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1 **Title**

2 Benthic prey production index estimated from trawl survey supports the food limitation hypothesis in
3 coastal fish nurseries

4

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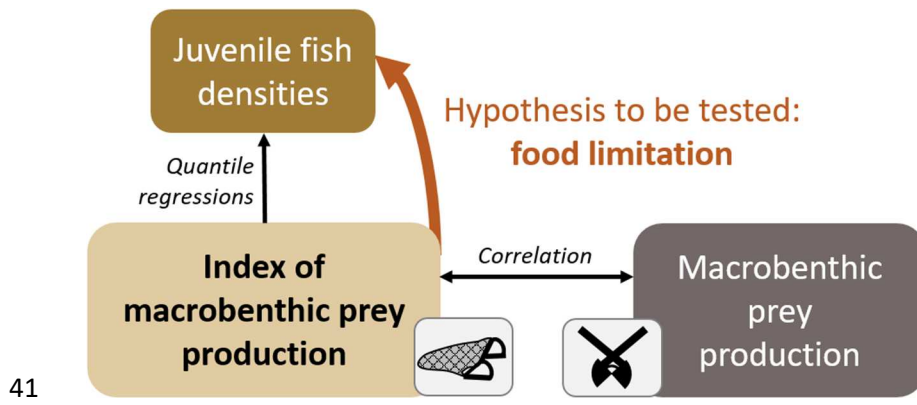
16

17 **Keywords:** young-of-the-year fish, macrobenthic production, trawl, grab, Bay of Biscay, quantile
18 regression

19 **Abstract**

20 Coastal and estuarine habitats function as nurseries for many commercial marine species. In these
21 ecosystems, the hypothesis that food supply limits juvenile fish density and survival has been widely
22 debated. Direct approaches that test this hypothesis in temperate soft-bottom nurseries are data-
23 intensive as they rely on beam trawl to collect juvenile fish *and* grab or core to collect their prey within
24 the macrobenthic community. Thus, application has often been limited to a few sampling stations and
25 temporal snapshots. However, scientific beam trawl surveys, conducted periodically in nurseries,
26 sample, besides juvenile fish, benthic invertebrates including potential prey species. Using data
27 collected solely from beam trawl surveys, we tested whether food supply limits juvenile fish densities
28 in several French nurseries. First, we validated that data of benthic invertebrates from bottom trawl
29 surveys could be used to estimate an index of benthic prey production, by comparing data collected
30 by grabs and trawls at the same sampling locations. Using this index on an extended trawl dataset, we
31 estimated inter-annual variability of benthic prey production among several nurseries along the coast
32 of the Bay of Biscay. Estimates of benthic prey production index were similar among nurseries,
33 although, these nurseries displayed different local hydrological patterns (currents and residence time).
34 The index was finally used to investigate whether benthic prey production limits young-of-the-year
35 fish density using quantile regressions. We found a significant and positive relationship between the
36 benthic prey production index and young-of-the-year fish densities, including flatfish and round fish
37 species. Hence, our study supports the hypothesis that trophic limitation occurs for juvenile fish in
38 coastal and estuarine nurseries during their first year of life, although other factors likely limit them
39 locally.

40 Graphical abstract



42 1 Introduction

43 Estuaries and coastal areas are among the most productive ecosystems in the world (Costanza et al.,
44 1997; Schelske and Odum, 1962). They function as nurseries for many marine fish species by
45 supporting production of juveniles, which replenish adult stocks offshore (Beck et al., 2001; Dahlgren
46 et al., 2006; Seitz et al., 2014). Recruitment (*i.e.* entry of young individuals into the fishery) of these
47 nursery-dependent species is most likely regulated during their juvenile stage (Myers and Cadigan,
48 1993; Ustups et al., 2013) by multiple limiting factors (Gibson, 1994). Wouters and Cabral (2009)
49 suggested that nurseries concentrate more macrobenthic prey for demersal juvenile fish than do
50 surrounding habitats. Hence, juveniles concentrate in nurseries, which leads to density-dependent
51 mortality that cause a “bottleneck” effect in the number of fish recruited to the stock (Craig et al.,
52 2007; Iles and Beverton, 2000). Although the density-dependent processes that influence recruitment
53 remain under debate, some studies suggested that prey production may be limiting (Le Pape and
54 Bonhommeau, 2015; Nash et al., 2007; van der Veer et al., 2016). Prey production in nurseries
55 becomes limiting when demand exceeds production, resulting in potential mortality and competition
56 among predators.

57

58 Several approaches have been used to test the food-limitation hypothesis for juvenile marine fish in
59 coastal and estuarine nurseries. Direct approaches usually compare prey production to food
60 requirements or consumption of juvenile fish. They have been performed using data from
61 experimental ponds (Craig et al., 2007) or directly collected in the field (Tableau et al., 2019), and
62 usually calculated the ratio of benthic prey consumption by juvenile fish to benthic prey biomass or
63 production using trophic models (Chevillot et al., 2019) or bioenergetic approaches (Tableau et al.,
64 2019; Vinagre and Cabral, 2008). These studies yielded conflicting results and remained cautious in
65 their conclusions, as they were generally based on a temporal snapshot (*i.e.* one year). These
66 approaches are effort-intensive because they require the biomass of both prey and predator to

67 estimate prey production and juvenile consumption (e.g. Bennett and Branch, 1990; Collie, 1987;
68 Vinagre and Cabral, 2008).

69

70 Another approach to test the food-limitation hypothesis is to analyse time series of predator and prey
71 data (Beaugrand et al., 2003; Crawford and Dyer, 1995; Okamoto et al., 2012). For instance, analyses
72 of predator-prey time series showed a relationship between inter-annual fluctuations in anchovy
73 biomass and the number of nesting seabirds (Crawford and Dyer, 1995). Although not demonstrating
74 a causal relationship, the analysis supported the hypothesis that when food supply is low, birds are
75 unlikely to allocate energy to breeding. Similarly, along the North Sea coast, a long-term dataset
76 showed a decrease in nutrient loading, which presumably caused a change in the spatial distribution
77 of *Pleuronectes platessa* juveniles (Støttrup et al., 2017). Joint analysis of predator and prey could
78 provide arguments in the debate on food limitation, especially when it is performed in a causation
79 context (Kato and Sasaki, 2017). Quantile regressions used in this context may be very helpful in
80 identifying limiting factors (Cade and Noon, 2003; Planque and Buffaz, 2008), since the food-limitation
81 hypothesis can be tested by examining several quantiles of the predator-prey relationship (Tableau et
82 al., 2016).

83

84 A long time series for juvenile fish and their prey is rare in temperate soft-bottom nurseries, especially
85 because benthic prey are commonly sampled using gears deployed over small spatial scales, such as
86 grabs or cores (Bennett and Branch, 1990; Collie, 1987; Eleftheriou, 2013; Tableau et al., 2015) and
87 because several replicates are required to obtain relevant estimates. The spatial (several km) and
88 temporal scales (several seasons or years) required when sampling to investigate variability in benthic
89 prey production and its consequences on juvenile fish often preclude acquisition of such data.
90 Alternatively, trawl surveys in nurseries also sample invertebrate species and are performed annually
91 across the French coast (Brind'Amour et al., 2009). Grabs and trawls sample two distinct portions (> 1
92 mm for grab; depending on mesh size and degree of clogging for trawl) of the same benthic

93 invertebrate community (Eleftheriou, 2013), and the overlap between them is assumed to contain prey
94 items that may be consumed by juvenile fish.

95

96 We investigated whether benthic prey production limits the density of juvenile fish in coastal and
97 estuarine nurseries using data collected solely from trawl surveys. First, we verified that data from
98 bottom trawl surveys could be used to estimate an index of benthic prey production, which is
99 traditionally assessed using grab samples. Second, using this index, we estimated inter-annual
100 variability in benthic prey production among several nurseries. Third, we used quantile regressions to
101 test the hypothesis that trophic limitation occurs in young-of-the-year (YOY) benthic-demersal fish
102 density in nurseries. This potential limitation was tested for a variety of YOY fish, including flatfish and
103 round fish species.

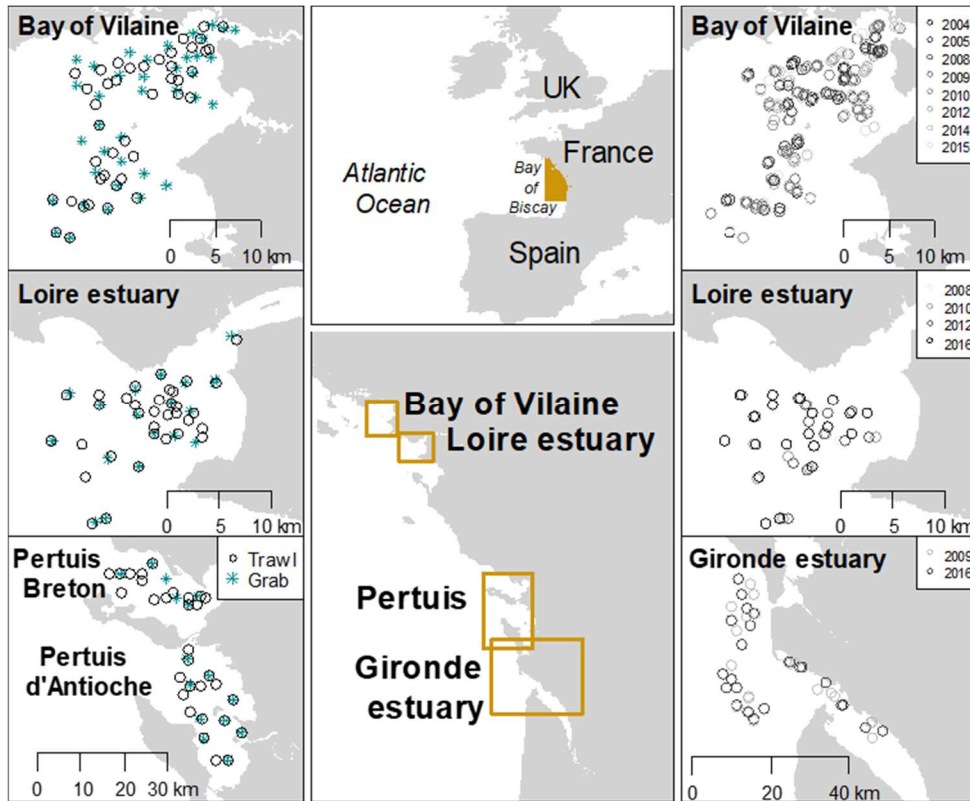
104 2 Materials and methods

105 2.1 Data collection

106 2.1.1 Nurseries surveyed

107 The study included nurseries located along the French coast of the Bay of Biscay (Figure 1; Table 1)
108 that were previously identified as important grounds for juvenile flatfish (Le Pape et al., 2003;
109 Trimoreau et al., 2013). The Bay of Vilaine, the outer Loire estuary, and two semi-enclosed bays
110 (Pertuis Breton and Pertuis d'Antioche) were sampled concurrently using a beam trawl and grab in late
111 summer 2008, 2016 and 2015, respectively (Figure 1, left panel). These data were used to meet the
112 first objective of the study (*i.e.* verify that beam trawl data could be used to estimate an index of
113 benthic prey production).

114



115

116 Figure 1. Location of the study sites along the French coast of the Bay of Biscay (middle panel).

117 Locations of the sampling stations with the two sampling gears, grabs and trawls (mean location), in

118 2008 in the Bay of Vilaine, in 2016 in the Loire estuary and in 2015 in both Pertuis stations (left panel).

119 Locations of the sampling stations with only trawls deployed (grey circles) in the Bay of Vilaine (8

120 years), the Loire estuary (4 years), and the Gironde estuary (2 years) (right panel).

121 These nurseries differed environmentally in sediment composition and bathymetry (Table 1). The Bay

122 of Vilaine is mainly a muddy nursery with sampling stations of varying depths (1-35 m), whereas the

123 two Pertuis are half-muddy and half-sandy shallow nurseries, and the outer Loire estuary is mainly

124 sandy with a gradient of depths (Table 1). Each nursery surveyed was divided into strata defined by

125 the bathymetry and the size distribution of sediments (assessed using the grab samples, Supp. Mat.

126 A). Thus, three bathy-sediment strata were defined in the Bay of Vilaine (V1, V2 and V3, from upstream

127 to downstream), three others in the outer Loire estuary (L1, L2 and L3), and two at each Pertuis site

128 (PA1, PA2 and PB1, PB2). The number in each code corresponds to the distance from the mouth of the

129 estuary (1 = upstream, 3 = offshore).

130

131 Table 1. Description of the nurseries and sampling design used to define the benthic production index,
132 including the mean bathymetry and mean percentages of mud (< 63 µm), sand (> 63 µm and < 500
133 µm), and gravel (> 500 µm) contents of the sediment of the nurseries.

Characteristic	Bay of Vilaine (V)	Outer Loire estuary (L)	Pertuis Breton (PB)	Pertuis Antioche (PA)
Sampling year	2008	2016	2015	2015
Mean mud percentage (%)	70.0	10.5	52.7	53.7
Mean sand percentage (%)	25.0	86.0	41.2	40.5
Mean (\pm 1 SD) depth (m)	15.4 \pm 0.5	11.0 \pm 0.4	5.9 \pm 0.4	7.5 \pm 0.3
Number of strata	3	3	2	2
Total number of trawl stations (and by stratum)	42 (V1: 17, V2: 8, V3: 17)	34 (L1: 2, L2: 25, L3: 7)	15 (PB1: 7, PB2: 8)	16 (PA1: 3, PA2: 13)
Total number of grab stations (and by stratum)	36 (V1: 17, V2: 6, V3: 15)	19 (L1: 3, L2: 11, L3: 5)	6 (PB1: 3, PB2: 3)	9 (PA1: 3, PA2: 6)

134

135 In addition to the surveys during which grab and trawl samples were collected, annual nursery-
136 dedicated trawl surveys were performed irregularly from 2004-2016 in late summer/early autumn
137 (Delaunay and Brind'Amour, 2018). During this period, the following three nurseries were sampled at
138 least 2 times: the Bay of Vilaine (8 years), the outer Loire estuary (4 years), and the outer Gironde
139 estuary (2 years; Figure 1, right panel). Benthic invertebrates and YOY fish collected during the 14
140 surveys (nursery-years) were used to meet the two last objectives of the study (i.e. estimate inter-
141 annual variability in benthic prey production index and test the trophic limitation hypothesis in YOY
142 fish).

143 2.1.2 Grab data collection

144 Grab samples were collected using a 0.1 m² Van Veen grab, with three replicates at each sampling
145 station. Once aboard, the grab content was sieved through a 1 mm grid mesh and kept in a 7% formalin
146 solution in plastic zip-top bags. In the laboratory, organisms were rinsed and sieved with fresh water
147 in a column of five successive sieves with square mesh sizes ranging from 16 to 1 mm. Organisms

148 retained in each sieve were then stored separately in a 70% ethanol solution, keeping in mind that
149 handling, fixing samples with formalin and storing with ethanol likely led to underestimate biomasses
150 (Gaston et al., 1996; Wetzel et al., 2005). Invertebrates from each sieve were identified to the lowest
151 taxonomic level, counted and weighed. Biomass per taxa was determined as wet mass (WM) and then
152 converted into ash-free dry mass (AFDM) using specific coefficients from a global database of
153 conversion factors (Brey et al., 2010). When no conversion factor was available at the species level,
154 the conversion factor for the next highest taxonomic level was used. Data from replicates of each
155 sampling station were summed, and biomass was standardized based on the area sampled (*i.e.* 3
156 replicates \times 0.1 m²). The sampling design is detailed in Table 1.

157 2.1.3 Trawl data collection

158 Bottom trawl samples were collected using a 2.9 m wide and 0.5 m high beam trawl with a 20 mm
159 stretched mesh size in the cod end. Trawls were performed during daylight hours at a mean speed of
160 2.5 knots for 15 min. Trawled benthic invertebrates were rinsed aboard, identified to the lowest
161 taxonomic level, counted and weighed. Biomass per taxa was determined as WM, which was
162 converted into AFDM as described in section 2.1.2. Trawled fish were collected, identified, counted,
163 measured and weighed at the species level, with 494 stations sampled during the 14 surveys (nursery-
164 years).

165 2.2 Select YOY fish

166 The fish selected were the eight marine nursery-dependent species with the highest biomass: four
167 flatfish species (*Arnoglossus laterna*, *Dicologlossa cuneata*, *Pleuronectes platessa*, *Solea solea*) and
168 four “round” fish species (*Merlangius merlangus*, *Mullus surmuletus*, *Trisopterus luscus*, *Callionymus*
169 *lyra*). The eight species represented an average of 68% of the total biomass in each nursery-year.
170 Length-frequency distributions were used to identify age groups in the survey. Gaussian distributions
171 were fit to cumulative length-frequencies over the years. The maximum length associated with each

172 Gaussian distribution was used to categorise a presumed year-class of all individuals captured. This
173 procedure was performed using the *Mclust* function of the *mclust* package (Scrucca et al., 2016) of R
174 software (R Core Team, 2019). YOY individuals (*i.e.* the first Gaussian distribution) were selected. Then,
175 a minimum and maximum lengths of 7 and 15 cm, respectively, were set to select individuals that feed
176 almost exclusively on macrobenthic invertebrate prey within the size range of the fish cohort (see
177 Supp. Mat. C). These size thresholds for individual fish assumed that fish smaller than the minimum
178 length (7 cm) prey on pelagic and benthic invertebrates that our sampling device could not capture
179 (*e.g.* copepods), whereas individuals larger than the maximum threshold (15 cm) have a high
180 proportion of small fish in their diet (Tableau et al., 2015). When length data were missing (as for *C.*
181 *lyra* before 2008), mean individual mass (total biomass divided by the number of individuals) was
182 converted into mean individual length using the coefficients a and b from the size-weight relationship
183 estimated for each species with all length data available in the data set from 2004-2016. Only
184 individuals whose mean individual length met the size ranges of the species were kept in the analyses.
185 Relative YOY fish density (number of individuals.ha⁻¹) was estimated at each station from catches
186 without correcting for catch efficiency.

187 2.3 Select potential benthic prey for YOY fish

188 First, as habitat-forming species are known to shape the habitat and strongly influence the benthic
189 community (Chaalali et al., 2017), the sampling stations (grab and trawl) dominated by those species
190 (*Haploops nirae*, *Crepidula fornicata* and *Ampelisca spinipes*) were excluded from the analyses. Rare
191 species, defined as species found only once in a nursery-year or with a biomass lower than 0.1% of the
192 total biomass of the nursery-year, were also excluded from the analyses as they add little to the
193 analysis.

194 Then, benthic organisms from the grab and trawl samples were selected independently to match the
195 species composition of the potential benthic prey of the YOY fish community. It was assumed that YOY
196 fish are opportunistic feeders that consume a variety of benthic prey no larger than a certain size

197 (Besyst et al., 1999; Griffin et al., 2012). Hence, a benthic invertebrate was identified as potential prey
198 if it was smaller than the maximum mouth height of a juvenile fish. Data on mouth heights of the three
199 most abundant species (*M. merlangus*, *S. solea* and *T. luscus*) in the studied areas were used to define
200 a mean height of 20 mm (unpublished data). As benthic organisms collected with trawl were not sized,
201 but only counted and weighted, we decided to select potential prey of the YOY fish using a filter based
202 on mean individual mass. To set the threshold under which an invertebrate can be considered as prey
203 for YOY fish, we used the benthic organisms collected with grab and categorised into size classes
204 described previously (section 2.1.2). Mean individual body mass of the organisms retained in each
205 mesh size was calculated. A threshold of 0.66 g WM.ind⁻¹ (*i.e.* ~0.1 g AFDM.ind⁻¹), corresponding mainly
206 to benthic organisms smaller than 16 mm (the largest mesh size), was identified as potential prey. This
207 threshold was applied to select potential prey from benthic invertebrates using the grab and the beam
208 trawl. Once applied to the grab data, the rare species and mean individual body mass filters selected
209 73.3% of the total biomass in the entire dataset (*i.e.* from all three nurseries where grab and trawl
210 were deployed concomitantly). Once applied to the trawled benthic species, 10.3% of the total
211 biomass of the entire dataset was retained. The benthic organisms included in those percentages
212 (respectively 73.3% and 10.3%) were considered as potential prey and were used to estimate
213 respectively benthic prey production using grab data and benthic prey production index using trawl
214 data.

215 2.4 Data analysis

216 2.4.1 Estimate benthic prey production (from grab data)

217 Benthic prey production was estimated by multiplying mean annual biomass by the annual production-
218 to-biomass ratio (P:B), which was calculated for each taxon at each station using the artificial neural
219 network model developed by Brey (2012). The input data for this model are 17 categorical parameters
220 that describe biological and functional traits (*e.g.* taxon, habitat, feeding and mobility), depth,
221 temperature and individual mean body mass. The parameters required by the model were collated

222 according to Saulnier et al. (2018) and supplemented with data from an online resource (Biological
 223 Traits Information Catalogue of The Marine Life Information Network
 224 <http://www.marlin.ac.uk/biotic/>). The bathymetry for each station was extracted from the General
 225 Bathymetric Chart of the Oceans 30 arc-second grid (GEBCO_2014, version 20150318,
 226 <http://www.gebco.net>, Weatherall et al., 2015). Mean annual bottom temperature for each nursery-
 227 year was extracted from a multi-decadal hindcast of a physical-biogeochemical model of the Bay of
 228 Biscay (Huret et al., 2013). Individual mean body mass was calculated by dividing each taxon's mean
 229 annual biomass by its mean annual abundance.

230 Benthic prey production was first calculated at the scale of the sampling station (P_k , in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$):

231

$$232 \quad P_k = CR * \sum_i [B_{i,k} * E_i * \left(\frac{P}{B}\right)_{i,k}] \quad \text{Equation 1}$$

233

234 where k is the station, i is the species, CR is a coefficient (unitless) that accounts for seasonality in the
 235 macrobenthic biomass (set to 0.7; Tableau et al., 2015), B is the biomass (in g AFDM) sampled during
 236 the survey (grab or trawl), E is the energy density (in $\text{kJ}\cdot\text{g AFDM}^{-1}$) obtained from a general database
 237 (Brey et al., 2010) and $P:B$ is the production-to-biomass ratio (in y^{-1}) detailed at the beginning of the
 238 subsection. The distribution of biomass and estimates of production are shown in Supp. Mat. B.

239

240 The patchy spatial distribution of benthic invertebrates led us to consider multiple sampling stations
 241 within a similar habitat. Therefore, benthic prey production was finally estimated at the scale of each
 242 stratum, as it is likely that, at this scale, the benthic communities are composed of species with similar
 243 environmental requirements. Total prey production per unit area in each stratum (P_s , in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$)
 244 equalled the sum of each sampling station:

245

$$246 \quad P_s = \frac{\sum_{k \text{ in } s} P_k}{\sum_{k \text{ in } s} A_k} \quad \text{Equation 2}$$

247

248 where, s is the stratum and A is the total area sampled at each station k by the grab ($\sim 0.1 \text{ m}^2$).

249 2.4.2 Estimate benthic prey production **index** (from trawl data)

250 To verify whether the beam trawl data could be used as an index of benthic prey production, we
251 filtered the benthic organisms captured by the trawl, as it was done for the grab data, to keep only the
252 potential prey. An index of benthic prey production was then estimated at the scale of the stratum by
253 applying Eq. 1 and 2 to the filtered trawl data.

254 To test the trophic limitation hypothesis in YOY fish, the index was calculated at the scale of the
255 nursery, instead of the stratum, as the objectives of this part of the study was first to explore spatio-
256 temporal variability in prey production among nurseries. Moreover, YOY fish may move among strata
257 during their first year of life and do not necessarily feed where they were caught; thus, the nursery
258 scale was deemed more relevant. To raise to the nursery scale, the index was calculated by applying
259 Eq. 1 and then, based on Eq. 2, the total benthic prey production index per unit area in each nursery
260 (P_n , in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$):

261

$$262 \quad P_n = \frac{\sum_{k \text{ in } s} P_k}{\sum_{k \text{ in } s} A_k} \quad \text{Equation 3}$$

263 where, n is the nursery and A is the total area sampled at each station k by the trawl ($\sim 4000 \text{ m}^2$).

264 2.4.3 Determine the reliability of bottom trawl data for estimating an index of benthic prey 265 production

266 The linear relationship between the estimates of benthic prey production using grab data and the
267 estimates of benthic prey production index using trawl data was done by calculating Pearson
268 correlation on the log-transformed benthic prey production.

269 2.4.4 Investigate whether benthic prey production limits YOY fish density using quantile
270 regressions

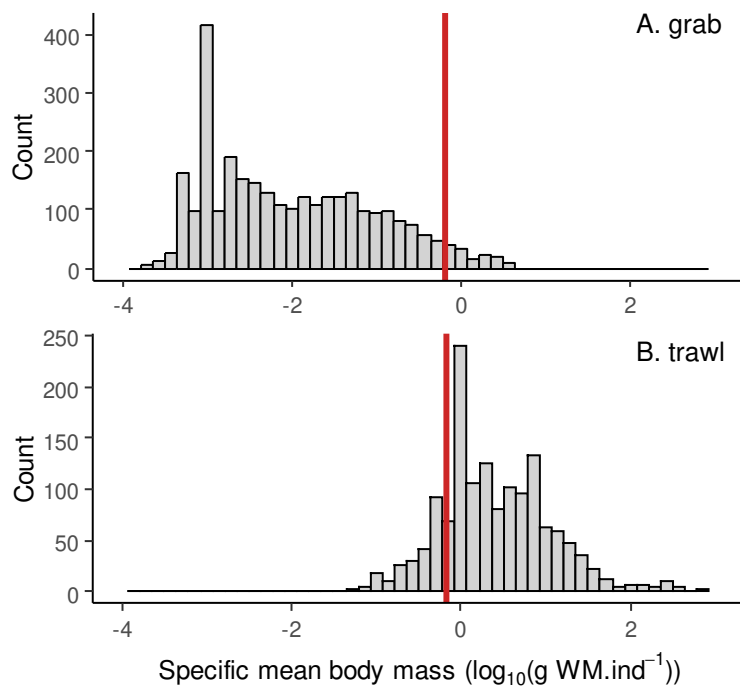
271 Quantile regressions were used to assess the relationship between benthic prey production index (log-
272 transformed to be consistent with the previous section) and the density of juvenile fish. This approach
273 is useful when testing the effect of a potential limiting factor but not measuring other factors (Cade
274 and Noon, 2003; Tableau et al., 2016). A limiting factor is detected when higher quantiles have
275 significant regressions and steeper slopes than lower quantiles. We hypothesised that benthic
276 production limits the density of juvenile fish. Lower and upper quantiles (10th and 90th) were tested by
277 performing bootstrap analyses with 1000 replicates (Supp. Mat. E2). The null hypothesis (H_0) was that
278 the relationship between benthic prey production index and juvenile fish abundance did not differ
279 from a randomly generated relationship. When the mean of the distribution of p -values was less than
280 0.05, H_0 was rejected and the regression was considered significant. Rejecting H_0 for both quantiles
281 would indicate potential limitation by the prey production or that an indirect factor influenced both
282 compartments. Rejecting H_0 for only the upper quantile would indicate that the prey production may
283 be limiting but that other factors most likely also interacted (see Tableau et al. (2016) for more details
284 on assumptions associated with quantile regressions and trophic limitation). The quantile regressions
285 were performed using the *quantreg* package (Koenker, 2018) of R software at the species, species
286 group (flat or round fish), and YOY community scales. Other quantiles (80th and 85th for upper quantiles
287 and 5th and 15th for lower ones) were also tested but are not shown, as the results were similar to those
288 presented in here.

289 3 Results

290 3.1 Trawl and grab: two correlated characterisations of benthic prey production

291 The two gears sampled different but complementary body mass spectra in the benthic community in
292 the four nurseries in the Bay of Biscay (Figure 2). As expected, the beam trawl sampled larger
293 individuals (mostly epibenthic megafauna) than the grab (mostly endobenthic macrofauna). The
294 overlap between the two body mass spectra showed that the trawl also sampled potential prey (10.3%
295 of total catches by biomass and 35.2% by abundance for the entire dataset). The communities of
296 invertebrates sampled with both gears had similarities, with *Owenia fusiformis* dominating the two
297 communities (from grab and trawl collection) in stratum V1, *Abra alba* in strata V3 and L3, and *Corbula*
298 *gibba* in stratum PA2 (Table 2, Supp. Mat. D). Although the proportion and abundance of species
299 caught with each gear differed, the two body mass spectra and the identity of the species support the
300 hypothesis that the two gears sampled complementary parts of the same large community of benthic
301 invertebrates in the nurseries. The part of the body mass spectrum from trawl data not considered as
302 potential prey (*i.e.* the right side of the vertical line, Figure 2B) contained small individuals of motile
303 epibenthic species, such as *Crangon crangon* and *Liocarcinus holsatus*, and larger benthic species not
304 consumed by YOY (Supp. Mat. D).

305

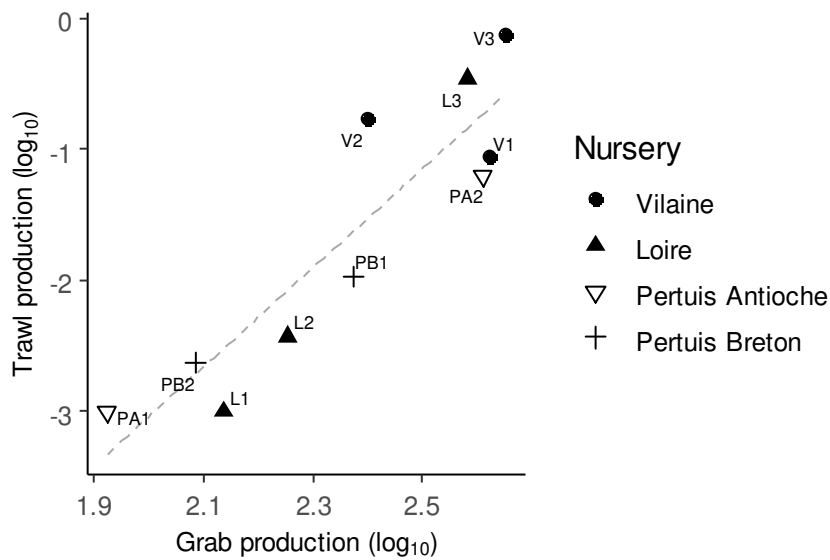


306

307 Figure 2. Weight spectra of station-specific mean body mass of benthic invertebrates in the four coastal
 308 areas of the Bay of Biscay sampled by (A) grab and (B) trawl. Data are \log_{10} -transformed. The red
 309 vertical line shows the threshold of mean body mass (*i.e.* 0.66 g wet mass (WM).ind⁻¹ – see section 2.1
 310 for details on the setting of the threshold value) used to identify potential prey of juvenile fish.

311 Benthic prey production index estimated from trawl data in the four nurseries studied ranged from 0
 312 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (strata in which no selected organisms were present) to $0.75 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$. Estimated of benthic
 313 prey production from grab data ranged from 84.2 to $675.6 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Figure 3). Annual production rates
 314 for potential prey from grab data were ~1000 times as high as those from trawl data. Nevertheless,
 315 the benthic prey production estimated by the two sampling gears were positively and significantly
 316 correlated (Pearson's $r = 0.90$, $p < 0.01$, Figure 3). This relationship was also observed using estimates
 317 of the biomass of potential prey (Pearson's $r = 0.77$, $p < 0.01$). Based on the strong correlation, the
 318 benthic prey production index estimated from trawl data was could be used and applied to the time
 319 series collected in the selected nurseries.

320



321

322 Figure 3. Log-linear relationship between annual prey production estimated from trawl and grab data
323 for each stratum in the four nurseries studied. Symbols are labelled with the names of the strata in
324 each nursery. Production estimates are in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$.

325 The site and sediment effects could not be statistically tested given the small number of points in each
326 nursery. Nevertheless, the description of the sites showed that three strata in the Bay of Vilaine had
327 the highest estimates of potential prey production for both gears. According to the bathy-sediment
328 conditions in each stratum, the highest productions ($> 400 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) occurred in sandy mud, except
329 in the outer estuary of the Loire, where environmental constraints such as low salinity or maximum
330 estuarine turbidity may restrict production (Table 2).

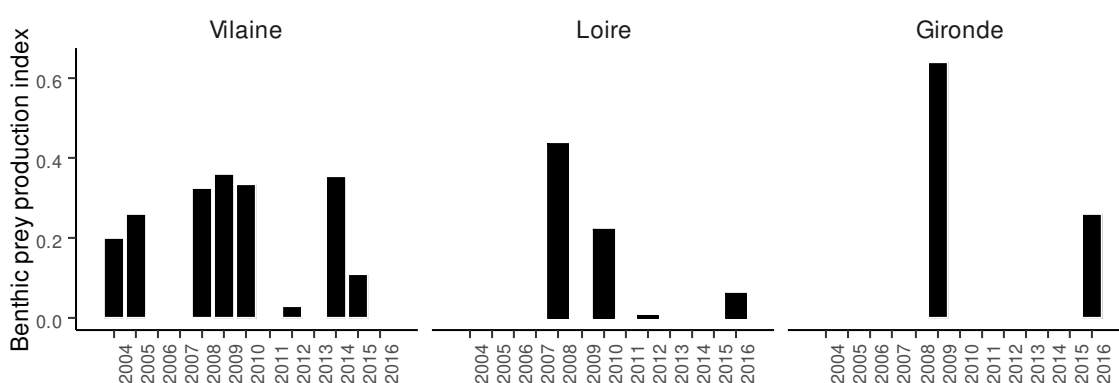
331 Table 2. Sediment type (according the typology of Chassé and Glémarec (1976)) of each stratum associated with dominant prey species using the two sampling
 332 methods (macrofauna: grab sampling; megafauna: trawl sampling, Supp. Mat. D), and the total production estimated from grab samples and detailed mean
 333 characteristics (sediment fractions and depth).

Sediment type / Stratum	Dominant prey species		Total production in grab (k J.m ⁻² .y ⁻¹)	Sediment fraction (%) (mean ± SD)			Depth (mean ± SD)	Number of grab stations	
	collected in grab samples	collected in trawl samples		Mud	Fine sand	Coarse sand and Gravel			
Mud	PA1	<i>Sternaspis scutata</i>	---	84.2	97.5 ± 0.6	2.1 ± 1.1	0.3 ± 0.4	5.2 ± 0.5	3
	V2	<i>Sternaspis scutata</i> , <i>Amphiura filiformis</i>	<i>Nucula</i> spp., <i>Philine aperta</i>	251.8	90.0 ± 5.3	7.2 ± 5.1	2.8 ± 1.5	11.4 ± 2.2	6
	PB1	<i>Sternaspis scutata</i> , <i>Spisula subtruncata</i>	<i>Corbula gibba</i> , <i>Ophiura</i> spp.	237.4	91.2 ± 5.4	7.6 ± 5.5	1.0 ± 1.1	4.8 ± 3.1	3
Sandy mud	V1	<i>Owenia fusiformis</i>	<i>Owenia fusiformis</i>	417.3	65.3 ± 26.0	22.6 ± 14.0	12.0 ± 22.4	7.9 ± 2.2	17
	V3	<i>Abra alba</i> , <i>Owenia fusiformis</i>	<i>Ophiura</i> spp., <i>Abra alba</i>	446.7	67.3 ± 17.2	20.7 ± 11.2	11.8 ± 11.7	22.8 ± 6.2	15
	L1	<i>Limecola balthica</i>	---	137.1	39.7 ± 3.8	58.0 ± 4.9	2.4 ± 2.4	6.4 ± 0.6	3
	PA2	<i>Corbula gibba</i>	<i>Ophiura</i> spp., <i>Corbula gibba</i>	406.8	31.8 ± 22.1	58.6 ± 27.9	2.2 ± 2.5	9.0 ± 4.3	6
Muddy sand	L3	<i>Spisula elliptica</i> , <i>Abra alba</i> , <i>Lagis koreni</i>	Annelida	382.3	14.0 ± 13.0	51.5 ± 23.4	34.3 ± 33.6	19.4 ± 2.6	5
	PB2	<i>Spisula solida</i>	<i>Alcyonium</i> spp., <i>Ophiura</i> spp.	121.9	14.1 ± 11.3	59.5 ± 14.6	23.9 ± 4.7	7.0 ± 5.0	3
Sand	L2	<i>Spisula solida</i>	<i>Asterias rubens</i>	179.3	1.0 ± 1.0	62.9 ± 33.4	35.5 ± 33.5	9.1 ± 3.3	11

334

335 3.2 Inter-annual variations in the benthic prey production index

336 Inter-annual variations in the benthic prey production index were quantified (Figure 4). Estimates for
337 the Bay of Vilaine (8 years sampled) ranged from 0.029 to 0.362 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ in 2012 and 2014,
338 respectively. Estimates for the outer Loire estuary (4 years sampled) ranged from 0.001 to 0.433 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$
339 in 2012 and 2008, respectively. Estimates for the outer Gironde estuary (2 years sampled) ranged
340 from 0.259 to 0.642 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ in 2016 and 2009, respectively.



341
342 Figure 4. Inter-annual variations in the benthic prey production index. Note the irregular frequency of
343 sampling. Benthic prey production index is in $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$.

344 Dominant prey species from the trawl data were similar among the three nurseries and were also
345 similar to those in the communities described in the trawl data used for the index. *Ophiura ophiura*
346 had the highest occurrence (93% of the case studies, *i.e.* 13 of 14), while *A. alba*, *Ophiura albida*,
347 *Amphiura filiformis*, *Lagis koreni*, and *Philine aperta* occurred in more than 70% of the case studies.
348 Motile epibenthic species were also observed, such as *C. crangon* and Amphipoda (in 64% and 38% of
349 the nursery-years studied, respectively).

350 3.3 Relationships between benthic prey production index and juvenile fish density

351 When investigating the relationship between benthic prey production index and YOY fish density, the
352 slopes of the upper quantiles (90th) always differed significantly from 0 for all species except *T. luscus*.

353 When *T. luscus* was kept in the analysis, slopes of the upper quantiles (90th) did not differ from 0 for
 354 the round fish group and the YOY community. *T. luscus* was the dominant species in the YOY
 355 community in number so it highly drove the results for the round fish group or the community of YOY
 356 fish. After removing *T. luscus* from the analysis, slopes of all fish groups (flatfish, round fish groups, and
 357 YOY community) differed significantly from 0 (Table 3, Supp. Mat. E1). Conversely, the lower quantiles
 358 (10th) were non-significant for all species.

359

360 Table 3. Slopes of quantile regressions of YOY fish density (no.ha⁻¹) at three scales as a function of the
 361 benthic prey production index (log scale) for lower (10th) and upper (90th) quantiles. Asterisks indicate
 362 slopes that differed significantly ($p < 0.05$) from 0. The percentage of non-empty stations (out of 494
 363 stations sampled in the 14 nursery-years) is indicated in the last column. “---” indicates species for
 364 which the number of empty stations was greater than 10% and 90% of the dataset for the lower and
 365 upper quantile regressions, respectively. “NS” indicates non-significant results.

Scale	10 th quantile	90 th quantile	Percentage of non- empty stations
YOY community	NS	NS	95%
YOY community without <i>Trisopterus luscus</i>	NS	120.7*	92%
Round fish group	NS	NS	92%
<i>Trisopterus luscus</i> – Pouting	---	NS	60%
<i>Merlangius merlangus</i> – Whiting	---	44.5*	62%
<i>Callionymus lyra</i> – Common dragonet	---	52.9*	49%
<i>Mullus surmuletus</i> – Striped red mullet	---	4.5*	32%
Flatfish group	---	33.8*	55%
<i>Solea solea</i> – Common sole	---	29.1*	45%
<i>Pleuronectes platessa</i> – European plaice	---	2.8*	13%
<i>Dicologlossa cuneata</i> – Wedge sole	---	---	6%

<i>Arnoglossus laterna</i> – Mediterranean scaldfish	---	1.8*	15%
--	-----	-------------	-----

366

367 4 Discussion

368 We hypothesised trophic limitation by macrobenthic prey production on YOY of benthic-demersal fish
 369 species. To test this hypothesis, we developed a benthic prey production index and validated it using
 370 data from grabs and trawls in four coastal nurseries. This index was then calculated from data collected
 371 using trawls in nurseries in the Bay of Biscay to estimate and describe prey production in each nursery,
 372 and investigate whether microbenthic prey production limits the YOY fish community. Results
 373 indicated that benthic prey production significantly influenced YOY fish density (except that of *T.*
 374 *luscus*), suggesting that benthic prey production may regulate juvenile fish density, although other
 375 factors likely limit them locally such as abiotic parameters (Trimoreau et al., 2013) or predation
 376 pressure (Ellis and Gibson, 1995; Leopold et al., 1998).

377 4.1 Selected trawled benthic invertebrate production: a macrobenthic prey production 378 index

379 The benthic communities captured by trawl and grab gears have been previously compared to assess
 380 regional biodiversity patterns (Rufino et al., 2017) and congruence of biodiversity structure among
 381 ecosystem components (Karakassis et al., 2006), but never, to the best of our knowledge, to calculate
 382 a benthic production index. However, Le Pape et al. (2007) included some benthic megafauna collected
 383 from trawl surveys classified into trophic guilds to improve their fish habitat models. The beam trawl
 384 can be considered a "generalist" gear because it samples large areas, motile or slightly motile benthic-
 385 demersal fish and invertebrates, and sessile invertebrates buried to different depths in the substrate,
 386 depending on the degree of compaction of the substrate. The beam trawl can cover several types of
 387 sediment. The size of the smallest benthic organisms captured depends on the mesh size at the cod

388 end (here, 20 mm) and whether it becomes partially clogged. The grab can be considered a more
389 "specialist" gear because it targets soft bottom small areas and often a single sediment type, and
390 slightly motile and sessile epi- and endo-invertebrates. The size of organisms is determined by the size
391 of the mesh in which grab contents are sieved (1 mm).

392

393 In this study, the benthic organisms sampled with the grab and the beam trawl belonged to two
394 overlapping size components of the same benthic community. The similarity in species composition
395 for both gears at the stratum scale supported this hypothesis. The same environmental factors –
396 sediment type, bathymetry, and hydrological conditions – likely shaped these two components (Rufino
397 et al., 2017). Since juvenile fish species can target only some small individuals of invertebrates in trawl
398 samples as prey, only the organisms overlapping in size (defined using a threshold of mean individual
399 body mass) in the two gears were analysed. The biomass threshold of $0.1 \text{ g AFDM.ind}^{-1}$ ($0.66 \text{ g WM.ind}^{-1}$
400 ca) is the largest prey that juvenile fish can catch given their mouth size (Tableau et al., 2015, 2016).
401 This threshold is certainly species-specific, but as the study was performed at the community level,
402 using the mean mouth size of several fish species (Hiddink et al., 2016; Tableau et al., 2015) likely
403 smoothed interspecific differences. We cannot exclude that other prey characteristics could influence
404 the prey selection by fish juveniles (texture, activity; van der Veer et al., 2016) but, to our best
405 knowledge, such data are missing in the literature for the fish studied.

406

407 The benthic prey production index included taxonomic groups (bivalves, polychaetes, ophiurids, and
408 crustaceans) matching the dominant potential prey found in grabs. The species in the grab and trawl
409 samples were consistent with the YOY diet in the nurseries (Pasquaud et al., 2008; Tableau et al., 2015).
410 For instance, both samples contained *P. aperta*, which are consumed by YOY *S. solea* in the Bay of
411 Vilaine (Kopp et al., 2013), and small echinoderms (*Ophiura* spp., *A. filiformis*), which can be grazed by
412 flatfish and round fish species (Duineveld and Van Noort, 1986; Ntiba and Harding, 1993; van der Veer
413 et al., 1990). Analysis of the potential prey species sampled by the trawl highlighted taxonomic

414 differences in the same size distributions that the grab had sampled. The trawl also sampled motile
415 suprabenthic organisms such as small *C. crangon*, which escape more easily from the grab via flushing.
416 Flatfish such as *P. platessa* and *S. solea* may feed on small individuals of these suprabenthic species
417 (Amara et al., 2001; Pasquaud et al., 2008), as may round fish such as *T. luscus* in the Loire estuary
418 (Robin and Marchand, 1986) or *M. merlangus* (Demain et al., 2011). However, defining potential prey
419 using only mean body mass resulted in many trawl stations that contained no potential prey, and
420 benthic prey production estimates from grab and trawl samples that differed by three orders of
421 magnitude, as the trawl sampled mainly larger individuals. Nevertheless, the two communities
422 represented by each gear were significantly and highly correlated, suggesting that production
423 estimates based on trawled benthic invertebrates can be a reliable index of benthic prey production
424 for juvenile fish.

425

426 According to the sediment types in the strata, sandy mud was more productive than other sediments.
427 Areas of sandy muds have been described as having the highest biomass along the coast of the Bay of
428 Biscay (Chassé and Glémarec, 1976b) and in the Pertuis (Hily, 1976). Benthic community composition
429 in sandy mud areas differed: *O. fusiformis* dominated the estuarine community of the Vilaine site, *A.*
430 *alba* dominated the offshore strata community of the Vilaine site, and *C. gibba* dominated the sandy
431 mud of the Pertuis d'Antioche. However, they also had common species such as *O. fusiformis* and
432 *Ophiura* spp. The most estuarine stratum of the Loire estuary was also composed of sandy muds but
433 had lower production than the other three strata. This estuarine habitat may be influenced by
434 maximum turbidity, which could reduce macrobenthic biomass and juvenile fish density (Marchand,
435 1993). However, this estuarine habitat was sampled on 3 stations which was the lowest number of
436 stations of the sampling design and could lead to a potential underestimation of benthic prey
437 production because of the patchy spatial distribution of benthic invertebrates. Moreover, it is
438 noteworthy that sites were sampled in different years, when climatic conditions may have differed,
439 which may have caused confounded site effect with year effect.

440

441 We caution against using the benthic prey production index calculated from beam trawl samples as an
442 absolute measure of production; instead, we recommend using the index only as a relative estimate
443 of the benthic prey production available. Indeed, the order of magnitude of the index's absolute values
444 cannot be compared to those obtained using another type of gear. The index was designed and
445 validated with data from temperate coastal and estuarine nurseries in the Bay of Biscay. It would be
446 informative and useful to increase the number of case studies, in particular in other geographical
447 context to see if the strong correlation still holds.

448 4.2 Variability in macrobenthic prey production among nurseries: potential influences

449 Coastal nurseries along the Bay of Biscay have a similar range of depths (Table 1) and temperature, but
450 differences in local hydrodynamics influence the main sediment characteristics. For instance, the
451 intensity of currents and water discharges in the outer Loire and Gironde estuaries is ~10 times as high
452 as that in the Bay of Vilaine. Mean annual flow is ~75 m³.s⁻¹ for the Vilaine River vs. ~850 and ~780
453 m³.s⁻¹ in the Loire estuary and Gironde estuary, respectively (Romero et al., 2013).

454

455 It might be expected that the higher river discharges and thus higher nutrient loads (Romero et al.,
456 2013) from the two large estuaries would produce more benthic prey than in the Bay of Vilaine. Yet,
457 according to the index, benthic prey production in the Bay of Vilaine is in the same order of magnitude
458 as those in the outer estuaries of Loire and Gironde. These similarities in prey production might be
459 related to the longer residence time of water in the Bay of Vilaine (Obaton and Garreau, 1999) than in
460 the two other nurseries (Lazure and Salomon, 1991). We hypothesized that a longer residence time
461 would allow primary producers to take up more terrestrial nutrients and organic matter, which could
462 benefit secondary producers and the rest of the coastal food web as shown in wetlands (Sierszen et
463 al., 2006). Conversely, the higher river discharges in the Loire and Gironde estuaries flush nutrients
464 and organic matter out to the ocean, resulting in prey production similar to that estimated in the Bay

465 of Vilaine. Nevertheless, our data did not enable us to explain that pattern and it would be interesting
466 to use a larger dataset to properly explore the potential drivers of inter-annual and inter-site variability
467 in benthic prey production.

468 4.3 Macrobenthic prey production limits YOY fish density

469 The hypothesis that YOY fish density was higher in years and sites with higher benthic prey production
470 was supported by the quantile regressions. Unlike the mean of a distribution, upper quantiles can
471 indicate that a tested limiting factor (here, available food resources) may be acting on the same
472 processes as other unknown limiting factors (Cade and Noon, 2003). These models have been used to
473 investigate the influence of food supply on demersal fish abundance around the Balearic Islands in the
474 western Mediterranean (Johnson et al., 2012). Significant relationships at the upper quantile in the
475 present study suggest that benthic prey production limits YOY fish density in coastal and estuarine
476 nurseries along the Bay of Biscay.

477
478 Food limitation for juvenile fish in nurseries has been widely debated (Le Pape and Bonhommeau,
479 2015). In this study, years with low benthic prey production index had lower juvenile fish density, while
480 years with high benthic prey production index had a wider range of densities, including the highest
481 densities. This suggests that the prey production likely plays a role in regulating juvenile fish density at
482 our study nurseries. This result agrees with those of Tableau et al. (2016) in the Bay of Vilaine that
483 showed that juvenile fish biomass overlapped benthic prey production spatially. Available food
484 resources that do not meet the energy needs of all individuals can result in trophic competition and
485 thus trophic limitation. This was presumably the case in another French nursery (the Bay of the Seine),
486 where consumption of YOY of several fish species followed benthic prey production over a three-year
487 period (Saulnier, 2019). Other studies, including this one, confirm the importance of trophic limitation
488 mechanisms in the first year of life for fish in coastal nurseries (Tableau et al., 2019; van der Veer et

489 al., 2016). Frequency and intensity of food limitation may differ among nurseries and periods of the
490 year, but this could not be tested due to our unbalanced dataset coming from annual surveys.

491

492 All YOY fish species showed a positive relationship with the benthic prey production index at the upper
493 quantile, except *T. luscus*, which may have different feeding or behaviour ecology. This species seems
494 to have an aggregative behaviour that is not exclusive to soft bottoms (Reubens et al., 2011), which
495 could partly explain the highest densities sampled at certain stations in the three nurseries. Moreover,
496 *T. luscus* is a suprabenthic feeder that targets Amphipoda, Mysidacea, and epibenthic Decapoda
497 (França et al., 2004; Hamerlynck and Hostens, 1993; Robin and Marchand, 1986), and the latter two
498 orders were sampled less by the grabs. YOY *M. merlangus* has similar feeding habits (Hamerlynck and
499 Hostens, 1993), but showed a positive relationship to the benthic prey production index, perhaps
500 because its juveniles settle in sand (Demain, 2010).

501

502 The non-significant lower quantile suggests that other untested factors likely limit fish density in the
503 nurseries. Abiotic factors such as bathymetry, sediments, and wave exposure partly determine the
504 distribution of juvenile flatfish in coastal nurseries (Le Pape et al., 2003; Trimoreau et al., 2013). Local
505 abiotic conditions may not be suitable for juveniles even if benthic prey production at the nursery scale
506 is high. Moreover, contamination and pollution in nurseries can influence juvenile growth and survival
507 (Gilliers et al., 2006; Marchand et al., 2003). Also, although juvenile fish experience less predation in
508 nurseries (Gibson, 1994), they have several potential predators, such as predatory invertebrates (Choy,
509 1986), other fish species (Ellis and Gibson, 1995) and sea birds (e.g. cormorants, Leopold et al., 1998).
510 Because this study showed a trophic limitation of juvenile fish by prey production, it emphasised
511 bottom-up regulation of the fish by their prey. However, top-down processes can also influence
512 populations of juvenile fish (Baker and Sheaves, 2009; van der Veer and Bergman, 1987). Moreover,
513 predation and food limitation are not opposing processes and may interact in regulating fish
514 populations (Hixon and Jones, 2005). For instance, starvation can increase fish activity, leading to

515 greater exposure to predation (Biro et al., 2003; Myers and Cadigan, 1993). Greater predation can then
516 become an indirect consequence of food limitation.

517

518 Finally, juvenile marine fish concentrate on nursery grounds (Iles and Beverton, 2000) where the
519 available food may be limiting during their first year of life. The index of benthic prey production
520 provided in here will give the opportunity to nursery-dedicated surveys to investigate the relative
521 variability of the benthic production of their nurseries, thereby contributing to the understanding of
522 the regulation of juvenile fish and hence variability in fish recruitment for commercially important
523 species.

524

525

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531

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