
<i>Genidens genidens</i>	-	-	-	-	-	-	-	-	5	12.11(1.78)	-17.24(0.83)	2.88	5	10.46(0.35)	-18.64(0.80)	2.99

<i>Menticirrhus</i> sp.	-	-	-	-	1	11.05	-18.47	3.48	3	11.44(0.48)	-16.50(0.65)	2.88	-	-	-	-
<i>Isopisthus parvipinnis</i>	-	-	-	-	2	10.98(0.77)	-18.43(1.41)	2.99	-	-	-	-	-	-	-	-
<i>Mola mola</i>	-	-	-	-	1	10.50	-16.89	2.68	-	-	-	-	-	-	-	-
<i>Nebris micro</i>	1	11.30	-16.87	3.22	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oligoplites saurus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	10.15	-17.14	3.06
<i>Orthopristis ruber</i>	1	11.01	-17.26	3.08	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paralonchurus brasiliensis</i>	-	-	-	-	1	11.55	-18.57	3.48	2	11.88(0.41)	-16.58(0.25)	2.85	-	-	-	-
<i>Pellona harroweri</i>	-	-	-	-	2	11.79(0.09)	-16.84(0.17)	2.90	2	11.65(00.2)	-18.03(0.06)	2.93	-	-	-	-
<i>Polydactylus virginicus</i>	2	11.70(0.14)	-17.51(0.39)	3.12	-	-	-	-	-	-	-	-	1	11.80	-16.95	3.02
<i>Prionotus punctatus</i>	2	11.60(0.40)	-17.07(0.21)	3.10	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rypticus saponaceus</i>	-	-	-	-	1	8.64	-23.52	2.67	-	-	-	-	-	-	-	-
<i>Selene setapinis</i>	1	9.79	-18.13	3.03	-	-	-	-	-	-	-	-	-	-	-	-
<i>Selene vomer</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	10.02(0.45)	-15.81(0.63)	2.73
<i>Sphoeroides greeleyi</i>	-	-	-	-	4	10.08(1.06)	-16.69(0.83)	2.88	-	-	-	-	-	-	-	-
<i>Sphoeroides testudineus</i>	-	-	-	-	-	-	-	-	3	10.76(0.20)	-16.19()	2.89	3	9.96(1.62)	-16.38(0.59)	2.88
<i>Stellifer rastrifer</i>	4	12.02(0.04)	-16.45(0.76)	3.18	5	10.91(0.28)	-16.82(0.65)	2.90	6	12.53(0.60)	-17.55(0.50)	2.96	9	11.22(0.41)	-17.11(0.66)	2.88
Cetacea:	-	-	-	-	-	-	-	-	-	-	-	-	1	15.06	-16.67	3.73
<i>Sotalia guianensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S2. Population metrics (Layman et al. 2007) of the main jellyfish (in bold) and their potential competitors from the Cananéia Lagoon Estuarine System, grouped by clusters (see Fig 3). NR = $\delta^{15}\text{N}$ range; CR = $\delta^{13}\text{C}$ range; TA = convex hull total area (δ^2 units); CD = mean distance to centroid; MNND = Mean Nearest Neighbor Distance; SDNND = standard deviation of mean nearest neighbor distance.

	SEA _c (δ units ²)	Cluster	NR	CR	TA	CD	MNND	SDNND
<i>Olindias sambaquiensis</i> (N=7)	5.07	B1	2.77	3.56	5.93	1.59	0.92	0.52
<i>Stellifer rastriker</i> (N=24)	1.61	B1	2.50	2.86	3.93	0.90	0.28	0.16
<i>Lolliguncula brevis</i> (N=10)	2.20	B1	3.24	2.48	4.30	0.97	0.69	0.39
Other consumers of B1 (<i>Paralichthys</i> + <i>Cathorops</i>) (N=8)	3.39	B1	2.65	2.75	4.28	1.35	0.64	0.49
<i>Pellona harroweri</i> (N=4)	0.23	B1	0.24	1.35	0.14	0.60	0.19	0.09
<i>Lychnorhiza lucerna</i> (N=30)	2.46	B2	3.69	3.25	8.84	1.16	0.31	0.37
<i>Chrysaora lactea</i> (N=17)	3.08	B2	2.46	4.09	6.41	1.36	0.46	0.30
<i>Chloscombrus chrysurus</i> (N=16)	2.16	B2	3.23	2.45	4.43	1.07	0.44	0.31
<i>Genidens genidens</i> (N=10)	2.68	B2	2.69	2.91	4.14	1.32	0.55	0.23
<i>Achirus lineatus</i> (N=12)	3.45	B2	2.31	4.80	6.13	1.41	0.63	0.34
<i>Peisos petrunkevitchi</i> (N=6)	1.68	B2	2.74	1.22	1.74	0.87	0.67	0.75
<i>Mnemiopsis leidyi</i> (N=22)	2.07	D	3.80	3.11	6.42	0.99	0.45	0.32

Supplementary figure 1. Relationships between body size (cm) (as bell diameter, for medusae, oral-aboral length for the ctenophore *Mnemiopsis leidyi*, total body length for fish and the shrimp *Xiphopenaeus kroyeri*, and carapace length for the crab *Callinectes danae*) and trophic level (as $\delta^{15}\text{N}$), of gelatinous zooplankton*, fish ** and crustaceans ***.

DISCUSSÃO GERAL E CONCLUSÕES

Mudanças ontogenéticas morfológicas e funcionais: consequências para os mecanismos e hábitos alimentares

Enquanto os adultos de cifomedusas possuem planos corporais altamente diversos, as éfiras possuem morfologia muito similar (Russell, 1970). Neste trabalho são descritos o desenvolvimento e a mecânica funcional de natação e alimentação, ao longo do crescimento de éfiras de medusas de Rhizostomeae. Éfiras de poucos milímetros vivem em um ambiente fluido onde as forças de viscosidade são igualmente importantes em relação as forças inerciais (Feitl *et al.* 2009; Higgins *et al.* 2008), o que afeta seu modo natatório, comportamental e de captura de alimentos. Em um ambiente viscoso, o impulso natatório cessa imediatamente após a contração da umbrela. O deslocamento gerado pela contração umbrelar da éfira é diretamente proporcional a amplitude do deslocamento da margem umbrelar (Vogel, 1994; Blough *et al.*, 2011). Para se obter maior deslocamento, éfiras de *L. lucerna* invertem sua umbrela e exibem um maior ângulo de contração do que a medusa adulta, onde a contração é restrita a uma pequena porção distal da margem. Conforme as éfiras crescem e aumentam a força de contração umbrelar, passam por uma mudança no regime de fluidos circundantes, pelo aumento da importância das forças inerciais. Com isso, o hidrodinamismo do corpo e a conservação do impulso se tornam mais importantes (Vogel, 1994). Para atender às demandas desse ambiente em transição, o plano corporal da éfira de *L. lucerna* muda, com a umbrela tornando-se mais alta e hemisférica (com menor arrasto hidrodinâmico) e a frequência de pulsação diminui das éfiras (5 Hz) para os indivíduos adultos (2-3 Hz).

O aumento do tamanho corporal e da força da natação também afetam os modos alimentares. Embora tenha se atribuído um papel relevante dos movimentos natatórios na produção de correntes alimentares em éfiras (Sullivan *et al.*, 1997; Gordoia *et al.*, 2014), os baixos números de Reynolds ($Re < 100$) em seu ambiente fluido viscoso sugerem que o transporte de fluidos (e presas) seja pouco eficiente neste estágio. Éfiras não criam vórtices circulatórios através das pulsações da umbrela (Feitl *et al.*, 2009), e quando o fazem os mesmos são rapidamente dissipados em indivíduos juvenis (Hamlet *et al.*, 2011). O uso da técnica da velocimetria por imagem de partículas no presente trabalho demonstrou que toda a aceleração dos fluidos gerada pela pulsação umbrelar

é rapidamente dissipada em éfiras (6 mm de diâmetro umbrelar) sendo ineficiente para o transporte de presas para suas superfícies distais nos braços orais. Tal mecanismo de formação dos vórtices só foi observado a partir do aumento ontogenético da força da pulsação da umbrela (<10 mm) em um ambiente dominado pelas forças inerciais ($Re > 300$).

Com o aumento ontogenético na força da pulsação umbrelar, os vórtices produzidos permanecem mais tempo transportando fluidos em direção às superfícies de captura de presas. Higgins *et al.* (2008) sugerem que isso ocorre em paralelo ao desenvolvimento distal das estruturas de captura de presas em *C. capillata*. Dessa forma, o organismo investiria energia na produção de tecido para desenvolver longos tentáculos e braços orais, somente após a força de suas pulsações produzir vórtices capazes de transportar presas distalmente para tais estruturas. Essa possível sincronia no desenvolvimento hidrodinâmico e morfológico pode ser um padrão universal entre cifomedusas, uma vez que o alongamento e ramificação dos braços orais de *L. lucerna* também ocorre em paralelo com o aumento ontogenético na força dos vórtices. Em indivíduos maiores de *L. lucerna*, enquanto a medusa inicia um ciclo de contração da umbrela, os vórtices produzidos pelas pulsações anteriores, continuam a transportar fluidos para as regiões distais dos braços orais. Medusas adultas de muitas espécies Semaestomeae (*e.g. Cyanea* spp; *Chrysaora* spp.) possuem braços orais que excedem em diversas vezes o diâmetro de sua umbrela (Kramp, 1961; Russell, 1970). Nesses organismos vórtices produzidos por sucessivas pulsações umbrelares continuam a transportar presas para os braços orais (Ford *et al.*, 1997), otimizando assim o contato entre braços orais e tentáculos com os fluidos transportados pelos vórtices.

A ineficiência do transporte de fluidos em éfiras pode resultar em limitações ecológicas para o consumo de presas sensíveis e evasivas como larvas de decápodes e copépodes calanóides. A análise da dieta e seletividade alimentar de éfiras de *Aurelia* sp. (Sullivan *et al.*, 1994; 1997) bem como experimentos em aquários (Riisgard & Madsen, 2011) indicam que devido às capacidades sensíveis e evasivas de presas como copépodes calanóides esses itens não são eficientemente capturados por éfiras da espécie. Portanto neste estágio de vida, presas pouco evasivas como outros organismos gelatinosos e rotíferos seriam mais importantes na dieta, do que os crustáceos evasivos, mesmo que esses últimos sejam os itens mais abundantes no ambiente natural (Sullivan *et al.*, 1994; 1997). Infelizmente a coleta de éfiras para a análise de conteúdos estomacais e de isótopos estáveis não foi possível neste estudo, devido às dificuldades

inerentes ao método de coleta (na superfície da água e com redes de arrasto) e também devido à baixa abundância de éfiras nos ambientes estudados (Tronolone *et al.*, 2002). No entanto, éfiras e juvenis de *L. lucerna* também se alimentam de éfiras de outras cifomedusas em laboratório (Schiariti *et al.*, *in prep.*), o que pode indicar que presas pouco evasivas como outros organismos gelatinosos, sejam de fato um item alimentar importante para estágios juvenis de muitas outras espécies de Scyphozoa.

Ao contrário de outras espécies de cifomedusas que expandem o número de taxa ingeridos e a diversidade de sua dieta ao longo do crescimento (Graham & Kroutil 2001; Riascos *et al.*, 2014), *L. lucerna* diminui a diversidade de sua dieta, tornando-se mais especializada na alimentação sobre copépodes calanóides que chegam a representar >90% da abundância numérica e da composição em carbono de sua dieta. O aumento ontogenético na força dos vórtices produzidos pela pulsação umbrelar, permite a captura de presas mais evasivas em *L. lucerna*. Dentro do intervalo de tamanho de medusas analisadas para o estudo de conteúdo estomacal (5–30 cm) com o aumento do tamanho da medusa, foi observada uma tendência de aumento na proporção de copépodes calanóides na dieta e também um aumento no tamanho de copépodes (*Acartia* spp. e *Paracalanus* spp.), relativo ao tamanho desses mesmos itens em campo. No entanto, a simples comparação entre velocidades dos fluxos marginais e as velocidades de fuga das presas para uma avaliação da probabilidade de captura (Costello & Colin, 1994), pode ser insuficiente para explicar certos padrões já que outros fatores (*e.g.* capacidade de detecção, descarga de nematocistos) também influenciam essas interações predador-presa.

A análise de isótopos estáveis dos tecidos de *L. lucerna* (2–25 cm) revelaram aumentos sutis em seu nível trófico (avaliados pelos valores de $\delta^{15}\text{N}$) os quais poderiam ser atribuídos ao aumento na força das correntes alimentares propiciando a captura de itens de mais elevado nível trófico (*e.g.* zooplâncton carnívoro, crustáceos maiores) em decorrência do desenvolvimento ontogenético. Apesar desse aumento no nível trófico, a espécie ainda manteve uma posição trófica semelhante a outros organismos zooplânctívoros (peixes e outros gelatinosos). O resultado dos isótopos estáveis corroborou os dados do conteúdo estomacal, que foi composto basicamente de componentes do mesozooplâncton. Apesar de parecer óbvio que o pequeno tamanho das bocas em medusas de Rhizostomeae limite o tamanho das presas ingeridas à escala do mesozooplâncton (Larson, 1991; Lee *et al.*, 2008), estudos da dieta de outras espécies do grupo demonstraram distintos padrões de seletividade alimentar sobre

presas mesozooplancônicas. Enquanto *Stomolophus meleagris* aparentemente consome baixas proporções de copépodes (Larson, 1991; Padilla-Serrato *et al.*, 2013), *Pseudorhiza haeckeli* possui seletividade positiva para copépodes calanóides (Fancett 1988). Diatomáceas foram o item mais abundante em *Rhizostoma pulmo* e *Cotylorhiza tuberculata* (Pérez-Ruzafa *et al.*, 2002), porém foram pouco importantes para outras espécies (Fancett, 1988; Larson, 1991; este estudo). Dessa forma, devem existir especializações alimentares em medusas de Rhizostomeae que ainda necessitam ser investigadas para uma melhor compreensão de seu papel trófico. A hipótese da descarga seletiva de nematocistos (Hanson & Kiørboe, 2006), pode determinar padrões alimentares e deve ser quantitativamente investigada para espécies onde foi demonstrada seletividade negativa na dieta (*e.g.* cladóceros *Penilia avirostris*). Vídeos de *L. lucerna* revelaram a ausência de reação de captura pelos *digitata*, para diatomáceas, semelhante ao demonstrado em pólipos de *Aurelia* sp. (Huang *et al.*, 2014) e para a hidromedusa *Aglaura hemistoma* (Colin *et al.*, 2005) e portanto, deve ser investigado quantitativamente no futuro.

A estrutura e o mecanismo bombeador filtrador de medusas de Rhizostomeae

Em medusas Rhizostomeae, pouca importância foi dada a descrição dos característicos braços orais filtradores, em sua estrutura tridimensional, utilizando organismos em postura de vida. Em parte, essa falta de informações se deve à maior ênfase dada aos canais umbrelares e seu padrão de desenvolvimento, como características de valor taxonômico e sistemático, como propõe o sistema de Stiasny (1921). Trabalhos que descrevem detalhes dos braços orais e das aberturas bucais (Huxley 1849; Haeckel, 1880; Mayer, 1910; Russell, 1970; Thiel, 1970; Mianzan & Cornelius, 1999; Lee *et al.*, 2008) se basearam em exemplares já preservados, os quais encolhem e perdem seu arranjo tridimensional. Detalhes dessa estrutura em animais vivos podem ser analisados em descrições dos estágios iniciais do desenvolvimento da boca da éfira para a formação dos primórdios dos braços orais (Claus, 1883; 1884; Uchida, 1925; Sugiura, 1966; Kawahara *et al.*, 2006; Holst *et al.*, 2008). Com base nessas descrições e observações do desenvolvimento dos braços orais em *L. lucerna* sugere-se que a forma da estrutura dos braços orais ao nível dos *digita* (comprimento e espaçamento) e dos poros filtradores (diâmetro e formato do poro) são conservados entre as espécies analisadas. Tal semelhança estrutural se deve provavelmente a

restrições mecânicas para o funcionamento eficiente dos braços orais como uma estrutura filtradora no ambiente fluido desses organismos.

O plano corporal de medusas Rhizostomeae é muito diverso considerando-se proporções no tamanho da umbrela e braços orais, e sua disposição espacial (Mayer, 1910, Mianzan & Cornelius, 1999). Tais diferenças afetam o modo de interação entre os vórtices produzidos pelas pulsações umbrelares e os braços orais, portanto afetando o modo pelo qual presas são retidas. Em *Cassiopea* sp., que possui braços orais de maior projeção lateral em relação ao eixo de simetria, todo o vórtice adentra os braços orais (Hamlet *et al.* 2011; Santhanakrishnan *et al.* 2012). Já em *L. lucerna*, os vórtices formados pela pulsação umbrelar se dividem ao atingir os braços orais, enquanto a região central do vórtice roda livremente, perpendicular à margem da umbrela e fora do espaço ocupado pelos braços orais, a região periférica dos vórtices adentra o espaço dos braços orais pela altura de sua inserção, no disco oral. Em função dessa divisão dos fluidos do vórtice dois modos de retenção de presas foram observados: *i*- adesão, em que o centro do vórtice gira fora do braço oral e arremessa presas de encontro a superfície do braço oral, que por sua vez, são retidas após o contato com os *digitata*; e *ii*- peneiramento, em que o fluido que adentra o centro do braço oral pela região proximal, tanto durante a expansão quanto durante a contração da umbrela, flui em direção ao exterior e as presas maiores do que os poros filtradores são retidas.

Em *Aurelia* sp. a captura de microzooplâncton ocorre em toda a superfície do corpo através de um muco aderente, que é transportado por correntes ciliares até os braços orais onde são ingeridos (Southward, 1955; Stoecker *et al.*, 1987). Nas sequências de vídeo de capturas de presa em *L. lucerna* todas as reações de retenção, foram realizadas pelos *digitata*, e não por cordões de muco supostamente aderentes, como especulou Phillips *et al.*, (1969) para *S. meleagris*. Shanks & Graham (1988) demonstraram que o muco é produzido por *S. meleagris* em resposta a predadores. Grandes concentrações de muco não foram observados em campo nos braços orais de *L. lucerna*, assim como em *S. meleagris* (Larson, 1991) e são provavelmente produzidos como uma reação ao estresse mecânico e pelo manuseio (Larson, 1991; Graham *et al.*, 2003). Porém não se descarta, um possível mecanismo semelhante ao de *Aurelia* sp. e ainda não descrito para medusas de Rhizostomeae, para a retenção e o transporte de microzooplâncton.

Soluções para o problema de se encontrar alimento em um meio onde o mesmo encontra-se esparsamente distribuído, são diversas entre organismos que

desenvolveram mecanismos bombeadores e filtradores (Rubenstein & Koehl, 1977; Riisgård & Larsen 2010). Cifomedusas porém foram um dos primeiros metazoários a realizar esse bombeamento por meio de força muscular (Costello *et al.*, 2008). *L. lucerna*, assim como outras medusas de Rhizostomeae, possuem maiores frequências de pulsação da umbrela do que outras cifomedusas (Costello & Colin 1994; 1995; D'Ambra *et al.*, 2001). Em *L. lucerna*, ambos os movimentos de contração e expansão da umbrela são mais rápidos do que em *Aurelia* sp. e *C. quinquecirrha*. A umbrela de medusas Rhizostomeae expande mais rápido provavelmente devido a propriedades mecânicas de sua mesoglêia, que possui até seis vezes mais colágeno (*Cotylorhiza tuberculata* e *Rhizostoma pulmo*) do que outras cifomedusas (*Aurelia* sp. e *Pelagia noctiluca*) (Addad *et al.* 2011). Esse colágeno da mesoglêia umbrelar, na forma de feixes, armazena a energia potencial elástica gerada pela contração e age em ação antagônica à musculatura subumbrelar, para a recuperação da forma inicial da umbrela (Muskatine & Lenhoff, 1974; Shaposhnikova *et al.*, 2005). Tal propriedade mecânica da umbrela de medusas Rhizostomeae propicia maiores volumes de água transportados contra os braços orais, e assim aumenta o volume filtrado (Acuña *et al.*, 2011; Katija *et al.* 2011).

O papel ecológico de *Lychnorhiza lucerna*

Existe um extenso debate sobre interações antagônicas (predação e competição) entre organismos gelatinosos (particularmente cnidários e ctenóforos pelágicos) e peixes (revisado em Purcell & Arai, 2001). Os primeiros são frequentemente apontados como grandes responsáveis pela redução de estoques pesqueiros devido a predação sobre ovos e larvas de peixes (Möller, 1980; 1984; Purcell, 1985; Mills, 1995). Para *L. lucerna*, ovos e larvas de peixes foram itens pouco importantes nos conteúdos estomacais e também ocorreram em baixíssimas densidades em campo durante as coletas. Devido aos altos valores isotópicos ($\delta^{15}\text{N} \approx 13$) em ovos de peixes, semelhante aos de peixes adultos e superiores aos de *L. lucerna* ($\delta^{15}\text{N} \approx 10$), exclui-se a possibilidade de que esses itens sejam importantes para a dieta da medusa. Ocorrendo sobreposição temporal e espacial entre *L. lucerna* e ovos e larvas de peixes esses últimos provavelmente seriam consumidos, uma vez que para outras medusas de Rhizostomeae (*e.g.* *Phyllorhiza punctata*; *P. haeckeli*; *S. meleagris*) ovos e larvas de peixe representaram grande proporção de sua dieta (15–65,3%) (Fancett, 1988; Graham *et al.*, 2003; Padilla–Serrato *et al.*, 2013).

Existem poucos dados sobre taxas alimentares individuais de medusas Rhizostomeae (Fancett & Jenkins, 1988; Larson, 1991; Garcia & Durbin, 1993). Essas medusas são apontadas como predadores pelágicos fundamentais, devido ao seu tamanho e padrão de natação robusto, que seria energeticamente custoso, demandando maiores taxas alimentares do que para outras cifomedusas (Purcell *et al.*, 2010). As taxas individuais de ingestão (copépodes ingeridos*medusa⁻¹*dia⁻¹) de *L. lucerna*, quantificadas neste estudo com base em conteúdo estomacal, foram maiores do que as de medusas semeostomátidas *Aurelia* sp., *C. capillata* e *C. quinquecirrha*, porém similares e menores do que as de *Aurelia* sp. do Japão (Purcell, 2009). Em uma aplicação das taxas individuais de ingestão quantificadas neste estudo, para a estimativa de impacto predatório, verificou-se que a agregação de *L. lucerna* (14 medusas 100 m⁻³) reportada por Colombo *et al.* (2003) no estuário do Rio da Prata (Argentina), poderia consumir entre 6 a 12 % da população de copépodes por dia, baseando-se em dados da densidade de copépodes aproximados do local (Viña *et al.*, 2002). Esse valor é inferior às maiores estimativas de impactos predatórios já quantificadas com base em conteúdos estomacais, como os de *Aurelia* sp. (26%) no mar do Japão (Uye & Shimauchi, 2005), *Chrysaora melanaster* (~33%) no Mar de Bering (Brodeur *et al.*, 2002), *Aurelia* sp. (~66%) no Mar Báltico (Schneider & Behrends, 1994) e *Aurelia* sp. (50%) no Canadá (Matsakis & Conover, 1991). Deve-se considerar porém, que a população de *L. lucerna* no estuário do Rio da Prata, era formada por indivíduos relativamente pequenos (moda= 11 cm de diâmetro umbrelar), e que medusas acima de 25 cm podem ter taxas individuais de ingestão até sete vezes maiores. Mesmo assim, esses dados destacam o grande potencial predatório dessa espécie, que ocorre sazonalmente em grande biomassa na costa sul e sudeste do Brasil e no norte da Argentina (Branco & Verani, 2006; Nogueira Jr. 2006; Schiariti *et al.*, 2008; Nagata *et al.*, 2009; Morandini, dados não publicados). Mesmo com este avanço no conhecimento da biologia alimentar de *L. lucerna*, ainda são necessários dados quantitativos de parâmetros populacionais para a espécie (*e.g.* capacidade reprodutiva, densidades, sazonalidade e distribuição vertical e batimétrica), os quais são fundamentais para avaliações mais abrangentes sobre seu potencial papel predatório e competidor.

Os valores isotópicos ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) de tecidos de animais podem ser usados como coordenadas para a delimitação de seu “nicho isotópico” (*sensu* Newsome *et al.*, 2007), que por sua vez, é uma representação do nicho trófico dos organismos (Peterson & Fry 1987; Post 2002; Bearhop *et al.*, 2004; Newsome *et al.*, 2007). A delimitação do

nicho isotópico pode evidenciar relações tróficas como partições no uso de recursos alimentares (Vaudo & Heithaus, 2011; Jackson *et al.*, 2011; Newsome *et al.*, 2012). Neste trabalho foi demonstrado que *L. lucerna*, e outros gelatinosos zooplancívoros (*Mnemiopsis leidyi* e *Chrysaora lactea*), sobrepõem seus nichos isotópicos com juvenis de peixes co-ocorrentes (*Chloroscombrus chrysurus*, *Genidens genidens*) em decorrência de hábitos alimentares semelhantes. Peixes porém aumentam seu nível trófico, possivelmente devido a inclusão de itens como macro-invertebrados e outros peixes em suas dietas (*e.g.* Bond 1996; Silva & Lopes, 2002). Contrariamente, não foi observado aumento ontogenético nos níveis tróficos de organismos gelatinosos mesmo quando houve ampla variação no tamanho corporal de organismos analisados. Em geral, espécies de peixes são zooplancívoras em seus estágios larvais e juvenis, mudando seus hábitos alimentares quando adultos (Deudero *et al.*, 2004; Layman *et al.*, 2005; Trueman *et al.*, 2005). A sobreposição na dieta ou em valores isotópicos entre peixes e gelatinosos (Purcell & Sturdevant, 2001; Brodeur *et al.*, 2008; Shoji *et al.*, 2009) representa apenas a partição de recursos alimentares e não necessariamente a competição. Nunca foi demonstrada a competição entre cifomedusas e peixes, pois isso depende da ocorrência de: *i*- sobreposição espaço-temporal entre competidores; e *ii*- partição de recursos limitantes. Essa última é muito mais difícil de se demonstrar, pois depende do conhecimento de taxas alimentares dos consumidores e sobre a produtividade do ecossistema (Purcell & Arai, 2001; Purcell, 2012), sendo somente avaliada entre hidromedusas e larvas de peixes (Purcell & Grover, 1990)

Em ecossistemas impactados pela sobrepesca, como o norte da Corrente de Bengala, o Mar de Bering e o Mar do Japão, o colapso de populações de peixes planctívoros (anchovas, sardinha e arenque) coincidiram com aumentos populacionais de medusas planctívoras (*Chrysaora fulgida*, *Chrysaora melanaster*, *Aurelia* sp., *Nemopilema nomurai*) (Brodeur *et al.*, 1999; Lynam *et al.*, 2006; Richardson *et al.*, 2009; Uye, 2011). No entanto, na Corrente de Humboldt o colapso de estoques de *anchoveta* peruana na década de 1970, coincidiram com aumentos nos estoques de sardinha (Alheit & Niquen, 2004). Richardson *et al.* (2009) especularam que populações de gelatinosos tenderiam a aumentar após declínios de peixes planctívoros, somente se outras espécies planctívoras de rápida resposta não ocuparem o nicho desocupado pela população colapsada. Regiões subtropicais do Oceano Atlântico possuem maior diversidade de espécies de peixes, do que regiões de maiores latitudes (40–60°) (Macpherson, 2002), dessa forma existe um maior número de espécies

potencialmente capazes de ocupar o nicho deixado pela espécie em declínio (Frank *et al.*, 2007). Mesmo assim, deve-se ressaltar que organismos gelatinosos que aqui ocorrem (*L. lucerna*, *M. leidy*, *Rhacostoma atlanticum*, *Chrysaora lactea*) são taxonomicamente e funcionalmente semelhantes a espécies causadoras de *blooms* em outras regiões costeiras, o que os coloca como candidatos à substituição de espécies com nichos similares. Para melhor compreender características funcionais que provêm as cifomedusas tamanha capacidade competidora e seu sucesso ecológico em ambientes perturbados e em rápida transição, mais estudos sobre sua performance reprodutiva, alimentar ainda devem ser realizados.

Apesar de o conhecimento sobre cifomedusas no Brasil ser razoável do ponto de vista taxonômico, ainda restam lacunas para serem preenchidas como comentado anteriormente em áreas como biologia reprodutiva e alimentar *in situ*. No entanto, este estudo promoveu avanços no sentido de melhor compreender o papel ecológico da espécie *Lychnorhiza lucerna* e sua importância/relevância nos ambientes costeiros estudados. O estudo de conteúdo estomacal da espécie forneceu informações importantes para estimar qual o impacto de *blooms*. Juntamente com os resultados da abordagem de isótopos estáveis foi possível verificar a sobreposição de nicho entre os gelatinosos e peixes juvenis. Isso reforça a idéia de que as medusas podem sim ocupar os eventuais nichos deixados por determinadas espécies de peixes, cujos estoques possam colapsar devido a sobrepesca, eutrofização e outras mudanças ambientais. A possível competição por recursos alimentares, que ocorre em estágios juvenis dos peixes pode reduzir ainda mais o recrutamento destas espécies. A abordagem metodológica empregada na quantificação de conteúdos estomacais em regiões corporais, propôs uma metodologia baseada em subamostragem que permitirá futuramente a redução de tempo de estudos futuros, sem que a qualidade seja comprometida. A abordagem biomecânica sobre a espécie *Lychnorhiza lucerna* ao longo da diferenciação ontogenética (éfira→medusa) é inovadora sendo a única em Rhizostomeae a combinar diversas técnicas videográficas para a quantificação de parâmetros biomecânicos e interações com presas. A morfologia dos braços e organização dos *digitata* cria um aparato filtrador e sua interação com vórtices produzidos pela pulsação umbrelar permite capturar até mesmo presas de alta capacidade escapatória. As informações sobre morfologia, mecânica de natação-alimentação reforçaram as observações dos dados de dieta e isótopos de que a espécie é eficaz na predação de copépodes mesozooplancônicos. As observações detalhadas

sobre a morfologia dos braços orais e mecanismos de captura de presas são essenciais para a compreensão do padrão generalizado para o grupo, apesar de mais observações em diferentes espécies serem necessárias. Pouco se sabe sobre dinâmicas compensatórias em ecossistemas costeiros subtropicais. No entanto, devido a sua biomassa, hábitos alimentares generalistas e seu impacto predatório, *L. lucerna* é um forte candidato a repor estoques de peixes em declínio, de nicho trófico similar.

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RESUMO

Nas últimas duas décadas, esforços têm sido direcionados para se compreender o papel ecológico de medusas de Scyphozoa, devido a aumentos populacionais e intensos *blooms* ao redor do mundo. Apesar de medusas de Rhizostomeae, causarem os mais intensos *blooms* recentemente reportados, quase nada se conhece sobre seu papel ecológico. O objetivo desta tese foi descrever as bases morfológicas e funcionais da alimentação de *Lychnorhiza lucerna* Haeckel, 1880 (Rhizostomeae), para se compreender seu papel predatório e suas interações tróficas. O projeto investigou (i) o desenvolvimento inicial de medusas de *L. lucerna*, com foco nos mecanismos locomotor-alimentar (ii) a dieta, seletividade alimentar e os potenciais impactos predatórios da espécie e (iii) a estrutura trófica de um sistema estuarino conservado, para compreender o papel ecológico e relações tróficas entre organismos gelatinosos e peixes. A abordagem metodológica envolveu: *i*- métodos videográficos em alta velocidade, para a quantificação de parâmetros biomecânicos em animais de diferentes estágios de desenvolvimento; *ii*- coletas de animais e plâncton na superfície da água para a quantificação de conteúdos estomacais no estudo de dieta, seletividade e taxas alimentares ao longo do litoral do estado São Paulo e Paraná; e *iii*- a análise de isótopos estáveis ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) de tecidos de consumidores (mesozooplâncton, gelatinoso, outros invertebrados e peixes) do estuário de Cananéia, São Paulo.

A ontogenia inicial de éfiras de *L. lucerna* envolve mudanças na umbrela e o desenvolvimento dos braços orais filtradores. No ambiente fluido ao redor das éfiras (<6 mm de diâmetro umbrelar) as forças de viscosidade são relativamente importantes ($Re < 100$). Por isso, os fluxos gerados pelas pulsações umbrelares rapidamente se dissipam, antes de atingirem as superfícies distais nos braços orais. O mecanismo de transporte de presas através das pulsações da umbrela só foi observado a partir do aumento ontogenético da força da pulsação (>10 mm) proporcionando um ambiente dominado pelas forças inerciais ($Re > 300$). Em adultos, as pulsações umbrelares produzem vórtices que escoam fluidos para os braços orais, os quais retêm partículas através de um mecanismo aderente e filtrador. Medusas de Rhizostomeae possuem as pulsações de umbrela mais robustas entre as cifomedusas, porém as velocidades máximas dos vórtices ($\sim 10 \text{ cm} \cdot \text{s}^{-1}$) de *L. lucerna* (<7 cm) são de 3 a 5 vezes menores que a velocidade de escape dos copépodes calanóides. Embora essa diferença possa sugerir sucesso aos copépodes para escapar, tanto as sequências de vídeo, quanto os conteúdos estomacais demonstraram que essas presas podem ser capturadas e ingeridas em quantidades similares às suas densidades no ambiente. Copépodes podem falhar na detecção do predador, sendo transportados contra as estruturas de captura de presas, mesmo se tiverem velocidades que permitiriam sua fuga. A interação de presas com os vórtices das pulsações é complexa e presas podem saltar em ângulos que resultam em captura pelos braços orais.

Através da análise de conteúdo estomacal foram encontrados 43 taxa compondo a dieta de *L. lucerna*, dos quais, copépodes representaram $\sim 80\%$ da composição numérica. A medusa é um predador generalista, com a dieta predominantemente similar à disponibilidade de mesozooplâncton. A capacidade de *L. lucerna* capturar os evasivos copépodes calanóides (*Paracalanus* spp. e *Acartia* spp.) aumenta com seu tamanho, devido ao aumento na força de suas correntes alimentares. Taxas alimentares da medusa variaram de 110 a 102871 copépodes ingeridos medusa⁻¹ dia⁻¹. Com essas taxas, estimou-se que uma agregação de *L. lucerna* reportada no norte da Argentina (14 indiv. 100 m⁻³) poderia ingerir de 6 a 12% do estoque de copépodes dia⁻¹, demonstrando o potencial impacto predatório de *blooms* da espécie. Aumentos populacionais de *L.*

lucerna certamente seriam deletérios para o recrutamento de diversas espécies de peixes, que habitam águas costeiras estuarinas quando juvenis. A análise de isótopos estáveis revelou que o nicho isotópico ocupado por *L. lucerna* e o de outros gelatinosos zooplancívoros, se sobrepõe aos nichos de peixes e outros consumidores de hábito alimentar semelhante. Pouco se sabe sobre dinâmicas compensatórias em ecossistemas costeiros subtropicais. No entanto, devido a sua biomassa, hábitos alimentares generalistas e seu impacto predatório, *L. lucerna* é um forte candidato a repor estoques de peixes em declínio, de nicho trófico similar.

Atualmente não existem indícios de que populações de *L. lucerna* estejam aumentando. As informações aqui apresentadas representam um avanço no conhecimento da biologia alimentar da espécie e sobre suas interações, que são essenciais para se conhecer as consequências de seus *blooms* e de possíveis aumentos populacionais. No entanto, muitas outras informações abordando outros aspectos (*e.g.* reprodutivos) e em escala populacional (*e.g.* biomassa, sazonalidade) ainda são necessários para uma compreensão mais completa sobre o papel da espécie no ecossistema.

Palavras chave: biologia alimentar, biomecânica, papel trófico, águas-vivas.

ABSTRACT

During the past three decades, efforts have been focused in order to understand the ecological role of scyphomedusae, due to population increases around the world. Despite Rhizostomeae medusae cause the most intense recently reported blooms, almost nothing is known about their feeding mechanisms, their trophic impacts and their ecological role. The goal of this thesis was to describe the morphological and functional bases of feeding in *Lychnorhiza lucerna* Haeckel, 1880 (Rhizostomeae), in order to understand its predatory role and trophic interactions. The project investigated: *i*- the early development of *L. lucerna*, focusing on swimming-feeding mechanisms; *ii*- the diet, prey selectivity, and the potential predatory impact of this species, and (*iii*) the trophic structure of a relatively pristine ecosystem, in order to understand trophic relationships between gelatinous zooplankton species and fish. The methodological approach included: *i*- high-speed videography for quantification of biomechanical parameters of swimming medusae at a range of developmental stages; *ii*- samplings of animals and plankton in surface waters for quantification of gut contents, prey selectivity and feeding rates along the coast of São Paulo and Paraná states; and *iii*- stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in tissues of consumers (mesozooplankton, gelatinous, other invertebrates and fish) in the estuary of Cananéia, São Paulo.

The early ontogeny of ephyrae involves changes in bell and development of filter-feeding oral arms. In the fluid environment around the ephyrae (<6mm bell diameter) the viscous forces are relatively important ($Re < 100$). Therefore, the flows generated by bell pulsations quickly dissipate before reaching the distal surfaces of the oral arms. The transport mechanism via bell pulsations was not observed until ontogenetic increase in the strength of the pulsations (>10mm) providing an environment dominated by inertial forces ($Re > 300$). In adults bell pulsations produce vortices that induce flows through oral arms, which retain particles by sticking and sieving mechanisms. Rhizostomeae jellyfish have the most robust bell pulsations among scyphomedusae, but maximum velocities of the vortices ($\sim 10\text{cm s}^{-1}$) of *L. lucerna* (<70mm) are still 3 to 5 times slower than escape velocity of calanoid copepods. Although this difference may suggest success for copepods to escape, both video sequences, and gut contents revealed that these prey can be captured and eaten at similar proportions as their field density. Copepods may fail to detect the predator, being transported against prey capture structures, even if they perform velocities that usually allow escaping. The interaction of prey with vortices is complex and prey may jump at angles that result in captures by oral arms.

Through the analysis of gut contents (N=40) 43 taxa were found composing the diet of *L. lucerna*, of which, copepods comprised $\sim 80\%$ of numerical abundance. This medusa is a generalist predator, since its diet was mostly similar to field mesozooplankton availability. Its ability to capture evasive calanoid copepods (*Paracalanus* spp. and *Acartia* spp.) increases with medusa size, as a consequence of increasingly stronger feeding currents. Feeding rates ranged from 110 to 102871 copepods eaten medusa $^{-1}$ day $^{-1}$. At these rates, it was estimated that an aggregation of *L. lucerna* reported in northern Argentina (14 ind. 100 m $^{-3}$) could consume 6-12% of the copepods standing stock day $^{-1}$, demonstrating the potential predatory impact of the species' blooms. Population increases of *L. lucerna* would certainly be detrimental to the recruitment of many fishes that inhabit estuarine coastal waters when juveniles. Stable isotope analyses revealed that the isotopic niche occupied by *L. lucerna* and by other gelatinous zooplanktivores, overlaps with niches of fishes, and other consumers of similar feeding habits. Little is known about compensatory dynamics in subtropical

coastal ecosystems. However, due to its biomass, generalist feeding habits, and predatory impact, *L. lucerna* is a strong contender to replace depleted fish stocks of similar trophic niche.

Currently there is no evidence that *L. lucerna* populations are increasing. The information presented here represents an advance in the knowledge of the species, its interactions, which are key in order to understand the consequences of its blooms and of possible population increases. However, many other information addressing other aspects (*e.g.* reproduction) and at population level (*e.g.* seasonality, biomass) are needed for a more complete understanding of the species role in the ecosystem.

Keywords: feeding biology, biomechanics, trophic role, stable isotopes, jellyfish.