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

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11

12 **Highlights**

13 Changes in fish functional groups biomass over 6 years were observed on artificial reefs

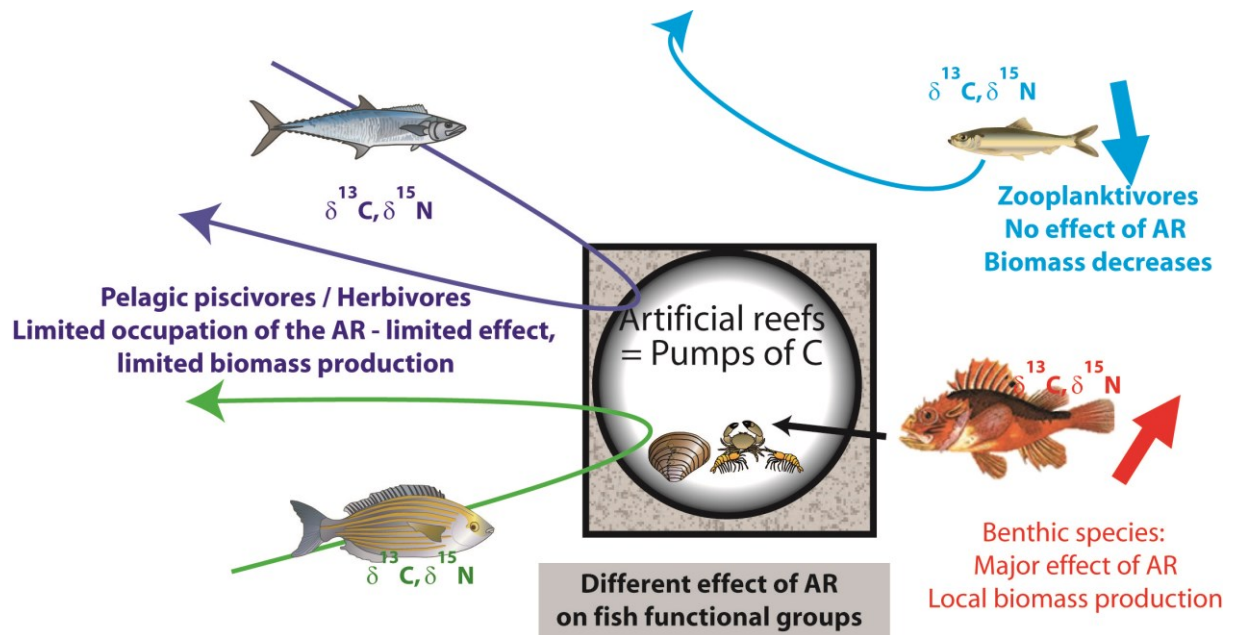
14 No robust pattern of change at assemblage level; 3 patterns for functional groups

15 Increase of biomass through production only for benthic fish species

16 Isotopic functional indices testify community maturation

17 Functional approach is powerful to ascertain biomass production

18



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.

Keywords: artificial reefs; Mediterranean Sea; fish biomass production; isotopic functional indices

1. Introduction

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

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

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

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

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

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

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

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

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

2. Material and methods

2.1. Underwater surveys

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

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

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

2.2. Fish sampling and stable isotope analysis.

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

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

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

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

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

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

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

2.3. Isotopic functional indices

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

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

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

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

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

2.4. Statistical analyses

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

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

3. Results

3.1. Biomass composition of the community

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

3.2. Isotopic composition of the community

Functional groups displayed significant differences (ANOVA, $p < 10^{-3}$) for the descriptors ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and trophic level) used (Table 1). For $\delta^{13}\text{C}$, the major difference was observed between zooplanktivores ($-19.75 \pm 0.37\text{‰}$) and other groups, with a 2.1‰ difference between minimal and maximal values when all species were considered, but only ~1‰ when zooplanktivores were excluded (Table 1). For $\delta^{15}\text{N}$ and trophic level, zooplanktivores and herbivores had the lowest values ($8.28 \pm 0.51\text{‰}$ 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 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 level).

3.3. Temporal and seasonal changes in biomass

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

3.4. Interannual variability in the community functional structure

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

4. Discussion

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

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

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

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

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

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

4.3. No effect of ARs on zooplanktivores

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

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

4.4. A functional traits-based monitoring of ARs

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

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

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

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

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

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

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

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

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Authors contribution

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

Data accessibility

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

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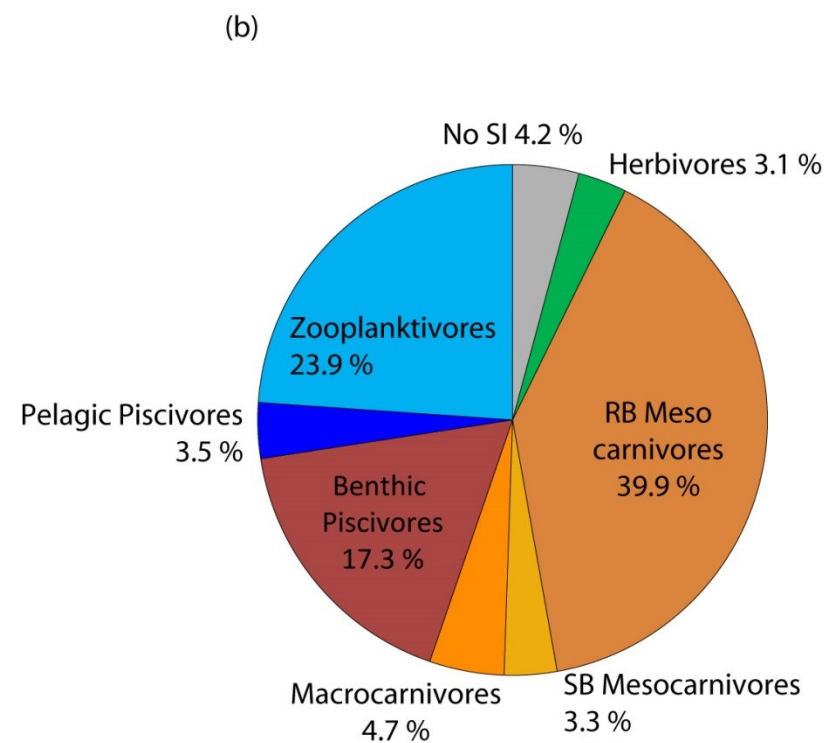
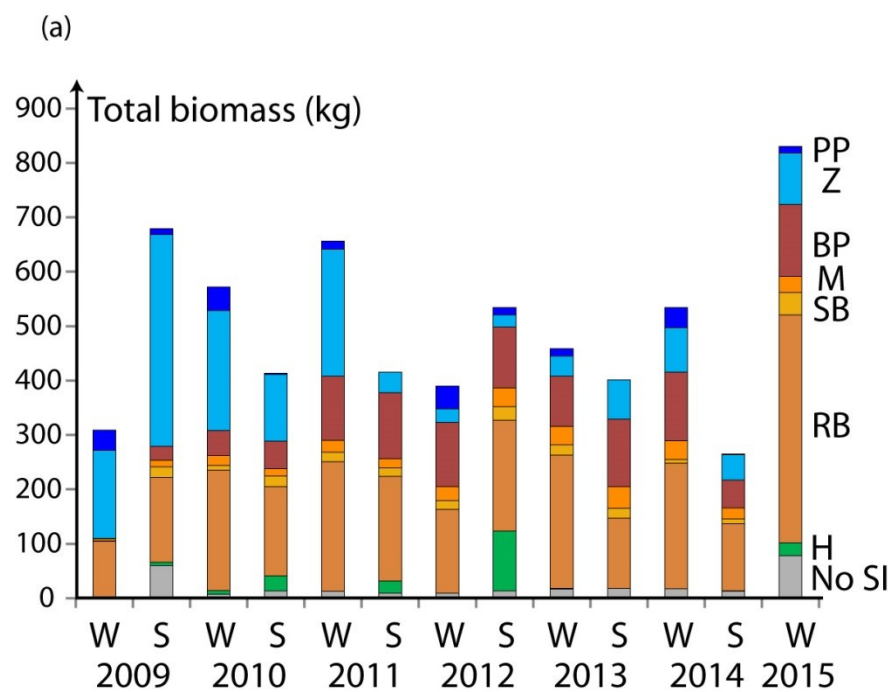


Fig. 1: (a) Biomass of fish assemblages per functional trophic group (H: herbivores, RB: Rocky- bottom mesocarnivores, SB: soft- bottom mesocarnivores, M: macrocarnivores, BP: benthic piscivores, PP: pelagic piscivores, Z: zooplanktivores, No SI: species with undetermined stable isotope (SI) ratio);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

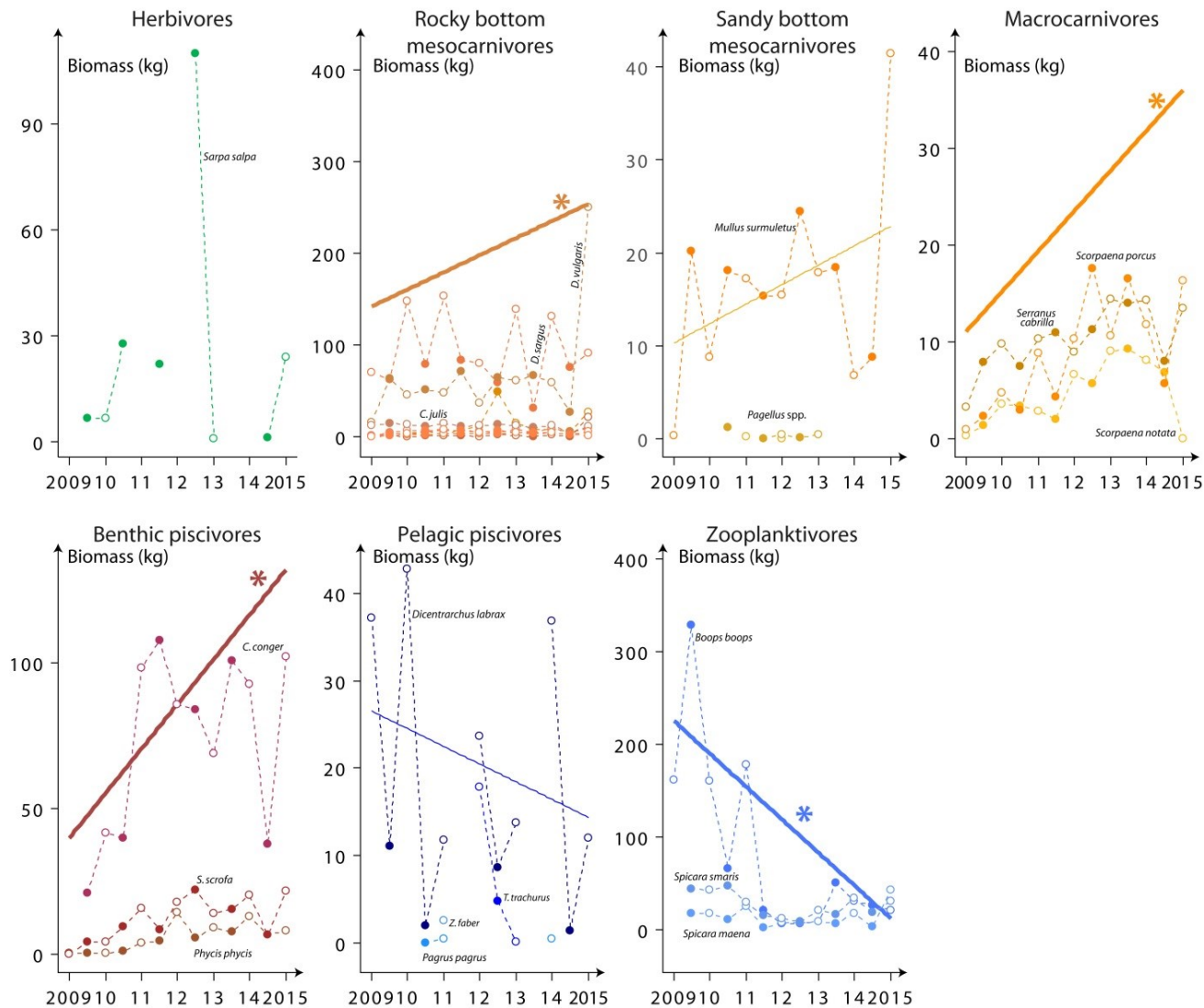


Fig. 2: Seasonal changes (dotted lines) in species biomasses per functional group. Solid lines represent results from linear regression analyses performed, for each functional group, on the total species biomass (with * when significant, see Table 2). Empty and filled symbols represent winter and summer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

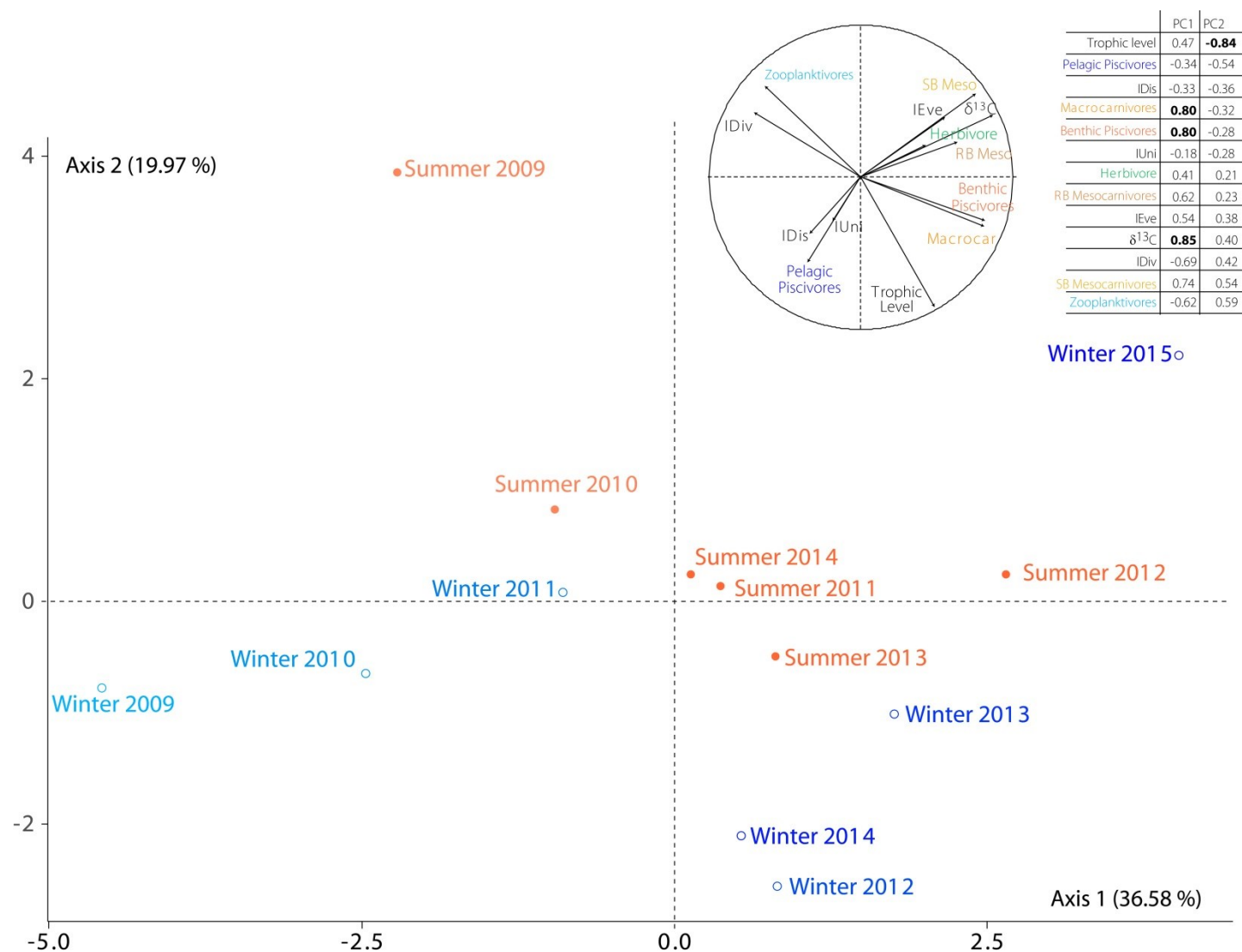


Fig. 3: PCA-biplot (axis 1: 36.58%, axis 2: 19.97%) based on isotopic functional indices, trophic descriptors ($\delta^{13}C$ and trophic level) and the total biomass of each functional trophic group. Correlations between each variable and the two first principal components are reported in the upper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

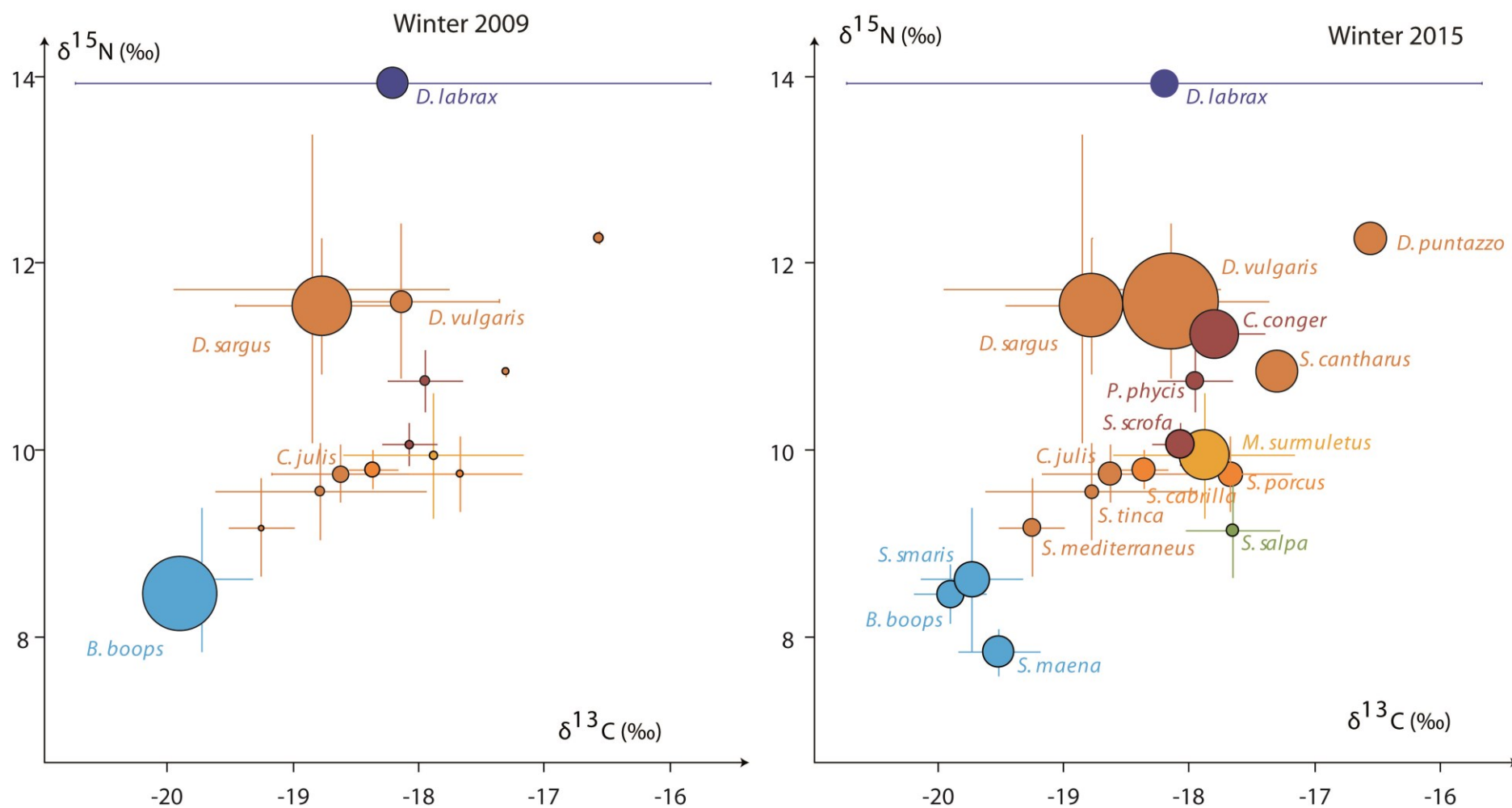


Fig. 4: Isotopic biplots of the community for the first (winter 2009, left panel) and last (winter 2015, right panel) surveys. Bubbles are proportional to the relative biomass of each species. Each color corresponds to a given functional group (green: herbivores; light blue: zooplanktivores; orange: 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 ± 0.38 ^{bcd}	9.13 ± 0.50 ^{ab}	2.53 ± 0.10 ^a
Zooplanktivores	3	-19.75 ± 0.37 ^a	8.28 ± 0.51 ^a	2.59 ± 0.30 ^a
Macrocarivores	3	-17.91 ± 0.50 ^{cd}	9.89 ± 0.43 ^b	3.39 ± 0.13 ^b
Benthic piscivores	3	-18.03 ± 0.24 ^{cd}	10.27 ± 0.43 ^b	3.50 ± 0.13 ^b
Pelagic piscivores	4	-18.32 ± 1.75 ^{bc}	13.63 ± 2.28 ^d	4.49 ± 0.67 ^c
RB Mesocarnivores	8	-18.62 ± 0.95 ^b	10.97 ± 1.49 ^c	3.29 ± 0.33 ^b
SB Mesocarnivores	3	-17.82 ± 0.62 ^d	10.33 ± 0.73 ^a	3.52 ± 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

Appendix 1: Is a seasonal-once sampling sufficient to depict community trophic functioning?

C and N isotopic ratios were used in the present study to depict functional trophic structure of the fish community on the artificial reefs of the Bay of Marseilles. The major patterns derived from stable isotopes are pretty robust to minor changes, as we did in the present study (Jabot et al., 2017). Nevertheless, three major factors may alter fish isotopic ratios. Their potential effect on the present results and conclusions are discussed here.

Isotopic ratio of a fish is directly dependent upon the isotopic ratio of the trophic baseline, *i.e.* the ratio of the primary production at the base of the food web it belongs to. Using an inappropriate baseline is a major and well-known pitfall of isotopic ecology (*e. g.* Jennings and van der Molen, 2015). If baseline isotopic ratio is changing, an artefactual change in fish isotopic ratio would occur but without any ecological or biological changes. Here, considering one stable isotope ratio value by species may prevent this bias.

The second factor that may affect fish isotopic ratios would be linked with dietary changes, notably considering that diet would be altered by the deployment of artificial reefs. Results of stomach contents performed on fish sampled on artificial reefs refuted this hypothesis, as diet of fish on artificial reefs was pretty similar with fish diets in other Mediterranean rocky reefs, with >10 year lag between the studies (Cresson et al., 2014b and references therein). Thus, it would be reasonable to consider no diet changes during the study period, and thus no effect on isotopic ratios.

The third factor that may drive changes in fish isotopic ratios would be an alteration of the main source of organic matter to the community, driven by the deployment of artificial reefs. Results of the present and past studies demonstrated that artificial reefs increase the importance of pelagic subsidies into the benthic community, through increased pelago-benthic coupling, notably as a result of the filtering activity of suspension feeders dominating the artificial reef community (Cheung et al., 2010; Cresson et al., 2014a; Dewsbury and Fourqurean, 2010). Such an effect here would result in an increase of the pelagic feature of fish isotopic ratios.

But pelagic primary production is largely demonstrated as the major source of organic matter in quite all Mediterranean fish communities, either in coastal soft-bottom systems (Carlier et al., 2007), rocky reefs (Belloni et al., 2019; Jennings et al., 1997) or *Posidonia oceanica* seagrass meadows (Ourgaud, 2015; Pinnegar and Polunin, 2000). Isotopic ratios measured for fish in the early stage of artificial reefs deployment are consistent with this trend and largely explained by their belonging to a food web based on pelagic subsidies. Functional changes in the fish community caused by artificial reefs deployment do not modify the nature of OM fluxes but only their intensity. No major changes in fish isotopic ratios can thus be expected after artificial reef deployment and community maturation.

Thus, we feel pretty confident on the robustness of isotopic ratios measured in 2010 to describe the trophic structure of the community and its temporal changes over the 6-year period of the study.

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Appendix 2: Detailed protocol for the average percentage method

To clarify the procedure, we used the following case study:

Time period	Observations
March 2012	471
June 2012	480
September 2012	492
December 2012	520
March 2013	427
June 2013	463
September 2013	484
December 2013	494
March 2014	425
June 2014	462
September 2014	463
December 2014	499

Step 1: for each year, we calculated annual means

2012 (annual mean)	2013 (annual mean)	2014 (annual mean)
490.75	467	462.25

Step 2: For a given period p of a given year y , we expressed the observation $x_{p,y}$ as the proportion $P_{p,y}$ of the annual mean \bar{x} of the year y . Therefore, for March 2012:

$$P_{march,2012} = \frac{x_{march,2012}}{\bar{x}_{2012}} = \frac{471}{490.75} = 0.9598$$

Time period	Observations	Proportions
March 2012	471	0.9598
June 2012	480	0.9781
September 2012	492	1.0025
December 2012	520	1.0596
March 2013	427	0.9143
June 2013	463	0.9914
September 2013	484	1.0364
December 2013	494	1.0578
March 2014	425	0.9194
June 2014	462	0.9995
September 2014	463	1.0016
December 2014	499	1.0795

Step 3: For each period p (or season), we computed the index S , i.e. the average proportion of each period. For example, for March:

$$S_{march} = \frac{0.9598+0.9143+0.9194}{3} = 0.9312$$

Seasonal indices			
March	June	September	December
0.9312	0.9897	1.0135	1.0656

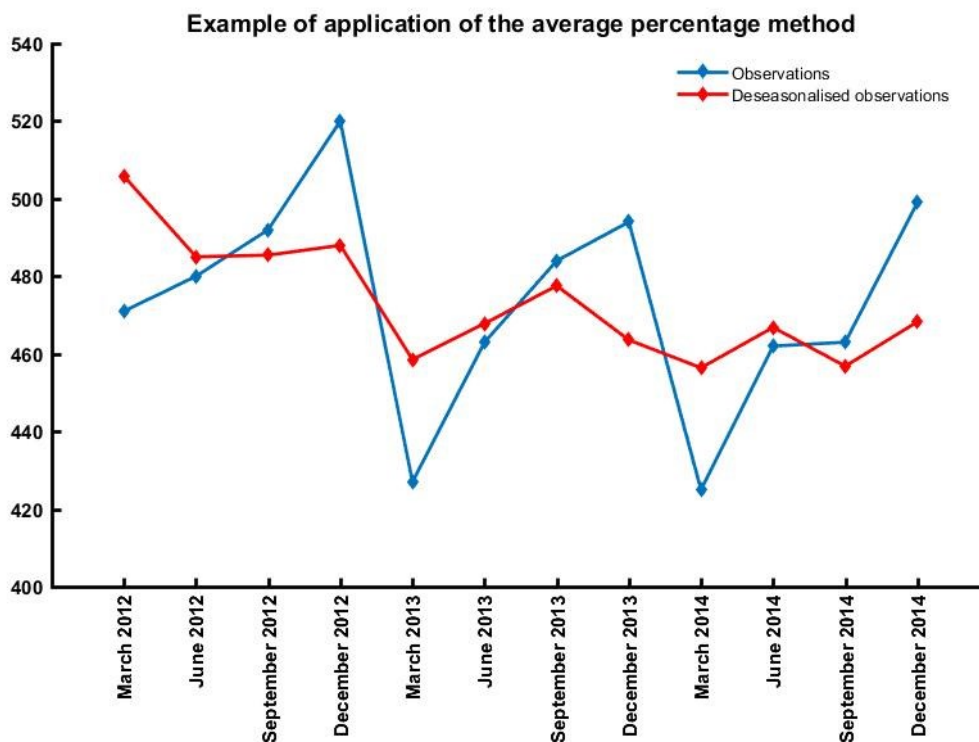
Step 4: Seasonal indices S are then used to smooth/deseasonalise the observations x , as follows:

For a given period p of a given year y , we expressed the observation $x_{p,y}$ as the proportion $P_{p,y}$ of the annual mean \bar{x} of the year y . Therefore, for March 2012:

$$xd_{march,2012} = \frac{x_{march,2012}}{S_{march}} = \frac{471}{0.9312} = 505.80$$

with $xd_{p,y}$ the deseasonalised observation at the given period p (here, in march) of the given year y (here, in 2012).

Time period	Observations	Proportions	Deseasonalised observations
March 2012	471	0.9598	505.80
June 2012	480	0.9781	485.01
September 2012	492	1.0025	485.45
December 2012	520	1.0596	487.97
March 2013	427	0.9143	458.55
June 2013	463	0.9914	467.82
September 2013	484	1.0364	477.54
December 2013	494	1.0578	463.57
March 2014	425	0.9194	456.40
June 2014	462	0.9995	466.83
September 2014	463	1.0016	456.82
December 2014	499	1.0795	468.26



Example of application of the average percentage method on a seasonal time series (March 2012 – December 2014, in blue) that allows to compute the deseasonalised time series (in red).

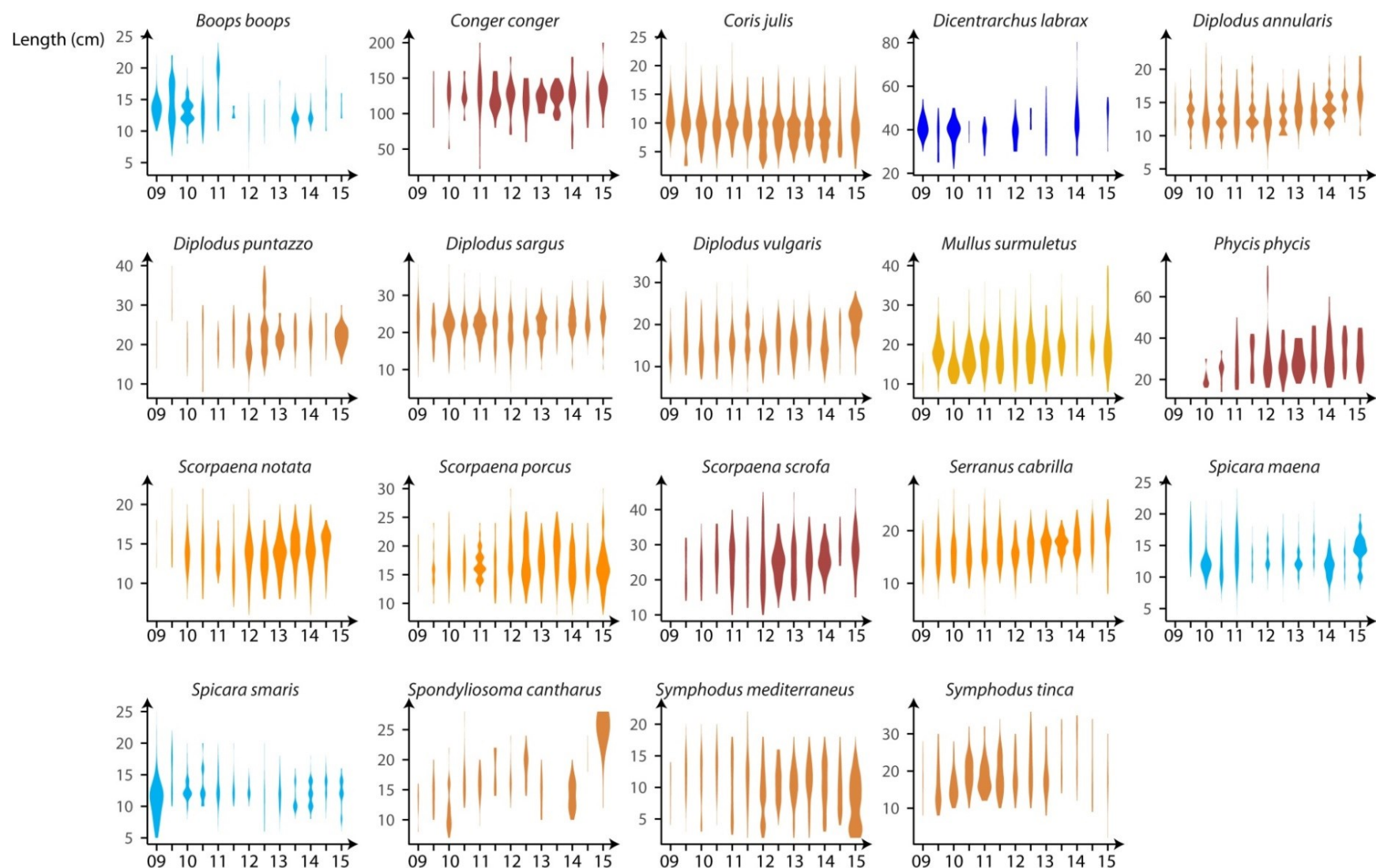


Figure S1: Temporal changes in species length. For each period, the mean length of species is represented by the bulge in the violin, its variability being indicated by the tails. Colors indicate functional trophic groups (green: herbivores; light blue: zooplanktivores; orange: Rocky-Bottom mesocarnivores; yellow: Soft-Bottom mesocarnivores; red: benthic piscivores; dark blue: pelagic piscivores).

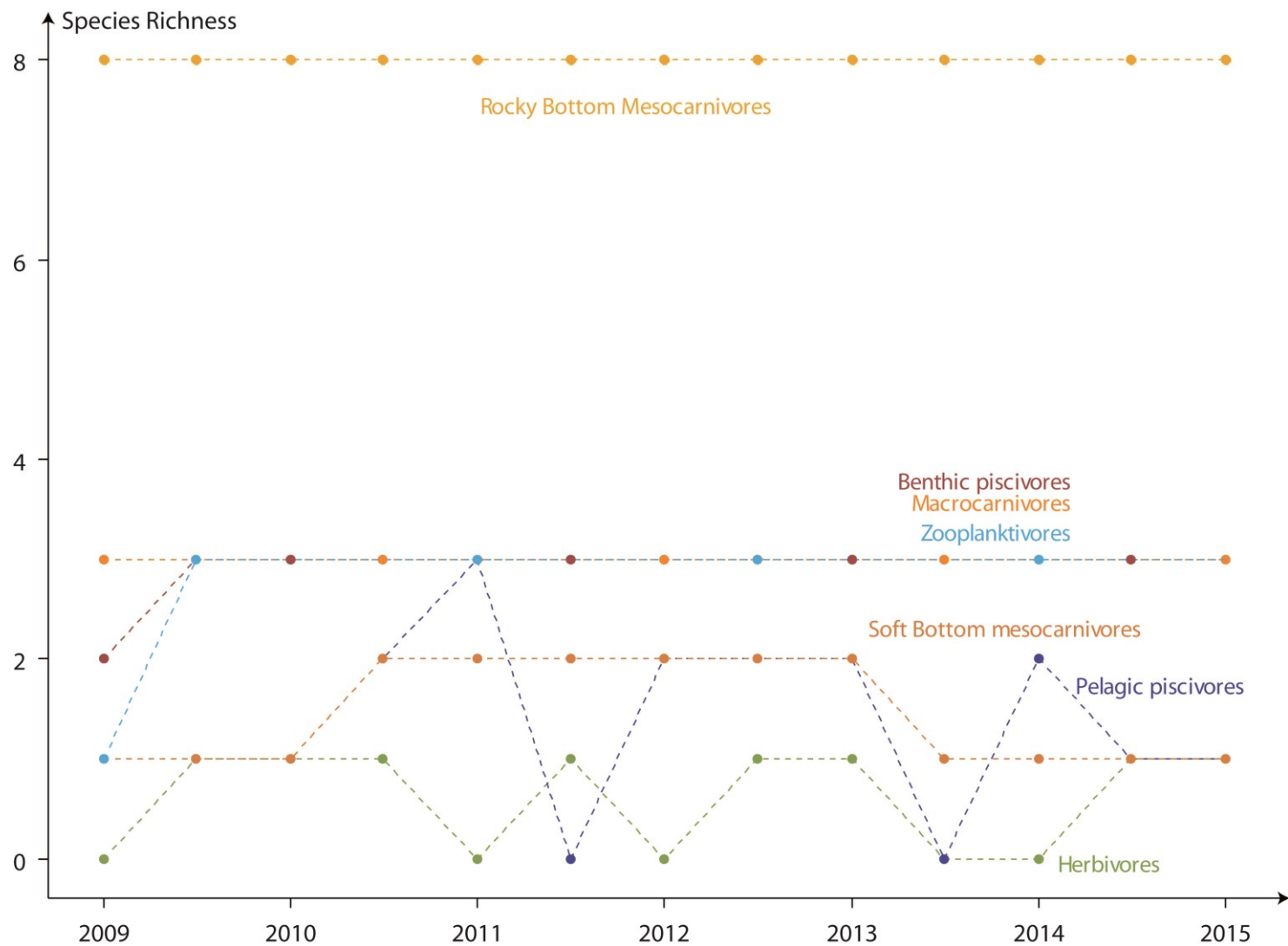


Fig. S2: Temporal trends of species richness within each trophic group. Lines for benthic piscivores, macrocarivores and zooplanktivores are mostly confounded.

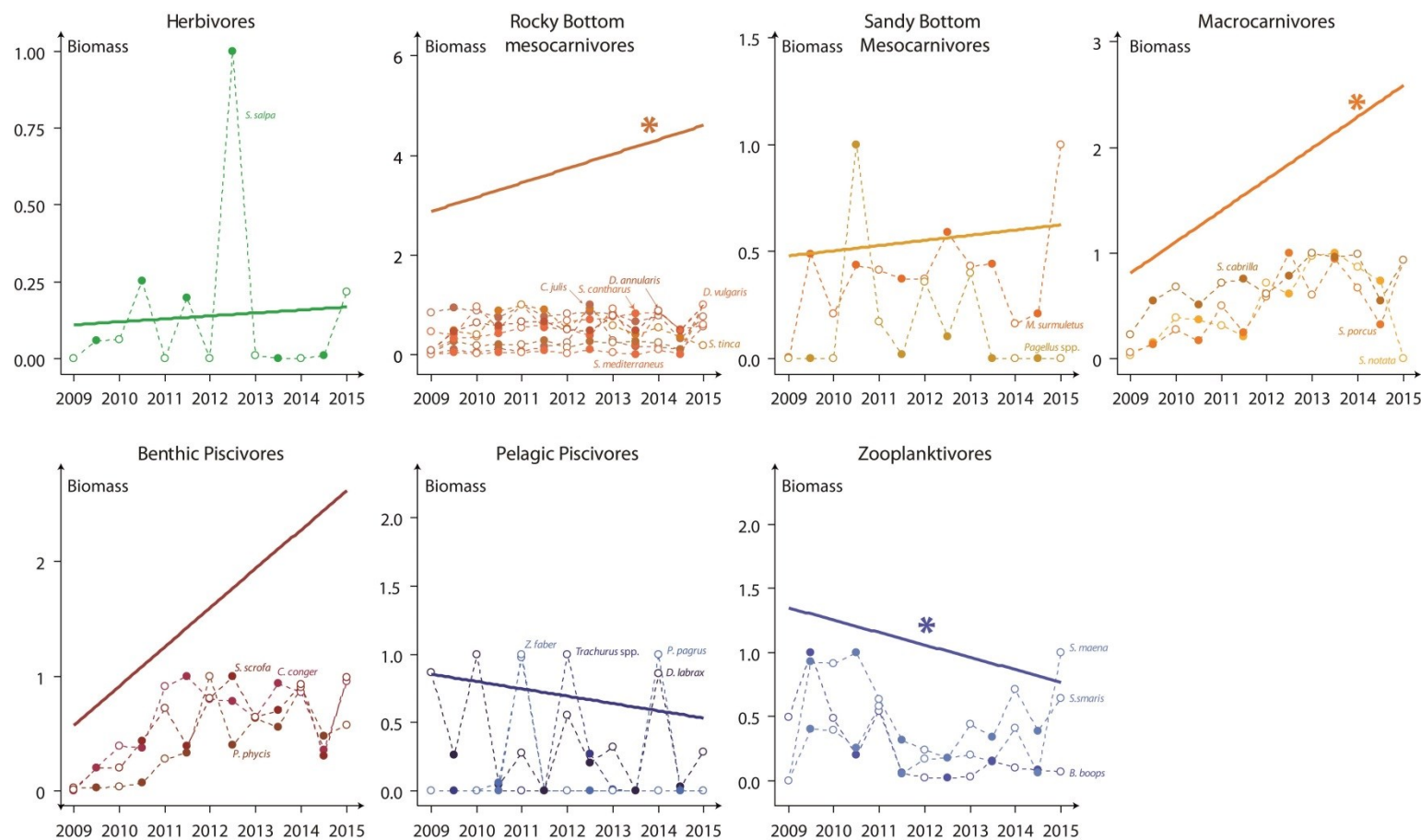


Figure S3: Seasonal changes (dotted lines) in species standardized biomass per functional group. Solid lines are regression for the total biomass per group (with * when significant, see Table 2). Empty and filled symbols represent winter and summer observations, respectively. Scales between panels are not comparable.

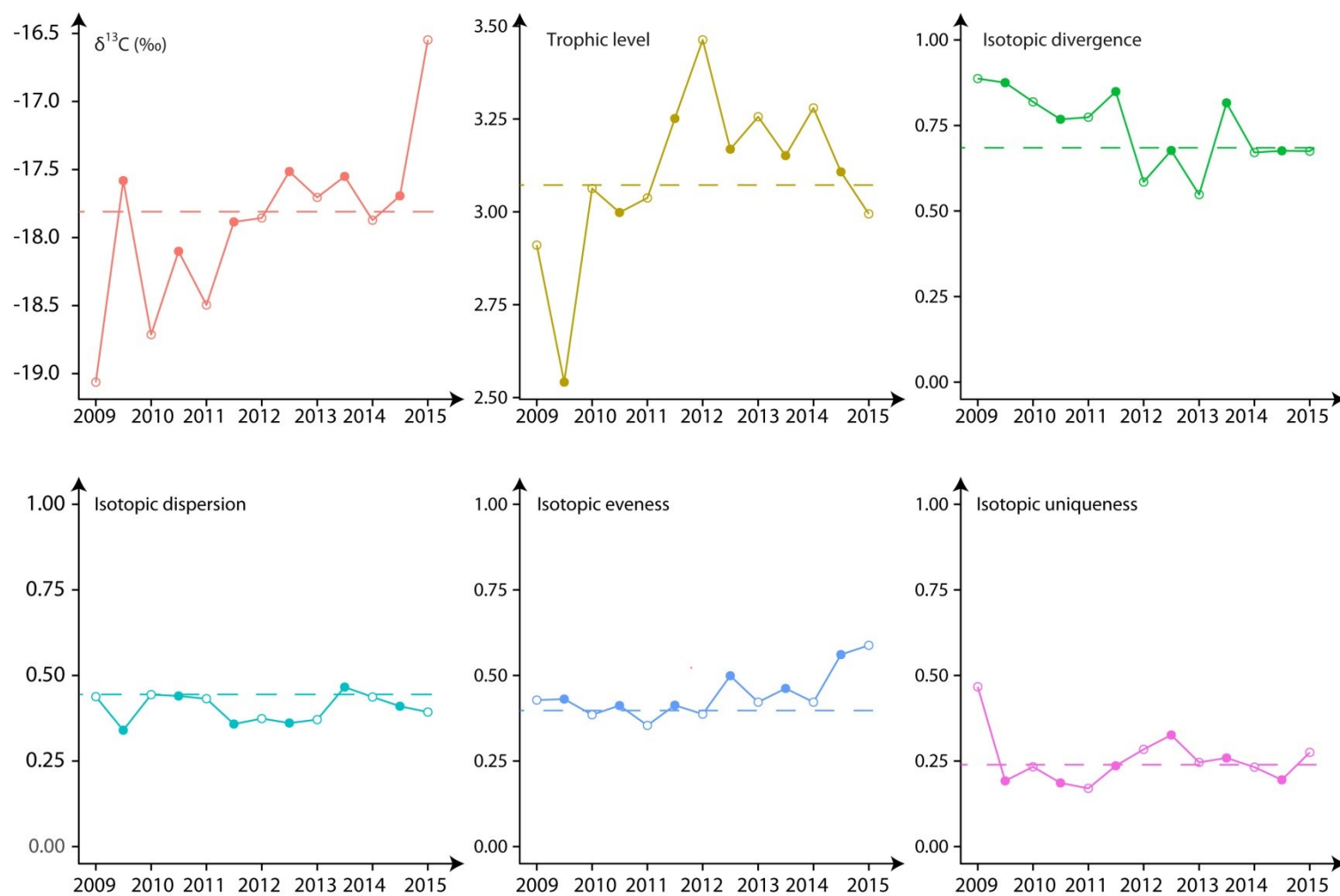


Figure S3: Temporal changes in isotopic indices for the period 2009-2015. Filled circles indicate summer values and empty circles are for winter. Dotted lines show the average value of each index.

Table S1: Isotopic ratios for primary producers and organic matter pools. Details about sampling can be found in dedicated papers

OM source	$\delta^{13}\text{C}$ (mean \pm sd)	$\delta^{15}\text{N}$ (mean \pm sd)	Explanation	Source
Microphytoplankton	$-22.70 \pm 0.76 \text{ ‰}$	$3.17 \pm 1.25 \text{ ‰}$	Cells size : > 10 μm	Darnaude et al (2004),
Nanophytoplankton	$-25.23 \pm 1.16 \text{ ‰}$	$1.77 \pm 0.25 \text{ ‰}$	Cells size : 2 – 10 μm	Rau et al (1990)
Macroalgae	$-21.09 \pm 2.41 \text{ ‰}$	$3.74 \pm 0.81 \text{ ‰}$	Average values measured for 18 species	present study ; Cresson et al.(2014)
<i>Posidonia oceanica</i> leaves	$-15.44 \pm 1.03 \text{ ‰}$	$3.74 \pm 0.90 \text{ ‰}$	Average values for leaves, excluding epibionts, and dead and senescent tissues	present study; Cresson et al.(2014)
Terrigenous inputs	$-26.25 \pm 0.51 \text{ ‰}$	$4.48 \pm 0.41 \text{ ‰}$	Average value of 4 sampling during flooding events	present study; Cresson et al.(2012)
Sewage outfall	$-25.06 \pm 0.23 \text{ ‰}$	$-0.01 \pm 0.14 \text{ ‰}$		Topçu et al. (2010)
	$-25.50 \pm 0.62 \text{ ‰}$	$-0.58 \pm 0.82 \text{ ‰}$		Bănaru et al (2014)

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Tab. S2: Composition of fish assemblages on artificial reefs in the Bay of Marseille. Standard length (SI): average length (in cm) of the individuals used for stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Length (survey): average length (in cm) of individuals observed during underwater surveys. Relative biomass (in kg) is the biomass of each species divided by the total biomass of the community. Note that the sum of mean biomass is not equal to 100%, as isotopic ratios are not determined for all the species of the assemblages. Species are sorted in descending order following their relative biomass. sd: standard deviation. RB: rocky bottom. SB: soft-bottom. NA: length not available for *Conger conger* as the caudal fin of the individual was too damaged.

Species	Functional trophic group	Standard length (SI-cm)		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Trophic level	Length (survey - cm)		Biomass	
		mean \pm sd	min-max	mean \pm sd	mean \pm sd		mean \pm sd	min-max	Total (kg)	Relative
<i>Diplodus sargus</i> (Linnaeus, 1758)	RB mesocarnivores	16 \pm 2	14 - 20	-18.77 \pm 0.69	11.54 \pm 0.73	3.25 \pm 0.21	23 \pm 4	7-38	1202.31	18.6%
<i>Boops boops</i> (Linnaeus, 1758)	Zooplanktivores	16 \pm 2	13 - 22	-19.90 \pm 0.29	8.46 \pm 0.32	2.34 \pm 0.10	14 \pm 3	6-24	1063.78	16.5%
<i>Conger conger</i> (Linnaeus, 1758)	Benthic piscivores	NA	-	-17.80 \pm 0.41	11.24 \pm 0.03	3.79 \pm 0.12	126 \pm 25	60-180	880.36	13.6%
<i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817)	RB mesocarnivores	12 \pm 2	7-17	-18.14 \pm 0.78	11.59 \pm 0.83	3.26 \pm 0.24	15 \pm 4	4-34	863.13	13.4%
<i>Spicara smaris</i> (Linnaeus, 1758)	Zooplanktivores	14 \pm 1	12-15	-19.73 \pm 0.41	8.61 \pm 0.77	3.01 \pm 0.23	13 \pm 3	6-22	315.60	4.9%
<i>Mullus surmuletus</i> Linnaeus, 1758	SB mesocarnivores	14 \pm 2	9-22	-17.88 \pm 0.72	9.94 \pm 0.67	3.40 \pm 0.20	19 \pm 5	8-40	213.06	3.3%
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	Pelagic piscivores	33 \pm 6	27-43	-18.20 \pm 2.53	13.92 \pm 0.60	4.57 \pm 0.18	41 \pm 9	25 - 80	201.00	3.1%
<i>Sarpa salpa</i> (Linnaeus, 1758)	Herbivores	23 \pm 2	27-32	-17.65 \pm 0.38	9.13 \pm 0.50	2.53 \pm 0.10	27 \pm 5	20-35	198.73	3.1%
<i>Spicara maena</i> (Linnaeus, 1758)	Zooplanktivores	13 \pm 2	10-17	-19.51 \pm 0.33	7.83 \pm 0.25	2.78 \pm 0.07	14 \pm 3	7-24	164.39	2.5%
<i>Scorpaena scrofa</i> Linnaeus, 1758	Benthic piscivores	18 \pm 4	12-22	-18.07 \pm 0.22	10.06 \pm 0.23	3.44 \pm 0.07	26 \pm 7	10-45	161.12	2.5%
<i>Coris julis</i> (Linnaeus, 1758)	RB mesocarnivores	11 \pm 2	07-14	-18.62 \pm 0.55	9.74 \pm 0.31	3.34 \pm 0.09	11 \pm 4	2-24	153.65	2.4%
<i>Diplodus puntazzo</i> (Walbaum, 1792)	RB mesocarnivores	9 \pm 0	-	-16.56 \pm 0.02	12.27 \pm 0.06	3.46 \pm 0.02	22 \pm 4	8-32	148.67	2.3%
<i>Serranus cabrilla</i> (Linnaeus, 1758)	Macrocarivores	14 \pm 1	11-17	-18.36 \pm 0.20	9.79 \pm 0.21	3.36 \pm 0.06	17 \pm 3	4-28	133.99	2.1%
<i>Scorpaena porcus</i> Linnaeus, 1758	Macrocarivores	14 \pm 4	8-25	-17.67 \pm 0.49	9.74 \pm 0.41	3.34 \pm 0.12	17 \pm 4	8-30	112.97	1.7%
<i>Diplodus annularis</i> (Linnaeus, 1758)	RBmesocarnivores	12 \pm 2	9-19	-18.85 \pm 1.10	11.72 \pm 1.65	3.30 \pm 0.48	14 \pm 3	5-22	79.12	1.2%
<i>Phycis phycis</i> (Linnaeus, 1766)	Benthic piscivores	33 \pm 0	33 - 34	-17.95 \pm 0.30	10.73 \pm 0.33	3.64 \pm 0.10	29 \pm 9	15 - 60	75.64	1.2%
<i>Scorpaena notata</i> Rafinesque, 1810	Macrocarivores	11 \pm 2	7-15	-17.66 \pm 0.39	10.15 \pm 0.50	3.46 \pm 0.15	14 \pm 3	6-22	58.91	0.9%
<i>Symphodus tinca</i> (Linnaeus, 1758)	RB mesocarnivores	16 \pm 5	12-21	-18.78 \pm 0.84	9.55 \pm 0.52	3.29 \pm 0.15	18 \pm 6	2-36	56.89	0.9%
<i>Symphodus mediterraneus</i> (Linnaeus, 1758)	RB mesocarnivores	11 \pm 1	10-13	-19.25 \pm 0.26	9.17 \pm 0.52	3.18 \pm 0.15	10 \pm 4	2-20	41.06	0.6%
<i>Spondyliosoma cantharus</i> (Linnaeus, 1758)	RB mesocarnivores	12 \pm 0	-	-17.30 \pm 0.02	10.83 \pm 0.05	3.66 \pm 0.02	16 \pm 5	8-28	32.21	0.5%
<i>Trachurus</i> spp. (Steindachner, 1868)	Pelagic piscivores	26 \pm 2	24 - 28	-18.74 \pm 0.77	14.87 \pm 2.98	4.85 \pm 0.88	28	20-28	22.70	0.4%

<i>Zeus faber</i> Linnaeus, 1758	Macrocarviores	26 ± 0	-	-17.97 ± 0.06	10.80 ± 0.04	3.66 ± 0.01	50	-	2.51	0.0%
<i>Pagellus</i> spp.	SB mesocarnivores	15 ± 2	10-19	-17.77 ± 0.26	10.81 ± 0.60	3.66 ± 0.18	19 ± 1	18 - 20	2.11	0.0%
<i>Pagrus pagrus</i> (Linnaeus, 1758)	Macrocarviores	31 ± 0	-	-17.73 ± 0.04	11.04 ± 0.03	3.73 ± 0.01	22 ± 5	16 - 25	1.16	0.0%

Table S2: Changes in biomass (in kg) for the period 2009-2015 estimated from the difference between the final biomass (BM_{final}) measured in winter 2015 and the initial biomass ($BM_{initial}$) in winter 2009 (except *C. conger*, *S. maena*, *S. smar*is and *S. salpa* for which the summer 2009 value was used) and calculated as follows:

$$Change = \frac{BM_{Final} - BM_{initial}}{BM_{initial}}$$

Values were not calculated for species with less than three occurrences or with irregular distribution. Species richness is the total number of species observed on artificial reefs, considered or not for stable isotope analyses.

Functional trophic group	Species	2009		2010		2011		2012		2013		2014		2015	Change
		Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	
SBMeso	<i>Mullus surmuletus</i>	0.26	20.15	8.77	18.13	17.22	15.36	15.47	24.43	17.90	18.40	6.80	8.72	41.47	159.71
RBMeso	<i>Spondyllosoma cantharus</i>	0.16	0.71	0.66	1.01	0.99	1.77	0.54	2.19	0.70	0.09	1.97	0.21	21.19	130.05
BenthicP	<i>Scorpaena scrofa</i>	0.19	4.33	4.31	9.57	15.83	8.55	17.79	22.07	14.15	15.50	20.38	6.74	21.72	111.90
RBMeso	<i>Diplodus puntazzo</i>	1.06	4.57	1.97	6.17	2.88	7.79	11.59	49.38	14.25	8.25	8.42	5.15	27.20	24.64
BenthicP	<i>Phycis phycis</i>	0.37	0.37	0.43	0.96	4.01	4.67	14.33	5.65	9.00	7.91	12.92	6.81	8.21	21.29
Macrocar	<i>Scorpaena porcus</i>	0.99	2.31	4.76	2.98	8.82	4.31	10.32	17.52	10.61	16.56	11.77	5.67	16.35	15.52
RBMeso	<i>Diplodus vulgaris</i>	16.21	63.62	45.91	51.73	48.34	71.28	36.32	64.51	61.80	66.76	59.47	27.18	250.00	14.43
RBMeso	<i>Diplodus annularis</i>	0.82	4.73	6.67	6.04	6.73	6.77	5.15	4.90	8.05	4.90	9.03	4.98	10.35	11.68
RBMeso	<i>Symphodus mediterraneus</i>	0.46	1.76	1.90	2.30	2.92	3.26	3.64	3.79	4.09	4.34	4.56	2.71	5.34	10.57
BenthicP	<i>Conger conger</i>	0.00	21.02	41.49	39.76	98.33	107.81	85.70	84.08	68.93	100.60	92.61	37.75	102.28	3.87
Macrocar	<i>Serranus cabrilla</i>	3.27	7.91	9.81	7.41	10.33	10.98	8.91	11.29	14.45	13.96	14.27	7.94	13.46	3.12
Zoopk	<i>Spicara maena</i>	0.00	17.05	16.97	10.72	25.04	2.31	7.29	7.41	8.46	6.10	17.47	2.59	42.97	1.52
RBMeso	<i>Symphodus tinca</i>	0.68	3.73	3.10	6.96	7.88	7.03	4.15	7.18	4.65	3.13	4.25	2.75	1.39	1.04
RBMeso	<i>Diplodus sargus</i>	69.68	62.03	147.71	78.79	153.21	83.06	80.20	58.64	139.58	31.52	131.17	75.40	91.32	0.31
RBMeso	<i>Coris julis</i>	12.66	14.18	13.23	11.25	15.02	11.51	12.39	13.03	12.32	9.83	11.82	4.90	11.52	-0.09
Zoopk	<i>Spicara smar</i> is	0.00	43.56	42.97	47.05	29.63	14.98	11.35	8.41	20.52	15.84	33.34	17.93	30.01	-0.31
PelagicP	<i>Dicentrarchus labrax</i>	37.18	11.03	42.81	1.96	11.81	0.00	23.66	8.56	13.78	0.00	36.86	1.33	12.02	-0.68
Zoopk	<i>Boops boops</i>	161.55	328.73	160.63	65.28	178.25	20.45	6.60	6.64	8.04	49.90	30.89	25.77	21.05	-0.87
Macrocar	<i>Scorpaena notata</i>	0.27	1.39	3.56	3.41	2.87	1.95	6.62	5.69	9.00	9.25	8.07	6.80	0.03	-0.88

Herbiv	<i>Sarpa salpa</i>	0.00	6.56	6.75	27.58	0.00	21.87	0.00	109.94	0.98	0.00	0.00	1.13	23.91	-
PelagicP	<i>Pagrus pagrus</i>	0.00	0.00	0.00	0.03	0.45	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00	-
PelagicP	<i>Trachurus</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	17.79	4.77	0.14	0.00	0.00	0.00	0.00	-
PelagicP	<i>Zeus faber</i>	0.00	0.00	0.00	0.00	2.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
SBMeso	<i>Pagellus</i> spp.	0.00	0.00	0.00	1.13	0.20	0.02	0.40	0.12	0.45	0.00	0.00	0.00	0.00	-
	All species	305.81	619.76	564.42	400.22	643.28	405.71	380.22	520.18	441.86	382.84	516.51	252.47	751.80	1.46
Total species richness		25	33	33	33	33	31	33	29	30	27	29	26	35	

Table S3: Results from statistical analyses performed to assess trends in species biomass at the species level. r_s : Spearman's correlation coefficient. p-value: probability value associated with Mann Kendal (MK) and Mann Whitney (MW) tests.

Species	Functional trophic group	Trend				Seasonality		
		Sen's slope	MK p-value	Spearman correlation		Mean winter index (%)	Mean summer index (%)	MW p-value
				r_s	p-value			
<i>Sarpa salpa</i>	Herbivores	-0.41	0.707	-0.09	0.750	19.95	80.05	0.080
<i>Coris julis</i>	RB mesocarnivores	-0.24	0.009	-0.75	0.003	55.48	44.52	0.026
<i>Diplodus annularis</i>	RB mesocarnivores	0.34	0.024	0.59	0.062	49.15	50.85	0.394
<i>Diplodus puntazzo</i>	RB mesocarnivores	1.46	0.012	0.64	0.026	35.73	64.27	0.026
<i>Diplodus sargus</i>	RB mesocarnivores	-1.1	0.583	-0.19	0.518	64.30	35.70	0.002
<i>Diplodus vulgaris</i>	RB mesocarnivores	2.34	0.059	0.56	0.070	43.41	56.59	0.180
<i>Spondyliosoma cantharus</i>	RB mesocarnivores	0.17	0.161	0.28	0.300	48.68	51.32	0.818
<i>Symphodus mediterraneus</i>	RB mesocarnivores	0.35	0	0.84	0.003	45.59	54.41	0.180
<i>Symphodus tinca</i>	RB mesocarnivores	-0.14	0.669	-0.12	0.709	42.72	57.28	0.180
<i>Mullus surmuletus</i>	SB mesocarnivores	0.76	0.360	0.26	0.359	36.44	63.56	0.015
<i>Pagellus spp.</i>	SB mesocarnivores	--	--	0	1	--	--	--
<i>Scorpaena notata</i>	Macrocarivores	0.62	0.059	0.46	0.113	47.39	52.61	0.394
<i>Scorpaena porcus</i>	Macrocarivores	1.19	0.004	0.78	0.004	50.39	49.61	0.937
<i>Serranus cabrilla</i>	Macrocarivores	0.67	0.012	0.68	0.015	48.98	51.02	0.937
<i>Phycis phycis</i>	Benthic piscivores	0.88	0.002	0.83	0.003	52.97	47.03	0.623
<i>Scorpaena scrofa</i>	Benthic piscivores	1.59	0.009	0.70	0.012	44.62	55.38	0.589
<i>Conger conger</i>	Benthic piscivores	6.37	0.100	0.47	0.102	43.49	56.51	0.485
<i>Dicentrarchus labrax</i>	Pelagic piscivores	-1.38	0.180	-0.45	0.132	90.45	9.55	0.002
<i>Pagrus pagrus</i>	Pelagic piscivores	--	--	0	1	--	--	--
<i>Trachurus spp.</i>	Pelagic piscivores	--	--	0	1	--	--	--
<i>Zeus faber</i>	Pelagic piscivores	--	--	0	1	--	--	--
<i>Boops boops</i>	Zooplanktivores	-12.57	0.044	-0.62	0.023	52.00	48.00	0.699
<i>Spicara maena</i>	Zooplanktivores	0.12	0.855	0.13	0.732	57.94	42.06	0.394
<i>Spicara smaris</i>	Zooplanktivores	-0.08	1	-0.04	0.854	48.84	51.16	0.394

