Trophic web and carrying capacity in a pearl oyster farming lagoon (Takapoto, French Polynesia)

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Abstract – Data concerning the planktonic food web and the farmed pearl oysters of the lagoon of Takapoto Atoll were assembled into a steady state model of carbon flows. A method of optimisation, using constraints from the literature, called 'inverse analysis' was chosen as the numerical tool for estimating the missing flow values. The resulting food web is characterised by: 1) high primary production, achieved by low phytoplankton biomass, 2) high production of non-living matter, especially as dissolved organic carbon, 3) low bacterial production, 4) zooplankton dominated by protozoa (biomass and processes) and mesozooplankton (processes), and 5) very low consumption of plankton by farmed bivalves compared to planktonic fluxes. When considering the whole lagoon, the farmed oysters (*Pinctada margaritifera*) and associated bivalves (*Pinctada maculata*) consume 0.24% of the planktonic gross primary production. In addition, the consumption by natural populations of the main benthic bivalves in this lagoon (*Chama iostoma*, *Arca ventricosa*, *Pinctada margaritifera* and *Pinctada maculata*) is also low compared to the high planktonic primary production (4.1%). The oyster farming in this lagoon is thus very far from being food-limited. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

atoll lagoon / food web / plankton / *Pinctada margaritifera* / steady state model

Résumé – Étude du réseau et de la capacité trophique d'un lagon d'atoll (Takapoto, Polynésie française) par rapport à l'huître perlière. Les données concernant le réseau trophique planctonique et les huîtres en culture dans le lagon de Takapoto ont été rassemblées dans un modèle à l'équilibre des flux de carbone. L'outil numérique employé pour estimer les flux inconnus, appelé « analyse inverse », est une méthode d'optimisation prenant en compte des contraintes tirées de la littérature. Le réseau trophique obtenu se caractérise par : 1) une forte production primaire comparée à la biomasse phytoplanctonique, 2) une forte production de matière détritique, en particulier dissoute, 3) une faible production bactérienne, 4) un zooplancton dominé par les protozoaires, tant en terme de biomasse que de flux de carbone, et le mésozooplancton pour ce qui concerne les flux et 5) une consommation du plancton par les bivalves cultivés très faible comparée aux processus planctoniques. En considérant le lagon dans son ensemble, les huîtres perlières (*Pinctada margaritifera*) et les bivalves associés (*Pinctada maculata*) consomment 0,24% de la production primaire planctonique brute. De plus, les principales populations naturelles de bivalves benthiques de ce lagon (*Chama iostoma*, *Arca ventricosa*, *Pinctada margaritifera* et *Pinctada maculata*) présentent, elles-aussi, une consommation de carbone peu élevée par rapport à la production primaire planctonique (4,1%). Le lagon est donc loin d'un état où la consommation des huîtres cultivées serait limitée. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

lagon / réseau trophique / plancton / *Pinctada margaritifera* / modèle à l'équilibre

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1. INTRODUCTION

Since 1980, the aquaculture of pearl oysters has played an increasing economic role in French Polynesia. Today, the production is approximately six metric tons of pearls (i.e. about 170 million €). After a large-scale mortality that decimated the farmed pearl oysters in several atolls in 1985, the French Polynesian authorities decided to set up a General Research Programme on Pearl Oysters (PGRN). The main objective of PGRN was to assess the carrying capacity of a lagoon for pearl oyster farming. Takapoto Lagoon (Tuamotu Archipelago, French Polynesia) was chosen as the study site. This study took place in the scientific context of a large reflection on carrying capacity, which led to the publication of numerous studies aiming at re-defining this notion and discussing it through a large inter-ecosystem comparison (e. g. Prins and Smaal, 1994; Prins et al., 1996; Bacher et al., 1997; Smaal and Zurburg, 1997; Dame and Prins, 1998; Prins and Dame, 1998).

The black pearl oyster, *Pinctada margaritifera* (Linnaeus, 1758) var. *cumingi* (Reeve) was one of the most abundant bivalves in the natural benthic fauna of most Polynesian atoll lagoons. The development of pearl oyster farming moved these benthic bivalves to the pelagic environment, since the farming technique consists of down lines suspended on subsurface long lines. Thus, understanding the relationships between farmed pearl oysters and the pelagic food web is essential to determine the carrying capacity of a lagoon in term of pearl oysters.

The planktonic studies in Takapoto Lagoon during the first part of the PGRN (PGRN I, 1991–1995) led to the building of a first model of the planktonic food web (Niquil et al., 1998). Using new experimental techniques and simultaneous measurements of several planktonic stocks and flows, Sakka et al. (2001) modified this first quantification of the planktonic food web in Takapoto.

The above papers focused on the planktonic community of Takapoto Atoll without taking into account the farmed pearl oysters. Simultaneously, Pouvreau et al. (2000) published an ecophysiological growth model of farmed *Pinctada margaritifera*, but they did not formally connect this model to the pelagic food web. For that reason, we propose a new food web model for the pelagic community, derived from Niquil et al. (1998), including the new field estimates of several planktonic processes from Sakka et al. (2001) and the farmed pearl oysters. As in our first model, we use inverse analysis to obtain a complete food web in which all the flows are quantified. The description of the resulting flow scheme leads to the characterization of the trophic capacity of the lagoon. This characterization is completed by a comparison with the consumption of the main benthic bivalves (not included in the pelagic food web model), which are supposed to compete for food with the farmed oysters.

2. MATERIAL AND METHODS

2.1. Study site

Takapoto Atoll is located in the northwest of the Tuamotu Archipelago (145°10'W, 14°40'S; *figure 1*). The surface area of the lagoon in 81 km2 (Andrefouët, 1998), and its mean depth is 25 m. It is characterised by an almost closed reef rim that strongly isolates the lagoon from the ocean despite a few shallow channels (< 50 cm deep) where currents are generally weak (Sournia and Ricard, 1976). The residence time of water in the lagoon is ca. 4 years (Sournia and Ricard, 1976). There are subsurface pinnacles with a strong cover of molluscs and corals above the sandy bottom (Pirazzoli and Montaggioni, 1984). Water is transparent, and the compensation depth always exceeds the maximum depth of the lagoon (Charpy et al., 1992). Nitrate, phosphate and silicate concentrations that are often lower than in the surrounding ocean (Charpy, 1996) provide evidence for strong oligotrophy in the lagoon. Water motion is mainly driven by regular east–northeastern trade winds (Rougerie, 1979) that homogenise the water mass of the lagoon.

Pearl oyster farming has been extensively developed in the lagoon since 1970, and it is now the main economic activity on the atoll (Salvat and Richard 1985).

2.2. Plankton analysis

Plankton studies conducted during the first phase of the PGRN (1991–1995) showed the lack of spatial or temporal variations in the water column (Charpy, 1996). Consequently, the study of the planktonic system, during the second phase of the programme
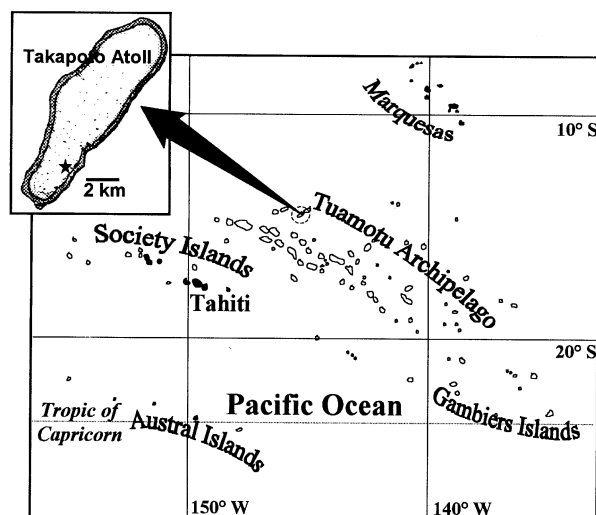
Figure 1. French Polynesia and location of Takapoto Atoll. High islands are in black and atolls in white. Star: location of our study site in Takapoto Lagoon.

(1995–1999), was limited to one sampling station and 4 depths (*figure 1*). The field project included two diel studies, in April 1996 and April 1997. Bacteria, phytoplankton, and proto- and metazooplankton were identified, counted and measured (except for bacteria) for conversion to biovolumes and masses of carbon. Production of dissolved organic carbon (DOC) by phytoplankton was estimated by ^{14}C incubations. Grazing on three size classes of phytoplankton and protozoa < 35 μm was estimated, in presence and absence of protozoa > 35 μm, using the dilution technique with in situ incubations (Sakka et al., 2000). The sinking of particles was estimated by sediment traps. The methods are fully described in Sakka et al. (2000) and values are presented in *tables I* and *II*.

For complementary information on metazooplankton metabolism, we also included in the present model the results of experiments conducted in November 1993 and February 1994 at the same sampling station. Nine incubation experiments were performed with eleven replicates to determine the excretion of total dissolved nitrogen and phosphorus and oxygen uptake. Production rates (*PR*) of micro- and mesozooplankton were calculated from their excretion rates (*ER*) and net growth efficiency, using the *C:N:P* ratios of zooplankton body constituents, metabolic end-products, assimilation efficiency and food, according to Le Borgne (1978). Carbon production rates were calculated from nitrogen and phosphorus production rates using the *C:N* or *C:P* ratios of the zooplankton constituents. Ingestion rate (*IR*) was calculated using the equation $IR = (PR + ER) / D$, where the assimilation efficiency *D* was calculated from the organic constituents of faeces and seston (Conover, 1966). Excretion and respiration rates were determined from 12 h long incubations experiments according to the methods described in Le Borgne et al. (1989) for atoll lagoons zooplankton. The resulting values were used as production to biomass, ingestion to biomass and respira-

Table I. Stocks of the different planktonic compartments integrated over the 25 m water column.

Compartments	Symbol	Stocks (mg C·m^{-2})
Cyanobacteria, assimilated to phytoplankton <1 μm	ph1	308
Picoeukaryotes, or phytoplankton from 1 to 3 μm	ph2	126
Macroalgae, or phytoplankton >3 μm	ph3	323
Protozoa < 35 μm	pz1	307
Protozoa > 35 μm	pz2	498
Metazoan zooplankton < 250 μm	mic	54
Metazoan zooplankton > 250 μm	mes	165
Heterotrophic bacteria	bac	477
Detritus (non-living carbon > 0.7 μm)	det	2789
Dissolved organic carbon (< 0.7 μm)	doc	33 400

From Sakka et al., 2001.

Table II. Flows from or between planktonic compartments, integrated over the 25 m water column.

Compartments	Flows (mg C·m^{-2}·day^{-1})
Detritus sinking	524
Net particulate primary production:	
ph1	468
ph2	97
ph3	150
Consumption:	
ph1 by pz1	130
ph2 by protozoa	53
ph3 by protozoa	145
bacteria by pz1	19
pz1 by pz2	92
Bacterial production	74
Production of DOC by phytoplankton	660
Production of mesozooplankton	263
Ingestion of mesozooplankton	1256
Respiration of mesozooplankton	435
Production of microzooplankton	72
Ingestion of microzooplankton	188
Respiration of microzooplankton	48

From Sakka et al., 2001.

tion to biomass ratios, that were applied to the biomass observed during the two diel studies. The resulting flow values are given in *table II*.

2.3. Bivalves consumption

Bivalves were integrated in the present food web model using clearance rates, retention efficiency and stock assessments acquired during the second phase of PGRN program. We decided to consider the two species of bivalves present on the long lines, i.e. not only the pearl oyster *Pinctada margaritifera*, but also the associated species *Pinctada maculata*, which densely colonizes the lines. The consumption by benthic bivalves was calculated, but not integrated in the model because of the lack of knowledge of the main benthic processes.

Bivalve populations (on the long lines or benthic) were assessed using appropriate sampling schemes. The abundance of farmed *Pinctada margaritifera* was estimated to be 2 millions (Prou et al., 1999). Assuming that the associated *Pinctada maculata* was approximately 5 times more abundant than pearl oysters, the population of this bivalve was estimated to be ca. 10 million on the farming lines (*table III*).

The stocks of natural communities of benthic bivalves were estimated by Addessi (1999) to be 635 million of *Arca ventricosa*, 53 million of *Chama iostoma* and 31 million of *Pinctada maculata*. The natural benthic population of *Pinctada margaritifera* was estimated to be 4 million (Zanini and Salvat, 2000).

The clearances rates and retention efficiency of the farmed *Pinctada margaritifera* were determined by

Table III. Data concerning the stocks and physiology of the bivalves.

Population of bivalves	Stock ($\times 10^6$)	Individual clearance rate ($L^{-1} \cdot h^{-1}$)	Retention efficiency spectrum (%)	Reference
Stocks on system culture				
Cultivated pearl oyster (*P. margaritifera*):	2			
Age-group I	0.9	$25.83\ W^{0.57}$	$100 / (1.0 + 52.2 \times 0.137^S)$	1
Age-group II	0.4	$25.83\ W^{0.57}$	$100 / (1.0 + 52.2 \times 0.137^S)$	1
Age-group III	0.4	$25.83\ W^{0.57}$	$100 / (1.0 + 52.2 \times 0.137^S)$	1
Associated trophic competitors (*P. maculata*)	10	$29.63\ W^{0.84}$	$100 / (1.2 + 124.7 \times 0.202^S)$	2
Natural stocks on bottom				
Natural pearl oyster (*P. margaritifera*)	4	$25.83\ W^{0.57}$	$100 / (1.0 + 52.2 \times 0.137^S)$	1
Other bivalves:				
Arca ventricosa	635	$3.91\ W^{0.46}$	$78.9 \times (1 - e^{-1.2\ (S - 1.05)})$	2
Pinctada maculata	31	$25.83\ W^{0.57}$	$100 / (1.2 + 124.7 \times 0.202^S)$	2
Chama iostoma	53	$7.63\ W^{0.71}$	not determined	2

A ratio of 1:10 was assumed between farmed pearl oysters and *Pinctada maculata*, on the long line systems. Because, the retention efficiency spectrum was not determined for *Chama iostoma*, that of *Pinctada margaritifera* was used, assuming that it was nearly the same. *W*: tissue dry weight (in grams), *S*: size of particles (in micrometres). References: (1) Pouvreau et al., 1999a; (2) Addessi 1999.

Pouvreau et al. (1999a, 1999b). Using the same methods, Addessi (1999) also estimated these two physiological functions for *Arca ventricosa*, *Chama iostoma* and *Pinctada maculata*. A brief review of these studies is given in *table III*. Carbon consumption (or filtration rate, *FR*, in milligrams of carbon per hour) for each of these bivalve populations, i, was calculated as follows, taking into account the different planktonic compartments, j:

$$FR_i = CR_i \times \sum_j (\ POC_j \times RE_{ij})$$

where:
– CR_i is the clearance rate (in litre per hour) for each bivalve species i, according to the medium size of individuals in each population. For the farmed *Pinctada margaritifera*, the population was divided into three age classes.
– POC_j is the particulate organic carbon biomass (in milligrams of carbon per litre) of each compartment j.
– RE_{ij} is the retention efficiency (percent) of each compartment j (taking into account its mean size) for each bivalve species i.

2.4. Food web quantification

The organic carbon stocks were aggregated into eight living and two non-living compartments, which structure the ecosystem on the basis of processes and sizes. The living compartments were: bacteria, ph1 (phytoplankton < 1 μm, i.e. autotrophic prokaryotes), ph2 (phytoplankton from 1 to 3 μm, i.e. picoeukaryotes), ph3 (phytoplankton > 3 μm, or microalgae), pz1 (protozoa < 35 μm), pz2 (protozoa > 35 μm), microzooplankton (metazoa < 250 μm) and mesozooplankton (metazoa from 250 to 2000 μm). Values of the flows between planktonic compartments were partly determined by field experiments (*table II*). The flows from planktonic compartments to the bivalves were fully

determined using the equations in *table III*. We thus obtained a partial quantification of the food web, which was completed by inverse analysis (Vézina and Platt, 1988). This numerical approach, whose algorithm is described in Vézina (1989), aims at determining the missing flow values as realistically as possible using a steady state assumption and thresholds for physiological rates. The thresholds used were the same as those determined by Vézina and Platt (1988, *table IV*). The choice of flows considered as being possible in Takapoto Lagoon is described in Niquil et al. (1998).

3. RESULTS

3.1. Characteristics of the planktonic food web

The food web model resulting from inverse analysis (*figure 2*, *table V*) represents an average state of the 25 m water column at the studied station of the lagoon.

The input of carbon into the system occurs mainly through gross planktonic primary production (1.6 gC·m^{-2}·day^{-1}). It is mainly (49%) due to the smallest phytoplankton (ph1). The remaining primary production is equally distributed between medium sized (ph2: 25%) and large (ph3: 26%) phytoplankton. The second input of organic carbon is through the consumption of carbon from benthic or terrestrial origin by mesozooplankton (659 mg C·m^{-2}·day^{-1}). This input is necessary because the estimated carbon ingestion by mesozooplankton is high (ingestion to biomass = 7.6 day^{-1}, determining a flow of 1256 mg C·m^{-2}·day^{-1}) and cannot be sustained by the sole phytoplankton production.

The output of carbon from the system involves three processes: 1) respiration of each living compartment, 2) sinking of detritus and 3) export of mesozooplankton production to non-planktonic systems (fish or benthic consumers). Among these outputs,

Table IV. List of the lower and upper bounds used as biological constraints for the inverse analysis.

Biological constraints	Lower bound	Upper bound
Respiration		
Phytoplankton	5% of gross primary production	30% of gross primary production
Protozoa	$0.064 \times B \times \exp(0.0693\ T)$	none
Microzooplankton	$0.072 \times B \times \exp(0.0693\ T)$	none
Mesozooplankton	$0.023 \times B \times \exp(0.0693\ T)$	none
Excretion		
Phytoplankton	10% of gross primary production	50% of gross primary production
Protozoa	33% of respiration	100% of respiration
Microzooplankton	33% of respiration	100% of respiration
Mesozooplankton	33% of respiration	100% of respiration
Assimilation efficiency		
Protozoa	50%	90%
Microzooplankton	50%	90%
Mesozooplankton	50%	90%
Net production efficiency		
Bacteria	10%	60%
Gross production efficiency		
Protozoa	10%	60%
Microzooplankton	10%	60%
Mesozooplankton	None	40%
Ingestion		
Protozoa	None	$5.46 \times B \times \exp(0.0693\ T)$
Dissolution		
Oxidation of detritus		1%

Modified from Vézina and Platt, 1988. B: Biomass of the considered compartment (in milligrams C per square metre). T: mean annual water temperature (28°C in Takapoto Lagoon). The lower and upper bounds are expressed as inequalities involving the concerned flow, sum of flows, or rate.
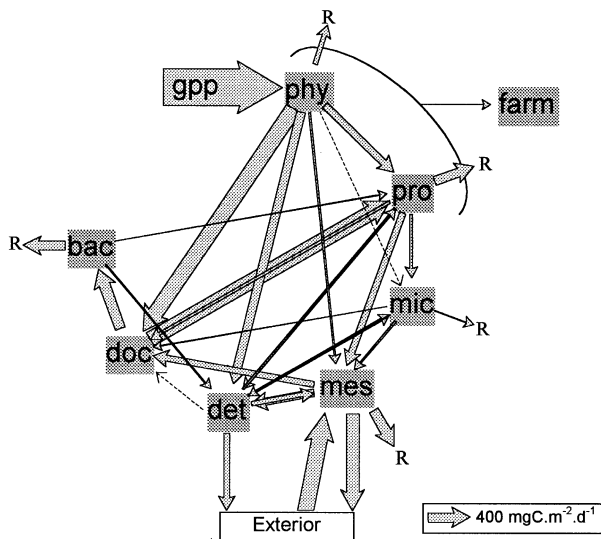
Figure 2. Graphic representation of the flows of the steady state model of the pelagic food web in the lagoon of Takapoto Atoll (numerical values are given in *table V*). Each carbon flow is represented by an arrow (the width of each arrow is proportional to the calculated value). Symbols of plankton compartments are given in *table I*; farm: farmed oysters (*Pinctada margaritifera*) and associated bivalves (*Pinctada maculata*), gpp: gross primary production; R: respiration.

the sinking process shows the highest value (524 mg C·m^{-2}·day^{-1}), followed by the respiration of mesozooplankton (435 mg C·m^{-2}·day^{-1}), and protozoa and bacteria (385 and 376 mg C·m^{-2}·day^{-1}, respectively).

The flows within the food web are dominated by three processes: 1) production of DOC by the phytoplankton (660 mg C·m^{-2}·day^{-1}), 2) DOC consumption by protozoa (612 mg C·m^{-2}·day^{-1}), and 3) phytoplankton mortality forming detritus (363 mg C·m^{-2}·day^{-1}). The grazing flows among living compartments are lower. The main grazing flows are the consumption of phytoplankton by protozoa (289 mg C·m^{-2}·day^{-1}) – especially the consumption of small phytoplankton (ph1) by small protozoa (pz1, 105 mg C·m^{-2}·day^{-1}) - and the consumption of protozoa by mesozooplankton (278 mg C·m^{-2}·day^{-1}).

The overall functioning of the planktonic food web is characterised by the fact that only 22% of the input of carbon reaches the second trophic level through a direct pathway (herbivory). The remaining carbon is driven into DOC (42%) or particulate detritus (23%), or is respired (12%).

The carbon throughput, i.e. the sum of all carbon flows entering each compartment (*table V*, last column) quantifies the role of each compartment in the processing of carbon. The mesozooplankton compartment has the highest throughput value

Table V. Steady-state model of the pelagic food web in the lagoon of Takapoto Atoll.

Input	res	los	ph1	ph2	ph3	pz1	pz2	mic	mes	bac	farm	det	doc	Total
ext	–	–	768	390	407	–	–	–	659	–	–	–	–	2224
ph1	38	–	–	–	–	105*	–	–	–	–	0.03*	363	262	768
ph2	98	–	–	–	–	19	33	0	45	–	0.03*	0	195	390
ph3	54	–	–	–	–	59	73	0	17	–	0.51*	0	204	407
pz1	147	–	–	–	–	–	78	56	147	–	0.49*	53	48	529
pz2	238	–	–	–	–	–	–	39	131	–	0.79*	54	78	541
mic	48*	–	–	–	–	–	–	–	72	–	0.09*	52	16	108
mes	435*	263*	–	–	–	–	–	–	–	–	–	299	259	1256
bac	376	–	–	–	–	19*	–	–	–	–	0.01*	55	–	450
farm	–	3.82	–	–	–	–	–	–	–	–	–	–	–	3.82
det	–	524*	–	–	–	29	43	93	185	–	1.89*	–	0	876
doc	–	–	–	–	–	299	313	–	–	450	–	–	–	1062
Total	1433	791	768	390	407	529	541	188	1256	450	3.82	876	1 062	8710

The lines refer to the origin of the flows and the columns to their fate. Cells with a – are flows that were not considered as being possible in the a priori model. The flow values (expressed in milligrams C per square metres and per day) were either determined in the field experiments (*) or calculated using inverse analysis. Symbols of plankton compartments are given in *table I*; farm: farmed oysters (*P. margaritifera*) and associated bivalves (*P. maculata*); ext: source of carbon outside the system; res: respiration; los: other outputs from the system.

(1256 mg C·m^{-2}·day^{-1}), followed by the DOC compartment (1062 mg C·m^{-2}·day^{-1}). The aggregated throughput of the two protozoa compartments has a similar value (1070 mg C·m^{-2}·day^{-1}).

3.2. Role of the farmed bivalves and associated trophic competitors

The total consumption by farmed bivalves (*Pinctada margaritifera*) and associated trophic competitors (*Pinctada maculata*) is very low (4 mg C·m^{-2}·day^{-1}), compared to the carbon flows through planktonic compartments (*table V*). In the whole lagoon, the farmed pearl oysters consumed 0.31 t C·day^{-1}. This consumption represents 0.24% of total gross planktonic primary production. The consumption flow of each compartment never exceeds 0.4% of its throughput. The total consumption by the farmed bivalves (their throughput) is equal to 5% of the throughput of mesozooplankton and 7% of the throughput of microzooplankton.

Considering that the bivalves are opportunistic and select their food on size criteria only, the main consumed compartments are particulate detritus (det, 49% of the consumed carbon), protozoa > 35 μm (pz2, 21%) and phytoplankton > 3 μm (ph3, 13%). Bacteria and the two smallest phytoplankton compartments are little used by the bivalves because of their small sizes (Pouvreau et al. 1999a), so that they account for less than 2% of the carbon consumed. Microzooplankton are consumed by bivalves, but their overall contribution is small (2%) because of their low stock (*table V*).

3.3. Comparison with benthic bivalves

The total consumption by the four benthic bivalves (65 mg C·m^{-2}·day^{-1}, *table V*), which are considered to be the main competitors of the farmed *Pinctada margaritifera*, is equal to 4% of planktonic gross primary production. Because their selection of food particles is based on the size only and we considered the 4 bivalves as being opportunistic, the most heavily consumed compartment is that of particulate detritus, representing 48% of the total carbon consumed by the four species. As for the pearl oysters, we assumed that bacteria, the two smallest phytoplankton compartments (ph1 and ph2) and microzooplankton are little consumed by bivalves.

The main competitor for the farmed pearl oyster is *Arca ventricosa*, which is responsible for 66% of the consumption by the four benthic bivalves. Its consumption represents 2.7% of gross phytoplankton production. *Arca ventricosa* mostly consumes particulate detritus. The main living compartment consumed by *Arca ventricosa* is that of the largest protozoa (pz2), with a flow corresponding to 2.4% of the throughput of pz2. The consumption of other competitors is low, i.e. 0.6% of total planktonic primary production for *Chama iostoma*, 0.5% for *Pinctada maculata*, and 0.2% for the natural *Pinctada margaritifera*.

4. DISCUSSION

4.1. Characteristics of the planktonic system and interaction with the farmed bivalves

The characteristics of the modelled planktonic food web, which concerns one sampling station and several sampling periods, will be considered to represent the entire Takapoto Lagoon because the absence of variability of the planktonic variables has been demonstrated in space (Sakka et al., 2001) and time (Charpy, 1996).

The planktonic community of Takapoto Lagoon is characterised by a high gross primary production (1.6 g C·m^{-2}·day^{-1}) in an oligotrophic environment (low nutrients concentrations). The turnover of the phytoplankton biomass is very rapid, (0.47 day). This high value is due to the high net production of both particulate carbon (715 mg C·m^{-2}·day^{-1}) and DOC (660 mg C·m^{-2}·day^{-1}). The value of net particulate production estimated by Sakka et al. (2001) is close to the previous estimate of Charpy et al. (1992, 820 mg C·m^{-2}·day^{-1}), and in the upper range of values published by Sorokin (1973) for several coral reef systems (20–720 mg·m^{-2}·day^{-1}). Phytoplankton < 1 µm, mostly cyanobacteria, account for 49% of gross primary production, i.e. slightly less than previously reported for Takapoto (60%, Charpy et al. 1992).

The non-living compartments dominate the modelled planktonic food web. This is especially true for the DOC compartment, which presents the second highest total flow of carbon (throughput), following mesozooplankton. DOC plays a larger role than in the previous published model (Niquil et al., 1998) in which the production of DOC by phytoplankton was estimated by inverse analysis, because it had not been determined in the field. When considering only particulate matter, the detritus compartment is the main stock and the total flow through it is large. The role of detritus had already been stressed by Niquil et al. (1998), leading to a high complexity of the system in which heterotrophic organisms can exploit multiple food sources (Niquil et al., 1998, 1999).

The bacterial compartment is characterised by low production, which contrasts a high carbon stock. This feature of the microbial food web in Takapoto Atoll, and more generally in Tuamotu atolls, has already been stressed by Torréton et al. (1997), who proposed the explanation of a bacterial production being bottom–up controlled, probably by P limitation. The absence of a top–down control is shown by the low grazing pressure of protozoa on bacteria (Sakka et al., 2000).

Zooplankton are dominated by mesozooplankton with a very high ingestion rate, and by the protozoa in terms of both stocks and flows. The value of the carbon stock (805 mg C·m^{-2} or 32 mg C·m^{-3}) is much higher than previous values published for coral reefs (46 mg C·m^{-2} in Tikehau Atoll, Charpy and Charpy-Roubaud, 1990; 5.7 mg C·m^{-3} in Uvea Atoll, Le Borgne et al. 1997; 7 to 13 mg C·m^{-3} in Bora Bay, Miyako Island, Ferrier-Pagès and Gattuso, 1998). The previous model published for Takapoto Lagoon (Niquil et al., 1998) found a larger role for metazoa than protozoa, but the latter had not then been investigated in the field using direct approaches.

The planktonic food web of Takapoto Lagoon is characterised by a high activity directly based on primary production, contrasting with low activity in the bacterial compartment. Protozoa processed a significant part of the carbon, mainly by consuming phytoplankton < 1 µm (cyanobacteria) and non-living matter. This carbon flows towards mesozooplankton, which actively graze the protozoa. The pattern of the planktonic food web in Takapoto Lagoon does not fit the continuum of food webs described by Legendre and Rassoulzadegan (1995), which extends from food webs dominated by the microbial loop to those based on the 'classical' herbivorous food chain. Microbes dominate the planktonic food web in Takapoto, but only through the production of cyanobacteria because the activity of the heterotrophic bacteria is low.

Quantitatively, the carbon flows from plankton to bivalves are very low, when averaged over of the entire lagoon, compared to the carbon flows within the planktonic community. The farmed bivalves have little effect on the food web, as their consumption represents low fractions of primary production and of the total carbon flow through each of their prey. Qualitatively (size classes), the role of bivalves in the food web is rather surprising, as the plankton are dominated by picoparticles that are not efficiently retained by bivalves. For *Pinctada margaritifera*, this low efficiency is partly explained by the absence on the gills of eu-latero–frontal cirri, which are known to contribute to the retention of small particles (Pouvreau et al., 1999b). It is also presumably the case for the other species of bivalves studied, but this needs to be confirmed.

4.2. Limits of the model due to methodological choices

The exchanges between the planktonic subsystem and the remainder of the ecosystem are highly simplified in our model. They are reduced to the sinking of detritus, the grazing of mesozooplankton on benthic material, and the consumption of mesozooplankton production by external predators. An overall approach to the carrying capacity of the lagoon, integrating the benthic competitors and farmed oysters into a single scheme, should take into account the coupling between benthic and pelagic processes. In order to do so, better knowledge of benthic processes would be necessary. For example, the data on benthic primary production are incomplete (Sournia and Ricard, 1976). In addition, the fish community, at least the planktonophagous species, would also need to be investigated.

The fate of the DOC compartment is not well constrained in our model. Phytoplankton produces a great amount of DOC, but this carbon cannot be used by bacteria because of their low production. This results in a very high consumption of DOC by protozoa, which is possible (Sherr, 1988), but remains to be demonstrated in the lagoon.

A last limitation of the present model concerns the calculation of the consumption of each planktonic compartment by the bivalves. Bivalves are considered to be opportunistic, selecting their food on size criteria only, but Loret et al. (2000) have shown that a taxonomic selection could also occur. However, a

different selection process would not greatly change the values of consumption estimated, and our conclusion on the carrying capacity of the lagoon discussed below remains valid.

4.3. Carrying capacity of Takapoto Lagoon

The aim of the present study was to assess the carrying capacity of the lagoon of Takapoto Atoll. The food web model integrating the farmed bivalves (*Pinctada margaritifera* and associated *Pinctada maculata*) into the pelagic system, shows their insignificant role compared to the high productivity of the planktonic system. Total consumption by the farmed bivalves is 0.24% of the gross primary production (*table VI*), which leads to rejection of the hypothesis of a risk of overstock inside the lagoon, proposed to explain the mortality event of 1985 (Charpy et al., 1997).

In order to compare the Takapoto shellfish ecosystem with other ones, we calculated the three indices described by Dame and Prins (1998): 1) the water residence time i.e. "the theoretical time it takes for the volume of water within a basin to be replaced with water from outside the system", 2) the primary production time i.e. " the ratio of averages of phytoplankton biomass to phytoplankton primary production", and 3) the clearance time i.e. "the time that is theoretically needed for the total bivalve filter feeder biomass, within an ecosystem, to filter particles from a volume of water equivalent to the total system volume". Compared to the 11 ecosystems studied by Dame and Prins (1998), the lagoon of Takapoto is characterised by the highest water residence time, the lowest primary production time and the highest farmed bivalve clearance time (*table VII*). The latter two characteristics confirm the small role of the farmed bivalves in the functioning of the system. The lagoon of Takapoto is a quite natural ecosystem, compared to some of the exploited temperate ecosystems considered by Dame and Prins (1998). When taking into account the natural benthic bivalves, the clearance time of Takapoto is reduced to 73 days, which stresses the dominance of the natural over farmed bivalves.

Table VI. Consumption on each planktonic compartment of the benthic bivalves that are potential competitors of the farmed *Pinctada margaritifera*.

Compartments	*C. iostoma*	*A. ventricosa*	Natural *P. margaritifera*	Natural *P. maculata*	Total
bac	0.06	0.00	0.02	0.00	0.08
ph1	0.12	0.00	0.04	0.04	0.20
ph2	0.12	0.49	0.04	0.04	0.69
ph3	1.24	6.20	0.44	1.18	9.06
pz1	1.18	5.89	0.42	1.12	8.61
pz2	1.91	9.55	0.69	1.82	13.97
mic	0.21	1.04	0.07	0.20	1.52
det	5.27	19.59	1.89	4.13	30.88
Total	10.11	42.76	3.61	8.53	65.01
Total for the lagoon	0.82	3.46	0.29	0.69	5.27

Values are in milligrams of carbon per square metre per day. The last line is the total value integrated over the surface of the lagoon (in tons of carbon per day). Symbols are given in *table I*.

Table VII. Turnover rates of the water mass, the phytoplankton and the seston eaten by the farmed bivalves, in Takapoto Lagoon and 11 ecosystems.

System	Water residence time	Primary production time	Bivalve clearance time	Cultivated species
North Inlet (USA)	1.0	0.82	0.7	*Crassostrea virginica*
South San Francisco Bay (USA)	11.1	1.10	0.7	Various
Marennes-Oléron (France)	7.1	10.00	2.7	*Crassostrea gigas + Mytilus edulis*
Oosterschelde (Netherlands)	40.0	3.08	3.7	*Mytilus + Cerastoderma*
Sylt (Königshafen, Germany)	0.5	0.78	4.0	*Mytilus cerastoderma*
Westen Wadden Sea (Netherlands)	10.0	0.97	5.8	*Mytilus*
Ria de Arosa (Spain)	23.0	0.63	12.4	*Mytilus edulis*
Narragansett Bay (USA)	26.0	1.68	25.0	*Mercenaria mercenaria*
Chesapeake Bay (USA)	22.0	0.94	325	*Crassostrea virginica*
Carlingford Lough (Ireland)	65.8	16.90	490.2	*Crassostrea gigas + Mytilus edulis*
Delaware Bay (USA)	97.0	7.40	1278	*Crassostrea virginica*
Takapoto Atoll Lagoon	1460	0.47	1321	*Pinctada margaritifera*

Rates are in days. The 11 ecosystems were studied by Dame and Prins (1998). For Takapoto, the bivalve clearance time was calculated for the farmed *P. margar*itifera and associated *P. maculata*.

Even if our approach provides a significant insight into the carrying capacity of the whole Takapoto Lagoon, it is not enough to assess the effects of local concentrations and possible food depletion for the farmed bivalves (Prins and Dame, 1998). Moreover, our approach did not take into account a possible modification, when increasing the stock of farmed bivalves, of inter-specific competitive relationships within the phytoplankton. Because the filtration of oysters is selective (Loret et al., 2000), it could lead to the dominance of potentially blooming species (Prins and Dame, 1998). Further studies should explore these two questions.

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