Novel approach for testing the food limitation hypothesis in estuarine and coastal fish nurseries

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ABSTRACT: Survival success of early life stages of fish is regulated by density-dependent effects, but the limiting factors explaining these effects have not been well identified. In coastal habitats, juveniles of many fish species occur in high concentrations and possibly compete for food resources. This study compared the ratio of food consumption to benthic prey production to test whether food availability is a major factor defining the carrying capacity of fish nurseries. We developed a method to quantify the exploitation efficiency (also called ecotrophic efficiency) of the juvenile fish feeding on benthic prey, expressed as a ratio of food consumption to food production. This method includes many sources of uncertainty and a key parameter of prey accessibility. Applied to the case study of the Bay of Vilaine (north Bay of Biscay), results suggest food limitation for juvenile fish. The generic nature of this method supports its wide application in various nursery habitats. As food limitation is a density-dependent process having a dampening effect on recruitment variability, examining its occurrence over time and space will improve our comprehension of nursery-dependent fish dynamics.

KEY WORDS: Exploitation efficiency · Predator–prey relationship · Food consumption · Fish juvenile · Nursery habitat · Bioenergetics · Density dependence · Carrying capacity · Secondary production

1. INTRODUCTION

Estuarine and coastal habitats are suitable nurseries for a large proportion of demersal and benthic fish species (Seitz et al. 2014, Brown et al. 2018) and are thus considered essential for completing their life cycle (Peterson et al. 2000, Beck et al. 2001, Fulford et al. 2011). Coastal nursery dependent species congregate at the juvenile stage in these spatially restricted habitats that supply abundant food resources and act as a potential refuge from predators (Gibson 1994, Gibson et al. 2002). This fish concentration is suspected to result in density-dependent processes, limiting the growth (Bacheler et al. 2012), survival, and thus recruitment of fish populations (Iles & Beverton 2000, Minto et al. 2008). The positive relation-

ship between surface areas of nursery habitats and the resulting average recruitment (Rijnsdorp et al. 1992, Kostecki et al. 2010, Wetz et al. 2011) supports this hypothesis. However, demonstration of density dependence does not indicate the cause of the limitation (Sinclair & Pech 1996). Even though some critical environment conditions can severely impact the carrying capacity of nursery habitats (e.g. van der Veer et al. 2000), the underlying processes remain poorly understood. Competition for food is assumed to be a key process (i.e. Gibson 1994), but the causal link between density-dependent survival and food is still debated (Le Pape & Bonhommeau 2015). Some studies suggest that benthic invertebrate populations are only minimally impacted by their predators (e.g. Gee et al. 1985, Shaw & Jenkins 1992); consequently, sur-

vival of juvenile fish would not be dependent on food availability (Ross 2003, Hampel et al. 2005, Vinagre & Cabral 2008). However, other studies propose that the distribution of benthic invertebrates can be regulated by their predators in estuarine and coastal ecosystems. Food availability would then be a factor limiting the survival of juvenile fish in nursery habitats (Nash & Geffen 2000, Nash et al. 2007, Craig et al. 2007): this is the food limitation hypothesis (Le Pape & Bonhommeau 2015).

Two approaches are commonly used to test whether food is limiting in coastal areas. The indirect approach focuses on growth variations. It assumes that the *in situ* growth rate would decrease with the density of juveniles if they compete for food (e.g. van der Veer & Witte 1993, Craig et al. 2007). However, this approach could lead to the erroneous rejection of the hypothesis of food limitation. Indeed, even in a food limitation context, the apparent growth of a juvenile fish population could remain maximal because of the highly size-selective mortality of juvenile fish: larger individuals have a higher survival than smaller ones (Sogard 1997, Levin et al. 1997, Le Pape & Bonhommeau 2015). Alternatively, the direct approach quantifies the exploitation pressure applied by consumers on their prey. Exploitation efficiency (EE; also called ecotrophic efficiency) is the ratio of food consumed by the juvenile fish community to the food supply represented by the production of the benthic invertebrate community (Collie 1987, Vinagre & Cabral 2008). This ratio is an intermediate component to compute ecological efficiency, which quantifies energy transfer among trophic levels (Lindeman 1942). It directly quantifies the portion of benthic production consumed by their predators; thus, it is an indicator of predation pressure. In this context, the food limitation hypothesis would be accepted if EE is high over years and/or over nursery habitats.

Few studies have carried out the direct approach to assess the predation pressure applied by one ecological guild on another. This method requires collecting a large amount of quantitative data on many marine species, including both the marine juvenile fish community and their benthic prey. Generally, one of the 2 following methods are used to estimate food consumption (FC). First, the gut-content method, which is a flux analysis requiring time-consuming experimental work. Gut contents must be weighed at constant intervals to determine the evacuation rate of each fish species (Elliott & Persson 1978). This method likely underestimates FC, as regurgitation often occurs soon after fish capture (e.g. Elliott &

Hemingway 2002, Vignon & Dierking 2011).The second approach is based on bioenergetics and estimates FC from fish growth. The energy conversion process can be more or less exhaustive; e.g. ranging from a very detailed approach using bioenergetics models (e.g. dynamic energy budget [DEB] theory; Kooijman 2009) to a largely simplified one, using mass-balanced trophic models (e.g. the Ecopath framework; Christensen et al. 2005). Assessing the quantity of food that is ingested to obtain annual fish production requires a compromise between (1) an exhaustive description of the processes involved in the conversion of ingested food into fish biomass and (2) the availability of reliable data to describe this conversion process. This compromise precludes the systematic use of bioenergetics models. DEB models have been used successfully to estimate juvenile food limitation for a well-studied coastal nursery dependent species (van der Veer et al. 2010, 2016). However, the DEB approach requires data and knowledge on a variety of fine metabolic processes that are mostly undescribed for marine juvenile fish, preventing its use in a multispecific approach. Mass-balanced trophic models are used to estimate flows between functional groups in an ecosystem (Christensen et al. 2005). These models, also based on bioenergetics, estimate the total EE of prey. However, mass-balanced models use an oversimplified description of growth and are not well suited to analyze short-term processes (i.e. turnover rate of prey production in coastal and estuarine systems; Ritter et al. 2005). Hence, these 2 families of models are not designed to focus on the food limitation hypothesis in estuarine and coastal fish nurseries. Therefore, we need a method that is based on bioenergetics, but less complex than a full DEB calculation.

The few studies that focus on predation of benthivorous fish generally estimate a low EE of the benthic prey, indexing low predation pressure (e.g. Vinagre & Cabral 2008). However, they do not necessarily conclude that there is an absence of food limitation (Collie 1987). Indeed, benthic production is shared by many fish species in coastal nursery habitats (McLusky & Elliott 2004, Nicolas et al. 2010). By considering only a few consumer species, most studies assess only a small part of the total EE of prey production. This key point underlines the need to account for a representative part of the consumers relying on the same pool of prey in order to fully evaluate the food limitation hypothesis.

The limits of the existing approaches to assess fish consumption emphasize the need to develop a bioenergetics-based approach responding to the con-

straints induced by data availability, but also sufficiently precise to quantify predation pressure and thus deal with the food limitation hypothesis in multispecies fish nurseries. In this paper, we developed a method to quantify energy flow between 2 compartments: the benthic invertebrate community and the benthivorous juvenile fish community. This methodology aims to estimate the ratio of FC of juvenile fish to benthic food production (FP) by quantifying 2 key intermediate components: fish production and prey production (Fig. 1). This approach accounts for prey accessibility and quantifies the uncertainty associated with input parameters. We applied this methodology to the Bay of Vilaine nursery ground (Bay of Biscay, Western Europe) to test the food limitation hypothesis.

shallow water habitats, as they migrate to deeper waters as adults (Seitz et al. 2014). In this context, the production-to-biomass ratio, referring mostly to an entire population in the literature, is not appropriate to estimate juvenile fish production within nursery habitats. Moreover, as fish feed on benthic macroinvertebrates for only a limited period of the juvenile stage, the time window must be properly delimited. Both arguments lead to estimate FC from mortality and growth rates. Data collection is detailed in Supplement S2 at www.int-res.com/articles/suppl/m629 p117_supp.pdf.

The biomass production (P, in weight yr^{-1} or weight surface^{-1} yr^{-1}) of a juvenile cohort during the growth period is estimated as:

$$P = \int_{t=t_0}^{t=T} n(t) \cdot \frac{dw}{dt} \cdot dt \tag{1}$$

2. MATERIALS AND METHODS

2.1. Computing EE

Our objective was to quantify energy flow between benthic macroinvertebrates and benthivorous fish living in estuarine and coastal nursery ecosystems — a community mostly dominated by juvenile fish (Gibson 1994). We estimated EE, which is the ratio of juvenile fish FC to benthic FP. EE is a baseline for the analysis of the food limitation hypothesis in fish nursery habitats (Fig. 1).

2.2. FC

The FC metric estimates the quantity of food consumed annually by a community of consumers. The bioenergetics approach computes fish production to then determine the FC of juvenile fish. For a single individual, annual production refers to its growth over 1 yr. Extrapolation to the population level is carried out either by integrating over time the product between instantaneous fish number and instantaneous growth rate, or by using its production-to-biomass ratio, which integrates both. Unlike macrobenthic invertebrates, a large proportion of fish species are not resident in coastal
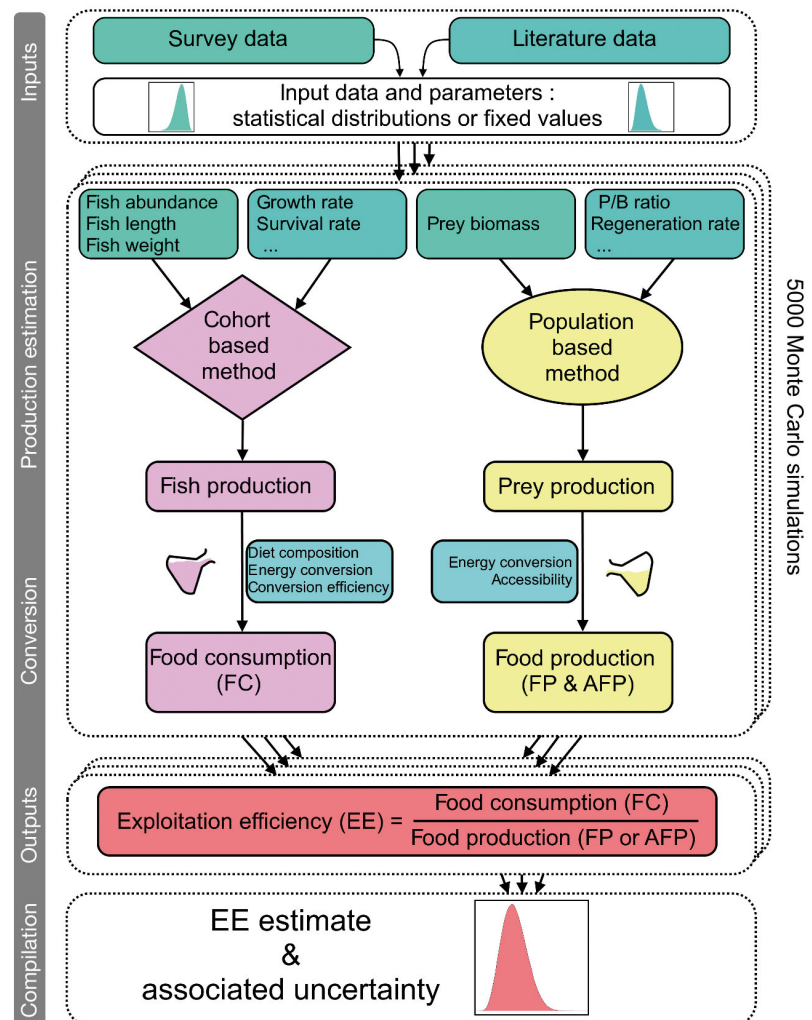

Fig. 1. Computational flowchart used to estimate exploitation efficiency (EE), including uncertainty analysis with Monte Carlo sampling. AFP: accessible food production

where t_0 and T, respectively, refer to the beginning and end of the growth period when juvenile fish feed on benthic macroinvertebrates and water temperature is correspondingly higher; n(t) is the number of individuals at time t; and $\frac{dw}{dt}$ is the instantaneous growth rate.

As the integration in Eq. (1) is not straightforward, it is discretized through a daily basis in Eq. (2) to estimate P of a juvenile cohort (in weight yr^{-1}, or in weight $surface^{-1}$ yr^{-1}):

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

where d_0 and D, respectively, are the first and last day of the growth period; n_d is the number of individuals in the middle of day d; and w_d and w_{d-1} are the individual weights at the end of day d and day d−1. The difference between the 2 weights provides the individual production for day d. The 2 components of Eq. (2) (n_d and w_d) can be computed using survey data, daily growth rate, and daily mortality rate. n_d is estimated as:

$$n_d = \frac{c_s}{q} \cdot e^{-(d-s)\cdot z} \qquad (2.1)$$

where s is an index of the survey date; c_s is fish abundance in number or number $surface^{-1}$; q is catch efficiency; and z is daily mortality (in d^{-1}). w_d is estimated as:

$$w_d = a \cdot [L_s + (d + 1/2 - s) \cdot G]^b \qquad (2.2)$$

where G is the daily growth rate of the studied species observed in the literature (Supplement S2); L_s is the average fish length of a single cohort observed in the survey at day s; and a and b are parameters of the length–weight relationship. d_0 (Eq. 2.3) is the day when an individual fish reaches the minimum size to actually feed on macrofauna:

$$d_0 = \frac{L_{d_0} - L_s}{G} + s \qquad (2.3)$$

where G (defined above) is assumed to be constant during the main growth period; L_s is as defined above; and L_{d_0} is the average fish length corresponding to a diet shift towards macroinvertebrates, defined from gut content analyses (Tableau et al. 2015).

P can then be expressed from Eqs. (2), (2.1), (2.2), and (2.3) as follows:

$$P = \frac{c_s}{q} \cdot e^{s \cdot Z} \cdot a \cdot \sum_{d \in d_0:D} e^{-d \cdot Z} [(L_s + (d+1/2-s) \cdot G)^b \qquad (3)$$
$$- (L_s + (d-1/2-s) \cdot G)^b]$$

where D, the end of the main growth period, occurs in late fall in temperate ecosystems (Hamerlynck &

Hostens 1993). FC is then derived from P. As the bioenergetics approach refers to energy units, P must be converted into energy production. To do so, we used data on gross conversion efficiency (K) (Hidalgo et al. 1987), defined as the quantity of ingested energy required to produce one energy unit of juvenile fish. As macroinvertebrates may represent only a part of the diet of some roundfish species (Hamerlynck & Hostens 1993), only that part of the production must be considered. Therefore FC of the benthivorous fish community, expressed in energy yr^{-1} or energy $surface^{-1}$ yr^{-1}, is calculated as:

$$FC = \sum_{i \in 1:I^{th} \text{ fish cohort}} P_i \cdot DC_i \cdot E_i \cdot \frac{1}{K_i} \qquad (4)$$

where P_i is the biomass production of fish cohort i; DC_i is the proportion of benthic macroinvertebrates in the diet estimated using stomach contents; and E_i is the energy density gathered from the literature (Supplement S2).

2.3. Benthic FP

Benthic invertebrate species were considered potential prey if they have been observed in juvenile fish gut contents (determined from literature studies on juvenile diet or from our own observations; see details in Tableau et al. 2015 and Supplement S2). Since benthivorous juvenile fish are considered to be opportunistic feeders (De Vlas 1979, Hampel et al. 2005, van der Veer et al. 2011, Schückel et al. 2012), FC cannot be partitioned among prey species. For consistency, the biological productions of all macrobenthic prey species are summed to estimate FP. As the mobility of benthic invertebrate prey is limited, one can assume that they remain in the coastal nursery all their lives. Thus, production-to-biomass ratio data referring to entire populations can be used to compute their production (Brey 2001). The 'available benthic energy coefficient' (ABEC) was developed for this purpose (Tableau et al. 2015). The Brey Model was used because it the most accurate model, especially for marine assemblages (Brey 2012). Since the benefits of a correction coefficient suggested in Brey (2012) remain an open question, we chose not to use it. As ABEC is only applicable to average annual biomasses, biomasses observed during the survey were corrected. The resulting biomass production was converted into energy by a species-specific coefficient, since energy density varies widely among invertebrate species. For instance, energy density is 1.02 kJ g^{-1} for the bivalve *Corbula gibba*, whereas it is 5.84 kJ g^{-1} for the polychaete *Lumbrineris* sp. and 8.19 kJ g^{-1} for *Ampelisca*

sp. (Brey et al. 2010). FP is expressed in energy yr^{-1} or energy surface^{-1} yr^{-1} as follows:

$$FP = \sum_{j\in 1:J^{th}\text{ prey species}} CR \cdot B_j \cdot P{:}B_j \cdot (1+R_j) \cdot E_j = \sum_{j\in 1:J^{th}\text{ prey species}} CR \cdot B_j \cdot ABEC_j \quad (5)$$

where CR is a ratio converting the biomass observed during a survey at a given period of the year into average annual biomass (Tableau et al. 2015); B_j is the biomass observed during a survey (in weight or weight surface^{-1}); $P{:}B_j$ the production-to-biomass ratio estimated from an empirical model accounting for water temperature, but which does not account for regeneration after sublethal fish cropping (Brey 2012) (in yr^{-1}); R_j is a regeneration coefficient (Tableau et al. 2015) accounting for somatic regeneration (i.e. production-to-biomass must be raised by 15% for *Amphiura filiformis* to account for regeneration; Skold et al. 1994); and E_j is the energy density (in energy weight^{-1}) for the jth prey species.

Only accessible prey matters for a predator (Tableau et al. 2015, van der Veer et al. 2016). ABEC (Tableau et al. 2015) allows us to weight the FP of a species by an accessibility coefficient based on observed juvenile fish prey catch rates. According to Tableau et al. (2015), 2 accessibility categories can be statistically identified; the authors suggested setting 1 as the coefficient of easily accessible prey and 0.11 as the coefficient of hardly accessible prey. When included in the FP equation (Eq. 5), the accessibility coefficient (A_j) gives the accessible FP (AFP):

$$AFP = \sum_{j\in 1:J^{th}\text{ prey species}} CR \cdot B_j \cdot P{:}B_j \cdot (1+R_j) \cdot E_j \cdot A_j \quad (6)$$

2.4. Partial uncertainty analyses

The computation of EE requires a large amount of data and parameters, usually at the species level (Table 1). Since quality of information can be poor on some parameters and data, uncertainty analyses were carried out. To do so, we classified the data and parameters following their quality in 3 categories, each of which were treated differently (Table 1).

Table 1. Categorization for the data and parameters. A resolution at the species level (yes, Y) associated with negligible uncertainty (Y) leads to the use of fixed values. When data and parameters are not defined at the species level (no, N) and/or have high uncertainty (N), there are 2 possibilities: if several sources are available (Y), values are defined with an associated distribution; if the uncertainty is unknown (N), a conservative approach is used. N*: data are unavailable for some fish cohorts, but the latter are still informed using data from other fish species. /: not applicable

Parameter	Description	Sources of information	Information at species level	Negligible uncertainty	Known uncertainty	Category of uncertainty	Statistical distribution
Food consumption in energy (fish data)							
C_s	Fish abundance	Surveys	Y	N	Y	2-distribution	Gamma
s	Survey date index		Y	Y	/	1-fixed data	/
L_s	Fish length		Y	Y	/	1-fixed data	/
a	Length–weight parameter	Deduced from surveys	Y	Y	/	1-fixed data	/
b	Length–weight parameter		Y	Y	/	1-fixed data	/
L_{d_0}	Diet shift length		Y	Y	/	1-fixed data	/
d_0	Diet shift date index	Deduced from surveys	N*	N	N	3-conservative	/
D	Growth end index	and literature	N	N	N	3-conservative	/
q	Catch efficiency		N*	N	N	3-conservative	/
Z	Mortality rate		N*	N	N	3-conservative	/
G	Growth rate		N*	N	N	3-conservative	/
DC	Diet composition	Literature	Y	N	N	3-conservative	/
E	Energy density		N	N	Y	2-distribution	Gamma
K	Gross efficiency		N	N	Y	2-distribution	Inverse gamma
Food production in energy (prey data)							
B	Invertebrate biomass	Surveys	Y	N	Y	2-distribution	Gamma
CR	Conversion ratio	Deduced from surveys	N	N	Y	2-distribution	Beta
A	Accessibility		N	N	Y	2-distribution	Beta
P:B	Production-to-biomass ratio		Y	N	Y	2-distribution	Lognormal
R	Regeneration rate	Literature	N	N	N	3-conservative	/
E	Energy density		Y	Y	/	1-fixed data	/

• 1st category: data and parameters with negligible uncertainty. Information comes from the studied species. Values are defined as fixed values. Typically, fish length can be considered in this category.

• 2nd category: data and parameters with highly quantified uncertainty. Information comes from the studied species but is uncertain given observation error (e.g. data on density), given the region and/or life stage at which the information is gathered, or because it is inferred from species taxonomically and functionally close to those observed in the data set (e.g. parameters on mortality rate). For this category, uncertainty is considered as known and/or estimated from the different sources of information. Each data point or parameter is defined using a statistical distribution (see Table 1 and Supplement S1 for details on the distributions).

• 3rd category: data and parameters with highly unquantified uncertainty. Unlike the 2nd category, there is a lack of knowledge and references to inform the values of this category. A conservative approach is needed. It consists of selecting, in a large range of uncertainty, the value of the data or parameter leading to a minimal EE. When at least one parameter is defined in that category, only a minimum threshold estimate of the EE is estimated.

EE was computed using the Monte Carlo method (Metropolis & Ulam 1949). Random sampling in parameter distributions were repeated 5000 times to build the final distributions (Fig. 1).

2.5. Application to a temperate nursery habitat: the Bay of Vilaine, France

2.5.1. Study site

The Bay of Vilaine is a soft-bottom habitat under estuarine influence that is used as a nursery by several benthic and demersal fish species of commercial interest (Le Pape et al. 2003). It has been studied for more than 30 yr, with valuable knowledge gained regarding its fish (Nicolas et al. 2007, Kopp et al. 2013) and benthic invertebrate communities (Le Bris & Glemarec 1995, Brind'Amour et al. 2014).
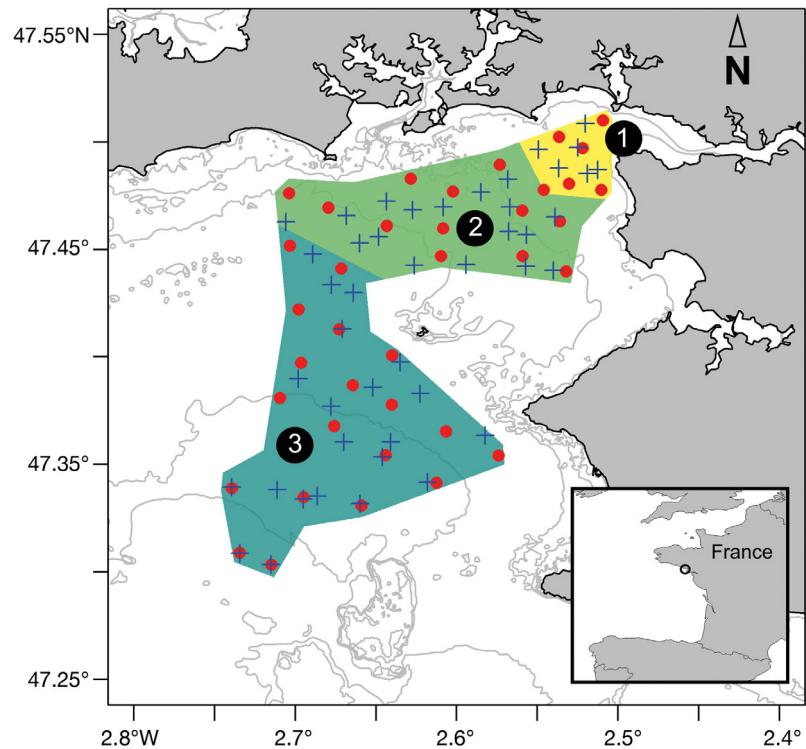

Fig. 2. Sampling design in the Bay of Vilaine. Red dots and blue crosses: grab and trawl sampling stations, respectively; 3 zones: the 3 main subtidal soft-bottom habitats along the bathymetric gradient. The C-shape of the area is due to a non-sampled rocky habitat on the east side of the bay

Given such data and knowledge-rich context, the bay constitutes a relevant framework in which to analyze predator–prey relationships (Le Pape et al. 2003, Kostecki et al. 2010, Tableau et al. 2016). The studied area covers the subtidal zone located from 5 to 30 m depth and consists mostly of sandy mud sediments (Le Bris & Glemarec 1995). It was stratified into 3 zones along the bathymetric gradient (see Supplement S2 for details). All samples were collected exclusively on this type of sediment, explaining the shape of the geographic domain of the study (Fig. 2).

2.5.2. Survey data

A survey was performed in late September 2008 targeting juvenile fish and benthic macroinvertebrates. This season was selected because, for most of the local fish species, juveniles born in spring are large enough to avoid selectivity issues and size-dependent catch efficiency, and also because this period is just before their autumnal migration towards deeper grounds after the growth period

(Dorel et al. 1991, Le Pape et al. 2007). Both protocols are detailed in Tableau et al. (2015). For fish sampling, most of the catches corresponded to benthic and demersal juvenile fish species belonging to the age groups 0 and 1 yr (G0 and G1). Fish species feeding at least partially on benthic macroinvertebrates were selected for this case study: 3 flatfish (benthic) species (*Solea solea*, *Dicologlossa cuneata*, and *Pleuronectes platessa*) and 4 roundfish (benthic or benthopelagic) species (*Merlangius merlangus*, *Merluccius merluccius*, *Mullus surmuletus*, and *Trisopterus luscus*). They represent 71% of the total fish abundance in this area. Ninety-four taxa were considered potential prey for the benthivorous fish community based on gut content analyses. They represent 96% in weight of the collected benthos. See Tableau et al. (2015) for further details on that selection.

2.5.3. Data inputs

Data and parameters are shown in Table 1. The detailed methodology for each data component is fully detailed in Supplement S2. Out of 14 parameters used to compute FC, 6 are described using the conservative approach, i.e. we select the value of the data or parameter leading to a minimal EE. For FP, 1 parameter out of 6 used the conservative approach.

3. RESULTS

3.1. FP and FC

The total FP in 2008 averaged over the 3 zones was 8120 MJ ha^{-1} yr^{-1} (~812 kJ m^{-2} yr^{-1}) and varied from 5850 to 8620 MJ ha^{-1} yr^{-1} among zones (Fig. 3a). When that FP is weighted by the accessibility coefficient (i.e. AFP), it is lowered to an average of 1110 MJ ha^{-1} over the 3 zones (Fig. 3b), corresponding to 14% of total FP.

The spatial distribution of the FC (Fig. 3c) is more contrasted than the AFP (e.g. 2 times higher in zone 3 than in zone 2). Total FC in 2008 averaged among the 3 zones is estimated at 485 MJ ha^{-1} yr^{-1} for the whole bay. The main consumers are 2 exclusive benthivorous fish cohorts (G1 [1-yr age group] of *Solea solea* and G1 of *Dicologlossa cuneata*) and 2 partial benthivorous cohorts (G0 of *Trisopterus luscus*, and G0 of *Merlangius merlangus*). The consumption of the G0 of *S. solea* and G0 of *Pleuronectes platessa* is concentrated in zone 1, which is a shallow area (5 to 13 m depth).
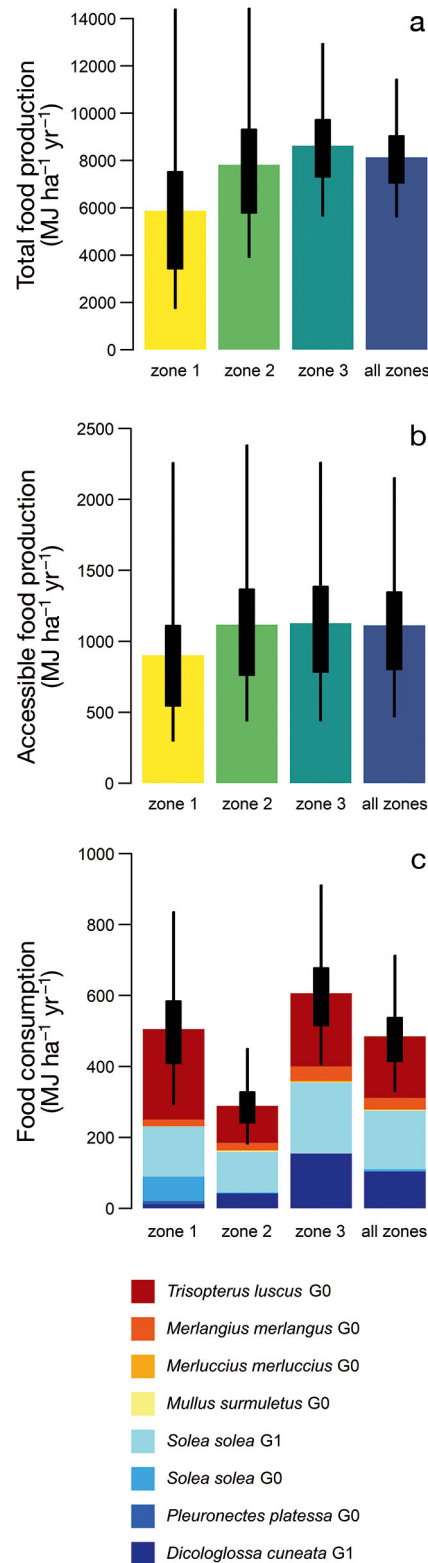

Fig. 3. (a) Total and (b) available food production and (c) food consumption, displayed by fish cohort (G0: young of the year; G1: 1 yr old) in the bay of Vilaine. Boxes: 50% confidence intervals; lines: 95% confidence intervals
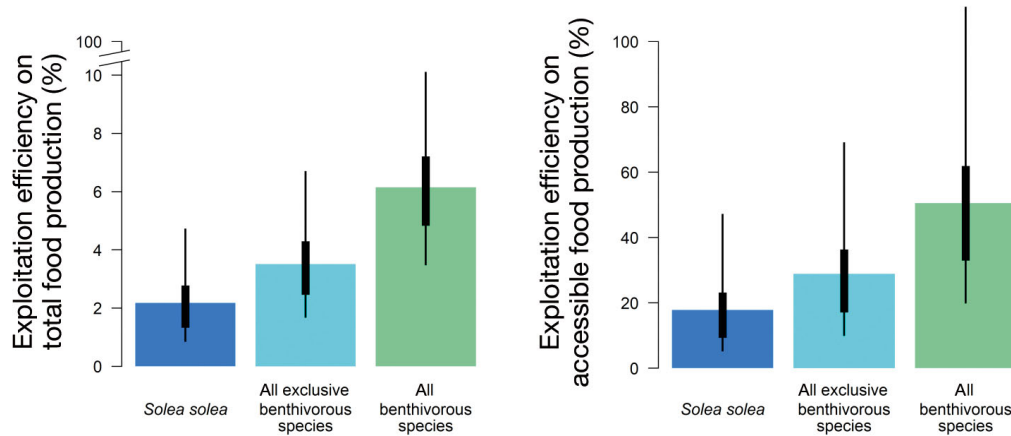
Fig. 4. Exploitation efficiency of total and accessible benthic production in 2008. Exclusive benthivorous species are the flatfish *Solea solea*, *Dicologlossa cuneata*, and *Pleuronectes platessa* and the roundfish *Mullus surmuletus*. All benthivorous species include also *Merluccius merluccius*, *Merlangius merlangus*, and *Trisopterus luscus*. Boxes: 50% confidence intervals; lines: 95% confidence intervals

3.2. EEs

The EE (Fig. 4) of the main benthivorous species (*S. solea*) on total FP is 2.1%. When all benthivorous species are considered, the estimate is 3.5% and increases to 6.1% when partial benthivorous species are also included. When only AFP is considered, the estimate of EE is far higher, ranging from 17.7% for *S. solea* to 50.0% for all species. Uncertainties around these estimates are very large, especially when only AFP is considered.

4. DISCUSSION

This study demonstrates a method of computing the EE of fish juveniles feeding on benthic prey in nursery habitats. Properly estimating EE is essential to better understand the functioning of marine ecosystems (Libralato et al. 2008, Watson et al. 2014), and more specifically, to investigate the food limitation hypothesis within fish nursery habitats (Le Pape & Bonhommeau 2015).

4.1. The food limitation hypothesis: preliminary insights

Coastal nursery habitats present generally high FP and a refuge from predators (Wouters & Cabral 2009, Ryer et al. 2010, Nash & Geffen 2012). The underlying aim of the food limitation hypothesis is to determine predation pressure in order to understand the level of food limitation (Le Pape & Bonhommeau 2015). Defining different food limitation

scenarios can help in interpreting the EE value for juvenile fish:

• No food limitation: food is abundant, and juvenile fish can invest negligible time and energy in foraging. The size of the juvenile population is either defined by factors affecting mortality in previous life stages (e.g. spawner condition affects offspring condition and survival, Hare 2014; larval predation, Houde 2008) or by other factors that occur during the juvenile stage (e.g. predation mortality, competition for space, Sheaves et al. 2015). Under the 'no food limitation' condition, the EE (EE_0) varies over time (inter-annual independence between FP and FC) but remains close to 0. The reciprocal to this causal relationship is not always true: EE can be close to 0 at the scale of the entire nursery with food limitation that occurs locally if there is a lot of spatial heterogeneity of fish and prey distributions.

• 1st level of food limitation: FP supports normal growth of the juvenile fish community, but overdispersed prey force the fish to invest a significant amount of time and energy in foraging. This behavioral response increases the vulnerability of juvenile fish and, consequently, their mortality (Gibson 1994, Biro et al. 2003). This EE (EE_1) is significantly above 0, but depends on density-dependent predation pressure (Johnson 2007, Cebrian 2015). This limiting effect, called predation-sensitive foraging (Sinclair & Arcese 1995) or risk effect (Heithaus et al. 2008), is typically a combination of food limitation and predation.

• 2nd level of food limitation: FP is temporarily not sufficient for all fish juveniles (van der Veer et al. 2016). Juvenile fish must invest a lot of time in find-

ing food, and thus instantaneous vulnerability is exacerbated. One main difference between this and the 1st level of food limitation is that some individuals have a lower body condition and remain small. Paradoxically, a decrease of the apparent growth of the population is rarely observed even though this level of food limitation is suspected to occur frequently (Walters & Juanes 1993, Fiksen & Jørgensen 2011, Le Pape & Bonhommeau 2015). Indeed, small size implies vulnerability to predators that leads to size-dependent mortality (Sogard 1997), the apparent growth is thus maintained at a maximum. If this level of food limitation unfailingly occurs, the EE (EE_2) consistently, and over years, reaches a higher value than EE_1 (which is, however, still unknown).

• 3rd level of food limitation: long-term FP is insufficient for juvenile fish. Consequently, individuals frequently starve to death (Gibson 1994). This has been verified in experiments (Edwards et al. 1970), but has not been observed in natural environments. Indeed, food deprivation in the wild, leading to poor condition, increases vulnerability to diseases and predation (Vethaak 1992) and leads to rapid and massive mortality (Juanes 2007) in the short term. This EE (EE_3) is expected to reach values near 100% if all benthic invertebrate consumers are considered or if the EE is estimated from AFP when only juvenile fish are considered.

Consequently, juvenile fish communities are affected by the lack of food availability before full exploitation at the scale of the fish nursery (Heath 2005). Moreover, low EE does not exclude a high level of food limitation as predicted by the foraging arena theory (Walters & Juanes 1993). Indeed, high predation pressure on fish juveniles prevents them from leaving their shelter to reach better feeding areas and forces them to feed in very restricted areas that are then potentially overexploited. Nevertheless, as nursery habitats are considered to be shelters for juvenile fish (Gibson 1994, Wouters & Cabral 2009), EE could potentially be high. Thus, the remaining problem is to assess the thresholds of EE above which food limitation is temporarily (2nd level) or ongoingly (3rd) insufficient (i.e. EE_2 and EE_3, respectively). The 3rd level could be reached before an EE of 100%. Indeed, significant levels of exploitation below 100% could lead to a collapse in prey availability. For instance, the uptake of 50% of the available production in an ecosystem (e.g. combination of invasive species and shellfish farming on primary production; Arbach Leloup et al. 2008) could lead to a dramatic shift in the trophic chain and a strong limitation of food availability for natural consumers (Rai-

monet & Cloern 2017). Moreover, considering the widely studied fisheries exploitation, the sustainable level of EE at an ecosystem scale is estimated to be around only 15% (Libralato et al. 2008, Watson et al. 2014, Zhou et al. 2015). At this rate, transfer efficiency of benthic production in shallow coastal and estuarine nursery grounds could be limited (Arbach Leloup et al. 2008, Raimonet & Cloern 2017). The specificities of the communities of these ecosystems, i.e. the quality paradox (Elliott & Quintino 2007), with a large number of immature individuals and high levels of mortality, leads to moderate sustainable levels of transfer losses, and thus low potential EE. As these considerations concern overall EE, including predation by competitors, the maximal level of EE by juvenile fish is probably dramatically lower (see Table 2), far below 100%.

The estimates established in the Bay of Vilaine suggest that at least the 1st level of food limitation occurred in 2008. The spatial overlap between the biomass of the juvenile fish community and FP (macrobenthic prey) over the Bay of Vilaine (Tableau et al. 2016) supports this hypothesis. The high EE estimate on AFP suggests that the 2nd level of food limitation might be reached in some sectors of the bay. The potentially large underestimation of the level of EE and previous considerations on the likely moderate threshold of lasting food limitation (i.e. EE_3) lead us to conclude that the 3rd level of food limitation could potentially be reached. An investigation over several years would be required to determine if there is consistency over time. The large uncertainties estimated in the present study would be drastically reduced by conducting at least 2 surveys (at the beginning and end of the main growth period) instead of one, as this increase in data would provide better estimates of fish growth, fish mortality (Nash & Geffen 2000), average benthic invertebrate biomass (Saulnier et al. 2019), and accessibility coefficients. Even if the food limitation hypothesis is investigated at the fish community scale, we assume that the density-dependent response to a lack of food availability would vary from one fish species to another. For instance, we expect that an exclusive benthic feeder would be more sensitive to a lack of benthic invertebrate availability than a partial benthic feeder, which can adapt its diet.

4.2. Conservative (under)estimation of EE

The proposed method provides an estimate of the EE that integrates available ecological knowledge

about the various species included in this case study. Input values can be derived either from *in situ* data (whenever possible) or from the literature. With regards to the assessment of their reliability, they are either fixed values or defined as statistical distributions. Unfortunately, available information on some uncertain parameters is too scarce and/or unreliable to define a statistical distribution. This limitation was overcome by using a conservative approach. Parameter values were chosen to provide a minimum estimate of FC. Improving these parameters would bring the estimate closer to the actual EE.

Several other shortcomings of the approach lead to an underestimation of EE:

• Fish biomass: the use of a beam trawl minimizes the uncertainty of benthic and juvenile fish catch per trawled area (Dorel et al. 1991). However, estimation methods used in the literature often only provide maximum catch efficiencies (e.g. Reiss et al. 2006), thus minimum estimates of fish biomass. Moreover, fish species selected in the analysis account for 71% of the catch, not the overall amount that fish consumed.

• One parameter using the conservative approach is diet composition. Macrobenthic proportion in the diet is defined with the smallest values observed in the literature (Supplement S2). A source of underestimation of FC is that some fish cohorts are present in the bay only during one season. Consequently, they are not observed in some surveys, and are therefore not considered (e.g. G1 of *Pleuronectes platessa* in early summer, Desaunay et al. 1981). Moreover, the considered growth period is restricted to a time window corresponding to only the maximum growth period (Hamerlynck & Hostens 1993). Feeding activity during the winter period is not estimated. Juveniles of the selected species move progressively to deeper water in winter, but the corresponding consumption during this migration cannot be estimated as the apparent mortality rate (reflecting both mortality and migration rates) is not available. Consumption by the resident fish species, present in the remaining 29% of the survey catch, likely occurs (Fonds et al. 1992).

• The consumption of benthic production was estimated for fish species only, whereas other non-fish consumers (e.g. the brown shrimp *Crangon crangon*), sometimes occurring at high biomass, may also feed on the same pool of prey (Jung et al. 2017).

• The parameter converting energy production into energy consumption is defined and does not account for indigestible parts of ingested prey.

All of these shortcomings most likely lead to an underestimate of FC occurring in the natural environment. The actual EE value is higher than the estimate provided. This (under)estimate is valuable in the context of the food limitation hypothesis, but associated conclusions need to account for this conservative methodology.

4.3. Community scale and prey accessibility: 2 keys of investigation

The 2008 FP in the bay of Vilaine is in the production range of similar habitats (Burd et al. 2012, Bolam et al. 2014). When only the dominant benthivorous species is considered, the EE on the FP is low (~2%). This result is in the range of studies focusing on a single fish species (Table 2). However, since the carrying capacity of a population is determined by the strength of interspecific density-dependence (Brown et al. 2019), a community approach was adopted. When more of the benthivorous fish community was considered, the EE was far higher (~6%). This result underlines the need to account for a maximum of species preying on the same community (Vinagre & Cabral 2008). The EE of the juvenile fish of the selected species is in the range of the results of Ecopath applications in nursery habitats (Table 2). However, these models were not built to assess the food limitation hypothesis and face several shortcomings (i.e. the total biomass of a fish species is sometimes estimated from trawl catch without accounting for the catch efficiency, Rybarczyk & Elkaïm 2003); the lack of knowledge regarding production-to-biomass ratios for juvenile fish is also a major concern (Mackinson & Daskalov 2007). The present estimate of EE is also close to Pihl (1985), who used a similar approach in a more restricted area (1.5 ha; Table 2).

Pihl (1985) also stated that the production of some prey species is fully consumed and that half of total prey production is consumed (Table 2), suggesting food competition, and consequently, potential food limitation. Similarly, the Ecopath-based approach estimates the overall EE as ranging from 20 to 99%. This indicates that considering the juvenile fish community is relevant, but not sufficient, as other predators may feed on the same pool of prey. The EE estimates would thus benefit from considering additional megabenthic invertebrate consumers, such as large echinoderms (e.g. starfish *Asterias rubens*) or crustaceans (swimming crab *Liocarcinus holsatus*, and the brown shrimp *Crangon crangon*). However, some key parameters referring to these species, such as

Table 2. Estimates of exploitation efficiency (EE; ratio of benthic production consumed by their predators to the total benthic production) in temperate marine ecosystems: habitat, scale, number of species, method, habitat features (area, bathymetry) and location

Main scale production of food estimation	No. of fish cohorts / species	Method of food consumption estimation	Surface area (ha)	Bathymetry (m)	EE by fish (%)	EE by all consumers (%)	Location	Study
Nursery habitat								
Species	7	Bioenergetics	19351	5–30	6.2	?	Bay of Vilaine, France	This study
Species	3	Evacuation rate	1.5	<1	6.8	50.8	Gullmarsvik, Sweden	Pihl (1985)
Taxonomic groups	2	Evacuation rate	2400	1.6	<1.0	?	Tagus estuary, Portugal	Vinagre & Cabral (2008)
Taxonomic groups	1	Evacuation rate	4600	4.4	<1.0	?	Tagus estuary, Portugal	Vinagre & Cabral (2008)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	>10000	?	24	99	Narragansett Bay, USA	Monaco & Ulanowicz (1997)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	>10000	?	4	99	Delaware Bay, USA	Monaco & Ulanowicz (1997)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	>10000	?	11	94	Cheasapeake Bay, USA	Monaco & Ulanowicz (1997)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	650000	0–20	10	78	Seine Bay, France	Tecchio et al. (2015)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	450000	0–10	1	20	Gironde estuary, France	Lobry et al. (2008)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	5000	0 (intertidal)	6.9	76	Bay of Somme, France	Rybarczyk et al. (2003)
Ecological guilds	Whole fish community	Bioenergetics (Ecopath)	3500	0–5	18	72	Seine estuary, France	Rybarczyk & Elkaïm (2003)
Adult habitat								
Species	2	Bioenergetics	3.6	<1	9	?	Kvarnbukten Bay, Sweden	Evans (1983)

the gross conversion efficiency, are unknown, which prevents the inclusion of such consumers in this application.

Van der Veer et al. (2016, p. 105) emphasized that 'for a predator only harvestable prey matters'. Even though some prey species belong to the hyperbenthos, a large part of the benthic macrofauna live partly or totally burrowed in the sediment, so access to prey items is a factor that potentially heavily impacts the food quantity that is harvestable by juvenile fish (Tableau et al. 2015). Indeed, the EE could never reach 100% even if juvenile fish were the only consumers. Considering total FP instead of AFP would fail to test the food limitation hypothesis (Vinagre & Cabral 2008). To our knowledge, this study is the first attempt to investigate the food limitation hypothesis by accounting quantitatively for food accessibility. The application to the bay of Vilaine in 2008 shows that at least 20% of the FP accessible to juvenile fish is consumed, and does not exclude that the entire accessible production is consumed (cf. the uncertainty intervals; Fig. 3). Accounting for prey accessibility significantly increases the EE estimate by including additional information that is essential to investigate the food limitation hypothesis. The accessibility coefficient provided by Tableau et al. (2015) is, however, a large source of uncertainty and requires further investigation (e.g. seasonal prey availability and ontogenetic variations, Beukema et al. 2014, van der Veer et al. 2016; species-specific behavior, de Groot 1969).

4.4. Future considerations

Moving forward, it would be fruitful to compare EE between nursery habitats over time, especially in areas with large differences in juvenile fish abundance. Indeed, as an EE value of 100% is unlikely, EEs significantly

different from 0% and consistent among nursery habitats with contrasted fish juvenile abundance would support a general food limitation effect. In this context, the environmental factors influencing benthic invertebrate production may also contribute to density-dependent survival explaining recruitment variations (Salen-Picard et al. 2002). As predators of juvenile fish influence fish juvenile densities, EEs could provide indirect information about these predators. According to the foraging arena theory applied to 2 nurseries monitored over several years, the maximum EE value reached in a nursery more exposed to large predators is expected to be lower than in the more protected nursery. Therefore, the maximum EE value for a nursery over a time series would reflect the quality of shelter of that nursery from predators of the juvenile fish.

The present method was developed to test the food limitation hypothesis in a temperate coastal nursery context, but this framework is sufficiently generic and could be applied to a broad latitudinal range of coastal habitats (tropical, subarctic). However, parameters that vary with latitude (e.g. duration of growth period, Freitas et al. 2012) and/or at small spatial scales (e.g. growth rate, Ciotti et al. 2014), would have to be properly defined.

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