

Geographic variation in stable isotopic and fatty acid composition of three families of anguilliform leptocephali and particulate organic matter (POM) in the western South Pacific

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Camilla Liénart, Eric Feunteun, Michael J. Miller, Jun Aoyama, Jean-Michel Mortillaro, et al.. Geographic variation in stable isotopic and fatty acid composition of three families of anguilliform leptocephali and particulate organic matter (POM) in the western South Pacific. Marine Ecology Progress Series, 2016, 544, pp.225-241. 10.3354/meps11575 . hal-01243513

HAL Id: hal-01243513 https://hal.science/hal-01243513

Submitted on 15 Dec 2015 $\,$

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Running Heading: Variation in leptocephalus composition in western South Pacific.

47 ABSTRACT: The feeding ecology of leptocephali has remained poorly understood because they apparently feed on particulate organic matter (POM), which varies in composition, and it 48 is unclear which components of the POM they assimilate. The δ^{13} C and δ^{15} N stable isotope 49 (SI) and fatty acid (FA) compositions of 3 families of leptocephali and POM were compared in 50 3 latitudinal current zones of the western South Pacific. The $\delta^{15}N$ signatures of both 51 leptocephali and POM overlapped, with both having their lowest values in the southern current 52 53 zone. POM contained 38 FAs and was rich in saturated FAs (SFA) (16:0, 18:0, 14:0), while leptocephali contained 50 FAs, with high proportions of 16:0, and higher contributions of 54 22:6ω3, 20:5ω3, 18:1ω9, 16:1ω7 and other FAs than the POM. Serrivomeridae leptocephali in 55 the north had higher δ^{15} N signatures and were also distinguished from Nemichthyidae and 56 Muraenidae larvae by their FA compositions (higher SFAs, lower 22:6 ω 3 and 20:5 ω 3). 57 Although SI signatures of the Serrivomeridae larvae did not clearly vary with size, 16:0 and 58 59 18:0 FA proportions decreased with increasing larval size, and 22:6 ω 3 and 16:1 ω 7 increased in 60 larger larvae. Correspondences between the latitudinal variations in nitrogen SI signatures and FA compositions of POM with those of leptocephali and the presence of FA markers of both 61 62 autotrophic and heterotrophic organisms were consistent with leptocephali feeding on POM. 63 POM can contain various materials from primary producers and heterotrophic microorganisms, but differences in the SI signatures and FA compositions in leptocephali remain to be 64 65 explained through further research.

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KEYWORDS: Leptocephali, fatty acids, stable isotopes, biomarkers, trophic ecology, oceaniccurrents.

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70 **INTRODUCTION**

71 Leptocephali are the larvae of approximately 15 families of anguilliform fishes and 72 their close relatives, which are widely distributed in the oceans from low-latitude temperate zones to tropical latitudes (Böhlke 1989, Miller & Tsukamoto 2004; Miller 2009). They have 73 74 highly laterally-compressed, transparent bodies and a unique physiology compared to other fish larvae (Pfeiler 1999, Bishop et al. 2000). All eel families except the Anguillidae are 75 almost exclusively marine and live in habitats ranging from the meso- and bathy- pelagic zones 76 77 (e.g., Nemichthyidae, Serrivomeridae) to coastal areas (e.g., Muraenidae) (Miller & Tsukamoto 2004). All leptocephali however, are present together in the near the surface to 300 m depth 78 zone of oceanic areas (Castonguay & McCleave 1987, Miller 2009). Dependent on their taxa 79

and adult habitats, the pelagic phase lasts for several months to more than a year before the
larvae undergo metamorphosis into juveniles (Marui et al. 2001).

Despite their wide distributions and the extensive literature on their morphology (e.g., 82 Böhlke 1989), the feeding ecology of leptocephali is still poorly resolved. During their larval 83 feeding and growth period, leptocephali accumulate energy storage compounds such as lipids 84 85 and glycosaminoglycans (GAG) in a gelatinous body matrix, which are then used for building new tissues during metamorphosis (Padrón et al. 1996, Pfeiler 1999, Pfeiler et al. 2002). A few 86 87 studies have examined the gut contents of leptocephali and have observed materials that resemble particulate organic matter (POM) such as marine snow, discarded appendicularian 88 89 houses or faecal pellets (Otake et al. 1993, Mochioka & Iwamizu 1996, Miller et al. 2011). 90 Carbon and nitrogen stable isotope studies of leptocephali indicate they feed at a low trophic 91 level (Otake et al. 1993, Miyazaki et al. 2011, Feunteun et al. 2015), which was confirmed 92 using amino acid nitrogen isotopes (Miller et al. 2013).

93 Other observations have suggested that leptocephali might also feed on microplanktonic organisms such as protozoans (Tanaka et al. 1995, Govoni 2010) and the DNA sequences of 94 95 various organisms including gelatinous zooplankton have been detected in leptocephalus 96 stomach contents (Riemann et al. 2010). Marine snow however, can be composed of multiple 97 materials and/or organisms, due to both aggregation and colonization processes (Alldredge & 98 Silver 1988, Shanks & Walters 1997, Kiørboe 2000). Therefore, the hypothesis that 99 leptocephali feed on POM and assimilate some of the components of marine snow, including colonising microorganisms, appears most likely (Deibel et al. 2012, Miller et al. 2013, 100 101 Feunteun et al. 2015). Differences in the isotopic compositions of leptocephali taxa have been 102 detected and clear correspondences between POM signatures and expected enrichment values in leptocephali have not always been observed (Miyazaki et al. 2011, Feunteun et al. 2015). 103 104 Thus, it is unclear if leptocephali feed on POM opportunistically or if there are selective differences in the types of POM consumed and/or the types of compounds assimilated from 105 ingested POM between different taxa. 106

An important component of the POM and organisms that potentially contribute to the diet of leptocephali are lipids, but only a few studies have examined the lipid content of leptocephali (Padrón et al. 1996, Deibel et al. 2012). Lipids are important for marine organisms because they are their major metabolic energy reserves (Falk-Petersen et al. 2000, Lee et al. 2006) and play key roles in cell structure and metabolism (Dalsgaard et al. 2003). Fatty acids (FAs) are a specific class of lipids that are energy rich molecules (Dalsgaard et al. 113 2003). Most consumers are unable to synthetize essential FAs (EFAs: $20:4\omega 6$, $20:5\omega 3$, 114 22:6 $\omega 3$), which are polyunsaturated FAs (PUFAs) with a terminal end omega-3 ($\omega 3$) or 115 omega-6 ($\omega 6$), due to their lack of specific enzymes and therefore they acquire these EFA 116 molecules exclusively from the food they eat (Canuel et al. 1995, Styrishave & Andersen 2000, 117 Meziane et al. 2002, Dalsgaard et al. 2003).

118 Biochemical tracers such as FAs and stable isotope ratios (SI) are commonly used in 119 trophic ecology studies because they provide information about the food sources that are assimilated by the organism over time (Pitt at al. 2009). SI ratios of carbon (δ^{13} C) and nitrogen 120 $(\delta^{15}N)$ are used to evaluate the food sources of organisms (Fry & Sherr 1984, Canuel et al. 121 1995) and to characterize organic matter transfer through food webs (Fry & Sherr 1984, Canuel 122 et al. 1995, Abrantes & Sheaves 2009). FAs can be used as biomarkers of specific organisms 123 (Meziane et al. 2007), or to determine the food sources exploited by consumer organisms 124 125 (Meziane et al. 1997, Meziane & Tsuchiya 2000, Mortillaro et al. 2015). They can also be used to follow organic matter transfer through food webs (Dalsgaard et al. 2003, Budge et al. 126 2006, Hall et al. 2006) and can provide information on larval ontogenetic changes (Plante et al. 127 128 2006).

This study used bulk SI and FA composition to provide information on the possible food sources of leptocephali and was specifically intended to investigate: (1) How leptocephali, belonging to three families, may assimilate POM and the associated microorganisms colonizing POM (protozoa, microalgae, bacteria, etc.) (2) Whether the diet of leptocephali changes with size and/or with latitude and/or current systems in the western South Pacific Ocean?

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136 MATERIALS AND METHODS

137 Study area and sample collection

Leptocephali were collected in the western South Pacific (WSP) during Leg 1 of the 138 KH-13-2 research cruise of the research vessel (R/V) Hakuho Maru from 4-24 February 2013. 139 140 Thirty-four stations were sampled at every 2° of latitude/longitude between 5°S-30°S and 165°E–175°W, in the region that includes New Caledonia, Fiji and Samoa (Figure 1A). 141 Leptocephali were collected using an Isaacs-Kidd midwater trawl (IKMT) with an 8.7 m² 142 143 mouth opening and 0.5 mm mesh. Sampling at each station was conducted following two 144 strategies: during the night a step tow fished in the upper 120 m (10 min. steps at 120 m, 70 m and 50 m), and during the day an oblique tow fished from the surface to 200 m, with both types 145

of tows taking less than 1 hour. Temperature, conductivity, depth (CTD) profiles were made at
21 of the stations to a depth of 500 m.

Leptocephali from each IKMT sample were sorted fresh, measured and identified to the 148 149 lowest possible taxonomic level according to Miller & Tsukamoto (2004). A total of 538 leptocephali from 13 families were collected, but only the 3 most abundant families were 150 151 analysed in this study. After identification and measurement, specimens to be used for SI and 152 FA analyses were stored at -80°C. In this study, family is the only taxonomic level considered, and 101 leptocephali from the 3 most abundant families; Muraenidae (n=27; length 25.3-83.0 153 mm, mean±S.D.= 50.1±13.4 mm), Nemichthyidae (n=28; length 30.0–259.0 mm, 122.0±60.5) 154 155 and Serrivomeridae (n=46; length 9.2-62.0 mm, 28.4±14.4 mm) were analysed for SI and FA 156 composition (Figure 1). Five samples of the Serrivomeridae larvae samples consisted of 2 of the smallest larvae (< 10 mm) pooled together to obtain enough tissue for analysis. Each 157 158 leptocephalus specimen or pooled sample was used for both SI and FA analyses. 159 Serrivomeridae larvae were used to examine differences in SI and FA composition in relation to leptocephalus size, because of the insufficient specimens of different sizes of Muraenidae 160 161 and Nemichthyidae larvae, and the Serrivomeridae larvae were mostly from the same current 162 zone.

Seawater samples were collected in triplicate at 13 stations (Figure 1A) in 12 L Niskin 163 164 bottles attached to the CTD rosette multisampler at the depth of the chlorophyll maximum as measured by a fluorometer on the CTD were used for POM analyses. The depth of the 165 chlorophyll maximum differed depending on the station, and was chosen because it is likely to 166 167 have high concentrations of particulate material that may be suitable for feeding by leptocephali. No POM was sampled at the first CTD station in the southwest due to its 168 proximity to the start of the cruise. POM was collected by filtering each 12 L of seawater 169 170 sample through separate pre-combusted glass fibre filters (GF/F, 47 mm diameter, 0.7 µm Large organisms such as copepods were removed manually and filters were 171 mesh). immediately stored frozen at -80°C until analysed. 172

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174 Stable isotopes analysis

175 All samples were lyophilised before analysis. GF/F filters were fumigated with 10% 176 HCl for 4 h to remove inorganic carbon (Lorrain et al. 2003). Leptocephali samples were 177 weighed. Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) SI analysis were performed by the UC 178 Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, 179 Davis, California) using a PDZ Europa ANCA-GSL elemental analyser for leptocephali analysis (half body, excluding the head region except for the smallest larvae) and an Elementar 180 Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, 181 182 Germany) for the GF/F filter POM samples (half filter). Each elemental analyser was interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, 183 UK). Isotopic data are reported using standard delta notation (δ^{13} C or δ^{15} N), defined as parts 184 per thousand deviation (‰) from an international standard (Vienna Peedee belemnite for $\delta^{13}C$ 185 and atmospheric N₂ for δ^{15} N) as defined by the equation: 186

 δ^{13} C or δ^{15} N =[($R_{sample}/R_{standard}$)-1]x1000

Where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$ of the sample or standard (Peterson & Fry 1987). The analytical precision (standard deviation for repeated measurements of internal standards) was $\pm 0.2\%$ and $\pm 0.3\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. All mean values of SI and FA data are expressed as mean \pm standard deviation (S.D.).

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194 Fatty acid analysis

195 Lipids were extracted following Meziane et al. (2007). Briefly, lipid samples (half bodies or filters) were extracted twice with a mixture of distilled water, MeOH and CHCl₃ 196 197 (1:2:1, v:v:v). Saponification and methylation were performed successively under reflux according to Meziane & Tsuchiya (2000). Saponification was achieved using a 2 M 198 NaOH:MeOH solution (1:2, v:v) and methylation with 1 ml of 14% BF₂-MeOH. The fatty 199 acid methyl esters (FAMEs) were separated and quantified by Gas Chromatography (Varian 200 CP-3800) using a flame ionisation detector at the National Museum of Natural History 201 (MNHN-Paris, Resaqua Laboratory). Separation was performed with an Agilent J&W GC 202 203 VF-WAXms column (30 m x 0.25 mm i.d.; 0.25 µm film thickness) with He as carrier gas. Most of FAs peaks were identified by comparing their retention times with those of known 204 standards (SupelcoTM 37 FAME mix; Sigma-Aldrich[®]) and confirmed with a GC-mass 205 206 spectrometer (Varian 450-GC 220-Ion Trap MS; He as carrier gas). FAs are designated as X:Y ω Z, where X is number of carbon atoms, Y is number of double bonds and Z is the 207 position of the ultimate double bond with respect to the terminal methyl group. 208 The 209 concentration of each FA was calculated using 23:0 as an internal standard according to Schomburg (1987): $C_{FA}=A_S/A_{IS} \times C_{IS}/W_S$, where A_S is the peak area of the FA, A_{IS} the peak 210

area of the internal standard, C_{IS} the concentration of the standard and W_S the dry weight of sample.

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214 Latitudinal regions of the study area

215 The study area was located within the northwestern part of the WSP subtropical gyre 216 (Qiu & Chen 2004). The water temperature in this region decreases from the north to south 217 (Miller et al. 2006) and during the survey it ranged from 29°C (surface) and 21–23°C (200 m) at northern stations (8°N) to 25°C and 18°C respectively in the south (24°S). This region 218 includes 3 main surface currents at different latitudes, which are the westward South Equatorial 219 Current (SEC, Equator to 20°S), the narrow eastward South Equatorial Countercurrent (SECC) 220 at 5 to 10°S (between two branches of the SEC), and the eastward South Tropical 221 222 Countercurrent (STCC) at latitudes south of Fiji and north of New Zealand (Qiu & Chen 2004; 223 Ganachaud et al. 2014). The SECC was present north of 10°S according to ADCP 224 observations made during the cruise, with mixed westward flow at central latitudes and mixed eastward flow in the south (Otake et al. unpubl. cruise report). 225 The assemblages of 226 leptocephali vary latitudinally in this region, with Serrivomeridae larvae being most abundant 227 in the north, species such as Muraenidae being abundant at central latitudes, and Nemichthyidae being more equally distributed across latitudes (Miller et al. 2006) as they were 228 229 during the present survey (Figure 1B-D). According to the general pattern of currents, the cruise stations were separated into 3 latitudinal zones for analyses of SI and FA compositions 230 231 of leptocephali and POM, which generally correspond with the SECC, SEC, and STCC current 232 systems (Figure 1B).

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234 Data analysis

All SI and FA data are expressed as mean values \pm standard deviation (S.D.). Prior to statistical comparison, data were first evaluated for homocedasticity (Bartlett test) and normalality of distribution (Shapiro-Wilk test), which were not attained in most cases. Therefore, non-parametric Kruskal-Wallis (KW) tests were used to compare FA and SI group values, followed by pairwise comparisons with Mann–Whitney Wilcoxon (MWW) tests and Bonferroni correction to correct significance thresholds. When the sample size in a current zone was too low, only KW tests were used.

All FAs were used in the analyses and no transformations were performed on the dataset to prevent excessive weighting of low proportion FAs. Data matrices (% TFA per

244 sample) were used to create triangular dissimilarity matrices with the Bray-Curtis dissimilarity coefficient, followed by non-metric multidimensional scaling (n-MDS). Stress values < 0.2245 were considered robust (Clarke 1993). Groups used as factors for the analysis were family 246 247 (Muraenidae, Nemichthyidae, Serrivomeridae) and size groups (≤10.0, 10.1–20.0, 20.1–40.0, 40.1-60.0 mm, Serrivomeridae only), as well as current zones (SEC, SEC, STCC) for both 248 leptocephali and POM. Differences in FAs composition among groups was statistically tested 249 250 using separate one-way analysis of similarity (ANOSIM) computed after 5000 permutations. Average dissimilarity (AD) between groups was determined by SIMilarity of PERcentage 251 (SIMPER) analysis (PRIMER[®]5 software module) was used to identify which fatty acids 252 determine the observed differences within or between groups. 253

Multivariate analyses were performed with PRIMER[®]5 software (Clarke & Warwick,
2001) and univariate tests using R software (R development Core Team 2014, Vegan package,
Oksanen et al. 2014). For all univariate tests, the probability α was set at 0.05.

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258 **RESULTS**

Isotopic and fatty acids composition of Particulate organic matter and leptocephali 260

Particulate organic matter (POM). SI values of POM (Figure 2) ranged from -27.8‰ 261 to -25.0% for δ^{13} C (mean±S.D. = -26.6±0.7%) and from 2.5% to 10% for δ^{15} N (6.1±2.3%) 262 (Table 1). A total of 38 FAs were identified in the POM (Table 1). Average saturated fatty 263 acid (SFAs) contribution to POM was 75.2±4.6% of total FAs, with 16:0 showing the highest 264 contribution (35.9±2.3%). The main monounsaturated fatty acids (MUFAs) were 18:1ω9 265 $(5.3\pm1.1\%)$ and $16:1\omega7$ ($4.4\pm0.9\%$). All relative contributions of polyunsaturated fatty acids 266 (PUFAs) were low with maximum values of $1.7\pm0.4\%$ for $16:2\omega4$, $1.7\pm0.8\%$ for $22:6\omega3$ and 267 268 1.7±0.5% for 18:4ω3. Similarly, EFAs 20:5ω3 and 20:4ω6 had low contributions to TFAs (about or $\leq 1\%$). Contributions of branched-chain fatty acid (BrFAs) were 2.4 \pm 0.4% of TFAs. 269

Leptocephali. For the 3 families of leptocephali (Figure 2), δ^{13} C stable isotope values ranged from -23.1‰ to -18.8‰ and from 0.7‰ to 14.5‰ for δ^{15} N (Table 1). There was a significant difference in δ^{13} C composition between Serrivomeridae (-21.0±0.8‰) and Nemichthyidae (-19.9±0.8‰) leptocephali (KW: *p*<0.001; followed by MWW: *p*<0.001). δ^{15} N signatures were significantly different among each of the 3 families (KW: *p*<0.001; MWW: *p*<0.01) with an average δ^{15} N of 4.7±3.3‰ for Nemichthyidae, 6.7±2.7‰ for Muraenidae and 10.9±1.9‰ for Serrivomeridae. A total of 50 FAs was identified in leptocephali (Table 1), with a large contribution of SFAs, MUFAs, and PUFAs to TFAs. The same 6 FAs (16:0, $16:1\omega7$, 18:0, $18:1\omega9$, $20:5\omega3$ and $22:6\omega3$) were most abundant in all 3 families, with all the other FAs each contributing less than about 4% to the TFAs. Muraenidae had higher levels of FAs by weight ($11.7\pm7.4 \text{ mg g}^{-1}$) than Nemichthyidae ($5.2\pm2.5 \text{ mg g}^{-1}$) and Serrivomeridae ($5.4\pm4.0 \text{ mg g}^{-1}$).

The 3 families also showed differences regarding their FAs compositions (ANOSIM: 282 283 p < 0.001), with Muraenidae showing no overlap with the Serrivomeridae and Nemichthyidae, which overlapped to some degree in the n-MDS plot (Figure 3). FAs profiles of leptocephali 284 exhibited average dissimilarity values (AD; SIMPER analysis) that were more similar between 285 Muraenidae and Serrivomeridae (16.6%) than between Muraenidae and Nemichthyidae 286 (14.3%) and between Nemichthyidae and Serrivomeridae (14.6%). The observed differences 287 were mostly due to the relative contributions of 16:0, $16:1\omega7$, 18:0, $18:1\omega9$, $20:5\omega3$ and 288 289 22:6\omega3 to TFAs (Table 1). SFAs contributed a higher proportion of TFAs in Serrivomeridae 290 leptocephali (44.8±7.5%) than PUFAs (33.8±5.7%), whereas the PUFAs contribution was slightly higher in Muraenidae and Nemichthyidae (42.3±3.7% and 39.4±4.2%, respectively) 291 292 than SFAs contribution (38.5 \pm 3.7% and 37.4 \pm 4.2%, respectively) (Figure 4A.B). The total ω 3 293 FAs contribution were significantly different (KW: p<0.001; MWW: p<0.05) for the 3 families, ranging from 23.7±5.5% for Serrivomeridae to 32.5±3.8% for Muraenidae (Figure 294 295 4C). BrFAs contributed less than 1% of TFAs, but differed significantly in their contribution to TFAs (KW: p < 0.001; MWW: p < 0.001) between Muraenidae (0.5±0.1%) and the other 296 families (Nemichthyidae: 0.8±0.1% and Serrivomeridae: 0.9±0.2%) (Figure 4D). 297

Fatty acid trophic markers (FATMs) of the leptocephali included two predominant 16:0 and 22:6 ω 3 FAs, which contributed on average 40% of the TFAs (Table 1). Proportions of the PUFAs 20:5 ω 3 and 22:6 ω 3 were lower for Serrivomeridae (5.1±2.1% and 14.8±3.2%, respectively) than for the two other families (KW *p*<0.001; MWW: *p*<0.001). Muraenidae had the highest percentage of 22:6 ω 3 of the 3 families. The contribution of 18:1 ω 9 to TFAs was lower for Muraenidae (5.8±0.9%; KW: *p*<0.001; MWW: *p*<0.001) than Nemichthyidae and Serrivomeridae (8.3±1.7% and 8.8±1.3%, respectively).

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306 FA compositions and SI signatures of Serrivomeridae size groups

The 4 size groups of Serrivomeridae leptocephali were compared for their FAs and SI signatures. No significant differences were found between size groups for $\delta^{15}N$ (Table 2) and

 δ^{13} C values were only significantly different for ≤ 10 mm larvae (-19.9±0.6‰) and 40–60 mm 309 larvae (-21.4±0.5‰) (KW: p<0.01; MWW: p<0.05). 310

The FA compositions of the Serrivomeridae leptocephali showed various percentage 311 312 changes with increasing size, with SFAs and BrFAs tending to decrease, and MUFAs and PUFAs tending to increase with increasing leptocephali size (Table 2). The total weight of FA 313 in the body of the leptocephali tended to decrease only slightly from the smallest to largest size 314 classes (5.8 to 4.4 mg g^{-1}) but differences were not significant. The 40–60 mm and <10 mm 315 sizes classes were significantly different in FA composition (ANOSIM: p < 0.05; n-MDS), 316 Figure 5) with an AD of 23.2%. The SFAs contribution to ≤ 10 mm larvae was higher 317 318 (56.7±0.9%) and PUFAs contribution was lower (25.2±0.6%) than in 40-60 mm larvae (37.1±0.3% for SFAs and 39.0±0.4% for PUFAs) mainly due to the contribution of the SFAs 319 16:0 and 18:0, the MUFA 16:107 and the PUFAs 22:603 and 20:503 (Table 2). The 320 321 contribution of ω 3 FAs increased with size, from 16.4±1.0% for <10 mm to 30.0±0.7% for 40– 322 60 mm larvae.

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POM and leptocephali SI signatures in current zones

The POM exhibited variation in δ^{15} N values, which ranged from 7.7±2.3‰ in the 325 SECC in the north, to 4.1±1.0‰ in the STCC in the southeast (Table 3), although the SEC 326 values overlapped with those of the other zones (Figure 6D). The δ^{13} C values showed less 327 variation with mean values that ranged from -27.0±0.2‰ to -26.2±0.9‰, but some of the 328 SECC values were lower (Figure 6D). When FA compositions of POM were separated 329 according to the 3 current zones, samples from the SECC (5–15°S) were significantly different 330 (ANOSIM: p < 0.05) from those of both the SEC (15–20°S) and STCC (20–30°S) with an AD 331 of 12.5% between the SECC and SEC, and 13.2% between SECC and STCC. These 332 333 differences mostly resulted from variations in the proportions of the SFAs 18:0, 16:0 and 14:0 (AD between 1.4 and 2.6%), the MUFAs $18:1\omega9$ and $16:1\omega7$ (AD between 0.9 and 0.7%) and 334 PUFAs 22:6 ω 3 and 18:4 ω 3 (AD between 0.8 and 0.5%). In the SECC, the SFA contribution 335 336 was higher (78.8±3.9%) and MUFA and PUFA contributions lower (11.7±2.9% and 7.1±1.4%) than in the other zones (Table 3). 337

Leptocephali also showed differences in isotopic signatures between the 3 current 338 zones, with δ^{15} N values being different (KW and MWW: p < 0.05). Some separation of the 339 δ^{15} N signatures in the 3 zones was also seen within families, except there was only one 340 Serrivomeridae larva analysed from the STCC (Figure 6A-C). For Serrivomeridae 341

leptocephali there was no significant difference in δ^{13} C values between larvae caught in the 342 different current zones, whereas δ^{15} N signatures were different between larvae from the SECC 343 and SEC (t-test: p < 0.05) (Figure 6C). Muraenidae from the SEC and SECC had different in 344 both their δ^{13} C and δ^{15} N values (KW and MWW: p < 0.05) (Figure 6B). There were also 345 differences in the δ^{13} C and δ^{15} N signatures of Nemichthyidae found in the STCC and those in 346 the SECC and SEC, respectively (KW and MWW: p < 0.05) (Figure 6A). FA profiles for the 347 leptocephali caught in the three different currents were not significantly different (KW and 348 MWW: *p*>0.1). 349

350

351 **DISCUSSION**

352 FA and SI signatures of leptocephali and POM

This study examined the variation of the FA profiles and SI signatures of 3 families of leptocephali and their likely food source of POM. Samples were collected across a wide range of latitudes and longitudes of the WSP. Previous studies in the western North Pacific (Miyazaki et al. 2011) and western Indian Ocean (Feunteun et al. 2015) analysed leptocephali and POM from much more limited areas of the ocean.

358 The chemical composition of the different taxa of leptocephali is generally comparable (Pfeiler 1999, Bishop et al. 2000) as confirmed by the FA profiles of the 3 families of 359 360 leptocephali studied in the WSP that show many similarities. There were however, also some differences. The Nemichthyidae, Muraenidae, and Serrivomeridae larvae had the same number 361 of major FAs and categories of FAs markers showed similar proportions. Deibel et al. (2012) 362 also found similar FA compositions for 6 other taxa of leptocephali (Congridae, 363 Muraenesocidae, Ophichthidae) from coastal, shelf or deep slope habitats off northwest 364 Australia. However, despite these overall similarities, the present study found small but 365 significant differences between the FA profiles of Muraenidae larvae and those of 366 Nemichthyidae and Serrivomeridae. The similarities in FAs compositions of the 3 families 367 were largely due to the FAs that were present in large proportions: $16:0, 18:0, 22:6\omega 3, 20:5\omega 3$, 368 369 $16:1\omega7$, and $18:1\omega9$. The same 6 FAs also had the highest proportions in leptocephali from northwestern Australia (Deibel et al. 2012). 370

371 SFAs 16:0 and 18:0 (mean ~24% and 8% of TFAs in all 3 families of leptocephali) are 372 the most abundant FAs in nature as they are products of lipogenesis in all organisms (Dewick 373 1997). Similarly, ω 3 FAs are abundant in marine zooplankton (Lee et al. 2006) and fish larvae 374 (Grote et al. 2011), as they were in the leptocephali, where they represented 24 to 33% of total 375 FAs depending on family. Amongst ω 3, the EFAs 20:5 ω 3 and 22:6 ω 3 are major components of cell membrane phospholipids (Sargent et al. 1993) and are also important for larval growth 376 and development (Sargent et al. 1993, Furuita et al. 2006, Grote et al. 2011). Marine 377 378 consumers however, cannot synthetize essential ω 3 and ω 6 PUFAs (Dalsgaard et al. 2003, Lee 379 et al. 2006, Kattner et al. 2007) so they need to obtain them through feeding (Canuel et al. 380 1995, Styrishave & Andersen 2000, Meziane et al. 2002). Thus, high proportions of ω 3 and 381 $\omega 6$ in leptocephali suggest that leptocephali feed on material containing or originating from autotrophic organisms or primary consumers in which ω 3 and ω 6 are abundantly present (Scott 382 et al. 2002, Dalsgaard et al. 2003, Lee et al. 2006). There is also the possibility that 383 384 leptocephali, as do some heterotrophic organisms (Dalsgaard et al. 2003, Canuel et al. 1995), synthesize these FAs from a precursor such as $18:1\omega9$. This MUFA is abundant in 385 leptocephali (mean of 7.6±1.6% for the 3 families combined in this study, and 6.4±1.3% in 386 387 Deibel et al. 2012) and can be obtained from feeding on zooplankton or other heterotrophic 388 sources in pelagic food webs (Dalsgaard et al. 2003, Lee et al. 2006).

In this study, POM was characterized by a strong contribution of SFAs (~75% of TFAs) 389 390 and a low contribution of $\omega 3$ (~5%), MUFAs (~13%) and PUFAs (~9%), which typically 391 indicates a low nutritional quality for the bulk organic matter, as suggested by other studies in 392 diverse aquatic systems (e.g., North Sea, Boon & Duineveld 1996; Amazon River, Mortillaro 393 et al. 2011). Interestingly, the important FATMs 18:109 and 16:107 (markers of heterotrophs and autotrophic microplankton, respectively) were the main unsaturated FAs that contributed 394 to the TFAs of POM (~5 and 4%, respectively). Also, BrFA markers made a low contribution 395 396 to TFAs ($\sim 2\%$) in POM. Most of these FATMs are typically biosynthesized in large amounts by bacteria (Kaneda 1991, Ederington et al. 1995, Meziane & Tsuchiya 2000) and because 397 decaying bulk POM is rapidly colonised by bacteria (Skerratt et al. 1995, Najdek et al. 2002), it 398 would be expected to be rich in these BrFAs. Thus, the FA composition may indicate that the 399 POM sampled within the chlorophyll maximum layer during this study is likely to be 400 composed of a large non-living POM fraction (detritus, faecal pellets, etc.) with a low bacterial 401 402 influence and to a lesser extent of living organic material (autotrophic and heterotrophic microplankton) that leptocephali would preferentially assimilate. 403

The diet of an organism can usually be examined by assuming a mean isotopic trophic enrichment of 1‰ in δ^{13} C (DeNiro & Epstein 1978, Rau et al. 1983) and of 3.4‰ in δ^{15} N (DeNiro & Epstein 1981, Minagawa & Wada 1984) from food source to consumer. The δ^{15} N values of POM (2.5 to 12‰) and leptocephali (0.5 to 13‰) in the present study heavily

overlapped, so no clear trophic enrichment between $\delta^{15}N$ signatures of POM and leptocephali 408 was evident, except perhaps for Serrivomeridae. One explanation for this is that there could be 409 410 a mismatch between the POM sampled on the filters and the types of POM that leptocephali 411 consume and what they assimilate from this, as mentioned above and described further below. A similar result was also described by Otake et al. (1993), who found that the δ^{15} N signature of 412 Congridae leptocephali (Conger myriaster) overlap with that of POM (~11-13‰). A wide 413 range of POM δ^{15} N values overlapping with those of leptocephali was also seen in studies in 414 the western North Pacific (Miyazki et al. 2011) and western Indian Ocean (Feunteun et al. 415 2015). Other studies examining geographic variations in SI signatures of POM and organisms 416 found similarly high values of δ^{15} N for POM (Waite et al. 2007, Lorrain et al. 2015). This is 417 presumably a result of regional variations that occur globally in the $\delta^{15}N$ values of primary 418 producers that contribute to POM, with some areas such as parts of the South Pacific likely 419 having higher values than other regions of the world (Somes et al. 2010). The δ^{13} C gap of 420 about 7‰ between mean values (2‰ gap for closest values) of POM and leptocephali is also 421 clearly larger than the expected 1‰ gap if leptocephali were consuming POM within the 422 chlorophyll maximum and assimilating all of it. The values of δ^{13} C of the POM we collected 423 within the chlorophyll maximum (about -25 to -27‰) were lower than those usually reported 424 for oceanic environments (e.g. Waite et al. 2007, Hwang et al. 2009, Miyazki et al. 2011). 425 However, values of δ^{13} C of bulk POM as low as -25 to -29‰ have been reported at similar 426 depths in several offshore areas (Jeffrey et al. 1983, Durffel et al. 2003, Feunteun et al. 2015, 427 Soares et al 2015). These low δ^{13} C bulk POM values are measured within or just below the 428 depth of the chlorophyll maximum and this may be a common pattern in the open ocean 429 (Jeffrey et al. 1983, Durffel et al. 1998, Hwang et al. 2009, Close et al. 2014). Moreover, POM 430 is considered to be organic material that usually forms bigger particles commonly called 431 432 "marine snow" that contains various living organisms (Alldredge & Silver 1988, Shanks & Walters, 1997, Kiørboe, 2000). Therefore, bulk POM composition in the open ocean likely 433 depends on plankton communities but also on the non-living degraded part of the organic 434 435 matter as well as bacterial communities. Isotopic fractionation and thus the signature of the bulk POM can differ due to variations in physiological processes between phytoplanktonic 436 groups (metabolic ¹³C enrichment, C-fixation) that are related to cell size, physiology and 437 growth rate (Goericke & Fry 1994, Popp et al. 1998). POM with widely varying δ^{13} C and δ^{15} N 438 signatures can be found at different depths (Jeffrey et al. 1983, Waite et al. 2007, Miyazki et al. 439 2011, Feunteun et al. 2015), so our POM isotopic values may be related to the specific 440

signatures within the chlorophyll maximum, which is not targeted in studies that only sample at
particular depths. Or they could be partly related to aspects of the biological communities in
our study area, which have not yet been studied. These factors might explain the large range of
values in carbon and nitrogen signatures of POM in the WSP.

It is also possible that leptocephali do not feed exclusively within the chlorophyll 445 446 maximum or consume every type of POM. It is more likely that leptocephali select specific types of POM particles to eat, such as some types of marine snow or the appendicularian 447 houses that have been directly observed in the intestines of leptocephali (Mochioka and 448 Iwamizu 1996, Miller et al. 2011). In addition, some materials such as zooplankton faecal 449 pellets observed in gut contents (Otake et al. 1993, Miller et al. 2011) are unlikely to be 450 451 digested. Further differences between the SI signatures of the POM sample collected on a filter and those that leptocephali consume and assimilate might be related to the transparent 452 453 exopolymer particles (i.e. TEP; Passow 2002) produced by microorganisms (phytoplankton, 454 bacteria) that aggregate within POM. TEPs are mainly composed of carbohydrate molecules that aggregate into marine snow (Holloway and Cowen 1997, Skoog et al. 2008, Engel et al. 455 456 2012) and are at the interface between dissolved and particulate organic carbon (Passow 2002). 457 Therefore, a significant fraction of TEP is likely not retained on the GF/F filters used to collect POM from the water samples, leading to these compounds being only partially included in 458 459 POM carbon measurements; whereas they would have been present in the POM materials assimilated by leptocephali. In addition, carbohydrates are molecules having no nitrogen, only 460 the $\delta^{13}C$ signature of these compounds would be reflected in leptocephali if they were 461 462 assimilated (Feunteun et al. 2015). Also, leptocephali have a long larval duration, so as previous studies have pointed out, larger larvae could be transported into collection areas after 463 originating from other areas where they have fed on POM with different isotopic signatures 464 465 (Myazaki et al. 2011, Feunteun et al. 2015).

466

467 Feeding ecology of leptocephali

468 Considering the various possible factors discussed above, the SI and FA analyses of this 469 study may still be generally consistent with the hypothesis that leptocephali feed on POM, 470 which has been indicated by direct observations of their gut contents (Otake et al. 1993, Miller 471 et al. 2011) and an analysis of their trophic position (Miller et al. 2013). The observational 472 studies of the gut contents of leptocephali that have found POM components such as 473 amorphous materials, appendicularian and other zooplankton fecal pellets, and discarded

474 appendicularian houses (Otake et al. 1993, Mochioka & Iwamizu 1996, Miller et al. 2011), provide direct evidence of POM consumption by a variety of eel larvae taxa. Also, Feunteun et 475 al. (2015) characterised SI signatures of many taxa of zooplankton along with 12 taxa of 476 477 leptocephali and POM and did not find evidence of leptocephali feeding on zooplankton. 478 However, as in previous SI studies (Miyazaki et al. 2011, Feunteun et al. 2015) it remains 479 unclear what types and components of POM are used by various taxa of leptocephali, and 480 methodological issues related to the filtration and analysis of POM may make it difficult to see 481 clear linkages using SI analyses.

The FATM compositions determined in the present study and those of Deibel et al. 482 (2012) indicate that leptocephali obtain their nutrition from various sources that include both 483 484 phytoplankton (16:1 ω 7, 20:5 ω 3), dinoflagellates (22:6 ω 3) and heterotrophic microorganisms such as bacteria and protozoans (18:1 ω 9) (Dalsgaard et al. 2003), all of which are likely to 485 486 contribute to POM composition (Alldredge & Silver 1988, Shanks & Walters, 1997, Kiørboe, 487 2000). As explained above and also suggested in other studies (Dalsgaard et al. 2003, Pitt el al. 2009), the composition of the food contents in the intestines of leptocephali could be different 488 489 from what they assimilate from ingested food. Our FA results suggest that it is the materials 490 from living organisms associated with POM that are mainly assimilated by leptocephali (e.g. 491 FATM of autotrophic and heterotrophic organisms). Indeed, Muraenidae larvae were rich in 492 PUFAs and ω 3 meaning even they feed on FA poor food source, they are able to preferentially assimilate and store FAs-rich components of the POM. Conversely, Serrivomeridae larvae had 493 the highest SFA and lowest PUFAs and ω 3 proportions, which suggests that they may feed on 494 495 POM opportunistically, with no selective assimilation or FA storage.

496

497 FA and SI composition of Serrivomeridae size classes

Although no major differences were found in the isotopic compositions of the 4 size classes of Serrivomeridae leptocephali, clear changes in their FA composition were detected. The only significant SI differences were that δ^{13} C values differed between the largest (-21.4‰) and smallest (-19.9‰) size classes, but no significant differences were found in δ 15N values. In contrast, all the major categories of FAs showed at least minor changes with size, either increasing MUFA and PUFA or decreasing SFA contributions to TFAs.

The dynamic nature of lipid metabolism and the influence of dietary lipids when larvae first feed can cause FA composition shifts during ontogeny (Wiegand 1996, Rainuzzo et al. 1997, Plante et al. 2006, Grote et al. 2011), and shifts in the growth strategies of leptocephali 507 when they reach large sizes may result in physiological changes (Pfeiler 1999, Bishop et al. 2000). The decrease in percentage of SFAs in larger Serrivomeridae larvae might be caused by 508 16:0 and 18:0 being used as a major substrates for energy production (Sargent 1995). MUFAs 509 510 and PUFAs are energy sources for development and growth especially during the larval stage when fish need energy for organogenesis, fast growth and basal metabolism (Abi-ayad et al. 511 512 2004, Plante et al. 2006) and these tended to increase in proportion in the leptocephali. 513 Moreover, the PUFA 20:5 ω 3 is an important energy substrate, as well as the 22:6 ω 3, which is also one of the principal components of cell membranes (Dalsgaard et al. 2003). 514 In Serrivomeridae, the increase of MUFAs and PUFAs percentages with size suggest that these 515 516 energetically rich FAs are not preferentially used to provide energy during larval growth. Thus, 517 larvae may be preferentially storing energy dense FAs such as long chain FAs and PUFAs that they cannot synthesize and which are in low concentrations in POM, to support the later high-518 519 energy requirements of metamorphosis or to use during the early juvenile stage, when food 520 availability may be uncertain. In bonefish leptocephali, SFA, MUFA, and PUFA FAs were used during metamorphosis (e.g., 30% use of 16:0, 12% of 16:1 ω 7, 7% of 18:5 ω 3), but most of 521 522 22:6ω3 was conserved (Padrón et al. 1996). More species of leptocephali including those that 523 reach larger sizes than the Serrivomeridae should be examined to further evaluate how FA 524 compositions changes during growth and metamorphosis.

525

526 **Regional differences in leptocephali and POM**

The isotopic signatures of leptocephali in the 3 current zones showed variations that 527 appeared to be related to the POM signatures in each zone. Both $\delta^{15}N$ and $\delta^{13}C$ values of 528 Nemichthyidae and Muraenidae larvae decreased to some extent from north (SECC) to south 529 (STCC) and the same pattern was seen in POM signatures, especially for $\delta^{15}N.$ The 530 531 compositions of the FAs of POM and leptocephali also varied significantly among the current zones. This suggests there is regional variability in the nutritional quality (SFA and $22:6\omega3$ 532 contributions) and availability ($18:1\omega9$, $16:1\omega7$ and $18:4\omega3$) of POM. For example, the SECC 533 534 POM had the highest percentage of SFAs and the lowest percentage of MUFAs and PUFAs, which indicates a lower nutritional quality. This may be reflected in the FA compositions of 535 Serrivomeridae larvae that were mostly collected in the SECC, since they also had high SFA 536 537 contents and low contents of PUFAs compared to the other more widely distributed families. In contrast, the SEC and STCC tended to have POM with higher nutritional quality with larger 538 539 PUFA and ω 3 contributions.

540 These observed differences in POM may have affected the composition of the leptocephali, because many studies indicate that diversity and bioavailability of POM plays a 541 key role in ecosystem functioning by supporting the trophic network (Grémare et al. 1997, 542 543 Carlier et al. 2007), with regional variability in trophic resources being reflected in the consumers (Cartes et al. 2014, Chouvelon et al. 2014). Our sampling was spread across 20 544 degrees of latitude and crossed 3 current systems, so it is not surprising that geographic 545 546 variations were observed in both the SI signatures and FA compositions of POM and leptocephali. This variation was likely due to latitudinal differences in planktonic community 547 structure in the different current systems and temperature regimes, because differences in the 548 $\delta^{15}N$ of primary producers can cause variations in the $\delta^{15}N$ values of POM and organisms 549 between regions (Somes et al. 2010, Cartes et al. 2014, Lorrain et al. 2015, Soares et al. 2015). 550 Longitudinal differences in the δ^{15} N of mesozooplankton have also been observed around New 551 Caledonia (Hunt et al. 2015). 552

553 It is clear though, that questions remain about the feeding ecology of leptocephali, because this study and the study in the western Indian Ocean (Feunteun et al. 2015) have found 554 differences in the compositions of other taxa of leptocephali collected from the same area. 555 Feunteun et al. (2015) found that Nemichthyidae leptocephali had lower $\delta^{15}N$ values than 556 Muraenidae and Serrivomeridae leptocephali (and other families), and similar differences were 557 seen between Nemichthyidae and Muraenidae larvae in the STCC zone in the present study. 558 Similar $\delta^{15}N$ differences were also seen between Anguilla japonica and Congridae larvae of the 559 genus Ariosoma (Miyazaki et al. 2011) in the western North Pacific. Possible reasons 560 proposed for these differences are similar to those already discussed above, such as different 561 types of POM being selected, the taxa feeding at different depths where the POM is slightly 562 different, differences in assimilation of materials from the POM, or physiological differences 563 564 among leptocephalus taxa (Miyazaki et al. 2011, Feunteun et al. 2015). To begin to evaluate these possibilities, more research is needed using SI and FA analyses of leptocephali and other 565 food web components in a wider range of areas to gain a better understanding of the feeding 566 567 ecology of these fish larvae.

568

Acknowledgements. This project was realized thanks to the help of the captain, crew and technicians of the R/V *Hakuo Maru*. We also thank the other scientific members for assistance with sampling and plankton sorting. Fatty acid analyses were performed at the French National History Museum of Paris (MNHN-ResAqua), especially with help from Najet Thiney. Thanks also to Régis Gallon, Anthony Acou and Emmanuelle Sultan (MNHN, station marine
de Dinard), to Christel Lefrançois (University of La Rochelle, LIENs, DYFEA Team), Thierry
Wirth (MNHN – EPHE, France) as well as Paco Rodriguez Tress for helping on the project
and Dave T. Welsh (Griffith University) for a final editing.

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Isotopes/ FA	POM (n=39)	MR (n=27)	NM (n=28)	SR (n=41)		POM (stn=13)	MR (n=27)	NM (n=28)	SR (n=41)
Stable Isotopes		(()	(Polyunsat.	(*******)	()	(
$\delta^{15}N$	6.1 ± 2.3	6.7 ± 2.7	4.7 ± 3.3	10.9 ± 1.9	16:2@4	1.7 ± 0.41	0.57 ± 0.19	0.61 ± 0.17	$0.72 \hspace{0.2cm} \pm \hspace{0.2cm} 0.33$
$\delta^{13}C$	-26.6 ± 0.7	-20.5 ± 1.1	-19.9 ± 0.8	-21.0 ± 0.8	16:2ω6	- ± -	0.05 ± 0.02	$0.09 \hspace{0.2cm} \pm \hspace{0.2cm} 0.02$	0.04 ± 0.02
Saturated					16:4 w 3	0.22 \pm 0.06	0.05 ± 0.05	0.02 ± 0.03	0.05 ± 0.04
12:0	0.51 ± 0.25	0.08 ± 0.12	0.04 ± 0.06	0.07 \pm 0.1	18:2ω6	1.21 ± 0.26	$2.76 \hspace{0.2cm} \pm \hspace{0.2cm} 0.47$	$2.97 \hspace{0.2cm} \pm \hspace{0.2cm} 0.44$	2.55 ± 0.6
13:0	0.11 ± 0.03	0.02 ± 0.02	0.02 ± 0.01	0.03 \pm 0.1	18:3 ω 3	0.45 ± 0.09	1.15 ± 0.33	1.17 ± 0.56	0.8 \pm 0.28
14:0	$14.05 \hspace{0.2cm} \pm \hspace{0.2cm} 1.71$	3.99 ± 1.32	$4.63 \hspace{0.2cm} \pm \hspace{0.2cm} 0.86$	$4.12 \hspace{0.2cm} \pm \hspace{0.2cm} 0.6$	18:3ω6	0.42 ± 0.08	$0.28 \hspace{0.2cm} \pm \hspace{0.2cm} 0.06$	0.23 ± 0.06	$0.39 \hspace{0.1in} \pm \hspace{0.1in} 0.1$
15:0	1.7 ± 0.22	1.52 ± 0.23	1.71 ± 0.37	2.1 ± 0.2	18:4 ω 3	$1.69 \hspace{0.2cm} \pm \hspace{0.2cm} 0.52$	$1.24 \hspace{0.2cm} \pm \hspace{0.2cm} 0.26$	1.37 ± 0.44	1.16 ± 0.37
16:0	$35.91 \hspace{0.2cm} \pm \hspace{0.2cm} 2.28$	20.94 ± 2.44	24.04 ± 2.64	$26.63 \hspace{0.2cm} \pm \hspace{0.2cm} 4.3$	20:2\u00fc6	- ± -	0.24 ± 0.1	$0.11 \hspace{0.1in} \pm \hspace{0.1in} 0.05$	0.08 ± 0.05
17:0	0.67 \pm 0.11	1.73 ± 0.18	1.26 ± 0.18	1.75 ± 0.3	20:3	- ± -	$0.15 \hspace{0.2cm} \pm \hspace{0.2cm} 0.04$	$0.15 \hspace{0.2cm} \pm \hspace{0.2cm} 0.04$	$0.09 \hspace{0.2cm} \pm \hspace{0.2cm} 0.03$
18:0	$19.47 \hspace{0.2cm} \pm \hspace{0.2cm} 2.31$	9.32 ± 1.25	5.14 ± 1.7	9.1 ± 2.9	20:3ω6	- ± -	$0.37 \hspace{0.2cm} \pm \hspace{0.2cm} 0.08$	0.24 ± 0.06	0.27 \pm 0.1
19:0	0.46 ± 0.09	0.31 ± 0.1	0.2 ± 0.09	0.34 ± 0.2	20:4 w 3	0.09 ± 0.02	1.4 ± 0.77	0.86 ± 0.3	0.96 ± 0.69
20:0	0.85 ± 0.1	0.27 \pm 0.07	0.14 ± 0.03	0.35 ± 0.2	20:4\omega6	0.13 ± 0.04	$2.82 \hspace{0.2cm} \pm \hspace{0.2cm} 0.79$	$2.81 \hspace{0.2cm} \pm \hspace{0.2cm} 0.51$	3.49 ± 0.96
21:0	0.06 ± 0.02	0.04 ± 0.01	0.03 ± 0.05	0.03 ± 0	20:5 w 3	1.02 ± 0.22	$7.85 \hspace{0.2cm} \pm \hspace{0.2cm} 0.97$	$8.52 \hspace{0.2cm} \pm \hspace{0.2cm} 1.22$	5.05 ± 2.07
22:0	0.58 ± 0.13	0.19 ± 0.04	0.14 ± 0.03	0.17 ± 0.1	22:2@6	0.27 \pm 0.14	- ± -	- ± -	- ± -
24:0	0.58 ± 0.25	0.08 ± 0.06	0.04 ± 0.03	0.09 ± 0.1	22:4ω6	- ± -	0.36 ± 0.15	0.27 \pm 0.21	0.12 ± 0.13
Σ SFA (%)	75.23 ± 4.58	38.5 ± 3.65	37.41 ± 4.2	44.79 ± 7.5	22:5 ω 3	- ± -	$2.79 \hspace{0.2cm} \pm \hspace{0.2cm} 1.58$	0.95 \pm 0.51	$0.93 \hspace{0.2cm} \pm \hspace{0.2cm} 0.59$
Monounsat.					22:5\omega6	0.19 ± 0.11	2.18 ± 0.65	2.24 ± 0.37	2.34 ± 0.63
16:1ω5	0.07 ± 0.03	0.14 ± 0.03	0.15 ± 0.03	0.13 ± 0	22:6 ω 3	1.67 ± 0.79	18.1 ± 2.13	16.8 ± 2.58	14.8 ± 3.16
16:1ω7	$4.42 \hspace{0.2cm} \pm \hspace{0.2cm} 0.88$	5.71 ± 1.14	$7.6 \hspace{0.2cm} \pm \hspace{0.2cm} 1.77$	6.59 ± 1.3	Σ PUFA (%)	9.1 \pm 2.1	42 ± 3.7	39 ± 4.2	34 ± 5.7
16:1ω9	2.07 ± 0.5	0.54 ± 0.09	0.66 ± 0.13	0.63 ± 0.1	Branched-chain				
17:1ω7	0.37 ± 0.08	0.45 ± 0.12	0.49 ± 0.11	0.32 ± 0.1	14:0iso	0.35 ± 0.1	0.01 ± 0.01	0.22 ± 0.01	0.03 ± 0.01
17:1ω9	- ± -	0.45 ± 0.1	0.73 ± 0.15	0.75 ± 0.1	15:0anteiso	0.45 ± 0.06	0.03 ± 0.01	0.04 ± 0.02	0.05 ± 0.03
18:1ω5	- ± -	0.1 ± 0.03	0.1 ± 0.03	0.11 ± 0	15:0iso	0.37 ± 0.05	0.12 ± 0.03	0.14 ± 0.03	0.17 ± 0.05
18:1ω7	0.71 ± 0.16	4.18 ± 0.77	3.93 ± 0.63	2.82 ± 0.7	16:0iso	0.22 ± 0.04	0.08 ± 0.02	0.1 ± 0.04	0.13 ± 0.04
18:1 ω 9	5.3 ± 1.06	5.84 ± 0.94	8.33 ± 1.72	8.77 ± 1.3	17:0anteiso	0.68 ± 0.17	0.08 ± 0.02	0.1 ± 0.03	0.11 ± 0.04
19:1ω9	- ± -	0.03 ± 0.02	0.02 ± 0.02	0.03 ± 0	17:0iso	0.05 ± 0.01	0.12 ± 0.03	0.26 ± 0.05	0.27 \pm 0.06
20:1ω7	- ± -	0.18 ± 0.08	0.12 ± 0.04	0.09 ± 0.1	18:0iso	0.26 ± 0.09	0.07 ± 0.05	0.16 ± 0.06	0.13 ± 0.05
20:1ω9	- ± -	0.22 ± 0.21	0.13 ± 0.07	0.1 ± 0.1	Σ BrFA (%)	2.38 ± 0.3	0.5 ± 0.1	0.8 ± 0.1	0.9 ± 0.2
22:1 ω 11	0.38 ± 0.13	0.09 ± 0.1	0.03 ± 0.02	0.06 ± 0	Total FA (mg.g-1)	3.6 ± 0.97	11.7 ± 7.44	5.22 ± 2.51	5.41 ± 3.99
22:1ω9	- ± -	0.05 ± 0.02	0.01 \pm 0.01	0.02 ± 0	Σω3	5.14 ± 1.46	32.5 ± 3.77	29.7 ± 3.84	23.7 ± 5.51
24:1ω9	- ± -	0.08 ± 0.05	0.06 ± 0.05	0.07 ± 0.1	Σω6	1.95 ± 0.12	9.06 ± 1.44	8.96 ± 0.83	9.28 ± 1.62
Σ MUFA (%)	13.33 ± 2.66		22.38 ± 2.9	20.49 ± 2.5	Σ EFA	2.82 ± 0.35	$28.7 \hspace{0.2cm} \pm \hspace{0.2cm} 1.3$	$28.1 \hspace{0.2cm} \pm \hspace{0.2cm} 1.44$	$23.3 \hspace{0.1in} \pm \hspace{0.1in} 2.06$
(-3)									

Table 1. Fatty acid relative contribution (%) and Carbon (δ^{13} C) and Nitrogen (δ^{15} N) mean isotopic signature of Particulate Organic Matter (POM) for 13 stations (3 replicates per station) and all leptocephali tissues for the three families Muraenidae (MR), Nemichthyidae (NM) and Serrivomeridae (SR). All values are mean ± S.D. n is the number of samples.

Isotopes/ FA	$\leq 10 \text{ mm}$ (n=5)	10-20 mm (n=6)	20-40 mm (n=20)	40-60 mm (n=10)		$\leq 10 \text{ mm}$ (n=5)	10-20 mm (n=6)	20-40 mm (n=20)	40-60 mm (n=10)
Stable Isotopes					Polyunsat.				
δ^{15} N	11.1 ± 1.4	11.8 ± 0.8	10.6 ± 1.9	10.0 ± 2.3	16:2ω4	0.36 ± 0.21	0.83 ± 0.39	0.68 ± 0.3	0.94 ± 0.24
$\delta^{13}C$	-19.9 ± 0.57	-21.3 ± 1.0	-20.6 ± 0.8	-21.4 ± 0.5	16:2ω6	0.01 \pm 0.01	0.04 ± 0.02	0.04 ± 0.02	0.05 ± 0.03
Saturated					16:4ω3	0.05 ± 0.05	0.07 \pm 0.04	0.05 ± 0.04	0.03 ± 0.02
12:0	0.13 ± 0.11	0.06 ± 0.06	0.07 \pm 0.05	0.04 ± 0.02	18:2@6	$1.93 \hspace{0.1in} \pm \hspace{0.1in} 0.73$	2.81 ± 0.3	$2.78 \hspace{0.2cm} \pm \hspace{0.2cm} 0.26$	$2.25 \hspace{0.2cm} \pm \hspace{0.2cm} 0.82$
13:0	0.05 ± 0.02	0.04 ± 0.03	0.03 ± 0.01	0.03 \pm 0.01	18:3ω3	0.48 ± 0.3	0.76 ± 0.2	$0.79 \hspace{0.2cm} \pm \hspace{0.2cm} 0.26$	1.1 ± 0.2
14:0	$4.5 \hspace{0.2cm} \pm \hspace{0.2cm} 0.54$	3.84 ± 0.88	$3.99 \hspace{0.2cm} \pm \hspace{0.2cm} 0.55$	$4.35 \hspace{0.2cm} \pm \hspace{0.2cm} 0.61$	18:3@6	$0.32 \hspace{0.2cm} \pm \hspace{0.2cm} 0.05$	0.43 ± 0.06	0.42 ± 0.1	0.37 ± 0.14
15:0	$2.25 \hspace{0.2cm} \pm \hspace{0.2cm} 0.29$	2.07 ± 0.27	$2.16 \hspace{0.2cm} \pm \hspace{0.2cm} 0.16$	$1.95 \hspace{0.2cm} \pm \hspace{0.2cm} 0.12$	18:4 ω 3	$0.69 \hspace{0.2cm} \pm \hspace{0.2cm} 0.41$	$1.17 \hspace{0.1in} \pm \hspace{0.1in} 0.29$	$1.23 \hspace{0.1in} \pm \hspace{0.1in} 0.32$	$1.24 \hspace{0.1in} \pm \hspace{0.1in} 0.34$
16:0	$33.23 \hspace{0.2cm} \pm \hspace{0.2cm} 5.29$	$27.01 \hspace{.1in} \pm \hspace{.1in} 1.33$	27.22 ± 2.67	$21.95 \hspace{0.2cm} \pm \hspace{0.2cm} 1.67$	20:2ω6	0.1 \pm 0.12	0.06 ± 0.02	0.07 ± 0.02	$0.12 \hspace{0.2cm} \pm \hspace{0.2cm} 0.03$
17:0	1.79 ± 0.14	1.76 ± 0.24	1.83 ± 0.27	1.56 ± 0.21	20:3	0.07 ± 0.04	0.07 \pm 0.02	0.09 ± 0.02	$0.12 \hspace{0.2cm} \pm \hspace{0.2cm} 0.02$
18:0	13.18 ± 3.9	9.9 ± 2.25	$9.17 \hspace{0.2cm} \pm \hspace{0.2cm} 2.13$	6.42 ± 0.62	20:3ω6	0.16 ± 0.05	0.25 \pm 0.05	0.25 \pm 0.06	0.4 \pm 0.08
19:0	$0.69 \hspace{0.2cm} \pm \hspace{0.2cm} 0.24$	0.32 \pm 0.14	0.3 ± 0.09	0.24 ± 0.08	20:4ω3	$0.41 \hspace{0.2cm} \pm \hspace{0.2cm} 0.24$	$0.69 \hspace{0.2cm} \pm \hspace{0.2cm} 0.22$	0.67 \pm 0.16	1.96 ± 0.7
20:0	0.46 ± 0.15	0.48 ± 0.39	$0.31 \hspace{0.1in} \pm \hspace{0.1in} 0.07$	$0.32 \hspace{0.2cm} \pm \hspace{0.2cm} 0.09$	20:4ω6	3.73 ± 1.25	3.69 ± 0.77	3.89 ± 0.66	2.46 ± 0.74
21:0	0.04 ± 0.02	0.03 ± 0.01	0.04 ± 0.01	0.03 ± 0.01	20:5ω3	4.04 ± 1.55	5.02 ± 0.69	4.47 ± 2.42	6.75 ± 0.98
22:0	0.24 ± 0.07	0.16 ± 0.03	0.17 ± 0.03	0.14 ± 0.03	22:4ω6	0.03 ± 0.06	0.11 ± 0.11	0.09 ± 0.12	0.22 \pm 0.13
24:0	0.18 ± 0.08	0.13 ± 0.11	0.07 ± 0.06	0.08 ± 0.07	22:5ω3	0.44 \pm 0.17	0.66 ± 0.1	0.77 \pm 0.19	1.67 \pm 0.77
Σ SFA (%)	56.73 ± 0.91	$45.79 \hspace{0.1 in} \pm \hspace{0.1 in} 0.48$	45.36 ± 0.51	37.09 ± 0.3	22:5ω6	$2.12 \hspace{.1in} \pm \hspace{.1in} 0.68$	2.36 ± 0.4	$2.51 \hspace{0.2cm} \pm \hspace{0.2cm} 0.75$	2.08 ± 0.3
Monounsat.					22:6w3	10.25 ± 4.35	13.54 ± 1.81	14.99 ± 2.22	17.36 ± 1.95
16:1ω5	0.08 ± 0.04	0.13 ± 0.02	0.14 ± 0.03	$0.13 \hspace{0.1in} \pm \hspace{0.1in} 0.02$	Σ ΡυγΑ	25.17 ± 0.6	32.55 ± 0.32	33.78 ± 0.47	39.01 ± 0.44
16:1ω7	$4.95 \hspace{0.2cm} \pm \hspace{0.2cm} 0.81$	6.54 ± 1.14	$6.31 \hspace{0.1in} \pm \hspace{0.1in} 0.68$	8.01 ± 1.24	Branched-chain				
16:1ω9	0.49 ± 0.14	0.63 ± 0.05	0.65 ± 0.08	0.67 \pm 0.06	14:0iso	0.04 \pm 0.01	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
17:1ω7	0.3 ± 0.03	0.27 ± 0.07	0.34 ± 0.1	0.33 ± 0.08	15:0anteiso	$0.11 \hspace{0.1in} \pm \hspace{0.1in} 0.02$	0.05 ± 0.02	0.05 ± 0.02	0.03 ± 0.01
17:1ω9	0.6 ± 0.15	0.77 ± 0.08	0.73 ± 0.11	0.84 ± 0.09	15:0iso	0.21 \pm 0.07	0.15 ± 0.02	0.17 ± 0.04	0.18 ± 0.04
18:1 ω 5	0.05 ± 0.03	0.11 ± 0.01	0.11 ± 0.03	0.13 ± 0.02	16:0iso	0.17 ± 0.07	0.12 ± 0.02	0.13 ± 0.04	0.14 ± 0.03
18:1ω7	2.4 ± 0.3	2.77 ± 0.32	$2.63 \hspace{0.2cm} \pm \hspace{0.2cm} 0.78$	3.47 ± 0.38	17:0anteiso	0.15 ± 0.09	0.11 ± 0.03	0.1 ± 0.02	0.08 ± 0.02
18:1ω9	7.81 ± 2.11	9.33 ± 0.64	$8.76 \hspace{0.2cm} \pm \hspace{0.2cm} 1.23$	8.92 ± 0.94	17:0iso	0.27 \pm 0.05	0.25 \pm 0.04	0.27 \pm 0.07	0.29 \pm 0.05
19:1ω9	0.02 ± 0.02	0.03 ± 0.03	0.01 ± 0.02	0.06 ± 0.04	18:0iso	0.13 ± 0.05	0.12 ± 0.09	0.13 ± 0.05	0.14 ± 0.03
20:1@7	0.06 ± 0.02	0.06 ± 0.03	0.07 ± 0.02	0.15 ± 0.07	Σ BrFA (%)	1.07 ± 0.05	0.82 ± 0.03	0.88 ± 0.04	0.88 ± 0.03
20:1@9	0.07 ± 0.03	0.07 ± 0.04	0.08 ± 0.03	0.19 ± 0.12	Total FA (mg.g-1)	5.82 ± 1.08	5.19 ± 1.92	4.62 ± 1.41	4.36 ± 1.54
22:1 ω 11	0.08 ± 0.05	0.06 ± 0.03	0.06 ± 0.03	0.05 ± 0.02	Σω3	16.36 ± 1.01	$21.9 \hspace{0.2cm} \pm \hspace{0.2cm} 0.48$	22.97 ± 0.8	30.01 ± 0.71
22:1 ω 9	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.02	0.02 ± 0.01	Σω6	$8.39 \hspace{0.2cm} \pm \hspace{0.2cm} 0.37$	9.74 ± 0.22	$10.05 \hspace{0.2cm} \pm \hspace{0.2cm} 0.25$	7.95 ± 0.28
24:1ω9	0.1 ± 0.03	0.05 ± 0.04	0.07 \pm 0.05	0.07 \pm 0.07	Σ EFA	18.02 ± 2.38	$22.25 \hspace{0.2cm} \pm \hspace{0.2cm} 1.09$	$23.35 \hspace{0.2cm} \pm \hspace{0.2cm} 1.77$	$26.57 \hspace{0.1in} \pm \hspace{0.1in} 1.20$
Σ MUFA (%)	17.03 ± 0.27	20.84 ± 0.18	19.98 ± 0.23	23.02 ± 0.23					

Table 2. Fatty acid relative contribution (%) and Carbon (δ^{13} C) and nitrogen (δ^{15} N) mean isotopic signature of Serrivomeridae leptocephali from four different size groups ($\leq 10, 10.1$ -20.0, 20.1-40.0 and 40.1-60.0 mm). The 5 samples of ≤ 10 mm larvae each include 2 larvae pooled together. All values are mean \pm S.D. n is the number of samples.

Table 3: Fatty acid relative contribution (%) of particulate organic matter (POM) from three different currents (South Equatorial Countercurrent (SECC),

810 South Equatorial Current (SEC) and Sub-Tropical Countercurrent (STCC). All values are mean ± S.D. n is the number of samples.

Isotopes/ FA		POM in SECC (n=15)		POM in SEC (n=15)		POM in STCC (n=9)			POM in SE (n=15)				OM in SEC (n=15)		POM in STCC (n=9)				
Stable Isotopes $\delta^{15}N$ $\delta^{13}C$	7.7 -26.2	± ±	2.3 0.9	6.1 -26.6	± ±	2.2 0.5	4.1 -27.0	± ±	1.0 0.2	Polyunsat. 16:2ω4 16:4ω3	0.97 0.26	± ±	0.32 0.08	1.98 0.22	± ±	0.4 0.04	2.45 0.18	± ±	0.56 0.07
Saturated FA										18:2ω6	1.1	±	0.21	1.24	±	0.21	1.34	±	0.45
12:0	0.48	±	0.19	0.6	±	0.32	0.41	±	0.23	18:3 ω 3	0.44	±	0.07	0.44	±	0.08	0.49	±	0.14
13:0	0.1	±	0.03	0.13	±	0.03	0.07	±	0.01	18:3ω6	0.4	±	0.09	0.43	±	0.07	0.42	±	0.06
14:0	14.05	±	1.48	14.6	±	1.74	13.14	±	2.03	18:4 ω 3	1.16	±	0.24	1.93	±	0.55	2.16	±	0.92
15:0	1.71	±	0.25	1.64	±	0.25	1.8	±	0.11	20:4w3	0.09	±	0.03	0.08	±	0.01	0.1	±	0.03
16:0	37.75	±	1.9	34.87	±	2.43	34.59	±	2.63	20:4ω6	0.11	±	0.03	0.14	±	0.05	0.16	±	0.04
17:0	0.74	±	0.11	0.64	±	0.13	0.61	±	0.06	20:5ω3	0.88	±	0.21	0.9	±	0.18	1.43	±	0.3
18:0	21.31	±	2.2	18.29	±	2.56	19.53	±	2.08	22:2ω6	0.31	±	0.2	0.32	±	0.13	0.13	±	0.05
19:0	0.45	±	0.08	0.42	±	0.08	0.54	±	0.12	22:5ω6	0.21	±	0.15	0.15	±	0.08	0.21	±	0.11
20:0	0.94	±	0.13	0.79	±	0.08	0.79	±	0.08	22:6w3	1.17	±	0.51	1.71	±	0.76	2.43	±	1.31
21:0	0.06	±	0.02	0.07	±	0.02	0.05	±	0.02	Σ PUFA (%)	7.11	±	1.44	9.53	±	1.96	11.5	±	3.47
22:0	0.62	±	0.17	0.56	±	0.11	0.55	±	0.11	Branched-chain									
24:0	0.6	±	0.26	0.56	±	0.2	0.59	±	0.3	14:0iso	0.34	±	0.12	0.35	±	0.08	0.37	±	0.09
Σ SFA (%)	78.83	±	3.86	73.16	±	4	72.7	±	6.72	15:0anteiso	0.46	±	0.08	0.4	±	0.05	0.5	±	0.06
Monounsat.										15:0iso	0.39	±	0.06	0.34	±	0.04	0.37	±	0.04
16:1ω5	0.08	±	0.04	0.08	±	0.03	0.07	±	0.03	16:0iso	0.21	±	0.06	0.21	±	0.04	0.23	±	0.02
16:1ω7	3.62	±	0.73	5.62	±	1.1	3.76	±	0.75	17:0anteiso	0.64	±	0.18	0.99	±	0.26	0.23	±	0.02
16:1ω9	1.99	±	0.49	2.2	±	0.46	1.99	±	0.57	17:0iso	0.06	±	0.01	0.05	±	0.02	0.04	±	0.01
17:1ω7	0.39	±	0.1	0.34	±	0.04	0.37	±	0.12	18:0iso	0.23	±	0.09	0.28	±	0.06	0.29	±	0.13
18:1ω7	0.65	±	0.16	0.73	±	0.14	0.8	±	0.2	Σ BrFA (%)	2.34	±	0.46	2.62	±	0.36	2.03	±	0.08
18:1ω9	4.63	±	0.91	5.32	±	0.71	6.36	±	1.9	Total FA (mg.g-1)	2.86	±	0.83	4.49	±	0.77	3.33	±	1.53
22:1w11	0.36	±	0.11	0.39	±	0.12	0.42	±	0.17	$\Sigma \omega 3$	4.00	±	0.87	5.27	±	1.49	6.81	±	2.4
Σ MUFA (%)	11.71	±	2.87	14.68	±	2.1	13.8	±	3.32	$\Sigma \omega 6$	2.14	±	0.14	2.28	±	0.11	2.26	±	0.14
										ΣEFA	2.16	±	0.25	2.75	±	0.33	4.02	±	0.55

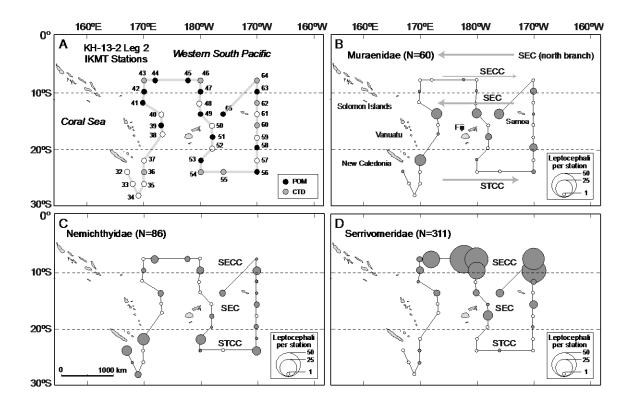


Figure 1: Maps of the KH-13-2 sampling survey of the R/V *Hakuho Maru* showing (A) the IKMT stations for collecting leptocephali (St. 32–65) and stations where particulate organic matter (POM) was analyzed (black circles) and where other CTD casts were made (shaded circles). The number of leptocephali caught per station of (B) Muraenidae (C) Nemichthyidae, and (D) Serrivomeridae are represented by the relative sizes of the shaded circles. The general locations of the South Equatorial Current (SEC), South Equatorial Countercurrent (SECC) and South Tropical Countercurrent (STCC) are shown with arrows, and the dotted lines separate the 3 current zones used for analyzing latitudinal differences in SI and FA compositions of leptocephali and POM.

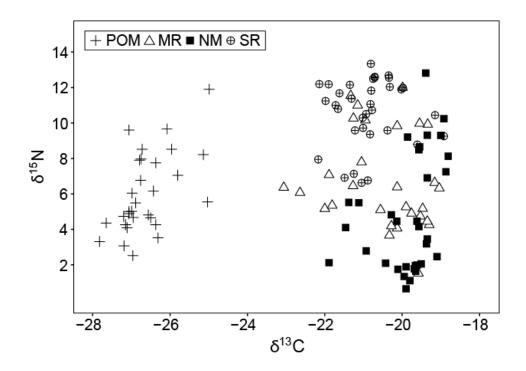


Figure 2. Carbon and nitrogen stable isotope values of particulate organic matter (POM) and the leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM).

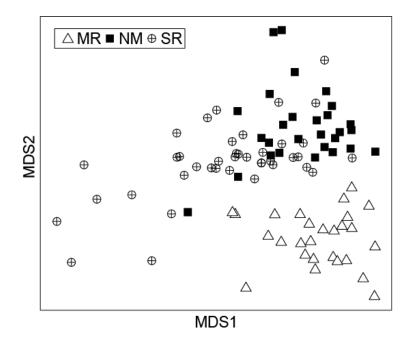


Figure 3. Non-metric multi-dimensional scaling (n-MDS) based on Bray-Curtis similarity distance of total fatty acid composition for leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM). Stress = 0.12.

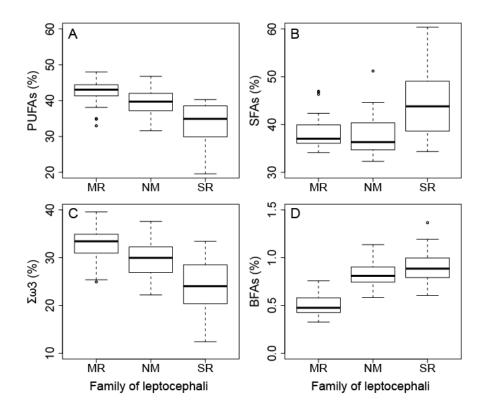


Figure 4. Fatty acids proportions (median, first and third quartiles) of (a) Polyunsatured Fatty Acids (PUFAs), (b) Saturated Fatty Acids (SFAs), (c) sum of ω 3 Fatty Acids ($\Sigma\omega$ 3), (d) Branched-chain Fatty Acides (BrFAs), for the leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM).

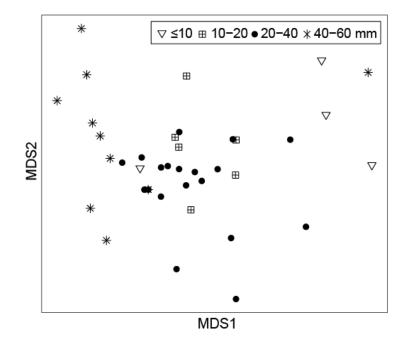


Figure 5. Non-metric MultiDimensional Scaling (n-MDS) based on Bray-Curtis similarity distance of total fatty acid concentration (mg g^{-1}) of Serrivomeridae leptocephali for 4 different size groups (see methods for exact size ranges). Stress = 0.08.

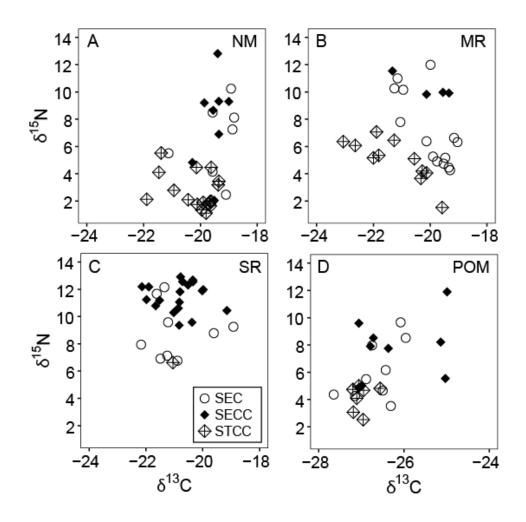


Figure 6. Carbon and nitrogen stable isotope values of (A) Nemichthyidae, (B) Muraenidae, (C) Serrivomeridae leptocephali and (D) POM from the 3 current zones of the South Equatorial Countercurrent (SECC), South Equatorial Current (SEC), and South Tropical Countercurrent (STCC).