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

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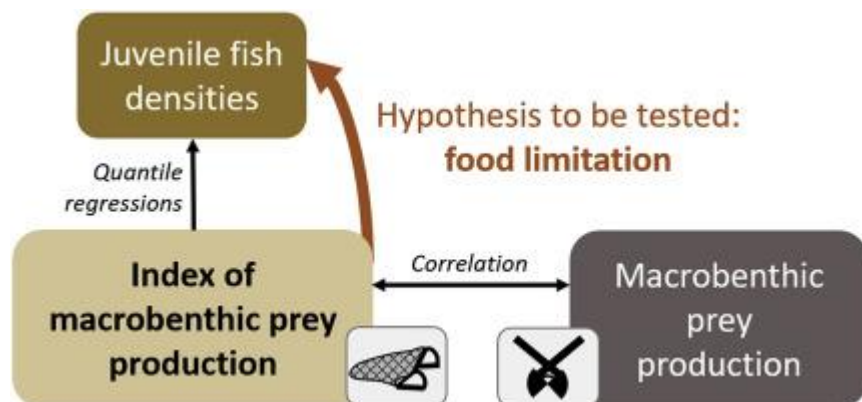
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Abstract :

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

Graphical abstract



Highlights

► Density of juvenile fish is limited by benthic prey production in nurseries. ► Data from bottom trawling can be used to estimate a benthic prey production index. ► Potential prey were selected using a mean individual body mass threshold.

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

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
53 recruitment remain under debate, some studies suggested that prey production may be limiting (Le
54 Pape and Bonhommeau, 2015; Nash et al., 2007; van der Veer et al., 2016). Prey production in
55 nurseries becomes limiting when demand exceeds production, resulting in potential mortality and
56 competition 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
71 prey data (Beaugrand et al., 2003; Crawford and Dyer, 1995; Okamoto et al., 2012). For instance,
72 analyses of predator-prey time series showed a relationship between inter-annual fluctuations in
73 anchovy biomass and the number of nesting seabirds (Crawford and Dyer, 1995). Although not
74 demonstrating a causal relationship, the analysis supported the hypothesis that when food supply is
75 low, birds are unlikely to allocate energy to breeding. Similarly, along the North Sea coast, a long-
76 term dataset showed a decrease in nutrient loading, which presumably caused a change in the
77 spatial distribution of *Pleuronectes platessa* juveniles (Støttrup et al., 2017). Joint analysis of predator
78 and prey could provide arguments in the debate on food limitation, especially when it is performed
79 in a causation context (Kato and Sasaki, 2017). Quantile regressions used in this context may be very
80 helpful in identifying limiting factors (Cade and Noon, 2003; Planque and Buffaz, 2008), since the
81 food-limitation hypothesis can be tested by examining several quantiles of the predator-prey
82 relationship (Tableau et al., 2016).

83

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

93 same benthic invertebrate community (Eleftheriou, 2013), and the overlap between them is assumed
94 to contain prey 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
103 and round fish species.

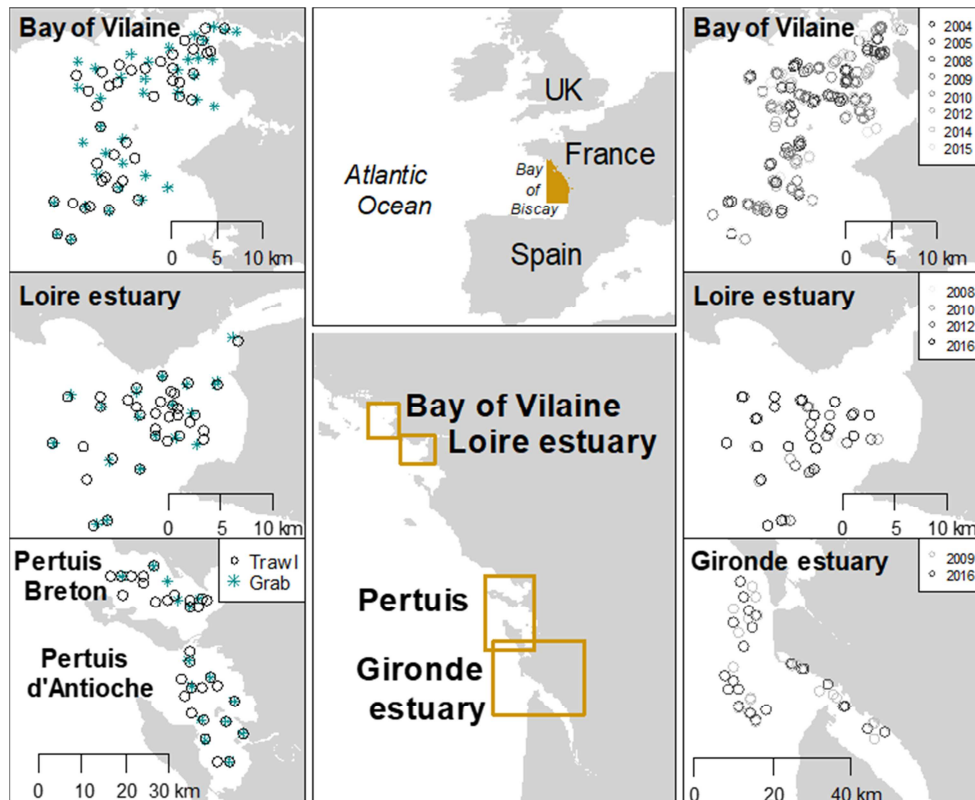
104 2 Materials and methods

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
111 late summer 2008, 2016 and 2015, respectively (Figure 1, left panel). These data were used to meet
112 the 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

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

120 Vilaine (8 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

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

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

129 mouth of the estuary (1 = upstream, 3 = offshore).

130

131 Table 1. Description of the nurseries and sampling design used to define the benthic production
 132 index, including the mean bathymetry and mean percentages of mud (< 63 μm), sand (> 63 μm and <
 133 500 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%
 146 formalin solution in plastic zip-top bags. In the laboratory, organisms were rinsed and sieved with
 147 fresh water in a column of five successive sieves with square mesh sizes ranging from 16 to 1 mm.

148 Organisms retained in each sieve were then stored separately in a 70% ethanol solution, keeping in
149 mind that handling, fixing samples with formalin and storing with ethanol likely led to underestimate
150 biomasses (Gaston et al., 1996; Wetzel et al., 2005). Invertebrates from each sieve were identified to
151 the lowest taxonomic level, counted and weighed. Biomass per taxa was determined as wet mass
152 (WM) and then converted into ash-free dry mass (AFDM) using specific coefficients from a global
153 database of conversion factors (Brey et al., 2010). When no conversion factor was available at the
154 species level, the conversion factor for the next highest taxonomic level was used. Data from
155 replicates of each sampling station were summed, and biomass was standardized based on the area
156 sampled (*i.e.* 3 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
164 (nursery-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.
175 Then, a minimum and maximum lengths of 7 and 15 cm, respectively, were set to select individuals
176 that feed almost exclusively on macrobenthic invertebrate prey within the size range of the fish
177 cohort (see Supp. Mat. C). These size thresholds for individual fish assumed that fish smaller than the
178 minimum length (7 cm) prey on pelagic and benthic invertebrates that our sampling device could not
179 capture (*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
183 relationship estimated for each species with all length data available in the data set from 2004-2016.
184 Only individuals whose mean individual length met the size ranges of the species were kept in the
185 analyses. Relative YOY fish density (number of individuals.ha⁻¹) was estimated at each station from
186 catches 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
192 the 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
196 YOY fish are opportunistic feeders that consume a variety of benthic prey no larger than a certain

197 size (Besyst et al., 1999; Griffin et al., 2012). Hence, a benthic invertebrate was identified as potential
198 prey if it was smaller than the maximum mouth height of a juvenile fish. Data on mouth heights of
199 the three most abundant species (*M. merlangus*, *S. solea* and *T. luscus*) in the studied areas were
200 used to define a mean height of 20 mm (unpublished data). As benthic organisms collected with
201 trawl were not sized, but only counted and weighted, we decided to select potential prey of the YOY
202 fish using a filter based on mean individual mass. To set the threshold under which an invertebrate
203 can be considered as prey for YOY fish, we used the benthic organisms collected with grab and
204 categorised into size classes described previously (section 2.1.2). Mean individual body mass of the
205 organisms retained in each mesh size was calculated. A threshold of $0.66 \text{ g WM.ind}^{-1}$ (*i.e.* $\sim 0.1 \text{ g}$
206 AFDM.ind^{-1}), corresponding mainly to benthic organisms smaller than 16 mm (the largest mesh size),
207 was identified as potential prey. This threshold was applied to select potential prey from benthic
208 invertebrates using the grab and the beam trawl. Once applied to the grab data, the rare species and
209 mean individual body mass filters selected 73.3% of the total biomass in the entire dataset (*i.e.* from
210 all three nurseries where grab and trawl were deployed concomitantly). Once applied to the trawled
211 benthic species, 10.3% of the total biomass of the entire dataset was retained. The benthic
212 organisms included in those percentages (respectively 73.3% and 10.3%) were considered as
213 potential prey and were used to estimate respectively benthic prey production using grab data and
214 benthic prey production index using trawl 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
218 production-to-biomass ratio (P:B), which was calculated for each taxon at each station using the
219 artificial neural network model developed by Brey (2012). The input data for this model are 17
220 categorical parameters that describe biological and functional traits (*e.g.* taxon, habitat, feeding and
221 mobility), depth, temperature and individual mean body mass. The parameters required by the

222 model were collated according to Saulnier et al. (2018) and supplemented with data from an online
 223 resource (Biological 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
 243 similar environmental requirements. Total prey production per unit area in each stratum (P_s , in
 244 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) 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
 252 the potential prey. An index of benthic prey production was then estimated at the scale of the
 253 stratum by 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

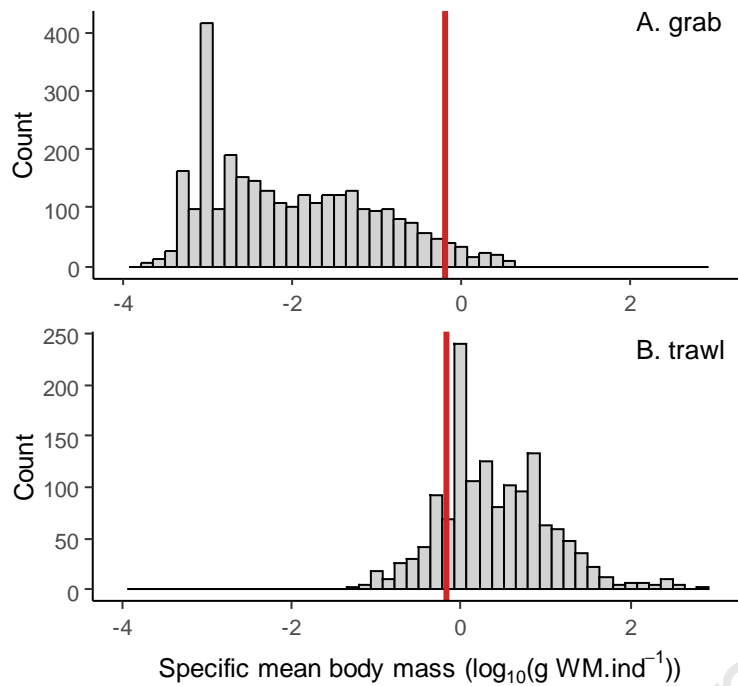
271 Quantile regressions were used to assess the relationship between benthic prey production index
272 (log-transformed to be consistent with the previous section) and the density of juvenile fish. This
273 approach is useful when testing the effect of a potential limiting factor but not measuring other
274 factors (Cade and Noon, 2003; Tableau et al., 2016). A limiting factor is detected when higher
275 quantiles have significant regressions and steeper slopes than lower quantiles. We hypothesised that
276 benthic production limits the density of juvenile fish. Lower and upper quantiles (10th and 90th) were
277 tested by performing bootstrap analyses with 1000 replicates (Supp. Mat. E2). The null hypothesis
278 (H_0) was that the relationship between benthic prey production index and juvenile fish abundance
279 did not differ from a randomly generated relationship. When the mean of the distribution of p -values
280 was less than 0.05, H_0 was rejected and the regression was considered significant. Rejecting H_0 for
281 both quantiles would indicate potential limitation by the prey production or that an indirect factor
282 influenced both compartments. Rejecting H_0 for only the upper quantile would indicate that the prey
283 production may be limiting but that other factors most likely also interacted (see Tableau et al.
284 (2016) for more details on assumptions associated with quantile regressions and trophic limitation).
285 The quantile regressions were performed using the *quantreg* package (Koenker, 2018) of R software
286 at the species, species group (flat or round fish), and YOY community scales. Other quantiles (80th
287 and 85th for upper quantiles and 5th and 15th for lower ones) were also tested but are not shown, as
288 the results were similar to those 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
295 (10.3% of total catches by biomass and 35.2% by abundance for the entire dataset). The communities
296 of invertebrates sampled with both gears had similarities, with *Owenia fusiformis* dominating the
297 two communities (from grab and trawl collection) in stratum V1, *Abra alba* in strata V3 and L3, and
298 *Corbula gibba* in stratum PA2 (Table 2, Supp. Mat. D). Although the proportion and abundance of
299 species caught with each gear differed, the two body mass spectra and the identity of the species
300 support the hypothesis that the two gears sampled complementary parts of the same large
301 community of benthic invertebrates in the nurseries. The part of the body mass spectrum from trawl
302 data not considered as potential prey (*i.e.* the right side of the vertical line, Figure 2B) contained
303 small individuals of motile epibenthic species, such as *Crangon crangon* and *Liocarcinus holsatus*, and
304 larger benthic species not consumed by YOY (Supp. Mat. D).

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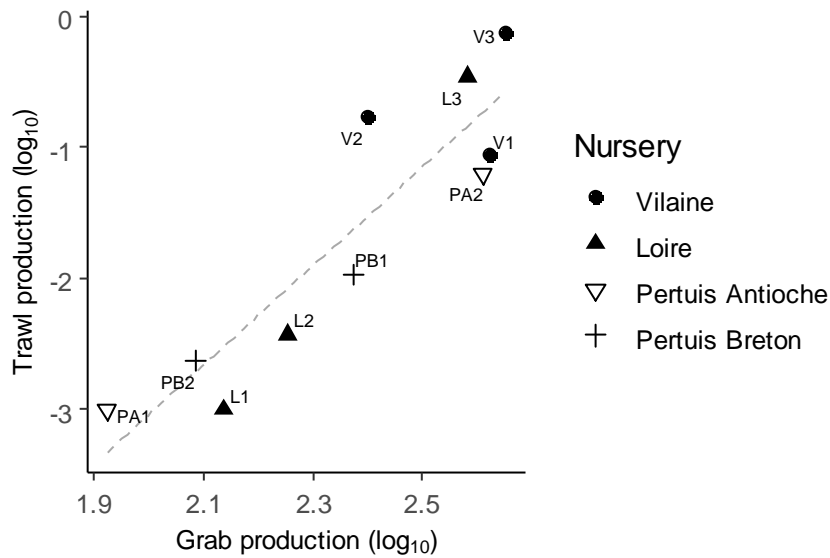


306

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

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

321



322

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

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

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

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

335

3.2 Inter-annual variations in the benthic prey production index

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



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

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

3.3 Relationships between benthic prey production index and juvenile fish density

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

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

360

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

367

368 4 Discussion

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

378 4.1 Selected trawled benthic invertebrate production: a macrobenthic prey 379 production index

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

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

393

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

407

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

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

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

441

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

449 **4.2 Variability in macrobenthic prey production among nurseries: potential influences**

450 Coastal nurseries along the Bay of Biscay have a similar range of depths (Table 1) and temperature,
451 but differences in local hydrodynamics influence the main sediment characteristics. For instance, the
452 intensity of currents and water discharges in the outer Loire and Gironde estuaries is ~10 times as
453 high as that in the Bay of Vilaine. Mean annual flow is ~75 m³.s⁻¹ for the Vilaine River vs. ~850 and
454 ~780 m³.s⁻¹ in the Loire estuary and Gironde estuary, respectively (Romero et al., 2013).

455

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

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

469 4.3 Macrobenthic prey production limits YOY fish density

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

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

491 among nurseries and periods of the year, but this could not be tested due to our unbalanced dataset
492 coming from annual surveys.

493

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

503

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

517 fish activity, leading to greater exposure to predation (Biro et al., 2003; Myers and Cadigan, 1993).
518 Greater predation can then become an indirect consequence of food limitation.

519

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

526

527

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533

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Highlights

- Density of juvenile fish is limited by benthic prey production in nurseries
- Data from bottom trawling can be used to estimate a benthic prey production index
- Potential prey were selected using a mean individual body mass threshold

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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:

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