
Functional traits unravel temporal changes in fish biomass production on artificial reefs

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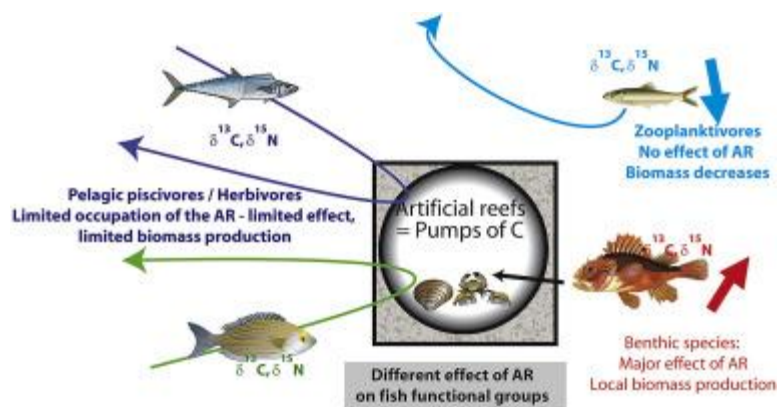
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Abstract :

Artificial reefs (ARs) are deployed worldwide as they are expected to support fisheries management. While the underlying mechanisms remain widely debated, production was recently determined as the most probable cause of increases in fish biomass. Changes in fish biomass in a temperate AR system were investigated from December 2008 to November 2015 by considering seven distinct functional groups, and isotopic functional indices were used to identify how these changes may have affected organic matter (OM) fluxes. Contrasting patterns of change were observed between functional trophic groups, highlighting that combining the biomass of all species present in a community is inappropriate for assessing AR-induced effects. Benthic sedentary species predominated (>75% of the total biomass) through massive production, with a 68-fold increase in mean biomass over the study period. Mobile species tended to vary seasonally, suggesting only a slight influence of AR. Zooplanktivores biomass decreased over the 6-year period, as a possible result of changes in environmental conditions. Isotopic indices helped to reveal both the community maturation and the importance of local OM sources not only in supporting fish biomass production but also in attracting pelagic species. Our results corroborate that production and attraction are two extremes of a range of contrasting patterns and highlight the importance of considering the specific responses of functional components of fish communities to accurately describe changes in AR functioning. Functional attributes such as trophic traits, habitat use and dispersal abilities must not be overlooked as they modulate fish species responses to the deployment of man-made rocky substrates.

Graphical abstract



Highlights

► Changes in fish functional groups biomass over 6 years were observed on artificial reefs. ► No robust pattern of change at assemblage level; 3 patterns for functional groups. ► Increase of biomass through production only for benthic fish species. ► Isotopic functional indices testify community maturation. ► Functional approach is powerful to ascertain biomass production.

Keywords : Artificial reefs, Mediterranean sea, Fish biomass production, Isotopic functional indices

45 1. Introduction

46 Biodiversity loss is one of the critical consequences of human-induced impacts on ecosystems
47 (Ceballos et al., 2015). A growing body of evidence has shown that overexploitation of resources and
48 habitat degradation are the major sources of disturbance in coastal marine regions (Halpern et al.,
49 2008). While the effects of fishing pressure on the structure and functioning of marine ecosystems
50 have been mostly assessed using biomass-derived indicators - as biomass can be easily estimated
51 from surveys or fisheries statistics (Coll et al., 2016) - recent theoretical developments demonstrate
52 the effectiveness of functional approaches in providing additional information for better detecting,
53 describing and explaining the overall impact of human pressures on marine environments (Mouillot
54 et al., 2013).

55 Functional ecology uses functional traits, *i.e.* any measurable biological characteristic that influences
56 species performance and survival: by considering functional traits in a quantitative way while taking
57 into account species biomass, Functional indices provide a meaningful framework to quantify how
58 disturbance affects ecosystems functioning (Mouillot et al., 2013) or to predict changes in ecosystem
59 processes (*e.g.* biogeochemical cycling; Naeem et al., 2012). Among the large range of morphological,
60 phenological and behavioral traits, trophic traits are the most intuitive and efficient discrete
61 attributes to (i) group species (e. g. Micheli and Halpern, 2005), (ii) capture and summarize
62 morphological, behavioral and interspecific interactions (Rigolet et al., 2015; Scharf et al., 2000;
63 Winemiller et al., 2015), (iii) reveal changes in food webs, trophic cascades, community structure and
64 ecosystem services (Coleman et al., 2015; Mouillot et al., 2013) and (iv) understand species-specific
65 responses and resilience to environmental heterogeneity (Coleman et al., 2015; Micheli and Halpern,
66 2005; Morris et al., 2018; Suzuki et al., 2018). Trophic diversity is therefore frequently used as a
67 proxy for functional diversity.

68 Stable isotopes are particularly suitable for defining trophic traits: carbon isotopic ratio ($\delta^{13}\text{C}$
69 hereafter) is classically used as a proxy for organic matter sources fueling food webs, while nitrogen
70 isotopic ratio ($\delta^{15}\text{N}$) is a relevant proxy for trophic level. Combining these two tracers was

71 demonstrated to be an efficient representation of species' ecological niche *sensu* Hutchinson, as the
72 "δ-space" ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) provide us insight on both resources type (the bionomic axis) and
73 species habitat (the scenopoetic axis), information commonly used to formalize the niche concept
74 (Bearhop et al., 2004; Jabot et al., 2017; Newsome et al., 2007). Isotopic indices, derived from the
75 dispersion and distribution of observations in the δ-space (Brind'Amour and Dubois, 2013), were thus
76 developed to describe communities' trophic structure, to quantify its total diversity or to estimate
77 trophic diversity (Layman et al., 2007). Despite the importance of taking into account biomass (or at
78 least estimation of abundance; Villéger et al., 2008) for good sets of metrics, and while biomass
79 weighted-functional indices are now commonly used in the literature, isotopic indices rarely
80 considered species-specific biomass in their calculation (Cucherousset and Villéger, 2015; Rigolet et
81 al., 2015). Such a limitation, except the faulty assumption that all species encountered within a
82 community have equal importance (Rigolet et al., 2015), may be related to the difficulty in collecting
83 species biomass and functional data simultaneously. This led researchers, in most cases, to ascribe
84 monitored biomass to species traits retrieved from global data aggregators such as FishBase (e. g.
85 Micheli and Halpern, 2005; Suzuki et al., 2018).

86
87 Artificial reefs (hereafter AR) have been used for centuries to manage coastal zones, to support
88 small-scale fisheries and restore degraded habitat (Becker et al., 2017; Claudet and Pelletier, 2004;
89 Neves Santos and Costa Monteiro, 1998). These structures are now a popular management tool, as
90 both professional and recreational fishermen seem satisfied with the increase in fish biomass and
91 catches at ARs (Tessier et al., 2015a). The origin of increasing biomass has been largely debated in
92 the literature and two main explanations have been proposed: while the first suggests that fish are
93 attracted from natural to artificial reefs, the second, the production hypothesis, states that fish
94 biomass increases are related to local production (e. g. Smith et al., 2016). Ecological mechanisms
95 behind these changes have been investigated in two distinct ways: some have scrutinized community
96 functioning (e.g. trophic relationships) without considering community composition nor long-term

97 changes (e. g. Relini et al., 2002; Scarcella et al., 2011) while others have measured changes in
98 biomass - sometimes in the same ARs -without thorough functional interpretation (Brickhill et al.,
99 2005; Relini et al., 1994). Investigating the relationships between organic matter fluxes and trophic
100 organization of fish communities, in addition to classical biomass measurement, may be a promising
101 scientific avenue to solve the old attraction/production controversy, notably by confirming that fish
102 and invertebrates communities of AR belong to the same food web (Powers et al., 2003; Brickhill et
103 al., 2005). While some studies have revealed that ARs favor biomass production (Champion et al.,
104 2015; Smith et al., 2016), most focused on single-time point surveys and overlooked long-term or
105 seasonal changes in fish communities; at best, 3 years of monitoring were investigated (Becker et al.,
106 2017). The massive amount of work required to monitor community composition and trophic
107 patterns may explain why such studies are rare.

108 From October 2007 to July 2008, more than 400 ARs were deployed in a 2km² area in the Bay of
109 Marseilles. This is the largest deployment of ARs in the Mediterranean Sea (Tessier et al., 2015b).
110 Reefs were constituted of metal frames, concrete piles and breeze blocks. Briefly, six types of
111 purpose-designed modules of different shapes and volumes were deployed and arranged in triangle-
112 shaped structures called “villages” at depth ranging from 25 to 35 meters(see Charbonnel et al., 2011
113 for a thorough description). After installation, both recreational and commercial fisheries were
114 forbidden in the zone. This deployment aimed to support artisanal fisheries and to restore adjacent
115 rocky reefs by fish biomass exportation, while being a great opportunity for researchers to examine
116 with special attention the “attraction versus production” hypotheses.

117 Here, based on our previous works carried out on this AR (see Table S1) and new analyses, we aimed
118 to better characterize its functioning and how it has evolved over the last years. To address this, we
119 followed a three-step procedure which builds on our knowledge of this system. First, a qualitative
120 investigation of system functioning was performed through measuring isotopic ratios all components
121 of the system. In the Bay of Marseilles, pelagic primary production dominated in both suspended and
122 sedimentary pools of organic matter (Cresson et al., 2012). Pelagic subsidies fueled the entire food

123 web, from suspension feeders to fish (Cresson et al., 2014a, 2016). Using stomach contents, we
124 corroborated the key role of AR as feeding areas: most important fish prey were invertebrate species
125 of the AR community. Secondly, the combination of these two sources of information, *i.e.* stable
126 isotopes and stomach contents, allowed determining 7 fish functional groups that share species with
127 similar functioning (Cresson et al., 2014a, 2014b); based on two seasons only, temporal variability
128 was not included however. To fill this gap, and thanks to the 6-year period of sampling, the temporal
129 modifications of the whole AR fish community were investigated, but also changes in each functional
130 trophic group. Thirdly, using Isotopic Functional Indices (IFI), calculated from both isotopic ratios and
131 individual biomass, we quantified how fish community maturation has affected the trophic structure
132 of the AR and its functioning over time, presumably as the coexistence of attraction and production
133 on the same maturing artificial reef system, mechanisms and processes being mainly related to fish
134 species life traits and strategies. IFI are notably expected to provide a synthetic vision of the
135 multifaceted changes of community composition as an ARs system matures, and to highlight the
136 coexistence of attraction and production on the same maturing artificial reef system, depending on
137 species habits.

138

139 **2. Material and methods**

140 **2.1. Underwater surveys**

141 Among the six AR types deployed in the bay of Marseilles, our study focused on the three largest
142 (2 - 6 m high, 75 - 187m³), *i.e.* metal basket, fakir basket and quarry rocks (Charbonnel et al., 2011).
143 These architectural types were selected because their species richness was the highest (GIS
144 Posidonie, unpubl. data). Fish species abundance and biomass on ARs were assessed seasonally from
145 December 2008 to November 2015 on each AR by underwater visual surveys performed on six
146 individual metal basket, six fakir basket and 12 quarry rocks individual modules, following the
147 methodology developed by Harmelin-Vivien et al (1985).

148 On each AR, two divers worked simultaneously for scientific and safety reasons. The first diver
149 went directly to the bottom to identify mobile and fast-moving species, mostly predators that may
150 be easily disturbed and missed. Before reaching the bottom, the second diver stayed at the surface
151 to count pelagic species. Then, both divers counted benthic species around the AR, each with their
152 own species list to avoid double-counting. Fish abundance was determined and individual size was
153 estimated to the nearest 2 cm. All underwater surveys were performed by the same team, to
154 preclude observer-induced bias. When performed by experienced scientific divers, as here, this
155 method allows assessing about more than half of the fish assemblage diversity, including most large
156 demersal and benthic species (Harmelin-Vivien et al., 1985). This method is less efficient for small
157 cryptic species, such as blenniids and gobids (Caldwell et al., 2016), and, as they are poorly sampled
158 by methods used for isotopic analyses, these species were not considered in the present study.

159 For consistency with the temporal resolution of stable isotope data (see below), months from
160 November to February were referred as “winter” and from May to August as “summer”.

161

162 **2.2. Fish sampling and stable isotope analysis.**

163 Carbon and nitrogen isotopic ratios were used to provide a qualitative picture of the trophic
164 functioning of AR fish assemblage. Samples for stable isotope analyses were collected in summer and
165 winter 2010. A seasonal once-only sampling strategy was sufficient to establish a representative
166 picture of the fish community functional structure, as (i) changes in stable isotope composition were
167 of negligible importance over a 6-year period, (ii) isotopic variability does not alter major patterns of
168 food-web structure derived from isotopic indices (Jabot et al., 2017) and (iii) species isotopic ratios
169 did not vary over the studied period, an assumption confirmed by isotopic values measured for the
170 same species in the Bay of Marseilles in 2012 and 2015 (Ourgaud, 2015; Belloni et al., 2019). Based
171 on this similarity, isotopic ratios measured for salemia *Sarpa salpa* in the Bay of Marseilles (Ourgaud,
172 2015) were added to our dataset, as underwater surveys revealed the relative sporadic importance
173 of this species. Consequences of this assumption are discussed in Appendix 1. By limiting the effect of

174 repeated lethal sampling on fish community abundance and diversity, a crucial question in a no-take
 175 area, this approach falls within a context of ethical research practices (Costello et al., 2016).

176

177 Sampling was consistent with classical methodology used for stable isotope analysis (see Cresson
 178 et al., 2014b). Dorsal muscle samples of 325 fish individuals were dissected, stored frozen, freeze
 179 dried and ground to a fine powder (Table S2). Powder was then analyzed with a flow mass
 180 spectrometer (Delta V advantage, Thermo Scientific). Stable isotope ratios were expressed following
 181 the classical δ notation:

$$182 \quad \delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 10^3 \quad (1)$$

183 where X is ^{13}C or ^{15}N and R the isotopic ratios $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. By applying a
 184 hierarchical cluster analysis based on the Euclidean similarity coefficient and Ward's algorithm
 185 calculated on the table encompassing stable isotope ratios and stomach contents obtained for each
 186 species, seven functional trophic groups were identified (see Cresson et al., 2014b). Pelagic piscivores
 187 included widely distributed demersal and pelagic species, that may prey on benthic or pelagic fish
 188 that mainly live in the water column, by as opposed to sedentary benthic piscivores such as *Conger*
 189 *conger* or *Scorpaena scrofa* that prey exclusively on benthic fish species and are generally gregarious.
 190 Clustering was consistent with the existing literature (e. g. Stergiou and Karpouzi, 2002; Karachle and
 191 Stergiou, 2017). Following Badalamenti et al (2000), trophic levels were based on individual's $\delta^{15}\text{N}$
 192 values:

$$193 \quad TL_i = \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{TB}}{TEF} + TL_{TB} \quad (2)$$

194 with TEF, the Trophic Enrichment Factor (i.e. the increase of $\delta^{15}\text{N}$ at each trophic level), set to 3.4‰.
 195 Two trophic baselines (TB) were used: nanophytoplankton ($\delta^{15}\text{N} = 1.77\text{‰}$ Rau et al., 1990) for most
 196 species and a proxy of benthic primary production ($\delta^{15}\text{N} = 3.91\text{‰}$; Cresson et al. 2014) for sparids, as
 197 applied in previous study (Cresson et al., 2014a). Trophic level of the baselines (TL_{TB}) was set to 1.

198

199 **2.3. Isotopic functional indices**

200 Biomass-weighted metrics were calculated following the methodology and scripts developed by
201 Cucherousset and Villéger (2015) and applied elsewhere (*e. g.* Chaalali et al., 2017; Rigolet et al.,
202 2015). This approach combined C and N isotopic ratios, as proxies of trophic functional diversity, and
203 community composition, assessed by species biomass. Biomass, rather than abundance, was chosen
204 to describe species assemblages (Villéger et al., 2008): by being directly related to metabolism and
205 secondary production, biomass performs better than abundance to resume species importance,
206 organic matter and energy fluxes within the community (Cucherousset and Villéger, 2015; Rigolet et
207 al., 2015). Biomass of each species was calculated from the length-mass relationship:

$$208 \quad M=a.L^b \quad (3)$$

209 where *a* and *b* are specific or allometric coefficients retrieved from the literature (Froese and Pauly,
210 2017). Biomass was calculated for all species observed on the ARs, whether their isotopic ratios were
211 measured or not. Seasonal relative biomasses-for species for which isotopic analysis were carried
212 out- were then calculated as the ratio between each species' biomass and the total fish biomass.
213 Species sampled for isotopic ratios represented more than 95% of the total biomass of the
214 community, with the exception of summer 2009 and winter 2015 when it was 91%. Species missing
215 stable isotope ratios had minor influences on the trophic organization of fish assemblage on ARs and
216 were: (i) pelagic vagrant species (*e.g. Mola mola, Sparus aurata* or *Seriola dumerili*) that occurred in
217 the AR zone for a very short period, (ii) small species (*e.g. Symphodus spp.*) with a relative biomass
218 close to 1% of the total biomass, and (iii) species observed once only (*e.g. Muraena helena* or
219 *Acantholabrus palloni*).

220 Average $\delta^{13}\text{C}$ and trophic level of the community were calculated as the sum of biomass-
221 weighted $\delta^{13}\text{C}$ and trophic levels for each species. Functional indices were computed on standardized
222 values (Cucherousset and Villéger, 2015; Jabot et al., 2017) to limit the influence of one isotope on
223 another, a well-known pitfall of isotopic metrics (Hoeinghaus and Zeug, 2008). Calculation details and
224 a full description of each index can be found in literature (Cucherousset and Villéger, 2015; Rigolet
225 et al., 2015) and their main rationale is only recalled here: functional divergence indices (Isotopic

226 Divergence 'IDiv' and Isotopic Dispersion 'IDis') provide information about isotopic richness, *i.e.* how
227 species diverge from the center of gravity of the community. High index values indicate most of the
228 biomass is dependant on alternative food sources (Chaalali et al., 2017). Functional evenness indices
229 (Isotopic Evenness 'IEve' and Isotopic Uniqueness 'IUni') describe the species distribution regularity
230 within the isotopic space. High values indicate communities dominated by a few specialist species
231 (Cucherousset and Villéger, 2015).

232

233 **2.4. Statistical analyses**

234 For each trophic group, temporal changes in biomass were first assessed by computing both
235 trend and seasonality for each time-series (December 2008-November 2015). Seasonality was
236 estimated by applying the average percentage method (Schwager and Etkorn, 2017) using median
237 values to alleviate potential biases related to extreme values (Spiegels and Stephens, 1999). Detailed
238 calculations are in Appendix 2. Three analyses were performed (*i*) non-parametric Mann-Kendall
239 (MK) statistical tests to assess the significance of each trend, (*ii*) Theil-Sen linear regressions to
240 quantify changes in species' biomass per unit time (Gilbert, 1987) and (*iii*) Mann-Whitney-Wilcoxon
241 (MW) non-parametric tests to estimate possible differences between summer and winter periods.
242 For each group, we also quantified whether trends were monotonically dependent on time by
243 performing Spearman's correlation permutation tests (999 permutations) with correction for
244 multiple comparisons (Legendre and Legendre, 2012). The closer r_s is to $|1|$ the stronger the
245 monotonic relationship (Table 2). This approach was applied on the whole community and to each
246 functional group and species. To consider a potential influence of predominating species when
247 estimating the total biomass of the seven functional groups, analyses were performed on observed
248 and standardized biomasses. Standardization (between 0 and 1, 0 being the biomass minimum and 1
249 the biomass maximum over the period December 2008 - November 2015) allowed to give equal
250 weight to each of the species within a given functional group. For each functional group that included
251 more than one species, a linear regression model was then applied, linear trends being represented

252 as solid lines. Isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and trophic level differences between functional groups were
253 estimated by means of ANOVA, including Tukey post-hoc tests. Inter-annual trends were summarized
254 by a Principal Component Analysis (PCA) performed on the matrix gathering the functional indices,
255 $\delta^{13}\text{C}$ values, trophic levels and total biomass per trophic group. Analyses and figures were performed
256 in R version 3.5.1 using the packages “car”, “FactoMineR”, “ggplot2”, “MASS” and “multcomp” (Fox
257 and Weisberg, 2010; Hothorn et al., 2008; Lê et al., 2008; R Core Team, 2018; Venables and Ripley,
258 2013; Wickham, 2009).

259

260 **3. Results**

261 **3.1. Biomass composition of the community**

262 From December 2008 to November 2015, the fish assemblage was dominated by benthic species
263 (herbivores, rocky- and soft-bottom mesocarnivores, macrocarnivores and benthic piscivores), that
264 represented more than 75% of the total biomass (Fig. 1). Rocky-bottom mesocarnivores (e.g labrids
265 and *Diplodus* spp.) were predominant and represented ~40% of the mean biomass, with seasonal
266 values ranging between 20-60%. Benthic piscivores were the second most important group (~20% of
267 the mean biomass) with high values related to large *Conger conger* individuals (Fig. S1). Low average
268 biomass (~5%) was measured for sandy bottom mesocarnivores (almost entirely one species *Mullus*
269 *surmuletus*) and for the herbivore *Sarpa salpa* (~3% of the mean biomass). Zooplanktivores
270 dominated pelagic species and represented ~25% of the mean biomass, but with high temporal
271 variability as their relative biomass ranged from 52% in winter 2009 to 3% in summer 2012. Pelagic
272 piscivores represented about 3% of the mean biomass, although especially high values were
273 observed in winter 2012 and 2014 (12 and 10%, respectively) because of the presence of mackerel
274 *Trachurus* spp. schools and large (36-50 cm) *Dicentrarchus labrax* individuals. Species richness within
275 each group remained constant during the studied period (Fig. S2)

276 **3.2. Isotopic composition of the community**

277 Functional groups displayed significant differences (ANOVA, $p < 10^{-3}$) for the descriptors ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$
278 and trophic level) used (Table 1). For $\delta^{13}\text{C}$, the major difference was observed between
279 zooplanktivores ($-19.75 \pm 0.37\text{‰}$) and other groups, with a 2.1‰ difference between minimal and
280 maximal values when all species were considered, but only $\sim 1\text{‰}$ when zooplanktivores were
281 excluded (Table 1). For $\delta^{15}\text{N}$ and trophic level, zooplanktivores and herbivores had the lowest values
282 ($8.28 \pm 0.51\text{‰}$ and $9.13 \pm 0.50\text{‰}$ for $\delta^{15}\text{N}$, 2.59 ± 0.30 and 2.53 ± 0.10 for trophic level respectively) while
283 pelagic piscivores clearly differed from all other groups ($13.63 \pm 2.28\text{‰}$ for $\delta^{15}\text{N}$, 4.49 ± 0.67 for trophic
284 level).

285 3.3. Temporal and seasonal changes in biomass

286 A general increase in biomass was detected from 2009 to 2015 (Fig. 2, Table S2) with an almost
287 doubling ($\times 1.5$) of the total biomass. When considering all species together however, we found that
288 this trend was not statistically significant (MK p-value = 0.951; Table 2). In comparing functional
289 groups, two patterns of changes were observed: a monotonous trend over the period 2009-2015 and
290 a marked seasonality. Major and significant biomass increases were observed for benthic piscivores
291 (Biomass $\times 68$; Sen's slope = 8.99, MK p-value = 0.01) and rocky-bottom mesocarnivores (Biomass \times
292 3; Sen's slope = 6.16, MK p-value = 0.2). These increasing trends were induced by the presence of
293 large individuals for *C. conger* and *Scorpaena scrofa* (Fig. S3, Table S3). Zooplanktivores displayed a
294 monotonous but decreasing trend, as evidenced by the steepest negative slope (Sen's slope = -12.43,
295 MK p-value = 0.16). Changes in herbivores, pelagic piscivores and sandy-bottom mesocarnivores
296 showed a strong seasonality with a high pelagic piscivore biomass in winter, but in summer for
297 herbivores and sandy-bottom mesocarnivores. While some species dominated the functional groups,
298 comparable results were obtained after standardization. Trends and seasonal patterns were similar
299 at both the species and functional group levels (Fig. S2, Table S3)

300 3.4. Interannual variability in the community functional structure

301 With two periods identified from winter 2009 to winter 2011 and from summer 2011 onwards, years
302 and both winter and summer seasons were well-separated on the PCA-biplot (Fig. 3), highlighting the
303 maturation of the fish community, functional changes over time, as well as a seasonal signal. The first
304 principal component (PC1, 37% of the explained variability) revealed the community maturation,
305 with increasing biomass in benthic species and decreasing biomass in pelagic species. As a result of
306 the decrease in pelagic species, a reduction in isotopic divergence and uniqueness, and an increase in
307 the mean $\delta^{13}\text{C}$ of the community were observed. The PC2 (20% of the total variability) detected
308 seasonality, this component being positively correlated with the community in summer, but
309 negatively in winter (except for winter 2015). This difference was mainly induced by the seasonal
310 occupation of artificial reefs by species with distinct trophic level (TL): herbivores with low TL in
311 summer and pelagic piscivores with high TL in winter. Herbivores in the summer community led to
312 high evenness values mainly because of the isotopic peculiarity of *S. salpa*. The unexpected position
313 of the community in winter 2015 was explained by a high value for isotopic evenness, as all groups
314 were present with slightly balanced biomass (Fig. 4). Examination of the second eigenvector
315 indicated that trophic level was highly negatively related to the PC2 (Fig. 3). While the position of
316 winter samples on the PCA-biplot was explained by high biomass of pelagic species, summer samples
317 were related to the presence of herbivores that induced low trophic level and high evenness values
318 (Figure S2).

319 **4. Discussion**

320 Over the last few decades, studies have largely focused on determining changes in fish biomass on
321 ARs, as fish biomass increases through production are crucial for ascertaining sustainable support to
322 fisheries (Powers et al., 2003). However, depending on species' life history strategies, contrasted
323 ecological responses to artificial habitats have emerged: benthic and sedentary species were largely
324 positively affected by AR deployment while no definite effect was observed for pelagic and mobile
325 species. These opposite patterns are typical in natural reefs but were seldom noticed in ARs (Morris
326 et al., 2018). They may explain and contribute to the attraction/production controversy: strong and

327 contrasting responses of fish to environmental heterogeneity were observed at the functional group-
328 level, which in turn generated noisy and non-significant trends in biomass at the community level
329 (Suzuki et al., 2018). Applying a functional approach and considering species on the basis of their
330 functional attributes therefore appears essential to adequately assess the ability of ARs to enhance
331 fish biomass.

332

333 **4.1. A major effect of ARs on benthic fish species production**

334 Predominance of benthic fish species in the AR community is consistent with most surveys
335 carried out on fish communities in natural and artificial reefs, in the Mediterranean Sea and
336 worldwide (Harmelin, 1987; Powers et al., 2003; Simon et al., 2011). Classically, these species show a
337 marked affinity for reefs, spending most of their life cycle on ARs and/or consuming food resources
338 there (Powers et al., 2003; Smith et al., 2016). The monotonous increasing trends as well as the
339 observation of larger individuals are also in line with actual biomass production linked to both an
340 increase in food resources and low fishing mortality. The ARs deployed in Marseilles were
341 intentionally designed to be complex habitats that provide shelter for these fish species and their
342 prey (Charbonnel et al., 2011). Increased accessibility to food resources, corroborated by the
343 presence in fish stomach contents of preys inhabiting AR (Cresson et al., 2014b), may enhance fish
344 growth rates (Scarcella et al., 2011). Fishing bans may also explain the occurrence of large benthic
345 piscivores, macro- and mesocarnivores individuals, usually prime targets of fisheries (Astruch et al.,
346 2018; Leleu et al., 2014). Important benthic species' biomasses and large individuals support that ARs
347 within marine protected areas are efficient in promoting biomass production and in spilling-over
348 larvae, juveniles and adults. This leads to the restoration of adjacent natural reefs and/or support for
349 fisheries (Harmelin-Vivien et al., 2008).

350 **4.2. A limited effect of ARs on species with a marked seasonal cycle**

351 The relative importance of soft- bottom mesocarnivores, herbivores and pelagic piscivores in the
352 assemblage and their notable seasonal variability demonstrated that ARs had a limited effect on
353 these species. Species included in these three functional groups only slightly contribute to the
354 community (3-5% of the average total biomass), which is consistent with their limited affinity for
355 rocky benthic artificial habitat. Large (up to 40cm in winter 2015; Table S2) *M. surmuletus* individuals
356 were unexpected as it is close to the largest size reported in the Mediterranean Sea (45 cm; Louisy,
357 2015). High *S. salpa* and *M. surmuletus* biomasses were observed on quarry rocks modules, *i.e.* rocks
358 deployed on the bottom, flat substrates covered by algal turf that may be grazed by *S. salpa* and on
359 which *M. surmuletus* may find its main prey, *e.g.* small crustaceans (Bautista-Vega et al., 2008). *Sarpa*
360 *salpa* species may also benefit from the adjacent *Posidonia oceanica* seagrass meadow to perform
361 seasonal displacements. A similar explanation can be given to pelagic piscivores that may use ARs to
362 predate on fish during some stages of their seasonal cycle only (Cresson et al., 2014b; Leitão et al.,
363 2008). High biomass of *D. labrax* in winter resulted from reproductive aggregations commonly
364 observed in coastal zones, independently of the presence of ARs. Finally, *D. labrax* and *M. surmuletus*
365 may also benefit from fishing closures as they are also targeted by fisheries. While both trophic and
366 protection effects of AR can be suggested for these species, their transient nature, with annual
367 displacement between AR and neighboring natural habitats was not influenced by AR deployment
368 and therefore restrain the influence of AR on biomass production.

369 **4.3. No effect of ARs on zooplanktivores**

370 The effect of ARs on zooplanktivores can be considered negligible as a low affinity for these structures
371 was expected (Powers et al., 2003). Most of the modules worldwide are too small to significantly
372 influence pelagic communities, whereas external forcing mainly impact zooplanktivores. This
373 decrease in zooplanktivores was already observed elsewhere in the Bay of Marseille and in the Gulf
374 of Lions (Brosset et al., 2016; Ourgaud et al., 2015). It was related to local drivers such as a decrease
375 of the organic matter available through improved sewage treatment (Ourgaud et al., 2015) and

376 global climatic forcing that may have affected small pelagic species through bottom-up trophic
377 cascades (Goberville et al., 2014). This hypothesis was strengthened by the recent local increase in
378 zooplanktivore biomass (L. Le Diréach, pers. obs.). While zooplanktivores have biological and
379 ecological peculiarities (e.g. transient nature, pelagic life, high sensitivity to environmental changes)
380 that may preclude a strong effect of ARs on their biomass, large modules may be beneficial as they
381 influence pelagic ecosystems (Champion et al., 2015). A positive effect can also be detected when
382 zooplanktivores show a strong association with reefs, *i.e.* when environmental conditions are optimal
383 to ensure efficient zooplankton supply (e.g reef's exposure to prevailing ocean currents; Champion et
384 al., 2015).

385 **4.4. A functional traits-based monitoring of ARs**

386 Our results provide useful insights to develop relevant indicators that assess the efficiency of ARs in
387 enhancing biomass production and to better manage these ecosystems. Structural and functional
388 community changes revealed that some functional groups displayed a clear increase in biomass in
389 response to an AR deployment while others did not, especially when the factors controlling changes
390 in biomass act at larger spatial or temporal scales. Differential responses of trophic groups to habitat
391 heterogeneity is common in coral reef fish community (Morris et al., 2018; Suzuki et al., 2018). Is it
392 thus relevant to assess the efficiency of ARs using biomass indicators based on the sum of all the
393 species present in a community? The different patterns of changes observed in natural and artificial
394 reefs - but also in estuarine ecosystems - confirmed that examining the functional groups of a
395 community separately provides essential information and may clarifies why inconclusive patterns
396 were observed when fish communities were considered as a whole (Morris et al., 2018; Nickerson et
397 al., 2018). The contrasted patterns detected for benthic and pelagic piscivores also demonstrated
398 that species diet must to be considered together with their habitat preferences. This can explain why
399 ambiguous patterns were identified in other AR systems when piscivorous species were pooled
400 (Neves dos Santos and Zalmon, 2015). Similarly, because species with significant responses to AR
401 deployment are mainly sedentary with narrow distributional range, we should ask if the use of

402 experimental fishing alone is well-adapted to estimate AR efficiency. These surveys usually use
403 passive devices (e.g. trammel nets) that mainly catch mobile species, *i.e.* the species the least
404 affected by AR deployment. A complete vision of ARs fish community may potentially require a
405 combination of pelagic and benthic nets specifically designed to catch sedentary species such as
406 scorpionfishes. Such a sampling procedure has proved useful for assessing the efficiency of ARs in
407 supporting fisheries (e. g. Neves Santos and Costa Monteiro, 1998). Underwater surveys, however,
408 by efficiently estimating benthic species biomass as well as invertebrate assemblages, seem well-
409 adapted to scientific issues such as estimating community composition and measuring ecological
410 efficiency.

411

412 **4.5. A modern vision of the attraction/production controversy based on Isotopic Functional** 413 **Indices**

414 Our study provides a new perspective on how ARs can produce fish biomass. Assuming that the
415 isotopic niche is a relevant proxy of the community's trophic niche (Newsome et al., 2007), isotopic
416 functional indices were recently shown to be reliable for measuring the main trophic fluxes within a
417 community (Chaalali et al., 2017; Jabot et al., 2017). Here, they allowed us to provide an innovative
418 vision of the temporal and functional components of the mechanisms of production involved in the
419 biomass increase in ARs.

420 Attraction and production were determined as two extremes of a wide range of ecological situations
421 (Brickhill et al., 2005; Svane and Petersen, 2001). Our results corroborate this assertion, while
422 highlighting that other dimensions, such as taxonomy, functional traits and temporal changes need
423 to be included in this continuum. Changes in Isotopic Divergence (IDiv) supported the importance of
424 considering time, at both seasonal and annual scales, in the attraction/production continuum. The
425 initial predominance of pelagic species with high displacement abilities and low affinity for ARs was
426 explained by fish attraction. Noticeable isotopic differences for pelagic piscivores are in line with the
427 consumption of prey from a remote food web, leading to high IDiv values in winter 2009 (Fig. 4).

428 Increasing IDiv values, which mirrored an increase in trophic diversity, can be interpreted as a proxy
429 of attraction. Contrarily, in winter 2015, the increase in benthic species biomass originating from
430 production led to a decrease of IDiv values: benthic species, all having similar isotopic values, have
431 benefited from production on AR. Such a result demonstrates the efficiency of stable isotopes as
432 tools to overcome difficulties related to fish displacement between artificial reefs and remote
433 habitats (Brickhill et al., 2005). By clustering biomass at the center of the isotopic space, the biplot
434 suggested that benthic species were mainly influenced by a common local organic matter source that
435 result from the pelagic-benthic coupling (*i.e.* downwards fluxes of pelagic organic matter) promoted
436 by AR (Cresson et al., 2014a). Since pelagic production is the main source of organic matter in almost
437 all Mediterranean ecosystems (Jennings et al., 1997; Pinnegar and Polunin, 2000), ARs did not modify
438 the natural functioning of Mediterranean communities. The nature of organic matter fluxes in
439 artificial reef fish community is comparable to that of natural communities. Time-repeated
440 measurements of isotopic ratios alone would therefore not be powerful enough to detect and
441 explain changes in community functioning, but the AR-driven coupling led to quantitative changes in
442 flux intensity, with an increasing amount of OM available for secondary production, as suggested by
443 changes in biomass and isotopic functional indices. The quite constant pattern of Isotopic Evenness
444 (IEve) index reflected the maturation of the fish community, with a switch from a pelagic-based
445 community to a benthic-based community, and most of the biomass shifting from the left to the
446 biplot center (Fig. 4). Seasonal variations in the IEve index highlighted the importance of herbivores
447 during summer. When food resources available on ARs were consumed by herbivores, the trophic
448 specialization of the community decreased, which in turn induced an increase in the IEve index
449 (Cucherousset and Villéger, 2015).

450

451 It is however important to stress that the attraction/production debate around AR or MPA efficiency
452 is mainly fishery-focused. Identifying and quantifying organic matter fluxes that support harvested

453 fish species emerges as crucial from an economic or management point of view but represents a
454 partial vision of ARs functioning only. By providing habitats for adults and juveniles, the fundamental
455 role of ARs is to support coastal benthic and demersal fish and macroinvertebrates populations to
456 benefit fisheries. Such structures are also relevant scientific tools that have contributed to better
457 identify and understand ecological mechanisms and processes behind changes in biomass (Miller,
458 2002). ARs may be seen as carbon pumps that contribute to increase OM fluxes in comparison to
459 previous barren substrates (Cresson et al., 2014a; Dewsbury and Fourqurean, 2010). It should be
460 kept in mind, however, that organic matter fluxes within AR communities as well as biomass
461 production are highly influenced by invertebrates; their preeminent role in these ecosystems should
462 not be overlooked. Future studies applying functional tools to the whole community present on ARs
463 is the next research step to accurately assess biomass fluxes in human-made rocky substrates.

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476 **Authors contribution**

477 PC, LLD, ER, PA, MO and MHV were involved in field sampling and laboratory analyses. PC, LLD, EG
478 and MHV analyzed the data. PC led the writing of the manuscript. All authors participated to
479 discussions about the results, contributed to the drafts and accepted the last submitted version of
480 the ms.

481 **Data accessibility**

482 Data are available from Seanoe digital repository <http://www.seanoe.org/data/00430/54118/>

483 **Bibliographical references**

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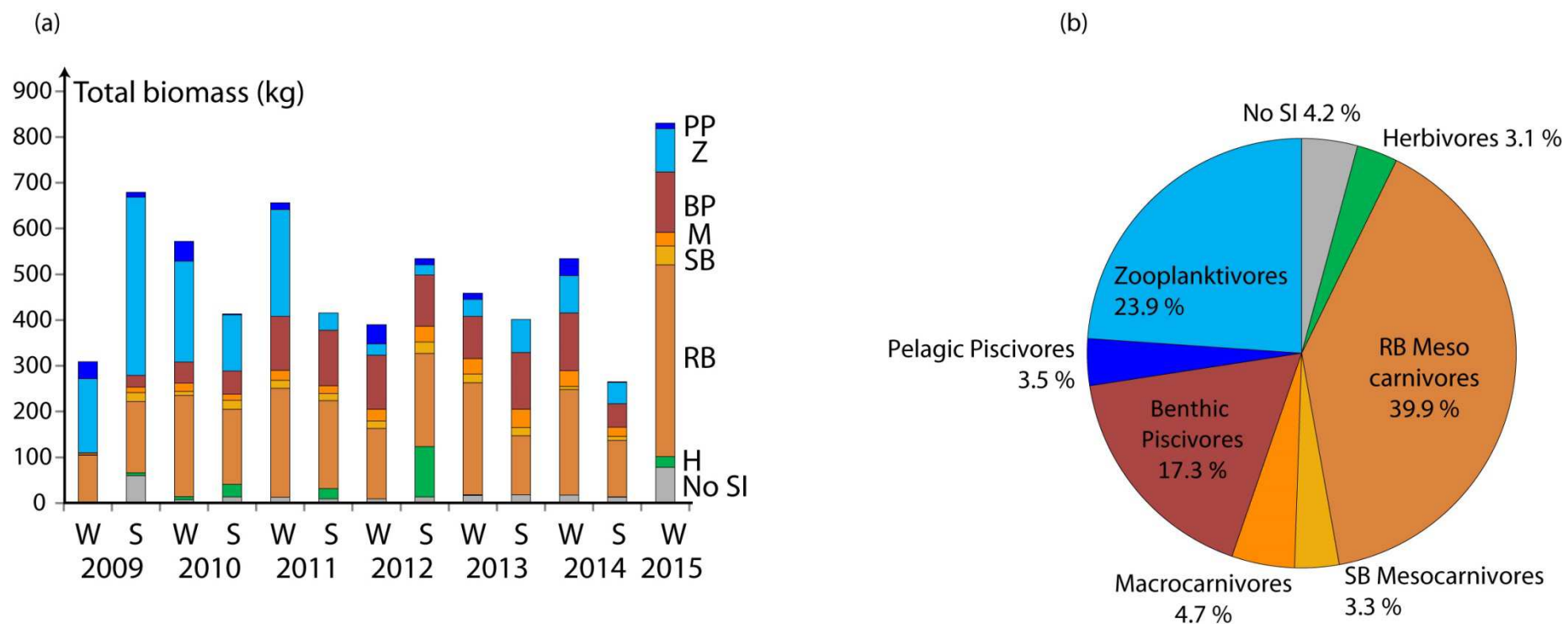


Fig. 1: (a) Biomass of fish assemblages per functional trophic group (H: herbivores, RB: Rocky- bottom mesocarnivores, SB: soft- bottom mesocarnivores, M: macrocarnivores, BP: benthic piscivores, PP: pelagic piscivores, Z: zooplanktivores, No SI: species with undetermined stable isotope (SI) ratio); (b) mean relative biomass of each trophic group over the sampling period

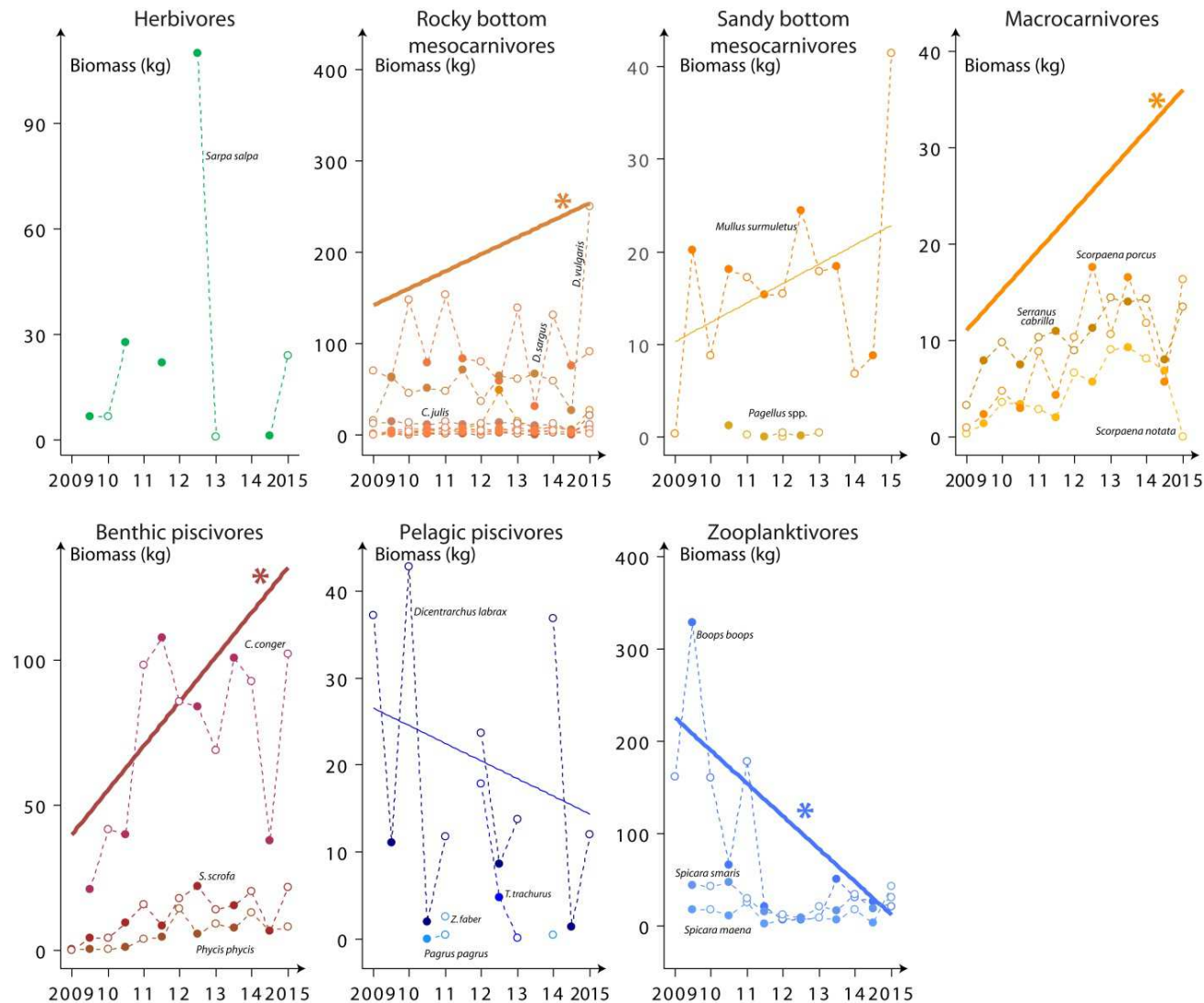


Fig. 2: Seasonal changes (dotted lines) in species biomasses per functional group. Solid lines represent results from linear regression analyses performed, for each functional group, on the total species biomass (with * when significant, see Table 2). Empty and filled symbols represent winter and summer observations, respectively. Scales between panels are not comparable. Data are provided in Table S2.

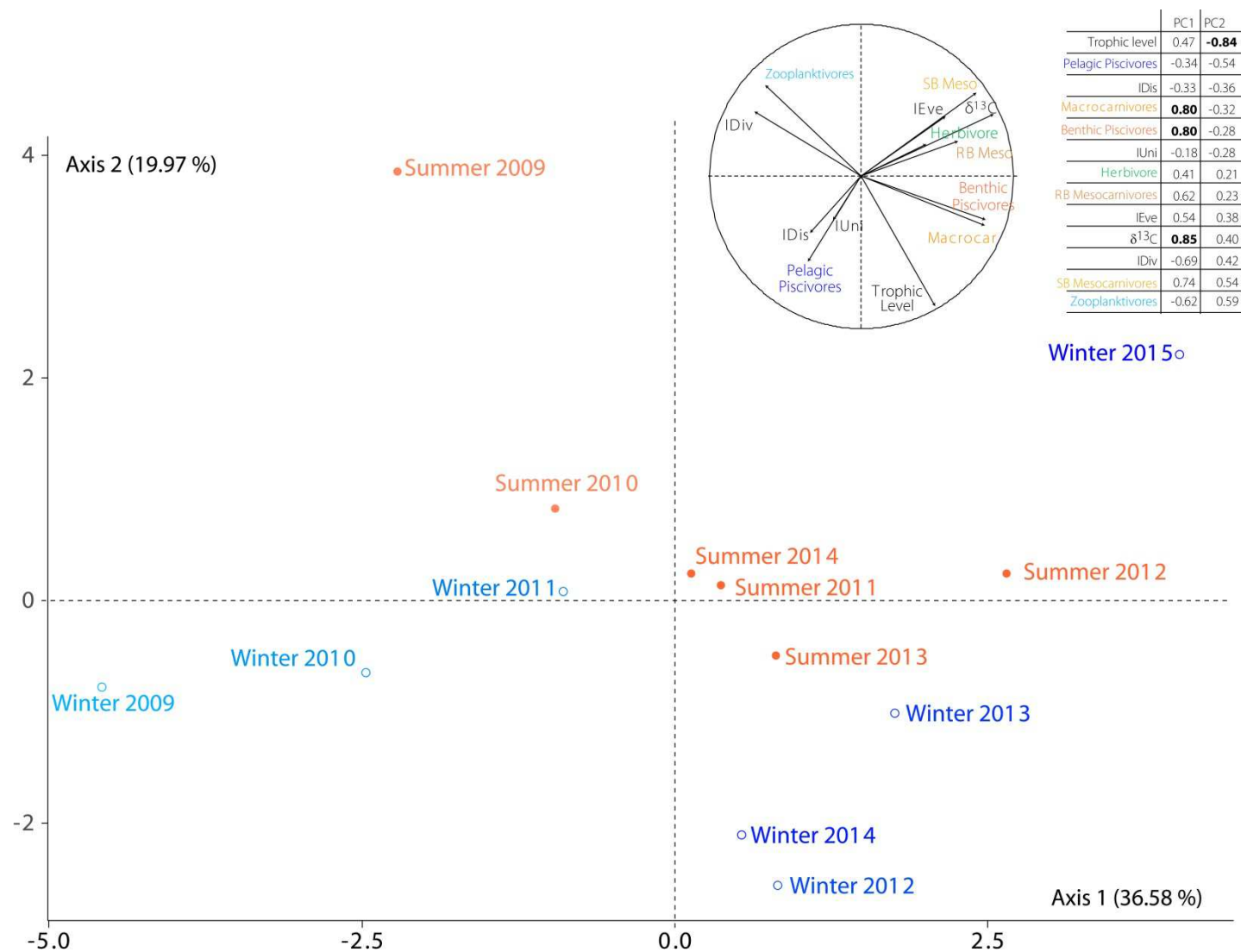


Fig. 3: PCA-biplot (axis 1: 36.58%, axis 2: 19.97%) based on isotopic functional indices, trophic descriptors ($\delta^{13}C$ and trophic level) and the total biomass of each functional trophic group. Correlations between each variable and the two first principal components are reported in the upper right table.

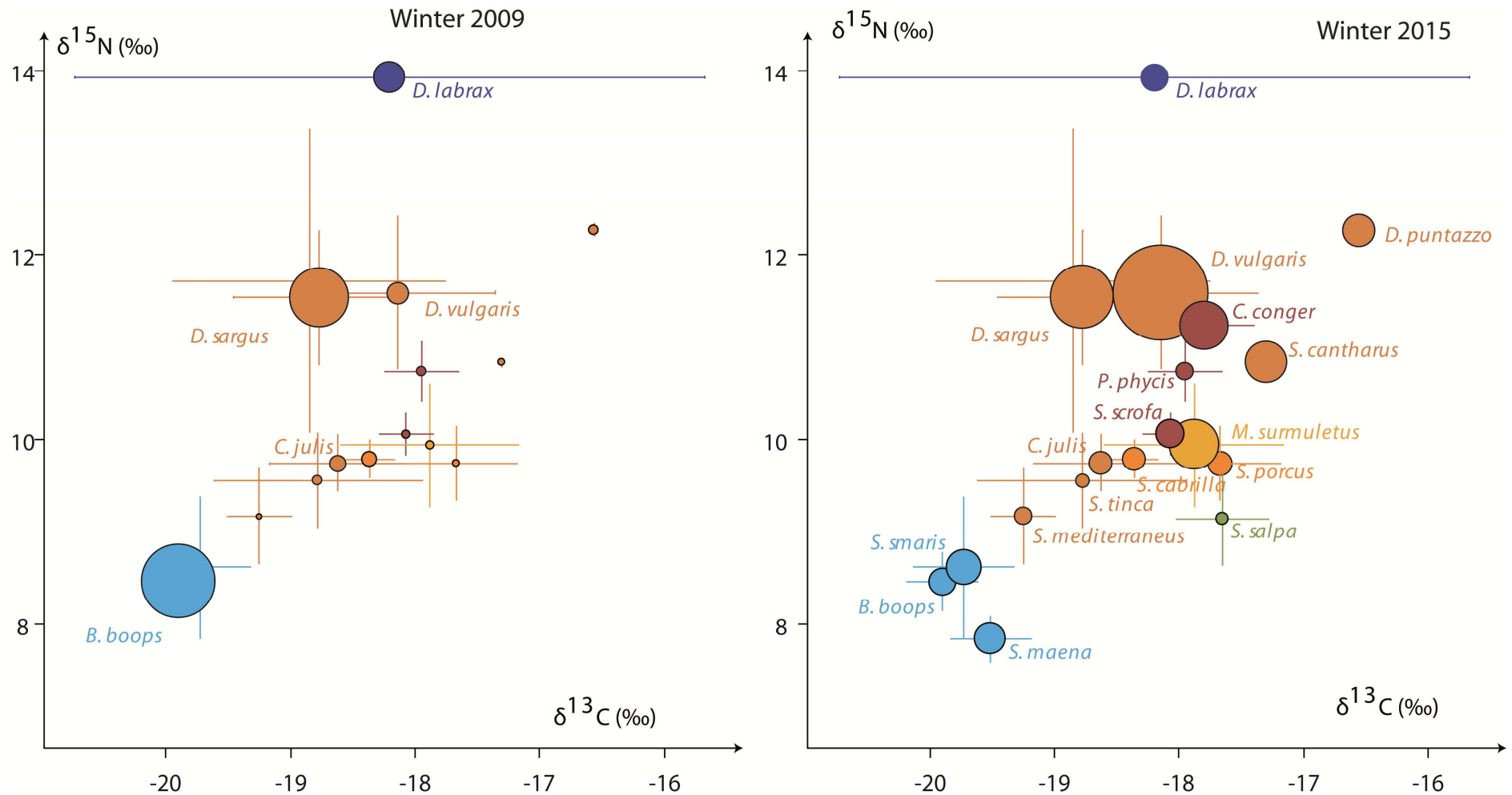


Fig. 4: Isotopic biplots of the community for the first (winter 2009, left panel) and last (winter 2015, right panel) surveys. Bubbles are proportional to the relative biomass of each species. Each color corresponds to a given functional group (green: herbivores; light blue: zooplanktivores; orange: RB mesocarnivores; yellow: SB mesocarnivores; red: benthic piscivores; dark blue: pelagic piscivores).

Table 1: Isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic levels of the functional groups and results of the ANOVA test. Values with different letters are significantly different.

Functional group	n species	$\delta^{13}\text{C}$ (mean \pm sd)	$\delta^{15}\text{N}$ (mean \pm sd)	Trophic level (mean \pm sd)
Herbivores	1	-17.65 \pm 0.38 ^{bcd}	9.13 \pm 0.50 ^{ab}	2.53 \pm 0.10 ^a
Zooplanktivores	3	-19.75 \pm 0.37 ^a	8.28 \pm 0.51 ^a	2.59 \pm 0.30 ^a
Macrocarivores	3	-17.91 \pm 0.50 ^{cd}	9.89 \pm 0.43 ^b	3.39 \pm 0.13 ^b
Benthic piscivores	3	-18.03 \pm 0.24 ^{cd}	10.27 \pm 0.43 ^b	3.50 \pm 0.13 ^b
Pelagic piscivores	4	-18.32 \pm 1.75 ^{bc}	13.63 \pm 2.28 ^d	4.49 \pm 0.67 ^c
RB Mesocarnivores	8	-18.62 \pm 0.95 ^b	10.97 \pm 1.49 ^c	3.29 \pm 0.33 ^b
SB Mesocarnivores	3	-17.82 \pm 0.62 ^d	10.33 \pm 0.73 ^a	3.52 \pm 0.21 ^b
ANOVA		F = 60.42, p < 0.001	F = 106.33, p < 0.001	F = 177.54, p < 0.001

Table 2: Results from statistical analyses performed to assess trends and seasonality in species biomass for each functional group. r_s : Spearman's correlation coefficient. p-value: probability value associated with Mann Kendal (MK) and Mann Whitney (MW) tests.

Functional group	Trend				Seasonality		
	Sen's slope	MK p-value	Spearman correlation r_s	p-value	Mean winter index (%)	Mean summer index (%)	MW p-value
Herbivores	-0.41	0.707	-0.12	0.753	19.95	80.05	0.080
RB Mesocarnivores	6.16	0.200	0.36	0.225	54.34	45.66	0.240
SB Mesocarnivores	0.76	0.360	0.28	0.412	36.45	63.55	0.015
Macrocarivores	2.49	0.006	0.76	0.003	48.74	51.26	0.937
Benthic piscivores	8.99	0.012	0.72	0.007	44.07	55.93	0.394
Pelagic piscivores	-1.15	0.143	-0.43	0.122	90.82	9.18	0.002
Zooplanktivores	-12.43	0.160	-0.56	0.065	55.05	44.95	0.818
All species pooled	-2.16	0.951	-0.03	0.951	52.15	47.85	0.588