# Food limitation of juvenile marine fish in a coastal and estuarine nursery

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**Abstract :**

Despite their importance for species conservation and sound management of exploited living resources, the density-dependent mechanisms that regulate wild populations are among the least understood process in ecology. In many marine fish species, there is strong evidence that regulation occurs at the juvenile stage, when individuals concentrate in spatially restricted nurseries. However, little is known about the underlying mechanisms. Whether competition for food resources determines fish growth and survival is particularly controversial. We investigated whether food supply may have limited juvenile fish production (integrating both growth and survival) in a coastal and estuarine nursery in western Europe. Using a recent bioenergetics-based approach, we calculated annual macrobenthic food production (FP) and annual food consumption (FC) by juvenile fish and predatory invertebrates for three consecutive years (2008–2010). We also calculated exploitation efficiency (FC:FP) and used it as an index of food limitation. Results revealed substantial interannual variations in FP (FP ~2–3 times higher in 2008 and 2010 than in 2009). FC by young-of-the-year fish followed a fairly similar pattern. In addition, predatory invertebrates consumed as much food as juvenile fish, highlighting the need to consider all dominant epibenthic predators when estimating the overall predation pressure on macrobenthic prey. Lastly, exploitation efficiency of the entire epibenthic predator community reached ~30% in 2009, which is relatively high despite the conservative modeling approach. Overall, these results suggest that food supply may have limited juvenile fish production during the study period, at least in 2009. Nonetheless, further studies based on longer time-series and/or other study sites are required to strengthen these findings.

**Graphical abstract**
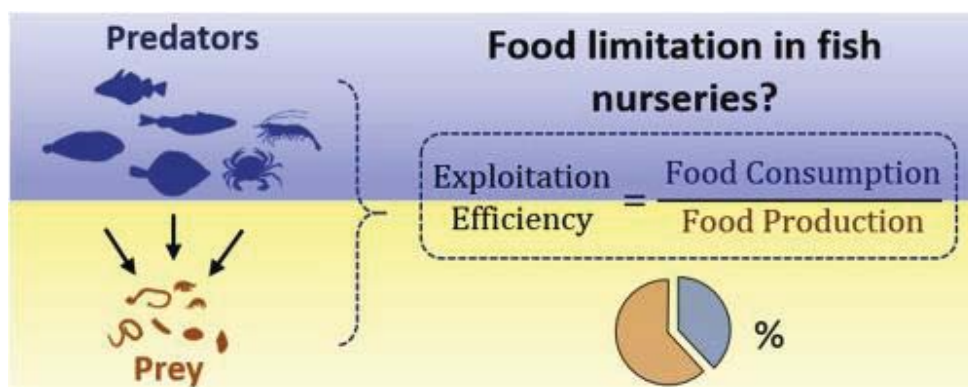


**Highlights**

► Annual macrobenthic food production varied greatly from 2008 to 2010. ► Food consumption by young-of-the-year fish followed a fairly similar pattern. ► Predatory invertebrates consumed as much food as juvenile fish. ► Exploitation efficiency of the epibenthic predator community reached ~30% in 2009. ► Food supply may limit juvenile fish production in the Seine nursery.

**Keywords** : Food limitation, nursery, juvenile fish, predatory invertebrates, macrofauna, English Channel

## 1. Introduction

Understanding the processes that regulate the abundance of wild populations is a primary goal in ecology, with direct implications for species conservation and sustainable management of exploited living resources (Hixon et al. 2002; Koons et al. 2015). In coastal and estuarine ecosystems, individuals from many fish species concentrate during the juvenile stage in spatially restricted nurseries (Beck et al. 2001). Although there is strong evidence that this concentration results in density-dependent regulation (Myers and Cadigan 1993; Iles and Beverton 2000; Minto et al. 2008), the underlying processes remain poorly understood (Hixon and Jones 2005; van Poorten et al. 2018). Competition for limiting resources and predation are often cited as the ultimate factors that cause density-dependent growth and survival (Post et al. 1999). Since predation pressure on juvenile fish is generally accepted as low in coastal nurseries (Bergman et al. 1988; Nash and Geffen 2000; Gibson et al. 2002; Litvin et al. 2018), competition for limiting resources, particularly food, seems more likely. Competition occurs when individuals of one or more species utilize common resources that are in short supply (Birch 1957). Hence, it is closely related to the carrying capacity of ecosystems (Hollowed et al. 2000), which is determined by the strength of intra- and interspecific density dependence (Brown et al. 2018). In marine ecosystems, most bentho-demersal fish species are considered opportunistic predators (Hunsicker et al. 2011). Even though food partitioning exists and may reduce competition among fish (Besyst et al. 1999; Darnaude et al. 2001), many species likely share a common pool of prey, particularly during their juvenile stage (Dolbeth et al. 2008; Schückel et al. 2012). Therefore, the amount of food available to each individual is ultimately affected by what the others consume, suggesting both intra- and interspecific competition in fish nurseries (Nunn et al. 2012). However, evidence that food supply actually limits juvenile fish production is rare, and the "food limitation hypothesis" remains controversial (Le Pape and Bonhommeau 2015).

In temperate ecosystems, juvenile marine fish concentrate in nursery grounds from late spring to early fall, when the biomass of macrobenthic prey peaks (Beukema 1974; Saulnier et al. 2019). Nonetheless, because the food supply varies annually, notably due to environmental fluctuations (Holland et al. 1987; Dolbeth et al. 2011), it may regulate production of juvenile fish, at least when settlement is high and/or prey availability is low (Nash et al. 2007; Le Pape and Bonhommeau 2015). Population regulation operates through changes in life-history traits such as growth, condition and survival (Andersen et al. 2017). Therefore, many studies investigated whether food was limiting by

88 comparing the growth rate observed in the field to optimal growth rates predicted by experimental or

89 bioenergetic models (Amara et al. 2001; van der Veer et al. 2010; Freitas et al. 2011; Selleslagh and

90 Amara 2013). However, this approach has some disadvantages. For example, observed growth rates

91 often remain nearly optimal, even when food is limiting, because slow-growing individuals have lower

92 survival and are thus rarely sampled (Le Pape and Bonhommeau 2015). Another approach is to

93 correlate time-series of food supply and fish abundance, fish condition or survival (Beaugrand et al.

94 2003; Okamoto et al. 2012; Latour et al. 2017), but long-term datasets with both prey and predator

95 indices are rarely available. Alternatively, the extent to which food is limiting can be inferred directly

96 from the proportion of prey production that is consumed by their predators (Evans 1983; Boisclair and

97 Leggett 1985; Collie 1987; Vinagre and Cabral 2008).

98     In the present study, we used this third approach to investigate whether competition for food

99 may limit juvenile fish production in coastal and estuarine nurseries. We focused on the outer Seine

100 estuary and the eastern Bay of Seine, in western Europe. This area is an important nursery ground for

101 many species that support commercial fisheries (Rochette et al. 2010, 2013; Archambault et al. 2016).

102 Like many estuarine ecosystems, this area experiences strong natural and anthropogenic stress

103 (Elliott and Quintino 2007), especially due to pollution and coastal development (Dauvin 2008; Tecchio

104 et al. 2015). In particular, its area of essential shallow and productive habitats has decreased

105 significantly over the past century due to the progressive extension of Le Havre harbor, dike

106 construction and channel dredging (Dauvin et al. 2006; Le Pape et al. 2007). Despite recent efforts to

107 reverse some anthropogenic changes (Ducrotoy and Dauvin 2008), this lasting morphological

108 alteration likely decreased the carrying capacity of the Seine estuary (e.g. for the common sole *Solea*

109 *solea*, Rochette et al. 2010, Archambault et al. 2018) and may have exacerbated competition among

110 juvenile fish.

111     To this case study, we applied a bioenergetics-based approach recently developed to

112 investigate the food limitation hypothesis in estuarine and coastal nurseries (Tableau et al. 2019).

113 Rather than searching for potential changes in life-history traits induced by food limitation (*e.g.*

114 condition, growth), this approach directly estimates whether the food supply is sufficient to support the

115 energy requirements of the predator community. Using literature and field data from scientific surveys,

116 we estimated an exploitation efficiency (EE), defined as the ratio of food consumption (FC) by

117 epibenthic predators to macrobenthic food production (FP). This ratio was used as index of food

118 limitation in coastal nurseries. While the method originally focused on juvenile fish, we extended it to

119 include the amount of food consumed by epibenthic predatory invertebrates commonly found in

120 estuarine and coastal ecosystems. Our goal was three-fold: (1) assess interannual (2008-2010) and

121 spatial (among strata) variations in FP and FC by epibenthic predators, (2) compare the FC by juvenile

122 fish and predatory invertebrates and (3) quantify how much food was consumed annually by the

123 epibenthic predator community, thus providing new insight into food limitation for juvenile fish in

124 coastal and estuarine nurseries.

125

126

## 2. Materials and methods

127

### 2.1. Study area

128

129 The outer Seine Estuary and the adjacent eastern Bay of Seine are located in the English

130 Channel on the northwest coast of France, western Europe (Fig. 1). This macrotidal area (the "Seine

131 nursery"), has a tidal range of ~7 m near Le Havre harbor and a mean river flow of ~470 $m^3.s^{-1}$ at the

132 entrance of the estuary, with high intra- and inter-annual variations in river discharge (Dauvin et al.

133 2017; Romero et al. 2018). The study site covers a subtidal shallow (mean depth = 8.2 m) area of 360

134 km², characterized by muddy-fine sand sediments and composed mostly of polyhaline waters in the

135 outer estuary and euhaline waters in the bay (Thiébaut et al. 1997; Savoye et al. 2003). The mean

136 annual sea bottom temperature during our study period was 12.8°C.

137

### 2.2. Data collection and selection

138

139 Epibenthic predators and their macrobenthic prey were sampled from 2008-2010 in late

140 summer using a stratified random sampling design, with stratification based on bathymetry and

141 sediment composition (Tecchio et al. 2015). The study site was divided into four strata that covered

142 the area sampled each year from 2008-2010: FN and FS in the outer Seine estuary and E4 and E14 in

143 the eastern Bay of Seine (Fig. 1). The navigation channel, separating FN and FS, was excluded since

144 it was sampled only in 2008. All strata were sampled using both grab and trawl devices.
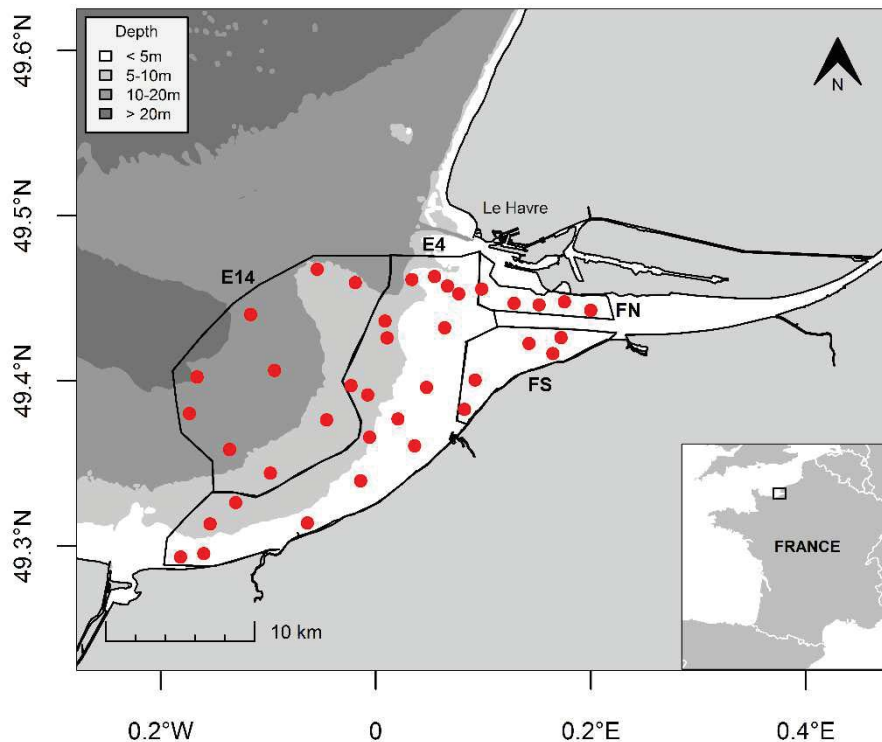
Fig. 1. Location of the sampling stations (n = 38) in the four strata of the study site: FN, FS (outer Seine estuary), E4 and E14 (eastern Bay of Seine). Red dots indicate the mean coordinates of each trawl haul, where the grab was deployed.

**2.2.1. Grab sampling survey**

Macrobenthic invertebrates were sampled using a 0.1 m² grab (Van Veen or Smith-MacIntyre) at 38 stations in 2008 (early October) and 2009 (early September) and 32 stations in 2010 (12 in early September, 20 in late November). Three to five replicates were collected at each station and sieved on board through a 1 mm mesh sieve using seawater. The material retained was fixed with a 10% buffered formaldehyde solution. In the laboratory, retained organisms were identified to the lowest possible taxonomic level (usually species), counted and weighed. Dry mass per taxon was determined by weighing the samples after drying at 60°C for 72 h. Then, ash-free dry mass (AFDM) was determined as dry mass minus ash mass after combusting the dried samples in a muffle furnace at 500°C for 6 h. Biomass and abundance were recorded in 2008 and 2010, while only abundance was recorded in 2009. Thus, biomass per taxon in 2009 was estimated for each sample as $B_i = A_i \cdot W_i$, where $B_i$ and $A_i$ are the biomass and abundance of taxon i, respectively, and $W_i$ is the mean individual body mass of taxon i averaged over all samples collected in both 2008 and 2010. Replicates

6

163    were pooled for each station, and biomass was expressed as g AFDM.m$^{-2}$ and abundance as

164    individuals.m$^{-2}$. We verified that the results obtained in 2009 were robust and were not an artefact of

165    the method used to estimate the macrobenthic biomass that year (Supplement S1).

166

167    **2.2.2. Prey selection**

168        Juvenile fish and epibenthic invertebrate predators are considered opportunistic feeders

169    (Besyst et al. 1999; Cabral et al. 2002; van der Veer et al. 2011). Thus, we used a conservative

170    approach by considering all macrobenthic taxa found in grab samples as potential prey, except for

171    *Asterias rubens*, *Echinocardium cordatum*, and *Crepidula fornicata*, which were never observed in gut

172    contents (unpubl. data). We also excluded rare taxa (sampled at a single station and/or during a single

173    year), which added little to the analysis. We also excluded shrimp-like species (e.g. *Crangon crangon*,

174    *Processa* spp.), even though these taxa were more frequent (occurrence ≥ 2), because their

175    abundance and biomass were always extremely low due to grab's difficulty in catching these mobile

176    invertebrates. Finally, we excluded taxa with a mean body mass ≥ 0.1 g AFDM (~ equivalent to a

177    length ≥ 16 mm; Supplement S2) at each station since they were considered too large to be prey

178    (Tableau et al. 2015). Overall, we retained 147 prey taxa that represented, on average, 81% by mass

179    and 99% by abundance of the total catch (excluding *A. rubens*, *E. cordatum* and *C. fornicata*).

180

181    **2.2.3. Trawl sampling survey**

182        The epibenthic predator community was sampled at 38 stations using a 2.9-m beam trawl with

183    a 20-mm mesh in the cod-end and one tickler chain (in late September in 2008 and 2009, and late

184    August in 2010). Each haul, performed during daytime with the same trawl towed by a research vessel

185    at a mean speed of 2.5 knots, covered a mean area of 3250 m², except in the FN strata, where it was

186    replaced with a 2-m beam trawl with the same characteristics (20-mm mesh in the cod-end, 1 tickler

187    chain) to sample four shallow stations. In 2009, the hauling operation failed at one station, and the

188    corresponding haul was thus excluded. All individuals caught in the net were identified, counted and

189    weighed by species on board. Fish were measured to the nearest 1 cm total length and separated into

190    age groups by reading otolith increments (for commercial species) or using length-frequency

191    distributions (Supplement S5).

192

193    **2.2.4. Predator selection**

194          We focused on the dominant epibenthic predators of the Seine nursery that feed at least partly

195    on macrobenthic invertebrates. To this end, we selected seven bentho-demersal fish species

196    (common sole *S. solea,* European plaice *Pleuronectes platessa,* common dab *Limanda limanda,*

197    common dragonet *Callionymus lyra*, whiting *Merlangius merlangus*, bib *Trisopterus luscus* and sand

198    goby *Pomatoschistus minutus*) observed mostly at the juvenile stage (young-of-the-year (G0) and G1)

199    and seven predatory invertebrate species (common sea star *A. rubens,* brown shrimp *C. crangon,*

200    shore crab *Carcinus maenas,* swimming crabs *Liocarcinus holsatus, Liocarcinus vernalis* and

201    *Liocarcinus depurator,* and velvet crab *Necora puber*). These species represented, on average, 80%

202    and 90% of the total catch of bentho-demersal fish and predatory invertebrates by mass, respectively.

203    For fish species, we restricted analysis to the size range corresponding to the period during which fish

204    actively feed on macrofauna. FC by fish < 5 cm was thus ignored, since they feed primarily on

205    meiofauna (Pihl 1985; Gee 1989; del Norte-Campos and Temming 1994; Amara et al. 2001). All

206    predatory invertebrates caught in the net were assumed to be large enough to feed actively on

207    macrofauna.

208

209    **2.3. Estimating macrobenthic food production**

210          FP of macrobenthic prey (kJ.yr$^{-1}$) was estimated as follows:

$$FP = \sum_{j \in 1:J^{th} \text{ prey species}} CR \cdot B_j \cdot P{:}B_j \cdot (1 + R_j) \cdot E_j$$

211    where CR is a seasonal ratio (unitless) that converts macrobenthic biomass into mean annual biomass

212    (estimated from Saulnier et al. 2019; Supplement S3), $B_j$ is the total biomass observed during the

213    survey (g AFDM), $P{:}B_j$ is the production-to-biomass ratio (yr$^{-1}$) estimated using an empirical model

214    (Brey 2012), $R_j$ is a regeneration coefficient (unitless) that represents somatic regeneration after

215    sublethal predator cropping (Tableau et al. 2015) and $E_j$ is the energy density (kJ.g AFDM $^{-1}$) from a

216    global database (Brey et al. 2010) that converts biomass into energy for prey species j.

217    For each species j, total biomass $B_j$ (g AFDM) in the study area was estimated as follows:

218          $B_j = \sum_{k \in 1:4} \overline{B}_{j,k} \cdot \alpha_k$

8

219 where $\overline{B}_{j,k}$ is the mean biomass (g AFDM.m$^{-2}$) of species j recorded during the survey in stratum k,

220 and $\alpha_k$ is the area (m$^2$) of stratum k.

221 To calculate FP, we implicitly assumed that juvenile fish and large epibenthic invertebrates shared a

222 single pool of macrobenthic prey, since these predatory species are considered opportunistic feeders

223 (van der Veer et al. 2011).

224

**2.4. Estimating food consumption by epibenthic predators**

226 FC corresponds to the amount of macrobenthic food items consumed annually by the

227 epibenthic predators in the nursery grounds. FC (kJ.yr$^{-1}$) is derived from the production of each

228 predator and the proportion of macrofauna in its diet, as follows:

$$FC = \sum_{i \in 1:I^{th}\ predator} P_i \cdot DC_i \cdot E_i \cdot \frac{1}{K_i}$$

229 where $P_i$ is the production of predator i (g.yr$^{-1}$), $DC_i$ is the proportion of benthic macrofauna in its diet,

230 $E_i$ is its energy density (kJ.g$^{-1}$) and $K_i$ is its gross conversion efficiency, defined as its

231 production:consumption ratio (Christensen et al. 2005). Parameters $DC_i$, $E_i$ and $K_i$ were derived from

232 the literature (Table 1, Supplement S6). Two methods were used to calculate the $P_i$ of juvenile fish and

233 predatory invertebrates, depending on their residence time in the nursery and the availability of cohort

234 data.

235

**2.4.1. Production of juvenile fish**

237 Many fish species use coastal shallow waters as a nursery ground during the juvenile stage

238 before moving offshore after maturation (Beck et al. 2001). They feed on macrobenthic prey only

239 during a certain period. For instance, they prey primarily upon meiofauna shortly after settlement and

240 progressively shift to macrofauna as they grow (e.g. Gee 1989; Amara et al. 2001). Following Tableau

241 et al. (2019), we calculated fish production using a cohort-based method that explicitly includes

242 ontogenic feeding shifts and residence time in the nursery. The P (g.m$^{-2}$) of each fish cohort in the

243 nursery was calculated as follows:

$$P = \sum_{d \in d_0:D} \frac{n_{d+1} + n_d}{2} \cdot (w_{d+1} - w_d)$$

9

244  where $d_0$ and $D$ are the first and the last day of its growth period, respectively, during which fish feed

245  on macrofauna, $n_{d+1}$ and $n_d$ are the number of individuals (m$^{-2}$) on days $d+1$ and $d$, and $w_{d+1}$ and

246  $w_d$ are mean individual body weight (g) on the same consecutive days.

247  Date $d_0$ was estimated as:

$$d_0 = \frac{L_{d_0} - L_s}{G} + s$$

248  where $s$ is the date of the survey, $L_{d_0}$ is the mean length (mm) of a fish cohort on day $d_0$, $L_s$ is its

249  mean length (mm) observed on day $s$ and $G$ is the mean daily growth rate (mm.day$^{-1}$) of the fish

250  species derived from the literature (Table 1, Supplement S6).

251  Date $D$ corresponds to the end of the main growth period in the nursery, which is autumn in temperate

252  ecosystems (van der Veer et al. 1990; Rogers 1994; Bouchereau and Guelorget 1998) and was set to

253  31 October (Jung et al. 2017). Length $L_{d_0}$ was set to 50 mm for G0 fish (see section 2.2.). Assuming

254  negligible growth during winter, $L_{d_0}$ of G1 fish was set to the $L_D$ of G0 fish in the previous year, where

255  $L_D$ is the length estimated on day $D$ for each species. Since no data were available in 2007, $L_{d_0}$ of G1

256  fish in 2008 was set to the $L_D$ of G0 fish averaged over 2008-2010.

257  For each cohort, the number of individuals $n_d$ and mean body weight $w_d$ on day $d$ were calculated

258  using catch efficiency, daily growth rate and daily mortality rate from the literature (Table 1,

259  Supplement S6) and survey data, as follows:

$$n_d = \frac{C_s}{q} \cdot e^{-(d-s).Z}$$

260  where $C_s$ is the total number of individuals in the study area on day $s$, $q$ is the catch efficiency

261  (unitless) and $Z$ is the daily mortality rate (day$^{-1}$).

262  The total number of individuals $C_s$ in the study area was estimated as follows:

263  $\qquad C_s = \sum_{k \in 1:4} \overline{C}_{s,k} \cdot \alpha_k$

264  where $\overline{C}_{s,k}$ is the mean density (ind.m$^{-2}$) recorded during the survey in stratum k and $\alpha_k$ is the area of

265  stratum k (m$^2$).

266  Mean body weight $w_d$ (g) was calculated as follows:

$$w_d = a.[L_s + (d-s).G]^b$$

267      where $a$ and $b$ are coefficients of the length-weight relationship estimated using local survey data, $L_s$

268      is the mean length (mm) of a fish cohort collected during the survey on day $s$, and $G$ is the mean daily

269      growth rate of a fish species during its main growth period (mm.day$^{-1}$).

270

271      **2.4.2. Production of epibenthic predatory invertebrates**

272      Unlike the size of juvenile fish, that of epibenthic predatory invertebrates was not measured

273      during the surveys, which prevented application of a cohort- or size-based method to calculate their

274      annual production. Instead, we calculated the annual production P (g.y$^{-1}$) of each invertebrate species

275      using a population-based method, as follows:

$$P = \frac{1}{q} \cdot B \cdot P{:}B$$

276      where $q$ is catch efficiency (unitless) obtained from the literature (Table 1, Supplement S6), $B$ is the

277      total biomass of the species in the study area during the survey (g) and $P{:}B$ is its production-to-

278      biomass ratio (y$^{-1}$) estimated using an empirical model (Brey 2012; Supplement S4).

279      For each species, total biomass $B$ (g) in the study area was estimated as:

280      $$B = \sum_{k \in 1:4} \overline{B}_k \cdot \alpha_k$$

281      where $\overline{B}_k$ is mean biomass (g.m$^{-2}$) of the species recorded during the survey in stratum $k$ and $\alpha_k$ is the

282      area (m$^2$) of stratum $k$.

283      Unlike the biomass of macrobenthic prey, that of predatory invertebrates recorded in late summer was

284      not corrected for seasonality since it was unclear whether it varies seasonally in nearshore areas (Hinz

285      et al. 2004; Reiss and Kröncke 2004, and local unpubl. data).

286

287      **2.5. Exploitation efficiency and uncertainty analysis**

288      We quantified the percentage of macrobenthic production consumed annually by the main

289      epibenthic predators from 2008-2010 as EE (%), equal to $(FC/FP) \cdot 100$. We also performed Monte-

290      Carlo simulations to quantify uncertainty in estimates of EE. Variables and parameters used to

291      estimate EE were separated into three categories (Tableau et al. 2019). Those with high and

292      quantifiable uncertainty were defined using probability distributions (Supplement S7). They included

293      fish abundance Cs, biomass B and P:B ratios of invertebrate predators and macrobenthic prey, the

294      seasonal coefficient CR, and the energy density E and gross conversion efficiency K of epibenthic

predators. Other variables or parameters were set to fixed values, either because their uncertainty was assumed to be low (e.g., local survey data collected at the species level; second category) or not quantifiable due to the lack of literature data (third category). For the third category, we used a conservative approach by selecting values that would underestimate EE. Finally, we calculated EE by randomly sampling from the probability distributions of each variable and parameter (10 000 iterations). We calculated EE of the young-of-the-year fish community (G0), all juvenile fish (G0 and G1) and all epibenthic predators (fish and invertebrates). All analyses were performed using the statistical software R (version 3.3.3, R Core Team 2017).

Table 1. Parameters used to calculate food consumption by epibenthic predators. Most data came from Tableau et al. (2019), Jung et al. (2017), Reiss et al. (2006), and references therein. See Supplement S6 for details. DC: proportion of benthic macrofauna in the diet, E: energy density, K: gross conversion efficiency, q: catch efficiency, G: daily growth rate, and Z: daily mortality rate. DC, K and q are unitless.

| Group | Species | Age group | DC | E (kJ.g$^{-1}$) | K | q | G (mm.d$^{-1}$) | Z (d$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Fish | *Solea solea* | 0 - I | 0.95 | 5.74 | 0.197 | 0.257 | 0.057 | 0.0179 - 0.0103 |
| | *Pleuronectes platessa* | 0 - I | 0.95 | 5.74 | 0.316 | 0.380 | 0.060 | 0.0171 - 0.0096 |
| | *Limanda limanda* | 0 - I | 0.95 | 5.74 | 0.316 | 0.380 | 0.049 | 0.0187 - 0.0115 |
| | *Callionymus lyra* | 0 - I | 0.95 | 5.78 | 0.321 | 0.450 | 0.052 | 0.0151 - 0.0099 |
| | *Pomatoschistus minutus* | I | 0.35 | 5.78 | 0.321 | 0.580 | 0.015 | 0.0128 |
| | *Trisopterus luscus* | 0 | 0.15 | 4.66 | 0.385 | 0.500 | 0.083 | 0.0077 |
| | *Merlangius merlangus* | 0 | 0.15 | 4.66 | 0.385 | 0.500 | 0.079 | 0.0076 |
| Invertebrates | *Asterias rubens* | - | 0.30 | 2.41 | 0.330 | 0.46 | - | - |
| | *Crangon crangon* | - | 0.30 | 4.13 | 0.201 | 0.40 | - | - |
| | *Carcinus maenas* | - | 0.40 | 3.22 | 0.258 | 0.20 | - | - |
| | *Liocarcinus* spp. | - | 0.40 | 3.22 | 0.258 | 0.20 | - | - |
| | *Necora puber* | - | 0.30 | 3.22 | 0.258 | 0.20 | - | - |

## 3. Results

### 3.1. Macrobenthic food production

314    Macrobenthic FP showed a clear interannual pattern from 2008-2010 in the Seine nursery,

315    being ~2-3 times higher in 2008 and 2010 (752 and 673 kJ.m$^{-2}$.yr$^{-1}$, respectively) than in 2009 (262

316    kJ.m$^{-2}$.yr$^{-1}$). This pattern was relatively pronounced but observed in all strata (Fig. 2) and obvious at

317    the scale of the study site (Fig. 3a). The largest variation in FP was recorded in stratum E4, which was

318    the most productive (FP of ~1100 kJ.m$^{-2}$.yr$^{-1}$ in 2008 and 2010). Since stratum E4 is also the largest

319    (160 km$^2$), it produced most of the macrobenthic food (62-74% of total FP from 2008-2010).

320    In addition to its spatial heterogeneity, FP also showed strong dominance of certain taxa (Fig.

321    2, Fig. 3a), especially annelids (mainly sedentary polychaetes) and, to a lesser extent, mollusks

322    (mainly bivalves). Hence, the interannual pattern in FP observed from 2008-2010 was driven by

323    interannual variations of a few macrobenthic species (Table S4), especially the tube-dwelling

324    polychaete *Owenia fusiformis*, whose production represented 45%, 23% and 60% of total FP in 2008,

325    2009 and 2010, respectively. Collectively, the polychaetes *Lagis koreni*, *Magelona johnstoni* and

326    *Lanice conchilega* and the bivalves *Abra alba* and *Phaxas pellucidus* also represented a high

327    percentage of total FP in the Seine nursery (19%, 31% and 14% in 2008, 2009 and 2010,

328    respectively). Conversely, the FP of crustaceans (e.g. amphipods) and echinoderms (e.g. ophiurids)

329    was marginal (< 6% and < 3%, respectively, from 2008-2010).

330
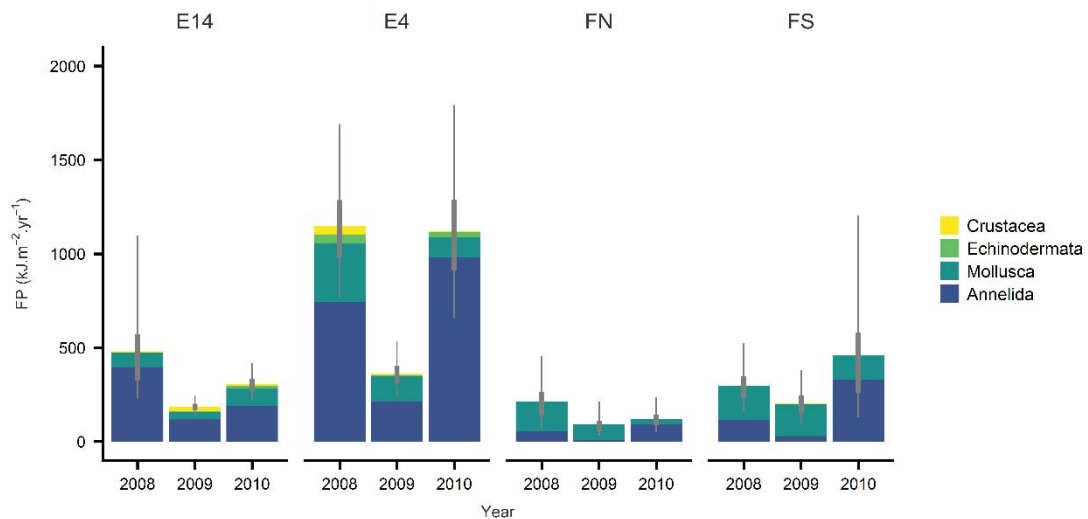


331

332    Fig. 2. Food production (FP, kJ.m$^{-2}$.yr$^{-1}$) by taxon in each stratum of the study site from 2008-2010.

333    Thick and thin gray lines represent 50% and 95% confidence intervals, respectively, estimated using

334    Monte-Carlo simulations.

335

336 **3.2. Food consumption by epibenthic predators**

337    FC by epibenthic predators showed significant but contrasting interannual variations among

338 predator groups (fish vs. invertebrates) and fish cohorts (G0 vs. G1). Interestingly, the pattern of FC by

339 G0 fish was relatively similar to that of FP (Fig. 3a, b), marked by a ~6-fold decrease from 2008 to

340 2009 (down to 5.2 kJ.m$^{-2}$.yr$^{-1}$ in 2009), followed by a ~2-fold increase from 2009 to 2010. Conversely,

341 the FC by G1 fish had an opposite pattern, peaking at 30.3 kJ.m$^{-2}$.yr$^{-1}$ in 2009 (Fig. 3d), while the FC

342 by predatory invertebrates gradually increased from 29.2 kJ.m$^{-2}$.yr$^{-1}$ in 2008 to 49.8 kJ.m$^{-2}$.yr$^{-1}$ in 2010

343 (Table 2, Fig. 3c). This latter increase in FC by predatory invertebrates occurred in all strata (Fig. S4).

344 Conversely, interannual variations in FC by the fish community (G0 and G1) showed no common

345 pattern among strata (results not shown).

346    Like their prey, the epibenthic predator community was dominated by a few species. FC by the

347 dragonet *C. lyra* was the highest among fish for all years and both cohorts, representing 46-66% and

348 53-60% of total FC by G0 and G1 fish, respectively, from 2008-2010. The European plaice *P. platessa*

349 and common sole *S. solea* were the second and third greatest fish consumers, respectively, followed

350 by the common dab *L. limanda.* FC by these three flatfish represented 32-49% and 39-45% of total FC

351 by G0 and G1 fish, respectively, from 2008-2010. Bib *T. luscus* and whiting *M. merlangus* were

352 observed only at the G0 stage, and their combined FC was extremely low (< 5%) from 2008-2010.

353 Since the gobies *P. minutus* were < 5 cm at the G0 stage, only their FC at the G1 stage was

354 estimated. It represented 8% of total FC by G1 fish in 2008 but was marginal (< 1%) from 2009-2010

355 (Fig. 3d). For predatory invertebrates, the common sea star *A. rubens* was the greatest consumer,

356 with FC ranging from 53-69% of total FC by invertebrate species from 2008-2010, followed by

357 swimming crabs *Liocarcinus* spp., shore crab *C. maenas* (particularly in 2010) and, to a lesser extent,

358 the brown shrimp *C. crangon* and velvet crab *N. puber* (Fig. 3c).

359    FC was distributed heterogeneously across the study site, and its spatial distribution varied

360 among species (Supplement S9). FC by the fish *C. lyra* and *L. limanda* and the invertebrates *A.*

361 *rubens*, *Liocarcinus* spp. and *N. puber* was concentrated in the bay (strata E4 and E14), while that by

362 the invertebrates *C. crangon* and *C. maenas* occurred mostly in the outer estuary (strata FN and FS).

363 FC by the flatfish *P. platessa* and *S. solea* varied spatially among years, species and cohorts (G0 vs.

364 G1) (e.g. generally concentrated in the bay in 2009 at the G1 stage but in the outer estuary at the G0

365 stage, especially for the common sole) (Fig. S5, S6).

14

Interestingly, FC by predatory invertebrates lay in the same order of magnitude as that by juvenile fish (G0 and G1) and represented 44-63% of total FC from 2008-2010 (Table 2).
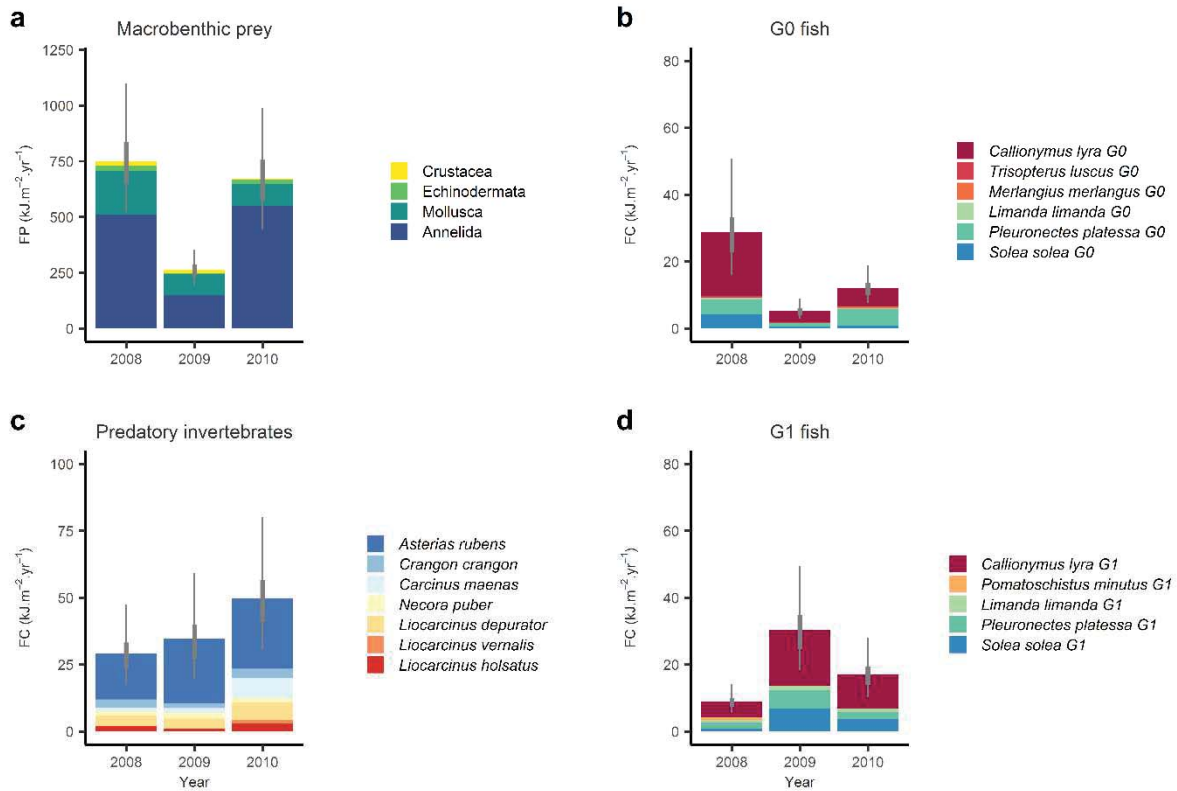


Fig. 3. Food production (FP, kJ.m$^{-2}$.yr$^{-1}$) by (a) taxon and food consumption (FC, kJ.m$^{-2}$.yr$^{-1}$) by (b) young-of-the-year G0 fish, (c) predatory invertebrates, and (d) G1 fish in the Seine nursery from 2008-2010. Thick and thin gray lines represent 50% and 95% confidence intervals, respectively, estimated by Monte-Carlo simulations.

Table 2. Food consumption (FC) by juvenile fish (G0 and G1) and predatory invertebrates in the Seine nursery from 2008-2010.

| Year | FC by juvenile fish (kJ.m$^{-2}$.yr$^{-1}$) | FC by predatory invertebrates (kJ.m$^{-2}$.yr$^{-1}$) | Relative FC by predatory invertebrates (%) |
|------|------|------|------|
| 2008 | 37.6 | 29.2 | 44 |
| 2009 | 35.5 | 34.6 | 49 |
| 2010 | 29.1 | 49.8 | 63 |

**3.3. Exploitation efficiency**

EE of the epibenthic predators on their macrobenthic prey varied considerably depending on the predator group (Fig. 4), ranging from 2-4% for G0 fish, 5-14% for all fish (G0 and G1) and 9-27% for all predators (fish and invertebrates). Interannual variations in EE also depended greatly on the predator group. EE of G0 fish decreased ~2-fold from 2008-2009 but remained stable from 2009-2010 (Fig. 4). Conversely, EE of all fish and of all predators were ~2-3 times higher in 2009 than in 2008 and 2010.
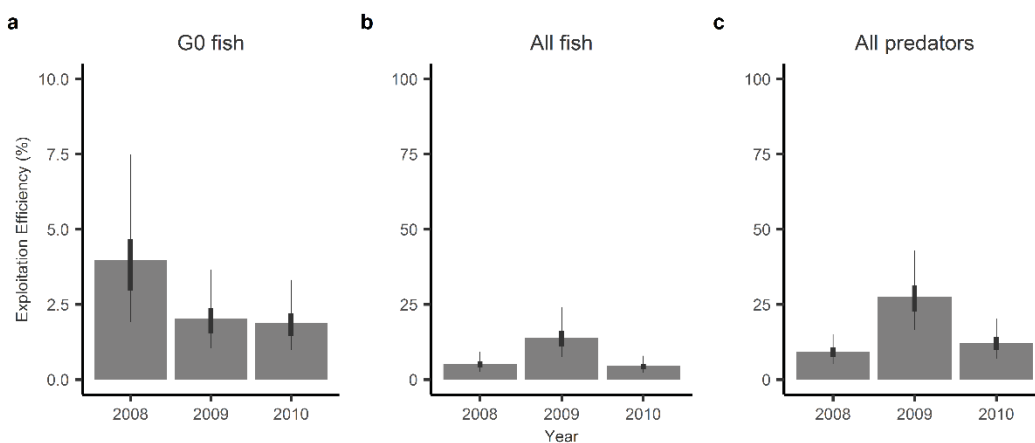


Fig. 4. Exploitation efficiency (EE, %) of (a) young-of-the-year G0 fish, (b) all fish and (c) all predators on their macrobenthic prey in the Seine nursery from 2008-2010. Thick and thin black lines represent 50% and 95% confidence intervals, respectively, estimated by Monte-Carlo simulations. Note the smaller scale of the y-axis of plot (a).

## 4. Discussion

Using a recent bioenergetics-based approach, we investigated whether food supply could limit juvenile fish production in three consecutive years (2008-2010) in the Seine nursery, western Europe. Our main results revealed a similar interannual pattern in FP and FC by G0 fish and highlighted the large amount of food consumed annually by the dominant predatory invertebrates. We also showed that the EE of the entire epibenthic predator community reached ~30% in 2009. Overall, these results suggest that food was likely limiting in the Seine nursery, given our conservative approach.

**4.1. Food production: a temporally variable but spatially stable pattern**

402    Over the past three decades, the macroinvertebrate community in the eastern Bay of Seine

403    and the outer Seine estuary has been studied extensively (Ménard et al. 1989; Dauvin and Gillet 1991;

404    Thiébaut et al. 1997; Mouny et al. 1998; Ghertsos et al. 2001; Dauvin 2008; Dauvin et al. 2017). The

405    spatio-temporal patterns in macrobenthic production (as measured by FP) from 2008-2010 are

406    strongly consistent with those previously reported, even though most studies focused on macrobenthic

407    abundance or biomass. For instance, the estuarine stratum FN, which had the lowest FP estimates

408    among the four strata (Fig. 2), has had long-lasting low macrobenthic abundance and biomass (Mouny

409    et al. 1998; Dauvin 2008), likely related to the high environmental (salinity variations) and

410    anthropogenic (pollution, harbor extension) stresses that occur in this area (Tecchio et al. 2015).

411    Conversely, high macrobenthic abundance and biomass values have been recorded at sampling

412    stations located mainly in marine stratum E4 (Dauvin and Gillet 1991; Thiébaut et al. 1997), where FP

413    was the highest each year in the present study (Fig. 2). Estimates of FP in the Seine nursery were

414    consistent with macrobenthic production estimates reported in several other temperate marine and

415    coastal ecosystems (20-850 kJ.m$^{-2}$.yr$^{-1}$: Reiss et al. 2009; Bolam et al. 2010; Brey 2012 and

416    references therein).

417    In addition to its stable spatial pattern across the years studied, the macrobenthic community

418    remained remarkably dominated by the same few taxa for 25 years, especially annelids (Dauvin et al.

419    2017). In particular, *O. fusiformis* was the most abundant species from 1986-1988 and in 1991

420    (Thiébaut et al. 1997). We showed that two decades later, annelids still largely dominated the

421    macrobenthic community (Figs. 2 and 3), with *O. fusiformis* still the most abundant and productive

422    species (as measured by FP, Table S4). Mechanisms that could explain the stability in spatial

423    organization and species dominance of the Seine macrobenthic community include larval retention

424    near adult populations, sediment stabilization caused by high densities of *O. fusiformis* and the salinity

425    gradient off the Seine estuary (Thiébaut et al. 1994, 1997).

426    Nonetheless, our results revealed substantial year-to-year variations in FP from 2008-2010 at

427    both population and community levels (Fig. 3, Table S4). Mean annual Seine River flow decreased

428    significantly from 2008 (525 m$^3$.s$^{-1}$) to 2009 (352 m$^3$.s$^{-1}$) and then increased moderately in 2010 (414

429    m$^3$.s$^{-1}$). The present study did not identify the exact causes of the macrobenthic variations from 2008-

430    2010. They may have been caused by variations in local environmental conditions (e.g. river flow,

431    wind regime) that determined larval drift and recruitment success of the dominant macrobenthic taxa,

17

432  which have a bentho-pelagic life cycle (Ménard et al. 1989; Thiébaut et al. 1992, 1996, Dauvin et al.

433  1993, 2017; Thiébaut 1996). Density-dependent mortality caused by competition for limited resources

434  among macrobenthic populations likely also had an influence (e.g. Thiébaut et al. 1997; Henderson et

435  al. 2006). Conversely, top-down regulation exerted by epibenthic predators (juvenile fish, predatory

436  invertebrates) has rarely been suggested as a cause for the interannual variations in the Seine

437  nursery. However, dominant macrobenthic species are important prey for several juvenile fish. Gut

438  content analyses revealed that these dominant species (e.g. *O. fusiformis*, *L. koreni*, *L. conchilega*, *A.*

439  *alba*) are major prey items for juvenile fish (especially plaice *P. platessa*, sole *S. solea* and dab *L.*

440  *limanda*) in the Seine nursery (Morin et al. 1999 and unpubl. data), and in several other coastal areas

441  in western Europe (Amara et al. 2001; Darnaude et al. 2001; Schückel et al. 2012). Local data on

442  predatory invertebrates' diets are lacking; however, these epibenthic predators likely consume

443  dominant macrobenthic prey as well, given their opportunistic feeding behavior (Norman and Jones

444  1992; van der Veer et al. 2011) and results from gut content analyses reported elsewhere (e.g. Allen

445  1983; Choy 1986; del Norte-Campos and Temming 1994; Freire 1996). Further local gut content

446  and/or stable isotope analyses would be useful to improve current FP estimates, and provide an in-

447  depth knowledge of food availability in the Seine nursery.

448

449  **4.2. Relating food production to food consumption by epibenthic predators**

450      Surprisingly, few studies have attempted to relate spatio-temporal patterns of the

451  macrobenthic community to those of higher trophic levels in the Seine nursery. For instance, the

452  abundance of several macrobenthic species decreased greatly in the eastern Bay of Seine from 2008-

453  2009 (Dauvin et al. 2017), but its potential effect on the epibenthic predator community was not

454  investigated. Several trophic models (Ecopath, EwE; Christensen et al. 2005) have quantified energy

455  flows between multiple functional groups in the eastern Bay of Seine and the outer Seine estuary, but

456  none focused on the nursery function of this ecosystem. This modeling approach was useful for

457  understanding overall trophic functioning of the Bay of Seine and the Seine estuary (Rybarczyk and

458  Elkaım 2003; Tecchio et al. 2015) and for assessing past and future impacts of human activities

459  (Raoux et al. 2017; Pezy et al. 2017). Nonetheless, such trophic models are not appropriate for

460  investigating fine-scale and short-term (e.g. year-to-year) variations in predator-prey interactions

461  (Tableau et al. 2019), as done in the present study.

462    Given the dramatic variations in annual prey production observed from 2008-2010, correlating

463    FP and FC may provide information about the food limitation hypothesis, despite the short duration of

464    the present study (3 years). In particular, the similar interannual patterns in FP and FC by G0 fish

465    suggest that food was limiting in the Seine nursery, at least at the G0 stage. These patterns in FP and

466    FC were mainly driven by variations in prey biomass and fish abundance, but also accounted for

467    interannual variations in mean body weight of each species. We acknowledge that estimates of FC by

468    fish may have been less accurate, especially due to the lack of local length data for the dragonet *C.*

469    *lyra* and goby *P. minutus* (Supplement S5), and because the beam trawl survey did not cover the

470    entire spatial distribution of common sole *S. solea*. Common sole was also found in the upper estuary

471    and on intertidal mud flats during high tide, particularly at the G0 stage (Morin et al. 1999).

472    Nonetheless, the interannual pattern in FC by G0 fish was considered similar to that in FP, given the

473    limitations of our dataset. The similarity was particularly high for plaice *P. platessa* (Fig. 3), which is a

474    main consumer of *O. fusiformis* in the Seine nursery (Ménard et al. 1989; Morin et al. 1999).

475    Interestingly, G1 fish showed an opposite interannual pattern, which is consistent with the

476    patterns in FP and in FC by G0 fish with a one-year lag. This agrees with the hypothesis that the year-

477    class strength is determined at the G0 stage on nursery grounds, or even earlier, at the pelagic phase

478    (Hjort 1914; van der Veer 1986; Leggett and Deblois 1994; Houde 2008). This opposite pattern could

479    also suggest competition for food between G0 and G1 fish, with lower survival of and thus lower FC by

480    G0 fish when the FC by G1 fish is high, as in 2009. However, correlation does not imply causation

481    (Hilborn 2016). Hence, the lower FC by G0 fish in 2009 could have been due to lower food supply

482    (bottom-up control), higher competition with G1 fish, higher predation pressure on G0 fish in the

483    nursery (top-down control), lower fish larval supply caused by higher mortality during early-life stages

484    (eggs and larvae) or a combination of some or all of these processes, which can occur simultaneously

485    (Hixon and Jones 2005). The dataset and short duration of the present study did not enable us to

486    distinguish these potential causes.

487    The completely different interannual variations in FC by predatory invertebrates was no

488    surprise, because macrobenthic prey likely represent a much smaller percentage of predatory

489    invertebrates' diets (Table 1, Supplement S6). In addition, FC by predatory invertebrates was clearly

490    dominated by the common sea star *A. rubens*, which can live at least five years in the wild (Guillou

491    1983). Thus, even though macrobenthic food resources in the Seine nursery could limit the sea star

492    population, the correlation between annual FP and annual FC would likely be weak because the

493    population response would aggregate variations in food supply over several years.

494         Interannual variations in FC by G0 fish were generally the same among strata and in the entire

495    study site (Fig. S5). This observation held for FC by predatory invertebrates in all strata and by G1 fish

496    in marine strata (E4 and E14) (Fig. S4, S6). Conversely, species composition differed significantly

497    among strata, especially according to the salinity tolerance of each species. For instance, euryhaline

498    species such as the common sole *S. solea*, brown shrimp *C. crangon*, and shore crab *C. maenas*

499    were found mainly in the outer estuary (FN and FS), while the common sea star *A. rubens*, common

500    dab *L. limanda* and dragonet *C. lyra*, which tolerate salinity less, were concentrated in the bay (E4 and

501    E14). However, spatial variations in the FC estimated in the present study must be interpreted with

502    caution. Species distribution is not driven by a single factor (e.g. salinity) but instead results from the

503    combination of several forces, both external (e.g. environmental forcing, food availability) and internal

504    (e.g. population size) to the populations (Planque et al. 2011). Since these forces change throughout

505    the year, the spatial distribution of mobile epibenthic predators changes accordingly. Predatory

506    invertebrates likely move much less than juvenile fish, but do move, particularly in late winter and late

507    summer, when they migrate (Venema and Creutzberg 1973; Boddeke 1976; Hinz et al. 2004).

508

509    **4.3. Including predatory invertebrates doubled estimates of food consumption**

510         Given the high density of predatory invertebrates generally observed in coastal and estuarine

511    nurseries (Pihl and Rosenberg 1984; van der Veer et al. 2011), they can exert substantial predation

512    pressure on macrobenthic prey, even though macrofauna are a moderate percentage of their diet

513    (Evans 1983; Pihl 1985; Jung et al. 2017). Our results agree with these previous findings. We showed

514    that FC by predatory invertebrates lay in the same order of magnitude as FC by juvenile fish from

515    2008-2010 in the Seine nursery. Including the FC by predatory invertebrates provided a larger and

516    probably more realistic estimate than that obtained for juvenile fish alone, as originally presented by

517    Tableau et al. (2019).

518         However, the approach we developed to estimate FC by predatory invertebrates has some

519    limitations. In particular, FC is derived from an estimate of production that may be inaccurate.

520    Empirical models, such as the one we used to estimate production (Brey 2012), perform relatively well

521    for an assemblage of species, but may have high prediction error for a single population (Brey 2001,

522 2012). Additionally, the same problem holds for macrobenthic prey, given the strong dominance of few

523 species. To our knowledge, however, empirical models remain the best approach currently available

524 for estimating secondary invertebrate production when data preclude the use of classic direct

525 methods. Moreover, Brey models (2001, 2012) were shown to perform as well or even better than

526 others (Cusson and Bourget 2005; Dolbeth et al. 2005; Petracco et al. 2012). Also, if production

527 estimates of predatory invertebrates were inaccurate, they would more likely be underestimated rather

528 than overestimated because only the larger individuals remained in the net. Since mean individual

529 weight and P:B ratios are negatively correlated (Schwinghamer et al. 1986), P:B ratios were much

530 lower than those generally found in the literature (e.g. Kuipers and Dapper 1981; Pihl and Rosenberg

531 1984; Pihl 1985). Consequently, they likely resulted in underestimating FP and FC, which is in

532 accordance with the conservative approach used in this study. Additionally, we used Monte-Carlo

533 simulations to include the uncertainty in estimates of FP and to estimate prediction error, unlike most

534 previous studies (e.g. Evans 1983, 1984; Pihl 1985; Collie 1987).

535

536 **4.4. Food limitation: lessons from exploitation efficiency**

537 Collectively, juvenile fish and predatory invertebrates consumed a large percentage of

538 macrobenthic prey production in the Seine nursery, as revealed by calculating EE. First, EE

539 automatically increased with the number of predators (G0 fish vs. all fish vs. all predators) for a given

540 year because FC increased accordingly, while FP remained unchanged (Fig. 4). As previously

541 suggested (Collie 1987; Vinagre and Cabral 2008; Tableau et al. 2019), these results highlighted the

542 importance of including all dominant benthic-feeding predators to estimate the overall predation

543 pressure on macrobenthic prey when testing the food limitation hypothesis in coastal and estuarine

544 nurseries. The interannual stability in EE of G0 fish from 2009-2010 logically results from the similarity

545 of the interannual pattern of FP and that of FC (G0 fish), strengthening the idea that the food supply

546 may have been limiting. In 2008, EE of all juvenile fish (5%) was similar to that (6%) in another French

547 coastal nursery (the Bay of Vilaine) observed in the same year and calculated using the same

548 approach (Tableau et al. 2019).

549 When all dominant predators were considered, our results revealed that EE on total prey

550 production (as measured by FP) could be as high as ~30%. This consumption level might have been

551 high enough to indicate that food limitation occurred (Collie 1987). In addition, the true EE was likely

552  much higher, since EE was estimated using a conservative approach. In particular, FC by epibenthic

553  predators was underestimated for several reasons. First, estimates of FC by juvenile fish were based

554  only on their requirements during the growing season, thus ignoring maintenance requirements for the

555  rest of the year. Even though requirements in winter are generally assumed to be much lower, they

556  may still be significant (Creutzberg and Witte 1989; van der Veer et al. 1990). Second, most gross

557  conversion efficiency estimates (K) found in the literature were obtained from laboratory experiments.

558  Thus, they were expected to be slightly higher than those in the wild, leading to underestimates of FC

559  and thus EE (Tableau et al. 2019). Third, catch efficiency estimates (q) were overestimated because

560  they came from beam trawl surveys using a 4 mm mesh liner in the cod-end (e.g. Reiss et al. 2006),

561  unlike scientific surveys performed in the Seine nursery that used a larger mesh (20 mm). Fourth, FC

562  by G2 fish was not considered because few G2 individuals were found in the net, since they probably

563  moved to deeper and offshore water before the scientific surveys occurred. Nonetheless, G2 fish may

564  exert significant predation pressure on macrobenthic prey earlier in the year. Lastly, FC by predatory

565  invertebrates was also likely underestimated, as explained. Hence, EE on total prey production likely

566  exceeded 30% in 2009 in the Seine nursery.

567  It is unlikely that EE reaches 100% even when food limitation occurs, since predators can

568  access only a portion of macrobenthic prey. For instance, a previous study estimated that juvenile fish

569  in coastal nurseries in the Wadden Sea could access only 10% of the total macrobenthic biomass (van

570  der Veer et al. 2011). Similarly, Tableau et al. (2015) estimated that the FP accessible to juvenile fish

571  in another French coastal nursery (the Bay of Vilaine) was approximately one-eighth that of total FP in

572  2008. These values were likely overestimated, at least for the entire predator community in the Seine

573  nursery. Predatory invertebrates likely access prey that are not accessible to juvenile fish given their

574  different prey-handling abilities, and previous estimates of prey accessibility considered only juvenile

575  fish (van der Veer et al. 2011; Tableau et al. 2015). However, even a much lower and more

576  reasonable ratio of total to accessible FP (e.g. 3) would lead to an EE close to 100% in 2009,

577  indicating strong competition for food that year. Thus, we cannot exclude the possibility that food was

578  limiting in the Seine nursery. In particular, the combination of a significant decrease in food supply (as

579  measured by FP) and a significant increase in food consumption by epibenthic predators may have

580  induced food limitation in 2009.

581       We focused mainly on annual FP and FC in the entire nursery. However, food limitation can

582     be restricted to specific areas and/or periods of the year (e.g. Walters and Juanes 1993). Since the

583     Seine nursery has been described as a mosaic of habitats (Tecchio et al. 2015), we estimated EE in

584     each stratum (Fig. S7). The analysis revealed that EE varied among strata (up to 37% in E14 in 2009

585     and 76% in FN in 2010), but caution in interpretation is required, since epibenthic predators move

586     among habitats throughout the year. The annual scale may not be the most appropriate one at which

587     to test the food limitation hypothesis. Resources may be limiting only during certain periods of the

588     year, such as the sensitive post-settlement phase (Geffen et al. 2007, 2011). Nevertheless, focusing

589     on this early-life stage is more challenging, especially when sampling prey and predators, but seems

590     crucial given its potential effect on fish recruitment (Nash and Geffen 2012; Nagelkerken et al. 2015).

591     A decline in growth rate of juvenile plaice *P. platessa* during late summer was also broadly reported

592     (Freitas et al. 2012; Ciotti et al. 2013b), and could be related to intra- or interspecific competition for

593     food (Ciotti et al. 2013a; van der Veer et al. 2016). However, the underlying causes of that pattern

594     remain unclear (Ciotti et al. 2014).

595       In conclusion, two main findings suggest that food supply may have limited juvenile fish

596     production in the Seine nursery, at least in 2009: (1) the similarity in the interannual patterns in FP and

597     FC by G0 fish and (2) the relatively high EE estimated for all predators in 2009 (~30%) given the

598     conservative calculation. Firmly validating or refuting the food limitation hypothesis in the Seine

599     nursery lies beyond the scope of this study, and further studies are required to reach a conclusion. To

600     this end, applying the bioenergetics-based approach to longer time-series and/or other nurseries

601     would be useful (Tableau et al. 2019). Finally, prey accessibility remains a key parameter that is

602     particularly challenging to calculate; however, estimating it is critical to better understand food

603     limitation (Boisclair and Leggett 1985).

604

the COLMATAGE project from which most data came, as well as Le Havre harbor for providing

additional grab data collected in 2010.

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**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: