

The mosaic of habitats of the Seine estuary: Insights from food-web modelling and network analysis

Tecchio Samuele^{1,*}, Rius Antonio¹, Dauvin Jean-Claude², Lobry Jérémy³, Lassalle Géraldine³, Morin Jocelyne⁴, Bacq Nicolas⁵, Cachera Marie⁶, Chaalali Aurélie^{1,7}, Villanueva Ching-Maria⁸, Niquil Nathalie¹

¹ Normandie Univ UNICAEN, UMR BOREA, MNHN, UPMC, CNRS 7208, IRD 207, F-14000 Caen, France.

² Normandie Univ UNICAEN, UMR M2C, UCBN, UR, CNRS 6143, F-14000 Caen, France.

³ IRSTEA, UR EABX Aquat Ecosyst & Global Changes, F-33612 Cestas, France.

⁴ IFREMER, F-14520 Port En Bessin, France.

⁵ Grp Interet Publ Seine Aval, F-76100 Rouen, France.

⁶ IFREMER, Lab Ressources Halieut, F-62321 Boulogne Sur Mer, France.

⁷ IFREMER, Fisheries Ecol & Modeling Dept, F-44311 Nantes 3, France.

⁸ IFREMER, Lab Biol Halieut, F-29280 Plouzane, France.

* Corresponding author : Samuele Tecchio, email address : samuele.tecchio@unicaen.fr

Abstract :

Ecological network analysis was applied in the Seine estuary ecosystem, northern France, integrating ecological data from the years 1996 to 2002. The *Ecopath with Ecosim* (EwE) approach was used to model the trophic flows in 6 spatial compartments leading to 6 distinct EwE models: the navigation channel and the two channel flanks in the estuary proper, and 3 marine habitats in the eastern Seine Bay. Each model included 12 consumer groups, 2 primary producers, and one detritus group. Ecological network analysis was performed, including a set of indices, keystone, and trophic spectrum analysis to describe the contribution of the 6 habitats to the Seine estuary ecosystem functioning. Results showed that the two habitats with a functioning most related to a stressed state were the northern and central navigation channels, where building works and constant maritime traffic are considered major anthropogenic stressors. The strong top-down control highlighted in the other 4 habitats was not present in the central channel, showing instead (i) a change in keystone roles in the ecosystem towards sediment-based, lower trophic levels, and (ii) a higher system omnivory. The southern channel evidenced the highest system activity (total system throughput), the higher trophic specialisation (low system omnivory), and the lowest indication of stress (low cycling and relative redundancy). Marine habitats showed higher fish biomass proportions and higher transfer efficiencies per trophic levels than the estuarine habitats, with a transition area between the two that presented intermediate ecosystem structure. The modelling of separate habitats permitted disclosing each one's response to the different pressures, based on their a priori knowledge. Network indices, although non-monotonously, responded to these differences and seem a promising operational tool to define the ecological status of transitional water ecosystems.

Highlights

► Six food web models of the Seine estuary, 15 groups each, for the years 1996–2002. ► Network and keystone analysis performed by functional habitats. ► Construction works and maritime traffic identified by network stress levels. ► Structural and functional differences along the salinity gradient. ► Subdivision in habitats improves interpretation in ecological network analysis.

Keywords : Trophic network, Estuary, Ecological network analysis, *Ecopath with Ecosim*, Food web, Ecosystem health indicators

48 1. INTRODUCTION

49 Estuaries are at the interface of marine and freshwater ecosystems, and are usually characterised
50 by high human activities and, accordingly, by high levels of anthropogenic pressure (Fairbridge,
51 1980; McLusky and Elliott, 2004). At the same time, they are among the most productive water
52 ecosystems, of extreme importance for biogeochemical cycles and for marine resources exploitation
53 (Wilson, 2002). The importance of studying the effects of anthropogenic impact on estuarine
54 ecosystems has increased in the last decade, especially in light of the Water Framework Directive,
55 which mandates achieving “good environmental status” of all European water bodies by 2015–
56 2021. However, the methods for evaluating environmental status are varied, addressing the issue at
57 different scales (i.e. from populations to ecosystems), while a standardized methodology is still
58 under discussion.

59 The Estuarine Quality Paradox refers to the issue of discerning human-driven stress in estuarine
60 ecosystems, which are by baseline subject to high levels of natural environmental stress (Dauvin,
61 2007; Elliott and Quintino, 2007). Stress, in this context, is defined as a modification of ecosystem
62 processes due to a response to an extended pressure from an external event or variable change
63 (Odum, 1985). The paradox was identified particularly in the use of benthic community indicators,
64 which are based on biodiversity assessments (Dauvin and Ruellet, 2009). In addition, the
65 complexity of an estuary calls for a comprehensive consideration of both its internal dynamics and
66 its ecological connections with the proximal marine biota (Able, 2005; Vinagre and Costa, 2014). A
67 possible solution is the application of the ecosystem approach to ecological analysis, by which all
68 species in the system are considered together, along with all flows and processes. Most often, food-
69 web modelling uses a series of linear equations to estimate values of all carbon flows occurring in a
70 natural system, which can then be analysed with Ecological Network Analysis (ENA) indicators.
71 The holistic ENA indices derived from food-web models were shown to partially discriminate
72 natural from human pressures, and their use has been successfully applied in estuaries around

73 European seas ([Baird and Ulanowicz, 1993](#); [Christian et al., 2005](#); [Lobry et al., 2008](#); [Patrício and](#)
74 [Marques, 2006](#)).

75 The Seine estuary is a mega-tidal estuary located in northern France, the third largest estuarine
76 ecosystem in the country after the Gironde and Loire along the French Atlantic coast, discharging
77 its waters into the English Channel ([Meybeck et al., 1998](#)). Anthropogenic pressures in the forms of
78 water pollutants, landscape engineering, bridges and port building works, have all been identified as
79 major shapers of the Seine estuary macrofauna assemblages ([Dauvin et al., 2010](#); [Dauvin et al.,](#)
80 [2008](#)). The Seine is the most polluted river in France, receiving human pressures from a highly-
81 industrialised watershed, with important agricultural activities and inhabited by approximately 17
82 million people. The Seine estuary represents a typical estuarine ecosystem, highly stressed both by
83 natural fluctuations and anthropogenic pressures, while at the same time hosting high levels of
84 productivity ([Dauvin and Desroy, 2005](#)). A large part of the mouth of the estuary is included in a
85 Natura2000 common interest area of the European Union and in a national natural Reserve;
86 however, no particular restrictions are in effect in the area. In addition, a new expansion of the Le
87 Havre harbour (Port 2000) was built in recent years, further eroding the surface of intertidal zones
88 and increasing maritime traffic. Using ecological quality indicators, a previous assessment provided
89 no definite findings on ecological status and concluded on the inability of discriminating between
90 human pressures and habitat characteristics ([Blanchet et al., 2008](#)).

91 Various modelling efforts related to the English Channel have been performed over the years. In
92 2003, a first estimation of the trophic flows and biomasses in the Seine estuary was published,
93 representing the state of the coastal system in the years 1996–1999 ([Rybarczyk and Elkaïm, 2003](#)).
94 Their results showed a highly-productive ecosystem, far from ecological maturity as indicated by
95 network analysis – an indication of stress ([Christensen, 1995](#)) – and more dependent than other
96 estuaries on external sources such as river discharge. [Rybarczyk et al. \(2003\)](#) applied the same
97 modelling approach in the Bay of Somme, another large estuarine system along the French coast of
98 the eastern part of the English Channel. Another inverse modelling effort studied the whole eastern

99 English Channel, finding a dominance of benthic carnivores in the food web, and evidences of
100 differences in ecosystem functioning when the sediment benthic habitats were taken into account
101 (Garcia et al., 2011). In particular, productivity and biological richness of estuaries were related to
102 the capacity of their mosaic of habitats to perform functions essential to the life cycles of species
103 inhabiting them (McLusky and Elliott, 2004). However, a more detailed analysis of the various
104 habitats forming the Seine estuary, working at the ecosystem scale, has not been performed to date.
105 Moreover, the use and applicability of ENA to discern natural from anthropogenic stress, and thus
106 their capability of circumventing the estuarine-quality paradox, although promising, has not been
107 unequivocally demonstrated yet (Niquil et al., 2012).

108 In this work, we first describe the set up and balancing of 6 food-web models for different
109 habitats of the Seine estuary, northern France, using the *Ecopath with Ecosim* approach. Modelling
110 an ecosystem as a mosaic of habitats has been infrequently attempted (Baird et al., 2007; Vinagre
111 and Costa, 2014). Then, we perform ENA on the resulting flow webs, to: (a) analyse the
112 contribution of habitats and their key roles to the Seine estuary functioning, and (b) discuss the
113 goodness of fit of ENA indices to environmental and anthropogenic stress and their use for
114 ecosystem health management. This second objective is timely to recent European Union calls on
115 assessing the applicability of ENA as ecosystem health indicators, considering the particular
116 situation and scale of the Seine estuary as a case-study.

117

118 **2. MATERIALS AND METHODS**

119 **2.1 Study area**

120 The Seine estuary and the adjacent western part of the Seine Bay were split into 6 spatial
121 compartments, which were modelled separately (Figure 1). Within the downstream part of the
122 estuary proper, we identified three estuarine habitats, i.e. the northern channel (*Fosse Nord*, FN),
123 the southern channel (*Fosse Sud*, FS) and the central navigation channel (*Chenal*, CH). Extending
124 into the eastern Seine Bay, we identified 3 other spatial marine compartments based on their

125 sediment composition and benthic habitat type (E4, E14, and E2), following guidelines by the
126 European Union Nature Information System (EUNIS classification of benthic habitats). Due to the
127 general current regimes in the Bay, and as the discharge plume of the Seine river flows primarily
128 adjacent to the southern coast, the marine habitats under its influence were mainly E4 and E14,
129 while the E2 was considered the habitat under the least influence of the plume (Salomon and
130 Breton, 1991). We will refer to “habitats” from now on as the modelled spatial compartments,
131 which represent homogenous zones from the hydro-sedimentary and salinity points of view. To
132 better disclose this, we identified and summarised the levels of external pressures on each of the 6
133 habitats, by using a qualitative scale that ranged from – (no impact) to +++ (very high impact),
134 according to both a literature review and the expert judgement of J.C. Dauvin.

135 The construction of the Le Havre harbour extension, called Port2000, started in the year 2002
136 and finished in 2005. As our objective was to exclude the impact of the harbour construction, which
137 will be evaluated at a later date, models were set up representing the condition of each spatial
138 compartment in the years before Port2000 construction, i.e. 1996–2002, for which an extensive
139 dataset is available. The qualitative recollection of data above described was also relative on the
140 same period.

141

142 **2.2 Modelling approach**

143 We used the *Ecopath with Ecosim* approach and software to estimate the carbon flows in the
144 food webs. Ecopath is a mass-balance, single-solution model that uses linear equations to estimate
145 flows between a number of functional groups established a priori (Christensen and Walters, 2004).
146 Each group is parameterised with, at least, its biomass (B , gC m^{-2}), its production rate over biomass
147 (P/B , year^{-1}), its consumption rate over biomass (Q/B , year^{-1}), its assimilation efficiency (or
148 excretion rate, U/Q), and the interactions with its prey and predators in the form of a diet matrix
149 (DC), which also establishes the identity of the trophic flows (Christensen and Pauly, 1992). Two
150 linear equations for each functional group are solved to ensure mass and energy balance (Figure 2)

151 (Christensen and Walters, 2004). Equation 1 expresses production (P) as a function of predation,
 152 fishing mortality (Y), net migration (E), biomass accumulation (BA), and natural mortality.
 153 Equation 2 ensures energy balance, calculating consumption of the i^{th} group (Q) as the sum of its
 154 production, respiration (R), and excretion (U).

$$155 \quad B \left(\frac{P}{B} \right)_i = \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ij} + Y_i + E_i + BA_i + B_i \left(\frac{P}{B} \right)_i (1 - EE_i) \quad (\text{Eq. 1})$$

$$156 \quad Q_i = P_i + R_i + U_i \quad (\text{Eq. 2})$$

157 The models were considered at steady state, thus biomass accumulations and net migration rates
 158 were considered negligible compared to the rest of the flows and were set to zero. Each model
 159 included 15 functional groups, including one detritus group and two primary producers, i.e.
 160 phytoplankton and microphytobenthos. Consumer groups included bacteria, zooplankton,
 161 meiofauna, four benthic invertebrates groups, four fish groups, and seabirds. The groups were
 162 represented in all habitats to allow comparability.

163 Table 1 and 2 show the input parameters used for all functional groups in the 6 habitats.
 164 Production, consumption, and excretion rates were obtained from literature, or from empirical
 165 equations (Pauly, 1980; Pauly et al., 1993) when data were available. All source data used for
 166 obtaining model parameters are listed in Supplementary Material Table 1. The maximum level of
 167 detail was available for fish and benthic invertebrates groups, as source data for biomasses and diets
 168 was compiled from a series of past research projects conducted in the area. Biomasses of fishes,
 169 which were generally available as wet weight (kg), were converted to carbon content (gC m^{-2}) using
 170 a conversion factor of 0.11 from Oguz et al. (2008). For benthic invertebrates, biomasses were
 171 converted from ash-free dry weight to carbon content using a conversion factor of 0.518 (Brey,
 172 2001).

173 We also summarised the quality of source data for biomasses, P/B, Q/B, and diet compositions
 174 into the Pedigree routine, which calculates a value between 0 and 1 related to the overall quality of

175 the data (with 0 indicating that data is of low quality, and 1 indicating that data is highly precise and
176 fully rooted in local studies).

177 All models had to be manually and slightly modified in their input data to equalize the mass
178 balances. The balancing approach was top-down, starting modifications from top predators down to
179 the lowest trophic levels. Balancing was performed taking into account the quality of source data as
180 described by the Pedigree. When modifications had to be made, diet compositions were varied
181 before other parameters. Each model was considered balanced when: (a) it did not violate mass
182 balance, i.e. all EE were < 1 , (b) it did not violate energy balance, and (c) metabolic coefficients
183 were reasonably within the known limits for each group (respiration/biomass ratio of 1–10 for
184 fishes, and food-conversion efficiencies in the range 0.1–0.3 for consumers in general).

185

186 **2.3 Network analysis**

187 After models were balanced, the trophic level (TL) of each functional group (i) was calculated as
188 the weighted average of the trophic levels of its prey (j), according to:

$$189 \quad TL_i = 1 + \sum_{j=1}^N DC_{ij} TL_j \quad (\text{Eq. 3})$$

190 and considering primary producers and detritus groups as having a base TL of 1.

191 Ecological network analysis (ENA) was performed directly within the EwE software, using the
192 network analysis plugin. For each habitat, we calculated the sum of all flows (T., $\text{gC m}^{-2} \text{y}^{-1}$), the
193 sum of all consumption flows, the sum of all exports, the sum of all respirations, and the sum of all
194 flows to detritus. We also calculated the proportion between biomass of fish groups and biomass of
195 invertebrate groups, considering as invertebrates the megabenthic, macrobenthic (suprabenthos),
196 and meiofauna groups. The ENA indices calculated were the total transfer efficiency (TE,
197 [Lindeman, 1942](#)), the Finn's Cycling Index (FCI) and the related Average Path Length (APL, [Finn,](#)
198 [1980](#)), the System Omnivory Index (SOI, [Libralato, 2008](#)), and the relative Redundancy (R/C) as
199 the proportion of redundant flows in the network, derived from the Ascendency theory ([Ulanowicz,](#)
200 [1986, 2009](#)). The formulae used for calculations are described in Supplementary Material Table 2.

201 The keystone index was calculated for each functional group and model, according to the
202 formula by [Libralato et al. \(2006\)](#), to study potential differences in key roles between habitats. This
203 analysis uses the mixed trophic impact matrix to calculate an index summarising the impact that a
204 minimal variation of biomass of a particular group would have on the biomasses of the other groups
205 in the system.

206 The smoothed continuous distribution of biomass by trophic level was also calculated for each
207 habitat, once all biomasses and trophic levels were estimated by the balanced models. The TL-
208 biomass graph, which considers trophic levels starting from 2, is useful to identify the levels of
209 trophic build-up in each habitat, and it can also be used as a coarse detector of ecosystem stress
210 ([Gascuel et al., 2005](#)). To check the effective trophic position of the most important groups in the
211 system, we added a novel decomposition spectrum using a TL-keystone diagram, based on the
212 same rationale as the biomass trophic spectrum for its interpretation.

213

214 **3. RESULTS**

215 **3.1 Quality of data and parameterisation**

216 The calculated Pedigree index for all models was 0.635, at the highest range of values reported
217 in literature ([Morissette, 2007](#)). This was mostly due to the biomass data sources, which were
218 obtained from local, highly replicated, and detailed samplings, and diet compositions of fish and
219 macrobenthic groups that came primarily from stomach content studies in the English Channel
220 (Supplementary Material Table 1).

221 In the majority of cases, biomasses were integrated and did not need to be estimated by the
222 model to the exception of habitats where microphytobenthos was supposed to be present only in a
223 reduced area and for which no stock data was available. As such, the biomass of microphytobenthos
224 was estimated by the model by using a fixed ecotrophic efficiency, $EE = 0.99$. These biomass
225 estimates were always considerably lower than in other areas where field biomasses were measured,
226 confirming the initial assumption of reduced prevalence. More generally, as biomass estimations are

227 obtained from the mass balance equations, this accordance between assumption and estimation
228 suggests a correct parameterisation of the predatory flows through the whole food web.

229

230 **3.2 Ecosystem flow structure**

231 Trophic levels (TL) ranged from 1.0 to a maximum of 4.1, represented in all models by fish
232 piscivores that can be thus considered as top predators in the area (Figures 3 and 4). Also at the top
233 of the food webs were seabirds, which however acquired a large percentage of their diet from
234 external sources. Trophic levels varied slightly between habitats, maintaining however the same
235 rank order between functional groups. This shows that the balancing procedures did not change the
236 relative importance of prey/predator interactions introduced with the diet matrix.

237 The majority of the functional groups maintained approximately the same omnivory between
238 habitats, with the widest variations in omnivory index between habitats shown by the benthic
239 predators (0.11–0.52). The groups with the highest omnivory were seabirds, fish planktivores, and
240 fish benthos feeders, while the most specialised groups in terms of trophic habits were fish
241 piscivores and, to a lesser degree, benthic deposit feeders (Supplementary Material Table 3).
242 Meiofauna also showed low omnivory, due to them feeding mainly on detrital sources.

243 In terms of ENA overall indices, the total ecosystem activity (measured with the sum of all
244 flows, T..) was the highest in the Southern Channel, mainly due to high values of export and flows
245 to detritus (Table 3). The rest of the habitats had comparable activity levels, ranging from 1161 to
246 $1826 \text{ gC m}^{-2} \text{ y}^{-1}$. The net system production and the ratio of primary production over total biomass
247 were however the lowest in the Southern Channel, suggesting a less efficient utilisation of the
248 inputted production, compared to the other modelled areas. The highest production over total
249 biomass ratio was found in the central Navigation Channel, where the total biomass was the lowest.

250 The ratio of fish biomass over invertebrate biomass was reduced in the estuarine zones compared
251 to the marine zones, with values ranging 1.14–1.48 in the former while ranging 2.27–4.56 in the
252 Seine Bay. The total transfer efficiency (TE) between discrete trophic levels behaved similarly, with

253 the estuarine zones (CH, FN, and FS) having overall lower efficiencies than the 3 marine habitats.
254 The mean TE for the estuarine habitats was 5.50 ± 1.17 %, while in the marine habitats it was
255 8.80 ± 1.27 %. Zooming on the Southern Channel, its TE was 6.8 %, the highest of the 3 estuarine
256 habitats.

257 The system omnivory index (SOI) ranged 0.160–0.193, at the lower end of the range for marine
258 ecosystems of the northern Europe (0.14–0.36, Mackinson and Daskalov, 2007). Omnivory was
259 highest in the FN, was lowest in the FS and E2 habitats, and showed comparable intermediate
260 values in the other habitats. High system omnivory in FN was mainly caused by high omnivory of
261 benthic predators, while the lower SOI in FS and E2 were caused by lower contributions of benthic
262 filter feeders and benthic predators, respectively. Finn's cycling index (FCI) was the index with the
263 widest range between habitats. FCI ranged from 3.65 % to 20.65 %, with the highest values present
264 in the E2 and FN sites, while being lowest in the FS. The average path length, which is calculated
265 using the same logic as FCI, showed again higher values in the E2 and FN while being the lowest in
266 the FS; path length in general ranged between 2.63 and 4.33. The relative redundancy index
267 evidenced a single habitat, FS, which showed the lowest value (0.380) while the rest of the habitats
268 with values comprised between 0.535 and 0.590, presenting more than half of their flow paths in
269 parallel.

270

271 **3.3 Ecological roles**

272 Trophic spectrum of biomass showed differences mainly between the estuarine and the marine
273 zones, with the latter showing biomass peaks at approximately one quarter of trophic level higher
274 than the estuarine systems (Figure 5a). The biomass peak of the second-order consumers was
275 located at TL 2.75–2.95 for the three estuarine habitats, whereas it was visible at TL 3.05–3.15 for
276 the marine habitats. These peaks were mainly produced by invertebrate benthic predators, in all
277 habitats but the CH, where it was caused by increased biomass of suprabenthos (mainly due to the
278 decapod *Palaemon longirostris*). The peaks for top predators were also shifted toward the same

279 direction, but more overlapped due to their reduced contribution in biomass. The highest levels of
280 keystoneity were concentrated in all habitats in a peak at $TL = 2.5$, and at $TL > 3.5$ (Figure 5b).
281 Between these two peaks, the CH habitat behaved differently from all others, decreasing only down
282 to -0.3 . The biomass peak of second-order consumers was therefore not reflected in a higher trophic
283 impact of their components over the rest of the food web, as the peaks of the two spectra did not
284 superpose.

285 Keystoneity patterns showed variations between the different food webs (Figure 6). Fish
286 piscivores were always present at the highest positions in all 6 habitats, along with seabirds.
287 Seabirds had the highest keystoneity in all habitats except E4, where they stand considerably
288 lower, and CH, where they had similar position as meiofauna. The northern channel (FN) had also
289 zooplankton and phytoplankton occupying the third and fourth position, respectively, following
290 seabirds and fish piscivores.

291 In the marine habitats, key roles were subject to wider variations, and benthic predators showed
292 high keystoneity. However, they appeared as structuring species rather than keystone, due to their
293 high biomass in all three habitats. This was especially evident in E4, where benthic predators
294 dominated the biomass along with benthic deposit feeders, and both showed high values of
295 keystoneity.

296

297 **4. DISCUSSION**

298 **4.1 Advantages and limitations of the models**

299 The usefulness of comparing snapshot ecosystem models, representing different habitats of a
300 same biogeographical region, became evident over the last decade (Baeta et al., 2011; Baird et al.,
301 2007; Lassalle et al., 2013; Patrício et al., 2004). In this study, we presented the most updated and
302 comprehensive modelling effort for the Seine estuary food web. The models were rooted in high-
303 quality source data as evidenced by the high Pedigree value, compared to literature, and by the
304 consistent estimates of the missing biomasses. Also, by studying a continuum of estuarine and

305 marine habitats (in the proximity of the Seine Bay) this approach provided one of the first insights
306 of the differences between food-web structure and function along the estuarine-coastal gradient,
307 from which future studies of inter-habitat connectivity through flows of energy will be possible.

308 The sampling programs used as biomass source data focused particularly on benthic megafauna
309 and fishes. Small-sized trophic groups, such as bacteria, microphytobenthos, and meiofauna, were
310 mainly parameterised using data from other models of the same area or of similar regions (see
311 Supplementary Table 1). However, the same pattern of knowledge was available for all six habitats,
312 thus permitting relevant comparisons between them.

313 Estuarine and marine habitats are known to have ostensibly different abiotic conditions between
314 them and, following from it, different community structures and functions (Fairbridge, 1980; Heip
315 and Herman, 1995; Wilson, 2002). For this reason, it is pivotal to characterise each habitat along an
316 estuarine-coastal gradient as it would provide useful information for spatial management planning.
317 In addition, setting a baseline of ecological index values will allow for subsequent before/after
318 impact evaluations, such as in the case of the construction of Port2000 harbour extension. Using
319 models to represent a mean multi-annual condition also helps reducing noise from low-scale
320 temporal trends, and will allow for a more thorough observation of long-term patterns.

321

322 **4.2 Characterisation of habitats in the Seine estuary**

323 In the central navigation channel (CH) meiofauna was shown to play a keystone role, indicating
324 an increased importance of substrate processes. In fact, the sediment of CH is constantly reactivated
325 due to high levels of resuspension caused by the year-round maintenance dredging to keep the
326 channel navigability and by maritime traffic for the Rouen harbour 120 km upstream (Dauvin and
327 Desroy, 2005). Maintenance dredging causes smothering and removal of bed organisms, and
328 increased turbidity with impact to fishes (Elliott and Hemingway, 2002). In fact, the biomass of
329 both fishes and macrobenthic invertebrates in the CH was the lowest of the estuary, leaving detritus-
330 driven dynamics as the main active compartment. To better disclose this process, more detailed

331 approaches should be undertaken: to date, the *Ecopath* approach does not allow focusing on the fine
332 details of flows to and from detritus, and the bacterial dynamics are also modelled in coarse detail
333 ([Christensen and Walters, 2004](#)). More complex inverse modelling techniques, possibly coupled
334 with *in-situ* measurements of sediment community functioning and quantification of uncertainty,
335 might be better suited to solve this critical issue in terms of system productivity.

336 In the keystone analysis, two habitats – FN and E4 – behaved differently from the rest. The
337 highest levels of impact were registered in the FN according to ENA, which is in reality a
338 combination of both anthropogenic and environmental stress (Table 4). The highest levels of system
339 omnivory (SOI) and high carbon recycling (FCI) compared to the other estuarine habitats logically
340 revealed that FN is therefore a highly impacted area, where benthic invertebrate predators dominate
341 the community, and where the food web is associated with a more web-like structure.

342 In E4, top-down control was reduced by the low keystone of seabirds and by the increased
343 importance of phytoplankton. This evidences a particularly interesting condition, with E4 being a
344 possible ecotone and mediating the transition from estuarine to marine environments by hosting
345 changes in keystone species with respect to the neighbouring habitats. The Seine estuary is
346 particular in the sense that the gradient of salinity is limited than in other estuaries and it is
347 concentrated at the mouth of the estuary, while the fluvial part of the watershed is shifted up flow
348 ([Meybeck et al., 1998](#)). In addition, estuarine and marine zones differed in their overall community
349 composition and discrete trophic levels structure: the estuarine habitats hosted a lower proportion of
350 fish biomass over invertebrate biomass than the marine habitats, and lower transfer efficiency
351 between trophic levels. A difference between these two regions suggested that the E4 habitat might
352 indeed be considered as a transition, ecotone-like, zone. Apart from their ecological interest,
353 estuarine ecotones are considered as key areas for stability and functioning of water ecosystems
354 ([Elliott and Whitfield, 2011](#)) and thus host interesting conditions to be specifically tested by means
355 of ENA.

356 In the analysis of the biomass trophic spectrum, a movement of biomass peaks towards lower
357 trophic levels would theoretically indicate a response to stress (Gascuel and Pauly, 2009). However,
358 this paradigm was studied in relation to fishing impact, where the removal of biomass of high TL
359 would shift the structure of the community “down” the food web (Pauly et al., 1998). In this study,
360 the second-order consumers indeed occupied slightly lower trophic positions, evidencing a response
361 from stress with respect to the marine habitats. However, it is unlikely that this response is caused
362 by fishing because the estuarine habitats are subjected to considerably less fishing effort than the
363 marine ones, apart from the fishery on the decapod *Crangon crangon*. More generally, the Seine
364 estuary is the ecosystem least exploited by fishing in the southern English Channel (Martin et al.,
365 2009). Rather, it is more probable that this analysis can evidence multiple stresses with potential
366 synergistic effects, such as the ones caused by wide-spread anthropogenic disturbance from
367 construction, marine traffic, and water pollution. In fact, the peak of second-order consumers was
368 mainly caused by suprabenthos in the CH, while benthic predators dominated the peak in all other
369 habitats, in accordance to what was found in a more extended study of the English Channel (Garcia
370 et al., 2011). This confirms results from the keystone analysis, and further suggests the
371 particular importance of sediment community processes in the CH habitat.

372

373 **4.3 Fitting stress to ENA**

374 The ENA indices usually respond to stress, defined as a negative response from disturbance
375 produced by an external pressure (Odum, 1985). When an ecosystem is influenced by an external
376 pressure, its response depends on its levels of resistance, defined as the extent of functioning
377 variations, and resilience, corresponding to the time needed to return to a comparable state (Pimm,
378 1991). ENA indices can, with varying sensitivities, inform on these two characteristics of marine
379 ecosystems and provide a numerical basis for comparing between habitats. However, for systems
380 that are already under stress such as estuaries, the differences may be subtle or at least masked by
381 the baseline effects of natural disturbance (Dauvin, 2007; Elliott and Quintino, 2007). Here, we

382 collected qualitative data on current knowledge of the levels of stress in the 6 studied habitats
383 (Table 4), to perform a first, although still coarse, analysis of the fitting of ENA to anthropogenic
384 and natural impact levels.

385 As previously described, the Seine estuary is one of the most man modified and contaminated
386 estuary in France. As expected, the Northern Channel habitat (FN) evidenced the highest levels of
387 ecological stress, according to ENA values. The indices that most captured this stressed condition
388 were FCI and SOI, in accordance to the classical interpretation of ecosystem responses with stress,
389 i.e. higher recycling and shorter food chains in stressed areas (McCann and Hastings, 1997; Odum,
390 1985; Scharler and Baird, 2005). The second-most impacted area in the Seine estuary appears to be
391 the highly-dredged navigation Channel (CH), where maritime traffic is present year-round, the
392 substrate is constantly resuspended, and a constant maximum turbidity zone is present. In addition,
393 central channels in estuaries usually present high levels of natural variability, especially close to the
394 mouth where tidal forces and water mixing are maximal (McLusky and Elliott, 2004). Here,
395 indications of system immaturity were found, such as high net system production and keystone
396 species shifts, while overall ENA indices did not completely reflect this condition.

397 Low-to-intermediate levels of physical disturbance, such as those found in the Southern Channel
398 (FS), are known to increase benthic diversity and complexity and, consequently, favour an increase
399 of ecosystem activity (Baeta et al., 2011; Hall, 1994). The FS also hosts a wide intertidal area, a
400 trait that might probably increase ecosystem activity. This is indeed what was evidenced by T..., the
401 highest levels of biomass, the high trophic specialisation compared to other areas (shown by SOI),
402 and low system stress (indicated by lower FCI and R/C).

403 Concerning the ENA indicators applied in this study, we found an acceptable fitting of SOI, FCI,
404 and to a lesser extent R/C to the levels of supposed stress of each spatial compartment. SOI was
405 already identified as a relevant indicator of stress in a previous meta-analysis of estuarine food webs
406 (Selleslagh et al., 2012). A general trend for system omnivory in estuaries is, however, still to be
407 determined. In this study, values of SOI were generally considerably higher, for instance, to those

408 found in the Mondego estuary, Portugal, which however did not consider the fish community in the
409 model (Baeta et al., 2011). These indices have been recently proposed as possible methods to
410 comply the EU mandate as ecological status indicators (Niquil et al., 2012). Although the results
411 presented here are promising, however, a more specific analysis will be necessary in this sense,
412 including statistically-testable comparisons and possibly considering other ENA candidate indices
413 such as Ascendency and its derived indicators (Ulanowicz and Abarca-Arenas, 1997). Furthermore,
414 the average path length (APL) did respond to the same gradients as FCI, thus suggesting that either
415 index would be sufficient for ecological status studies.

416 Another important reason to model separate habitats can be drawn from comparing these results
417 with a previous food-web model of the Seine estuary (Rybarczyk and Elkaïm, 2003). This previous
418 model is approximately overlapping with the three estuarine habitats considered here (CH, FN, FS)
419 using the same number of functional groups, although with different subdivisions between them and
420 not considering bacteria which can influence recycling estimations. In the 2003 study, SOI and
421 R/DC indices showed values outside the range showed in the present study (SOI = 0.11 and R/DC =
422 0.281, Rybarczyk and Elkaïm, 2003) while other two indices, FCI and T., which here responded to
423 the levels of habitat pressure, had values inside the range obtained in this study (FCI = 16.1 and T..
424 = 3603 gC m⁻² y⁻¹ in the 2003 study). Differences are then present between considering separate
425 habitats and a larger area, and might change the direction and interpretation of results especially in
426 relation to assessing the ecological status.

427

428 **4.4 Conclusions**

429 In this study, an analysis of the contribution of the Seine habitats and their key roles to the
430 estuary functioning was done based on the analysis of emergent ENA properties. The two habitats
431 with a functioning most related to a stressed state were the northern and central navigation channels,
432 where building works and constant maritime traffic are considered major anthropogenic stressors.
433 Regarding our second objective, the combined use of ENA indices and keystone analysis can

434 respond fairly adequately to the distinct levels of pressure in an estuarine ecosystem, seeming thus a
435 promising candidate indicator of “ecosystem health status”. The ENA response alone was not
436 completely unequivocal, meaning that further studies are needed to fully disclose the response
437 patterns of ENA indices to the levels of ecosystem stress. Furthermore, while acknowledging that a
438 holistic approach considering the whole estuary might disclose previously unknown properties,
439 results here point to a spatial complexity of the Seine estuary ecosystem, where distinct habitats
440 present distinct emergent traits. In the framework of assessing environmental status of ecosystems
441 subject to the European Union Water Framework Directive, we argue for including the habitat-level
442 spatial observation when planning conservation strategies.

443

444 **ACKNOWLEDGEMENTS**

445 This work was funded by the project ANTROPOSEINE (G.I.P. Seine-Aval, 5th programme,
446 France). We also acknowledge, for their help in compiling the dataset and for giving specific expert
447 advices: Aurore Raoux (UMR BOREA Caen), Chloé Dancie (CSLN Le Havre), Philippe Riou and
448 Mathilde Schapira (IFREMER Port-en-Bessin), Anik Brind’Amour (IFREMER Nantes), Bruno
449 Ernande (IFREMER Boulogne-sur-Mer), Sami Souissi (Station Marine de Wimereux), Sandrine
450 Alizier (UMR LOG Wimereux), Stella Marmin (UMR M2C Caen), Franck Gentil and Eric
451 Thiébaud (Station Biologique de Roscoff), Nicolas Desroy (IFREMER Dinard), and the Port
452 Authorities of Le Havre and Rouen.

453

454

BIBLIOGRAPHY

- 455
456
457 Able, K.W., 2005. A re-examination of fish estuarine dependence: Evidence for connectivity between
458 estuarine and ocean habitats. *Est Coast Shelf Sci* 64, 5-17.
- 459 Baeta, A., Niquil, N., Marques, J.C., Patrício, J., 2011. Modelling the effects of eutrophication, mitigation
460 measures and an extreme flood event on estuarine benthic food webs. *Ecol Model* 222, 1209-1221.
- 461 Baird, D., Asmus, H., Asmus, R., 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø
462 Bight ecosystem, northern Wadden Sea. *Mar Ecol Prog Ser* 351, 25-41.
- 463 Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem
464 properties of four tidal estuaries. *Mar Ecol Prog Ser* 99, 221-237.
- 465 Blanchet, H., Lavesque, N., Ruellet, T., Dauvin, J.-C., Sauriau, P.G., Desroy, N., Desclaux, C., Leconte, M.,
466 Bachelet, G., Janson, A.-L., Bessineton, C., Duhamel, S., Jourde, J., Mayot, S., Simon, S., de
467 Montaudouin, X., 2008. Use of biotic indices in semi-enclosed coastal ecosystems and transitional waters
468 habitats—Implications for the implementation of the European Water Framework Directive. *Ecol Ind* 8,
469 360-372.
- 470 Brey, T., 2001. Population dynamics in benthic invertebrates. A Virtual Handbook., [http://thomas-](http://thomas-brey.de/science/virtualhandbook)
471 [brey.de/science/virtualhandbook](http://thomas-brey.de/science/virtualhandbook).
- 472 Christensen, V., 1995. Ecosystem maturity - towards quantification. *Ecol Model* 77, 3-32.
- 473 Christensen, V., Pauly, D., 1992. ECOPATH II - a software for balancing steady-state ecosystem models and
474 calculating network characteristics. *Ecol Model* 61, 169-185.
- 475 Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol Model*
476 172, 109-139.
- 477 Christian, R.R., Baird, D., Luczkovich, J., Johnson, J.C., Scharler, U.M., Ulanowicz, R.E., 2005. Role of
478 network analysis in comparative ecosystem ecology of estuaries, in: Belgrano, A., Scharler, U.M., Dunne,
479 J., Ulanowicz, R.E. (eds.), *Aquatic Food Webs*. Oxford University Press, Oxford, UK, pp. 25-40.
- 480 Cuvilliez, A., Deloffre, J., Lafite, R., Bessineton, C., 2009. Morphological responses of an estuarine
481 intertidal mudflat to constructions since 1978 to 2005: The Seine estuary (France). *Geomorphology* 104,
482 165-174.

483 Dauvin, J.-C., 2007. Paradox of estuarine quality: Benthic indicators and indices, consensus or debate for the
484 future. *Mar Pollut Bull* 55, 271-281.

485 Dauvin, J.-C., Alizier, S., Vallet, C., Ruellet, T., 2010. Does the Port 2000 harbour construction have an
486 effect on the Seine estuary suprabenthic community? *Est Coast Shelf Sci* 86, 42-50.

487 Dauvin, J.-C., Desroy, N., 2005. The food web in the lower part of the Seine estuary: a synthesis of existing
488 knowledge. *Hydrobiologia* 540, 13-27.

489 Dauvin, J.-C., Fisson, C., Garnier, J., Lafite, R., Ruellet, T., Billen, G., Deloffre, J., Verney, R., 2008. A
490 report card and quality indicators for the Seine estuary: From scientific approach to operational tool. *Mar*
491 *Pollut Bull* 57, 187-208.

492 Dauvin, J.-C., Pezy, J.-P., 2013. Long-term changes of the Seine estuary suprabenthos (1996–2012). *J Exp*
493 *Mar Biol Ecol* 448, 93-103.

494 Dauvin, J.-C., Ruellet, T., 2009. The estuarine quality paradox: Is it possible to define an ecological quality
495 status for specific modified and naturally stressed estuarine ecosystems? *Mar Pollut Bull* 59, 38-47.

496 Dauvin, J.C., Desroy, N., Janson, A.L., Vallet, C., Duhamel, S., 2006. Recent changes of estuarine benthic
497 and suprabenthic communities in response to harbour infrastructural development. *Mar Pollut Bull* 53, 80-
498 90.

499 Elliott, M., Hemingway, K. (eds.) 2002. *Fishes in Estuaries*. Blackwell Science, Oxford 636 pp.

500 Elliott, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the
501 difficulty of detecting anthropogenic stress in naturally stressed areas. *Mar Pollut Bull* 54, 640-645.

502 Elliott, M., Whitfield, A.K., 2011. Challenging paradigms in estuarine ecology and management. *Est Coast*
503 *Shelf Sci* 94, 306-314.

504 Fairbridge, R., 1980. The estuary: its definition and geodynamic cycle, in: Olausson, E., Cato, I. (eds.),
505 *Chemistry and Geochemistry of Estuaries*. John Wiley and Sons, New York, pp. 1-35.

506 Finn, J.T., 1980. Flow analysis of models of the Hubbard Brook ecosystem. *Ecology* 61, 562-571.

507 Garcia, C., Chardy, P., Dewarumez, J.-M., Dauvin, J.-C., 2011. Assessment of benthic ecosystem
508 functioning through trophic web modelling: the example of the eastern basin of the English Channel and
509 the Southern Bight of the North Sea. *Mar Ecol* 32 (Suppl. 1), 72-86.

510 Gascuel, D., Bozec, Y.-M., Chassot, E., Colomb, A., Laurans, M., 2005. The trophic spectrum: theory and
511 application as an ecosystem indicator. *ICES J Mar Sci* 62, 443-452.

512 Gascuel, D., Pauly, D., 2009. EcoTroph: modelling marine ecosystem functioning and impact of fishing.
513 *Ecol Model* 220, 2885-2898.

514 Guezennec, L., 1999. Seine Aval: un estuaire et ses problèmes. *Seine-Aval Scientific Report 1.1*, France 29
515 pp.

516 Hall, J.S., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments.
517 *Oceanogr Mar Biol Annu Rev* 32, 179-239.

518 Heip, C.H.R., Herman, P.M.J., 1995. Major biological processes in European tidal estuaries. *Hydrobiologia*
519 311, 1-266.

520 Lassalle, G., Lobry, J., Le Loc'h, F., Mackinson, S., Sanchez, F., Tomczak, M.T., Niquil, N., 2013.
521 Ecosystem status and functioning: searching for rules of thumb using an intersite comparison of food-web
522 models of Northeast Atlantic continental shelves. *ICES J Mar Sci* 70, 135-149.

523 Le Hir, P., 2001. Courants, vagues et marées: les mouvements de l'eau. *Seine-Aval Scientific Report 1.2*,
524 France 32 pp.

525 Libralato, S., 2008. System Omnivory Index, in: Jørgensen, S.E., Fath, B.D. (eds.), *Ecological Indicators*,
526 vol. 4 of *Encyclopedia of Ecology*. Elsevier, Oxford, pp. 3472-3477.

527 Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web
528 models. *Ecol Model* 195, 153-171.

529 Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399-417.

530 Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and stability of an
531 estuarine trophic network. *Mar Ecol Prog Ser* 358, 13-25.

532 Mackinson, S., Daskalov, G., 2007. An ecosystem model of the North Sea to support an ecosystem approach
533 to fisheries management: description and parameterisation, *Science Series Technical Report*. Cefas,
534 Lowestoft, p. 142.

535 Marmin, S., Dauvin, J.C., Lesueur, P., 2014. Collaborative approach for harbour dredged sediment
536 management in the Bay of Seine (France). *Ocean Coast Manage* 102, 328-339.

537 Martin, C.S., Carpentier, A., Vaz, S., Coppin, F., Curet, L., Dauvin, J.-C., Delavenne, J., Dewarumez, J.-M.,
538 Dupuis, L., Engelhard, G., Ernande, B., Foveau, A., Garcia, C., Gardel, L., Harrop, S., Just, R., Koubbi, P.,
539 Lauria, V., Meaden, G.J., Morin, J., Ota, Y., Rostiaux, E., Smith, R., Spilmont, N., Vérin, Y., Villanueva,
540 C., Warembourg, C., 2009. The Channel habitat atlas for marine resource management (CHARM): an aid
541 for planning and decision-making in an area under strong anthropogenic pressure. *Aquat Living Resour* 22,
542 499-508.

543 McCann, K.S., Hastings, A., 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proc R*
544 *Soc B* 264, 1249-1254.

545 McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: ecology, threats and management*. Oxford
546 University Press, USA, New York 214 pp.

547 Meybeck, M., de Marsily, G., Fustec, É. (eds.) 1998. *La Seine en son bassin: fonctionnement écologique*
548 *d'un système fluvial anthropisé*. Elsevier, Paris 749 pp.

549 Morin, J., Duhamel, S., De Roton, G., 2010. *Poissons, habitats & ressources halieutiques: cas de l'estuaire de*
550 *la Seine*. Seine-Aval Scientific Report 2.5, France 75 pp.

551 Morissette, L., 2007. *Complexity, cost and quality of ecosystem models and their impact on resilience: a*
552 *comparative analysis, with emphasis on marine mammals and the Gulf of St. Laurence*, *Zoology*.
553 University of British Columbia, Vancouver BC, Canada.

554 Niquil, N., Chaumillon, E., Johnson, G.A., Bertin, X., Grami, B., David, V., Bacher, C., Asmus, H., Baird,
555 D., Asmus, R., 2012. The effect of physical drivers on ecosystem indices derived from ecological network
556 analysis: Comparison across estuarine ecosystems. *Est Coast Shelf Sci* 108, 132-143.

557 Odum, E.P., 1985. Trends expected in stressed ecosystems. *BioScience* 35, 419-422.

558 Oguz, T., Fach, B., Salihoglu, B., 2008. A coupled plankton-anchovy population dynamics model assessing
559 nonlinear controls of anchovy and gelatinous biomass in the Black Sea. *Mar Ecol Prog Ser* 369, 229-256.

560 Patrício, J., Marques, J.C., 2006. Mass balanced models of the food web in three areas along a gradient of
561 eutrophication symptoms in the south arm of the Mondego estuary (Portugal). *Ecol Model* 197, 21-34.

562 Patrício, J., Ulanowicz, R.E., Pardal, M.A., Marques, J.C., 2004. Ascendency as an ecological indicator: a
563 case study of estuarine pulse eutrophication. *Est Coast Shelf Sci* 60, 23-35.

564 Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean
565 environmental temperature in 175 fish stocks. *CIEM* 39, 175-192.

566 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs.
567 *Science* 279, 860-863.

568 Pauly, D., Soriano-Bartz, M., Palomares, M.L.D., 1993. Improved construction, parametrization and
569 interpretation of steady-state ecosystem models, in: Christensen, V., Pauly, D. (eds.), *Trophic models of*
570 *aquatic ecosystems*. ICLARM conference proceedings, vol. 26, pp. 1-13.

571 Pimm, S.L., 1991. *The Balance of Nature? Ecological issues in the conservation of species and communities*.
572 The University of Chicago Press, London 434 pp.

573 Rybarczyk, H., Elkaïm, B., 2003. An analysis of the trophic network of a macrotidal estuary: the Seine
574 Estuary (Eastern Channel, Normandy, France). *Est Coast Shelf Sci* 58, 775-791.

575 Rybarczyk, H., Elkaïm, B., Ochs, L., Loquet, N., 2003. Analysis of the trophic network of a macrotidal
576 ecosystem: the Bay of Somme (Eastern Channel). *Est Coast Shelf Sci* 58, 405-421.

577 Salomon, J.C., Breton, M., 1991. Courants résiduels de marée dans la Manche. *Oceanol Acta* 14, 47.

578 Scharler, U.M., Baird, D., 2005. A comparison of selected ecosystem attributes of three South African
579 estuaries with different freshwater inflow regimes, using network analysis. *J Mar Syst* 56, 283-308.

580 Selleslagh, J., Lobry, J., Amara, R., Brylinski, J.-M., Boët, P., 2012. Trophic functioning of estuarine
581 ecosystems along a gradient of anthropogenic pressures: a French case study with emphasis on a small and
582 low impacted estuary. *Est Coast Shelf Sci* 112, 73-85.

583 Ulanowicz, R.E., 1986. *Growth and development: Ecosystems phenomenology*. Springer-Verlag, New York,
584 USA.

585 Ulanowicz, R.E., 2009. The dual nature of ecosystem dynamics. *Ecol Model* 220, 1886-1892.

586 Ulanowicz, R.E., Abarca-Arenas, L.G., 1997. An informational synthesis of ecosystem structure and
587 function. *Ecol Model* 95, 1-10.

588 Vinagre, C., Costa, M.J., 2014. Estuarine-coastal gradient in food web network structure and properties. *Mar*
589 *Ecol Prog Ser* 503, 11-21.

590 Wilson, J.G., 2002. Productivity, fisheries and aquaculture in temperate estuaries. *Est Coast Shelf Sci* 55,
591 953-968.

592 **FIGURE LEGENDS**

593 **Figure 1.** Map of the study area in the Seine estuary, northern France, with bathymetry and
594 showing the subdivision of the six modelled habitats. Sources: Le Havre and Rouen port authorities,
595 SHOM, and GIP Seine-Aval.

596 **Figure 2.** Conceptual diagram explaining how Ecopath splits the production flows into the energy
597 balance, and how the various functional groups (represented by the pies) are connected, as
598 production for a prey is consumption for a predator. In our work, harvest (Y in Equation 1) was
599 assumed zero.

600 **Figure 3.** Flows and biomasses of the three estuarine habitats (CH, FN, FS). Flows values by diet
601 are indicated by the colour scale, while group biomasses are logarithmically proportional to the area
602 of their respective circles. Groups are vertically positioned by their calculated trophic level.

603 **Figure 4.** Flows and biomasses of the three marine habitats (E4, E14, E2). Flows values by diet are
604 indicated by the colour scale, while group biomasses are logarithmically proportional to the area of
605 their respective circles. Groups are vertically positioned by their calculated trophic level.

606 **Figure 5.** Continuous trophic analysis of (a) biomass and (b) keystoneindex, by trophic levels, for
607 the six modelled habitats of the Seine Bay. Grey rectangles indicate the position of peaks identified
608 in (a) as second-order consumers, and are repeated in (b) for reference. The first grey bar represents
609 the peak of second-order consumers in estuarine habitats and the second one the peak in marine
610 habitats.

611 **Figure 6.** Keystoneindex by [Libralato et al. \(2006\)](#) by functional group for each of the six
612 modelled habitats (indicated also by colour codes). The area of circles is proportional to each group
613 biomass, relative to its habitat. Only groups with high keystoneindex (> 0.55) are represented.

614

Table 1. Biomass values, and production, consumption, and assimilation rates for the 6 modelled ecosystems after balancing. When a range is given, it means that values were changed during balancing and between models according to general species composition. Biomass values estimated by the model are indicated in bold.

		Biomass (gC m ⁻²)						P/B (year ⁻¹)	Q/B (year ⁻¹)	U/Q
		CH	FN	FS	E4	E14	E2			
1	Seabirds	0.633	0.633	0.633	0.300	0.300	0.300	0.013	0.325	0.20
2	Fish, piscivores	0.019	0.055	0.057	0.143	0.103	0.264	0.480–0.587	3.50	0.20
3	Fish, planktivores	0.040	0.075	0.027	0.043	0.026	0.032	0.800–0.960	6.70	0.20
4	Fish, benthos feeders	0.012	0.038	0.230	0.560	0.244	0.554	1.360	7.83	0.20
5	Fish, endobenthic feeders	0.015	0.035	0.045	0.141	0.123	0.175	1.038–1.280	4.57	0.20
6	Benthic predators	0.155	11.150	8.530	5.950	5.230	2.202	1.19–1.40	5.95–7.00	0.20
7	Benthic filter feeders	0.442	1.900	15.087	3.580	3.810	8.710	1.04–1.12	5.21–5.34	0.30
8	Benthic deposit feeders	0.146	1.760	3.850	6.134	6.134	4.255	1.56–1.76	7.85	0.30
9	Suprabenthos	2.208	2.380	3.700	4.320	6.290	7.160	5.95–6.60	27–33	0.30
10	Meiofauna	0.427	0.119	0.400	0.377	0.402	0.167	12–16	60–75	0.30
11	Zooplankton	1.720	1.720	1.850	1.720	1.720	1.620	38.4–52.5	128–150	0.40
12	Bacteria	1.020	2.800	2.800	2.800	1.910	0.600	26.8–125	53.5–250	0.35
13	Microphytobenthos	0.094	1.725	1.720	0.309	0.374	0.384	33–35		
14	Phytoplankton	3.300	1.126	1.470	2.220	3.240	1.627	150		
15	Detritus	19.000	19.000	19.000	19.000	19.000	19.000			

Table 2. Common diet matrix used as input for the 6 modelled habitats. Diets, which are presented by predator (columns) and sum to 1, were slightly modified to balance the equations in each model.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12
1 Seabirds												
2 Fish, piscivores	0.050											
3 Fish, planktivores	0.050	0.300										
4 Fish, benthos feeders		0.100	0.020	0.040								
5 Fish, endobenthic feeders		0.140	0.020									
6 Benthic predators	0.100	0.280	0.010	0.280	0.070							
7 Benthic filter feeders	0.100	0.040		0.050	0.290	0.250						
8 Benthic deposit feeders	0.100	0.060	0.090	0.310	0.260	0.120						
9 Suprabenthos		0.080	0.165	0.100	0.150	0.180			0.100			
10 Meiofauna			0.040		0.060	0.250	0.050	0.050				
11 Zooplankton			0.355	0.070	0.020	0.050	0.100	0.050	0.400	0.050		
12 Bacteria							0.050	0.100		0.050		
13 Microphytobenthos						0.050	0.100	0.200	0.200	0.100		
14 Phytoplankton			0.300				0.600	0.100		0.100	0.650	0.100
15 Detritus				0.150	0.150	0.100	0.100	0.500	0.300	0.700	0.350	0.520
Import	0.600											0.380

Table 3. General system statistics and ecological network analysis (ENA) indices of the 6 modelled ecosystems in the Seine Bay.

	CH	FN	FS	E4	E14	E2	
Model area	24	25	28	270	232	90	km ²
Sum of all consumption	413.05	575.62	706.82	633.78	703.92	697.84	g m ⁻² y ⁻¹
Sum of all exports	123.14	100.81	1681.98	183.34	300.59	84.54	g m ⁻² y ⁻¹
Sum of all respiratory flows	123.14	188.65	257.83	220.56	258.82	232.21	g m ⁻² y ⁻¹
Sum of all flows into detritus	535.92	295.98	1938.30	417.92	563.11	356.79	g m ⁻² y ⁻¹
Total system throughput (T..)	1469.04	1161.05	4584.92	1455.60	1826.44	1371.39	g m ⁻² y ⁻¹
Sum of all production	635.75	417.10	492.31	541.72	707.27	483.24	g m ⁻² y ⁻¹
Calculated total net primary production	498.10	229.34	280.70	343.82	499.31	256.71	g m ⁻² y ⁻¹
Total primary production/total respiration	2.59	1.22	1.09	1.56	1.93	1.11	
Net system production	374.97	40.70	22.87	123.26	240.50	24.50	g m ⁻² y ⁻¹
Total primary production/total biomass	48.68	8.99	6.95	12.02	16.68	9.15	
Total biomass/total throughput	0.007	0.022	0.009	0.020	0.016	0.020	
Total biomass (excluding detritus)	10.23	25.52	40.40	28.60	29.94	28.05	g m ⁻²
Fish biomass / invertebrate biomass	1.48	1.17	1.14	4.36	2.27	4.56	%
Total transfer efficiency	4.50	5.20	6.80	9.10	7.40	9.90	%
System Omnivory index (SOI)	0.184	0.193	0.160	0.186	0.177	0.160	
Finn's cycling index (FCI)	8.52	18.94	3.65	13.86	11.23	20.65	% of T..
Average path length (APL)	2.825	4.011	2.634	3.604	3.265	4.330	
Relative redundancy (R/C)	0.556	0.535	0.380	0.580	0.590	0.542	

Table 4. Qualitative analysis of impacts for each of the 6 modelled habitats. Categories ranged from – for no impact to +++ for very high impact.

	CH	FN	FS	E4	E14	E2	References
Dredging	+++	-	-	-	-	-	Marmin et al. (2014)
Deposit	+	+++	-	+++	-	-	Marmin et al. (2014)
Dyke	+++	++	++	-	-	-	Guezennec (1999) ; Cuvilliez et al. (2009)
Loss of intertidal zones	-	+++	-	-	-	-	Cuvilliez et al. (2009) ; Dauvin and Desroy (2005)
Shrimp fishing	+	+	+	+++	-	-	Morin et al. (2010)
Other commercial trawling	-	-	+	++	++	++	Morin et al. (2010)
Granulate extraction	-	-	-	-	-	+	Marmin et al. (2014)
Salinity decrease	+++	++	+	+	-	-	Dauvin and Pezy (2013)
Port construction	+	+++	-	-	-	-	Dauvin et al. (2006)
Bridge construction	-	+++	-	-	-	-	Cuvilliez et al. (2009)
Siltation (arrival of fine terrestrial particulate)	+	+	++	+++	-	-	Guezennec (1999)
Increase in sandy sediments	-	+++	+	-	-	-	Cuvilliez et al. (2009) ; Dauvin et al. (2006)
Presence of maximal turbidity zone	+++	+	+	++	-	-	Guezennec (1999)
Residual currents (disturbance)	+++	+++	++	+	+	+	Le Hir (2001)

Figure 1
[Click here to download high resolution image](#)

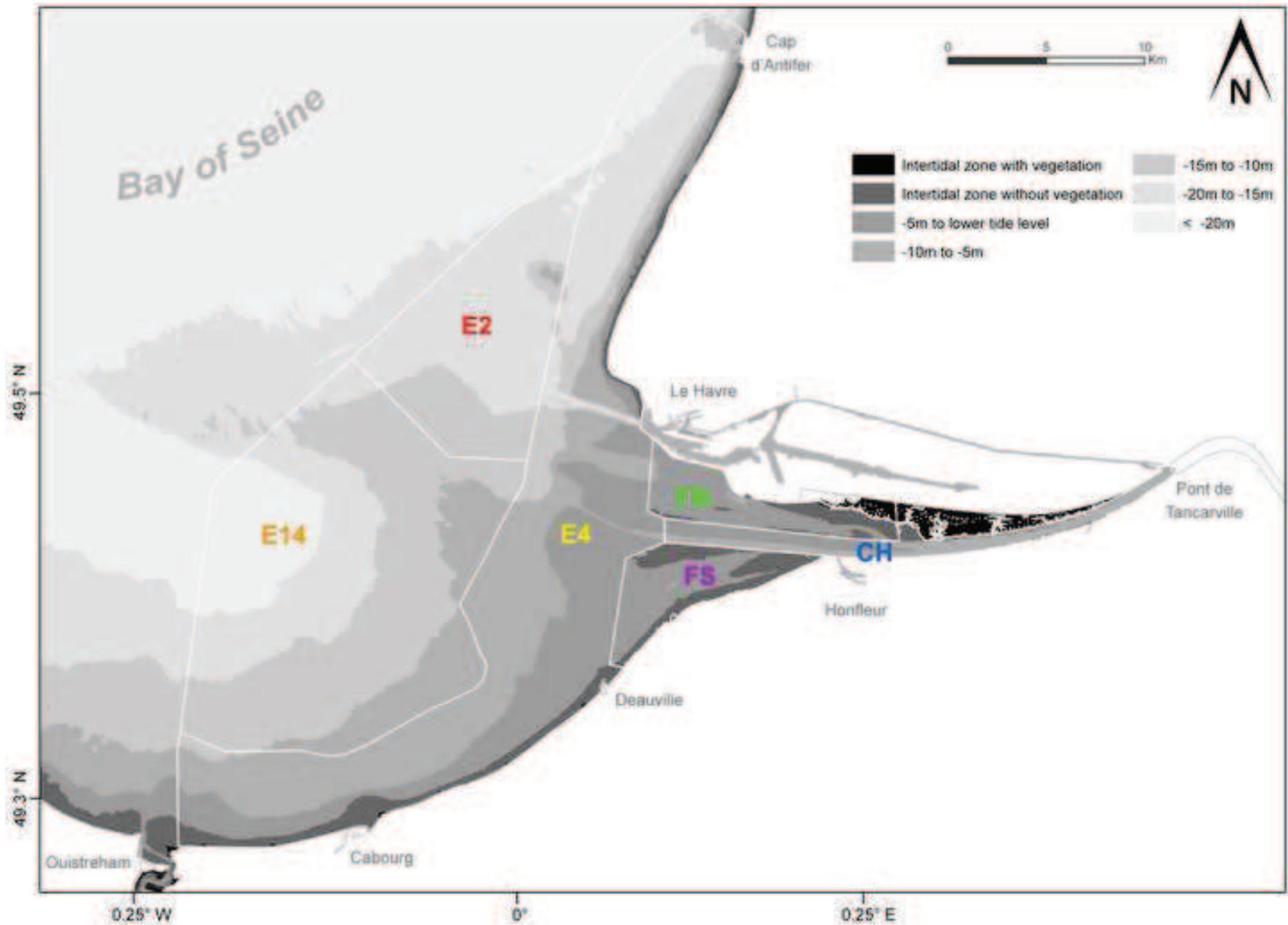


Figure 2
[Click here to download high resolution image](#)

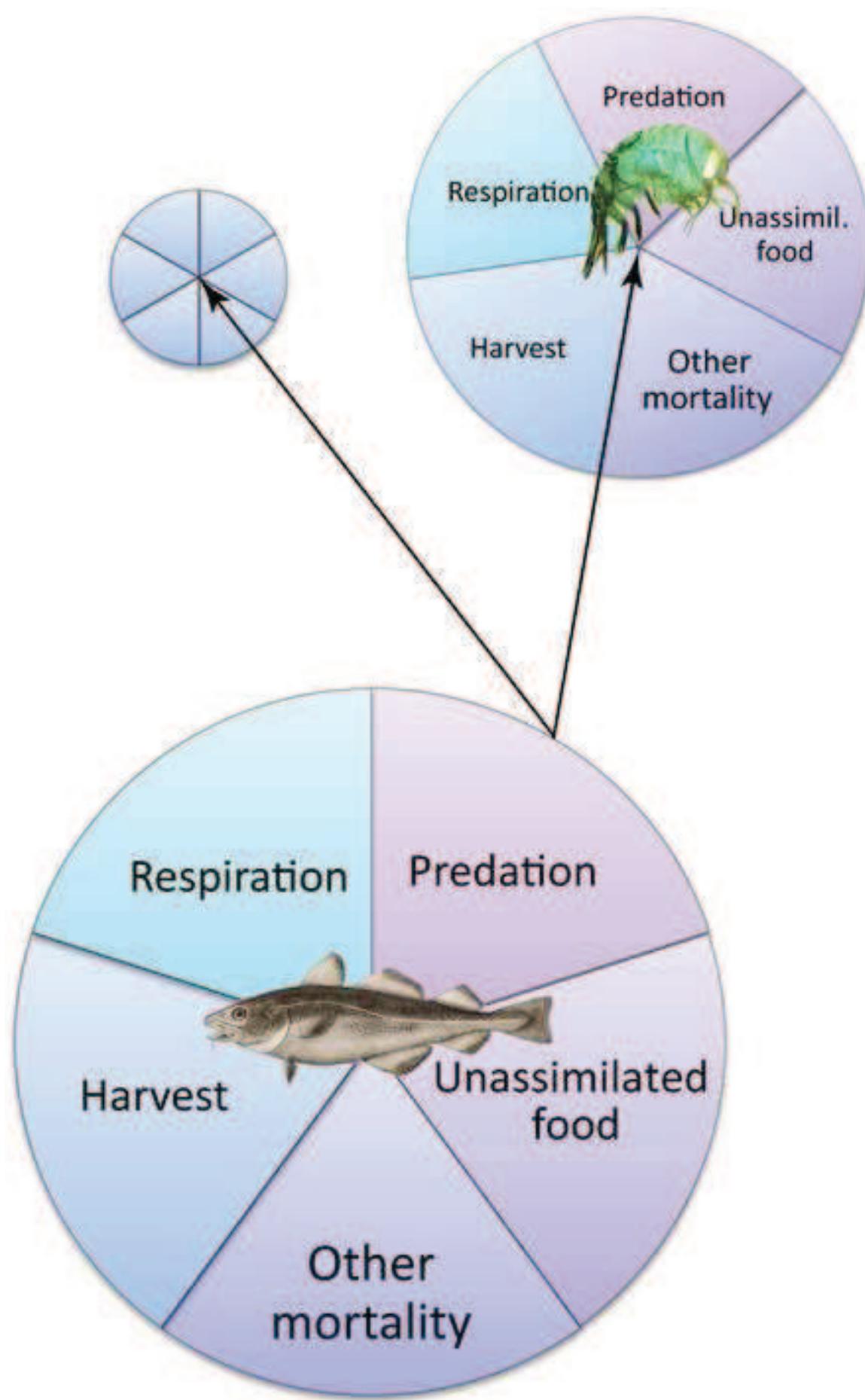
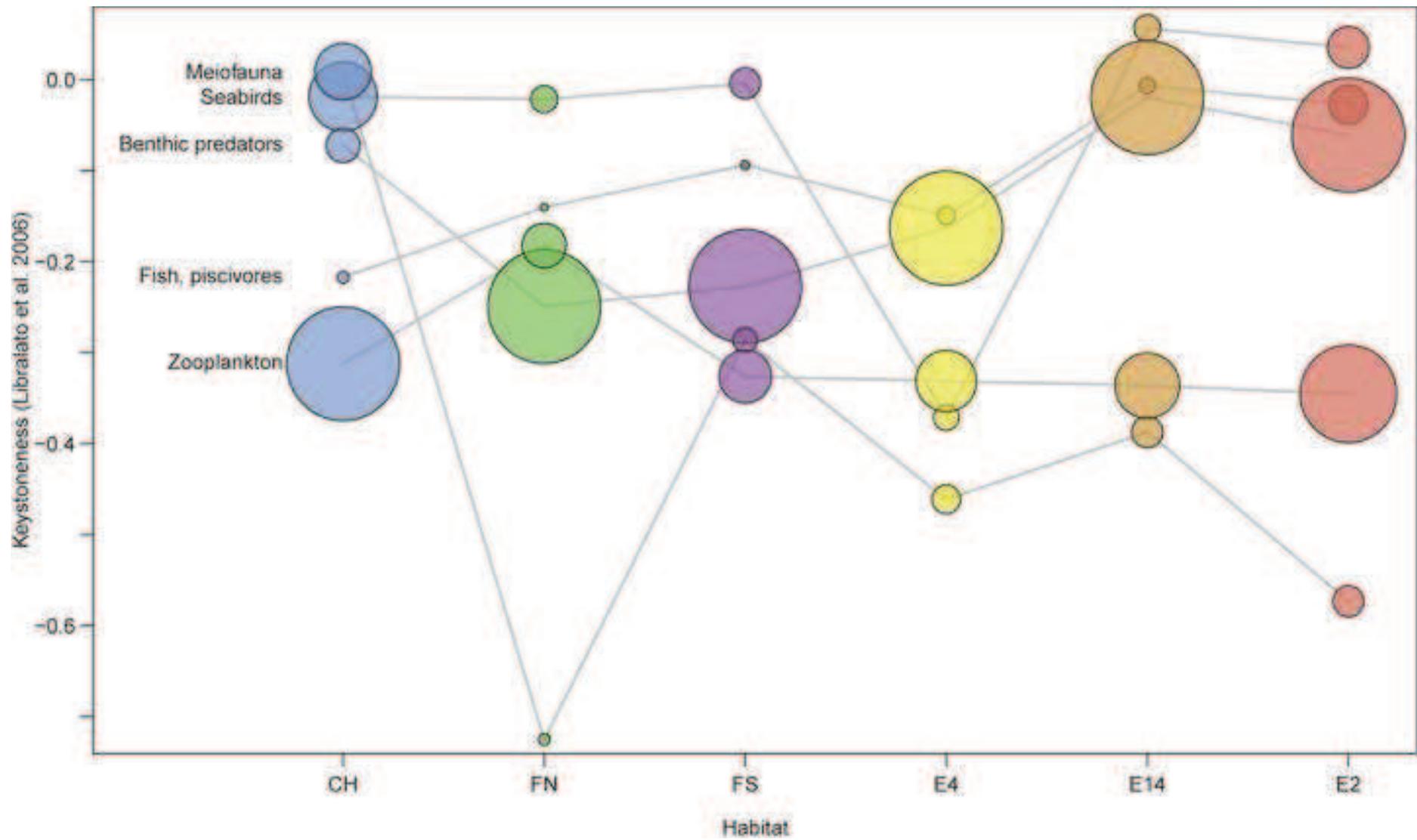


Figure 4
[Click here to download high resolution image](#)



Figure 6

[Click here to download high resolution image](#)



Supplementary material for online publication only

[Click here to download Supplementary material for online publication only: Supplementary material EwE Seine.pdf](#)

Manuscript with track-change (for review only)

[Click here to download Supplementary material for online publication only: Tecchio et al - Seine habitats - v2 - TrackChange.doc](#)