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ORIGINAL PAPER

Trophic relationships between the large scyphomedusa *Chrysaora plocamia* and the parasitic amphipod *Hyperia curticephala*

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Abstract Scyphozoan jellyfish develop dramatic population blooms, which may significantly alter marine food webs. In turn, hyperiid amphipods parasitising jellyfish can occur in such great numbers that they represent an important trophic link to diverse species of fish, and may contribute to the decline of their host populations. Therefore, there is an urgent need to assess the trophic function and energy transfer through jellyfish and their parasites. We studied the isotopic composition (i.e. $\delta^{13}C$ and $\delta^{15}N$) of *Chrysaora plocamia*, the largest and most abundant scyphozoan jellyfish in the Humboldt Current System of Chile and Peru, and of its associated hyperiid parasite *Hyperia curticephala*. The isotopic composition of *C. plocamia* changed with body size, suggesting that that the diet of this species may include both pelagic and benthic prey as a consequence of the vertical distribution patterns observed. Although the density and intensity of infection of the parasite *H. curticephala* changed with the size of the host, their isotopic composition showed little variation, suggesting no shifts in the use of resources by the parasite. In contrast to other hyperiid parasites, reported to shift to a benthic mode of life when their hosts are lacking or in low abundance, the isotopic composition of *H. curticephala* revealed that their food source is mainly pelagic.

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Introduction

Although it remains controversial at a global level (Condon et al. 2013), several authors have associated anthropogenic perturbation of coastal upwelling ecosystems with shifts from fish to jellyfish-dominated systems (Lynam et al. 2006; Richardson et al. 2009). Given the recent increased interest in jellyfish, and their potential keystone role in ecosystem functioning (Doyle et al. 2014), there is an urgent need to assess the trophic function and energy transfer through jellyfish in marine systems. Of particular concern are scyphozoan jellyfish which, owing to their metagenic life history, are able to develop dramatic population blooms (Hamner and Dawson 2009) that can significantly alter marine food webs (Pauly et al. 2009; Condon et al. 2011).

Among coastal upwelling ecosystems, the Humboldt Current System (HCS) shows an exceptionally high productivity: covering less than 1 % of the world's ocean, it provides more than 10 % of global fish catches, based mainly on the Peruvian anchovy (Chavez et al. 2008; Montecino and Lange 2009; Weimerskirch et al. 2012). As in other upwelling systems, the pelagic food web in the HCS is characterised by short trophic pathways and the fish community is abundant but shows reduced diversity. Apart

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from zooplankton, only three trophic levels of consumers are typically distinguished: small-size planktivorous fish (mainly the anchovy *Engraulis ringens* and the Pacific sardine *Sardinops sagax*), larger fish predators (including the jack mackerel *Trachurus murphyi*, the hake *Merluccius gayi* and cephalopods) and top predators (mainly tuna *Thunnus orientalis*, swordfish *Xiphias gladius*, southern sea lions *Otaria flavescens* and seabirds) (see Thiel et al. 2007 and references therein). Although jellyfish may form dense aggregations and exert significant trophic impacts on copepods (Pagès et al. 2001), fish eggs (Riascos et al. 2014) and benthic fauna (Ceh et al. 2015), they are rarely considered in trophic web models (Pauly et al. 2009). Among schyphozoan jellyfish, *Chrysaora plocamia* is the most conspicuous and abundant in the HCS, whose seasonal proliferation affect human activities, including fisheries, aquaculture, desalination plants and tourism (Mianzan et al. 2014).

Perspectives on the trophic function of jellyfish have progressed from an old view which considered them as trophic dead ends (e.g. Verity and Smetacek 1996) to the recognition that trophic interactions with fishes and invertebrates are diverse and ecologically relevant (Ohtsuka et al. 2009; Riascos et al. 2013; D'Ambra et al. 2015). Among the taxa associated with jellyfish, parasitic hyperiid amphipods are of special importance: most of the ~ 250 hyperiid species described are symbiotically associated with different groups of gelatinous animals (Laval 1980; Vinogradov et al. 1996), and they may be an important trophic link channelling energy to diverse fish species (Riascos et al. 2012). Hyperiids have been distinctly considered as parasites, parasitoids and micropredators (Ohtsuka et al. 2009; Oliva et al. 2010) because they can occur in great numbers and may contribute to the decline of host populations (Mills 1993; Pitt et al. 2014).

Assessing trophic relationships between taxa can be difficult. Gut or stomach content data represent snapshots in time of an individual's diet, which can be highly variable; data may be biased towards recently ingested and slowly digested prey. A review of the diet composition of medusae in the genus *Chrysaora* shows that holoplanktonic crustaceans and fish eggs represent between 52 and 99 % of the diet (Riascos et al. 2014). However, experimental work indicates that these animals voraciously prey on gelatinous items, which are often difficult to identify in gastric pouches (Morandini et al. 2004). A previous study shows an age-related spatial segregation in *C. plocamia*: adult medusae consistently inhabit surface waters, while juveniles are mainly found in deeper waters or near the bottom (Zeballos et al. 2008). This raises the question—do size-dependent vertical distribution patterns of *C. plocama* allow for exploitation of both benthic and pelagic resources? Assessing trophic relationships between hyperiid parasites and their host using gut content analysis is challenging due to the small size of hyperiids and their prey. According to Laval (1980), hyperiids may directly consume host tissues or their prey, depending on host life stage and changes in hyperiid density, a view supported by a recent study using stable isotopes (Fleming et al. 2014). Therefore, assessment of trophic function should integrate this spatial–temporal variability in food sources for both parasitic hyperiids and their hosts.

Stable isotope ratios provide an opportunity to develop a time-integrated assessment of diet, as the isotope values of a consumer's tissues reflect that of the animal's diet while that tissue was being metabolised (West et al. 2006). In this context, we investigated three hypotheses regarding trophic interactions of *C. plocamia* and the parasitic amphipod *Hyperia curticephala*. Firstly, the isotopic composition of *C. plocamia* tissues should change with body size, reflecting the depth segregation and thus different putative diet patterns between adult and juvenile medusae. Secondly, we hypothesised that the infection intensity of *Hyperia curticephala* affects its trophic patters. Following this reasoning, we evaluated the hypothesis that the isotopic composition of *H. curticephala* is similar to that of host's tissues (mesoglea and gonad) reflecting the grazing on the host, instead of external food sources.

Materials and methods

Sample collection

Sampling was conducted in Mejillones Bay (22°57′9–23°05′8S; 70°20′–70°32′W), northern Chile. This is a small bay considered an important upwelling area in northern Chile which, due to the high primary productivity, significantly contributes to total fisheries in the country (Thiel et al. 2007). In Mejillones Bay, the medusa stage of *C. plocamia* generally occurs between late in the Austral spring and early autumn (November–March; Riascos et al. 2013). At the start of the pelagic season, the population is comprised mainly of large adult medusae; at the end, juvenile medusae are more common due to high adult mortality (Ceh et al. 2015). Additionally, the burden of hyperiids was found to be high in the middle of the pelagic season of *C. plocamia* (Riascos et al. 2012). Therefore, sampling was performed on 23 January 2012 to obtain the widest possible size range of *C. plocamia* (9–39 cm). Adult, sexually mature medusae (bell diameter ≥27 cm; $N = 8$) were collected in surface waters up to 9 m depth, and juvenile medusae (bell diameter <27 cm; $N = 11$) were collected in deeper waters (15–25 m depth). The relationship between sexual maturity and body size of *C. plocamia,* described by a logistic model [% of maturity $= 0.098/1 + e^{(15.855-0.551\ \text{bell diameter})}$] (see Ceh et al. 2015 for details), was used to

classify individuals as adults or juveniles. Each animal was captured using a plastic bag to preserve associated hyperiids, stored on ice and immediately transported to the laboratory.

Considering that pelagic phytoplankton, macroalgae and benthic microalgae are the main sources of primary production in this area (Reddin et al. 2015) and the fact that *C. plocamia* (Ceh et al. 2015) and hyperiid amphiods (Fleming et al. 2014) may use benthic resources, samples of macroalgae, particulate organic matter (POM) and benthic algae/biofilm were collected from subtidal locations on the Mejillones peninsula adjacent to Mejillones Bay to include them as potential energy sources in our analysis. Epilithic biofilm was scraped from rocks using a metal spatula, a 5 l water sample was collected for POM, and fronds of the dominant brown alga (*Lessonia nigrescens*) were collected, with tissue taken from frond areas of recent growth. All samples of primary producers were transported to the laboratory on ice and frozen at −20 °C, except water samples which were held at 4 °C prior to filtration.

Laboratory processing

Due to the recognised effects of preservation on jellyfish isotope values (Fleming et al. 2011), jellyfish were not preserved prior to processing in the laboratory. Each medusa was rinsed thoroughly in filtered seawater, and all hyperiids larger than 0.2 mm (length from the anterior edge of the head to the telson tip) were sorted, their number registered and pooled as a single sample for each individual medusa. Thereafter, mesoglea and gonad tissue were separated from the rest of the body. Finally, for each medusa the dry mass of pooled hyperiids, mesoglea, gonad and remaining tissues was determined by drying the samples in an oven at 65 °C until constant weight. All tissues were desiccated for 24 h before being weighed to prevent the absorption of water vapour during cooling.

Macroalgal samples were cleaned of surface epiphytes, rinsed with filtered seawater and dried at 65 °C for 48 h. Water samples for POM analyses were filtered through pre-combusted (550 °C for 5 h) 0.7-µm Whatman GF/F filters and then dried at 65 °C for 48 h. Epilithic biofilm samples were split in two (ca. 5 mg each). One part, for analysis of $\delta^{15}N$, was untreated. The other part, for analysis of $\delta^{13}C$, was decalcified to prevent potential contamination with ^{13}C-enriched inorganic C by application of 10 % hydrochloric acid drop by drop until bubbling ceased (Carabel et al. 2006). The decalcified sample was then dried again and homogenised before being stored in a new container. The biofilm was decalcified as it potentially includes a range of different taxa (and particles) that may include inorganic C and previous work has shown (e.g. Ng et al. 2007) that it can (relative to other putative sources of primary production, e.g. macroalgae) have significant inorganic C component.

Samples of hyperiids, jellyfish mesoglea and gonad tissues, and macroalgae and epilithic biofilm were ground to a fine powder using an agate pestle and mortar, and a subsample was encapsulated and weighed (±0.01 mg) in tin capsules (6 × 4 mm, Sercon Ltd.) prior to analysis. Samples were combusted in an elemental analyser (Carlo-Erba Instruments EA1110, Milan, Italy) coupled to a continuous flow isotope ratio mass spectrometer (Europa Scientific) at OEA Labs Ltd., Callington, Cornwall, UK. Analytical error (1 SD) estimates for both $\delta^{13}C$ and $\delta^{15}N$ based on repeated analysis of an internal bovine liver standard were less than 0.2 ‰.

Data analyses

To analyse the relationship between the isotopic composition of *C. plocamia* and body size, we used LOESS (locally weighted scatterplot smoothing) a nonparametric regression (Trexler and Travis 1993) to evaluate possible relationships between *C. plocamia* body size (as dry mass) and isotopic ($\delta^{13}C$ and $\delta^{15}N$) and elemental (C:N) composition of mesogleal and gonadal tissues. Paired t tests were used to assess differences in isotopic values between mesogleal and gonadal tissues, after checking for the assumptions of this test. We used LOESS regression to examine the hypothesis that the isotopic composition of *H. curticephala* changes with host body size. Next, we examined how parasite infection intensity (number of parasites per host) and infection density (number of parasites per gram of host dry mass) varied with host body mass. Finally, we examined whether there was a relationship between parasite density and isotopic composition of pooled parasites using LOESS regression.

To test the third hypothesis, we performed comparisons of $\delta^{13}C$ and $\delta^{15}N$ values between *C. plocamia* and *H. curticephala* and between tissues (mesoglea–gonad, for *C. plocamia*) using a single-factor PERMANOVA. PERMANOVA is a nonparametric probability-based analogue of analysis of variance between two or more groups based on a distance measure (Anderson 2001). For this, similarity matrices based on Euclidean distance were created from untransformed $\delta^{13}C$ and $\delta^{15}N$ values. We also used paired *t* tests to examine inter-tissue differences in $\delta^{13}C$ and $\delta^{15}N$ in individual jellyfish.

To examine the relative importance of host tissues to the long-term diet of *H. curticephala*, we estimated the relative contribution of four different putative foods [combined *C. plocamia* tissues, POM, epilithic biofilm and macroalgae (*L. nigrescens*)] to the assimilated diet of *H. curticephala* using the SIAR, a mixing model based on a Bayesian approach (Parnell et al. 2010) implemented in the software package SIAR, running under R (R Development Core Team 2009). Benthic sources were included following a

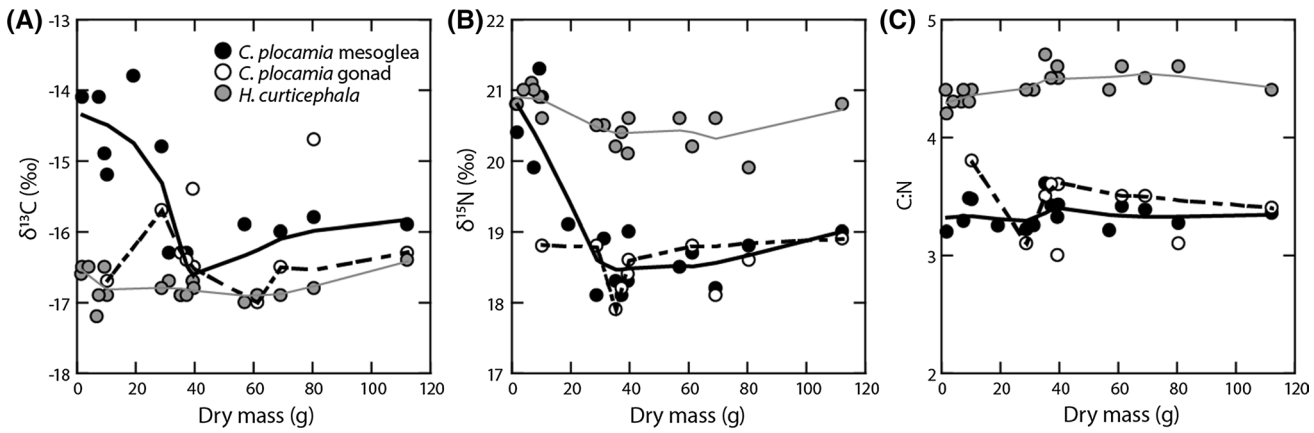

Fig. 1 Variation in **a** $\delta^{13}C$, **b** $\delta^{15}N$ and **c** C:N values with *Chrysaora plocamia* dry mass of mesoglea and gonads and *Hyperia curticephala*. *Lines* LOESS (stress = 0.5)

recent report of their contribution to *Hyperia* in a coastal system in the North-East Atlantic (Fleming et al. 2014) as well as our interest in the potential shift in host habitat use with size. $\delta^{13}C$ and $\delta^{15}N$ values for *H. curticephala* were adjusted for trophic fractionation (isotopic difference between a consumer and their prey) using three different trophic enrichment factors (TEFs). Given the unusual TEFs reported for amphipods (Fleming et al. 2014), we used three different TEFs to examine the sensitivity of the mixing model to variation in this important factor. We used TEFs from Fleming et al. (2014) who estimated TEFs based on a review of studies focused on trophic enrichment in amphipods, which resulted in an unusual negative TEF for Δ13C (mean ± SD TEF, =−1.5 ± 3.0 ‰) and a relatively low $\Delta^{15}N$ (1.4 ± 1.3 ‰). We also included TEFs from two major reviews of trophic enrichment across different taxa (Post (2002): $\Delta^{13}C = 0.4 \pm 1.3$ ‰, $\Delta^{15}N = 3.4 \pm 1.0$ ‰; McCutchan et al. (2003): $\Delta^{13}C = 0.5 \pm 1.3$ ‰, $\Delta^{15}N = 2.3 \pm 1.5$ ‰). Using the concentration-dependent routine of SIAR, we estimated the relative contribution of *C. plocamia* mesoglea and gonad tissue, the dominant macroalgae (*L. nigrescens*), which form large stands in the study area, and could potentially subsidise pelagic consumers, pelagic POM and epilithic benthic biofilm (the latter two being shown by Fleming et al. (2014) to contribute significantly to *Hyperia* assimilated diet in the NE Atlantic).

Results

Changes in isotopic composition of *C. plocamia* with body size

Both $\delta^{13}C$ and $\delta^{15}N$ values of mesoglea tissues of *C. plocamia* were nonlinearly and negatively related to dry mass (Fig. 1a, b), indicating that small *C. plocamia* (dry mass <30–40 g) had higher mesoglea $\delta^{13}C$ and $\delta^{15}N$ values, while individuals with greater body mass showed little variation in $\delta^{13}C$ and in $\delta^{15}N$. Variations in gonad $\delta^{13}C$ or $\delta^{15}N$ values were small in comparison with those of mesoglea. There was no evidence for size-based variation in C:N values in either gonad or mesoglea tissue (Fig. 1c).

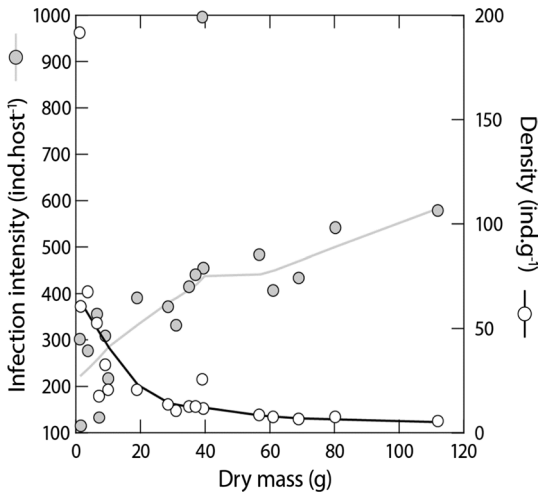

Fig. 2 Relationship between *Chrysaora plocamia* size (dry mass) and infection intensity (*grey markers*, *left* y-axis) and density (*white markers*, *right* y-axis) of *Hyperia curticephala*. *Lines* LOESS (stress = 0.5)

Assessing isotopic composition of the parasite *H. curticephala*

H. curticephala infection intensity increased with host dry mass (Fig. 2; infection intensity: median ± IQR = 388 ± 148; range 112–993 ind. host^{-1}). However, parasite density was negatively associated with *C. plocamia* mass, indicating that the number of parasites decreased with increasing dry mass

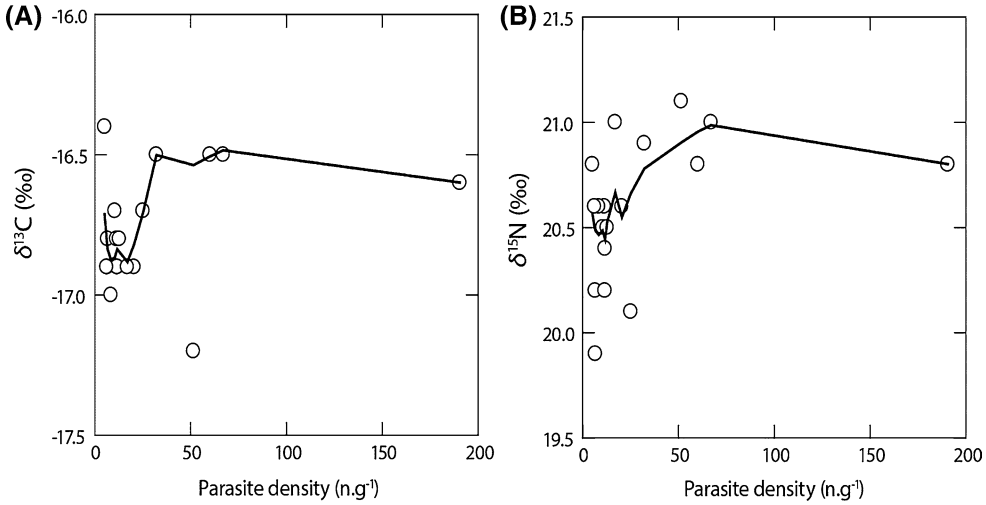

Fig. 3 Variation in **a** δ^{13}C and **b** δ^{15}N of *Hyperia curticephala* living at different densities in the scyphozoan jellyfish *Chrysaora plocamia*

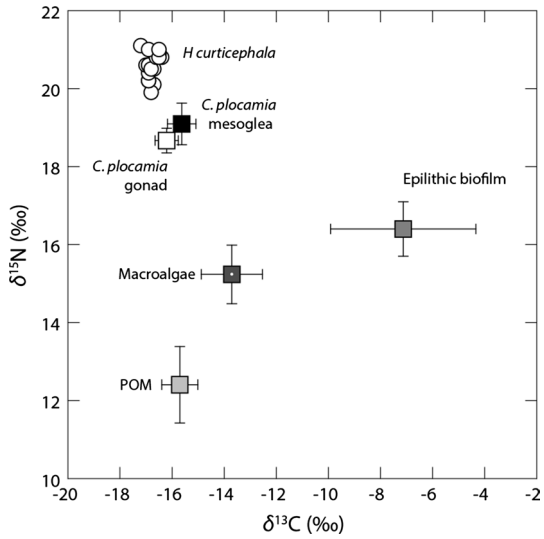

Fig. 4 Isotopic biplot showing variation in mean ± 95 % CI δ^{13}C and δ^{15}N values recorded from *Hyperia curticephala* and *Chrysaora plocamia* (gonads and mesoglea) and particulate organic matter, macroalgae and epilithic biofilm as key sources of energy potentially contributing to *Hyperia* diet

of medusae. There was little evidence for isotopic differences in parasites living in hosts of different sizes (Fig. 1a, b) or at different densities (Fig. 3). Moreover, pooled samples of *H. curticephala* showed little isotopic variation (Fig. 4; Table 1): δ^{13}C values ranged between −17.2 and −16.4 ‰, while δ^{15}N values varied between 19.9 and 21.1 ‰. C:N values varied between 4.2 and 4.7.

Dietary composition of *Hyperia curticephala*

Tissues of *C. plocamia* showed variation in isotopic composition (Table 1): mesoglea δ^{13}C values varied between −16.9 and −13.8, and mesoglea δ^{15}N values varied between 18.1 and 21.3 ‰. Gonadal tissue δ^{13}C ranged between −17.2 and −14.7 ‰ and gonad δ^{15}N values between 17.9 and 19.7. Paired *t* tests revealed no evidence for differences in δ^{13}C ($t = 0.79$, $df = 10$, $p = 0.45$) or δ^{15}N (1.49, $df = 10$, $p = 0.17$) between *C. plocamia* mesogleal and gonadal tissues. A similar comparison showed that C:N ratios were similar in the two tissues ($t = 0.67$, $df = 10$, $p = 0.52$).

Table 1 Estimates of mean (±SD) δ^{13}C, δ^{15}N and C:N for different taxa and tissues

Taxon/tissue	*n*	δ^{13}C	δ^{15}N	C:N
Chrysaora plocamia				
Mesoglea	19	−15.6 (1.0)	19.1 (1.0)	3.3 (0.1)
Gonads	13	−16.2 (0.7)	18.7 (0.5)	3.4 (0.3)
Combined	33	−15.9 (1.0)	19.0 (0.9)	3.3 (0.2)
Hyperia curticephala	19	−16.8 (0.2)	20.6 (0.3)	4.4 (0.1)
Particulate organic matter	18	−15.7 (1.4)	12.4 (1.9)	5.1 (1.0)
Epilithic biofilm	9	−7.0 (3.6)	16.4 (0.9)	8.5 (1.0)
Macroalgae	7	−13.7 (1.2)	15.2 (0.8)	16.7 (1.9)

n indicates sample size. Smaller *N* for gonad tissue for *C. plocamia* reflects the lack of gonad tissues in smaller individuals

A comparison of δ^{15}N-δ^{13}C centroids using PERMANOVA showed isotopic differences between *H. curticephala,* and their hosts (*C. plocamia*) (Pseudo-$F_{1,49} = 21.23$; $p = 0.0001$). *H. curticephala* were ^{13}C depleted by ca. 1 ‰ compared to their hosts (tissues combined), and ^{15}N enriched by ca. 1.6 ‰ (Fig. 4, Table 1). A visual comparison of *H. curticephala* isotope values relative to the three different energy sources (POM, macroalgae and epilithic biofilm) indicated that they were largely fuelled by pelagic-derived materials (Fig. 4). Comparisons of host and parasite isotope values using Pearson's correlation showed little evidence for a relationship between host and *Hyperia* δ^{13}C values (mesoglea:

$r = 0.28$, $n = 15$, $p = 0.31$; gonad: $r = -0.15$, $n = 12$, $p = 0.65$). However, there was evidence for a relationship between host and *Hyperia* δ^{15}N values (mesoglea: $r = 0.58$, $n = 15$, $p = 0.022$; gonad: $r = 0.67$, $n = 12$, $p = 0.022$).

Estimates of the relative importance of different putative sources to the assimilated diet of *Hyperia* were generated using the SIAR mixing model. Three separate model runs using different TEFs (Post 2002; McCutchan et al. 2003; Fleming et al. 2014) all indicated that *C. plocamia* provided the bulk of the assimilated diet (Fig. 5) of *H. curticephala*, with modal values varying between 69 and 96 % of the diet. Modal estimates of the contribution of POM varied considerably between runs, with the Fleming et al. (2014) TEF resulting in an estimate of only 1 %. The modal estimate using the Post (2002) TEF was 28 % which fell slightly when the McCutchan et al. (2003) TEF was used (13 %). Under each of the three model runs, there was no support for any contribution from either epilithic biofilm (mean modal estimate = 0 %) or macroalgae (mean modal estimate = 1 %) to the assimilated diet of *Hyperia*.

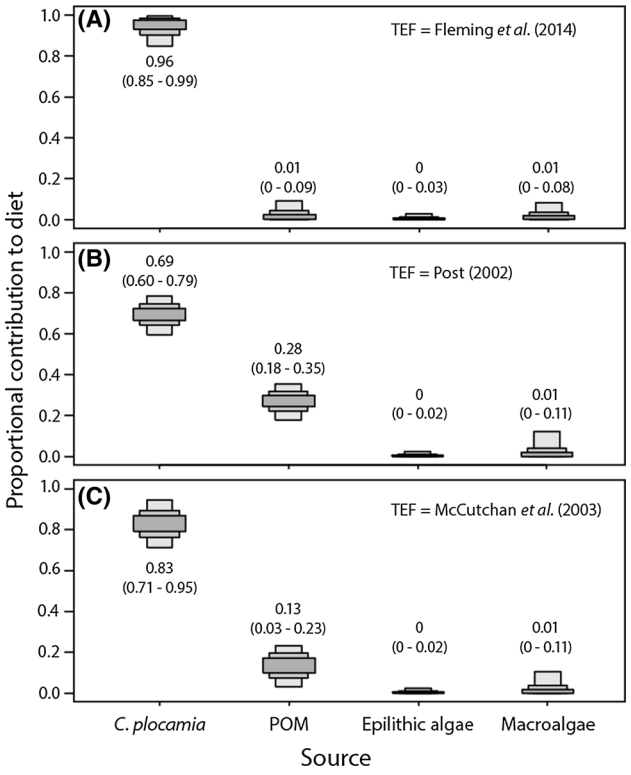

Fig. 5 Outputs of SIAR mixing model showing the estimated contribution of different putative foods to the assimilated diet of *Hyperia curticephala*. *Boxes* relate to 25, 75 and 95 % Bayesian credibility intervals. *Numbers* given in each figure include modal (*no parentheses*) and 5–95 % credibility limits (*in parentheses*) for estimates of each source when three different TEFs are used. NB, *Chrysaropa plocamia* values estimated from combined mesoglea and gonadal tissues

Discussion

Intraspecific niche partitioning in food sources during the pelagic life phase of *C. plocamia*

Recent findings show that scyphozoan jellyfish display patterns in vertical movement that are characteristic of cruising predators and can control their position in the water column (Hays et al. 2012). Our results showed changes in isotopic composition of *C. plocamia* with body size. This suggest that intraspecific depth segregation, with juveniles occupying deeper water than adults (Zeballos et al. 2008), has important consequences in terms of niche partitioning in food sources. The fact that juvenile medusae tend to have higher δ^{13}C and δ^{15}N values than their adult counterparts indicates that they feed on ^{13}C-enriched prey typically found in benthic or inshore areas (France 1995; Mallela and Harrod 2008) and higher trophic level prey. Therefore, our results support the hypothesis that depth segregation between juveniles and adult *C. plocamia* is reflected in intraspecific niche partitioning in food sources. This result is in line with recent reports describing the ability of jellyfish to actively control their position near the sea bed (Hays et al. 2012) and the presence of abundant large emergent benthic food in jellyfish gut contents (Pitt et al. 2008), which suggest that this species may be able to exploit different food sources through its pelagic life.

Gonad δ^{13}C and δ^{15}N did not change with dry mass. This may be related to the fact that small medusae (<12 g dry mass or <15 cm bell diameter) had no gonad tissue or it is difficult to recognise. Thus, the size range available to assess these relationships in mesoglea was between 9 and 39 cm, whereas for gonad tissue, it was between 15 and 39 cm. Alternatively, this could be related to our finding of no significant differences in δ^{13}C and δ^{15}N values between gonad and mesoglea tissues, which is surprising because previous studies have shown that scyhozoan gonads are lipid rich and have therefore lower δ^{13}C than other tissues (Milisenda et al. 2014; D'Ambra et al. 2015). Conversely, our comparison of C:N ratios in the two tissues indicates that at the time of sampling, lipid contents were similar. This may be explained by the finding that in the study area, sexually mature *C. plocamia* mainly occurs between October and December, with their numbers decreasing rapidly thereafter (Ceh et al. 2015). Therefore, gonad tissue of medusae collected in January may be relatively depleted in lipids.

Use of resources by *H. curticephala* is independent of intra-host density

Our results on the parasite *H. curticephala* demonstrated that they were more crowded in small hosts, which could

be related to the reproductive strategy of the parasite. According to Laval (1980), different females demarsupiate larvae among newly available hosts, and thereafter, the number of hatched juveniles decreases rapidly because they escape to other hosts. This is supported by data showing that juvenile *C. plocamia* harbour mainly small hyperiids, whereas adult medusae harbour hyperiids across the whole size range (Online resource 1). In conclusion, our data indicate that the short term high rate of the parasite infestation does not play a crucial role in defining shifts in predatory behaviour within the host.

There was little support for any relationship between isotopic composition of *H. curticephala* and intra-host density (Fig. 3), and the parasites showed very little isotopic variation (Fig. 4). This indicates that parasites living on hosts of different sizes, which harbour parasites at different densities, have similar diet patterns. Moreover, this is in line with the fact that *C. plocamia* showed no significant isotopic variation between mesoglea and gonad, because juveniles commonly feed on mesoglea and adults subsequently feed mainly on gonads (see Laval 1980; Riascos et al. 2012), which could represent a source of variability in isotopic composition of the parasite (see Towanda and Thuesen 2006). Therefore, our second hypothesis can be rejected.

Food sources of *Hyperia curticephala* comprise pelagic-derived materials

Laval (1980) described hyperiid amphipods as "the descendants of benthic crustaceans which have developed a benthic-like existence on the pelagic substratum provided by gelatinous animals of the zooplankton". This premise suggests that these animals had developed a feeding strategy allowing them to feed on the resources provided by their pelagic hosts. This has been confirmed for hyperiid parasites in stable isotope studies: Towanda and Thuesen (2006) showed that $\delta^{13}C$ and $\delta^{15}N$ values for *Hyperia medusarum* fell in the range of those of the scyphozoan *Phacellophora camtschatica*, indicating a trophic reliance on their host. But this is not always true; based on field and isotopic data, Dittrich (1988) and Fleming et al. (2014) demonstrated that the association of the hyperiid *Hyperia galba* with different medusae is restricted to the season of high host abundance, after which they shift to a benthic mode of life. Two lines of evidence suggest that this is not the case for *H. curticephala* and that food is mainly derived from the pelagic realm. Firstly, $\delta^{13}C$ values of *H. curticephala* differed substantially from that of macroalgae and epilithic biofilm (Fig. 4), key putative sources of energy and nutrients for benthic consumers in the HCS (Thiel et al. 2007). Secondly, different SIAR mixing model runs using a range of TEFs consistently indicated that *C. plocamia* provided the bulk of the assimilated diet of *H. curticephala*. Moreover, hyperiid amphipods are commonly associated with different gelatinous hosts (see Laval 1980) including holoplanktonic species, which would allow them to spend their life in the pelagic environment.

Laval (1980) showed that hyperiids had developed specialised structures to attach to their host and prey on the host's food. Riascos et al. (2014) revealed the importance of fish eggs and larvae to *C. plocamia* diet, and it is possible that *H. curticephala* display kleptoparasitism (a form of competition that involves the stealing of already-procured items; Iyengar 2008). We did not have stable isotope data for fish eggs and larvae and could not directly test this hypothesis in *H. curticephala*. Indirect evidence suggests against kleptoparasitism as a major source of energy and nutrients for *H. curticephala*: the isotopic differentiation between the parasite and the host fits well with the TEFs estimated by Fleming et al. (2014), and consumption of a lower trophic level prey would result in more depleted $\delta^{15}N$ values in *H. curticephala* than those observed here. However, for a full test of putative kleptoparasitism, future studies should include the putative prey of the host population.

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References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Carabel S, Godínez-Domínguez E, Verísimo P, Fernández L, Freire J (2006) An assessment of sample processing methods for stable isotope analyses of marine food webs. J Exp Mar Biol Ecol 336:254–261

Ceh J, Gonzalez JE, Pacheco AS, Riascos JM (2015) The elusive life cycle of scyphozoan jellyfish: metagenesis revisited. Sci Rep 5:12037. doi:10.1038/srep12037

Chavez FP, Bertrand A, Guevara-Carrasco R, Soler P, Csirke J (2008) The northern Humboldt Current System: brief history, present status and a view towards the future. Prog Oceanogr 79:95–105

Condon RH, Steinberg DK, del Giorgio PA, Bouvier TC, Bronk DA, Graham WM, Ducklow HW (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc Nat Acad Sci 108:10225–10230

Condon RH, Duarte CM, Pitt KA, Robinson KL, Lucas CH, Sutherland KR, Mianzan HW, Bogeberg M, Purcell JE, Decker MB, S-i Uye, Madin LP, Brodeur RD, Haddock SHD, Malej A, Parry GD, Eriksen E, Quiñones J, Acha M, Harvey M, Arthur JM, Graham WM (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Nat Acad Sci 110:1000–1005

D'Ambra I, Graham WM, Carmichael RH, Hernandez FJ Jr (2015) Fish rely on scyphozoan hosts as a primary food source: evidence from stable isotope analysis. Mar Biol 162:247–252

Dittrich B (1988) Studies on the life cycle and reproduction of the parasitic amphipod *Hyperia galba* in the North Sea. Helgol Mar Res 42:79–98

Doyle TK, Hays GC, Harrod C, Houghton JDR (2014) Ecological and societal benefits of jellyfish. In: Lucas CH, Pitt KA (eds) Jellyfish blooms. Springer, Germany

Fleming N, Houghton J, Magill C, Harrod C (2011) Preservation methods alter stable isotope values in gelatinous zooplankton: implications for interpreting trophic ecology. Mar Biol 158:2141–2146

Fleming NEC, Harrod C, Griffin DC, Newton J, Houghton JDR (2014) Jellyfish provide short-term reproductive habitat for hyperiid amphipods in a temperate near-shore environments. Mar Ecol Prog Ser 510:229–240

France R (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307–312

Hamner WM, Dawson MN (2009) A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. In: Pitt KA, Purcell JE (eds) Jellyfish blooms: causes, consequences, and recent advances. Springer, Netherlands, pp 161–191

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Levy searches: jellyfish can search the water column like fish. Proc R Soc Ser B Lon 279:465–473

Iyengar EV (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biol J Linnean Soc 93:745–762

Laval P (1980) Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanogr Mar Biol Ann Rev 18:11–56

Lynam CP, Gibbons MJ, Axelsen BE, Sparks CA, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. Curr Biol 16:R492–R493

Mallela J, Harrod C (2008) $\delta^{13}C$ and $\delta^{15}N$ reveal significant differences in the coastal foodwebs of the seas surrounding Trinidad and Tobago. Mar Ecol Progr Ser 368:41–51

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390

Mianzan H, Quiñones J, Palma S, Schiariti A, Acha EM, Robinson KL, Graham WM (2014) *Chrysaora plocamia*: a poorly understood jellyfish from South American waters. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Netherlands, pp. 219–236

Milisenda G, Rosa S, Fuentes VL, Boero F, Guglielmo L, Purcell JE, Piraino S (2014) Jellyfish as prey: frequency of predation and selective foraging of *Boops boops* (Vertebrata, Actinopterygii) on the mauve stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). PLoS ONE 9:e94600

Mills CE (1993) Natural mortality in NE Pacific coastal hydromedusae: grazing predation, wound healing and senescence. Bull Mar Sci 53:194–203

Montecino V, Lange CB (2009) The Humboldt Current System: ecosystem components and processes, fisheries, and sediment studies. Progr Oceanogr 83:65–79

Morandini AC, Da Silveira FL, Jarms G (2004) The life cycle of *Chrysaora lactea* Eschscholtz, 1829 (Cnidaria, Scyphozoa) with notes on the scyphistoma stage of three other species. Hydrobiologia 530:347–354

Ng JSS, Wai T-C, Williams GA (2007) The effects of acidification on the stable isotope signatures of marine algae and molluscs. Mar Chem 103:97–102

Ohtsuka S, Koike K, Lindsay D, Nishikawa J, Miyake H, Kawahara M, Mujiono N, Hiromi J, Komatsu H (2009) Symbionts of marine medusae and ctenophores. Plankton Benthos Res 4:1–13

Oliva ME, Maffet A, Laudien J (2010) Asociación entre *Chrysaora plocamia* (Cnidaria, Scyphozoa) e *Hyperia curticephala* (Peracarida: Amphipoda) en Bahía de Mejillones, norte de Chile. Rev Biol Mar Oceanogr 45:127–130

Pagès F, González HE, Ramón M, Sobarzo M, Gili JM (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by Bassia bassensis (Siphonophora: Calycophorae). Mar Ecol Prog Ser 210:13–24

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672

Pauly D, Graham W, Libralato S, Morissette L, Palomares MLD (2009) Jellyfish in ecosystems, online databases and ecosystem models. Hydrobiologia 616:67–85

Pitt KA, Clement AL, Connolly RM, Thibault-Botha D (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic–pelagic coupling. Estuar Coast Shelf Sci 76:827–833

Pitt KA, Budarf AC, Browne JG, Condon RH (2014) Bloom and bust: why do blooms of jellyfish collapse? In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Netherlands, pp. 79–103

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reddin CJ, Docmac FM, O'Connor NE, Bothwell JH, Harrod C (2015) Coastal upwelling drives intertidal community composition and trophic ecology. PloS ONE 10(7):e0130789. doi:10.1371/journal.pone.0130789

Riascos JM, Vergara M, Fajardo J, Villegas V, Pacheco AS (2012) The role of hyperiid parasites as a trophic link between jellyfish and fishes. J Fish Biol 81:1686–1695

Riascos JM, Villegas V, Cáceres I, Gonzalez JE, Pacheco AS (2013) Patterns of a novel association between the scyphomedusa *Chrysaora plocamia* and the parasitic anemone *Peachia chilensis*. J Mar Biol Assoc UK 93:919–923

Riascos JM, Villegas V, Pacheco AS (2014) Diet composition of the large scyphozoan jellyfish *Chrysaora plocamia* in a highly productive upwelling centre off northern Chile. Mar Biol Res 10:791–798

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Thiel M, Macaya E, Acuña E, Arntz W, Bastias H, Brokordt K, Camus P, Castilla J, Castro L, Cortés M, Dumont C, Escribano R, Fernández M, Gajardo J, Gaymer C, Gomez I, González A, González H, Haye P, Illanes J, Iriarte J, Lancellotti D, Luna-Jorquera G, Luxoro C, Manríquez P, Marín V, Muñoz P, Navarrete S, Perez E, Poulin E, Sellanes J, Sepúlveda H, Stotz W, Tala F, Thomas A, Vargas C, Vasquez J, Alonso-Vega J (2007) The Humboldt Current System of Northern and Central Chile—oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol Ann Rev 45:195–344

Towanda T, Thuesen EV (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. Mar Ecol Progr Ser 315:221–236

Trexler JC, Travis J (1993) Nontraditional regression analyses. Ecology 74:1629–1637

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Progr Ser 130:277–293

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperiidea) of the World Oceans. Science Publishers Inc, Enfield

Weimerskirch H, Bertrand S, Silva J, Bost C, Peraltilla S (2012) Foraging in Guanay cormorant and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System. Mar Ecol Progr Ser 458:231–245

West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's ecological recorders. Trends Ecol Evol 21:408–414

Zeballos J, Arones I, Cabrera A, Galindo O, Lorenzo A, Quiñones J, Zavala J, Flores D, Carbajo L (2008) Informe de las actividades desarrolladas durante el año 2007. Instituto del Mar del Perú, Laboratorio Costero de Pisco, Perú