

1 **Life strategies and habitat preferences of Bythitidae and Zoarcidae, specialized**
2 **fishes with particular life histories, in the Mediterranean deep sea**

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12 **Abstract**

13 Deep-sea habitats are home for a variety of yet poorly known fish species, some of
14 which display specialized life strategies, as is the case of Bythitidae and Zoarcidae.

15 With the purpose of elucidating biological and ecological aspects of representatives of
16 these families in NW Mediterranean waters, a large dataset based on 599 specimens of

17 *Cataetyx alleni*, 30 *C. laticeps* and 284 *Melanostigma atlanticum* captured during the

18 last 30 years within the framework of different research projects was used to address

19 their geographical and bathymetric distribution, population structure, reproduction,

20 trophic ecology, parasitism and enzymatic markers in the Balearic basin. Present

21 outcomes revealed a patchy distribution mostly for *M. atlanticum*, possibly related to

22 aggregation during reproduction and to the association with specific sediments. For the

23 three species, higher densities occurred in the mainland vs. the insular margin, and a

24 diminishing trend in estimated densities over the last decades was observed for *C. alleni*

25 and *M. atlanticum* likely linked to climatic oscillations. Trophic data indicated that the

26 two *Cataetyx* species inhabit the water-sediment interface and mainly feed on
27 suprabenthic prey, while *M. atlanticum* inhabits the water column near the bottom
28 preying on pelagic organisms and moving towards the seabed during reproduction.
29 These results were supported by the parasitological assessment, which revealed that
30 parasite communities were moderately diverse and abundant for *Cataetyx* spp. while
31 being highly depauperate for *M. atlanticum*. Present outcomes confirmed reproduction
32 of *C. alleni* during autumn-winter and of *M. atlanticum* during summer. Spawning of
33 the former species may occur in winter-spring, as suggested by the finding, by the first
34 time, of two females captured in March with fully-developed embryos inside. Levels of
35 enzymatic markers quantified in muscle were provided for *C. alleni* and *M. atlanticum*
36 for the first time. The special interactions found between the distribution and biology of
37 Bythitidae and Zoarcidae and the sedimentary bottoms that they inhabit indicates that
38 such *conventional* habitats are more heterogeneous than it is generally assumed and
39 deserve higher attention for future protection.

40 **Keywords:** deep-sea, Bythitidae, Zoarcidae, viviparism, *Cataetyx*, *Melanostigma*

51 **1. Introduction**

52 The deep sea constitutes a vast space making up 75% of the global biosphere (Angel,
53 1997; Della Torre et al., 2010) and fish are an important part of this huge ecosystem, to
54 which they contribute with an enormous overall abundance and biomass (Drazen and
55 Sutton, 2017). Due to the increasing exploitation of deep-dwelling living resources
56 (Morato et al., 2006; Watson and Morato, 2013) and the necessity to have information
57 on deep-sea commercial fish life cycles, distribution and abundance, the life history of
58 some of these species is reasonably well known. This is, for instance, the case of
59 gadiforms, one of the major groups exploited in deep waters (Koslow et al., 2000) for
60 which information on depth distribution, reproductive potential, trophic ecology or
61 parasites has been provided in many studies (e.g. see Atkinson (1995), Carrassón and
62 Matallanas (2002a) and Constenla et al. (2015) for macrourids, Dallarés et al. (2014,
63 2016) for the common mora *Mora moro* (Risso, 1810) and the greater forkbeard *Phycis*
64 *blennoides* (Brünnich, 1768), respectively, or Sweetman et al. (2018) for the blue
65 grenadier *Macruronus novaezelandiae* (Hector, 1871)). These deep-living species are
66 abundant in their habitats and in the context of an environment with low food
67 availability, they display what we could catalogue as a “conventional” life cycle with
68 oviparism and free-pelagic larvae.

69 However, deep-sea habitats are also home for other “less conventional” fish species
70 with more specialized life strategies and for which life cycle and possible adaptations to
71 such a particular environment are not well known yet. These species with particular
72 traits receive, in general, less attention than commercial ones they coexist with, but can
73 even be moderately abundant in local fish communities (e.g. Chlorophthalmidae or
74 Nothacanthidae in the western Mediterranean (Stefanescu et al., 1992a). They often
75 show curious anatomical adaptations to the extreme habitat in which they dwell

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76 (Ebeling and Cailliet, 1974; Warrant and Locket, 2004) and particular trophic habits
77 (e.g. the shortfin spiny eel *Notacanthus bonaparte* Risso, 1840 feeds on coral polyps
78 (Rodríguez Romeu et al., 2016)), life strategies or reproductive features (Koslow et al.,
79 2000).
80 Viviparous brotula (Bythitidae) constitute a moderately diversified family distributed in
81 a wide range of habitats, including freshwater, coastal regions and the deep sea (Nelson,
82 2006). Specifically, the genus *Cataetyx* is worldwide distributed in tropical and
83 temperate waters and is represented by two species in the deep Mediterranean, *C. alleni*
84 (Byrne, 1906) and *C. laticeps* Koefoed, 1927 (Matallanas, 1990). Like all members of
85 the family, males of these species bear an intromittent organ and females release larvae
86 after internal fertilization and egg hatching (Follesa et al., 2011). Other Bythitidae living
87 in Mediterranean waters are rarer than *Cataetyx* spp., such as *Bellottia apoda* Giglioli,
88 1883 or *Grammonus ater* (Risso, 1810) (Matallanas, 1990); the latter living in littoral
89 caves (Gerovasileiou et al., 2015).
90 Some eelpouts (Zoarcidae) are also viviparous (Mead et al., 1964), but most of the ca.
91 60 recognized species of the family are oviparous and can be found from the intertidal
92 zone to the continental slope, with some species (e.g. *Thermarces cerberus* Rosenblatt
93 and Cohen, 1986 or *T. pelophilum* Geistdoerfer, 1999) also associated to hydrothermal
94 vents and cold seeps down to depths of 2300 m (Geistdoerfer, 1996, 1999). In the deep
95 Mediterranean, a single zoarcid can be found, the Atlantic soft pout *Melanostigma*
96 *atlanticum* Koefoed, 1952 (Stefanescu et al., 1992a). This species displays a singular
97 reproductive strategy, since adults develop benthic habits during the spawning period
98 and egg fertilization takes place in burrows (mud pockets) at 15–30 cm below the
99 seafloor surface (Markle and Wenner, 1979; Silverberg et al., 1987).

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100 *Cataetyx alleni*, *C. laticeps* and *M. atlanticum* share characteristic features of K-
101 strategists, as is common for many deep-sea fishes (Koslow et al., 2000; Laptikhovsky,
102 2006). Eggs are protected and kept safe from predators by their keeping either inside the
103 female's body or in subterranean burrows, as explained above. Furthermore, for *M.*
104 *atlanticum*, rather reduced broods (i.e. 36-56 eggs/female) alongside with large eggs (up
105 to four mm) have been reported, as well as parental care behavior (Silverberg et al.,
106 1987; Silverberg and Bossé, 1994).
107 Unfortunately, several gaps exist on the knowledge of the life history and ecology of
108 these curious species. In the NW Mediterranean, Stefanescu et al. (1992b) determined
109 their bathymetric distribution and addressed depth-size trends for *C. alleni* and *C.*
110 *laticeps*. Besides these studies, for *C. alleni*, the best characterized species of the three
111 addressed herein, studies on diet and trophic features (Carrassón and Cartes, 2002;
112 Carrassón and Matallanas, 1990, 1994, 2002b) and reproduction (Fernandez-Arcaya et
113 al., 2016; Follesa et al., 2011; Relini Orsi, 1974) in the Mediterranean area have been
114 performed. Notes on growth were provided by Morales-Nin (1990) and larval
115 characterization of *Cataetyx* (authors could not determine if belonging to *C. alleni* or *C.*
116 *laticeps*) by Sabatés and Fortuño (1988). For *C. laticeps*, available information is much
117 scarcer. Notes on direct *in situ* observations were provided by Galil (2004), Gates et al.
118 (2012), Saldanha (1994) and Saldanha and Biscoito (1997). The latter authors also
119 provided a brief list of prey recovered from gut contents of a few large specimens.
120 Parasites infecting *C. laticeps* have been recorded by Bray (1996), Bray et al. (1999)
121 and Costa et al. (2016). Finally, some brief comments on its biology were provided by
122 Stefanescu et al. (1990). Reproductive aspects are scarcely known for this species,
123 although some observations on size and morphology for oocytes and larvae were
124 provided by Rannou (1975) and more detailed data on oocytes size, ovarian

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125 organization and fecundity by Fernandez-Arcaya et al. (2016). Regarding *M.*
126 *atlanticum*, reproductive aspects such as eggs size, breeding season and benthic
127 spawning behavior were dealt with by Markle and Wenner (1979) (these authors also
128 provided a few preliminary data on parasites and diet), Silverberg and Bossé (1994) and
129 Silverberg et al. (1987). Finally, Møller and Jørgensen (2000) studied the distribution
130 and abundance of this species in north Atlantic waters, also providing a brief note on
131 reproductive aspects.

132 The present study aims to shed light on the biology and ecology of *C. alleni*, *C. laticeps*
133 and *M. atlanticum*, as examples of specialized fish adapted to extreme environments.
134 Samples collected in the Balearic Sea (NW Mediterranean Sea) during the last three
135 decades are devoted to address geographical and bathymetric patterns in their
136 distribution, population structure, reproduction, trophic ecology, parasitism and
137 physiological markers of these deep-sea fish in order to define better their habitat
138 preferences and ecological requirements.

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140 **2. Materials and methods**

141 *2.1. Study area and sample collection*

142 A total of 582 specimens of *C. alleni*, 25 *C. laticeps* and 284 *M. atlanticum* were
143 collected from the Balearic basin (NW Mediterranean Sea), both over the mainland and
144 insular slopes, during the three last decades within the framework of five different
145 research projects: RECOMARES (cruises were carried out in winter 2020 at 400 – 2300
146 m depth off the central and southern Catalan coasts and west Mallorca island),
147 ANTROMARE (cruises performed in summer 2010 and 2011 and autumn 2011 at 400
148 – 2200 m depth off the central Catalan coast and north Ibiza and Mallorca islands),
149 BIOMARE (cruises performed in all seasons of 2007 and in winter 2008 at 50 – 1700 m

150 depth off the central Catalan coast), RETRO (cruises performed in spring and winter
151 1991 and in summer 1992 at 400 – 1900 m depth off the central Catalan coast),
152 ABISMAR (cruises performed in autumn 1989 at 1200 – 1800 m depth in the central
153 region of the Balearic basin and off Valencia) and BATIMAR (cruises performed in
154 summer 1987 and 1988 and autumn 1988 at 950 – 2200 m depth off the central Catalan
155 coast and north Mallorca island). Given the rarity and low abundance of these species,
156 especially *C. laticeps* and *M. atlanticum*, we compiled for this study data from all
157 available sampling series. Table S1, provided as electronic supplementary material,
158 shows detailed sampling data for specimens collected.

159 After capture, total length (TL), preanal length (PL) and total weight (TW) were
160 measured for each fish. Once in the laboratory, fish were eviscerated, liver and gonads
161 weighed to the nearest 0.001 g, and the rest of the specimen was frozen at –20 °C for
162 further dietary and parasitological studies. In the case of fish from project
163 ANTROMARE, a piece of gonad of *C. alleni* specimens was fixed in formalin for
164 further histological analysis, and a piece of axial musculature of 14 *C. alleni* and 13 *M.*
165 *atlanticum* specimens was dissected and kept at –20 °C for biochemical analyses.

166 In the case of fish from project BATIMAR, they were freshly fixed in buffered formalin
167 for further dietary, histological and parasitological studies, and standard length (SL) and
168 eviscerated weight (EW) were recorded instead. Table S2, provided as electronic
169 supplementary material, shows number of specimens of each species collected,
170 measured, weighed and sexed according to seasons and depth ranges.

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172 *2.2. Assessment of reproductive aspects (gonad histology and estimation of fecundity*
173 *and eggs diameter)*

174 All fish were sexed macroscopically and/or microscopically, when possible. Gonads of
175 444 *C. alleni*, five *C. laticeps* and 42 *M. atlanticum* from BATIMAR and
176 ANTROMARE projects were fixed in formalin. Gonadal development was studied from
177 gonadal histological sections of a total of 38 *C. alleni* (24 males and 14 females), four
178 *C. laticeps* (one male and three females) and seven *M. atlanticum* (one male and six
179 females). In these cases, one gonad was processed by routine histological techniques,
180 embedded in paraffin, sectioned at 4–8 μm and stained with hematoxylin-eosin or
181 Mallory's trichrome stain.
182 Fecundity was estimated from maturing and mature ovaries (i.e. with oocytes in
183 vitellogenic and ripe stages) of 34 females of *C. alleni*, one of *C. laticeps* and 16 of *M.*
184 *atlanticum*. To calculate absolute fecundity (i.e. number of oocytes that a female
185 produces in a breeding season), all oocytes of one of the two ovaries, previously
186 weighed, of each female were counted under a stereomicroscope. The second ovary was
187 also weighed and then its number of vitelline oocytes estimated from the n° of oocytes-
188 weight relationship obtained in the first ovary. Total number of vitelline and hydrated
189 oocytes present in both ovaries was then calculated to estimate fish absolute fecundity.
190 Relative fecundity was calculated as absolute fecundity/TL (in mm). Nomenclature
191 relative to oocytes developmental stages follows Carrassón and Bau (2003).
192 Egg diameter was measured directly from fixed gonads using a calibrated stage
193 micrometer incorporated to the microscope lens.

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195 2.3. Dietary study

196 A total of 109 specimens of *C. alleni* and 30 of *M. atlanticum* were used for the trophic
197 study, while only nine specimens were available for *C. laticeps*. The level of treatment
198 of trophic information for each species depended of the available information on this

199 topic from previous studies by present authors in the area. In the present study, seasonal
200 information on the feeding capacity (fullness) and diet of *C. alleni*, and of prey-parasite
201 relationships following the approach adopted by Dallarés et al. (2014, 2016) for other
202 fishes such as *M. moro* or *P. blennoides*, are provided. In contrast, gut fullness and diet
203 of *M. atlanticum* are described herein by the first time. For comparative purposes, the
204 dietary information available for *C. laticeps* is also briefly described.

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206 *2.4. Parasitological study*

207 A total of 101 whole specimens of *C. alleni*, six *C. laticeps* and 28 *M. atlanticum*
208 belonging to RETRO, BIOMARE and ANTROMARE projects were examined for
209 parasites. Regarding BATIMAR project, intestines of 60 specimens of *C. alleni* and 11
210 *M. atlanticum* were also examined for parasites.

211 Parasitological examination was performed according to a standardized protocol.

212 Briefly, once in the laboratory, fish were thawed and all external surfaces and buccal
213 cavity were carefully inspected for ectoparasites to the naked eye and with a
214 stereomicroscope. Fish were then dissected and all organs and musculature checked for
215 endoparasites using a stereomicroscope. Parasites were collected and preserved in 70%
216 ethanol. For their identification, plathyhelminths were stained with iron acetocarmine,
217 dehydrated through a graded ethanol series, cleared in clove oil or dimethyl phthalate
218 and examined as permanent mounts in Canada balsam. Nematodes and copepods were
219 cleared in glycerine and examined as semi-permanent mounts. All parasites were
220 identified to the lowest possible taxonomic level.

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222 *2.5. Enzymatic determinations*

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223 From each muscle sample, a portion of about 0.3 g was used for acetylcholinesterase
224 (AChE), lactate dehydrogenase (LDH) and citrate synthase (CS) determinations. Each
225 muscle portion was homogenised in a 50 mM buffer phosphate (pH 7.4) in a 1:5
226 (weight:volume) ratio using a polytron® blender. The homogenate was centrifuged at
227 10,000 g × 30 min and the supernatant (S10) was used for biochemical determinations.
228 A range of six concentrations of acetylthiocholine iodide (ATC) from 0.05 to 10 mM
229 was used to determine kinetic constants such as Vmax and Km of AChE in each species
230 and catalytic efficiency measured as Vmax/Km. For determination of AChE activity in
231 samples, substrate (ATC) concentration selected was 1 mM, as described in Solé et al.
232 (2010). Acetylcholinesterase activity was assayed according to the principle of Ellman
233 et al. (1961) at 405 nm using 1:5 (*C. alleni*) and 1:10 (*M. atlanticum*) diluted original
234 sample. Lactate dehydrogenase activity was determined at 340 nm according to the
235 method developed by Vassault (1983), modified to 96-well microplate format, with the
236 reactive quantities described in Dallarés et al. (2014) and using 1:160 diluted original
237 sample. For CS assay, the protocol used was based on Childress and Somero (1979) at
238 412 nm and final conditions were: 0.1 mM of dithiobisnitrobenzoic acid solution in 50
239 mM Tris-HCl buffer (pH 8) were mixed with 25 µl of 1:5 diluted sample, 0.1 mM acetyl
240 CoA and 0.5 mM oxaloacetate in each microplate well.
241 In all determinations, reading was performed in triplicate in a microplate reader
242 (TECAN Infinite 200) during 5 min at 25 °C. Activity was expressed in nmol/min/mg
243 protein and in µmol/min/g wet weight of tissue.
244 Total protein content in the S10 fraction was determined by the Bradford (Bradford,
245 1976) method using bovine serum albumin as standard (BSA 0.05–0.5 mg/ml).
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247 *2.6. Data analyses*

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248 Plots displaying distributions of hauls included in the present study were generated
249 using the mapping free software QGIS v.3.12. For each sampling location, a buffer area
250 proportional in size to fish density estimated in that location (i.e. number of fishes
251 captured on a given haul by the swept area (in ha) during that haul) was added. This was
252 done separately for each of the three species addressed. In the case of *M. atlanticum*,
253 fish density data was log-transformed due to the high variability observed for this
254 variable. Densities of this species in RETRO hauls are likely underestimated because a
255 different trawl system, with a larger mesh size, was used (MTS-25 instead of OTSB-14
256 trawl; see Cartes et al. (2009a) for further information). This could allow escape of
257 smallest captures, such as *M. atlanticum*. Despite this bias, data from RETRO hauls
258 were still used for *M. atlanticum* because its calculated densities were very high in some
259 cases. However, these hauls were highlighted in distribution maps for *M. atlanticum* in
260 order to make them visually distinguishable. Capture bias associated to MTS-25
261 (RETRO hauls) could not occur for *C. laticeps* due to its large size. Captures of *C.*
262 *alleni* with this trawl are not included in the present study since a high enough sample
263 size was achieved with OTSB-14 trawls.

264 In order to explore the influence of main spatial and temporal gradients on density
265 patterns of the three species, Generalized Linear Models (GZMs) with negative
266 binomial distribution were applied on haul density data setting “depth range” (i.e. upper
267 slope: 200 – 800 m, middle slope: 800 – 1400 m or lower slope: > 1400 m),
268 “mainland/insular” and “old/recent” (i.e. years 1988–1989/years 2007–2020) as factors.
269 Furthermore, a potential effect of the distance to submarine canyons on the mainland
270 slope was also tested through the same models.

271 Since a particular distribution of *M. atlanticum* in relation to submarine canyons was
272 visually identified (i.e. captures of this species seemed to be mostly associated to the

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273 SW side of canyons rather than to the NE side), differences in estimated mean density
274 between both sides of canyons were tested by Mann-Whitney U or one-sample Student t
275 tests (the latter was used when *M. atlanticum* was sampled in only one side of a given
276 canyon and thus data variance was 0 in the other side). For this purpose, submarine
277 canyons for which hauls were performed at both their NE and SW sides were selected
278 (i.e. Morràs, Berenguera and Foix canyons; see Figure 1B). For each haul, the closest
279 canyon was identified either visually or by measuring distances to the two nearby
280 canyons in case of doubt. Only hauls considered as being in the vicinity of the selected
281 canyons (less than *ca.* 15 km distance) were included in the analyses.

282 Fish condition was assessed by condition factor (CF, calculated as $(TW/TL^3) \times 100$),
283 hepatosomatic index (HSI, calculated as $(\text{liver weight}/TW) \times 100$) and gonadosomatic
284 index (GSI, calculated as $(\text{gonad weight}/TW) \times 100$), the latter only calculated for adult
285 specimens. Stomach/intestinal fullness (*%f*) were calculated using total content weight
286 (CW) in each case as $(CW/TW) \times 100$. Parasite prevalence (P) and abundance were
287 calculated following (Bush et al., 1997). Parasites displaying a total prevalence $\geq 10\%$
288 were considered non-accidental and are henceforth called common parasites. Diversity
289 of parasite infracommunities (i.e. all parasites of all taxa in an individual fish) was
290 estimated using Brillouin's diversity index (PRIMER v7; Anderson et al., 2008).

291 For *C. alleni*, General Linear Models (GLMs) were applied to test the effect of factors
292 seasonality and slope region simultaneously, as well as their interaction, on biological
293 indices (CF, HSI and GSI; males and females were treated separately in the two latter
294 cases). When no interaction between both factors was found, the effect of each was
295 tested separately. For *M. atlanticum*, only seasonality was tested using the same tests. In
296 the case of *C. alleni* and *M. atlanticum*, GZMs were used to test associations between
297 fish size, CF and HSI and the following parasitological descriptors: total parasite

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298 abundance, abundance of common parasites, parasite richness (i.e. number of different
299 parasite taxa in a given host) and presence/absence of total and common parasites in
300 individual fish. For individual parasite diversity, Spearman rank correlations were used
301 instead. Moreover, GZMs were also performed, including fish size as covariate, to test
302 differences between spring-summer and autumn-winter periods for parasite total
303 prevalence (TP), total mean abundance (TMA), mean species richness (MSR), and
304 prevalence and mean abundance of common parasites. Parasitological data from spring
305 and summer, and from autumn and winter were grouped due to the low number of
306 specimens available from the two former seasons and according to the high similarity in
307 overall parasite abundance observed between each of the two seasons grouped.
308 Differences in the same parasitological descriptors were also tested among slope regions
309 by GZMs. For mean parasite diversity, Mann-Whitney and Kruskal-Wallis tests were
310 used to test seasonal and bathymetric differences, respectively. Parasitological data of
311 *C. alleni* and *M. atlanticum* from BATIMAR project were treated separately because
312 they were restricted to intestinal samples, as highlighted in section 2.3., and were thus
313 not directly comparable to the rest of data. Seasonal and bathymetric differences were
314 also tested for these data from *C. alleni* by GZMs, as described above. For *C. laticeps*
315 no statistical tests were done on parasitological data or biological indices due to the
316 reduced sample size. In all cases, differences were tested only for groups with at least
317 five individual samples.
318 In order to find possible associations between diet items and common parasites, dietary
319 and parasitological data of 86 *C. alleni* and five *C. laticeps* were analysed by
320 multivariate canonical correspondence analysis (CCA) (Ter Braak, 1986). Data were
321 grouped by haul in the case of *C. alleni*, and data from hauls belonging to the same
322 season, depth and locality were also grouped (i.e. B2O3/O4/O5). CCA relates in this

323 case the abundance of common parasites with the abundance of each prey-species.

324 Arrows in CCA plots represent explanatory variables which are proportional in length
325 to their importance on the explained variable (Ter Braak, 1986; more details are
326 provided in Dallarés et al. (2014)).

327 Finally, a possible association between fish size and AChE, LDH and CS activities was
328 assessed through Pearson and Spearman bivariate correlation tests.

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330 **3. Results**

331 *3.1. Spatial and temporal trends on distribution and density patterns*

332 Maps showing distribution in the Balearic basin of *C. alleni*, *C. laticeps* and *M.*

333 *atlanticum* in hauls included in the present study are displayed in Figures 1 and 2.

334 The GZM testing the main spatial and temporal influences in the distribution of *C.*

335 *alleni* was overall highly significant (GZM, $\eta^2 = 125.873$, $p < 0.001$), with the three

336 chosen explanatory variables explaining a significant amount of variation of the density

337 patterns observed. In relation to spatial influences, a higher densities occurred in the

338 continental than in the insular margin of the Balearic basin (GZM, $\eta^2 = 51.505$, $p <$

339 0.001) and highest densities were observed in the middle slope (i.e. 800-1400 m depth)

340 (GZM, $\eta^2 = 97.206$, $p < 0.001$) (Fig. 2A). A temporal pattern also occurred, since

341 densities were generally higher in “old” hauls (years 1988–1989) than in recent ones

342 (years 2007–2020) (GZM, $\eta^2 = 5.379$, $p = 0.02$). Density values expressed as a function

343 of seasonality, displayed in Figure 3A, revealed highest densities in spring (March) and

344 autumn (October). A significant influence of distance to submarine canyons was not

345 detected (GZM, $p > 0.05$).

346 In the case of *C. laticeps*, the low number of hauls available yielded a rather incomplete

347 picture regarding its distribution and density patterns in comparison to the other two

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348 species addressed (Fig. 2B). However, a pattern of restricted distribution to the lower
349 slope (i.e. > 1400 m depth) and abyssal plain depths could be appreciated. The GZM
350 testing main spatial and temporal influences on the density distribution of this species
351 explained a significant amount of the observed variation (GZM, $\eta^2 = 19.230$, $p < 0.001$)
352 and evidenced higher densities in the mainland than in the insular margin (GZM, $\eta^2 =$
353 7.684 , $p = 0.006$) and in recent than in old hauls (GZM, $\eta^2 = 12.656$, $p < 0.001$). In
354 relation to seasonality, highest densities were observed in spring (Fig 3A). A significant
355 influence of distance to submarine canyons was not detected (GZM, $p > 0.05$).
356 *Melanostigma atlanticum* was exclusively captured in the continental margin of the
357 Balearic basin (Fig. 1A). As for *Cataetyx* spp., the GZM testing main spatial and
358 temporal influences on density patterns was overall significant (GZM, $\eta^2 = 467.846$, p
359 < 0.001) and confirmed that, except for a few captures in the middle and even the lower
360 slopes, always associated to low fish density, *M. atlanticum* was mostly captured in the
361 upper slope (i.e. 200-800 m depth) below 400 m (GZM, $\eta^2 = 298.785$, $p < 0.001$) and
362 that densities were much higher in old than in recent hauls (GZM, $\eta^2 = 39.342$, $p <$
363 0.001). Regarding seasonal pattern, highest densities were detected in summer (July)
364 (old hauls, MTS-25 art) and autumn (October) (recent hauls, OSTB-14 art) (Fig. 3B).
365 Furthermore, higher densities of this species occurred closer to submarine canyons
366 (GZM, $\eta^2 = 128.368$, $p < 0.001$). In relation to this pattern, mean density of *M.*
367 *atlanticum* was significantly higher at the SW side of the Morràs and Berenguera
368 canyons (Mann-Whitney, $U = 58.5$, $p = 0.013$ and one sample t-test, $t = 14.291$, $p <$
369 0.001 , respectively). No significant differences between both sides were detected for the
370 Foix canyon ($p > 0.05$) although very few hauls were available for comparison at the
371 SW side and, in fact, this species was not detected at the NE side (Fig. 1B).
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373 3.2. Size distribution and trends on biological indices

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2 374 Size distribution plots (Fig. 4) revealed a bigger-deeper trend for *C. alleni* in spring,
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5 375 summer and autumn: in the upper slope captured individuals invariably measured less
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7 376 than 9 cm while most specimens exceeded this size in the lower slope. In the middle
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9 377 slope, TL of specimens captured was highly variable, especially in summer. In winter,
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11 378 high variability in fish TL was observed at the three depth strata. This positive
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13 379 relationship between size and depth was better fitted to a power regression, associated to
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15 380 a reasonably high determination coefficient and was observed for both sexes (Fig. 5A).
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17 381 For *C. laticeps*, most specimens were larger than 30 cm and a bigger-deeper trend was
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19 382 suspected for both sexes (Fig. 5B) although the very low sample size prevented from
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21 383 observing any clear trend. Regarding *M. atlanticum*, most specimens captured were
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23 384 adults larger than 10 cm. In this case, a shallower-smaller trend was rather observed,
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25 385 with large individuals encountered in the upper and middle slopes and small specimens
26
27 386 concentrated in the upper slope (Figs. 4 and 5C).
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29 387 Condition factor of *C. alleni* data was significantly higher in the upper and middle
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31 388 slopes than in the lower slope (GLM, $F_{(2, 133)} = 10.354$; $p < 0.001$) (Fig. 6A). Regarding
32
33 389 seasonality, CF significantly increased during spring and summer with respect to
34
35 390 autumn and winter (GLM, $F_{(3, 132)} = 5.491$; $p = 0.001$). HSI did not show significant
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37 391 bathymetric or seasonal differences in either males or females (GLM, $p > 0.05$) (Fig.
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39 392 6B). GSI of *C. alleni* displayed significant differences among seasons for both sexes,
40
41 393 with increasing values from summer to autumn (GLM, $F_{(1, 39)} = 45.628$; $p < 0.001$ for
42
43 394 males and $F_{(1, 23)} = 42.752$; $p < 0.001$ for females) (Fig. 6C). This index did not vary
44
45 395 significantly as a function of depth (GLM, $p > 0.05$ in both cases). For *C. laticeps*, low
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47 396 sample size prevented from observing seasonal or bathymetric trends. Specimens for
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49 397 which biological indices could be calculated ($n = 10$) were sexually immature
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398 individuals with GSI ranging from 0.06 to 1.50, HSI from 0.49 to 2.11 and CF from
399 0.37 to 0.79. Concerning *M. atlanticum*, specimens for which biological indices could
400 be calculated belonged almost entirely to the upper slope. Trends were thus assessed
401 seasonally although data were not available for all seasons. CF and females HSI
402 displayed higher values in summer than in spring (only CF) and autumn (both indices),
403 although this trend was not significant (GLM, $p > 0.05$) (Figs. 6D, E). In contrast,
404 females GSI hardly varied from summer to autumn (GLM, $p > 0.05$), while seasonal
405 differences for males GSI could not be tested due to low sample size (Fig. 6F).

406

407 *3.3. Reproductive aspects (gonadal development, fecundity and eggs diameter)*

408 Sex ratio for *C. alleni* was 1.28 (males:females, $n = 413$). Gonadal microscopic and
409 macroscopic examination for fishes of this species captured in July revealed that
410 females were either sexually mature or, most of them, in process of maturation, with
411 gonads containing oocytes showing different levels of yolk content (at vitellogenic
412 stage). Vitellogenesis started from an oocyte diameter of 0.30 mm. Females of October
413 and December were sexually mature (at late vitellogenic or ripe stage) and showed
414 fertilized gonads with sperm present in oviducts and ovarian lumen (Figs. 7A, B). A
415 rather synchronous group of maturing/mature oocytes, that conformed most of the
416 gonadal tissue, and a second very minority group consisting of some immature
417 oocytes at previtellogenic or early vitellogenic stages could be appreciated in all cases.
418 Exceptionally, two females from winter (March 2020) harbouring between ten and 15
419 hatched and still unhatched mature embryos ~6–8 mm in length were found (Fig 7C).
420 Unfortunately, condition indices for these females were not calculated because the
421 material from the corresponding hauls, belonging to RECOMARES project, was not
422 fully processed at the time in which the present study was carried out. In male gonads,

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423 an intense spermatogenic activity was observed in October, with spermatogonia,
424 spermatocytes, spermatids and spermatozoa. One male from July 2010 was immature,
425 only showing spermatogonia and spermatocytes.

426 Regarding *C. laticeps*, sex-ratio was 0.4 (males:females, n = 14). Two females from
427 July (SL < 22 cm) displayed immature ovaries containing oocytes in previtellogenic
428 state (Fig. 7D). Vitellogenesis started from an oocyte diameter of 0.2 mm. Another
429 female from the same month (SL = 39.7 cm) displayed mature ovaries with late
430 vitellogenic oocytes full of yolk granules and some interspersed previtellogenic oocytes.
431 One female from December displayed an empty ovary with atretic follicles and some
432 immature oocytes. The single male analysed was captured in October and displayed
433 immature gonads containing primary and secondary spermatogonia.

434 In the case of *M. atlanticum*, sex-ratio was 0.65 (males:females, n = 61). Four out of the
435 six females with gonads processed for histology (all from October) displayed oocytes at
436 advanced vitellogenic stages (Fig. 7E) while the other two were in early process of
437 maturation, with oocytes at cortical alveoli and vitellogenic stages. Vitellogenesis
438 started from an oocyte diameter of 0.4 mm. In contrast to *Cataetyx* species, fusion of
439 yolk granules was observed in mature oocytes. The single male examined had testes
440 containing primary and secondary spermatogonia and primary spermatocytes (Fig. 7F).
441 Mean absolute and relative fecundities, as well as mean diameter of early vitellogenic
442 and mature oocytes for adult females of the three species are displayed in Table 1.
443 Fecundity and egg size data are based on samples from Autumn 1988.

445 3.4. Dietary study

446 Diet of *C. alleni* was diverse, based on a high variety of suprabenthic organisms, mainly
447 natatory peracarids, polynoid polychaetes and decapod crustaceans (Fig. 8A). Among

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448 peracarids, mobile (swimming) species dominated (e.g. *Ilyarachna* spp. and
449 *Munnopsurus atlanticus* among asellote isopods, *Boreomysis arctica* among mysids).
450 Taxa usually linked to sediments, like cumaceans, contributed less. The biggest prey
451 (i.e. crabs, small lobsters) were consumed by larger specimens. Diet varied as a function
452 of season (see Carrassón and Matallanas (2002b) for detailed seasonal data). In brief, in
453 winter and spring Axiidae (*Calocarides coronatus* and *Calocaris macandreae*),
454 Polynoidae (*Harmothoe* spp.) and isopod asellotes were more abundant, while in
455 summer and autumn crabs (*Monodaeus couchi*) and shrimps (*Pandalina profunda*) were
456 the most important prey. Seasonal dynamics of stomach fullness evidenced highest
457 amount of food ingested in summer and lowest values in autumn (%*f* = 0.26 vs. 0.02,
458 respectively), while intermediate values were found in winter and spring (%*f* = 0.09 and
459 0.12, respectively). Due to the high vacuity coefficient (% specimens with empty
460 stomachs) in *C. alleni* (50.96 %), intestinal fullness was also estimated. In this case,
461 highest values were found in spring and lowest values in winter (%*f* = 0.27 vs. 0.07,
462 respectively). Intermediate values were detected in summer and autumn (%*f* = 0.16 and
463 0.10, respectively).
464 Based in a low number of samples examined, the diet of *C. laticeps* was represented, as
465 for *C. alleni*, by suprabenthic-nectobenthic prey (e.g. fish like *Coryphaenoides*
466 *guentheri* and *C. alleni*; shrimps like *Aristeus antennatus*, *Acantheephyra eximia* or
467 *Nematocarcinus exilis*) (Fig. 8B). However, prey were bigger than those found in *C.*
468 *alleni*. Among smallest individuals (three specimens between 5–7 cm TL), similar in
469 size to *C. alleni*, identical prey to those identified in *C. alleni* were found: polynoid
470 polychaetes and peracarids (e.g. Lysianassidae, *Rhachotropis* sp., *B. arctica*, etc.).
471 Vacuity coefficient was 10%. Total stomach fullness was very low (%*f* = 0.05) and
472 could not be analysed as a function of seasonality.

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473 Diet of *M. atlanticum* was almost exclusively based on pelagic prey (Alciopiidae,
474 Calanoidea, *Sergestes arcticus*, *Conchoecia* spp.), including a few suprabenthic prey
475 (Polynoidae) (Fig. 8C). Vacuity coefficient was 15.6%. Stomach fullness was very low
476 and decreased from summer to autumn (%*f* = 0.004 vs. 0.002). Actually, only a small
477 number of entire prey were found in a few guts. In most cases prey were only
478 represented by digested hard parts (e.g. polychaetes setae).

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480 3.5. Parasitological study

481 Complete specimens of *C. alleni* examined in the present study displayed a total
482 parasite prevalence of 31.68 % and harboured a total of ten different parasite taxa,
483 including two digeneans, one cestode, five nematodes, one copepod and one isopod.
484 Prevalence and mean abundance values for these parasites and descriptors of the
485 parasite community are provided in Table 2. Anisakid nematodes *Hysterothylacium*
486 *aduncum* and *Raphidascaris macrouri* were, by far, the most prevalent parasites (total P
487 = 14.85 % and 9.90 %, respectively) and were thus categorized as “common”, while the
488 rest were considered accidental infections. Nematodes classified as Anisakidae gen. sp.
489 and *Raphidascaris* sp. most probably belonged either to *H. aduncum* or to *R. macrouri*,
490 but a more accurate identification was not possible due to their bad condition.
491 Significant positive associations were found between fish TL and total parasite
492 abundance (GZM, $\chi^2 = 4.877$, $p = 0.027$), parasite diversity ($r_s = 0.208$, $p = 0.038$) and
493 abundance of *H. aduncum* (GZM, $\chi^2 = 5.251$, $p = 0.022$). No significant differences
494 among slope regions or between year periods were detected for parasitological
495 descriptors ($p > 0.05$).
496 Intestinal samples of *C. alleni* from the BATIMAR project displayed a total parasite P
497 of 28.33 %. Parasites recovered consisted in four nematode taxa (Table 2), of which

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498 common parasites were, again, the nematodes *H. aduncum* and *R. macrouri* (total P =
499 15.00 % and 13.33 %, respectively). In this case, no significant relationships were found
500 between parasitological descriptors or common parasites infection parameters and fish
501 size or biological indices ($p > 0.05$). Total mean abundance, MSR, P and abundance of
502 *H. aduncum*, and P and abundance of *R. macrouri* were significantly higher in autumn
503 than in summer (GZM, $\chi^2 = 4.647$, $p = 0.031$; $\chi^2 = 4.908$, $p = 0.027$; $\chi^2 = 6.093$, $p =$
504 0.014 ; $\chi^2 = 7.190$, $p = 0.007$; $\chi^2 = 3.885$, $p = 0.049$ and $\chi^2 = 4.967$, $p = 0.026$,
505 respectively). For the four former variables, a significant interaction between fish SL
506 and the factor season was found (GZM, $\chi^2 = 5.438$, $p = 0.020$; $\chi^2 = 5.292$, $p = 0.021$; χ^2
507 $= 6.141$, $p = 0.013$ and $\chi^2 = 7.824$, $p = 0.005$, respectively). Conversely, no significant
508 differences among slope regions were detected ($p > 0.05$).

509 Specimens of *C. laticeps* examined harboured a total of six different parasite taxa
510 including one digenean, two cestodes and three nematodes (Table 2). Cestode parasites
511 consisted in two larval forms with indeterminate identities due to their immature state.
512 These two forms, that could actually represent more than two species, differed in size
513 and morphology: a small uni-acetabulate form bearing a single apical sucker and a
514 bigger bothriate form bearing four bothridia and an apical sucker and assigned to *Scolex*
515 *pleuronectis*, a collective name applied to plerocercoids of cestodes of the order
516 Tetrphyllidea (Jensen and Bullard, 2010).

517 The CCA assessing relationships between main prey items and common parasites of *C.*
518 *alleni* and *C. laticeps*, shown in Figure 9, displayed a clear association of the parasites
519 *H. aduncum* and the two morphotypes of larval cestodes with *C. laticeps* and its main
520 prey (i.e. teleosts and large natantian decapods). Regarding the nematode *R. macrouri*,
521 only recovered from *C. alleni*, it was mainly associated to samples from the upper and

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522 middle slopes and small-sized crustaceans (e.g. *Rhachotropis* amphipods, cumaceans or
523 calanoid copepods) and polynoid polychaetes.
524 Complete specimens of *M. atlanticum* examined for parasites displayed a total P of 25
525 %. Two parasite taxa were recovered: the larval cestode *S. pleuronectis* and the
526 nematode *H. aduncum*, both considered common (total P = 10.71 % and 17.86 %,
527 respectively) (Table 2). Total parasite P, TMA and MSR displayed a significant positive
528 association to fish TL (GZM, $\chi^2 = 4.584$, $p = 0.032$; $\chi^2 = 6.033$, $p = 0.014$ and $\chi^2 =$
529 4.166 , $p = 0.041$, respectively). Moreover, these same descriptors were significantly
530 higher in spring-summer than in autumn-winter (GZM, $\chi^2 = 5.238$, $p = 0.022$; $\chi^2 =$
531 7.402 , $p = 0.007$ and $\chi^2 = 4.409$, $p = 0.036$, respectively).
532 A single parasite was recovered from intestinal samples of *M. atlanticum* from the
533 BATIMAR project, the cestode *S. pleuronectis* (Table 3).

534 535 3.6. Enzymatic determinations

536 Mean activity values and activity ranges for the enzymatic biomarkers analyzed in *C.*
537 *alleni* and *M. atlanticum* are displayed in Table 4. For AChE, K_m (substrate affinity)
538 was 0.1045 mM and V_{max} (maximal velocity) 149.25 nmol/min/mg prot for *C. alleni*
539 and K_m was 0.1154 mM and V_{max} 384.62 nmol/min/mg prot for *M. atlanticum*. No
540 significant associations were detected between activities of these enzymes and fish size
541 ($p > 0.05$).

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543 4. Discussion

544 4.1. Density and distribution of Bythitidae and Zoarcidae in the Balearic basin

545 One of the relevant features of present research is the long timespan (i.e. from 1987 to
546 present) covered, which allows observing interesting patterns in a long-time temporal

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547 scale. In this sense, one of the most evident patterns observed in the present study is a
548 diminishing trend in estimated fish densities over the last decades for *M. atlanticum* and
549 *C. alleni*. Indeed, mean density was 2.46 ind/ha for *M. atlanticum* and 1.36 ind/ha for *C.*
550 *alleni* in hauls from late 80s and early 90s, and decreased to 0.86 and 1.01 ind/ha,
551 respectively, in hauls from year 2007 on. These trends were already reported by Cartes
552 et al. (2009b), who noted a reduction in fish abundance and diversity during the period
553 1988 – 2007 and an increase of decapod crustaceans in the area. As explained by these
554 authors, this trend is mostly explained by climatic oscillations that favoured plankton-
555 suprabenthos feeders (such as *M. atlanticum* and *C. alleni*) in 1988–1992 in comparison
556 with the 2007–2008 period, in which benthos-feeders were favoured instead. This trend,
557 however, does not indicate a progressive decrease in diversity (which should be
558 addressed by a more complete sampling series) and can be rather linked to periodic
559 climatic oscillations, related, for instance, to NAO (North Atlantic Oscillation) indices
560 (Cartes et al., 2015).

561 Regarding geographical distribution, in deep-sea species it is mostly shaped by
562 environmental conditions that influence availability of trophic resources and also the
563 life cycle of species themselves (Cartes et al., 2018; Fanelli et al., 2013a; Papiol et al.,
564 2012). In relation to *C. alleni*, *C. laticeps* and *M. atlanticum*, studied herein, a patchy
565 distribution is evidenced by present results. Although this has already been argued for
566 the distribution of benthic organisms (e.g. in isopods, see Cartes and Figueroa (2020)),
567 in the present study this heterogeneity is identified for mobile species. This pattern is
568 especially strong for *M. atlanticum*, which shows a high swimming activity as deduced
569 from dietary and parasitological studies (see sections 4.2. and 4.3. below), and that
570 seems to aggregate as a result of its reproductive behavior. Indeed, an enormous
571 variability in population density was observed among hauls for this species, with some

1 572 exceptionally high density values (the highest one reaching 1826 individuals / km²) that
2 573 are suggestive of an aggregated pattern, consisting in high density patches in specific
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7 575 Another evident pattern, both for Bythididae and Zoarcidae, is the low/poor densities
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9 576 observed around insular areas. The fact that the three species analyzed herein (four,
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11 577 including *B. apoda*) are viviparous (in the case of Bythididae) and/or have big eggs and
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13 578 low number of larvae and, probably, big first larval stages display low mobility,
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15 579 accentuate difficulties in colonizing new areas around islands due to low larval
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17 580 dispersion. In addition, these species might not find their optimal habitats at insular
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19 581 habitats. In this sense, differences in the sediment nature in mainland vs. insular regions
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21 582 (Cartes and Figueroa, 2020) may play a relevant role. This same distribution pattern has
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23 583 been observed, not as drastically though, in some Gadiformes in the area. For instance,
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25 584 *P. blennoides* and the roughsnout grenadier *Trachyrincus scabrus* (Rafinesque, 1810)
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27 585 are more abundant in mainland than in insular slopes (Fanelli et al., 2013a) due to the
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29 586 availability of trophic resources.
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36 587 An interesting pattern found for *M. atlanticum* is that aggregation occurs in areas close
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38 588 to submarine canyons and, noteworthy, more in the S face of canyons (see below).
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41 589 Despite this pattern has not been statistically demonstrated for *Cataetyx* spp. in the
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43 590 present study, it applies to the other Bythitidae distributed in the deep Mediterranean, *B.*
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45 591 *apoda*, a very rare species (only seven specimens collected in all BIOMARE-
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47 592 ANTROMARE cruises) almost exclusively collected in submarine canyons (six
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49 593 specimens in Besós Canyon, at 480–678 m depth).
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53 594 In the case of *C. alleni* a clear bigger-deeper trend was observed, as already reported by
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55 595 Stefanescu et al. (1992b) and Moranta et al. (2004), and indicative of an ontogenic
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57 596 migration with age to deeper grounds. Unfortunately, more data would be needed to
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597 confirm a bathymetric migration linked to reproduction, as has been reported for *N.*
598 *bonaparte* in the same area (Rodríguez Romeu et al., 2016). The progressive increase of
599 GSI values in the middle slope from spring to autumn (mean GSI = 0.4 ± 0.5 in spring,
600 1.6 ± 1.1 in summer and 6.1 ± 2.2 in autumn) and in the lower slope from summer to
601 autumn (mean GSI = 1.7 ± 0.9 and 4.2 ± 1.4 , respectively), alongside with the
602 generalized absence of large individuals in the upper slope, seem to indicate that this
603 species does not migrate to deeper grounds during the reproductive season and that
604 other factors may explain the depth-size trend observed. Actually, species-specific depth
605 distributions are highly distinctive and mainly attributed to individual autoecological
606 traits, with a particular importance of factors related to food availability. The restricted
607 trophic environment found below 1000 m in the Catalan Sea favours small species, such
608 as *C. alleni*, which are able to satisfy their energy requirements in contrast to large
609 demersal fish with higher energy demands (Stefanescu et al., 1993). The almost
610 disappearance of *C. alleni* in the lower slope has been attributed to competition with
611 other fish showing similar mean weight (size) and diet and deeper mean distribution,
612 such as the smallmouth spiny eel *Polyacanthonotus rissoanus* (De Filippi and Verany,
613 1857; Rodríguez Romeu et al., 2016) or Günther's grenadier *Coryphaenoides guentheri*
614 (Vaillant, 1888) (Carrassón and Matallanas, 2002b; Rodríguez Romeu et al., 2016).
615 In the specific case of *M. atlanticum*, it is likely that its geographical distribution is
616 constrained by its particular reproductive behaviour. Since this is a digging species
617 whose reproduction takes place in burrows excavated below the seafloor (Silverberg et
618 al., 1987; Silverberg and Bossé, 1994), appropriate substrates must be a necessary
619 requisite for its occurrence. In this sense, *M. atlanticum* dwells in muddy bottoms, as
620 reported by different authors (Silverberg and Bossé, 1994) and confirmed by present
621 results. Interestingly, highest densities of this species were recorded in the S side of

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622 canyons, a pattern also identified in the distribution of bamboo corals *Isidella elongata*
623 (González Irusta et al., in prep.). Therefore, it is conceivable that *M. atlanticum* needs
624 some texture of deep sediments that is preferentially located in the S of transversal
625 canyons in the Balearic Basin. The general regime of current circulation both for
626 intermediate (Levantine Intermediate Water, down to approximately 600 m depth) and
627 deep waters (Western Mediterranean Deep Water, down to the seafloor) occurring from
628 NE to SW in the studied area (Millot, 1999) may contribute to accumulate softer
629 sediments in the S, probably more fluid muds, while dispersing and resuspending
630 sediments above the seafloor in the N of submarine canyons, where more compacted
631 sediments would be found. Carpine (1970) already classified different “muddy bottoms”
632 in the deep western Mediterranean. The special requirements of sediments/habitats of
633 particular characteristics shown by species addressed herein may further influence their
634 distribution at larger scales, e.g. avoiding insular areas, as described above. In the case
635 of *M. atlanticum*, its distributional pattern along the Mediterranean Spanish margin as
636 determined from MEDITS bottom trawl surveys, performed yearly since 1994 (Bertrand
637 et al., 2002) is not regular, and the species is, for example, entirely absent from the
638 Alboran Sea (García-Ruiz et al., 2015). A possible indirect effect by trawling through
639 resuspension of sediments, described within canyons (Paradis et al., 2017) cannot be
640 discarded as having some indirect influence on *M. atlanticum* mating/spawning on the
641 upper slope (trawlers operate in the area to ca. 800 m), though our sampling was mostly
642 from adjacent slopes. This is the shallowest occurring species of those addressed herein,
643 living at shallower grounds than *Cataetyx* spp.

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645 4.2. Habitat use inferred by diet

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646 Regarding the ecological niche occupied by *Cataetyx* spp., it seems confined to the
647 near-bottom water-sediment interface. The diet of *C. alleni*, although including some
648 infaunal prey, showed different aspects indicating that this species mainly catches
649 suprabenthic prey, distributed at *ca.* 0–0.5 m above the bottom, while buried organisms
650 are hardly consumed. This is deduced, for example, by the fact that most asellote
651 isopods consumed by this species beared paddle-shaped legs adapted to natatory activity
652 (Cartes and Figueroa, 2020), by the high proportion of amphipods also with natatory
653 capacity (e.g. *Rhachotropis* spp. or Lysianassidae), by the high presence of polynoids
654 among polychaetes consumed and by the low proportion of cumaceans, usually linked
655 to sediments. *Cataetyx laticeps* is very similar to *C. alleni* in terms of trophic ecology
656 and the main difference between both at this respect is that bigger prey (e.g. shrimps
657 and fish) are consumed by the former due to a larger body size.

658 *Melanostigma atlanticum* was considered a demersal species by Stefanescu et al.
659 (1992a), in contrast to Gordon and Duncan (1985) or Haedrich and Merrett (1988). The
660 former authors argued that this species approached the seabed not only when spawning,
661 but also when looking for food. However, present results rather suggested the contrary,
662 that *M. atlanticum* is in contact with the seafloor only when spawning since its diet is
663 almost exclusively based in pelagic prey. No data, however, are available on catches of
664 *M. atlanticum* in midwater. Therefore, the life cycle of this species probably develops in
665 the water column near the bottom, in the benthic boundary layer (BBL). In fact, not
666 only reproducers, but also smaller-sized individuals were collected by trawling in
667 present samplings, strengthening this hypothesis.

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669 4.3. Habitat use inferred by parasites and parasites transmission patterns

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670 Composition and structure of parasitological assemblages identified in *C. alleni*, *C.*
671 *laticeps* and *M. atlanticum*, which are herein described in full for the first time, reflect
672 the differences in habitat use already deduced from the dietary study. Notably,
673 parasitological descriptors of *Cataetyx* spp. were higher than in *M. atlanticum*, which is
674 likely explained by the different habitat distribution of these species. In general,
675 benthopelagic species such as *C. alleni* and *C. laticeps* are known to be infected by
676 more parasites than those with pelagic habits, which is indicative of exposure to a
677 broader spectrum of parasites through consumption of a variety of prey that can act as
678 potential transmitters (Campbell et al., 1980; Marcogliese, 2002). However, richness,
679 diversity and abundance of parasite assemblages of *Cataetyx* spp., and mostly for *C.*
680 *alleni*, were low compared to other deep-sea fish of the same waters (Constenla et al.,
681 2015; Dallarés et al., 2014, 2016, 2017; Pérez-i-García et al., 2015b, 2017). It could be
682 hypothesized that this may be partly related to the fact that Bythitidae are viviparous
683 (without free larvae exposed to external influences), which limits egg and larval
684 dispersion and thus colonization of different habitats and exposure to a wider array of
685 parasites. In the case of *C. laticeps*, although too few individuals were examined for
686 parasites (six individuals), it is noteworthy that relatively high total values for parasite
687 diversity, prevalence and abundance were obtained. This could be indicative that this
688 species harbors a more abundant and diverse parasite community than its congener *C.*
689 *alleni*. Although the diet of both fish is rather similar, as noted above, the consumption
690 of larger prey by *C. laticeps* could make the difference in this case. Indeed, *C. laticeps*
691 consumes prey at a higher trophic level than *C. alleni* ($\delta^{15}\text{N} = 11.82$ vs. ~ 10.50 ; Fanelli
692 et al., 2013b) and large prey generally transmit more parasites than smaller ones to their
693 predators due to their own higher position within food webs and higher vagility. By its
694 size, *C. laticeps* may thus accumulate the “parasitological history” of a wider array of prey,

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695 i.e. it has exposure to a wider array of parasites from different sources. For these
696 reasons, the much larger size of *C. laticeps* is also important in explaining these
697 patterns. In effect, the relevance of body size for explaining parasite infection patterns is
698 evidenced by significant associations found in the present study between this variable
699 and parasite abundance, richness and diversity in *C. alleni* and *M. atlanticum*. As the
700 host grows bigger, it is able to consume larger and more diverse prey, which will
701 increase parasite transmission, and may also accumulate parasites (especially larval
702 forms) that “wait” to be trophically transmitted onto their next host (Dallarés et al.,
703 2017). In relation to *M. atlanticum*, its depauperate parasite community is typical of fish
704 with a more pelagic distribution due to the lower availability of intermediate hosts on
705 the water column (Campbell et al., 1980; Marcogliese, 2002). Only larval parasites were
706 found, which indicates that *M. atlanticum* acts as intermediate or paratenic host for them
707 and has been linked to small body size (as is, indeed, observed for this species),
708 vulnerability to predation and, subsequently, a low trophic position within local food
709 web (Poulin and Leung, 2011).
710 Among the parasites recovered, it is noteworthy that the three species were infected by
711 the anisakid nematode *H. aduncum* at high prevalences. Indeed, this is a widespread
712 parasite both at the geographical and bathymetric scales that has been reported in a high
713 number of fishes and is known to use a wide variety of transmission routes (Køie,
714 1993). This parasite is basically associated to samples of *C. laticeps* in the CCA due to
715 the much higher abundances reached in this host. This leads to its linkage to *C. laticeps*
716 main prey, i.e. large natantian decapods and teleosts, which indeed could transmit this
717 parasite after becoming infected through consumption of its second intermediate or
718 transport hosts. As for *C. alleni*, for which relationships to *H. aduncum* are not
719 evidenced in the CCA, and *M. atlanticum*, not included in the analysis, small

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720 crustaceans and polychaetes (known first and second intermediate hosts, respectively,
721 for *H. aduncum*; Kjøie, 1993) constituting a significant part of their diet (Carrassón and
722 Matallanas, 2002b; present results) could transmit this parasite. The other parasite
723 commonly found in *C. alleni*, *R. macrouri*, is a recently described species that has been
724 reported at high prevalences in macrourid fishes in the same waters (Constenla et al.,
725 2015; Pérez-i-García et al., 2015a). Its importance also in parasite assemblages of *C.*
726 *alleni* may suggest a generalist infection pattern on deep-sea fishes at least in the NW
727 Mediterranean area with diverse infection routes. Actually, no reliable information is
728 available regarding the life cycle of this little-known parasite. Constenla et al. (2015)
729 suggested a potential transmission through suprabenthic peracarids (e.g. mysids), which
730 are also important in diet of *C. alleni*. Present CCA outcomes partially support this
731 hypothesis, linking *R. macrouri* to a variety of suprabenthic peracarids (other than
732 mysids) as well as to polynoid polychaetes. In any case, more studies on this species
733 need to be performed before drawing any conclusion on its transmission patterns.
734 Cestode larvae assigned to *S. pleuronectis* were also found infecting the three fish
735 species analysed herein, although only *C. laticeps* and *M. atlanticum* seemed to play an
736 important role in their life cycle. These larval forms typically exhibit euryxenous
737 specificity for their intermediate hosts and are thus broadly distributed, and infect
738 cetaceans or sharks as adults (Jensen and Bullard, 2010). As *H. aduncum*, they were
739 associated to main prey of *C. laticeps* in the CCA, which likely act as transmitters after
740 consuming a variety of intermediate or paratenic hosts.
741 Although the purpose of the present study was not to carry out a long-term
742 parasitological study, some interesting patterns can be outlined in relation to samples
743 from BATIMAR (years 1988–1989) vs. BIOMARE (years 2007–2008) and
744 ANTROMARE (years 2010–2011) hauls. In the case of *C. alleni*, intestinal samples

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745 from more recent and from older samples were characterized by the same common
746 parasites (i.e. *H. aduncum* and *R. macrouri*), indicating that the basic composition of the
747 parasite community of this host has not significantly varied in the last three decades.
748 Similarly, seasonal trends were somewhat similar in recent and old intestinal samples,
749 with the autumn-winter period displaying higher values for parasitological descriptors
750 than the spring-summer period (values for recent intestinal samples in spring-summer
751 and autumn-winter periods: TP = 18.52 and 25.53 %, TMA = 0.30 ± 0.72 and $0.34 \pm$
752 0.67 , MSR = 0.37 ± 0.78 and 0.55 ± 0.97 , respectively; see Table 1 for seasonal values
753 of old samples). This trend was, however, much more marked in old than in recent
754 intestinal samples, as evidenced by statistical results. In the case of *M. atlanticum*,
755 almost identical parasitological descriptors occurred in more recent vs. older autumn
756 samples. Overall, these results highlight the general stability of the composition and
757 seasonal trends of these parasite assemblages in the long-term.

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759 *4.4. Reproductive aspects and trends in biological indices*

760 According to Follesa et al. (2011), *C. alleni* probably reproduces in autumn-winter since
761 inseminated females were found in November and January, in correspondence with the
762 highest maturity of males. These data are in accordance with present results, since all
763 females captured in October 2011 displayed fertilized gonads and GSI for this species
764 peaked in autumn-winter for both sexes. Notably, densities estimated for this species
765 increased progressively during summer and reached highest values in October, possibly
766 associated to reproductive aggregation events. The GSI increase co-occurred with subtle
767 decreases of CF and HSI (the latter only for males), which can be used as a proxy for
768 indirectly estimating fish nutritional status and reserves accumulation (Schloesser and
769 Fabrizio, 2017), possibly indicating accumulation of energy reserves before the

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770 reproductive period. Stomach fullness seasonal trends paralleled those observed for CF
771 and HSI, likely evidencing reserves accumulation through higher food consumption.
772 These differences in gut fullness across the year are well explained by seasonal changes
773 of external conditions that determine food availability and that, therefore, regulate
774 reproduction (Papiol et al., 2014). Indeed, fish reproductive state is known to be
775 modulated by external factors (Bromage and Roberts, 1995).
776 This is the first time that mature embryos are found inside two female's body in this
777 species. The presence of some already hatched embryos indicates that these females,
778 captured in early March, were spawning or about to spawn, and that embryonic
779 development likely lasts a few months. High densities observed during this month for *C.*
780 *alleni*, after fairly sustained values during December and February, and just before a
781 steep decrease during spring months, point to a long reproductive period (as suggested
782 by Follesa et al. (2011)) probably characterized by aggregation of individuals. Low
783 fecundity found for *C. alleni* when compared to other deep-sea teleosts (Fernandez-
784 Arcaya et al., 2016) is one of the conservative reproductive features displayed by this
785 species. Indeed, some of the most effective adaptations to deep-sea living conditions are
786 those allowing a conservative (K-strategist) reproductive cycle focused on producing
787 few larvae in advanced stages (i.e. reduced broods and large eggs) that may ensure high
788 survival of next generations (D'onghia et al., 1998; Koslow et al., 2000; Laptikhovsky,
789 2006). Regarding *C. laticeps*, the release of a large quantity of live larvae 7–8 mm in
790 length (approximately the same size than embryos observed in *C. alleni*, present study)
791 from one female captured in August in the NW Mediterranean was reported by Rannou
792 (1975), indicating that spawning of *C. laticeps* takes place in summer in this area. It
793 could be suggested that this event extends through autumn as well, as suggested by the
794 finding, in the present study, of a female that had recently spawned in December. The

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795 finding of a few maturing females in July, alongside with an immature male in October,
796 might point to a long reproductive period for this species (as suggested for its congener
797 *C. alleni*; Follesa et al., 2011), with mating taking place around the spring-summer
798 period. However, the low number of specimens available does not allow to precisely
799 determining further reproductive timing of this species.

800 According to Markle and Wenner (1979), the spawning season of *M. atlanticum* extends
801 from July to at least September, as judged by oocyte diameters, with females in June
802 showing the initiation of egg maturation. Indeed, these and other authors reported mean
803 oocyte diameters far larger than 2.5 mm in females captured in North-Atlantic waters
804 from July to September (Markle and Wenner, 1979; McAllister and Rees, 1964;
805 Silverberg et al., 1987). Other periods sampled showed all females possessing small (<
806 1 mm) eggs. According to present results, reproductive timing for this species seems to
807 follow a different pattern in the Mediterranean Sea. Females collected in October
808 displayed small oocytes (< 1 mm diameter) full of yolk, as observed in histological
809 sections, but no postovulatory or atretic oocytes were observed, and males captured in
810 the same hauls displayed immature gonads without spermatozoa, which confirms that
811 reproduction does not take place at the time of capture but later. Despite the lack of
812 significant differences between summer and autumn mean GSI values for this species,
813 an increasing trend is observed, indicating that gonads are undergoing maturation
814 during these seasons. Increased captures of this species are expected during the
815 reproductive period, since association with the seafloor occurs during this time. As
816 noted by Silverberg and Bossé (1994), contact with the ocean bottom may be quite
817 prolonged, lasting as much as ten months between the descent of adults towards the
818 sediment in mid-summer and the return to the water column in early spring of small
819 juveniles. Indeed, highest estimated densities occurred in summer and autumn months,

1 820 when most adults were captured, and seemed to kept medium values until mid-spring,
2 821 when the smallest individual (3 cm) was just captured.
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7 823 *4.5. Biochemical indicators*
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9 824 This is the first time that enzymatic activities are reported for *C. alleni* and *M.*

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11 825 *atlanticum*. While no enzymatic data have been published to date for bythitids, zoarcids

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14 826 are better characterized at this respect. Regarding available data for comparison with

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17 827 present results, Drazen et al. (2015) reported muscular LDH and CS activities in several

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19 828 zoarcids off California and Hand and Somero (1983) published on muscular LDH levels

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21 829 on the hydrothermal vent zoarcid *T. cerberus*.

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24 830 Among the chosen enzymes, LDH and CS are used as a proxy for metabolic rate. While

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26 831 LDH is associated to anaerobic metabolism and burst-swimming activity, CS is

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29 832 involved in the Krebs cycle and acts as indicator of aerobic metabolism (Dalhoff, 2004).

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31 833 Metabolic rate and thus the activity of these two enzymes generally decline with depth

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34 834 in marine fishes, in parallel with a marked decrease in food availability (Dalhoff, 2004;

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36 835 Drazen and Seibel, 2007; Drazen et al., 2015). Compared to other benthopelagic deep-

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39 836 sea fish species in the Balearic basin inhabiting a similar depth range, *C. alleni*

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41 837 displayed rather similar LDH activity values to those reported in, for example, *N.*

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43 838 *bonaparte* or *P. rissoanus* (Rodríguez-Romeu et al., 2016), while showing markedly

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46 839 higher LDH activity than *L. lepidion* and *A. rostratus* (Koenig and Solé, 2014; Pérez-i-

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49 840 García et al., 2015). In the case of *M. atlanticum*, high LDH activity values when

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51 841 compared to species with similar distribution (e.g. *P. blennoides* or *M. moro*, Dallarés et

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54 842 al., 2014, 2016). Interestingly, Hand and Somero (1983) also noted that LDH activities

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56 843 in muscle of the zoarcid *T. cerberus* were very high compared to other deep-sea fishes

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58 844 and that they were within the range noted for many shallow-living demersal species.
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845 Present LDH and CS levels reported for *M. atlanticum* are in turn within the range
846 reported by Drazen et al. (2015) for several benthic zoarcids. As for the third enzyme
847 assessed, AChE, it is involved in neurotransmission and increased activity levels have
848 been linked to higher swimming activity and pelagic distribution (Solé et al., 2010).
849 Somewhat similar levels to those reported in other deep-sea species of similar
850 distribution were found for *C. alleni*, while *M. atlanticum* generally displayed fairly
851 higher values (Solé et al., 2010; Dallarés et al., 2014; Koenig and Solé, 2014;
852 Rodríguez-Romeu et al., 2016).
853 Indeed, a great variability (sometimes even more than an order of magnitude difference)
854 naturally occurs in the activities of the analysed enzymes in deep-sea species inhabiting
855 similar depths and habitats (e.g. see Solé et al., 2010 and Drazen et al., 2015). Apart
856 from depth and habitat, many other factors are known to affect responses of these
857 biomarkers. For instance, food availability, environmental variables, body size,
858 biological and/or ecological particularities of the studied organism and even
859 contaminants, among others (Dalhoff, 2004; Solé et al., 2010; Drazen et al., 2015). It is
860 thus usually difficult to identify the exact causes for the observed levels and their
861 variations, even more in samples obtained in the field. Adding further complexity,
862 tissue-specific responses, short-term variability due to external or biological factors, and
863 the choice of the most adequate biomarkers in each case must be taken into account
864 (Dalhoff, 2004). At this respect, it could be concluded that despite their interest, present
865 novel enzymatic data are based on a small sample of individuals obtained in similar
866 conditions and do not allow drawing firm conclusions regarding their main drivers.

868 **5. Conclusions**

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869 In conclusion, data on diet and parasites proved useful tools to deduce habitat use,
870 distribution and special habits of the “non-conventional” specialized fish like those
871 belonging to Bythitidae and Zoarcidae here analyzed. In particular, suprabenthic and
872 pelagic habits were confirmed for *Cataetyx* spp. and *M. atlanticum*, respectively,
873 although the latter species develops benthic habits during reproduction. The distribution
874 of the studied species is conditioned by their particular life histories. Low larval
875 dispersion could be a determining factor posing difficulties for colonizing neighbouring
876 habitats, as is the case of insular slopes. In addition, optimal substrate conditions may
877 not be found in these areas, which could also explain the patchy distribution over
878 sedimentary depths observed at different scales, probably conditioned by reproductive
879 features of e.g. the digging zoarcid *M. atlanticum*. The specialized life histories of the
880 Bythitidae and Zoarcidae here analyzed is indicating that the *conventional* sedimentary
881 areas (e.g. not necessarily occupied by any habitat forming species like corals) that they
882 inhabit are not as homogeneous as is often assumed, with small scale gradients that
883 provoke the irregular distribution of species and have influence in its biology. Such
884 special interactions should be argued for future protection strategies for such habitats.

885

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Table 1. Mean absolute and relative fecundities, as well as diameter of late vitellogenic and mature oocytes of *Cataetyx alleni*, *Cataetyx laticeps* and *Melanostigma atlanticum*. Data are provided as mean \pm standard deviation (min. - max., n).

	<i>Cataetyx alleni</i>	<i>Cataetyx laticeps</i>	<i>Melanostigma atlanticum</i>
Absolute fecundity (oocytes)	2125.58 \pm 741.10 (955 – 3769, n = 36)	34794 (n = 1)	98 \pm 72.85 (7 - 218, n = 12)
Relative fecundity (oocytes/mm of length)	21.32 \pm 7.51 (10.38 – 36.24, n = 36)	87.64 (n = 1)	0.95 \pm 0.72 (0.06 – 2.12, n = 12)
Diameter of late vitellogenic oocytes (mm)	0.63 \pm 0.12 (0.5 – 1.00, n = 33)	n.a.	0.55 \pm 0.10 (0.4 – 0.7, n = 21)
Diameter of mature oocytes (mm)	1.15 \pm 0.08 (1.07 – 1.22, n = 3)	0.70 (n = 1)	0.60 \pm 0.05 (0.55 – 0.65, n = 4)

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Table 3. Developmental stage, location within host, prevalence (P(%)) and mean abundance (MA) ± standard deviation (SD) of parasites recovered in whole specimens and in intestines (BATIMAR project, years 1988 and 1989) of *Melanostigma atlanticum* examined in the present study. Associated parasitological descriptors are shown below. N: sample size. Abbreviations for parasite developmental stages: L, larva; Pd, plerocercoid. Abbreviations for parasite locations: Ac, abdominal cavity; In, intestine; Li, liver; MS, mesenteries. Different superscript letters show significant differences between year periods for parasitological descriptors.

N			<i>Melanostigma atlanticum</i>				<i>M. atlanticum</i> (intestines, BATIMAR project)		
	Stage	Location	Spring-summer 12		Autumn-winter 16		Autumn 11		
			P (%)	MA ± SD	P (%)	MA ± SD	P (%)	MA ± SD	
Cestoda									
	<i>Scolex pleuronectis</i>	Pd	In	33.33	0.42 ± 0.67	6.25	0.06 ± 0.25	9.09	0.09 ± 0.30
Nematoda									
	<i>Hysterothylacium aduncum</i>	L3, L4	Ac, Ms, Li	25.00	0.67 ± 1.50	–	–	–	–
Total P (%)			50.00 ^a		6.25 ^b		9.09		
Total mean abundance			1.25 ± 1.81 ^a		0.06 ± 0.25 ^b		0.09 ± 0.30		
Species richness			2		1		1		
Mean species richness			0.67 ± 0.77 ^a		0.06 ± 0.25 ^b		0.09 ± 0.30		
Mean diversity (Brillouin's index)			0.06 ± 0.14		0.00 ± 0.00		0.00 ± 0.00		

1213 **Table 4.** Mean \pm standard deviations of enzymatic activity levels (AChE,
 1214 acetylcholinesterase; LDH, lactate dehydrogenase; CS, citrate synthase) assessed in
 1215 *Cataetyx alleni* and *Melanostigma atlanticum*. N: sample size.

	<i>Cataetyx alleni</i>	<i>Melanostigma atlanticum</i>
N	14	13
AChE (nmol/min/mg prot)	105.47 \pm 32.51 (61.60–169.75)	364.60 \pm 139.39 (135.87 - 584.07)
AChE (μmol/min/g wet weight)	1.23 \pm 0.34 (0.56-1.94)	2.37 \pm 0.90 (0.86-3.99)
LDH (nmol/min/mg prot)	6657 \pm 972 (4960 - 8696)	11742 \pm 3665 (5481 - 19849)
LDH (μmol/min/g wet weight)	77.37 \pm 5.73 (72.54-93.32)	72.71 \pm 23.84 (27.18-109.05)
CS (nmol/min/mg prot)	45.64 \pm 7.76 (27.98 - 61.46)	62.72 \pm 24.97 (23.59 - 111.49)
CS (μmol/min/g wet weight)	0.53 \pm 0.08 (0.35-0.65)	0.41 \pm 0.24 (0.12-0.93)

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1218 **Figure captions**

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2 1219 **Figure 1.** Distribution of hauls in which specimens of *Melanostigma atlanticum* were
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4 1220 captured in the Balearic basin (A) and in the Besós area (B). Hauls are represented by a
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6 1221 solid spot in the case of OTSB-14 hauls and by an empty spot in the case of MTS-25
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8 1222 hauls; see section 2.6. for explanations on both fishing gears. Besós area is depicted in
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10 1223 figure A by a rectangle delimited by a dashed line. A buffer area proportional in size to
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12 1224 estimated fish density (log-transformed), delimited by a solid line in the case of OTSB-
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14 1225 14 hauls and by a dashed line in the case of MTS-25 hauls, is displayed for each haul.
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16 1226 Hauls in which no captures of *M. atlanticum* were registered are represented by a cross
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18 1227 in the case of OTSB-14 hauls and by a triangle in the case of MTS-25 hauls. Axes of
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20 1228 submarine canyons for which differences in density of *M. atlanticum* were tested
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22 1229 between NE and SW sides are represented by solid lines in figure B.

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24 1230 **Figure 2.** Distribution of hauls in which specimens of *Cataetyx alleni* (A) and *C.*
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26 1231 *laticeps* (B) were captured in the Balearic basin. A buffer area proportional in size to
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28 1232 estimated fish density is displayed for each haul. Hauls in which no captures of
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30 1233 *Cataetyx* spp. were registered are represented by a cross.

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32 1234 **Figure 3.** Estimated mean densities throughout the year in captures of *Cataetyx alleni*,
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34 1235 *C. laticeps* and *Melanostigma atlanticum*. In the case of *M. atlanticum*, densities from
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36 1236 hauls performed with OTSB-14 and MTS-25 trawls are displayed separately (see
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38 1237 section 2.6. for explanations on both fishing gears).

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40 1238 **Figure 4.** Size distribution of *Cataetyx alleni*, *C. laticeps* and *Melanostigma atlanticum*.
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42 1239 Data are splitted into depth strata and seasons for *C. alleni* and *M. atlanticum*. N:
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44 1240 number of individuals; TL: total length.

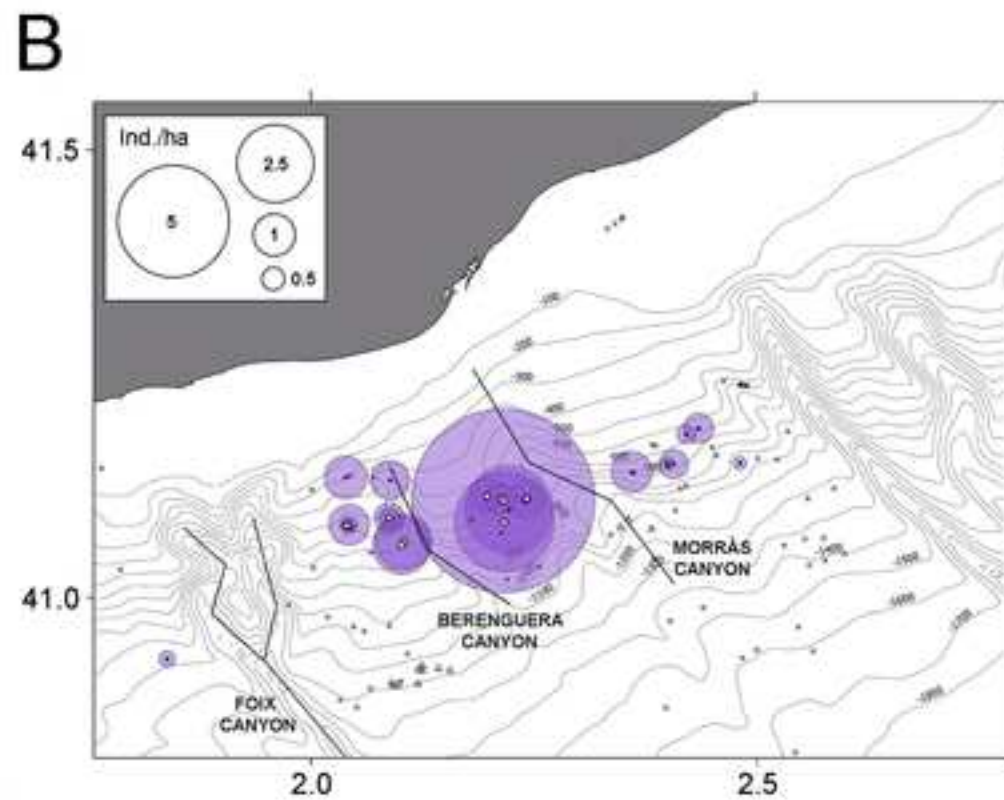
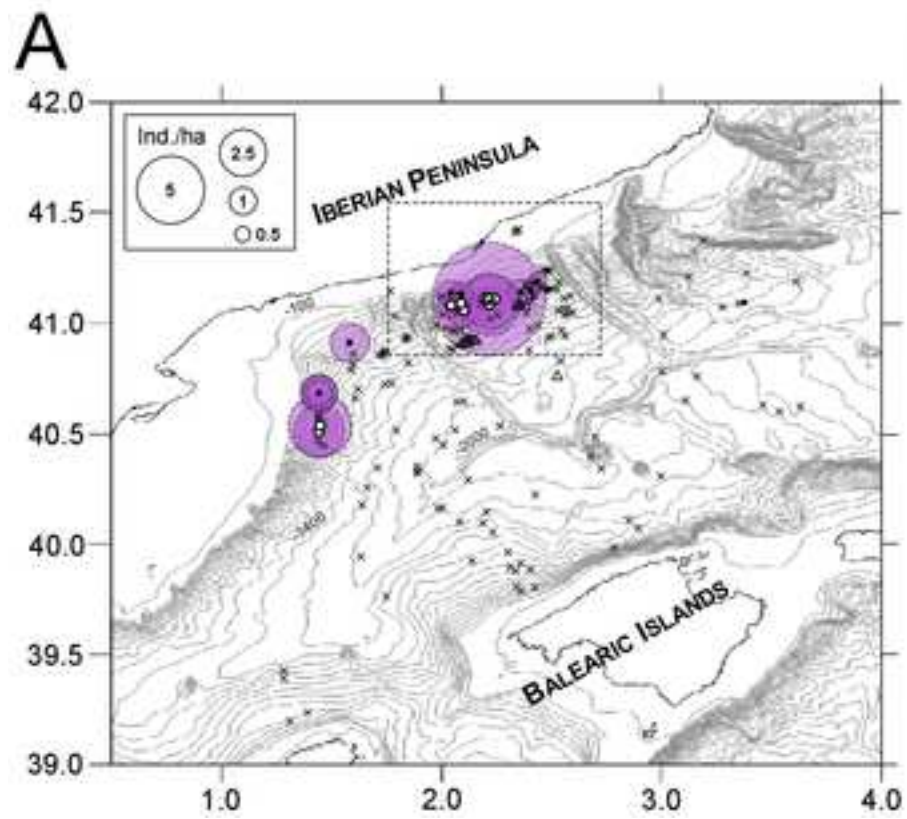
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46 1241 **Figure 5.** Size-depth relationships for males (●) and females (○) of *Cataetyx alleni* (A),
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48 1242 *C. laticeps* (B) and *Melanostigma atlanticum* (C). TL: total length.

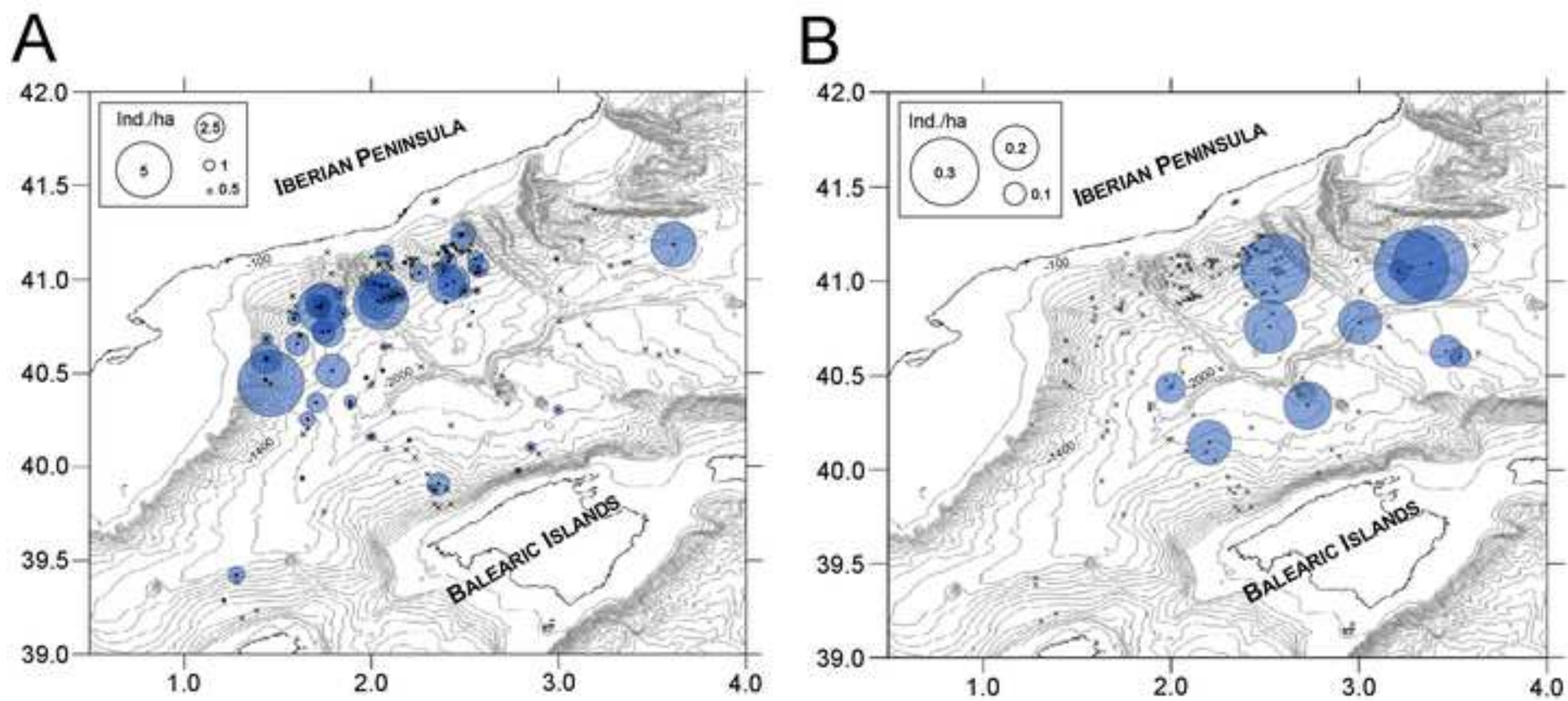
1243 **Figure 6.** Seasonal variability on mean values \pm standard deviations of Fulton's
1244 condition factor (K; A, D), hepatosomatic index (HSI; B, E) and gonadosomatic index
1245 (GSI; C, F) for *Cataetyx alleni* and *Melanostigma atlanticum*. HSI and GSI trends are
1246 displayed separately for males (●) and females (●). Different letters indicate significant
1247 differences across seasons. n: number of individuals.

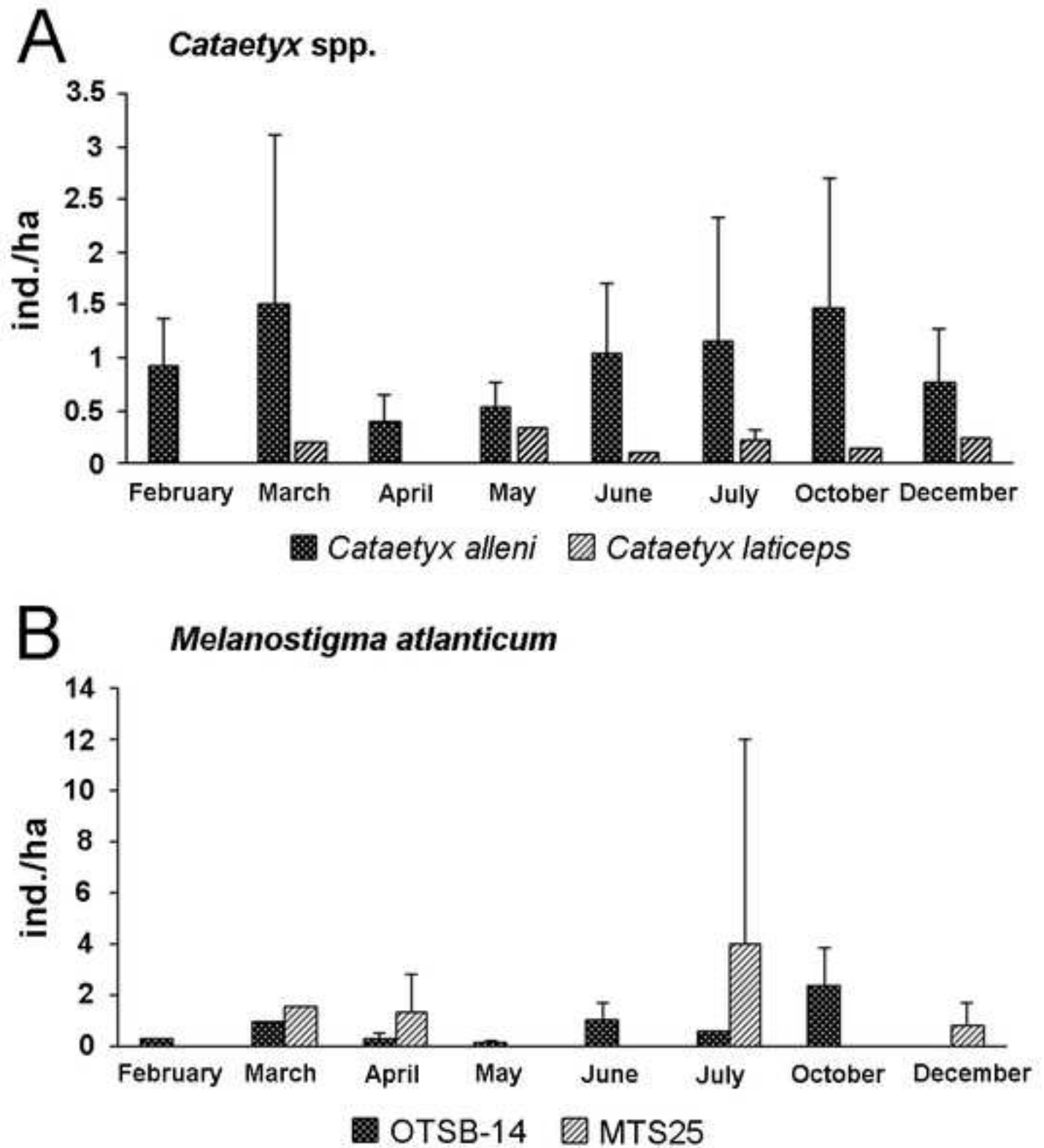
1248 **Figure 7.** Histological sections of gonads of *Cataetyx alleni* (A, B), *C. laticeps* (D) and
1249 *Melanostigma atlanticum* (E, F), and hatched (1) and unhatched (2) fully-developed
1250 embryos of *C. alleni* found within a female's gonad (C). O: oocyte; Sp: spermatozoa.
1251 Stains: hematoxylin-eosin and (A, B, E, F) and Mallory's trichrome stain (D).

1252 **Figure 8.** Contribution (%W) of main prey groups to diet of *Cataetyx alleni* (A), *C.*
1253 *laticeps* (B) and *Melanostigma atlanticum* (C). Data are splitted into seasons in the case
1254 of *C. alleni* and *M. atlanticum*.

1255 **Figure 9.** Plot of the canonical correspondence analysis relating common parasites
1256 (total prevalence \geq 10 %) to main prey groups of *Cataetyx alleni* and *C. laticeps*.
1257 Abbreviations for main prey groups: Alcio: Alciopiidae; Asell: Asellota; Axiid:
1258 Axiidae; Apseu: Apseudidae; Brach: Brachyura; Calan: Calanoidea; Cum: Cumacea;
1259 Cyprid: Cypridinidae; Gamm: other Gammaridea; Harp: *Harpinia* spp.; Isop: other
1260 Isopoda; Lysian: Lysianassidae; Mysida: Mysidacea (*Boreomysis arctica*); Natan:
1261 Decapoda Natantia; Osteych; Osteychthyes; Polyn: Polynoidae; Polych: other
1262 polychaeta; Rhach: *Rhachotropis* spp. Abbreviations for parasites: Cela: uni-acetabulate
1263 cestode larvae; Hyad: *Hysterothylacium aduncum*; Rama: *Raphidascaris macrouri*;
1264 Scpl: *Scolex pleuronectis*.

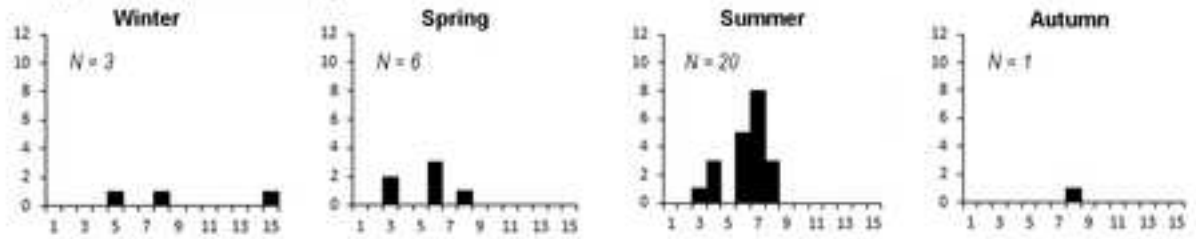




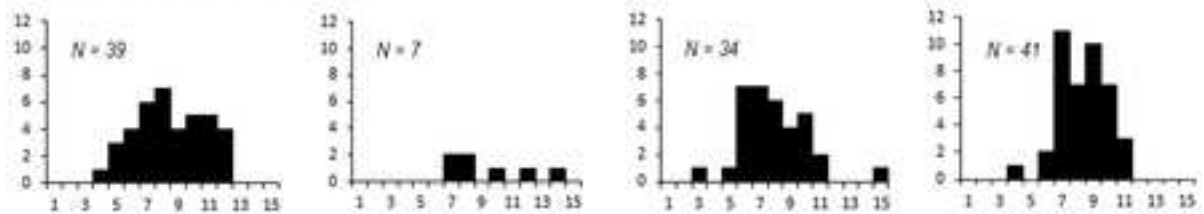


Cataetyx alleni

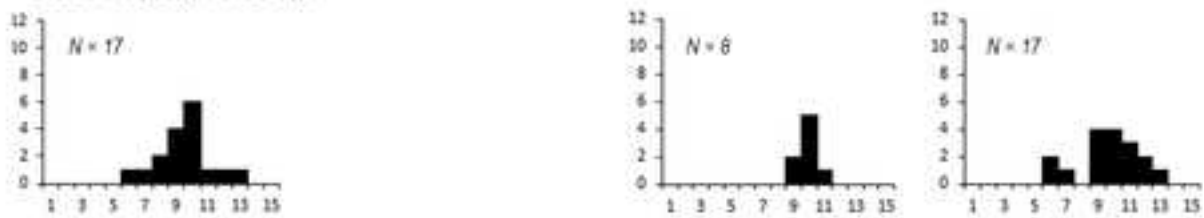
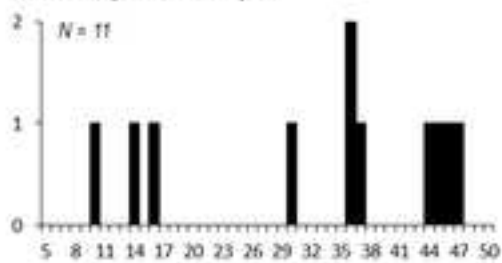
Upper slope (200-800 m)



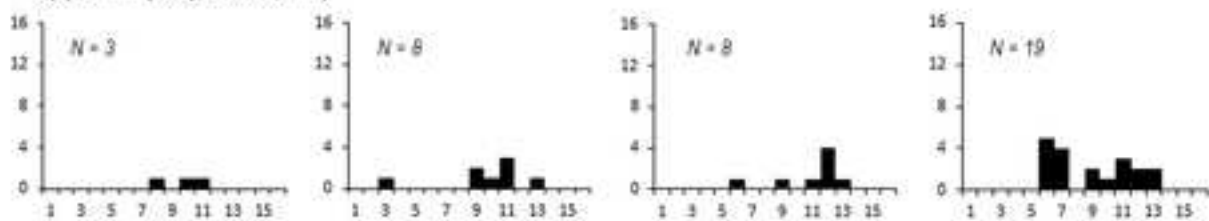
Middle slope (800-1400 m)



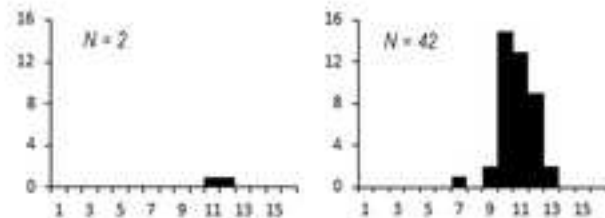
Lower slope (>1400 m)

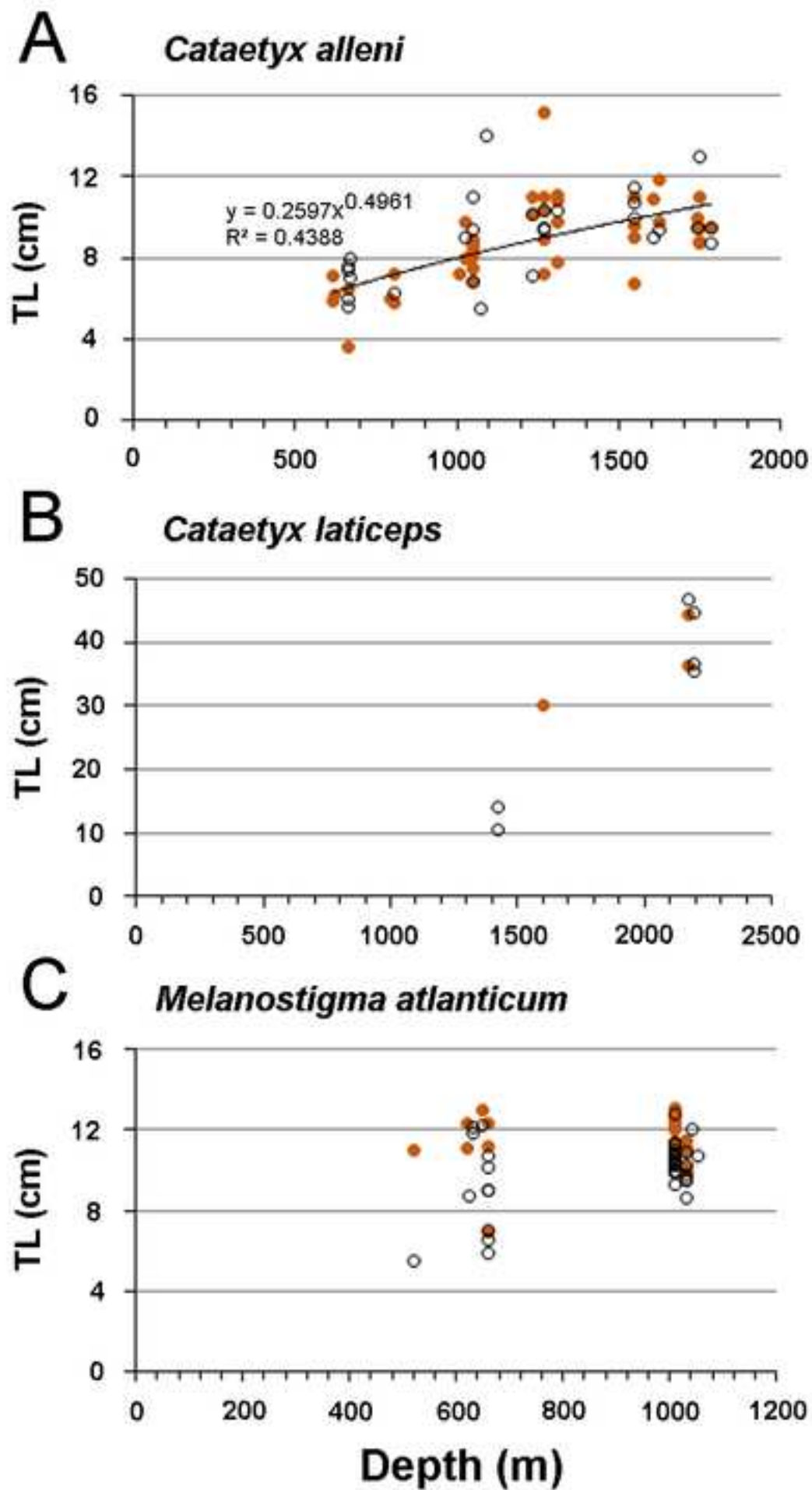
**N*****Cataetyx laticeps******Melanostigma atlanticum***

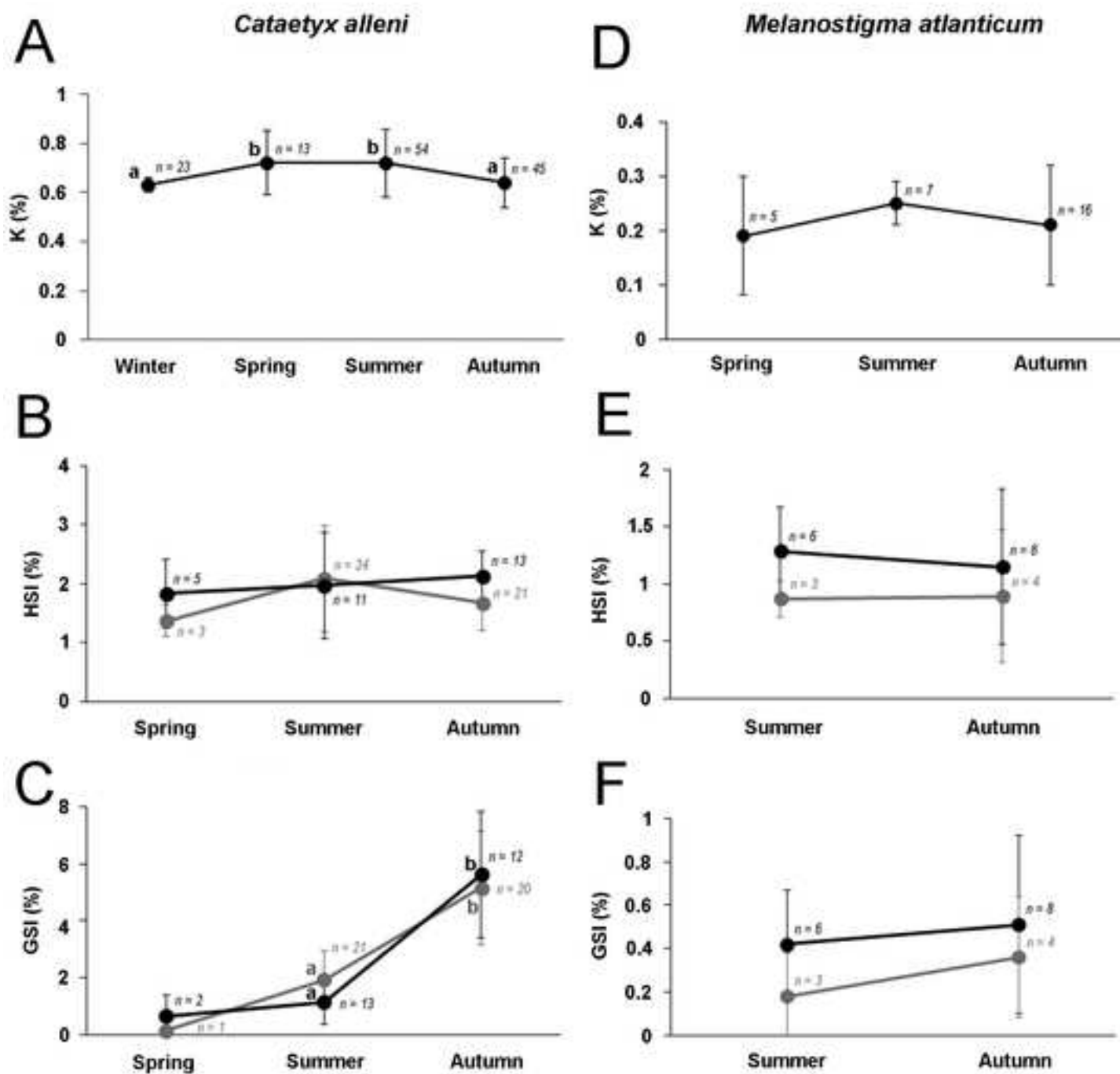
Upper slope (200-800 m)

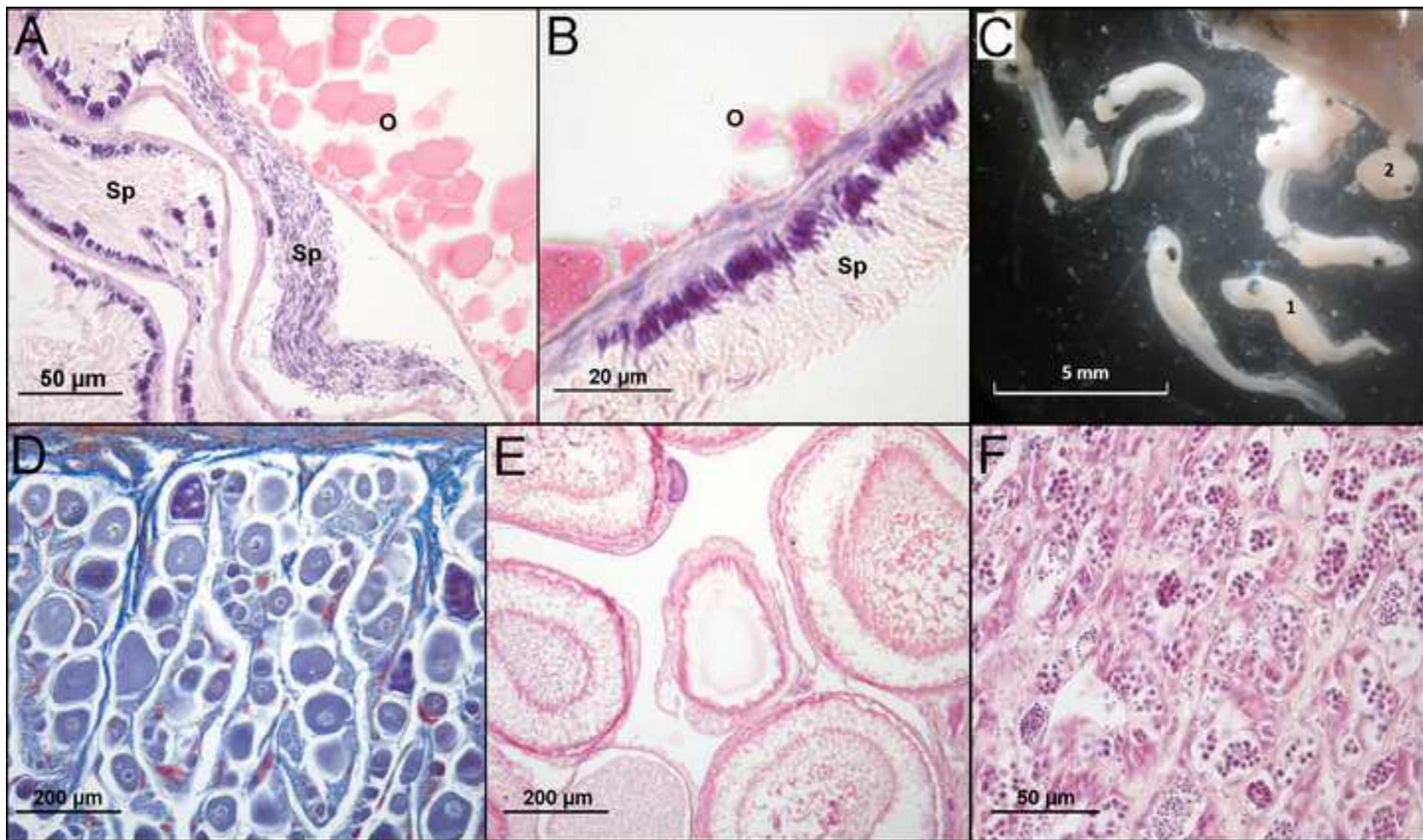


Middle slope (800-1400 m)

**TL (cm)**







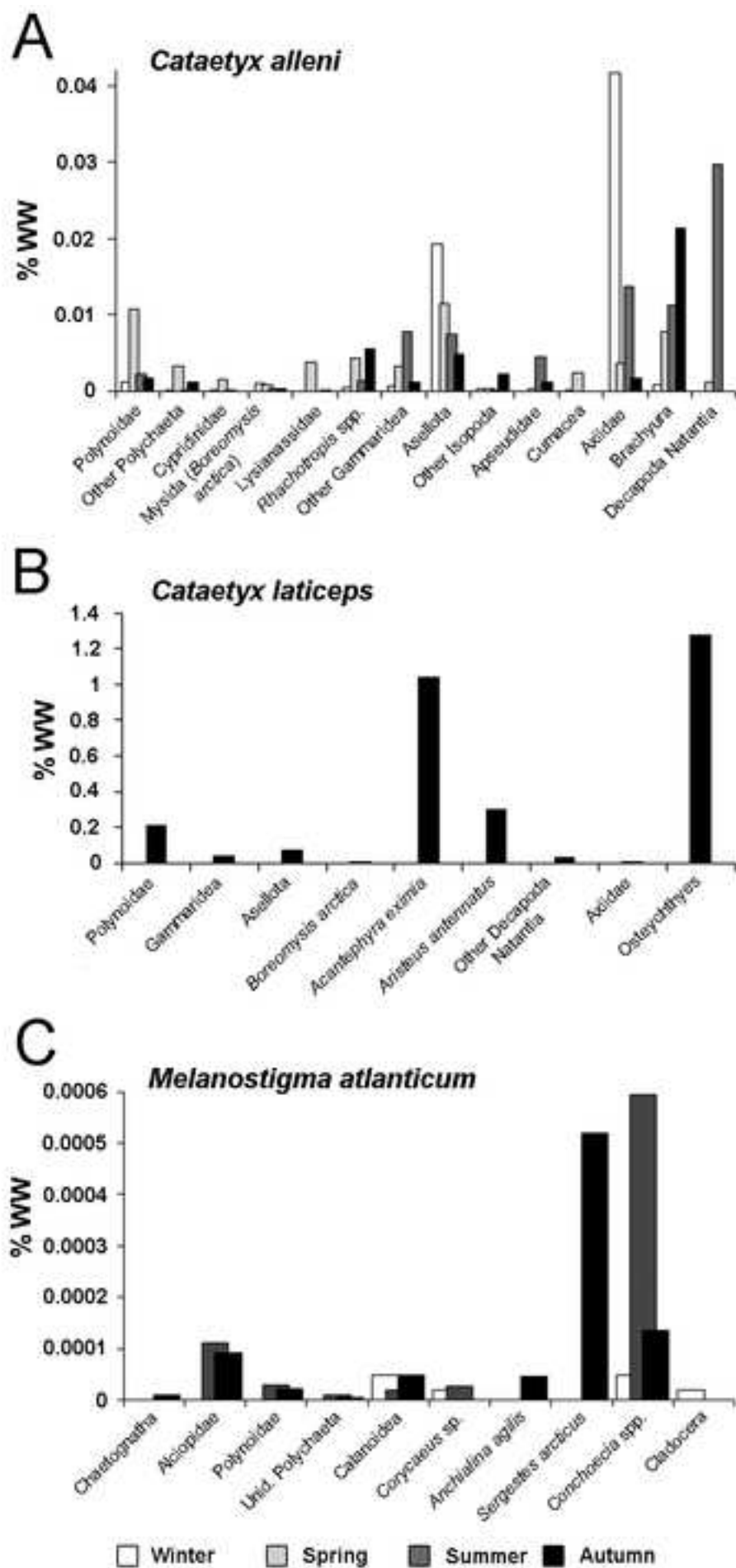


Figure 9

