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FEATURE ARTICLE

Fish rely on scyphozoan hosts as a primary food source: evidence from stable isotope analysis

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Abstract Predation of fish on their scyphozoan hosts has not been clearly defined using analysis of gut contents because gelatinous prey are difficult to visually detect and are dissolved by fixative solutions. Therefore, scyphomedusae have been generally considered not relevant in fish diet. To determine the contribution of their scyphozoan host tissue to the assimilated diet of age-0 *Chloroscombrus chrysurus*, we determined δ^{13}C and δ^{15}N of fish, their hosts (scyphomedusae *Aurelia* sp. and *Drymonema larsoni*) and their potential prey—small plankton (<200 µm) and mesozooplankton (>200 µm)—in the coastal waters of Alabama, USA. The diet of *C. chrysurus* was defined using the Bayesian mixing model Stable Isotope Analysis in R (SIAR). Models indicated that the scyphozoan hosts contributed on average ~90 % to fish assimilated diet. In contrast with previous dietary assessments based on analysis of gut contents, these results highlight that scyphozoans are important to the diet of fish associated with them. Because several ecologically and economically important fish species live in association with scyphomedusae, a redefinition of trophic links in marine food webs may be needed in light of the findings in this study.

Introduction

Interactions between fish and jellyfish (Phylum Cnidaria, Class Scyphozoa) are complex. Jellyfish can consume fish eggs and larvae, and they potentially compete with fish for plankton prey (reviewed in Purcell and Arai 2001). Early life stages of fishes (e.g. species from families Carangidae, Centrolophidae, Nomaeidae, Stromateidae and Tetragonouridae), however, school underneath the bell of scyphomedusae (Mansueti 1963; Arai 1988; Purcell and Arai 2001), presumably for protection from predators (Brodeur 1998; Purcell et al. 2000). This behaviour may increase survival during years of high abundance of scyphomedusae, compared with years of low jelly biomass (Lynam and Brierley 2007).

Whilst it is well documented that scyphomedusae both consume and shelter some fish species, predation of fish on their scyphozoan hosts is controversial. At least 124 species of fish prey on jellyfish (Purcell 2012), and based on visual observations, fish associated with scyphozoans appear to feed on their hosts (Mansueti 1963). However, gelatinous tissue has been rarely identified in gut contents of fish (Purcell and Arai 2001), and the low organic content of scyphozoans compared with other zooplankton (Pitt et al. 2009; Lucas et al. 2011) had generally lead to the conclusion that scyphozoan tissue is not relevant in the diet of fish (Purcell and Arai 2001).

Detecting gelatinous zooplankton in fish stomachs is difficult because digestion rates are relatively fast (Arai et al.

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2003) and gelatinous tissue is degraded by solutions used to preserve gut contents (Mianzan et al. 1996). As a consequence, predation rates on jellyfish likely have been underestimated (Arai 1988; Mianzan et al. 1996, 2001). To quantify fish predation rates on scyphozoans, additional approaches are needed to complement gut content analysis. Detecting nematocysts in the gut is a laborious procedure, which does not provide an estimate of the contribution of gelatinous prey to the diet of their predators (Sal Moyano et al. 2012). In contrast, stable isotope ratios allow for definition of the assimilated diet and food sources not detected visually (Peterson and Fry 1987). Using stable isotope analysis, Towanda and Thuesen (2006) defined that both the amphipod *Hyperia medusarum* and the crab *Cancer gracilis* (now *Metacarcinus gracilis*) fed on their host, the scyphomedusa *Phacellophora camtschatica*. The ingestion of their scyphozoan hosts tissue by the amphipod *Hyperia galba* has been recently determined using the same methodological approach in northern Ireland coastal waters (Fleming et al. 2014). These results highlight that jellyfish trophic links within marine food webs may be more complex than previously defined, and therefore, a reassessment of trophic interactions involving jellyfish is needed.

Age-0 Atlantic bumper *Chloroscombrus chrysurus* are found in association with *Chrysaora quinquecirrha* and *Stomolophus meleagris* in Mississippi Sound (Phillips et al. 1969), and with *Aurelia* sp. in Florida (Tolley 1987). *C. chrysurus* are one of the most abundant species in the Gulf of Mexico and serve an important ecological role as forage fish for high-trophic-level predators (Shaw and Drullinger 1990). Hence, understanding the ecology and food web links of their early life stages has important ecological and economic implications. Additionally, because the association between *C. chrysurus* and scyphomedusae in Alabama coastal waters may be considered representative of general fish–scyphozoan associations, defining trophic links between these species may be applicable to other fish–jellyfish associations in other systems.

Based on visual observations of *C. chrysurus* feeding on their scyphozoan hosts (Phillips et al. 1969), we hypothesised that gelatinous tissues were ingested and assimilated by fish. To test this hypothesis, we determined δ^{13}C and δ^{15}N of fish, the scyphomedusae *Aurelia* spp. and *Drymonema larsoni* associated with them along with their potential prey, small plankton (<200 µm) and mesozooplankton (>200 µm). The dietary composition of fish was defined using SIAR.

Materials and methods

Sample collection

Chloroscombrus chrysurus ($N = 33$) were collected with the scyphomedusae *Aurelia* sp. ($N = 23$) and *D. larsoni* ($N = 5$), in Alabama coastal waters from July to October 2009–2010 using a dip net. Fish and medusae were kept separately in buckets with filtered seawater from the collection site to allow for gut evacuation.

Potential prey of fish and medusae were collected simultaneously with predators. To isolate small plankton (<200 µm), water was collected using a 2-L Niskin bottle deployed below the surface (1 m depth), filtered on the boat through a 200-µm mesh and stored in bottles. Mesozooplankton (>200 µm) were collected using duplicate vertical tows (200-µm mesh, 0.5-m diameter, 1-m long plankton net) and transferred to plastic bottles. All samples were kept on ice during transport to the laboratory.

Sample processing

Fish length was measured as fork length (± 0.1 cm). Fish were deprived of the head, fins and skin and dried individually. Bell diameter of medusae was measured as the distance between opposite rhopalia (± 0.5 cm). To determine δ^{13}C and δ^{15}N of the scyphozoan hosts, a piece of the bell was isolated as representative of the whole organism and rinsed with ultra-pure water to remove plankton or detritus (D'Ambra et al. 2014). Small plankton were concentrated by filtering water samples through pre-ashed GF/F filters (4 h at 500 °C to remove organic C and N). Mesozooplankton samples were concentrated through a 200-µm sieve. All samples were oven-dried at 60 °C to prevent changes in the isotopic composition due to high temperatures; tissues and zooplankton samples were individually homogenised using mortar and pestle.

Stable isotope analysis

Given the low organic content of medusae (Pitt et al. 2009), an average of 4.0 ± 0.3 mg of dried medusae and 1.0 ± 0.2 mg of dried fish and plankton were sent to the Stable Isotope Facility at the University of California in Davis (USA) in 2009 and the Stable Isotope Facility for Environmental Research (SIRFER) at the University of Utah (USA) in 2010 for δ^{13}C and δ^{15}N. C and N stable isotope ratios were measured using a PDZ Europa ANCA-GSL elemental analyser interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK) at UC Davis and an isotope ratio mass spectrometer (Finnigen Delta Plus; Bremen, Germany) coupled with an elemental analyser (model 1110; Carlo Erba, Milan, Italy) through an open split interface (CONFLO III; Finnigan, Bremen, Germany) at SIRFER. During analyses, samples were interspersed with replicates of at least two different laboratory standards. These laboratory standards, which were selected to be compositionally similar to the samples being analysed, were previously calibrated against standard reference materials from the National Institute of Standards and Technology and International Atomic Energy Agency. Final δ values were expressed as ‰ relative to international standards VPDB (Vienna PeeDee Belemnite) for C and Air for N. The long-term standard deviations were 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$ at UC Davis and 0.1 ‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$ at SIRFER. To ensure measurements were comparable between the two laboratories, 15 samples were analysed in both laboratories and compared using a paired *t* test after testing for normality of data. The mean difference in $\delta^{13}C$ was 0.1 ‰ ($t_{27} = 0.42$, *P* value = 0.68) and the mean difference in $\delta^{15}N$ was 0.2 ‰ ($t_{27} = 0.71$, *P* value = 0.48), both falling in the range of within-facility instrument variation.

The effect of lipid content on $\delta^{13}C$ in tissues was corrected among tissues with C:N > 3.5 (Post et al. 2007) by applying the following equations, which were mathematically derived from lipid-extracted samples from the same sampling sites.

For small plankton and mesozooplankton (D'Ambra 2012),

$$\delta^{13}C = \delta^{13}C' - (-2.45 + 0.62 \times C:N) \qquad (1)$$

For scyphomedusae (D'Ambra et al. 2014),

$$\delta^{13}C = \delta^{13}C' - (-9.43 + 2.69 \times C:N) \qquad (2)$$

where $\delta^{13}C'$ is the bulk $\delta^{13}C$.

Data analysis

The dietary composition of *C. chrysurus* was defined using SIAR (version 2.13.1), a package in R (Comprehensive Archive Network site, http://cran.r-project.org/), using Bayesian mixing models (Parnell et al. 2010). Given that increasing size may result in a shift in trophic position (Fleming et al. 2011), we calculated Pearson's correlation coefficient between $\delta^{15}N$ and fish fork length and between $\delta^{15}N$ and scyphozoan bell diameter, respectively. Because we did not find a significant correlation between fork length and $\delta^{15}N$ of fish ($r_s = 0.28$, $N = 33$, $P = 0.11$) and between bell diameter of medusae and their $\delta^{15}N$ ($r_s = -0.17$, $N = 23$, $P = 0.45$ for *Aurelia* sp.; $r_s = -0.15$, $N = 5$, $P = 0.82$ for *D. larsoni*), fish and medusae were pooled by genera for SIAR analyses. Expected fractionation values ($\Delta^{13}C = 1.4 \pm 1.0$ ‰; $\Delta^{15}N = 3 \pm 1$ ‰; McCutchan et al. 2003, Vanderklift and Ponsard 2003) were applied to estimate the trophic shift between *C. chrysurus* and their prey. Because *D. larsoni* prey on *Aurelia* sp. (Bayha et al. 2012), two separate models were made to define the diet of *C. chrysurus:* model A for the diet of fish associated with *Aurelia* sp., where small plankton, mesozooplankton and *Aurelia* sp. were considered as potential prey of fish (Fig. 2a), and model B for the diet of fish associated with *D. larson*, where both size fractions of plankton and both species of medusae were included as potential prey (Fig. 2b).

Results

Chloroscombrus chrysurus (2.2 ± 0.9 cm fork length) in this study had higher $\delta^{15}N$ values and similar or lower $\delta^{13}C$ values compared with their hosts, *Aurelia* sp. (Figure 1a) and *D. larsoni* (Fig. 1b), respectively. Dietary composition defined using SIAR indicated that the scyphozoan hosts made the greatest contribution to diet of *C. chrysurus* (Fig. 2). *Aurelia* sp. provided 80–100 % to the assimilated diet of fish associated with them (Fig. 2a). When fish were associated with *D. larsoni*, the dietary composition was based on both scyphozoans, with the host providing 50–100 % and *Aurelia* sp. providing up to 40 % of the assimilated diet (Fig. 2b). Small plankton and mesozooplankton provided a minor contribution to the diet of fish in both models (Fig. 2).

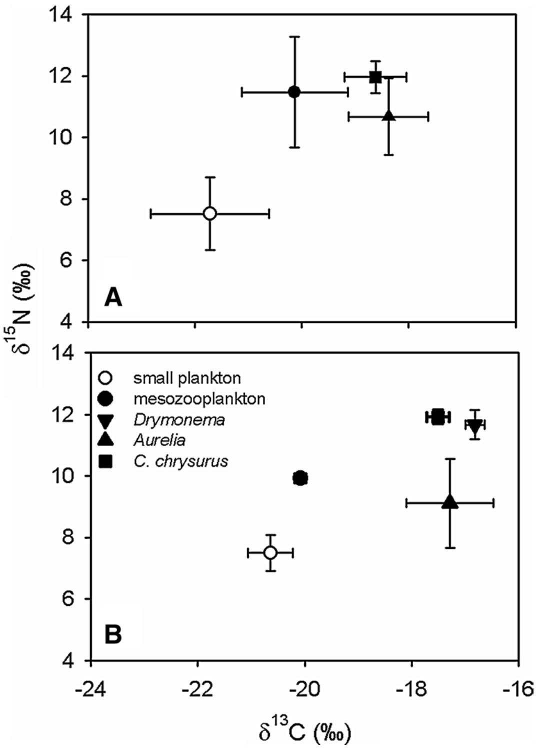

Fig. 1 $\delta^{15}N$ and $\delta^{13}C$ of *Chloroscombrus chrysurus* associated with **a** *Aurelia* sp. and **b** *Drymonema larsoni* along with their potential prey, small plankton (<200 μm) and mesozooplankton (>200 μm) collected in Alabama coastal waters from June to October 2009–2010

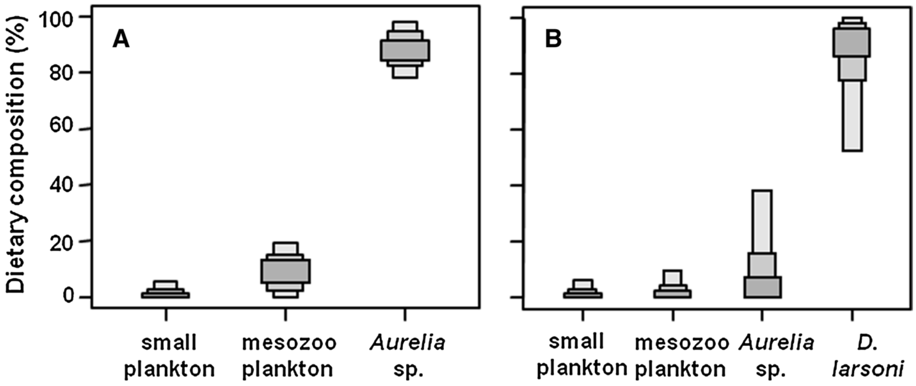

Fig. 2 Dietary composition (%) of *Chloroscombrus chrysurus* associated with **a** *Aurelia* sp. and **b** *Drymonema larsoni* calculated using SIAR. *Grey scale* (from *light to dark*) indicates 95, 75 and 25 % confidence intervals, respectively

Discussion

Trophic link between fish and their scyphozoan hosts

Overall, SIAR models indicated that the assimilated diet of age-0 *C. chrysurus* associated with scyphomedusae in Alabama coastal waters was based on scyphozoan host tissue. This finding highlights an aspect of the trophic ecology of fish associated with scyphomedusae that was not clearly defined in previous studies. Although visual observations indicated that fish may feed on their hosts (Mansueti 1963; Brodeur 1998), scyphozoans were considered irrelevant in the diet of fish because of their low organic content (Purcell and Arai 2001). Based on study of a few species, scyphomedusae are thought to have relatively low energy density, with remarkable species and tissue-specific differences (Doyle et al. 2007). However, the leatherback sea turtle, *Dermochelys coriacea*, which reaches considerable size, is dependent on a jelly-based diet (Bjorndal 1997; Arai 2005). The paradox of feeding on a low-energy-density diet has been explained as the result of an adaptation of the digestive tract to feed on gelatinous prey (Purcell and Arai 2001) and high predation rates for the leatherback sea turtle (Davenport 1998; Fossette et al. 2012). Recent studies suggest that jellyfish may have been underestimated in the diet of loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles (Cardona et al. 2012; González Carman et al. 2014). These observations, along with the findings in this study, suggest that the importance of jellyfish merits further evaluation as a component in the diet of fish.

Although the metabolic aspects are not clearly defined, feeding on a jelly-based diet may be simple and convenient for fish sheltering underneath scyphozoan bells, as they would have their prey available without energetic costs to pursue and capture it. In the perspective of more complex trophic interactions, feeding on jellyfish may be an advantage for fish in terms of competition for food resources. The northern Gulf of Mexico is a highly productive system (Grimes 2001), where the abundances of fish early life stages, including *C. chrysurus*, are often correlated with riverine discharge (Carassou et al. 2011). However, fish early life stages and macrozooplankton aggregate in the river plume, increasing mortality due to competition and predation (Grimes and Finucane 1991). Feeding on their host, age-0 *C. chrysurus* may enhance survival rates, allowing jelly-associated fish to exploit an under-utilised resource available to a limited number of predators. The increase in larval recruitment of whiting *Merlangius merlangus* in co-occurrence with high abundance of *Cyanea capillata* in the North Sea was explained as a result of the protection provided by scyphozoans to age-0 fish and an undefined potential commensalism between fish and their hosts (Lynam and Brierley 2007). Dietary definitions in this study suggest that scyphomedusae may play a key role as food source in the early life stages of fish sheltering underneath their bell and enhance survival rates of fish.

Limitations of the study

Our results indicate that scyphozoan tissue is important in the diet of fish associated with them, but dietary definitions need a refinement. SIAR mixing models are sensitive to the fractionation values used to interpret the trophic shift from predator to prey (Parnell et al. 2010). We used expected fractionation values for *C. chrysurus* because they encompass a variety of prey based on a literature review (McCutchan et al. 2003; Vanderklift and Ponsard 2003), but they are not specific for gelatinous prey. Given the low organic content of jellyfish (Pitt et al. 2009; Lucas et al. 2011), it is likely that their predators uptake all the organic matter available, reducing fractionation values (Peterson and Fry 1987). Hence, to obtain an accurate definition of the fish diet, laboratory experiments are needed to determine fractionation values from fish to medusae.

Milisenda et al. (2014) speculated that the bogue *Boops boops* may feed selectively on the gonads of the mauve stinger, *Pelagia noctiluca*, in the Strait of Messina, based on the biochemical composition of scyphozoan body parts, which indicated that gonads contain more lipids and carbohydrates than bell and oral arms of the scyphomedusa.

Determination of δ^{13}C and δ^{15}N in *Aurelia* sp. indicated that gonads have lower δ^{13}C than bell and oral arms due to their higher lipid content (D'Ambra et al. 2014). We could not analyse scyphozoan tissues individually due to the budgeting of this study. However, although using the isotopic values of the different body parts is a suitable approach to determine whether *C. chrysurus* feed on the gonads of their hosts, we suggest preliminary checking that the stable isotope values of the tissues differ remarkably to allow for a reliable source partitioning using mixing models (Parnell et al. 2010).

Conclusions

This study provide the first evidence that scyphomedusae are a primary food source for *C. chrysurus* early life stages. Previous studies emphasised the refuge function of fish–jellyfish associations, but our SIAR models highlight a close trophic link between *C. chrysurus* and scyphomedusae derived from this same behaviour. Our results suggest that the importance of jellyfish in the diet of fish has been generally underestimated due to limitations in the methodological approaches used. By feeding on their host, *C. chrysurus* (and potentially other jellyfish-associated species) exploit a resource restricted to few predators and thereby reduce competition for food resources, which may overcome energetic constraints associated with the lower quality of a gelatinous diet. The availability of food along with protection from predators may increase survival and subsequent recruitment, which suggests that fish associations with scyphomedusae should be considered in food web models and ecosystem assessments.

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