

l'institut Agro

#### AGRO CAMPUS OUEST

## THESE DE DOCTORAT DE

#### L'INSTITUT AGRO

ECOLE DOCTORALE N° 598 Sciences de la Mer et du littoral Spécialité : Écologie marine

Par

### Louise DAY

# Fonctionnement et capacité trophique des nourriceries côtières et estuariennes : exemple de la Seine

Thèse présentée et soutenue à Nantes, le 3 décembre 2020 Unité de recherche : UR EMH Ifremer - UMR ESE Institut Agro, INRAE Thèse N° : 2020-23 H-115

Rapporteurs avant soutenance :		Composition du Jury :		
		Rapporteurs		
Mireille HARMELIN-VIVIEN	Professeur, Université de Méditerranée	Mireille HARMELIN-VIVIEN	Professeur, Université de Méditerranée	
		Benjamin CIOTTI	Professeur, University of	
Benjamin CIOTTI	Professeur, University of Plymouth		Plymouth	
		Examinateurs		
		Frida BEN RAIS LASRAM	Maitre de conférences, Université Littoral Côte d'Opale	
		Jean-Michel OLIVIER	Ingénieur de recherche, Université Lyon 1	
		Directeurs de thèse		
		Hervé LE BRIS	Professeur, Institut Agro - INRAE	
		Anik BRIND'AMOUR	Cadre de recherche, lfremer	
		Président	Mireille HARMELIN-VIVIEN	

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#### **Avant-propos**

Cette thèse s'inscrit dans le cadre du projet GIP Seine-Aval 6- CAPES, « CApacité trophique des nourriceries de Poissons de l'Estuaire de Seine », coordonné par Anik Brind'Amour (IFREMER Nantes), en collaboration avec Hervé Le Bris (Agrocampus Ouest / INRAE), Pierre Cresson, Camille Vogel, Franck Maheux (IFREMER), Sylvain Duhamel et Bastien Chouquet (Cellule du Suivi du Littoral Normand), Jean-Claude Dauvin et Jean-Philippe Pézy (Université de Caen Normandie, UMR M2C / CNRS).

Elle s'est déroulée entre Octobre 2017 et Septembre 2020 au sein de l'unité EMH (Ecologie et Modèles pour l'Halieutique), Ifremer Nantes et de l'UMR ESE (Ecologie et Santé des Ecosystèmes), Institut Agro, INRAE, co-dirigée par Anik Brind'Amour (Ifremer Nantes) et Hervé Le Bris (Institut Agro / INRAE).

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#### Remerciements

Dans un premier temps, je tiens à remercier mes directeurs de thèse Anik Brind'Amour et Hervé Le Bris. Pendant ces trois années, vous avez toujours été présents, encourageants, passionnés et passionnants. J'ai beaucoup apprécié votre belle complémentarité scientifique, nos discussions constructives et bienveillantes, la confiance que vous m'avez accordée pendant ces trois années et vos précieuses qualités humaines. Je suis fière d'avoir été votre « troisième acte », pour reprendre l'expression d'Hervé, et je ne pouvais pas imaginer mieux comme encadrement.

Je continue en remerciant les membres de mon jury qui ont accepté d'évaluer mon travail de thèse : les rapporteurs Mireille Harmelin-Vivien et Benjamin Ciotti et les examinateurs Frida Ben Rais Lasram et Jean-Michel Olivier. Merci pour vos retours pertinents sur mon manuscrit et nos discussions lors de la soutenance. Je n'imaginais pas soutenir ma thèse en distanciel, je vous remercie pour votre adaptabilité et pour avoir rendu ce moment agréable et fluide, malgré les circonstances. Je tiens également à remercier particulièrement Mireille Harmelin-Vivien pour sa relecture attentive de mon manuscrit de thèse.

Je tiens à remercier l'IFREMER et le GIP Seine Aval qui ont financé ce travail, ainsi que tous les membres du projet CAPES pour leur implication dans la récolte des données, le tri, l'identification, la dissection, préparation des échantillons, etc. ainsi que la participation aux réunions du projet. Je remercie particulièrement les deux stagiaires, Andréa Lemoine et Alexandra Engler que j'ai eu le plaisir de co-encadrer avec Camille Vogel et Pierre Cresson respectivement. Merci à vous quatre pour nos nombreux échanges, ainsi que les moments conviviaux partagés toujours avec plaisir !

Je remercie Jérémy Lobry, Eric Thiébaut et Pierre Cresson (à nouveau !) qui ont accepté de faire partie de mon comité de thèse. Vous avez été de très bons conseils, à l'écoute et encourageants.

Merci à tous les membres du laboratoire EMH à Nantes de m'avoir chaleureusement accueilli. C'est un lieu où j'ai apprécié venir travailler et où je me sentais bien entourée. Un merci spécial pour Sigrid et Olivier qui sont venus le jour de ma soutenance et qui ont fait de cette soutenance en distanciel un excellent souvenir. Merci aux escaladeurs, Olivier, Youen, Sigrid, Camille, aux coureurs, Pascal dit Plaff, Stéphanie, Nico, Erwan, Fabien, Lucas, Youen, Sigrid, Anik, Léo, Damien aux copines Sophie, Angie, Amélie, Solène, aux copains anciens doctorants Erwan, Fab, Florianne, Pierre et aux nouveaux Baptiste, Jérôme, puis à Morgane, David, Agathe et Anne So, toujours de bons conseils ! Trois années

ponctuées de belles rencontres, en espérant pouvoir continuer de partager des soirées jeux, des sessions de surf, pêche ou escalade et des apéros !

Je remercie ensuite les collègues du laboratoire EH à Rennes avec qui j'ai passé de très bons moments lors de mes visites dont les footings le long de la Vilaine le midi mais surtout les fameux apéros du vendredi soir ! Merci à Cath et Kath, Etienne, Jérôme, Didier, Marie, Oliv, Thomas et aux plus jeunes, Hub (Anne et Anatole), PY, Auriane, Marine, JB Lecomte et Juliette !

Une grande pensée également aux copines nantaises, Adèle et Elsa qui étaient là pour décompresser, faire du yoga, rigoler et kayaker sur l'Erdre ! Je remercie aussi les amis plus éloignés géographiquement mais toujours partants pour des weekends ou vacances, à la mer, à la montagne ou à Paris : les copains du foyer (et bravo au premier docteur de la troupe : JC !), Mamou et Marion, Andréa, Clemao, Sophie, François et Otis ! Merci à la coloc des trois pierres blanches de m'avoir accueillie pendant les deux confinements, merci pour vos bons petits plats, les soirées brasero et les olympiades ! Un immense merci à Ségolène, mon acolyte du quotidien (#hangout), un soutien sans faille et bientôt de nouvelles aventures ensemble ! Je remercie spécialement mon super copain Flo pour son soutien et ce super montage vidéo de thèse (je ne pouvais pas imaginer un meilleur cadeau !).

Enfin, je remercie ma famille, mon socle solide et tout particulièrement mes sœurs et ma maman qui m'a gentiment accueillie durant les deux dernières années de ma thèse en m'offrant les meilleures conditions possibles.

Merci à tous !

#### Valorisations scientifiques

#### Articles publiés

**Day, L.**, Brind'Amour, A., Cresson P., Chouquet, B., Le Bris, H. (2020) Contribution of estuarine and coastal habitats within nursery to the diets of juvenile fish in spring and autumn. *Estuaries and Coasts*, DOI: 10.1007/s12237-020-00823-z

**Day, L.**, Le Bris, H., Saulnier, E., Pinsivy, L., Brind'Amour, A. (2020) Benthic prey production from trawl survey supports the food limitation hypothesis in coastal fish nurseries. *Estuarine and Coastal and Shelf Science*, DOI: 10.1016/j.ecss.2020.106594

#### **Communications orales**

**Day, L.**, Cresson, P., Le Bris, H., Brind'Amour, A. (2019). Is trophic capacity spatially variable in the bay of Seine? *CHEERS*, Bordeaux, France, November 4th-8th, 2019

Timmerman, C. A., **Day, L.**, Brind'amour, A., Cresson, P., Isotopic niche variation in plaice Pleuronectes platessa: diet, habitat or metabolic effect? *ICES Annual Science Conference 2019*, Gothenburg, Sweden, 9-12 September 2019

#### Posters

**Day, L.**, Cresson, P., Engler, A., Le Bris, H., Brind'Amour, A., Combining stable isotope mixing models and a bioenergetics-based approach to spatialize the exploitation efficiency of juvenile demersal fish a coastal nursery, *ICES Annual Science Conference 2019*, Gothenburg, Sweden, 9-12 September 2019

Lemoine, A., **Day, L.**, Brind'Amour, A., Vogel, C. Evolution saisonnière de la condition des juvéniles de plie (Pleuronectes platessa) en estuaire de Seine. *14e colloque de l'AFH* "Recherche Halieutique et Développement Durable". 26 au 28 juin 2019, Université de Caen Normandie.

Engler, A., **Day, L.**, Chouquet, B., Vogel, C., Brind'Amour, A., Cresson, P. Variations spatiales de l'alimentation des juvéniles de sole et de plie en Baie de Seine. *14e colloque de l'AFH* "Recherche Halieutique et Développement Durable". 26 au 28 juin 2019, Université de Caen Normandie.

**Day, L.**, Le Bris, H., Saulnier, E., Pinsivy, L., Brind'Amour, A., Can we use trawled benthic invertebrates as a surrogate of fish prey in coastal nurseries? *XVIth International Symposium on Oceanography of the Bay of Biscay (ISOBAY 16)*, 5-7 June 2018 (1<sup>st</sup> best poster award)

#### Abstract

Estuarine and coastal ecosystems fulfil a nursery function for many benthic and demersal fish species. These nursery-dependant species concentrate at the juvenile stage in these spatially limited habitats, resulting in density-dependent regulation affecting growth and survival according to the carrying capacity of estuarine and coastal nurseries. However, the underlying mechanisms that drive this capacity are still poorly understood and the limitation of the food supply on the juvenile fish remains a pending issue. Previous studies commonly tested the trophic limitation over the entire nursery (subtidal part) and at an annual scale. However, biological processes leading to trophic limitation (*e.g.* competition) can act on finer spatial and temporal scales. A first hypothesis would postulate that competition is stronger following the arrival of individuals, generally in spring, while a second hypothesis would postulate stronger competition at the end of the summer season, after the period of high production of trophic resources in spring. From a spatio-temporal point of view, some less productive habitats may be a place of trophic limitation, while others (*e.g.* intertidal areas) may provide a significant amount of food resources, at a given moment. Thus, it would be relevant to test the hypothesis of trophic limitation at these spatial and temporal scales.

The estuary and eastern bay of Seine (Eastern English Channel) is a nursery composed by several habitats offering diverse food resources. Over the last decades, important anthropogenic activities significantly reduced the surface, especially of mudflats, likely decreasing the gross production of this ecosystem. A recently developed bioenergetics-based approach allows the estimation the exploitation efficiency (EE), *i.e.* the part of the secondary production consumed by bentho-demersal juvenile fish. In this thesis, this approach was applied to habitats within the Seine nursery and at two important periods of their juvenile stage: the post-settlement period (early spring) and the end of the growth season (late summer).

In order to spatialize juvenile fish consumption over the habitats within the nursery, habitats' contribution to juvenile fish diet need to be estimated. Indeed, an underlying question related to the assumptions of the model in the thesis is to check if fish feed on their habitat of collection. This question is addressed in the first chapter, in a context of identification of essential feeding habitats within nursery for juvenile fish, using trophic tracers (stomach contents and stable isotopes) to quantify the contribution of each habitat to juvenile fish diet. This is addressed, thanks to stable isotopes mixing models, with primary consumers as sources in each habitat. Primary consumers have isotopic compositions more stable over time (compared to primary producers usually chosen as sources in this type of study) and, in this case, spatially distinct.

In the second chapter, estimates of EE (*i.e.* the part of the production consumed by the juveniles) at the habitat scale and at the beginning and the end of the growth season in the nursery, allow a better

understanding of the processes responsible of trophic competition and potential limitation. Nine benthodemersal fish species are included in the study and represent more than 80% of the total biomass of the bentho-demersal community of the Seine nursery. Prey production is estimated using benthic invertebrates from macrofauna community (spring and autumn) and harpacticoids copepods (spring). The end of the growth season (autumn) when benthic resources for juvenile fish are less abundant, individual fish energetic needs are higher (as fish are larger) and a potential higher interspecific competition (due to the presence of all species in the nursery) could thus constitute a period of trophic limitation.

The last chapter tests the trophic limitation in estuarine and coastal nurseries using time series of predator (juvenile fish densities) and prey (prey production) data. To do so, an index of benthic prey production is beforehand created and validated by comparing data punctually collected by grabs, a classic sampler for macrobenthic community studies with data from scientific beam trawl surveys, at the same periods. Quantile regressions between this index and the juveniles densities estimated over the time series suggest that production of benthic prey is a limiting factor in the nursery function.

Finally, this thesis challenges the scales at which to address the issue of trophic limitation in coastal and estuarine nurseries and provides elements supporting this hypothesis. Habitat and season scales seem relevant to study juvenile fish nursery functioning. This thesis also provides technical solutions for spatially and monthly adaptations of the bioenergetics-based approach developed at larger scales. Moreover, the knowledge acquired at fine scales can be more easily transferred to managers of coastal and estuarine areas where conflicts for spatial use with human activities are present and where protection and conservation of the nursery function is then essential.

# Chapitre 1.

Introduction générale



Illustration : L. Fleury

#### 1.1 Estuaires et baies côtières : des milieux productifs à préserver

#### 1.1.1 Estuaires et baies côtières

Le terme estuaire vient du latin *aestuarium* qui signifie « lieu où le flux pénètre ». À l'interface entre la mer, le fleuve et la terre, ses limites mouvantes ont conduit de nombreux scientifiques à proposer des définitions de cet écotone (*i.e.* zone de transition; Elliott and McLusky, 2002; Potter et al., 2010). Dans leur revue, Whitfield and Elliott (2011) définissent un estuaire comme « une masse d'eau côtière semi-fermée reliée à la mer de façon permanente ou périodique, qui a une salinité différente de celle de la haute mer adjacente en raison des apports d'eau douce et qui est caractérisé par un biote particulier ». L'estuaire est donc le lieu de rencontre entre deux masses d'eau : une masse d'eau douce, déversoir d'un bassin versant et une masse d'eau maritime. Il est alors soumis à de nombreux gradients naturels comme par exemple les gradients de salinité, de profondeur ou encore de température.

Certains estuaires se jettent dans la mer au niveau d'une baie côtière. Cet espace géographique correspond à une intrusion de la mer dans la côte. Une baie côtière peut accueillir un ou plusieurs estuaires, c'est le cas par exemple de la Baie de Seine (France) ou la baie de Lyme de l'autre côté de la Manche (Royaume Uni).

#### 1.1.2 Des milieux productifs soutenant un réseau trophique complexe

Les estuaires et les baies côtières sont souvent catégorisés parmi les écosystèmes les plus productifs de la planète (Schelske and Odum, 1961; Costanza *et al.*, 1997; Kennish, 2002). Les apports terrigènes et les conditions physiques favorables (faible profondeur qui laisse la lumière pénétrer et température plus élevée entre le printemps et l'automne) peuvent supporter une forte production primaire par photosynthèse (Heip *et al.*, 1995; Glé *et al.*, 2008). La production primaire des écosystèmes côtiers et estuariens est assurée par divers producteurs primaires tels que le phytoplancton, les macroalgues, les herbiers marins, le microphytobenthos ou les plantes vasculaires des marais (Montagna et al., 2013). Notons que les niveaux de production peuvent varier le long du gradient estuarien. Par exemple, la zone de turbidité maximale (ou bouchon vaseux) réduit l'apport en énergie lumineuse et peut créer des conditions d'anoxie (Marchand, 1993; Dauvin and Desroy, 2005).

Le phytoplancton marin et d'eau douce est alors soit directement consommé par les zooplanctivores (consommateurs primaires), soit sédimente. Une fois sédimenté, il peut entrer dans le réseau trophique par des voies détritiques ou être utilisé par des organismes filtreurs (Cloern, 2001 ; Montagna et al., 2013). Les faibles profondeurs des écosystèmes estuariens et côtiers renforcent le couplage benthopélagique et permet aux filtreurs et aux dépositivores benthiques de s'appuyer sur plusieurs sources primaires, pélagiques et benthiques (Guarini et al., 2004 ; Perissinotto et al., 2003). Ainsi, les producteurs primaires assimilent les nutriments et, avec les détritus et la matière organique d'origine terrestre, alimentent les réseaux trophiques côtiers. L'énergie circule ensuite vers les niveaux trophiques supérieurs : les invertébrés carnivores, les poissons adultes ou juvéniles, etc. (Pasquaud et al., 2008 ; Tableau et al., 2016). Cette description simplifiée des flux de nutriments et d'énergie à travers les écosystèmes côtiers et estuariens décrit les principaux processus allant des nutriments et de la matière organique aux juvéniles de poissons (Fig. 1).



Figure 1 : Exemple d'un réseau trophique d'un écosystème estuarien typique montrant les liens d'alimentation entre les principaux groupes trophiques. Les flèches noires indiquent le flux de nourriture de la source au consommateur. Figure extraite de (Day *et al.*, 2013).

#### 1.1.3 Des milieux fortement anthropisés à préserver

Le littoral a été occupé très tôt par les populations humaines et l'est encore aujourd'hui (Lotze, 2006). Il concentre les activités humaines avec 60% de la population mondiale vivant à moins de 100 km des côtes (Vitousek, 1997). Les nombreuses activités humaines impactent directement (industrialisation, activités portuaires, pêche, extraction de granulats, etc.) ou indirectement (impact induit par le changement climatique : réchauffement de l'océan, acidification) les zones côtières et estuariennes (Kennish, 2002; Lotze, 2006). Ces espaces sont également les déversoirs des bassins versants drainant toutes les substances et particules issues des agglomérations urbaines, de l'agriculture et de l'industrie. À titre d'exemple, le bassin versant de la Loire recouvre 1/5 du territoire métropolitain français. Celui de la Seine, plus petit est occupé par 30% de la population française.

Cette concentration d'activités soumet les écosystèmes à des pressions (Elliott and McLusky, 2002; Lotze, 2006; Crain *et al.*, 2009) affectant d'une part la qualité du milieu via la contamination chimique (Matthiessen and Law, 2002) ou des marées vertes (Quillien *et al.*, 2018; Kermagoret *et al.*, 2019) et d'autre part l'étendue de ces milieux par l'utilisation d'espace aquatique pour la construction de digues ou les aménagements portuaires par exemple (Dauvin *et al.*, 2006). Cette concentration d'activités conduit généralement à la dégradation et la perte d'habitats pour de nombreuses espèces engendrant donc des conflits d'usage entre activités humaines et utilisation de l'espace par des espèces y résidant de façon permanente ou partiellement (Brown *et al.*, 2018). Seitz et al. (2014) ont estimé que 44% des espèces évaluées par le CIEM<sup>1</sup> dépendent de ces habitats côtiers durant au moins une phase de leur cycle de vie, ce qui représente 77% des débarquements en volume. La dégradation des habitats entraîne la réduction de l'abondance des juvéniles de poissons y résidant (Lotze, 2006; Courrat *et al.*, 2009; Rochette *et al.*, 2010), impactant le futur recrutement<sup>2</sup> de ces populations.

Ainsi, pour maintenir cette fonction halieutique ainsi que les nombreuses autres fonctions soutenues par ces systèmes, il est nécessaire de préserver leur qualité, leur intégrité et leur connectivité avec les autres écosystèmes. La gestion de ces espaces impliquant de nombreux acteurs, l'exercice est d'autant plus délicat et revêt des dimensions écologiques, sociales et économiques. Il est donc nécessaire d'en comprendre mieux le fonctionnement et d'acquérir les connaissances fondamentales nécessaires pour pouvoir concilier les activités humaines et les usages par les autres espèces.

#### 1.2 Estuaires et baies côtières : dynamiques spatiales et temporelles

À l'interface entre terre et mer et entre eau salée et eau douce, les estuaires et les baies côtières sont soumis à une forte variabilité spatiotemporelle des paramètres physico-chimiques tels que la température, la salinité ou encore la concentration de matières en suspension (Heip *et al.*, 1995). Ces variables abiotiques structurent l'espace le long du gradient estuarien et sont contrôlées par deux processus hydrodynamiques principaux : la marée avec ses variations tidales (cycle de 12 h environ et variations de l'amplitude de marée) et le débit du cours d'eau avec ses variations saisonnières. L'oxygène en tant que paramètre essentiel à la vie des organismes est dépendant de ce contexte et présente dans ces écosystèmes de fortes variabilités spatio-temporelles.

#### 1.2.1 Estuaire : une mosaïque d'habitats

La niche écologique fondamentale d'une espèce peut être représenté comme un espace à plusieurs dimensions, chacune des dimensions représentant une variable environnementale, abiotique ou biotique (Hutchinson, 1957). Dans un estuaire, les espèces se répartissent selon leur capacité à supporter la dessalure, les variations de température, l'exondation, la turbidité ou encore l'anoxie, mais aussi les ressources alimentaires présentes. Ainsi, du fait de la présence de forts gradients environnementaux, les estuaires sont souvent décrits comme des mosaïques d'habitats connectés entre eux (Peterson, 2003;

<sup>&</sup>lt;sup>1</sup> CIEM : le Conseil International pour l'Exploration de la Mer (CIEM) ou The International Council For the Exploration of the Sea (ICES) est un organisme inter-gouvernemental qui coordonne la recherche sur les ressources et l'environnement marins dans l'Atlantique nord-est. Il est également en charge d'émettre des avis pour la gestion des ressources exploitées pour les stocks présents sur ce secteur.

<sup>&</sup>lt;sup>2</sup> Le recrutement correspond au nombre de juvéniles en âge de rejoindre la population adulte.

Sheaves *et al.*, 2015). Les communautés d'invertébrés benthiques sont structurées le long du gradient amont aval selon des variables physiques (Ysebaert *et al.*, 2003; Dutertre *et al.*, 2013; Dauvin *et al.*, 2017) avec des communautés marines euhalines en aval et des communautés plus tolérantes aux fortes variations environnementales en amont. L'estuaire de Seine illustre bien ce contraste avec la communauté à *Abra alba-Lagis koreni* dans la partie marine de l'estuaire et la communauté à *Limecola balthica* dans la zone poly/mésohaline (Thiébaut *et al.*, 1997; Morin *et al.*, 1999). La tolérance à l'exondation est également un critère déterminant, notamment dans la colonisation des vasières intertidales, ce qui en fait un habitat très particulier, avec un corridor d'espèces propres aux estuaires européens, par exemple *Hediste diversicolor, Corophium volutator, L. balthica, Scrobicularia plana, Cyathura carinata et Hydrobia ulvae* (Marchand, 1993; França *et al.*, 2009; Baffreau *et al.*, 2017). Ces zones situées à l'interface entre la terre et l'estuaire sont connectées à la partie subtidale par les mouvements d'eau. Des espèces mobiles profitent du jusant pour s'alimenter sur la zone intertidale (Cabral, 2000; Laffaille *et al.*, 2001). On retrouve également des successions d'assemblages d'espèces de poissons, selon les conditions supportées par chaque espèce et donc les niches écologiques des espèces (Marchand, 1993; Nicolas *et al.*, 2010).

Ces gradients de facteurs physiques structurent également spatialement le réseau trophique estuarien, de la production primaire et autres sources de matière organique jusqu'aux prédateurs supérieurs (Deegan and Garritt, 1997). À la base des réseaux trophiques, le gradient amont-aval se reflète dans les sources de matières avec un mélange de matière organique particulaire (MOP) d'origine terrestre et estuarienne en amont et des MOP marines en aval (Liénart *et al.*, 2017). Ce gradient peut être facilement caractérisé en mesurant la signature isotopique en carbone ( $\delta^{13}$ C, le ratio en C<sup>13</sup>/C<sup>14</sup>), avec la MOP marine enrichie en C<sup>13</sup> par rapport à la MOP d'origine terrestre (Darnaude *et al.*, 2004; Antonio *et al.*, 2010; Liénart *et al.*, 2017). Ces gradients isotopiques se répercutent ensuite sur les consommateurs supérieurs (Riera and Richard, 1996; Leakey *et al.*, 2008; Marley *et al.*, 2019).

Les différents habitats sont connectés entre eux par les mouvements hydrodynamiques qui déplacent la matière en suspension comme du microphytobenthos mis en suspension (Kang et al., 2015; Yokoyama et al., 2009. Ils sont également connectés par les organismes mobiles prédateurs (Laffaille *et al.*, 2001; Marley *et al.*, 2019). De plus, cette structure spatiale est très dynamique dans le temps et elle subit de fortes variations, notamment le rythme saisonnier du débit du fleuve. Par exemple, en période estivale où le débit est le plus bas, l'estuaire du Tage supporte deux réseaux trophiques localisés. L'automne et les changements de débit engendrent de forts mouvements qui rétablissent la connectivité entre ces deux réseaux trophiques pour n'en former plus qu'un (Vinagre *et al.*, 2011b).

#### 1.2.2 Dynamiques saisonnières

S'ajoutant à ces contrastes spatiaux marqués, les estuaires sont marqués par des variations saisonnières associées aux dynamiques fluviales liées aux précipitations et à la fonte des neiges. En zone tempérée,

les débits sont les plus importants en saison hivernale (Marchand, 1993; Romero *et al.*, 2016), la période Novembre-Avril concentrant en moyenne les deux tiers du débit annuel (Romero *et al.*, 2013). Les débits apportent les nutriments et apports terrigènes à la base des réseaux trophiques estuariens, un des facteurs de la saisonnalité de la production primaire estuarienne avec la lumière et la température (Heip *et al.*, 1995; Cloern, 2001; Glé *et al.*, 2008). Ainsi, au printemps, avec l'augmentation des températures, les fortes concentrations en nutriments et l'allongement des jours, on observe souvent un bloom de production primaire. Les faibles apports liés aux débits estivaux limitent la production dans cette saison. L'augmentation du débit à l'automne augmente l'apport de nutriments, mais la baisse d'énergie lumineuse et/ou de la température limite la production à cette période.

Les communautés animales suivent aussi cette saisonnalité. On peut citer par exemple, le patron de saisonnalité de la macrofaune benthique (Beukema, 1974; Saulnier *et al.*, 2019) supportée par la saisonnalité de la production primaire et des apports terrigènes de matière organique, les changements saisonniers dans les communautés de poissons et de crustacés (Maes *et al.*, 1998; Selleslagh *et al.*, 2012) ; les arrivées et départs d'oiseaux migrateurs pour les estuaires situés sur les voies de migration de ces espèces, par exemple, l'estuaire de Seine avec 100 000 oiseaux s'arrêtant chaque année pour s'alimenter et se reposer (Dauvin and Desroy, 2005). Les dynamiques saisonnières des communautés sont en partie expliquées par la variabilité des variables physico-chimiques, mais également par les changements dans les interactions trophiques entre les différents compartiments biologiques (Selleslagh *et al.*, 2012).

#### **1.2.3** Dynamiques interannuelles

Enfin, les estuaires et les baies côtières fluctuent à une échelle temporelle plus large. Le débit, variable structurante de ces écosystèmes, peut montrer une variabilité interannuelle forte (Romero *et al.*, 2016) avec des années à fort débit et des années à faible débit. Ces changements de régime hydrologique modifient le gradient de salinité pouvant provoquer des changements importants dans la composition des communautés benthiques (Chang *et al.*, 2018), leurs biomasses et leurs abondances dues aux variations d'apports par le fleuve (Salen-Picard *et al.*, 2002). Ces variations se répercutent sur les réseaux trophiques. Kostecki et al. (2010) montrent que les fluctuations interannuelles du débit de la Vilaine (France) impactent les signatures isotopiques de la matière organique, se propageant jusqu'aux consommateurs secondaires, les juvéniles de sole commune.

#### 1.3 Fonction de nourricerie des estuaires et baies côtières

#### **1.3.1** Définition de la nourricerie

Le rôle et l'utilisation des estuaires et baies côtières pour les espèces de poissons sont étudiés surtout depuis le siècle dernier, et en particulier pour le rôle qu'ils jouent pour les juvéniles des espèces marines. D'après la revue de Kenneth Able (2005), les premières observations consignées dans une revue scientifique de l'utilisation des habitats côtiers par les juvéniles d'espèces marines remontent aux travaux de Gunter (1945) : "the young of many animals usually thought of as marine, require areas of low salinity for nursery grounds". Le cycle de vie de ces espèces est caractérisé par une ségrégation spatiale entre les différentes phases du cycle de vie (Gibson, 1994). Les adultes vivent au large, sur le plateau continental où ils se reproduisent pendant l'hiver. Les œufs puis les larves sont pélagiques et se déplacent passivement avec les courants océaniques et les vents, puis activement vers les baies côtières et les estuaires (Gibson, 2005). Au moment de la métamorphose, ses larves passent d'une vie pélagique à une vie benthique et les juvéniles s'installent alors dans des zones côtières et estuariennes à la fin du printemps ou au début de l'été (Gibson, 2005). Ils se nourrissent et grandissent jusqu'à la fin de la saison de forte croissance (en automne). Ensuite, pendant encore un ou deux ans selon les espèces, les juvéniles passent le printemps et l'été dans les estuaires et les baies côtières peu profondes pendant la saison de forte croissance et rejoignent les eaux plus profondes l'hiver. Enfin, ils rejoignent la population adulte au large.

Les termes 'estuaire-dépendance' et 'nourricerie' ont été largement utilisés sans définition formelle et avec confusion (Beck *et al.*, 2001; Able, 2005). Certains chercheurs considéraient l'ensemble de l'estuaire comme une nourricerie (Able, 2005) quand d'autres faisaient référence seulement à certaines zones spécifiques telles que les marais salants, les mangroves et les herbiers sous-marins (Beck *et al.*, 2001). Le manque d'une définition claire est source de contradictions et désaccords freinant la gestion et la conservation de ces zones. Beck et al. (2001) conceptualisent le terme « *nourricerie* » dans leur revue ; cette définition fait office de référence encore aujourd'hui. Un habitat est une nourricerie pour une espèce donnée si sa contribution par unité de surface à la production d'individus qui rejoignent le stock adulte est supérieure en moyenne à la production des autres habitats que les juvéniles occupent. Ainsi, pour être qualifié de nourricerie, un habitat doit supporter des densités de juvéniles de poissons supérieures aux autres habitats, mais également de meilleurs taux de survie et de croissance, ainsi que de permettre le déplacement vers les habitats adultes.

Ces habitats sont en partie caractérisés par des facteurs abiotiques. Par exemple, les espèces de poissons plats dans les nourriceries du golfe de Gascogne sont préférentiellement situées sur des fonds vaseux peu profonds (< 30 m), et faiblement exposés aux vagues (Le Pape *et al.*, 2007a; Trimoreau *et al.*, 2013). Une quantité suffisante de nourriture pour soutenir la croissance et un faible nombre de prédateurs pour

maintenir le taux de survie sont également essentiels (Gibson, 1994; Beck et al., 2001; Wouters and Cabral, 2009).

# **1.3.2** Evolution du concept de nourricerie et notamment sur des aspects spatiaux et temporels

Bien que faisant office de définition officielle, la définition de Beck et al. (2001) a été affinée, notamment dans une optique de gestion et de conservation. Dahlgren et al. (2006) constatent que, dans certains cas, la définition n'inclut pas certains secteurs essentiels dans le renouvellement de la population de l'espèce étudiée : un secteur avec une contribution totale élevée, mais très grand aura une contribution par mètre carré faible alors qu'il supporte largement la production de recrues. Ainsi, ils introduisent le concept d'Habitat Effectif des Juvéniles *"as a habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage"*. Ce concept est essentiel pour une conservation efficace des zones côtières impliquées dans la production de juvéniles dans un but de maintien ou la restauration des stocks adultes. Dans ce même contexte, Sheaves et al. (2015) soulignent qu'ignorer la complexité de ces habitats, les processus agissants et les effets sur la fonction de nourricerie peut engendrer une mauvaise définition des zones essentielles à protéger. Par exemple, l'accès à des zones riches en nourriture peut être limité par la présence de prédateurs (compromis nourriture/prédateur). Les zones de transition entre zones de refuge et zones d'alimentation peuvent alors représenter des goulots d'étranglement écologiques.

Enfin, Nagelkerken et al. (2015) proposent une définition dynamique et intégrée de nourricerie : une unité marine spatialement explicite consistant en une mosaïque d'habitats connectés fondée sur des processus écologiques dérivant du comportement des espèces. Ils la conceptualisent par le terme '*seascape nursery*'. Cette unité est dynamique dans le temps, via les variations des variables environnementales les définissant ainsi que l'ontogénie des juvéniles de poissons.

#### 1.4 Capacité d'accueil et facteurs de régulation des populations

#### 1.4.1 Mortalité densité-dépendante et capacité d'accueil des nourriceries

Le renouvellement des populations marines est dépendant du recrutement. Le recrutement des espèces nourricerie-dépendantes<sup>3</sup> exploitées comme la sole ou la plie est moins variable que celui des autres espèces marines, par exemple la sardine (Archambault *et al.*, 2014). Or, le recrutement découle des taux de mortalité subie pendant les premières phases de vie qui sont le stade œuf, le stade larvaire et le stade

<sup>&</sup>lt;sup>3</sup> Espèces dont la phase juvénile a lieu sur les nourriceries côtières alors que les phases œufs, larves et adultes sont au large.

juvénile. Pour les espèces nourricerie-dépendantes les premiers stades, œuf et larves, sont caractérisés par un taux de mortalité élevé et ils sont soumis à des processus densité-indépendants liés à la variabilité environnementale et au climat influençant sur les courants ou la température de l'eau (Ohlberger *et al.*, 2014; Archambault *et al.*, 2018). Ces processus densité-indépendants génèrent de la variabilité (interannuelle) dans l'abondance de la cohorte (Fig. 2) et donc sur le nombre de larves arrivant sur les nourriceries côtières (Le Pape and Bonhommeau, 2015; Archambault *et al.*, 2018).

Le stade juvénile est caractérisé par des processus de mortalité densité-dépendante (Nash and Geffen, 2012; Le Pape and Bonhommeau, 2015). Plus le nombre de larves arrivant sur les zones de nourricerie est grand, plus le taux de mortalité est grand, atténuant la variabilité tel un goulot d'étranglement (Fig. 2). Ainsi, le recrutement de ces espèces est déterminé par le stade juvénile (Myers *et al.*, 2001; Ustups *et al.*, 2013). L'hypothèse de concentration décrite par Iles and Beverton (2000) énonce que, pour les populations qui se concentrent sur les zones de nourriceries pendant leur première année, une limitation de la taille de la population peut découler de l'atteinte de la capacité d'accueil de ces habitats.



Figure 2 : Evolution du nombre d'individus (et variabilité) au cours des premières phases du cycle de vie des espèces nourriceries-dépendantes. Pendant les stades œuf et larve, pélagiques, le taux de mortalité est le plus élevé et la variabilité, générée par l'hydrodynamisme principalement est grande. Les larves s'installent sur les nourriceries côtières âgées de quelques mois et adoptent une vie démersale et/ou benthique (métamorphose pour les poissons plats). Ces habitats agissent comme goulot d'étranglement pour la dynamique de ces populations et atténuent la forte mortalité des stades précédents. Le taux de mortalité y est toujours élevé, mais moins que pour les stades larvaires. Adaptée de Le Pape and Bonhommeau (2015) et Nash and Geffen (2012).

La notion de capacité d'accueil est souvent utilisée dans la communauté scientifique, mais reste élusive et controversée, car elle a été utilisée de différentes façons (Dhondt, 1988; del Monte-Luna *et al.*, 2004). Del Monte-Luna et al. (2004) propose la définition suivante : *'the limit of growth or development of each and all hierarchical levels of biological integration, beginning with the population, and shaped by processes and interdependent relationships between finite resources and the consumers of those* 

*resources*'. Ainsi, inhérent à cette notion, on retrouve l'idée d'une population maximale qui peut être supportée par un environnement donné avec des ressources données dans une certaine fenêtre temporelle (del Monte-Luna *et al.*, 2004; Ayllón *et al.*, 2012). Une idée primordiale dans la notion de capacité d'accueil concerne ses variations spatio-temporelles (Ayllón *et al.*, 2012). La quantité et la qualité des ressources utilisées varient dans le temps, les besoins des individus évoluent avec les saisons, la compétition intra et inter spécifique connait également des fluctuations. C'est ce qu'ont démontré Luo et al. (2001) dans la baie de Chesapeake (Etats-Unis) à l'aide d'une approche spatialement et temporellement explicite liant un modèle de qualité de l'eau avec un modèle de bioénergétique.

Un des challenges de l'écologie estuarienne aujourd'hui est la détermination des facteurs influençant la capacité d'accueil (prédation, compétition pour l'espace, parasitisme, nourriture disponible, maladie, variabilité environnementale, etc.), leur importance relative les uns par rapport aux autres et leurs interactions (del Monte-Luna *et al.*, 2004).

Ainsi, de par leur surface restreinte et de la concentration des juvéniles dans ces zones, les habitats côtiers et estuariens jouent un rôle crucial dans la régulation de ces populations (Caddy, 2014) et dans le recrutement de ces espèces (van der Veer *et al.*, 2000) et donc dans le renouvellement des populations (Archambault *et al.*, 2018).

#### 1.4.2 Facteurs de mortalité des populations dans les nourriceries

Les facteurs de régulation densités-dépendants des populations dans les nourriceries induisent une mortalité pour les juvéniles de poissons, directement en affectant la survie ou indirectement en affectant d'abord la croissance et/ou la condition des individus (Martino and Houde, 2012).

Bien que les nourriceries soient souvent décrites comme des zones refuge face à la prédation pour les juvéniles de poissons (Gibson *et al.*, 2002; Able, 2005), il existe une certaine pression de prédation sur les juvéniles par des crevettes à l'arrivée des juvéniles (van der Veer and Bergman, 1987; van der Veer *et al.*, 1991; Geffen *et al.*, 2011), par des poissons adultes faisant intrusion dans les nourriceries côtières (par exemple, la morue, Gibson and Robb, 1996), par des oiseaux marins (par exemple, cormoran, Leopold et al., 1998) ou encore par des mammifères marins (par exemple, phoque commun, Aarts et al., 2019). La pression de prédation sur les juvéniles de poissons est taille-dépendante : plus les poissons grandissent, plus ils sont protégés d'une mort par prédation (Ellis and Gibson, 1995). La mortalité induite directement par la prédation est donc susceptible de se produire à la phase d'installation des juvéniles sur les nourriceries (van der Veer and Bergman, 1987).

Une forte pression de prédation à l'installation des juvéniles n'exclut pas la compétition trophique comme autre facteur de régulation des populations. Les ressources alimentaires sont en quantités finies sur les nourriceries côtières. Quand elles viennent à manquer, cela peut augmenter la compétition trophique intraspécifique et/ou interspécifique (van der Veer *et al.*, 2016). Le manque de nourriture

affecte alors dans un premier temps l'état physiologique des organismes : baisse de la condition traduisant une dégradation de l'état nutritionnel du poisson (Stowell *et al.*, 2019) ou encore une diminution de la croissance (Ciotti *et al.*, 2013b). Bien qu'il soit envisageable que le poisson amenuisé meurt d'inanition, il est probable que cet état conduise à une modification de son comportement l'exposant à un risque de prédation plus important (Sinclair *et al.*, 2006). Sa recherche de nourriture devient alors plus active ou dans des zones moins protégées (Myers *et al.*, 2001; Biro *et al.*, 2003). La limitation trophique induirait donc une hausse de la prédation et ainsi une chute du taux de survie.

La proximité entre individus induite par la concentration des individus sur une surface restreinte favorise la transmission de parasites ou de pathogènes (Durieux *et al.*, 2010). De plus, certains facteurs de régulation de ces populations sont densité-indépendants. Par exemple, la contamination chimique (via contact ou ingestion) peut engendrer une baisse de la croissance des juvéniles (Gilliers *et al.*, 2006). Cependant, ces facteurs de régulation des populations sont encore rarement étudiés dans un contexte d'espèces nourricerie-dépendantes.

L'hypothèse de la limitation trophique est une source de questionnements et de débats de par la difficulté à mesurer et quantifier ce phénomène proprement (Le Pape and Bonhommeau, 2015).

#### 1.5 Capacité vs limitation trophique dans les nourriceries

#### 1.5.1 Capacité trophique

La capacité trophique découle de l'interaction entre les ressources alimentaires disponibles et les consommateurs de ces ressources. En s'appuyant sur la définition de la capacité d'accueil de del Monte-Luna et al. (2004), la capacité trophique est donc le nombre maximal de consommateurs que peuvent supporter les ressources alimentaires d'un écosystème donné. Les consommateurs sont, dans notre cas, les juvéniles de poissons marins présents dans les habitats côtiers et estuariens. L'énergie consommée soutient la maintenance de l'organisme, sa croissance (puis soutiendra la maturation et la reproduction). Cette allocation de l'énergie est bien décrite, par exemple, dans les modèles individus-centrés de budget énergétique, Dynamic Energy Budget ou DEB (Kooijman, 2000), qui formalisent les flux d'énergie entrant, sortant et mis en réserve dans un organisme, en fonction de son environnement et au cours de son cycle de vie (par exemple pour la plie juvénile : van der Veer et al., 2010). Ainsi, l'énergie assimilée est allouée principalement à la croissance pour les juvéniles, une fois que la fonction de maintenance est assurée. Les ressources trophiques soutenant la production d'individus sont majoritairement les invertébrés benthiques constituant l'alimentation des juvéniles de poissons marins. Les régimes alimentaires se situent sur un gradient de strictement benthique à hyperbenthique voire pélagique. La sole commune (Solea solea), la plie (Pleuronectes platessa) ou encore le flet commun (Platichthys flesus) se nourrissent principalement d'invertébrés benthiques tels que des bivalves ou des polychètes (Le Mao, 1986; Amara *et al.*, 2001; Kostecki *et al.*, 2012; Kopp *et al.*, 2013). Le bar commun (*Dicentrarchus labrax*) est un prédateur hyperbenthique consommant majoritairement des invertébrés tels que des mysidacées, des amphipodes ou des crevettes (Laffaille *et al.*, 2001; Pasquaud *et al.*, 2010; Fonseca *et al.*, 2011). Les juvéniles de merlan (*Merlangius merlangus*) et de tacaud commun (*Trisopterus luscus*) sont décrits comme prédateurs de crustacés hyperbenthiques ou pélagiques (Mysidacées, crevettes) ou de petits poissons (Hamerlynck and Hostens, 1993; Morin *et al.*, 1999). Plus généralement, malgré ces différences spécifiques liées à leurs niches écologiques et à leur stratégie de chasse, les juvéniles sont également décrits comme opportunistes, se nourrissant des proies principalement présentes (Besyst *et al.*, 1999; Griffin *et al.*, 2012).

#### **1.5.2** Limitation trophique ?

Théoriquement, l'atteinte de la capacité trophique correspond à la consommation de toutes les ressources trophiques par les consommateurs. Le dépassement de la capacité trophique peut alors se traduire par le phénomène de limitation trophique où les consommateurs sont affectés par le manque de ressources trophiques : diminution de la condition physiologique, diminution de la croissance, mortalité. Comment alors discerner, la mettre en évidence voire tester la limitation trophique ?

#### Densité dépendance

Certaines études, en démontrant la mortalité densité-dépendante des juvéniles de poissons, proposent la limitation trophique comme mécanisme sous-jacent le plus probable de cette mortalité. Par exemple, Craig et al. (2007) ont démontré expérimentalement le caractère densité-dépendant de la mortalité et de la croissance des juvéniles de *Leiostomus xanthurus* (Sciaenidae nourricerie-dépendante de la côte ouest atlantique) et proposent la compétition trophique comme responsable.

La méthode du « self-thinning », d'abord développée en écologie végétale, puis ensuite testée et adaptée aux populations animales (Begon *et al.*, 1986), permet de tester si la capacité d'accueil est atteinte. Simplement, si la capacité d'accueil est atteinte, la mortalité des individus augmente par rapport à un contexte où la densité de juvénile est plus faible et n'atteint pas la capacité d'accueil.

En étudiant l'évolution de la croissance d'une cohorte en fonction de l'évolution de la densité de cette cohorte au cours de la saison de forte croissance où les juvéniles sont sur la nourricerie, la comparaison de la tangente de la pente obtenue avec une valeur théorique établie de -4/3 (Begon *et al.*, 1986) nous permet de diagnostiquer si la mortalité est densité-dépendante (Fig. 3).



Figure 3 : Trajectoires démographiques et de croissance de deux populations (A et B). Entre mai et juin, les individus s'installent sur la nourricerie et y grandissent, la densité et la croissance augmentent. Pendant l'été, ils continuent de grandir, mais leur nombre diminue (mortalité) puis en septembre, la densité chute plus fortement due à un départ de la zone. La population B atteint la capacité d'accueil (pente de la tangente égale à -4.3) alors que la population B ne l'atteint pas. Figure adaptée de (Nash *et al.*, 2007).

Nash et al. (2007) ont appliqué cette méthode aux juvéniles de plies sur deux nourriceries du nord de l'Europe et en concluent que la capacité d'accueil dans ces cas d'étude n'est atteinte qu'occasionnellement. Ils suggèrent que la limitation trophique pourra en être la cause dans certains cas.

#### Croissance et condition physiologique

Certaines approches proposent de tester l'influence de la qualité et de la qualité des proies sur les populations de juvéniles en s'intéressant aux effets sur la croissance et la condition des individus (Amara et al., 2001; van der Veer et al., 2010; Teal et al., 2012; Poiesz et al., 2018; Stowell et al., 2019). L'hypothèse est la suivante : le manque de ressources trophiques induit une baisse de la croissance et/ou de la condition en raison d'une augmentation de la compétition trophique. Cette baisse est caractérisée par la comparaison à une valeur optimale issue d'une relation entre croissance et température (Amara et al., 2001; Amara and Paul, 2003) ou bien issue de la prédiction de la croissance maximale par un modèle DEB (van der Veer et al., 2010; Poiesz et al., 2018) ou encore issue de valeurs métaboliques obtenues en conditions expérimentales sur un gradient de privation alimentaire (Hufnagl et al., 2010). Amara et Paul (2003) montrent que la croissance des plies dans l'estuaire de la Canche est inférieure aux prédictions issues d'un modèle juste après leur installation sur la nourricerie. Ils en concluent à une potentielle limitation trophique, en particulier sur les vasières intertidales où les juvéniles vont se nourrir, mais où ils rencontrent également des compétiteurs pour ces ressources. Une réduction de la croissance au cours de l'été est également régulièrement démontrée (Teal et al., 2008; van der Veer et al., 2010; Freitas et al., 2012; Poiesz et al., 2018). Cependant aucune de ces études n'a encore établi de lien direct entre la croissance ou l'état des poissons et la compétition trophique (Ciotti et al., 2014; van der Veer et al., 2016). De plus, Le Pape and Bonhommeau (2015) démontrent que seule la croissance apparente des individus survivants peut être mesurée, ce qui peut engendrer un biais dans les résultats obtenus.

#### Relation proie/prédateur

Des patrons de synchronies entre proies et prédateurs ou de cohérences spatiales entre proies et prédateurs peuvent indiquer une potentielle limitation trophique. Okamoto et al. (2012) montrent que la production de juvénile par adulte est déterminée par la quantité de nourriture (biomasse de proies). Plus récemment, le long de la côte de la mer du Nord, un changement dans la distribution spatiale des juvéniles de plie, *Pleuronectes platessa* (Støttrup *et al.*, 2017) est mis en relation avec la disponibilité de proies benthiques dont la productivité serait affectée par la diminution observée de l'apport de nutriments. Les études de synchronie entre proies et prédateurs sont robustes, mais souvent rares dans un contexte estuarien, car les suivis temporels de biomasse de proies sont coûteux.

Une congruence spatiale entre les patrons de distribution de proies et des juvéniles dans l'estuaire de la Vilaine en 2008 et la significativité des quantiles supérieurs et inférieurs entre les proies et les juvéniles de poisson viennent appuyer l'hypothèse de limitation trophique (Tableau *et al.*, 2016). Siddon et al. (2013) montrent alors qu'un « mismatch » ou décalage spatial entre la distribution des juvéniles de *Theragra chalcogramma* et la distribution des proies et de la température serait à l'origine d'un mauvais recrutement de l'espèce en 2005. À l'inverse, Yeung and Yang (2017) suggèrent que, pour les juvéniles de *Lepidopsetta polyxystra* et *Limanda aspera*, deux espèces de poissons plats sur la plate-forme côtière de la péninsule de l'Alaska, le mismatch spatial entre les juvéniles et leur proie indique que la disponibilité en proie n'est pas limitante pour ces espèces. Or, des effets densité-dépendants peuvent aussi être à l'origine de changements dans la distribution des individus vers des habitats moins favorables (Thorson *et al.*, 2016). De plus, l'étude des patrons spatiaux indique les lieux où les prédateurs se nourrissent, mais seule ne permet pas de tester la limitation trophique.

Théoriquement, on peut tester si la capacité trophique est atteinte en comparant l'offre et la demande. En d'autres termes, si le ratio de la demande énergétique des juvéniles sur l'offre de proies atteint la valeur théorique de 1, tout ce qui est produit est consommé. Au-delà, elle est dépassée et des phénomènes de limitation trophique peuvent être observés. En pratique, il est très difficile d'estimer ce ratio avec précision, car il est nécessaire d'inclure la liste exhaustive des prédateurs présents et d'obtenir de nombreuses données sur les espèces de proies et de prédateurs présentes dans l'aire d'étude : abondance, biomasse, capturabilité, besoin énergétique individuel, consommation, taux d'excrétion, productivité, etc. (*p. ex.* Bennett and Branch, 1990; Collie, 1987; Vinagre and Cabral, 2008). Ainsi, la comparaison à la valeur théorique de 1 est peu informative.

De nombreuses études concluent à la non-atteinte de la limitation trophique suite à la comparaison des compartiments offre et demande (Evans, 1983; Bennett and Branch, 1990; Vinagre and Cabral, 2008) quand d'autres soutiennent l'hypothèse d'une compétition trophique entre les prédateurs (Pihl, 1985). Une des raisons des faibles valeurs du ratio offre sur demande est la liste réduite des prédateurs inclus dans ces études (*e.g.* Collie (1987) s'intéresse seulement à la consommation de la limande à queue jaune,

*Limanda ferruginea*), car les modèles utilisés sont souvent très gourmands en données expérimentales (Evans, 1983; Collie, 1987; Vinagre and Cabral, 2008).

Face à ce constat, Tableau et al. (2019) ont développé un modèle bioénergétique pour estimer le ratio offre/demande, appelé d'efficacité d'exploitation (EE) de proies par les juvéniles de poisson et ainsi tester l'hypothèse de limitation trophique dans les nourriceries côtières pour les communautés de juvéniles de poissons bentho-démersaux. Ce modèle estime la production de proies et la consommation alimentaire à partir de données issues de campagnes et de paramètres sortis de la littérature. Ce modèle se veut générique et inclut la communauté de juvéniles de poissons marins bentho-démersaux consommant l'offre alimentaire disponible. À l'aide de cette approche, les auteurs ont pu quantifier l'efficacité d'exploitation dans l'estuaire de la Vilaine en 2008. En considérant les espèces strictement benthivores et partiellement benthivores, le ratio atteint ainsi 0.06. Dans l'attente de résultats issus de l'application du modèle à d'autres écosystèmes, Tableau et al. (2019) proposent une grille de lecture basée sur des scénarios pour interpréter les estimations du ratio demande sur offre qui combinent limitation trophique et prédation. Saulnier et al. (2020) appliquent ce modèle à l'estuaire de la Seine sur trois années consécutives et relèvent que, pour les juvéniles de moins d'un an  $(G0^4)$ , le ratio est constant autour de la valeur de 0.02. Cette relative stabilité interannuelle appuie l'hypothèse de limitation trophique. En effet, la stabilité des EE traduit que la consommation des juvéniles G0 suit les variations interannuelles de production de proies sur trois années. Il faudrait évidement confirmer ce patron avec une plus longue série temporelle.

#### 1.6 Capacité trophique : une question d'échelle ?

Le choix de l'échelle d'étude dans les interactions proie-prédateur est essentiel (Bailey *et al.*, 2010; Johnson *et al.*, 2013). Il est déterminant dans les résultats obtenus et dans les processus responsables de ce que l'on regarde (Feiner *et al.*, 2019). La capacité trophique est dynamique dans l'espace et le temps. L'offre alimentaire est hétérogène au sein de la nourricerie (Freitas *et al.*, 2016; Saulnier *et al.*, 2020) et les juvéniles de poissons n'utilisent pas les différents habitats avec la même intensité (James *et al.*, 2019). L'offre évolue également dans le temps avec la saisonnalité de la production benthique et pélagique. La demande varie avec l'augmentation des besoins individuels et les shifts ontogéniques alimentaires (Lawson *et al.*, 2018). Ainsi l'interaction entre proies et consommateurs varie avec la saison, mais également avec la marée qui donne accès aux ressources des zones intertidales.

<sup>&</sup>lt;sup>4</sup> Les juvéniles de poissons de moins d'un an *i.e.* nés dans l'année sont appelés G0. Ceux âgés d'un an seront appelés G1

#### 1.6.1 Variations dans l'espace de l'offre alimentaire et de la consommation

Les ressources trophiques ne se répartissent pas de façon homogène sur les différents habitats d'un estuaire. Le secteur marin de l'estuaire de Seine présente des niveaux de productions de proies macrobenthiques supérieurs aux autres habitats entre 2008 et 2010 (Saulnier et al., 2020). Beukema and Cadée (1997) montrent que, dans la mer de Wadden, le macrobenthos est limité par la quantité de nourriture à leur disposition seulement dans certaines zones. Les juvéniles de poissons exploitent ces ressources selon leur niche écologique et l'énergie déployée pour y accéder. L'« Optimal foraging theory » (MacArthur and Pianka, 1966; Werner and Hall, 1974), énonce que, dans le choix de recherche de nourriture, les organismes optimisent l'énergie nette gagnée (c'est-à-dire maximisent le rapport entre les avantages énergétiques et les coûts), et donc sélectionnent les habitats permettant cette optimisation. Les juvéniles des poissons plats ayant une mobilité restreinte, quelques centaines de mètres attribuées à leur capacité de mouvement et pas plus de 5 km par jour en incluant l'utilisation des courants pour se déplacer (Le Pape and Cognez, 2016), il est envisageable que la limitation trophique soit plus intense dans certains habitats. De plus, dans les estuaires tempérés, les vasières intertidales peuvent supporter des biomasses de proies élevées (Freitas et al., 2016) et sont utilisées par les juvéniles de poissons qui viennent s'y alimenter (Morin et al., 1999; Cabral, 2000; Laffaille et al., 2001).. Ainsi, la question des différences de capacité trophique à une échelle locale *i.e.* celle des habitats, semble pertinente. Walters and Juanes (1993) suggèrent que lors de l'étude de la régulation de la densité aux premiers stades de la vie des poissons, la notion d'utilisation de l'habitat doit être incluse. En outre, dans un contexte de perte d'habitat et de dégradation des côtes (Lotze, 2006), il est particulièrement important d'inclure la notion d'habitat dans l'étude de la fonction de nourricerie.

#### **1.6.2** Variations temporelles

Chevillot et al. (2017) et Pihl (1985) suggèrent que la capacité trophique n'est atteinte qu'à un certain moment de la saison de croissance, les variations saisonnières de l'offre trophique et de la demande des juvéniles engendrant des variations de la pression trophique au cours du temps. Par exemple, à leur première installation sur la nourricerie, les juvéniles sont limités par la taille de leur bouche pour se nourrir et se concentrent donc sur les petites proies. La méiofaune<sup>5</sup> constitue alors la majorité de leur alimentation (Gee, 1989; Coull, 1990). En grandissant, ils augmentent leur spectre de taille de proies et consomment alors de plus grandes proies, principalement issues de la macrofaune<sup>6</sup> (Pihl, 1985; Aarnio *et al.*, 1996).

Deux périodes sensibles ont été identifiées. Au printemps, les densités de juvéniles sont élevées dues à l'arrivée massive des larves (Nash and Geffen, 2012). Parallèlement, les conditions environnementales

<sup>&</sup>lt;sup>5</sup> Ensemble des invertébrés de moins d'1 mm

<sup>&</sup>lt;sup>6</sup> Ensemble des invertébrés de plus d'1 mm

favorisent la production d'invertébrés benthiques (proies des juvéniles). La fin de la saison estivale correspond à la fin de la période de production de proies macrobenthiques et au moment où les besoins énergétiques individuels sont élevés. Ces deux périodes pourraient alors engendrer une limitation trophique localisée dans le temps qu'une approche intégrée sur toute la période de croissance ne pourrait mettre en évidence.

Une meilleure identification de la période la plus sensible à la limitation trophique est une étape essentielle pour le suivi sur le long terme de ce processus de régulation des populations de juvéniles dans les zones côtières. De plus, étudier l'utilisation des habitats côtiers par les juvéniles à différentes échelles permet une compréhension plus fine et complémentaire des processus régissant ces populations (Litvin *et al.*, 2018). Enfin, dans un cadre d'une gestion du littoral, des échelles spatiales et temporelles fines sont plus informatives et en cohérence avec la gestion des activités humaines de ces zones.

#### 1.7 Objectifs et démarche de la thèse

#### 1.7.1 Objectifs

Dans ce contexte, l'objectif général de cette thèse est d'estimer l'efficacité d'exploitation des proies par les juvéniles au sein de nourriceries estuariennes et côtières et d'alimenter la réflexion sur le caractère limitant du facteur trophique dans leur fonctionnement. La démarche a été menée selon deux échelles spatio-temporelles : fine (habitat et période de croissance d'une nourricerie sur une année) et large (plusieurs nourriceries sur plusieurs années).

Ce travail de thèse s'articule autour de trois chapitres (Fig. 4). Le **chapitre 2** s'attache à identifier les habitats essentiels pour l'alimentation de quatre espèces bentho-démersales d'importance commerciale et majoritaires dans la communauté de juvéniles. Usuellement, les habitats essentiels à une espèce sont identifiés à l'aide de données de présence/absence (habitat potentiel) ou d'abondances (habitat réalisé) de l'espèce. L'abondance a l'avantage de donner une photo instantanée de la distribution spatiale de l'espèce. Les traceurs trophiques (contenus stomacaux, isotopes stables) permettent d'identifier les proies consommées par un individu, mais également, les habitats utilisés par un individu pour se nourrir à condition que ces habitats présentent des contrastes sur les traceurs étudiés. Par exemple, en comparant le contenu digestif d'un individu aux communautés issues de deux habitats contrastés, il est possible de déterminer le lieu d'alimentation. Ainsi, l'utilisation conjointe des contenus stomacaux et d'isotopes stables, traceurs complémentaires de l'alimentation en termes de temps d'intégration, permet de quantifier les habitats préférentiels. Ce travail a été effectué à deux périodes encadrant la phase de forte croissance : à la fin du printemps après l'installation des juvéniles sur la nourricerie et au début de l'automne.



Figure 4 : Questions de recherche et démarche de ce travail de thèse.

Le **chapitre 3** (Fig. 4) constitue le cœur de ce travail de thèse. Il s'attache à quantifier l'efficacité d'exploitation des proies benthiques par les juvéniles bentho-démersaux dans une nourricerie à des échelles spatio-temporelles fines, soit à l'échelle de l'habitat et aux deux périodes sensibles préalablement décrites. Pour ce faire, le modèle de capacité trophique (Tableau *et al.*, 2019b) a tout d'abord dû être ajusté à ces échelles, notamment en s'appuyant sur les résultats du premier chapitre en ce qui concerne la spatialisation de la consommation des juvéniles sur les différents habitats. La comparaison des valeurs d'efficacité d'exploitation (ratio en énergies de l'offre et de la demande) des proies par les juvéniles de poissons a ensuite permis de préciser la période et les habitats où la limitation trophique paraissait la plus forte.

Enfin, ce travail de thèse change d'échelle pour une analyse intégrant plusieurs nourriceries et sur plusieurs années et étudier la potentielle occurrence (et récurrence) de la limitation trophique. Le **chapitre 4** (Fig. 4) étudie alors la variabilité de l'offre alimentaire et son caractère limitant cette fois sur les densités de juvéniles de poissons. Pour ce faire, un proxy de la production de proies a été construit à partir des données collectées au chalut en comparaison des données issues d'échantillonnage à la benne quantitative. Le proxy est tout d'abord validé puis appliqué à une série de données d'une quinzaine d'années.

#### 1.7.2 Sites d'étude

Les deux premiers chapitres concernent l'estuaire de la Seine. Il est situé sur la côte nord-ouest française, débouchant dans la Manche (Fig. 5).



Figure 5 : Sites d'étude de de ce travail de thèse.

La Seine est le 4<sup>ième</sup> fleuve en termes de débit en Europe (Romero et al., 2013) avec un débit moyen de 470 m<sup>3</sup> s<sup>-1</sup> (moyenne entre 1970–2014) (Romero et al., 2016). Cet estuaire est représentatif de la situation globale des milieux estuariens-côtiers. Il a notamment subi des transformations morphologiques très importantes au cours du dernier siècle (Delsinne, 2005) : endiguement, industrialisation, chenal de navigation (axe de navigation majeur), etc. Plus récemment, un vaste chantier de rénovation et d'extension du port du Havre (Port 2000) dans les années 2000 au niveau de l'embouchure a encore modifié la morphologie de cet estuaire. Ces profondes modifications ont eu pour conséquences la réduction de l'espace disponible, la réduction des surfaces intertidales, la réduction du volume de l'estuaire, et un envasement significatif de l'estuaire aval. Les vasières intertidales occupaient environ 130 km<sup>2</sup> en 1850 et sont réduites à 30 km<sup>2</sup> au début du 21<sup>ième</sup> siècle (Dauvin et al., 2006). Or, cet estuaire assure la fonction de nourricerie pour des populations de Manche Est, dont la population de sole commune. La perte d'habitat a pour conséquence directe une diminution de plus de 40% de la production de juvéniles de sole pour l'estuaire de Seine depuis 1850 (Rochette et al., 2010). La contribution de cette nourricerie au renouvellement de la population a donc largement diminué. Des scénarios de rénovation de cet estuaire montrent qu'elle pourrait induire une augmentation des captures potentielles pour les populations adjacentes (Archambault et al., 2018).

#### Chapitre 1. Introduction générale



Figure 6 : L'embouchure de l'estuaire de Seine et ses lieux dits. Réalisation : GIP Seine Aval 2015. Source de données : IGN, GPMH, GPMR, SANDRE.

Les communautés benthiques sont conditionnées par le gradient de salinité estuarien ainsi que les infrastructures morphologiques (Fig. 6). On y retrouve alors une communauté dans les sables de la partie marine de l'embouchure dominée par *Abra alba* et *Lagis koreni*. La communauté estuarienne vaseuse de l'embouchure est dominée par *Limecola balthica* (Thiébaut *et al.*, 1997; Morin *et al.*, 1999). La vasière intertidale nord est caractérisée par la communauté à *Hediste diversicolor* et *Corophium volutator* (Baffreau *et al.*, 2017). Ces communautés offrent des niveaux de production de proies potentielles pour les juvéniles y résidant très variables (Saulnier *et al.*, 2020).

Le troisième chapitre concerne les nourriceries côtières de Vilaine, de Loire, Gironde et des pertuis charentais situées dans le golfe de Gascogne (Fig. 5). Ces écosystèmes côtiers ont été identifiés comme étant des nourricerie d'importance pour les juvéniles de populations marines du golfe de Gascogne (Le Pape *et al.*, 2003a; Trimoreau *et al.*, 2013).

#### 1.7.3 Cadre méthodologique

Comme évoqué dans la section de la démarche de ce travail de thèse, le modèle de capacité trophique développé par Tableau et al. (2019) a été choisi et adapté aux échelles de travail des deux premiers chapitres. Ce modèle estime l'efficacité d'exploitation (EE) de la production de proies par les juvéniles. Pour ce faire, un premier module estime la Production de proie (FP pour Food Production) qui est calculée à partir des biomasses des proies échantillonnées et de leur ratio spécifique P/B issu du modèle empirique de Brey (2012). La FP est ensuite convertie en énergie grâce à des coefficients de densité énergétique (Brey *et al.*, 2010). La FP est estimée à l'échelle de l'habitat. Le premier défi méthodologique pour ce travail de thèse est d'adapter cette estimation à une échelle saisonnière, le ratio P/B étant un ratio de productivité annuelle. Un second module estime la consommation des juvéniles de poissons (FC pour Food Consumption). La FC est estimée à partir de la production des prédateurs,

résultant majoritairement de la croissance pour les juvéniles immatures. La production est convertie en consommation par un facteur d'efficacité de conversion brut issu de la littérature (Tableau *et al.*, 2019b). Un dernier facteur s'ajoute pour prendre en compte la part de proies intégrées dans la FP dans le régime alimentaire de chaque cohorte (de chaque espèce). Le second défi méthodologique de ce travail de thèse a été de spatialiser la FC à l'aide de traceurs trophiques (contenus digestifs, isotopes stables du C et N), ainsi que son estimation à une échelle saisonnière. Enfin, pour pouvoir disposer de données de l'offre alimentaire sur le long terme et tester l'occurrence de la limitation trophique, le troisième défi a été de construire un indice de la production benthique de proies à partir de données récoltées au chalut lors du suivi annuel des abondances de juvéniles dans les nourriceries du golfe de Gascogne.

Enfin, l'hypothèse de limitation trophique est testée de deux manières : (1) via les estimations des EE par habitat et par période et la comparaison relative intersaison et inter-habitats et (2) à l'aide de régressions quantiles testant l'effet limitant de la production de proies benthiques sur les densités de juvéniles de poisson.

### Chapitre 2.

Contribution des habitats au sein d'une nourricerie côtière à l'alimentation des juvéniles de poissons à deux périodes : printemps et automne



Illustration : L. Fleury
Les estuaires sont composés d'une mosaïque d'habitats hétérogènes (Nagelkerken *et al.*, 2015) structurés par des variables abiotiques (salinité, température, profondeur, couverture sédimentaire, etc.) déterminant les communautés benthiques et les espèces capables de s'y installer et s'y développer. La concentration d'activités et de pressions anthropiques (Lotze, 2006) dans certains estuaires pousse à la compréhension la plus exhaustive possible du fonctionnement écologique des habitats et de leur degré de connexion pour assurer la protection ou la restauration des habitats essentiels aux fonctions écologiques, dont la fonction de nourricerie. Un habitat participe à la fonction de nourricerie s'il offre des ressources soutenant la croissance et la survie des juvéniles (Beck *et al.*, 2001; Wouters and Cabral, 2009). Dans une approche concentrée sur le rôle de l'offre alimentaire dans les nourriceries, un habitat essentiel est un habitat attractif pour les juvéniles de poissons par l'offre de proies disponibles (diversité d'espèces, productivité). Ainsi, tous les habitats ne participent pas avec la même intensité à la capacité trophique de la nourricerie.

Le premier chapitre de cette thèse s'intéresse alors au fonctionnement trophique au sein de la nourricerie, et plus particulièrement à l'importance relative de chaque habitat dans l'alimentation des juvéniles de 4 espèces de poisson. L'objectif est double : (1) examiner les stratégies d'alimentation de ces 4 espèces au regard de leurs niches écologiques et traits biologiques et (2) identifier les habitats essentiels d'un point de vue trophique pour les juvéniles de 4 espèces en estimant la contribution des différents secteurs à leur régime alimentaire et ainsi appréhender comment l'environnement (caractérisé par la diversité taxonomique ou isotopique des proies) se reflète dans l'alimentation des juvéniles de poissons, via leurs contenus stomacaux, ou leurs signatures isotopiques. L'analyse des contenus stomacaux permet une analyse précise de l'alimentation avec une identification taxonomique et un dénombrement des proies consommées sur une fenêtre temporelle courte (les dernières heures). L'approche isotopique se base sur l'intégration de la composition des proies dans les tissus du prédateur. Elle informe donc sur l'alimentation moyenne sur une période plus longue, en lien avec le temps de renouvellement cellulaire des tissus du prédateur. Elle a beaucoup été utilisée dans les estuaires pour discriminer les sources de matière organique entrant dans les réseaux trophiques, les ratios isotopiques du carbone ( $\delta^{13}$ C) signant pour les différentes sources (Le Pape *et al.*, 2013; Liénart *et al.*, 2017).

L'estimation du recouvrement des niches trophiques entre habitats à partir des deux traceurs trophiques nous permet d'appréhender les stratégies d'utilisation de l'espace estuarien par les 4 espèces. Un faible recouvrement inter-habitat indique une ségrégation alimentaire entre les individus des différents habitats alors qu'une fort recouvrement indique une utilisation similaire des ressources par les individus des différents habitats. Ensuite, nous avons d'une part comparé la diversité taxonomique des habitats avec celle des contenus digestifs et, d'autre part, utilisé des modèles de mélange isotopique pour estimer la contribution de chacun des habitats à l'alimentation des juvéniles. Le modèle de mélange permet usuellement de quantifier les proportions relatives de proies dans l'alimentation d'un prédateur. Dans ce chapitre, les habitats, caractérisés par la signature isotopique des invertébrés y résidant, sont utilisés comme sources des modèles de mélange pour quantifier leur contribution à l'alimentation des juvéniles. Ces différentes approches nécessitent de s'assurer que la communauté des proies potentielles montre des contrastes taxonomique et isotopique entre habitats, ce qui constitue la première étape de ce chapitre. Enfin, un objectif complémentaire de ce chapitre est l'obtention de coefficients qui permettront de spatialiser la consommation des juvéniles sur les habitats dans le modèle de capacité trophique, et de s'affranchir de l'hypothèse initiale selon laquelle les poissons consomment exclusivement dans les habitats où ils sont capturés. Contribution of estuarine and coastal habitats within nursery to the diets of juvenile fish in spring and autumn

# Authors

Louise Day<sup>a,b</sup>, Anik Brind'Amour<sup>a</sup>, Pierre Cresson<sup>c</sup>, Bastien Chouquet<sup>d</sup>, Hervé Le Bris<sup>b</sup>

<sup>a</sup>IFREMER, EMH, Rue de l'île d'Yeu, B.P. 21105, 44311 Nantes, France

<sup>b</sup>ESE, Ecology and Ecosystems Health, Institut Agro, INRAE, 35042 Rennes, France

<sup>c</sup>IFREMER Laboratoire Ressources Halieutiques Manche Mer du Nord, 62200, Boulogne sur Mer, France

<sup>d</sup>Cellule de Suivi du Littoral Normand (CSLN), 76600 Le Havre, France

Published in Estuaries and Coasts (2020)

# 2.1 Abstract

Coastal and estuarine nurseries are composed of habitats with different biotic and abiotic features. Quantifying the contribution of different habitats within nurseries to juvenile fish feeding would help identify those that are essential in the completion of their life cycle, by providing food resources that maximise growth and survival. Essential habitats for four bentho-demersal fish species (whiting, sea bass, plaice and common sole) in an estuarine nursery were identified using gut contents and stable isotopes. Habitats differed in isotopic ratios and benthic communities. The estuarine gradient defined the macrofauna communities and sources of organic matter used by primary consumers. Trophic niche overlaps and trophic contribution of habitats highlighted that the species used both intertidal and subtidal habitats as feeding grounds. Flatfish were local feeders and fed on prey available mainly in the habitat in which they were caught, suggesting feeding behaviour that required little energy for movement. Sea bass were concentrated in upstream habitats, with intertidal mudflats contributing for nearly half of its diet. Whiting had a ubiquitous feeding strategy, suggesting that it may target prey with the most energetic gain in the habitats. Hence, habitats were used simultaneously during the same season or asynchronously throughout the year by the juvenile fish studied, suggesting no preference for a specific habitat at the community scale. Finally, both trophic tracers demonstrated the trophic importance of intertidal mudflats, especially for the sea bass and common sole, with contributions up to the half and two-third of their diet respectively.

Keywords: trophic tracers, isotopic ratios, gut contents, Seine estuary, young-of-the-year



# **Graphical abstract**

# 2.2 Introduction

Coastal and estuarine areas act as nurseries for several marine species. The nursery concept has evolved throughout time, gaining accuracy in both spatial and temporal aspects of species utilization (Heck *et al.*, 1997; Beck *et al.*, 2001; Able, 2005; Nagelkerken *et al.*, 2015; Sheaves *et al.*, 2015). Beck et al. (2001) formalised the concept and suggested quantitative ways of identifying nursery habitats for juvenile fish. According to these authors, a nursery is an area that has higher fish density, growth rates and survival rates than those in other coastal and estuarine areas. It is also physically connected to adult habitats and thus a major contributor to recruitment of adult stock. Following that definition, nurseries can be identified at different nested spatial scales: between areas at very broad geographic scale (100 to 1000 km, Le Pape et al. 2003; Morat et al. 2014) and within a single zone like an estuary (Vinagre *et al.*, 2009a; De Raedemaecker *et al.*, 2012). In either cases, the ultimate contribution of nursery habitats to adult stock is determined by their ability to provide suitable conditions for juveniles (Morat *et al.*, 2014): sufficient resources (food, temperature and low predation) to maximise growth and survival at the juvenile stage (Gibson, 1994; Beck *et al.*, 2009), which may influence juvenile fish populations and, ultimately, recruitment (Johnson *et al.*, 1998; Courrat *et al.*, 2009).

At a nursery scale (*e.g.* within an estuary or coastal bay), not all habitats provide the same amounts of resources for juvenile fish (Freitas *et al.*, 2016; Saulnier *et al.*, 2020). Nagelkerken et al. (2015) refined the nursery concept by integrating landscape mosaics and temporal dynamics, considering the spatial and temporal variability, respectively. Juvenile fish may use connected habitats within the nursery (Baltz *et al.*, 1993; Dance and Rooker, 2015; Perry *et al.*, 2018; James *et al.*, 2019). For instance, the sparid fish *Rhabdosargus halubi* uses a variety of habitats (*i.e.* seagrass, sand and mudflats) to meet its dietary needs while in the nursery (James *et al.*, 2019). Habitat uses within nurseries can also vary interannually (Le Pape *et al.*, 2003b) or seasonally (van der Veer *et al.*, 2001; França *et al.*, 2009; Primo *et al.*, 2013). In the Wadden Sea, newly settled *Pleuronectes platessa* (Linnaeus 1758) use the intertidal habitat for one month before moving into deeper habitats (van der Veer *et al.*, 2001).

At the community scale, different fish species may occupy different habitats within a nursery, given their morphological, physiological, behavioural or ecological differences. According to the optimal foraging theory (MacArthur and Pianka, 1966; Werner and Hall, 1974), organisms select habitats while searching for food to optimize the net energy gained (*i.e.* maximise the ratio energy benefit over costs). Hence, regarding energy requirements, species may forage to different extents in certain areas and have different abilities to catch specific prey, as fish morphology influences swimming abilities and prey catchability directly (Ohlberger *et al.*, 2006). Understanding spatio-temporal patterns and processes in nursery habitats used by juvenile fish in coastal ecosystems is fundamental to ecology (Perry *et al.*,

2018) and supports spatial planning and management of coastal areas. Ignoring the complexity of these areas composed by multiple habitats can lead to a misidentification of the critical areas to be urgently protected (Sheaves *et al.*, 2015).

To identify nursery habitats within coastal and estuarine areas, studies commonly sample juvenile fish in different locations to determine their spatial distribution. They associate a species' distribution with the factors that influence it, relying on the assumption that high fish densities reveal essential nursery habitats (Baltz *et al.*, 1993; Allen and Baltz, 1997; De Raedemaecker *et al.*, 2012). This assumption can be verified for species with low swimming capabilities. For instance, Solea solea (Linnaeus 1758) was found to concentrate in specific part of the Tagus estuary (Portugal) and spatial distribution of fish densities in such case help in identifying essential habitats (Vinagre *et al.*, 2009a). Many studies combine distribution and environmental data to develop habitat models at fine spatial scales (Maes *et al.*, 2004). This last option is informative but data-intensive, as it often describes an integrated view (*i.e.* including several years of data) of fish spatial distribution. Moreover, estuaries often contain different types of habitats (*e.g.* subtidal/intertidal, vegetated/unvegetated/soft/rocky) that may require different gears to sample, which makes comparing them challenging (Beck *et al.*, 2001).

We hypothesised that juvenile fish select feeding habitats that maximise their survival and growth. Therefore, if we quantify the contribution of nursery habitats to feeding, we will identify those that benefit juveniles most and, consequently, contribute to their recruitment in fisheries. Fish feeding habitats are commonly identified using trophic tracers such as stable isotopes (Vinagre et al., 2011a; Green et al., 2012; McCauley et al., 2012; Carlisle et al., 2015), gut contents (Kuipers, 1973; Wirjoatmodjo and Pitcher, 1984; James et al., 2019) or natural tags such as parasites (Durieux et al., 2010), as long as habitats differ sufficiently (e.g. isotopically or taxonomically; Litvin et al. 2014; McCauley et al. 2012). Trophic markers trace the contribution of habitats to fish feeding within a nursery, even of habitats that cannot be sampled using the same gear (Beck et al., 2001). For instance, in temperate estuaries, several studies used trophic tracers to highlight the trophic contribution of intertidal mudflats to fish nurseries (Kostecki et al. 2012; Le Pape et al. 2013), while fish were sampled only in the subtidal part of the areas studied. These studies used stable isotopic ratios to assess the contribution of microphytobenthos (MPB) in the diet of S. solea, with the underlying hypothesis that MPB sign for intertidal mudflats. Likewise, this method is used in other ecosystems (e.g. coastal temperate lagoon) to trace the fate of continental particulate organic matter (POM) in juvenile fish food web (Escalas et al., 2015). The common element of the aforementioned studies is that they are based on isotopic ratios measured for primary producers or organic matter pools to trace juvenile fish diet. However, isotope signatures of primary producers can be very variable (Cabana and Rasmussen, 1996). In addition, primary production is not entirely integrated in food webs and most of the primary production channels towards detrital pathway. Quantifying the contribution of a specific habitat to juvenile fish diet using such unstable sources is often challenging. On the contrary, using consumers is

largely advocated in marine systems (*e.g.* Jennings and van der Molen 2015). In here, we decided to use the primary consumers in each habitat in order to quantify their relative contribution of habitats to juvenile fish diets within the nursery. Most commonly, coupling trophic tracers is recognised powerful to elucidate trophic relationships in marine systems, as gut content and stable isotopes reflect diet over different periods of time (Pethybridge *et al.*, 2018). Gut contents reflect the recent diet, while stable isotopes provide integrated information about the diet over the previous few weeks (Herzka, 2005). Combining both types of information may help identify feeding habitats and detect recent movements of juvenile fish. Differences between gut contents and stable isotope analyses may indicate recent changes in habitat use, whereas similar patterns from both approaches may suggest that individuals consistently feed in the same habitat (Herzka, 2005; Dale *et al.*, 2011).

In this study, we identified essential feeding habitats for four bentho-demersal fish species of commercial importance (whiting, *Merlangius merlangus* (Linnaeus 1758), sea bass, *Dicentrarchus labrax* (Linnaeus 1758), plaice, *P. platessa* and common sole, *S. solea*) in a coastal-estuarine nursery using gut contents and stable isotopes approaches. We notably verified whether juvenile fish fed ubiquitously in all habitats in the nursery or had feeding preferences for specific habitats. The four species had contrasting swimming abilities (flatfish *vs.* roundfish), feeding behaviours and ecological preferences. Using both approaches, we (*i*) compared the trophic niches for each species in the habitat in which it was collected to those from the other habitats, (*ii*) estimated the contribution of each habitat to the diet of juveniles of each species and (*iii*) identified preferential feeding habitats based on the largest dietary contributions. Before conducting these analyses, we verified that the benthic habitats had contrasting environmental conditions, isotopic ratios and macrofaunal compositions. We ultimately discuss the ecological and energy requirements of the four juvenile fish species in light of optimal foraging theory and consolidate the knowledge on feeding behaviour of the different juveniles studied.

# 2.3 Material and methods

# 2.3.1 Sampling site

The Seine is a major river in south-western Europe with the fourth largest river flow (Romero *et al.*, 2013): mean river flow of 470 m<sup>3</sup> s<sup>-1</sup> (from 1970 to 2014) and high inter- and intra-annual variations (Romero *et al.*, 2016). The Seine estuary is located on the northwest coast of France and opens into the English Channel (Fig. 1). It has experienced major morphological alterations over the past century to facilitate navigation and commercial activities. The changes in estuary morphology have resulted in a decrease in intertidal areas, from ~130 km<sup>2</sup> in 1850 to 30 km<sup>2</sup> at the beginning of the 21<sup>st</sup> century (Dauvin *et al.*, 2006). These changes in morphology, along with a drastic reduction in the area of certain habitats,

altered the nursery function of this estuary, as well as its support of adult fish populations (Le Pape *et al.*, 2007b; Rochette *et al.*, 2010).



Figure 1: Locations of the sampling stations (star: grab station and line: trawl station) in the four subtidal habitats (grab and trawl; EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel) and the intertidal habitat (grab only; IM: intertidal mudflats).

In this study, the Seine nursery, composed of lower estuary and outer mouth (eastern bay of Seine) of the river, was divided into five sectors (hereafter, 'habitats'): four subtidal habitats (Fig. 1), adapted from Tecchio et al. (2015), and an intertidal habitat. The estuary mouth is the largest marine habitat (115 km<sup>2</sup>). The navigation channel (17 km<sup>2</sup>) is regularly dredged to allow access to Rouen harbour and has strong currents from the river. It is surrounded by the southern channel (33 km<sup>2</sup>) and northern channel (16 km<sup>2</sup>). The northern channel is contiguous with Le Havre harbour and intertidal mudflats (5 km<sup>2</sup>), which are located upstream, on the north coast. Subtidal benthic communities of the study site are often described as two major communities: a fine sand *Abra alba-Lagis koreni* community in the marine portion of the bay (~estuary mouth) and a muddy *Limecola balthica* community in the poly/mesohaline area (~southern channel, northern channel) (Thiébaut *et al.*, 1997; Morin *et al.*, 1999). The intertidal mudflats (Baffreau *et al.*, 2017).

#### 2.3.2 Data collection

In 2017, sampling surveys targeting benthic invertebrates communities in the five habitats were conducted in spring (between 18 May and 25 May) and autumn (between 19 September and 12 October). Surveys targeting fish associated with the four subtidal habitats were also conducted in spring (between 10 June and 17 June) and autumn (between 10 October and 14 October).

## Macrofauna, meiofauna and suprabenthos sampling

Benthic macrofauna (> 1 mm) and meiofauna (< 1 mm) were sampled at 25 stations in the Seine nursery (5 stations per habitat). Sampling was conducted using a 0.1 m<sup>2</sup> Van Veen grab with 5 replicates at each station. Three replicates were used to estimate density and biomass of macrofauna and meiofauna, and the two others were kept for isotope analysis. These two replicates were kept frozen until identification in the laboratory. A core sample (3.6 cm in diameter, 8 cm high) was extracted from each replicate and placed in a 4% formaldehyde solution for meiofauna biomass estimation. The first three replicates were sieved through a 1 mm grid mesh and kept in a 4% formaldehyde solution diluted in marine water. In the laboratory, macrofaunal organisms were sorted from residual sediments, identified to the lowest taxonomic level, counted and weighed. Biomass per taxa was determined as ash-free dry weight. Data from the three replicates from each sampling station were summed, and abundance and biomass were standardised based on the area sampled (*i.e.* three replicates of 0.1 m<sup>2</sup> expressed per squared meter). Meiofauna samples were sieved (38  $\mu$ m grid mesh), and biomass was estimated for each station.

The suprabenthos was also sampled twice in 2017 (May/June and September) at one station (three replicates) per habitat, using a suprabenthic sledge, which consisted of a single  $0.18 \text{ m}^2$  box ( $0.6 \times 0.3 \text{ m}$ ) designed to filter the water 0.10-0.40 m above the sea bed. The box was equipped with a WP2 suprabenthos net with a 0.5 mm mesh. Sampling was conducted at a mean speed of ~1.5 knots for 5 min. Organisms were washed and frozen on board. In the laboratory, samples were identified to the genus level and counted. Counts were expressed per cubic meter of water sampled.

## **Fish sampling**

Fish were sampled in the four subtidal habitats using a 2 m wide and 0.3 m high beam trawl with a 5 mm mesh stretched in the cod end. Hauls were performed at a mean speed of 2.5 knots in the opposite direction of the tide for 10 min during daylight hours. The number of hauls in each habitat was proportional to its area. A multi-parameter probe was used to measure bottom salinity and temperature before each haul. Fish were identified, counted, weighed and measured by species on board at each station. They were selected for further isotope and gut content analyses. The selected individuals were kept in a cooler and then frozen upon arrival at the laboratory. Additionally, intertidal mudflats were sampled in both seasons using fyke and trammel nets, to collect *D. labrax* juveniles.

# Fish species and young-of-the-year selection

We selected four marine nursery-dependent species, including two flatfish species – *S. solea* (common sole) and *P. platessa* (plaice) – and two roundfish species – *M. merlangus* (whiting) and *D. labrax* (sea bass). On average, these four species represented 65 and 56% of the total catch of bentho-demersal fish by weight in spring and autumn, respectively. Young-of-the-year fish (YOY) were selected visually using size spectra (Fig. S1). Size thresholds used to identify YOY (first mode of the size spectra) were

defined by season and species. When necessary, unpublished fish data from monthly survey of the same area were used (Fig. S1).

The four species selected are known to feed on a variety of prey, including benthic meiofauna, macrofauna and small fish species. YOY *S. solea* and *P. platessa* feed mainly on benthic invertebrates such as bivalves and polychaetes but also for small sizes on copepod harpacticoides (Amara *et al.*, 2001; Kostecki *et al.*, 2012; Kopp *et al.*, 2013). YOY *M. merlangus* feed on crustaceans and small fish (Bromley, 1997; Demain *et al.*, 2011b; Day *et al.*, 2019), along with a small proportion of benthic invertebrates (Morin *et al.*, 1999; Demain *et al.*, 2011b). YOY *D. labrax* is a suprabenthos feeder that preys on copepods, mysids and crustaceans (Laffaille *et al.*, 2001).

# 2.3.3 Gut content analysis

After thawing fish in the laboratory, their guts (stomach and intestine) were extracted and then fixed and stored in a 4% formaldehyde solution diluted in marine water until analysis. For analysis, the guts were rinsed with water and then emptied into water in a Petri dish. Contents were analysed under a stereomicroscope and/or an optic microscope, depending on the size of the prey item observed. Prey items were identified to the lowest taxonomic level possible and then counted. Prey occurrence and abundance, the most robust variables (Baker *et al.*, 2014), were recorded. The sampling design for gut contents is detailed in Table S1. The percentage of prey identified to the species or genus level varied among species: 26 and 17% for *M. merlangus*, 30 and 24% for *D. labrax*, 41 and 36% for *S. solea* and 60 and 70% for *P. platessa* in spring and autumn, respectively.

# 2.3.4 Stable isotope analysis

In the laboratory, a sample of white dorsal muscle (~1 mg) was dissected from the individuals already dissected for their gut contents. The sampling design for stable isotope analysis of YOY fish is detailed in Table S2. Although *S. solea* was collected in the estuary mouth in spring, no isotopic samples were collected. For benthic invertebrates, when individuals were large enough, they were dissected to collect the most suitable tissue (*e.g.* mantle of bivalves) or to remove tissue that can bias isotope analysis (*e.g.* crustacean cuticle or stomach). When individuals were too small for individual analysis or dissection, several individuals were pooled to reach the amount of matter required for analyses. All samples were then frozen (-80°C for 24 h and then stored at -30°C) before being freeze-dried (at least 24 h) and ground into a homogeneous powder. Samples that resulted from pooling and/or that contained carbonates were acidified, by subsequent addition of 1% HCl in excess, then rinsed with MiliQ water and freeze-dried again.

Nitrogen and carbon isotopic ratios were determined using a Thermo Fisher Scientific Delta V Plus mass spectrometer, coupled to a Flash 2000 elemental analyser with a Conflow IV interface. Stable isotope

values were expressed in  $\delta$  notation, which was calculated using the following equation:  $\delta X = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000 (in \%_0)$ , where X is <sup>13</sup>C or <sup>15</sup>N, and R<sub>sample</sub> and R<sub>standard</sub> are the <sup>13</sup>C:<sup>12</sup>C or <sup>15</sup>N:<sup>14</sup>N ratio of the sample and the international standard, respectively (Vienna-Pee Dee Belemnite for  $\delta^{13}$ C and atmospheric nitrogen for  $\delta^{15}$ N). Accuracy of the analyses was verified by repeated measurements of internal acetanilide standards. The measurement error was less than 0.2‰ for both elements. Carbon and nitrogen contents were measured in all samples using the elemental analyser to calculate C:N ratios, which are usually considered a proxy of lipid content. Following the classic approach,  $\delta^{13}$ C values measured in samples with C:N ratios greater than 3.5 were normalised according to the following equation (Post *et al.*, 2007):  $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$ .

# 2.3.5 Data analysis

# Differences in benthic communities among habitats

To determine whether benthic macrofauna composition (as potential juvenile prey) varied among the habitats in the Seine estuary, we used an unconstrained ordination method – non-metric multidimensional scaling (nMDS; Kruskal, 1964) – using the R package 'vegan' (Oksanen *et al.*, 2019). Abundance data were square-root transformed, and the Bray–Curtis dissimilarity index was calculated to create a resemblance matrix. Stations whose benthic macrofauna compositions were the most similar lay closest to each other on the nMDS plane (Oksanen *et al.*, 2019). Two-dimensional representations were considered valid below a stress threshold of 0.3. We also calculated the mean density and biomass per habitat of the macrofauna community, the mean density per habitat of the suprabenthos community and the mean biomass per habitat of the meiofauna community. The genus richness per habitat was estimated from the macrofauna and suprabenthos communities. We also verified graphically that the isotopic ratios of sessile or low-mobility primary consumers varied among habitats, which is an essential prerequisite for stable isotope mixing models.

#### Juvenile fish use of the habitats

To assess whether YOY fish collected from different habitats fed on the same mixture of prey, we estimated the trophic niche of each fish species in each habitat and then the overlap among them using both isotopic and gut content results.

# Isotopic approach:

Isotopic niches were estimated using the corrected Standard Ellipse Area (SEAc), *i.e.* the ellipse that contains ~40% of the data in the isotopic  $\delta^{13}$ C- $\delta^{15}$ N plane (Jackson *et al.*, 2011). The isotopic niche overlap between two habitats (A and B) was estimated by the mean overlap between their SEAc, according to the following equation:

# $Isotopic \ overlap = mean(\frac{overlap(A,B)}{total \ area \ A}, \frac{overlap(A,B)}{total \ area \ B}),$

Overlaps were estimated using the 'maxLikOverlap' function of the R package 'SIBER' (Jackson *et al.*, 2011), which uses the estimated means and covariance matrices (from Maximum Likelihood optimisation) of two habitats to calculate the area of overlap between them. Then, for each species and each season, a specific overlap index was calculated as the mean of all of the inter-habitat overlaps. A higher specific overlap index indicated greater similarity among isotopic niches of the habitats and suggested that the species probably fed on the same mixture (*i.e.* same isotopic ratios) regardless of the habitat in which it was collected (*i.e.* ubiquitous feeder).

# Gut content approach:

Overlaps among trophic niches were estimated from gut contents of YOY fish using the Schoener index (Schoener, 1970):

Schoener Index = 
$$1 - 0.5(\sum_{i=1}^{n} |p_{i,A} - p_{i,B}|)$$

where  $p_{i,A}$  and  $p_{i,B}$  are relative abundances of prey item *i* for the same fish species collected in habitats *A* and *B*, respectively. The index ranges from 0 (no niche overlap) to 1 (full niche overlap). A mean specific diet overlap of the habitats was also calculated, as it was done for overlaps calculated for isotopic niches.

# Contribution of the habitats to YOY diets

Stable isotopes and gut contents were used to quantify the relative contributions of the habitats to juvenile fish.

# Isotopic approach:

Stable isotope mixing models estimate the posterior distribution of the relative contributions of sources (often prey) in a consumer's (predator's) diet from the isotopic ratio of the prey and the predator (Parnell *et al.*, 2013). MixSIAR stable isotope mixing models (Stock *et al.*, 2018) were run to estimate the relative contribution of each habitat to YOY fish diets. For each habitat, we calculated an isotopic ratio representative of benthic primary consumers, mostly deposit-feeder and filter-feeder guilds (*i.e.* potential prey for YOY fish), considering invertebrate species in each habitat and those composed the fish diet. The navigation channel was not considered a feeding habitat, as its prey abundance and biomass were low, regular dredging causing defaunation (Lu and Wu, 2000). Representative isotopic values of habitats were used as source inputs in the isotopic mixing model. Isotopic contrast among sources is an important prerequisite for stable isotope mixing models. It was verified graphically in the  $\delta^{13}C-\delta^{15}N$  space (Phillips *et al.*, 2014).

Trophic discrimination factors (TDF) - the isotopic difference between a consumer and its diet - are key parameters for quantifying diet using stable isotope mixing models (Bond and Diamond, 2011; Barton et al., 2019) as they indicate that consumers do not assimilate isotopes in the same proportions as the proportions of the sources. Consumers generally have a higher ratio of heavy isotopes to light isotopes (DeNiro and Epstein, 1978; Phillips et al., 2014). To the best of our knowledge, TDF for carbon and nitrogen have never been determined experimentally for the four species studied. Hence, we used values that are commonly used for marine organisms (Vander Zanden and Rasmussen, 2001): 3‰ for  $\delta^{15}$ N and 1‰ for  $\delta^{13}$ C between two successive trophic levels. To test the sensitivity of our results to these parameters, we used six combinations of different values instead of one value for each element. For YOY S. solea, P. platessa and M. merlangus, we used one trophic level TDF, as macrobenthic primary consumers (i.e. sources of mixing models) can be considered the principal prey (Amara et al., 2001; Demain *et al.*, 2011b):  $2.5 \pm 1\%$ ,  $3.0 \pm 1\%$  and  $3.5 \pm 1\%$  for  $\delta^{15}$ N and  $0.5 \pm 0.5\%$  and  $1.0 \pm 0.5\%$  for  $\delta^{13}$ C. For YOY *D. labrax*, we used TDF values that represented one to two trophic levels, as *D. labrax* consume prey located one (small fish and crustaceans) or two (primary consumers) trophic levels below:  $4.5 \pm 1\%$ ,  $5.0 \pm 1\%$  and  $5.5 \pm 1\%$  for  $\delta^{15}$ N and  $1.0 \pm 0.5\%$  and  $1.5 \pm 0.5\%$  for  $\delta^{13}$ C. Mean contributions and their standard deviations were calculated from the medians estimated using all combinations of  $\delta^{15}$ N TDF and  $\delta^{13}$ C TDF (*i.e.* six per trophic level).

Before running MixSIAR, potential sources (with TDF added) and consumers were plotted in the  $\delta^{13}$ C– $\delta^{15}$ N space to verify that consumers' values were surrounded by those of sources (an assumption of the model) for each combination of TDF. The model could not be run if this assumption were not met.

#### Gut content approach:

Gut contents and the environment were compared based on the percentage of prey items (mainly macrofauna and suprabenthos) in the mean gut content of a given species from a given habitat and in a given season that could potentially occur in each habitat:

$$SI = \frac{n_{A \subset B}}{n_A}$$

where  $n_{A \subset B}$  ('A is a subset of B') is the number of prey items for a fish species in habitat A whose taxa match those found in the list of local benthic invertebrates (*i.e.* macrofauna and suprabenthos) in habitat B, and  $n_A$  is the number of prey items in the mean gut content. Only taxa identified to genus or species were used; those identified only to order or class were removed.

All analyses were performed using R software (R Core Team, 2019).

# 2.4 Results

# 2.4.1 Differences in benthic communities among habitats

The estuary mouth had high macrofauna biomass and density in spring and autumn, and high genus richness in autumn (Table 1). The meiofauna biomass in this habitat was lowest in spring compared with others and remained low in autumn. The suprabenthos density was at an intermediate level in spring and dropped drastically in autumn, as in all other habitats (Table 1). The southern channel had intermediate levels of benthic invertebrates but high macrofauna biomass in autumn (Table 1) because one station (out of five) contained many common cockles (*Cerastoderma edule*). The navigation channel had the lowest macrofauna biomass and density in both seasons, high meiofauna biomass in spring and high suprabenthos density in autumn. The northern channel had the highest meiofauna biomass and second-highest density of macrofauna invertebrates in autumn. Intertidal mudflats had the highest temperature (Table 1). They also had the lowest density and biomass of all compartments in autumn but had the highest density of suprabenthos (Table 1).

	Season	Estuary mouth	Southern Navigation channel channel		Northern channel	Intertidal mudflats
(°O)	Spring	$17.7\pm0.6$	$18.4 \pm 0.3$	18.5±0.3	$17.8\pm0.3$	$21.9\pm0.8$
Temperature (°C)	Autumn	$19.9\pm0.3$	$20.0\pm0.1$	$19.8 \pm 0.3$	$19.7\pm0.2$	$17.0 \pm 0.4$
$G_{1}$ $(1)$ $(1)$ $(1)$	Spring	$27.3\pm2.4$	$27.4\pm0.6$	$24.8 \pm 2.7$	$26.9 \pm 1.2$	$15.1\pm8.7$
Samily (700)	Autumn	$26.7\pm1.4$	$27.0\pm0.3$	25.1±1.9	$25.9 \pm 1.4$	$14.5\pm8.5$
Macrofauna biomass	Spring	$16.1\pm16.3$	$11.2 \pm 19.5$ 0.02±0.01		$1.5 \pm 2.5$	$8.6\pm7.0$
(g AFDM m <sup>-2</sup> )	Autumn	$23.6\pm23.4$	$27.3\pm24.9$	$0.08 \pm 0.1$	$22.9\pm44.8$	$5.3 \pm 5.1$
Macrofauna density	Spring	$4238\pm3096$	$1126 \pm 1089$	$47\pm56$	$234\pm223$	$4606\pm3912$
(ind m <sup>-2</sup> )	Autumn	$6033 \pm 8595$	$1882 \pm 1155$	10± 10	$2995\pm3698$	$1640 \pm 1460$
Meiofauna biomass	biomass Spring $19.6 \pm 14$ .		$22.9 \pm 14.4$	$59.1{\pm}40.8$	$33.4\pm10.0$	$66.7\pm34.0$
(g AFDM m <sup>-2</sup> )	Autumn	$20.7\pm15.5$	$28.6\pm21.2$	13.6± 17.5	$68.3\pm25.3$	$35.8\pm9.5$
Suprabenthos density	os density Spring 2862		1192	1119	2558	4874
(ind m <sup>-3</sup> )	Autumn	39	28	1074	620	1555
Genus richness	Spring	103	67	22	25	19
(macrofauna)	(macrofauna) Autumn 105		62	9	44	24
Genus richness	Spring	4	8	13	7	8
(suprabenthos)	Autumn	2	5	9	12	8

 Table 1 : Mean (±1 standard deviation, when shown) of characteristics of the habitats in spring and autumn

 2017 (AFDM: ash-free dry matter)

Strong differences among benthic macrofauna communities were highlighted by little overlap among the polygons that represented habitats on the nMDS plane for the two seasons (Fig. 2). Intertidal mudflats were distinct from the other habitats in both seasons. In autumn, the gradient from upstream (intertidal mudflats) to downstream (estuary mouth) was observed on the first axis of the nMDS, while southern and northern channels partly overlapped, revealing similarities between the two benthic communities. In spring, the navigation channel polygon had the largest area on the nMDS plane. This pattern resulted from its contiguity with the other four habitats and its lower mean abundance (47 ind m<sup>-2</sup>) than those of the other habitats (Table 1). Notably, invertebrates were not found at two of its five stations in autumn. It also partly overlapped with the northern channel (Fig. 2).



Figure 2: Two-dimensional ordination based on non-metric multidimensional scaling (nMDS) of habitats (coloured polygons) from square-root transformed density data of benthic macroinvertebrate species grabsampled at 25 stations in the Seine River estuary; EM: estuary mouth; SC: southern channel; NC: northern channel; NAV: navigation channel; IM: intertidal mudflats. Stress = 0.117 in spring and stress = 0.20 in autumn

# 2.4.2 Isotopic differences between habitats

For both seasons, isotopic ratios of primary consumers in the benthic community (particulate-feeder and filter-feeder guilds) differed among habitats (Fig. 3). The estuary mouth had the highest  $\delta^{13}$ C values, whereas intertidal mudflats had the highest  $\delta^{15}$ N values. Northern and southern channels overlapped completely in both seasons (Fig. 3). These habitats were thus merged into a single habitat source in the stable isotope mixing models (*i.e.* southern/northern channels).

Some species collected in several habitats differed in isotopic ratio among habitats (Fig. S2): the bivalve *Limecola balthica* in all five habitats in spring and autumn (except in the estuary mouth in autumn); the bivalves *Cerastoderma edule*, *Abra alba* and *Donax vittatus* in the estuary mouth and southern/northern channels in spring; and the bivalves *Abra alba* and *Spisula subtruncata* and polychaetes *Owenia fusiformis* and *Lagis koreni* in the estuary mouth and southern/northern channels in autumn.



Figure 3: Stable isotope bi-plots ( $\delta^{13}$ C and  $\delta^{15}$ N) of benthic primary consumers (means ± standard deviations, triangles and crosses respectively) and young-of-the-year fish isotopic niches represented by corrected Standard Ellipse Areas (SEAc) and each individual fish (points) within each habitat (EM: estuary mouth; SC: southern channel; NC: northern channel; IM: intertidal mudflats) in spring and autumn

# 2.4.3 YOY fish density within habitats

*M. merlangus* was collected in the four subtidal habitats in spring and autumn. Its density was highest in the estuary mouth in spring and in the navigation channel in autumn and lowest in the northern channel in both seasons (Fig. 4). Like *M. merlangus*, *S. solea* was collected in the four subtidal habitats in both seasons (Fig. 4), with high densities in all habitats in spring, and in the southern channel in autumn. In spring, *D. labrax* was not collected in the four subtidal habitats, but was collected in the mudflats. In autumn, it was collected in the southern/northern channels, with on average more individuals in the southern channel (Fig. 4). *P. platessa* was collected in all habitats except the navigation channel (Fig. 4). The two flatfish species had lower densities in autumn than in spring, suggesting that their juveniles experienced high mortality during summer.



Figure 4: Mean young-of-the-year fish densities in the four subtidal habitats (EM: estuary mouth; SC: southern channel; NAV: navigation channel; NC: northern channel) in spring and autumn. Error bars indicate  $\pm$  0.5 standard deviation

# 2.4.4 Inter-habitat YOY fish niche overlaps

Generally speaking, niche overlap among habitats was higher for *M. merlangus* and *D. labrax* than for flatfish, using both isotopic and gut content approaches.

The isotopic niches of *M. merlangus* overlapped greatly among habitats, with mean values of 0.48 and  $0.54\%^2$  in spring and autumn, respectively (Table 2). The overlap was especially large in the lower section of the estuary, with values reaching  $0.70\%^2$  in the northern, southern and navigation channels (Fig. 3; Table S2). The same pattern was observed for gut contents: its mean inter-habitat Schoener index was 0.53 in autumn (with overlaps between the navigation channel and estuary mouth and between the southern and northern channels greater than 0.6 -Table S3). Inter-habitat overlaps of gut contents were smaller in spring than in autumn, but they remained among the largest overlaps (0.73 between northern and navigation channels) obtained for any species (Table 2).

In spring, *D. labrax* was collected only in the intertidal mudflats; therefore, we could not estimate its inter-habitat overlap. In autumn, its isotopic niches overlapped moderately, with a mean inter-habitat overlap of  $0.48\%^2$  (Table 2). This overlap was influenced greatly by one individual from the northern channel highly enriched in  $\delta^{15}$ N (Fig. 3). When it was removed, mean inter-habitat overlap increased to  $0.60\%^2$ , with particularly high overlap between the northern channel and intertidal mudflats. Its Schoener overlap was 0.18 which was the second lowest overlap in autumn (Table 2).

*P. platessa* isotopic niches had a mean inter-habitat overlap of  $0.25\%^2$  in spring and  $0.39\%^2$  in autumn (Table 2). The latter overlap was influenced by two individuals in the southern channel; when they were removed, mean overlap decreased to  $0.20\%^2$ . The mean inter-habitat Schoener overlap was 0.25 in spring and 0.04 in autumn, which was the smallest in the entire dataset (Table 2). Its inter-habitat Schoener indexes were also low (Table S3).

Season	Mean inter-habitat overlap	Solea solea	Pleuronectes platessa	Dicentrarchus labrax	Merlangius merlangus	
	Isotopic niches	0.11	0.25		0.48	
Spring	Schoener index	0.28	0.25		0.33	
	Number of habitats	3(SI) – 4 (GC)	3	1	4	
	Isotopic niches	0.06	0.39	0.48	0.54	
Autumn	Schoener index 0.34		0.04	0.18	0.53	
	Number of habitats	4	3	3	4	

Table 2: Mean inter-habitat niche overlaps for each young-of-the-year fish species in each season according to the stable isotopic (SI) approach (inter-habitat isotopic niche overlap) and gut content (GC) approach (inter-habitat Schoener index). The number of habitats in which the species was collected is also indicated

For *S. solea*, the isotopic niches among the habitats were the most isolated, especially in autumn, when overlap values rarely differed from 0 (except between the navigation and northern channels, Fig. 3; Table S2), indicating that individuals from different areas fed on different prey mixtures. The mean Schoener overlaps were 0.28 and 0.34 (like for *D. labrax*), in spring and autumn, respectively (Table 2). In autumn, however, the Schoener index between the navigation and northern channels was 0.68 (Table S3) due to consumption predominantly of the polychaete *Polydora ciliata* and the amphipod *C. volutator* by individuals collected in these habitats (Table S4).

# 2.4.5 Contributions of habitats to YOY fish diets

Generally, TDF influenced mixing model outputs for *D. labrax* and *M. merlangus* greatly, as indicated by the overlapping habitat contributions as a function of the combinations of TDF tested (Fig. 5). Differences in TDF did not influence the results for *S. solea* (except for the northern channel in autumn) or *P. platessa* (except for the southern channel in autumn) (Fig. 5; Fig. S3.1).

In spring, *M. merlangus* most likely fed in the estuary mouth (mean contributions of 49-65%, Fig. S3.2) or in the southern/northern channels (mean contributions of 30-47%, Fig. S3.2) and avoided the intertidal mudflats to feed (Fig. 5). Gut contents and local benthic invertebrates had few similarities (Fig. 6). In autumn, contributions to its diet from all habitats ranged from 19 to 50% regardless of where it had been collected (Fig. 5). The same pattern was observed when comparing its gut contents with local benthic invertebrates (Fig. 6). TDF had a particularly strong influence on the outputs for this species. However, they indicated that individuals from different habitats had diets with similar isotopic ratios: for a given TDF pair, the contribution of the habitats to the *M. merlangus* diet remained similar, regardless of where the individual had been collected (Fig. 6).



Figure 5: Relative contributions (0-100%) of habitats (EM: estuary mouth; SNC = southern/northern channels combined ; IM: intertidal mudflats) to isotopic ratios of young-of-the-year fish from stable isotope mixing models by species and season (in columns) and the habitat from which individuals were collected (in rows). In each radar graph, the vertices of coloured triangles correspond to medians of the posterior distribution of habitat contributions based on the six combinations of trophic discrimination factors tested. The vertices of black triangles correspond to means of the medians. Empty cells represent habitats in which no fish of that species were sampled. *D. labrax* was absent from all of the habitats in spring except for the intertidal mudflats; however, its  $\delta^{13}$ C values there were extremely negative and likely came from an unidentified source

In autumn, intertidal mudflats contributed greatly to the *D. labrax* diet. Regardless of the habitat in which the individual had been collected, intertidal mudflats always contributed at least 40%, on average (Fig. 5; Fig. S3.2). The diet was thus supplemented by local feeding in the habitat of collection. Gut contents revealed that 58 and 21% of prey items of *D. labrax* from the northern channel and intertidal mudflats, respectively, could have been found in the intertidal mudflats (Fig. 6). No result is shown for spring, although *D. labrax* was collected in the intertidal mudflats (Fig. 3) as  $\delta^{13}$ C values in the individuals collected in this habitat were extremely depleted (-26.0 to -19.5‰). Gut contents indicated that *D. labrax* fed mainly on copepods (Calanoida, Harpacticoida and other non-identified Copepoda;

Table S4) in spring, which could have come from southern/northern channels or the estuary mouth (Fig. 6).



0 25 50

Figure 6: Similarity between juvenile fish gut contents and local benthic invertebrates (macrobenthos and suprabenthos), which corresponds to the percentage of prey (numbers in cells) that the juveniles from a given habitat could have found in another habitat (EM: estuary mouth; SC: southern channel; NC: northern channel; NAV: navigation channel; IM: intertidal mudflats). Empty cells correspond to habitats in which no fish of that species were collected. Black-bordered squares on the diagonal represent local feeding

In spring, mixing model outputs for *P. platessa* showed an upstream-downstream gradient: upstream, intertidal mudflats contributed  $\sim 50\%$  of the diet of juvenile fish collected in the northern channel, while downstream, the estuary mouth contributed 52% of the diet of juvenile fish collected in the estuary mouth (Fig. 5, Fig. S3.2). Similarities between gut contents and local benthic invertebrates were also high (84-98%) (Fig. 6). Gut contents of *P. platessa* collected in the northern channel had the highest similarities with benthic invertebrates in the northern channel, southern channel and estuary mouth. The similarity was lower with benthic invertebrates in the intertidal mudflats (29%, Fig. 6). This pattern may be related to the unusual gut contents of one plaice individual, which ate 33 Mya spp. prey, even though this bivalve species was not observed in the mudflats but instead in the southern/northern channels and estuary mouth. When this individual was removed, the similarity between gut contents from the northern channel and local benthic invertebrates in the intertidal mudflats increased to 60%. In autumn, results of the mixing model highlighted that P. platessa from the estuary mouth and the northern channel fed preferentially in the estuary mouth (mean contribution of 60 and 68%, respectively) (Fig. 5; Fig. S3.2),

while *P. platessa* from the southern channel fed in the southern/northern channels (mean contribution of 53%) (Fig. 5; Fig. S3.2). Gut contents were most similar to benthic invertebrates of the estuary mouth for fish collected in the estuary mouth (98%), and of the southern/northern channels for fish collected in the southern channel (94%) (Fig. 6). Individuals from the northern channel fed in the estuary mouth and southern/northern channels.

Like *P. platessa*, *S. solea* seemed to feed locally, *i.e.* in the habitat in which they were collected or near it (Figs. 5 and 6). Based on mixing model outputs, intertidal mudflats were exploited by *S. solea* from the northern channel in spring and from the northern and navigation channels in autumn (Fig. 5). Prey in the gut contents of *S. solea* collected in the northern and navigation channels were relatively similar to local benthic invertebrates in the intertidal mudflats (similarities of ~60 and ~40%, respectively).

# 2.5 Discussion

Essential habitats within a nursery should provide sufficient resources and environmental conditions to maximise the growth and survival of YOY fish (Gibson, 1994; Beck *et al.*, 2001). In this study, we did not measured growth nor fitness of YOY fish but hypothesised, according to optimal foraging theory, that individuals in a population would search for food and feed in habitats that optimise their net rate of energy intake to increase fitness, and that these habitats would thus contribute more to the adult stock (MacArthur and Pianka, 1966). Feeding is optimal when prey in local benthic communities are either abundant or of high energy intake). Using trophic tracers integrating at two different time scales, we quantified the trophic dependency of four species to different habitats within the Seine estuary. We discuss YOY feeding preference in relation with their morphology and potential growth performance.

#### 2.5.1 Contrasting benthic macrofauna composition and isotopic ratios among habitats

Estuaries and coastal bays are often composed of different types of habitats. The varying depth and flow of rivers influence the salinity and sediment gradients that partly shape benthic communities (Ysebaert *et al.*, 2003; Dutertre *et al.*, 2013; Dauvin *et al.*, 2017). The segregation in benthic macrofauna communities observed between habitats along the salinity gradient was thus expected. The intertidal mudflats differed from the other habitats in both seasons, as they contained mainly species that tolerate desalination and lengthy exondation (*e.g. H. diversicolor, C. volutator, L. balthica*). In autumn, benthic macrofauna communities in the southern and northern channels could not be distinguished, although they were distinct in spring. This lack of contrast in autumn could have been due to low river flow in summer 2017, which was half the mean flow observed in summer from 2000 to 2017 (http://www.hydro.eaufrance.fr). The unusual water regime of that year may have enabled a potential

effect of marine water intrusion on the benthic macrofauna composition (Chang *et al.*, 2018) and on the food web structure within the estuary (Vinagre *et al.*, 2011b).

Isotopic ratios of the primary consumers also differed among habitats in both seasons. This may be related to the isotopic gradient of primary producers usually observed in estuaries, from a mixture of terrestrial/riverine POM upstream to marine POM downstream (Liénart et al., 2017). This gradient appears in the  $\delta^{13}$ C values of estuarine POM, with terrestrial POM more  $\delta^{13}$ C-depleted than marine POM (Darnaude et al., 2004; Antonio et al., 2010; Liénart et al., 2017). Upstream POM and benthic primary consumers had lower  $\delta^{13}$ C values than their downstream counterparts (Riera and Richard, 1996; Leakey *et al.*, 2008). This pattern was the same in samples from the estuary mouth, which had higher  $\delta^{13}$ C values than the southern and northern channels. Isotopic ratios of the latter two overlapped, likely because they were located at the same point on this gradient, with primary consumers that fed on the same mixture of primary producers of mixed origins. This similarity in isotopic ratios supported merging them into a single source in the mixing model. Primary consumers from intertidal mudflats were easily identified on the isotopic estuarine gradient, as their  $\delta^{15}$ N values were higher, presumably due to the integration of MPB in the food web they belong to. MPB is a major food resource for macrofauna in estuaries (Herman *et al.*, 2000) that has high  $\delta^{15}$ N values (Kostecki *et al.*, 2012). Moreover, as isotope signatures of primary consumers vary less than those of primary producers, our sources most likely remained constant over time (Cabana and Rasmussen, 1996).

# 2.5.2 Feeding habitats: influence of ecological requirements and swimming ability

The search for food influences the spatial distribution of fish. It is associated mainly with the energy requirements of a species, biotic interactions with other individuals or species and the environmental conditions (*i.e.* abiotic factors) a species can tolerate physiologically. For instance, low salinity tolerance influences a species' ability to feed in estuarine intertidal mudflats (Champalbert *et al.*, 1992). We hypothesised that species morphology influences swimming ability and the range of feeding habitats. Therefore, flatfish would feed in habitats where they were collected, whereas roundfish would feed ubiquitously among habitats. One difference between flat and roundfish was the level of identification of prey, perhaps due in part to differences in anatomy. The stomach of flatfish is more difficult to distinguish from the intestine (De Groot, 1971), and based on our observations, *D. labrax* and *M. merlangus* have a stronger stomach that can grind prey more strongly. Hence, the gut contents of flatfish and roundfish should be compared cautiously.

# S. solea and P. platessa: high site fidelity

Flatfish species had the lowest inter-habitat overlaps in both seasons and at both temporal scales of integration (*i.e.* gut contents and stable isotopes), especially *S. solea*. The reduced feeding mobility observed for the two flatfish species (Burrows et al. 2004; Le Pape and Cognez 2016) could also explain

the high feeding fidelity, which has been observed for *S. solea* in many estuaries, such as those of the Thames (Leakey *et al.*, 2008), Gironde (Selleslagh *et al.*, 2015) and Vilaine (Kopp *et al.*, 2013). Hence, *S. solea* individuals feed in a small range around their habitat of collection, and this range is maintained over time, given the difference in integration time between the trophic tracers. Among the habitats studied, intertidal mudflats contributed more than 50% of the diet of *S. solea* collected in the most estuarine habitats. High trophic contribution of intertidal habitats to the diet of juvenile *S. solea* was highlighted in the Tagus estuary in Portugal (Cabral, 2000) and in the Seine estuary 20 years ago (Morin *et al.*, 1999). Moreover, *S. solea* was present in all habitats in both seasons and fed in both intertidal and subtidal habitats. Besides its food requirements, tolerance for low salinity may also explain the presence of *S. solea* in estuarine habitats (Champalbert *et al.*, 1992).

*P. platessa* also had a feeding range close to its habitat of collection, with the highest contributions coming from nearby habitats. Capture-mark-recapture experiments with wild *P. platessa* showed that plaice had high site fidelity within nursery habitats (Burrows *et al.*, 2004). However, *P. platessa* from the southern channel in spring fed preferentially in intertidal mudflats (highest mean contribution calculated by the isotopic mixing model) or in estuary mouth and channels (highest similarity between invertebrates in gut contents and the local benthic community). As the integration time of the trophic tracers differs (weeks *vs.* several hours), YOY *P. platessa* collected in the southern channel most likely fed in the intertidal mudflats immediately after they arrived in the estuary, and then migrated to and fed in the marine habitats. Future studies based on a multi-tissue isotopic approach could provide additional information to support this hypothesis (*e.g.* Guelinckx et al., 2008). Unlike *S. solea*, *P. platessa* was not collected in the navigation channel, where prey abundance was low and salinity was lower than that in other subtidal habitats. YOY *P. platessa* is described as more marine than estuarine (Gibson, 1973; Poxton and Nasir, 1985).

# M. merlangus: mobile ubiquitous feeder

Unlike flatfish, *M. merlangus* has morphological features that facilitate its movement among habitats (Ohlberger *et al.*, 2006). This greater mobility requires expending large amounts of energy. In addition, its growth rate is ~30% higher than those estimated for *P. platessa* and *S. solea* (Hamerlynck and Hostens, 1993; Amara, 2004). Thus, it may explore larger areas to target higher energy prey to satisfy its energy demand (*i.e.* have a ubiquitous feeding strategy in multiple habitats).

The highest inter-habitat overlaps, observed for *M. merlangus* trophic niches, indicated that individuals collected in different habitats fed on the same prey items or mixture of prey. Its prey seemed to come mainly from subtidal habitats in spring, while subtidal and intertidal habitats contributed equally to its diet in autumn. However, posterior contributions of the mixing models varied according to the TDF. As key parameters in stable isotope mixing models, TDF can strongly influence model results (Bond and Diamond, 2011). Assuming a constant diet over time (*i.e.* integration time of the trophic markers), we

had hoped to use the results of gut content analysis to determine a realistic range of values for specific TDF. Unfortunately, gut contents were not as informative as expected (low percentages of taxa identified to the genus or species level), with little similarity between them and local benthic invertebrates. Moreover, these invertebrates represented only some of the *M. merlangus* diet (Demain *et al.*, 2011b). We decided to use means of the median contributions estimated from the six combinations of TDF tested in realistic ranges, which are usually used (Vander Zanden and Rasmussen, 2001), considering that the uncertainty around the means was high for *M. merlangus*. Two hypotheses not mutually exclusive were generated from this result: *M. merlangus* (1) is highly mobile, facilitating the foraging of a wide range of habitats to feed (Leakey *et al.*, 2008) and (2) feeds on mobile prey (Bromley 1997; Demain et al. 2011) which isotopic ratios reflect a mixture of the prey living in the various habitats in the estuary. Additionally, as its highest densities observed in the higher salinity habitats confirm its avoidance of water of low salinity levels (Potter *et al.*, 1988), it could not feed in the intertidal desalinated mudflats.

## D. labrax: dependent on intertidal mudflats

In spring, D. labrax YOY were collected only in riparian habitats near the intertidal mudflats. Individuals were strongly  $\delta^{13}$ C-depleted, indicating that they fed on  $\delta^{13}$ C-depleted prev such as terrestrial insects or amphipods such as Orchestia sp. as observed in the gut contents where copepods were also found. The occurrence of two types of prey illustrates the feeding behaviour already observed by Laffaille et al. (2001) showing its opportunistic behaviour with amphipod foraged rather during ebb period and copepods during flood periods. As mentioned, similarities with local benthic fauna should be interpreted with caution. It is thus likely that D. labrax fed in its habitat of collection, intertidal mudflats. Moreover, as tides influence gut contents greatly (Kuipers, 1973; Rountree and Able, 1992; Laffaille et al., 2001), the timing of sampling could have influenced our observations. In autumn, YOY D. labrax still fed in intertidal mudflats, especially individuals collected in the northern channel and intertidal mudflats as already observed in the same study site by Morin et al. (1999). However, D. labrax collected in the southern channel also fed in northern/southern channels, as confirmed by intermediate inter-habitat overlaps of trophic niches. In the Thames estuary, isotopic ratios of D. labrax testified the trophic importance of estuarine resources for individuals collected in the estuary and of coastal and estuarine resources when collected in the coastal area, which was facilitated by its high mobility (Leakey et al., 2008). As D. labrax tolerates lower salinity levels, and had even an increased growth in low salinities (9-11) conditions (Boeuf and Lasserre, 1978), it can stay and feed in the upper section of the estuary what *M. merlangus* cannot.

# 2.6 Conclusion and perspectives

The habitats studied were used either simultaneously in the same season or asynchronously throughout the year, suggesting no preference for a specific habitat at the community scale. YOY *S. solea* and *P.* 

*platessa*, which have similar growth rates, adopted a local feeding strategy when they encountered specific ecological conditions. YOY *M. merlangus* had a ubiquitous feeding strategy and foraged among all habitats, which may be related to their higher energy demand for growth and movement, while YOY *D. labrax* fed most often in subtidal habitats and estuarine intertidal thanks to its tolerance to low salinities.

Our conclusions are based on a single year with unusually low river flow. River flow is known to influence estuarine and coastal food webs (Kostecki *et al.*, 2010; Vinagre *et al.*, 2011b) and habitat use by juvenile fish (Le Pape *et al.*, 2003b). Increased occurrence of summer drought is expected in the context of climate change (Vinagre *et al.*, 2019). The pattern observed in 2017 is thus expected to occur repeatedly in the years to come. Identifying the feeding habitats of juvenile fish in coastal nurseries requires studying fish foraging throughout the growing season. Our results highlight that the two flatfish species studied have a high feeding fidelity on the nursery habitats within a given season, but they did not enable us to assess habitat use or inter-habitat movements between spring and autumn. Additionally, these results may help solve one of the main challenges in estimating the trophic capacity of YOY fish nurseries at relevant spatial scales (Saulnier *et al.*, 2020). Indeed, one major assumption of the approach is that fish feed in the habitat in which they are collected. Our study provided information for reallocating fish consumption to the actual feeding habitats of the species studied.

Estuarine and coastal areas are zones in which human activities can conflict with environmental objectives, such as functioning as a nursery for juvenile fish (Le Pape et al. 2007; Rochette et al. 2010). Integrated coastal zone management requires coordinated application of policies that influence the coastal zone and helps mitigate impacts of coastal activities by respecting natural resources and ecosystem functions in both time and space. Such integrated management requires better understanding of key habitats that juvenile fish need to complete their life cycles (Levin and Stunz, 2005). The Seine estuary can be considered a landscape of habitats that needs to be preserved. Nearly 45% of its intertidal and subtidal zones were lost due to continental development from 1850 to 2003, and intertidal mudflats represented more than 80% of that loss (Delsinne, 2005) consistently with global trends (Murray et al., 2019). Intertidal mudflats appeared to be attractive to YOY fish for their (i) high biomass and abundance of small prey, which gather at high densities and most likely decreases YOY foraging time (Toole, 1980); (ii) warmer spring temperature than in subtidal habitats; and (iii) contribution to predator avoidance (Gibson et al. 2002). It is likely that a combination of these factors explains the attractiveness of intertidal mudflats, although prey availability may be the most plausible explanation (Tableau *et al.*, 2016). Our results confirm the urgent need to protect and preserve this essential habitat, especially for the feeding (and ultimately growth) of YOY fish species.

# 2.7 References

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# 2.8 Supplementary material

**Fig. S1** Length distributions for each species in each season (all habitats combined). The vertical orange line separates the first cohort (young-of-the-year) from older individuals

#### a. Data in this study



**b**. Data from previous sampling every month from 2000-2015 collected in the context of "Port 2000" building (Le Havre harbour) using beam trawl.



Analyses of length-distribution were preferred to size gathered from the literature as length-age relationships are spatially-dependent and vary with latitude (Vinagre *et al.*, 2009b; Ciotti *et al.*, 2013a).

Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013. Spatial variation in growth rate of early juvenile European plaice Pleuronectes platessa. Mar. Ecol. Prog. Ser. 475, 213–232. https://doi.org/10.3354/meps10087

Vinagre, C., Ferreira, T., Matos, L., Costa, M.J., Cabral, H.N., 2009. Latitudinal gradients in growth and spawning of sea bass, Dicentrarchus labrax, and their relationship with temperature and photoperiod. Estuar. Coast. Shelf Sci. 81, 375–380. https://doi.org/10.1016/j.ecss.2008.11.015 **Fig. S2** Inter-habitat variability (mean  $\pm 1$  SD) of  $\delta^{13}$ C and  $\delta^{15}$ N (‰) values of invertebrate species collected in different habitats (EM: estuary mouth, SC: southern channel, NC: northern channel, IM: intertidal mudflats). ABRAALB: *Abra alba*, LAGIKOR: *Lagis koreni*, LIMEBAL: *Limecola balthica*, OWENFUS: *Owenia fusiformis*, SPISSUB: *Spisula subtruncata*, CERSEDU: *Cerastoderma edule* 



**Fig S3.** Contribution of habitats (EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats) to juvenile fish diets (calculated from median contributions of posterior distributions estimated using stable isotope mixing models and several TDF combinations)









**Table S1** Sampling design for gut content and stable isotope analysis (SIA) of the four species by habitat(EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM:intertidal mudflats) and season

		Sp	oring	Autumn			
Species	Habitat	Non-empty guts	Fish SIA samples	Non-empty guts	Fish SIA samples		
	EM	0	0	0	0		
Dicentrarchus labrax	SC	0	0	43	10		
	NC	0	0	45	10		
	NAV	0	0	0	0		
	IM	18	17	50	9		
	EM	45	10	47	10		
Marlangius marlangus	SC	12	10	42	10		
mertangtus mertangus	NC	10	9	45	10		
	NAV	9	7	39	10		
Pleuronectes platessa	EM	19	10	19	11		
	SC	24	10	15	16		
	NC	12	8	8	12		
	NAV	0	0	0	0		
Solea solea	EM	24	samples lost	19	12		
	SC	20	6	20	11		
	NC	22	8	22	12		
	NAV	21	5	18	13		

**Table S2** Isotopic niche overlaps among habitats (EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats) for juvenile fish of each species. Overlap between habitat 1 and habitat 2 is the mean percentage overlap of the ellipse of niche 1 by niche 2 and the percentage overlap of the ellipse of niche 2 by niche 1. NA: not applicable

Species	Spring						Autumn				
Dicentrarchus	NA						Autumn	SC	NC	IM	
labrax							SC		0.47	0.51	
							NC			0.48	
											_1
Merlangius	Spring	EM	SC	NC	NAV		Autumn	EM	SC	NC	NAV
merlangus	EM		0.58	0.34	0.50		EM		0.32	0.36	0.41
	SC			0.52	0.56		SC			0.73	0.69
	NC				0.41		NC				0.71
Pleuronectes	Spring	EM	SC	NC			Autumn	EM	SC	NC	
platessa	EM		0.26	0	_		EM		0.51	0.29	
	SC			0.50			SC			0.37	
									•		_
Solea solea	Spring	SC	NC	NAV			Autumn	EM	SC	NC	NAV
	SC		0	0			EM		0	0	0
	NC			0.34	1		SC			0	0
					-		NC				0.03
**Table S3** Diet overlaps among habitats (EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats) for juvenile fish of each species estimated using the Schoener index. NA: not applicable

Species			Spring					A	utumn		
Dicentrarchus	NA					A	Autumn	FS	SC	IM	
labrax						S	SC		0.34	0.16	
						١	NC			0.04	
										-	_
Merlangius	Spring	EM	SC	NC	NAV	A	Autumn	EM	SC	NC	NAV
merlangus	EM		0.38	0.19	0.08	F	EM		0.44	0.40	0.63
	SC			0.29	0.29	S	SC			0.65	0.49
	NC				0.73	١	NC				0.54
Pleuronectes	Spring	EM	SC	NC		I	Autumn	EM	SC	NC	
platessa	EM		0.15	0.46		F	EM		0.07	0.02	
	SC			0.15		S	SC			0.03	
											_
Solea solea	Spring	EM	SC	NC	NAV	A	Autumn	EM	SC	NC	NAV
	EM		0.27	0.41	0.20	I	EM		0.18	0.14	0.03
	SC			0.33	0.14	S	SC			0.42	0.59
	NC				0.33	١	NC				0.68
											I

**Table S4** Mean number of prey (by taxon) in gut contents per individual fish by species and habitat (EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats)

## <u>Spring</u>

Predator	Prey	EM	SC	NAV	NC	IM
Dicentrarchus labrax	Acartia					0.02
Dicentrarchus labrax	Amphipoda					0.33
Dicentrarchus labrax	Animalia					0.02
Dicentrarchus labrax	Calanoida					4.63
Dicentrarchus labrax	Cirripedia					0.06
Dicentrarchus labrax	Copepoda					2.29
Dicentrarchus labrax	Harpacticoida					0.02
Dicentrarchus labrax	Lekanesphaera rugicauda					0.12
Dicentrarchus labrax	Malacostraca					0.02
Dicentrarchus labrax	Pseudocalanus					0.57
Merlangius merlangus	Actinopterygii	0.18	0.08	0.29	0.11	
Merlangius merlangus	Amphipoda	0.07	0.08	0.29	0.11	
Merlangius merlangus	Animalia	0.31	0.5	0.14	0.22	
Merlangius merlangus	Bivalvia	0.02	0	0	0	
Merlangius merlangus	Brachyura	5.84	0	0	0	
Merlangius merlangus	Calanoida	3.78	1.58	0	0	
Merlangius merlangus	Carcinus maenas	0.13	0	0	0	
Merlangius merlangus	Caridea	0.07	0.08	0	0	
Merlangius merlangus	Centropages typicus	0	0.08	0	0	
Merlangius merlangus	erlangius merlangus Copepoda		0	0	0.11	
Merlangius merlangus	rlangius merlangus Crangon crangon		0	0	0.11	
Merlangius merlangus	Merlangius merlangus Cumacea		0	0	0	
Merlangius merlangus	Aerlangius merlangus Decapoda		0	0	0.11	
Merlangius merlangus	s merlangus Eumalacostraca		0	0	0.11	
Merlangius merlangus	ingus Euterpina		0	0	0	
Merlangius merlangus	verlangus Gobiidae		0	0	0	
Merlangius merlangus	us Malacostraca		0.08	0	0	
Merlangius merlangus	Mysidacea	1.07	0.67	3	1.11	
Merlangius merlangus	Pisidia longicornis	0.04	0	0	0	
Pleuronectes platessa	Abra alba	0.05	0		0	
Pleuronectes platessa	Ampelisca sp	0.05	0		0	
Pleuronectes platessa	Ampharete lindstroemi	0.05	0		0	
Pleuronectes platessa	Ampharetidae	0.05	0		0	
Pleuronectes platessa	Annelida	0.11	0.08		0.17	
Pleuronectes platessa	Aphroditidae	0	0		0.08	
Pleuronectes platessa	Arthropoda	0.16	0.08		0	
Pleuronectes platessa	Balanidae	0	0.04		0	
Pleuronectes platessa	Bivalvia	9.47	0.96		0.42	
Pleuronectes platessa	Carcinus maenas	0	0.29		0	
Pleuronectes platessa	Cerastoderma edule	0	10.92		0.17	
Pleuronectes platessa	Corophium volutator	0	0		0.92	
Pleuronectes platessa	Crangon crangon	0.05	0.33		0.25	
Pleuronectes platessa	Decapoda	0.05	0		0.08	
Pleuronectes platessa	Diastylis sp	0.37	0		0	
Pleuronectes platessa	Eteone longa	0.05	0		0	
Pleuronectes platessa	Eudorella truncatula	0.05	0		0	
Pleuronectes platessa	Foraminifera	0.05	0.08		0.08	
Pleuronectes platessa	Gastrosaccus sp	0.05	0		0	
Pleuronectes platessa	Harpacticoida	0.05	0.17		0	
Pleuronectes platessa	Hediste diversicolor	0	0		0	

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Pleuronectes platessa	Hydrozoa	0.05	0.04		0	
Pleuronectes platessa	Kurtiella bidentata	0	0.04		0	
Pleuronectes platessa	Lagis koreni	0.42	0.79		0	
Pleuronectes platessa	Lanice conchilega	0.11	0		0	
Pleuronectes platessa	Limecola balthica	0	0.04		0.08	
Pleuronectes platessa	Lutraria sp	5.32	0.04		0	
Pleuronectes platessa	Macropodia linaresi	0	0		0.08	
Pleuronectes platessa	Mactridae	0.32	0		0	
Pleuronectes platessa	Magelona sp	0.05	0		0	
Pleuronectes platessa	Mya sp	20.58	0.33		2.75	
Pleuronectes platessa	Mysidae	0	0		0.08	
Pleuronectes platessa	Mytilus edulis	0	0		0.08	
Pleuronectes platessa	Nephtys sp	0.26	0.17		0.08	
Pleuronectes platessa	Nereididae	0	0.04		0	
Pleuronectes platessa	Ostracoda	0.05	0.08		0	
Pleuronectes platessa	Pariambus typicus	0.32	0		0	
Pleuronectes platessa	Phaxas pellucidus	17.84	1.13		0	
Pleuronectes platessa	Phyllodocidae	0.05	0		0.08	
Pleuronectes platessa	Polychaeta errantia	0.05	0		0	
Pleuronectes platessa	Polydora ciliata	0.16	0.17		0.17	
Pleuronectes platessa	Portunidae_larve	0	0.08		0	
Pleuronectes platessa	Pseudocuma sp	0.05	0		0	
Pleuronectes platessa	Pseudopolydora pulchra	0.05	0		0	
Pleuronectes platessa	Pygospio elegans	0.16	0.33		0.17	
Pleuronectes platessa	Sabellidae	0.05	0		0	
Pleuronectes platessa	Spionidae	0.79	0.79		0.17	
Pleuronectes platessa	Spisula subtruncata	0.95	0.29		0	
Solea solea	Abra alba	0.75	0	0	0	
Solea solea	Acari	0.04	0	0	0	
Solea solea	Actinopterygii	0.04	0.05	0.05	0	
Solea solea	Amphipoda	0.04	0	0.14	0	
Solea solea	Annelida	0.04	0	0.67	0	
Solea solea	Aphroditidae	0	0.05	0	0	
Solea solea	Arthropoda	0.13	0.05	0	0.05	
Solea solea	Balanidae	0.08	0	0	0	
Solea solea	Bivalvia	2.96	3.55	0.29	0.32	
Solea solea	Bivalvia_larve	0	0	0.1	0.23	
Solea solea	Bryozoa	0	0.05	0	0	
Solea solea	Cardiidae	0.17	0	0.1	0.09	
Solea solea	Cerastoderma edule	0.17	0	0	0.27	
Solea solea	Corophium volutator	0	0	1.19	1.77	
Solea solea	Crangon crangon	0	0	0	0.09	
Solea solea	Cumacea	0.04	0	0	0	
Solea solea	Decapoda	0	0.05	0	0	
Solea solea	Diastylis sp	0.25	0	0	0	
Solea solea	Divers	0.04	0	0.1	0	
Solea solea	Foraminifera	0.13	0.1	0.05	0.27	
Solea solea	Gammarus sp	0	0	0	0.09	
Solea solea	Gnathiidae	0	0	0	0.05	
Solea solea	Harpacticoida	1	0.25	27.48	1.27	
Solea solea	Hediste diversicolor	0	0	0.1	0.45	
Solea solea	Hydrozoa	0	0	0.05	0	
Solea solea	Kurtiella bidentata	0.38	0	0	0.09	
Solea solea	Limecola balthica	0	0.1	0	0	
Solea solea	Mactridae	0.17	0	0	0	
Solea solea	Melita hergensis	0	0.05	0	0	
Solea solea	Nephtys sp	0.25	0.35	0	0.23	
Solea solea	Nototropis falcatus	0.04	0	0	0	
Solea solea	Ostracoda	0.38	0	0.05	0.09	

Solea solea	Pharidae	0.21	0	0	0	
Solea solea	Phaxas pellucidus	0.04	0.15	0.05	0	
Solea solea	Polydora ciliata	0.08	1.5	1.9	0.64	
Solea solea	Polynoidae	0	0	0.1	0.05	
Solea solea	Pontocrates altamarinus	0.13	0	0	0	
Solea solea	Pseudocumatidae	0.04	0	0	0	
Solea solea	Pygospio elegans	0	0.25	0	0	
Solea solea	Sabellidae	0.04	0	0	0	
Solea solea	Spionidae	0.67	0.35	0	0.55	
Solea solea	Veneridae	0.5	0	0	0	

## Autumn

Predator	Prey	EM	SC	NAV	NC	IM
Dicentrarchus labrax	Actinopterygii		0.23		0.22	0.06
Dicentrarchus labrax	Amphipoda		0.21		0.07	0.16
Dicentrarchus labrax	Animalia		0.35		0.2	0.08
Dicentrarchus labrax	Araneae		0		0	0.02
Dicentrarchus labrax	Bivalvia		0.05		0	0
Dicentrarchus labrax	Brachyura		0.02		0.02	0
Dicentrarchus labrax	Carcinus maenas		0		0.02	0.02
Dicentrarchus labrax	Caridea		0		0	0.02
Dicentrarchus labrax	Cirripedia		1.07		0	0
Dicentrarchus labrax	Copepoda		0		0	0.02
Dicentrarchus labrax	Corophium volutator		0		0.2	0
Dicentrarchus labrax	Crangon crangon		0.09		0.11	0.02
Dicentrarchus labrax	Crangonidae		0.05		0.07	0
Dicentrarchus labrax	Decapoda		0.02		0.07	0.02
Dicentrarchus labrax	Echinodermata		0		0.02	0
Dicentrarchus labrax	Echinozoa		0		0.02	0
Dicentrarchus labrax	Eteone longa		0		0.02	0
Dicentrarchus labrax	Eumalacostraca		0.05		0.02	0.02
Dicentrarchus labrax	Foraminifera		0.14		0	0
Dicentrarchus labrax	Gammaridea		0.35		0	5.26
Dicentrarchus labrax Hydrozoa			0.07		0	0
Dicentrarchus labrax	Insecta		0		0	0.06
Dicentrarchus labrax	Isaeidae		0		0	0.02
Dicentrarchus labrax	Isopoda		0		0	0.06
Dicentrarchus labrax	Lagis koreni		0.07		0.02	0
Dicentrarchus labrax	Lekanesphaera rugicauda		0		0	1.84
Dicentrarchus labrax	Lumbrineris cingulata		0		0	0.02
Dicentrarchus labrax	Malacostraca		0.21		0.04	0.08
Dicentrarchus labrax	Mysidacea		0.35		0.29	0
Dicentrarchus labrax	Nephtyidae		0		0.04	0.04
Dicentrarchus labrax	Polychaeta		0.14		0.13	0.04
Dicentrarchus labrax	Rhodophyta		0.05		0	0
Dicentrarchus labrax	Schistomysis kervillei		0.33		0	0
Dicentrarchus labrax	Talitridae		0		0	1.56
Merlangius merlangus	Actinopterygii	0.68	0.88	0.38	0.51	
Merlangius merlangus	Animalia	0.28	0.24	0.23	0.38	
Merlangius merlangus	Annelida	0	0	0.03	0	
Merlangius merlangus	Brachyura	0.04	0.02	0.03	0.02	
Merlangius merlangus	Carcinus maenas	0	0.02	0	0	
Merlangius merlangus	Caridea	0.02	0.05	0.13	0.02	
Merlangius merlangus	Cirripedia	0.02	0	0	0	
Merlangius merlangus	Clupeidae	0.06	0	0	0.04	
Merlangius merlangus Crangon crangon		0.02	0.24	0.21	0.2	

Merlangius merlangus	Crangonidae	0.06	0.19	0.03	0.07	
Merlangius merlangus	Decapoda	0.04	0.21	0.1	0.09	
Merlangius merlangus	Eumalacostraca	0.02	0.05	0.05	0.13	
Merlangius merlangus	Gobiidae	0	0.05	0.21	0.2	
Merlangius merlangus	Hydrozoa	0	0.02	0	0	
Merlangius merlangus	Malacostraca	0.04	0.19	0.05	0.11	
Merlangius merlangus	Mysidacea	0.23	0.05	0.46	0	
Merlangius merlangus	Pomatoschistus	0	0	0.03	0	
Merlangius merlangus	Senticaudata	0	0.02	0	0	
Pleuronectes platessa	Abra alba	0.11	0		0	
Pleuronectes platessa	Ampharete lindstroemi	0.16	0		0	
Pleuronectes platessa	Annelida	0.05	0.53		0.38	
Pleuronectes platessa	Arthropoda	0.16	0.13		0	
Pleuronectes platessa	Balanidae	0	0.07		0	
Pleuronectes platessa	Bivalvia	0.26	5.6		0	
Pleuronectes platessa	Cerastoderma edule	0	8.4		0	
Pleuronectes platessa	Copepoda	0	0.07		0.13	
Pleuronectes platessa	Crangon crangon	0.11	0		0	
Pleuronectes platessa	Divers	0	0		0	
Pleuronectes platessa	Elysia viridis	0	0.33		0	
Pleuronectes platessa	Fabulina fabula	0.05	0		0	
Pleuronectes platessa	Hediste diversicolor	0	0.13		0	
Pleuronectes platessa	Hydrozoa	0.11	0.13		0	
Pleuronectes platessa	Kurtiella bidentata	0.05	0		0	
Pleuronectes platessa	Lagis koreni	0.05	0.07		0	
Pleuronectes platessa	Limecola balthica	0	0.07		0	
Pleuronectes platessa	Liocarcinus pusillus	0.05	0		0	
Pleuronectes platessa	Melinna palmata	0.11	0		0	
Pleuronectes platessa	Mysidae	0.05	0		0	
Pleuronectes platessa	Nephtys assimilis	0	0.2		0	
Pleuronectes platessa	Nephtys hombergii	0	0.27		0	
Pleuronectes platessa	Nephtys kersivalensis	0	0.07		0	
Pleuronectes platessa	Nephtys sp	0.74	0.27		0	
Pleuronectes platessa	Nereididae	0	0		0.25	
Pleuronectes platessa	Nucula sp	0.05	0		0	
Pleuronectes platessa	Owenia fusiformis	3.42	0		0	
Pleuronectes platessa	Pariambus typicus	0.05	0		0	
Pleuronectes platessa	Phaxas pellucidus	2.47	0		0	
Pleuronectes platessa	Phyllodocidae	0	0.07		0	
Pleuronectes platessa	Polydora ciliata	0.05	0.2		0.38	
Pleuronectes platessa	Spionidae	0.11	0.07		0.25	
Pleuronectes platessa	Spisula subtruncata	0.11	0.27		0	
Solea solea	Abra alba	0	0	0.11	0	
Solea solea	Alitta succinea	0	0	0.06	0	
Solea solea	Ampelisca sp	0	0	0	0.05	
Solea solea	Ampharete lindstroemi	0.11	0	0	0.05	
Solea solea	Ampharetidae	0.21	0.05	0	0	
Solea solea	Amphipoda	0.16	0	0	0	
Solea solea	Animalia	0	0.1	0	0	
Solea solea	Annelida	0.16	0.05	0	0.14	
Solea solea	Aphroditiformia	0.05	0	0	0.05	
Solea solea	Arthropoda	0.21	0.25	0.17	0.14	
Solea solea	Bivalvia	1.16	0.85	0	0	
Solea solea	Bivalvia_larve	0	0.05	0.06	0	
Solea solea	Boccardiella ligerica	0	0	0.28	0.23	
Solea solea	Brachyura	0.05	0	0	0	
Solea solea	Carcinus maenas	0	0	0	0.05	
Solea solea	Copepoda	0.05	0.05	0	0	
Solea solea	Corophium volutator	0	0	12.72	3.86	

Solea solea	Crangon crangon	0.42	0.1	0.17	1.05	
Solea solea	Crangonidae	0.21	0	0	0	
Solea solea	Cyathura carinata	0	0	0	0.41	
Solea solea	Diastylis bradyi	1.84	0	0	0	
Solea solea	Diastylis sp	0.32	0	0	0	
Solea solea	Ericthonius punctatus	0	0	0.06	0	
Solea solea	Eurytemora affinis	0	0	0	0.09	
Solea solea	Hediste diversicolor	0	0.05	0	0.73	
Solea solea	Hydrozoa	0.05	0.05	0	0	
Solea solea	Kurtiella bidentata	0	0	0.22	0	
Solea solea	Lagis koreni	0.16	0.8	0	0	
Solea solea	Lanice conchilega	0.11	0	0	0	
Solea solea	Leucothoe incisa	0.05	0	0	0	
Solea solea	Liocarcinus sp	0.05	0	0	0	
Solea solea	Melinna palmata	0.32	0	0	0	
Solea solea	Mya sp	0.26	0	0	0	
Solea solea	Nephtys sp	0.37	0.15	0	0.23	
Solea solea	Nereididae	0	0.35	0.39	0.41	
Solea solea	Ostracoda	0.37	0.1	0	0.18	
Solea solea	Owenia fusiformis	0.26	0	0	0	
Solea solea	Pariambus typicus	0.11	0	0	0	
Solea solea	Perioculodes longimanus	0.05	0	0	0	
Solea solea	Pholoe inornata	0.05	0	0	0	
Solea solea	Photis longicaudata	0.11	0	0	0	
Solea solea	Phyllodocidae	0.32	0.25	0.06	0.05	
Solea solea	Plantae	0	0	0	0.09	
Solea solea	Polydora ciliata	0.11	4.35	18.72	3.36	
Solea solea	Polydorinae	0	0.05	0	0	
Solea solea	Polynoidae	0	0.1	0	0	
Solea solea	Portunidae	0.05	0	0	0	
Solea solea	Pseudocuma longicorne	0.11	0	0	0	
Solea solea	Pseudopolydora pulchra	0.11	0	0.06	0	
Solea solea	Sabellaria spinulosa	0	0	0	0.05	
Solea solea	Spionidae	0.16	0.05	0	0.05	
Solea solea	Spisula subtruncata	0.11	0	0	0	

## Chapitre 3.

Capacité trophique à fines échelles dans les nourriceries côtières estuariennes : focus sur le début et la fin de la période de forte croissance des juvéniles de poissons et sur les habitats de l'estuaire de la Seine



Illustration L. Fleury

Le chapitre précédent confirme l'hétérogénéité des habitats au sein de l'estuaire, tant d'un point de vue des variables abiotiques que biotiques. Ces contrastes ont permis de mettre en évidence des stratégies d'alimentation propres à chaque espèce, avec une consommation « locale » pour les poissons plats et une exploration des différents habitats par les poissons ronds. Nous avons aussi souligné l'importance des vasières intertidales comme habitat d'alimentation essentiel pour les juvéniles de bar et de sole. Enfin, la contribution des habitats a été estimée par espèce et au printemps et à l'automne, entourant la période de forte croissance des juvéniles.

L'objectif de ce chapitre est d'estimer la capacité trophique via les Efficacité d'Exploitation (EE) *i.e.* le ratio entre la demande énergétique des juvéniles et l'offre alimentaire à l'échelle des habitats de l'estuaire de Seine et aux deux périodes potentiellement sensibles pour les juvéniles de poissons : juste après leur arrivée sur la nourricerie (fin du printemps) et à la fin de la saison de forte croissance (automne). Les estimations de consommation par habitat sont couplées avec les estimations de contributions de chacun des habitats à l'alimentation des juvéniles (chapitre 2) pour réallouer la consommation de manière la plus réaliste possible.

Chapitre 3. Capacité trophique à fines échelles

Trophic carrying capacity in estuarine nurseries: focus on fish juveniles' growing period and habitats of the estuary of Seine

Preliminary results –

## Authors

Louise Day<sup>a,b</sup>, Anik Brind'Amour<sup>a</sup>, Pierre Cresson<sup>c</sup>, Camille Vogel<sup>d</sup>, Bastien Chouquet<sup>e</sup>, Sylvain Duhamel<sup>e</sup>, Jean-Claude Dauvin<sup>f</sup>, Jean-Philippe Pézy<sup>f</sup>, Hervé Le Bris<sup>b</sup>

<sup>a</sup>IFREMER, EMH, Rue de l'île d'Yeu, B.P. 21105, 44311 Nantes, France

<sup>b</sup>Institut Agro, INRAE, ESE, Ecology and Ecosystems Health, 35042 Rennes, France

<sup>c</sup>IFREMER Laboratoire Ressources Halieutiques Manche Mer du Nord, 62200, Boulogne sur Mer, France

<sup>d</sup>IFREMER, Ctr Manche Mer-du-Nord, Laboratoire de Ressources Halieutiques, F-14520, Port en Bessin, France

<sup>e</sup>Cellule de Suivi du Littoral Normand (CSLN), 76600 Le Havre, France

<sup>f</sup>Normandie Univ., UNICAEN, UNIROUEN, CNRS UMR 6143 M2C, Laboratoire Morphodynamique Continentale et Côtière, 24 rue des Tilleuls, 14000 Caen, France

## **3.1** Abstract

Estuarine and coastal ecosystems are composed of spatially restricted habitats fulfilling a nursery function for many demersal fish species. These nursery-dependant species concentrate at the juvenile stage in these habitats, resulting in density-dependent regulation affecting growth and survival. However, the underlying mechanisms are still poorly understood and the limitation of the food supply on the juvenile fish remains a pending issue. The Seine estuarine and coastal ecosystem (Eastern English Channel) is a nursery composed of a mosaic of habitats offering diverse food resources. Over the last decades, important anthropogenic activities significantly reduced the surface, especially of mudflats, likely reducing the gross production of this ecosystem. In here, we aim at assessing the trophic contribution of the different habitats to different nursery-dependant fish juveniles at two important periods of their juvenile stage: the post-settlement period (early spring) and the end of the growth season (late summer), using a recently developed bioenergetics-based approach. This approach estimates in each habitat the exploitation efficiency (EE), *i.e.* the part of the production consumed by the juveniles, assuming that the consumption occurs locally, *i.e.* is restricted to the habitat in which the fish was captured. We challenged that assumption by weighting the fish consumption with the estimated habitat contribution from stable isotopes mixing models outputs to re-allocate fish consumption over the habitats. The comparison of the EE assessed in different habitats identifies trophically-limited habitats and highlights the functional role of the intertidal mudflats in the assessment of the trophic capacity of the bay of Seine. These results likely support the integrated coastal zone management of this highly man-shaped ecosystem.

## Keywords

Food limitation, habitat scale, growth season, Bay of Seine

## 3.2 Introduction

Estuarine and coastal areas support essential ecological functions and concentrate many humans' activities. This duality often lead to conflicts between anthropogenic use of coastal waters and marine species living or partly living in these ecosystems. Among them, bentho-demersal nursery-dependant species concentrate within estuarine and coastal areas during their juvenile stage (Iles and Beverton, 2000). The life cycle of these species is characterized by a spatial segregation among stages (Gibson, 1994). Adults live in deeper coastal shelf waters and often reproduce at the end of winter. Eggs then larvae are pelagic and move passively with ocean currents and winds and then actively towards the coastal bays and estuaries (Gibson, 2005). Larvae move from a pelagic to a more or less benthic life with the metamorphosis and juvenile settled then in coastal and estuarine areas called nurseries at the end of spring/early summer (Gibson, 2005). They feed and grow fast until early autumn. Then for another 1 or 2 years according to the species, juvenile fish move into shallow nursery during the growth season before recruiting to the adult population offshore.

Hence, juvenile stage of nursery-dependant species is characterized by a concentration of individuals over spatially constrained nursery habitats. This concentration leads to density-dependence processes when the number of individuals within nursery is high (Beverton, 1995; Iles and Beverton, 2000), such as mortality (van der Veer *et al.*, 1991) or growth reduction as individuals reach the carrying capacity of the nursery. Concentration of juvenile fish on nurseries dampen the high variations induced by density-independent mortality affecting early-life stages (egg and larvae) and though control the recruitment level of these species (van der Veer *et al.*, 2000; Nash and Geffen, 2012; Le Pape and Bonhommeau, 2015). Because of the regulating role these habitats play for nursery-dependant species, among which highly economical valuable species for fisheries (*Solea solea, Pleuronectes platessa, Dicentrarchus labrax*), their identification and the processes that regulate these fish populations at the juvenile stage raise the interest of many stakeholders (scientists, managers, fishermen). However, the underlying causes of density-dependence processes (*e.g.* trophic competition, predation) are still poorly understood and the limitation of the food supply on the juvenile fish remains a pending issue (Le Pape and Bonhommeau, 2015).

Trophic carrying capacity and food limitation hypothesis have been widely studied in a variety of temperate estuarine and coastal nurseries (Le Pape and Bonhommeau, 2015 and reference therein). Principal methods used were indirect, based on the comparison of growth or condition index of juvenile with optimal parameter (Amara *et al.*, 2001; Teal *et al.*, 2008; van der Veer *et al.*, 2010; Freitas *et al.*, 2012; Ciotti *et al.*, 2013b; Poiesz *et al.*, 2018). Some studies demonstrated a summer reduction of growth (Teal *et al.*, 2008; van der Veer *et al.*, 2018; van der Veer *et al.*, 2018), but none of them linked growth or fish condition to trophic competition yet (Ciotti *et al.*, 2014; van der Veer *et al.*, 2016). Moreover, Le Pape and Bonhommeau (2015) highlighted that when measuring fish growth out in the

field, only apparent growth of survival individuals was reported which can hide a potential lethal effect of food limitation. Hence, direct approaches taking into account both compartments of trophic carrying capacity (*i.e.* prey and predator) could bring lights on the trophic limitation hypothesis. Indeed, it was demonstrated that the carrying capacity for bentho-demersal fish was reached using a mass-balanced model in the Gironde estuary (Chevillot *et al.*, 2019). A bioenergetics approach estimating prey production and consumption of epibenthic predators also concluded in interspecific competition for food resource on the Swedish coast (Pihl, 1985). However, some direct studies also reported low proportion of prey consumed by predators (Collie, 1987; Vinagre and Cabral, 2008). Mass-balanced models include the entire ecosystem but oversimplify it and are not designed to test the food limitation hypothesis while bioenergetics approach cited above are extremely data intensive and then only applied to a few species of predators. In this context, Tableau et al. (2019) developed a bioenergetics-based model to estimate whether or not trophic carrying capacity has been reached and test the food limitation hypothesis in coastal nurseries. This model estimates prey production and food consumption from data survey and parameters from the literature.

One explanation of the uncertainty around processes of juvenile fish populations' regulation in nurseries and the role of the trophic resources might be the scales at which the studies are undertaken (Pihl, 1985; Chevillot et al., 2017). More generally, choosing the appropriate scale is essential when studying the prey-predator interactions (Bailey et al., 2010). Food availability, fish consumption, and therefore trophic carrying capacity are likely to vary during the growth season of juvenile. Coastal benthic invertebrates, main prey of bentho-demersal fish in nurseries (Morin et al., 1999; Amara et al., 2001; Dolbeth et al., 2008), show seasonal variations in their biomass and production (Beukema, 1974; Saulnier et al., 2019). In spring, increasing temperature, day length and nutrients availability lead to an increase of primary production fuelling the secondary production of benthic invertebrates (combination of growth and recruitment). On the contrary, in autumn, a combination of weight loss, mortality and decrease of food resources result in a decline in benthic invertebrates production (Saulnier et al., 2019). Simultaneously, juvenile fish also show seasonal variations in their spatial distribution related to their ecological tolerance to the estuarine physico-chemical context (Amorim et al., 2018) as well as variations of their dietary preferences with ontogeny (Lawson et al., 2018). Primary producer blooms in early summer may also affect the structure of coastal and estuarine food web (Vinagre et al., 2012). Hence, it was suggested that the trophic carrying capacity has been reached only at some moment of the growth season (Pihl, 1985; Chevillot et al., 2017). The post-settlement period in nurseries is often described as highly sensitive for juvenile fish (Geffen et al., 2011). We assumed that massive arrival of juvenile fish in nurseries at the beginning of the growth season (late spring) could result in the reaching of the top of the trophic carrying capacity during this short period. Conversely, the end of the growth season (late summer-early autumn), with low food resources and demand of grown fish could also lead to food limitation.

In addition to strong temporal variations, nurseries are seascapes composed of a mosaic of habitats (Nagelkerken et al., 2015) shaped by environment gradients (Dauvin et al., 2017; Dutertre et al., 2013) and man-made modifications (Dauvin and Desroy, 2005). Environmental gradients cause spatial heterogeneity in basal sources of food web (Darnaude et al., 2004; Deegan and Garritt, 1997) and in benthic communities (Dauvin and Desroy, 2005). Habitats within an estuary provide different type and amount of resources for juvenile fish (Day et al., 2020a; Freitas et al., 2016; Shaw and Jenkins, 1992) which could imply difference in trophic carrying capacity at the habitat scale. Walters and Juanes (1993) suggested that when studying density-dependence regulation in early stages of fish, the notion of habitat use needed to be considered. Furthermore, in a context of habitat loss and coastal degradation (Lotze, 2006), it is particularly important to include the notion of habitats in the study of nursery function.

In this study, we quantified changes in trophic carrying capacity in juvenile fish nursery at fine spatiotemporal scales *i.e.* the scale of its various habitats at the beginning (after fish settlement on the nursery, in June) and at the end of the growth season (in October). Thus, the first aim of the study consisted in the adaptation of the bioenergetics-based model of trophic capacity (Tableau et al., 2019) to these scales. To do so, we combined this model with outputs from stable isotopes mixing models to re-allocate the fish consumption over the habitats according to our findings on the fish feeding preferences between habitats (Day et al., 2020a) and adapted parameters to match the monthly scale of our study. Secondly, we focussed on fish consumption and estimated its monthly dynamics over the growth season in 2017 to improve our understanding of the trophic carrying capacity variations between the two periods studied. Finally, we estimated exploitation efficiency of benthic prey by juvenile fish to evaluate whether or not the trophic carrying capacity has been reached at the beginning and the end the growth season and in each habitat composing the fish nursery.

## **3.3 Material and methods**

## 3.3.1 Sampling site

The Seine estuary is located on the northwest coast of France and opens into the English Channel (Fig. 1). It has experienced major morphological alterations over the past century: dikes, navigation channel and more recently, enlargement of Le Havre harbour in the estuary mouth (in 2000). These changes have notably caused significant habitat loss with a decrease in intertidal areas, from ~130 km<sup>2</sup> in 1850 to 30 km<sup>2</sup> at the beginning of the 21<sup>st</sup> century (Dauvin *et al.*, 2006) and decrease of total potential nursery ground of 33% (Rochette *et al.*, 2010). Direct consequence on juvenile fish have been reported with a decrease of 42 % of the production of *Solea solea* juvenile linked to surface loss (Rochette *et al.*, 2010). Moreover, the benthic communities are spatially heterogeneous, shaped by environmental gradients and

man-made infrastructures (Thiébaut *et al.*, 1997; Baffreau *et al.*, 2017) and offer highly variable levels of production from one habitat to another (Day et al., 2020a).

In this study, the Seine estuary was divided into five sectors (hereafter, "habitats", Fig. 1) adapted from Tecchio et al. (2015) and Dauvin and Desroy (2005): four subtidal habitats and an intertidal habitat. The estuary mouth is the largest marine habitat (115 km<sup>2</sup>). The navigation channel (17 km<sup>2</sup>) allows access to Rouen harbour. It is surrounded by the southern channel (33 km<sup>2</sup>) and northern channel (16 km<sup>2</sup>). The northern channel is contiguous to Le Havre harbour and intertidal mudflats (5 km<sup>2</sup>), which are located upstream, on the north coast.



Figure 1: Locations of the sampling stations (black stars: grab station and blue lines: trawl station) in the four subtidal habitats (grab and trawl; EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel) and the intertidal habitat (grab only; IM: intertidal mudflats). Solid lines are the trawl stations from the historic survey conducted monthly, dotted line are the trawl stations sampled in June and October 2017 for this study in addition.

#### **3.3.2** Data collection and selection

Data collection was realized in 2017. Sampling surveys targeting benthic invertebrates were conducted twice in the year: at the beginning (~ fish arrival on the nursery in June) and the end of the growth season (October) and in the five habitats. Sampling surveys targeting fish were conducted monthly between May and October according to an historic survey conducted monthly from 2000 to 2017 in the Seine estuary (solid lines in Fig. 1). To extent the spatial coverage of the study, additional trawl sampling points were added in the marine part of the estuary (dotted lines in Fig. 1) twice in 2017 (at the beginning and the end of the growth season). Fish surveys were conducted in the four subtidal habitats. All dates of data collection are detailed in Table S1.

## Macrofauna and meiofauna sampling

Benthic invertebrates were sampled applying the same protocol as in Day et al. (2020a). Benthic macrofauna (> 1 mm) and meiofauna (< 1 mm) were sampled at 25 stations in the Seine nursery (5

stations per habitat). Sampling was conducted using a 0.1 m<sup>2</sup> Van Veen grab with three replicates at each station. A core sample (3.6 cm in diameter, 8 cm high) was extracted from each replicate and placed in a 4% formaldehyde solution for meiofauna biomass estimation. The rest of the three replicates were sieved through a 1 mm grid mesh and kept in a 4% formaldehyde solution diluted in marine water. In the laboratory, macrofaunal invertebrates were sorted from residual sediments, identified to the lowest taxonomic level, counted and weighed. Biomass per taxa was determined as ash-free dry weight. Data from the three replicates from each sampling station were summed, and abundance and biomass were standardised based on the area sampled (*i.e.* three replicates of 0.1 m<sup>2</sup> expressed per m<sup>2</sup>). Meiofauna samples were sieved (38  $\mu$ m grid mesh) and organisms were separated from inorganic matter. Biomass was estimated for each station as ash-free dry weight.

## **Prey selection**

The prey selection within the macrofaunal benthic organisms was completed according to the same steps conducted in Day et al. (2020a) or Saulnier et al. (2020). First, rare species and species poorly sampled with the grab were excluded from the analyses as they add little to the analysis. After, all benthic invertebrates from macrofauna were *a priori* considered as potential prey for the community of juvenile fish according to their opportunistic feeding behaviour. Nevertheless, prey larger than the mouth size of biggest fish were excluded (Besyst et al., 1999; Johnson et al., 2012). Thus, according to Day et al. (2020b), Saulnier et al. (2020) and Tableau et al. (2015), species with mean individual body mass inferior to 0.1 g AFDM ind<sup>-1</sup> were kept as potential prey.

## **Fish sampling**

As done in Day et al. (2020a), fish were sampled in the four subtidal habitats using a 2 m wide and 0.3 m high beam trawl with a 5 mm mesh stretched in the cod end. Hauls were performed at a mean speed of 2.5 knots in the opposite direction of the tide for 10 min during daylight hours. The number of hauls in each habitat was proportional to its area. Fish were identified, counted, weighed and measured by species on board at each station.

## Fish species and young-of-the-year selection

We selected nine marine nursery-dependent species of fish at the G0 (young-of-the-year) and G1 (1year old) stages: *Solea solea* (common sole) and *Pleuronectes platessa* (plaice), *Limanda limanda* (dab), *Platichthys flesus* (European flounder), *Merlangius merlangus* (whiting), *Dicentrarchus labrax* (sea bass), *Trisopterus luscus* (bib), *Callionymus lyra* (dragonet) and *Pomatoschitus* sp. (sand gobies). On average, these species represented 81% and 87% of the total weight of bentho-demersal fish caught in spring and autumn, respectively. Size thresholds from monthly fish size spectra in 2017 were used to distinguished G0 from G1 stages and G1 from older fish for each month and species. When necessary, size fish data from the monthly historic survey were used.

G0 and G1 stages of the flatfish species (*S. solea*, *P. platessa*, *L. limanda* and *P. flesus*) and *C. lyra* consume mainly benthic macrofaunal invertebrates such as bivalves, crustaceans and polychaetes (Le Mao, 1986; Morin *et al.*, 1999; Amara *et al.*, 2001; Kostecki *et al.*, 2012). Small individuals (< 40 mm) also consume small prey from the meiofaunal invertebrates community such as copepods (Pihl, 1985; Gee, 1989; Coull, 1990). G0 stages of *M. merlangus*, *D. labrax* and *T. luscus* feed partly on benthic macrofauna whereas G1 stages of these species target small fish as prey (Morin *et al.*, 1999; Pasquaud *et al.*, 2008; Demain *et al.*, 2011b). Hence, only G0 stages of these three species were included as well as G0 and G1 stages of flatfish species and *C. lyra*.

## 3.3.3 Data analysis

Trophic carrying capacity of the nursery was computed using the bioenergetics-based model recently developed by Tableau et al. (2019) and refined by Saulnier et al. (2020). The bioenergetics-based model quantifies on the one hand, the energy supply of prey selected from the benthic invertebrate community called Food Production (FP) and, on the other hand, the dietary needs of benthivorous juvenile fish, the Food Consumption (FC) (Tableau *et al.*, 2019b). Trophic carrying capacity and food limitation were examined by estimating the ratio of juvenile fish FC to benthic FP: the Exploitation Efficiency of juvenile fish on the benthic invertebrate community.

The model was initially developed to estimate FP and FC at the scale of the whole growth period (~ integrated from May to October) and at the scale of the habitats and then summed over entire nursery area. Hence, the habitat scale was already implemented to estimate FC but was not relevant in the initial model as FC within a given habitat would result from fish only present on the habitat during data collection, which is most likely false. In this study, the model was adapted to be able to estimate trophic carrying capacity at fine spatio-temporal scales (the scale of the habitat and the period) in order to identify the period and the habitat most likely leading to trophic limitation (*e.g.* trophic competition).

This methodological adaptation involved three major changes:

- Estimate of FC at the period scale (~monthly scale)
- Estimate of FC on untrawled habitats (spatialization)
- Estimate of FP at the period scale (~monthly scale)

## Food Consumption (FC) and the beginning and end of the growth season

FC is the quantity of food consumed over a certain period by a community of consumers. First, the fish production is estimated and then converted into FC.

Fish production for a juvenile cohort was estimated as:

(1) 
$$\boldsymbol{P}_{h,p} = \overline{N}_{h,s} \times (\overline{w}_{p,d_0} - \overline{w}_{p,D})$$

with  $P_{h,p}$  the production over the period p in a the habitat h for a fish cohort,  $\overline{N}_{h,s}$  the mean density of fish cohort at the mean date of the survey s and in the habitat h,  $\overline{w}$  the mean individual body weight at the beginning of the period ( $d_0$ ) and at the end of the period (D). Both periods were set to 30 days in order to ease the comparison between them. The dates of beginning and end ( $d_0$  and D) for each period were set to 15 days before the mean date of the survey s and 15 days after.

Fish production using equation (1) assumes that the mean density of fish cohort was representative of the 30 days selected around the mean date of the survey. This means that fish density was considered constant over the 30 days even though it might have shown positive or negative linear tendency over the period. Given our dataset this assumption was difficult to verify.

Mean individual body weight was estimated as a function of fish length, growth and using the lengthweight relationship at the beginning of the period (eq. 2.1) and at the end of period (eq. 2.2):

(2.1) 
$$\bar{\boldsymbol{w}}_{p,d_0} = a \times (L_s - G_p \times (d_s - d_0))^k$$

(2.2) 
$$\overline{\boldsymbol{w}}_{p,D} = \boldsymbol{a} \times (L_s + G_p \times (D - d_s))^b$$

with *a* and *b* the coefficients of the length-weight relationship, *Ls* the length at the date of survey *s*,  $G_p$  the daily growth rate during the period *p*, *ds* the date of the survey *s*,  $d_0$  the date of the beginning of the period and *D* the date of the end of the period. The coefficients *a* and *b* were collected in the literature (Material S1).

Daily growth rates were estimated for each period, as this parameter is not constant over the growth season for juvenile fish. Indeed, during their first year, growth rate increases at the beginning of the growth season, then stabilises and finally declines until the end as reviewed for *P. platessa* (Ciotti *et al.*, 2014). This pattern was also observed for *S. solea* (Amara, 2003; Teal *et al.*, 2008) and *L. limanda* (Amara, 2003). Growth rates increases in spring to summer, diminishes until the winter and restarts in Marsh again (Amara, 2003). It also appeared that the timing of growth declines may vary spatially (Ciotti *et al.*, 2013b), with differences in timing among nurseries. Hence, we decided to use local data to estimate growth rates at the beginning and at the end of the growth period. We used length data from the monthly historic survey from 2000 to 2017 (unpublished data) which were collected as in the protocol described in this study. For each month and each year, we calculated the mean date of collection and the mean length.

Daily growth rates for each period were estimated by modelling the evolution of mean fish length as a function of time and extracting growth rates for each period. Different models were tested to model

growth over time: linear regressions (with time as continuous and time as factor) and nls with different growth equations (Von Bertalanffy and Gompertz growth functions and logistic regression). The best model was selected using AIC criterion and extracted of growth rates for each period using the coefficients estimated (in case of linear regression as the best model) or the derivative of the modelled function using estimated parameters (in case of nls as the best model). Details on the model selection are included in Material S2.

Finally, FC was estimated in each habitat h and at the two periods considered p as following:

(3) 
$$\boldsymbol{FC}_{h,p} = \sum_{i \in 1:I^{th} fish \ cohort} P_{i,h,p} \times \frac{1}{q_i} \times E_i \times \frac{1}{K_i} \times DC_{i,p}$$

with  $P_{i,h,p}$  the fish production for the fish cohort *i* in the habitat *h* for the period *p*, *q<sub>i</sub>* the catch efficiency of the trawl,  $E_i$  the energy density to convert fish production in energy units,  $K_i$  the gross conversion efficiency which converts fish production to fish consumption (the quantity of ingested energy required to produce one energy unit of juvenile fish), and  $DC_{i,p}$  the diet composition *i.e.* the proportion of benthic macrofauna and/or copepods harpacticoids in the diet. q, E and K were collected from the literature (Material S1).

Diet composition may vary along the growth period as fish diet changes with ontogeny (Aarnio *et al.*, 1996; Amara *et al.*, 2001) and according to prey availability (Molinero and Flos, 1992). Moreover, FP estimates were composed of proportion of macrofauna and/or proportion of harpacticoids (meiobenthic copepods) according to the species and period. Information of each species diet and its associated values (proportion of macrofauna and harpacticoids) were collected from the literature and details are presented in Material S3.

## **Spatialization of the Food Consumption**

FC was estimated at the habitat scale (Fig. 1). The only parameter in the FC equations which is spatially explicit is the mean density of fish. When computing FC of a habitat using mean density of fish from this habitat, it was assumed no movement of fish among habitats or that fish fluxes in and out are equal. Although flatfish species are known to have limited movements within nursery (< 10 km, Le Pape and Cognez, 2016), roundfish species may move from one habitat to another enabled by their swimming abilities. Furthermore, juvenile fish within nursery can use tidal movements to reach intertidal areas to feed at high tide (Cabral, 2000; Laffaille et al., 2001; Morin et al., 1999). Since beam trawl sampling in the intertidal mudflats was not technically feasible, no juvenile fish densities could be estimated whereas a part of the FC was probably realized in this habitat. Thus, FC was re-allocated over the habitat combining the FC estimates in each habitat and the outputs of SIMM from Day et al. (2020a) for G0 fish of *S. solea*, *P. platessa*, *M. merlangus* and *D. labrax*, we used their estimated  $\alpha$ . In the present study, thanks to N and C stable isotopic data available for June and October,  $\alpha$  were estimated for G1 according the same method. Several SIMM were run to take into account the uncertainty on the trophic

discrimination factors (key parameter of SIMM). The re-allocated FC were the matrix product of the non-re-allocation FC with the matrix of coefficients from the SIMM such as:

$$(4) \qquad \begin{bmatrix} FC(r)_{EM} & FC(r)_{SNC} & FC(r)_{IM} \end{bmatrix} = \begin{bmatrix} \alpha_{EM-EM} & \alpha_{EM-SNC} & \alpha_{EM-IM} \\ \alpha_{SNC-EM} & \alpha_{SNC-SNC} & \alpha_{SNC-IM} \\ \alpha_{NAV-EM} & \alpha_{NAV-SNC} & \alpha_{NAV-IM} \end{bmatrix} \mathbf{x} \begin{bmatrix} FC(nr)_{EM} \\ FC(nr)_{SNC} \\ FC(nr)_{NAV} \end{bmatrix}$$

with  $FC(r)_h$ , the FC re-allocated to the habitat h,  $FC(nr)_h$ , the FC non-re-allocation from the habitat h,  $\alpha_{h1-h2}$  the mean of the medians of the posterior distributions of the relative contribution of the habitat h1 on the diet of the fish from the habitat h2. Southern and northern channels were merged in SIMMs as they could not be differentiated in their isotopic compositions. Nevertheless, results were presented at the scale of the habitat (Fig. 1) to ease to comparison before and after the re-allocation.

For *P. flesus* and *L. limanda*, we used the same  $\alpha$  as *S. solea* as we assumed similar swimming abilities (Le Pape and Cognez, 2016) and feeding behaviour between the three species. Moreover, the distribution of *P. flesus* and *L. limanda* over the habitats was similar to that of *S. solea*. For *T. luscus*, we used the same  $\alpha$  as *M. merlangus*. We also assumed that as gadiforms, both species also have similar swimming abilities and feeding behaviour. For *C. lyra* and *Pomatoschistus* sp., we did not re-allocate the FC. *C. lyra* was concentrated in the estuary mouth and most likely stayed there to feed. Concurrently, we assumed very low mobility for the resident fish species, *Pomatoschistus* sp.

#### Monthly dynamics of Food Consumption

Monthly fish data were analysed to estimate monthly FC providing information on the dynamics of the FC between the two dates for which exploitation efficiency was estimated (beginning and end of the growth period). This was done using fish data collected monthly from historic survey (Fig. 1). FC was thus estimated monthly from May to October covering, however, a smaller geographic scale than the survey used in 2017 (Fig. 1). Estimates were realized at the bay scale without any food re-allocation, as we deemed the  $\alpha$  too uncertain for the months without isotopic sampling. The growth parameters (*G*, eq. 2.1 and 2.2) were extracted from the growth models described above. For the diet composition parameter (DC, eq. 3), the proportions of macrofauna and harpacticoids DC were selected as follows: for May and June, DC from the beginning of the growth period were attributed while for the other months, values from the end of the growth period were used.

## Food Production (FP) and the beginning and end of the growth season

FP is the quantity of food produced by benthic invertebrates over a certain period. Benthic invertebrates species from the macrofauna are commonly observed in juvenile fish stomach contents in temperate nursery (Le Mao, 1986; Morin *et al.*, 1999; Amara *et al.*, 2001; Dolbeth *et al.*, 2008), as well as meiofauna for smaller individuals (Pihl, 1985; Gee, 1989; Coull, 1990; Aarnio *et al.*, 1996; Andersen *et al.*, 2005). Hence, the FP was estimated from these two compartments of potential prey.

Meiofauna is roughly composed of nematodes and harpacticoids copepods. Even if nematodes are abundant in the environment they are not exploited by juvenile fish, like *S. solea* (Jinadasa *et al.*, 1991). Harpacticoids were collected in stomach content of small juvenile fish (Andersen *et al.*, 2005; Amara *et al.*, 2009) early in the growth season (between May and June). Moreover, *Pomatoschistus* sp. is also known as a meiofauna consumer (Pihl, 1985; Doornbos and Twisk, 1987; Salgado *et al.*, 2004). Harpacticoids were included in FP estimates by taking 2% of the total meiofauna biomass (Heip *et al.*, 1990; Chardy and Dauvin, 1992). To estimate production of harpacticoids, we needed individuals mean body weight which was found in the literature (~1  $\mu$ g, Heip et al., 1984; Smol et al., 1994; Widbom, 1984).

(5) 
$$FP_{h,p} = \sum_{j \in 1:J^{th} \text{ prey species }} B_{h,s,j} \times \left(\frac{P}{B_{p,j}} \times \beta_p\right) \times (1+R_j) \times E_j$$

with  $FP_{h,p}$ , the Food Production in each habitat *h* and period *p*,  $B_{h,s,j}$  the mean biomass observed at the date of the survey *s* in the habitat *h* and for the species *j*,  $P/B_{p,j}$ , the production-to-biomass ratio estimating from an empirical model (Brey, 2012) and  $\beta_p$  a seasonal coefficient to transform annual production-to-biomass ratio into monthly production-to-biomass ratio,  $R_j$  a regeneration coefficient as some species can regenerate from cropping (Tableau *et al.*, 2015) and  $E_j$  the energy density (Brey *et al.*, 2010).

Production-to-biomass ratio refers to the production of an entire population over a year (in yr<sup>-1</sup>). In this study, we needed to estimate FP at two specific periods (June and October) with one sample date per period. To do that, we estimated monthly production-to-biomass ratio using coefficients ( $\beta$ ). The production period (defined as  $\frac{dB}{dt} > 0$ ) in temperate estuary for benthic invertebrates lasts around seven months (March-April to September-October) (Beukema, 1974; Saulnier et al., 2019). The productionto-biomass ratio is likely not constant over this period. However, to our knowledge, there is no study on direct temporal variations of production-to-biomass ratio for benthic invertebrates in temperate estuaries. Given this, we decided to adopt a precautionary approach and elaborated several scenarios (Table 1). The first scenario (Sc1) assumed that production-to-biomass ratio was constant over time. The annual production-to-biomass ratio was divided by the number of months within the period of production (7 months). The second scenario (Sc2) assumed that production-to-biomass ratio varied according to the variations of the relative biomass (ratio of monthly estimate to annual mean) from the supplementary of Saulnier et al. (2020) based on the study of seasonality of benthic macrofauna biomass (Saulnier et al., 2019). For each month, we calculated the ratio of the relative biomass increase over the total relative biomass increase between April and September.  $\beta$  for the beginning of the growth season was the mean between this ratio in May and June (23 %) and  $\beta$  for the end of the growth season was the mean between this ratio in August and September (2.5 %). The rationale of Sc2 was to set  $\beta$  such as the production-to-biomass ratio would be at a higher value at the beginning of the growth season than at the end. In some studies, harpacticoids (meiobenthic copepods) showed a seasonality in the abundance

(Rutledge and Fleeger, 1993; Dahms and Qian, 2004) with highest densities in the warmer season (Dahms and Qian, 2004).  $\beta$  for harpacticoids were set similarly to  $\beta$  for macrofauna in Sc1 and Sc2. However, meiobenthic copepods have shorter turn-over and reproduce regularly (Coull and Vernberg, 1975). Hence, a third scenario (Sc3) assumed no seasonality in harpacticoids' productivity and seasonality in macrofauna invertebrates' productivity.

Table 1: Summary of the Food Production scenarios used with the  $\beta$  coefficients associated at the beginning and the end of the growth season. M: macrofauna; h: harpacticoids (meiobenthic copepods).

	Brief description		β	References
		Beginning	End	
Sc1	Productivity (P/B ratio) is	$\frac{1}{7}$ for both	h periods	
	constant over time <i>i.e.</i> no	M a	nd h	
	seasonality in the productivity			
Sc2	Productivity ratio varies over	23 %	2.5 %	Beukema, 1974; Dahms and Qian,
	time within the period of	M and h	M and h	2004; Saulnier et al., 2019
	production for M and h			
Sc3	Productivity ratio varies over	M: 23 %	M: 2.5 %	Beukema, 1974; Coull and
	time within the period of	h: $\frac{1}{7}$	h: $\frac{1}{7}$	Vernberg, 1975; Saulnier et al.,
	production only for M	,	/	2019

## Exploitation efficiency (EE) and uncertainty analysis

*EE* is the part of the *FP* which is consumed by juvenile fish, i.e. *EE* (in %) is the ratio of *FC* over the *FP*. We estimated EE for G0 and G1 as follows:

(6) 
$$EE(G0) = \frac{FC(G0)}{FP(M \text{ and } h)} \times 100 \text{ and } EE(G1) = \frac{FC(G1)}{FP(M)} \times 100$$

with FP(M and h) the FP of macrofauna invertebrates and harpacticoids, and FP(M) the FP of macrofauna invertebrates only.

Uncertainty in FP, FC and EE estimates were quantified through Monte-Carlo simulations (10000 iterations). Variables and parameters were divided into three categories (Tableau *et al.*, 2019b): (1) those with quantifiable and high uncertainty for which probability distributions were defined, (2) those with low uncertainty as they came from local surveys for which fixed values were used, and (3) those with unquantifiable uncertainty for which fixed values were also used adopting a conservative approach to minimize EE estimates. Details on uncertainty of variables and parameters are included in Material S4.

## 3.4 Results



## 3.4.1 2017: a year with low densities for many juvenile fish cohorts

Figure 2: Mean density (ind m<sup>-2</sup>) calculated as the average of the monthly means from May of October by fish species and cohort. Grey is for the 2000-2017 period and orange is for 2017 only.

Globally, 2017 was a year with densities of fish lower than the average estimated between the 2000-2017 period (Fig. 2). Densities were especially low in 2017 for both cohorts of *P. platessa* and G0 *T. luscus*. There were exceptions for *M. merlangus* G0 with mean densities in 2017 almost four times higher than the mean of the 2000-2017 period. *D. labrax* G1 also showed mean densities in 2017 higher than that of 2000-2017 period (Fig. 2).

## 3.4.2 Monthly dynamics of FC between May and October in 2017

FC at the scale of the bay of Seine was estimated between May and October using the monthly data collected within the historic survey area in 2017 (Fig. 3).

For the G0 fish community, the FC at the scale of the bay increased from May to October with the exception of September (Fig. 3A). FC resulted from the fish density and the individual body weight gain (the two parameters that vary monthly in the equation 2). Individual body weight gain increased from May to October as a function of fish length. In October, individual body weight is around five time higher than in May (Fig. 3B2). Mean fish density increased from May to a peak in August, dropped in September and rebounded slightly in October (Fig. 3B1). In parallel, all species (9 species included in the study) were present on the area studied from July. *C. lyra*, *D. labrax* and *L. limanda* were absent during the first months (Fig. 3B3).

For the G1 fish community, the FC at the scale of the bay was the highest in June (Fig. 3A). It drastically decreased in July and then stabilized for the rest of the studied period. Mean fish density also peaked in June and then decreased until October (Fig. 3B1). Individual body weight gain increased during the season for all species logically as fish grew (Fig. 3B2). The number of fish species present in the area was lower in August and September (*P. platessa* and *L. limanda* were absent).



B3. Number of species present (over the species studied)



Figure 3: Monthly dynamics between May and October of (A) the Food Consumption of G0 and G1 fish and the main factors which drive FC: (B1) Mean density of fish species in ind m<sup>-2</sup> (B2) mean individual body weight gain between the beginning and the end of the month in g ind<sup>-1</sup> and (B3) the number of species present on the area of study over the number of species included in the study (9 for G0 fish and 6 for G1 fish).

## 3.4.3 Spatially-explicit trophic carrying capacity in June and October 2017

## Food production in June and October

Scenarios on the seasonality of ratio P/B influenced greatly the FP estimates in both periods *i.e.* beginning and end of the growth season for juvenile fish in nursery (Fig. 4). Under Sc1 (no seasonality in the P/B ratio *i.e.*  $P/B_{june} = P/B_{october} = 1/7$  of the annual P/B), FP were of the same order of magnitude in both periods (Fig. 4). FP estimates at the end of the growth season were slightly higher than at the beginning. Under Sc2 (the ratio P/B varies seasonally) and Sc3 (the ratio P/B varies seasonally only for macrofauna species), FP estimates were largely higher at the beginning of the growth season than at the end. Differences between periods were accentuated under Sc2 as productivity of harpacticoids was also higher at the beginning of the growth season, contrary to Sc3 (Fig. 4).



Figure 4: Food production reported to the habitat area (in kJ m<sup>-2</sup> month<sup>-1</sup>) at the beginning and the end of the growth season for juvenile fish in nursery and by scenario of seasonality of production of macrofauna (brown) and harpacticoids from the meiofauna (blue). In October, food production is only macrofauna production. Thick black lines represent 50% of the confidence interval and thin black lines, the 95% confidence interval of total FP estimated by Monte Carlo simulations. The beginning of the growth season for juvenile fish in the nursery corresponds to end of May/June the end, to end of September/October.

FP, reported to the habitat area (kJ m<sup>-2</sup> month<sup>-1</sup>), was the highest in the intertidal mudflats at the beginning and at the end of the growth season with 42% to 44% according to FP scenarios, followed by the estuary mouth (Fig. 4). At the end of the growth season, FP was the highest in the estuary mouth under Sc1 and Sc2 (34% in both scenarios) and in northern channel under Sc3 (36%) (Fig. 4). The areas of the different habitat greatly vary from 5 km<sup>2</sup> (intertidal mudflats) to 110 km<sup>2</sup> (estuary mouth). When estimated for the entire area of each habitat, FP estimates were higher in the estuary mouth, which is also the largest habitat (Fig. S1).

The proportion of FP attributed respectively to macrofauna and harpacticoids varied among habitats and with the period, with the part of the macrofauna varying from 0 to 86% whereas the part of the harpacticoids between 14 to 100% (Table S2). The estuary mouth was the habitat with the highest macrofauna percentages, [51-86] %. The navigation channel was largely dominated by harpacticoids (Table S2). In the three other habitats, the composition varied with the period and the FP scenario.





Figure 5: Fish consumption (in GJ month<sup>-1</sup>) at the *beginning* and the *end* of the growth season for juvenile fish in nursery and by cohort (top) none re-allocated (*i.e.* estimated using densities of fish collected in each habitat) and (bottom) re-allocated (*i.e.* estimated combining outputs from SIMM with FC none re-allocated). Thick grey lines represent 50% of the confidence interval and thin grey lines, the 95% confidence interval of total FP estimated by Monte Carlo simulations. Note that the y scales are different for G0 (max = 300 GJ) and G1 (max = 2225 GJ).

FC reallocation allows the estimation of FC in the intertidal mudflats, where sampling could not have been done for fish. According to the values obtained, they were the second habitat in terms of FC at the beginning of the growth season for both G0 and G1 and at the end of the growth season for G0, with

around 20% of the total consumption realized by juvenile fish (Fig. 4B). FC estimates in the estuary mouth were the highest observed for all the cohorts notwithstanding the sampling periods (Fig. 4AB). The re-allocation of the FC in that habitat had the effect of decreasing the FC values of ~ 25% on average for all the cohorts from the two periods (Fig. 4B). Hence, the re-allocation of the FC had the effect of balancing contributions among habitats (except for the navigation channel), presumably representing the actual consumption of fish (Fig. 4B). FC re-allocation also affected the FC in the southern and northern channels: FC was higher in the southern channel before re-allocation and, on the contrary, it was higher in the northern channel after re-allocation (Fig. 4AB). Finally, in the cases of no re-allocation or re-allocation of FC, the FC estimates for G1 fish were higher than those for G0 fish at the beginning of the growth season, whereas the reverse was observed at the end of the growth season (Fig. 4B).



Figure 6: Fish consumption (re-allocated *i.e.* estimated combining outputs from SIMM with FC none reallocated) *reported to the habitat area* (in kJ m<sup>-2</sup> month<sup>-1</sup>) at the *beginning* and the *end* of the growth season for juvenile fish in nursery and by cohort. Note that the y scales are different for each panel.

As mentioned for the FP, the different habitats vary greatly in their total area (5 km<sup>2</sup> to 110 km<sup>2</sup>). When FC is reported to the habitat area (*i.e.* kJ.m<sup>-2</sup> month<sup>-1</sup>), the intertidal mudflats become the main contributor to FC with 53 % and 66 % respectively at the beginning and the end of the growth season for G0 fish community, and 83 % and 54 % respectively at the beginning and the end of the growth season for G1 fish community (Fig. 6).

The G0 fish FC split between the two prey compartments. At the beginning of the growth season, G0 fish FC on macrofauna was nearly equal to FC on meiofauna (Table S3). At the end of the growth season, only *Pomatoschistus* sp. had DC for harpacticoids with positives values which resulted in FC on meiofauna only by *Pomatoschistus* sp. It was then between 0 and 20% (Table S3).

#### Exploitation efficiency over the habitats in June and October

Generally, EE estimates were highest at the end of the growth period for G0 fish and the beginning for G1 fish (Fig. 7). The mean value of EE estimates over scenarios and habitats were 0.5 % and 7 % for G0 fish community and 21 % and 6 % for G1 fish, the beginning and the end of the growth period respectively.

In the detail, the G0 fish community show EE estimates between 5 to 20 times higher (depending on the FP scenario) at the end of the growth season than at its beginning: EE estimates never exceeded 1.5% in the beginning of the growth season whereas it reached for instance 42% in one of the FP scenario (Sc2). For G1 fish community, the differences between the two periods were most noticeable in Sc1 with EE sometimes reaching EE values ~ 70% (in the northern channel) in comparison to the two other scenarios where EE values were in the same order of magnitude (~ 40%; Fig. 7). It is worth mentioning that the results from Sc2 and Sc3 were very similar as only the FP from macrofauna species was included in the EE ratio of G1 fish community. The two scenarios are not equal due to Monte-Carlo simulations (Fig. Sc3).



Figure 7: Mean estimates of EE for G0 fish over both prey compartments (harpacticoids and macrofauna) and G1 over macrofauna prey in each habitat at the beginning (blue) and the end (gold) of the growth season by FP scenarios. The confidence intervals are not represented here for a better clarity in the figure but incertitude around EE estimates generated by Monte-Carlo simulations are presented in Figures S2A and S2B.

As FC of G0 fish was divided over both compartments of prey (*i.e.* harpacticoids and macrofauna), we also estimated EE for both compartments (Fig. S3). Thus, with mean values that did not exceeded 3%, EE estimates of G0 over harpacticoids were much lower than the ones over macrofauna, especially in northern part of the estuary at the end of the growth period where EE estimates reached almost 85% in the intertidal mudflats around 10% in the northern channel (under Sc2 and Sc3). Comparison of the EE

among the habitats showed the same pattern for the G0 and G1 fish communities, with higher EE values in the northern channel (NC) and intertidal mudflats (IM) at the beginning of the growth season and higher EE values in the intertidal mudflats at the end of the growth season (Figs. S2A and S2B).

FC re-allocation over the habitats modified the conclusions on EE spatial repartition (Fig. S4). When no re-allocation of FC is done, the navigation channel show artificially very high values of mean estimates of EE. This is especially observable for G1 as FP by macrofauna was very low in this habitat but FC was estimated high.

## 3.5 Discussion

# **3.5.1** Intertidal mudflats and subtidal marine habitat: main contributors to trophic carrying capacity

Assuming that habitats showing the highest FP and FC values are main contributors to the trophic carrying capacity, we then consider the estuary mouth and the intertidal mudflats as essential habitats contributing to the trophic carrying capacity of the bay of Seine.

## Estuary mouth and intertidal mudflats: food resource providers

The estuary mouth was the largest habitat and presented the highest production values at both periods whatever the FP scenario and even when reported to its area. Supported by the fine sand *Abra alba-Lagis koreni* community (Thiébaut *et al.*, 1997), it was already described as the most productive habitat at the annual scale (Saulnier *et al.*, 2020) or presenting the highest biomasses of macrobenthic invertebrates (Thiébaut *et al.*, 1997; Dauvin and Desroy, 2005). The average monthly production calculated (see Sc. 1) from the annual FP estimated for this habitat by Saulnier et al. (2020) between 2008 and 2010 ranged from 50 to 170 kJ m<sup>-2</sup>. The 2017 estimates in our study were in the same order of magnitude with 100 kJ m<sup>-2</sup> and 200 kJ m<sup>-2</sup> at the beginning and the end of the growth period respectively.

The intertidal mudflats was also a productive habitat relatively to its small area (20 times smaller than estuary mouth), especially at the beginning of the growth season. The production was dominated by *Hediste diversicolor* and *Corophium volutator*, the two main species composing intertidal mudflats community (Baffreau *et al.*, 2017). On the contrary, the navigation channel presented the lowest macrobenthic production values: that habitat is regularly dredged to allow access to Rouen harbour, a major French harbour. However, the harpacticoids production seemed less affected by the regular defaunation of the navigation channel.

## Contribution of harpacticoids copepods to FP

Harpacticoids production values were around the same order of magnitude of the macrobenthic production values in all habitats (except in the estuary mouth). These values are very high compared to literature data. Indeed, Heip et al. (1984) estimated that the production of macrofauna was similar to the total production of meiofauna, including nematodes and copepod harpacticoids (representing 2% of the meiobenthic community in here). Production stems from three main parameters: production-to-biomass ratio, mean individual body weight and biomass. Production-to-biomass ratio estimated for harpacticoids (Brey, 2012) was around 28 yr<sup>-1</sup> which is in the high range of literature data (Heip *et al.*, 1984, 1990) but still coherent for harpacticoids (Herman and Heip, 1985). Mean individual weight was also in the range of the values from the literature (Widbom, 1984; Smol *et al.*, 1994). Nevertheless, the biomass estimates of meiobenthic community were between 5 to 10 times higher than those measured in other European estuaries (Huys *et al.*, 1992; Smol *et al.*, 1994). Therefore, it is most likely that biomass values recorded during our study were or really very high or overestimated leading to caution considering this part of the food supply.

#### **Re-allocation of FC**

Before re-allocation, FC estimates assumed that fish collected in a habitat were the only ones that consumed within a habitat. The re-allocation of the FC over the habitats of the estuary made possible to go beyond this hypothesis and allowed the consumption of a habitat to come from individuals from other habitats. FC consumption was re-allocated combining the results obtained from the bio-energetic approach with the outputs from SIMM (Day et al., 2020a). The main effect of this re-allocation was the attribution of the FC of juvenile fish to the intertidal mudflats, where no sampling could have done but which was expected to constitute a major feeding habitat (Cabral, 2000; Day et al., 2020a; Laffaille et al., 2001; Morin et al., 1999). Choices made for SIMM affected the results of re-allocation. Primary consumers' stable isotopes ratios (i.e. sources of SIMM) from northern and southern channels overlapped which led to the merge of these habitats as a single habitat in SIMM (Day et al., 2020a). Hence, FC re-allocated to these two channels were a priori equally distributed. It also probably explained why the FC in the southern channel decreased after re-allocation whereas the one in the northern channel increased. We likely under-estimated the FC in the southern channel and overestimated it in the northern channel. One solution to overcome this issue could be the use other environmental markers. A Bayesian mixing model recently developed (Ballutaud et al., 2019), uses both stable isotopes and organic contamination and could improve the fine distribution of fish and then FC over southern and northern channels, the latter supposed to be more contaminated due to its proximity to Le Havre harbour.

When studying trophic carrying capacity, the community scale is recommended (Tableau et al., 2016) as the inclusion of all predators consuming benthic prey in FP improves the EE estimates. We chose to

re-allocate FC over habitats using SIMM. To do so, stable isotopic composition data were needed. Habitats' use within the estuary is specific, according to their ecological niches and their potential swimming abilities (Day et al., 2020a), but isotopic compositions were not assessed for some of them since they were not sampled. Hence, we used use  $\alpha$  parameters (re-allocation parameter) of *S. solea* for *P. flesus* and *L. limanda* and those of *M. merlangus* for *T. luscus*. The species for which specific isotopic compositions were obtained represented more than the half of the biomass of the juvenile fish community in 2017 (Day et al., 2020a) giving a good confidence to our results. Nevertheless, this extrapolation may be questionable particularly for *P. flesus* which exhibited high overlap of  $\delta^{13}$ C and  $\delta^{15}$ N ratios between three distinct areas in the Gironde estuary (Bay of Biscay), contrary to *S. solea* (Selleslagh et al., 2015). Moreover, G0's feeding may occur in the upstream part of estuaries as observed in the Lima estuary, Portugal (Mendes et al., 2020).

#### Relative spatial concordance between FP and FC, food limitation in upstream habitats?

After re-allocation, the consumption of juvenile fish was the highest in the habitats where prey production was also the highest *i.e.* the estuary mouth for the total consumption and the intertidal mudflats when reported to the habitat area. Thus, FP and FC coarsely coincide spatially. This result was also found in other coastal nurseries such as the bay of Vilaine (Tableau *et al.*, 2016).

It is noteworthy that EE estimates showed great differences among habitats, which means that the spatial agreement between both parts of EE was relative. EE estimates were particularly high in the intertidal mudflats and the northern channel. These two habitats are contiguous on the northern inner part of the estuary. At the beginning of the growth period, intertidal mudflats present higher temperature and high levels of prey biomass and density (Day et al., 2020a) as well as the highest prey production level of the estuary. The trophic argument is probably responsible for the attractiveness of this habitat. At the end of the growth period, the prey production in intertidal mudflats was not as attractive but the northern channel showed high prey production relatively to other habitats in October. It is then unclear why the intertidal mudflats supported a high predation pressure from juvenile fish at the end of the growth season but it anyhow resulted in very high EE estimates, in particular over the benthic macrofauna. The value of 85 % for the EE in intertidal mudflats based on the consumption of only G0 suggested that the trophic carrying capacity is likely to be reached there.

## 3.5.2 Identification of period most likely food-limited

#### G0 fish most likely food-limited at the end of the growth season

In the absence of threshold values ruling on trophic limitation, we used Tableau et al. (2019) interpretations and identified the highest values of EE (Chevillot et al., 2019) to identify the period and habitats under potential trophic limitation. For the G0 fish community, EE estimates were highest at the end of the growth period, notwithstanding the FP scenarios, suggesting that trophic limitation most

likely happened at the end of the growth period. This was reinforced by the fact that the two habitats that displayed the highest FC are also the two that supported the most important prey production.

G0 fish settle on nurseries in spring, early summer, according to hydrodynamics conditions during reproduction and early-life stages (Rochette et al., 2010). At their arrival on nursery, their individual energetic needs are very low (*i.e.* proportional to their size, < 30 mm) but they are numerous. During this period, feeding conditions seemed optimal with high food resources in early summer supported by high productivity of benthic invertebrates in temperate estuaries (Saulnier et al., 2019). Indeed, the time overlap between prey and predators when larvae settle is essential to the nursery function (Chevillot et al., 2017). The settlement (and metamorphosis for flatfish species) phase of juvenile fish in nursery is often described as very sensitive to density-dependence mortality (van der Veer et al., 1991) induced by predation (van der Veer et al., 1991; Geffen et al., 2011). In the Wadden and Irish seas nurseries, shrimps are apex predators for newly settle P. platessa and P. flesus (van der Veer and Bergman, 1987; van der Veer et al., 1991; Geffen et al., 2011). Hence, predation might be the main cause of direct mortality right after settlement for G0 fish, at the beginning of the growth period, dampening variability in yearclass strength (van der Veer and Bergman, 1987; van der Veer et al., 1991). It is noteworthy that predation occurred all along the growth period by crustaceans and fish (van der Veer and Bergman, 1987; Ellis and Gibson, 1995) at the beginning of the growth season and then by birds (Leopold et al., 1998) or seals in certain coastal bays (Aarts et al., 2019).

At the end of the growth season, EE estimates rose up to 7% at the bay scale but reached 85% for the macrofauna only in the intertidal mudflats. With mean individual body weight nearly five times higher than in early summer, G0 individual energetic needs and their consumption increased accordingly. In parallel, following the productivity seasonal hypotheses (Sc2 and Sc3), food production is reduced compared to the beginning of the growth season, thus generating a double penalty in autumn.

August corresponded to the peak of density for G0 juvenile fish resulting in FC at the scale of the entire bay almost as high as in October. In Port Erin Bay, *P. platessa* reached a peak in consumption rate at the end of July-August (Nash *et al.*, 2007). In parallel, this season was often characterized by a growth reduction, estimated from the comparison of optimal growth rate (under optimal food and temperature conditions) with realized growth rate by flatfish species in the Wadden Sea (Teal *et al.*, 2008; van der Veer *et al.*, 2010; Freitas *et al.*, 2012; Poiesz *et al.*, 2018). Some authors suggested that this was due to potential food limitation (Teal *et al.*, 2008) or reduction in prey activity during summer (van der Veer *et al.*, 2016). However, the link between summer growth reduction of juvenile fish and food has not been directly studied yet (Ciotti *et al.*, 2014). Estimates of FP in this season (for example end of July/beginning of August) would greatly help to understand if trophic limitation started in summer due to trophic competition leading to growth reduction and then, resulting in the observation of higher EE estimates in autumn.

In theory, flatfish G0 fish arrive in nursery ground at the beginning of the growth period and thus their abundances peak in May or June (Nash *et al.*, 2007). Abundance then decreases through the growth season with density-dependent mortality (van der Veer *et al.*, 1991) caused by predation and/or trophic limitation. At the end of the growth season, juvenile fish migrate out of the nursery ground for the winter. In this study, we observed, notably for *S. solea* (major species in 2017 and economically valuable) intermonth variations of abundance with abundance in July and October around the same value. It was also the case over the 15 last years. This species is euryhaline and its distribution may go beyond the study area over upstream estuary. It would be very informative to extend the area of survey to match better the area of distribution of species in order to have a better insight of the total number of individuals and avoid confusion between migration and mortality. With these data, we could use the sampling in October with the survivors from the growth season to estimate the number of fish initially present under optimal growth. We then could compare it to the actual number of fish at the beginning of the growth season.

#### G1 fish most likely food-limited at the beginning of the growth season

For G1 fish community, we observed the pattern opposite to that of G0 fish community: EE estimates were much higher at the beginning of the growth season (20%) than at the end although they were still high (6%). As for G0 fish, mechanisms that explained monthly variations of FC were growth resulting in an increase of individuals needs and fish density. In spring, G1 fish were already near or on the nursery ground with the peak of density in June. After, the density dropped which could be due to high mortality or emigration of fish to deeper areas. Emigration is more likely as (1) mortality decreases with fish length (Nash and Geffen, 2012) and (2) in July, trophic competition with G0 in the estuary may increase due G0 ontogenetic shift in diet (Aarnio *et al.*, 1996; Amara *et al.*, 2001).

However, even if G1 fish partly migrated towards deeper areas to feed, some individuals stayed on the area of study. With predatory benthic invertebrates (e.g. *Crangon crangon, Liocarcinus* spp.), they increased predation pressure on macrobenthic fauna (Pihl, 1985). Saulnier et al. (2020) estimated that the consumption of predatory invertebrates equalled the one of fish in the bay if Seine in 2008-2010. Moreover, in the intertidal mudflats, birds also exert predatory pressure and compete with juvenile fish for the macrofaunal resources (Rosa *et al.*, 2008; Horn *et al.*, 2017). This predation pressure has never been estimated for the Seine estuary to our best knowledge but could improve our understanding of trophic carrying capacity of intertidal mudflats in this ecosystem, which already seemed heavily used by fish.

#### Seasonal dynamics of production supported trophic carrying capacity in estuary

Both intertidal and subtidal habitats supported the production of prey of the nursery. Coarsely, local main primary producers of intertidal mudflats are microphytobenthos that is biofilm of microalgae, such as diatoms, and cyanobacteria, living associated with the sediment (Wohlgemuth, 1970). In the subtidal habitats, the main primary producer is pelagic with the phytoplankton. However, microphytobenthos is

also the source of carbon for consumers located in the subtidal part of tidal estuary, consumed through tidal exports of microphytobenthos to subtidal habitats (Yokoyama *et al.*, 2009; Kang *et al.*, 2015) or through the movements of motile consumers to intertidal part (Kang *et al.*, 2015). It highlighted the importance of integrate both compartments when studying trophic carrying capacity of nursey.

In spring, phytoplanktonic bloom (Heip *et al.*, 1995; Glé *et al.*, 2008) but also of microphytobenthos bloom (Savelli *et al.*, 2018) supported the secondary prey production, element of the trophic carrying capacity. Drivers of this production are mainly biotic : light, temperature, nutrients carried by river discharge (Heip *et al.*, 1995; Glé *et al.*, 2008). Another determinant in the seasonality of trophic carrying capacity is the synchrony between prey peak of production and fish demand in energy. In the Gironde estuary, Chevillot et al. (2017) demonstrated shift in the pelagic food web of the estuary caused by aa earlier peak in zooplankton production threatening the nursery sustainability.

## **3.5.3** Under estimations of EE by the model

EE were probably under-estimated as suggested by Tableau et al. (2019) and Saulnier et al. (2020). FC were under-estimated by choosing values which over-estimate catch efficiency (q) and gross efficiency (K). Moreover, all predators were not included (*i.e.* predatory invertebrates which can represent the half of the total consumption (Saulnier et al., 2020)). FP was over-estimated, especially as all macrobenthic invertebrates were considered available for the juvenile fish to feed. According to the optimal foraging theory (MacArthur and Pianka, 1966), a predator tends to maximise the ratio between energy benefice and handling and searching time. Hence, prey burrowed in the sediment or able to escape from predation are less available to juvenile fish (Tableau et al., 2015; van der Veer et al., 2016). Tableau et al. (2015) proposed a method to estimate prey accessibility to predator fish based on prey functional traits (burrowing depth and mobility) and gut contents. Taking into account this parameter led to a significant increase in EE estimates in the bay of Vilaine (Tableau et al., 2019b). Prey accessibility also depends on predator foraging behaviour. In gut contents of GO S. solea, only bivalve molluscs siphons were found whereas for P. platessa, bivalve were found whole (pers. comm. Bastien Chouquet, CSLN). Furthermore, accessibility is likely to vary with fish ontogeny and prey behavioural changes in the season, such as a summer reduction of prey activity resulting to a reduction in their availability to juvenile fish (van der Veer et al., 2016). Further investigations should be carry out to suggest seasonal coefficients of prey accessibility but would largely improve the estimation of exploitation efficiency by juvenile nurseries.

Finally, in this study we used growth rates varying with the season but estimated using mean fish length evolution with days over 15 years. Food limitation can affect individuals through reduction of growth. Hence, if food limitation occurred and affected growth rate of juvenile fish, by taking a mean growth rate over a 15 years period, we would have over-estimated this parameter. An over-estimation of growth rate would lead to an over-estimation of FC and thus higher EE estimates. This could be problematic as

we based our choices to under-estimate EE to be sure to estimate EE at its lowest value. Moreover, changes in mean length over the growth season can be associated to changes in growth rates (as we assumed) but also immigration of small fish and emigration of large fish at the beginning and the end of the growth period (Ciotti *et al.*, 2014), or apparent growth rates of survival fish (Le Pape and Bonhommeau, 2015). Individual growth predictions based on otoliths microstructure analysis would be a solution to overcome this issue and extract growth rates for each period (Poiesz *et al.*, 2018).

## 3.5.4 Conclusion

We studied the trophic carrying capacity during two potentially sensitive periods for juvenile fish within nurseries: post-settlement period at the beginning of the growth season on nursery and at the end of the growth season in nearly autumn. It appeared that if trophic limitation occurred, it would be more likely at the end of the growth season for G0 bentho-demersal fish community when food resources are low and individual needs are the highest and conversely at the beginning of the growth season for G1 benthodemersal fish when abundances are high before potential massive immigration. At the annual scale, recent studies also supported the trophic food limitation or the reach of trophic carrying capacity in several French estuaries (Chevillot et al., 2019; Tableau et al., 2019b; Saulnier et al., 2020). At the nursery scale, estuary mouth is the largest provider of food resources for juvenile fish although maximal trophic carrying capacity was probably not reached in that habitat. Intertidal mudflats are also habitats of food resources provider. Maximal trophic carrying capacity is most likely to be reached with the highest values of EE estimated in this habitat. Our conclusions are based on a single year. This particular year showed on average lower fish densities than the previous 15 years as well as levels of production in the same order of magnitude of 2008-2010 period (Saulnier et al., 2020). Hence, it could be expected that years with higher fish densities would induce more trophic competition leading to higher EE estimates.

Mechanisms controlling fish densities, *i.e.* trophic competition (intra- and/or inter-specific) and predation for the main ones, act at the fine scales studied in this study. Hence, we underline the importance and coherence of studying trophic carrying capacity at these scales. Our study provides EE estimates that tend to show that food limitation occurs for some habitat, period and age group community. Lastly, processes underlying density-dependence mortality are probably co-occurring and not exclusive (Walters and Juanes, 1993). If mortality through predation is a main factor of G0 fish density regulation just after settlement (van der Veer and Bergman, 1987; van der Veer *et al.*, 1991; Geffen *et al.*, 2011), it does not exclude also food-limitation which in turn can increase fish activity, leading to greater exposure to predation (Myers and Cadigan, 1993; Biro *et al.*, 2003).
# 3.6 Perspectives

Providing EE data at spatio-temporal scale, this study will enrich the previous ones using the same model of trophic carrying capacity (Tableau *et al.*, 2019b; Saulnier *et al.*, 2020) in order to define threshold values to rule on whether or not food limitation occurs. In the current absence of such a threshold the EE estimates could be linked to other data likely affected by food limitation. Food limitation can have non-lethal repercussions on juvenile fish (*e.g.* decline in growth or condition) and/or lethal implications (mortality). Assuming that food limitation caused growth decline or mortality, linking intensity of these processes to EE estimates would help to interpret absolute values.

Finally, in a context of climate and major environmental changes in a next step of this study would be to investigate and quantify the effect of the environment on the trophic carrying capacity. Climate change affect phenology of species (Durant *et al.*, 2007) and then could induce spatial and/or temporal mismatch in prey-predator relationship (Beaugrand *et al.*, 2003; Durant *et al.*, 2007; Siddon *et al.*, 2013; Chevillot *et al.*, 2017). By studying the link between trophic carrying capacity and environmental changes, we could attempt to predict changes in population of juvenile fish regulation in coastal and estuarine nurseries.

# **3.7 References**

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# 3.8 Supplementary material

# **Table S1**: Dates of data collection in 2017

# A. Prey: grab surveys

Periods selected to study	Days of data collection				
trophic capacity					
Fish arrival on nursery	17 and 18/05 in EM, SC and NC				
	17 to 25/05 in NAV and IM				
End of the growth season	19/09 in EM, SC and NC				
	8 to 12/10 in NAV and IM				

# B. Fish: trawl surveys

Months	Periods selected to study	Days of data collection for hauls in	Days of data collection for
	trophic capacity	the historic survey area	supplementary hauls in the marine part
May		9 and 10/05	
June	Fish arrival on nursery	10 and 14/06	17 and 18/06
July		13 and 17/07	
August		11 and 14/08	
September		5 and 7/09	
October	End of the growth season	10 and 12/10	13 and 14/10

**Table S2**: Composition of the Food Production in each habitat and by FP scenarios: macrofauna and harpacticoids (meiobenthic copepods) in percentages calculated using mean values of all parameters. EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats. S1: no seasonality in the ratio P/B *i.e.* P/B<sub>june</sub> = P/B<sub>october</sub> = 1/7 of the annual P/B, S2: the ratio P/B varies seasonally, S3: the ratio P/B varies seasonally only for macrofauna species.

Scenario	Habitat	Macrofauna- harpacticoids	Macrofauna- harpacticoids
		percentages at the	percentages at the end of
		beginning of the growth	the growth season (%)
		season (%)	
S1	EM	78 - 22	86 - 14
	SC	35 - 65	61 – 39
	NAV	0 - 100	0 - 100
	NC	8-92	53 - 47
	IM	52-48	46 - 54
S2	EM	78 - 22	86 - 14
	SC	35 - 65	61 – 39
	NAV	0-100	0 - 100
	NC	8-92	53 - 47
	IM	52 - 48	46 - 54
S3	EM	85 - 15	51 - 49
	SC	47 – 53	21 - 79
	NAV	0-100	0 - 100
	NC	13 - 87	17 – 83
	IM	64 - 36	13 - 87

**Table S3**: Percentages of macrofauna and harpacticoids (meiobenthic copepods) of the Food Consumption of G0 fish by habitat in June and October, calculated using mean values of all parameters. EM: estuary mouth, SC: southern channel, NC: northern channel, NAV: navigation channel, IM: intertidal mudflats.

Note that in October, only *Pomatoschistus* sp. consumed harpacticoids, whereas in June, *S. solea*, *P. platessa*, *P. flesus*, *L. limanda*, *D. labrax* and *Pomatoschistus* sp. consumed harpacticoids.

	Macrofauna- harpacticoids	Macrofauna- harpacticoids
percentages at the beginning of		percentages at the end of the
	the growth season (%)	growth season (%)
EM	49 - 51	96-4
SC	58-42	93 - 7
NAV	40 - 60	80 - 20
NC	59 - 41	97 – 3
IM	59-41	100 - 0

**Figure S1**: Food production (in GJ month<sup>-1</sup>) at the beginning and the end of the growth season for juvenile fish in nursery and by scenario of seasonality of production of macrofauna (brown) and harpacticoids from the meiofauna (blue). Thick black lines represent 50% of the confidence interval and thin black lines, the 95% confidence interval of total FP estimated by Monte Carlo simulations.



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**Figure S2**: Exploitation efficiency in each habitat at the beginning and the end of the growth season for juvenile fish in nursery by Food Production scenario (Sc1 to Sc3). Thick grey lines represent 50% of the confidence interval and thin grey lines, the 95% confidence interval of total FP estimated by Monte Carlo simulations. \**NAV*: EE estimates of G0 fish on macrofauna prey (D) were excluded from the figure to clarify it.

A. G0 fish



B. G1 fish



#### C. G0 fish (harpactocoids)



### C. G0 fish (macrofauna)



**Figure S3**: Mean estimates of EE for G0 over both prey compartments (A) FC of harpacticoids by G0 fish over FP of harpacticoids and (B) FC of macrofauna by G0 fish over FP of macrofauna in each habitat at the beginning (blue) and the end (gold) of the growth season by FP scenarios.

\**NAV*: EE mean values of G0 fish on macrofauna prey were excluded from the figure to clarify it; FP of macrofauna in NAV was extremely low in autumn and FC was only realized by species for which FC was not re-allocated from SIMM (*Pomatoschitus* sp. and *C. lyra*). The ratio of the two values resulted in extremely high values in autumn (between 200 and 1200 %) that cannot be interpreted.



**Figure S4**: Mean estimates of EE without FC re-allocation for G0 fish and G1 fish in each habitat at the beginning (blue) and the end (gold) of the growth season for juvenile fish in nursery by FP scenarios. EE for G0 fish is the ratio between the FC of G0 fish and the FP of both macrofauna species and harpacticoids (meiobenthic copepods). EE for G1 fish is the ratio between the FC of G1 fish and the FP of macrofauna species. Gr.Season.beginning is the beginning of the growth season for juvenile fish in the nursery (end of May/June) and Gr.Season.end is the end (end of September/October). The confidence intervals are not represented here for a better clarity in the figure.





Gr.Season.beginning

#### Materiel S1: Literature data collection for juvenile fish.

Literature data collection was based on the data collection realised by Tableau *et al.* (2019) and Saulnier *et al.* (2020). In this study, we added two species to the ones already present in these two studies: sea bass (*Dicentrarchus labrax*) and European flounder (*Platichthys flesus*). For each parameter, a brief description of the collection by Tableau *et al.* (2019) and Saulnier *et al.* (2020) was provided and the new values for sea bass and flounder were detailed.

#### Length-weight relationship coefficients a and b

a and b were estimated from local data i.e. the data collected in the historic survey area from 2000 to 2017 for each fish cohort as described by Tableau *et al.* (2019).

#### <u>E: Energy density (kJ.g<sup>-1</sup>)</u>

Energy density for fish was extracted from Spitz *et al.* (2010), following the procedure of data collection of Saulnier *et al.*, (2020). The values of mean and standard deviation for Perciformes were attributed to *D. labrax* and the values for Pleuronectiformes to *P. flesus*.

Table MS1.1: Energy	y density	$(E, kJ.g^{-1})$	) for	each t	taxa.
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Таха	Ε	E (sd)
	(mean)	
Pleuronectiformes	5.743	0.483
Gadiformes	4.66	0.587
Perciformes	5.783	0.606

#### K: Gross conversion efficiency

Tableau et al. (2019) collected 189 data of gross conversion efficiency of juvenile fish at optimal temperature from 31 references in aquaculture journals (see references in Supplement S2). Values were grouped at the family (Gadidae, Pleuronectidae, Soleidae) or order (Perciformes). The values of mean and standard deviation for Perciformes were attributed to *D. labrax* and the values for Pleuronectidae to *P. flesus*.

Taxa	K	K (sd)
	(mean)	
Soleidae	0.197	0.0675
Pleuronectidae	0.316	0.0792
Gadidae	0.385	0.072
Perciformes	0.321	0.0969

#### Table MS1.2: Gross conversion efficiency (K, unitless) for each taxa.

#### q: catch efficience

Data on catch efficiency were collected in the literature (Rogers and Lockwood, 1989; Hamerlynck and Hostens, 1993; Reiss *et al.*, 2006). We attributed the catch efficiency value (0.50) found for *T. luscus* and *M. merlangus* (Hamerlynck and Hostens, 1993) to *D. labrax* based on a criterion of close body shape which probably influence their escape probability from beam trawl. We attributed the catch efficiency value (0.38) found for *P. platessa* and *L. limanda* to *P. flesus* based on the same criterion.

#### Table MS1.3: catch efficiency (q, unitless) for each taxa.

Таха	q
Soleidae	0.275
Pleuronectidae	0.38
Gadidae and <i>D. labrax</i>	0.5
C. lyra	0.45
Pomatoschistus	0.58

#### Materiel S2: Model selection growth

During the first year of the nursery season, growth rate increases at the beginning, then stabilises and finally declines until the end as reviewed for *P. platessa* (Ciotti et al., 2014, Fig S2.1) and also described for other species (Amara, 2003; Teal *et al.*, 2008).



# Figure MS2.1: Growth rate evolution of juvenile plaice through the nursery season, from settlement to autumn (adapted from Ciotti et al., 2014).

As the timing of growth declines vary spatially (Ciotti *et al.*, 2013b), we decided to use local data to estimate growth rates at the beginning and at the end of the growth period. We used length data from the monthly historic survey from 2000 to 2017 (unpublished data yet). For each month and each year, we calculated the mean date of collection and the mean length.

Daily growth rates for each period were estimated by modelling the evolution of mean fish length as a function of time and extracting growth rates for each period. We tested different models to model length (L) evolution with time (t):

#### M1 assumed a constant growth rate over the year.

• M1: linear regression with the following equation:  $L(t) = \alpha + \beta(t) + \varepsilon_t \sim N(0,1)$ 

 $\alpha$  and  $\beta$  are the coefficients of the linear regressions and  $\epsilon$  are the residuals with the assumption that they are normally distributed.

M2, M3, M4 and M5 assumed a varying growth rate over the year.

• M2 linear regression with an effect period:  $L(t, p) = \alpha(p) + \beta(t) * \gamma(p) + \varepsilon_t \sim N(0, 1)$ 

The slope and the ordinate to the origin could vary between the two periods.

★ M3: Von Bertalanffy growth function with non-linear regression using non-linear least squares (nls) procedure:  $VB(t) = L \infty \cdot (1 - e^{-K(t - t_0)})$ 

 $L\infty$  is the asymptotic length, K the growth coefficient, t<sub>0</sub> the value used to calculate size when time is zero.

- ★ M4: Gompertz growth function with non-linear regression using non-linear least squares (nls) procedure:  $G(t) = L \infty \cdot e^{-\frac{1}{K} \cdot e^{-K(t-t_0)}}$
- ★ M5: logistic regression with non-linear regression using non-linear least squares (nls) procedure:  $LR(t) = \frac{\varphi_1}{1 + e^{-(\varphi_2 + \varphi_3 \cdot t)}}$

All models were run and models' assumptions (normality and variance homogeneity of the residuals) were verified graphically. Best model was selected using AIC criterion (see fish cohort details after Table S2.1). Growth rates were extracted for each period either the coefficients estimated (in case of M1 or M2 as the best model) or the derivative of the modelled function using estimated parameters (in case of M3, M4 or M5 as the best model). Growth rates estimated for each period are presented in Table S2.1.

Cohort	Species	$\hat{G}$ (beginning of the	$\hat{G}$ (end of the growth
		growth period)	period)
G0	Solea solea	0,0556	0,0421
	Pleuronectes platessa	0,0549	0,0211
	Limanda limanda	0,0452	0,0065
	Platichthys flesus	0,0353	0,0491
	Dicentrarchus labrax	0,0331	0,0474
	Callionymus lyra	0,0685	0,0088
	Merlangius merlangus	0,0313	0,0688
	Trisopterus luscus	0,0735	0,054
G1	Solea solea	0,0587	0,0376
	Pleuronectes platessa	0,0669	0,0153
	Limanda limanda	0,044	0,0268
	Platichthys flesus	0,0444	0,0444
	Dicentrarchus labrax	0,0555	0,0293
	Callionymus lyra	0,0552	0,0255

Table MS2.1: Estimated growth rates ( $\hat{G}$ ) at the beginning and the end of the growth period for fish cohort.

# P. platessa G0

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
<b>M1</b> lm (y ~ x)	Non-homogenous	276,8	0,0	426
<b>M2</b> lm (y ~ x * season)	Non-homogenous	266,7	0,0554	0,0223
<b>M3</b> nls (y ~ VB(x))	Non-homogenous	267,6	0,0564	0,027
<b>M3.log</b> nls ( <i>ln</i> (y) ~ <i>ln</i> (VB(x)))	ok	244	0,0513	0,0322
<b>M4</b> nls (y ~ G(x))	Non-homogenous	265,4	0,0581	0,0227
<b>M4.log</b> nls $(ln(y) \sim ln(G(x)))$	ok	240,6	0,0536	0,0264
<b>M5</b> nls (y ~ L(x))	Non-homogenous	264,3	0,0579	0,019
<b>M5.log</b> nls ( <i>ln</i> (y) ~ <i>ln</i> (L(x)))	ok	238,6	0,0549	0,0211

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# M5.log residuals



# M5.log curve



model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\widehat{G}$ (autumn)
<b>M1</b> lm (y ~ x)	ok	238,2	0,0	)56
<b>M2</b> lm (y ~ x * season)	ok	224,1	0,0424	0,0418
<b>M3</b> nls (y ~ VB(x))	ok	240,2	0,0574	0,0542
<b>M3.log</b> nls $(ln(y) \sim ln(VB(x)))$	ok	255,8	0,0525	0,0516
<b>M4</b> nls (y ~ G(x))	ok	231,8	0,0576	0,0481
<b>M4.log</b> nls $(ln(y) \sim ln(G(x)))$	ok	244,7	0,0487	0,063
<b>M5</b> nls (y ~ L(x))	ok	225,4	0,0556	0,0421
$M5.log$ nls $(ln(y) \sim ln(L(x)))$	ok	241	0,049	0,0541

### M5 residuals



#### M5 curve



### L. limanda G0

model	Residuals (visual check)	AIC	$\widehat{G}$ (spring)	$\hat{G}$ (autumn)
M1	Overestimations of low			
lm (y ~ x)	and high lengths	154,6	0,0	221
M2	ok			
lm (y ~ x * season)		142,4	0,0419	0,0094
M3	ok			
nls (y ~ VB(x))		141,8	0,0541	0,009
M3.log	ok			
nls $(ln(y) \sim ln(VB(x)))$		148,4	0,05	0,0102
M4	ok			
nls (y ~ $G(x)$ )		141,5	0,0487	0,0077
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		147,7	0,0462	0,0086
M5	ok			
nls (y ~ $L(x)$ )		141,4	0,0452	0,0065
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		147,2	0,0436	0,0071

# <u>M5 residuals</u>







model	Residuals (visual check)	AIC	$\widehat{G}$ (spring)	$\widehat{G}$ (autumn)
M1	Overestimations of low			
$lm (y \sim x)$	and high lengths	182,1	0,0	428
M2	ok			
lm (y ~ x * season)		177,5	0,032	0,041
M3	Convergence not achieved			
nls (y ~ VB(x))				
M3.log	Convergence not achieved			
nls $(ln(y) \sim ln(VB(x)))$				
M4	ok			
nls (y ~ $G(x)$ )		179,8	0,0391	0,0456
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		150,3	0,035	0,0518
M5	ok			
nls (y ~ $L(x)$ )		178,1	0,0384	0,0439
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		148,3	0,0353	0,0491

P. flesus G0

#### M5.log residuals







#### D. labrax G0

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
<b>M1</b> lm (y ~ x)	ok	175,7	0,0431	
M2 lm (y ~ x * season)	ok	157,3	-0,011	0,0399
<b>M3</b> nls (y ~ VB(x))	Convergence not achieved			
<b>M3.log</b> nls $(ln(y) \sim ln(VB(x)))$	Convergence not achieved			
<b>M4</b> nls (y ~ G(x))	ok	174,6	0,0329	0,0502
$\begin{array}{l} \textbf{M4.log}\\ nls \; (ln(y) \sim ln(G(x))) \end{array}$	Convergence not achieved			
<b>M5</b> nls (y ~ L(x))	ok	173,6	0,0331	0,0474
$\begin{array}{l} \textbf{M5.log} \\ nls \; (ln(y) \sim ln(L(x))) \end{array}$	Convergence not achieved			

Best model according to Akaike criteria was M2. However, using M2,  $\hat{G}$  at the beginning of the growth period was negative probably due to the few numbers of points and the potential inter-annual delay in G0 *D. labrax* arrival on nursery. Hence, we choose M5 to estimate growth rates for G0 *D. labrax*.

#### M5 residuals

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model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
M1	Underestimations of low and			
lm (y ~ x)	high lengths	285	0,0	559
M2	ak			
lm (y ~ x * season)	0K	279,1	0,0313	0,0688
M3	Convergence not achieved			
nls (y ~ VB(x))				
M3.log	Convergence not achieved			
nls $(ln(y) \sim ln(VB(x)))$				
M4	Convergence not achieved			
nls (y ~ $G(x)$ )				
M4.log	Convergence not achieved			
nls $(ln(y) \sim ln(G(x)))$				
M5	ok			
nls (y ~ $L(x)$ )		280,9	0,0428	0,0751
M5.log	Convergence not achieved			
nls $(ln(y) \sim ln(L(x)))$				

M. merlangus G0

#### M2 residuals







#### T. luscus G0

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\widehat{G}$ (autumn)
M1	Overestimations of low			
lm (y ~ x)	and high lengths	319,6	0,0	555
M2	ok			
lm (y ~ x * season)		317,6	0,0735	0,054
M3	ok			
nls (y ~ VB(x))		317,8	0,0672	0,0411
M3.log	ok			
nls $(ln(y) \sim ln(VB(x)))$		330,2	0,0712	0,0367
M4	ok			
nls (y ~ $G(x)$ )		320,1	0,0652	0,039
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		332	0,0736	0,0299
M5	ok			
nls (y ~ $L(x)$ )		322,5	0,062	0,0381
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		334,5	0,0744	0,0241

#### 117 M2 residuals









ed		Obs
	Fitted	4

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
M1	Overestimations of low			
$lm (y \sim x)$	and high lengths	101,6	0,0	)29
M2	Non homogenous			
lm (y ~ x * season)		93,4	0,1454	0,0153
M3	ok			
nls (y ~ VB(x))		86,1	0,3412	0,0099
M3.log	ok			
nls $(ln(y) \sim ln(VB(x)))$		83,7	0,3513	0,0096
M4	ok			
nls (y ~ $G(x)$ )		85,9	0,0805	0,0096
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		84	0,08	0,0091
M5	ok			
nls (y ~ $L(x)$ )		85,7	0,0683	0,0092
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		84,2	0,0685	0,0088

C.lyra G0

Best model according to Akaike criteria was M4.log. However, using M2.log,  $\hat{G}$  were very different (high value in spring and low value in autumn) which is far from what can be found in literature. This was also probably due to the few numbers of points at the beginning of the nursery season. Hence, we choose M5.log (with AIC just 0.2 superior to the one of M4.log) to estimate growth rates for G0 C. lyra.

#### M5.log residuals







# P. platessa G1

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
M1	Overestimations of low			
$lm (y \sim x)$	lengths	322,6	0,0	459
M2	ok			
$lm (y \sim x * season)$		312,3	0,059	0,0131
M3	ok			
nls (y ~ VB(x))		312,1	0,066	0,0231
M3.log	ok			
nls $(ln(y) \sim ln(VB(x)))$		315,2	0,0647	0,0245
M4	ok			
nls (y ~ $G(x)$ )		311,8	0,0667	0,0217
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		314,9	0,0655	0,0229
M5	ok			
nls (y ~ $L(x)$ )		311,6	0,0669	0,0153
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		314,8	0,0661	0,0213

# $\frac{1}{5}$ <u>M5 residuals</u>



# M5 curve



model	Residuals (visual check)	AIC	$\widehat{G}$ (spring)	$\widehat{G}$ (autumn)
$\frac{M1}{lm (v \sim x)}$	ok	221	0.0505	
$\frac{M2}{lm (y \sim x * season)}$	ok	215,7	0,0558	0,0377
$\frac{M3}{nls (y \sim VB(x))}$	ok	214	0,0592	0,0393
$\frac{\textbf{M3.log}}{nls (ln(y) \sim ln(VB(x)))}$	ok	212,7	0,0584	0,0404
<b>M4</b> nls (y ~ G(x))	ok	213,5	0,0593	0,0381
$\begin{array}{l} \textbf{M4.log} \\ nls \ (ln(y) \sim ln(G(x))) \end{array}$	ok	212,3	0,0586	0,0389
<b>M5</b> nls (y ~ L(x))	ok	215,3	0,0555	0,0295
$\frac{\textbf{M5.log}}{nls (ln(y) \sim ln(L(x)))}$	ok	211,9	0,0587	0,0376

S. solea G1

#### M5.log residuals



#### M5.log curve



### L. limanda G1

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
<b>M1</b> lm (y ~ x)	ok	244,5	0,0	275
<b>M2</b> lm (y ~ x * season)	ok	242	0,044	0,0268
<b>M3</b> nls (y ~ VB(x))	Convergence not achieved			
$\begin{array}{l} \textbf{M3.log} \\ nls \ (ln(y) \sim ln(VB(x))) \end{array}$	ok	248,8	0,0379	0,0132
<b>M4</b> nls (y ~ G(x))	ok	243,7	0,0367	0,0148
<b>M4.log</b> nls $(ln(y) \sim ln(G(x)))$	ok	248,9	0,0382	0,0126
<b>M5</b> nls (y ~ L(x))	ok	244,3	0,0369	0,0123
$\frac{\textbf{M5.log}}{\text{nls } (ln(y) \sim ln(L(x)))}$	ok	249	0,0384	0,0119

# M2 residuals

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# M2 curves



model	Residuals (visual check)	AIC	$\widehat{G}$ (spring)	$\widehat{G}$ (autumn)
<b>M1</b> lm (y ~ x)	ok	263,3	0,0444	
<b>M2</b> lm (y ~ x * season)	ok	265	0,0424	0,0364
<b>M3</b> nls (y ~ VB(x))	Convergence not achieved			
<b>M3.log</b> nls ( <i>ln</i> (y) ~ <i>ln</i> (VB(x)))	Convergence not achieved			
<b>M4</b> nls (y ~ G(x))	Convergence not achieved			
$\begin{array}{l} \textbf{M4.log} \\ nls \ (ln(y) \sim ln(G(x))) \end{array}$	Convergence not achieved			
<b>M5</b> nls (y ~ L(x))	ok	265,1	0,044	0,0372
<b>M5.log</b> nls $(ln(\mathbf{x}) \sim ln(\mathbf{L}(\mathbf{x})))$	ok	268.8	0.0448	0.0429

P. flesus G1

#### M1 residuals



#### M1 curve



# D. labrax G1

model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
M1	ok			
$lm (y \sim x)$	011	231,5	0,0	0501
M2	ok			
lm (y ~ x * season)	ŬK.	222,9	0,0414	0,0322
M3	Convergence not			
nls (y ~ VB(x))	achieved			
M3.log	Convergence not			
nls $(ln(y) \sim ln(VB(x)))$	achieved			
M4	ok			
nls (y ~ $G(x)$ )		230	0,0565	0,0409
M4.log	ok			
nls $(ln(y) \sim ln(G(x)))$		227,7	0,0518	0,047
M5	ok			
nls (y ~ $L(x)$ )		218,4	0,0555	0,0293
M5.log	ok			
nls $(ln(y) \sim ln(L(x)))$		226,5	0,0524	0,0449

# M5 residuals



# M5 curve



model	Residuals (visual check)	AIC	$\hat{G}$ (spring)	$\hat{G}$ (autumn)
M1	Overestimations of low			
lm (y ~ x)	lengths	269,7	0,0	297
M2	ok			
lm (y ~ x * season)		262,6	0,0552	0,0255
M3	Non homogenous			
nls (y ~ VB(x))		262,8	0,0471	0,0102
M3.log	Non homogenous			
nls $(ln(y) \sim ln(VB(x)))$		261,9	0,0468	0,01
M4	Non homogenous			
nls (y ~ $G(x)$ )		263,1	0,0479	0,0091
M4.log	Non homogenous			
nls $(ln(y) \sim ln(G(x)))$		262	0,0479	0,0087
M5	Non homogenous			
nls (y ~ $L(x)$ )		264,6	0,0517	0,0044
M5.log	Non homogenous			
nls $(ln(y) \sim ln(L(x)))$		262,2	0,0489	0,0075

C. lyra G1

#### M2 residuals



#### M2 curve



#### Materiel S3: DC monthly

Diet composition is the gravimetric proportion of macrobenthic invertebrates in the diet of each predator. It was collected from various sources by Saulnier *et al.* (2020). Hence, *S. solea*, *P. platessa*, *L. limanda* and *C. lyra* were considered as strictly benthic feeder feeding mainly on macrofauna (Le Mao, 1986; Morin *et al.*, 1999; Dolbeth *et al.*, 2008). *P. flesus* was also a benthic feeder largely preying on macrobenthic invertebrates (Mendes *et al.*, 2020). DC were set to 0.95 for these species. *M. merlangus* and *T. luscus* feed mainly on nekton like fish, shrimps and mysids (Hamerlynck and Hostens, 1993; Morin *et al.*, 1999). Benthic macrofauna (*e.g.* polychaetes, bivalves, amphipods) composed a low part of their diet (Demain *et al.*, 2011a). DC were set to 0.15 for these species. *D. labrax* juvenile is often described as a hyperbenthic feeder (Pasquaud *et al.*, 2008, 2010; Fonseca *et al.*, 2011). Its diet is composed of hyperbenthic invertebrates such as mysids, amphipods or shrimps (Pasquaud *et al.*, 2010). Benthic macrofauna was also present in lower proportion in its diet: *Corophium volutator* or annelids (Morin *et al.*, 1999). DC value was set to 0.15 as for *M. merlangus* and *T. luscus*.

Hence, these values were used for the end of the growth period. However, at the beginning of the growth season, smaller individuals fed partly on meiofauna (Pihl, 1985; Gee, 1989; Coull, 1990; Aarnio *et al.*, 1996; Andersen *et al.*, 2005). Ontogenetic diet shift from meiofauna to macrofauna appeared between 30 and 60 mm for flatfish species (Pihl, 1985; Gee, 1989; Coull, 1990; Aarnio *et al.*, 1996; Andersen *et al.*, 2005) and around 30 mm for *D. labrax* (Fonseca *et al.*, 2011). Hence, we set DC to meiofauna from fish mean length in June (Table MS3.1).

*Pomatoschistus* sp. were also a meiofauna consumer (Pihl, 1985; Doornbos and Twisk, 1987; Salgado *et al.*, 2004) with a the relative importance of macrofauna increasing for individuals from 30 mm (Salgado *et al.*, 2004; Jackson and Rundle, 2008). Hence, DC for harpacticoids was set according to mean fish length at the beginning and the end of the growth season (Table MS3.1).

**Table MS3.1**: Diet compositions (DC) for each fish cohort at the beginning and the end of the growth season. DC harpacticoids is the proportion of harpacticoids in fish diet (in %) and DC macrofauna, the proportion of macrobenthic invertebrates (in %).

Cohort	Species	Mean length at beginning	Beginning of the growth season		End of the growth season	
		of the growth	DC	DC	DC	DC
		season (cm)	harpacticoids	macrofauna	harpacticoids	macrofauna
G0	Solea solea	3.3	0.45	0.45	0	0.95
	Pleuronectes platessa	4.1	0.15	0.8	0	0.95
	Limanda limanda	1.9	0.8	0.1	0	0.95
	Platichthys flesus	3.7	0.45	0.45	0	0.95
	Dicentrarchus labrax	2.7	0.15	0.15	0	0.15
	Callionymus lyra	abs.	abs.	abs.	0	0.95
	Merlangius merlangus	7.6	0	0.15	0	0.15
	Trisopterus luscus	6.0	0	0.15	0	0.15
	Pomatoschistus spp.	3.3	0.6	0.2	0.2	0.35
G1	Solea solea	16.2	0	0.95	0	0.95
	Pleuronectes platessa	17.4	0	0.95	0	0.95
	Limanda limanda	13.7	0	0.95	0	0.95
	Platichthys flesus	12.5	0	0.95	0	0.95
	Dicentrarchus labrax	11.4	0	0.15	0	0.15
	Callionymus lyra	11.7	0	0.95	0	0.95

**Material S4**: Data sources and categorization of variables and parameters involved in the model of trophic carrying capacity. 'Y' means Yes and 'N' means No. Fixed data were attributed to parameter at the specific level resolution and with negligible uncertainty. Distributions of probability were attributed to parameters and variables with high uncertainty but known. Conservation approach was attributed to parameters with high uncertainty hardly quantifiable (see Tableau et al. 2019 and Saulnier et al. 2020 for more details)

	Data	Description	Sources of	Information	Category of	Statistical
			information	at species	uncertainty	distribution
				level		
Food consumption	$\overline{N}$	Fish abundance	Survey data	Y	2-distribution	Gamma
	d	Survey date		Ν	1-fixed data	-
	L	Fish length		Y	1-fixed data	-
	а	Length-weight param.	Deduced from	Y	1-fixed data	-
	b	Length-weight param.	survey data	Y	1-fixed data	-
	G	Growth rate		Y	1-fixed data	-
	q	Catch efficiency	Literature data	Ν	3-conservative	-
	DC	Diet composition		Y	3-conservative	-
	Е	Energy density		Ν	2-distribution	Gamma
	K	Gross efficiency		Ν	2-distribution	Inverse gamma
	α	Contribution of habitats	Isotopic data	Ν	3-conservative	-
		to diet				
Food production	В	Prey biomass	Survey data	Y	2-distribution	Gamma
	β	Seasonal P:B coefficient	Literature data	Ν	3-conservative	-
	P:B	Production-to-biomass	Empirical model	Y	2-distribution	Lognormale
	R	Regeneration rate	Literature data	Ν	3-conservative	-
	E	Energy density	1	Y	1-fixed data	-

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# Chapitre 4.

Occurrence de la limitation trophique : un indice de production de proies benthiques à partir d'échantillonnages au chalut pour appréhender les variations interannuelles de la relation proieprédateur sur les nourriceries côtières



Illustration : L. Fleury

Le chapitre précédent montre que la limitation trophique est plus probable à l'automne pour les juvéniles âgés de moins d'un an (G0), quand la production des ressources alimentaires est moins importante que plus tôt dans la saison et que les densités de juvéniles présentes exercent encore une forte pression de prédation sur la macrofaune benthique. Les vasières intertidales, habitat déjà identifié comme essentiel pour l'alimentation présentent des EE à l'automne très élevées suggérant une consommation d'une forte proportion des ressources qui y sont disponibles, accentuant leur caractère essentiel. Au printemps, les fortes productions d'invertébrés benthiques (copépodes harpacticoïdes et macrofaune benthique) supportent la consommation des G0. Les estimations de EE à cette saison sont pourtant élevées pour les juvéniles d'un an (G1), suggérant une forte pression de prédation locale. Les résultats indiquent que la capacité trophique est supérieure en début fin d'été / début d'automne pour les juvéniles G0, suggérant une limitation trophique. Cette période paraît ainsi appropriée pour s'intéresser à l'occurrence de ce processus à plus large échelle.

L'objectif de ce chapitre est d'étudier les variations interannuelles de la production de proies et d'explorer l'occurrence d'une potentielle limitation trophique en confrontant ces variations à l'évolution de densités de prédateurs sur les mêmes sites et aux mêmes années. Les données de production de macrofaune benthique et par conséquent des proies qui en sont issues sont très limitées en raison de la lourdeur d'analyse de ce compartiment classiquement échantillonné à benne quantitative. En revanche grâce aux échantillonnages effectués avec des chaluts à perche dans les suivis réguliers des nourriceries du golfe de Gascogne, des données de densité et de biomasse d'invertébrés sont disponibles, les plus petits individus pouvant être considérés comme des proies des juvéniles de poisson. L'analyse conjointe de ces deux sources de données (benne et chalut) issues des mêmes campagnes d'échantillonnage va permettre de valider un proxy ou indice de la production benthique des nourriceries côtières (niveaux de production et composition spécifique). Les variations annuelles de cet indice seront mises en relation avec les densités de juvéniles G0 de poissons dans des régressions quantiles permettant de tester l'aspect limitant de l'indice de production benthique sur les densités de juvéniles de poisson.

Chapitre 4. Variations interannuelles de la capacité trophique

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

# Authors

Louise Day<sup>a,b</sup>, Hervé Le Bris<sup>b</sup>, Erwan Saulnier<sup>a,b</sup>, Lucas Pinsivy<sup>b</sup>, Anik Brind'Amour<sup>a</sup>

<sup>a</sup>IFREMER, EMH, Rue de l'île d'Yeu, B.P. 21105, 44311 Nantes Cedex 03, France

<sup>b</sup>ESE, Ecology and Ecosystems Health, Agrocampus Ouest, INRAE, 35042 Rennes, France

Published in Estuarine, Coastal and Shelf Science (2020)

# 4.1 Abstract

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

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



### Graphical abstract

# 4.2 Introduction

Estuaries and coastal areas are among the most productive ecosystems in the world (Schelske and Odum, 1961; Costanza *et al.*, 1997). They function as nurseries for many marine fish species by supporting production of juveniles, which replenish adult stocks offshore (Beck *et al.*, 2001; Dahlgren *et al.*, 2006; Seitz *et al.*, 2014). Recruitment (*i.e.* entry of young individuals into the fishery) of these nursery-dependent species is most likely regulated during their juvenile stage (Myers and Cadigan, 1993; Ustups *et al.*, 2013) by multiple limiting factors (Gibson, 1994). Wouters and Cabral (2009) suggested that nurseries concentrate more macrobenthic prey for demersal juvenile fish than do surrounding habitats. Hence, juveniles concentrate in nurseries, which leads to density-dependent mortality that cause a "bottleneck" effect in the number of fish recruited to the stock (Iles and Beverton, 2000; Craig *et al.*, 2007). Although the density-dependent processes that influence recruitment remain under debate, some studies suggested that prey production may be limiting (Nash *et al.*, 2007; Le Pape and Bonhommeau, 2015; van der Veer *et al.*, 2016). Prey production in nurseries becomes limiting when demand exceeds production, resulting in potential mortality and competition among predators.

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

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

and Noon, 2003; Planque and Buffaz, 2008), since the food-limitation hypothesis can be tested by examining several quantiles of the predator-prey relationship (Tableau *et al.*, 2016).

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

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

### 4.3.1 Data collection

### Nurseries surveyed

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



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

These nurseries differed environmentally in sediment composition and bathymetry (Table 1). The Bay of Vilaine is mainly a muddy nursery with sampling stations of varying depths (1-35 m), whereas the two Pertuis are half-muddy and half-sandy shallow nurseries, and the outer Loire estuary is mainly sandy with a gradient of depths (Table 1). Each nursery surveyed was divided into strata defined by the

bathymetry and the size distribution of sediments (assessed using the grab samples, Supp. Mat. A). Thus, three bathy-sediment strata were defined in the Bay of Vilaine (V1, V2 and V3, from upstream to downstream), three others in the outer Loire estuary (L1, L2 and L3), and two at each Pertuis site (PA1, PA2 and PB1, PB2). The number in each code corresponds to the distance from the mouth of the estuary (1 = upstream, 3 = offshore).

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

	Bay of Vilaine	Outer Loire	Pertuis Breton	Pertuis Antioche
Characteristic	(V)	estuary (L)	(PB)	(PA)
Sampling year	2008	2016	2015	2015
Mean mud percentage (%)	70.0	10.5	52.7	53.7
Mean sand percentage (%)	25.0	86.0	41.2	40.5
Mean ( $\pm 1$ SD) depth (m)	$15.4\pm0.5$	$11.0\pm0.4$	$5.9 \pm 0.4$	$7.5 \pm 0.3$
Number of strata	3	3	2	2
Total number of trawl	42	34	15	16
stations (and by stratum)	(V1: 17, V2: 8,	(L1: 2, L2: 25,	(PB1: 7, PB2: 8)	(PA1: 3, PA2: 13)
	V3: 17)	L3: 7)		
Total number of grab	36	19	6	9
stations (and by stratum)	(V1: 17, V2: 6,	(L1: 3, L2: 11,	(PB1: 3, PB2: 3)	(PA1: 3, PA2: 6)
	V3: 15)	L3: 5)		

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

### Grab data collection

Grab samples were collected using a 0.1 m<sup>2</sup> Van Veen grab, with three replicates at each sampling station. Once aboard, the grab content was sieved through a 1 mm grid mesh and kept in a 7% formalin solution in plastic zip-top bags. In the laboratory, organisms were rinsed and sieved with fresh water in a column of five successive sieves with square mesh sizes ranging from 16 to 1 mm. Organisms retained in each sieve were then stored separately in a 70% ethanol solution, keeping in mind that handling, fixing samples with formalin and storing with ethanol likely led to underestimate biomasses (Gaston *et al.*, 1996; Wetzel *et al.*, 2005). Invertebrates from each sieve were identified to the lowest taxonomic level, counted and weighed. Biomass per taxa was determined as wet mass (WM) and then converted into ash-free dry mass (AFDM) using specific coefficients from a global database of conversion factors

(Brey *et al.*, 2010). When no conversion factor was available at the species level, the conversion factor for the next highest taxonomic level was used. Data from replicates of each sampling station were summed, and biomass was standardized based on the area sampled (*i.e.* 3 replicates  $\times$  0.1 m<sup>2</sup>). The sampling design is detailed in Table 1.

### **Trawl data collection**

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

### 4.3.2 Select YOY fish

The fish selected were the eight marine nursery-dependent species with the highest biomass: four flatfish species (Arnoglossus laterna, Dicologlossa cuneata, Pleuronectes platessa, Solea solea) and four "round" fish species (Merlangius merlangus, Mullus surmuletus, Trisopterus luscus, Callionymus lyra). The eight species represented an average of 68% of the total biomass in each nursery-year. Lengthfrequency distributions were used to identify age groups in the survey. Gaussian distributions were fit to cumulative length-frequencies over the years. The maximum length associated with each Gaussian distribution was used to categorise a presumed year-class of all individuals captured. This procedure was performed using the Mclust function of the mclust package (Scrucca et al., 2016) of R software (R Core Team, 2019). YOY individuals (i.e. the first Gaussian distribution) were selected. Then, a minimum and maximum lengths of 7 and 15 cm, respectively, were set to select individuals that feed almost exclusively on macrobenthic invertebrate prey within the size range of the fish cohort (see Supp. Mat. C). These size thresholds for individual fish assumed that fish smaller than the minimum length (7 cm) prey on pelagic and benthic invertebrates that our sampling device could not capture (e.g. copepods), whereas individuals larger than the maximum threshold (15 cm) have a high proportion of small fish in their diet (Tableau et al., 2015). When length data were missing (as for C. lyra before 2008), mean individual mass (total biomass divided by the number of individuals) was converted into mean individual length using the coefficients a and b from the size-weight relationship estimated for each species with all length data available in the data set from 2004-2016. Only individuals whose mean individual length met the size ranges of the species were kept in the analyses. Relative YOY fish density (number of individuals.ha<sup>-1</sup>) was estimated at each station from catches without correcting for catch efficiency.

### 4.3.3 Select potential benthic prey for YOY fish

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

Then, benthic organisms from the grab and trawl samples were selected independently to match the species composition of the potential benthic prey of the YOY fish community. It was assumed that YOY fish are opportunistic feeders that consume a variety of benthic prey no larger than a certain size (Besyst et al., 1999; Griffin et al., 2012). Hence, a benthic invertebrate was identified as potential prey if it was smaller than the maximum mouth height of a juvenile fish. Data on mouth heights of the three most abundant species (M. merlangus, S. solea and T. luscus) in the studied areas were used to define a mean height of 20 mm (unpublished data). As benthic organisms collected with trawl were not sized, but only counted and weighted, we decided to select potential prey of the YOY fish using a filter based on mean individual mass. To set the threshold under which an invertebrate can be considered as prey for YOY fish, we used the benthic organisms collected with grab and categorised into size classes described previously (section 2.1.2). Mean individual body mass of the organisms retained in each mesh size was calculated. A threshold of 0.66 g WM.ind<sup>-1</sup> (*i.e.* ~0.1 g AFDM.ind<sup>-1</sup>), corresponding mainly to benthic organisms smaller than 16 mm (the largest mesh size), was identified as potential prey. This threshold was applied to select potential prey from benthic invertebrates using the grab and the beam trawl. Once applied to the grab data, the rare species and mean individual body mass filters selected 73.3% of the total biomass in the entire dataset (i.e. from all three nurseries where grab and trawl were deployed concomitantly). Once applied to the trawled benthic species, 10.3% of the total biomass of the entire dataset was retained. The benthic organisms included in those percentages (respectively 73.3% and 10.3%) were considered as potential prey and were used to estimate respectively benthic prey production using grab data and benthic prey production index using trawl data.

#### 4.3.4 Data analysis

### **Estimate benthic prey production (from grab data)**

Benthic prey production was estimated by multiplying mean annual biomass by the annual productionto-biomass ratio (P:B), which was calculated for each taxon at each station using the artificial neural network model developed by Brey (2012). The input data for this model are 17 categorical parameters that describe biological and functional traits (*e.g.* taxon, habitat, feeding and mobility), depth, temperature and individual mean body mass. The parameters required by the model were collated according to Saulnier et al. (2018) and supplemented with data from an online resource (Biological Traits Information Catalogue of The Marine Life Information Network http://www.marlin.ac.uk/biotic/). The bathymetry for each station was extracted from the **Ge**neral **B**athymetric Chart of the Oceans 30 arc-second grid (GEBCO\_2014, version 20150318, http://www.gebco.net, Weatherall et al., 2015). Mean annual bottom temperature for each nursery-year was extracted from a multi-decadal hindcast of a physical-biogeochemical model of the Bay of Biscay (Huret *et al.*, 2013). Individual mean body mass was calculated by dividing each taxon's mean annual biomass by its mean annual abundance.

Benthic prey production was first calculated at the scale of the sampling station ( $P_k$ , in kJ.m<sup>-2</sup>.y<sup>-1</sup>):

$$P_{k} = CR * \sum_{i} [B_{i,k} * E_{i} * (\frac{P}{B})_{i,k}]$$
Equation 1

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

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

$$P_{s} = \frac{\sum_{k \text{ in } s} P_{k}}{\sum_{k \text{ in } s} A_{k}}$$
Equation 2

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

### Estimate benthic prey production index (from trawl data)

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

To test the trophic limitation hypothesis in YOY fish, the index was calculated at the scale of the nursery, instead of the stratum, as the objectives of this part of the study was first to explore spatio-temporal variability in prey production among nurseries. Moreover, YOY fish may move among strata during their first year of life and do not necessarily feed where they were caught; thus, the nursery scale was deemed more relevant. To raise to the nursery scale, the index was calculated by applying Eq. 1 and

then, based on Eq. 2, the total benthic prey production index per unit area in each nursery  $(P_n, in kJ.m^{-2}.y^{-1})$ :

$$P_{n} = \frac{\sum_{k \text{ in } s} P_{k}}{\sum_{k \text{ in } s} A_{k}}$$
 Equation 3

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

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

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

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

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

### 4.4 Results

### 4.4.1 Trawl and grab: two correlated characterisations of benthic prey production

The two gears sampled different but complementary body mass spectra in the benthic community in the four nurseries in the Bay of Biscay (Fig. 2). As expected, the beam trawl sampled larger individuals (mostly epibenthic megafauna) than the grab (mostly endobenthic macrofauna). The overlap between

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



Figure 2. Weight spectra of station-specific mean body mass of benthic invertebrates in the four coastal areas of the Bay of Biscay sampled by (A) grab and (B) trawl. Data are log10-transformed. The red vertical line shows the threshold of mean body mass (i.e. 0.66 g wet mass (WM) ind<sup>-1</sup> – see section 2.1 for details on the setting of the threshold value) used to identify potential prey of juvenile fish.

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

production index estimated from trawl data was could be used and applied to the time series collected in the selected nurseries.



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

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

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

Domir		Dominant	minort may anonica		Sediment fraction (%)				
		Dominant prey species		productio	(mean ± SD)		Depth	Number	
Sed ty Str	iment 7pe / ratum	collected in grab samples	collected in trawl samples	n in grab (k J.m <sup>-2</sup> .y <sup>-</sup> <sup>1</sup> )	Mud	Fine sand	Coarse sand and Gravel	(mean ± SD)	of grab stations
	PA1	Sternapsis		84.2	$97.5\pm0.6$	$2.1 \pm 1.1$	$0.3 \pm 0.4$	$5.2\pm0.5$	3
Mud	V2	scutata Sternapsis scutata, Amphiura	Nucula spp., Philine aperta	251.8	90.0 ± 5.3	$7.2 \pm 5.1$	2.8 ± 1.5	11.4 ± 2.2	6
	PB1	filiformis Sternaspis scutata, Spisula subtruncata	Corbula gibba, Ophiura spp.	237.4	91.2 ± 5.4	7.6 ± 5.5	1.0 ± 1.1	4.8 ± 3.1	3
	V1	Owenia	Owenia	417.3	65,3 ±	22.6 ±	12.0 ±	$7.9\pm2.2$	17
Sandy mud	V3	fusiformis Abra alba, Owenia	fusiformis Ophiura spp., Abra	446.7	26.0 67.3 ± 17.2	14.0 20.7 ± 11.2	22.4 11.8 ± 11.7	$22.8\pm6.2$	15
	L1	fusiformis Limecola balthica	alba 	137.1	39.7 ± 3.8	58.0 ± 4.9	2.4 ± 2.4	$6.4 \pm 0.6$	3
	PA2	Corbula gibba	Ophiura spp., Corbula gibba	406.8	31.8 ± 22.1	58.6 ± 27.9	2.2 ± 2.5	9.0 ± 4.3	6
	L3	Spisula	Annelida	382.3	14.0 ±	51.5 ±	34.3 ±	$19.4\pm2.6$	5
Muddy sand		elliptica, Abra alba, Lagis koreni			13.0	23.4	33.6		
	PB2	Spisula solida	Alcyonium spp., Ophiura spp.	121.9	14.1 ± 11.3	59.5 ± 14.6	23.9 ± 4.7	$7.0 \pm 5.0$	3
Sand	L2	Spisula solida	Asterias rubens	179.3	1.0 ± 1.0	62.9 ± 33.4	35.5 ± 33.5	9.1 ± 3.3	11

### 4.4.2 Inter-annual variations in the benthic prey production index

Inter-annual variations in the benthic prey production index were quantified (Fig. 4). Estimates for the Bay of Vilaine (8 years sampled) ranged from 0.029 to 0.362 kJ.m<sup>-2</sup>.y<sup>-1</sup> in 2012 and 2014, respectively. Estimates for the outer Loire estuary (4 years sampled) ranged from 0.001 to 0.433 kJ.m<sup>-2</sup>.y<sup>-1</sup> in 2012 and 2008, respectively. Estimates for the outer Gironde estuary (2 years sampled) ranged from 0.259 to 0.642 kJ.m<sup>-2</sup>.y<sup>-1</sup> in 2016 and 2009, respectively.



Figure 4. Inter-annual variations in the benthic prey production index. Note the irregular frequency of sampling. Benthic prey production index is in kJ.m<sup>-2</sup>.y<sup>-1</sup>.

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

### 4.4.3 Relationships between benthic prey production index and juvenile fish density

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

Table 3. Slopes of quantile regressions of YOY fish density (no ha<sup>-1</sup>) at three scales as a function of the benthic prey production index (log scale) for lower (10<sup>th</sup>) and upper (90<sup>th</sup>) quantiles. Asterisks indicate slopes that differed significantly (p < 0.05) from 0. The percentage of non-empty stations (out of 494 stations

	10 <sup>th</sup>	90 <sup>th</sup>	Percentage of non-
Scale	quantile	quantile	empty stations
YOY community	NS	NS	95%
YOY community without Trisopterus luscus	NS	120.7*	92%
Round fish group	NS	NS	92%
Trisopterus luscus – Pouting		NS	60%
Merlangius merlangus – Whiting		44.5*	62%
Callionymus lyra – Common dragonet		52.9*	49%
Mullus surmuletus - Striped red mullet		4.5*	32%
Flatfish group		33.8*	55%
Solea solea – Common sole		29.1*	45%
Pleuronectes platessa – European plaice		2.8*	13%
Dicologlossa cuneata – Wedge sole			6%
Arnoglossus laterna – Mediterranean scaldfish		1.8*	15%

sampled in the 14 nursery-years) is indicated in the last column. "---" indicates species for which the number of empty stations was greater than 10% and 90% of the dataset for the lower and upper quantile regressions, respectively. "NS" indicates non-significant results.

### 4.5 Discussion

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

# 4.5.1 Selected trawled benthic invertebrate production: a macrobenthic prey production index

The benthic communities captured by trawl and grab gears have been previously compared to assess regional biodiversity patterns (Rufino *et al.*, 2017) and congruence of biodiversity structure among ecosystem components (Karakassis *et al.*, 2006), but never, to the best of our knowledge, to calculate a benthic production index. However, Le Pape et al. (2007) included some benthic megafauna collected from trawl surveys classified into trophic guilds to improve their fish habitat models. The beam trawl

can be considered a "generalist" gear because it samples large areas, motile or slightly motile benthodemersal fish and invertebrates, and sessile invertebrates buried to different depths in the substrate, depending on the degree of compaction of the substrate. The beam trawl can cover several types of sediment. The size of the smallest benthic organisms captured depends on the mesh size at the cod end (here, 20 mm) and whether it becomes partially clogged. The grab can be considered a more "specialist" gear because it targets soft bottom small areas and often a single sediment type, and slightly motile and sessile epi- and endo-invertebrates. The size of organisms is determined by the size of the mesh in which grab contents are sieved (1 mm).

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

The benthic prey production index included taxonomic groups (bivalves, polychaetes, ophiurids, and crustaceans) matching the dominant potential prey found in grabs. The species in the grab and trawl samples were consistent with the YOY diet in the nurseries (Pasquaud *et al.*, 2008; Tableau *et al.*, 2015). For instance, both samples contained *P. aperta*, which are consumed by YOY *S. solea* in the Bay of Vilaine (Kopp *et al.*, 2013), and small echinoderms (*Ophiura* spp., *A. filiformis*), which can be grazed by flatfish and round fish species (Duineveld and Van Noort, 1986; van der Veer *et al.*, 1990; Ntiba and Harding, 1993). Analysis of the potential prey species sampled by the trawl highlighted taxonomic differences in the same size distributions that the grab had sampled. The trawl also sampled motile suprabenthic organisms such as small *C. crangon*, which escape more easily from the grab via flushing. Flatfish such as *P. platessa* and *S. solea* may feed on small individuals of these suprabenthic species (Amara *et al.*, 2001; Pasquaud *et al.*, 2008), as may round fish such as *T. luscus* in the Loire estuary (Robin and Marchand, 1986) or *M. merlangus* (Demain *et al.*, 2011a). However, defining potential prey using only mean body mass resulted in many trawl stations that differed by three orders of magnitude, as the trawl sampled mainly larger individuals. Nevertheless, the two communities represented by each

gear were significantly and highly correlated, suggesting that production estimates based on trawled benthic invertebrates can be a reliable index of benthic prey production for juvenile fish.

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

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

# 4.5.2 Variability in macrobenthic prey production among nurseries: potential influences

Coastal nurseries along the Bay of Biscay have a similar range of depths (Table 2) and temperature, but differences in local hydrodynamics influence the main sediment characteristics. For instance, the intensity of currents and water discharges in the outer Loire and Gironde estuaries is ~10 times as high as that in the Bay of Vilaine. Mean annual flow is ~75 m<sup>3</sup>.s<sup>-1</sup> for the Vilaine River vs. ~850 and ~780 m<sup>3</sup>.s<sup>-1</sup> in the Loire estuary and Gironde estuary, respectively (Romero *et al.*, 2013).

It might be expected that the higher river discharges and thus higher nutrient loads (Romero *et al.*, 2013) from the two large estuaries would produce more benthic prey than in the Bay of Vilaine. Yet, according to the index, benthic prey production in the Bay of Vilaine is in the same order of magnitude as those in the outer estuaries of Loire and Gironde. These similarities in prey production might be related to the

longer residence time of water in the Bay of Vilaine (Obaton and Garreau, 1999) than in the two other nurseries (Lazure and Salomon, 1991). We hypothesized that a longer residence time would allow primary producers to take up more terrestrial nutrients and organic matter, which could benefit secondary producers and the rest of the coastal food web as shown in wetlands (Sierszen *et al.*, 2006). Conversely, the higher river discharges in the Loire and Gironde estuaries flush nutrients and organic matter out to the ocean, resulting in prey production similar to that estimated in the Bay of Vilaine. Nevertheless, our data did not enable us to explain that pattern and it would be interesting to use a larger dataset to properly explore the potential drivers of inter-annual and inter-site variability in benthic prey production.

#### 4.5.3 Macrobenthic prey production limits YOY fish density

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

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

All YOY fish species showed a positive relationship with the benthic prey production index at the upper quantile, except *T. luscus*, which may have different feeding or behaviour ecology. This species seems to have an aggregative behaviour that is not exclusive to soft bottoms (Reubens *et al.*, 2011), which could partly explain the highest densities sampled at certain stations in the three nurseries. Moreover, *T.* 

*luscus* is a suprabenthic feeder that targets Amphipoda, Mysidacea, and epibenthic Decapoda (Robin and Marchand, 1986; Hamerlynck and Hostens, 1993; França *et al.*, 2004), and the latter two orders were sampled less by the grabs. YOY *M. merlangus* has similar feeding habits (Hamerlynck and Hostens, 1993), but showed a positive relationship to the benthic prey production index, perhaps because its juveniles settle in sand (Demain, 2010).

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

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

### Acknowledgements

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

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### 4.7 Supplementary materiel

Supplementary Material A: Bathy-sediment strata in the four coastal nurseries of the Bay of Biscay

For each nursery (the outer Loire estuary, the Bay of Vilaine, and the two semi-enclosed bays, Pertuis d'Antioche and Pertuis Breton), strata were defined based on the bathymetry and sediment composition.

Sediments were collected with a 0.1 m<sup>2</sup> Van Veen grab. A sample (~500 g) was extracted and then stored in a plastic bag (Twirl'em) at +4°C. In the laboratory, the samples were dried at 80°C in an oven during 48 hours. 100 g of the dried samples were then sieved in a column of 14 successive sieves with square mesh sizes ranging from 63 to 10000  $\mu$ m. Sediments were than categorized into four categories according to grain size: gravels with a diameter between 2000 and 10000  $\mu$ m, coarse sand between 500 and 2000  $\mu$ m, fine sand between 63 and 500  $\mu$ m and mud, inferior to 63  $\mu$ m.



## Figure A1. Sediment composition of each grab sampling station in 2008 in the Bay of Vilaine, 2016 in the Loire outer estuary and 2015 in both Pertuis.

We used four variables to define the strata (associated with each station sampled): bathymetry, distance to the mouth of the river, percentage of mud, and percentage of coarse sand. Clustering was performed using the R package *ClustGeo* (Chavent *et al.*, 2017). We used a ward-like hierarchical clustering algorithm that includes spatial/geographical constraints with two dissimilarity matrices (D0, based on the above variables, and D1, based on geographic distances only) and a mixing parameter  $\alpha$  [0;1], which sets the importance of each matrix. The number of clusters was chosen by visual inspection of the wardlike dendrogram from clustering on D0 (without the geographical constraint), and then the mixing parameter that was the best compromise between loss of bathy-sediment homogeneity and loss of geographical homogeneity was set. Strata were designed separately for each site.

		a (mixing	
Site	k (number of clusters)	parameter)	Strata description
Vilaine	4 (but only 3 strata, as the 4 <sup>th</sup>	0.1	<b>V1</b> : sandy mud estuarine stratum (<6 km from the river mouth),
	stratum consisted of 2		shallow (5-12 m deep)
	stations with coarser		V2: muddy coastal shallow stratum (8-14 m deep)
	sediments included in V1)		V3: sandy mud coastal deep stratum (>18 km from the mouth, 17-
			34 m deep)
Loire	3	0.2	L1: sandy mud estuarine shallow stratum (5-6 m deep)
			L2: sandy coastal shallow stratum (5-14 m deep)
			L3: sandy (but muddier than L2) coastal deep stratum (16-23 m
			deep)
Pertuis	2	0	<b>PB1</b> : muddy coastal (close to the continent) shallow stratum (2-8
Breton			m deep)
			<b>PB2</b> : coarse sediment coastal deep stratum (4-12 m deep)
Pertuis	2	0	<b>PA1</b> : muddy coastal (close to the mouth of the river) shallow
Antioche			stratum (4-5 m deep)
			PA2: sandy mud coastal (6-22 km from the mouth) deep stratum

Table A1. Clustering parameters and strata description for each nursery.

La mise à jour automatique des citations est désactivée. Pour voir la bibliographie, cliquez sur Actualiser dans l'onglet Zotero.Chavent, M., Kuentz-Simonet, V., Labenne, A., & Saracco, J. (2017). ClustGeo: an R package for hierarchical clustering with spatial constraints. *Computational Statistics*, 1-24. https://arxiv.org/pdf/1707.03897.pdf



Figure A2. Bathy-sediment strata in (a) 2008 in the Bay of Vilaine, (b) 2016 in the Loire outer estuary and (c) 2015 in both Pertuis stations. Locations of the sampling stations with grabs are indicated with the blue stars.

**Supplementary Material B:** Variability in biomass and production sampled by trawl and grab in nurseries along the Bay of Biscay within each bathy-sedimentary stratum



Figure B1. Boxplots of biomass of prey by station estimated from (top) grab and (bottom) trawl sampling in each bathy-sediment stratum. Biomass is in g AFDM m<sup>-2</sup>. For a greater clarity, y-axis has been cropped (bottom right) between 0 and 0.05 g AFDM m<sup>-2</sup>.



Figure B2. Boxplots of benthic prey production by station estimated from (top) grab and (bottom) trawl sampling in each bathy-sediment stratum. Production is in kJ m<sup>-2</sup> y<sup>-1</sup>. For a greater clarity, y-axis has been cropped (bottom right) between 0 and 1 kJ m<sup>-2</sup> y<sup>-1</sup>.

**Supplementary Material C:** Length-frequency distributions for each species and details on size selection procedures



Figure C1. Length-frequency distributions for each species using lengths collected between 2004 and 2016 (the period c. When several cohort could be distinguished, Gaussian distribution was used to determine the Young-of-the-year size class (vertical red line). Grey rectangles represent the second step of the fish selection: individuals that feed almost exclusively on macrobenthic invertebrate prey, which was set to [7 - 15] cm size range (see main text for more details). Finally, the red rectangles represent the final fish selection: Young-of-the-year within the [7 - 15] cm size range.

**Supplementary Material D:** Composition of potential prey sampled by grab and trawl in the three nurseries (V: Bay of Vilaine, L: outer Loire estuary, and G: outer Gironde estuary)



Figure D1. Composition (in production) of potential prey sampled by grab and trawl in the three nurseries (V: Bay of Vilaine, L: outer Loire estuary, and G: outer Gironde estuary).

**Supplementary Material E:** Quantile regressions (10<sup>th</sup> and 90<sup>th</sup>) for each species and each community level







Figure E1. Graphic representations of the quantile regressions (10<sup>th</sup> and 90<sup>th</sup>) of benthic food production index on fish density for each species and each community level. Black lines indicates 10<sup>th</sup> and 90<sup>th</sup> regression lines.

### 10<sup>th</sup> quantile



Figure E2. Distributions of p-values of the slope coefficient for lower and upper quantiles (10<sup>th</sup> and 90<sup>th</sup>) including the 1000 replicates of the bootstrap analyses. This was done to estimate the standard error associated with the slope coefficient.

### Chapitre 5.

Discussion générale



Illustration : L. Fleury

Le stade juvénile des espèces marines nourricerie-dépendantes est caractérisé par une forte concentration des individus dans les zones de nourricerie et ce stade est crucial pour le renouvellement de ces populations et pour le maintien des activités halieutiques qui en dépendent (sole, bar - ICES, 2017). Cependant, les processus de régulation densité-dépendants qui y ont lieu (Iles and Beverton, 2000; Ohlberger *et al.*, 2006; Archambault *et al.*, 2014) et plus précisément l'importance des différents mécanismes sous-jacents sont encore débattus, en particulier le rôle du facteur trophique (Le Pape and Bonhommeau, 2015).

L'objectif général de cette thèse était d'alimenter la réflexion sur la question de la capacité trophique des nourriceries côtières et de son caractère limitant pour les juvéniles. Une première approche s'est concentrée sur les processus ayant lieu à une fine échelle spatio-temporelle (l'échelle de l'habitat au sein de la nourricerie et l'échelle de la saison). Cette approche a été privilégiée pour deux raisons principales : (1) les estuaires et les baies côtières supportant la fonction de nourricerie sont des systèmes présentant de fortes variations spatiales (Peterson, 2003; Nagelkerken et al., 2015) et temporelles, en lien notamment avec l'hydrodynamisme saisonnier (Marchand, 1993; Romero et al., 2013) impliquant que (2) les processus et les variables responsables de la limitation trophique (comme la compétition trophique ou la production de proies) sont variables dans le temps et l'espace (Beukema, 1974; Lawson et al., 2018; Saulnier et al., 2019). Ainsi, on peut supposer si la capacité trophique du milieu est limitante, alors elle agirait à certaines saisons (Pihl, 1985; Chevillot et al., 2017) ou bien dans certains habitats spécifiques (Beukema and Cadée, 1997). De plus, ces fines échelles sont adaptées pour un dialogue avec les gestionnaires de ces milieux. Les conflits entre les activités humaines et les fonctions soutenues par ces écosystèmes font de la compréhension des processus à fines échelles un véritable enjeu pour la gestion. Une seconde approche a ensuite permis d'alimenter la réflexion sur la limitation trophique en testant l'occurrence potentielle de ce processus sur plusieurs années et différentes nourriceries.

Cette discussion présente et discute les principaux résultats de cette thèse. Elle s'alimente du contexte dans lesquels ils s'inscrivent, elle revient sur les principaux challenges méthodologiques de cette thèse et elle propose quelques pistes d'amélioration possibles ainsi que des perspectives dans la continuité de ce travail.

# 5.1 Fonctionnement trophique à fine échelle spatiale de la nourricerie de l'estuaire de la Seine

### 5.1.1 Intégration de la matière organique par les juvéniles le long du gradient du fleuve

Les sources de matière organique sur lesquelles s'appuient les réseaux trophiques estuariens sont multiples et diverses : matières vivantes (phytoplancton, microphytobenthos (MPB), macrophytes) et particules détritiques (Riera and Richard, 1996; Le Pape *et al.*, 2013). Le gradient estuarien structure le mélange de matière organique disponible (Liénart *et al.*, 2017). A. Engler<sup>7</sup>, dans le cadre de son stage de Master 2, a quantifié la contribution des sources primaires (MOP marine, MOP fluviale et microphytobenthos) dans le régime alimentaire des juvéniles de sole et de plie le long du gradient estuarien de la Seine à l'aide d'un modèle de mélange isotopique (Stock *et al.*, 2018) admettant comme co-variable le gradient estuarien (la distance au point le plus en amont de l'estuaire). Ce travail a permis de caractériser le gradient estuarien classique entre l'amont et l'aval de l'estuaire (Fig. 1).



# Figure 1 : Contribution des sources de matière organique dans l'alimentation des soles G0 au printemps et à l'automne le long du gradient estuarien (Amont-aval). Les zones grisées correspondent aux zones où aucun poisson n'a été échantillonné. Figure adaptée du rapport de stage d'A. Engler (2019).

Il a aussi mis en évidence des différences inter-saison concernant la MOP marine, largement dominante dans les secteurs avals (embouchure et fosse sud) au printemps (> 70 %) alors qu'à l'automne, sa contribution chutait et celle du MPB augmentait avec en moyenne 30 % de l'alimentation des juvéniles de plies et de soles (exemple de la sole Fig. 1). La forte contribution de la MOP marine au printemps

<sup>&</sup>lt;sup>7</sup> Alexandra Engler, stagiaire de Master 2 co-encadrée avec Pierre Cresson (unité HMMH, Ifremer Boulogne sur Mer)

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pourrait s'expliquer par un bloom phytoplanctonique dans la partie avale. L'importance du MPB à l'automne pourrait être due soit à l'export de la production de MPB des vasières intertidales via les courants (Yokoyama et al., 2009; Kang et al., 2015), soit à une production locale de MPB en partie avale (Rigolet et al., 2014) ou encore à la récente migration des poissons s'étant nourris en amont et dont la signature isotopique reflèterait encore la contribution des secteurs amont. Pour les individus issus du secteur amont, le MPB est une des sources principales de leur alimentation, notamment à l'automne, contribuant entre 20 et 40 % à leur alimentation, une contribution dans les mêmes ordres de grandeur que dans d'autres estuaires. Dans l'estuaire de la Vilaine, la contribution du MPB à l'alimentation des soles G0 a été estimée entre 25 et 45 % (Kostecki et al., 2010), tout comme dans d'autres systèmes (Baie du Mont Saint Michel, Tage, Charente) sauf dans le delta du Rhône (Le Pape et al., 2013) où les juvéniles de sole dépendent principalement de la matière d'origine fluviale et des apports terrigènes (Darnaude et al., 2004). Les caractéristiques propres au delta pourraient être à l'origine de cette différence. Kostecki et al. (2010) ont également montré que la contribution des différentes sources variait avec le débit. Celui de la Seine en 2017 étant particulièrement faible par rapport à la série (http://www.hydro.eaufrance.fr), la matière organique d'origine terrestre a vraisemblablement moins alimenté le réseau trophique que la moyenne. Ces résultats seront également à confirmer en utilisant les signatures isotopiques des sources directement issues de l'estuaire de Seine en 2017 (les valeurs actuelles sont issues de la littérature sur d'autres sites).

### 5.1.2 Caractérisation de l'utilisation des habitats d'alimentation par les juvéniles

Les sources de matière organique consommée par les juvéniles donnent un premier aperçu de l'hétérogénéité spatiale du fonctionnement trophique des nourriceries et de l'utilisation des ressources par les juvéniles de poissons. L'estuaire de la Seine est une mosaïque d'habitats structurés par des variables biotiques (salinité, profondeur, sédiment, morphologie) se traduisant dans les caractéristiques des communautés macrobenthiques (Thiébaut *et al.*, 1997; Baffreau *et al.*, 2017; Dauvin *et al.*, 2017). Dauvin and Desroy (2005) proposent une définition des grands habitats de la baie de Seine basés sur ces critères et adoptés par les gestionnaires de cet estuaire. Mieux comprendre la capacité trophique des nourriceries côtières nécessite une meilleure compréhension du fonctionnement trophique de l'estuaire et la quantification des liens trophiques entre ces habitats. Ces problématiques ont été abordées dans cette thèse sous l'angle de la contribution des habitats à l'alimentation des juvéniles, permettant ainsi de souligner le rôle trophique des habitats ainsi que leur connectivité. L'échelle de l'habitat permet alors de faciliter le dialogue avec les instances de gestion de l'estuaire qui utilisent ces mêmes repères spatiaux. En outre, l'estimation de la contribution des habitats à l'alimentation des juvéniles est une étape essentielle dans l'estimation de la capacité trophique.

Les habitats d'alimentation essentiels pour les 4 espèces de poissons marins nourricerie-dépendants sélectionnés traduisent à la fois les niches écologiques et les capacités de déplacement de ces espèces.

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Les juvéniles de sole et de bar supportent des dessalures (Boeuf and Lasserre, 1978; Champalbert *et al.*, 1992) et exploitent activement les habitats amont, et en particulier les vasières intertidales, alors que la plie, décrite comme une espèce plutôt marine exploite essentiellement les habitats marins (Gibson, 1973; Poxton and Nasir, 1985). Les capacités de déplacement des juvéniles de sole et de plie étant modérées (Le Pape and Cognez, 2016), ils montrent une stratégie d'alimentation « locale », *i.e.* proche de l'endroit où ils sont capturés. Les résultats du stage d'A. Engler ont également confirmé le caractère très opportuniste des juvéniles de sole (Darnaude *et al.*, 2001; Kopp *et al.*, 2013) et ont montré une forte affinité des juvéniles de plie pour les bivalves, espèces dominantes dans l'embouchure. Enfin, les juvéniles de merlan explorent les différents habitats au sein d'une nourricerie est aussi soulignée dans des écosystèmes de marais côtiers ('tidal marsh') et l'importance de considérer la nourricerie comme une mosaïque d'habitats, dynamique spatialement et temporellement, est essentielle pour la gestion de ces systèmes (Colombano *et al.*, 2020).

Les contenus stomacaux reflètent l'alimentation des dernières heures alors que la signature isotopique intègre le régime alimentaire sur une plus longue période, en lien avec le renouvellement cellulaire du tissu considéré (Tieszen *et al.*, 1983). Le renouvellement cellulaire pour le muscle est de l'ordre d'un à plusieurs mois (Buchheister and Latour, 2010). Pour les juvéniles de poissons dont la croissance est élevée, on peut supposer que la signature isotopique intègre en moyenne l'alimentation du dernier mois de vie. Ainsi, les traceurs trophiques utilisés ne permettent pas de connaitre l'utilisation des habitats par les juvéniles pendant la saison estivale, entre les deux périodes étudiées plus précisément. Le projet MODHANOUR<sup>8</sup> étudiait l'évolution au cours des mois du centre de gravité de la distribution spatiale des juvéniles de poissons dans l'estuaire de Seine. Il a montré plusieurs patrons de migrations saisonniers, dont un patron sortant et un patron sortant puis revenant en automne, notamment pour les soles et les plies G0 (Brind'Amour *et al.*, 2018). Explorer les raisons de cette migration (en lien avec la disponibilité alimentaire par exemple, ou l'activité des proies en été ; van der Veer et al., 2016) permettrait aussi de mieux comprendre le fonctionnement trophique de ce système et d'alimenter la réflexion sur la capacité trophique, si ces migrations sont liées à un facteur trophique.

### 5.1.3 Rôle trophique des habitats de la baie de Seine

L'utilisation des courants par les juvéniles pour accéder aux ressources trophiques des vasières intertidales avait déjà été démontrée dans l'estuaire de la Seine et dans d'autres estuaires (Morin *et al.*, 1999; Cabral, 2000; Laffaille *et al.*, 2001; Kostecki *et al.*, 2012; Le Pape *et al.*, 2013). Dans cette thèse, la contribution de cet habitat à l'alimentation des juvéniles a été quantifiée. Les ressources trophiques des vasières sont exploitées par les juvéniles de sole et de bar et elles contribuent au moins à la moitié

<sup>&</sup>lt;sup>8</sup> Porté par le GIP Seine-Aval (phase 5)
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de leur alimentation pour les individus situés dans les habitats proches des vasières. Les vasières intertidales semblent donc attractives pour les juvéniles pour une raison d'ordre trophique. Elles présentent un cortège d'espèces capables de supporter l'émersion comme l'amphipode Corophium volutator, la polychète Hediste diversicolor ou encore le bivalve Scrobicularia plana avec des productivités élevées (ratio P/B de C. volutator supérieur à 5 an<sup>-1</sup>) ou de fortes biomasses. Ce sont des espèces classiquement retrouvées dans les ensembles benthiques des vasières intertidales, comme dans l'estuaire du Tage (Moreira, 1995) ou encore dans la baie du Mont-Saint-Michel, où on observe également de fortes densités en juin/juillet (Meziane and Retière, 2001). Cette différence entre communauté intertidale et communauté subtidale se retrouve aussi dans les communautés de zooplancton pélagiques et avec les poissons zooplanctivores échantillonnés dans la zone subtidale se nourrissant sur les communautés intertidales comme décrit dans l'estuaire de la Gironde (David et al., 2016). Les températures plus élevées au printemps peuvent également expliquer la venue des juvéniles dans ces habitats. En 2017, cet habitat présentait les plus fortes valeurs de EE, notamment à l'automne pour les juvéniles G0 jusqu'à une moyenne de 85%. Sachant que d'autres prédateurs consomment potentiellement ces ressources (voir 5.3.2), il est fort probable qu'à cette saison, l'intégralité de la production de macrofaune de cet habitat soit consommée et que la capacité trophique soit atteinte. Cet habitat de faible surface joue donc un rôle primordial dans la capacité trophique de la nourricerie de Seine.

Parmi les habitats subtidaux, l'embouchure soutient également de fortes productions de proies, une forte consommation des juvéniles de poissons et montre des faibles valeurs de EE (la production de proies supporte largement la consommation des juvéniles), ce qui lui donne un rôle trophique de tout premier ordre. Cet habitat a la particularité d'être très vaste comparé aux autres, tout en restant productif. Cette forte production de proies est un pattern récurrent pour cet habitat (Saulnier *et al.*, 2020). C'est également un habitat avec une grande diversité d'espèces de macrofaune benthique, en 2017, mais déjà observé auparavant (Dauvin and Desroy, 2005), contrairement aux vasières intertidales qui présentent un corridor d'espèces plus étroit. Les fosses subtidales nord et sud sont moins productives que les deux autres habitats et présentent des niveaux de consommations également inférieurs, en particulier pour la fosse nord. Cette fosse est connue pour sa faible production benthique (Mouny *et al.*, 1998; Saulnier *et al.*, 2020), dont l'explication réside possiblement dans les fortes variations de salinité subies en fosse nord ou par sa proximité au port du Havre.

Finalement, les habitats présentés comme des entités distinctes présentent un certain degré de connectivité, via les mouvements des masses d'eau et les mouvements des espèces y résidant, et par la forte amplitude du marnage. Dans un système microtidal où les habitats sont plus isolés d'un point de vue hydrodynamique, la connectivité entre habitats d'un point de vue trophique est assurée par les prédateurs supérieurs (Marley *et al.*, 2019).

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#### 5.1.4 Rôle trophique dans un contexte de dégradation des habitats côtiers

Comme décrit dans l'introduction, l'estuaire de la Seine a subi de nombreuses modifications morphologiques au cours du siècle dernier, causant la dégradation et la perte d'habitats, en particulier la perte de vasières intertidales (Delsinne, 2005). Cette perte de surface se traduit par la perte de la fonction de nourricerie pour les juvéniles de sole (Rochette *et al.*, 2010; Archambault *et al.*, 2018) et par la diminution de la qualité des ressources (Le Pape *et al.*, 2007b). Ce contexte pousse les usagers de cet estuaire, ses gestionnaires et les scientifiques impliqués à mieux en comprendre le fonctionnement et l'importance des différents habitats pour préserver ou restaurer la fonction de nourricerie de l'estuaire. Une précédente étude avait déjà montré que les habitats de la fosse nord et du chenal de navigation présentaient des signes de stress (Tecchio *et al.*, 2015). Cette thèse s'inscrit dans la continuité de ces travaux en adaptant l'échelle d'étude à la gestion de l'écosystème.

En outre, on peut également s'attendre à des évolutions liées au changement climatique tels qu'une élévation du niveau de la mer ou une marinisation de l'écosystème (Harley *et al.*, 2006), pouvant à leur tour causer la perte ou la dégradation d'habitats essentiels et touchant tous les écosystèmes des plus dégradés aux plus préservés. Par exemple, dans les baies nord-américaines, l'augmentation du niveau de la mer pourrait engendrer une perte des habitats intertidaux de 20 à 70 % (Galbraith *et al.*, 2002).

# 5.2 Apports de la thèse dans le débat sur le caractère limitant de la capacité trophique des nourriceries pour les juvéniles

## 5.2.1 Capacité trophique à l'échelle des périodes encadrant la période forte croissance des juvéniles

La capacité trophique a été abordée à travers l'efficacité d'exploitation (EE) à deux périodes potentiellement sensibles dans les interactions proie-juvénile : la fin du printemps (~ juin), juste après l'installation des juvéniles sur la nourricerie et au début de l'automne (~octobre), soit la fin de la forte période de croissance des juvéniles. Au printemps, les estimations de EE pour les G0 sont plus faibles (en moyenne 0,5 %), malgré quelques disparités spatiales entre les habitats. Ceci suggère que la forte pression de prédation exercée par l'arrivée massive de juvéniles à la fin du printemps (par exemple pour la plie; Nash and Geffen, 2012) coïncide (« match ») avec la forte production de proies à cette même période. Au printemps, la quantité de nutriments accumulés pendant l'hiver , l'augmentation de la longueur des jours favorisent une forte production primaire et est caractérisée par des blooms phytoplanctoniques et microphytobenthiques (Heip *et al.*, 1995, p 1995; Glé *et al.*, 2008). Cette production primaire, accompagnée de matière organique apportée par le fleuve, soutient la production secondaire, soit les proies des juvéniles. L'arrivée des juvéniles est alors synchrone avec la forte production de proies. Ce synchronisme est favorisé notamment par la

saisonnalité des périodes de reproduction des espèces sous nos latitudes. À l'inverse, sous les tropiques, la production n'a pas de saisonnalité et les fraies s'étalent tout au long de l'année (Gibson, 2005). De plus, il semble que l'arrivée des juvéniles sur la nourricerie soit en léger décalage d'une espèce à l'autre. Comme A. Lemoine<sup>9</sup> a pu l'observer sur la nourricerie de la baie de Seine pour la période 2000-2015 pour les juvéniles de sole et de plie. En 2017, les plies G0 sont déjà présentes lors de la campagne du mois de mai alors que les soles G0 en sont encore absentes. Le pic de densité pour ces deux espèces est en juin. L'année 2017 est caractérisée par une installation précoce des soles G0 par rapport à la situation moyenne 2000-2015. Sous nos latitudes tempérées, la période de ponte de la plie précède celle la sole (Gibson, 2005). Cet étalement des arrivées des larves réduit probablement la pression de prédation exercée sur la communauté de proies. En effet, au printemps, les juvéniles se nourrissent principalement de méiofaune du fait de la taille de leur bouche (Gee, 1989; Coull, 1990; Aarnio et al., 1996). On peut supposer que les premiers arrivants se nourrissent de cette ressource puis en grandissant, accèdent à des proies de plus grande taille dont la proportion dans leur régime alimentaire s'accroît alors. Le passage (« shift ») alimentaire entre méiofaune et macrofaune est souvent décrit autour de 40 mm pour les poissons plats (Pihl, 1985; Gee, 1989; Coull, 1990; Aarnio et al., 1996; Andersen et al., 2005). Ainsi les changements ontogéniques dans l'alimentation, combinés à l'étalement des arrivées peuvent conduire à une réduction de la compétition interspécifique et ainsi à une réduction de la pression de prédation exercée sur un compartiment de proies.

À l'inverse des G0, les estimations de EE pour les G1 sont plutôt élevées au printemps (en moyenne 20 %). Les juvéniles G1 accèdent à des communautés de proies sensiblement différentes de celles des juvéniles G0 du fait de leur taille de bouche. Cette valeur de 20 % semble élevée comparée à la littérature : entre 2 et 16 % pour les G1 sur 3 années dans la baie de Seine (Saulnier *et al.*, 2020) ou autour de 5 % dans la baie de Vilaine (Tableau *et al.*, 2019b). De plus, cette valeur est probablement sous-estimée du fait de la non prise en compte de l'accessibilité des proies par les juvéniles (Tableau *et al.*, 2015). Néanmoins, il s'agit d'une valeur estimée sur un mois et non sur l'année comme pour les autres études citées ci-dessus. Ceci suggère que les juvéniles G1 exerceraient une très forte pression de prédation sur la macrofaune benthique à la fin du printemps. En juillet, les densités de G1 sur la zone d'étude diminuent brutalement (principalement pour la sole). Cette chute pourrait être liée à une offre alimentaire insuffisante induisant de la mortalité ou plus probablement à une migration vers d'autres zones (Nash and Geffen, 2012).

La période automnale était supposée être une période sensible, car l'offre en proies diminuant (Beukema, 1974; Saulnier *et al.*, 2019) et les températures baissant conduisent à un ralentissement de la croissance journalière. C'est notamment le cas chez la plie (Ciotti *et al.*, 2013b, 2014; van der Veer *et al.*, 2016). Les estimations de EE pour les G0 sont en effet supérieures par rapport à celles du printemps (~ 7 %,

<sup>&</sup>lt;sup>9</sup> Andréa Lemoine, stagiaire de Master 2 co-encadrée avec Camille Vogel (unité HMMH, Ifremer Port en Bessin)

jusqu'à 85 % localement dans les vasières intertidales). Les densités de juvéniles sont plus faibles à cette période, du fait de la mortalité des mois précédents, mais les besoins énergétiques individuels proportionnels à la taille induisent une demande et donc une consommation plus importante qu'au printemps. Ainsi, ces valeurs de EE peuvent traduire une limitation trophique pour les prédateurs étroitement dépendants des invertébrés macrobenthiques, comme les poissons plats ou le callionyme lyre. En outre, les estimations de EE pour les juvéniles G1 à cette même période sont du même ordre de grandeur que celles des G0. En cette période, les deux classes d'âge se partageraient davantage de proies.

Malgré l'effort pour estimer la capacité trophique sur deux saisons potentiellement sensibles, une incertitude persiste encore sur la saison estivale. On sait que la consommation des juvéniles G0 atteint un pic au mois d'août pour la baie de Seine en 2017. Le taux de consommation des juvéniles de plie atteint également un maximum en août sur la nourricerie de la baie de Port Erin (Nash *et al.*, 2007). Les patrons de migration saisonniers des juvéniles indiquent également que les poissons se déplacent vers l'aval de l'estuaire entre mai et octobre (Brind'Amour *et al.*, 2018). Enfin, de nombreuses études dans la mer de Wadden concluent à une diminution de la croissance en été en comparant la température et la croissance journalière estimée sous des conditions optimales de nourriture à la croissance observée (Teal *et al.*, 2008; van der Veer *et al.*, 2010; Freitas *et al.*, 2012; Poiesz *et al.*, 2018). Des hypothèses autour de la régulation par la nourriture ont été émises (Teal *et al.*, 2008; van der Veer *et al.*, 2016). La forte consommation des juvéniles en été nous amène à questionner le rôle du facteur trophique sur la croissance et *in fine* sur une potentielle diminution du taux de survie, par inanition ou par prédation résultat d'un comportement plus risqué de recherche de nourriture (Biro *et al.*, 2003; Sinclair *et al.*, 2006). Des estimations de l'offre alimentaire et de sa disponibilité pour les juvéniles en été permettraient de creuser cette hypothèse.

#### 5.2.2 La capacité trophique dans l'évolution du contexte climatique

Le changement climatique menace tous les écosystèmes mondiaux et les espèces y résidant. Les nourriceries côtières et leur fonctionnalité sont également affectées par ces changements (McLean *et al.*, 2018). Dans leur étude sur la baie de Somme, McLean et al. (2018) montrent un déclin d'environ 80 % de l'abondance des poissons dans cette nourricerie, et notamment les espèces dites à stratégie de reproduction *r*, soit les espèces décrites dans le cadre de cette thèse. Les changements de température et de salinité impactent également la productivité benthique, comme dans les zones côtières de la mer Baltique où on a constaté une altération de la productivité des zones entre 6 et 20 m de profondeur, pouvant engendrer un manque localisé de nourriture pour les poissons démersaux (Snickars *et al.*, 2015). Le changement climatique affecte également la phénologie des espèces (Harley *et al.*, 2006; Durant *et al.*, 2007; Nixon *et al.*, 2009). Puisqu'il impacte la phénologie des juvéniles et de leurs proies, on peut se demander comment cela se répercutera sur les interactions proies-prédateurs. Va-t-on vers un pic de méiobenthos avancé qui ne coïnciderait plus avec l'arrivée des juvéniles ? Cette dernière ne serait-elle

pas également avancée du fait d'une gamétogénèse accélérée des géniteurs, conduisant à une ponte plus précoce et une croissance larvaire plus courte ? Quelques éléments de réponse sont apportés dans l'estuaire de la Gironde où des changements de phénologie sont constatés pour les compartiments de proies (avancement du pic de production du zooplancton) et des prédateurs (avancement de l'arrivée des juvéniles de poissons pélagiques), mais où l'on observe également une réduction du temps de résidence conjoint des juvéniles avec leur proie (Chevillot *et al.*, 2017). Dans cette même nourricerie, la fonction de nourricerie est questionnée et la problématique de la capacité trophique atteinte a été soulevée par l'augmentation des valeurs d'Efficacité d'Exploitation estimées par plusieurs modèles Ecopath construits à trois périodes successives (Chevillot *et al.*, 2019). Ainsi, mieux comprendre la fonctionnalité des nourriceries est urgent pour prédire l'impact qu'aura le changement climatique sur ces écosystèmes et ses répercussions sur les populations (Chevillot *et al.*, 2017).

#### 5.2.3 Occurrence de la limitation trophique

Dans leurs thèses, A. Tableau et E. Saulnier soulignent la nécessité d'augmenter le nombre de cas d'étude pour interpréter les valeurs d'EE obtenues. C'est dans cet objectif que nous avons élargi l'échelle fine explorée dans l'estuaire de la Seine à celle du golfe de Gascogne sur deux décennies. Ce travail s'est avant tout centré sur la production de proies, première partie du modèle de Tableau et al., (2019) par le biais d'un indice établi à partir des données issues d'échantillonnage de chalut. Il a été confronté à la densité de juvéniles, métrique souvent mobilisée pour l'appréciation de la fonction de nourricerie (Le Pape et al., 2003b; van der Veer et al., 2011; Trimoreau et al., 2013), et pas à la consommation des juvéniles comme c'est le cas chez Tableau et al., (2019). L'effet limitant de la production de proies sur les densités de juvéniles a ainsi été montré via des régressions quantiles sur plusieurs années et plusieurs nourriceries. Une hypothèse proposée pour la variabilité de l'offre alimentaire observée serait une cascade trophique à partir de l'apport des nutriments et de matière organique qui supporterait ensuite les productions primaire et secondaire (développé plus amplement dans la partie 5.4.3). Le suivi régulier de ces nourriceries grâce aux campagnes Nurse (Brind'Amour et al., 2019) devrait continuer à fournir des données permettant d'affiner l'indice, de le confronter à l'estimation de la consommation des juvéniles, second volet du modèle de Tableau et al (2019) et d'apprécier le déterminisme des facteurs environnementaux dans les variations susceptibles d'être observées.

Des données de proies ont également été collectées dans l'estuaire de la Seine depuis les années 2000, donc conjointement à la série de données sur les juvéniles. Ces données, reçues tardivement dans le cadre de cette thèse, sont précieuses pour étudier l'occurrence voire la récurrence du phénomène de limitation trophique. On s'attend alors à ce que, si la limitation trophique est récurrente, les valeurs de EE entre les différentes années oscillent autour d'une valeur seuil. Si la limitation trophique est ponctuelle, on s'attend alors à plus de variations dans les valeurs de EE (Fig. 2).



Figure 2 : Exemple théorique de l'évolution de la production de proie (FP) et de la consommation des juvéniles (FC) sous l'hypothèse d'une limitation trophique récurrente et sous celle d'une limitation ponctuelle.

### 5.3 Adaptations méthodologiques et pistes d'amélioration

#### 5.3.1 Adaptation du modèle de capacité trophique

Le modèle de capacité trophique de Tableau et al. (2019) estime la pression de prédation des juvéniles sur les ressources alimentaires présentes dans les nourriceries côtières. Ce modèle intègre la production de proies et la consommation des juvéniles sur la saison de forte croissance. Il était donc nécessaire d'adapter ce modèle pour répondre à l'objectif d'estimation de la capacité trophique à l'échelle de l'habitat et de la période (~ mois).

La première étape de l'estimation de la consommation des juvéniles est le calcul de leur *production (i.e.* la quantité de matière constitutive produite). Le modèle initial suppose une décroissance exponentielle de l'abondance au cours de la saison de croissance, en lien avec la mortalité taille-dépendante (Nash and Geffen, 2012). Théoriquement, les juvéniles G0 arrivent sur la nourricerie entre mai et juillet puis leur nombre décroit en raison de la mortalité en fin de saison de forte croissance ou d'une migration vers des zones plus profondes. Or, les données mensuelles ne vérifiaient pas cette hypothèse notamment pour la limande ou la sole (Fig. 3). Ceci est vraisemblablement lié à un décalage entre aire d'étude et aire de distribution des juvéniles plutôt qu'à une variation de la capturabilité des poissons, les mailles du chalut étant de 1 cm étirées.



Figure 3 : Évolution de la densité de juvéniles par mois dans l'estuaire de la Seine pour 3 espèces la limande (*L. limanda*, la plie, *P. platessa*, et la sole commune, *S. solea*)

Ainsi, la production a été calculée à partir de l'abondance mesurée au milieu du mois, en faisant l'hypothèse d'une bonne estimation de l'abondance moyenne sur le mois. Le projet MODHANOUR a montré que pour certaines espèces, les aires de distribution dépassaient l'aire échantillonnée dans le suivi utilisé pour ce travail de thèse, comme pour la limande qui a une distribution étendue vers l'espace marin ou le flet qui remonte dans l'estuaire (Brind'Amour et al., 2018). S'appuyer sur des données avec une plus large couverture spatiale permettrait alors de mieux comprendre les processus de mortalité / immigration, pour les espèces clés de la nourricerie. La deuxième adaptation pour le calcul de la production des juvéniles concerne le paramètre de croissance. Le modèle initial suppose une croissance constante (1 paramètre par espèce) durant la période de forte croissance. Cependant, ce paramètre évoluant (Amara, 2003; Teal et al., 2008; Ciotti et al., 2014), des estimations mensuelles ont été faites à partir de la courbe de croissance pour estimer la croissance spécifique moyenne au cours de cette période. Selon les travaux de F. Quemper<sup>10</sup>, sur l'évolution mensuelle de la taille des juvéniles de plie et de sole entre 2000 et 2015, les plies montreraient une diminution du taux de croissance dans les années récentes à l'inverse des soles. Or, le fait de n'échantillonner que les « survivants » biaise probablement le taux de croissance observé (Le Pape and Bonhommeau, 2015) et le possible décalage entre aire d'étude et aire de distribution des espèces rend les interprétations délicates. Ainsi, l'utilisation des taux de croissance mensuels moyens paraissait la meilleure estimation pour ce paramètre.

Une fois la consommation des juvéniles estimée, la seconde amélioration consistait en sa spatialiser sur les différents habitats. Pour ce faire, les résultats du modèle non spatialisé ont été combinés avec les sorties des modèles de mélange isotopique estimant la contribution des habitats à l'alimentation des poissons. L'incertitude autour des taux de fractionnement<sup>11</sup> isotopique a conduit à utiliser plusieurs valeurs plausibles. Les résultats étaient robustes aux différentes valeurs de taux de fractionnement pour la plie et la sole, mais moins pour le bar et le merlan, ce qui est couramment le cas avec ce paramètre (Bond and Diamond, 2011). Une valeur moyenne a donc été choisie avec des résultats à interpréter avec

<sup>&</sup>lt;sup>10</sup> Florian Quemper, stagiaire de césure encadré par Anik Brind'Amour et Camille Vogel dans le cadre du projet CAPES en 2019.

<sup>&</sup>lt;sup>11</sup> Pour rappel, le taux de fractionnement correspond à la différence observée dans la signature isotopique entre une proie et son prédateur, résultant de la discrimination des isotopes en fonction de leur masse atomique lors des processus d'assimilation et d'excrétion.

précaution pour ces espèces-là. Finalement, un des intérêts des modèles de mélange bayésiens est l'obtention de la distribution associée aux paramètres estimés (ici, la contribution des habitats à l'alimentation des poissons, le paramètre  $\alpha$ ). Or dans un souci de temps, une valeur fixe a été utilisée pour la spatialisation (*i.e.* la médiane). La prise en compte de cette incertitude autour de ce paramètre devra être intégrée au modèle.

La troisième adaptation concerne la production de proies et plus particulièrement la mensualisation du ratio production sur biomasse. Au vu de la diversité d'espèces de la macrofaune benthique, le choix d'une mensualisation à l'échelle de la communauté est apparu comme le plus réaliste et parcimonieux. La littérature sur la saisonnalité des ratios P/B des populations et de la production de la macrofaune benthique à l'échelle de la communauté étant peu étoffée (Beukema, 1974; Saulnier *et al.*, 2019), différents scénarios ont été élaborés par précaution avec différentes valeurs de coefficients pour mensualiser le ratio P/B.

Enfin, la dernière adaptation a consisté en l'ajout du compartiment méiobenthique, et plus précisément des copépodes harpacticoides comme proies potentielles des juvéniles. Cet ajout était essentiel pour l'estimation de la capacité trophique au printemps, quand les poissons se nourrissent activement sur ce compartiment (Widbom, 1984; Coull, 1990; Aarnio *et al.*, 1996; Glé *et al.*, 2008). L'ajout du suprabenthos aurait aussi été un ajout notable, notamment pour les poissons « ronds » tels que le bar, les gobies ou les gadidés dont une partie de l'alimentation repose sur ce compartiment de proies (Hostens and Mees, 1999; Laffaille *et al.*, 2001) particulièrement abondantes dans le chenal de navigation de la baie de Seine (Mouny *et al.*, 1998; Dauvin and Desroy, 2005). Les fortes densités de merlan qui y ont été observées à l'automne 2017 pourraient être liées à cette abondance.

#### 5.3.2 Quid des compétiteurs des juvéniles ?

Certains invertébrés benthiques de la mégafaune, , tels que l'étoile de mer *Asterias rubens*, la crevette grise *Crangon crangon* ou encore des crabes *Liocarcinus* spp se nourrissent en partie de macrofaune benthique (Evans, 1983; Christianen *et al.*, 2017). Saulnier et al. (2020) montrent que la consommation de ces prédateurs est du même ordre de grandeur de celle de la communauté de juvéniles de poisson en baie de Seine entre 2008 et 2010, notamment pour l'étoile de mer *Asterias rubens*. Des doutes sur ces données en 2017 font qu'elles n'ont pas été et incluses dans les estimations, mais ces espèces représentent potentiellement une certaine pression de prédation sur les espèces consommées par les juvéniles de poisson.

Les oiseaux (échassiers, canards ou mouettes (Horn *et al.*, 2017)) exercent également une pression de prédation sur les proies macrobenthiques dans les zones où elles leur sont accessibles, particulièrement sur les vasières intertidales (Moreira, 1995; Rosa *et al.*, 2008; Horn *et al.*, 2017) à marée basse. L'utilisation des ressources macrobenthiques des vasières par les oiseaux est estimée par comptage

(Rosa *et al.*, 2008; Horn *et al.*, 2017), par observation du comportement des oiseaux et de leurs prélèvements de faune sur les vasières (Moreira, 1995) ou encore l'analyse des fèces (De Smet *et al.*, 2013). L'estuaire de la Seine abrite de nombreuses espèces d'oiseaux résidantes. Situé sur la voie de migration Ouest Paléarctique et Est Atlantique, il accueille également beaucoup d'espèces migratrices (200 espèces régulières ; Fisson et al., (2014)) en hiver (GIP Seine Aval and Maison de l'estuaire, 2010) pour se reposer ou s'alimenter. La perte d'habitats intertidaux affecte également la fréquentation de ces populations, comme cela a pu être observé pour l'avocette élégante (*Recurvirostra avosetta*) dont les effectifs ont drastiquement chuté depuis 1997 (GIP Seine Aval and Maison de l'estuaire, 2010).

#### 5.3.3 Indice de production benthique

Le suivi des évolutions temporelles des proies et prédateurs peut permettre de tester l'occurrence potentielle de la limitation trophique (Crawford and Dyer, 1995; Okamoto *et al.*, 2012). L'échantillonnage quantitatif (benne) de la macrofaune benthique est couteux en temps d'analyses et de mesures (tri, détermination, comptages, pesées). Ceci explique l'absence de séries temporelles d'abondances et de biomasses longues de macrofaune benthique, en parallèle de séries temporelles d'abondances et de biomasses de juvéniles de poissons. Les chaluts classiquement utilisés pour collecter les juvéniles de poissons échantillonnent également des invertébrés benthiques, dont les petits individus représentent les proies communément retrouvées dans les contenus digestifs. Ces individus ont été sélectionnés pour construire un indice de la production benthique selon une échelle spatiale qu'il a fallu délimiter. Les méthodes d'interpolation spatiale (construction de variogramme puis kriegage) s'avérant non concluantes en raison d'un nombre trop limité de stations d'échantillonnage (sites de la Loire et des Pertuis), l'agrégation à l'échelle de la strate bathy-sédimentaire est apparue comme le meilleur compromis en bonne correspondance de l'échelle des habitats au sein des estuaires ou des baies de l'étude.

La bonne correspondance, mais avec un facteur de l'ordre 10<sup>3</sup>, entre les estimations de productions *via* les données issues de bennes et celles issues des données sélectionnées des chaluts a permis de construire cet indice.

### 5.4 Perspectives de recherche

## 5.4.1 Compréhension plus fine du fonctionnement trophique des nourriceries : confrontation aux théories écologiques

La disponibilité en ressources trophiques est un des facteurs majeurs dans les choix des prédateurs et dans les interactions entre espèces (Stephens *et al.*, 2019; Francois *et al.*, 2020). Plusieurs théories écologiques peuvent expliquer le comportement de recherche de nourriture des espèces dans leur

environnement et les interactions entre espèces (Fig. 4). La théorie classique de la compétition trophique prévoit quant à elle que quand les ressources alimentaires sont abondantes, les prédateurs se nourrissent d'une plus grande diversité de proies, car la compétition interspécifique est faible. À l'inverse, quand les ressources se raréfient, la compétition augmente et on observe alors une diminution et une ségrégation interspécifique des niches trophiques. Cette ségrégation permet alors la coexistence des espèces dans un même environnement (Cloyed and Eason, 2017).

L'« Optimum Foraging Theory » (OFT), ou théorie de l'optimisation de la recherche alimentaire prédit qu'un individu maximise le gain net d'énergie, soit le ratio entre l'énergie dépensée pour chercher, capturer et digérer une proie et l'énergie assimilée une fois la proie consommée (MacArthur and Pianka, 1966). Les invertébrés benthiques n'ont pas tous la même densité énergétique, selon leur composition biochimique, i.e. de leur composition relative en lipides, glucides et protéines (Brey et al., 2010). Par exemple la densité énergétique des bivalves Abra alba et Scrobicularia plana est d'environ 1 kJ g<sup>-1</sup> quand celle du polychète Hediste diversicolor et des copépodes harpacticoides est supérieure à 3 kJ g-1 (Brey et al., 2010). Quand les ressources trophiques sont abondantes dans l'environnement, les prédateurs ciblent alors les proies présentant le meilleur gain net d'énergie. On s'attend alors à ce que la niche trophique soit étroite, constituée seulement des proies les plus énergétiques. Les stratégies de chasse varient selon les prédateurs ; les proies les plus intéressantes varient donc en fonction de l'espèce considérée. Par exemple, le turbot, Scophthalmus maximus, est décrit comme un prédateur exclusivement visuel alors que la plie, Pleuronectes platessa utilise la vue et l'olfaction pour trouver ses proies (De Groot, 1971). Quand les ressources alimentaires se raréfient, les différentes espèces de juvéniles élargissent leur assiette, car les proies à gain net énergétique élevé se font plus rares et demandent alors plus d'énergie pour être débusquées. La niche trophique est alors plus large et les recouvrements de niches inter-espèces potentiellement plus élevés.



Figure 4 : Prédictions de changement de la largeur de niche trophique et du recouvrement entre niches trophiques inter-espèces en fonction de la disponibilité alimentaire selon la théorie de la compétition trophique (CT) et celle de l'« optimum foraging theory » (OFT). Figure adaptée de Stephens et al. (2019) et Correa and Winemiller (2014).

Ces théories répondent différemment à la disponibilité en proie, mais ne sont pas exclusives. En effet, on peut supposer que dans un environnement riche en proies, deux espèces sélectionnent les proies les plus intéressantes énergétiquement alors que si l'environnement s'appauvrit, les prédateurs changent de type de proies pouvant mener à une ségrégation de leurs niches trophiques, permettant la coexistence de ces espèces dans cet écosystème. C'est le cas par exemple du tigre, du léopard et du dhole, trois carnivores top-prédateurs de l'Asie du Sud-Est (Steinmetz *et al.*, 2020), pour qui les proies préférentielles sont des ongulés, mais qui se spécialisent sur différentes proies alternatives dans un contexte de diminution de la densité d'ongulés.

Ces théories pourraient être testées à partir des données disponibles dans le cadre de cette thèse : les contenus stomacaux et les signatures isotopiques des juvéniles de poissons, celles de leurs proies, et les échantillonnages des différents compartiments de proies potentielles, avec le printemps considéré comme la saison de forte disponibilité en proies et l'automne, la saison moins productive et donc avec une offre alimentaire moins fournie. Darnaude et al. (2001) ont montré une ségrégation trophique entre 4 espèces de poissons plats dans en Méditerranée en se basant sur un indice de recouvrement de contenus stomacaux. Cette ségrégation est favorisée par les différences morphologiques et de rythme alimentaire des différentes espèces. Dans son stage, A. Engler a commencé à étudier ces questions et a trouvé une certaine partition des ressources entre les juvéniles de plie et de sole.

De plus, les individus d'une même espèce peuvent consommer différentes ressources : c'est ce qu'on appelle en écologie trophique la « Niche Variation Hypothesis » ou encore l'hypothèse de variation de niche (Van Valen, 1965). La niche peut varier en fonction de l'ontogénie par exemple. Cependant, on observe également des variations dans l'utilisation des ressources entre les individus du même âge, soit une spécialisation individuelle comme observé par Araújo et al. (2011). Ces derniers auteurs décrivent 3 causes possibles de la spécialisation individuelle : (1) une différence dans l'optimisation des ressources due à des variations individuelles phénotypiques, (2) une différence dans le critère d'optimisation des ressources et (3) une différence dans les capacités à atteindre le choix optimum (par exemple, à cause d'un statut social). Ces aspects pourraient également être étudiés pour approfondir l'écologie trophique des juvéniles de l'estuaire de Seine et mieux comprendre les mécanismes agissant sur leurs stratégies alimentaires pour in fine, analyser leur fonctionnement dans un contexte de potentielle limitation trophique.

#### 5.4.2 Combiner les approches pour appréhender la question de la limitation trophique ?

Ce travail de thèse supporte l'hypothèse de limitation trophique, plusieurs résultats la suggérant. Différentes approches pour tester la densité dépendance et estimer la capacité trophique dans une nourricerie sont répertoriées dans l'introduction de cette thèse. L'application de ces différentes approches conjointement à un cas d'étude pour lequel on dispose d'une grande diversité de données et de suivi sur plusieurs années pourrait grandement alimenter nos conclusions quant à la limitation Discussion générale

trophique dans les nourriceries côtières. Face à une question complexe, et notamment dans la recherche d'une relation de cause à effet dans un milieu naturel, le travail scientifique consiste souvent à collecter des preuves de différentes natures, agissant à différentes échelles spatiales et temporelles. La convergence des approches permettrait de vérifier avec plus de confiance que la limitation trophique est un processus régulateur déterminant dans la dynamique des populations de juvéniles de poissons.

La baie de Seine semble être un cas d'étude approprié pour ce travail multi-approches. En effet, avec la construction de l'extension du port du Havre dans les années 2000, l'estuaire a fait l'objet de nombreux suivis des compartiments biologiques pouvant être affectés par ces modifications. De plus, le GIP Seine-Aval, crée en 2003, centralise les connaissances acquises et les données collectées par les différents projets. Dans le cadre du projet MODANOUR, la méthode du « self-thinning » (Nash et al., 2007) a été appliquée à partir de la série temporelle de collecte mensuelle pour trois espèces de poissons plats. Cette méthode permet de conclure sur l'atteinte ou non de la capacité d'accueil en fonction de la mortalité densité-dépendante en suivant l'évolution du poids moyen individuel en fonction de l'évolution de la densité au cours de la saison de forte croissance (Begon et al., 1986; Nash et al., 2007). Ainsi, il semblerait que la capacité d'accueil soit régulièrement atteinte pour ces espèces dans la baie de Seine (Brind'Amour et al., 2018). La diminution du nombre d'individus pouvant également être due à un départ de la zone d'étude et non à de la mortalité, il faudrait s'assurer que l'analyse soit réalisée sur les cohortes dont la zone d'étude recoupe bien la distribution spatiale au long de la saison de forte croissance. Comme évoqué à la fin du paragraphe 5.2.3 (occurrence de la limitation trophique), des données de macrofaune benthique collectées dans la baie de Seine sur une quinzaine d'années viennent d'être récupérées. Les données de proies qui en découlent analysées conjointement avec celles des juvéniles de poissons permettraient alors l'estimation de la capacité trophique annuelle sur une longue série temporelle. L'évolution relative de ces estimations et leur mise en relation avec des variables environnementales, notamment le débit, pourraient nous aider à démontrer le caractère limitant ou non du facteur trophique dans cet écosystème et à en comprendre ses variables forçantes.

Enfin, si le processus responsable des phénomènes de mortalité densité-dépendante dans les nourriceries est la limitation trophique, on peut s'attendre à ce que la croissance ou la condition des individus soient affectées par ce manque de ressources trophiques. La question est de savoir si le ralentissement de croissance est détectable avec des échantillonnages mensuels de juvéniles de poissons. Si la détérioration de l'état physiologique du poisson est rapide, il ne survivra pas et seuls les individus en bonne condition seront échantillonnés (Le Pape and Bonhommeau, 2015). Dans le cadre de cette thèse, des données de croissances journalières issues de la lecture d'otolithes devaient être acquises. Les otolithes sont des pièces calcifiées situées dans l'oreille interne qui croissent en couches concentriques pendant toute l'ontogénèse et sans résorption (Campana and Neilson, 1985). Après avoir vérifié que le taux de croissance de l'otolithe (mesuré par la distance séparant 2 stries) peut être utilisé comme un proxy de la croissance de l'individu (*e.g.* Isnard et al., 2015; Le Luherne et al., 2017), on pourrait comparer celui

obtenu entre la naissance et le printemps pour les individus échantillonnés au printemps à celui des individus échantillonnés à l'automne. Une différence entre ces deux groupes pourrait traduire une sélection des individus. On s'attend à ce que les individus avec un plus fort taux de croissance aient survécu. Cependant, il est important de préciser qu'une détérioration de l'état physiologique des juvéniles de poissons n'implique pas forcément une limitation trophique. En effet, d'autres facteurs peuvent impacter la physiologie des individus comme par exemple la contamination chimique (Marchand *et al.*, 2003).

La mer intérieure de Wadden (Pays Bas) ou l'estuaire du Tage (Portugal) sont également des nourriceries très étudiées (van der Veer *et al.*, 1991, 2001; Vinagre and Cabral, 2008; França *et al.*, 2009; Vinagre *et al.*, 2009a; Freitas *et al.*, 2016; Jung *et al.*, 2017) seraient également des cas d'étude potentiels pour ce travail multi-approches, après recensement des données disponibles.

#### 5.4.3 Quel rôle du débit dans la variabilité interannuelle de la capacité trophique ?

Si le facteur trophique joue un rôle majeur dans la régulation des jeunes stades de poissons dans les nourriceries comme tend à le démontrer cette thèse, alors l'étape suivante est de comprendre ses variations et les facteurs environnementaux impliqués. Une relation positive entre l'abondance des poissons juvéniles dans les nurseries côtières et les facteurs environnementaux locaux tels que le débit du fleuve a été démontrée dans plusieurs cas (Loneragan and Bunn, 1999; Le Pape et al., 2003b; Taylor et al., 2010; Dutterer et al., 2013; Nyitrai et al., 2013). Cette variable de forçage mériterait particulièrement d'être explorée dans une éventuelle poursuite de nos travaux. Les changements de débit affectent ainsi le gradient de salinité, les courants, la stratification, les apports organiques et minéraux, la qualité de l'eau, autant de facteurs qui impactent ensuite les juvéniles de poissons (Drinkwater and Frank, 1994). L'explication du lien entre débit et abondance de juvéniles est alors complexe et de nombreuses hypothèses sont proposées dans les études s'attachant à cette tâche délicate. Un plus fort débit engendre des courants de surface vers le large. Ce mouvement entraine un mouvement antagoniste avec la masse d'eau proche du fond se déplaçant alors vers l'estuaire (Lazure and Salomon, 1991) pouvant permettre aux larves de rejoindre plus facilement les nourriceries (Le Pape et al., 2003b; Taylor et al., 2010). Un débit élevé peut aussi stimuler les déplacements ou les migrations des individus et ainsi augmenter leur capturabilité (Loneragan and Bunn, 1999). Le débit agit aussi sur l'habitat des juvéniles de poissons en réduisant la dessalure quand le débit diminue. Par la suite, ce phénomène peut avoir des répercussions sur la pêcherie (Rowell et al., 2005). Une autre hypothèse souvent proposée est la cascade trophique : le débit amène des nutriments et des matières organiques incorporés dans la chaîne trophique estuarienne, alimentant les juvéniles (Drinkwater and Frank, 1994; Loneragan and Bunn, 1999; Darnaude et al., 2004). Cette dernière hypothèse serait intéressante à tester dans l'étude des variations de la capacité trophique. L'apport de nutriments boosterait la production primaire sur laquelle s'alimente la production secondaire d'invertébrés benthiques. Cependant, la réponse de la production benthique secondaire aux apports de nutriments n'est pas forcément linéaire. Elle peut présenter un effet de seuil, ou montrer une forme de dôme (Josefson and Rasmussen, 2000; Abdelrhman and Cicchetti, 2012). Dans les estuaires danois, les apports en azote soutiennent ainsi la biomasse benthique jusqu'à un seuil audelà duquel elle diminue (Josefson and Rasmussen, 2000). En effet, l'apport en nutriments peut avoir un double effet : la stimulation de la production, mais également une surcharge organique causant par exemple des conditions anoxiques (Abdelrhman and Cicchetti, 2012; Dolbeth *et al.*, 2012). Ainsi, le débit est une variable structurante des écosystèmes côtiers et ses variations influencent très sûrement la capacité d'accueil des juvéniles. C'est également une variable très complexe agissant sur les différents compartiments physique et biologique du système. Elle doit donc être interprétée avec précaution.

#### 5.4.4 Lien avec le recrutement des espèces nourriceries-dépendantes

Le renouvellement des ressources marines exploitées dépend de la biomasse de géniteurs et de la mortalité lors des jeunes stades de vie, du stade œuf jusqu'au recrutement. Comprendre les variations du recrutement ainsi que les facteurs responsables de ses fluctuations est un grand défi de l'halieutique.

Dans le cas des espèces marines nourriceries-dépendantes, les œufs et larves sont pélagiques et les juvéniles se concentrent sur les nourriceries estuariennes et côtières. Rijnsdorp et al. (1992) ont également trouvé une relation positive avec le niveau de recrutement (moyen et maximal) et l'aire des nourriceries de soles. Les facteurs générant de la variabilité dans le recrutement agissent sur la phase larvaire pélagique alors que les facteurs la régulant sont prépondérants lors de la phase démersale juvénile (van der Veer *et al.*, 2000). Le recrutement est donc régulé dans la phase juvénile, sur les nourriceries côtières (van der Veer *et al.*, 2000; Ustups *et al.*, 2013; Le Pape *et al.*, 2020).

Les juvéniles de différentes nourriceries rejoignent la population adulte. Par exemple, le stock de la sole du golfe de Gascogne est alimenté par les juvéniles provenant des différentes nourriceries côtières le long du golfe. À partir des données issues des campagnes de suivi des nourriceries et des campagnes au large ciblant les adultes, il serait pertinent d'étudier la démographie de l'espèce et de suivre l'abondance d'une cohorte de l'âge 0 à son recrutement. L'incorporation des données de campagnes ciblant les juvéniles avant le recrutement dans la pêcherie semble en effet améliorer l'évaluation du recrutement (Le Pape *et al.*, 2020).

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## DOCTORAT SCIENCES BRETAGNE DE LA MER LOIRE ET DU LITTORAL





Titre : Fonctionnement et capacité trophique des nourriceries côtières et estuariennes : exemple de la Seine

Mots clés : Limitation trophique, Habitats, Juvéniles, Bioénergétique

Résumé : Les zones côtières et estuariennes remplissent la fonction de nourricerie pour de nombreuses espèces de poissons démersaux. Ces zones étant limitées spatialement, elles disposent de ressources finies où les juvéniles de poissons se concentrent, engendrant de la régulation densitédépendante. On parle alors de capacité d'accueil des nourriceries. La prépondérance des mécanismes sous-jacents à cette mortalité, dont notamment la limitation trophique, est encore source de débat dans la communauté scientifique. L'objectif général de cette thèse est d'estimer la capacité trophique au sein des nourriceries estuariennes et côtières et d'alimenter la réflexion sur le caractère limitant du facteur trophique dans leur fonctionnement. La démarche a été menée selon deux échelles spatio-temporelles : fine sur l'estuaire de la Seine (habitats de la nourricerie et

périodes de croissance des juvéniles de poissons) et large sur le golfe de Gascogne (plusieurs nourriceries sur deux décennies). Les résultats soutiennent le rôle du facteur trophique de certains habitats clés de la nourricerie de la baie de Seine, en particulier son embouchure et ses vasières intertidales. Ces dernières étant largement réduites dans cet estuaire, une attention particulière pourra leur être portée dans le cadre de la restauration de la fonction de nourricerie. Par ailleurs, les juvéniles âgés de moins d'un an sont plus susceptibles de souffrir du manque de ressources alimentaires à la fin de la forte période de croissance (automne). Les résultats sur le golfe de Gascogne supportent l'occurrence de ce processus, même s'il interagit très probablement avec d'autres, dans ces écosystèmes complexes et dynamiques.

Title: Functioning and trophic capacity of coastal and estuarine nurseries: example of the Seine estuary and eastern bay

**Keywords:** Food limitation, Habitats, Juvenile fish, Bioenergetics

**Abstract:** Estuarine and coastal ecosystems are composed of spatially restricted habitats fulfilling a nursery function for many demersal fish species. These nursery-dependant species concentrate at the juvenile stage in these habitats, resulting in densitydependent regulation. The predominance of the mechanisms underlying this mortality is still a source of debate in the scientific community, in particular trophic limitation. The overall goal of this thesis is to estimate the trophic carrying capacity within estuarine and coastal nurseries and to provide food for thought on the limiting nature of the trophic factor in their functioning. The approach was carried out on two spatio-temporal scales: fine on the Seine estuary (nursery habitat and. growth periods of juvenile fish) and wide on the Bay

of Biscay (several nurseries over two decades). Results (fine scale) support the importance of the trophic factor of key habitats in the nursery function of the Bay of Seine, including the estuary mouth and the intertidal mudflats. As these are largely degraded in this estuary, special attention may be given within the framework of the restoration the nursery function. Moreover, young of the year juvenile fish are more likely to suffer from a lack of food resources at the end of their first growth period (autumn). Results (wide scale) on the Bay of Biscay also support the occurrence of this trophic limitation, even though it most probably interacts with others, in these complex and dynamic ecosystems.