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Not all jellyfish are equal: isotopic evidence for inter- and intraspecific variation in jellyfish trophic ecology

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Jellyfish are highly topical within studies of pelagic food-webs and there is a growing realisation that their role is more complex than once thought. Efforts being made to include jellyfish within fisheries and ecosystem models are an important step forward, but our present understanding of their underlying trophic ecology can lead to their over-simplification in these models. Gelatinous zooplankton represent a polyphyletic assemblage spanning >1,400 species that inhabit coastal seas to the deep-ocean and employ a wide variety of foraging strategies. Despite this diversity, many contemporary modelling approaches include jellyfish as a single functional group feeding at one or two trophic levels at most. Recent reviews have drawn attention to this issue and highlighted the need for improved communication between biologists and theoreticians if this problem is to be overcome. We used stable isotopes to investigate the trophic ecology of three co-occurring scyphozoan jellyfish species (*Aurelia aurita*, *Cyanea lamarckii* and *C. capillata*) within a temperate, coastal food-web in the NE Atlantic. Using information on individual size, time of year and $\delta^{13}C$ and $\delta^{15}N$ stable isotope values we examined: (1) whether all jellyfish could be considered as a single functional group, or showed distinct inter-specific differences in trophic ecology; (2) Were size-based shifts in trophic position, found previously in *A. aurita*, a common trait across species?; (3) When considered collectively, did the trophic position of three sympatric species remain constant over time? Differences in $\delta^{15}N$ (trophic position) were evident between all three species, with size-based and temporal shifts in $\delta^{15}N$ apparent in *A. aurita* and *C. capillata*. The isotopic niche width for all species combined increased throughout the season, reflecting temporal shifts in trophic position and seasonal succession in these gelatinous species. Taken together, these findings support previous assertions that jellyfish require more robust inclusion in marine fisheries or ecosystem models.

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Introduction

Jellyfish (here considered as Phylum Cnidaria; Class Scyphozoa) are a conspicuous, yet long-overlooked component of pelagic marine systems. In recent years the notion of gelatinous species as merely carbon sinks, or trophic dead ends has become largely obsolete (Arai 2005; Hansson & Norrman 1995; Sweetman et al. 2014). Besides obligate predators of jellyfish such as leatherback turtles (*Dermochelys coriacea*; see also Houghton et al. 2006), Arai (2005) drew attention to a wide range of opportunistic carnivores such as molluscs, arthropods, reptiles and birds that feed upon gelata episodically and recently opportunist scavenging has been observed in the deep-sea (Sweetman et al. 2014). From a perspective of top-down control, it is also known that the collective prey-consumption rates of gelatinous aggregations can be so high that predation can directly or indirectly control the population size of other zooplanktonic organisms including larval fish (Nielsen et al. 1997; Purcell 1992). Moreover, evidence of sized-based shifts in the moon jellyfish *Aurelia aurita* (Linnaeus, 1758) (Fleming et al. 2011; Graham & Kroutil 2001) and suggest that jellyfish could themselves exhibit size-associated shifts in trophic ecology, *e.g.* similar to those shown by fishes (Graham et al. 2007).

Prompted by a growing body of evidence, Pauly *et al*. (2009) stressed that gelatinous taxa require more robust inclusion in marine fisheries or ecosystem models. At present, such species are typically considered as a single functional group or an 'average' group of animals, feeding on the same prey throughout their life history (Boero et al. 2008; Pauly et al. 2009). Indeed, out of 100 models considered, only 23 % incorporated jellyfish as a distinct functional group (normally feeding at a single trophic level) and only 4 % of models considered them in any greater detail (e.g. deeding at two trophic levels) (Pauly et al. 2009; Ruzicka et al. 2012). Consequently, seasonal or ontogenetic shifts in diet (Fleming et al. 2011), intra-specific differences in prey types (Fancett 1988; Graham & Kroutil 2001)

and intra-guild predation (Bayha et al. 2012; Robison 2004; Titelman et al. 2007) are sometimes over-simplified or disregarded entirely. Pauly et al. (2009) and Doyle et al. (2014) make a number of suggestions for researchers working with gelatinous species on how to generate data that are useful to theoreticians. These studies highlight the fact that the ecological-modelling community cannot be expected to consider jellyfish in adequate detail if the required data are not provided by other researchers (Doyle et al. 2014). This is a valid point, but until recently many questions surrounding the trophodynamics of gelatinous species appeared intractable given the spatial and temporal variability of aggregations (Doyle et al. 2007; Houghton et al. 2007), the broad-scale over which they can occur (Doyle et al. 2008) and methodological limitations (Purcell 1992).

Within this broad context, the aim of this study was to examine trophic variation in three sympatric jellyfish species (*Aurelia aurita* (Linnaeus, 1758), *Cyanea lamarckii* (Péron & Lesueur, 1810) and *C. capillata* (Linnaeus, 1758)) in a temperate coastal marine system. Strangford Lough in Northern Ireland was identified as an ideal study system as it supports an annual succession of gelatinous zooplankton species from early May to late August (Fleming et al. 2013). We used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to consider size-based and temporal shifts in the trophic ecology of the three jellyfish species, both individually and collectively as a dominant large gelatinous zooplankton community. Such isotopic approaches have been used widely to examine the trophic ecology of marine and estuarine systems (Peterson & Fry 1987) in general, and are gathering momentum for the study of gelatinous species (Kogovšek et al. 2014; Nagata et al. 2015; Pitt et al. 2008). To provide data that might aid the further inclusion of jellyfish into ecosystem models, our analyses were aligned to examine three specific questions: (1) Could all jellyfish be considered as a single functional group or was there evidence for distinct inter-specific differences in trophic ecology? (2) Were size-based shifts in trophic ecology found previously in *A. aurita* a common trait across species? and (3) When

considered collectively, did the trophic position and isotopic niche of three sympatric species remain constant over time?

MATERIALS & METHODS

Collection and processing

Strangford Lough (54° 28' 20.98"N 5° 35' 10.60"W) in County Down, Northern Ireland is a large, semi-enclosed coastal embayment (150 km^2) that flows into the northern Irish Sea (see Maloy et al. 2013 for a description). Three scyphozoan jellyfish species are persistently present in the lough but their relative abundance varies over time. In May, the community is dominated by *Aurelia aurita*, with an increase in *Cyanea lamarckii* in early June and *Cyanea capillata* in July (Fleming et al. 2014). All three species disappear from the water column in the same order from late July onwards (Fleming et al. 2013; 2014). Jellyfish medusae were sampled monthly from Strangford Lough (May 2010 to September 2010). All jellyfish were collected near the surface from a small boat using a dip net (mesh size 1 mm) for smaller jellyfish and a larger net (5 mm mesh size) for larger individuals. Sampling was conducted in a non-random manner, as our aim was to collect sufficient individuals to allow for balanced statistical comparisons (e.g. across months). Unfortunately, owing to temporal variation in the abundance of the different species, and often challenging weather conditions, it was not possible to ensure a balanced number of samples per species. Filter-feeding bivalves (*Mytilus* spp.) and grazing gastropods (*Littorina saxatilis* (Olivi)) were sampled over the study period from intertidal areas adjacent to the jellyfish sampling sites over the same period (Woodland et al. 2012) to provide a measure of isotopic baselines of the pelagic (bivalve) and benthic (gastropods) primary production pathways (Mallela & Harrod 2008; Post 2002).

Laboratory and SIA analysis

All jellyfish samples were collected and processed immediately to prevent potentially marked preservation effects (Fleming et al. 2011). Scyphozoan jellyfish (*A. aurita, C. lamarckii* and *C. capillata*) were weighed and measured (wet mass: ± 1g; bell diameter: ± 1cm). Jellyfish medusae were rinsed thoroughly in filtered seawater, after which bell (mesoglea) tissues were separated and dried at 60°C in a drying oven following Fleming et al. (2011). Samples were weighed into tin cups prior to stable isotope analysis. Previous preliminary analyses revealed that optimal sample mass for mass spectrometry varied between taxa *i.e. A. aurita* ≈ 12 mg; *C. lamarckii* ≈ 2.4 mg, *C. capillata* ≈ 5.1 mg and other taxa ≈ 0.8 mg). Samples were analysed for $\delta^{13}C$, $\delta^{15}N$ and C:N at the East Kilbride Node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility via continuous flow isotope ratio mass spectrometry using an ECS 4010 elemental analyser (Costech, Milan, Italy) interfaced with a Delta XP mass spectrometer (Thermo Electron, Bremen, Germany). The standard deviation of multiple analyses of an internal gelatine standard was ~ 0.1 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Statistical analysis

Prior to analysis the bell mass, diameter and stable isotope data were $\log_{10}$-transformed to improve normality and reduce heteroscedasticity ($\delta^{13}C$ data were $\log_{10}+40$ transformed due to their negative values). We used various statistical approaches to characterise and compare the trophic ecology of the different jellyfish species. To examine whether bell $\delta^{13}C$ and $\delta^{15}N$ values differed by species or sample month, we used permutational ($n_{permutations}$ = 9,999) multivariate analysis of variance (PERMANOVA) in PRIMER 6.1.12 (Clarke & Gorley 2006; Clarke & Warwick 2001) to examine variation in the location of centroids of log-$_{10}$transformed $\delta^{15}N$-$\delta^{13}C$ data, based on a Euclidean similarity matrix (Anderson 2001; Anderson et al. 2008). Here, it is assumed that where $\delta^{15}N$-$\delta^{13}C$ centroids overlap (i.e. are not significantly different), then trophic ecology is similar e.g. between species or survey month.

As some small ($n \leq 3$) sample sizes were recorded for each species across the different survey months (*C. capillata* in May; *A. aurita* and *C. lamarckii* in August), it was not possible to make a balanced two-way analysis for the entire study period and interaction terms were not included in the analysis. A full two way PERMANOVA examining isotopic variation associated with Species and Month (and the Species x Month interaction) was only conducted for June and July.

A two way PERMANOVA was used to examine how variation in baseline $\delta^{15}N$ associated with the pelagic and benthic pathways varied over time. We compared $\log_{10}$-transformed $\delta^{15}N$ data from filter feeding bivalves (pelagic) and grazing gastropods (benthic), with the factors Functional Group and Month. We also examined the associated interaction between these two factors.

Normal linear least-squares regression was used to examine how $\log_{-10}$ transformed stable isotope values ($\delta^{13}C$ data were $\log_{10}+40$ transformed) varied with individual size (bell wet mass and diameter).

In stable isotope studies, consumer trophic position is typically estimated from $\delta^{15}N$ data, which are corrected for baseline variation and trophic fractionation (Post 2002). Although we had reliable data on pelagic and benthic $\delta^{15}N$ baselines (see above), jellyfish trophic enrichment factors (TEFs) are unknown. D'Ambra et al (2014) recently provided TEFS for *A. aurita* in what represents the only experimental estimate of jellyfish trophic fractionation in the literature. The mean ± SD TEFs estimated for *A. aurita* ($\Delta^{13}C = 4.3 \pm 0.2‰$; $\Delta^{15}N = 0.1 \pm 0.2‰$) are unusual and contrast with the average TEFS more commonly seen in the literature (e.g. Post (2002): $\Delta^{13}C = 0.4 \pm 1.3‰$; $\Delta^{15}N = 3.4 \pm 1‰$; McCutchan et al. (2003) (Δ13C = 0.5 ± 1.3‰, Δ15N =2.3 ± 1.5‰). As use of the jellyfish specific TEFs provided by D'Ambra (2014) resulted in unfeasibly high trophic positions for the

jellyfish species, including *A. aurita*, we did not make direct estimates of trophic position, but provide indirect estimates by presenting $\delta^{15}N$ data.

As jellyfish are often considered as a single functional group, we examined how an indicator of community level trophic position varied across the survey period at the level of the whole community level, by pooling $\delta^{15}N$ data from all three jellyfish species and conducting a univariate PERMANOVA with month as a fixed independent factor, both for individual species and for the dominant gelatinous zooplankton community as a whole (species pooled).

We used the SIBER procedure (Stable Isotope Bayesian Ellipses in R) within the R package SIAR (Jackson et al. 2011) to examine variation in jellyfish isotopic niche space. This approach relies on the concept that that multiple stable isotope ratios measured from consumers represents niche dimensions, *e.g.* variation in $\delta^{13}C$ reflects use of different energy sources, or habitats, while $\delta^{15}N$ can provide information on the trophic level at which a consumer feeds (Peterson & Fry 1987). This so called 'isotopic niche' or 'δ-space' (Newsome et al. 2007) is thought to reflect the trophic niche of groups of consumers (Bearhop et al. 2004; Layman et al. 2007), where more isotopic variation reflects a larger consumer isotopic niche, assuming that spatial or temporal variation in baseline isotopic values is considered. Here we use Bayesian Standard Area Ellipses (SEA_B), as the use of Bayesian inference allows the incorporation of uncertainty such as small sample sizes (Jackson et al. 2011). This iterative approach uses Monte Carlo Markov-Chain simulation to construct ellipses characterising isotopic variation that provide a robust indicator of isotopic niche width. Here, we used this technique to characterise temporal variation in the trophic niche of the three jellyfish species, as well as overlap between species. We also examined temporal variation in SEA_B values calculated for the jellyfish community as a whole (i.e. all three species of jellyfish combined). In order to examine the differences

in isotopic niche area (SEA_B) between different consumer groups, we calculated probabilities from posterior distributions (based on 100,000 draws) of the parameters of model *M* given the prior data *D* (Pr(*M*|*D*)). These maximum likelihood comparisons provide direct probabilities of differences rather than the traditional frequentist test of a null-hypothesis. In order to differentiate these comparisons, maximum-likelihood probabilities are reported here as percentages.

Statistical analyses were conducted using routines in PRIMER-E 6 (Clarke & Gorley 2006) and SYSTAT 13.1 (SYSTAT Software Inc 2009). SIBER analyses (Jackson et al. 2011)were conducted using SIAR (Parnell et al. 2010) in R version 3.1.2 (R Development Core Team 2014).

RESULTS

Inter-specific variation

Three species of scyphozoan jellyfish were collected from Strangford Lough Between May and August 2010. A total of 122 medusae were collected from the surface of the water column comprising *Aurelia aurita* (n = 43), *Cyanea lamarckii* (n = 36) and *C. capillata* (n = 43). Data collected across the entire study for the three jellyfish species (Fig. 1) showed considerable intraspecific variation and apparent isotopic overlap between the species. However, when $\delta^{15}N$ and $\delta^{13}C$ data for individual species were compared over time, distinct differences appeared (Table 1; Fig. 2). A full two-way PERMANOVA comparing the influence of survey month and species was only possible for all three species in the months of June and July when medusae of all species were present. The analysis of $\log_{10}$-transformed data revealed that $\delta^{15}N$-$\delta^{13}C$ centroid location varied significantly between the three jellyfish species (Pseudo-$F_{2,71}$ = 5.01, P = 0.006) and survey month (Pseudo-$F_{1,71}$ = 5.1, P = 0.02). However, there was no interaction between species and survey month ($F_{2,71}$ = 0.25, P = 0.82) indicating that temporal shifts in $\delta^{13}C$-$\delta^{15}N$ isotope values were similar across the three scyphozoan species in June and July. Pairwise comparisons showed that *A. aurita* were isotopically distinct from both *Cyanea* species in June (*C. lamarckii* P ≤ 0.0043; *C. capillata* P = 0.02), and *C. lamarckii* in July (P = 0.03). The $\delta^{15}N$-$\delta^{13}C$ centroids of the two *Cyanea* species overlapped during these months (June: P = 0.89; July: P = 0.43).

Next, we considered inter-specific differences in isotopic niche width over time (Fig. 3). Between species comparisons (data pooled from all months) showed that *C. capillata* had the largest mean (95 % credibility limits) isotopic niche width of 6.9 (4.95 - 9.03) ‰^{2}, compared to *A. aurita* (4.94 (3.55 - 6.46) ‰^{2}) or *C. lamarckii* (5.49 (3.84 - 7.32) ‰^{2}). Maximum-likelihood pairwise comparisons indicated a borderline (P = 94 %) probability that across the entire study the isotopic niche width of *C. capillata* was larger than that of *A. aurita*. There was no statistical support (P = 85 %) for differences

196 between *C. capillata*, and its congeneric *C. lamarckii* over the same period. There was a 67 %
197 probability of differences in isotopic niche width size between *A. aurita* and *C. lamarckii*.
198
199 **Intra-specific variation**
200 Both *A. aurita* and *C. capillata* showed positive linear relationships (Table 2: Fig. 4) between $\log_{10}$-
201 transformed $\delta^{13}C$ and wet mass (*A. aurita* $F_{1,41} = 26.9$, $R^2 = 0.40$, $P < 0.001$; *C. capillata* $F_{1,41} = 16.1$,
202 $R^2 = 0.28$, $P < 0.001$) and bell diameter (*A. aurita* $F_{1,41} = 26.3$, $R^2 = 0.39$, $P < 0.001$; *C. capillata* $F_{1,41} =$
203 19.1, $R^2 = 0.32$, $P < 0.001$), indicating a shift in dietary source with size in these species. However,
204 there was no evidence for any such relationship in *C. lamarckii* for wet mass ($F_{1,35} = 0.71$, $R^2 = 0.02$, P
205 = 0.405) or bell diameter ($F_{1,35} = 0.85$, $R^2 = 0.02$, P = 0.363), indicating that individuals of all sizes
206 assimilated carbon from a similar range of sources. $\delta^{15}N$ increased with size (Fig. 4 & Table 2) in both
207 *A. aurita* ($\log_{10}$-transformed wet mass $F_{1,41} = 48.8$, $R^2 = 0.54$, $P < 0.001$; bell diameter $F_{1,41} = 46.2$, R^2
208 = 0.53, P = <0.001) and *C. capillata* (wet mass $F_{1,41} = 22.1$, $R^2 = 0.35$, P = <0.001; bell diameter $F_{1,41} =$
209 22.0, $R^2 = 0.34$, $P < 0.001$). In all cases, the slope of the $\log_{10}$-$\log_{10}$ relationship was < 1 (Table 2). As
210 in the case of $\delta^{13}C$, *C. lamarckii* showed no evidence of any size-based shift in $\delta^{15}N$ (wet mass = $F_{1,35} =$
211 1.50, $R^2 = 0.04$, P = 0.229; bell diameter $F_{1,35} = 2.4$, $R^2 = 0.06$, P = 0.131).
212
213 Although individual *A. aurita* were captured in each of the survey months (Fig. 2), sufficient samples
214 for analysis were not recorded in August (n = 2), and statistical comparisons here are limited to the
215 period May-July (See Table 1 for sample sizes). During this period, the location of *A. aurita* $\delta^{15}N$-$\delta^{13}C$
216 centroids varied significantly (One way PERMANOVA Pseudo-$F_{2,38} = 15.19$, P = 0.0001), indicating
217 that *A. aurita* underwent an isotopic shift over the study period. Pairwise tests showed that $\delta^{15}N$-$\delta^{13}C$
218 centroids shifted between May and both June (t = 4.49, P = 0.0002) and July (t = 4.77, P = 0.0001).
219 $\delta^{15}N$-$\delta^{13}C$ values overlapped in June and July (t = 1.6, P = 0.12). The difference between May and the

220 other months reflected enrichment in ^{13}C and ^{15}N (to a lesser degree than for C) from May to the later
221 months. Sample sizes in *C. lamarckii* were relatively low throughout the study, with large numbers
222 only being encountered in June (Table 1).
223
224 *C. lamarckii* showed significant temporal shifts in the location of the $\delta^{15}N$-$\delta^{13}C$ centroids (May – July:
225 Pseudo-$F_{2,31} = 15.46$, $P = 0.0001$). Pairwise tests revealed that centroids differed between May and both
226 June ($t = 5.15$, $P = 0.0002$) and July ($t = 6.58$, $P = 0.001$), but overlapped between June and July ($t =$
227 0.63, $P = 0.56$). Isotopically, *C. lamarckii* became increasingly ^{13}C and ^{15}N enriched over the survey
228 period (Fig. 2, Table 1).
229
230 Only two *C. capillata* were available for analysis in May, but in the following months, $\delta^{15}N$-$\delta^{13}C$
231 centroids for this species changed significantly (June-August: Pseudo-$F_{2,38} = 4.44$, $P = 0.008$). Pairwise
232 tests indicated that this shift was relatively gradual, with isotopic overlap in June and July ($t = 1.87$, $P =$
233 0.06) and July-August ($t = 1.22$, $P = 0.22$). Isotopic differences were most marked at the extremes of
234 the collection period: June – August ($t = 2.79$, $P = 0.003$).
235
236 Bayesian estimates of isotopic niche width (SEA_B) showed significant variation within species during
237 the study period (Table 3 & Fig. 3). Pairwise comparisons showed that *A. aurita* mean isotopic niche
238 width was lower in May relative to other months (Table 3, Fig. 3), with a 95 % probability of a
239 difference with June and a 98 % probability of a difference with July. The isotopic niche width of *C.*
240 *lamarckii* was reduced in May relative to June (probability = 99 %) and July (96 %), there were no
241 obvious differences in isotopic niche width in *C. lamarckii* in June and July (P = 46 %). *C. capillata*
242 was not recorded in sufficient numbers in May to allow analyses, but showed a generally similar
243 isotopic niche width through the June - August period (P range 50 – 60 %).

244

245 **Variation at a whole community level**

246 Baseline $\delta^{15}N$ values recorded from filter feeding and grazing molluscs were consistent across the
247 study period (PERMANOVA on log10-transformed $\delta^{15}N$ data; Month: Pseudo-$F_{2,108}$ = 0.48, P =
248 0.725), but differed between the two functional groups (Pseudo-$F_{1,108}$ = 59.57, P = 0.0001) with benthic
249 grazers (mean ± SD $\delta^{15}N$ = 11.2 ± 1.08, n = 58) being ^{15}N enriched by 1.5 ‰ relative to filter feeding
250 bivalves (bivalve = 9.7 ± 0.7, n = 56). However, the lack of an interaction between the two factors
251 (Month x Functional Group: Pseudo-$F_{2,108}$ = 0.087, P = 0.91) indicated that the difference between the
252 two functional groups remained constant over time.

253

254 As $\delta^{15}N$ baselines were consistent over time, we were able to use $\delta^{15}N$ as an indirect indicator of
255 changes in whole community trophic position over time. $\delta^{15}N$ values for the GZ community varied
256 over the study period (One way PERMANOVA Pseudo-$F_{3,119}$ = 36.9, P = 0.0001; Fig. 2), and showed
257 relative increases in trophic position over time. Pairwise tests showed May was lower than all other
258 months (June, t = 6.2, P = 0.0001; July, t = 10.6, P = 0.0001; August , t = 13.3, P = 0.0001). June $\delta^{15}N$
259 values were higher than May, but lower than subsequent months (May, t = 6.2, P = 0.0001; July, t =
260 3.1, P = 0.0027; August, t = 4.4, P = 0.002). There was no measurable difference in whole community
261 $\delta^{15}N$ values in July and August (t = 1.9, P = 0.07; Fig. 2).

262

263 We also examined temporal variation in the isotopic niche width by pooling values from the three
264 jellyfish species (See all GZ values in Fig. 3). Mean (95 % credibility limits) jellyfish isotopic niche
265 width in May was lower than in June, July or August (P = 100 % in all cases). However, isotopic niche
266 for the combined jellyfish species began to change in position and width as the season progressed with
267 an increase in isotopic niche ($‰^2$ 95% credibility limits) from May = 2.05 (1.31 – 2.89) to Aug = 5.72

(3.49 – 8.3), suggesting a broader trophic niche in the latter months and was similar in the following months (P July > June = 54 %; P August > June = 76 %; P August > July = 70 %).

Discussion

Pauly et al. (2009) described jellyfish as arguably the most important predators in the sea. There is little ambiguity in this statement which, in part, prompted the present study. Rational thought regarding jellyfish ecology is very much needed if we are to avoid the trap of viewing such species as merely unnatural and unwanted constituents of our oceans (Doyle et al. 2014). There is no doubt that the potential expansion of jellyfish in highly depleted oceans is a matter of grave concern (Lynam et al. 2006; Purcell et al. 2007), but we must also acknowledge that this threat is often driven by our own actions e.g. overfishing, eutrophication and translocation (Arai 2001; Graham & Bayha 2007; Hay 2006), or climatic oscillations (Condon et al. 2013) rather than the species in question. Tackling such issues requires an underlying knowledge of how jellyfish function within marine systems, so that long-standing trends in populations and communities can be teased apart from shifts in ecosystem structure. Stable isotope analysis offers a powerful biochemical approach to the estimation of trophic and dietary composition of individuals through to communities (Bearhop et al. 2004; Bolnick et al. 2011; Bolnick et al. 2003) and the results presented here support the idea that jellyfish play a more complex trophic role than once envisaged.

Inter-specific differences in trophic position

Distinct isotopic differences were evident between all three jellyfish species (*A. aurita*, *C. lamarckii* and *C. capillata*) with variation in $\delta^{13}C$ and $\delta^{15}N$ values and niche width inferring differences in their capacity to capture and ingest a range of prey items (Figs 2 & 3). Typically, scyphozoan jellyfish encounter rather than detect and pursue prey and use both 'passive ambush feeding' and 'feeding current feeding' with direct interception and filtering through tentacles being used in both cases (Kiørboe 2011). Feeding currents are generated by pulsation of the bell which varies in shape and size between species; with slower velocities normally associated with smaller individuals (Costello & Colin

1994; 1995; Kiørboe 2011). Depending on the escape velocities of putative prey, differences in feeding current velocity between different jellyfish species might lead to different prey being captured and ingested; although further work is required to link trophic position with morphological characteristics in an empirical manner.

The total complement of nematocysts or 'cnidome' (Peach & Pitt 2005) also plays a part in prey capture (Costello et al. 2008), and this 'cnidome' varies with the individual and species. *A. aurita* have a reduced cnidome (Shostak 1995) and a much reduced capture surface (short tentacles) which may account again for the low trophic position and narrowest niche width of this species in the present study. By comparison, the congenerics *C. lamarckii* and *C. capillata* have similarities in both nematocyst complement (Ostman & Hydman 1997; Shostak 1995) and morphology (Holst & Laakmann 2013), yet differed here with regard to their $\delta^{13}C$ and $\delta^{15}N$ values and niche widths. While both *Cyanea* species conform to the same body plan, there is a large disparity in the maximum size, and therefore capture surface that can be attained by the two species. More specifically, *C. lamarckii* rarely exceeds 20 cm (max. 30 cm; Russell 1970), whereas *C. capillata* has been observed as large as 85 cm (max. 90 cm in British waters; Russell 1970) in this system (Fleming pers. obs.). There are also size related differences in toxicity; although *C. lamarckii* is as venomous as *C. capillata* (Helmholz et al. 2007), as both species increase in size so too do the size of their nematocysts (Ostman & Hydman 1997), these differences may account for the higher $\delta^{15}N$ values and broader niche width observed in *C. capillata*.

The isotopic variation found between three co-occurring species in this study suggests niche partitioning and represents a host of differences in morphology, bell pulsation strength, prey capture techniques and nematocyst composition that enable differential prey capture (Bayha & Dawson 2010;

Costello & Colin 1994; Peach & Pitt 2005). Taking into account such isotopic variation between three co-occurring species in a single system, caution must clearly be taken to avoid over-simplification of jellyfish in ecosystem models. In a broader context, as gelatinous zooplankton span >1,400 species, occupying habitats ranging from the deep ocean through to shallow water near-shore environments, the inclusion of an 'average' jellyfish in such models is likely to underestimate the collective impact in terms of energy flow or consumption of prey (Pauly et al. 2009).

Intra-specific differences in trophic ecology

A. aurita and *C. capillata* shifted their use of both energy source and trophic position ($\delta^{13}C$ and $\delta^{15}N$) with increasing body size, independent of time (Fig. 4). This suggests different sized jellyfish medusae, present in the water column at the same time and with access to the same prey field, feed at different positions in the food chain (Fleming et al. 2011; Graham & Kroutil 2001). The simultaneous presence of different sized medusae appears to be a consistent trait across a range of species at temperate latitudes (Houghton et al. 2007) suggesting that jellyfish reproductive cohorts are often poorly defined with a marked overlap within given seasons. The third jellyfish species examined, *C. lamarckii*, did not exhibit a size-based shift in trophic position with increasing body size. This most likely reflects the comparatively narrow size range of the medusae sampled (3.5 - 20 cm), with the species rarely exceeding a bell diameter of 30 cm (Russell 1970). By comparison, *C. capillata* medusae spanned a far broader size range (6 - 85 cm) allowing size related shifts in diet to be more easily identified. These findings suggest that body size in jellyfish may, to some extent, underpin their capacity to feed at multiple trophic levels through ontogeny. There are some clear exceptions to this rule e.g. small gelatinous species (<12 cm bell diameter) such as box jellyfish *Chironex fleckeri* and *Carukia barnesi* have extraordinarily powerful stings that enable them to capture relatively large prey such as larval and small fishes (Carrette et al. 2002; Kintner et al. 2005; Underwood & Seymour 2007).

The trophic position of the jellyfish community over time

When considered as a whole, the $\delta^{15}N$ values of the scyphozoan jellyfish community in Strangford Lough increased as the season progressed (Fig. 2). Given that $\delta^{15}N$ baselines were constant across the study period, this indicates that trophic position increased over time. In terms of isotopic niche width there was an interesting dissimilarity between the start of the season (May) and the following months (June, July and August) suggesting a shift to a broader dietary niche in the latter months (Fig. 3). This increased resource utilisation is consistent with previous studies that suggested jellyfish dietary niches are extremely broad, with species operating as generalists (Dawson & Martin 2001; Ishii & Båmstedt 1998; Schneider & Behrends 1998) feeding opportunistically across a range of plankton (Båmstedt et al. 1997; Titelman et al. 2007). Therefore, our data suggest that a different and possibly constrained resource pool is being exploited at the beginning of the 'jellyfish season'. The sequential change in species composition seen in Strangford Lough could, in part, be the result of intra-guild predation (Bayha et al. 2012; Robison 2004; Titelman et al. 2007) which may contribute to the observed broadening in isotopic niche. Additionally, the collective increase in trophic position over time may reflect species succession in the lough with a general shift from an *A. aurita* dominated in system in May through to a *C. capillata* dominated system in August (Fleming et al. 2014). Most likely our results reflect interplay of these two scenarios but highlight the problems associated with assuming that different jellyfish species occupy a single trophic position or ecological niche (Boero et al. 2008; Pauly et al. 2009). Interspecific and temporal variation in jellyfish isotopes values can be put into deeper ecological context through the use of models to estimate trophic position (Post 2002) and consumption patterns (Parnell et al. 2010). However, the use of these for jellyfish both require reliable estimates of trophic enrichment factors. We welcome the recent TEF estimates made by D'Ambra et al. (2014) for *Aurelia* sp., however, we found that the use of their TEFS resulted in unfeasibly high trophic positions

368 for the *Aurelia* and other jellyfish in our system. For example, using Post's (2002) basic model for
369 tropic position resulted in a mean jellyfish trophic position of 17, with the baseline provided by our
370 mean *Mytilus* $\delta^{15}N$ values. As such, estimates of trophic level and consumption (e.g. mixing models)
371 by jellyfish made using tools requiring accurate TEFS remain problematic. We therefore call for more
372 experimental work to characterise jellyfish TEFs.
373
374 **Conclusions**
375 Size-based shifts in $\delta^{13}C$ and $\delta^{15}N$ values were evident in two of the three jellyfish species examined
376 here, leading to an inference that variation body size in some way dives variation in the trophic ecology
377 of a particular species. When considered over time, distinct differences in $\delta^{13}C$ and $\delta^{15}N$ values were
378 found within and between species, with evidence of niche segregation between the two *Cyanea*
379 species. Niche width for all species combined increased considerably throughout the season, reflective
380 of a possible interplay of intra-guild predation and species succession reflecting temporal shifts in $\delta^{13}C$
381 and $\delta^{15}N$ values and the seasonal succession in gelatinous species.
382
383 Taken together, these lines of evidence reinforce the idea that scyphozoan jellyfish require more
384 elegant inclusion in ecosystem or fisheries-based models. The salient point here is that jellyfish should
385 not be averaged or defined as a single amorphous group with little reference to temporal and allometric
386 shifts in individual species or gelatinous communities alike.

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389

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393

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Figure captions

Figure 1: Variation in $\delta^{13}C$ and $\delta^{15}N$ shown in three species of jellyfish over the whole study period. (See Table 1 for summary statistics).

Figure 2: Box-whisker plots showing variation in $\delta^{13}C$ (upper panel) and $\delta^{15}N$ (lower panel) in the three jellyfish species, and within the dominant GZ community (GZ; all three species combined) over the study period. See Table 1 for sample sizes and other summary statistics. NB: Baseline $\delta^{15}N$ values remained constant over this period, indicating that the increase in $\delta^{15}N$ values reflected a shift in trophic position rather than seasonal shifts at the base of the foodweb. Boxes show inter-quartile range, and the bold horizontal bar indicates the median value. Whiskers reflect values 1.5 x the interquartile range.

Figure 3: Variation in isotopic niche width (SEAB) between species (A. a = *A. aurita*; C. l = *C. lamarckii*; C. c = *C. capillata*)) and within the dominant GZ community (GZ; all three species combined) sampled over the survey period. Boxes represent the 50, 75 and 95 % Bayesian credibility intervals estimated from 100,000 draws. Samples marked with *included less than 10 individuals (see Parnell et al. 2010). See Table 3 for statistical comparisons.

Figure 4: Variation in bell $\delta^{13}C$ (A & B) and $\delta^{15}N$ (C & D) with bell diameter (A & C) and wet mass (B & D). Note use of logarithmic scale on x-axes.

Table 1(on next page)

Summary statistics

Table 1: Summary statistics for bell stable isotope and C:N ratios.

2

Species	***n***	**$\delta^{13}C$ (± SD) ‰**	**$\delta^{15}N$ (± SD) ‰**	**C:N (± SD)**
Aurelia aurita **May**	16	-20.3 (0.5)	8.5 (1.1)	3.8 (0.1)
Aurelia aurita **June**	18	-18.2 (0.5)	10.3 (1.5)	3.5 (0.4)
Aurelia aurita **July**	9	-18.1 (0.7)	11.5 (1.5)	3.5 (0.4)
Aurelia aurita **August**	2	-17.3 (0.1)	11.8 (1.7)	3.7 (0.1)
Overall mean *A. aurita*	43	-19.0 (1.2)	9.7 (1.6)	3.6 (0.2)
Cyanea lamarckii **May**	7	-21.4 (0.2)	8.6 (0.6)	3.9 (0.1)
Cyanea lamarckii **June**	21	-19.5 (0.7)	11.5 (1.5)	3.7 (0.4)
Cyanea lamarckii **July**	5	-19.4 (0.8)	12.1 (1.3)	3.7 (0.3)
Cyanea lamarckii **Aug**	3	-19.2 (0.8)	11.5 (0.8)	3.7 (0.2)
Overall mean *C. lamarckii*	36	-19.8 (1.0)	11.0 (1.8)	3.7 (0.3)
Cyanea capillata **May**	2	-21.4 (0.1)	7.7 (0.1)	3.8 (0.1)
Cyanea capillata **June**	13	-19.5 (1.2)	11.0 (2.1)	3.6 (0.4)
Cyanea capillata **July**	14	-19.4 (1.1)	12.8 (1.3)	3.6 (0.2)
Cyanea capillata **Aug**	16	-18.7 (1.6)	13.3 (1.1)	3.5 (0.3)
Overall mean *C. capillata*	43	-19.7 (1.3)	12.4 (1.8)	3.6 (0.1)

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Table 2 (on next page)

Summary statistics for least squares regressions

Table 2: Summary statistics for least squares regressions examining relationships between individual jellyfish size and bell stable isotope ratios (mass, length and $\delta^{15}N$ data $\log_{10}$ transformed, $\delta^{13}C$ data $\log_{10}+40$ transformed). NB: in all cases slopes were significantly different from 1.

2

Species	Isotope	Comparison	Intercept (± SE)	Slope (± SE)	R^2	F	P
A. aurita	$\delta^{13}C$ (-21.1 to -17.2 ‰)	Bell diameter (6 to 36 cm)	1.224 (0.019)	0.079 (0.015)	0.39	$F_{1,41} = 26.3$	< 0.001
A. aurita	$\delta^{15}N$ (6.7 to 14.8 ‰)	Bell diameter (6 to 36 cm)	0.609 (0.056)	0.305 (0.045)	0.53	$F_{1,41} = 46.2$	< 0.001
A. aurita	$\delta^{13}C$ (-21.1 to –17.2 ‰)	Wet mass (12 – 1 702 g)	1.256 (0.013)	0.029 (0.006)	0.40	$F_{1,41} = 26.9$	< 0.001
A. aurita	$\delta^{15}N$ (6.7 to 14.8 ‰)	Wet mass (12 – 1 702 g)	0.730 (0.038)	0.111 (0.016)	0.54	$F_{1,41} = 48.8$	< 0.001
C. lamarckii	$\delta^{13}C$ (-21.6 to -18.5 ‰)	Bell diameter (4 to 20 cm)	1.287 (0.019))	0.018 (0.019)	0.02	$F_{1,35} = 0.85$	= 0.363
C. lamarckii	$\delta^{15}N$ (7.7 to 15.8 ‰)	Bell diameter (4 to 20 cm)	0.939 (0.067)	0.103 (0.066)	0.06	$F_{1,35} = 2.4$	= 0.131
C. lamarckii	$\delta^{13}C$ (-21.6 to -18.5 ‰)	Wet mass (3 to 493 g)	1.293 (0.013)	0.006 (0.007)	0.02	$F_{1,35} = 0.71$	= 0.405
C. lamarckii	$\delta^{15}N$ (7.7 to 15.8 ‰)	Wet mass (3 to 493 g)	0.985 (0.047)	0.030 (0.025)	0.04	$F_{1,35} = 1.50$	= 0.229
C. capillata	$\delta^{13}C$ (-21.8 to -17.2 ‰)	Bell diameter (6 to 85 cm)	1.233 (0.020)	0.062 (0.014)	0.32	$F_{1,41} = 19.1$	< 0.001
C. capillata	$\delta^{15}N$ (7.6 to 16.1 ‰)	Bell diameter (6 to 85 cm)	0.876 (0.046)	0.157 (0.034)	0.34	$F_{1,41} = 22.0$	< 0.001
C. capillata	$\delta^{13}C$ (-21.8 to -17.2 ‰)	Wet mass (19 to 23 680 g)	1.259 (0.015)	0.020 (0.005)	0.28	$F_{1,41} = 16.1$	< 0.001
C. capillata	$\delta^{15}N$ (7.6 to 16.1 ‰)	Wet mass (19 to 23 680 g)	0.931 (0.035)	0.055 (0.012)	0.35	$F_{1,41} = 22.1$	< 0.001

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Table 3(on next page)

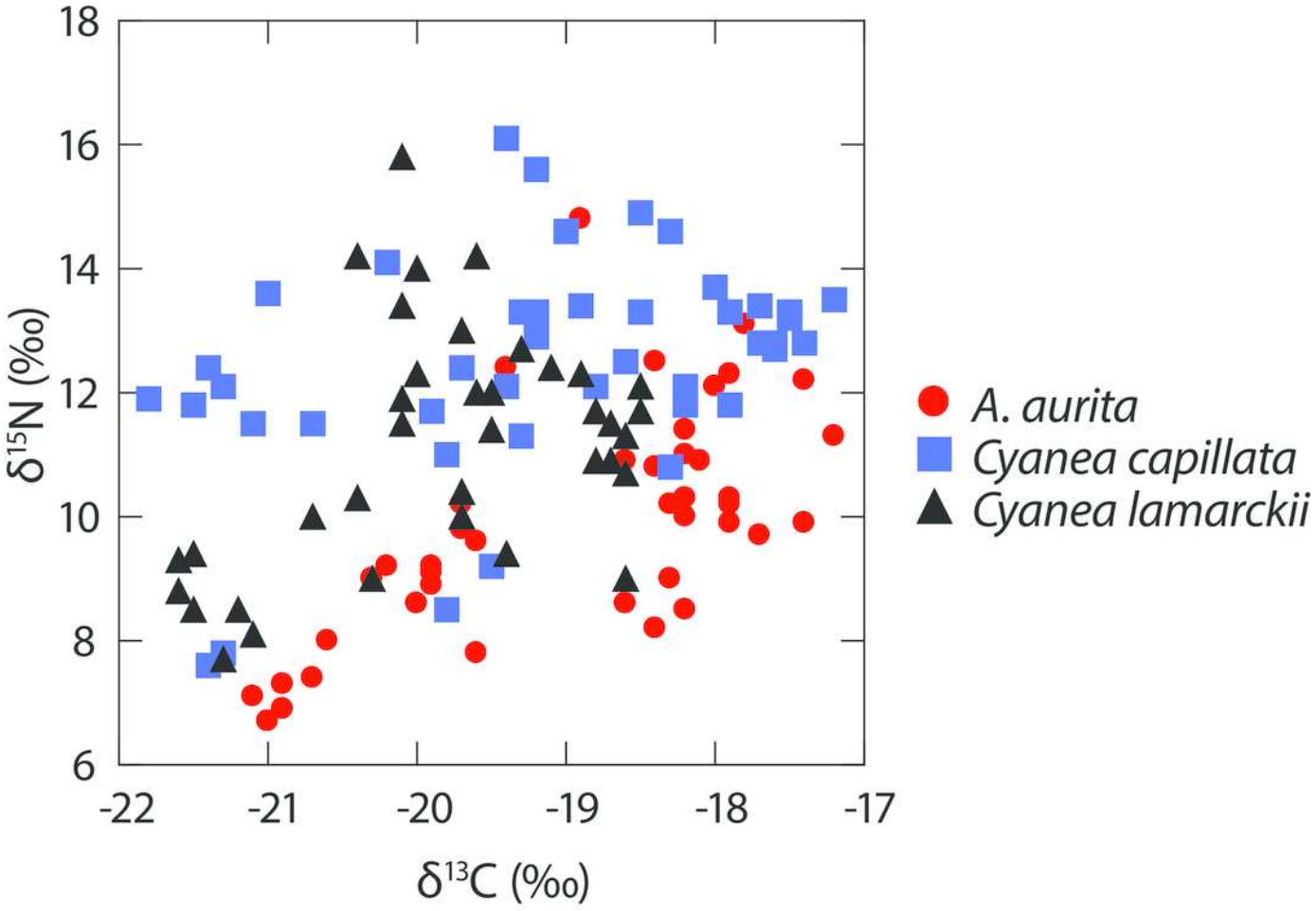
Bayesian comparisons of isotopic niche width (SEAB) between different jellyfish species and survey months

Table 3: Table showing results of Bayesian comparisons of isotopic niche width (SEAB) between different jellyfish species and survey months. Probabilities (based on 100,000 draws) that isotopic niche area in Group A is larger than the comparative value in Group B (A>B) are shown. Species codes: *A. a* = *A. aurita*; *C. l* = *C. lamarckii*; *C. c* = *C. capillata*). Groups marked with * reflect samples sizes < 10.

Group		*Group A*								
		A. a May	*A.a* June	*A. a* July*	*C. l* May*	*C. l* June	*C. l* July*	*C. c* June	*C. c* July	*C. c* August
	A. a May	—	0.951	0.980	0.388	0.996	0.969	0.998	0.999	0.999
	A. a June		—	0.756	0.062	0.855	0.728	0.927	0.938	0.969
	A. a July*			—	0.029	0.540	0.496	0.697	0.703	0.775
	C. l May*				—	0.988	0.964	0.993	0.994	0.997
Group B	*C. l* June					—	0.460	0.713	0.722	0.821
	C. l July*						—	0.683	0.688	0.754
	C. c June							—	0.497	0.596
	C. c July								—	0.609
	C. c August									—

Isotopic variation in 3 species of co-occuring jellyfish

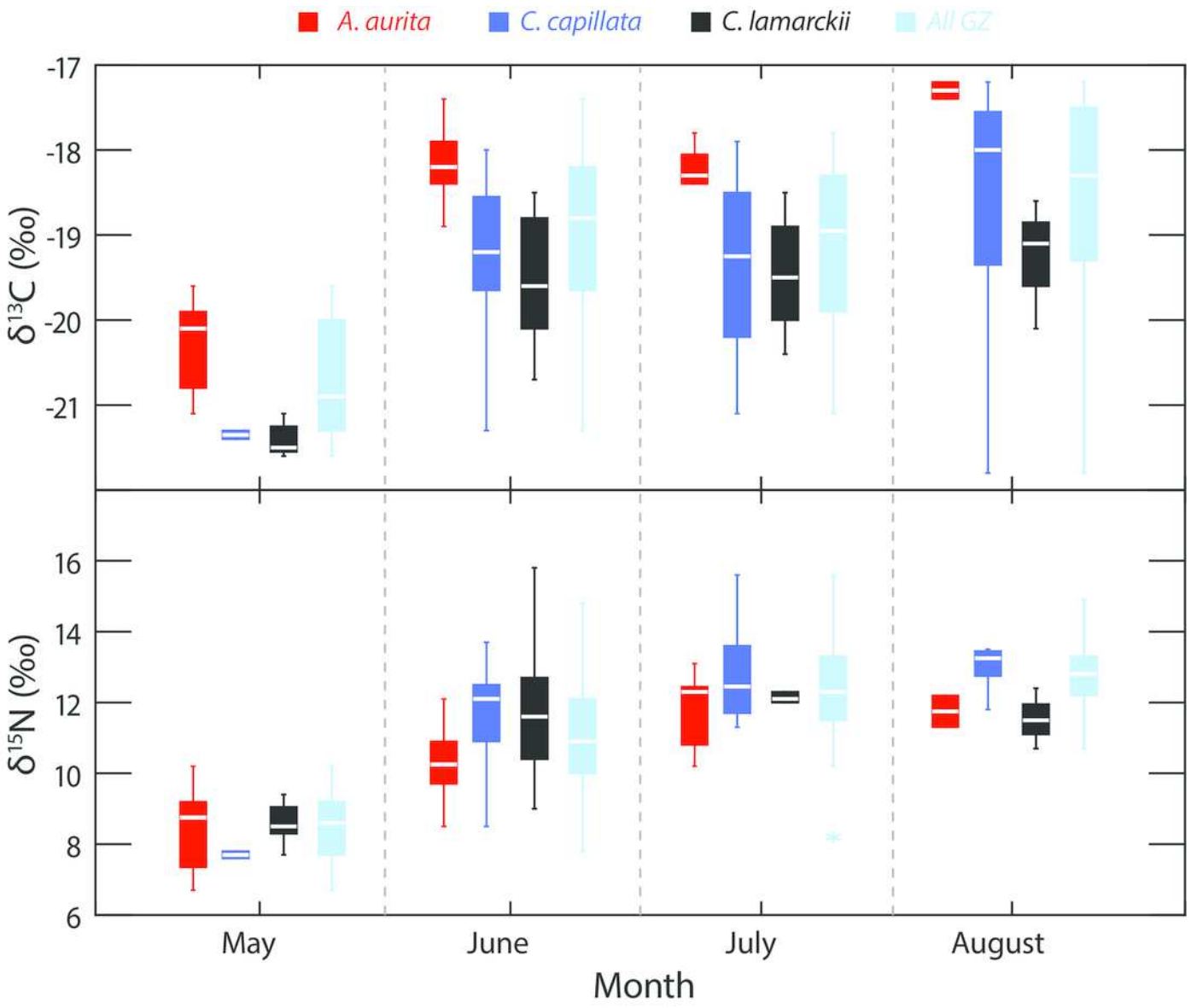
Figure 1: Variation in $\delta^{13}C$ and $\delta^{15}N$ shown in three species of jellyfish over the whole study period. (See Table 1 for summary statistics).



2

Temporal variation in jellyfish $\delta^{13}C$ and $\delta^{15}N$

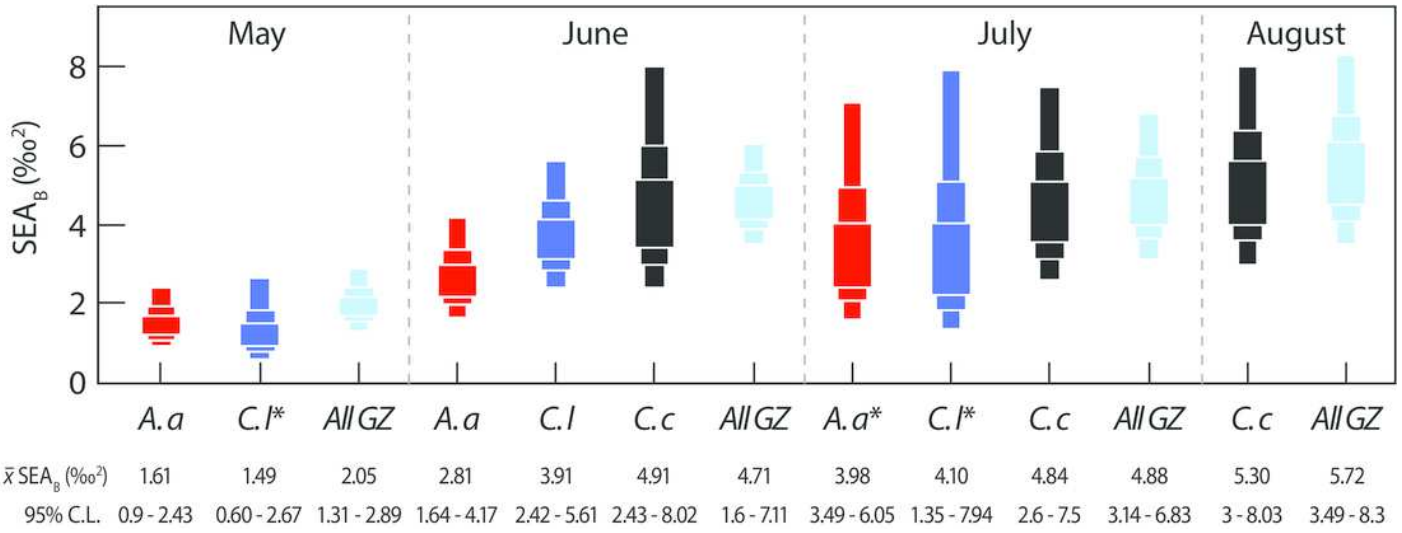
Figure 2: Box-whisker plots showing variation in $\delta^{13}C$ (upper panel) and $\delta^{15}N$ (lower panel) in the three jellyfish species, and within the dominant gelatinous zooplankton community (GZ; all three species combined) over the study period. See Table 1 for sample sizes and other summary statistics. NB: Baseline $\delta^{15}N$ values remained constant over this period, indicating that the increase in $\delta^{15}N$ values reflected a shift in trophic position rather than seasonal shifts at the base of the food web. Boxes show inter-quartile range, and the bold horizontal bar indicates the median value. Whiskers reflect values 1.5 x the interquartile range.



3

Variation in isotopic niche width (SEA_B) between species

Figure 3: Variation in isotopic niche width (SEA_B) between species (*A. a = A. aurita*; *C. l = C. lamarckii*; *C. c = C. capillata*)) and within the dominant gelatinous zooplankton community (GZ; all three species combined) sampled over the survey period. Boxes represent the 50, 75 and 95 % Bayesian credibility intervals estimated from 100,000 draws. Samples marked with *included less than 10 individuals (see Parnell et al. 2010). See Table 3 for statistical comparisons.



4

Figure showing isotopic variation with size

Figure 4: Variation in bell $\delta^{13}C$ (A & B) and $\delta^{15}N$ (C & D) with bell diameter (A & C) and wet mass (B & D). Note use of logarithmic scale on x-axes.