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How trophic impasses structure coastal food webs? Insights from ECOPATH modelling

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Abstract :

Fluxes of organic matter are the foundation of the functioning of ecosystems and the understanding of their origin, production and their uses by biological and ecological processes is therefore essential. In anthropized systems, such as coastal ecosystems, disruptions caused by human activities at different scales can mobilize a significant part of the organic matter, which is no longer available locally for natural processes. As many coastal and marine ecosystems, the megatidal bay of Saint-Brieuc (BSB) faces cumulated impacts of strong anthropogenic pressures, mainly eutrophication-related proliferation of green algae, invasive species (slipper limpet) and shellfish farming. To assess these cumulative impacts, this study performs a quantitative assessment of the food web using the mass balanced Ecopath model, at two spatial scales: the whole Bay vs its intertidal fraction. Models outputs demonstrate the importance of the spatial scale considered on conclusions drawn. The global model showed that invasive species constitute a non-negligible trophic impasse. The intertidal submodel evidenced the effects of both green algae (trophic impasse) and farmed mussels (export), i.e. main producers and consumers, respectively, as additional bottlenecks limiting the trophic transfer. The BSB is thus characterized by tidal flats approaching their productive carrying capacity and low trophic transfer, hindered by three main trophic impasses.

Highlights

► Ecopath modelling is used to achieve a quantitative evaluation of the food web. ► The bay of Saint-Brieuc ecosystem is characterized by three trophic impasses. ► Green algae proliferations impact the productivity of phytoplankton. ► Farmed mussels are important competitors and consume a high part of phytoplankton. ► The slipper limpet is an important competitor but locally and patchily distributed.

Keywords : Ecopath, food web, shellfish farming, green algae, invasive species, Bay of Saint-Brieuc

1. Introduction

Marine and coastal ecosystems host complex ecological processes supporting a high productivity and crucial ecosystem services such as carbon sequestration, coastal protection and food supply (Claudet and Fraschetti, 2010; Selleslagh et al., 2012). The increase in anthropogenic pressures on nearshore areas has growing impacts on biodiversity and ecosystem services (Airoldi and Beck, 2008; Halpern et al., 2012; Gamfeldt et al., 2015). It is necessary to better take into consideration anthropogenic pressures to estimate the impact of these activities in order to estimate the resistance and resilience of the ecosystems and improve their conservation and management.

Fluxes of organic matter are the foundation of the ecosystems functioning, in particular food webs, and many biological (predation, filtration, nutrients uptake) and abiotic (sedimentation, diffusion, resuspension) processes control these fluxes. Although many studies have addressed the response of species and communities to anthropogenic pressures (Griffiths et al., 2017; Couce et al., 2020), less have focused on the impacts on the processes supporting ecosystems functioning [e.g. energy and mass transfers, biogeochemical cycles (Griffiths et al., 2017; Kemp et al., 2005)]. Yet, anthropogenic pressures such as nutrients inputs or fishing activities can influence fluxes of organic matter within coastal ecosystems (Griffiths et al., 2017; Cloern et al., 2016; Kemp et al., 2005).

Phytoplankton has a major role in supporting food webs (Sarker and Wiltshire, 2017; Cloern, 1996; Salmaso et al., 2012). Its abundance and composition are sensitive to environmental changes (Cloern et al., 2016, Salmaso et al., 2012).

Increasing nutrient concentration enhances phytoplankton production (Cloern, 2001), and sometimes leads to proliferations of green algae that can compete with other primary producers for nutrients (Fong et al., 1993; Sun et al., 2018). In addition, aquaculture, like shellfish farming, can modify the availability of primary production and result in food web modifications (Cugier et al., 2010; Inglis et al., 2000; Smaal and Van Duren, 2019; McKindsey et al., 2011). This is especially critical in ecosystems under strong human influence and/or with limited productivity, where human activities can impact or mobilize a significant part of organic matter, which is no longer available locally for natural communities. This can potentially lead to an overuse of the organic matter and a modification of energy pathways.

Productive carrying capacity is the maximum density and/or biomass of farming organisms an ecosystem can support. This parameter, often used to manage shellfish farming, does not include ecological impact considerations (MPO, 2015; Byron et al., 2011; Smaal and Van Duren, 2019). It needs to be backed by the ecological carrying capacity, which corresponds to the maximum biomass of shellfish farming that an ecosystem can support, without any major ecological change (MPO, 2015; Byron et al., 2011; Smaal and Van Duren, 2019). In order to evaluate the ecological carrying capacity, the whole ecosystem has to be considered as well as all the culture and fishing activities (McKindsey et al., 2006). The depletion of feeding resources can be helpful to evaluate the carrying capacity (MPO, 2015; Jiang and Gibbs, 2005; Byron et al., 2011; Filgueira et al., 2021).

In the English Channel, the Bay of Saint-Brieuc (BSB) is characterized by a diversified and abundant benthic fauna (Sturbois et al., 2021ab), among which suspension feeders such as cockles [*Cerastoderma edule* (Ponsero et al., 2022)] or scallops [*Pecten maximus* (Fifas and Caroff, 2014)]. It hosts a marine nature reserve covering part of its intertidal flats. Yet it is affected by numerous anthropogenic activities, including shellfish farming of mussels (*Mytilus edulis*) and fishing. The bay hosts significant populations of the invasive slipper limpets (*Crepidula fornicata*), which can compete for food with native and farmed suspension-feeders (Blanchard and Hamon, 2006). In addition, the BSB is characterized by seasonal green algae (*Ulva spp*.) proliferations [e.g. 12682 in 2021 (Ballu, pers.com.; Charlier et al., 2006; Gravier, 2012)]. The subtidal part of the bay hosts one of the important scallop fisheries in France which, together with eutrophication, has been observed to induce long-term modifications in the structure of benthic assemblages (Sturbois et al., 2021ab). Aforementioned studies highlighted a strong variability between intertidal and subtidal parts of the bay in the anthropogenic drivers of ecological changes*.*These changes highlight the need for a better understanding of the functioning of this area in order to improve its conservation and management.

The diversity of natural and anthropogenic processes involving the use of primary production within the BSB raises the question of potential interferences among them, and ultimately of the carrying capacity of the ecosystem. In this context, this study aims to answer the following questions: (1) What are the respective levels of production from the different primary producers, and of consumption/production from the faunal compartments? (2) Which part of primary production is consumed by production activities (mussel farming) and invasive species (dominated by the slipper limpet, *C. fornicata* and the Japanese oyster *Magallana gigas*), in comparison with natural compartments? (3) How do green tides, invasive species and shellfish farming influence the system?

This study aims to achieve a quantitative evaluation of the food web within the Bay of Saint-Brieuc, from the sources of primary production uses (phytoplankton, microphytobenthos, salt marsh, green tides) to consumers and upper trophic levels, at different spatial scales, using Ecopath modelling. Different faunistic compartments (wild, invasive and farmed benthic invertebrates, higher trophic levels) and activities (fishing and aquaculture) were considered. The Ecopath program is a simple way of modelling (Polovina, 1984; Christensen and Pauly, 1992), largely used in marine trophic ecology (Heymans et al., 2016; https://Ecopath.org/). Ecopath models consider all functional groups, from primary producers to apex predators, and allows to answer a wide range of scientific questions, usually about fishing management (Christensen et al., 2005; Araújo et al., 2008), but also related to impacts of shellfish farming and biological invasions (Arbach Leloup et al., 2008), or efficiency of protected marine area (Valls et al., 2012). A model was developed and declined at two complementary spatial scales (bay vs intertidal fraction), to answer the questions of the study.

2. Materials and methods

2.1. Study area

The BSB is located on the French coast of the western part of the English Channel (Fig. 1). This bay is a megatidal system, characterized by a tidal range approaching 13 meters during spring tides. The study area includes a variety of benthic habitats, such as salt marshes (125 ha) and different habitats with various sediment structure, both intertidal (4325 ha) and subtidal (10940 ha).

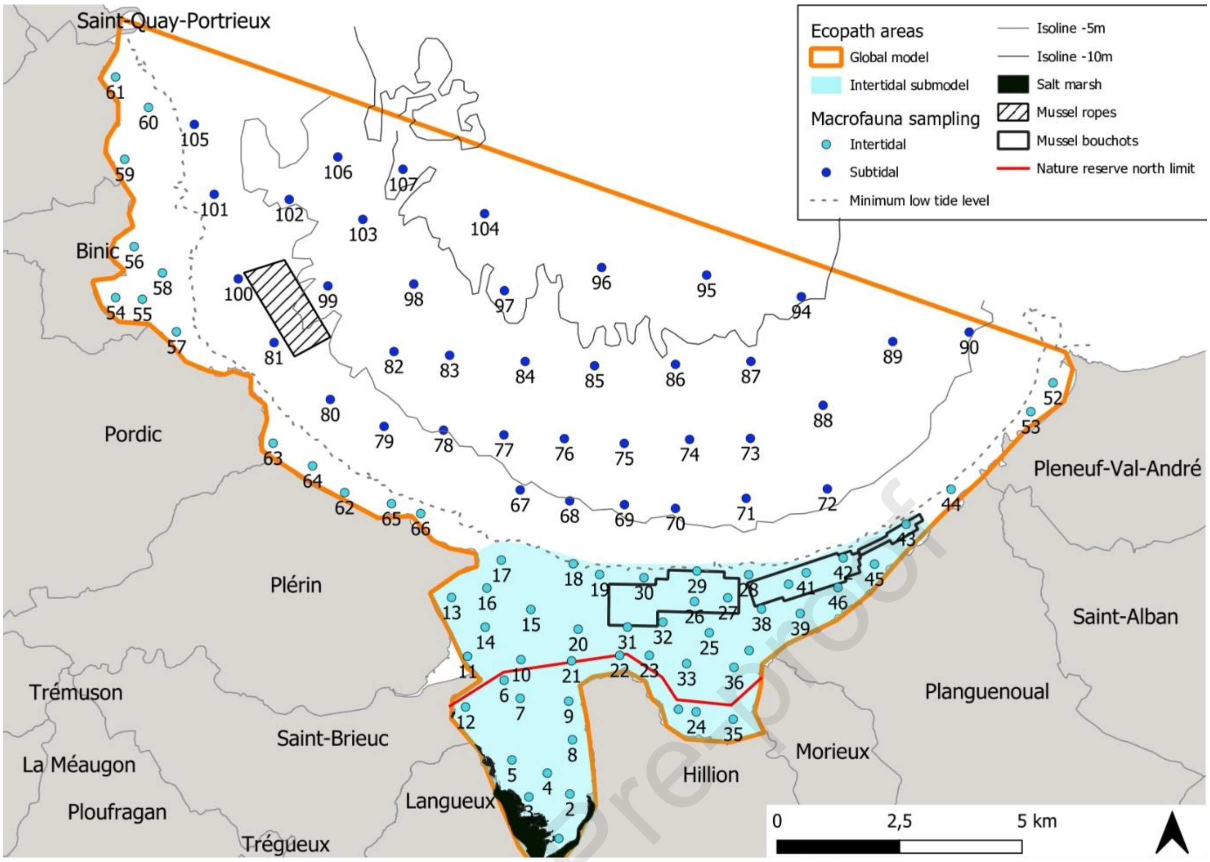


Fig. 1: Study areas in the bay of Saint-Brieuc and stations sampled by Sturbois et al. (2021ab).

The BSB is a productive and diversified ecosystem which supports an abundant benthic macrofauna (Sturbois et al., 2021ab), and especially important scallops (*Pecten maximus*, Fifas and Caroff, 2014), and cockles (*Cerastoderma edule*, Ponsero et al., 2009a) populations. The high diversity of birds, notably shorebirds during stopover or overwintering (Sturbois and Ponsero, 2018; Ponsero et al., 2016) have led to classify a fraction of its intertidal areas as national nature reserve since 1998, over 1140 ha (Fig. 1). This marine protected area is divided in two coves (Yffiniac on the western part and Morieux on the eastern part) characterized by differences in sedimentary parameters, benthic resources, shorebirds community and anthropogenic context. The western part of the intertidal area concentrates the benthic macrofauna biomass, wader abundance and professional and recreational cockles fishing while intertidal Mussels (*Mytilus edulis*) shellfish farming on bouchot (93 km of linear rows on 300 ha, about 4000 tons) is limited to the eastern part (Ponsero et al., 2016; Sturbois et al., 2021b). In the subtidal area, the bentho-demersal fish and cephalopod community is characterized by low diversity and abundance and mainly forages on benthic resources (Sturbois et al., 2022b). The site also hosts activities such as tourism, fishing and shellfish farming on ropes (10 strings, about 80 tons) (Fig. 1). Some shellfish species (clams, scallops) are also targeted by professional fishermen.

Two species with strong invasive dynamics were introduced in the 1960 in BSB: the slipper limpet (*Crepidula fornicata*) (Blanchard and Hamon, 2006) and the Japanese oyster (*Magallena gigas*) (Miossec et al, 2009; Simonin, 2012). The BSB also suffers from eutrophication, resulting in strong green macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2006; Gravier 2012) with ecological impacts (Le Luherne et al., 2016 and 2017).

2.2. Ecopath modelling approach

A mass-balanced trophic model was constructed using the Ecopath with Ecosim software [EwE (Christensen et al., 2005; Christensen and Pauly, 1992)]. The core Ecopath routine of EwE, derived from Polovina (1984), was used to model the fluxes between the different compartments of the system, based on a system of linear equations for ensuring the mass-balance hypothesis, i.e. input fluxes of a group are equals to its output fluxes (Christensen and Pauly, 1992):

$$\left(\frac{P}{B}\right)_i . B_i . EEi - \sum_{j=1}^{n2} \left(\frac{Q}{B}\right)_j . B_j . DC_{i,j} - Y_i = 0$$

Where, for i = 1 to n_1 functional groups and j = 1 to n_2 ($<n_1$) predators groups: B = biomass; P/B = production / biomass ratio, which represents biomass turn-over; EE = ecotrophic efficiency, the fraction of production consumed, fished or exported out the system; Y = catches by human activities; $DC_{i,j}$ = fraction of a prey i in the diet of a predator j.

For each of the n_1 compartments of the system, at least three of the parameters EE, Q/B, P/B and B are required by the model as initial input. The model estimates the n_1 unknown parameters from the system of linear equations (n_1 equations) with respect to the mass-balance between groups. To ensure the mass-balanced hypothesis, the ecotrophic efficiency for each group must be lower than 1, which means that for a given group, catches, consumption and export cannot be higher than its production (Heymans et al., 2016; Christensen et al., 1992; Darwall et al., 2010).

The core Ecopath routine is based on a second equation named the consumption equation. The consumption by predators can be described by the energy-balance equation:

Consumption = production + respiration + unassimilated food

The Ecopath model also requires input of the diet composition of each trophic group. Finally, catches/human extraction have also to be filled out for the concerned groups.

2.3. Models structure and input data

The Ecopath modelling has been performed at two complementary spatial scales (Fig. 1): (1) scale of the study area (whole model, 15390 ha) including the intertidal (4450 ha) and the subtidal zones (10940 ha); and (2) scale of the tidal flat in the intertidal area (submodel, 2900 ha). These two spatial scales were studied to (i) have a global vision of the trophic web with the whole model, and (ii) focus with the submodel on the tidal flat where green tides and shellfish farming are located. As usual (Christensen and Pauly, 1992), both models were constructed on an annual period. The reference year was 2019, due to the amount of data available for this year (Sturbois, 2021). Trophic fluxes and basic inputs were estimated in tons of fresh mass of flesh per km².

2.3.1. Whole model

The food web of the BSB was described through 17 trophic groups (Table 1). Species were grouped based on their trophic and production characteristics [similar preys, predators, turnover rate (Christensen et al., 2005)]:

- (a) four primary producer (phytoplankton, microphytobenthos, green algae, salt marshes);
- (b) zooplankton;
- (c) five groups for the indigenous macrobenthic fauna. Zoophagous (including carnivorous and necrophagous) and filter feeders were considered separately on intertidal and subtidal areas, but deposit feeders were considered as a unique group in the bay for the sake of parcimony, due to their weaker link with the objective of the study;
- (d) two groups of farmed macrofauna (subtidal and intertidal farmed mussels);
- (e) two groups of invasive macrofauna (slipper limpet and Japanese oyster);

- (f) fish and cephalopods, (g) herbivorous anatidae and (h) zoophagous birds.

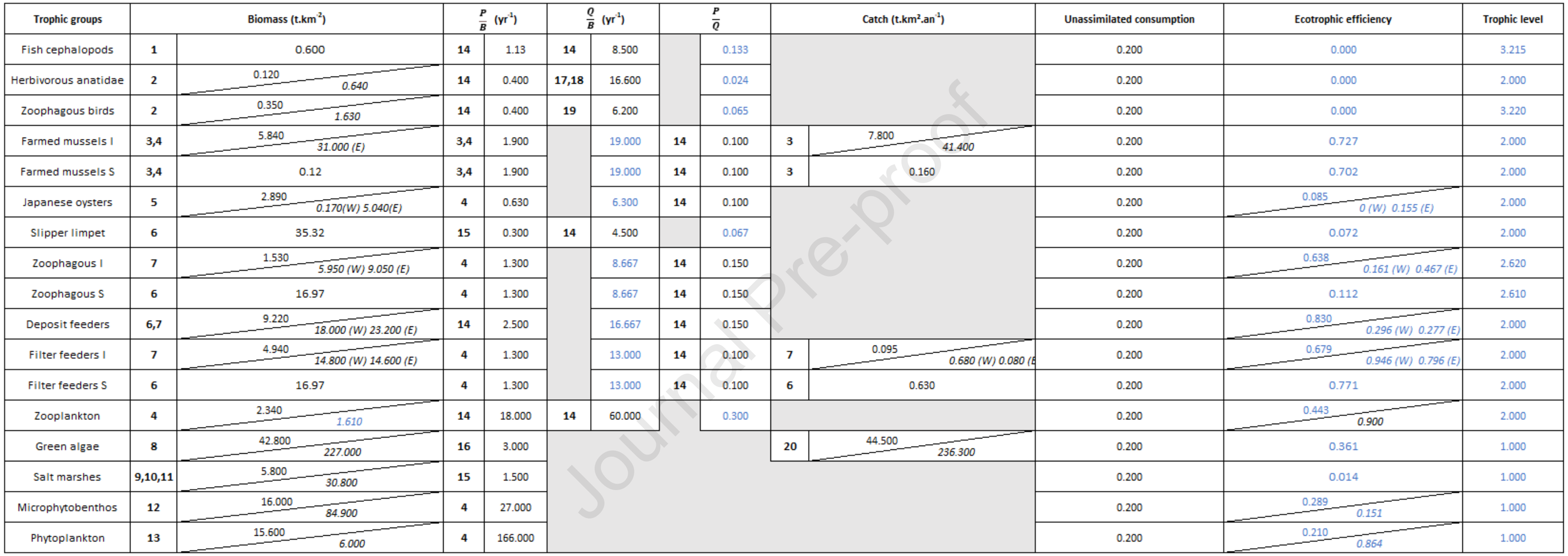
2.3.2. Submodel

The upper intertidal food web, called submodel, was described through the same trophic groups, except fish and cephalopods and slipper limpets, absent from this zone. The predation pressure of fish and cephalopods on the intertidal zone at open sea was nevertheless considered in the submodel for the concerned compartments. The indigenous benthic macrofauna groups were distinguished between western and eastern coves. For phytoplankton and zooplankton, biomasses were calculated in proportion to the volume of water overlying the tidal flat.

2.3.3. Data origin

The major part of data related to biomass were collected from studies conducted mainly locally, and mostly in 2019 (Table 1). Biomass, production and consumption data not available from BSB were collected from other studies, conducted in the bay of Mont Saint-Michel (Arbach Leloup et al., 2008) and the English Channel (Stanford and Pitcher, 2004). Biomass for each group was averaged annually, including migrating groups (zoophagous birds, herbivorous anatidae). To convert biomasses of macrobenthos from dry mass to fresh mass, the coefficients of Ricciardi and Bourget (1998) were used. The absolute biomass of fish and cephalopod estimated from scientific trawl surveys was adjusted with a factor of 5 to approximate the real biomass (Le Pape, pers.com.; Reiss et al., 2006; Kuipers, 1975; Kaiser et al., 1994). Catches were obtained from shellfish fisheries data (recreational and professional shellfish fishing for cockles and clams, professional shellfish fishing for scallops, Table 1) and mussel farming production data (CRC, www.crcbn.com/).

Table 1: Basic estimates of the whole model (straight) and the submodel (italic). In black, the input parameters and in blue the parameters estimated by Ecopath. The bold numbers correspond to the bibliography. I = Intertidal area, S = subtidal area, W = Western part, E = Eastern part.



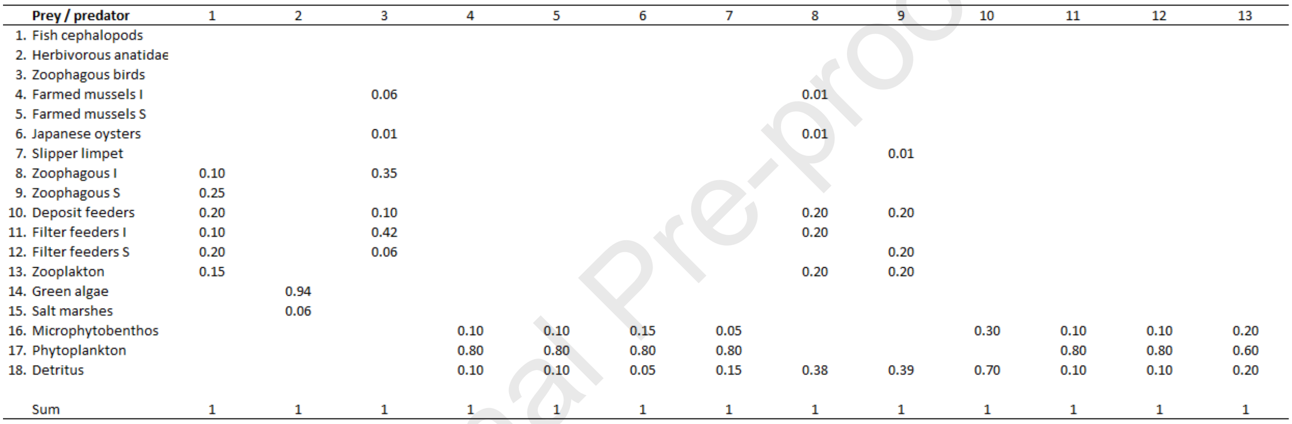
Trophic groups	**Biomass (t.km^{-2})**		**$\frac{P}{B}$ (yr^{-1})**		**$\frac{Q}{B}$ (yr^{-1})**		**$\frac{P}{Q}$**		**Catch (t.km^{2}.an^{-1})**		**Unassimilated consumption**	**Ecotrophic efficiency**	**Trophic level**
Fish cephalopods	**1**	0.600	**14**	1.13	**14**	8.500		0.133			0.200	0.000	3.215
Herbivorous anatidae	**2**	0.120 / *0.640*	**14**	0.400	**17,18**	16.600		0.024			0.200	0.000	2.000
Zoophagous birds	**2**	0.350 / *1.630*	**14**	0.400	**19**	6.200		0.065			0.200	0.000	3.220
Farmed mussels I	**3,4**	5.840 / *31.000 (E)*	**3,4**	1.900		19.000	**14**	0.100	**3**	7.800 / *41.400*	0.200	0.727	2.000
Farmed mussels S	**3,4**	0.12	**3,4**	1.900		19.000	**14**	0.100	**3**	0.160	0.200	0.702	2.000
Japanese oysters	**5**	2.890 / *0.170(W) 5.040(E)*	**4**	0.630		6.300	**14**	0.100			0.200	0.085 / *0 (W) 0.155 (E)*	2.000
Slipper limpet	**6**	35.32	**15**	0.300	**14**	4.500		0.067			0.200	0.072	2.000
Zoophagous I	**7**	1.530 / *5.950 (W) 9.050 (E)*	**4**	1.300		8.667	**14**	0.150			0.200	0.638 / *0.161 (W) 0.467 (E)*	2.620
Zoophagous S	**6**	16.97	**4**	1.300		8.667	**14**	0.150			0.200	0.112	2.610
Deposit feeders	**6,7**	9.220 / *18.000 (W) 23.200 (E)*	**14**	2.500		16.667	**14**	0.150			0.200	0.830 / *0.296 (W) 0.277 (E)*	2.000
Filter feeders I	**7**	4.940 / *14.800 (W) 14.600 (E)*	**4**	1.300		13.000	**14**	0.100	**7**	0.095 / *0.680 (W) 0.080 (E*	0.200	0.679 / *0.946 (W) 0.796 (E)*	2.000
Filter feeders S	**6**	16.97	**4**	1.300		13.000	**14**	0.100	**6**	0.630	0.200	0.771	2.000
Zooplankton	**4**	2.340 / *1.610*	**14**	18.000	**14**	60.000		0.300			0.200	0.443 / *0.900*	2.000
Green algae	**8**	42.800 / *227.000*	**16**	3.000					**20**	44.500 / *236.300*	0.200	0.361	1.000
Salt marshes	**9,10,11**	5.800 / *30.800*	**15**	1.500							0.200	0.014	1.000
Microphytobenthos	**12**	16.000 / *84.900*	**4**	27.000							0.200	0.289 / *0.151*	1.000
Phytoplankton	**13**	15.600 / *6.000*	**4**	166.000							0.200	0.210 / *0.864*	1.000

1: Sturbois et al., 2022a; 2: bimonthly counts of birds in the nature reserve of the BSB; 3: https://www.crcbn.com/; 4: Arbach Leloup et al., 2008; 5: Simonin, 2012; 6: Sturbois et al., 2021a; 7: Sturbois et al., 2021b; 8: https://www.ceva-algues.com/; 9: Sturbois and Bioret, 2019; 10: Bouchard and Lefeuvre, 2000; 11: Lefeuvre et al., 2000; 12: Davoult et al., 2009; 13: https://marc.ifremer.fr/; 14: Stanford and Pitcher, 2004; 15: Blanchard and Hamon, 2006; 16: Patrício and Marqués, 2006; 17: Ponsero et al., 2009b; 18: Mayhew, 1988; 19: Ponsero and Le Mao, 2011; 20: Saint-Brieuc Armor Agglomération, comm. pers.

The biomass of green algae collected by local authorities as part of precautionary sanitary measures was also considered as anthropogenic exportations in the models.

Diet compositions (Table 2) were compiled from previous studies in the BSB, available literature and expert knowledge (Sturbois et al., 2022b; Arbach Leloup et al., 2008; Rybarczyk et al., 2003; Ponsero et al., 2009b).

Table 2: Diet matrix of the whole model. The same matrix, spatially adjusted, was used in the submodel. I = Intertidal and S = Subtidal.



Prey / predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Fish cephalopods													
2. Herbivorous anatidae													
3. Zoophagous birds													
4. Farmed mussels I			0.06					0.01					
5. Farmed mussels S													
6. Japanese oysters			0.01					0.01					
7. Slipper limpet									0.01				
8. Zoophagous I	0.10		0.35										
9. Zoophagous S	0.25												
10. Deposit feeders	0.20		0.10					0.20	0.20				
11. Filter feeders I	0.10		0.42					0.20					
12. Filter feeders S	0.20		0.06						0.20				
13. Zooplakton	0.15							0.20	0.20				
14. Green algae		0.94											
15. Salt marshes		0.06											
16. Microphytobenthos				0.10	0.10	0.15	0.05			0.30	0.10	0.10	0.20
17. Phytoplankton				0.80	0.80	0.80	0.80				0.80	0.80	0.60
18. Detritus				0.10	0.10	0.05	0.15	0.38	0.39	0.70	0.10	0.10	0.20
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

2.4. Food web analysis

2.4.1. Balancing and validation

The models were balanced and their reliability was tested. Balancing an Ecopath model requires the adjustments of input parameters, by focusing on the data characterized by low confidence level (Christensen et al., 2005). The confidence level of input data and parameters were estimated and the overall confidence level of the model was estimated from its pedigree (Morissette, 2007; Christensen and Walter, 2004).

The realism of the production level of the different sources of primary production was checked from literature (Arbach Leloup et al., 2008; Rybarczyk et al., 2003; Migné et al., 2009; Ní Longphuirt et al., 2007; Hily, 1991; Cugier et al., 2005; Ballu pers.com.).

To validate the models, the thermodynamic and ecological rules of Darwall et al. (2010) were checked. For every trophic group: the EE has to be lower than 1, the gross food efficiency (P/Q) between 0.1 and 0.3 (except for groups with very low production such as top predators), the net efficiency higher than the gross food efficiency, the respiration / assimilation ratio lower than 1, the respiration / biomass ratio of fish between 1 and 10 yr^{-1} and the production / respiration ratio lower than 1 (Darwall et al., 2010).

2.4.2. Ecopath output

Ecopath provides estimates on production, mortality sources, consumption, net conversion efficiency, and the required primary production [quantification of the fluxes in primary production equivalent (Christensen and Pauly, 1993)]. The software also aggregates the functional groups in trophic level (*sensu* Lindeman,1942; *sensu* Odum and Heald, 1975) which allows estimation of fluxes of organic matter to detritus and upper trophic levels.

The software also calculates different parameters informing on the maturity of the system (Odum, 1969):

- (i) the ratio of net primary production to total biomass (PP/B) and to total respiration (PP/R),

- (ii) both the Finn's cycling index (fraction of ecosystem's throughput that is recycled) and Finn's mean path length (Christensen and Pauly, 1993),

- (iii) the ascendency, i.e., an estimation of the complexity of the trophic relations and the stability of the system, which increase with its maturity (Odum, 1969; Ulanowicz,1986)

- (iv) the system omnivory index (SOI), describing both the structure and the complexity of the food web (Pauly et al., 1993).

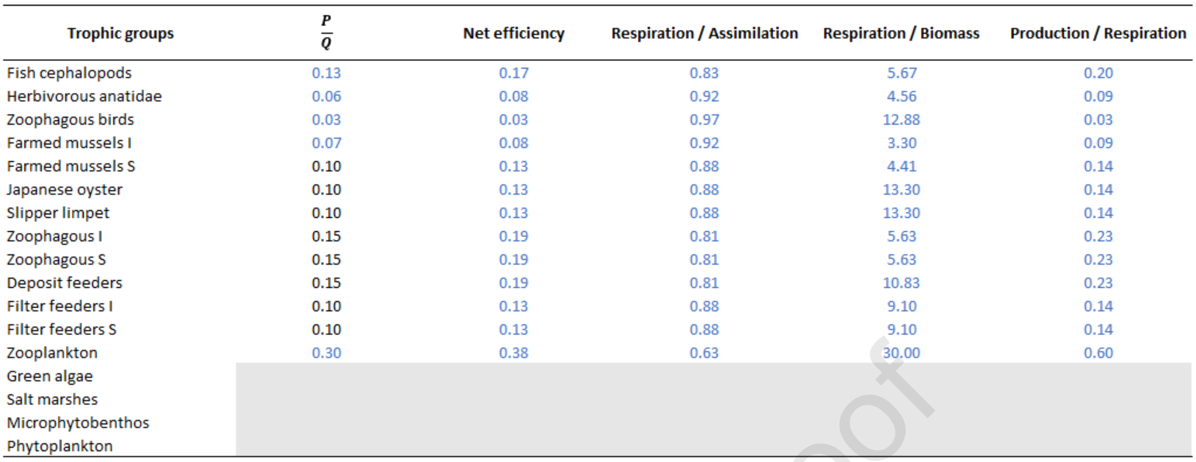
3. Results

3.1. Balancing and validating the models

In the whole model, predation pressure of zoophagous groups was adjusted according to expert knowledge and literature (Sturbois pers.com., Stanford and Pitcher, 2004; Arbach Leloup et al., 2008; Rybarczyk et al., 2003). In the intertidal submodel, the EE of zooplankton was set at 0.9 and the biomass was left to be estimated by the model (Essington, 2007; Heymans et al., 2016).

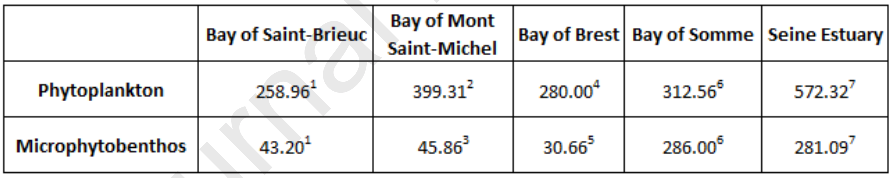
These options being retained, both the models fit with the mass-balanced hypothesis. Then both (i) thermodynamic and ecological rules (Table 3) and (ii) production levels of both primary producers (Table 4) allow the validation of the two models.

Table 3: Validation of the thermodynamic and ecological rules defined by Darwall et al., (2010).



Trophic groups	$\frac{P}{Q}$	Net efficiency	Respiration / Assimilation	Respiration / Biomass	Production / Respiration
Fish cephalopods	0.13	0.17	0.83	5.67	0.20
Herbivorous anatidae	0.06	0.08	0.92	4.56	0.09
Zoophagous birds	0.03	0.03	0.97	12.88	0.03
Farmed mussels I	0.07	0.08	0.92	3.30	0.09
Farmed mussels S	0.10	0.13	0.88	4.41	0.14
Japanese oyster	0.10	0.13	0.88	13.30	0.14
Slipper limpet	0.10	0.13	0.88	13.30	0.14
Zoophagous I	0.15	0.19	0.81	5.63	0.23
Zoophagous S	0.15	0.19	0.81	5.63	0.23
Deposit feeders	0.15	0.19	0.81	10.83	0.23
Filter feeders I	0.10	0.13	0.88	9.10	0.14
Filter feeders S	0.10	0.13	0.88	9.10	0.14
Zooplankton	0.30	0.38	0.63	30.00	0.60
Green algae					
Salt marshes					
Microphytobenthos					
Phytoplankton					

Table 4: Production levels of primary producers (tC.km^2.an^{-1}) in different bays, numbers in exponent correspond to the bibliography indicated below.



	Bay of Saint-Brieuc	Bay of Mont Saint-Michel	Bay of Brest	Bay of Somme	Seine Estuary
Phytoplankton	258.96[1]	399.31[2]	280.00[4]	312.56[6]	572.32[7]
Microphytobenthos	43.20[1]	45.86[3]	30.66[5]	286.00[6]	281.09[7]

1: This study; 2: Arbach Leloup et al., 2008; 3: Migné et al., 2009; 4: Hily, 1991; 5: Ni Longhuirt et al., 2007; 6: Rybarczyk et al., 2003; 7: Rybarczyk and Elkaïm, 2003.

Phytoplanktonic production in the BSB was lower than in other bays of the English Channel [*e.g.* 399.31 in the bay of Mont Saint-Michel (Arbach Leloup et al., 2008); 571.9 tC.km^2.an^{-1} in the bay of Seine (Rybarczyk and Elkaïm, 2003) or 312.56 tC.km^2.an^{-1} in the bay of Somme, (Rybarczyk et al., 2003)].

The pedigree of the BSB model is equal to 0.553, which indicated a right of quality in data source (Morissette, 2007).

3.2. Primary production

3.2.1. Sources

In the whole model (Fig. 2a), the dominant source of primary production was the phytoplankton (2589.6 t.km^{-2}.yr^{-1}, 82% of the total primary production). In the submodel, the microphytobenthos was dominant (55.7%, 472.5 t.km^{-2}.yr^{-1}), phytoplankton representing only 26.5% of the total primary production on the tidal flat (Fig. 2b). Green algae were not a dominant source in the whole model, while they represented 16.7% of the primary production in the submodel (Fig. 2). Salt marshes production was low in both models compared to the other sources.

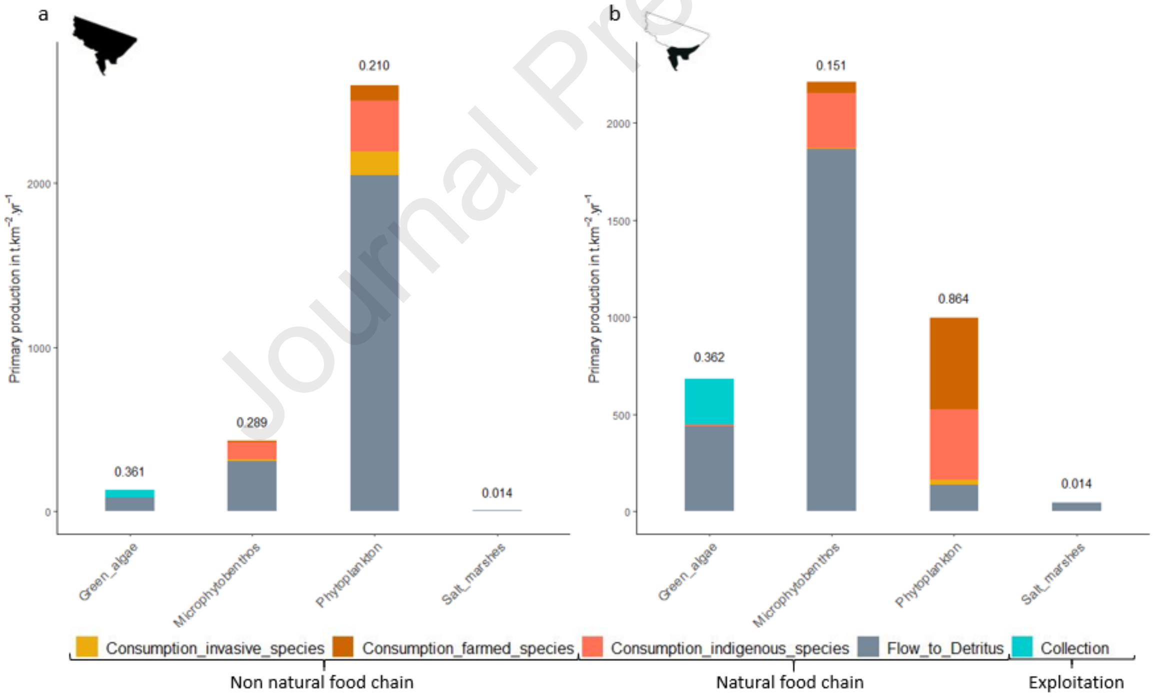


Fig. 2. Levels of fluxes and source of mortalities for the different sources of primary production. a: Whole model. b: Submodel. Numbers correspond to the ecotrophic efficiency of each compartment.

3.2.2. Destination of primary production

Despite the high proportion of the phytoplankton production in the whole model, only a small proportion was consumed (EE = 0.210, Fig. 2a). This consumption was mainly due to natural species (Fig. 2a). In contrast, at the submodel scale, phytoplankton production was largely consumed (EE = 0.864), especially by farmed species (Fig. 2b). The other sources of primary production were weakly consumed. Despite green algae being consumed by herbivorous anatidae, it concerns a very low part compared to its annual production; excluding the sanitary removal, the algae ecotrophic efficiency was only 0.015.

3.2.3. Consumption

In the whole model, wild subtidal filter feeders were the strongest consumers of the primary production (Fig. 3a), with 29.7% of the consumption by the indigenous benthic macrofauna (55.6% of the consumption of the subtidal area). The slipper limpet is the second consumer of the primary production (Fig. 3a), with 20.2% of the total consumption by the indigenous benthic macrofauna (37.9% in the subtidal area). The Japanese oyster represented a very low part of the consumption of primary production.

The total consumption of primary production by the wild benthic compartments was 286 t.km^{-2}.yr^{-1} for the intertidal area (4450 ha) and 309 t.km^{-2}.yr^{-1} for the subtidal area (10940 ha). Integrating introduced species and farmed mussels, the total consumption of primary production was 691.2 t.km^{-2}.yr^{-1} in the intertidal area and 502.2 t.km^{-2}.yr^{-1} in the subtidal area (Fig. 3a).

In the intertidal submodel (tidal flat, 2900 ha), farmed mussels mainly consumed the primary production (Fig. 3b): 46.9% of the total consumption, and

61.9% in the eastern part were where mussels are exclusively bred. The EE of phytoplankton (0.864) in the submodel, was only 0.391 when farmed mussels were excluded. Within the submodel, the eastern part was characterized by 73% of the consumption fluxes of primary production by the intertidal macrozoobenthos, including farmed and introduced bivalves. Excluding mussels and Japanese oysters, the levels of consumption are relatively similar between the western and eastern parts for the deposit feeders (respectively 300 $t.km^{-2}.yr^{-1}$ and 386 $t.km^{-2}.yr^{-1}$) and for the filter feeders (respectively 192.38 $t.km^{-2}.yr^{-1}$ and 188.96 $t.km^{-2}.yr^{-1}$) (Fig. 3b).

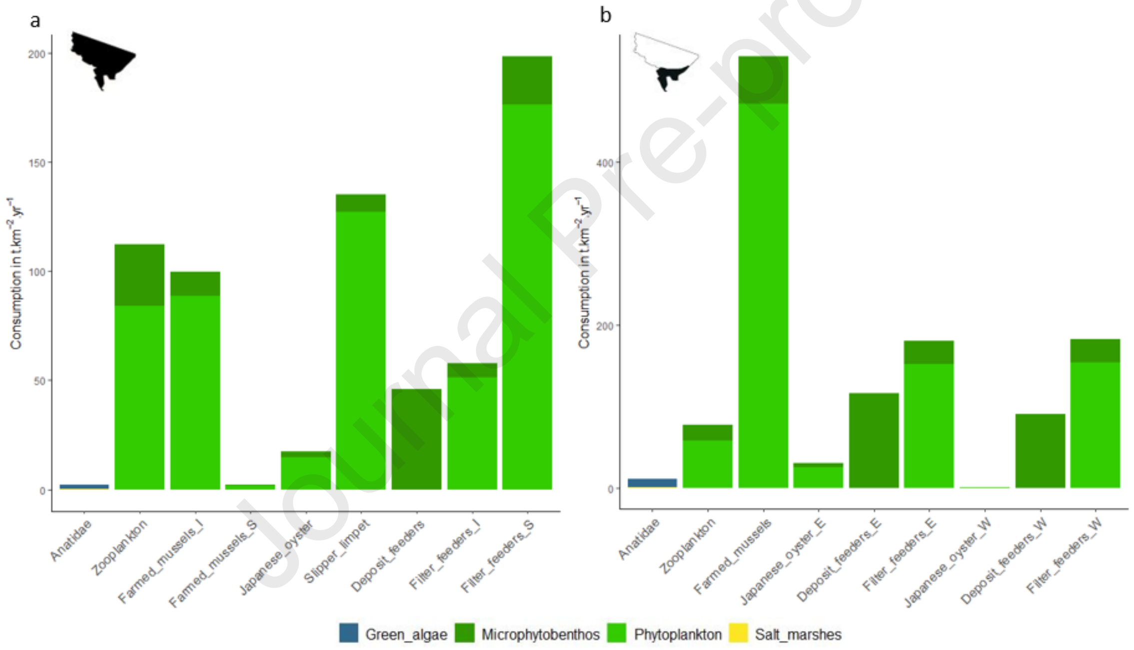


Fig. 3. Consumption of the different compartments of primary production by the faunal compartments. a: Whole model, I = intertidal and S = Subtidal. b: Submodel, E = Eastern part, W = Western part.

3.3. Secondary production and food chain

3.3.1. Faunal compartments

Within the whole area (15 390 ha), zoophagous macrozoobenthos represented 29.3% of the subtidal benthic fauna biomass, filter feeders, 56.5% and deposit feeders, 14.2%. In the intertidal area, macrozoobenthic biomass was composed of 13.4% of zoophagous, 43.1% of filter feeders and 43.5% of deposit feeders (Fig. 4c). In the submodel which concerns the tidal flat in the intertidal area, zoophagous correspond to 15.3% of the benthic fauna biomass in the western part and 19.3% in the eastern part. Filter feeders and deposit feeders respectively represented 38.2% and 46.5% of the biomass in the western part and 31.2% and 49.5% in the eastern part (Fig. 4d).

In the whole model, the zooplankton represented the largest secondary producer (32.2% of the total secondary production), before subtidal filter feeders and deposit feeders (Fig. 4a). In the intertidal submodel, filter feeders and zooplankton productions were lower than those of farmed mussels and deposit feeders [23.4%, 23% and 17.9% of the total secondary production, respectively (Fig. 4b)].

3.3.2. Destination of secondary production

The production of wild organisms was partially consumed by higher trophic levels. EE presented a wide range of values depending on the compartments (Fig. 4). In the global model, deposit feeders (EE = 0.830), subtidal filter feeders (EE = 0.771) and intertidal filter feeders (EE = 0.649) were the most consumed compartments (Fig. 4a). In the submodel, the most consumed compartments were filter feeders (0.946 in the eastern part and 0.796 in the western part), excluding the zooplankton for which the EE has been set at 0.9 (Fig. 4b).

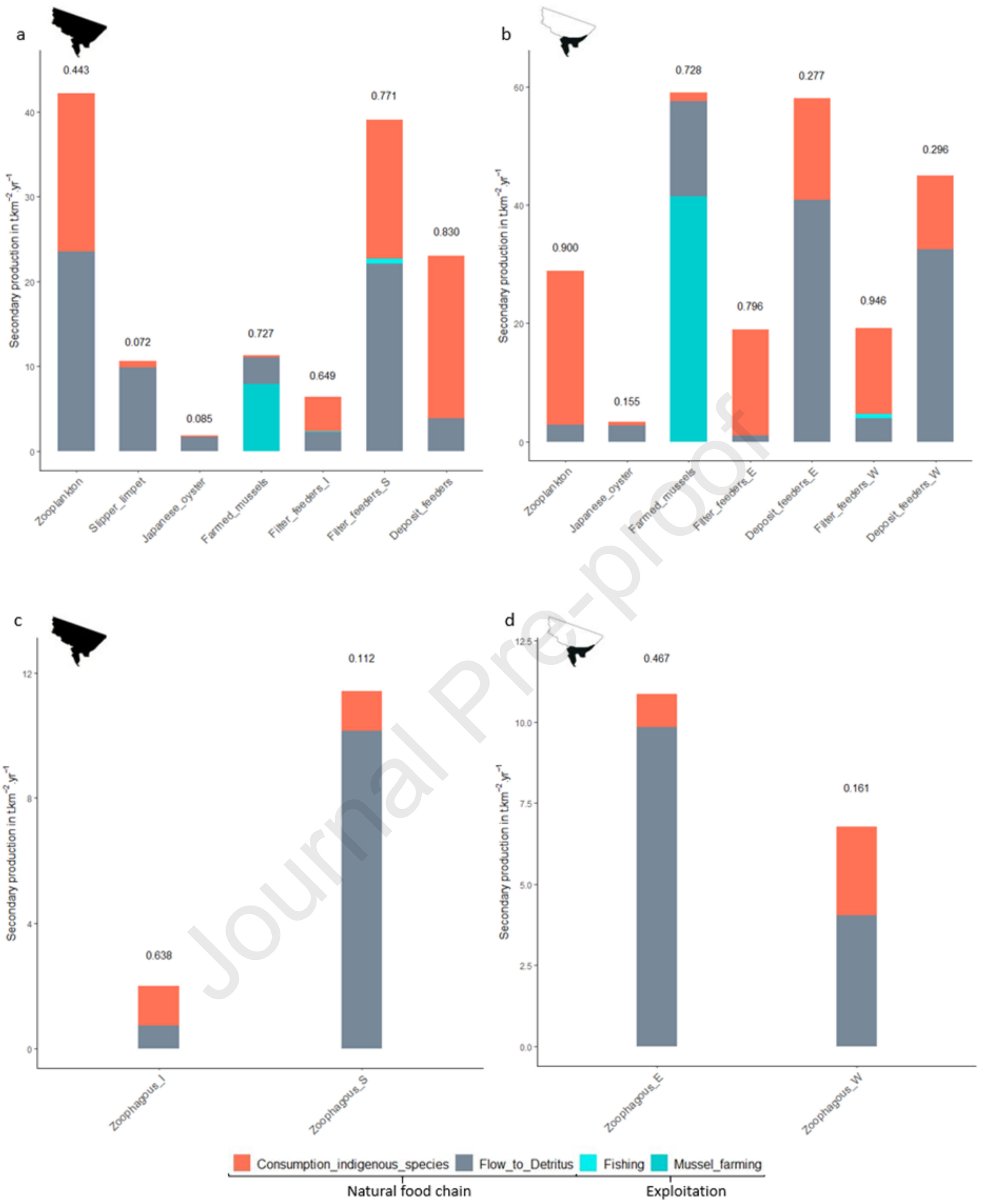


Fig. 4. Levels of fluxes and sources of mortalities for faunal compartments. a: trophic level 2 of the whole model, b: trophic level 2 of the submodel, c: trophic level 2+ of the whole model, d: trophic level 2+ of the submodel. I = intertidal, S = Subtidal. W = Western part, E = Eastern part. Values correspond to the EE of each compartment.

3.4. Main characteristics of the food web

This system was characterized by a total throughput of 6824 $t.km^{-2}.yr^{-1}$, with 14% devoted to consumption, 37% to export (catch) and 40% to flow to detritus (Table 5). Some of the general parameters, i.e., total primary production / total respiration, total primary production / total biomass, Finn's index and ascendency appeared low regarding general insights for coastal ecosystems (Table 5).

The BSB food web was characterized by three trophic impasses. The first one originated from green algae. Although Brent goose and European wigeon consumed 290 tons of fresh matter per year (Fig. 5), green algae were weakly consumed with respect to their total production. Detritus coming from salt marshes were also few consumed but they represented a very low production level. The second one was related to the two invasive species, slipper limpet in the subtidal area and Japanese oyster in the intertidal area. Invasive species were an important source of biomass and consumed a significant part of the primary production (Fig. 5). Congruently with its lower biomass compared to the slipper limpet, Japanese oyster had a lower consumption of primary production (Fig. 5). These two introduced species, weakly consumed by higher trophic levels (Fig. 5), only provide a low transfer rate of organic matter in the food web.

Farmed mussels were the third impasse. At the scale of the whole model, their biomass and consumption were relatively low compared to invasive and wild species, but in the intertidal submodel, their influence was dramatically higher (Fig. 5). This compartment was exported by mussel farmers and not transferred to higher trophic levels (Fig. 5).

Table 5: General parameters of the whole model of the BSB and some Ecopath models of others sites. The absence of values for some sites means that they are not available or are not comparable because of the unit used. Numbers in exponent correspond to the bibliography indicated below.

Parameters	Units	BSB[1]	Dublin bay[2]	Curonian Lagoon[3]	Parnü bay[3]	Moroccan Atlantic coast[4]	Gran Canaria coast[5]	Bay of Somme[6]	Bay of Mont-Saint-Michel[7]	Narragansett bay[8]	Delaware bay[8]	Gulf of Maine[9]
Fluxes and general characteristics												
Sum of all consumption	t.km^{-2}.yr^{-1}	968.038	-	-	-	4191.040	-	-	1090.000	-	-	6968.827
Sum of all exports	t.km^{-2}.yr^{-1}	2515.954	-	-	-	5748.100	-	-	3700.000	-	-	4211.147
Sum of all respiratory flows	t.km^{-2}.yr^{-1}	642.747	-	-	-	2937.900	-	-	730.000	-	-	5245.491
Sum of all flows into detritus	t.km^{-2}.yr^{-1}	2697.742	-	-	-	6370.730	-	-	3880.000	-	-	5182.244
Total system throughput (TST)	t.km^{-2}.yr^{-1}	6824.480	-	-	-	19248.770	-	-	9400.000	-	-	21.408
Total catch	t.km^{-2}.yr^{-1}	53.185	-	-	-	-	-	-	15.900	-	-	2.671
Total biomass (excluding detritus)	t.km^{-2}	169.236	-	-	-	274.470	-	-	180.000	-	-	487.390
Sum of all production	t.km^{-2}.yr^{-1}	3290.384	-	-	-	9636.110	-	-	4570.000	-	-	10.899
Net system production	t.km^{-2}.yr^{-1}	2515.953	-	-	-	5725.110	-	-	3700.000	-	-	3984.242
Calculated total net primary production	t.km^{-2}.yr^{-1}	3158.700	-	-	-	8663.010	-	-	4430.000	-	-	9229.733
Indices												
Total primary production/total respiration (PP/R)		4.914	-	10.851	1.054	2.950	2.172	15.509	6.100	1.300	1.300	1.760
Total primary production/total biomass (PP/B)		18.664	-	108.212	5.814	31.560	8.647	21.816	24.600	24.200	28.200	18.937
Total biomass/total throughput		0.025	-	0.005	0.040	0.010	0.035	0.012	0.019	0.041	0.035	0.023
System Omnivory Index (SOI)		0.041	-	0.165	0.050	0.200	0.340	0.009	0.058	0.300	0.300	0.290
Ascendency												
Ascendency (A)	t.km^{-2}.yr^{-1}	8123.000	-	-	-	-	-	-	-	-	-	-
Development capacity (C)	t.km^{-2}.yr^{-1}	22221.000	-	-	-	-	-	-	-	-	-	-
System overhead (O)	%	61.990	-	-	-	59.000	74.500	-	-	-	-	-
Relative ascendency (A/C)	%	36.560	42.200	69.000	34.000	41.000	25.500	35.000	47.700	33.500	33.400	-
Cycling												
Average path length		2.161	-	2.055	4.285	2.220	12.600	-	2.100	-	-	2.313
Finn's index (FCI)	%	1.050	31.900	0.580	24.640	1.360	3.253	12.200	0.640	48.200	48.200	3.360

1: this study; 2: Wilson and Parkes, 1998; 3: Tomczak et al., 2009; 4: Essekhyr et al., 2019; 5: Couce-Montero et al., 2015; 6: Rybarczyk et al, 2003; 7: Arbach Leloup et al., 2008; 8: Monaco et Ulanowicz, 1997; 9: Zhang and Chen, 2007.

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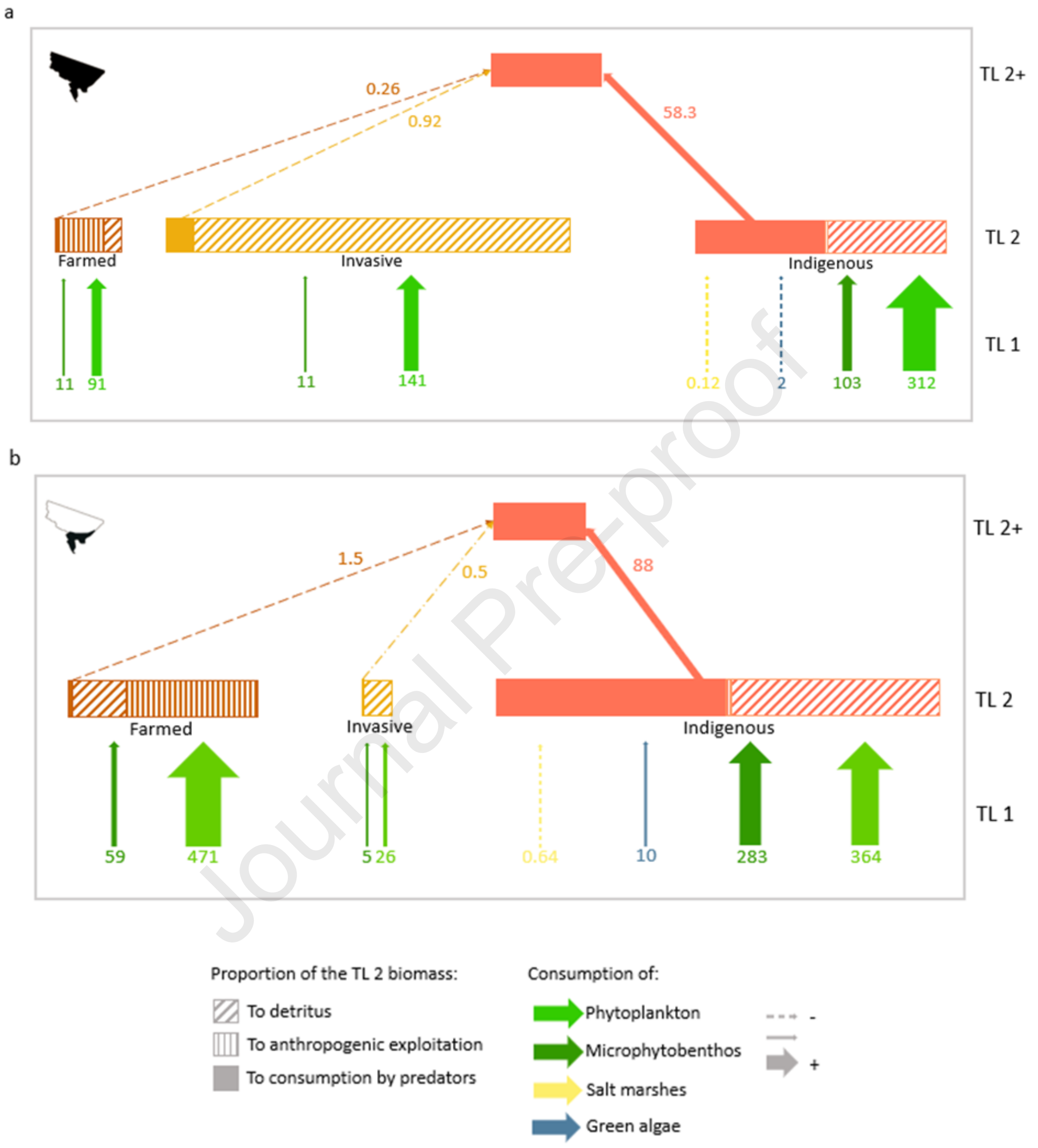

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432 Fig. 5. Food web of BSB. Numbers correspond to the consumption flow size (t.km^{-2}.yr^{-1}). The 433 boxes size is proportional to the biomass of each compartment in the bay. TL = Trophic 434 level. a: Food web of the whole model (15 390 ha). b: Food web of the submodel (2 900 ha).

4. Discussion

4.1. General description of the food web

Odum (1969) described the maturity as resulting from successive stages of the system leading to a « climax » which results in a balance between fluxes of energy linked to respiration and production of biomass, an in an increase of both the stable trophic relations and the the detritus path. This maturity can be characterized by several parameters calculated by Ecopath. However, the comparison of several Ecopath models remains complicated because of difference in the representation of the food webs (Heymans et al., 2016). Moreover, the interpretation of some indices is discussed (e. g. FCI; Heymans and Baird, 2000).

Although the BSB appeared as a productive system (TST = 6824 $t.km^{-2}.yr^{-1}$), the Ecopath model underlined its immaturity and instability (Table 5). The PP/R index, indicator of the maturity of a system, was particularly high in the BSB (4.91). According to Odum (1969), the mature and stable systems present a ratio near to 1, contrary to the immature ones characterized by elevated ratios. The Finn's cycling index generally ranges between 4 and 15% in coastal ecosystems (Heymans and Baird, 2000). In BSB, Finn's cycling index value was very low (1.05%), which confirms the immaturity of the system. The SOI and the average path length pointed the simplicity of the trophic web (Ulanowicz, 1986; Odum, 1969).

Similar results evidenced the immaturity of other shallow macrotidal bays (Table 5): the bay of Somme (Rybarczyk et al., 2003), the bay of Seine (Raoux et al, 2020), the bay of Mont Saint-Michel (Arbach Leloup et al., 2008) or the Canche estuary (Selleslagh et al., 2012). In contrast, other macrotidal systems were characterized by an intermediate level of maturity and stability such as the Gulf of Maine (Zhang and

Chen, 2007) or even presented complex and resilient food webs, such as the Delaware and Narragansett Bay bays (Monaco and Ulanowicz, 1997).

As estuaries, regarded as environmentally naturally stressed areas because of the high degree of variability in their physico-chemical characteristics (Elliott and Quintino, 2007), macrotidal coastal ecosystems are considered as naturally immature, because of the perturbation caused by the tides cycle and the seasonality of fresh water loadings (Odum, 1969). This partly explains the frequent conclusion about immaturity of such ecosystems based on trophic models.

However, the accumulation of biomass in certain compartments and their non-exploitation could flourish the instability and immaturity of such ecosystems (Selleslagh et al., 2012; Ullah et al., 2012). In the Bay of Saint-Brieuc, the accumulation of slipper limpets could partly explain immaturity, as demonstrated in the Bay of Mont-Saint-Michel (Arbach Leloup et al., 2008). In addition, green algae, very few consumed, induce similar consequences. Finally, the aquaculture can also play an important role in modifying availability of primary production and bentho-pelagic relationships (Leguerrier et al., 2004; Brzeski and Newkirk, 1997). The impact of mussel farming has already been demonstrated in the Mont Saint-Michel Bay study (Arbach Leloup et al., 2008). The high production and the non-exploitation of these three compartments (mussels, slipper limpet and green algae) limit the transfer of organic matter in the food web, impact trophic relationships and food availability, playing a role in the observed immaturity and instability.

4.2. A bay characterized by major trophic impasses

4.2.1. On intertidal flats

Green algae

The annual production of phytoplankton in BSB was lower than the production observed in other sites (Table 4). Such a depletion in the BSB can be partly explained by the severe annual green algae proliferations (Ménesguen, 1998). Using the same resources, green algae monopolizes nutrients during their proliferation stages and consequently reduces the phytoplankton productivity (Cloern, 1996; Fong et al., 1993). Recognized as better competitors than phytoplankton under conditions of high nutrient input, green algae develop *pro parte* at the expense of phytoplankton (Ménesguen, 1998; Fong et al., 1993). Although algae production was not dominant in the whole model (15 390 ha), green tides may however influence the total phytoplankton production. This effect was enhanced in the intertidal submodel (2 900 ha) where the major part of the phytoplankton was consumed by filter feeders in relation to a lower production compared to the whole model.

Despite their important biomass, green algae were weakly consumed by herbivorous anatidae and this consumption did not regulate the green algae stock in the water column (Ponsero et al., 2009b). Although green algae support an herbivorous anatidae population during winter (B. goose and E. wigeon), they remain an important trophic impasse due the high concerned production whom only 1.5% is transferred to higher trophic levels. Green algae are for an important part (around 30%) collected and eliminated by local authorities. Remaining algae are left in place and contribute to the detrital pool with a limited influence on the intertidal and subtidal food webs (Sturbois et al, 2021b; Sturbois et al., 2022a).

Sites suffering from green algae proliferations exhibit simplified trophic webs, and seasonal changes in diet for some species during green algae blooms (Patrício et al., 2004; Patrício and Marques, 2006; Quillien et al., 2016). In the BSB, no seasonal diet shift could be detected (Sturbois et al., 2022b) nor widespread consequences of hypoxic episodes (Fong et al., 1993), spatially limited in the bay because of the collection of green algae and hydrodynamics (Sturbois et al., 2022b). The impact of green tides in the BSB thus results in competition with other sources of primary production for nutrients and an important trophic impasse with additional consequences on essential fish habitat suitability (Le Luherne et al., 2016).

Mussel farming

Despite a high value of EE (due to their exportation by farmers), farmed mussels were identified as a trophic impasse. The consumption by laridae, sea bream (*Spondyliosoma cantharus*) and gilthead bream (*Sparus aurata*), lacking local data were not integrated in our models, and the predation on mussels may have been underestimated. However, only a small part of mussel biomass is consumed by predators and integrates the food web.

Considering the low level of production of the mussels farming on ropes in the subtidal area compared to others faunal compartments, the consumption of primary production by farmed species in the whole model is mostly due to mussels farming on bouchot in the intertidal area. Although they represented a low rate of consumption at the scale of the 15 390 ha in the whole model, farmed mussels were the most important consumers in the intertidal submodel. In farming areas, they are known to be an important competitor with respect to native species (Han et al., 2017). After exclusion of mussels from the submodel, phytoplankton was only consumed up to 39%

(against 86% in the presence of mussels). Such values are in accordance with results reported by Cugier et al. (2010) in the Mont Saint-Michel bay, showing the primary production depletion where mussels are farmed.

Bouchot mussel farming in the BSB currently experience growth issues, leading to a higher proportion of mussels under the commercial size and so a decrease in production and profitability (Sturbois pers. com.). With regard to biomass of farmed mussels, the question of the ecological carrying capacity can be raised for the tidal flat of the BSB (MPO, 2015; Byron et al., 2011). The carrying capacity is a complex notion that can vary over time and space, depending on environmental conditions (Chapman and Byron, 2017; Filgueira et al., 2021). Ecopath modelling does not consider seasonal variations, but an overall average over one year (Christensen et Pauly, 1992). However, it could be useful as a first approach to estimate the carrying capacity (Jiang and Gibbs, 2005; Byron et al., 2011; Zhao et al., 2022). The primary production required (PPR), in comparison with total primary production, can be used to evaluate the carrying capacity (Christensen and Pauly, 1993 and 1995). In the tidal flat submodel, the PPR of mussels farmed on bouchot was 16%, which represents a high level of PPR in contrast with the 8% assessed for fishing activities (Christensen and Pauly, 1995). Moreover, according to the submodel, phytoplankton would be over-consumed (EE>1) if the biomass of mussels was increased from 31 t.km^{-2} to 39.8 t.km^{-2} only (for a PPR of 21%). On the contrary, in the whole model, the PPR of mussels (considering the ones farmed on ropes in the subtidal area and the ones on bouchot in the tidal flat) was equal to 3%, which confirms that at the larger spatial scale, mussels have a limited impact.

In the BSB, the combined effect of green tides and mussel's consumption (Smaal, 1991; Han et al., 2017; Newell, 2004) limits phytoplankton biomass (respectively by reducing the production and increasing the consumption) in the intertidal area. This phytoplankton limitation is noticeable at certain times of the year depending on the seasonality of green algae bloom and mussel's growth, seasonality that cannot be reflected in an Ecopath model (Heymans et al., 2016).

4.2.2. Introduced slipper limpet and consumption in the subtidal zone

The slipper limpet is abundant in the BSB and represents the second most important consumer after the "subtidal filter feeders" group. Although this species is frequently known to be a major competitor of native species (Blanchard and Hamon, 2006; Dupouy and Latrouite, 1979), competition for feeding resources with native species had not been demonstrated systematically. For example, in the bay of Brest (Iroise sea), slipper limpets are more in competition for space than for food resources (Thouzeau et al., 2000; Ménesguen and Grégoris, 2018). However, in some site like the bay of Mont Saint-Michel, slipper limpet represents 50% of the total biomass of organisms of trophic level 2 and 40% of the consumption of the primary production (Arbach Leloup et al., 2008; Cugier et al., 2010), *i.e.* twice as much as in the BSB. Very few consumed by predators, this species represents a significant trophic impasse (Blanchard and Hamon, 2006). Moreover, in the BSB, slipper limpet is locally and patchily distributed (Blanchard and Hamon, 2006; Sturbois et al., 2021a), and would rather compete locally with native species, and especially the scallop *Pecten maximus,* of main interest for fisheries.

4.3. Strengths, limitations and insights for management

Our Ecopath model of the BSS constitutes a valuable and explicit synthesis, which improved our current knowledge of the trophic structure and pathways and also evidenced system data gaps. Strength of the Ecopath model performed in the BSB is that it is based on data acquired locally and recently (Pedigree = 0.554, Morissette, 2007; Christensen and Walters, 2004): biomasses used in the model come from studies conducted during the year 2019 (Sturbois, 2021). When data were not available, they were collected from studies in similar sites or, as a last resort, from other sites located in the English Channel. As a direct consequence, some data were less reliable, as the microphytobenthos production taken from the bay of Mont Saint-Michel (Davoult et al., 2009) and probably overestimated in the models. Despite these data-dependent limitations, this Ecopath model provides a relevant and valuable tool to evidence trophic pathways and anthropogenic impacts and support decision making in such a complex and dynamic coastal ecosystems (Christensen and Pauly, 1992; Colléter et al., 2015; Watson et al., 2020). The modeling approach confirms the importance of considering trophic modelling at several complementary spatial scales for the better understanding and conservation of such complex ecosystems under natural dynamics and anthropogenic influence (Arbach Leloup et al., 2008; Cugier et al., 2010; Ferreira et al., 2008).

This modelling approach has been performed in response to the questions of the marine protected area managers about trophic functioning for a conservation purpose. By quantifying trophic fluxes, the Ecopath modelling complemented the local recent intertidal and subtidal trophic studies based on stable isotope compositions. A major conclusion remains that the phytoplankton availability could reach a threshold limit. For instance, the productivity and growth of Mussels is a major concern in the study area. It led professionals to ask for an extension of the farming area to compensate for economic loss. Our conclusions suggest that it would constitute a counterproductive strategy with potential trophic cascade effects by: (1) exacerbating productivity problems, (2) increasing the trophic competition with the natural local macrofauna which constitute notably preys for waders that justify the creation of the nature reserve. Such considerations are all the more crucial because local authorities act to decrease nutrient fluxes in the bay of Saint-Brieuc in order to limit the recurring eutrophication processes. Next step must concern the integration of this information in future governance rounds to mirror economic and conservation issues and improve scientific-based decision making.

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Table 1

Trophic groups	Biomass (t.km^{-2})		$\frac{P}{B}$ (yr^{-1})		$\frac{Q}{B}$ (yr^{-1})		$\frac{P}{Q}$		Catch (t.km^{-2}.an^{-1})		Unassimilated consumption	Ecotrophic efficiency	Trophic level
Fish cephalopods	**1**	0.600	**14**	1.13	**14**	8.500		0.133			0.200	0.000	3.215
Herbivorous anatidae	**2**	0.120 *0.640*	**14**	0.400	**17,18**	16.600		0.024			0.200	0.000	2.000
Zoophagous birds	**2**	0.350 *1.630*	**14**	0.400	**19**	6.200		0.065			0.200	0.000	3.220
Farmed mussels I	**3,4**	5.840 *31.000 (E)*	**3,4**	1.900		19.000	**14**	0.100	**3**	7.800 *41.400*	0.200	0.727	2.000
Farmed mussels S	**3,4**	0.12	**3,4**	1.900		19.000	**14**	0.100	**3**	0.160	0.200	0.702	2.000
Japanese oysters	**5**	2.890 *0.170(W) 5.040(E)*	**4**	0.630		6.300	**14**	0.100			0.200	0.085 *0 (W) 0.155 (E)*	2.000
Slipper limpet	**6**	35.32	**15**	0.300	**14**	4.500		0.067			0.200	0.072	2.000
Zoophagous I	**7**	1.530 *5.950 (W) 9.050 (E)*	**4**	1.300		8.667	**14**	0.150			0.200	0.638 *0.161 (W) 0.467 (E)*	2.620
Zoophagous S	**6**	16.97	**4**	1.300		8.667	**14**	0.150			0.200	0.112	2.610
Deposit feeders	**6,7**	9.220 *18.000 (W) 23.200 (E)*	**14**	2.500		16.667	**14**	0.150			0.200	0.830 *0.296 (W) 0.277 (E)*	2.000
Filter feeders I	**7**	4.940 *14.800 (W) 14.600 (E)*	**4**	1.300		13.000	**14**	0.100	**7**	0.095 *0.680 (W) 0.080 (E)*	0.200	0.679 *0.946 (W) 0.796 (E)*	2.000
Filter feeders S	**6**	16.97	**4**	1.300		13.000	**14**	0.100	**6**	0.630	0.200	0.771	2.000
Zooplankton	**4**	2.340 *1.610*	**14**	18.000	**14**	60.000		0.300			0.200	0.443 *0.900*	2.000
Green algae	**8**	42.800 *227.000*	**16**	3.000					**20**	44.500 *236.300*	0.200	0.361	1.000
Salt marshes	**9,10,11**	5.800 *30.800*	**15**	1.500							0.200	0.014	1.000
Microphytobenthos	**12**	16.000 *84.900*	**4**	27.000							0.200	0.289 *0.151*	1.000
Phytoplankton	**13**	15.600 *6.000*	**4**	166.000							0.200	0.210 *0.864*	1.000

Table 2

	Prey / predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1.	Fish cephalopods													
2.	Herbivorous anatidae													
3.	Zoophagous birds													
4.	Farmed mussels I			0.06					0.01					
5.	Farmed mussels S													
6.	Japanese oysters			0.01					0.01					
7.	Slipper limpet									0.01				
8.	Zoophagous I	0.10		0.35										
9.	Zoophagous S	0.25												
10.	Deposit feeders	0.20		0.10					0.20	0.20				
11.	Filter feeders I	0.10		0.42					0.20					
12.	Filter feeders S	0.20		0.06						0.20				
13.	Zooplankton	0.15							0.20	0.20				
14.	Green algae		0.94											
15.	Salt marshes		0.06											
16.	Microphytobenthos				0.10	0.10	0.15	0.05			0.30	0.10	0.10	0.20
17.	Phytoplankton				0.80	0.80	0.80	0.80				0.80	0.80	0.60
18.	Detritus				0.10	0.10	0.05	0.15	0.38	0.39	0.70	0.10	0.10	0.20
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 3

Trophic groups	$\frac{P}{Q}$	Net efficiency	Respiration / Assimilation	Respiration / Biomass	Production / Respiration
Fish cephalopods	0.13	0.17	0.83	5.67	0.20
Herbivorous anatidae	0.06	0.08	0.92	4.56	0.09
Zoophagous birds	0.03	0.03	0.97	12.88	0.03
Farmed mussels I	0.07	0.08	0.92	3.30	0.09
Farmed mussels S	0.10	0.13	0.88	4.41	0.14
Japanese oyster	0.10	0.13	0.88	13.30	0.14
Slipper limpet	0.10	0.13	0.88	13.30	0.14
Zoophagous I	0.15	0.19	0.81	5.63	0.23
Zoophagous S	0.15	0.19	0.81	5.63	0.23
Deposit feeders	0.15	0.19	0.81	10.83	0.23
Filter feeders I	0.10	0.13	0.88	9.10	0.14
Filter feeders S	0.10	0.13	0.88	9.10	0.14
Zooplankton	0.30	0.38	0.63	30.00	0.60
Green algae					
Salt marshes					
Microphytobenthos					
Phytoplankton					

Table 4

	Bay of Saint-Brieuc	Bay of Mont Saint-Michel	Bay of Brest	Bay of Somme	Seine Estuary
Phytoplankton	258.96[1]	399.31[2]	280.00[4]	312.56[6]	572.32[7]
Microphytobenthos	43.20[1]	45.86[3]	30.66[5]	286.00[6]	281.09[7]

Table 5

Parameters	Units	BSB[1]	Dublin bay[2]	Curonian Lagoon[3]	Parnü bay[3]	Moroccan Atlantic coast[4]	Gran Canaria coast[5]	Bay of Somme[6]	Bay of Mont-Saint-Michel[7]	Narragansett bay[8]	Delaware bay[8]	Gulf of Maine[9]
Fluxes and general characteristics												
Sum of all consumption	$t.km^{-2}.yr^{-1}$	968.038	-	-	-	4191.040	-	-	1090.000	-	-	6968.827
Sum of all exports	$t.km^{-2}.yr^{-1}$	2515.954	-	-	-	5748.100	-	-	3700.000	-	-	4211.147
Sum of all respiratory flows	$t.km^{-2}.yr^{-1}$	642.747	-	-	-	2937.900	-	-	730.000	-	-	5245.491
Sum of all flows into detritus	$t.km^{-2}.yr^{-1}$	2697.742	-	-	-	6370.730	-	-	3880.000	-	-	5182.244
Total system throughput (TST)	$t.km^{-2}.yr^{-1}$	6824.480	-	-	-	19248.770	-	-	9400.000	-	-	21.408
Total catch	$t.km^{-2}.yr^{-1}$	53.185	-	-	-	-	-	-	15.900	-	-	2.671
Total biomass (excluding detritus)	$t.km^{-2}$	169.236	-	-	-	274.470	-	-	180.000	-	-	487.390
Sum of all production	$t.km^{-2}.yr^{-1}$	3290.384	-	-	-	9636.110	-	-	4570.000	-	-	10.899
Net system production	$t.km^{-2}.yr^{-1}$	2515.953	-	-	-	5725.110	-	-	3700.000	-	-	3984.242
Calculated total net primary production	$t.km^{-2}.yr^{-1}$	3158.700	-	-	-	8663.010	-	-	4430.000	-	-	9229.733
Indices												
Total primary production/total respiration (PP/R)		4.914	-	10.851	1.054	2.950	2.172	15.509	6.100	1.300	1.300	1.760
Total primary production/total biomass (PP/B)		18.664	-	108.212	5.814	31.560	8.647	21.816	24.600	24.200	28.200	18.937
Total biomass/total throughput		0.025	-	0.005	0.040	0.010	0.035	0.012	0.019	0.041	0.035	0.023
System Omnivory Index (SOI)		0.041	-	0.165	0.050	0.200	0.340	0.009	0.058	0.300	0.300	0.290
Ascendency												
Ascendency (A)	$t.km^{-2}.yr^{-1}$	8123.000	-	-	-	-	-	-	-	-	-	-
Development capacity (C)	$t.km^{-2}.yr^{-1}$	22221.000	-	-	-	-	-	-	-	-	-	-
System overhead (O)	%	61.990	-	-	-	59.000	74.500	-	-	-	-	-
Relative ascendency (A/C)	%	36.560	42.200	69.000	34.000	41.000	25.500	35.000	47.700	33.500	33.400	-
Cycling												
Average path length		2.161	-	2.055	4.285	2.220	12.600	-	2.100	-	-	2.313
Finn's index (FCI)	%	1.050	31.900	0.580	24.640	1.360	3.253	12.200	0.640	48.200	48.200	3.360

Highlights

- Ecopath modelling is used to achieve a quantitative evaluation of the food web
- The bay of Saint-Brieuc ecosystem is characterized by three trophic impasses
- Green algae proliferations impact the productivity of phytoplankton
- Farmed mussels are important competitors and consume a high part of phytoplankton
- The slipper limpet is an important competitor but locally and patchily distributed

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: