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2 **Geographic variation in stable isotopic and fatty acid composition**
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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
48 they apparently feed on particulate organic matter (POM), which varies in composition, and it
49 is unclear which components of the POM they assimilate. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope
50 (SI) and fatty acid (FA) compositions of 3 families of leptocephali and POM were compared in
51 3 latitudinal current zones of the western South Pacific. The $\delta^{15}\text{N}$ signatures of both
52 leptocephali and POM overlapped, with both having their lowest values in the southern current
53 zone. POM contained 38 FAs and was rich in saturated FAs (SFA) (16:0, 18:0, 14:0), while
54 leptocephali contained 50 FAs, with high proportions of 16:0, and higher contributions of
55 22:6 ω 3, 20:5 ω 3, 18:1 ω 9, 16:1 ω 7 and other FAs than the POM. Serrivomeridae leptocephali in
56 the north had higher $\delta^{15}\text{N}$ signatures and were also distinguished from Nemichthyidae and
57 Muraenidae larvae by their FA compositions (higher SFAs, lower 22:6 ω 3 and 20:5 ω 3).
58 Although SI signatures of the Serrivomeridae larvae did not clearly vary with size, 16:0 and
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
61 FA compositions of POM with those of leptocephali and the presence of FA markers of both
62 autotrophic and heterotrophic organisms were consistent with leptocephali feeding on POM.
63 POM can contain various materials from primary producers and heterotrophic microorganisms,
64 but differences in the SI signatures and FA compositions in leptocephali remain to be
65 explained through further research.

66

67 **KEYWORDS:** Leptocephali, fatty acids, stable isotopes, biomarkers, trophic ecology, oceanic
68 currents.

69

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

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

82 Despite their wide distributions and the extensive literature on their morphology (*e.g.*,
83 Böhlke 1989), the feeding ecology of leptocephali is still poorly resolved. During their larval
84 feeding and growth period, leptocephali accumulate energy storage compounds such as lipids
85 and glycosaminoglycans (GAG) in a gelatinous body matrix, which are then used for building
86 new tissues during metamorphosis (Padrón et al. 1996, Pfeiler 1999, Pfeiler et al. 2002). A few
87 studies have examined the gut contents of leptocephali and have observed materials that
88 resemble particulate organic matter (POM) such as marine snow, discarded appendicularian
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
94 organisms such as protozoans (Tanaka et al. 1995, Govoni 2010) and the DNA sequences of
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, Kjørboe 2000). Therefore, the hypothesis that
99 leptocephali feed on POM and assimilate some of the components of marine snow, including
100 colonising microorganisms, appears most likely (Deibel et al. 2012, Miller et al. 2013,
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
103 in leptocephali have not always been observed (Miyazaki et al. 2011, Feunteun et al. 2015).
104 Thus, it is unclear if leptocephali feed on POM opportunistically or if there are selective
105 differences in the types of POM consumed and/or the types of compounds assimilated from
106 ingested POM between different taxa.

107 An important component of the POM and organisms that potentially contribute to the
108 diet of leptocephali are lipids, but only a few studies have examined the lipid content of
109 leptocephali (Padrón et al. 1996, Deibel et al. 2012). Lipids are important for marine
110 organisms because they are their major metabolic energy reserves (Falk-Petersen et al. 2000,
111 Lee et al. 2006) and play key roles in cell structure and metabolism (Dalsgaard et al. 2003).
112 Fatty acids (FAs) are a specific class of lipids that are energy rich molecules (Dalsgaard et al.

113 2003). Most consumers are unable to synthesize essential FAs (EFAs: 20:4 ω 6, 20:5 ω 3,
114 22:6 ω 3), which are polyunsaturated FAs (PUFAs) with a terminal end omega-3 (ω 3) or
115 omega-6 (ω 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, Styrihave & 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
120 assimilated by the organism over time (Pitt et al. 2009). SI ratios of carbon ($\delta^{13}\text{C}$) and nitrogen
121 ($\delta^{15}\text{N}$) are used to evaluate the food sources of organisms (Fry & Sherr 1984, Canuel et al.
122 1995) and to characterize organic matter transfer through food webs (Fry & Sherr 1984, Canuel
123 et al. 1995, Abrantes & Sheaves 2009). FAs can be used as biomarkers of specific organisms
124 (Meziane et al. 2007), or to determine the food sources exploited by consumer organisms
125 (Meziane et al. 1997, Meziane & Tsuchiya 2000, Mortillaro et al. 2015). They can also be
126 used to follow organic matter transfer through food webs (Dalsgaard et al. 2003, Budge et al.
127 2006, Hall et al. 2006) and can provide information on larval ontogenetic changes (Plante et al.
128 2006).

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

135

136 **MATERIALS AND METHODS**

137 **Study area and sample collection**

138 Leptocephali were collected in the western South Pacific (WSP) during Leg 1 of the
139 KH-13-2 research cruise of the research vessel (R/V) *Hakuho Maru* from 4–24 February 2013.
140 Thirty-four stations were sampled at every 2° of latitude/longitude between 5°S–30°S and
141 165°E–175°W, in the region that includes New Caledonia, Fiji and Samoa (Figure 1A).
142 Leptocephali were collected using an Isaacs-Kidd midwater trawl (IKMT) with an 8.7 m²
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
145 and 50 m), and during the day an oblique tow fished from the surface to 200 m, with both types

146 of tows taking less than 1 hour. Temperature, conductivity, depth (CTD) profiles were made at
147 21 of the stations to a depth of 500 m.

148 Leptocephali from each IKMT sample were sorted fresh, measured and identified to the
149 lowest possible taxonomic level according to Miller & Tsukamoto (2004). A total of 538
150 leptocephali from 13 families were collected, but only the 3 most abundant families were
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,
153 and 101 leptocephali from the 3 most abundant families; Muraenidae ($n=27$; length 25.3–83.0
154 mm, $\text{mean}\pm\text{S.D.}= 50.1\pm 13.4$ mm), Nemichthyidae ($n=28$; length 30.0–259.0 mm, 122.0 ± 60.5)
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
157 the smallest larvae (< 10 mm) pooled together to obtain enough tissue for analysis. Each
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
160 to leptocephalus size, because of the insufficient specimens of different sizes of Muraenidae
161 and Nemichthyidae larvae, and the Serrivomeridae larvae were mostly from the same current
162 zone.

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

173

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 ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) 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
180 analysis (half body, excluding the head region except for the smallest larvae) and an Elementar
181 Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau,
182 Germany) for the GF/F filter POM samples (half filter). Each elemental analyser was
183 interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire,
184 UK). Isotopic data are reported using standard delta notation ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$), defined as parts
185 per thousand deviation (‰) from an international standard (Vienna Peedee belemnite for $\delta^{13}\text{C}$
186 and atmospheric N_2 for $\delta^{15}\text{N}$) as defined by the equation:

$$187 \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

188

189 Where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$ of the sample or standard (Peterson & Fry 1987). The
190 analytical precision (standard deviation for repeated measurements of internal standards) was
191 $\pm 0.2\text{‰}$ and $\pm 0.3\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. All mean values of SI and FA data are
192 expressed as mean \pm standard deviation (S.D.).

193

194 **Fatty acid analysis**

195 Lipids were extracted following Meziane et al. (2007). Briefly, lipid samples (half
196 bodies or filters) were extracted twice with a mixture of distilled water, MeOH and CHCl_3
197 (1:2:1, v:v:v). Saponification and methylation were performed successively under reflux
198 according to Meziane & Tsuchiya (2000). Saponification was achieved using a 2 M
199 NaOH:MeOH solution (1:2, v:v) and methylation with 1 ml of 14% BF_3 -MeOH. The fatty
200 acid methyl esters (FAMES) were separated and quantified by Gas Chromatography (Varian
201 CP-3800) using a flame ionisation detector at the National Museum of Natural History
202 (MNHN-Paris, Resaqua Laboratory). Separation was performed with an Agilent J&W GC
203 VF-WAXms column (30 m x 0.25 mm i.d.; 0.25 μm film thickness) with He as carrier gas.
204 Most of FAs peaks were identified by comparing their retention times with those of known
205 standards (SupelcoTM 37 FAME mix; Sigma-Aldrich[®]) and confirmed with a GC-mass
206 spectrometer (Varian 450-GC 220-Ion Trap MS; He as carrier gas). FAs are designated as
207 X:Y ω Z, where X is number of carbon atoms, Y is number of double bonds and Z is the
208 position of the ultimate double bond with respect to the terminal methyl group. The
209 concentration of each FA was calculated using 23:0 as an internal standard according to
210 Schomburg (1987): $C_{\text{FA}} = A_{\text{S}}/A_{\text{IS}} \times C_{\text{IS}}/W_{\text{S}}$, where A_{S} is the peak area of the FA, A_{IS} the peak

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

213

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)
218 at northern stations (8°N) to 25°C and 18°C respectively in the south (24°S). This region
219 includes 3 main surface currents at different latitudes, which are the westward South Equatorial
220 Current (SEC, Equator to 20°S), the narrow eastward South Equatorial Countercurrent (SECC)
221 at 5 to 10°S (between two branches of the SEC), and the eastward South Tropical
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
225 eastward flow in the south (Otake et al. unpubl. cruise report). 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
228 Nemichthyidae being more equally distributed across latitudes (Miller et al. 2006) as they were
229 during the present survey (Figure 1B-D). According to the general pattern of currents, the
230 cruise stations were separated into 3 latitudinal zones for analyses of SI and FA compositions
231 of leptocephali and POM, which generally correspond with the SECC, SEC, and STCC current
232 systems (Figure 1B).

233

234 **Data analysis**

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

242 All FAs were used in the analyses and no transformations were performed on the
243 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
245 coefficient, followed by non-metric multidimensional scaling (n-MDS). Stress values < 0.2
246 were considered robust (Clarke 1993). Groups used as factors for the analysis were family
247 (Muraenidae, Nemichthyidae, Serrivomeridae) and size groups (≤ 10.0 , 10.1–20.0, 20.1–40.0,
248 40.1–60.0 mm, Serrivomeridae only), as well as current zones (SEC, SEC, STCC) for both
249 leptocephali and POM. Differences in FAs composition among groups was statistically tested
250 using separate one-way analysis of similarity (ANOSIM) computed after 5000 permutations.
251 Average dissimilarity (AD) between groups was determined by SIMilarity of PERcentage
252 (SIMPER) analysis (PRIMER[®]5 software module) was used to identify which fatty acids
253 determine the observed differences within or between groups.

254 Multivariate analyses were performed with PRIMER[®]5 software (Clarke & Warwick,
255 2001) and univariate tests using R software (R development Core Team 2014, Vegan package,
256 Oksanen et al. 2014). For all univariate tests, the probability α was set at 0.05.

257

258 **RESULTS**

259 **Isotopic and fatty acids composition of Particulate organic matter and leptocephali**

260

261 **Particulate organic matter (POM).** SI values of POM (Figure 2) ranged from -27.8‰
262 to -25.0‰ for $\delta^{13}\text{C}$ (mean \pm S.D. = -26.6 \pm 0.7‰) and from 2.5‰ to 10‰ for $\delta^{15}\text{N}$ (6.1 \pm 2.3‰)
263 (Table 1). A total of 38 FAs were identified in the POM (Table 1). Average saturated fatty
264 acid (SFAs) contribution to POM was 75.2 \pm 4.6% of total FAs, with 16:0 showing the highest
265 contribution (35.9 \pm 2.3%). The main monounsaturated fatty acids (MUFAs) were 18:1 ω 9
266 (5.3 \pm 1.1%) and 16:1 ω 7 (4.4 \pm 0.9%). All relative contributions of polyunsaturated fatty acids
267 (PUFAs) were low with maximum values of 1.7 \pm 0.4% for 16:2 ω 4, 1.7 \pm 0.8% for 22:6 ω 3 and
268 1.7 \pm 0.5% for 18:4 ω 3. Similarly, EFAs 20:5 ω 3 and 20:4 ω 6 had low contributions to TFAs
269 (about or \leq 1%). Contributions of branched-chain fatty acid (BrFAs) were 2.4 \pm 0.4% of TFAs.

270 **Leptocephali.** For the 3 families of leptocephali (Figure 2), $\delta^{13}\text{C}$ stable isotope values
271 ranged from -23.1‰ to -18.8‰ and from 0.7‰ to 14.5‰ for $\delta^{15}\text{N}$ (Table 1). There was a
272 significant difference in $\delta^{13}\text{C}$ composition between Serrivomeridae (-21.0 \pm 0.8‰) and
273 Nemichthyidae (-19.9 \pm 0.8‰) leptocephali (KW: $p < 0.001$; followed by MWW: $p < 0.001$).
274 $\delta^{15}\text{N}$ signatures were significantly different among each of the 3 families (KW: $p < 0.001$;
275 MWW: $p < 0.01$) with an average $\delta^{15}\text{N}$ of 4.7 \pm 3.3‰ for Nemichthyidae, 6.7 \pm 2.7‰ for
276 Muraenidae and 10.9 \pm 1.9‰ for Serrivomeridae.

277 A total of 50 FAs was identified in leptocephali (Table 1), with a large contribution of
278 SFAs, MUFAs, and PUFAs to TFAs. The same 6 FAs (16:0, 16:1 ω 7, 18:0, 18:1 ω 9, 20:5 ω 3
279 and 22:6 ω 3) were most abundant in all 3 families, with all the other FAs each contributing less
280 than about 4% to the TFAs. Muraenidae had higher levels of FAs by weight (11.7 ± 7.4 mg g⁻¹)
281 than Nemichthyidae (5.2 ± 2.5 mg g⁻¹) and Serrivomeridae (5.4 ± 4.0 mg g⁻¹).

282 The 3 families also showed differences regarding their FAs compositions (ANOSIM:
283 $p<0.001$), with Muraenidae showing no overlap with the Serrivomeridae and Nemichthyidae,
284 which overlapped to some degree in the n-MDS plot (Figure 3). FAs profiles of leptocephali
285 exhibited average dissimilarity values (AD; SIMPER analysis) that were more similar between
286 Muraenidae and Serrivomeridae (16.6%) than between Muraenidae and Nemichthyidae
287 (14.3%) and between Nemichthyidae and Serrivomeridae (14.6%). The observed differences
288 were mostly due to the relative contributions of 16:0, 16:1 ω 7, 18:0, 18:1 ω 9, 20:5 ω 3 and
289 22:6 ω 3 to TFAs (Table 1). SFAs contributed a higher proportion of TFAs in Serrivomeridae
290 leptocephali ($44.8\pm 7.5\%$) than PUFAs ($33.8\pm 5.7\%$), whereas the PUFAs contribution was
291 slightly higher in Muraenidae and Nemichthyidae ($42.3\pm 3.7\%$ and $39.4\pm 4.2\%$, respectively)
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
294 families, ranging from $23.7\pm 5.5\%$ for Serrivomeridae to $32.5\pm 3.8\%$ for Muraenidae (Figure
295 4C). BrFAs contributed less than 1% of TFAs, but differed significantly in their contribution
296 to TFAs (KW: $p<0.001$; MWW: $p<0.001$) between Muraenidae ($0.5\pm 0.1\%$) and the other
297 families (Nemichthyidae: $0.8\pm 0.1\%$ and Serrivomeridae: $0.9\pm 0.2\%$) (Figure 4D).

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

305

306 **FA compositions and SI signatures of Serrivomeridae size groups**

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

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

311 The FA compositions of the Serrivomeridae leptocephali showed various percentage
312 changes with increasing size, with SFAs and BrFAs tending to decrease, and MUFAs and
313 PUFAs tending to increase with increasing leptocephali size (Table 2). The total weight of FA
314 in the body of the leptocephali tended to decrease only slightly from the smallest to largest size
315 classes (5.8 to 4.4 mg g^{-1}) but differences were not significant. The 40–60 mm and ≤ 10 mm
316 sizes classes were significantly different in FA composition (ANOSIM: $p < 0.05$; n-MDS),
317 Figure 5) with an AD of 23.2%. The SFAs contribution to ≤ 10 mm larvae was higher
318 ($56.7 \pm 0.9\%$) and PUFAs contribution was lower ($25.2 \pm 0.6\%$) than in 40–60 mm larvae
319 ($37.1 \pm 0.3\%$ for SFAs and $39.0 \pm 0.4\%$ for PUFAs) mainly due to the contribution of the SFAs
320 16:0 and 18:0, the MUFA 16:1 ω 7 and the PUFAs 22:6 ω 3 and 20:5 ω 3 (Table 2). The
321 contribution of ω 3 FAs increased with size, from $16.4 \pm 1.0\%$ for ≤ 10 mm to $30.0 \pm 0.7\%$ for 40–
322 60 mm larvae.

323

324 **POM and leptocephali SI signatures in current zones**

325 The POM exhibited variation in $\delta^{15}\text{N}$ values, which ranged from $7.7 \pm 2.3\text{‰}$ in the
326 SECC in the north, to $4.1 \pm 1.0\text{‰}$ in the STCC in the southeast (Table 3), although the SEC
327 values overlapped with those of the other zones (Figure 6D). The $\delta^{13}\text{C}$ values showed less
328 variation with mean values that ranged from $-27.0 \pm 0.2\text{‰}$ to $-26.2 \pm 0.9\text{‰}$, but some of the
329 SECC values were lower (Figure 6D). When FA compositions of POM were separated
330 according to the 3 current zones, samples from the SECC ($5\text{--}15^\circ\text{S}$) were significantly different
331 (ANOSIM: $p < 0.05$) from those of both the SEC ($15\text{--}20^\circ\text{S}$) and STCC ($20\text{--}30^\circ\text{S}$) with an AD
332 of 12.5% between the SECC and SEC, and 13.2% between SECC and STCC. These
333 differences mostly resulted from variations in the proportions of the SFAs 18:0, 16:0 and 14:0
334 (AD between 1.4 and 2.6%), the MUFAs 18:1 ω 9 and 16:1 ω 7 (AD between 0.9 and 0.7%) and
335 PUFAs 22:6 ω 3 and 18:4 ω 3 (AD between 0.8 and 0.5%). In the SECC, the SFA contribution
336 was higher ($78.8 \pm 3.9\%$) and MUFA and PUFA contributions lower ($11.7 \pm 2.9\%$ and $7.1 \pm 1.4\%$)
337 than in the other zones (Table 3).

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

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

350

351 **DISCUSSION**

352 **FA and SI signatures of leptocephali and POM**

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

358 The chemical composition of the different taxa of leptocephali is generally comparable
359 (Pfeiler 1999, Bishop et al. 2000) as confirmed by the FA profiles of the 3 families of
360 leptocephali studied in the WSP that show many similarities. There were however, also some
361 differences. The Nemichthyidae, Muraenidae, and Serrivomeridae larvae had the same number
362 of major FAs and categories of FAs markers showed similar proportions. Deibel et al. (2012)
363 also found similar FA compositions for 6 other taxa of leptocephali (Congridae,
364 Muraenesocidae, Ophichthidae) from coastal, shelf or deep slope habitats off northwest
365 Australia. However, despite these overall similarities, the present study found small but
366 significant differences between the FA profiles of Muraenidae larvae and those of
367 Nemichthyidae and Serrivomeridae. The similarities in FAs compositions of the 3 families
368 were largely due to the FAs that were present in large proportions: 16:0, 18:0, 22:6 ω 3, 20:5 ω 3,
369 16:1 ω 7, and 18:1 ω 9. The same 6 FAs also had the highest proportions in leptocephali from
370 northwestern Australia (Deibel et al. 2012).

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 $\omega 3$, the EFAs 20:5 $\omega 3$ and 22:6 $\omega 3$ are major components
376 of cell membrane phospholipids (Sargent et al. 1993) and are also important for larval growth
377 and development (Sargent et al. 1993, Furuita et al. 2006, Grote et al. 2011). Marine
378 consumers however, cannot synthesize essential $\omega 3$ and $\omega 6$ 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 $\omega 3$ and
381 $\omega 6$ in leptocephali suggest that leptocephali feed on material containing or originating from
382 autotrophic organisms or primary consumers in which $\omega 3$ and $\omega 6$ are abundantly present (Scott
383 et al. 2002, Dalsgaard et al. 2003, Lee et al. 2006). There is also the possibility that
384 leptocephali, as do some heterotrophic organisms (Dalsgaard et al. 2003, Canuel et al. 1995),
385 synthesize these FAs from a precursor such as 18:1 $\omega 9$. This MUFA is abundant in
386 leptocephali (mean of 7.6 \pm 1.6% for the 3 families combined in this study, and 6.4 \pm 1.3% in
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).

389 In this study, POM was characterized by a strong contribution of SFAs (~75% of TFAs)
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 18:1 $\omega 9$ and 16:1 $\omega 7$ (markers of heterotrophs
394 and autotrophic microplankton, respectively) were the main unsaturated FAs that contributed
395 to the TFAs of POM (~5 and 4%, respectively). Also, BrFA markers made a low contribution
396 to TFAs (~2%) in POM. Most of these FATMs are typically biosynthesized in large amounts
397 by bacteria (Kaneda 1991, Ederington et al. 1995, Meziane & Tsuchiya 2000) and because
398 decaying bulk POM is rapidly colonised by bacteria (Skerratt et al. 1995, Najdek et al. 2002), it
399 would be expected to be rich in these BrFAs. Thus, the FA composition may indicate that the
400 POM sampled within the chlorophyll maximum layer during this study is likely to be
401 composed of a large non-living POM fraction (detritus, faecal pellets, etc.) with a low bacterial
402 influence and to a lesser extent of living organic material (autotrophic and heterotrophic
403 microplankton) that leptocephali would preferentially assimilate.

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

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

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

445 It is also possible that leptocephali do not feed exclusively within the chlorophyll
446 maximum or consume every type of POM. It is more likely that leptocephali select specific
447 types of POM particles to eat, such as some types of marine snow or the appendicularian
448 houses that have been directly observed in the intestines of leptocephali (Mochioka and
449 Iwamizu 1996, Miller et al. 2011). In addition, some materials such as zooplankton faecal
450 pellets observed in gut contents (Otake et al. 1993, Miller et al. 2011) are unlikely to be
451 digested. Further differences between the SI signatures of the POM sample collected on a
452 filter and those that leptocephali consume and assimilate might be related to the transparent
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
455 that aggregate into marine snow (Holloway and Cowen 1997, Skoog et al. 2008, Engel et al.
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
458 POM from the water samples, leading to these compounds being only partially included in
459 POM carbon measurements; whereas they would have been present in the POM materials
460 assimilated by leptocephali. In addition, carbohydrates are molecules having no nitrogen, only
461 the $\delta^{13}\text{C}$ signature of these compounds would be reflected in leptocephali if they were
462 assimilated (Feunteun et al. 2015). Also, leptocephali have a long larval duration, so as
463 previous studies have pointed out, larger larvae could be transported into collection areas after
464 originating from other areas where they have fed on POM with different isotopic signatures
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),
475 provide direct evidence of POM consumption by a variety of eel larvae taxa. Also, Feunteun et
476 al. (2015) characterised SI signatures of many taxa of zooplankton along with 12 taxa of
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.

482 The FATM compositions determined in the present study and those of Deibel et al.
483 (2012) indicate that leptocephali obtain their nutrition from various sources that include both
484 phytoplankton (16:1 ω 7, 20:5 ω 3), dinoflagellates (22:6 ω 3) and heterotrophic microorganisms
485 such as bacteria and protozoans (18:1 ω 9) (Dalsgaard et al. 2003), all of which are likely to
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 et al.
488 2009), the composition of the food contents in the intestines of leptocephali could be different
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
493 assimilate and store FAs-rich components of the POM. Conversely, Serrivomeridae larvae had
494 the highest SFA and lowest PUFAs and ω 3 proportions, which suggests that they may feed on
495 POM opportunistically, with no selective assimilation or FA storage.

496

497 **FA and SI composition of Serrivomeridae size classes**

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

504 The dynamic nature of lipid metabolism and the influence of dietary lipids when larvae
505 first feed can cause FA composition shifts during ontogeny (Wiegand 1996, Rainuzzo et al.
506 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.
508 2000). The decrease in percentage of SFAs in larger Serrivomeridae larvae might be caused by
509 16:0 and 18:0 being used as a major substrates for energy production (Sargent 1995). MUFAs
510 and PUFAs are energy sources for development and growth especially during the larval stage
511 when fish need energy for organogenesis, fast growth and basal metabolism (Abi-ayad et al.
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
514 also one of the principal components of cell membranes (Dalsgaard et al. 2003). In
515 Serrivomeridae, the increase of MUFAs and PUFAs percentages with size suggest that these
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
518 they cannot synthesize and which are in low concentrations in POM, to support the later high-
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
521 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
522 22:6 ω 3 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**

527 The isotopic signatures of leptocephali in the 3 current zones showed variations that
528 appeared to be related to the POM signatures in each zone. Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of
529 Nemichthyidae and Muraenidae larvae decreased to some extent from north (SECC) to south
530 (STCC) and the same pattern was seen in POM signatures, especially for $\delta^{15}\text{N}$. The
531 compositions of the FAs of POM and leptocephali also varied significantly among the current
532 zones. This suggests there is regional variability in the nutritional quality (SFA and 22:6 ω 3
533 contributions) and availability (18:1 ω 9, 16:1 ω 7 and 18:4 ω 3) of POM. For example, the SECC
534 POM had the highest percentage of SFAs and the lowest percentage of MUFAs and PUFAs,
535 which indicates a lower nutritional quality. This may be reflected in the FA compositions of
536 Serrivomeridae larvae that were mostly collected in the SECC, since they also had high SFA
537 contents and low contents of PUFAs compared to the other more widely distributed families.
538 In contrast, the SEC and STCC tended to have POM with higher nutritional quality with larger
539 PUFA and ω 3 contributions.

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

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

568

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577

578

579 **LITERATURE CITED**

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Table 1. Fatty acid relative contribution (%) and Carbon ($\delta^{13}\text{C}$) and Nitrogen ($\delta^{15}\text{N}$) 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 \pm S.D. n is the number of samples.

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									
$\delta^{15}\text{N}$	6.1 \pm 2.3	6.7 \pm 2.7	4.7 \pm 3.3	10.9 \pm 1.9					
$\delta^{13}\text{C}$	-26.6 \pm 0.7	-20.5 \pm 1.1	-19.9 \pm 0.8	-21.0 \pm 0.8					
Saturated									
12:0	0.51 \pm 0.25	0.08 \pm 0.12	0.04 \pm 0.06	0.07 \pm 0.1	16:2 ω 4	1.7 \pm 0.41	0.57 \pm 0.19	0.61 \pm 0.17	0.72 \pm 0.33
13:0	0.11 \pm 0.03	0.02 \pm 0.02	0.02 \pm 0.01	0.03 \pm 0.1	16:2 ω 6	- \pm -	0.05 \pm 0.02	0.09 \pm 0.02	0.04 \pm 0.02
14:0	14.05 \pm 1.71	3.99 \pm 1.32	4.63 \pm 0.86	4.12 \pm 0.6	16:4 ω 3	0.22 \pm 0.06	0.05 \pm 0.05	0.02 \pm 0.03	0.05 \pm 0.04
15:0	1.7 \pm 0.22	1.52 \pm 0.23	1.71 \pm 0.37	2.1 \pm 0.2	18:2 ω 6	1.21 \pm 0.26	2.76 \pm 0.47	2.97 \pm 0.44	2.55 \pm 0.6
16:0	35.91 \pm 2.28	20.94 \pm 2.44	24.04 \pm 2.64	26.63 \pm 4.3	18:3 ω 3	0.45 \pm 0.09	1.15 \pm 0.33	1.17 \pm 0.56	0.8 \pm 0.28
17:0	0.67 \pm 0.11	1.73 \pm 0.18	1.26 \pm 0.18	1.75 \pm 0.3	18:3 ω 6	0.42 \pm 0.08	0.28 \pm 0.06	0.23 \pm 0.06	0.39 \pm 0.1
18:0	19.47 \pm 2.31	9.32 \pm 1.25	5.14 \pm 1.7	9.1 \pm 2.9	18:4 ω 3	1.69 \pm 0.52	1.24 \pm 0.26	1.37 \pm 0.44	1.16 \pm 0.37
19:0	0.46 \pm 0.09	0.31 \pm 0.1	0.2 \pm 0.09	0.34 \pm 0.2	20:2 ω 6	- \pm -	0.24 \pm 0.1	0.11 \pm 0.05	0.08 \pm 0.05
20:0	0.85 \pm 0.1	0.27 \pm 0.07	0.14 \pm 0.03	0.35 \pm 0.2	20:3	- \pm -	0.15 \pm 0.04	0.15 \pm 0.04	0.09 \pm 0.03
21:0	0.06 \pm 0.02	0.04 \pm 0.01	0.03 \pm 0.05	0.03 \pm 0	20:3 ω 6	- \pm -	0.37 \pm 0.08	0.24 \pm 0.06	0.27 \pm 0.1
22:0	0.58 \pm 0.13	0.19 \pm 0.04	0.14 \pm 0.03	0.17 \pm 0.1	20:4 ω 3	0.09 \pm 0.02	1.4 \pm 0.77	0.86 \pm 0.3	0.96 \pm 0.69
24:0	0.58 \pm 0.25	0.08 \pm 0.06	0.04 \pm 0.03	0.09 \pm 0.1	20:4 ω 6	0.13 \pm 0.04	2.82 \pm 0.79	2.81 \pm 0.51	3.49 \pm 0.96
Σ SFA (%)	75.23 \pm 4.58	38.5 \pm 3.65	37.41 \pm 4.2	44.79 \pm 7.5	20:5 ω 3	1.02 \pm 0.22	7.85 \pm 0.97	8.52 \pm 1.22	5.05 \pm 2.07
Monounsatur.					22:2 ω 6	0.27 \pm 0.14	- \pm -	- \pm -	- \pm -
16:1 ω 5	0.07 \pm 0.03	0.14 \pm 0.03	0.15 \pm 0.03	0.13 \pm 0	22:4 ω 6	- \pm -	0.36 \pm 0.15	0.27 \pm 0.21	0.12 \pm 0.13
16:1 ω 7	4.42 \pm 0.88	5.71 \pm 1.14	7.6 \pm 1.77	6.59 \pm 1.3	22:5 ω 3	- \pm -	2.79 \pm 1.58	0.95 \pm 0.51	0.93 \pm 0.59
16:1 ω 9	2.07 \pm 0.5	0.54 \pm 0.09	0.66 \pm 0.13	0.63 \pm 0.1	22:5 ω 6	0.19 \pm 0.11	2.18 \pm 0.65	2.24 \pm 0.37	2.34 \pm 0.63
17:1 ω 7	0.37 \pm 0.08	0.45 \pm 0.12	0.49 \pm 0.11	0.32 \pm 0.1	22:6 ω 3	1.67 \pm 0.79	18.1 \pm 2.13	16.8 \pm 2.58	14.8 \pm 3.16
17:1 ω 9	- \pm -	0.45 \pm 0.1	0.73 \pm 0.15	0.75 \pm 0.1	Σ PUFA (%)	9.1 \pm 2.1	42 \pm 3.7	39 \pm 4.2	34 \pm 5.7
18:1 ω 5	- \pm -	0.1 \pm 0.03	0.1 \pm 0.03	0.11 \pm 0	Branched-chain				
18:1 ω 7	0.71 \pm 0.16	4.18 \pm 0.77	3.93 \pm 0.63	2.82 \pm 0.7	14:0iso	0.35 \pm 0.1	0.01 \pm 0.01	0.22 \pm 0.01	0.03 \pm 0.01
18:1 ω 9	5.3 \pm 1.06	5.84 \pm 0.94	8.33 \pm 1.72	8.77 \pm 1.3	15:0anteiso	0.45 \pm 0.06	0.03 \pm 0.01	0.04 \pm 0.02	0.05 \pm 0.03
19:1 ω 9	- \pm -	0.03 \pm 0.02	0.02 \pm 0.02	0.03 \pm 0	15:0iso	0.37 \pm 0.05	0.12 \pm 0.03	0.14 \pm 0.03	0.17 \pm 0.05
20:1 ω 7	- \pm -	0.18 \pm 0.08	0.12 \pm 0.04	0.09 \pm 0.1	16:0iso	0.22 \pm 0.04	0.08 \pm 0.02	0.1 \pm 0.04	0.13 \pm 0.04
20:1 ω 9	- \pm -	0.22 \pm 0.21	0.13 \pm 0.07	0.1 \pm 0.1	17:0anteiso	0.68 \pm 0.17	0.08 \pm 0.02	0.1 \pm 0.03	0.11 \pm 0.04
22:1 ω 11	0.38 \pm 0.13	0.09 \pm 0.1	0.03 \pm 0.02	0.06 \pm 0	17:0iso	0.05 \pm 0.01	0.12 \pm 0.03	0.26 \pm 0.05	0.27 \pm 0.06
22:1 ω 9	- \pm -	0.05 \pm 0.02	0.01 \pm 0.01	0.02 \pm 0	18:0iso	0.26 \pm 0.09	0.07 \pm 0.05	0.16 \pm 0.06	0.13 \pm 0.05
24:1 ω 9	- \pm -	0.08 \pm 0.05	0.06 \pm 0.05	0.07 \pm 0.1	Σ BrFA (%)	2.38 \pm 0.3	0.5 \pm 0.1	0.8 \pm 0.1	0.9 \pm 0.2
Σ MUFA (%)	13.33 \pm 2.66	18.69 \pm 1.15	22.38 \pm 2.9	20.49 \pm 2.5	Total FA (mg.g ⁻¹)	3.6 \pm 0.97	11.7 \pm 7.44	5.22 \pm 2.51	5.41 \pm 3.99
					Σ ω 3	5.14 \pm 1.46	32.5 \pm 3.77	29.7 \pm 3.84	23.7 \pm 5.51
					Σ ω 6	1.95 \pm 0.12	9.06 \pm 1.44	8.96 \pm 0.83	9.28 \pm 1.62
					Σ EFA	2.82 \pm 0.35	28.7 \pm 1.3	28.1 \pm 1.44	23.3 \pm 2.06

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Table 2. Fatty acid relative contribution (%) and Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) mean isotopic signature of Serrivomeridae leptocephali from four different size groups (≤ 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.

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

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809 **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 \pm S.D. n is the number of samples.
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Isotopes/ FA	POM in SECC (n=15)	POM in SEC (n=15)	POM in STCC (n=9)	POM in SECC (n=15)	POM in SEC (n=15)	POM in STCC (n=9)	
Stable Isotopes			Polyunsat.				
$\delta^{15}\text{N}$	7.7 \pm 2.3	6.1 \pm 2.2	4.1 \pm 1.0	16:2 ω 4	0.97 \pm 0.32	1.98 \pm 0.4	2.45 \pm 0.56
$\delta^{13}\text{C}$	-26.2 \pm 0.9	-26.6 \pm 0.5	-27.0 \pm 0.2	16:4 ω 3	0.26 \pm 0.08	0.22 \pm 0.04	0.18 \pm 0.07
Saturated FA			18:2 ω 6	1.1 \pm 0.21	1.24 \pm 0.21	1.34 \pm 0.45	
12:0	0.48 \pm 0.19	0.6 \pm 0.32	0.41 \pm 0.23	18:3 ω 3	0.44 \pm 0.07	0.44 \pm 0.08	0.49 \pm 0.14
13:0	0.1 \pm 0.03	0.13 \pm 0.03	0.07 \pm 0.01	18:3 ω 6	0.4 \pm 0.09	0.43 \pm 0.07	0.42 \pm 0.06
14:0	14.05 \pm 1.48	14.6 \pm 1.74	13.14 \pm 2.03	18:4 ω 3	1.16 \pm 0.24	1.93 \pm 0.55	2.16 \pm 0.92
15:0	1.71 \pm 0.25	1.64 \pm 0.25	1.8 \pm 0.11	20:4 ω 3	0.09 \pm 0.03	0.08 \pm 0.01	0.1 \pm 0.03
16:0	37.75 \pm 1.9	34.87 \pm 2.43	34.59 \pm 2.63	20:4 ω 6	0.11 \pm 0.03	0.14 \pm 0.05	0.16 \pm 0.04
17:0	0.74 \pm 0.11	0.64 \pm 0.13	0.61 \pm 0.06	20:5 ω 3	0.88 \pm 0.21	0.9 \pm 0.18	1.43 \pm 0.3
18:0	21.31 \pm 2.2	18.29 \pm 2.56	19.53 \pm 2.08	22:2 ω 6	0.31 \pm 0.2	0.32 \pm 0.13	0.13 \pm 0.05
19:0	0.45 \pm 0.08	0.42 \pm 0.08	0.54 \pm 0.12	22:5 ω 6	0.21 \pm 0.15	0.15 \pm 0.08	0.21 \pm 0.11
20:0	0.94 \pm 0.13	0.79 \pm 0.08	0.79 \pm 0.08	22:6 ω 3	1.17 \pm 0.51	1.71 \pm 0.76	2.43 \pm 1.31
21:0	0.06 \pm 0.02	0.07 \pm 0.02	0.05 \pm 0.02	Σ PUFA (%)	7.11 \pm 1.44	9.53 \pm 1.96	11.5 \pm 3.47
22:0	0.62 \pm 0.17	0.56 \pm 0.11	0.55 \pm 0.11	Branched-chain			
24:0	0.6 \pm 0.26	0.56 \pm 0.2	0.59 \pm 0.3	14:0iso	0.34 \pm 0.12	0.35 \pm 0.08	0.37 \pm 0.09
Σ SFA (%)	78.83 \pm 3.86	73.16 \pm 4	72.7 \pm 6.72	15:0anteiso	0.46 \pm 0.08	0.4 \pm 0.05	0.5 \pm 0.06
Monounsatur.			15:0iso	0.39 \pm 0.06	0.34 \pm 0.04	0.37 \pm 0.04	
16:1 ω 5	0.08 \pm 0.04	0.08 \pm 0.03	0.07 \pm 0.03	16:0iso	0.21 \pm 0.06	0.21 \pm 0.04	0.23 \pm 0.02
16:1 ω 7	3.62 \pm 0.73	5.62 \pm 1.1	3.76 \pm 0.75	17:0anteiso	0.64 \pm 0.18	0.99 \pm 0.26	0.23 \pm 0.02
16:1 ω 9	1.99 \pm 0.49	2.2 \pm 0.46	1.99 \pm 0.57	17:0iso	0.06 \pm 0.01	0.05 \pm 0.02	0.04 \pm 0.01
17:1 ω 7	0.39 \pm 0.1	0.34 \pm 0.04	0.37 \pm 0.12	18:0iso	0.23 \pm 0.09	0.28 \pm 0.06	0.29 \pm 0.13
18:1 ω 7	0.65 \pm 0.16	0.73 \pm 0.14	0.8 \pm 0.2	Σ BrFA (%)	2.34 \pm 0.46	2.62 \pm 0.36	2.03 \pm 0.08
18:1 ω 9	4.63 \pm 0.91	5.32 \pm 0.71	6.36 \pm 1.9	Total FA (mg.g-1)	2.86 \pm 0.83	4.49 \pm 0.77	3.33 \pm 1.53
22:1 ω 11	0.36 \pm 0.11	0.39 \pm 0.12	0.42 \pm 0.17	Σ ω 3	4.00 \pm 0.87	5.27 \pm 1.49	6.81 \pm 2.4
Σ MUFA (%)	11.71 \pm 2.87	14.68 \pm 2.1	13.8 \pm 3.32	Σ ω 6	2.14 \pm 0.14	2.28 \pm 0.11	2.26 \pm 0.14
				Σ EFA	2.16 \pm 0.25	2.75 \pm 0.33	4.02 \pm 0.55

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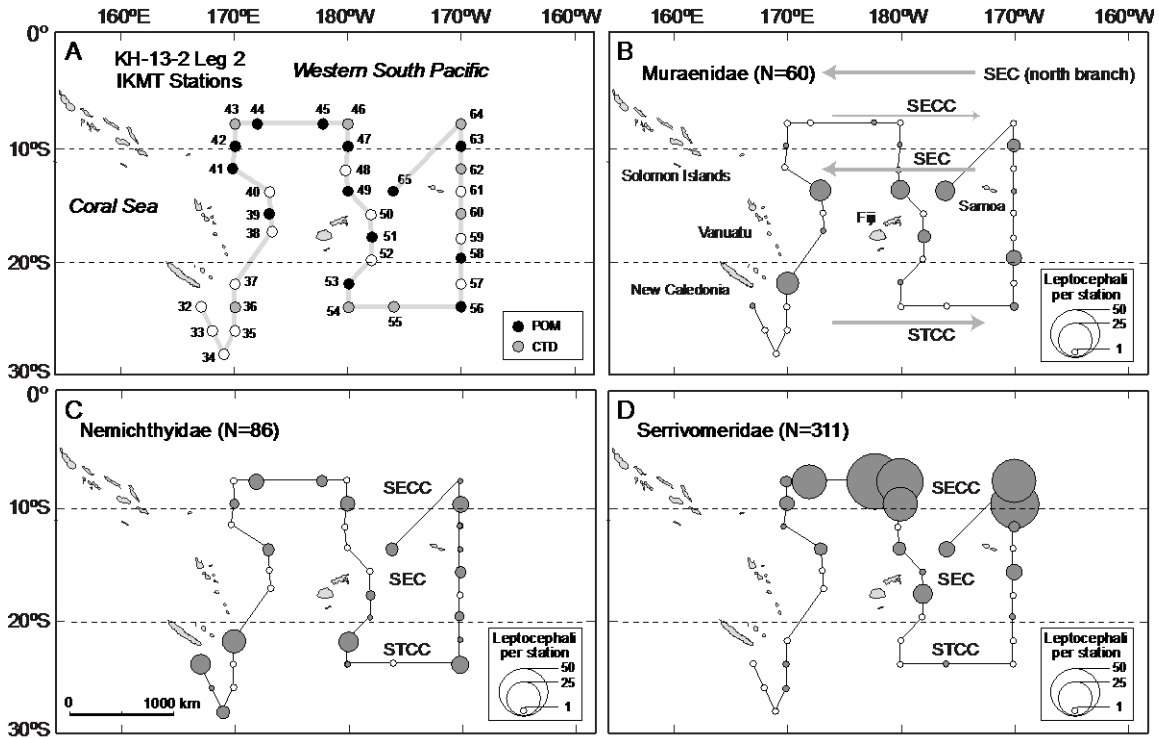


Figure 1: Maps of the KH-13-2 sampling survey of the R/V *Hakuho Maru* showing (A) the IKMT stations for collecting leptocephali (St. 32–65) and stations where particulate organic matter (POM) was analyzed (black circles) and where other CTD casts were made (shaded circles). The number of leptocephali 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.

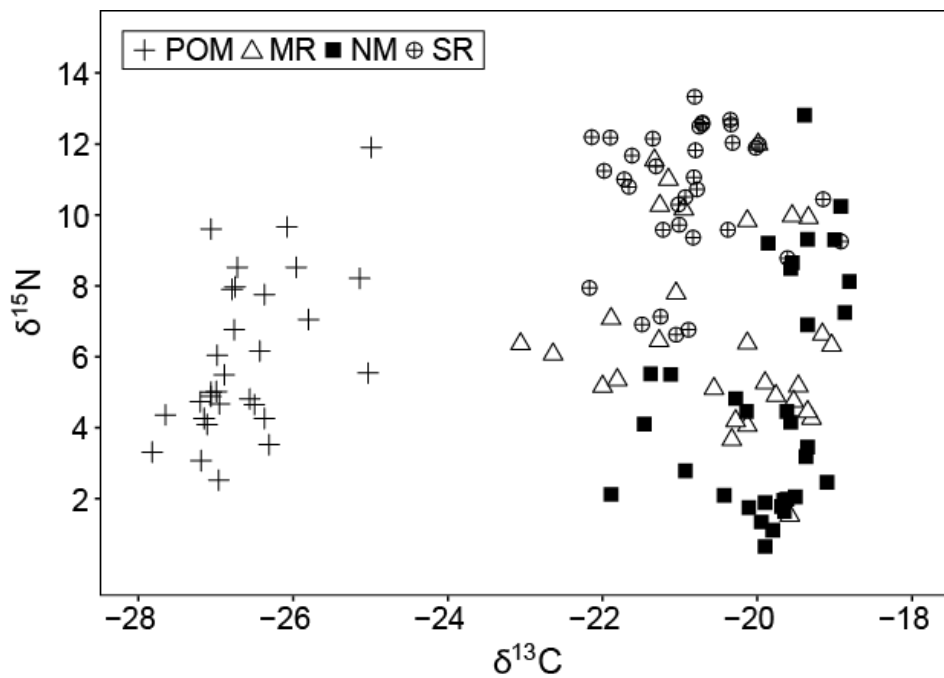


Figure 2. Carbon and nitrogen stable isotope values of particulate organic matter (POM) and the leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM).

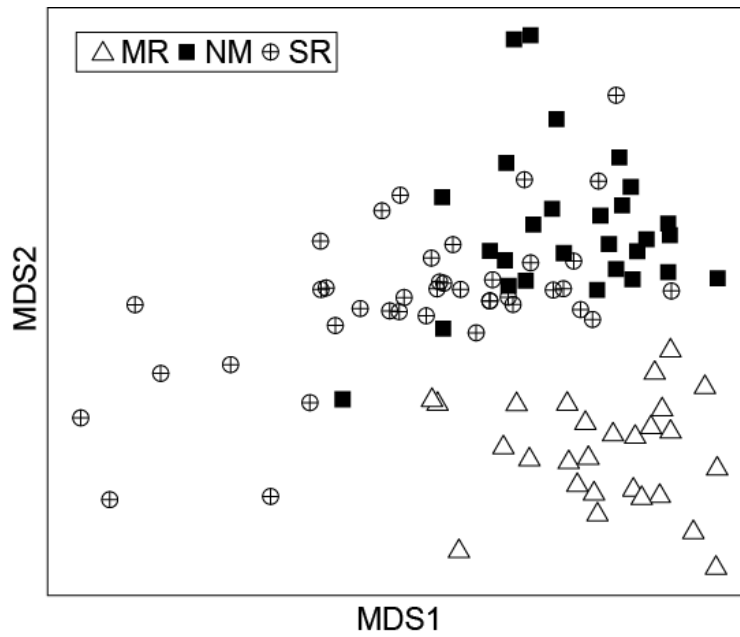


Figure 3. Non-metric multi-dimensional scaling (n-MDS) based on Bray-Curtis similarity distance of total fatty acid composition for leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM). Stress = 0.12.

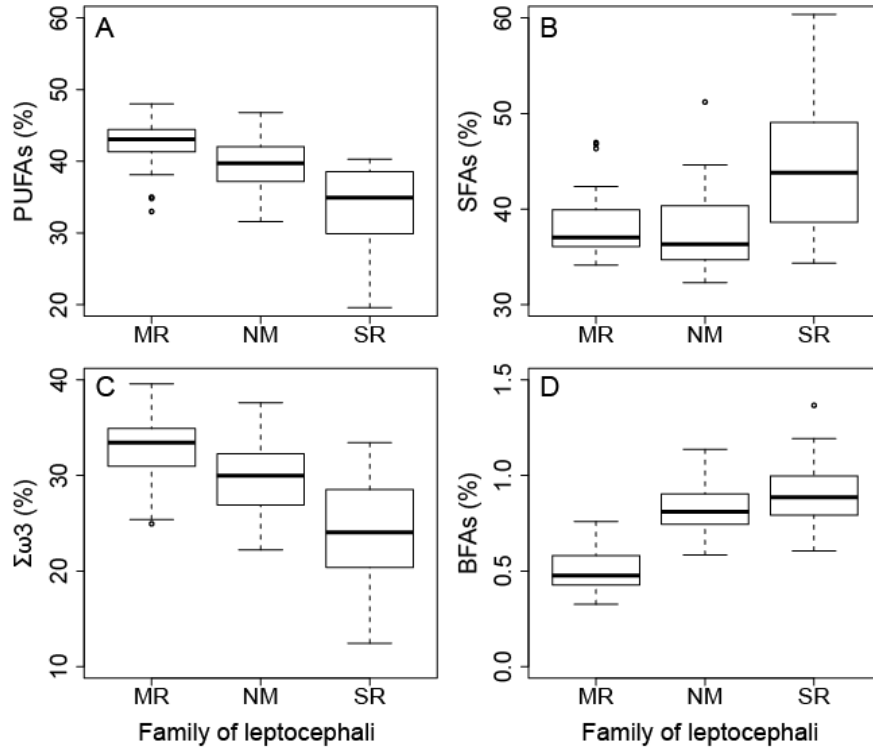


Figure 4. Fatty acids proportions (median, first and third quartiles) of (a) Polyunsaturated Fatty Acids (PUFAs), (b) Saturated Fatty Acids (SFAs), (c) sum of $\omega3$ Fatty Acids ($\Sigma\omega3$), (d) Branched-chain Fatty Acides (BrFAs), for the leptocephali of the Muraenidae (MR), Serrivomeridae (SR) and Nemichthyidae (NM).

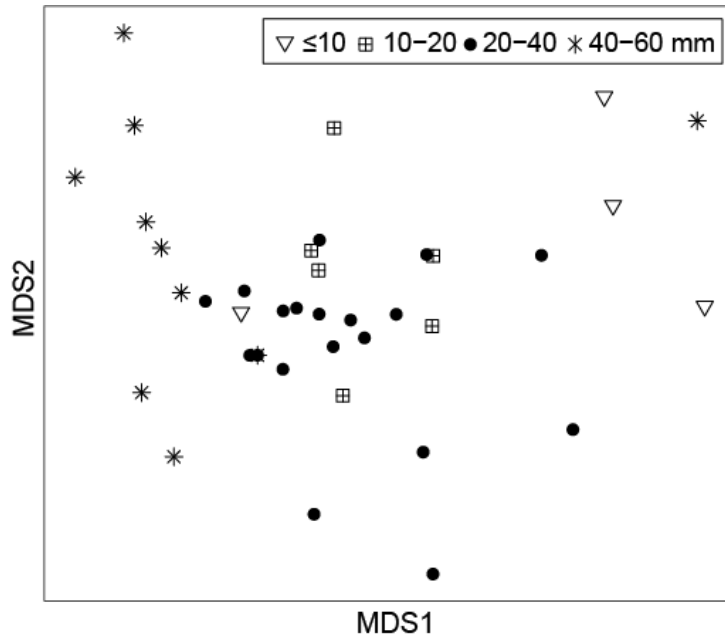


Figure 5. Non-metric MultiDimensional Scaling (n-MDS) based on Bray-Curtis similarity distance of total fatty acid concentration (mg g^{-1}) of Serrivomeridae leptocephali for 4 different size groups (see methods for exact size ranges). Stress = 0.08.

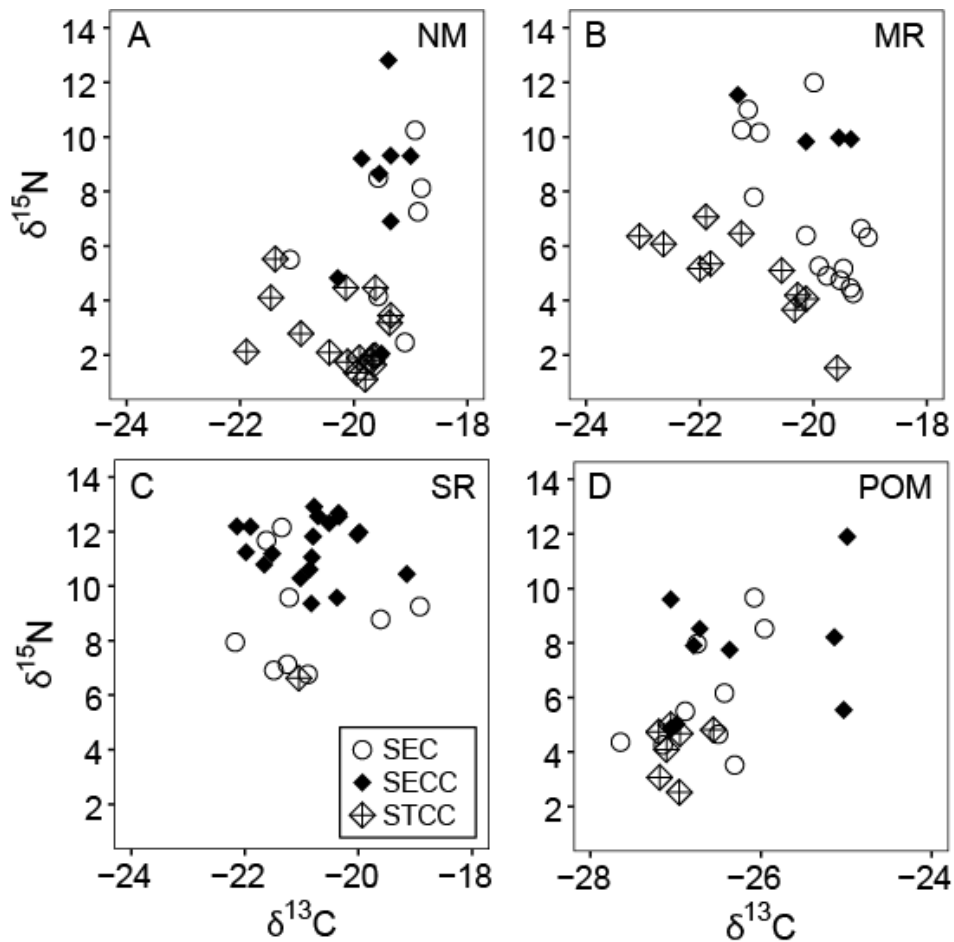


Figure 6. Carbon and nitrogen stable isotope values of (A) Nemichthyidae, (B) Muraenidae, (C) Serrivomeridae leptocephali and (D) POM from the 3 current zones of the South Equatorial Countercurrent (SECC), South Equatorial Current (SEC), and South Tropical Countercurrent (STCC).