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Ontogenetic and seasonal shifts in diets of sharptail mola *Masturus lanceolatus* in waters off Taiwan

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ABSTRACT: Sharptail mola *Masturus lanceolatus* share a circumglobal distribution with ocean sunfish *Mola mola* and are typically regarded as gelatinous plankton feeders. Both species are frequently captured as bycatch in the same areas, but sharptail mola are often targeted and heavily harvested in certain regions. However, the diet of sharptail mola remains poorly described. We examined the foraging habits and trophic dynamics of sharptail mola from waters off eastern Taiwan using stomach content analysis (SCA; n = 162), bulk tissue stable isotope analysis (SIA; n = 213), and compound-specific isotope analysis of amino acids (CSIA-AA; n = 10). Results demonstrated that sharptail mola mainly consumed tunicates, with lower dietary proportions of diverse prey from epi- and mesopelagic, coastal, and benthic habitats. The diet of sharptail mola changed significantly with size; small mola (<80 cm) had lower $\delta^{15}N$ and $\delta^{13}C$ values and fed on more pteropods and Salpidae, while large mola (>80 cm) fed on more *Pyrosoma* spp., cephalopods, and benthic organisms living on sandy substrates, with larger individuals having correspondingly higher isotope values and trophic positions. Diet compositions and $\delta^{13}C$ values also showed seasonal variations across body size, suggesting that sharptail mola might undergo seasonal migrations with changing availability of food resources. The results provide insights into the trophic dynamics of sharptail mola and suggest that their foraging behavior varies across life-history stages and seasons.

KEY WORDS: Pelagic food web · Feeding ecology · Gelatinous prey · Resource partitioning · Niche overlap

1. INTRODUCTION

Members of the family Molidae (genera *Mola*, *Masturus*, and *Ranzania*) are distributed worldwide from tropical to temperate regions. The family includes the world's heaviest bony fish, the bumphead sunfish *Mola alexandrini*, which weighs up to 2.7 t (Gomes-Pereira et al. 2023). The Molidae play an important ecological role as predators in the gelatinous food web (Grémillet et al. 2017), and most *Mola* species were regarded as obligate gelativores that typically feed on scyphozoan jellyfish (Fraser-Brunner 1951, Hooper et al. 1973). However, recent studies using stomach content analysis (SCA) and bulk tissue stable isotope analysis (SIA) have revealed a wider range of prey items consumed by ocean sunfish *Mola mola*, including pelagic and neritic prey such as crab megalops and amphipods (Syväranta et

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al. 2012, Harrod et al. 2013, Nakamura & Sato 2014). Using DNA metabarcoding, SIA, and compound-specific isotope analysis of amino acids (CSIA-AA), researchers found evidence of an ontogenetic shift in the diets of ocean sunfish. Small-sized individuals were found to have a mixed diet of both benthic and pelagic prey, while larger individuals occupied a higher trophic position and fed primarily on pelagic-derived prey (Sousa et al. 2016, Phillips et al. 2020). These observations might reflect ontogenetic dietary changes or could be related to seasonal migration patterns (Dewar et al. 2010, Chang et al. 2021) and variability in foraging behaviors across region and/or life stage. For instance, small ocean sunfish off Japan stayed near the shallow seabed, whereas larger individuals moved back and forth between surface and deeper waters (Nakamura & Sato 2014).

Sharptail mola *Masturus lanceolatus* share a circumglobal distribution with ocean sunfish (Caldera et al. 2020). They have similar physical features as well as behavioral and movement patterns, including migration patterns and depth distributions (Seitz et al. 2002, Dewar et al. 2010, Chang et al. 2020). Sharptail mola are captured as bycatch globally (Nyegaard et al. 2018, Arostegui et al. 2020) and are targeted for human consumption regionally (e.g. Taiwan, average annual catch: 436 t in 2006–2019; Fisheries Agency 2020). While the International Union for Conservation of Nature (IUCN) assessed the conservation status of the sharptail mola as 'Least Concern' in 2015, this was largely based upon lack of available data (Leis et al. 2015). Broadly, limited data are available on sharptail mola, and their diets are poorly described. Bakenhaster & Knight-Gray (2016) noted that remains of fishes and some invertebrates were found in the stomach contents of 2 sharptail mola from waters off Florida (USA). In addition, sand and leaves were discovered in the stomach of 1 stranded sharptail mola in Japan (Sawai et al. 2019), although this likely reflects ingestion of these items during stranding. Overall, it is difficult to characterize sharptail mola diet due to lack of data and the highly digested nature of their gut contents. As such, more robust diet studies are required to understand the trophic ecology of this species and how it partitions the environment with the closely related ocean sunfish.

Coupling SCA and SIA provides insight into the feeding habits of sharptail mola across ontogeny and habitats. SCA provides a detailed snapshot of dietary information that reflects recent foraging (i.e. hours to days/weeks; Cortés 1997), whereas SIA can provide information on the sources of primary production that support their diet and their trophic relationships integrated over longer time scales. Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$; $\delta^{13}C$ and $\delta^{15}N$) in predator tissues reflect their diets over the previous weeks, months, or >1 yr, depending on the tissue examined and its isotopic incorporation rate (Madigan et al. 2021). In particular, $\delta^{15}N$ values increase significantly (2~4‰) with each trophic level (Vander Zanden & Rasmussen 2001, Post 2002), and as a result are frequently used to examine trophic dynamics and trophic position of animals. However, it can be challenging to distinguish the relative importance of variation in baseline $\delta^{15}N$ values of the food web from increases in $\delta^{15}N$ associated with feeding at higher trophic levels. CSIA-AA is a more recently developed tool that overcomes these limitations of bulk SIA. The $\delta^{15}N$ values in 'source' amino acids (e.g. lysine, phenylalanine, serine, tyrosine, and sometimes glycine) change little with increasing trophic level and reflect the baseline of food webs, whereas other amino acids, in particular the 'trophic' amino acids (e.g. alanine, glutamic acid, leucine, proline, valine), which exhibit high isotope fractionation, reflect an organism's trophic level (McClelland & Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Therefore, $\delta^{15}N$ values of amino acids retain information about isotopic baselines and trophic isotope fractionation. Differences in $\delta^{15}N$ values of source and trophic amino acids can thus be used to determine both the $\delta^{15}N$ values at the base of the food web and trophic positions of animals (McClelland & Montoya 2002, Bradley et al. 2015).

In this study, we used SCA, bulk SIA, and CSIA-AA to reveal the trophic ecology of sharptail mola. We aimed to explore (1) whether sharptail mola feed mainly on Scyphozoa, other gelatinous taxa, or on more diverse prey, and (2) potential ontogenetic or seasonal shifts in sharptail mola diet. The results will provide new insights into the trophic ecology of sharptail mola in oceanic food webs.

2. MATERIALS AND METHODS

2.1. Sample collection

We collected tissue and stomach samples from sharptail mola at fish markets in eastern Taiwan from 2017 to 2021. All sharptail mola were caught off eastern Taiwan by set-net and longline fisheries (Fig. 1), preserved on ice, and brought back to local fish markets for sale on the same day. Total length (TL, from the tip of the snout to the end of the caudal fin) and standard length (SL, from the tip of the snout to the

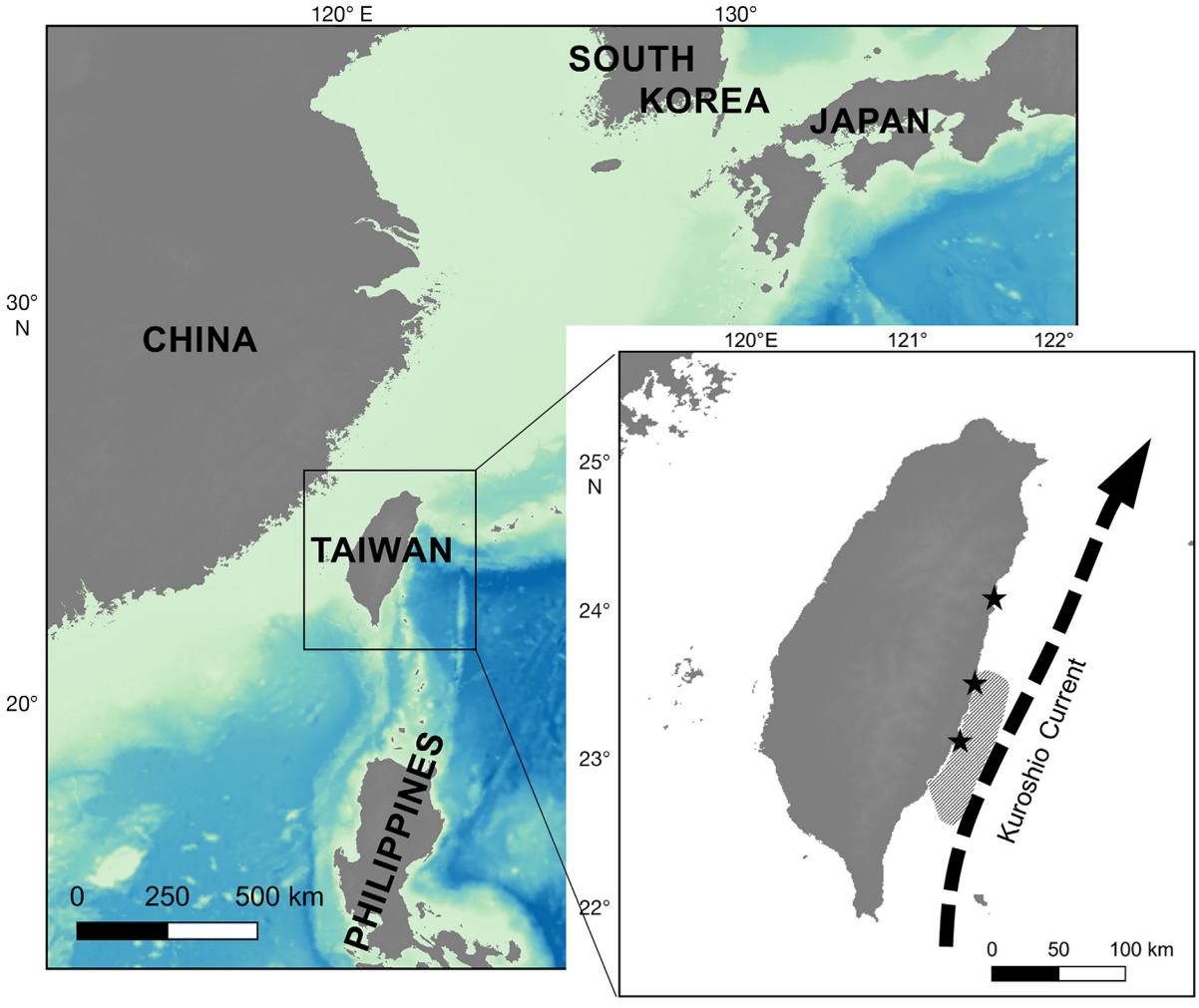

Fig. 1. Sharptail mola fishing grounds for set-net (stars) and longline (hatched area) fishing operations in eastern Taiwan

line in front of the caudal fin) were measured. We used SL in analyses here, as in some cases, caudal fins had been removed and discarded before landing. Stomach contents (n = 162) and white muscle samples (n = 213, collected from the abdomen) were collected, and muscle samples were frozen at −80°C. Stomach contents were processed immediately due to the rapid digestion of gelatinous prey (Arai et al. 2003).

Prey items for SIA were collected to match, as closely as possible, prey found in stomach contents of sharptail mola. Scyphozoa (*Atolla* spp.) (n = 8) were collected with hand-nets from a boat during the summer in the waters off eastern Taiwan in 2019, and the whole body was processed immediately. Cephalopods (n = 4) were collected from fish markets in eastern Taiwan from the same fishing regions as those for sharptail mola. Mantle tissues of cephalopods were taken and frozen at −80°C until processing. Undigested tunicates (*Pyrosoma* spp. and Salpidae, n = 16), amphipods *Phronima* spp. (n = 7), and pteropods (n = 10) were collected directly from stomach contents of sharptail mola and preserved at −80°C for processing.

2.2. Stomach content analysis

In the laboratory, prey items were identified to the lowest possible taxon, and their abundance and weight were measured. Cephalopods were identified from beaks. After measurement, the prey items were preserved in 95% ethanol. All prey items were categorized into 9 functional groups based on their habitat and taxon (Table S1 in the Supplement at www.int-res.com/articles/suppl/m715p113_supp.pdf). Unidentified items, sand, and plastics were not included in these functional groups and the analyses, and a

stomach without any prey was counted as an empty stomach.

2.3. Bulk tissue stable isotope analysis

Sharptail mola muscle tissue and prey items were rinsed with distilled water and dried for 48 h at 60°C and then ground into a homogeneous powder. Approximately 0.4–0.8 mg (depending on the species) of powder were packed into ultra-clean tin capsules. Pteropods and *Phronima* spp. were weighed into silver cups and acidified with 10% HCl for removing the carbonate, after which the samples were dried for 24 h at 60°C. $\delta^{13}C$ and $\delta^{15}N$ values were determined using an elemental analyzer (Costech ECS 4010 Elemental Combustion System using a Zero Blank Autosampler) and mass spectrometer (Thermo-Delta V Advantage). The bulk isotope values were expressed in standard ‰ notation relative to Vienna Pee Dee belemnite (V-PDB) for carbon and atmospheric N_2 for nitrogen. The analytical error derived from multiple analyses of reference materials for both $\delta^{13}C$ and $\delta^{15}N$ was <0.2‰. Because lipids have lower $\delta^{13}C$ values relative to other animal tissues, and the variability in tissue lipid content can affect $\delta^{13}C$ values (Focken & Becker 1998), the $\delta^{13}C$ values of sharptail mola muscle (C:N > 3.5) and invertebrate prey items (C:N > 3.8) were normalized using lipid normalization algorithms for muscle from Atlantic bluefin tuna *Thunnus thynnus* (Logan et al. 2008) and from zooplankton (Syväranta & Rautio 2010), respectively.

2.4. Nitrogen isotope analysis of individual amino acids

Ten sharptail mola across size classes were selected for CSIA-AA. The preparation for CSIA-AA followed the methods of Hannides et al. (2009). Approximately 10–15 mg of homogenized white muscle tissue were hydrolyzed, then esterification and trifluoroacetylation were undertaken. The $\delta^{15}N$ values of individual amino acids were analyzed using a Delta V Plus mass spectrometer interfaced to a Trace GC gas chromatograph. All samples were analyzed in triplicate, and measured $\delta^{15}N$ values were corrected relative to the known $\delta^{15}N$ values of a norleucine internal reference. Standard deviation for triplicate injections of each sample averaged 0.55‰ (±0.3‰) and ranged from 0.03 to 1.95‰. Three trophic amino acids (alanine, leucine, glutamic acid) and 3 source amino acids (glycine, phenylalanine, lysine) were selected to calculate a weighted average for trophic position (TP) estimation based on Bradley et al. (2015).

2.5. Data analysis

To classify sharptail mola into ecologically relevant size groupings, we used LOESS smoothing and a piecewise linear regression model in R version 4.0.4 ('fANCOVA' and 'segmented' packages) (Cleveland et al. 1992, Muggeo 2008) to find breakpoints in the relationship between isotopic data and body size of sharptail mola. The discontinuous values in $\delta^{13}C$ and $\delta^{15}N$ implied a change in diet of sharptail mola across size, with breakpoints found at approximately 80 and 120 cm for both $\delta^{13}C$ and $\delta^{15}N$ values (Fig. S1). Thus, sharptail mola were categorized into 3 size classes: Class I (<80 cm SL), Class II (80–120 cm SL), and Class III (>120 cm SL). Subsequent diet compositions and isotopic values of sharptail mola were analyzed by these 3 size classes. The analysis did not include the interannual variation in diets of sharptail with the assumption of similar prey availability across years.

For SCA, 5 diet indices were calculated: frequency of occurrence (%FO) as the proportion of predator stomachs containing a prey item; gravimetric importance (%W) as the proportion of the weight of a prey item in the total weight of stomach contents; numerical abundance (%N) as the proportion of the number of a prey item in the total number of all prey; the index of relative importance (IRI) as an index of the combination of these 3 metrics (Pianka 1973); and %IRI as the proportion of IRI of a prey item in the sum of all IRI values. The indices for prey composition and proportion for functional prey groups among each size class and seasons of sharptail mola were calculated. Diets (%N and %W) among size classes and seasons were compared using a percent similarity index (PSI, Hurlbert 1978). Cumulative prey curves were used to determine whether there was a sufficient number of stomach samples across size and seasons to describe the diet of sharptail mola. The diet compositions (%N and %W) of sharptail mola across all size classes and seasons were compared using a 2-way nested analysis of similarities (ANOSIM, 9999 permutations) with pairwise tests, all based upon a Bray-Curtis similarity matrix. This analysis was done using PRIMER software (version 6, Plymouth Marine Laboratory; Clarke 1993).

For bulk SIA, nonlinear regression was used to test the relationships between $\delta^{13}C$ and $\delta^{15}N$ values and

SL for sharptail mola. Differences in $\delta^{13}C$ and $\delta^{15}N$ values between body size and seasons were tested using ANOVA (mixed design; Underwood 1997), with size class and season as fixed effects, and Tukey's post hoc test in R version 4.0.4. The differences in $\delta^{13}C$ and $\delta^{15}N$ values among prey categories and sharptail mola were tested using 1-way ANOVA with Tukey's post hoc tests in R version 4.0.4.

TP_{bulk} using bulk $\delta^{15}N$ values was estimated using the equation:

$$TP_{bulk} = TP_{base} + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{TDF} \quad (1)$$

where $\delta^{15}N_{consumer}$ represents the $\delta^{15}N$ value of sharptail mola and $\delta^{15}N_{baseline}$ represents the baseline species $\delta^{15}N$ values. Here, we used $\delta^{15}N$ values (5.1‰) of zooplankton from the waters off Taiwan as $\delta^{15}N_{baseline}$ and a trophic level of 2 (TP = 2) for TP_{base} (Weng et al. 2015). The trophic discrimination factor (TDF) for ocean sunfish muscle (3‰) was used (Phillips et al. 2020). Differences in TP across size classes were tested using 1-way ANOVA in R version 4.0.4.

Due to the high variability in bulk $\delta^{15}N$ values of zooplankton as the base of food webs, CSIA-AA was used to estimate a more accurate TP for sharptail mola. TP_{AA} using $\delta^{15}N$ values of amino acids was estimated using the equation:

$$TP_{AA} = 1 + \frac{\delta^{15}N_{Trp} - \delta^{15}N_{Src} - \beta}{TDF_{AA}} \quad (2)$$

where $\delta^{15}N_{Trp}$ and $\delta^{15}N_{Src}$ are the weighted averages of selected trophic and source amino acids. β (3.6‰; Bradley et al. 2015) represents the difference between the $\delta^{15}N$ values of trophic and source amino acids in primary producers. TDF_{AA} (5.7‰; Bradley et al. 2015) represents the TDF for the $\delta^{15}N$ values of trophic (alanine, leucine, glutamic acid) and source (glycine, phenylalanine, lysine) amino acids for each trophic level.

The Bayesian mixing model in the 'MixSIAR' package (Stock & Semmens 2013) was applied in R version 3.6.0 to estimate relative contributions of prey taxa to each sharptail mola size class. The most common prey items found in the stomach contents of sharptail mola were used, including *Phronima* spp. (n = 7), tunicates (*Pyrosoma* spp. and Salpidae, n = 16), and pteropods (n = 10). Scyphozoa (*Atolla* spp.; n = 8) were selected because Scyphozoa are regarded as the major food source for other molids. *Pyrosoma* spp. and Salpidae had similar isotopic values and ecological niche. They were weighted equally in calculated tunicate values. Cephalopods (n = 4) were used because the proportion of cephalopods in the gut contents of sharptail mola increased with size, reflecting increased contribution to the diets of large sharptail mola. Gravimetric importance (%W) represents the total mass or energy transferred from prey to sharptail mola. We constructed the informative priors based on the diet compositions (by %W) of sharptail mola in this study. The informative priors were scaled to have a total weight equal to the number of sources (Stock et al. 2018). We used bulk tissue TDF values for ocean sunfish, where $\Delta^{13}C = 2 \pm 1.3$‰ and $\Delta^{15}N = 3 \pm 1.2$‰ (Phillips et al. 2020). For model inputs, Markov chain Monte Carlo was set to normal length. Both Gelman-Rubin (Gelman et al. 2013) and Geweke diagnostics (Geweke 1991) were used to test for model convergence.

Stable Isotope Bayesian Ellipses in R version 4.0.4 (SIBER; Jackson et al. 2011) was used to calculate the isotopic niche width among 3 size classes. Specifically, we estimated trophic niche metrics including a convex hull (Layman et al. 2007), a corrected standard ellipse area (SEA_c), and a Bayesian standard ellipse area (SEA_b) (Jackson et al. 2011, 2012).

3. RESULTS

3.1. Diet composition across size classes

A total of 162 stomachs of sharptail mola were collected, of which 57 were empty (35%). A wide variety of prey taxa were identified in stomachs, including gelatinous organisms, mollusks, crustaceans, and fishes (Table 1). One of the stomach samples was excluded from analysis because it contained a relatively large abundance of flying fish eggs compared to other stomachs, which led to a disproportionate influence of this single fish on overall diet estimates. Tunicates (both salps and pyrosomes), *Phronima* spp. amphipods, and pteropods were the most frequently consumed prey. Pteropods (35%N) and tunicates (29%N) were the most numerically abundant. Based on weight, all predators fed predominantly on epi- and mesopelagic tunicates (Pyrosomatidae: 48%W; Salpidae: 33%W) that made up a total of 80% in weight and 75% in %IRI of the prey.

Cumulative prey curves indicated that sample size for sharptail mola <80 cm and 80–120 cm reached an asymptotic relationship (Fig. S2A). Thus, the sample sizes were sufficient to describe the diets of sharptail mola <120 cm. The stomach samples of sharptail mola >120 cm were probably not adequate to fully describe the diets. Sharptail mola diet compositions by %N (ANOSIM: R = 0.78, p = 0.001) and %W (R =

Table 1. Prey items of collected sharptail mola with stomach content. Five diet indices were calculated: %FO: frequency of occurrence; %N: numerical abundance; %W: gravimetric importance; IRI: index of relative importance; %IRI: proportion IRI of a prey item relative to the sum of all IRI values

Prey item	%FO	%N	%W	IRI	%IRI
SCYPHOZOA					
Atollidae — *Atolla* spp.	10.48	1.03	3.10	43.35	0.52
MOLLUSCS					
Cephalopoda					
Ommastrephidae (beak)	7.62	0.38	0.51	6.77	0.08
Gonatidae (beak)	0.95	0.05	0.00	0.05	0.00
Pen of unidentified cephalopod	1.90	0.09	0.00	0.18	0.00
Eye lens of unidentified cephalopod	12.38	1.60	0.12	21.23	0.26
Hook of unidentified cephalopod	0.95	1.46	0.09	1.47	0.02
Pteropoda					
Cavoliniidae — *Diacavolinia longirostris*	36.19	13.91	1.02	540.45	6.54
Cavoliniidae — *Cavolinia* spp.	10.48	2.30	0.16	25.78	0.31
Cavoliniidae — *Diacria costata*	6.67	0.42	0.01	2.87	0.03
Creseidae — *Creseis conica*	27.62	11.00	0.82	326.22	3.95
Cliidae — *Clio pyramidata*	2.86	0.14	0.00	0.41	0.00
Carinariidae — *Carinaria* spp.	23.81	5.50	0.61	145.46	1.76
Atlantidae	17.14	1.60	0.08	28.76	0.35
Gastropoda					
Benthic gastropod (unidentified)	3.81	0.23	0.02	0.96	0.01
Heteropoda					
Heteropod radula	12.38	4.28	0.18	55.18	0.67
TUNICATES					
Salpidae	60.95	15.55	32.81	2948.11	35.67
Pyrosomatidae — *Pyrosoma* spp.	52.38	13.67	48.02	3231.48	39.09
Pyrosomatidae — *Pyrosomella* spp.	0.95	0.05	0.03	0.07	0.00
CRUSTACEANS					
Amphipoda					
Phronimidae — *Phronima* spp.	47.62	11.56	3.56	719.82	8.71
Hyperiidae — *Hyperia* spp.	4.76	0.23	0.00	1.12	0.01
Euphausiacea					
Euphausiidae — *e*uphausiids	1.90	0.38	0.02	0.76	0.01
Decapoda					
Gnathophausia sp.	0.95	0.05	0.16	0.20	0.00
Shrimp (unidentified)	14.29	1.79	0.26	29.25	0.35
Crab megalopa (unidentified)	0.95	0.09	0.01	0.10	0.00
Scyllaridae phyllosoma	10.48	1.46	0.49	20.39	0.25
Crab zoea (unidentified)	3.81	0.23	0.01	0.95	0.01
FISH					
Scombridae	0.95	0.05	1.19	1.18	0.01
Lutjanidae	0.95	0.05	0.68	0.69	0.01
Lutjanidae (teeth)	1.90	0.09	0.01	0.19	0.00
Exocoetidae (egg)	12.38	4.79	0.39	64.23	0.78
Fish (unidentified)	1.90	0.09	0.73	1.58	0.02
Otolith of unidentified fish	1.90	0.19	0.00	0.36	0.00
Bone of unidentified fish	4.76	1.08	0.03	5.28	0.06
OTHER					
Sand	1.90	–	4.49	8.55	0.10
Plastics	6.67	3.95	0.05	26.68	0.32
Unidentified organisms	5.71	0.66	0.32	5.61	0.07
TOTAL	105	2128	821 g		

0.09, p = 0.017) showed significant differences among size classes (Table 2a). The diets were more similar across all size classes by %N (higher PSI values) than %W (Table 2a). Sharptail mola <80 cm fed mainly on prey from offshore, epi- and mesopelagic habitats, and sharptail mola >80 cm fed on prey from coastal, benthic, and epi- and mesopelagic habitats (Fig. 2). Tunicates were the most important prey in diets of sharptail mola across size groups. Within this prey category (epi-/mesopelagic tunicates), small sharptail mola (<80 cm) fed mainly on Salpidae (57 %W) compared to larger individuals (80–120 cm: 40 %W; >120 cm: 5 %W), which primarily fed on Pyrosoma (80–120 cm: 38 %W; >120 cm: 79 %W) (Table S2). The weight proportions of pteropods and amphipods Phronima spp. (epi/mesopelagic crustaceans) in diets decreased with increasing sharptail mola size. The occurrences and abundances of crustacean juveniles were mainly composed of crab zoea in the guts of sharptail mola >120 cm and were mainly composed of phyllosoma in the guts of mola <80 cm. Sharptail mola 80–120 cm fed more on fish (Scombridae and Lutjanidae) than those <80 cm and >120 cm. In addition, sharptail mola >80 cm individuals foraged more on cephalopods than those <80 cm, although they were still only a minor component of the diet. A large amount of sand was found in stomachs of sharptail mola >120 cm (20 % FO, Table S2).

3.2. Seasonal trend in diet composition across size classes

Cumulative prey curves indicated that sample size for sharptail mola in autumn, summer, and spring were sufficient to describe their diet (Fig. S2B). Overall, the diets of all sharptail mola showed seasonal variations by %N (R = 0.17, p = 0.002) and %W (R = 0.18, p = 0.001) (Table 2b). Summer diets were similar to autumn diets with high PSI values (%W: 72.5; %N: 63.3), and sharptail mola consumed more crustacean juveniles and cephalopods than during other seasons (Fig. S3). Most of the flying fish eggs were consumed in sum-

Table 2. Percent similarity index (PSI) values among size classes of sharptail mola and seasons; measured in terms of prey numbers (%N, below diagonal dashes) and weights (%W, above diagonal dashes). Comparisons do not include unidentified organisms, plastics, and sand. *significant differences in ANOSIM results ($p < 0.05$) between groups in terms of %N and %W

(a) Size class (ANOSIM: $p < 0.05$)

	<80 cm	80–120 cm	>120 cm
<80 cm	–	76.6*	33.4*
80–120 cm	58.9*	–	44.3*
>120 cm	59.8*	51.2*	–

(b) Season (ANOSIM: $p < 0.05$)

	Spring	Summer	Autumn	Winter
Spring	–	37.9	55.9*	26.9
Summer	64.7	–	72.5	57.3
Autumn	50.5*	63.3	–	60.0*
Winter	38.8	48.3	50.3	–

(c) <80 cm (ANOSIM: $p < 0.05$)

	Spring	Summer	Autumn	Winter
Spring	–	66.4	61.7*	37.4
Summer	22.4	–	81.5*	36.8
Autumn	43*	29*	–	40.5*
Winter	23.7	21.5*	30.1*	–

(d) 80–120 cm (ANOSIM: $p < 0.05$)

	Spring	Summer	Autumn	Winter
Spring	–	44.7	38.9	63.6
Summer	26.9	–	78.5	63.2
Autumn	44.6*	56	–	57.3
Winter	40	45.9	57.7	–

(e) >120 cm (ANOSIM: $p > 0.05$)

	Spring	Summer	Autumn	Winter
Spring	–	12.4	5.7	–
Summer	12.9	–	76.1	–
Autumn	3	56.9	–	–
Winter	–	–	–	–

mer and autumn, including the one stomach sample with a large abundance of eggs. Autumn diets differed from spring diets in terms of %W (ANOSIM pairwise-test: $R = 0.235$, $p = 0.007$) and %N ($R = 0.328$, $p = 0.002$), and sand was found in the stomachs of sharptail mola in summer and autumn.

Seasonal variation in sharptail mola diets was examined by size group. The diet composition of sharptail mola <120 cm displayed seasonal variation (%N, 80 cm: $R = 0.32$, $p = 0.005$, 120 cm: $R = 0.16$, $p = 0.013$; %W, 80 cm: $R = 0.2$, $p = 0.01$, 120 cm: $R = 0.15$, $p = 0.039$) whereas that of mola >120 cm did not (%N, $R = 0.17$, $p = 0.227$; %W, $R = 0.1$, $p = 0.281$) (Table 2c–e). In sharptail mola <80 cm, most diets were distinct among seasons (%N, $R = 0.316$, $p < 0.001$; %W, $R = 0.198$, $p = 0.01$) (Table 2c). The proportion of pteropods was lower in summer diets than in other seasons in terms of %N (Fig. 3). Few crustacean juveniles (predominately phyllosoma) were found in summer and autumn diets, and a high mass of *Phronima* spp. was found in winter diets. In diets of sharptail mola

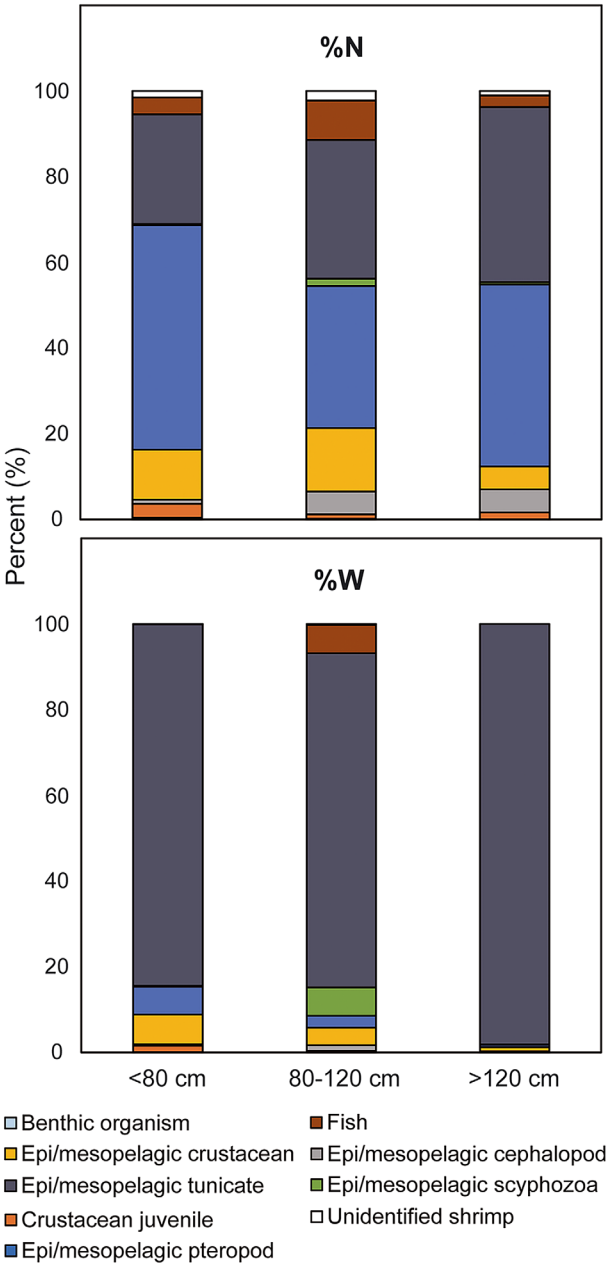

Fig. 2. Numerical (%N) and gravimetric (%W) diet compositions of sharptail mola for each size class (sample sizes: <80 cm, n = 34; 80–120 cm, n = 61; >120 cm, n = 10). Prey items were categorized into different functional groups

80–120 cm, spring diets significantly differed from autumn diets in terms of numerical index (R = 0.162, p = 0.013); these fish fed on numerous tunicates in spring and shifted to pteropods in summer, autumn, and winter. Numerous cephalopods and fish were also found during summer, autumn, and winter. The %W of Scyphozoa was higher in summer, autumn, and winter compared to spring.

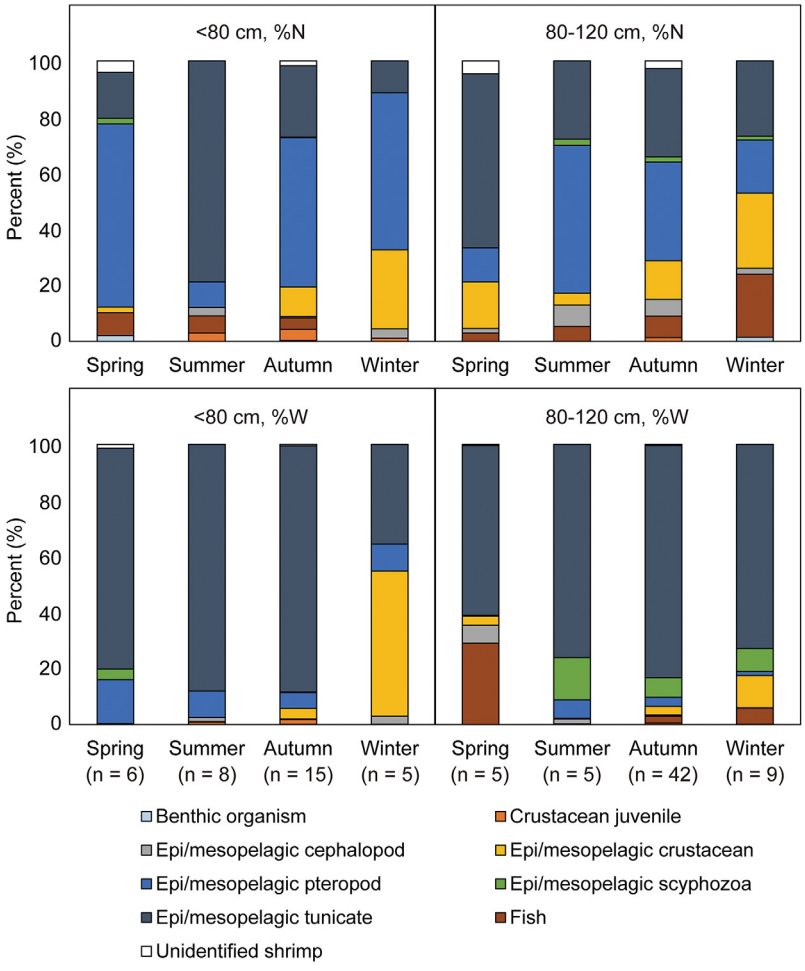

Fig. 3. Seasonal diet composition of sharptail mola <80 cm and 80–120 cm in terms of numerical (%N) and gravimetric (%W) indices. Sample size (n) represents sample size for each size class in each season. Individuals >120 cm were excluded because their diet compositions were not significantly different among seasons (p > 0.05)

3.3. Seasonal variation in bulk isotope values across size classes

Isotopic compositions of carbon and nitrogen in bulk tissues were positively related to body size of sharptail mola (nonlinear regression: $\delta^{13}C$: R^2 = 0.07, p = 0.007; $\delta^{15}N$: R^2 = 0.14, p < 0.001). The $\delta^{15}N$ values for sharptail mola >80 cm were significantly higher than those for mola <80 cm (ANOVA: $F_{2, 202}$ = 4.646, p = 0.011), and values did not differ across seasons ($F_{3, 202}$ = 1.074, p = 0.361) with no interaction between size and season ($F_{5, 202}$ = 0.75, p = 0.587). $\delta^{13}C$ values significantly differed across size groups, increasing with body size ($F_{2, 202}$ = 4.164, p = 0.017). $\delta^{13}C$ values also differed significantly across seasons ($F_{3, 202}$ = 5.777, p = 0.001). $\delta^{13}C$ values in spring were the highest and those in autumn were the lowest across all size classes. Seasonal patterns of $\delta^{13}C$ values in sharptail mola evaluated by size groups showed significant seasonal variations in individuals <120 cm (<80 cm: $F_{3, 45}$ = 4.897, p = 0.005; 80–120 cm: $F_{3, 114}$ = 3.001, p = 0.034). In mola <80 cm, $\delta^{13}C$ values in spring were significantly higher than the values in autumn (post hoc test: p = 0.004), whereas in mola 80–120 cm, none of the pairwise tests between seasons showed significant differences.

3.4. $\delta^{15}N$ values of amino acids and TP estimates

Similar to observed patterns for bulk $\delta^{15}N$ values, mean $\delta^{15}N$ values of trophic and source amino acids in sharptail mola slightly increased with size, from 21.5 to 23.6‰, and from 3.2 to 4‰, respectively (Table 3). TP_{AA} across size classes of sharptail mola were consistent with TP_{bulk} estimates. Mola >120 cm had higher mean TP than size classes of 80–120 cm and <80 cm (Table 3). Mean TP_{bulk} showed significant differences across size class ($F_{2, 210}$ = 11.601, p < 0.001), whereas mean TP_{AA} did not ($F_{2,7}$ = 1.658, p = 0.26). Mean $\delta^{15}N$ values of all prey items (except for cephalopods) were significantly lower than those of sharptail mola ($F_{5, 252}$: 77.811, p < 0.001; post hoc test: p < 0.05) (Fig. 4A). Across prey items, the lowest mean $\delta^{15}N$ value and TP_{bulk} were observed in *Phronima* spp., and the highest values and TP_{bulk} were observed in cephalopods (Fig. 4B). The lowest mean $\delta^{13}C$ values were found in pteropods, and the highest $\delta^{13}C$ values were found in *Atolla* spp. (epi-/mesopelagic Scyphozoa).

Table 3. Mean ± SD $\delta^{15}N$ values of trophic ($\delta^{15}N_{Trp}$) and source amino acids ($\delta^{15}N_{Src}$), and trophic positions (TPs) estimated by isotopic data from individual amino acids (TP_{AA}) and bulk tissues (TP_{bulk}) across size classes of sharptail mola

Size class	$\delta^{15}N_{Trp}$ (‰)	$\delta^{15}N_{Src}$ (‰)	TP_{AA}	TP_{bulk}
<80 cm	21.49 ± 1.4	3.51 ± 0.2	3.5 ± 0.3	3.5 ± 0.4
80–120 cm	22.00 ± 2.0	3.48 ± 3.8	3.6 ± 0.4	3.7 ± 0.3
>120 cm	24.41 ± 1.0	4.52 ± 1.1	3.9 ± 0.2	3.8 ± 0.3

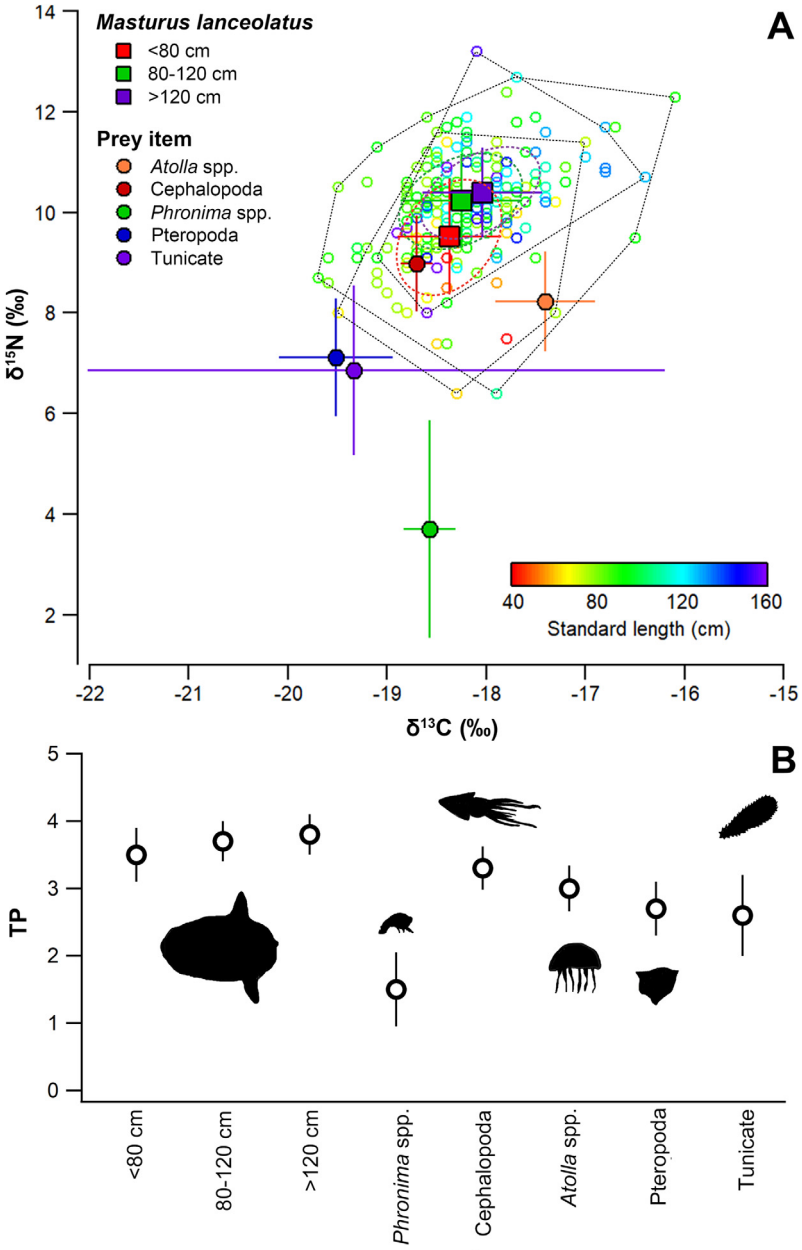

Fig. 4. (A) Biplot of $\delta^{13}C$ and $\delta^{15}N$ values from sharptail mola and their prey items (mean ± 1 SD) off eastern Taiwan and (B) trophic position (TP) estimates in bulk tissues of sharptail mola and their prey items. Isotopic niche for sharptail mola across size classes in (A) shows corrected standard ellipse areas (SEAc, dashed lines) and total area of convex hull (dotted lines). Open circles in (A) represent the $\delta^{13}C$ and $\delta^{15}N$ values for all specimens of sharptail mola

3.5. Isotopic niche width across size classes

Results of isotopic niche area across 3 size classes of sharptail mola, calculated using SEA_c and SEA_b, were similar (Fig. 4A). The trophic isotopic niche decreased gradually with increasing size (SEA_c: <80 cm: 1.85, 80–120 cm: 1.72, >120 cm: 1.56) (Fig. S4). The overlap in SEA_c among the 3 size classes was high, with overlap percentage estimates between <80 cm and 80–120 cm, 80–120 cm and >120 cm, and <80 cm and >120 cm of 78, 85, and 70%, respectively.

3.6. Mixing models

Mixing model results indicated that prey contributions varied across size classes of sharptail mola (Fig. 5). The most important prey items for all size classes were tunicates, with decreasing proportions (median) with increasing size (92, 82, and 75% for <80, 80–120 and >120 cm size classes, respectively). The relative proportion of cephalopods increased across mola size, from 0.4% in fish <80 cm to 10 and 17% in fish 80–120 and >120 cm, respectively. The contributions of *Atolla* spp., pteropods, and *Phronima* spp. to the diets of sharptail mola were low for all 3 size groups (Fig. 5).

4. DISCUSSION

Sharptail mola from waters off Taiwan fed extensively on gelatinous organisms, similar to observations of diet in other molids. However, unlike other molids that typically feed on scyphozoans, tunicates were the most important gelatinous prey in the diets of sharptail mola in this study. The TP estimated from $\delta^{15}N$ values in bulk tissues and amino acids slightly increased with the increase in size, suggesting a continuous ontogenetic shift in their diet.

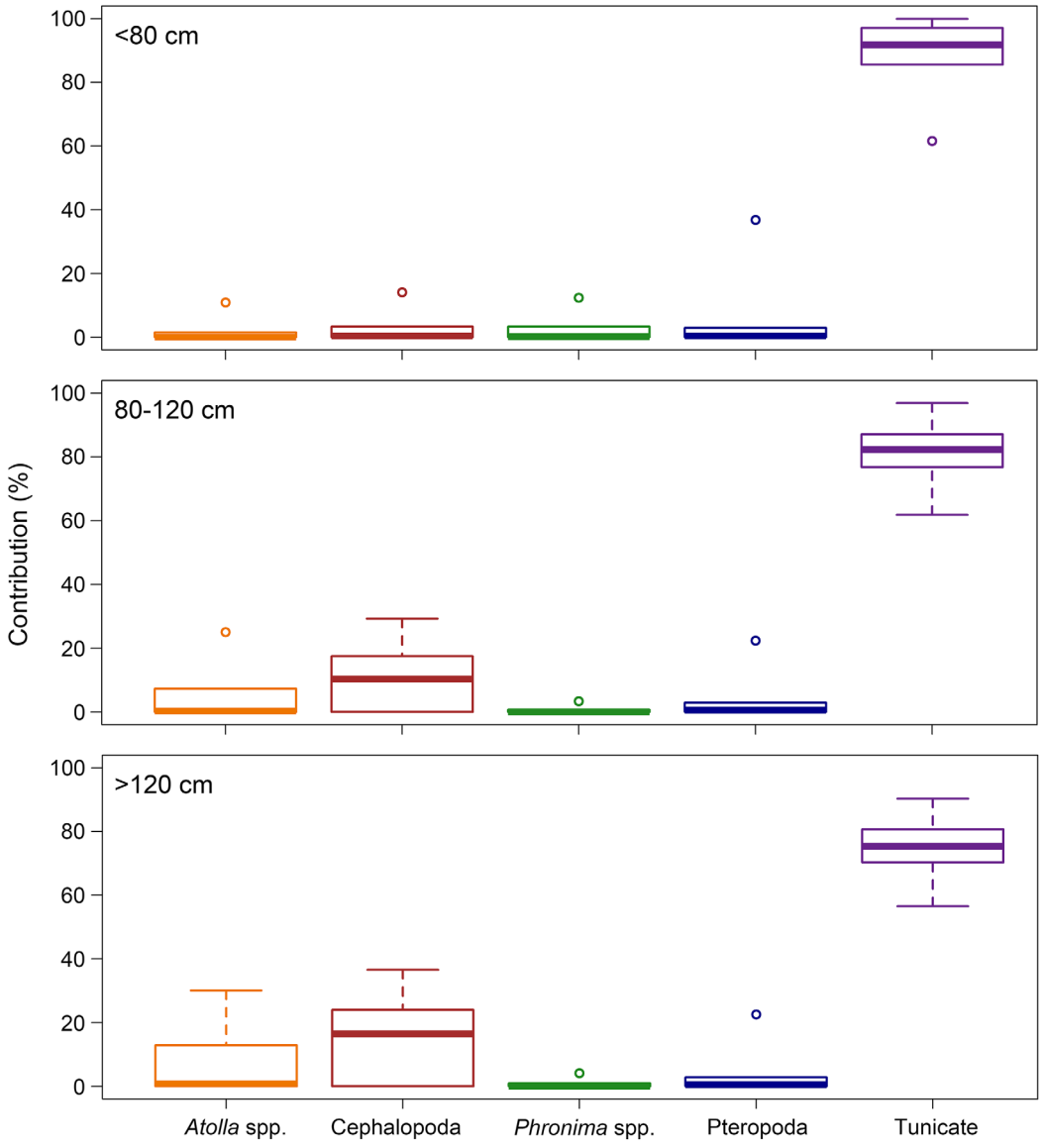

Fig. 5. Estimated contribution of common prey species to sharptail mola diet based on Bayesian isotope mixing models. Informative priors were based on diet compositions (by % weight, %W) of sharptail mola. Boxplots represent the 25th, median, and 75th quartiles of data; whiskers represent 1.5× the interquartile range; and open circles represent outliers

4.1. Diets of sharptail mola

Sharptail mola principally fed on gelatinous prey, mainly salps and pyrosomes, which corroborates sparse prior observations and suggests that they are selective and targeted predators (Harbison & Janssen 1987, Bakenhaster & Knight-Gray 2016). This feeding strategy is similar to other molids with described diets, such as the ocean sunfish (Pope et al. 2010). In our study, sharptail mola principally consumed tunicates, but also salps and pyrosomes, as demonstrated by SCA and SIA. Typically, due to high water content, gelatinous species have low energy density and are regarded as unfavorable foods in pelagic food webs (Larson 1986). However, some studies (Davenport & Balazs 1991, Davenport 1998, Doyle et al. 2007) have indicated that leatherback sea turtles *Dermochelys coriacea* are able to consume enough Scyphozoa daily to maintain sufficient energy intake. Like sea turtles, sharptail mola consume huge quantities and biomass of gelatinous food (tunicates) which are likely their main energy source.

Sharptail mola mainly consumed gelatinous prey but augmented their diet with various other prey from epi- and mesopelagic, coastal, and benthic habitats, suggesting they search for prey sources in

various habitats and thus expand their feeding niche. Similar dietary observations were reported for 2 stranded sharptail mola on the Atlantic coast of Florida, which fed on prey from pelagic (tunicates) and benthic habitats (various invertebrates) (Bakenhaster & Knight-Gray 2016). Foraging in diverse habitats (from epi- to mesopelagic, and from pelagic to benthic) might be relevant to the wide-ranging vertical movement behavior of sharptail mola, which potentially track prey on the seafloor, surface, and deep water (Cartamil & Lowe 2004, Dewar et al. 2010). These vertically variable foraging strategies have been observed in other molids and in other consumers of gelatinous prey, such as loggerhead sea turtles *Caretta caretta* and leatherback sea turtles, that search for prey in various habitats (Houghton et al. 2006, Marshall et al. 2012, Nakamura & Sato 2014).

While both sharptail mola and ocean sunfish are gelativores, their diets and habitat uses across ontogeny differ. Notably, a small amount of Scyphozoa was found in the stomachs of sharptail mola across size groups, in contrast to the diets of ocean sunfish, which are dominated by this prey group (Pope et al. 2010, Nakamura & Sato 2014). There are 2 possible explanations for this difference. One is that sharptail mola have a selective preference for other gelatinous species and invertebrates, suggesting potential resource partitioning from ocean sunfish. Indeed, tunicates have rarely been found in the stomachs of *Mola* spp. captured in the same location off east Taiwan (C.-T. Chang unpubl. data). Another reason might be underestimation of Scyphozoa from stomach contents. Systematically underestimating soft-bodied prey is a well-documented problem in diet studies based on SCA (Symondson 2002). However, such prey are regularly recognized in ocean sunfish stomachs, suggesting they would be present in sharptail mola stomachs if they were being consumed. Further, the low contribution of Scyphozoa from Bayesian mixing models indicated minimal importance of Scyphozoa in sharptail mola diet, so the lack of Scyphozoa in stomachs might not be due to poor preservation but to actual infrequency in overall diet.

4.2. Size effects

Size-related changes in sharptail mola diets suggest intraspecific resource partitioning. In our study, the diet composition of sharptail mola changed with increasing sizes from low-mobility prey (e.g. small invertebrates) to include more active prey (e.g. cephalopods and fish), from epi- and mesopelagic habitats to pelagic, benthic, and coastal regions. These changes are likely related to body size and swimming performance of sharptail mola. Molas are thought to be suction feeders (Gregory 1933), and prey availability is constrained by gape size, similar to tunas (Ménard et al. 2006). Increased swimming ability of fish may enable them to forage in various habitats or on higher-mobility prey (Sánchez-Hernández et al. 2019). Further increasing body size may increase competitive performance and decrease predation risk, thus expanding the habitats (pelagic, benthic, and coastal habitats) within which they can forage. Similar patterns were found in studies of ocean sunfish, with small fish targeting a mixed diet in nearshore waters and large individuals exploiting prey from a broad depth range from epipelagic to mesopelagic zones (Nakamura & Sato 2014, Sousa et al. 2016, Phillips et al. 2020).

Despite these slight but significant changes in diet with size, all sharptail mola predominately fed on tunicates. Little variance in niche width across sharptail mola size groups also suggested high similarity of food sources (gelatinous prey) at all life stages, and the $\delta^{15}N_{Src}$ values suggest they feed from the same habitats, similar to sea turtles, which have been shown to feed mainly on Scyphozoa throughout their lifespans (Pate & Salmon 2017). This high utilization of gelatinous prey regardless of size was also demonstrated in mixing model diet estimates, which suggested dominance of tunicates across sizes. Large sharptail mola did have slightly higher TPs (in both TP_{AA} and TP_{bulk}) and $\delta^{15}N_{Trp}$ values than small individuals, which may result from their ability to capture slightly higher quantities of higher-mobility prey of higher TP.

4.3. Seasonal effect

Seasonal shifts in diets and isotopic compositions of sharptail mola were observed, suggesting that sharptail mola may adjust their diets to seasonally abundant or particularly energy-rich prey when they are available. During spring, $\delta^{13}C$ values of mola were highest, and the very high mass of tunicates found (especially for small mola) suggests that they fed on these filter-feeding prey during the high-productivity spring season (González et al. 2000, Czudaj et al. 2020, Lan et al. 2020). Moreover, a regular seasonal bloom of tunicates occurs on the waters off Taiwan in the high-productivity season, suggesting that sharp-

tail mola may advantageously feed on highly abundant prey when available (Kuo et al. 2015, Franco et al. 2016, 2019), similar to observations of mesopelagic fishes (Cailliet 1972). During summer and autumn, sharptail mola had low $\delta^{13}C$ values, suggesting feeding in different habitats or on different seasonally available resources. This difference was consistent with SCA results that showed mola feeding on more pelagic prey in winter and spring and more coastal, benthic, and pelagic prey in summer and autumn. Additionally, the fact that most flying fish eggs were found in summer and autumn diets is further evidence for opportunistic feeding on pulses of available prey abundance; similar foraging patterns were observed in green turtles *Chelonia mydas* off Taiwan, which fed on eggs during flying fish egg-harvest seasons (Ng et al. 2014). We propose that in high-productivity seasons (spring and winter), sharptail mola (especially larger individuals) can obtain adequate energy from tunicates from pelagic regions. In low-productivity seasons (summer and autumn), they might move closer inshore, where productivity is higher (Guo 1991, Chung et al. 2007), or move back and forth between the surface and benthic habitats to expand available prey resources.

Additionally, seasonal shifts in $\delta^{13}C$ values of sharptail mola might be affected by the seasonal variability in the carbon isotopic composition of lower trophic level prey or particulate organic matter (POM). The $\delta^{13}C$ values of POM showed seasonal variations due to different oceanographic processes near the waters surrounding Taiwan (Lin et al. 2014, Ho et al. 2021). The seasonal variabilities in the base of the food web propagate to the consumer, i.e. mola, via foraging.

4.4. Integrating SCA and SIA in estimating diets of sharptail mola

There were some discrepancies between SCA and SIA that highlighted the differences in dietary resolution between the 2 approaches and the importance of integrating them in studying foraging ecology. The importance of tunicates in diets of sharptail mola were shown in both approaches, whereas other organisms like cephalopods or benthic organisms were shown only using SCA. SCA results can provide a snapshot of diets but cannot reflect long-term dietary prey proportions (e.g. %N or %W) because of variability in digestibility of prey items. In addition, multiple indices (number, weight, occurrence, IRI, PSI) and approaches (ANOSIM) were combined and used to fully describe the diet composition in SCA due to the high variability of gut contents between individual fish. In diet compositions of sharptail mola, some groups' diets had high/low PSI but significant/non-significant differences in ANOSIM. It may seem counterintuitive that the diet between groups with low PSI (low overlap) would not have a significant difference and vice versa. This could be due to inherent differences in both approaches. PSI is a comparison of diet overlap between groups using overall %N or %W values (Hurlbert 1978), while ANOSIM uses all diet data, including the variability, in a statistical test (Anderson & Walsh 2013). When a group's diets has low PSI values but the result of ANOSIM is non-significant, it implies a large variation in diets within the group. Therefore, a lower overlap (low PSI values) may not accurately reflect the diets.

SIA results provide time-integrated information on assimilated prey and their energy contribution (Peterson & Fry 1987). For example, in our study, cephalopods contributed little to the diets (based on %FO, %N, and %W) of large sharptail mola because they were only occasionally observed and highly digested. However, SIA results indicated that cephalopods were more important to the long-term diet of large sharptail mola than apparent from SCA. The inconsistency between SIA and SCA was also found in the trophic niche widths across the size of sharptail mola. The decrease in trophic niche widths with body size was not shown in the SCA results in our study. Instead, large sharptail mola exploit their diets in different habitats. Newsome et al. (2007) mentioned that the limitation of an SIA-derived niche is that a small niche width of a consumer would result from consumers feeding on varied resources that have similar isotopic compositions. These types of discrepancies have also been described in studies of apex predators (Chiang et al. 2020, Petta et al. 2020). Thus, integrating the SCA and SIA provides a more holistic view of the trophic ecology of sharptail mola.

There are some limitations in this study. First, we did not explore the interannual variation in diets due to the small sample size, and we assumed that prey availabilities are similar across years. Second, the sample sizes in different seasons across all size groups were unbalanced because of the seasonal occurrence of sharptail mola in waters off Taiwan. However, an unbalanced design might decrease the statistical power and the robustness (Anderson & Walsh 2013), and increasing the sample size would improve the robustness of the method. Additionally, some gut contents were not identifiable because they were highly digested. DNA metabarcoding could be used to cope with unidentified prey and improve the

accuracy of the diet estimates in future work. Last, similar isotopic values of tunicates and pteropods contribute to the uncertainties of the mixing model results (Phillips et al. 2005). The model can perform well when prey sources have dissimilar isotopic values, and vice versa. If tunicates and pteropods, which have similar isotopic values, are combined (resulting in a total of 4 prey sources), the contribution of tunicates is slightly higher than the results with 5 prey sources due to the increase in the percentage of tunicates + pteropods (%W). However, in the present study, we chose not to combine these 2 prey sources because of the differences in their trophic niche and taxonomy.

5. CONCLUSION

We found that sharptail mola predominately fed on tunicates, although increasing diet diversity with increasing body size and seasonal shifts in diet suggest the possibility of reducing intra- and inter-specific competition for prey resources. Sharptail mola diets differed unexpectedly from co-occurring ocean sunfish in that they did not feed extensively on scyphozoans, suggesting a potential for resource or trophic niche partitioning among Molidae. The present study further describes the resource use and ecological role of the poorly studied sharptail mola, adding to the understanding of trophic interactions of Molidae in marine ecosystems. Understanding pelagic predator feeding strategies helps clarify how species modify diet and behavior across ontogeny and seasons, identifying key prey species and feeding habitat that may be integrated into more holistic population assessments and conservation and management initiatives.

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LITERATURE CITED

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574

Arai MN, Welch DW, Dunsmuir AL, Jacobs MC, Ladouceur AR (2003) Digestion of pelagic Ctenophora and Cnidaria by fish. Can J Fish Aquat Sci 60:825–829

Arostegui MC, Braun CD, Woodworth-Jefcoats PA, Kobayashi DR, Gaube P (2020) Spatiotemporal segregation of ocean sunfish species (Molidae) in the eastern North Pacific. Mar Ecol Prog Ser 654:109–125

Bakenhaster MD, Knight-Gray JS (2016) New diet data for *Mola mola* and *Masturus lanceolatus* (Tetraodontiformes: Molidae) off Florida's Atlantic coast with discussion of historical context. Bull Mar Sci 92:497–511

Bradley CJ, Wallsgrove NJ, Choy CA, Drazen JC, Hetherington ED, Hoen DK, Popp BN (2015) Trophic position estimates of marine teleosts using amino acid compound specific isotopic analysis. Limnol Oceanogr Methods 13: 476–493

Cailliet GM (1972) The study of feeding habits of two marine fishes in relation to plankton ecology. Trans Am Microsc Soc 91:88–89

Caldera EJ, Whitney JL, Nyegaard M, Ostalé-Valriberas E, Kubicek L, Thys TM (2020) Genetic insights regarding the taxonomy, phylogeography and evolution of the ocean sunfishes (Molidae: Tetraodontiformes). In: Thys TM, Hays GC, Houghton JDR (eds) The ocean sunfishes: evolution, biology and conservation. CRC Press, Boca Raton, FL, p 37–54

Cartamil DP, Lowe CG (2004) Diel movement patterns of ocean sunfish *Mola mola* off southern California. Mar Ecol Prog Ser 266:245–253

Chang CT, Lin SJ, Chiang WC, Musyl MK and others (2020) Horizontal and vertical movement patterns of sunfish off eastern Taiwan. Deep Sea Res II 175:104683

Chang CT, Chiang WC, Musyl MK, Popp BN and others (2021) Water column structure influences long-distance latitudinal migration patterns and habitat use of bumphead sunfish *Mola alexandrini* in the Pacific Ocean. Sci Rep 11:21934

Chiang WC, Chang CT, Madigan DJ, Carlisle AB and others (2020) Stable isotope analysis reveals feeding ecology and trophic position of black marlin off eastern Taiwan. Deep Sea Res II 175:104821

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y and others (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr Methods 7: 740–750

Chung IC, Hwang RL, Lin SH, Wu TM and others (2007) Nutrients, temperature, and salinity as primary factors influencing the temporal dynamics of macroalgal abundance and assemblage structure on a reef of Du-Lang Bay in Taitung in southeastern Taiwan. Bot Stud 48: 419–433

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Cleveland WS, Grosse E, Shyu WM (1992) Local regression models. In: Chambers JM, Hastie TJ (eds) Statistical models in S. Wadsworth & Brooks/Cole, Pacific Grove, CA, p 309–376

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54: 726–738

Czudaj S, Giesemann A, Hoving HJ, Koppelmann R, Lüskow F, Möllmann C, Fock HO (2020) Spatial variation in the trophic structure of micronekton assemblages from the eastern tropical North Atlantic in two regions of differing productivity and oxygen environments. Deep Sea Res I 163:103275

Davenport J (1998) Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. Brit Herp Soc Bull 62:4–8

Davenport J, Balazs GH (1991) 'Fiery bodies' — Are pyrosomas an important component of the diet of leatherback turtles? Brit Herp Soc Bull 37:33–38

Dewar H, Thys T, Teo SLH, Farwell C and others (2010) Satellite tracking the world's largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific. J Exp Mar Biol Ecol 393:32–42

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays GC (2007) The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. J Exp Mar Biol Ecol 343:239–252

Fisheries Agency (2020) Fisheries statistical yearbook — Taiwan, Kinmen and Matsu Area, 2020. Fisheries Agency, Council of Agriculture, Taipei

Focken U, Becker K (1998) Metabolic fractionation of stable carbon isotopes: implications of different proximate compositions for studies of the aquatic food webs using $\delta^{13}C$ data. Oecologia 115:337–343

Franco P, Chen HJ, Hwang JS (2016) Taxonomic composition and seasonal distribution changes of pelagic tunicates in the waters off nuclear power plants in northern Taiwan in relation to environmental conditions. Zool Stud 55:e28

Franco P, Dahms HU, Hwang JS (2019) Pelagic tunicates at shallow hydrothermal vents of Kueishantao. PLOS ONE 14:e0225387

Fraser-Brunner A (1951) The ocean sunfishes (Family Molidae). Bull Br Mus Nat Hist 1:87–121

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis. CRC Press, Boca Raton, FL

Geweke J (1991) Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. Research Department Staff Report 148. Federal Reserve Bank of Minneapolis, Minneapolis, MN

Gomes-Pereira JN, Pham CK, Miodonski J, Santos MAR and others (2023) The heaviest bony fish in the world: a 2744 kg giant sunfish *Mola alexandrini* (Ranzani, 1839) from the North Atlantic. J Fish Biol 102:290–293

González HE, Sobarzo M, Figueroa D, Nöthig EM (2000) Composition, biomass and potential grazing impact of the crustacean and pelagic tunicates in the northern Humboldt Current area off Chile: differences between El Niño and non-El Niño years. Mar Ecol Prog Ser 195: 201–220

Gregory WK (1933) Fish skulls: a study of the evolution of natural mechanisms. The American Philosophical Society, Philadelphia, PA

Grémillet D, White CR, Authier M, Doremus G, Ridoux V, Pettex E (2017) Ocean sunfish as indicators for the rise of slime. Curr Biol 27:R1263–R1264

Guo YJ (1991) The Kuroshio. Part II. Primary productivity and phytoplankton. Oceanogr Mar Biol Annu Rev 29: 155–189

Hannides CCS, Popp BN, Landry MR, Graham BS (2009) Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. Limnol Oceanogr 54:50–61

Harbison GR, Janssen J (1987) Encounters with a swordfish (*Xiphias gladius*) and sharptail mola (*Masturus lanceolatus*) at depths greater than 600 meters. Copeia 1987: 511–513

Harrod C, Syväranta J, Kubicek L, Cappanera V, Houghton JDR (2013) Reply to Logan & Dodge: 'Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators'. J Fish Biol 82:10–16

Ho PC, Okuda N, Yeh CF, Wang PL, Gong GC, Hsieh CH (2021) Carbon and nitrogen isoscape of particulate organic matter in the East China Sea. Prog Oceanogr 197:102667

Hooper SN, Paradis M, Ackman RG (1973) Distribution of trans-6-hexadecenoic acid, 7-methyl-7-hexadecenoic acid and common fatty acids in lipids of ocean sunfish *Mola mola*. Lipids 8:509–516

Houghton JDR, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87:1967–1972

Hurlbert SH (1978) The measurement of niche overlap and some relatives. Ecology 59:67–77

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLOS ONE 7:e31757

Kuo CY, Fan TY, Li HH, Lin CW, Liu LL, Kuo FW (2015) An unusual bloom of the tunicate, *Pyrosoma atlanticum*, in southern Taiwan. Bull Mar Sci 91:363–364

Lan KW, Lian LJ, Li CH, Hsiao PY, Cheng SY (2020) Validation of a primary production algorithm of vertically generalized production model derived from multi-satellite data around the waters of Taiwan. Remote Sens 12:1627

Larson RJ (1986) Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. J Exp Mar Biol Ecol 99:107–120

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Leis JL, Matsuura K, Shao KT, Hardy G and others (2015) Sharptail mola *Masturus lanceolatus* (errata version published in 2017). The IUCN Red List of Threatened Species: e.T193634A115330232. https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T193634A2250642.en

Lin HY, Lin PY, Chang NN, Shiao JC, Kao SJ (2014) Trophic structure of megabenthic food webs along depth gradients in the South China Sea and off northeastern Taiwan. Mar Ecol Prog Ser 501:53–66

Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. J Anim Ecol 77: 838–846

Madigan DJ, Snodgrass OE, Hyde JR, Dewar H (2021) Stable isotope turnover rates and fractionation in captive California yellowtail (*Seriola dorsalis*): insights for application to field studies. Sci Rep 11:4466

Marshall CD, Guzman A, Narazaki T, Sato K, Kane EA, Sterba-Boatwright BD (2012) The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): implications for durophagy in neritic, benthic habitats. J Exp Biol 215:4166–4174

McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology 83:2173–2180

Ménard F, Labrune C, Shin YJ, Asine AS, Bard FX (2006) Opportunistic predation in tuna: a size-based approach. Mar Ecol Prog Ser 323:223–231

Muggeo VMR (2008) Segmented: an R package to fit regression models with broken-line relationships. R News 8: 20–25

Nakamura I, Sato K (2014) Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. Mar Biol 161:1263–1273

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5: 429–436

Ng KY, Chen TH, Balazs GH (2014) Flying fish egg harvest off Keelung, Taiwan uncovers occurrence of pelagic-phase green turtles. Mar Turtle Newsl 143:14–15

Nyegaard M, Loneragan N, Hall S, Andrew J, Sawai E, Nyegaard M (2018) Giant jelly eaters on the line: species distribution and bycatch of three dominant sunfishes in the Southwest Pacific. Estuar Coast Shelf Sci 207:1–15

Pate JH, Salmon M (2017) Ontogenetic niches and the development of body shape in juvenile sea turtles. Chelonian Conserv Biol 16:185–193

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Petta JC, Shipley ON, Wintner SP, Cliff G, Dicken ML, Hussey NE (2020) Are you really what you eat? Stomach content analysis and stable isotope ratios do not uniformly estimate dietary niche characteristics in three marine predators. Oecologia 192:1111–1126

Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. Oecologia 144:520–527

Phillips ND, Elliott Smith EA, Newsome SD, Houghton JDR and others (2020) Bulk tissue and amino acid stable isotope analyses reveal global ontogenetic patterns in ocean sunfish trophic ecology and habitat use. Mar Ecol Prog Ser 633:127–140

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Evol Syst 4:53–74

Pope EC, Hays GC, Thys TM, Doyle TK and others (2010) The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives. Rev Fish Biol Fish 20:471–487

Popp BN, Graham BS, Olson RJ, Hannides CCS and others (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson TE, Siegwolf RTW (ed) Stable isotopes as indicators of ecological change. Elsevier, Amsterdam, p 173–190

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

Sánchez-Hernández J, Nunn AD, Adams CE, Amundsen PA (2019) Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. Biol Rev Camb Philos Soc 94:539–554

Sawai E, Hibino Y, Iwasaki T (2019) A rare river stranding record of sharptail sunfish *Masturus lanceolatus* in Fukuoka Prefecture, Japan. Biogeography 21:27–30

Seitz AC, Weng KC, Boustany AM, Block BA (2002) Behaviour of a sharptail mola in the Gulf of Mexico. J Fish Biol 60:1597–1602

Sousa LL, Xavier R, Costa V, Humphries NE and others (2016) DNA barcoding identifies a cosmopolitan diet in the ocean sunfish. Sci Rep 6:28762

Stock BC, Semmens BX (2013) MixSIAR GUI user manual: version 3.1. https://github.com/brianstock/MixSIAR/

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Symondson WOC (2002) Molecular identification of prey in predator diets. Mol Ecol 11:627–641

Syväranta J, Rautio M (2010) Zooplankton, lipids and stable isotopes: importance of seasonal, latitudinal, and taxonomic differences. Can J Fish Aquat Sci 67: 1721–1729

Syväranta J, Harrod C, Kubicek L, Cappanera V, Houghton JDR (2012) Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators. J Fish Biol 80:225–231

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46:2061–2066

Weng JS, Lee MA, Liu KM, Hsu MS, Hung MK, Wu LJ (2015) Feeding ecology of juvenile yellowfin tuna from waters southwest of Taiwan inferred from stomach contents and stable isotope analysis. Mar Coast Fish 7: 537–548

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