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Reply to Logan & Dodge: ‘Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators’

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Syväranta *et al.* (2012) recently provided stable-isotope data from eight small-bodied ocean sunfish *Mola mola* (L. 1758) captured from the Italian fishing port of Camogli on the Ligurian coast. Representative data were also given for members of pelagic and neritic–coastal food webs. The level of ^{13}C and ^{15}N enrichment shown by *M. mola* relative to their putative obligate diet of gelatinous zooplankton (gelata) (based on the locally dominant *Pelagia noctiluca* and literature data) was used to question their obligate consumption of such prey. Furthermore, the *M. mola* were isotopically more similar to neritic rather than pelagic fishes captured locally, prompting the suggestion that juvenile *M. mola* may not be obligate predators of gelata, but functionally, they might be part of the neritic and coastal food web.

In their comment, Logan & Dodge (2013) have produced a detailed critical analysis of Syväranta *et al.*’s (2012) approach, results and conclusions. They are thanked for furthering a much needed debate regarding *M. mola*. Here, a response is made to their comments with the provision of additional quantitative analysis that strengthen the original conclusions.

Logan & Dodge (2013) provide an excellent summary of isotopic variation in gelata across different marine areas worldwide. Although their summary of data from the north-east Pacific and north-west Atlantic Oceans are of great value to workers interested in gelatinous zooplankton, their relevance to Mediterranean *M. mola* is limited and they are not considered further here. As Logan & Dodge (2013) suggest, however, the *M. mola* sampled by Syväranta *et al.* (2012) may have migrated to the Mediterranean Sea from the north-east Atlantic Ocean prior to capture; therefore, their summaries from the Mediterranean Sea (where the *M. mola* were captured) and

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from the north-east Atlantic Ocean were utilized here. It is felt that this is unlikely (see below), but if, as Logan & Dodge (2013) suggest, *M. mola* are obligate consumers of gelata, then their muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values should be closely associated to that of their putative prey from the north-east Atlantic Ocean.

Logan & Dodge's (2013) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were combined with other available values for gelata in the Mediterranean Sea and the north-east Atlantic Ocean, and a similar dataset was built from the literature for neritic benthic invertebrates from both areas. Briefly, published summary values [mean, s.d. (or s.e.) and n] were taken for gelata and benthic invertebrates from both areas and representative individual data were generated using the random sampling function of Systat 13.1 (SYSTAT Software Inc.; www.systat.com). Data were then pooled to provide an overall estimated mean \pm s.d. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for gelata (Logan & Dodge, 2013; A. Malej, pers. comm.) and benthic invertebrates for the Mediterranean Sea (Jennings *et al.*, 1997; Pinnegar & Polunin, 2000; Revelles *et al.*, 2007; Wangensteen *et al.*, 2011) and similar taxa from the north-east Atlantic Ocean (Das *et al.*, 2003; Goll ty *et al.*, 2010; Schaal *et al.*, 2011). This approach provided sufficient sample sizes to allow the calculation of robust estimates of mean \pm s.d. values for these two broad categories of putative prey representing the wider Mediterranean Sea [Fig. 1(a); n gelata = 67, n benthic invertebrates = 262] and north-east Atlantic Ocean regions (n gelata = 100, n benthic invertebrates = 442). Note that the isotope data for gelata or neritic invertebrates from Syv ranta *et al.* (2012) were not included in these pooled samples.

These results [Fig. 1(a)] show that, as discussed by Logan & Dodge (2013), taxonomically and functionally similar taxa in the Mediterranean Sea and north-east Atlantic Ocean are isotopically distinct: gelata were typically ^{13}C depleted relative to that of benthic invertebrates as expected (France, 1995; Mallela & Harrod, 2008), although the relative difference between the two marine areas varied. In terms of the juvenile *M. mola*, even after extending the gelata dataset, they remained isotopically closest to neritic benthic invertebrates from the Mediterranean Sea, once trophic enrichment is considered.

The probable consumption patterns of the eight juvenile *M. mola* were examined using a four-source Bayesian isotope mixing model (SIAR; Parnell *et al.*, 2010). Mean \pm s.d. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for gelata and neritic benthic invertebrates from the Mediterranean Sea and the north-east Atlantic Ocean were used as putative trophic sources. Mean \pm s.d. trophic enrichment factors for fish muscle tissue ($\Delta^{13}\text{C} = 1.3 \pm 1.3\text{‰}$, $\Delta^{15}\text{N} = 2.9 \pm 1.2\text{‰}$) were taken from McCutchan *et al.* (2003). The model provided mean and 95% credibility estimates of the relative combined assimilation of C and N from gelata and neritic benthic macroinvertebrates from both the Mediterranean Sea (where the fish were captured) and the north-east Atlantic Ocean [where Logan & Dodge (2013) suggested they may have migrated from].

The results [Fig. 1(b)] clearly indicate that juvenile *M. mola* were unlikely to have exclusively consumed gelata, but in support of the previous conclusion (Syv ranta *et al.*, 2012), the model suggested that the *M. mola* had assimilated C and N from both neritic (c. 40%) and gelatinous prey (c. 40%) from the Mediterranean Sea. There was little support for Logan & Dodge's (2013) suggested migration of *M. mola* from the north-east Atlantic Ocean. In the following sections, various other aspects of Logan & Dodge's (2013) criticism of Syv ranta *et al.* (2012) are responded to.

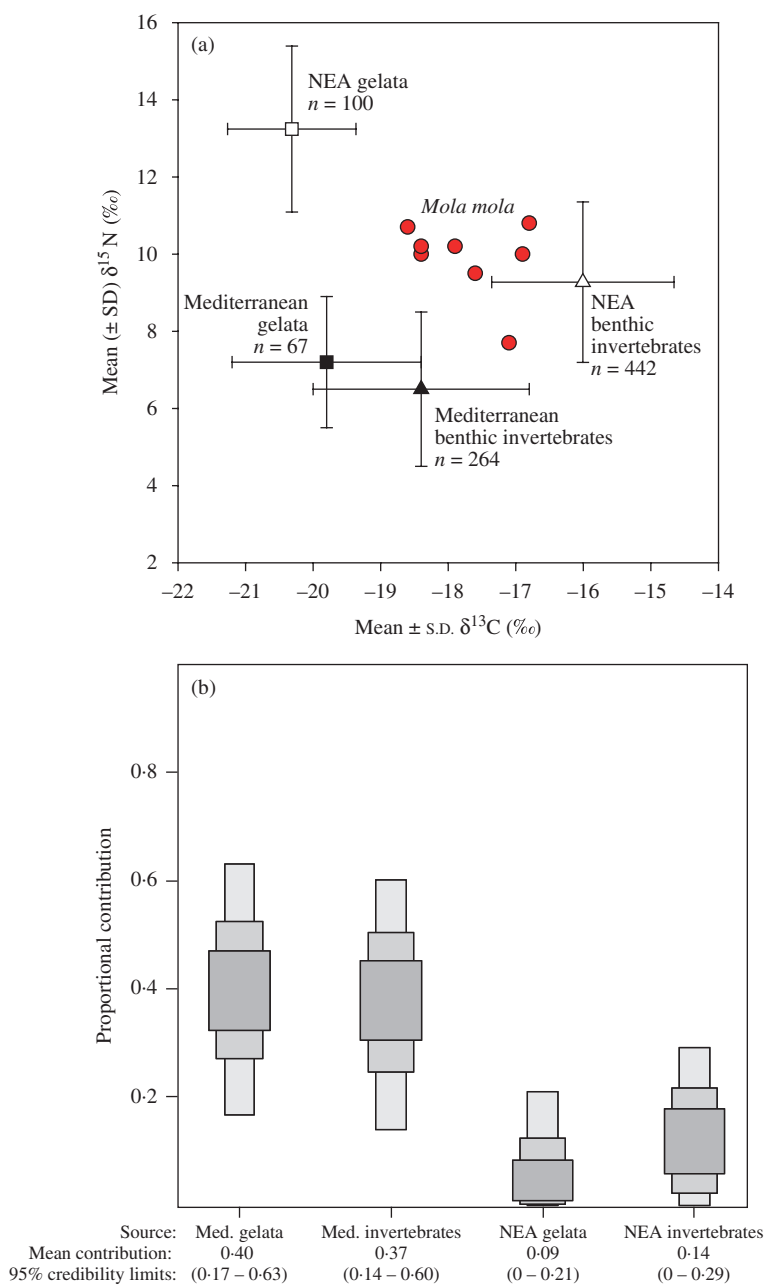


FIG. 1. (a) Isotope biplot showing variation in juvenile *Mola mola* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (●) relative to mean \pm s.d. values estimated for their putative gelatinous zooplankton (gelata) prey and possible neritic benthic invertebrate prey from the Mediterranean Sea (Med.) and the north-east Atlantic Ocean (NEA). (b) Visual representation of the output of the Bayesian mixing model showing 25, 50 and 95% credibility intervals of predicted proportional consumption of each of the four potential sources to the diet of the juvenile *M. mola*. This indicates that the juvenile *M. mola* were resident in the Mediterranean Sea where they consumed a mixture of gelatinous (mean = 40%) and neritic (37%) prey.

Logan & Dodge (2013) suggest that the isotopic differences reported by Syväranta *et al.* (2012) probably reflected the lack of a comprehensive dataset where the absence of high trophic-level species probably accounted for the large differences in $\delta^{15}\text{N}$ between *M. mola* and their putative gelata prey. Representative samples of *P. noctiluca*, however, were collected, which at the time of sampling was the locally dominant jellyfish, during what was the probable period of maximum growth for *M. mola*. As such, it is reasonable to expect an obligate predator of gelata to consume these jellyfish, and their tissues to reflect this isotopically.

The values of Syväranta *et al.* (2012) were also compared with data that were available in the literature, and they were shown to be isotopically similar to the *P. noctiluca* sampled. Logan & Dodge (2013) rightly highlighted, however, the fact that other Mediterranean Sea jellyfish data were available, *e.g.* where $\delta^{15}\text{N}$ were higher than in those values shown in Syväranta *et al.* (2012). Some of these data were not available in the literature (A. Malej, B. Cermelj, S. Lojen & C. Milos, unpubl. data), but have now been included in the analyses.

Even though there are some individual cases of ^{15}N -enriched jellyfish in the Mediterranean Sea, they are not common, and on average, *M. mola* remain enriched in ^{15}N relative to the mean $\delta^{15}\text{N}$ value for gelatinous zooplankton in the region. The large differences in $\delta^{13}\text{C}$ between *M. mola* and that of gelata in either the Mediterranean Sea or the north-east Atlantic Ocean remain an issue that has to be considered by those who suggest that the species consumes only gelatinous zooplankton. Assuming that the estimates of trophic fractionation are correct for *M. mola*, there is still a large difference in $\delta^{13}\text{C}$ values between predator and their presumed obligate prey. The use of mixing models [Fig. 1(b)] indicates that at least in the case of the juvenile *M. mola* examined here, they feed on a similar proportion of pelagic and neritic prey.

Logan & Dodge (2013) note that isotopic overlap does not strictly reflect dietary overlap. This is an important point, and there are manifold ways by which a consumer's tissues can attain a certain stable-isotope value. Isotopic overlap is, however, used throughout the isotope ecology literature as an indication of possible similarities in trophic ecology or habitat use. One of the strengths of stable-isotope analysis is its capacity to reveal otherwise hidden features of consumer trophic ecology or habitat use (Harrod *et al.*, 2005, 2010). For example, unusual levels of isotopic overlap or even the lack of overlap where it is expected can drive further, more focused investigations. This should be undertaken with regard to *M. mola*.

Logan & Dodge (2013) suggested that the unusual isotopic values of juvenile *M. mola* in Syväranta *et al.* (2012) might be indicative of migration from outside of the study area and that individuals were yet to reach isotopic equilibrium with their gelatinous zooplankton prey in the study area. More specifically, the authors implied that individuals may have migrated from the north-east Atlantic Ocean, where $\delta^{15}\text{N}$ baselines are notably ^{15}N enriched relative to those from the Mediterranean Sea [Fig. 1(a)]. This behaviour seems unlikely for several reasons. Firstly, Logan & Dodge (2013) point to Sims *et al.* (2009) as evidence that *M. mola* could potentially move between the north-east Atlantic Ocean and Mediterranean Sea. The potential for such long-distance movement is undeniable, yet the authors overlook an important point with respect to timing. Sims *et al.* (2009) tracked a single sunfish from Irish waters in August 2007, with two others tracked from Portugal in February of the same year. All three animals followed a seasonal pattern of increasing latitude from late winter to summer and decreasing latitude from late summer into autumn.

In other words, *M. mola* in the north-east Atlantic Ocean may adhere to the classic north–south migratory paradigm displayed by leatherback sea turtles *Dermochelys coriacea*, and many fishes that seasonally forage in warm temperate waters during summer (Leggett, 1977). The juvenile *M. mola* sampled by Syväranta *et al.* (2012) were also encountered during summer months, but in the Mediterranean Sea, indicating that a north–south seasonal migration similar to Sims *et al.* (2009) had not occurred during that year. Logan & Dodge (2013) argue that such migrations in *M. mola* are common, but there are only a few tracking studies conducted to date, which prevents a meaningful extrapolation into the Mediterranean Sea. Indeed, migration is a plastic behaviour in many species with animals moving between sites only if there is a distinct benefit in doing so (Bauer *et al.*, 2009). For example, Sims *et al.* (2009) argue that *M. mola* leave temperate latitudes in the autumn for one of two reasons: decreasing water temperature or seasonal reductions in prey, or a combination of both. In this context, it is logical to ask why individuals would migrate away from the warm, jellyfish-rich waters of the Mediterranean Sea (Goy *et al.*, 1989; CIESM, 2001) in the months leading up to, or during, summer. Secondly, the suggestion of a north-east Atlantic Ocean–Mediterranean Sea seasonal migration (or one way ontogenic emigration) is logical but is not supported by either the raw isotope data [Fig. 1(a)] or the Bayesian mixing model outputs. *Mola mola* are located in isotopic space different from that expected if they were consuming north-east Atlantic Ocean jellyfish, and the mixing model indicates that they are members of the Mediterranean Sea food web.

Logan & Dodge (2013) rightly note that only bell tissues from *P. noctiluca* were sampled. They then suggest that Syväranta *et al.* (2012) may have therefore biased the estimates of jellyfish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and in turn those of *M. mola* consumption. This is possible, but work elsewhere has shown that although statistical differences can be apparent between the different components of the jellyfish (*e.g.* oral arms, gonads and bell), they are not typically of a level to account for the differences shown between the *M. mola* and their putative gelatinous zooplankton prey [Syväranta *et al.* (2012); Fig. 1(a)]. Furthermore, many isotope ecologists working with gelatinous zooplankton use bell tissues (Pitt *et al.*, 2009), and it is probable that many of the estimates included by Logan & Dodge (2013) in their tables were from bell tissues.

As a final comment, many of the points made by Logan & Dodge (2013) are important. The brevity required by the Brief Communication format of the original paper, however, may have led to some misunderstanding. For clarity, the notion that *M. mola* eat jellyfish was not challenged, nor was extrapolation of the findings to adults or populations in other regions sought. Simply, their classification as ‘obligate predators of jellyfish’ was challenged as this phrase implies that they are ‘restricted, constrained or compelled’ to feed on such prey (Oxford English Dictionary Online; www.oed.com). In Syväranta *et al.* (2012), this line of argument was supported with empirical evidence from the literature (*i.e.* gut content analysis) that suggested predation on non-gelatinous species was not an aberration. Viewed independently of the isotopic data, these much overlooked findings are grounds alone for challenging the idea of exclusive jellyfish predation (Pope *et al.*, 2010). Yet, the opening paragraphs to many studies still present *M. mola* and leatherback sea turtles *D. coriacea* as a couplet of obligate predators inferring a comprehensive understanding of the former’s trophic ecology (Pope *et al.*, 2010). Put simply, this understanding is currently unavailable, a point raised both by Syväranta *et al.* (2012) and Logan & Dodge

(2013), highlighting some important common ground. In this context, the extremely useful summary of isotopic data for gelata supplied by Logan and Dodge (2013) has enabled a relatively robust examination of the probable consumption patterns of a small sample of juvenile *M. mola* to be made. By comparing the isotopic data for the eight individuals previously detailed in Syväranta *et al.* (2012), it was possible to show that: (1) they probably consumed a combination of pelagic and neritic prey and (2) it was extremely unlikely that they had been feeding in the north-east Atlantic Ocean. Taken together, these findings support the original conclusion (Syväranta *et al.* 2012) that predation upon gelatinous species by *M. mola* is not the entire story.

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