Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France)

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Abstract

To ensure sustainable uses of the coastal zone, an integrated ecosystemic approach and ecosystem models are required to frame ecological processes and evaluate environmental impacts. Here, a mass-balance trophic (Ecopath) model of the Mont Saint Michel Bay (MSMB) was developed, to analyze the bay's functioning as an ecosystem. This bay, intensively exploited by fishing and for shellfish farming, is also suffering from the proliferation of the gastropod *Crepidula fornicata*, an exotic species.

The MSMB model has 18 compartments, from the primary producers to top predators, and emphasizes the large biomass of filter feeders. The model identified the MSMB as a highly productive ecosystem controlled largely from the bottom-up, and strongly impacted by huge biomasses of filter feeders. However, the low transfer efficiency rates imply that a large part of the primary production is not transferred upward to higher trophic levels, but is lost in high hydrodynamic exchanges and in the trophic impasse represented by a large biomass of *Crepidula fornicata*.
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1. Introduction

Coastal areas are productive ecosystems that host a large part of the world's living marine resources and have the highest biological diversity of any part of the sea (Costanza et al., 1997). Despite of these ecological (Beck et al., 2001; Hugues et al., 2005), economical and social (Balmford et al., 2002) largely irreplaceable benefits, these ecosystems have been increasingly subjected to a large number of human pressures, leading to major environmental problems, such as, eutrophication and pollution, over-exploitation, invasions by alien species, etc. (Antunes and Santos, 1999; Costanza, 1999; Hugues et al., 2005).

In this context, ecosystem models may be used as a tool for resolving patterns, indicative of the key ecosystem responses (Fulton et al., 2005). Using such models, analysis of the effects of disturbance and measure of the ecosystem stability and resilience become possible (Perez-Espana and Arreguin-Sanchez, 2001). Within the last few decades, the number of ecosystem models in existence has rapidly grown (Fulton et al., 2003), especially trophic or food web models, notably through the wide availability and acceptance of the Ecopath with Ecosim (Ewe) software (Christensen and Walters, 2004).

Here, Ecopath was used to organize information on the functioning of the food web of the Mont Saint Michel Bay (MSMB), located on the north coast of France. The site is famous for its abbey, built on a hill in the intertidal zone, so that both the buildings and the vast productive mudflats surrounding it have been recognized for their cultural and ecological interest and, since 1979, is listed in the World Heritage Sites

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(UNESCO). The MSMB hosts intensive shellfish farming enterprises. Also, for the last decades, it has been facing an invasion of the American slipper limpet *Crepidula fornicata* (Blanchard, 1997). Measures designed to mitigate these various problems became unavoidable to ensure the conservation of wildlife and associated habitats (Lefeuvre and Bouchard, 2002), and the sustainable development of local economical activities (e.g. tourism, shellfish farming and fishing; Le Mao et al., 2004). Therefore the MSMB was selected, in 2001, as a study site by the French national program of coastal environment (PNEC).

The present study, carried out in the framework of the PNEC, examined the trophic functioning of the MSMB with regards to human activities and recent environmental changes. The ultimate objective was to analyze different interactions between the biological components of the MSMB, and to assess the values of consumption and production fluxes of its food web. An Ecopath model, representing a mass-balance budget of production, consumption, fish farming and fishing in the food web was constructed. It considers all functional groups in this system, from primary producers to apex predators, including the large biomass of natural, farmed and exotic filter feeders. Information on ecosystem structure and function provided by inferred biomass transfers between functional groups can then be used to evaluate the likely impact of changes in the abundance of selected groups, and examine how such changes are impacting the whole ecosystem via different links of the food web (Ulanowicz, 1986).

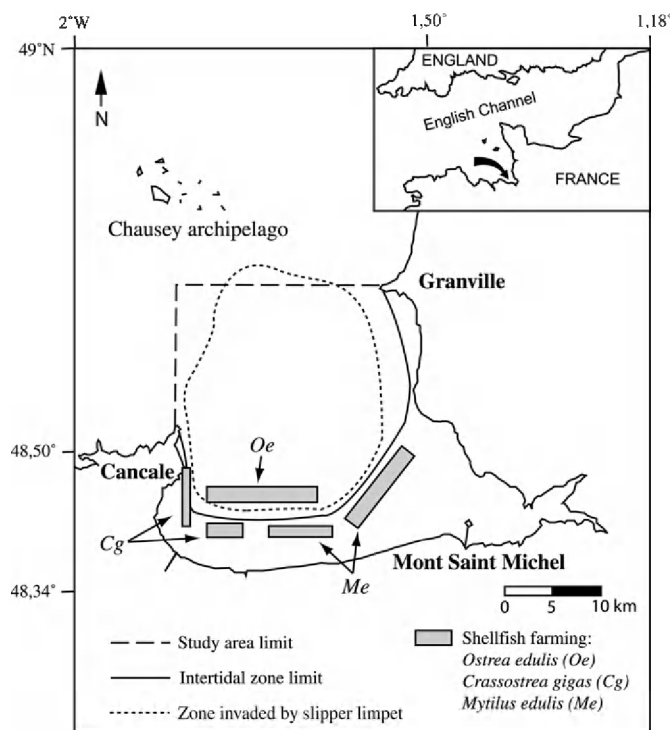Fig. 1. General location and details of the study area within the Mont Saint Michel Bay, France (geographic coordinates are in decimal degrees).

2. Materials and methods

2.1. Study site

The MSMB is located in France, in the western part of the English Channel (48°30′N−1°40′W; Fig. 1). This bay is a semi-diurnal macrotidal system characterized by the second highest tidal range in Europe (10−11 m on average, with a maximum of 15.5 m). The intertidal zone covers 250 km^2 and includes 210 km^2 of mudflats and 40 km^2 of salt marshes.

The MSMB is host to a high biodiversity (Lefeuvre and Bouchard, 2002), notably:

- one of the largest salt marshes of the French coast;
- one of the main nurseries of the English Channel coast for many fish species of commercial interest (Lafaille et al., 2000) such as sea bass (*Dicentrarchus labrax*), whiting (*Merlangius merlangius*), flatfishes (common sole *Solea solea* and plaice *Pleuronectes platessa*), clupeids (*Sardina pilchardus*, *Clupea harengus* and *Sprattus sprattus*), and elasmobranchs (*Raja* spp.);
- thousands of over-wintering birds and birds resting while on their migrations;
- honeycomb reef-like structures built by the polychaete *Sabellaria alveolata*.

This site also hosts activities such as tourism, fishing and shellfish farming (Le Mao et al., 2004). Three bivalves are farmed (Fig. 1): (1) the Japanese oyster (*Crassostrea gigas*) in the intertidal mudflat of Cancale Bay (about 345 ha), (2) the European flat oyster (*Ostrea edulis*), farmed in the subtidal domain (880 ha) and (3) the common mussel (*Mytilus edulis*) reared on poles arranged in linear rows on the intertidal mudflat (total length of the rows: 272 km). The American limpet, *Crepidula fornicata*, which was introduced about 60 years ago, is now increasingly found, and currently represents the highest biomass of filter feeders within the bay (Loomis and VanNieuwenhuyze, 1985; Blanchard, 1997; Blanchard and Ehrhold, 1999).

2.2. Model approach

A mass-balanced trophic model was constructed using EwE (Christensen and Walters, 2004). The core Ecopath routine of EwE, derived from Polovina (1984), was applied to balance the energy budget of the different compartments of the system. The model is structured around a system of linear equations for ensuring mass-balance, which can be expressed (Christensen and Walters, 2004) as follows:

$$B_i \times \left(\frac{P}{B}\right)_i \times \mathrm{EE}_i = Y_i + \sum_j^n B_j \times \left(\frac{Q}{B}\right)_j \times \mathrm{CR}_{ij} \qquad (1)$$

where, for $i = 1$ to n functional groups and $j = 1$ to n predators, B is the biomass in a given period of time; P/B the production/biomass ratio, which is equivalent to the instantaneous rate of total mortality, Z, under equilibrium (Allen, 1971); EE

the ecotrophic efficiency (the fraction of production consumed, fished or exported out the system); Y the fishery yield; Q/B the consumption/biomass ratio and CR_{ij} the fraction of i in the diet of j.

Ecopath sets up a system containing as many linear equations as groups present within a system (n). The model can estimate one of the four parameters (n equations for n unknown parameters) as long as any three of these parameters are known, *viz.* B, P/B, Q/B or EE.

After the missing parameters have been estimated (with respect to the mass-balance between groups), consumption by predators can be described by the energy-balance equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \tag{2}$$

2.3. Input data and model structure

The study area of the model included 380 km² of subtidal domain and 210 km² of intertidal mudflats (Fig. 1). To simplify the model, the salt marshes, connected to trophic network in the bay by the organic matter exported to the tidal system (Lafaille et al., 1998), were included in the model only as imported production.

The food web of the MSMB was described through 18 trophic groups, with the grouping of taxa being based on their similar trophic properties (preys, predators, turnover rate; Christensen and Walters, 2004). This resulted in two primary producer compartments (phytoplankton and microphytobenthos), three groups of cultivated filter feeders (European flat oyster, Japanese oyster and common mussel), *Crepidula fornicata*, zooplankton, meiofauna, small fishes (small species and other juvenile fish), three groups of macrobenthic fauna (carnivorous and necrophagous macrobenthic fauna, intertidal and subtidal filter feeders), mullets, three groups targeted by fisheries (cephalopods, large crustaceans and adult fishes), birds and marine mammals (Table 1).

The major part of data related to biomass, production and consumption (Table 2) were collected from studies conducted within the framework of the PNEC on the MSMB during the reference year 2003 (Table 1), taken as reference because several sampling surveys were performed in the bay during that year. When they were not available from this program, data were collected from various other sources (Table 1), particularly a model developed on the western Channel (Stanford and Pitcher, 2004). Commercial yields were taken from producer statistics for all cultivated species and from official records on statistical rectangle 28E6 of the ICES system, used for European fisheries data collection. Diet compositions (Table 3) were compiled from available literature but mainly from expert knowledge, after discussion with the specialists who provided the survey data (Table 1). Biomasses for each group are averaged on an annual period: if a group is present only during a part of the year, and eats elsewhere during the rest of the time, its biomass when present is multiplied by the proportion of time of presence to estimate the average annual biomass. It is the reason why no imported food is mentioned in the diet matrix (except for detritus that include organic matter coming from the salt marshes). Trophic fluxes between the different compartments of the trophic model were estimated in tonnes (t) of fresh weight of flesh per km².

2.4. Network analysis

Once the model was balanced, various parameters and indices were generated using the EwE software (Christensen and Walters, 2004). Trophic interactions between groups and the effects of exploitation were compared using EE, trophic levels (TL, computed from the mean TL of prey + 1; Christensen and Pauly, 1998), consumption rates, predation mortality and the primary production required (PPR) to sustain consumption by the various compartments of the model, and the extraction by humans.

Direct and indirect trophic interactions were analyzed using the mixed trophic impact routine of EwE, inspired by the Leontief matrix (Ulanowicz and Puccia, 1990), and which reflect both the impact of prey over their predators and predators over their preys (Pace et al., 1999).

Finally, the system was examined as a whole using the model's global parameters. With Ecopath, functional groups are aggregated into discrete trophic levels *sensu* Lindeman (1942) as suggested by Ulanowicz (1995), which allows estimation of flows to detritus and upper trophic levels, and of transfer efficiencies. Some network attributes (Ulanowicz, 1986; Ulanowicz and Kay, 1991) and flow indexes were analyzed to describe holistic properties of the system, i.e., total system throughput (T, sum of all flows through all compartments), Finn's (Finn, 1976) cycling index (FCI, fraction of ecosystem's throughput that is recycled), and Finn's mean path length (average size of the path length following for these transfers). The ratio of Net Primary Production to Total Biomass (PP/B) and to Total Respiration (PP/R) was also examined, as it is an important index of system maturity (Odum, 1969).

3. Results

3.1. Balancing the model

The Ecopath Eq. (1) states that each group must be mass-balanced, i.e., for one group, catches, consumption, biomass accumulation and export must not exceed production. Balancing an Ecopath model requires to adjust the input parameters such that none of the EE values exceeds 1 (Christensen and Walters, 2004; Kavanagh et al., 2004).

Here, the biomasses of many predator groups (cephalopods, large crustaceans, carnivorous and necrophagous macrobenthic fauna, adult fishes and small/juveniles fishes) were preliminarily adjusted according to expert estimates. A first attempt at balancing the model showed that the demand from these predator groups exceeded the production of most of the prey groups (meiofauna, carnivorous and necrophagous macrobenthic fauna, intertidal and subtidal filter feeders). Thus, to achieve mass-balance, an ecotrophic efficiency of 0.9 was applied to these groups, and the biomass of predator groups targeted by fisheries was left to be estimated by the model (Table 2).

Table 1

Input data values for the Mont Saint Michel Bay Ecopath model obtained mostly from the French national program of coastal environment on the Mont Saint Michel Bay (PNEC). The model refers to the year 2003, as most of the data used for its construction were based on sampling conducted in 2003. Choices of parameter values were also informed by the February 17–20, 2000. Ecopath workshop conducted in the Agrocampus, Rennes (D. Pauly and G. Fontenelle, unpublished data)

Trophic group	Biomass	Production/biomass (P/B)	Consumption/biomass (Q/B)	Production/consumption (P/Q)
Birds	Le Mao et al. (2006)	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Marine mammals	G. Gautier, DIREN Basse Normandie,[a] (PNEC); C. Liret, Océanopolis (unpublished data)	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Cephalopods	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Large crustaceans	Model estimate	D. Latrouite, IFREMER (unpublished data)	Stanford and Pitcher (2004)	
Adult fishes	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Small and juvenile fishes	Model estimate		Lafaille et al., 1998	Palomares et al. (1993)
Mullets	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Zooplankton	QUADRIGE II database, IFREMER	Christensen (1995)	Christensen (1995)	
Carnivorous and necrophagous macrobenthic fauna	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Intertidal filter feeders	J. Trigui and E. Thiebaut, Univ. Paris 6 (PNEC); N. Toupoint, Museum National d'Histoire Naturelle (unpublished data); Zwarts et al. (1996), Dubois (2002), Dubois et al. (2006)	Dauvin (2000), Ropert and Dauvin (2000)		Stanford and Pitcher (2004)
Subtidal filter feeders	F. Olivier, MNHN (PNEC); E. Thiebaut and C. Guichardière, Univ. Paris 6 (PNEC); Zwarts et al. (1996)	Dauvin (2000), Ropert and Dauvin (2000)		Stanford and Pitcher (2004)
Meiofauna	K. Seznec, Univ. Paris 6 (PNEC)	Le Loc'h (unpublished data)		Le Loc'h (unpublished data)
Slipper limpets	Blanchard and Ehrhold (1999)	Blanchard and Ehrhold (1999)	Blanchard and Ehrhold (1999)	
European flat oyster	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Japanese oyster	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Common mussel	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Phytoplankton	QUADRIGE II database, IFREMER	C. Struski, IFREMER (PNEC)		
Microphytobenthos	D. Davoult, Univ. Paris 6 (PNEC)	D. Davoult, Univ. Paris 6 (PNEC)		

[a] Institutional affiliation of data providers (unpublished data) are all located in France.

Table 2

Input and calculated (in **bold**) parameters for the Ecopath model of the Mont Saint Michel Bay. Catches and biomasses are expressed in t km^{-2} (fresh weight). The production/biomass (*P/B*) and consumption/biomass (*Q/B*) ratios are in year^{-1}. The production/consumption (*P/Q*) ratio, trophic level (TL) and ecotrophic efficiency (EE) are dimensionless. Data in *italics* originate from 2003 studies of the French national program of coastal environment on the Mont Saint Michel Bay (PNEC). Values in bold are computed from the Ecopath with Ecosim software

Trophic group	Catch	Troph	Biomass	P/B	Q/B	EE	P/Q
Birds	0.002	**3.01**	*0.263*	0.400	*14.000*	**0.019**	**0.029**
Marine mammals		**4.12**	0.027	0.310	13.900	**0.000**	**0.022**
Cephalopods	0.480	**3.79**	**0.230**	2.5	15.000	0.900	**0.167**
Large crustaceans	0.450	**2.69**	**1.767**	0.500	4.000	0.900	**0.125**
Adult fishes	0.150	**3.16**	**3.501**	0.800	6.000	0.900	**0.133**
Small and juvenile fishes	0.160	**2.82**	**1.088**	**6.600**	22.000	0.900	0.300
Mullets	0.002	**2.10**	**0.088**	0.500	5.000	0.900	**0.100**
Zooplankton		**2.00**	2.460	18.000	60.000	**0.257**	0.300
Carnivorous and necrophagous macrobenthic fauna	3.000	**2.08**	**13.615**	1.300	**6.500**	0.900	0.200
Intertidal filter feeders		**2.00**	*12.350*	1.300	**13.000**	**0.877**	0.100
Subtidal filter feeders	1.500	**2.00**	*6.450*	1.300	**13.000**	**0.808**	0.100
Meiofauna		**2.00**	*0.700*	10.000	**50.000**	**0.348**	0.200
Slipper limpets	3.050	**2.00**	*91.100*	0.300	*4.500*	**0.140**	**0.067**
European flat oyster	0.150	**2.00**	*0.410*	*0.400*	**4.000**	**0.915**	0.100
Japanese oyster	0.760	**2.00**	*1.350*	*0.630*	**6.300**	**0.894**	0.100
Common mussel	6.150	**2.00**	*4.600*	*2.000*	**20.000**	**0.854**	0.100
Phytoplankton		**1.00**	*24.055*	*166.000*	−	**0.166**	−
Microphytobenthos		**1.00**	*16.000*	*27.000*	−	**0.382**	−

3.2. Trophic structure of the MSMB

3.2.1. A large proportion of filter feeders

Input values and output estimates after balancing the model were summarized in Table 2 and ecosystem statistics in Table 4. The MSMB is characterized by a high productivity, with an overall production of about 4600 t km^{-2} year^{-1}, and the large biomass of filter feeders (65% of total biomass), with *Crepidula fornicata* as most dominant species (51% of total biomass). Fig. 2a, representing biomasses at different trophic levels, illustrates that there is a substantial lower biomass above the filter feeders (TL = 2).

3.2.2. Contrast in efficiencies of trophic transfers

In the model, the productions (Fig. 2b) and EE values (Table 2) showed a wide range of variation, reflecting the unequal trophic roles of various compartments.

Table 3

Predator–prey matrix of the ecosystem in the Mont Saint Michel Bay. Data in *italics* originate from 2003 studies of the French national program of coastal environment on the Mont Saint Michel Bay (PNEC)

Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Birds																
2. Marine mammals																
3. Cephalopods		0.1														
4. Large crustaceans			0.1						0.1							
5. Adult fishes		0.8	0.6	0.1					0.2							
6. Small and juvenile fishes					0.3				0.1							
7. Mullets		0.1														
8. Zooplankton					0.2	0.3										
9. Carnivorous and necrophagous macrobenthic fauna	*0.15*		0.3	0.3	0.2	0.2										
10. Intertidal filter feeders	*0.6*				0.1	0.2			0.05							
11. Subtidal filter feeders				0.1	0.1	0.1										
12. Meiofauna						0.1	0.1									
13. Slipper limpets				0.1												
14. European flat oyster																
15. Japanese oyster																
16. Common mussel	*0.25*			0.1												
17. Phytoplankton								0.4		0.8	0.8		*0.8*	*0.8*	*0.8*	*0.8*
18. Microphytobenthos						0.5		0.4	0.15	0.1	0.1	0.8	*0.05*	*0.15*	*0.15*	*0.1*
19. Detritus			0.3	0.1	0.1	0.4	0.2		0.4	0.1	0.1	0.2	*0.15*	*0.05*	*0.05*	*0.1*

Table 4
Summary statistics for the Mont Saint Michel Bay model

Parameter	Units	Value
Sum of all consumption	$t\,km^{-2}\,year^{-1}$	1090
Sum of all exports	$t\,km^{-2}\,year^{-1}$	3700
Sum of all respiratory flows	$t\,km^{-2}\,year^{-1}$	730
Sum of flows into detritus	$t\,km^{-2}\,year^{-1}$	3880
Total system throughput	$t\,km^{-2}\,year^{-1}$	9400
Sum of all production	$t\,km^{-2}\,year^{-1}$	4570
Mean trophic level of catch		2.11
Gross efficiency (catch/net P.P)		0.00358
Calculated total Net Primary Production	$t\,km^{-2}\,year^{-1}$	4430
Total primary production/total respiration		6.1
Net system production	$t\,km^{-2}\,year^{-1}$	3700
Total primary production/total biomass		24.6
Total biomass/total throughput		0.019
Total biomass (excluding detritus)	$t\,km^{-2}$	180
Total catches	$t\,km^{-2}\,year^{-1}$	15.9
Connectance index		0.17
System omnivory index		0.058
Finn cycling index	%	0.64
Finn mean path length		2.1

First, a large break in the pyramid of production is observed between TL1 and 2 (6%), indicating that little of the primary production in the system is utilized. This is matched by low EE values for phytoplankton and microphytobenthos, which indicate that only a small proportion of their production is grazed within the water column, or in the benthic domain.

In contrast, in the next step of the trophic chain (TL2/TL3), the transfer efficiency is quite high (18%). This corresponds to high values of EE for farmed and 'natural' inter- and subtidal filter feeders, whose production is largely used by shellfish farming (70% of the mortality for oysters and mussels) or consumed by predators (89% of the mortality of 'natural' filter feeders is caused by predators).

The slipper limpets (*Crepidula fornicata*) is an exception: only 14% of its production is utilized by higher trophic level animals and the fisheries. Moreover, even this is too high, as the catch of slipper limpets is discarded as it is due to dredging operations to limit its extend. The consumption of primary production by slipper limpets is four times higher than for cultivated mollusks. When the surface areas covered by the organisms are taken into account, the impact of farmed shellfish remains 2.5 times lower than those due to the slipper limpet. Requiring the highest PPR in the model (17%), slipper limpets appear as a large trophic impasse in the system: although this species represents 41% of the total consumption of primary production and detritus, its trophic efficiency when discards are removed is lower than 3%.

Hence, in the MSMB, the trophic chain is shorten at TL2 by two different processes, extraction by shellfish farming but, mainly, large production of slipper limpets, not exploited by higher trophic levels (Fig. 3).

Finally, in the residual natural trophic chain, transfers to top predators are efficient (12%), as also indicated by high EE values.

3.2.3. Influence of shellfish farming on yields

PPR for current total catches ($15.9\,t\,km^{-2}\,year^{-1}$) corresponds to 15% of the Net Primary Production; the 'catch' has a mean trophic level of 2.11. This low value is due to the intensity of shellfish farming, which contributes the major part of withdrawals by humans. However, the trophic role due to fishing activities proper is far more important than that due to shellfish farming: the PPR to sustain fishing activities is seven times higher than for shellfish farming.

3.2.4. Convergent signals indicating a bottom-up, productive immature system

Results of Leontief matrix routine underline the positive impacts of phytoplankton and microphytobenthos on the other groups of the system (Fig. 4). Primary producers provide a key food supply for filter feeders (second trophic level), which constitute the preys of higher-order consumers.

Total system throughput (Table 4) reached 9400 t $km^{-2}\,year^{-1}$, of this, 12% is devoted to consumption, 8% to respiration, 41% to flows to detritus and 39% to exports (equivalent to yield and/or net system production).

Total primary production/total biomass ($PP/B = 25\,year^{-1}$) and total primary production/respiration ($PP/R = 6$) had high values. The omnivory index of the MSMB model, of about 0.06, identifies the food web as very simple; consistently, the FCI is very low (0.64%) and the Finn's mean path length very short (2.1; Table 4).

4. Discussion

The model developed in this study was mainly based on the data collected from studies conducted on the MSMB during the reference year 2003. After that the biomass of predator groups targeted by fisheries was left to be estimated by the model, this Ecopath model was equilibrated. As (1) input data were based on *in situ* surveys, (2) none of the EE values exceeds 1 (Christensen and Walters, 2004) and (3) estimated annual productions ($B \times P/B$) were realistic with regards to catches and fishing pressures for groups in which biomasses are calculated from the mass-balance procedure, this model was considered as realistic. Even if this model is based on an annual mass-balance, and does not reproduce the large seasonal variations, and seasonal contrasted trophic situations, it can be used to analyze the system on this annual scale.

(a) Biomasses

(b) Production

Trophic level 4+
Trophic level 3
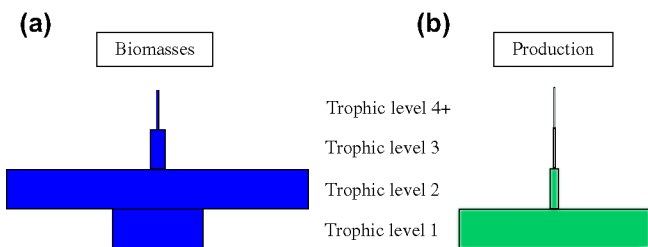Trophic level 2
Trophic level 1

Fig. 2. Pyramids of (a) biomass and (b) productivity characterizing the Mont Saint Michel Bay ecosystem (relative scales).
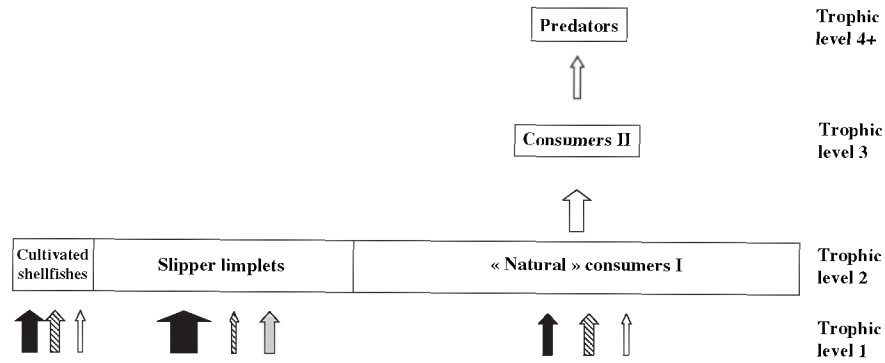
Fig. 3. Pyramids of consumption characterizing the Mont Saint Michel Bay with details on trophic level 2 (respective levels of consumption by farmed shellfish, slipper limpet and "natural" consumers, and origin of this consumption (primary production by phytoplankton (black arrow) or phytobenthos (cross-hatched arrow), or detritus (grey arrow))).
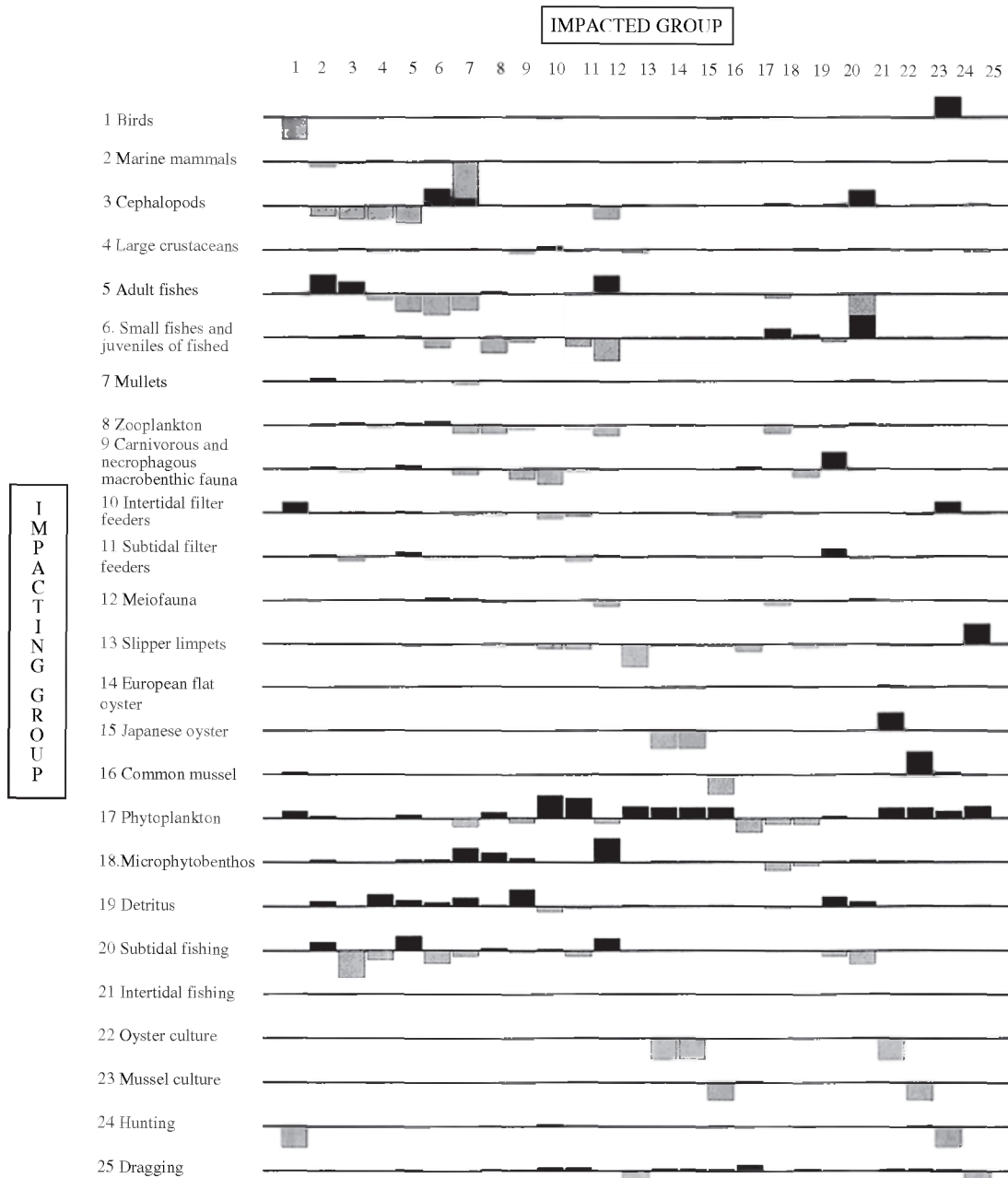

Fig. 4. Mixed trophic impacts between groups of the Mont Saint Michel Bay ecosystem. Bars represent the direct and indirect trophic impacts that the groups' lines have on the columns groups. Black bars indicate a positive impact and white bars a negative impact. The impacts are relative and comparable to each other.

This model has highlighted the main features of the MSMB: a very high production, associated with a low efficiency of transfer from primary production to higher trophic levels, partly due to a large biomass of filter feeders not available for consumption within the system. Also, the system is profoundly impacted by the invasive mollusk *Crepidula fornicata*.

4.1. A general description of the trophic web

4.1.1. Low rate of transfer of the high primary production in the trophic chain

In spite of a moderate production of microphytobenthos, MSMB is highly productive, the primary production being essentially supported by phytoplankton, whose concentration remains high through the summer (Hoch and Garreau, 1998). As in coastal lagoons, the strong tidal currents in this bay enhance the production rate (Comin and Valiela, 1993), by injecting regenerated nutrients into the euphotic zone (Hoch and Garreau, 1998).

However, an adverse effect of hydrodynamics in the MSMB is that the tidal currents lead to exchanges with adjacent shelf waters and to huge loss of organic matter via phytoplankton export (Le Pape and Menesguen, 1997). As a consequence, the primary production cannot be fully exploited by the bay's consumers (Le Pape et al., 1999; Rybarczyk et al., 2003; Riera, 2007).

4.1.2. The large influence of filter feeders

The model highlights the importance of filter feeders in the trophic network in the MSMB, which is locally called "filter feeders' bay." Such role for filter feeders frequently occurs in highly productive coastal systems, as high primary production results in higher food availability favorable to filter feeding (Le Pape et al., 1999; Grall and Chauvaud, 2002).

However, one of the specific features of the MSMB is that a large proportion of these filter feeders consists of *Crepidula fornicata*: its consumption reaches more than 40% of consumptions at TL2, but it is not exploited by human nor by the food chain; hence, it represents a large trophic impasse (Fig. 3).

4.2. A global evaluation of the system

The model identified the MSMB as a highly productive ecosystem and the Leontief matrix routine demonstrated that it is largely controlled from the bottom-up. However, global indicators (high PP/*B* and PP/*R*, low omnivory and low Finn cycling index and mean path length) suggest that the MSMB ecosystem is immature, in line with Odum (1969), Finn (1976) and Ulanowicz (1986, 1995). Low maturity status is common in megatidal coastal and estuarine systems, as the bay of Somme (Rybarczyk et al., 2003), or the Seine estuary (Rybarczyk and Elkaim, 2003), with relation to the low rate of transfer of primary production (Le Pape and Menesguen, 1997). Even if it is sometimes difficult to compare different systems from different degree of compartments aggregation

in models, very low values of cycling index in the MSMB reflect an especially immature system.

The immaturity of the MSMB trophic network may be explained, if partly, by the intensive human exploitation of the bay, through shellfish farming and fishing activities. Yields represent 15% of the Net Primary Production in the MSMB, i.e., a high rate of exploitation (Pauly and Christensen, 1995; Christensen and Pauly, 1998), especially when the large losses of primary production due to hydrodynamic exchanges (Le Pape et al., 1999) are considered.

However, the immaturity status is also due to the high biomass of *Crepidula fornicata*, which represents 50% of the biomass at TL = 2, and 40% of the consumption of the primary production, but which causes a trophic impasse and reduces the efficiency of overall trophic interactions in the system.

In conclusion, the MSMB trophic network appears to be segmented in three trophic sub-systems, partly disconnected (Fig. 3):

- A short shellfish farming chain (TL2), whose trophic influence on the system is moderate;
- A short chain (TL2), based on *Crepidula fornicata*, which consumes a large part of the, mainly planctonic, primary production (Riera, 2007);
- A residual 'natural' exploited system, with a high transfer efficiency.

4.3. The determining influence of Crepidula fornicata

Coastal and estuarine areas are among the most biologically invaded systems in the world, especially by mollusks (Grosholz, 2002; Reise et al., 2006), with grave consequences for the invaded ecosystems. Cloern (1982) demonstrated the large influence of the exotic clam *Potamocorbula amurensis* in San Francisco Bay, which now diverts to itself the major part of primary production. Ecological consequences of invasions into coastal habitats can affect the entire ecosystem (Grosholz, 2002) and, in several cases, as in the San Francisco Bay after the introduction of *P. amurensis* (Bax et al., 2003), the collapse of fisheries.

However, Crooks and Khim (1999) suggested that the effects of habitat structural changes could compensate for the effect of invasive species on food webs. Thus, *Crepidula fornicata* modifies physical characteristics of benthic habitats: (1) by accumulating chain-shaped colonies which carpet the sea bottoms (Thieltges et al., 2003), and (2) as other filter feeding invasive species do (Daunys et al., 2006), by the excessive sedimentation associated with its excretion and by modification of hydrodynamics in the boundary layer flow (Ehrhold et al., 1998). Such habitat changes have been demonstrated to alter the nursery function of coastal areas (Le Pape et al., 2004).

Reise et al. (2006), who reviewed the problem of introduced species in European coastal ecosystems, are globally less alarmist, asserting that there is no evidence that alien species generally impair biodiversity and ecosystem functioning.

Similarly, de Montaudouin and Sauriau (1999) found that bio-mass, abundance and species richness of benthic macrofauna were enhanced in the presence of *Crepidula fornicata*, whose shells increase the heterogeneity of the substrate (Attrill et al., 1996). MSMB hence appears as an inverse example, where the consequences of the massive invasion of slipper limpet appear very important with, as in the San Francisco Bay, a large (40%) diversion of the consumed primary production.

4.4. Investigation of future changes in the system and management measures

One aim of the PNEC program in the MSMB was to de-velop knowledge in order to create reliable tools for manage-ment. Since the present study is not predictive, the question of the future of the bay remains open. Possible scenarios include: (1) changes in shellfish farming distribution and intensity, and/or (2) changes in the distribution of *Crepidula fornicata* in-cluding those due to control measures. These changes could be in part simulated using Ecosim (Christensen and Walters, 2004), which simulated biomass dynamics based on the pa-rameters derived from the Ecopath model. However, this pro-cedure implies the setting of a vulnerability rate to simulate the top-down versus bottom-up control; the problem is that the results are very sensitive to the vulnerability values chosen (Christensen and Walters, 2004). Without time series data, it was not possible to tune these parameters and the simulations will remain very sensitive to the initial settings, particularly the spatial biogeochemical dynamics. Nevertheless, additional mass-balance sub-models, as the one used to analyze the con-sumption of primary production by slipper limpets in the area covered by cultivated mollusks (cf. Section 3.2.2.) can provide information on contrasted situations. This sub-model has al-lowed to demonstrate that the impact of the slipper limpet is still higher than this of farmed shellfish when farming areas only are taken into account. It would be possible to develop comparable sub-models to investigate other questions.

The next steps in this study should thus involve developing an alternative spatial biogeochemical dynamic model, taking into account the filtering pressure of mollusks. An alternative approach would consist of assembling suitable time series, taking into account possible changes in biomass and diet ma-trix, and also investigating the use of Ecospace, which also uses parameters from Ecopath (Walters et al., 1998; Pauly et al., 2000).

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