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Before-After analysis of the trophic network of an experimental dumping site in the eastern part of the Bay of Seine (English Channel)

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ABSTRACT

3 An experimental study was conducted to assess the physical and biological impacts of muddy fine sand
4 dredged material dumped on a medium sand site MACHU offshore the Seine Estuary. Complementary
5 trophic web modelling tools were applied to the MACHU ecosystem to analyse the effects of dumping
6 operations. Results show that, after the dumping operations, the biomass of fish increased while
7 invertebrate biomass remained relatively stable through time. Nevertheless, the biomasses of benthic
8 invertebrates, omnivores/scavengers and predators showed some increases, while non-selective
9 deposit feeders and filter feeders decreased. At the ecosystem level, results show that the total
10 ecosystem activity, the ascendancy and the overall omnivorous character of the food-web structure
11 increased after dumping operations, whereas recycling subsequently decreased. Finally, the fine and
12 medium sand habitat offshore from the Seine estuary, which undergoes regular natural physical
13 perturbations, shows a high resilience after a short dumping phase.

Keywords: Ecopath; trophic model; Ecological Network Analysis; dredged material disposal; Bay of Seine

1. Introduction

14

15 To enable their economic development, harbours are required to maintain their maritime access
16 conditions. The need for dredging has resulted from increased marine transportation requirements
17 and vessel size, and modifications in the sedimentation patterns of estuaries and rivers due to harbour
18 and industrial developments as well as urbanization (Messieh et al., 1991; Marmin et al., 2014). As a
19 consequence, navigation channels are regularly dredged to ensure sufficient depth for a large variety
20 of vessels including the largest container ships. According to their low chemical hazard for the
21 environment, dredged materials have been mainly disposed of on sea often outside marine protected
22 areas, by overflowing during dredging, dumping in authorized zones or brought ashore for storage or
23 treatment (Marmin et al., 2014). Deposition on land remains an alternative which is obligatory for
24 contaminated sediment but which requires large storage spaces not used by other human activities.
25 In the case of 'clean' sand sediment (i.e. without high % of mud), the dredged material can be used for
26 the creation of artificial wetland areas or beach nourishment. However, nowadays, for economic
27 reasons, most dredged material is disposed of in coastal zones in open water (Marmin et al., 2014).

28 The Seine estuary is one of the main estuaries on the northwest European continental shelf and is
29 economically important for France, due to the presence of two maritime harbours: Grand Port
30 Maritime du Havre (GPMH) at the entrance of the estuary and the upstream Grand Port Maritime de
31 Rouen (GPMR). The watershed of the Seine covers an area of $\sim 79,000 \text{ km}^2$ with a population of ~ 16
32 million inhabitants, accounting for $\sim 50 \%$ of the river traffic in France, $\sim 40 \%$ of the country's economic
33 activity and $\sim 30 \%$ of its agricultural activities (Dauvin, 2006). The GPMR, which is the most important
34 French inland harbour, is located in the freshwater part of the Seine estuary at $\sim 120 \text{ km}$ from the sea.
35 Its access is ensured by regular maintenance and permanent dredging of the navigation channel,
36 mainly in the lower part of the Seine estuary between the Normandy Bridge and the open sea. Each
37 year, the GPMR dredges between 4 and 4.5 million cubic meters of sediment, which is dumped on the
38 disposal site called Kannik commissioned in 1977 in the Northern Channel of the Seine estuary (Marmin
39 et al., 2014, 2016) (Fig. 1). Moreover, the GPMH dredges between 2 and 2.5 million cubic metres of
40 sediment each year in the harbour basins and deposits this material in an offshore deposit zone named
41 Octeville (Fig. 1) (Marmin et al., 2014).

42 The dumping of dredged material represents one of the most important problems in coastal zone
43 management and leads to a major disturbance of the environment (Marmin et al., 2014). The type and
44 severity of the impact of dumping of dredged material on benthic macrofauna depend on many
45 factors: 1) the physico-chemical characteristics and the volume of sediment deposited; 2) the physical
46 conditions of the depositional environment: water depth, sediment and hydrodynamic regime; 3) the
47 season and the similarity between sediment of the dredging area and in the dumping area; 4) the

48 contamination of dredged materials; 5) the methods of dumping; 6) the adaptation of organisms to
49 the local sedimentary regime and 7) the structure and composition of the benthic community in the
50 dumping area and neighbouring sites (Marmin, 2013). Furthermore, numerous studies have been
51 conducted to investigate the effects of dumping on benthic macrofauna (for example see Van Dolah
52 et al., 1984; Harvey et al., 1998; Roberts et al., 1998; Smith and Rule, 2001; Witt et al., 2004). In many
53 cases, these studies focused on the structure of benthic invertebrate communities to assess the
54 impacts and/or recovery from this activity, i.e. the resistance and resilience of benthic habitats to the
55 stress due to the sediment deposit. Few studies dealt with the assessment of functional changes of
56 such benthic habitats (Wilber et al., 2007; Bolam et al., 2011; Bolam, 2012; Bolam et al., 2016). In
57 addition, dumping operations can generate negative impacts on fish eggs and larvae: i.e. Messieh et
58 al. (1991) showed that sediment deposited on herring spawn increase egg mortality. Changes in
59 species composition can be observed, and this has an impact on the food-web structure and
60 functioning (Messieh et al., 1991).

61 Under European Union pressure, the French administration and non-governmental environmental
62 protection organizations require that maritime harbours take account of the Integrated Coastal Zone
63 Management (ICZM) of the Seine estuary in the context of their economic development project
64 (Marmin et al., 2014). Among the requests, the Scientific Committee of the Seine Estuary (SCSE), which
65 was created in 2008 to help the French State and port authorities to promote the sustainable
66 development of the Seine estuary, has asked the GPMR to find a new sediment dumping area outside
67 the Seine estuary.

68 The SCSE studies led to validation of the Machu site, composed of fine to medium sand located in
69 the eastern part of the Bay of Seine (Marmin, 2013; Marmin et al., 2014, 2016) (Fig. 1). In 2012-2013,
70 experimental dumping operations were carried out to better understand the impacts of the deposition
71 of sediments from the navigation channel onto the morphosedimentary seabed and benthic habitats
72 of the Machu site using a Before-After-Control Impact approach (Marmin, 2013; Marmin et al., 2014,
73 2016).

74 In this study, we develop a holistic view of the impact of dumping operations on ecosystem
75 functioning through the use of trophic web modelling tools. Trophic models describe the interaction
76 between biological compartments at different trophic levels and are based on the quantification of
77 energy flow and matter in ecosystems. These models make use of numerical methods to characterize
78 the emergent properties of ecosystems, by application of Ecological Network Analysis (ENA)
79 (Ulanowicz, 1986). This type of joint analysis has been frequently applied to coastal and marine
80 systems to assess changes in their functioning in response to environmental perturbations (Ortiz and
81 Wolff 2002; Rybarczyk et al., 2003; Niquil et al., 2012; Tecchio et al., 2013, 2015). ENA indices have

82 also been proposed as trophic descriptors of ecosystem health for the EU Marine Strategy Framework
83 Directive (Niquil et al., 2012; Niquil et al., 2014).

84 Various modelling studies related to the eastern part of the Bay of Seine and the Seine estuary
85 have been implemented over the two last decades. The structure and functioning of the Seine estuary
86 was investigated by Rybarczyk and Elkaim (2003), who considered it as a single spatial compartment
87 and then by Tecchio et al. (2015; 2016), who divided it into six spatial compartments.

88 Assuming that dumping operations represent a stress for the ecosystem, such as other natural and
89 anthropogenic stresses (granulate extraction, fish trawling, harbour works, etc.), we use the ENA
90 approach here to test its efficiency in detecting functional changes of benthic habitats. Thus, this study
91 is focused on the following objectives: 1) to characterize the trophic network of the Machu site before
92 experimental deposition, 2) to determine the effect of sediment dumping on the structure of the food
93 web, and thus 3) to evaluate the interest of the ENA approach in a context of inherently stressed
94 environments. To address these questions, several ECOPATH models are constructed which are
95 defined and described in the following sections.

96

97 **2. Materials and methods**

98

99 *2.1. Study area*

100 The Bay of Seine forms an approximate quadrilateral of 5,000 km², with water depths never
101 exceeding 30 m. In this macrotidal environment (tidal ranges of up to 7.5 m at Le Havre), tidal currents
102 average between 1 and 2 knots in the southern sector of the bay, and their intensity gradually
103 diminishes towards the eastern part of the Bay of Seine (Salomon and Breton, 1991, 1993). These
104 currents play an essential role in the distribution of sediments (Larsonneur et al., 1982) and benthic
105 communities (Gentil and Cabioch, 1997). Lesourd (2003) provided the last map of sedimentary facies
106 across the eastern Bay of Seine before the 'Port 2000' construction (2002-2005), and identified an
107 offshore-inshore gradient; the offshore sediments generally consist of gravel and coarse sand, while
108 sediments just at the mouth of the Seine Estuary, are mainly fine sand and silty/muddy fine sands.
109 Moreover, seasonal variations in the sedimentary regime in the mouth of the macrotidal Seine estuary,
110 are described in Lesourd et al. (2003). The most recent map of the distribution of superficial sediments
111 in the mouth of the Seine estuary and the eastern part of the Bay of Seine shows a high diversity of
112 facies mainly in the North Channel (Lesourd et al., 2016). A general overview shows: broad sand bars
113 on both sides of the entry of the navigation channel; extensive development of sandy mud facies (25
114 to 75% of silt and clay); an area of muddy sand facies juxtaposing coarse sand in the shallower waters
115 of the Bay of the Seine and the persistence of medium sand in the offshore Machu area, with a weak
116 influence of fine particle coming from the estuary.

117 The chosen Machu experimental disposal site is located in the eastern part of the Bay of Seine (Fig.
 118 1) at a mean water depth of ~ 20-25 m. Two million cubic metres of dredged sediment coming from
 119 the maintenance of the navigation channel of the Seine estuary were dumped on the experimental
 120 disposal area in 2012-2013 (Marmin et al., 2016). The first million cubic metres were deposited
 121 between May 13th 2012 and December 15th 2012 on the MASED site (Fig. 1). This site corresponds to a
 122 single point forming a conical deposit equivalent to 7 months of dumping activities. A second million
 123 cubic meters of sediment was deposited between 16th April 2012 and 21th February 2013 on the MABIO
 124 site (Fig. 1). The dumping operations were carried out four times, corresponding to the deposition of
 125 250 000 m³ of sediment per season on rectangular area of about 100 ha (Marmin et al., 2016).

126

127 *2.2. Modelling approach*

128

129 The Ecopath with Ecosim (EwE) software suite (Polovina, 1984, Christensen and Walters, 2004,
 130 Christensen et al., 2008) is used here to model the food web at the Machu site before (2010-2011 data)
 131 and after (2013-2014) the dumping operations (spring 2012-winter 2013) to evaluate the impacts of
 132 short-term deposition on the food-web structure and functioning. The modelling suite is composed of
 133 three modules: Ecopath, which provides mass-balanced snapshot of the system, Ecosim, a time-
 134 dynamic extension and Ecospace, a temporal-spatial model. Ecopath is a mass-balance (i.e. neglecting
 135 year-to-year changes in biomass compared to flows), single-solution model (i.e. returning only one
 136 value per flow), that estimates flows between a set of established trophic compartments. Each
 137 compartment is parameterized using its biomass data (B , gC.m⁻²), its production to biomass ratio (P/B ,
 138 year⁻¹), its production to consumption ratio (P/Q , year⁻¹) or its consumption to biomass ratio (Q/B ,
 139 year⁻¹), and a diet matrix (DC_{ij}) which establishes the interactions between predators and preys in the
 140 system (Christensen and Walters, 2004).

141 The parameterization of an Ecopath model is based on satisfying two equations. The first equation
 142 (Eq. 1) describes the production for each compartment in the system as a function of the consumption
 143 to biomass ratio (Q/B) of its predators (j), the fishing mortality (Y_i , gC.m⁻²), the net migration (E_i ;
 144 emigration – immigration, year⁻¹), the biomass accumulation (BA_i , year⁻¹) and its natural mortality ($1 -$
 145 EE_i). The Ecotrophic Efficiency (EE) is the fraction of total production that is consumed in the system
 146 (by fishing activity or by predators). Its value can never exceed 1. $(1 - EE_i)$ represents the fraction of
 147 mortality not explained by the model, such as mortality due to old age or diseases.

$$148 \quad B \left(\frac{P}{B} \right)_i = \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ij} + Y_i + E_i + BA_i + B_i \left(\frac{P}{B} \right)_i (1 - EE_i) \quad (\text{Eq. 1})$$

149 The second equation (Eq. 2) describes the energy balance within a compartment, which expresses
 150 consumption (Q_i) as the sum of production (P_i), respiration (R_i , gC.m⁻²) and unassimilated food (U_i).

151
$$Q_i = P_i + R_i + U_i \quad (\text{Eq. 2})$$

152

153 *2.3. Functional groups*

154

155 The selection and aggregation of functional groups included in the Ecopath model is based on
156 the biological and ecological characteristics of the species or groups of species, such as their food
157 preference, as well as on data availability. On this basis, 15 functional groups are selected (Table 1, Fig.
158 2), including fish, seven invertebrate groups, zooplankton, primary producers, bacteria and detritus.

159

160 *2.3.1. Fish compartments*

161

162 Fish data were collected by the Cellule de Suivi du Littoral Normand (CSLN) from bottom otter
163 trawl surveys at night. The available data was collected from a total of 8 beam trawl campaigns carried
164 out before the dumping operations in April, July, October 2010 and in January 2011, and then after the
165 dumping operations in April, July, October 2013 and in January 2014. Fish were divided into 4
166 functional groups: piscivorous, demersal, benthic- feeding and planktivorous.

167 For each campaign, total biomasses in wet weight are divided by the number of individuals of
168 each species to obtain the individual wet weight. A conversion factor of 0.35 is used to convert both
169 wet weights into dry weights and into carbon contents (Boët et al., 1999). For each trophic
170 compartment, the mean biomasses were calculated. Q/B and P/B ratios are taken from Mackinson and
171 Daskalov (2007). The diet matrix is constructed mainly using the stomach contents given in literature
172 data from the eastern part of the English Channel (Cachera, 2013).

173

174 *2.3.2. Invertebrates compartments*

175

176 *2.3.2.1. Cephalopods*

177

178 Biomass data (in kg.km⁻²) for cephalopods were also obtained from beam trawl CSLN surveys.
179 Q/B and P/B ratios were taken from Sanchez and Olaso (2004). Diet compositions are compiled from
180 the literature (De Pierrepont et al., 2005; Daly et al., 2001).

181

182 *2.3.2.2. Benthic invertebrates*

183

184 Benthic invertebrates were sampled with a 0.1 m² Van Veen grab (three replicates at each
185 station). Before the dumping operations, the macrobenthos data were collected from the sampling of

186 17 stations in 2010-2011. The Machu habitat is associated with the medium-to-fine sand *Ophelia*
187 *borealis* community (Gentil and Cabioch, 1997), but is partially influenced by a mixing between *Ophelia*
188 *borealis* and *Abra alba-Lagis koreni* communities in its southern part (Marmin, 2013). The data after
189 the end of the deposition phase (spring 2013 to spring 2014) were collected by sampling 17 stations in
190 the Machu site (unpublished data). Species are grouped into 5 compartments:
191 “omnivores/scavengers”, “predators”, “filter feeders”, “selective deposit feeders”, and “non-selective
192 deposit feeders”. Ash-free dry weights are converted to carbon contents using a conversion factor of
193 0.518 (Brey, 2001). P/B and Q/B ratios are taken from Le Loc’h (2004) and Brey (2001), and diet
194 compositions from Rybarczyk and Elkaim (2003).

195

196 2.3.2.3. Meiofauna

197

198 The mean annual biomasses of meiofauna, as well as the P/B and Q/B ratios are obtained from the
199 literature for a similar sediment habitat in the English Channel (Rybarczyk and Elkaim, 2003; Garcia et
200 al., 2011).

201

202 2.3.3. Zooplankton

203

204 Mean annual biomasses of zooplankton are collected from another study focused on the Seine
205 Estuary (Rybarczyk and Elkaim, 2003). The P/B and Q/B ratios are obtained from the literature (Wang,
206 2005).

207

208 2.3.4. Bacteria

209

210 The benthic bacterial biomasses, as well as P/B and Q/B ratios are taken from Chardy (1987) and
211 McIntyre (1978) for a similar sediment habitat in the English Channel.

212

213 2.3.5. Phytoplankton

214

215 The phytoplankton biomass and P/B ratios are from Rybarczyk and Elkaim (2003) and Hoch (1998),
216 respectively.

217

218

219

220

221 2.2.6. Detritus

222

223 The mean annual biomass of dead organic matter is obtained from the formula of Pauly et al.
224 (1993).

225

226 *2.4. Balancing the Ecopath model*

227

228 The models are considered balanced when the EE values of each group is lower than 1 (i.e. mass
229 balance is reached) and no violations of energy balance are observed. We also check that physiological
230 rates are within the known limits for each functional group: i) P/Q of 0.1–0.3 for consumers, and ii)
231 respiration/biomass (R/B) ratios of 1–10 for fish groups. The EwE pedigree routine is used to quantify
232 the input parameter uncertainties (Christensen and Walters, 2004). It helps to identify the least certain
233 parameters that should be modified first to achieve mass balance. The balancing approach used here
234 is top-down, starting with the top predator groups and moving down the food web to smooth out
235 inconsistencies. When modifications of the data are required, diet compositions (DC) are modified
236 first, and then the P/B and Q/B ratios. Biomasses (B) are considered as less uncertain, and are thus
237 modified during the last step of the balancing process.

238 Biomasses of the small pelagic fish are left to be estimated by the model after setting their
239 Ecotrophic Efficiency at 0.93. The estimated biomasses are higher than the input data first entered
240 during model construction. This can be partly explained by the fact that the bottom-trawl deployed
241 during the CSLN survey was not fully adapted to capture these species, the abundance of which is thus
242 likely to be underestimated. The biomass of the meiofauna is also left to be estimated by the model
243 after setting their Ecotrophic Efficiency at 0.97.

244

245 *2.5. Analysing ecosystem organization, major interactions and emergent properties*

246

247 For the two Ecopath models (before and after the dumping operations), the trophic level of each
248 functional group is calculated from its diet composition matrix. It is computed as the weighted average
249 of the trophic levels of its prey, with primary producers and non-living material being set at a trophic
250 level of 1:

$$251 \quad TL_j = 1 + \sum_{i=1}^N DC_{ji} TL_i \quad (\text{Eq. 3})$$

252

253 where DC_{ij} is the fraction of the prey i in the diet of predator j .

254

255 Ecological Network Analysis (ENA) indices are calculated using the network analysis plug-in
256 included in *EwE* (Christensen and Walters, 2004). The following ENA indices are adopted:

- 257 • The Total System Throughflow (T..) is calculated as the sum of all the flows in the food web. It
258 characterizes the overall activity and measures the size of the ecosystem (Latham, 2006).
- 259 • The Transfer Efficiency (TE) is the fraction of total flows of each discrete trophic level that
260 throughput into the next level (Lindeman, 1942).
- 261 • Finn's Cycling Index (FCI) gives the percentage of all flows generated by cycling (i.e. the
262 percentage of carbon flowing in circular pathways) (Finn, 1980).
- 263 • The System Omnivory Index (SOI) is calculated as the average of the OIs of the individual group,
264 weighted by the logarithm of each consumer intake (Pauly et al., 1993, Christensen and
265 Walters, 2004). It is an indicator of the structure and complexity of the food web that measures
266 how the interactions are distributed among trophic levels (Christensen and Walters, 2004).
267 High values of SOI correspond to a web-like structure, whereas low values of SOI correspond
268 to a chain-like structure (Libralato, 2008).
- 269 • The ascendancy (A) is a measure of the system activity (Total System Throughput) linked to its
270 degree of organization (Average Mutual Information; AMI) (Ortiz and Wolff, 2002). This index
271 is related to the developmental status or maturity of an ecosystem (Ulanowicz, 1986).
- 272 • Relative redundancy (R/DC) measures the fraction of internal flows in proportion to total
273 development capacity. It corresponds to an indicator of the inefficiency of the network (Saint-
274 Béat et al., 2013) as it measures the number of parallel trophic itineraries connecting the
275 different trophic compartments (Rybarczyk and Elkaïm, 2003).

276

277 The Mixed Trophic Impact (MTI) routine is applied to evaluate the impacts of direct and indirect
278 interactions in the food web. This analysis shows the theoretical effect that a slight increase in the
279 biomass of one group would have on the biomasses of all the other groups in the system (Ulanowicz
280 and Puccia, 1990). The Keystoneness Index is calculated for each functional group, to identify those
281 groups having a high overall effect on the other groups compared to their relatively low biomass.
282 Calculations are performed according to the index defined by Libralato et al. (2005, 2006). The
283 Detritivory/Herbivory ratio (D/H) is the ratio between detritivory flows (from detritus to trophic level
284 II) and herbivory flows (from primary producers to trophic level II) (Ulanowicz, 1992). The ratio of
285 biomass of fish groups to the biomass of invertebrate groups is also calculated.

286

287

288

289 **3. Results**

290

291 The calculated Pedigree index for the models is 0.5.

292

293 *3.1. Structure and functioning of the ecosystem before dumping operations*

294

295 Phytoplankton is the dominant functional group in the biomass, representing 39.5% of the
296 total living biomass of the system (Table 1). The other major groups of the system are benthic
297 invertebrates, filter feeders (mostly composed of the Terebellidae Polychaete *Lanice conchilega*) and
298 non-selective deposit feeders (mostly composed of the sea urchin *Echinocardium cordatum*), making
299 up 22.6% and 17.6% of the living biomass, respectively.

300 The Trophic Level of the functional groups ranges from TL=1 for primary producers and
301 detritus, as imposed by construction, to a maximum of 4.4 for cephalopods that can be thus considered
302 as top predators in the area (Table 1). Demersal fish rank just below with a trophic level of 4.1. The
303 omnivorous feeding mode of the functional groups, estimated by the omnivory index (OI), is comprised
304 between 0.1 and 0.709. The groups with the highest OI values are cephalopods (OI =0.709), followed
305 by benthic invertebrate omnivores/scavengers (OI = 0.439) and demersal fish (OI = 0.435), while the
306 most specialized group is made up of planktivorous fish (OI = 0.0885).

307 The MTI analysis (Fig. 3) indicates that demersal fish exert a widespread influence on the
308 trophic web, due to the wide diversity of prey items. In fact, demersal fish negatively affect benthic
309 invertebrate selective deposit feeders, planktivorous fish and benthic-feeding fish. Other predators
310 such as cephalopods, also feeding on these compartments, respond negatively to an increase of
311 demersal fish biomass. The MTI analysis also shows that benthic invertebrate predators negatively
312 affect benthic invertebrates (non-selective and selective deposit feeders, omnivores/scavengers).
313 They also negatively affect cephalopods and benthic-feeding fish, which have some preys in common
314 with benthic predators.

315 The keystone index is highest for zooplankton (-0.145), benthic invertebrate predators (-
316 0.196) and demersal fish (-0.201) (Fig. 4).

317

318 *3.2 Ecosystem structure and changes of functioning after dumping operations*

319

320 After the dumping operations, the phytoplankton remains the dominant functional group of
321 the total living biomass of the system, followed by benthic invertebrates and filter feeders (Table 1).
322 The biomass of demersal fish (dominated by the pouting *Trisopterus luscus*), benthic-feeding fish
323 (dominated by the flatfish *Pleuronectes platessa*) and planktivorous fish (dominated by the mackerel

324 *Scomber scombrus*) increases by factors of 4.7, 8.4 and 6, respectively (Table 1). The biomasses of
325 benthic invertebrate omnivores/scavengers (dominated by the decapod *Liocarcinus marmoreus*) and
326 predators (dominated by the sea star *Asterias rubens*) also increase by factors of 3.3 and 3.5,
327 respectively (Table 1). By contrast, cephalopods and benthic invertebrate non-selective deposit
328 feeders show a strong decline with a 98 % and 66% reduction in their biomass, respectively (Table 1).
329 The biomass of cephalopods and benthic invertebrate filter feeders also decreases after the dumping
330 operation. Results also indicate the presence of a new functional group after the dumping operations,
331 i.e. piscivorous fish, but with a very low biomass of 0.0039 gC m⁻² (Table 1). The ratio of fish biomass
332 to invertebrate biomass increases approximately sevenfold between both periods (Machu After /
333 Machu Before). This is related to the strong increase in fish biomass that rises by a factor of
334 approximately 8 after the dumping operations, while invertebrate biomass remains relatively stable
335 through time.

336 The Keystoneness patterns show variations between the two periods (Fig. 4). Before the
337 dumping operations, zooplankton was the functional group with the highest keystone index, with
338 benthic invertebrate predators occupying the second rank followed by demersal fish. However, after
339 the dumping operations, the piscivorous fish became the functional group with the highest
340 keystone index (0.003), followed by the zooplankton (0.141) and cephalopods (-0.167). Benthic
341 invertebrate predators and demersal fish remain at a lower rank, since they occupy the fifth and the
342 fourth rank, respectively.

343 Between the two periods, the total ecosystem activity (T.), representing the sum of all flows
344 in the system, increases by 1.3% (Table 2). The System Omnivory index (SOI) increases by 13.34% (from
345 0.22 to 0.25) between the two periods, while Finn's Cycling Index (FCI) decreases by 16.4% (Table 2).
346 The ascendancy (A) increases by 0.7%. The relative redundancy and the detritivory/herbivory ratio
347 (D/H) remain stable between the two periods (Table 2). The transfer efficiencies (TE) show a similar
348 pattern between the periods, decreasing as a function of TL in both models (Fig. 5).

349

350 The system overall EE (the percentage of total production consumed by predators) increases
351 by 19.5% between the two periods (Table 1). For instance, the EE of Benthic invertebrate
352 omnivores/scavengers, filter feeders and non-selective deposit feeders increases by a factor of 1.5, 3,
353 and 6, respectively (Table 1).

354

355

356 4. Discussion

357

358 4.1- Effects of dumping operations on the sediments

359

360 The dumped muddy fine sand formed a conical pile at the MASED site and a wide and irregular
361 elongated dump mound at the MABIO site; in both cases, a depression due to the settling of dredged
362 material persisted at the sea bottom throughout the surveys (Marmin et al., 2016), this morphometry
363 can provide a favourable habitat for demersal fishes. The superficial sediments at the MACHU site
364 show a fining tendency with time due to the experimental deposition of estuarine sediments (with an
365 effect limited to 500 m around the impacted stations), but the stations surrounding the MACHU site
366 do not record any significant changes (Marmin et al., 2016). After deposition, during the year following
367 the survey, a small proportion (5-20%) of the accumulated material was lost, either due to erosion and
368 transport away from the site, or due to consolidation. At the same time, a progressive recovery of the
369 sea bed is suggested at some stations: the multimodal grain-size distribution reflects mixing of part of
370 the dumped sands with shelf material (Marmin et al., 2016).

371

372 4.2- Demersal fish and benthic response to dumping activities

373

374 For demersal fish, the four years of monitoring reveal an attraction for, or at least a higher
375 concentration of three flatfish species: *Solea solea*, *Pleuronectes platessa* and *Limanda limanda* at the
376 experimental site of Machu during and after the deposit operations. More particularly, the study of
377 demersal fish shows a high concentration of individuals belonging to these three flatfish species during
378 the experimental dumping and up to 9 months after cessation for *L. limanda* and up to 27 months for
379 *P. platessa*. The response to experimental dumping reflects a spatial differentiation, with an attractive
380 effect over the entire experimental area or over only a part. The morpho-sedimentary changes induced
381 by dumping therefore seem to create an attractive environment for *L. limanda*, *S. solea* and *P. platessa*
382 (adult fish of a year). This may occur for trophic reasons, including the input of macrozoobenthos
383 during dumping. The dumping operations generate a new source of food in the ecosystem. Possibly
384 due to the biomass modifications, EE values (the percentage of production consumed by predators) of
385 the whole ecosystem show an increase of 20.5%. The macrozoobenthos provided by dumping could
386 increase the fish predation.

387

388 For the benthic compartment, a small variation of biomass is observed between the different
389 trophic groups. However, taxa diversity and changes in communities are perceptible during the
390 experiment, as has been observed in several studies (Bolam et al., 2006; Ware et al., 2010). While 164
390 taxa are recorded at the Machu site, 102 taxa show a decrease in their abundance and 43 taxa are no

391 longer sampled after dumping. Conversely, after dumping, 57 taxa show an increase in their
392 abundance and 30 new taxa are recorded. This increase/decrease in abundance is the result of a
393 community change. Before the dumping operation, there was a typical medium sand *Nephtys cirrosa*
394 community characterized by the polychaetes (*Magelona filiformis/johnstoni*, *Nephtys cirrosa*) and
395 amphipods (*Megaluropus agilis*, *Urothoe elegans*, etc.) found in the eastern part of the Bay of Seine
396 (Marmin, 2013), in the eastern part of the English Channel (Prygiel, 1987) and in the southern North
397 Sea (Desroy et al., 2002; Van Hoey et al., 2004). After dumping, the Machu site corresponded to a mix
398 of the *Nephtys cirrosa* and *Abra alba* communities of medium and muddy fine sand (with the bivalves
399 *Phaxas pellucidus*, *Spisula subtruncata*, and the polychaete *Owenia fusiformis*, etc.). The *Abra alba*
400 community of the Bay of Seine shows the richest abundance and biomass for the European seas
401 (Thiébaud et al, 1997; Dauvin and Desroy, 2005). Results show a faunal modification before/after the
402 experiment, but no change is observed in the total biomass before/after dumping. Indeed, the biomass
403 decrease in the benthic invertebrate non-selective deposit feeders is offset by an increase in the
404 biomass of the benthic invertebrate omnivores/necrophages and predators.

405 The species established in the *Nephtys cirrosa* community at the Machu site are adapted to an
406 unstable environment characterized by a strong hydrodynamic activity, with increased sedimentation
407 and resuspension leading to natural sediment instability (Marmin, 2013). These species can tolerate
408 sedimentation rates caused by anthropogenic activities such as dumping (see for example Newell et
409 al., 1998; Roberts et al, 1998; Prevedelli et al., 2001; Bolam et al, 2016). Bolam and Rees (2003) showed
410 that invertebrate recolonization in stable marine environments can take several years, whereas it takes
411 place only on the order of several months in naturally disturbed environments (strong hydrodynamics,
412 polyhaline habitats, etc.). In the case of naturally perturbed environments, the community structure is
413 generally less complex and, as a result, ecological succession levels are lower, which ultimately leads
414 to shorter recovery periods (Diaz, 1994). The medium sand *Nephtys cirrosa* community appears to
415 have a great capacity for restoration after disturbance in relation to the annual recruitment of benthic
416 macrofauna. After the dumping, the spring-summer recruitment of the dominant benthic species (*Abra*
417 *alba-Lagis koreni* muddy fine sand community, which shows a benthic-pelagic cycle) ensures a rapid
418 increase in the abundance in the area impacted area by the deposition. This is in agreement with the
419 high ranking of zooplankton in the keystone index, suggesting that the food web is bottom-up
420 controlled. Moreover, adult migration coupled with a strong hydrodynamic regime, such as occurring
421 with the bivalve *Abra alba* (Olivier et al., 1996, Marmin, 2003), also contributes to the recovery of the
422 stressed environment (see Powilleit and Kube, 1999; Zajac et al., 1998). This adult migration
423 demonstrates the important role of the areas around a disturbed site in macrofauna recovery. The
424 presence of nearby non impacted areas provides a source of drifting migrating adults that leads to a
425 much quicker recovery of the impacted site due to the juvenile recruitment (Zajac and Whitlatch 2001;

426 Diaz, 1994). The important resilience of the Machu site is due to physical parameters: a particular
427 hydrodynamic environment with strong tidal flow and flow currents faster than ebb currents, which
428 maintain the ecosystem in a stressed state.

429 The Machu site seems to be a resilient ecosystem, which can be explained by the limited impacted
430 area (500 m around the impacted station) and by the presence of a non-impacted zone serving as a
431 reserve for the colonization of macrozoobenthic invertebrates on the impacted zone. This colonization
432 is made possible by the drift of the post-larvae, juveniles and adults living near the impacted zone
433 during a tidal cycle and on a large spatial scale (the whole community), as observed by Olivier et al
434 (1996) in the *Abra alba* community of the eastern part of the Bay of Seine, including two benthopelagic
435 cycle species with massive recruitment capacities: *Owenia fusiformis* and *Pectinaria koreni* (Thiébaut,
436 1994; Thiébaut et al., 1992). The resilience of an ecosystem impacted by dumping has also been
437 studied in the Mediterranean Sea (Hermand, 2008). This author observed a colonization of cuttings in
438 less than 6 months (with a specific richness higher than at the control stations) and a total restoration
439 of the ecosystem in 18 months (Hermand, 2008).

440

441 4.3- Strengths and drawbacks of model construction

442 In this study, we have investigated the trophic web of the Machu site one year before and two
443 years after the dumping operations. From a methodological point of view, the models were based on
444 high quality source data as evidenced by the high value of the pedigree index and compared to the
445 pedigree values distribution for pre-existing models (Morissette, 2007). In fact, the pedigree index (0.5)
446 was in the highest part of the range (0.164 to 0.676) reported in Morissette (2007). In the majority of
447 cases, biomasses were integrated and did not need to be estimated by the model. This was mostly due
448 to the biomass data sources, which were obtained from local, highly replicated, and detailed samplings
449 through a Before-After-Control-Impact (BACI) approach from April 2010 to April 2014. In addition, the
450 diet compositions of the fish species came from stomach content studies performed in the eastern
451 English Channel.

452 The model developed in this study was atypical due to its intrinsic small spatial scale with one
453 on the main drawbacks being the fact that the population dynamics and home range of mobile species
454 vastly exceed the limits of the Machu site. As a partial solution, we consider trophic transfers outside
455 the area of the Machu site for fish by setting import entries in the diet composition matrix. This
456 limitation is common to all small-scale Ecopath models (e.g. marine protected areas or offshore wind
457 farms (Albouy et al., 2010; Colléter et al., 2012; Valls et al., 2012; Raoux et al., 2017).

458

459

460

461 *4.4- Changes in ENA indices related to stress*

462 Ecological Network Analysis indices are powerful tools because they can link system
463 architecture to system functioning and can reveal emergent properties (Ulanowicz, 2004). These
464 indices have been commonly used in coastal and marine systems to assess changes in their functioning
465 in response to perturbations (Tomczak et al., 2013; Tecchio et al., 2015; Raoux et al., 2017) and as
466 ecosystem health indicators (Bondavalli et al., 2006; Niquil et al., 2012; Niquil et al., 2014). In fact,
467 several emergent properties of ecological functioning can change under stress (Mukherjeer et al.,
468 2015; Tecchio et al., 2015).

469 In the present study, the ENA indices are calculated to analyse the status of the Machu site
470 ecosystem as regards resisting stress. According to our models, one year of dumping operations
471 appears to have a relatively limited impact on the structure and flow pattern of the local food web. In
472 fact, only small variations between the two periods are revealed by a comparison of ENA indices (total
473 ecosystem activity (T..), ascendancy (A), Finn's Cycling Index (FCI), system omnivory index (SOI) and
474 relative redundancy (R/DC) before and after the dumping operations.

475 Results show that the total activity of the Machu site ecosystem, as measured with T..,
476 increased after the dumping operations. This could be partly explained by the sampling of a new fish
477 compartment after the dumping operations, which led to an increase in fish diversity and complexity
478 consequently favouring an increase of ecosystem activity (Baeta et al., 2011; Hall, 1994).

479 Ascendancy, which measures the developmental status or maturity of an ecosystem
480 (Ulanowicz, 1986), also increased after the dumping operations. As an ecosystem matures, it goes
481 through successive stages (Odum, 1969) associated with a shift from opportunist to specialist species
482 (Walker and Salt 2006). According to Ulanowicz et al. (1997), the ascendance should increase as the
483 system becomes more specialist. Moreover, these authors state that, on the contrary, ascendancy is
484 supposed to change and more particularly decrease if a system is affected by disturbance. Other
485 authors agree with Ulanowicz et al. (1997), maintaining that low ascendancy indicates a stressed or
486 immature system (Ortiz and Wolff, 2002; Patricio et al., 2006; Baird et al., 2009). Our results suggest
487 that the dumping operations will not act as a stress for the Machu site ecosystem which shows high
488 resilience.

489 In a similar way, the decreasing trend in Finn's Cycling Index (proportion of all flows generated
490 by cycling) tends to confirm that the ecosystem was not perturbed after the dumping operations. In
491 fact, the FCI index is often considered as a possible indicator of stress, and an increase in recycling is
492 usually interpreted as a response to stress (Odum, 1985; Scharler and Baird, 2005; Tecchio et al., 2015).
493 Under stress, cycling can act as a buffer during perturbation and increase the ability of the system to
494 resist changes (Saint-Béat et al., 2015).

495 After the dumping operations, we observed an increase in SOI. This increase can be partly
496 explained by the sampling of piscivorous fish, which led to a change in the system from a chain-like to
497 a web-like structure. The SOI index has also been described as a relevant indicator of stress (Lobry et
498 al., 2008; Selleslagh et al., 2012). As omnivory enhances flexibility of the system, more omnivorous
499 systems are able to absorb perturbations and recover more rapidly afterwards (Fagan, 1997; Libralato,
500 2008). In addition, according to Fagan (1997), an increase in the degree of omnivory has a stabilizing
501 role on the system. This index can be associated with the redundancy (Williams and Martinez, 2004).

502 Concerning the relative redundancy (parallel trophic pathways) index, our results show that
503 this index remained the same between the two periods, suggesting that the non-organized part of the
504 system appears to remain at the same level. As with SOI, relative redundancy brings flexibility to the
505 system by allowing reorganization in the case of disturbance (Ulanowicz, 2009).

506 Furthermore, the transfer efficiencies (TE) decreased in parallel with TL in the two sampling
507 periods indicating that the compartments behave functionally in a similar way before and after
508 dumping operations. In fact, Coll et al. (2009) observed that marine ecosystems undergoing a
509 perturbation such as fishing activities showed breaks in the typical decreasing pattern of TE. These
510 observations are in line with the results mentioned above, and suggest that the dumping operations
511 act as a limited stress for the Machu site ecosystem which shows high resilience.

512 The ENA results from the Machu model before and after the dumping operations can be
513 compared with other ecosystems studied with the same methodology (Ecopath) and located in the
514 same biome such as the Seine Estuary (Rybarczyk and Elkaim, 2003; Tecchio et al., 2015). The ENA
515 indices before and after the dumping operations are of the same order of magnitude as the other
516 models developed in the Bay of Seine, suggesting no major trophic structural and functional shift after
517 the dumping operations. This result can be explained by the fact that the Bay of Seine is historically
518 characterized by a high level of human activities (pollution, transport, fishing, aquaculture, harbour
519 development, aggregate extraction, sediment dredging and deposition) (Dauvin, 2015) which have led
520 to an increase in resilience through time to face these multiple pressures.

521

522 **5. Conclusion,**

523 In this study, we use trophic modelling based on the analysis of emergent ENA properties to
524 study a local stress (dumping operations during one year) on the Machu food web. Our results show a
525 combination of changes in the food-web structure and functioning, but reveal the high resilience of
526 the Machu site after a short dumping phase. This high resilience can be explained by the fact that this
527 ecosystem is subject to regular natural physical perturbations and is historically characterized by a high
528 level of human activities. In addition, our study only concerns the dumping of one million cubic metres
529 of sediment in two zones (MABIO and MABES), while up to 4-4.5 million cubic metres of sediment are

530 extracted and dumped each year to ensure the access of GPMR (Marmin et al., 2016). More
531 representative experiments need to be conducted to provide further information on the capacity of
532 the ecosystem to resist dumping operations in the long-term. Following the BACI approach, such
533 modelling studies will be carried out both during and at the end of the dumping operations which have
534 a duration of ten years.

535 One major recommendation of the GPRM is to exploit the future dumping site with alternating
536 strips (Marmin, 2013). The dumping site would be divided into strips oriented parallel to the current
537 direction. The strips would be used by alternating a dumping phase with a recovery phase in order to
538 promote biological recovery processes ensuring the colonization of dumped sediment and the
539 restoration of benthic communities.

540

541

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543

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557

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776

777 **Figure captions**

778

779 **Fig. 1.** Location of the existing Octeville and Kannick as well as the future Machu dumping sites in the
780 eastern part of the Bay of Seine, with outlines of the Natura 2000 site and marine harbour waiting
781 areas.

782

783 **Fig. 2.** Flows and biomasses of the ecosystem before the dumping operations

784

785 **Fig. 3.** Mixed Trophic Impact (MTI) analysis performed on the trophic web before dumping operations.
786 Overall impacts are represented as negative (black circles) or positive (white circles).

787

788 **Fig. 4.** Keystoneness index calculated for the two Ecopath models (before and after dumping
789 operations; Machu Before model is shown in blue and Machu After scenario in green). The size of the
790 circles is proportional to the functional group biomass.

791

792 **Fig. 5.** Transfer efficiencies for discrete trophic levels used in the two Ecopath models (before and after
793 dumping operations; Machu Before model is shown in black and Machu After scenario in grey).

794 **Table 1**

795 Biomass values, production to biomass ratios (P/B), consumption to biomass ratios (Q/B), Ecotrophic
 796 Efficiencies (EE) and trophic level (TL) before and after the dumping operations.

797

	Biomass gC m ⁻²		P/B (year ⁻¹)		Q/B (year ⁻¹)		EE		TL	
	Before	After	Before	After	Before	After	Before	After	Before	After
Cephalopods	0.0050	0.00005	2.80	2.80	15.00	15.00	0.27	0.27	4.39	4.33
Piscivorous fish	-	0.00		0.87		5.11		0.03	-	3.96
Demersal fish	0.02	0.11	2.43	2.43	10.31	10.31	0.32	0.01	4.08	3.91
Benthic-feeding fish	0.17	1.41	0.81	0.81	3.80	3.79	0.42	0.29	3.35	3.32
Planktivorous fish	0.00	0.03	1.04	1.04	8.38	8.38	0.93	0.93	3.15	3.15
Benthic invertebrates, Omnivore/Necrophage	0.67	2.22	4.72	4.72	23.60	23.60	0.66	0.99	3.11	3.14
Benthic invertebrate predators	0.44	1.57	5.64	5.64	28.20	28.20	0.94	0.99	3.26	3.14
Benthic invertebrate filter feeders	4.69	4.28	4.97	4.97	19.88	19.88	0.34	0.99	2.27	2.27
Benthic invertebrates, sDF	0.15	0.17	7.37	7.40	36.85	37.00	0.92	0.99	2.22	2.22
Benthic invertebrates, nsDF	3.64	1.23	6.60	6.60	33.00	33.00	0.16	0.99	2.19	2.22
Meiofauna	0.43	0.84	35.00	35.00	140.00	140.00	0.97	0.97	2.26	2.25
Zooplankton	1.72	1.72	7.59	7.59	36.14	36.14	0.94	0.97	2.15	2.15
Bacteria	0.60	0.60	125.42	125.42	250.84	250.84	0.68	0.80	2.00	2.00
Phytoplankton	8.18	8.18	31.89	31.89			0.58	0.56	1.00	1.00
Detritus	9.05	9.05					0.74	0.80	1.00	1.00

798

799

800

801 **Table 2**

802 ENA indices for the two models before and after the dumping operations. The Total System
803 Throughput (T., gC m⁻² year⁻¹) is calculated as the sum of all the flows in the food web. Finn's Cycling
804 Index (FCI) gives the percentage of all flows generated by cycling. The Ascendancy (A) is a measure of
805 the system activity (Total System Throughput) linked to its degree of organization (Average Mutual
806 Information) and is expressed in gC m⁻² year⁻¹. The System Omnivory Index (SOI) is calculated as the
807 average of the OIs of the individual group, weighted by the logarithm of each consumer intake. The
808 Relative redundancy (R/DC) measured the fraction of internal flows as a proportion of total
809 development capacity

810

ENA	Before	After
T..	1130.13	1144.76
FCI	11.82	9.88
Ascendance	1129.90	1137.70
SOI	0.22	0.25
R/DC	0.59	0.59

811

812

813 **Table 3.** General system statistics and ENA indices for the Machu models compared to values obtained
 814 for similar systems. The Total System Throughput (T., gC m⁻² year⁻¹) is calculated as the sum of all the
 815 flows in the food web. The Ascendency (A) is a measure of the system activity (Total System
 816 Throughput) linked to its degree of organization (Average Mutual Information) and is expressed in gC
 817 m⁻² year⁻¹. Finn's Cycling Index (FCI) gives the percentage of all flows generated by cycling. The System
 818 Omnivory Index (SOI) is calculated as the average of the OIs of the individual group, weighted by the
 819 logarithm of each consumer intake.

820

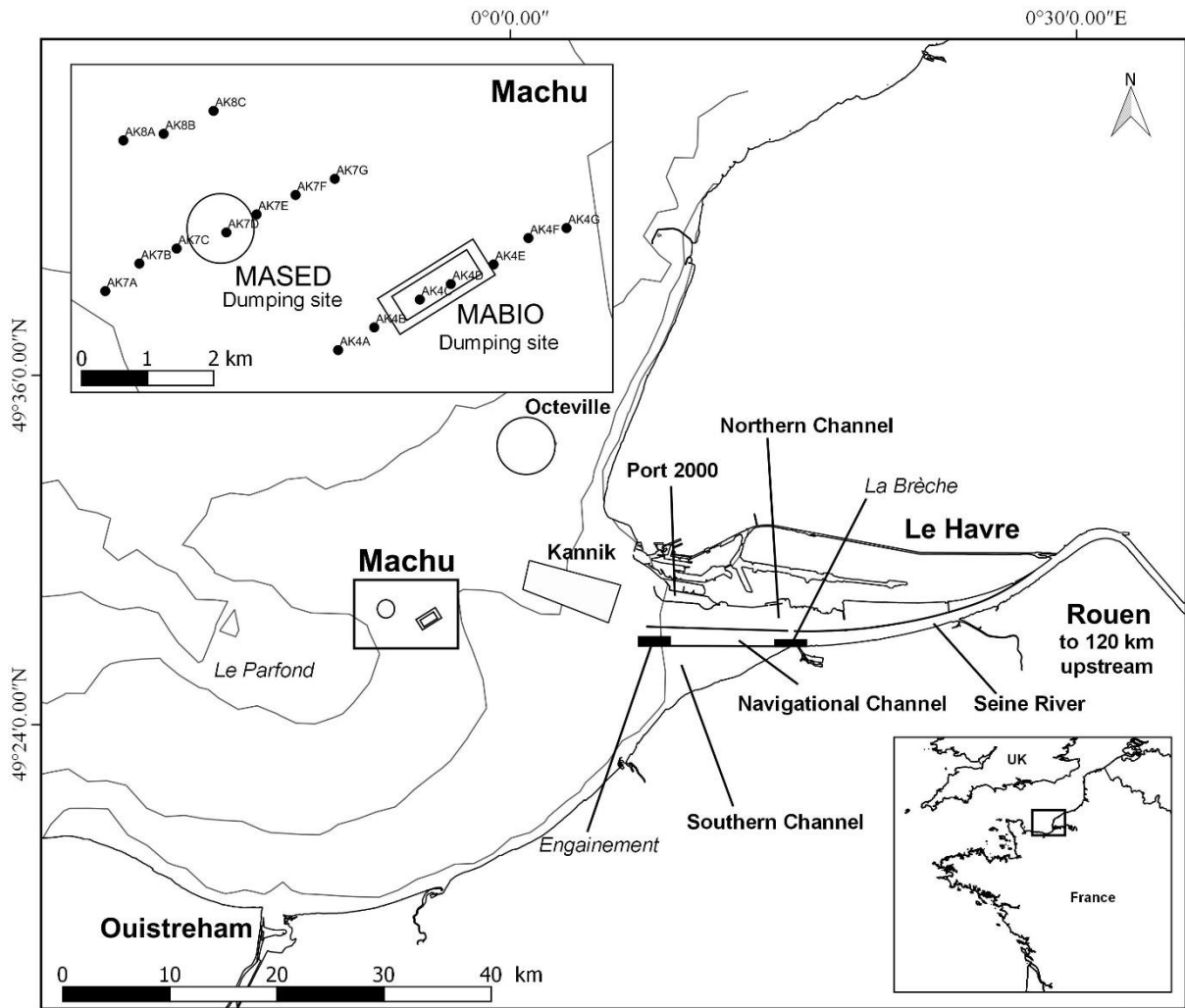
Ecosystems	T.	A	FCI	SOI	Reference for Ecopath models
Seine estuary	3603.22	3944.3	16.1	0.11	Rybarczyck and Elkaim, 2003
Seine estuary	4584.92 - 1161.05	1442.6-6058.6	3.65 -20.65	0.160-0.193	Tecchio et al., 2015
Machu Before	1130.13	1129.90	11.82	0.22	This study
Machu After	1144.76	1137.7	9.88	0.25	This study

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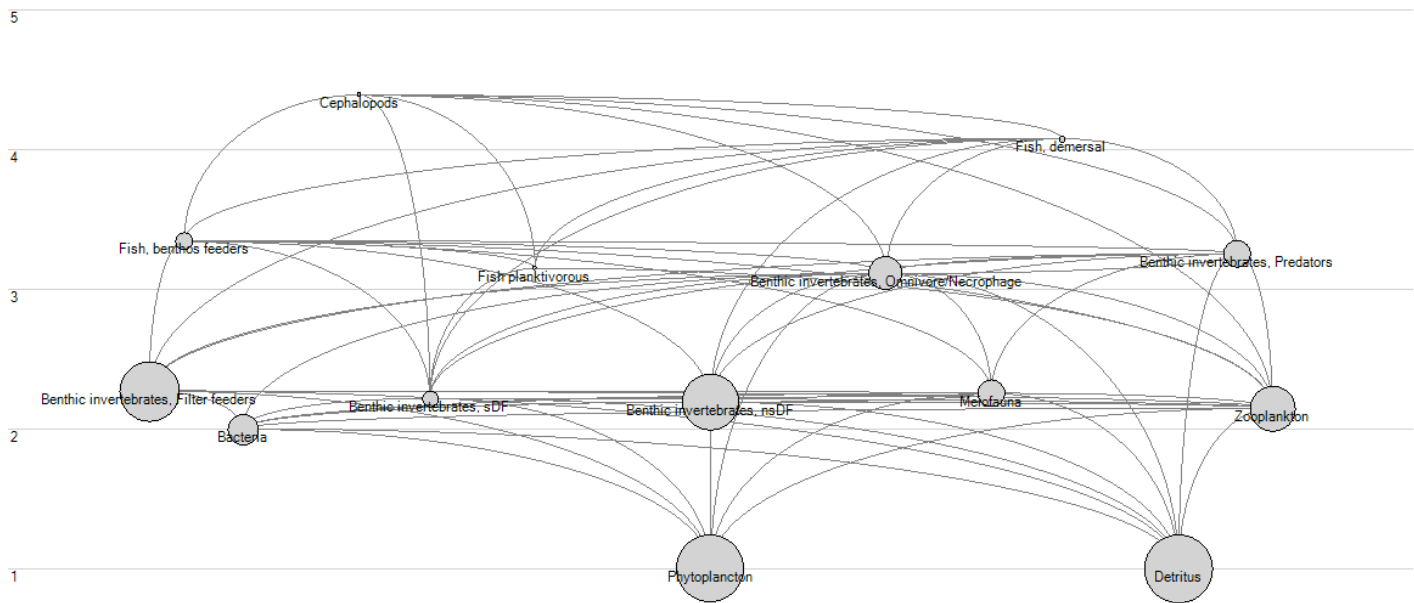
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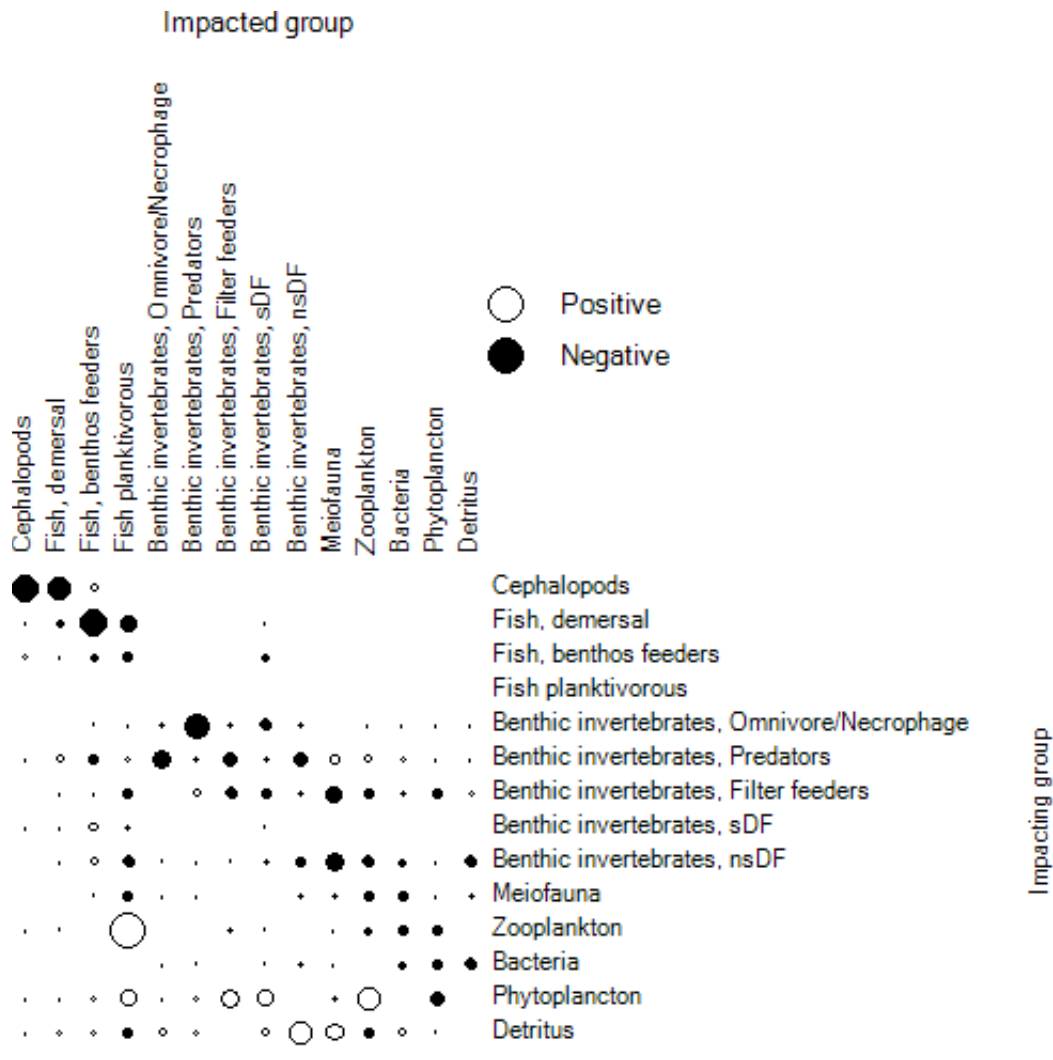


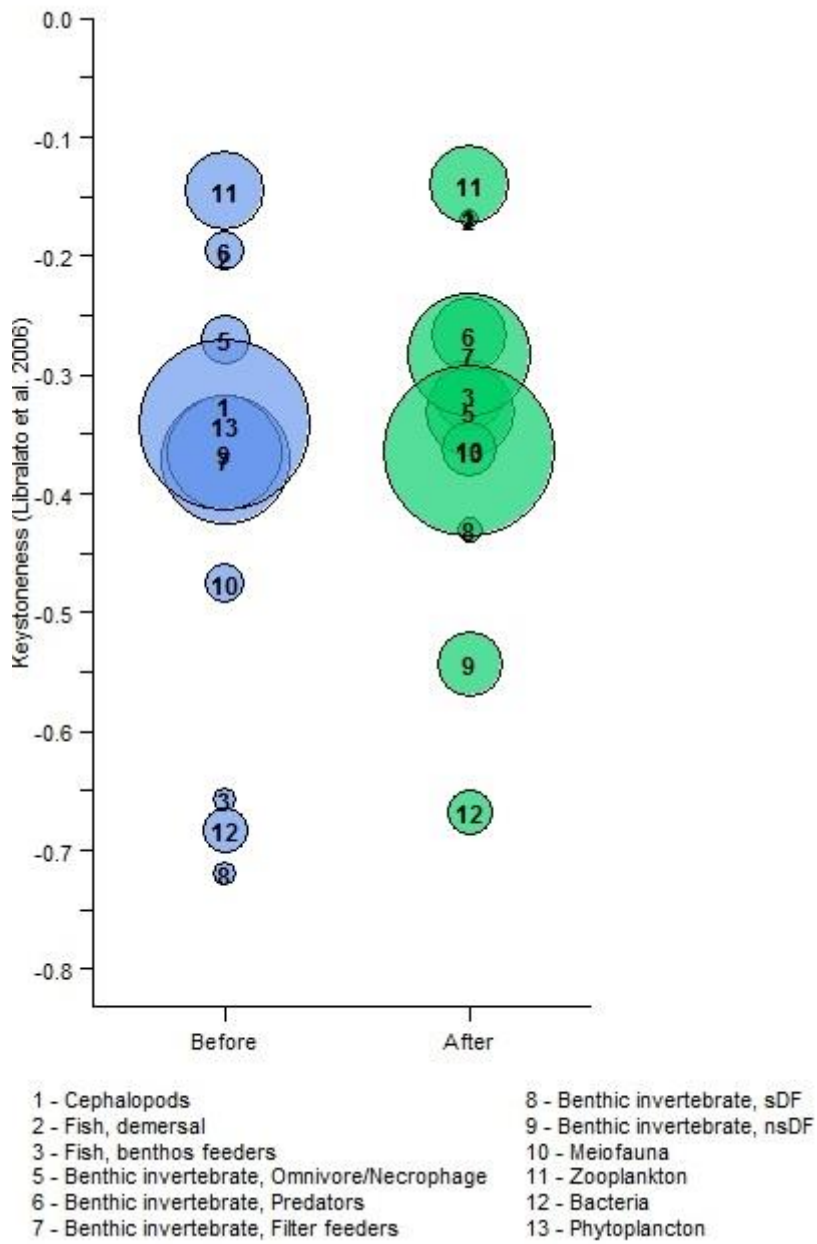
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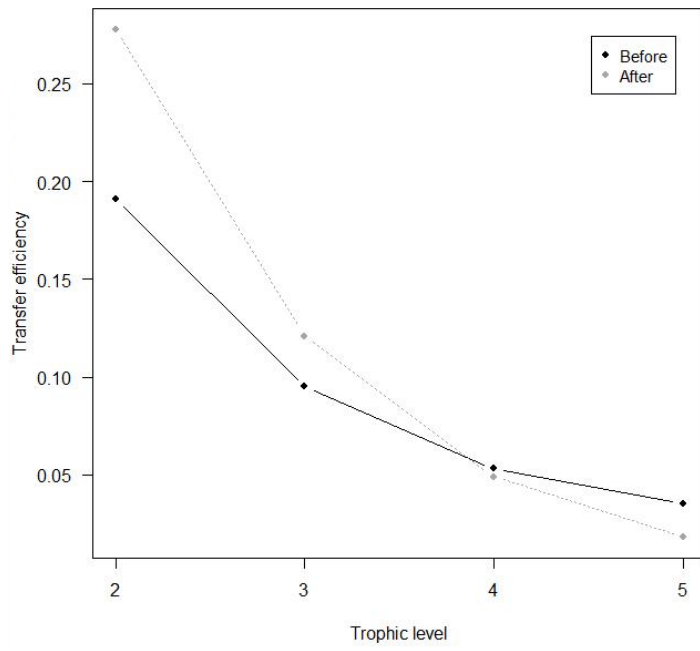
826 [Correction on figure: engainment → channel entry]







832 **Figure 5.**



833