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

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Highlights

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

Abstract

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

1. Introduction

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

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

88 comparing the growth rate observed in the field to optimal growth rates predicted by experimental or
89 bioenergetic models (Amara et al. 2001; van der Veer et al. 2010; Freitas et al. 2011; Selleslagh and
90 Amara 2013). However, this approach has some disadvantages. For example, observed growth rates
91 often remain nearly optimal, even when food is limiting, because slow-growing individuals have lower
92 survival and are thus rarely sampled (Le Pape and Bonhommeau 2015). Another approach is to
93 correlate time-series of food supply and fish abundance, fish condition or survival (Beaugrand et al.
94 2003; Okamoto et al. 2012; Latour et al. 2017), but long-term datasets with both prey and predator
95 indices are rarely available. Alternatively, the extent to which food is limiting can be inferred directly
96 from the proportion of prey production that is consumed by their predators (Evans 1983; Boisclair and
97 Leggett 1985; Collie 1987; Vinagre and Cabral 2008).
98 In the present study, we used this third approach to investigate whether competition for food
99 may limit juvenile fish production in coastal and estuarine nurseries. We focused on the outer Seine
100 estuary and the eastern Bay of Seine, in western Europe. This area is an important nursery ground for
101 many species that support commercial fisheries (Rochette et al. 2010, 2013; Archambault et al. 2016).
102 Like many estuarine ecosystems, this area experiences strong natural and anthropogenic stress
103 (Elliott and Quintino 2007), especially due to pollution and coastal development (Dauvin 2008; Tecchio
104 et al. 2015). In particular, its area of essential shallow and productive habitats has decreased
105 significantly over the past century due to the progressive extension of Le Havre harbor, dike
106 construction and channel dredging (Dauvin et al. 2006; Le Pape et al. 2007). Despite recent efforts to
107 reverse some anthropogenic changes (Ducrotoy and Dauvin 2008), this lasting morphological
108 alteration likely decreased the carrying capacity of the Seine estuary (e.g. for the common sole *Solea*
109 *solea*, Rochette et al. 2010, Archambault et al. 2018) and may have exacerbated competition among
110 juvenile fish.
111 To this case study, we applied a bioenergetics-based approach recently developed to
112 investigate the food limitation hypothesis in estuarine and coastal nurseries (Tableau et al. 2019).
113 Rather than searching for potential changes in life-history traits induced by food limitation (*e.g.*
114 condition, growth), this approach directly estimates whether the food supply is sufficient to support the
115 energy requirements of the predator community. Using literature and field data from scientific surveys,
116 we estimated an exploitation efficiency (EE), defined as the ratio of food consumption (FC) by
117 epibenthic predators to macrobenthic food production (FP). This ratio was used as an index of food

limitation in coastal nurseries. While the method originally focused on juvenile fish, we extended it to include the amount of food consumed by epibenthic predatory invertebrates commonly found in estuarine and coastal ecosystems. Our goal was three-fold: (1) assess interannual (2008-2010) and spatial (among strata) variations in FP and FC by epibenthic predators, (2) compare the FC by juvenile fish and predatory invertebrates and (3) quantify how much food was consumed annually by the epibenthic predator community, thus providing new insight into food limitation for juvenile fish in coastal and estuarine nurseries.

2. Materials and methods

2.1. Study area

The outer Seine Estuary and the adjacent eastern Bay of Seine are located in the English Channel on the northwest coast of France, western Europe (Fig. 1). This macrotidal area (the "Seine nursery"), has a tidal range of ~7 m near Le Havre harbor and a mean river flow of ~470 $m^3.s^{-1}$ at the entrance of the estuary, with high intra- and inter-annual variations in river discharge (Dauvin et al. 2017; Romero et al. 2018). The study site covers a subtidal shallow (mean depth = 8.2 m) area of 360 km^2, characterized by muddy-fine sand sediments and composed mostly of polyhaline waters in the outer estuary and euhaline waters in the bay (Thiébaut et al. 1997; Savoye et al. 2003). The mean annual sea bottom temperature during our study period was 12.8°C.

2.2. Data collection and selection

Epibenthic predators and their macrobenthic prey were sampled from 2008-2010 in late summer using a stratified random sampling design, with stratification based on bathymetry and sediment composition (Tecchio et al. 2015). The study site was divided into four strata that covered the area sampled each year from 2008-2010: FN and FS in the outer Seine estuary and E4 and E14 in the eastern Bay of Seine (Fig. 1). The navigation channel, separating FN and FS, was excluded since it was sampled only in 2008. All strata were sampled using both grab and trawl devices.

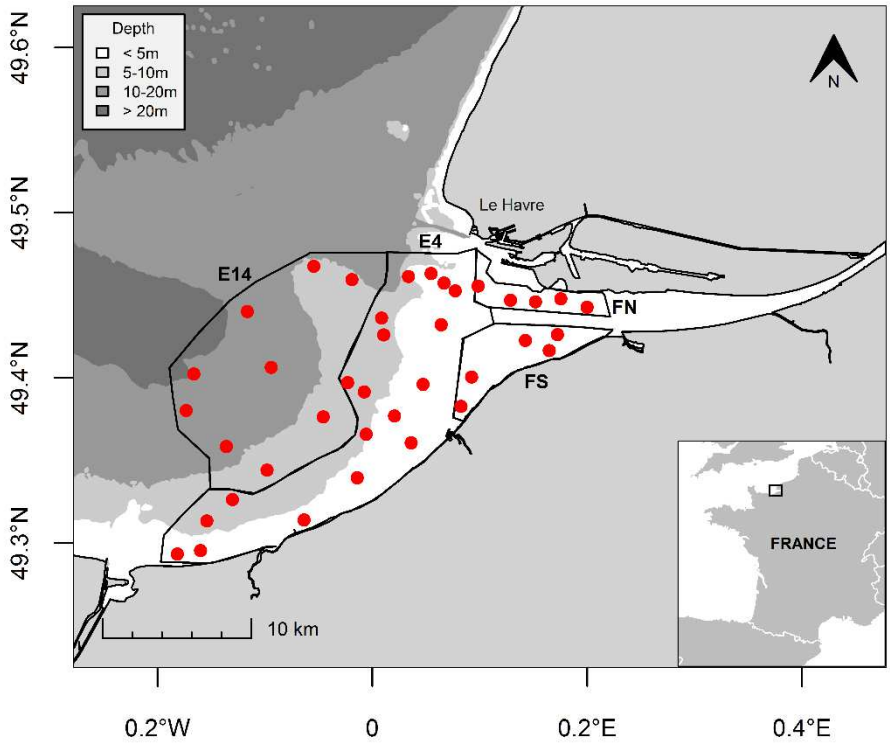


Fig. 1. Location of the sampling stations (n = 38) in the four strata of the study site: FN, FS (outer Seine estuary), E4 and E14 (eastern Bay of Seine). Red dots indicate the mean coordinates of each trawl haul, where the grab was deployed.

2.2.1. Grab sampling survey

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

were pooled for each station, and biomass was expressed as g AFDM.m^{-2} and abundance as individuals.m^{-2}. We verified that the results obtained in 2009 were robust and were not an artefact of the method used to estimate the macrobenthic biomass that year (Supplement S1).

2.2.2. Prey selection

Juvenile fish and epibenthic invertebrate predators are considered opportunistic feeders (Besyst et al. 1999; Cabral et al. 2002; van der Veer et al. 2011). Thus, we used a conservative approach by considering all macrobenthic taxa found in grab samples as potential prey, except for *Asterias rubens*, *Echinocardium cordatum*, and *Crepidula fornicata*, which were never observed in gut contents (unpubl. data). We also excluded rare taxa (sampled at a single station and/or during a single year), which added little to the analysis. We also excluded shrimp-like species (e.g. *Crangon crangon*, *Processa* spp.), even though these taxa were more frequent (occurrence ≥ 2), because their abundance and biomass were always extremely low due to grab's difficulty in catching these mobile invertebrates. Finally, we excluded taxa with a mean body mass ≥ 0.1 g AFDM (~ equivalent to a length ≥ 16 mm; Supplement S2) at each station since they were considered too large to be prey (Tableau et al. 2015). Overall, we retained 147 prey taxa that represented, on average, 81% by mass and 99% by abundance of the total catch (excluding *A. rubens*, *E. cordatum* and *C. fornicata*).

2.2.3. Trawl sampling survey

The epibenthic predator community was sampled at 38 stations using a 2.9-m beam trawl with a 20-mm mesh in the cod-end and one tickler chain (in late September in 2008 and 2009, and late August in 2010). Each haul, performed during daytime with the same trawl towed by a research vessel at a mean speed of 2.5 knots, covered a mean area of 3250 m², except in the FN strata, where it was replaced with a 2-m beam trawl with the same characteristics (20-mm mesh in the cod-end, 1 tickler chain) to sample four shallow stations. In 2009, the hauling operation failed at one station, and the corresponding haul was thus excluded. All individuals caught in the net were identified, counted and weighed by species on board. Fish were measured to the nearest 1 cm total length and separated into age groups by reading otolith increments (for commercial species) or using length-frequency distributions (Supplement S5).

193 **2.2.4. Predator selection**

194 We focused on the dominant epibenthic predators of the Seine nursery that feed at least partly
195 on macrobenthic invertebrates. To this end, we selected seven bentho-demersal fish species
196 (common sole *S. solea,* European plaice *Pleuronectes platessa,* common dab *Limanda limanda,*
197 common dragonet *Callionymus lyra*, whiting *Merlangius merlangus*, bib *Trisopterus luscus* and sand
198 goby *Pomatoschistus minutus*) observed mostly at the juvenile stage (young-of-the-year (G0) and G1)
199 and seven predatory invertebrate species (common sea star *A. rubens,* brown shrimp *C. crangon,*
200 shore crab *Carcinus maenas,* swimming crabs *Liocarcinus holsatus, Liocarcinus vernalis* and
201 *Liocarcinus depurator*, and velvet crab *Necora puber*). These species represented, on average, 80%
202 and 90% of the total catch of bentho-demersal fish and predatory invertebrates by mass, respectively.
203 For fish species, we restricted analysis to the size range corresponding to the period during which fish
204 actively feed on macrofauna. FC by fish < 5 cm was thus ignored, since they feed primarily on
205 meiofauna (Pihl 1985; Gee 1989; del Norte-Campos and Temming 1994; Amara et al. 2001). All
206 predatory invertebrates caught in the net were assumed to be large enough to feed actively on
207 macrofauna.

208

209 **2.3. Estimating macrobenthic food production**

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

211 $$FP = \sum_{j \in 1:J^{th}\ \text{prey species}} CR \cdot B_j \cdot P{:}B_j \cdot \left(1 + R_j\right) \cdot E_j$$

212 where CR is a seasonal ratio (unitless) that converts macrobenthic biomass into mean annual biomass
213 (estimated from Saulnier et al. 2019; Supplement S3), B_j is the total biomass observed during the
214 survey (g AFDM), $P{:}B_j$ is the production-to-biomass ratio (yr^{-1}) estimated using an empirical model
215 (Brey 2012), R_j is a regeneration coefficient (unitless) that represents somatic regeneration after
216 sublethal predator cropping (Tableau et al. 2015) and E_j is the energy density (kJ.g AFDM $^{-1}$) from a
217 global database (Brey et al. 2010) that converts biomass into energy for prey species j.
218 For each species j, total biomass B_j (g AFDM) in the study area was estimated as follows:

219 $$B_j = \sum_{k \in 1:4} \overline{B}_{j,k} \cdot \alpha_k$$

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

To calculate FP, we implicitly assumed that juvenile fish and large epibenthic invertebrates shared a single pool of macrobenthic prey, since these predatory species are considered opportunistic feeders (van der Veer et al. 2011).

2.4. Estimating food consumption by epibenthic predators

FC corresponds to the amount of macrobenthic food items consumed annually by the epibenthic predators in the nursery grounds. FC (kJ.yr^{-1}) is derived from the production of each predator and the proportion of macrofauna in its diet, as follows:

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

where P_i is the production of predator i (g.yr^{-1}), DC_i is the proportion of benthic macrofauna in its diet, E_i is its energy density (kJ.g^{-1}) and K_i is its gross conversion efficiency, defined as its production:consumption ratio (Christensen et al. 2005). Parameters DC_i, E_i and K_i were derived from the literature (Table 1, Supplement S6). Two methods were used to calculate the P_i of juvenile fish and predatory invertebrates, depending on their residence time in the nursery and the availability of cohort data.

2.4.1. Production of juvenile fish

Many fish species use coastal shallow waters as a nursery ground during the juvenile stage before moving offshore after maturation (Beck et al. 2001). They feed on macrobenthic prey only during a certain period. For instance, they prey primarily upon meiofauna shortly after settlement and progressively shift to macrofauna as they grow (e.g. Gee 1989; Amara et al. 2001). Following Tableau et al. (2019), we calculated fish production using a cohort-based method that explicitly includes ontogenic feeding shifts and residence time in the nursery. The P (g.m^{-2}) of each fish cohort in the nursery was calculated as follows:

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

where d_0 and D are the first and the last day of its growth period, respectively, during which fish feed on macrofauna, n_{d+1} and n_d are the number of individuals (m^{-2}) on days $d+1$ and d, and w_{d+1} and w_d are mean individual body weight (g) on the same consecutive days.

Date d_0 was estimated as:

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

where s is the date of the survey, L_{d_0} is the mean length (mm) of a fish cohort on day d_0, L_s is its mean length (mm) observed on day s and G is the mean daily growth rate ($mm.day^{-1}$) of the fish species derived from the literature (Table 1, Supplement S6).

Date D corresponds to the end of the main growth period in the nursery, which is autumn in temperate ecosystems (van der Veer et al. 1990; Rogers 1994; Bouchereau and Guelorget 1998) and was set to 31 October (Jung et al. 2017). Length L_{d_0} was set to 50 mm for G0 fish (see section 2.2.). Assuming negligible growth during winter, L_{d_0} of G1 fish was set to the L_D of G0 fish in the previous year, where L_D is the length estimated on day D for each species. Since no data were available in 2007, L_{d_0} of G1 fish in 2008 was set to the L_D of G0 fish averaged over 2008-2010.

For each cohort, the number of individuals n_d and mean body weight w_d on day d were calculated using catch efficiency, daily growth rate and daily mortality rate from the literature (Table 1, Supplement S6) and survey data, as follows:

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

where C_s is the total number of individuals in the study area on day s, q is the catch efficiency (unitless) and Z is the daily mortality rate (day^{-1}).

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

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

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

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

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

where a and b are coefficients of the length-weight relationship estimated using local survey data, L_s is the mean length (mm) of a fish cohort collected during the survey on day s, and G is the mean daily growth rate of a fish species during its main growth period ($mm.day^{-1}$).

2.4.2. Production of epibenthic predatory invertebrates

Unlike the size of juvenile fish, that of epibenthic predatory invertebrates was not measured during the surveys, which prevented application of a cohort- or size-based method to calculate their annual production. Instead, we calculated the annual production P ($g.y^{-1}$) of each invertebrate species using a population-based method, as follows:

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

where q is catch efficiency (unitless) obtained from the literature (Table 1, Supplement S6), B is the total biomass of the species in the study area during the survey (g) and $P{:}B$ is its production-to-biomass ratio (y^{-1}) estimated using an empirical model (Brey 2012; Supplement S4).

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

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

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

Unlike the biomass of macrobenthic prey, that of predatory invertebrates recorded in late summer was not corrected for seasonality since it was unclear whether it varies seasonally in nearshore areas (Hinz et al. 2004; Reiss and Kröncke 2004, and local unpubl. data).

2.5. Exploitation efficiency and uncertainty analysis

We quantified the percentage of macrobenthic production consumed annually by the main epibenthic predators from 2008-2010 as EE (%), equal to $(FC/FP) \cdot 100$. We also performed Monte-Carlo simulations to quantify uncertainty in estimates of EE. Variables and parameters used to estimate EE were separated into three categories (Tableau et al. 2019). Those with high and quantifiable uncertainty were defined using probability distributions (Supplement S7). They included fish abundance Cs, biomass B and P:B ratios of invertebrate predators and macrobenthic prey, the seasonal coefficient CR, and the energy density E and gross conversion efficiency K of epibenthic

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

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

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

3. Results

3.1. Macrobenthic food production

Macrobenthic FP showed a clear interannual pattern from 2008-2010 in the Seine nursery, being ~2-3 times higher in 2008 and 2010 (752 and 673 $kJ.m^{-2}.yr^{-1}$, respectively) than in 2009 (262 $kJ.m^{-2}.yr^{-1}$). This pattern was relatively pronounced but observed in all strata (Fig. 2) and obvious at the scale of the study site (Fig. 3a). The largest variation in FP was recorded in stratum E4, which was the most productive (FP of ~1100 $kJ.m^{-2}.yr^{-1}$ in 2008 and 2010). Since stratum E4 is also the largest (160 km^2), it produced most of the macrobenthic food (62-74% of total FP from 2008-2010).

In addition to its spatial heterogeneity, FP also showed strong dominance of certain taxa (Fig. 2, Fig. 3a), especially annelids (mainly sedentary polychaetes) and, to a lesser extent, mollusks (mainly bivalves). Hence, the interannual pattern in FP observed from 2008-2010 was driven by interannual variations of a few macrobenthic species (Table S4), especially the tube-dwelling polychaete *Owenia fusiformis*, whose production represented 45%, 23% and 60% of total FP in 2008, 2009 and 2010, respectively. Collectively, the polychaetes *Lagis koreni*, *Magelona johnstoni* and *Lanice conchilega* and the bivalves *Abra alba* and *Phaxas pellucidus* also represented a high percentage of total FP in the Seine nursery (19%, 31% and 14% in 2008, 2009 and 2010, respectively). Conversely, the FP of crustaceans (e.g. amphipods) and echinoderms (e.g. ophiurids) was marginal (< 6% and < 3%, respectively, from 2008-2010).

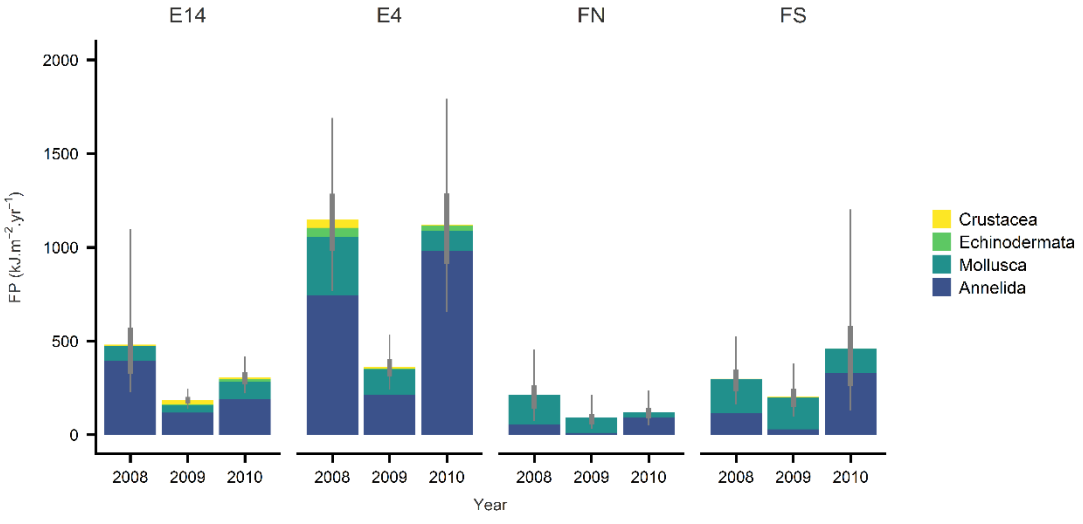


Fig. 2. Food production (FP, $kJ.m^{-2}.yr^{-1}$) by taxon in each stratum of the study site from 2008-2010. Thick and thin gray lines represent 50% and 95% confidence intervals, respectively, estimated using Monte-Carlo simulations.

343 **3.2. Food consumption by epibenthic predators**

344 FC by epibenthic predators showed significant but contrasting interannual variations among
345 predator groups (fish vs. invertebrates) and fish cohorts (G0 vs. G1). Interestingly, the pattern of FC by
346 G0 fish was relatively similar to that of FP (Fig. 3a, b), marked by a ~6-fold decrease from 2008 to
347 2009 (down to 5.2 $kJ.m^{-2}.yr^{-1}$ in 2009), followed by a ~2-fold increase from 2009 to 2010. Conversely,
348 the FC by G1 fish had an opposite pattern, peaking at 30.3 $kJ.m^{-2}.yr^{-1}$ in 2009 (Fig. 3d), while the FC
349 by predatory invertebrates gradually increased from 29.2 $kJ.m^{-2}.yr^{-1}$ in 2008 to 49.8 $kJ.m^{-2}.yr^{-1}$ in 2010
350 (Table 2, Fig. 3c). This latter increase in FC by predatory invertebrates occurred in all strata (Fig. S4).
351 Conversely, interannual variations in FC by the fish community (G0 and G1) showed no common
352 pattern among strata (results not shown).

353 Like their prey, the epibenthic predator community was dominated by a few species. FC by the
354 dragonet *C. lyra* was the highest among fish for all years and both cohorts, representing 46-66% and
355 53-60% of total FC by G0 and G1 fish, respectively, from 2008-2010. The European plaice *P. platessa*
356 and common sole *S. solea* were the second and third greatest fish consumers, respectively, followed
357 by the common dab *L. limanda*. FC by these three flatfish represented 32-49% and 39-45% of total FC
358 by G0 and G1 fish, respectively, from 2008-2010. Bib *T. luscus* and whiting *M. merlangus* were
359 observed only at the G0 stage, and their combined FC was extremely low (< 5%) from 2008-2010.
360 Since the gobies *P. minutus* were < 5 cm at the G0 stage, only their FC at the G1 stage was
361 estimated. It represented 8% of total FC by G1 fish in 2008 but was marginal (< 1%) from 2009-2010
362 (Fig. 3d). For predatory invertebrates, the common sea star *A. rubens* was the greatest consumer,
363 with FC ranging from 53-69% of total FC by invertebrate species from 2008-2010, followed by
364 swimming crabs *Liocarcinus* spp., shore crab *C. maenas* (particularly in 2010) and, to a lesser extent,
365 the brown shrimp *C. crangon* and velvet crab *N. puber* (Fig. 3c).

366 FC was distributed heterogeneously across the study site, and its spatial distribution varied
367 among species (Supplement S9). FC by the fish *C. lyra* and *L. limanda* and the invertebrates *A.*
368 *rubens*, *Liocarcinus* spp. and *N. puber* was concentrated in the bay (strata E4 and E14), while that by
369 the invertebrates *C. crangon* and *C. maenas* occurred mostly in the outer estuary (strata FN and FS).
370 FC by the flatfish *P. platessa* and *S. solea* varied spatially among years, species and cohorts (G0 vs.
371 G1) (e.g. generally concentrated in the bay in 2009 at the G1 stage but in the outer estuary at the G0
372 stage, especially for the common sole) (Fig. S5, S6).

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

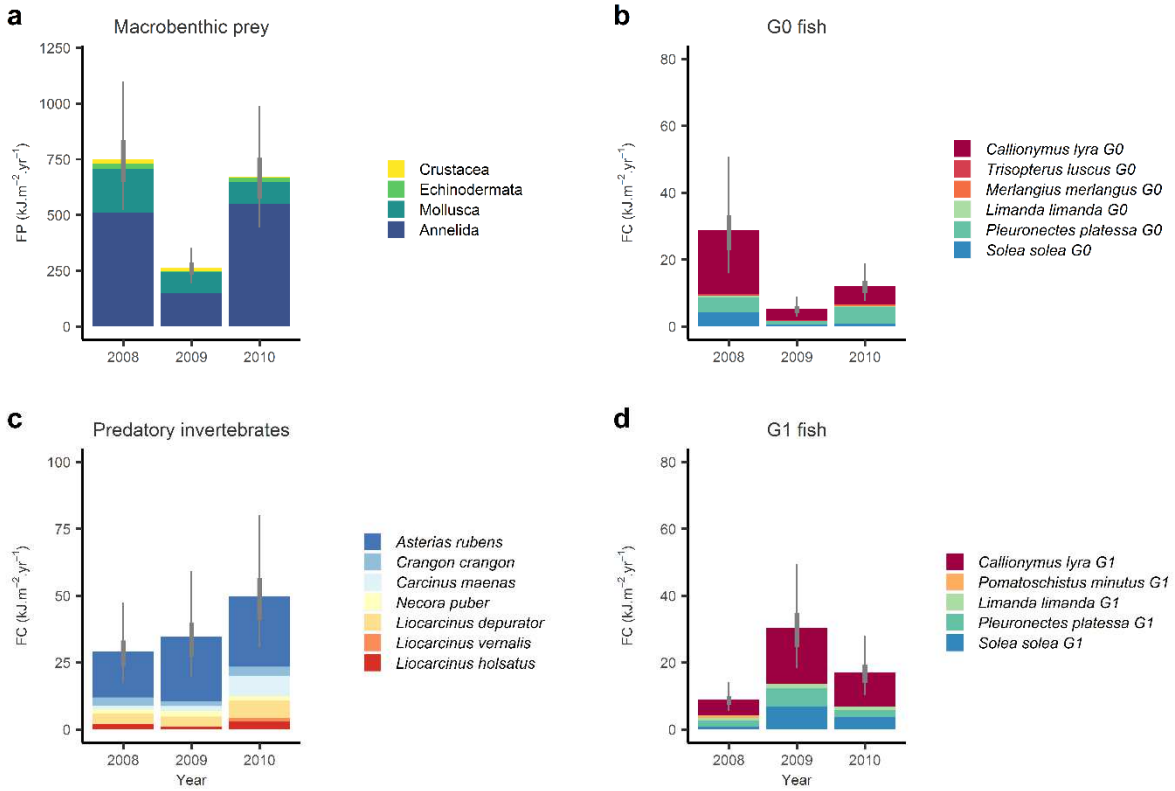


Fig. 3. Food production (FP, $kJ.m^{-2}.yr^{-1}$) by (a) taxon and food consumption (FC, $kJ.m^{-2}.yr^{-1}$) by (b) young-of-the-year G0 fish, (c) predatory invertebrates, and (d) G1 fish in the Seine nursery from 2008-2010. Thick and thin gray lines represent 50% and 95% confidence intervals, respectively,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

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

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

3.3. Exploitation efficiency

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

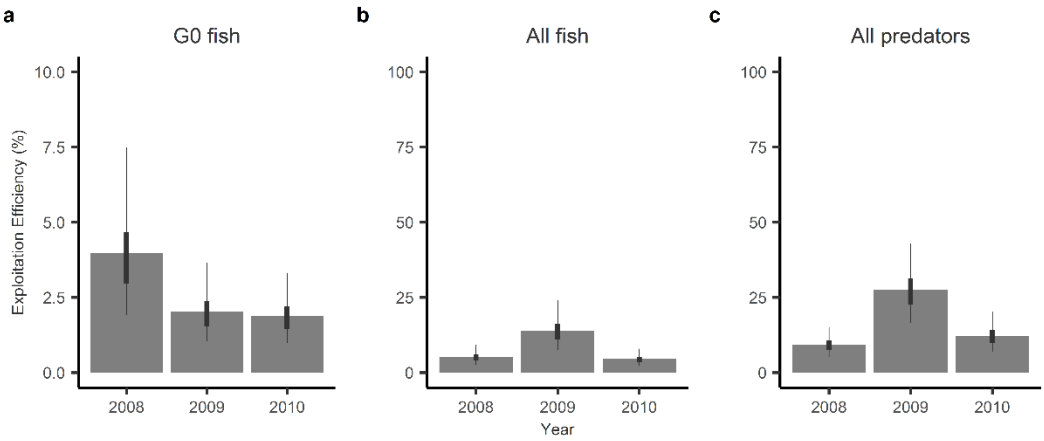


Fig. 4. Exploitation efficiency (EE, %) of (a) young-of-the-year G0 fish, (b) all fish and (c) all predators on their macrobenthic prey in the Seine nursery from 2008-2010. Thick and thin black lines represent 50% and 95% confidence intervals, respectively, estimated by Monte-Carlo simulations. Note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

4. Discussion

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

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

Over the past three decades, the macroinvertebrate community in the eastern Bay of Seine and the outer Seine estuary has been studied extensively (Ménard et al. 1989; Dauvin and Gillet 1991; Thiébaut et al. 1997; Mouny et al. 1998; Ghertsos et al. 2001; Dauvin 2008; Dauvin et al. 2017). The spatio-temporal patterns in macrobenthic production (as measured by FP) from 2008-2010 are strongly consistent with those previously reported, even though most studies focused on macrobenthic abundance or biomass. For instance, the estuarine stratum FN, which had the lowest FP estimates among the four strata (Fig. 2), has had long-lasting low macrobenthic abundance and biomass (Mouny et al. 1998; Dauvin 2008), likely related to the high environmental (salinity variations) and anthropogenic (pollution, harbor extension) stresses that occur in this area (Tecchio et al. 2015). Conversely, high macrobenthic abundance and biomass values have been recorded at sampling stations located mainly in marine stratum E4 (Dauvin and Gillet 1991; Thiébaut et al. 1997), where FP was the highest each year in the present study (Fig. 2). Estimates of FP in the Seine nursery were consistent with macrobenthic production estimates reported in several other temperate marine and coastal ecosystems (20-850 $kJ.m^{-2}.yr^{-1}$: Reiss et al. 2009; Bolam et al. 2010; Brey 2012 and references therein).

In addition to its stable spatial pattern across the years studied, the macrobenthic community remained remarkably dominated by the same few taxa for 25 years, especially annelids (Dauvin et al. 2017). In particular, *O. fusiformis* was the most abundant species from 1986-1988 and in 1991 (Thiébaut et al. 1997). We showed that two decades later, annelids still largely dominated the macrobenthic community (Figs. 2 and 3), with *O. fusiformis* still the most abundant and productive species (as measured by FP, Table S4). Mechanisms that could explain the stability in spatial organization and species dominance of the Seine macrobenthic community include larval retention near adult populations, sediment stabilization caused by high densities of *O. fusiformis* and the salinity gradient off the Seine estuary (Thiébaut et al. 1994, 1997).

Nonetheless, our results revealed substantial year-to-year variations in FP from 2008-2010 at both population and community levels (Fig. 3, Table S4). Mean annual Seine River flow decreased significantly from 2008 (525 $m^3.s^{-1}$) to 2009 (352 $m^3.s^{-1}$) and then increased moderately in 2010 (414 $m^3.s^{-1}$). The present study did not identify the exact causes of the macrobenthic variations from 2008-2010. They may have been caused by variations in local environmental conditions (e.g. river flow, wind regime) that determined larval drift and recruitment success of the dominant macrobenthic taxa,

439 which have a bentho-pelagic life cycle (Ménard et al. 1989; Thiébaut et al. 1992, 1996, Dauvin et al.
440 1993, 2017; Thiébaut 1996). Density-dependent mortality caused by competition for limited resources
441 among macrobenthic populations likely also had an influence (e.g. Thiébaut et al. 1997; Henderson et
442 al. 2006). Conversely, top-down regulation exerted by epibenthic predators (juvenile fish, predatory
443 invertebrates) has rarely been suggested as a cause for the interannual variations in the Seine
444 nursery. However, dominant macrobenthic species are important prey for several juvenile fish. Gut
445 content analyses revealed that these dominant species (e.g. *O. fusiformis*, *L. koreni*, *L. conchilega*, *A.*
446 *alba*) are major prey items for juvenile fish (especially plaice *P. platessa*, sole *S. solea* and dab *L.*
447 *limanda*) in the Seine nursery (Morin et al. 1999 and unpubl. data), and in several other coastal areas
448 in western Europe (Amara et al. 2001; Darnaude et al. 2001; Schückel et al. 2012). Local data on
449 predatory invertebrates' diets are lacking; however, these epibenthic predators likely consume
450 dominant macrobenthic prey as well, given their opportunistic feeding behavior (Norman and Jones
451 1992; van der Veer et al. 2011) and results from gut content analyses reported elsewhere (e.g. Allen
452 1983; Choy 1986; del Norte-Campos and Temming 1994; Freire 1996). Further local gut content
453 and/or stable isotope analyses would be useful to improve current FP estimates, and provide an in-
454 depth knowledge of food availability in the Seine nursery.
455
456 **4.2. Relating food production to food consumption by epibenthic predators**
457 Surprisingly, few studies have attempted to relate spatio-temporal patterns of the
458 macrobenthic community to those of higher trophic levels in the Seine nursery. For instance, the
459 abundance of several macrobenthic species decreased greatly in the eastern Bay of Seine from 2008-
460 2009 (Dauvin et al. 2017), but its potential effect on the epibenthic predator community was not
461 investigated. Several trophic models (Ecopath, EwE; Christensen et al. 2005) have quantified energy
462 flows between multiple functional groups in the eastern Bay of Seine and the outer Seine estuary, but
463 none focused on the nursery function of this ecosystem. This modeling approach was useful for
464 understanding overall trophic functioning of the Bay of Seine and the Seine estuary (Rybarczyk and
465 Elkaım 2003; Tecchio et al. 2015) and for assessing past and future impacts of human activities
466 (Raoux et al. 2017; Pezy et al. 2017). Nonetheless, such trophic models are not appropriate for
467 investigating fine-scale and short-term (e.g. year-to-year) variations in predator-prey interactions
468 (Tableau et al. 2019), as done in the present study.

469 Given the dramatic variations in annual prey production observed from 2008-2010, correlating
470 FP and FC may provide information about the food limitation hypothesis, despite the short duration of
471 the present study (3 years). In particular, the similar interannual patterns in FP and FC by G0 fish
472 suggest that food was limiting in the Seine nursery, at least at the G0 stage. These patterns in FP and
473 FC were mainly driven by variations in prey biomass and fish abundance, but also accounted for
474 interannual variations in mean body weight of each species. We acknowledge that estimates of FC by
475 fish may have been less accurate, especially due to the lack of local length data for the dragonet *C.*
476 *lyra* and goby *P. minutus* (Supplement S5), and because the beam trawl survey did not cover the
477 entire spatial distribution of common sole *S. solea*. Common sole was also found in the upper estuary
478 and on intertidal mud flats during high tide, particularly at the G0 stage (Morin et al. 1999).
479 Nonetheless, the interannual pattern in FC by G0 fish was considered similar to that in FP, given the
480 limitations of our dataset. The similarity was particularly high for plaice *P. platessa* (Fig. 3), which is a
481 main consumer of *O. fusiformis* in the Seine nursery (Ménard et al. 1989; Morin et al. 1999).
482 Interestingly, G1 fish showed an opposite interannual pattern, which is consistent with the
483 patterns in FP and in FC by G0 fish with a one-year lag. This agrees with the hypothesis that the year-
484 class strength is determined at the G0 stage on nursery grounds, or even earlier, at the pelagic phase
485 (Hjort 1914; van der Veer 1986; Leggett and Deblois 1994; Houde 2008). This opposite pattern could
486 also suggest competition for food between G0 and G1 fish, with lower survival of and thus lower FC by
487 G0 fish when the FC by G1 fish is high, as in 2009. However, correlation does not imply causation
488 (Hilborn 2016). Hence, the lower FC by G0 fish in 2009 could have been due to lower food supply
489 (bottom-up control), higher competition with G1 fish, higher predation pressure on G0 fish in the
490 nursery (top-down control), lower fish larval supply caused by higher mortality during early-life stages
491 (eggs and larvae) or a combination of some or all of these processes, which can occur simultaneously
492 (Hixon and Jones 2005). The dataset and short duration of the present study did not enable us to
493 distinguish these potential causes.
494 The completely different interannual variations in FC by predatory invertebrates was no
495 surprise, because macrobenthic prey likely represent a much smaller percentage of predatory
496 invertebrates' diets (Table 1, Supplement S6). In addition, FC by predatory invertebrates was clearly
497 dominated by the common sea star *A. rubens*, which can live at least five years in the wild (Guillou
498 1983). Thus, even though macrobenthic food resources in the Seine nursery could limit the sea star

499 population, the correlation between annual FP and annual FC would likely be weak because the
500 population response would aggregate variations in food supply over several years.

501 Interannual variations in FC by G0 fish were generally the same among strata and in the entire
502 study site (Fig. S5). This observation held for FC by predatory invertebrates in all strata and by G1 fish
503 in marine strata (E4 and E14) (Fig. S4, S6). Conversely, species composition differed significantly
504 among strata, especially according to the salinity tolerance of each species. For instance, euryhaline
505 species such as the common sole *S. solea*, brown shrimp *C. crangon*, and shore crab *C. maenas*
506 were found mainly in the outer estuary (FN and FS), while the common sea star *A. rubens*, common
507 dab *L. limanda* and dragonet *C. lyra*, which tolerate salinity less, were concentrated in the bay (E4 and
508 E14). However, spatial variations in the FC estimated in the present study must be interpreted with
509 caution. Species distribution is not driven by a single factor (e.g. salinity) but instead results from the
510 combination of several forces, both external (e.g. environmental forcing, food availability) and internal
511 (e.g. population size) to the populations (Planque et al. 2011). Since these forces change throughout
512 the year, the spatial distribution of mobile epibenthic predators changes accordingly. Predatory
513 invertebrates likely move much less than juvenile fish, but do move, particularly in late winter and late
514 summer, when they migrate (Venema and Creutzberg 1973; Boddeke 1976; Hinz et al. 2004).
515

516 **4.3. Including predatory invertebrates doubled estimates of food consumption**

517 Given the high density of predatory invertebrates generally observed in coastal and estuarine
518 nurseries (Pihl and Rosenberg 1984; van der Veer et al. 2011), they can exert substantial predation
519 pressure on macrobenthic prey, even though macrofauna are a moderate percentage of their diet
520 (Evans 1983; Pihl 1985; Jung et al. 2017). Our results agree with these previous findings. We showed
521 that FC by predatory invertebrates lay in the same order of magnitude as FC by juvenile fish from
522 2008-2010 in the Seine nursery. Including the FC by predatory invertebrates provided a larger and
523 probably more realistic estimate than that obtained for juvenile fish alone, as originally presented by
524 Tableau et al. (2019).

525 However, the approach we developed to estimate FC by predatory invertebrates has some
526 limitations. In particular, FC is derived from an estimate of production that may be inaccurate.
527 Empirical models, such as the one we used to estimate production (Brey 2012), perform relatively well
528 for an assemblage of species, but may have high prediction error for a single population (Brey 2001,

529 2012). Additionally, the same problem holds for macrobenthic prey, given the strong dominance of few
530 species. To our knowledge, however, empirical models remain the best approach currently available
531 for estimating secondary invertebrate production when data preclude the use of classic direct
532 methods. Moreover, Brey models (2001, 2012) were shown to perform as well or even better than
533 others (Cusson and Bourget 2005; Dolbeth et al. 2005; Petracco et al. 2012). Also, if production
534 estimates of predatory invertebrates were inaccurate, they would more likely be underestimated rather
535 than overestimated because only the larger individuals remained in the net. Since mean individual
536 weight and P:B ratios are negatively correlated (Schwinghamer et al. 1986), P:B ratios were much
537 lower than those generally found in the literature (e.g. Kuipers and Dapper 1981; Pihl and Rosenberg
538 1984; Pihl 1985). Consequently, they likely resulted in underestimating FP and FC, which is in
539 accordance with the conservative approach used in this study. Additionally, we used Monte-Carlo
540 simulations to include the uncertainty in estimates of FP and to estimate prediction error, unlike most
541 previous studies (e.g. Evans 1983, 1984; Pihl 1985; Collie 1987).
542
543 **4.4. Food limitation: lessons from exploitation efficiency**
544 Collectively, juvenile fish and predatory invertebrates consumed a large percentage of
545 macrobenthic prey production in the Seine nursery, as revealed by calculating EE. First, EE
546 automatically increased with the number of predators (G0 fish vs. all fish vs. all predators) for a given
547 year because FC increased accordingly, while FP remained unchanged (Fig. 4). As previously
548 suggested (Collie 1987; Vinagre and Cabral 2008; Tableau et al. 2019), these results highlighted the
549 importance of including all dominant benthic-feeding predators to estimate the overall predation
550 pressure on macrobenthic prey when testing the food limitation hypothesis in coastal and estuarine
551 nurseries. The interannual stability in EE of G0 fish from 2009-2010 logically results from the similarity
552 of the interannual pattern of FP and that of FC (G0 fish), strengthening the idea that the food supply
553 may have been limiting. In 2008, EE of all juvenile fish (5%) was similar to that (6%) in another French
554 coastal nursery (the Bay of Vilaine) observed in the same year and calculated using the same
555 approach (Tableau et al. 2019).
556 When all dominant predators were considered, our results revealed that EE on total prey
557 production (as measured by FP) could be as high as ~30%. This consumption level might have been
558 high enough to indicate that food limitation occurred (Collie 1987). In addition, the true EE was likely

559 much higher, since EE was estimated using a conservative approach. In particular, FC by epibenthic
560 predators was underestimated for several reasons. First, estimates of FC by juvenile fish were based
561 only on their requirements during the growing season, thus ignoring maintenance requirements for the
562 rest of the year. Even though requirements in winter are generally assumed to be much lower, they
563 may still be significant (Creutzberg and Witte 1989; van der Veer et al. 1990). Second, most gross
564 conversion efficiency estimates (K) found in the literature were obtained from laboratory experiments.
565 Thus, they were expected to be slightly higher than those in the wild, leading to underestimates of FC
566 and thus EE (Tableau et al. 2019). Third, catch efficiency estimates (q) were overestimated because
567 they came from beam trawl surveys using a 4 mm mesh liner in the cod-end (e.g. Reiss et al. 2006),
568 unlike scientific surveys performed in the Seine nursery that used a larger mesh (20 mm). Fourth, FC
569 by G2 fish was not considered because few G2 individuals were found in the net, since they probably
570 moved to deeper and offshore water before the scientific surveys occurred. Nonetheless, G2 fish may
571 exert significant predation pressure on macrobenthic prey earlier in the year. Lastly, FC by predatory
572 invertebrates was also likely underestimated, as explained. Hence, EE on total prey production likely
573 exceeded 30% in 2009 in the Seine nursery.

574 It is unlikely that EE reaches 100% even when food limitation occurs, since predators can
575 access only a portion of macrobenthic prey. For instance, a previous study estimated that juvenile fish
576 in coastal nurseries in the Wadden Sea could access only 10% of the total macrobenthic biomass (van
577 der Veer et al. 2011). Similarly, Tableau et al. (2015) estimated that the FP accessible to juvenile fish
578 in another French coastal nursery (the Bay of Vilaine) was approximately one-eighth that of total FP in
579 2008. These values were likely overestimated, at least for the entire predator community in the Seine
580 nursery. Predatory invertebrates likely access prey that are not accessible to juvenile fish given their
581 different prey-handling abilities, and previous estimates of prey accessibility considered only juvenile
582 fish (van der Veer et al. 2011; Tableau et al. 2015). However, even a much lower and more
583 reasonable ratio of total to accessible FP (e.g. 3) would lead to an EE close to 100% in 2009,
584 indicating strong competition for food that year. Thus, we cannot exclude the possibility that food was
585 limiting in the Seine nursery. In particular, the combination of a significant decrease in food supply (as
586 measured by FP) and a significant increase in food consumption by epibenthic predators may have
587 induced food limitation in 2009.

We focused mainly on annual FP and FC in the entire nursery. However, food limitation can be restricted to specific areas and/or periods of the year (e.g. Walters and Juanes 1993). Since the Seine nursery has been described as a mosaic of habitats (Tecchio et al. 2015), we estimated EE in each stratum (Fig. S7). The analysis revealed that EE varied among strata (up to 37% in E14 in 2009 and 76% in FN in 2010), but caution in interpretation is required, since epibenthic predators move among habitats throughout the year. The annual scale may not be the most appropriate one at which to test the food limitation hypothesis. Resources may be limiting only during certain periods of the year, such as the sensitive post-settlement phase (Geffen et al. 2007, 2011). Nevertheless, focusing on this early-life stage is more challenging, especially when sampling prey and predators, but seems crucial given its potential effect on fish recruitment (Nash and Geffen 2012; Nagelkerken et al. 2015). A decline in growth rate of juvenile plaice *P. platessa* during late summer was also broadly reported (Freitas et al. 2012; Ciotti et al. 2013b), and could be related to intra- or interspecific competition for food (Ciotti et al. 2013a; van der Veer et al. 2016). However, the underlying causes of that pattern remain unclear (Ciotti et al. 2014).

In conclusion, two main findings suggest that food supply may have limited juvenile fish production in the Seine nursery, at least in 2009: (1) the similarity in the interannual patterns in FP and FC by G0 fish and (2) the relatively high EE estimated for all predators in 2009 (~30%) given the conservative calculation. Firmly validating or refuting the food limitation hypothesis in the Seine nursery lies beyond the scope of this study, and further studies are required to reach a conclusion. To this end, applying the bioenergetics-based approach to longer time-series and/or other nurseries would be useful (Tableau et al. 2019). Finally, prey accessibility remains a key parameter that is particularly challenging to calculate; however, estimating it is critical to better understand food limitation (Boisclair and Leggett 1985).

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619

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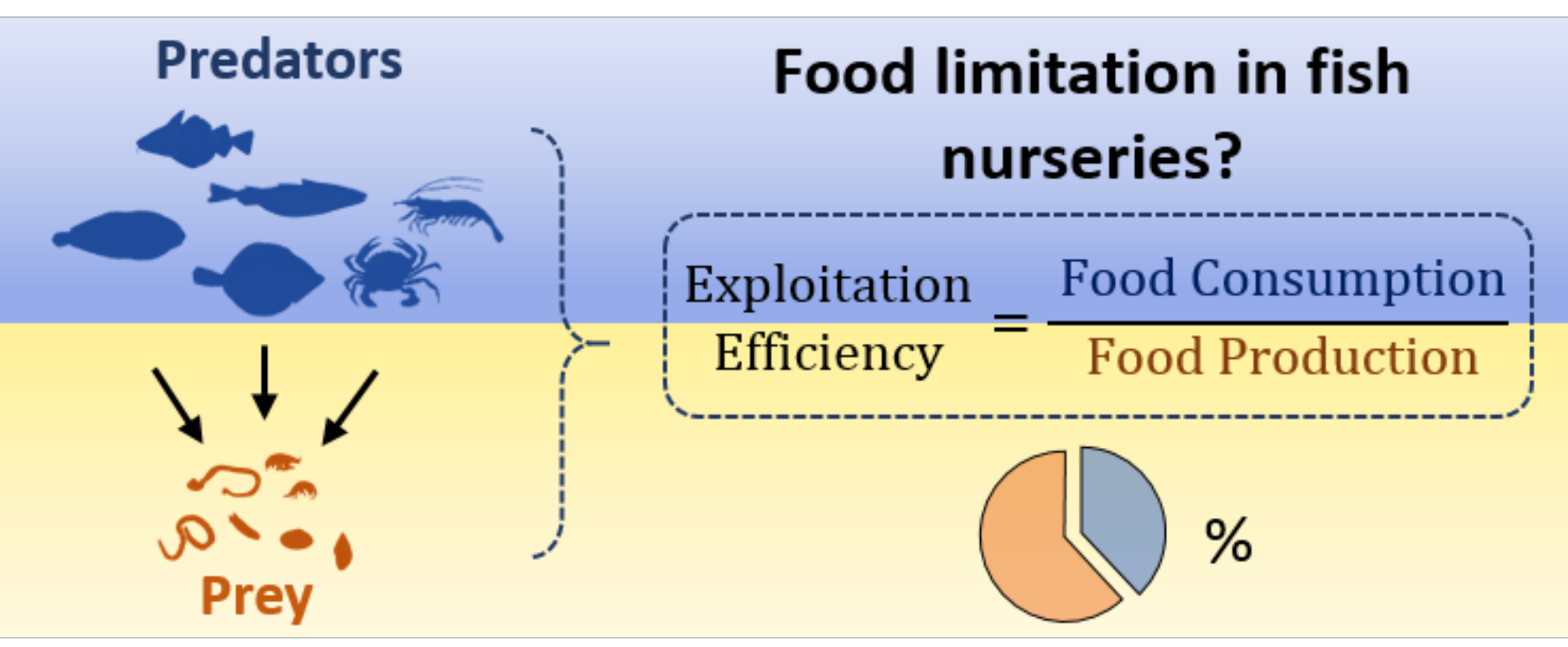
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Predators
Prey
Food limitation in fish nurseries?
Exploitation Efficiency = Food Consumption / Food Production
%