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

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Title

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Authors

Louise Day[a,b]*, Hervé Le Bris[b], Erwan Saulnier[a,b], Lucas Pinsivy[b], Anik Brind'Amour[a]

[a]IFREMER, EMH, Rue de l'île d'Yeu, B.P. 21105, 44311 Nantes Cedex 03, France

[b]ESE, Ecology and Ecosystems Health, Agrocampus Ouest, INRAE, 35042 Rennes, France

E-mail addresses:

* Corresponding author, L. Day: louise.day@ifremer.fr

H. Le Bris: herve.le.bris@agrocampus-ouest.fr

E. Saulnier: erwan.saulnier@agrocampus-ouest.fr

L. Pinsivy: lucas.pinsivy@ifremer.fr

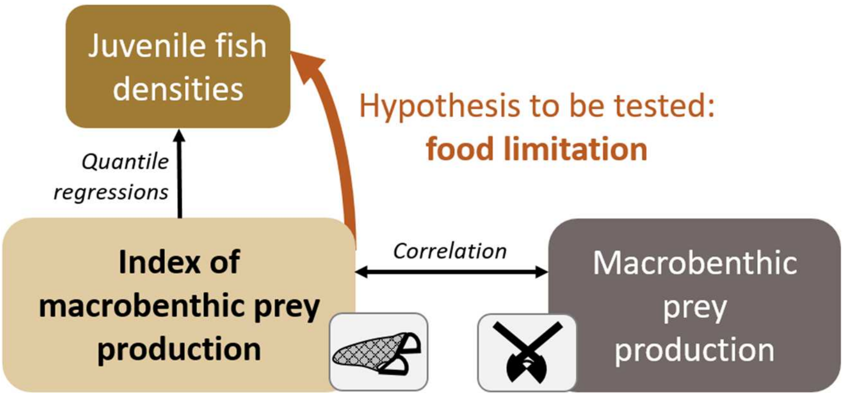
A. Brind'Amour: anik.brindamour@ifremer.fr

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

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 finnaly 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



1 Introduction

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

Several approaches have been used to test the food-limitation hypothesis for juvenile marine fish in coastal and estuarine nurseries. Direct approaches usually compare prey production to food requirements or consumption of juvenile fish. They have been performed using data from experimental ponds (Craig et al., 2007) or directly collected in the field (Tableau et al., 2019), and usually calculated the ratio of benthic prey consumption by juvenile fish to benthic prey biomass or production using trophic models (Chevillot et al., 2019) or bioenergetic approaches (Tableau et al., 2019; Vinagre and Cabral, 2008). These studies yielded conflicting results and remained cautious in their conclusions, as they were generally based on a temporal snapshot (*i.e.* one year). These approaches are effort-intensive because they require the biomass of both prey and predator to estimate prey production and juvenile consumption (*e.g.* Bennett and Branch, 1990; Collie, 1987; Vinagre and Cabral, 2008).

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

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

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

2 Materials and methods

2.1 Data collection

2.1.1 Nurseries surveyed

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

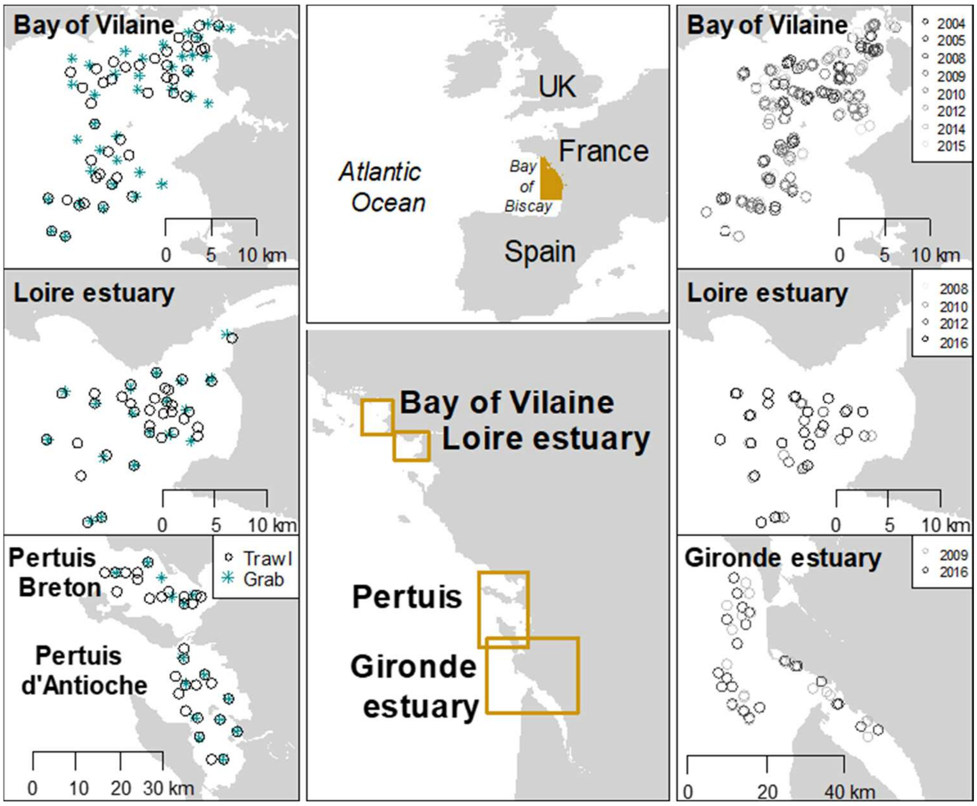


Figure 1. Location of the study sites along the French coast of the Bay of Biscay (middle panel). Locations of the sampling stations with the two sampling gears, grabs and trawls (mean location), in 2008 in the Bay of Vilaine, in 2016 in the Loire estuary and in 2015 in both Pertuis stations (left panel). Locations of the sampling stations with only trawls deployed (grey circles) in the Bay of Vilaine (8 years), the Loire estuary (4 years), and the Gironde estuary (2 years) (right panel).

These nurseries differed environmentally in sediment composition and bathymetry (Table 1). The Bay of Vilaine is mainly a muddy nursery with sampling stations of varying depths (1-35 m), whereas the two Pertuis are half-muddy and half-sandy shallow nurseries, and the outer Loire estuary is mainly sandy with a gradient of depths (Table 1). Each nursery surveyed was divided into strata defined by the bathymetry and the size distribution of sediments (assessed using the grab samples, Supp. Mat. A). Thus, three bathy-sediment strata were defined in the Bay of Vilaine (V1, V2 and V3, from upstream to downstream), three others in the outer Loire estuary (L1, L2 and L3), and two at each Pertuis site (PA1, PA2 and PB1, PB2). The number in each code corresponds to the distance from the mouth of the estuary (1 = upstream, 3 = offshore).

Table 1. Description of the nurseries and sampling design used to define the benthic production index, including the mean bathymetry and mean percentages of mud (< 63 µm), sand (> 63 µm and < 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 (± 1 SD) depth (m)	15.4 ± 0.5	11.0 ± 0.4	5.9 ± 0.4	7.5 ± 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)

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

2.1.2 Grab data collection

Grab samples were collected using a 0.1 m² Van Veen grab, with three replicates at each sampling station. Once aboard, the grab content was sieved through a 1 mm grid mesh and kept in a 7% formalin solution in plastic zip-top bags. In the laboratory, organisms were rinsed and sieved with fresh water in a column of five successive sieves with square mesh sizes ranging from 16 to 1 mm. Organisms retained in each sieve were then stored separately in a 70% ethanol solution, keeping in mind that handling, fixing samples with formalin and storing with ethanol likely led to underestimate biomasses (Gaston et al., 1996; Wetzel et al., 2005). Invertebrates from each sieve were identified to the lowest taxonomic level, counted and weighed. Biomass per taxa was determined as wet mass (WM) and then converted into ash-free dry mass (AFDM) using specific coefficients from a global database of conversion factors (Brey et al., 2010). When no conversion factor was available at the species level, the conversion factor for the next highest taxonomic level was used. Data from replicates of each sampling station were summed, and biomass was standardized based on the area sampled (*i.e.* 3 replicates × 0.1 m^2). The sampling design is detailed in Table 1.

2.1.3 Trawl data collection

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

2.2 Select YOY fish

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

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

2.3 Select potential benthic prey for YOY fish

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

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

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

2.4 Data analysis

2.4.1 Estimate benthic prey production (from grab data)

Benthic prey production was estimated by multiplying mean annual biomass by the annual production-to-biomass ratio (P:B), which was calculated for each taxon at each station using the artificial neural network model developed by Brey (2012). The input data for this model are 17 categorical parameters that describe biological and functional traits (*e.g.* taxon, habitat, feeding and mobility), depth, temperature and individual mean body mass. The parameters required by the model were collated according to Saulnier et al. (2018) and supplemented with data from an online resource (Biological Traits Information Catalogue of The Marine Life Information Network http://www.marlin.ac.uk/biotic/). The bathymetry for each station was extracted from the General Bathymetric Chart of the Oceans 30 arc-second grid (GEBCO_2014, version 20150318, http://www.gebco.net, Weatherall et al., 2015). Mean annual bottom temperature for each nursery-year was extracted from a multi-decadal hindcast of a physical-biogeochemical model of the Bay of Biscay (Huret et al., 2013). Individual mean body mass was calculated by dividing each taxon's mean annual biomass by its mean annual abundance.

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

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

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

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

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

where, s is the stratum and A is the total area sampled at each station k by the grab (~0.1 m^2).

2.4.2 Estimate benthic prey production index (from trawl data)

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

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

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

where, n is the nursery and A is the total area sampled at each station k by the trawl (~4000 m^2).

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

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

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

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

3 Results

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

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

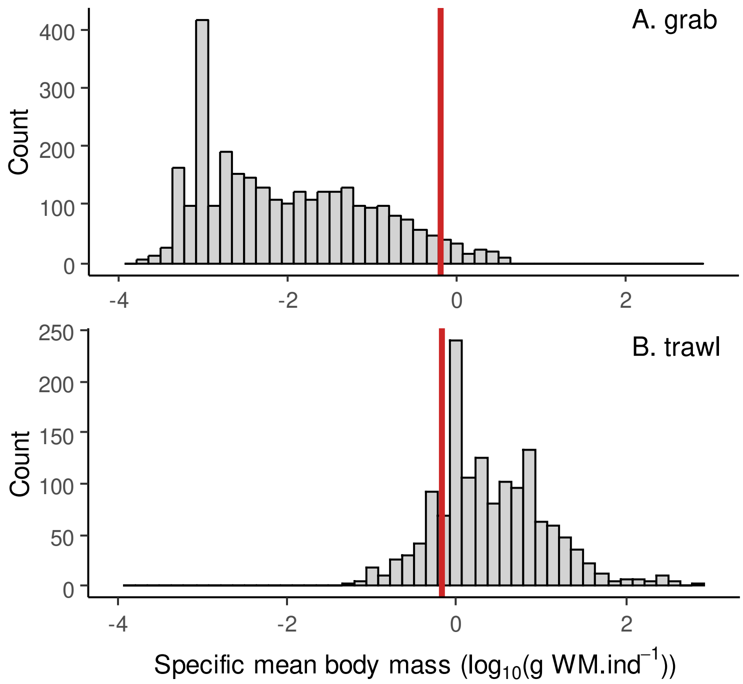


Figure 2. Weight spectra of station-specific mean body mass of benthic invertebrates in the four coastal areas of the Bay of Biscay sampled by (A) grab and (B) trawl. Data are log_{10}-transformed. The red vertical line shows the threshold of mean body mass (*i.e.* 0.66 g wet mass (WM).ind^{-1} – see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

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

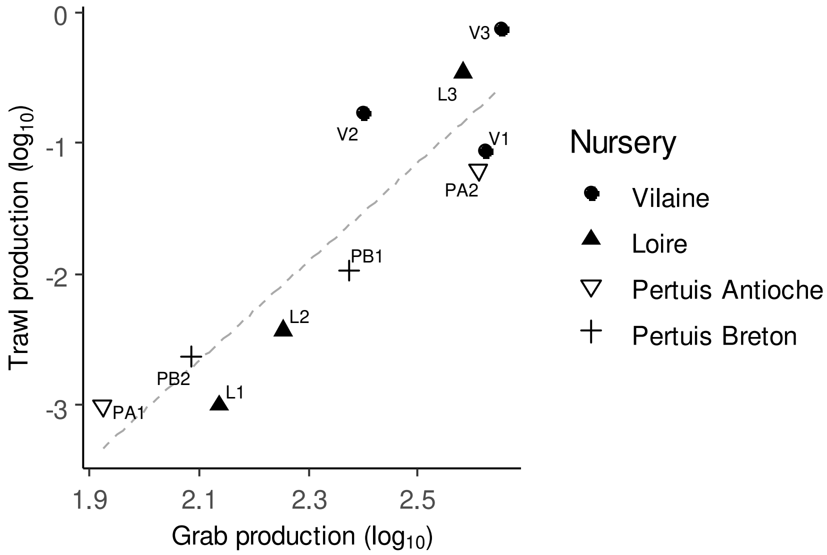


Figure 3. Log-linear relationship between annual prey production estimated from trawl and grab data for each stratum in the four nurseries studied. Symbols are labelled with the names of the strata in each nursery. Production estimates are in $kJ.m^{-2}.y^{-1}$.

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

Table 2. Sediment type (according the typology of Chassé and Glémarec (1976)) of each stratum associated with dominant prey species using the two sampling methods (macrofauna: grab sampling; megafauna: trawl sampling, Supp. Mat. D), and the total production estimated from grab samples and detailed mean 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	*Sternapsis scutata*	---	84.2	97.5 ± 0.6	2.1 ± 1.1	0.3 ± 0.4	5.2 ± 0.5	3
	V2	*Sternapsis scutata, Amphiura filiformis*	*Nucula* spp., *Philine aperta*	251.8	90.0 ± 5.3	7.2 ± 5.1	2.8 ± 1.5	11.4 ± 2.2	6
	PB1	*Sternaspis scutata*, *Spisula subtruncata*	*Corbula gibba*, *Ophiura* spp.	237.4	91.2 ± 5.4	7.6 ± 5.5	1.0 ± 1.1	4.8 ± 3.1	3
Sandy mud	V1	*Owenia fusiformis*	*Owenia fusiformis*	417.3	65,3 ± 26.0	22.6 ± 14.0	12.0 ± 22.4	7.9 ± 2.2	17
	V3	*Abra alba, Owenia fusiformis*	*Ophiura* spp., *Abra alba*	446.7	67.3 ± 17.2	20.7 ± 11.2	11.8 ± 11.7	22.8 ± 6.2	15
	L1	*Limecola balthica*	---	137.1	39.7 ± 3.8	58.0 ± 4.9	2.4 ± 2.4	6.4 ± 0.6	3
	PA2	*Corbula gibba*	*Ophiura* spp., *Corbula gibba*	406.8	31.8 ± 22.1	58.6 ± 27.9	2.2 ± 2.5	9.0 ± 4.3	6
Muddy sand	L3	*Spisula elliptica*, *Abra alba, Lagis koreni*	Annelida	382.3	14.0 ± 13.0	51.5 ± 23.4	34.3 ± 33.6	19.4 ± 2.6	5
	PB2	*Spisula solida*	*Alcyonium* spp., *Ophiura* spp.	121.9	14.1 ± 11.3	59.5 ± 14.6	23.9 ± 4.7	7.0 ± 5.0	3
Sand	L2	*Spisula solida*	*Asterias rubens*	179.3	1.0 ± 1.0	62.9 ± 33.4	35.5 ± 33.5	9.1 ± 3.3	11

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 $kJ.m^{-2}.y^{-1}$ in 2012 and 2014, respectively. Estimates for the outer Loire estuary (4 years sampled) ranged from 0.001 to 0.433 $kJ.m^{-2}.y^{-1}$ in 2012 and 2008, respectively. Estimates for the outer Gironde estuary (2 years sampled) ranged from 0.259 to 0.642 $kJ.m^{-2}.y^{-1}$ in 2016 and 2009, respectively.

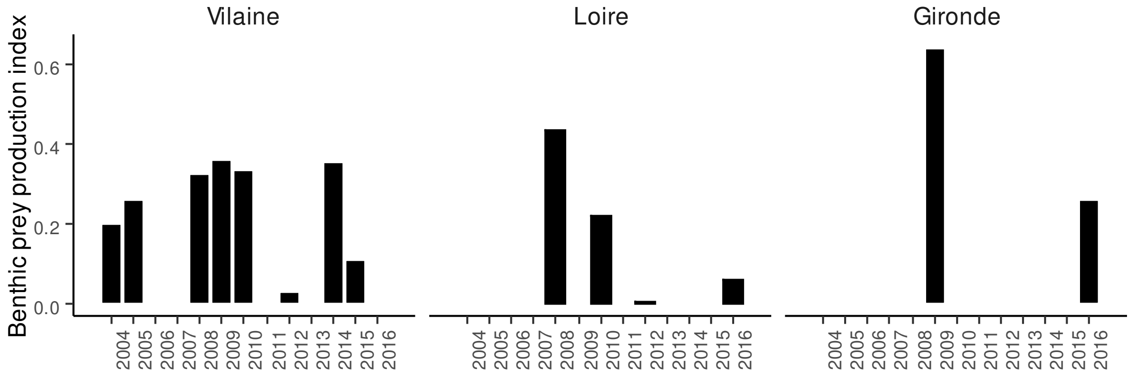


Figure 4. Inter-annual variations in the benthic prey production index. Note the irregular frequency of sampling. Benthic prey production index is in $kJ.m^{-2}.y^{-1}$.

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 (90^{th}) always differed significantly from 0 for all species except *T. luscus*.

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

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

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

Arnoglossus laterna – Mediterranean scaldfish	---	**1.8***	15%

4 Discussion

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

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

The benthic communities captured by trawl and grab gears have been previously compared to assess regional biodiversity patterns (Rufino et al., 2017) and congruence of biodiversity structure among ecosystem components (Karakassis et al., 2006), but never, to the best of our knowledge, to calculate a benthic production index. However, Le Pape et al. (2007) included some benthic megafauna collected from trawl surveys classified into trophic guilds to improve their fish habitat models. The beam trawl can be considered a "generalist" gear because it samples large areas, motile or slightly motile bentho-demersal fish and invertebrates, and sessile invertebrates buried to different depths in the substrate, depending on the degree of compaction of the substrate. The beam trawl can cover several types of sediment. The size of the smallest benthic organisms captured depends on the mesh size at the cod end (here, 20 mm) and whether it becomes partially clogged. The grab can be considered a more "specialist" gear because it targets soft bottom small areas and often a single sediment type, and slightly motile and sessile epi- and endo-invertebrates. The size of organisms is determined by the size of the mesh in which grab contents are sieved (1 mm).

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

The benthic prey production index included taxonomic groups (bivalves, polychaetes, ophiurids, and crustaceans) matching the dominant potential prey found in grabs. The species in the grab and trawl samples were consistent with the YOY diet in the nurseries (Pasquaud et al., 2008; Tableau et al., 2015). For instance, both samples contained *P. aperta*, which are consumed by YOY *S. solea* in the Bay of Vilaine (Kopp et al., 2013), and small echinoderms (*Ophiura* spp., *A. filiformis*), which can be grazed by flatfish and round fish species (Duineveld and Van Noort, 1986; Ntiba and Harding, 1993; van der Veer et al., 1990). Analysis of the potential prey species sampled by the trawl highlighted taxonomic differences in the same size distributions that the grab had sampled. The trawl also sampled motile suprabenthic organisms such as small *C. crangon*, which escape more easily from the grab via flushing. Flatfish such as *P. platessa* and *S. solea* may feed on small individuals of these suprabenthic species (Amara et al., 2001; Pasquaud et al., 2008), as may round fish such as *T. luscus* in the Loire estuary (Robin and Marchand, 1986) or *M. merlangus* (Demain et al., 2011). However, defining potential prey using only mean body mass resulted in many trawl stations that contained no potential prey, and benthic prey production estimates from grab and trawl samples that differed by three orders of magnitude, as the trawl sampled mainly larger individuals. Nevertheless, the two communities represented by each gear were significantly and highly correlated, suggesting that production estimates based on trawled benthic invertebrates can be a reliable index of benthic prey production for juvenile fish.

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

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

4.2 Variability in macrobenthic prey production among nurseries: potential influences

Coastal nurseries along the Bay of Biscay have a similar range of depths (Table 1) and temperature, but differences in local hydrodynamics influence the main sediment characteristics. For instance, the intensity of currents and water discharges in the outer Loire and Gironde estuaries is ~10 times as high as that in the Bay of Vilaine. Mean annual flow is ~75 $m^3.s^{-1}$ for the Vilaine River vs. ~850 and ~780 $m^3.s^{-1}$ in the Loire estuary and Gironde estuary, respectively (Romero et al., 2013).

It might be expected that the higher river discharges and thus higher nutrient loads (Romero et al., 2013) from the two large estuaries would produce more benthic prey than in the Bay of Vilaine. Yet, according to the index, benthic prey production in the Bay of Vilaine is in the same order of magnitude as those in the outer estuaries of Loire and Gironde. These similarities in prey production might be related to the longer residence time of water in the Bay of Vilaine (Obaton and Garreau, 1999) than in the two other nurseries (Lazure and Salomon, 1991). We hypothesized that a longer residence time would allow primary producers to take up more terrestrial nutrients and organic matter, which could benefit secondary producers and the rest of the coastal food web as shown in wetlands (Sierszen et al., 2006). Conversely, the higher river discharges in the Loire and Gironde estuaries flush nutrients and organic matter out to the ocean, resulting in prey production similar to that estimated in the Bay of Vilaine. Nevertheless, our data did not enable us to explain that pattern and it would be interesting to use a larger dataset to properly explore the potential drivers of inter-annual and inter-site variability in benthic prey production.

4.3 Macrobenthic prey production limits YOY fish density

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

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

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

The non-significant lower quantile suggests that other untested factors likely limit fish density in the nurseries. Abiotic factors such as bathymetry, sediments, and wave exposure partly determine the distribution of juvenile flatfish in coastal nurseries (Le Pape et al., 2003; Trimoreau et al., 2013). Local abiotic conditions may not be suitable for juveniles even if benthic prey production at the nursery scale is high. Moreover, contamination and pollution in nurseries can influence juvenile growth and survival (Gilliers et al., 2006; Marchand et al., 2003). Also, although juvenile fish experience less predation in nurseries (Gibson, 1994), they have several potential predators, such as predatory invertebrates (Choy, 1986), other fish species (Ellis and Gibson, 1995) and sea birds (e.g. cormorants, Leopold et al., 1998). Because this study showed a trophic limitation of juvenile fish by prey production, it emphasised bottom-up regulation of the fish by their prey. However, top-down processes can also influence populations of juvenile fish (Baker and Sheaves, 2009; van der Veer and Bergman, 1987). Moreover, predation and food limitation are not opposing processes and may interact in regulating fish populations (Hixon and Jones, 2005). For instance, starvation can increase fish activity, leading to greater exposure to predation (Biro et al., 2003; Myers and Cadigan, 1993). Greater predation can then become an indirect consequence of food limitation.

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

Acknowledgements

The authors thank people involved in the collection and identification of the benthic invertebrates and the captain and the crew during NURSE surveys. We also thank two anonymous reviewers for their helpful comments on an earlier version of the manuscript. A Ph.D. grant (SA6-CAPES-1) from the GIP Seine Aval and IFREMER financially supported this study.

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