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Jessica Salaün, Aurore Raoux, Jean-Philippe Pezy, Jean-Claude Dauvin, Sylvain Pioch. Structural and functional changes in Artificial Reefs ecosystem stressed by trophic modelling approach: Case study in the Bay of Biscay. *Regional Studies in Marine Science*, 2023, 65, pp.103100. <10.1016/j.rsma.2023.103100>. <hal-04248150>

HAL Id: hal-04248150

<https://normandie-univ.hal.science/hal-04248150v1>

Submitted on 13 Jan 2025

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1 **Structural and functional changes in Artificial Reefs ecosystem stressed by**
2 **trophic modelling approach: case study in the Bay of Biscay**

3
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12
13
14 **ABSTRACT:**

15 Artificial Reefs (ARs) are commonly cited as a tool used for increasing fishery production and
16 reinstating ecosystem functionalities. The assessment of AR deployment is mostly based on analysis
17 of the evolution of fish communities. Recently, studies have focused on trophic modelling to
18 understand the functioning of such ecosystems in a more holistic approach. Trophic models are able to
19 address this concern by describing the interaction between species at different trophic levels and based
20 on the quantification of energy and matter flows through ecosystems. These models allow the
21 application of numerical methods - also called Ecological Network Analysis (ENA) - to characterize
22 emergent properties of the ecosystem. Usually, ENA indices are proposed as indicators of ecosystem
23 health as they are sensitive to different impacts on marine ecosystems. In the present study, the
24 Ecopath software is used to build an ecosystem model composed of 23 compartments, from detritus
25 and phytoplankton to mammals, to describe the situation “before” and “after” the deployment of ARs
26 in the south of the Bay of Biscay along the Landes coast. In addition, ENA indices are calculated for
27 two periods, “before” and “after” the deployment of artificial reefs, to compare network functioning
28 and the overall properties of the structural trophic network. Our results show little structural change in
29 the ecosystem, with a rearrangement of the trophic levels and a simultaneous increase in biomass and
30 system maturity. These preliminary results evidently need to be confronted with other environmental
31 factors such as, for instance, substrate composition, proximity to natural reefs and larval supply...
32 Nonetheless, we consider that the maturity index could be used as a new indicator to assess the
33 evolution of ARs with specific management objectives.

34
35 **KEYWORDS:** Trophic network; Before/After approach; Maturity indicator; Eopath with Ecosim
36 software;

39 •

40 **1 Introduction**

41 Artificial Reefs (ARs) are human made voluntarily submerged structures created “to mimic certain
42 functions of a natural reef such as protecting, regenerating, concentrating, and/or enhancing
43 populations of marine resources” (FAO, 2015). Despite some controversial debates about the effects
44 of production and concentration (Osenberg *et al.*, 2002; Pickering et Whitmarsh, 1997), ARs are
45 commonly considered to be relevant tools for increasing fisheries production and supporting
46 commercial or recreational fishing activities, if they are properly managed (Seaman *et al.*, 2000;
47 Santos et Monteiro, 1997). Therefore, they are used worldwide with fish production being the main
48 objective (Lacroix *et al.*, 2002; Jensen, 2002; Baine, 2001). Recently and to an increasing extent, ARs
49 are also deployed to rehabilitate marine ecosystems (coral, rocky or algae substrata) and their
50 functionalities (*e.g.* nursery, feeding or reproductive), or to mitigate the effects of anthropogenic
51 impacts (Seaman, 2019; Patranella, et al., 2017; Pioch et al., 2011). Although the general objectives of
52 AR projects are frequently defined in terms of production, protection or recreational activities, there is
53 a lack of information on the precise objectives with specific indicators (Becker *et al.*, 2018, Claudet *et*
54 *al.*, 2006). Thus, suitable criteria and quantitative indicators need to be developed to assess the
55 attainment of AR objectives (Hammond *et al.*, 2020).

56 Despite the worldwide deployment of ARs and the increasing research on their design, performance
57 and management, knowledge of their efficiency remains largely insufficient regarding the production
58 and protection aspects (Lee *at al.*, 2018; Lima *et al.*, 2020). As their main goal is to enhance fish
59 biomass, studies have focused predominantly on the variation of certain ecological components such
60 as fish assemblages, abundance and species richness (Véron *et al.*, 2008; Folpp *et al.*, 2011; Neves dos
61 Santos and Zalmon, 2015; Becker *et al.*, 2018). Moreover, ARs create new hard substrates to be
62 colonized by sessile fauna and consequently provide new food resources that are non-pre-existent on
63 soft bottoms (Baine, 2001). The feeding relations have been recently explored to demonstrate the real
64 contribution to fish production as a function of the attraction effect of ARs using stable isotopic ratios
65 to characterize the trophic network (Cresson *et al.*, 2019). These results open new perspectives using
66 trophic analysis as a tool to understand the overall functioning of AR systems from the primary
67 producers to the top predators, while providing original new metrics to improve the effectiveness
68 assessment of ARs.

69 Trophic analyses were firstly developed to evaluate ecosystem-based management of fisheries
70 (Polovina, 1984; Christensen and Pauly, 1992; Gascuel, 2019). For this purpose, models using the
71 Ecopath with Ecosim software (EwE) have been intensively used and developed over the last three
72 decades (Colléter *et al.*, 2015; Drouineau *et al.*, 2006; Chouvelon, 2011; Moullec, 2015; Guénette and
73 Gascuel, 2012; Halouani, 2016). These joint trophic approach have been recently applied to coastal
74 and marine systems to assess changes in their functioning in response to environmental perturbations
75 such as Offshore Wind Farm (OWF), marine aggregates exploitation, harbour construction and

76 dumping of dredged materials (Raoux *et al.*, 2017; Pezy *et al.*, 2017) as well as specific regulations for
77 Marine Protected Areas (MPA) (Prato, 2016; Valls *et al.*, 2012; Wallmo and Kosaka, 2017; Fulton *et*
78 *al.*, 2015). These studies based on Ecological Network Analysis (ENA) provide metrics that could be
79 used to define the state of marine ecosystems and assess the effectiveness of conservative management
80 tools. Hence, this approach has led to the development of indicators for stakeholders and decision
81 makers, allowing them to build up and enrich Ecosystem Based Management (Safi *et al.*, 2019; Fath *et*
82 *al.*, 2019). Applied to ARs, this would be an innovative approach to assess positive or negative
83 changes in ecosystems associated with the deployment of ARs.

84 Other engineering infrastructures can act as ARs, such as shipwrecks, oil platforms or Offshore Wind-
85 Farms (OWF). These artificial structures also induce an increase of fish biomass, species diversity and
86 provide shelter against predators. Several surveys on fish and macro-invertebrates indicate that these
87 structures also give rise to reef effects (Glarou *et al.*, 2020; Ajamian *et al.*, 2015; Picken *et al.*, 2000).
88 Therefore, this innovative approach, which consists of comparing the state of an ecosystem before and
89 after a few years of AR deployment by using trophic modelling, could provide an effective overview
90 of the ecological effects of ARs and other artificial structures on the marine ecosystem (Conner *et al.*,
91 2016; Raoux *et al.*, 2017).

92 The present study tries to apply the trophic framework approach to validate that ARs can contribute to
93 enhancing an ecosystem. In this study, we build Ecopath ecosystem models, composed of 23
94 compartments, ranging from detritus and phytoplankton to marine mammals, to describe the situation
95 “before” and “after” the deployment of ARs in the southern part of the Bay of Biscay along the Landes
96 coast. These ARs were deployed by an association named “Atlantique Landes Récifs” with the aim of
97 creating a protected area for growing fishes after observing a decrease of catches along the coast
98 (ALR, 1998). For this purpose, all marine activities are prohibited on the site and three types of AR
99 have been deployed to offer refuges, habitats and food supply for demersal and pelagic fishes. The
100 hypothesis tested in this study is that ARs modify the structure and functioning of the trophic network.
101 Moreover, our study focuses on the identification of emergent properties that evolve with the
102 deployment of ARs and proposes the use of ecological indicators to monitor the progress of AR
103 projects in reaching their objectives.

104

105 **2 Materials and methods**

106 **2.1 Study area**

107 In France, ARs were deployed since 1968 throughout more than fifty sites, firstly in the aim to
108 develop or protect fisheries resources and, since a decade, to restore marine ecosystems (Salaün *et al.*,
109 2022b). The study area is located in the south of the Bay of Biscay, a large gulf on the French Atlantic
110 coast characterized by a continental shelf that decreases in width from the North (150 km) to the South
111 (12 km) (Borja *et al.*, 2019). The south of the continental shelf is incised by the Capbreton Canyon
112 whose head is situated only 250 m off the Landes coast (Mazières *et al.*, 2015). The study area is

113 exposed to strong swell that transports around 1,000 m³ per year of sediment to the south (Abadie *et*
114 *al.*, 2006). Spring upwelling occurs in the area (Planque *et al.*, 2004) and the sediment habitat
115 correspond to fine sand with wave influence (Borja *et al.*, 2019) associated with *Nephtys cirrosa*
116 benthic communities (after Monbet, 1972). Boreal and subtropical fish species are distributed across

117 this rich ecosystem (Authier *et al.*, 2018) and top predators such as marine mammals and seabirds are
 118 attracted (Planque *et al.*, 2004; Sanchez and Santurtun, 2013).
 119

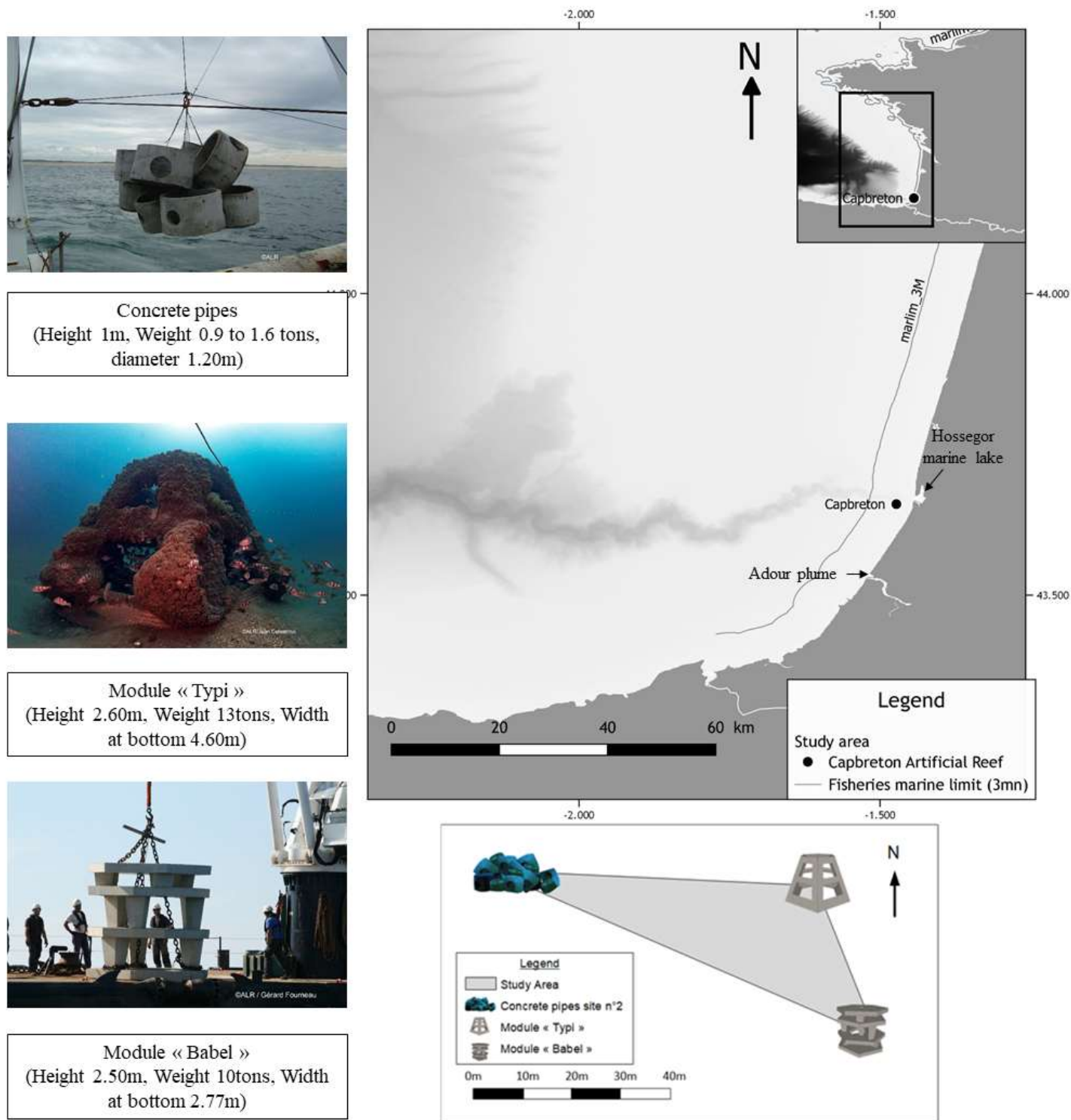


Figure 1 : Location of the Capbreton Artificial Reef study site and photographs of the three artificial reefs modules forming a triangle

120 ARs have been implemented off Capbreton to create hard bottom habitats for fisheries production
121 (Salaün *et al.*, 2022); this location was chosen for many reasons, including the proximity of Capbreton
122 harbour and the coastline (2.2 km offshore on a sandy bottom at 20 m depth), the gentle slope of the
123 continental shelf (<0.8 %) and the supply of organic matter from the Hossegor marine lake and the
124 Adour plume (Biosub, 1999; Mazière *et al.*, 2015) (Figure 1). Three types of ARs were deployed by
125 the association “Atlantique Landes Récifs”, with clusters of concrete Bonna® pipes being emplaced in
126 1999 at three sites of around 200 m² each. The “Typi” modules were deployed in 2010 with a 11 m²
127 footprint and the “Babel” modules in 2015 with a 5 m² footprint (Figure 1). Rapidly, two ARs sites
128 with Bonna pipes were buried. The study focused on the three remaining ARs sites that forms a
129 triangle covering an area of 900 m², with one peak corresponding to site n°2 with clusters of concrete
130 pipes, and the other two peaks corresponding to the sites with Typi and Babel modules. Also, the total
131 ARs surface footprint covered 102 m², the total surface colonized represented 3 656 m² and the
132 volume formed were 830 m³.

133

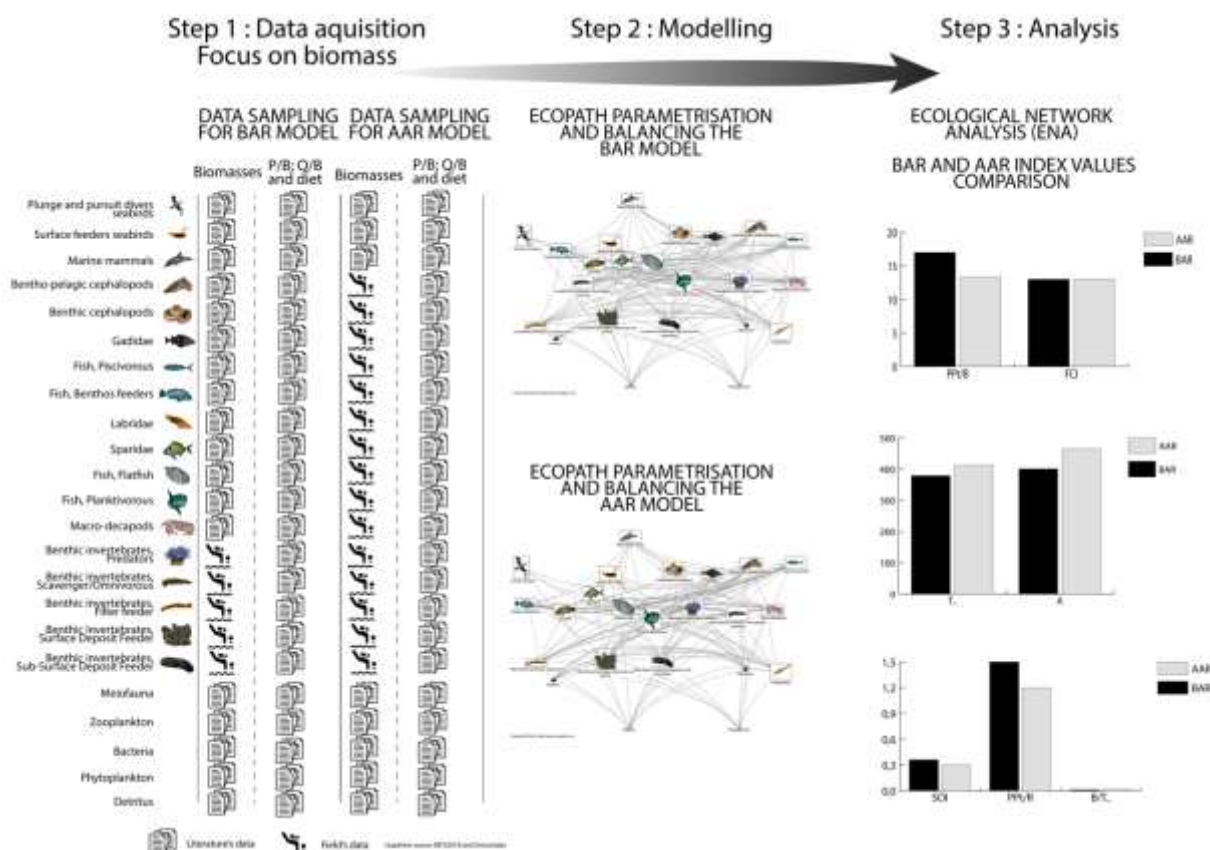
134 **2.2 Trophic network modelling framework**

135

136 In this study, we use the Ecopath with Ecosim (EwE) approach and software (Polovina, 1984;
137 Christensen and Pauly, 1992) to model the trophic network before and after the placement of three
138 ARs in the Capbreton Artificial Reef study site. Thus, the two Ecopath models called BAR (Before
139 AR deployment) and AARs (After AR deployment) based on data collected on the three artificial reefs
140 of the Capbreton study site were created. To ensure statistical robustness a minimum of five years’
141 data for each model were addressed. Therefore, the BAR model covered the period from 1997 to 2002
142 and the AAR model covered for ten years from 2010 to 2020. Despite the overlapping of the BAR
143 period and the first AR deployment occurring in 1999, the data considered to represent this period
144 were carefully selected to minimize the possibility that ARs deployment had an influence on it.

145 Ecopath modelling is based on functional groups that constitute the trophic network units. A
146 functional group could include several species or individual ones that have similar habitat and
147 ecological characteristics (growth rates, diets, predators, consumption). Whereas detritus group is
148 essential, the number of groups are not limited (Heymans *et al.*, 2016). The Ecopath model requires
149 inputs for each functional group that are information on the biomass, the diet composition and other
150 ecological parameter such as the Production-Biomass ratio, the Consumption-Biomass ratio and the
151 Ecotrophic Efficiency. The inputs are based on the individual species information (Step 1 in Figure 2)
152 that are weighted by their relative biomass to calculate a single functional group parameter (Step 2 in
153 Figure 2). Then, the models are analysed and compared using ecological index (Step 3 in Figure 2).
154 However, the index is related to the model structural parameters, such as the number of groups, that
155 could make comparisons between models difficult to interpret (Pinnegar *et al.*, 2005).

156 To make the static Ecopath models more comparable, we chose to fix the number and the type of the
 157 functional groups, but the species including in these groups could be different over models. Thus, we
 158 selected 23 functional groups based on heightened species interest referenced in our study site (e.g.,
 159 commercial species, cultural value species, reef species) that range from detritus and phytoplankton to
 160 top predators such as marine mammals or diving seabirds. Whereas ecological parameters are
 161 relatively easy to estimate with literature values, the biomass is more space related. We chose to focus
 162 our sampling strategy on the local biomass data acquisition considering our allocated time and funds.



163
 164 *Figure 2: Trophic network modelling framework apply to model before and after the ARs deployment in Capbreton*

165
 166

167 **2.3 Biomass sampling strategy**

168

169 The biomass data intended to represent the stable state of relationships in the ecosystem before and
 170 after ARs deployment and overview their ecological effect. The biomass sampling strategy were made
 171 to this end: (1) on-site collection of fish and benthic invertebrates of soft bottom and hard substrate
 172 was privileged, as they are the faunal communities the most impacted by ARs deployment (Fabi *et al.*,
 173 2006); (2) the biomass data for the other fauna groups were taken from the literature (details given on
 174 Table 1); (3) the same biomass data were used for meiofauna, zooplankton, phytoplankton and
 175 bacteria groups before and after ARs deployment because ARs deployment was assumed to have no
 176 effect on their biomass and production (Miller and Falace, 2000) and (4) the same biomass data were

177 used for marine mammals and birds groups due to the low surface-area of ARs (in m²) compared to
178 their predation areas (in km²), ARs were assumed to have little influence on the biomass of these top
179 predators (Castège and Milon, 2018). As a result, other external factors that could influence the
180 parameter fluctuation such as temperature growth were limited and top-down and bottom repercussion
181 due to ARs deployment were strengthened.

182

183 The biomass sampling was carried out using multi-tool surveys:

- 184 • Soft bottom benthic fauna sampling (Before and After AR deployment);
- 185 • Hard bottom benthic fauna sampling (on Artificial Reef);
- 186 • Underwater visual census of fishes, macro-decapods and cephalopods (only After AR
187 deployment).

188 The annual average representation of exchanges in the ecosystem was made with available data
189 covering a minimum of five years as possible (Table 1). To be able to compare data from various
190 numbers of samples and different method, all data were express into mean annual biomass by square
191 meter implemented on the surface triangle (900 m²).

192 *Table 1: The periods and locations of the data collected for the functional groups included in the two models (BAR: Before*
193 *Artificial Reef and AR: After Artificial Reef)*

194

| | BAR | AAR |
|-----|--|---|
| | Periods and location for biomass data | Periods and location for biomass data |
| 195 | | |
| 196 | | |
| 197 | | |
| 198 | Plunge and pursuit divers? seabirds | 1999-2004 (Bay of Biscay surveys) |
| 199 | Surface feeders seabirds | |
| 200 | Marine mammals | |
| 201 | Benthopelagic cephalopod | 1997-2002 (South of Bay of Biscay surveys) |
| 202 | Benthic cephalopod | 2010-2020 (this study coupled with older ARs surveys) |
| 203 | Gadidae | |
| 204 | Fish piscivorous | |
| 205 | Fish, benthos feeders | |
| 206 | Labridae | |
| 207 | Sparidae | |
| 208 | Fish flatfish | |
| 209 | Fish planctivorous | |
| 210 | Macro-decapods | |
| 211 | Predators | 2000 (Capbreton survey) |
| 212 | Scavengers /omnivorous | 2019-2020 (this study) |
| 213 | Filters feeders | |
| 214 | Surface Deposit Feeders | |
| 215 | Sub surface Deposit Feeders | |
| | Meiofauna | 1981 (Galicia survey) |
| | Zooplankton | 1999-2006 (Bay of Biscay surveys) |
| | Bacteria | 1994-2002 (Bay of Biscay surveys) |
| | Phytoplankton | 1999-2000 (Bay of Biscay surveys) |
| | Détritus | 1994-2002 (Bay of Biscay surveys) |

2.3.1 Soft bottom benthic fauna sampling

Hand box-corer samplers and a grab of 0.02 m² were used to sample the soft bottom benthic fauna.

The corer used is 25 cm long and has a diameter of 16 cm, with a cap to limit loss of material. The opening of the grab is 20 cm long and 10 cm wide.

The first soft bottom benthic fauna sample campaign was conducted by scuba-divers in May 2000, just after the first deployment of ARs, on 12 stations located along the four cardinal directions at distances of 1 m, 5 m and 10 m from the AR site (Ferrou, 2000; Figure 3). Two replicates of 0.02 m² each were sampled with the hand box-corer at each station. A grab was operated for the furthest stations at 30 m from site n°2 for one sample (Ferrou, 2000). To be able to use these data in the BAR model, we selected only those stations furthest from the AR placement site (5m, 10m and 30 m). This allows us to avoid considering the recent influence of ARs on the soft bottom benthic community mainly concentrated around the AR footprints (Créocéan, 2008). Therefore, the total sampling effort used for the BAR model corresponds to a coverage of around 0.4 m².

The second soft bottom benthic fauna sample campaign was conducted by scuba-divers in September 2019 and 2020 on 12 stations located along each cardinal direction 20 m from the three ARs (Figure 3). Between three to six replicates of 0.02 m² were collected at each station with the hand-box corer.

232 The total sampling effort was around 0.9 m² and the collected samples were used for the After
233 Artificial Reefs model (AAR).

234 To ensure comparison, the data collected for BAR and AAR model were expressed into mean annual
235 biomass by square meter implemented on the surface triangle (900 m²) using the method described
236 below.

237 The sediment collected was sieved through a 0.1-mm mesh. All samples were preserved in 10 %
238 formaldehyde solution before being sorted. The species were counted under a binocular microscope
239 and identified at the lowest taxonomic level needed to classify them into functional groups. The
240 biomass of species collected for the BAR model was calculated based on the abundance of the benthic
241 species present and their individual weight referenced by Pezy (2017). The species collected for the
242 AAR model were placed in a drying oven at 60°C for the duration needed to ensure drying of the
243 sample (around 48h to 96h). Then, the samples were weighed to determine dry weight (DW) before
244 being put into another oven for 5 hours at 500°C. The ash-free dry weight (AFDW) was obtained by
245 subtracting ash weight from DW. For benthic invertebrates, the biomass was converted from AFDW
246 to carbon content using a conversion factor of 0.518 (Brey, 2001). Then the biomass was reported on
247 the studied triangle site (900 m²).

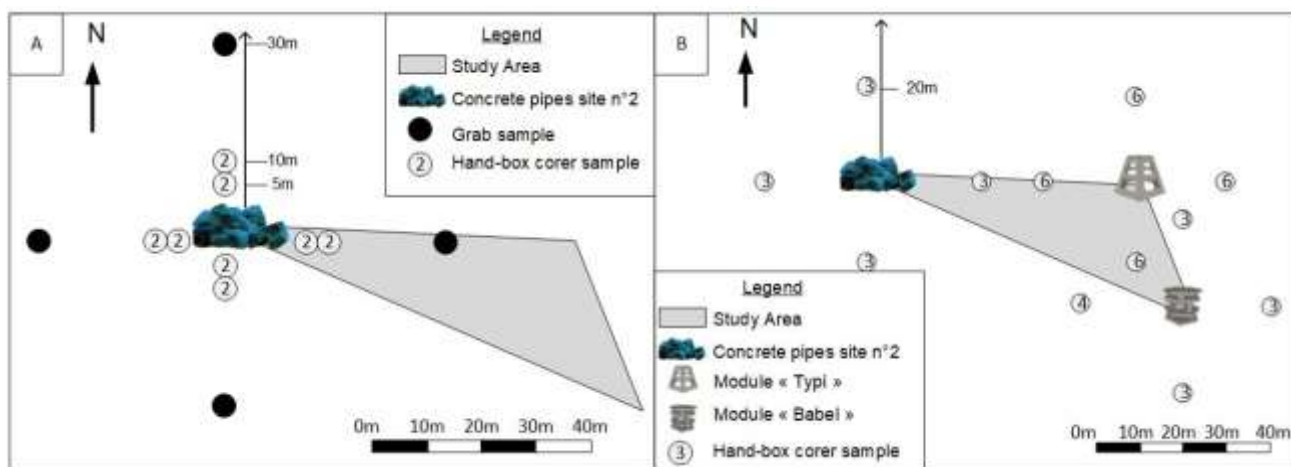


Figure 3: Number of soft bottom benthic fauna sampling in 2000 (A) and 2019-2020 (B)

248

249

250 2.3.2 Hard bottom benthic fauna sampling

251 The Scraping method is commonly used to analyse benthic fauna communities on hard substrates
252 (FAO, 2015) and was applied in this study to ARs. The difficulty of this technique is to be able to
253 collect all organisms, especially those of small size, when there is underwater current (FAO, 2015).

254 Samples of benthos were collected in summer 2019 and winter 2020. Six scrape samples at different
255 AR positions (inside, below, North, East, West and South) were collected by divers on each AR

256 module type, using a quadrat sampler of 20 x 20cm for 2019 and 30 x 30cm for 2020, a putty knife
257 and a net bag (<1 mm mesh size). A total area of 0.553 m² was sampled in summer 2019 and 0.819 m²
258 in winter 2020, thus providing mean annual biomass for the After Artificial Reefs model (AAR).

259 All samples were preserved in 10 % formaldehyde solution before being sorted. The species were
260 counted under a binocular microscope and identified at the lowest taxonomic level needed to classify
261 them into functional groups. The mean annual biomass was then obtained using the AFDW
262 determined from the sampled surface for each species extending to the entire ARs colonisable surface
263 (3 656 m²) and was converting to carbon content using a conversion factor of 0.518 (Brey, 2001). To
264 ensure a comparable data on two dimensional, the biomass obtained was then reported on the total
265 ARs surface footprint (102 m²) and then on the studied triangle site (900 m²).

266

267 **2.3.3 Fishes, macro-decapods and cephalopods underwater visual census**

268

269 Underwater visual census (UVC) is commonly used as a non-destructive survey method for assessing
270 fish assemblages (Kulbicki and Sarramégn. 1999). This method was adapted to ARs using both
271 stationary point and belt transect counts to record fast moving species and then benthic and cryptic
272 species (Cresson *et al.*, 2018; Lowry *et al.*, 2011, Charbonnel *et al.*, 1997; Labrosse *et al.*, 2011). The
273 survey covered the surface of ARs footprints. UVC campaigns were conducted when possible each
274 year between May to September on each ARs. For the AAR model, we selected 120 counts carried out
275 during the last ten years: 58 on the concrete pipes at site n°2 (2010, 2011, 2012, 2013, 2015, 2016,
276 2018 and 2019), along with 49 on the Typi (2010, 2011, 2012, 2013, 2015, 2016, 2018, 2019 and
277 2020) and 13 on the Babel module types (2015, 2016, 2018, 2019 and 2020). This selection that
278 covers several years allows a better representation of the mean annual biomass of fishes, macro-
279 decapods and cephalopods.

280 The data was derived from underwater visual census observations of scientific divers and trained
281 volunteer divers following the recommendations of Harmelin-Vivien *et al.* (1985). Abundances of
282 populations were counted individually up to 10 individuals, whereas larger populations were estimated
283 using abundance classes reviewed in the literature (11–30; 31–50; 51–200; 201–500; 500-1000; >1000
284 individuals). The total length of fish was evaluated in cm. The wet weight was then obtained using the
285 length-weight relationship $W = a \times TL^b$, where W is the wet weight in grams, TL is the average total
286 length of the size class in cm, while a and b are species-specific constants obtained from the data
287 available in Fishbase (Froese and Pauly, 2019) and selected in the vicinity of the study area. As the
288 survey covered only the surface of ARs footprints, the average biomass was calculated for each
289 species (fish, cephalopods and decapods) using the footprint of ARs. Conversion factors of 0.192 and
290 0.402 were used to convert cephalopod wet weights into dry weights and then into carbon contents,
291 respectively, while 0.35 was used for fishes and 0.518 for decapods (Brey *et al.*, 2010; Brey, 2001). To

292 maintain the proportion between the surface covered by ARs and the triangle studied surface, the mean
293 annual biomass obtained was then reported on the studied triangle site (900 m²) with no extrapolation.

294

295 **2.3.4 Collected data from literature**

296

297 According to the literature, two trophic networks on the continental shelf of the Bay of Biscay have
298 already been established by Lassalle *et al.* (2011) and Moullec *et al.* (2017). Data were extracted from
299 these models by preferentially selecting coastal data in the vicinity of the study area.

300 For the BAR model, the biomasses of fishes, macro-decapods and cephalopods were estimated from
301 bottom-trawl surveys carried out by IFREMER since 1997 in the Bay of Biscay in the context of the
302 EVHOE cruises for the West Europe fisheries evaluation (Evaluation Halieutique Ouest de l'Europe;
303 Devreker and Lefebvre, 2018; Mahé and Poulard, 2005). Only the southeast coastal surveys were
304 selected. In order to ensure a better statistical overview, the period selected for representing the state
305 before ARs were extending to 2002. The distance from the trawl surveys selected after the first ARs
306 deployment in 1999 and the study sites (around 65 km) allowed to consider the fish macro-decapods
307 and cephalopods biomass were not influenced by the 1999 ARs deployment. The data captured from
308 these thirteen selected trawl transects during the period 1997-2002 were averaged with respect to the
309 survey surface-area over the five years selected (1997, 1998, 1999, 2001 and 2002). Conversion
310 factors of 0.192 and 0.402 were used to convert cephalopod wet weights into dry weights and then into
311 carbon contents, respectively, with 0.35 used for fishes and 0.518 for decapods (Brey *et al.*, 2010;
312 Brey, 2001).

313 The collection of data for top predators is derived from aerial strip-transect surveys, named ROMER
314 and ATLANCET, conducted from 2001 to 2004 in the Bay of Biscay (Certain *et al.*, 2008). Annual
315 average abundances were converted into biomass using weight referenced by species for sea birds and
316 marine mammals (Spitz *et al.*, 2018; Anonymous, 2008; ICES, 2000; Hunt *et al.*, 2005). Conversion
317 factors of 0.3 and 0.4 were used to convert wet weights into dry weights and then into carbon contents,
318 respectively, for sea birds (Lassalle *et al.*, 2011) and a coefficient of 10% is used to convert directly
319 wet weights into carbon contents for marine mammals (Bradford-Grieve *et al.*, 2003).

320 Meiofauna data were selected from a site located in Galicia, Spain, where benthic habitat
321 characteristics are closely similar to the Capbreton site (Tenore *et al.*, 1984). The biomasses of the
322 benthic macrobenthic invertebrates were converted from AFDW to carbon content using a conversion
323 factor of 0.518 (Brey, 2001).

324 Zooplankton data were taken from BIOMAN campaigns conducted in the Bay of Biscay from 1999 to
325 2006 (Irigorien *et al.*, 2008). The phytoplankton data used were acquired in the south of the Bay of
326 Biscay as far as the 100 m isobath (zone known as “Gironde Interne”) for the period 1999-2000
327 (Lampert *et al.*, 2001). Then, the data were normalized to the depth of the study (20 m) and the
328 chlorophyll-a were converted into carbon content using a factor 40 (Chardy and Dauvin, 1992). The

329 bacteria and detritus biomass were derived from the Ecopath model of the Bay of Biscay built by
330 Lassalle (2011).

331

332 **2.4 Trophic network modelling**

333

334 **2.4.1 Ecopath equation-based modeling**

335

336 Ecopath is a mass-balance single-solution model that uses linear equations to estimate flows between a
337 number of functional groups established *a priori* (Christensen and Walters, 2004). The
338 parameterization of an Ecopath model is based on satisfying two equations. The first equation (Eq. 1)
339 describes the production of each compartment in the system as a function of the consumption to
340 biomass ratio (Q/B) of its predators (j), the fishing mortality (Y_i , $\text{gC}\cdot\text{m}^{-2}$), the net migration (E_i ;
341 emigration – immigration, year^{-1}), the biomass accumulation (BA_i , year^{-1}) and its natural mortality
342 ($1-EE_i$). The Ecotrophic Efficiency (EE) is the fraction of total production consumed in the system
343 (by fishing activities or by predators). Its value can never exceed unity. $(1-EE_i)$ represents the fraction
344 of mortality not explained by the model, such as mortality due to old age or diseases.

$$345 \quad B \left(\frac{P}{B} \right)_i = \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ij} + Y_i + E_i + BA_i + B_i \left(\frac{P}{B} \right)_i (1 - EE_i) \quad (\text{Eq. 1})$$

346 The second equation (Eq. 2) ensures energy balance, calculating consumption of the i^{th} group (Q) as
347 the sum of its production, respiration (R), and excretion (U)

$$348 \quad Q_i = P_i + R_i + U_i \quad (\text{Eq. 2})$$

349 **2.4.2 Ecopath model parametrisation**

350

351 The two models developed in this study are composed of 23 functional groups or compartments
352 ranging from seabirds and mammals to detritus. Seabirds are divided into two groups, according to
353 their feeding strategies. The "plunge and pursuit divers" group is mainly composed of gannets and the
354 "surface feeders" are mainly composed of gulls and kittiwakes. Marine mammals (*Delphinus delphis*,
355 *Stenella coeruleoalba* and *Tursiops truncatus*) are placed together in one group. Cephalopods are
356 divided into two groups: the benthopelagic group mainly composed of *Loligo vulgaris* and the benthic
357 group mainly composed of *Sepia officinalis*. The model also comprises seven groups of fish (Gadidae,
358 piscivorous, benthos feeders, Labridae, Sparidae, flatfish and planktivorous). Gadidae, Labridae and
359 Sparidae are not aggregated with the other compartments to allow a detailed analysis of the potential
360 impact of the reef effect on these three groups which also include commercial species. Benthic
361 invertebrates are divided into six groups (macro-decapods, predators, scavengers/omnivores, filter
362 feeders, surface deposit feeders and subsurface selective feeders). Finally, the model also comprises

363 one group of zooplankton, one group of bacteria, one group of phytoplankton and one group of
364 detritus.

365 The source data used for obtaining the model parameters (Biomass, P/B, Q/B, diet and conversion
366 factor) are listed in Supplementary material (Table 1). The dietary preferences for multi-species
367 groups are weighted by the relative biomass contribution of each species (Supplementary material,
368 Tables 2 and 3). Besides, considering the study site as an open system, the diet import was added in
369 proportion of time spent outside the system (Christensen and Walters, 2004).

370 The two models comparison aimed to reveal what modification on the structure and functioning of the
371 trophic network ARs modify. The differences in the fishing activity between BAR and AAR model
372 (all activities were restricted) conduct to add a MPA effect on the system. Therefore, to highlight
373 mostly ARs effect, the fishing mortality in the BAR model represented by Y was not considered.

374

375 **2.4.3 Balancing the Ecopath model**

376

377 To equalize the mass balances, the input data to the models had to be manually and slightly calibrated.
378 The balancing approach was top-down, starting modifications from top predators down to the lowest
379 trophic levels. Balancing was performed taking into account the quality of the diet data source. Due to
380 a lack of data, the biomass of planctivorous fish and flatfish were left to be estimated by the model
381 after setting their Ecotrophic Efficiency at 0.95 (Christensen and Walters, 2004). In the same way, the
382 biomass of macro-decapods and benthic invertebrate filter feeders were also estimated by Ecopath
383 using an EE of 0.95. The consistency of the model was checked with the Ecopath PREBAL tool (Link,
384 2010).

385

386 **2.5 Analysis of the ecosystem organization and maturity**

387

388 Ecological network analysis (ENA) was performed to reveal the emergent properties of the trophic
389 network using the plug-in included in EwE software (Christensen and Walters, 2004). Thus, for both
390 models, we made use of the Total System Throughput (T.), which corresponds to the sum of all flows
391 occurring in the system (Latham, 2006), and the System Omnivory Index (SOI), which provides a
392 measure of the trophic specialization of predators in terms of trophic levels and an indicator of the
393 structure and complexity of a trophic network (Libralato, 2008). We also calculated the Finn's Cycling
394 Index (FCI), which represents the fraction of the flows in the system generated by recycling (Finn,
395 1980) and the Ascendency, which is a measure of the growth and the flow coherence of the system,
396 integrating its size and organization (Ulanowicz and Abarca-Arenas, 1997; González *et al.*, 2016;
397 Nogues *et al.*, 2021). In addition, the maturity status of the ecosystems (Odum, 1969) was also
398 assessed using the following ratios: the total primary production/total respiration (PPt/R), the total

399 primary production/total biomass (PPt/B) and the total biomass/total system throughput (B/T..)
400 (Christensen *et al.*, 2005).

401 The trophic level (TL) of each functional group (i) was calculated as the weighted average of the
402 trophic levels of its prey (j), according to the following equation:

$$TL_j = 1 + \sum_{i=1}^N DC_{ji} TL_i$$

403 where DC_{ji} is the fraction of prey i in the diet of predator j.

404 It is noteworthy that the EwE software is a single solution model and statistical comparisons between
405 models are not possible (Christensen and Walters, 2004).

406 **3 Results**

407 **3.1 Functional group biomass profiles and trophic levels**

408

409 Results show that, before the deployment of the ARs, Phytoplankton is the dominant functional group
410 in the biomass, representing approximately 28 % of the total living biomass of the system (Table 2).

411 The other major groups of the system are benthic invertebrates, scavengers/omnivores and bacteria,
412 making up approximately 17 % and 8 % of the total living biomass, respectively (Table 2).

413 After the deployment of the artificial reef, the phytoplankton remains the dominant functional group of
414 the total living biomass of the system, followed by the benthic invertebrate filter feeders (mostly
415 composed of the barnacles *Balanus* spp.) and the predators of benthic invertebrates (mostly composed
416 of the gastropod *Natica*), representing approximately 22 %, 19 % and 10 % of the total living biomass,
417 respectively (Table 2). Results show that the total living biomass is higher after deployment of the
418 artificial reefs. In fact, the total living biomass increases by approximately 28 % after deployment of
419 the three artificial reefs on the Capbreton site. This increase of biomass is mostly due to the macro-
420 decapods and benthic invertebrate filter feeders, whose biomass increases by a factor of approximately
421 5 and 4, respectively, after the installation of the ARs. From another perspective, the Labridae and
422 benthos feeder fish are the functional groups that experienced the greatest proportional increases
423 (increase by a factor of 10 and 7 respectively).

424 Three notable changes in the species composition of functional group occurred with the ARs
425 deployment and modified consequently the Q/B data input. The fish piscivorous functional group
426 biomass was dominated by 93% of *Trachurus trachurus* (Linnaeus, 1758) in the BAR model while in
427 the AAR it was dominated by 72% of *Conger conger* (Linnaeus, 1758). The fish benthos feeder's
428 functional biomass group was mainly represented by 47% of *Trachinus draco*, (Linnaeus, 1758), 24%
429 of *Chelon ramada* (Risso, 1827) and 16% of *Mullus surmuletus* (Linnaeus, 1758) while with ARs the
430 functional group biomass was composed by 90% of *Umbrina canariensis* (Valenciennes, 1843). The
431 biomass of Sparidae functional group evolved from 67% of *Boops boops* (Linnaeus, 1758), to 27% of

432 *Diplodus sargus* (Linnaeus, 1758), 29% *Diplodus vulgaris* (Geoffroy Saint Hilaire, 1817) and 37%
 433 *Spondylisoma cantharus* (Linnaeus, 1758).

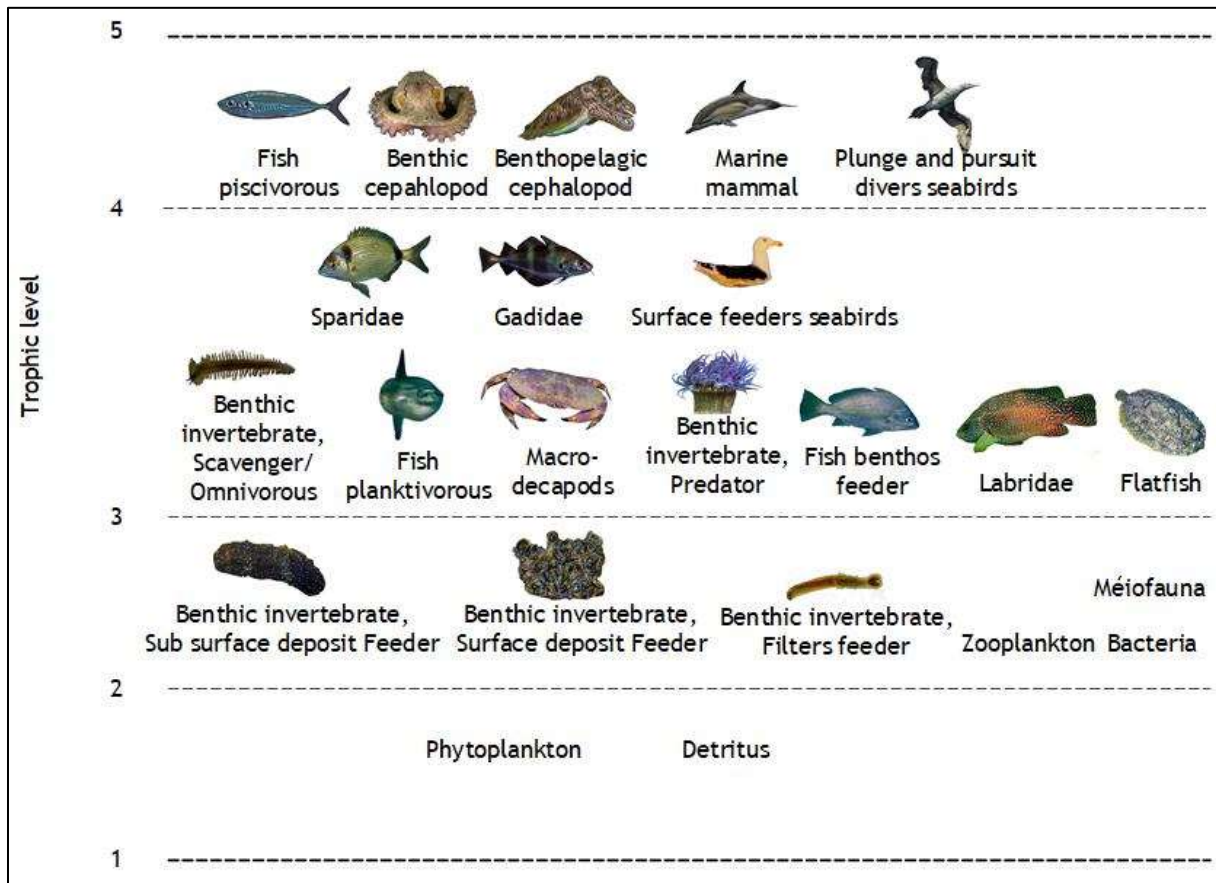
434 Table 2 : Biomass values (gC.m⁻², Trophic Levels, production over biomass (P/B) ratios, consumption over biomass (Q/B)
 435 ratios, in the two Ecopath models ("before" (BAR) and "after" (AAR) the construction of the artificial reef). Major changes
 436 were highlighted in bold and dominant living functional group were indicated by *.

| Functional groups | Biomass | | Trophic Level | | P/B | | Q/B | | EE | |
|---------------------------------------|------------------------|---------------------------|---------------|-----------|-----------|-----------|-------------|-------------|-----------|-----------|
| | BAR model | AAR model | BAR model | AAR model | BAR model | AAR model | BAR model | AAR model | BAR model | AAR model |
| Plunge and pursuit diver's seabirds | 0.0001 | 0.0001 | 4.06 | 4.11 | 0.09 | 0.09 | 70.4 | 70.4 | 0 | 0 |
| Surface feeders seabirds | 0.0001 | 0.0001 | 3.93 | 3.94 | 0.09 | 0.09 | 74.94 | 74.94 | 0 | 0 |
| Marine mammals | 0.0018 | 0.0018 | 4.85 | 4.83 | 0.08 | 0.08 | 42.5 | 42.5 | 0 | 0 |
| Benthopelagic cephalopods | 0.0096 | 0.0037 | 4.31 | 4.17 | 2.71 | 2.71 | 14.54 | 14.54 | 0.86 | 0.95 |
| Benthic cephalopods | 0.0240 | 0.0371 | 4.10 | 4.06 | 3.5 | 3.5 | 15 | 15 | 0.68 | 0.95 |
| Gadidae | 0.0487 | 0.0409 | 4.03 | 4.00 | 0.75 | 0.75 | 5.1 | 5.1 | 0.86 | 0.98 |
| Fish, piscivorous | 0.1758 | 0.3065 | 3.98 | 4.20 | 0.6 | 0.55 | 5.9 | 4.1 | 0.90 | 0.98 |
| Fish, benthos feeders | 0.0246 | 0.1705 | 3.78 | 3.43 | 0.93 | 1.17 | 7.71 | 3.96 | 0.94 | 0.99 |
| Labridae | 3,9 x 10 ⁻⁶ | 4x 10⁻⁵ | 3.51 | 3.31 | 1.3 | 1.3 | 10.38 | 10.38 | 0.92 | 0.95 |
| Sparidae | 0.0263 | 0.0089 | 3.56 | 3.62 | 0.55 | 1.38 | 2.45 | 6.05 | 0.93 | 0.99 |
| Fish, flatfish | 0.0208 | 0.0672 | 3.53 | 3.36 | 0.78 | 0.88 | 3.01 | 3.28 | 0.95 | 0.95 |
| Fish, planktivorous | 0.2231 | 0.2670 | 3.15 | 3.15 | 1.09 | 1.092 | 7.73 | 7.73 | 0.95 | 0.95 |
| Macro-Decapods | 0.0322 | 0.1543 | 3.13 | 3.12 | 1.18 | 1.01 | 5.9 | 5.05 | 0.95 | 0.95 |
| Benthic invertebrates, Predators | 0.2920 | 0.6161* | 3.16 | 3.22 | 2.35 | 2.1 | 11.75 | 10.5 | 0.96 | 0.95 |
| Benthic invertebrates, Scv/O | 0.8228* | 0.2827 | 3.14 | 3.20 | 0.55 | 0.66 | 2.75 | 3.3 | 0.95 | 0.98 |
| Benthic invertebrates, Filter feeders | 0.3073 | 1.2196* | 2.28 | 2.32 | 2.46 | 2.8 | 9.84 | 11.2 | 0.95 | 0.91 |
| Benthic invertebrates, sDF | 0.2690 | 0.3366 | 2.44 | 2.36 | 2.8 | 3.11 | 14 | 15.55 | 0.94 | 0.95 |
| Benthic invertebrates, ssDF | 0.2883 | 0.4126 | 2.22 | 2.22 | 3.12 | 2.6 | 15.6 | 13 | 0.92 | 0.91 |
| Meiofauna | 0.2642 | 0.2642 | 2.29 | 2.21 | 15 | 15 | 60 | 60 | 0.86 | 0.92 |
| Zooplankton | 0.3600 | 0.3600 | 2.15 | 2.15 | 11 | 11 | 52.38 | 52.38 | 0.96 | 0.90 |
| Bacteria | 0.3940* | 0.3940 | 2.02 | 2.02 | 115 | 125 | 230 | 250 | 0.26 | 0.20 |
| Phytoplankton | 1.3800* | 1.3800* | 1 | 1 | 61.2 | 61.2 | | | 0.44 | 0.53 |
| Detritus | 2.8467 | 2.8467 | 1 | 1 | | | | | 0.47 | 0.52 |

437

438 In both models (BAR and AAR), the trophic levels (TL) of the functional groups range from 1 for
 439 primary producers and detritus to a maximum of 4.8 for marine mammals that could be considered as
 440 top predators in this area (Table 3; Figure 4). As mentioned below, TL 1 is composed of two groups
 441 (primary producers and detritus, as imposed by the model structure) and represents approximately 54
 442 % and 46 % of the total biomass in the BAR and AAR models, respectively. TL 2 is composed of six
 443 functional groups (bacteria, zooplankton, benthic invertebrate subsurface and surface deposit feeders
 444 and filter feeders) making up approximately 23 % and 29 % of the total biomass in the BAR and AAR
 445 models, respectively. TL 3 incorporates the major part of the fish functional group (such as flatfish,
 446 benthos feeders, planktivorous and Sparidae) and is composed of nine functional groups. It represents
 447 16 and 18 % of the total biomass in the BAR and AAR model, respectively. Finally, TL 4 is composed

448 of five functional groups in the BAR model and six functional groups in the AAR model. TL 4
 449 corresponds to top predators and represents only 8 and 7% of the total biomass in the BAR and AAR
 450 models, respectively. Thus, TL2 is the trophic level contributing most to the total living biomass in
 451 both models.



452

453 *Figure 4: Trophic levels of the 23 groups in the AAR models*

454

455 *Table 3: Percentage of the biomass for each Trophic Level in the two models Ecopath models: “before” (BAR) and “after”*
 456 *(AAR) the construction of the artificial reef.*

457

| Trophic Levels | BAR | AAR |
|----------------|------|------|
| >TL 4 | 8 % | 7 % |
| TL 3 | 16 % | 18 % |
| TL 2 | 23 % | 29 % |
| TL 1 | 54 % | 46 % |

458

459

460

461

462

463 **3.2 Ecological Network Analysis and time-evolution of ecosystems**

464

465 The results obtained from Ecological Network Analysis (ENA) show that the activity of the
 466 ecosystems studied here, as indicated by the Total System Throughput and Ascendency, is relatively
 467 lower than other estuarine French models as well as other coastal models (Table 4). The System
 468 Omnivory Index shows that, in both models, the trophic networks have a complex “web-like” structure
 469 before and after AR deployment (Libralato, 2008). Finn’s Cycling Index obtained for both models
 470 points towards a medium recycling system and the PPt/R ratio suggests that the systems are immature.
 471 Any comparison between the ENAs of different models should be performed with caution because
 472 some indicators are specific to the topology of the model, such as the number of functional groups and
 473 the distribution of species (Heymans *et al.*, 2016). Table 4 presents the ENA of similar ecosystems
 474 characteristics, i.e. coastal and sandy sediment in order to place the results in context.

475 *Table 4: Comparison of indices of network analysis for various French estuary ecosystems reef deployment put in context*
 476 *with other Ecopath models. N (number of functional group), Total System Throughput (T., gC.m-2. Year-1); Ascendency (A,*
 477 *flowbits); System Omnivory Index (SOI, %), Finn Cycle Index (%), Biomass total (excluding detritus) (Bt, gC.m-2. Year-1), Total*
 478 *primary production/total respiration (PPt/R), Total biomass/total throughput (B/T..) and Total primary production/total*
 479 *biomass (PPt/B)*

| Ecosystem | BAR Landes Coast | AAR Landes Coast | Seine estuary (France) | St Michel bay (France) | Loire estuary (France) | Gironde estuary (France) | Galicia coast (Spain) | Lithuanian coast |
|-----------|------------------------|------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|-------------------------------|------------------------------|
| Reference | This study | This study | Selleslagh <i>et al.</i> , 2012 | Selleslagh <i>et al.</i> , 2012 | Selleslagh <i>et al.</i> , 2012 | Selleslagh <i>et al.</i> , 2012 | Paradell <i>et al.</i> , 2020 | Tomczak <i>et al.</i> , 2009 |
| N | 23 | 23 | 15 | 19 | 19 | 18 | 23 | 12 |
| T.. | 379 | 413 | 3603.22 | 376.00 | 635.35 | 744.30 | / | 900 |
| A | 401 | 465 | 3944.3 | 451.6 | 647.0 | 939.5 | 1239 | 1084 |
| SOI | 0.36 | 0.302 | 0.11 | 0.06 | 0.12 | 0.12 | 0.205 | 0.059 |
| FCI | 13 | 13 | 16.10 | 0.64 | 0.19 | 3.99 | 19.4 | 2.55 |
| Bt | 5 | 6.33 | 22.30 | 7.20 | 4.14 | 2.12 | / | 20.98 |
| PPt/R | 1.5 | 1,2 | 1.37 | 6.10 | 139.59 | 1.05 | 1.758 | 3.397 |
| B/T.. | 0.013 | 0.015 | 0.01 | 0.02 | 0.01 | 0.003 | 0.017 | 0.023 |
| PPt/B | 17.01 | 13.35 | 38.26 | 24.60 | 76.26 | 21.52 | 18.34 | 18.351 |

480

481 **4 Discussion**

482 **4.1 Structural comparison with natural reef**

483

484 ARs have been mainly deployed to mimic the ecological functionalities of natural reefs and/or sustain
 485 artisanal fisheries (Pioch, 2008, Salaün *et al.*, 2022a). Over the past decade, studies of ARs have been
 486 focused on demonstrating their real contribution to the production of commercial fishes in the context

487 of fish assemblage analysis; their similitude to natural reef assemblages has been defined as a goal to
488 reach (Simon *et al.*, 2013; Perieira *et al.*, 2016; Streich *et al.*; 2018, Wu *et al.*, 2019). The results of
489 this study showed that fish assemblages of ARs are dominated by piscivorous, planktivorous and
490 benthos feeder fish (representing 86 % of the total biomass). This range of results is similar to other
491 studies conducted in the Mediterranean Sea (Cresson *et al.*, 2017; Koeck *et al.*, 2014; Leitao *et al.*,
492 2013) but also in the Yellow sea, South-West Atlantic and the Pacific (Wu *et al.*, 2019; Hackradt *et*
493 *al.*, 2011; Smith *et al.*, 2016; Hylkema *et al.*, 2020). However, despite the similarity with other fish
494 assemblages in ARs system, it seems weak to use this indicator to assess the efficiency of ARs.
495 Firstly, in this study, the comparison with natural reef were not possible because the study site is
496 surrounded by soft-bottom and the first natural reef is 20km away and represents a rocky shore
497 ecosystem (Castège *et al.*, 2016).
498 Secondly, there is no consensus among the scientific community about using fish assemblages to
499 indicate whether ARs are successful in acting as natural reefs. Some studies highlight the performance
500 of ARs in providing the same assemblage as a natural reef over a short period of time (Wu *et al.*,
501 2019). However, other studies conclude that equivalence cannot be achieved on a long time scale (100
502 years) (Simon *et al.*, 2013). Besides, this criterion of performance seems to be influenced by other
503 parameters such as the size of the ecosystem, as well as the localisation, substrate features and
504 roughness of the habitat (Lopez de Oliveira, 2016). But remarkably, it seems that the distance between
505 ARs and natural reefs does not impact the fish assemblage of ARs. (Simon *et al.*, 2013).
506 Therefore, to provide robust indicators, scientific studies highlight the need to use functional
507 approaches to provide indicators to assess the effects of ARs on communities (Cresson *et al.*, 2014). In
508 this way, trophic network studies, isotopic analysis and modelling approaches provide functional
509 description of ARs system based on biomass evolution and this criterion could be used to assess the
510 ARs productivity to support fisheries (Roa-Ureta, *et al.*, 2019; Cresson *et al.*, 2019; Smith *et al.*, 2016;
511 Mavraki *et al.*, 2021).

512

513 **4.2 Functional evolution using biomass indicators**

514

515 The deployment of three types of ARs along the Landes coast offered new hard substrates for sessile
516 fauna, notably invertebrate filter feeders, thus promoting their development within the ecosystem
517 (Raoux, 2017; Cresson, 2013). The benthic community of the BAR system is mainly composed of
518 benthic detritivorous species (41 %) with a small proportion of filter-feeder organisms (16 %). The
519 fish assemblage is dominated by planktivorous and piscivorous fish. With the deployment of ARs, the
520 total biomass of the system is increased by 14 %. Filter feeders become the predominant benthic taxa
521 in the system (62 %). This result needs to be qualified by the fact that the biomasses of filter feeders is
522 calculated by the model.

523 The presence of filter feeders and grazer communities on ARs is considered essential to transfer the
524 energy from the water column to the macro-invertebrates and fish communities (Bortone *et al.*, 2000).
525 Their dominance in the benthic community has been demonstrated by various studies on artificial
526 structures (Cresson, 2013; Boaventura *et al.*, 2006; Wetzel *et al.*, 2014). The dominance of filter
527 feeder species such as barnacles and mussels has been described as an initial condition for the
528 colonization of artificial structures before the establishment of a more heterogeneous community
529 (Boaventura *et al.*, 2006; Wetzel *et al.*, 2014, Cresson, 2013, Monteiro and Santos, 2000). A similar
530 benthic composition was expected for the ARs on the Capbreton site.

531 We find a major difference in the composition of the benthic community compared to other artificial
532 structures such as offshore wind farms (OWF). On OWF foundations located in the Baltic Sea, the
533 biomass of blue mussels is totally predominant and accounts for more than 97 % of the total biomass
534 of the benthic fauna (Maar *et al.*, 2009). The enhanced concentration of blue mussels observed on a
535 pillar near the surface is about 7 to 18 times higher than on scour protection (Maar *et al.*, 2009). A
536 very different composition is found on the studied ARs along the Landes coast, where the mussel
537 biomass is very low and represents less than 1 % of the invertebrate filter feeders. This major
538 difference could be explained by the distinct difference in size between the two structures and the
539 different environmental context (Degraer *et al.*, 2020). While OWFs make use of monopiles placed on
540 a soft bottom habitat and which reach up to the sea-surface, ARs do not reach the surface and have
541 little influence on the water column (in this study, ARs have a height of around 2.6 m). Besides, the
542 Baltic Sea bottom is covered by extensive blue mussel beds, whereas, along the Landes coast, the
543 nearest mussel beds are located at distances of 3 km and then 20 km from the Capbreton Artificial
544 Reef study site (Figure 1). Therefore, the larval flow of mussels is reduced. Compared to OWFs, the
545 small effect on filter feeder biomass is due to the light colonization of this species (blue mussel) from
546 the water column (Degraer *et al.*, 2020). Instead of blue mussels, another trophic competitor has
547 colonized the Capbreton ARs: barnacles account for around 52 % of benthic community on ARs.
548 Despite of the presence of barnacle, in comparison with other similar ARs, the filter feeder biomass
549 still is lower by a factor of 10 (Wetzel *et al.*, 2014).

550 The benthic fauna represents the primary prey of reef fishes. As the benthic fauna increases, it is
551 expected that fishes will come to feed on the ARs and thus contribute to increase in production around
552 ARs (Fabi *et al.*, 2006). However, we need to analyse gut contents to confirm this hypothesis. Indeed,
553 some species such as planktivorous fish, do not feed on the ARs benthic fauna, but can nevertheless be
554 attracted onto ARs by the zooplankton exposure due to the ocean (Cresson *et al.*, 2019). A similar
555 study conducted in Hong Kong simulated the reef effect after the implantation of ARs (Pitcher *et al.*,
556 2002). With ARs covering 3 % of the Marine Protected Areas of Hong Kong, the fish biomass is
557 estimated to have increased by 30 % corresponding to 247 t (Xu *et al.*, 2019). In the current study,
558 ARs represent 11 % of the studied area that could be taken as equivalent to an MPA because of the
559 restricted access established over the entire area. The fish biomass has increased by 67 %, but this

560 represents only 460 kg. Based on the biomass evolution between BAR and AAR system, the increase
561 of benthic fauna and fish community could be interpreted as a success of ARs biomass production.
562 Nevertheless, ARs are known to have attraction function, and their contribution to biomass production
563 may be local (Cresson *et al.*, 2019). Exploring the bottom trawl survey data carried out by IFREMER
564 in the Bay of Biscay in 2016, using a proximal trait to the study site (7km), and compare it to the BAR
565 data (from the same IFREMER survey but in 1999-2002), the results showed little biomass variation
566 that could be an increase or decrease depending on the species (e.g. *Trachinus Draco*: -3%). This
567 comparison, using only one data campaign, supports the local trends in ARs contribution.
568 The comparison with other ARs systems could give a scale of effectiveness but need to integrate local
569 characteristics. Several factors could influence the biomass production of fish and epifauna: reef
570 shape, size, volume, relief, roughness, substrate composition, kelp density, invertebrate density, reef
571 age, proximity to natural reefs and larval supply (Granneman *et al.*, 2015, Moschella *et al.*, 2005;
572 Baine, 2001; Abelson *et al.*, 2002). The complexity of a module is a function of its shape, roughness,
573 porosity and the size of cavities that it contains (Riera, 2020). An indicator was used to classify
574 modules in function of their objective and the fauna characteristics. Two of the three ARs deployed in
575 the present study can be characterized as follows (following Bouchard, 2018):
576 1) The Bonna pipe module is described as a “box” structure with a large hole on the top and a small
577 hole at the side. The surface specific deployed seems sufficient for settled benthic fauna and to provide
578 wide shelter for demersal fishes.
579 2) The Typi module is a « cage » type structure that is not suitable for demersal fishes because of the
580 lack of shelters. The size and the volume of these modules deployed in the studied area (102 m² and
581 830 m³) may be too small to sufficiently enhance biodiversity and biomass (Hackradt *et al.*, 2011).
582 Environmental criteria also influence the efficiency of ARs. In fact, the diversity of fauna communities
583 depends on the larval flow and is affected by ocean dynamics and the connectivity with other hard
584 substrates (Svane and Petersen 2001; Koeck *et al.* 2011, De Bie *et al.* 2012). As already highlighted,
585 the studied sector is 20 km away from a natural rocky habitat. But the shipwrecks and harbour
586 channels near the studied area act as transitory hard substrates which could ensure the connectivity
587 between these features (Pastor, 2008). The site is not only subject to local upwelling carrying primary
588 producers but also intensive storms that damage reefs by smoothing (Hylkema *et al.*, 2020). All these
589 local factors make it difficult to compare the productivity based on the biomass indicator between
590 different ARs at various localities (Baine, 2001).

591

592 **4.3 Ecological Network Analysis provide new indicators to assess ARs effectiveness**

593

594 The changes in ecosystems over time can only be described when ecosystem topologies remain
595 similar. The Before/After analysis used in our study has the advantage of providing two similar
596 ecosystem topologies for the Ecological Network Analysis (ENA). ENA provides indicators that

597 enable us to link the ecosystem structure and its functionalities (Ulanowicz, 1986). Then, these
598 evolving trends can be compared to other types of ecosystems. In our study, the trends in Total
599 ecosystem activity and Ascendency (A) between the two periods show an increase of approximately 9
600 and 16 %, respectively (Table 5). These rising rates are similar to those simulated in the English
601 Channel for a system before and after OWF deployment (Raoux *et al.*, 2017). Conversely, the System
602 Omnivory Index (SOI) decreases between the two periods, and this trend was also observed in
603 Laizhou Bay following AR deployment (Table 4). Finally, the results also highlight that Finn's
604 Cycling Index remains mostly stable between the two periods.

605 Results concerning the other ecosystem attributes show that the ratios PPt/R, PPt/B and the B/T.. vary
606 between the two systems, but this is not the case for the simulation of ARs deployment in Bohai Bay
607 (Table 5). In fact, the PPt/R ratio decreases between the BAR model and the AAR model by
608 approximately 20 %. This trend is also observed in Laizhou Bay as well as in the English Channel, but
609 is the opposite of the change occurring in the ecosystem of the Yellow sea with OWF deployment
610 (Table 5). A similar pattern is observed for the PPt/B ratio, which shows a decrease of approximately
611 22 % between the BAR model and the AAR model (Table 5). By contrast, the B/T.. increases between
612 the BAR model and the AAR model by approximately 15 %, in accordance with the change in the
613 ecosystem of the English Channel (Table 4).

614 The maturity of a system can be assessed using several indices. The PPt/R index is the ratio between
615 the energy used for biomass production (total primary production) and the energy used for maintaining
616 stability of the system (total respiration) (Christensen *et al.*, 2005). When the system is growing,
617 generally in a "young system", production exceeds the respiration and the PPt/R index is higher than
618 unity. On the contrary, when the system is mature, the system tends to balance the use of energy
619 related to both production and consumption (Odum, 1969). The B/T.. ratio is an index that increases
620 with the maturity of the system. Regarding these indicators used by Odum (1969), there is a good
621 correlation between the decrease in PPt/R, PPt/B, net community production and the increase of B/T
622 (Table 5). Since there are identical input data of primary producers in both models, the PPt/R and
623 PPt/B metrics inevitably decrease, because the primary production stays the same whereas biomass
624 increases. The B/T.. ratio, which is not directly related to primary production, could better be used in
625 this study to describe the change in maturity of the system. Thus, the B/T.. ratio shows an increase in
626 system maturity with the deployment of ARs. Mature and young systems have been described by
627 Odum (1969) as extreme opposites of an ecosystem. While young systems are characterized by
628 production in terms of growing and abundance, mature systems yield indicators, such as B/T... but also
629 A and SOI index, that reflect the stability of a complex web-like system. The increase of system
630 maturity showed by B/T.. is confirmed by the Ascendency increase (Ulanowicz, 1997) and the SOI
631 index trend that indicates evolution to a more complex system (Libralato, 2008). Thus, in our case,
632 the deployment of ARs changes the structure of the ecosystem towards a more complex system and its
633 functionality towards a more stable system.

634 However, the study is based on observation of the last two years of the benthic community and ten
635 years of fish assemblages. By averaging ten years of surveys, we can smooth out the inter-annual
636 variations in biomass. While communities associated with ARs could rapidly become a stable system
637 (Scarcella *et al.*, 2015), the ARs of Capbreton could have been a production system during the initial
638 period before becoming more mature. Compared to other trophic modelling simulations on ARs (Guan
639 *et al.*, 2016; Xu *et al.*, 2019) or other artificial structures such as OWFs, (Raoux *et al.*, 2017), the
640 increase of maturity seems to be a criteria of reef effect based on the B/T., PPt/R or PPt/B metrics
641 (Table 5). In addition, Wang *et al.*, (2019) used the System Omnivory Index to measure the increase of
642 maturity with OWF deployment in the Yellow Sea. This index describes the complexity of the system
643 and also provides the characteristics of a mature stage (trophic food chains represented as a web-like
644 system).

**Références
for Ecopath
models**

This study

Guan et al 2016

Xu et al., 2019

Wang et al. 2019

Raoux et al., 2017

| <i>Models</i> | BAR | AAR | | BAR in Bohai Bay | Simulation of AR in Bohai Bay | | BAR in Laizhou* | AAR in Laizhou* | | Before OWF in Yellow sea* | OWF in Yellow sea * | | Before OWF in English channel | Simulation of OWF in English channel | |
|------------------------|-------|-------|-------|------------------|-------------------------------|---------|-----------------|-----------------|-------|---------------------------|---------------------|-------|-------------------------------|--------------------------------------|----------|
| <i>Number of group</i> | 23 | 23 | / | 13 | 13 | / | 13 | 17 | / | 14 | 14 | / | 37 | 37 | / |
| <i>T..</i> | 379 | 413 | +9 % | / | / | / | 4721,2 | 3924,49 | -17 % | / | / | / | 1607,62 | 1831,93 | +13,95 % |
| <i>A</i> | 401 | 465 | +16 % | / | / | / | / | / | / | 7 195 | 8677 | +21% | 1869,1 | 2156,9 | +15,40% |
| <i>SOI</i> | 0,36 | 0,302 | -16% | 0,0379 | 0,0379 | 0% | 0,23 | 0,188 | -18% | / | / | / | 0,173 | 0,199 | +15,03% |
| <i>FCI</i> | 13 | 13 | 0% | 0,25 | 0,25 | 0% | 9,035 | 16,84 | +86% | 3,899 | 8,448 | +117% | / | / | / |
| <i>PPt/R</i> | 1,5 | 1,2 | -20% | 3,1088 | 3,1087 | 0% | 1,724 | 0,665 | -61% | 1,47 | 1,784 | +21% | 1,72 | 1,12 | -34,88% |
| <i>B/T..</i> | 0,013 | 0,015 | +15% | 0,0105 | 0,0105 | 0% | 0,01 | 0,045 | +350% | / | / | / | 0,03 | 0,04 | +33,33% |
| <i>PPt/B</i> | 17,01 | 13,35 | -22% | 42,399 | 42,3987 | -0,001% | 27,54 | 3,145 | -89% | 52,281 | 67,737 | +30% | / | / | / |

645

646 *Table 5: Comparison between ENA indicators of Before/After analysis with other Ecopath models. Total System Throughput (T., gC.m-2. Year-1; * t.km-2. Year-1); Ascendency (A, flowbits);*
 647 *System Omnivory Index (SOI, %), FCI (%), Total primary production/total respiration (PPt/R), Total biomass/total throughput (B/T..) and Total primary production/total biomass (PPt/B)*

648

649 Others model parameters also help us understand the functioning of AR systems. Ascendency
650 represents the level of the system activity and its organization (Ulanowicz, 1986). The increase of
651 Ascendency also indicates a higher activity in the system, which is characteristic of a maturity stage
652 (Ulanowicz, 1997). Regarding the modelling of Wang *et al.*, (2019) and Raoux *et al.*, (2017), this
653 parameter increases respectively after eight and thirty years of OWF deployment. This result should be
654 qualified by the unchanged value of the FCI (percentage of all flow in the system) before and after AR
655 deployment (Finn, 1980). Thus, the low boosting of activity corroborates the local effect of ARs on
656 the Capbreton site, without any strong modification in the system structure and functioning.

657
658 The indicators suggested to detect changes in ecosystems in this study are based on studies conducted
659 to highlight the relevant ENA indicators (Safi *et al.*, 2019; Fath *et al.*, 2019). By analysing the
660 ecosystem functioning and structure, ENA provides holistic indicators to assess the impact of human
661 activities and environmental management measures such as ARs deployment. In fact, the ecological
662 effects expected from the deployment of ARs were listed by Claudet and Pelletier (2004), but no
663 details were given about the quantified objectives to be attained. As a result, only indicators showing
664 the trend of the system towards the general objectives could be used by managers to monitor the
665 performance of ARs. Coupled before/after analysis with trophic modelling approach allows indicators
666 that reveal structural and functional changes in the ecosystem with ARs deployment and could be used
667 by managers to assess the effectiveness of ARs.

668 The growth in the use of the trophic modelling approach reflects the emerging need for indicators for
669 managers (Heymans *et al.*, 2016; Pezy *et al.*, 2017; Raoux *et al.*, 2017; Guan *et al.*, 2016; Wang *et al.*
670 2019; Xu *et al.*, 2019; Prato *et al.* 2016; Valls *et al.* 2012; Hermosillo-Núñez *et al.*, 2018). The current
671 study is embedded in this approach, with the aim of highlighting the effect of AR deployment on
672 ecosystems.

673

674 **4.4 Limitations of the trophic modelling approach**

675

676 Trophic modelling is based on large amounts of biological data for each functional group chosen.
677 Besides, diet is a key parameter in the trophic modelling approach. In this study, the BAR model is
678 largely inspired by the data selected from coastal areas of the southern part of the Bay of Biscay
679 (Lassalle *et al.*, 2011) and information on diet is drawn from the literature. In this study, the models
680 were based on available data as proximate to the study as possible that lead to differences in the
681 sampling efficiency (such as between bottom trawl data and scuba diver surveys) and the period
682 covered up. As a consequence, our trophic models should be considered as a first approach to
683 providing an overview of the evolution of AR systems. Artificial reefs are known to attract a high
684 abundance of fish, which could potentially increase the local production. Thus, there is a need to
685 investigate the feeding ecology and trophic diet of fish that occur abundantly on artificial reefs by

686 analysing stable isotopes and stomach contents to examine the short- and long-term trophic diet
687 composition (Bentorcha *et al.*, 2017).

688 The difficulty and cost of such extensive data collection could be an obstacle when applying the
689 trophic approach to coastal management. Prato *et al.* (2014) suggested carrying out a prior survey of
690 the most important and less documented functional groups. In this how, we chose to focus on benthic
691 invertebrates and fish biomass surveys and fixed the upper and lower trophic groups biomasses.
692 Consequently, the direct biomass trends of these groups could not be analysed. However, they still
693 were integrated in the trophic modelling as a part of the system, and the flows tendencies were
694 investigated.

695 Finally, ENA is clearly dependent on the model structure and comparisons between trophic models
696 could be hazardous (Prato 2016; Fath *et al.*, 2019; Christensen *et al.*, 2005). Equivalent models need to
697 be favoured to assess the effect or evolution of coastal management tools within the ecosystem, i.e.
698 models based on the same number of functional groups and the same composition of these groups.

699

700 **5 Conclusion**

701

702 The ARs assessment still remains a challenge for marine managers who are required to monitor the
703 objectives of maintaining or enhancing fisheries production, with the aim of readjusting human
704 pressures on the ecosystems (Salaün *et al.*, 2022a). At the same time, trophic modelling has been
705 developed over many decades and applied to monitor various marine ecosystems around the world.
706 This approach has been used to understand the effect of fisheries on the entire ecosystem. Recently, it
707 was extended to other research domains such as the management of MPAs (Hermosillo-Núñez *et al.*,
708 2018) and the simulation of the effect of OWFs on the ecosystem (Raoux *et al.*, 2017; Pezy *et al.*,
709 2017). Our study represents a new investigation of the use of trophic modelling, based on a
710 comparison of the system before and after the deployment of ARs.

711 Like OWFs, ARs are mostly deployed on soft bottom habitats. So, they create hard substrates that
712 become colonized by various communities. With the deployment of ARs, the total biomass of the
713 system increases and the dominant fauna changes from detritivores to invertebrate filter feeders.
714 However, the reef effect is restricted to its vicinity and the low increase in biomass should rather be
715 linked to the environmental context of the studied area (a sandy coast with low connectivity with hard
716 substrates). In this case, the deployment of ARs has little influence on the ecosystem structure and
717 biomass production.

718 By using ENA metrics on AR systems, it is possible to highlight the trophic modifications linked to
719 the introduction of hard substrates on soft habitats. Our study highlights a positive effect with an
720 increase in system maturity through ARs deployment; this finding has emerged by using ENA
721 indicators, such as B/T., PPt/R, PPt/B and SOI. In accordance with other studies, this related change

722 in maturity seems to be a criterion reflecting the effect of artificial structures. Thus, our results
723 demonstrate the interest of using a large set of ENA indicators to characterize different trophic
724 functioning attributes. This is essential for an effective overview of the induced changes. By the end,
725 ENA provides indicators that could be used by managers to monitor the temporal colonization and
726 evolution of ARs, and assess performances objectives, to appreciate the pertinence of their
727 deployment.

728 **6 Acknowledgements**

729
730 This work was co-funded by the National Association for Technical Research and Atlantique Landes
731 Récifs (ALR). For their help in compiling the datasets and giving expert advice, we also acknowledge:
732 Eric Charbonnel, Philippe Lenfant, Nelly Ferrou-Rocher, Andréa Bayens, and all ALR volunteers.
733 Dr M.S.N. Carpenter post-edited the English style and grammar.

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