**Aquatic
Living
Resources**

Trophic model of lagoonal communities in a large open atoll (Uvea, Loyalty islands, New Caledonia)⋆

Yves-Marie Bozec[1,2,a], Didier Gascuel[1] and Michel Kulbicki[2]

[1] Département Halieutique, UPR Mesh, Ensar, 65 rue de St-Brieuc, CS 84215, 35042 Rennes Cedex, France
[2] Unité de recherche CoRéUs, Institut de recherche pour le développement (IRD), BP A5, 98848 Nouméa Cedex, New Caledonia

Abstract – A mass-balanced trophic model was developed for the coral reef lagoon of Uvea atoll (New Caledonia) using the Ecopath software. The model accounts for both pelagic and soft-bottom communities to describe the whole trophic structure and biomass flows in the shallowest part of the atoll lagoon. Phytoplankton production approximately equals the benthic primary production. Benthic biomass accounts for more than 80% of the total living biomass in the shallow lagoon. The benthic domain requires input of food from the pelagic system (mainly zooplankton) and from adjacent areas to sustain the biomass of predatory fishes. Predation pressure was found to be a major force structuring the food web, but it is also suggested that water circulation within the lagoon influences the amount of primary resources, such as plankton, benthic microphytes and detritus.

Key words: Atoll lagoon / Food web / Trophic structure / Pelagic and demersal fishes / Soft-bottom communities

Résumé – Modèle trophique des communautés lagonaires dans un atoll ouvert de grande taille (Ouvéa, îles Loyautés, Nouvelle-Calédonie). Un modèle trophique utilisant le logiciel Ecopath a été développé sur les communautés biologiques du lagon de l'atoll d'Ouvéa (Nouvelle-Calédonie). Le modèle intègre les communautés benthiques et pélagiques pour la description de la structure trophique de la zone lagonaire peu profonde de l'atoll. La production phytoplanctonique est du même ordre de grandeur que la production primaire benthique. La biomasse du domaine benthique représente 80 % de la biomasse totale de cette partie du lagon, et nécessite des apports provenant du système pélagique (principalement du zooplancton) et des habitats adjacents pour soutenir la consommation des poissons prédateurs. La prédation exerce une pression majeure sur la structure trophique, mais la circulation des eaux lagonaires est également supposée contrôler la quantité des ressources primaires, telles que le plancton, le microphytobenthos et les détritus.

1 Introduction

Coral reef ecosystems are very productive and support a high concentration of life (Odum and Odum 1955). As shown in other marine ecosystems, fishing activities may strongly affect the biological interactions between reef organisms (e.g., Hughes 1994; Roberts 1995). This challenges the understanding of the structure and dynamics of those complex ecosystems, in order to develop an ecosystem-based approach for the management of coral reef resources.

Several comprehensive studies on the trophic interactions between reef organisms have been conducted using an ecosystem modelling approach (e.g., Polovina 1984; Opitz 1993; Johnson et al. 1995; Arias-González 1997; Tudman 2001).

⋆ Appendix C is only available in electronic form at
http://www.edpsciences.org/alr

ᵃ Corresponding author: bozec@roazhon.inra.fr

Such studies have focused on the most productive zones, i.e., the hard substrate of coral reefs, whereas sandy bottoms of the reef-protected lagoons have received far less attention (Johnstone 1990; Niquil et al. 1999). In some atoll lagoons, the planktonic food web was intensively studied (Niquil et al. 1999), but comprehensive studies coupling the benthic and the pelagic systems are scarce (but see Charpy and Charpy-Roubaud 1990, 1991). Above all, fish communities are seldom included, leading to an incomplete description of the whole trophic structure of lagoonal systems.

One limitation of ecosystem-based research on coral reefs is that information is often missing for some ecological compartments. An extensive ecological survey was conducted by IRD on the reef and lagoon areas of Uvea atoll (New Caledonia) in the early 90s. This provided information for most ecological compartments of this ecosystem. The present study applies a mass-balanced trophic model to the biological

communities of the shallowest part of Uvea lagoon, using the Ecopath software (Christensen and Pauly 1992). As a first step, we focused our model on the shallow lagoon where the sampling effort was optimal. By doing so, some parameters can be calibrated and used in a future work for studying the whole ecosystem. Our model of trophic interactions aimed at (1) integrating scientific data on functional groups (both benthic and pelagic) into a cohesive framework (2) complementing current knowledge on atoll lagoons by quantifying biomass, production and consumption rates, and (3) stating hypotheses on the trophic links between the shallow lagoon and the surrounding habitats of the atoll.

2 Material and methods

2.1 Study site

Uvea is a large open atoll (872 km^2, Kulbicki 1995) located in the northern part of the Loyalty Archipelago (north east of New Caledonia). The lagoon is triangular in shape (Fig. 1) and encircled by a barrier reef topped by a set of low coral islets (the Northern and Southern Pleiades). The lagoon bottom is formed by an homogeneous fine sediment layer (Chevillon 1994) covering a fairly smooth limestone tab (Garrigue et al. 1998). Sediment thickness is generally low (averaging 5.4 cm depth) and hard substrates (limestone tab with scattered small coral patches) cover 30% of the lagoon bottom (Garrigue et al. 1998). The main island closes the lagoon in the eastern part, whereas the barrier is intersected by reef-flat spillways and passes which promote water exchanges with the surrounding ocean. A previous study of hydrological parameters (Le Borgne et al. 1993, 1997) has underlined that Uvea lagoon is highly oligotrophic with fairly homogeneous waters. The close values of temperature, salinity and nutrient inside and outside the lagoon, and the low values of biomass of phytoplankton and zooplankton indicate that water exchanges between the two environments are important (Le Borgne et al. 1997). The atoll has a well marked east-to-west slope which results in an increasing depth from the main island to Anemata pass, a wide deep pass in the western part. A fault line divides the lagoon in two parts, one on each side of the 20-m isobath: (1) a shallow lagoon on the east, protected from trade winds by the main island; (2) a deeper zone on the west, largely opened towards the ocean. The present study concerns the shallow lagoon only, which accounts for 3/4 of the whole lagoonal surface.

2.2 Basic modelling

The Ecopath modelling approach (Christensen and Pauly 1992; Christensen and Walters 2004) is based on the assumption of mass-balance, i.e. flows to and from each group of the model are balanced as follows:

$$P_i = Y_i + B_i M2_i + E_i + BA_i + B_i M0_i \qquad (1)$$

where P_i is the production rate for the group i, Y_i the total fishery catch of i, B_i the total biomass of i, $M2_i$ the mortality
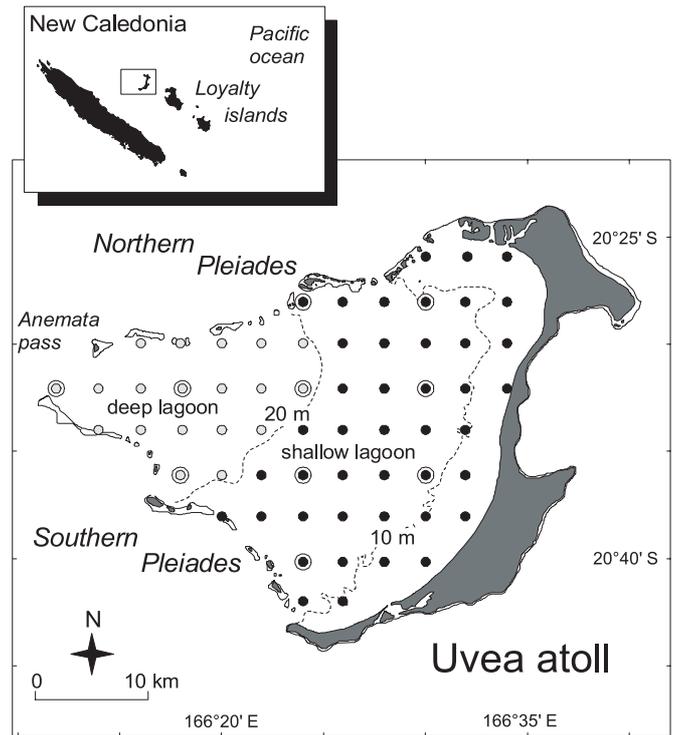
Fig. 1. Map of Uvea atoll showing the distribution of benthic sampling stations in the shallow lagoon (solid black circles, $n = 43$), delimited for the needs of the present study by the 20-m isobath. Grey circles refer to deep lagoon sampling stations, whereas doubled circles indicate stations where pelagic sampling was also conducted ($n = 6$).

rate of i by predation, E_i the net migration rate of i (emigration less immigration), BA_i the biomass accumulation rate for i, and $M0_i$ the "other mortality" rate for i. The predation mortality rate expresses the trophic link between the group i and its predators j as follows:

$$M2_i = \Sigma B_j (Q/B)_j DC_{ji}$$

where B_j is the biomass for a predator j, $(Q/B)_j$ the consumption/biomass ratio for the given predator j and DC_{ji} the contribution of i to the diet of the predator j. The "other mortality" includes all mortality not elsewhere included (e.g., natural mortality, mortality by starvation, etc.) and is internally computed from:

$$M0_i = (1 - EE_i)(P/B)_i$$

where $(P/B)_i$ is the production/biomass ratio of i and EE_i the trophic efficiency defined as the proportion of the production of i that is utilized in the system (i.e., through predation by j, fishing or migration).

The Ecopath software solves the set of Eq. (1) (one for each group i) for one of the following parameters: B, P/B, Q/B and EE. Hence, at least three of these four parameters are required as input. A second assumption is that energy balance of a group is ensured as follows:

$$Q_i = P_i + R_i + GS_i \qquad (2)$$

Table 1. Source of input data values for the Uvea shallow lagoon model. Calculations are detailed in Appendix A.

Trophic group	Biomass	P/B	Q/B
PF Large piscivores	*in situ* estimation (Kulbicki et al. 1994)	Empirical relationships (Pauly 1980)	Empirical relationships (Palomares and Pauly 1999; Froese and Pauly 2000)
PF Large planktivores			
PF Small pelagics	**Model estimation**	Polovina (1984)	Polovina (1984)
DF Sharks	Gribble 2000	Gribble (2000)	Gribble (2000)
DF Demersal fishes (8 groups)	*in situ* estimation (Kulbicki et al. 1994)	Empirical relationships (Pauly 1980)	Empirical relationships (Palomares and Pauly 1999; Froese and Pauly 2000)
Cephalopods	**Model estimation**	Opitz (1993)	Opitz (1993)
Macrobenthic invertebrates (5 groups)	*in situ* estimation (Clavier et al. 1992)	Allometric relationships (Banse and Mosher 1980)	Empirical relationships (Appendix A)
Meiofauna	*in situ* estimation (Boucher, unpubl. data)	Buat (1996)	**Model estimation**
Zooplankton	*in situ* measurements (Le Borgne et al. 1993)	Estimated from excretion (Le Borgne et al. 1993; Le Borgne 1978)	Estimated from excretion (Le Borgne et al. 1993; Le Borgne 1978)
Corals-zooxanthellae	*in situ* estimation of coral cover (Kulbicki et al. 1993) and empirical relationship (Odum and Odum 1955)	Sorokin (1993)	Sorokin (1993)
Phytoplankton	*in situ* Chl *a* concentrations (Le Borgne et al. 1993)	*in situ* experimentations (Le Borgne et al. 1993)	
Benthic macrophytes	*in situ* estimation (Clavier et al. 1992)	**Model estimation**	
Benthic microphytes	*in situ* Chl *a* concentrations (Clavier and Boucher, unpubl. data)	*in situ* measurement (Clavier, unpubl. data)	
Detritus (column)	*In situ* estimation (Le Borgne et al. 1993)		
Detritus (sediment)	*In situ* estimation (Boucher, unpubl. data)		

PF: pelagio fish; DF: demersal fish.

where R_i is the respiration of group i and GS_i is the part of consumption that is not assimilated defined as:

$$GS_i = Q_i (1 - AE_i)$$

where AE_i is the assimilation efficiency of group i.

2.3 Input data and model structure

The data were collected during cruises conducted from 1991 to 1992, except for meiofauna (Boucher, unpubl. data) and benthic primary production (Clavier, unpubl. data) assessed in 1994. The parametrization is based on an assumption of mass-balance over the 1991-92 period. Instead we mainly used as input parameters averaged values over a one-year period which is usually applied in Ecopath models.

We decided to describe the trophic structure of Uvea shallow lagoon through 25 trophic groups (Fig. 4), based on taxonomic criteria, trophic role, size and quality of field data. We thus defined two detrital compartments (in the sediment and water column), and the following 23 living groups (Table 1): pelagic fishes (3 groups), demersal fishes (8 groups), cephalopods (mainly squids), macrobenthic invertebrates (5 groups), meiofauna, zooplankton, corals,

phytoplankton, benthic macrophytes and benthic microphytes. Values of group biomass were estimated from in situ observations, except for two groups (cephalopods and small pelagics). Production and consumption were derived from empirical relationships or from various sources (Table 1). All calculations for the estimation of input values are listed and detailed in Appendix A.

2.4 Strategy for model balancing

The first Ecopath Eq. (1) states that each group must be mass-balanced, i.e., catches, consumption, biomass accumulation and export do not exceed production for a group. Therefore, balancing the model requires to adjust the input parameters in a manner that *EE* do not exceed 1. This manual procedure relies on knowledge to decide which adjustments have to be done (Kavanagh et al. 2004), and must be rigorously applied according to realistic hypotheses. If *EE* is less than 1 for a group, this indicates an excess of biomass at the end of the considered period (one year in our case), that may accumulate in the system, migrate out the system, or be lost by other mortality. For the present model, we stated that no accumulation of biomass may occur during one year for any

groups: although fluxes of water coming into the lagoon are unknown, the water circulation is expected to export living or detrital matter out of the lagoon. Therefore, a group with a low *EE* was expected to lose biomass through the water fluxes passing over the lagoon.

We apply the following strategy to achieve mass-balance for all groups. First, adjustments of diets were privileged since feeding habits of some organisms are highly labile and mainly depend on food sources that are available in the ecosystem. In a second step, we gave preference to the adjustments of parameters that were not estimated in the field. Finally, if necessary, we included a term of imported food in the diet of a given group, indicating that this group consumes preys that are not part of the defined system.

3 Results

3.1 Balancing the model

The first attempt in balancing the Uvea shallow lagoon model revealed that demand from fish predators exceeded the production of most prey groups (small demersal fish and macrobenthic invertebrates). Therefore, a general bottom-up approach was applied to adjust diets in order to relieve predation pressure on these groups. As a result, predation by large pelagic piscivorous fishes was displaced towards cephalopods and small pelagics. During the balancing process, there was a danger of placing an overly predator demand on these two pelagic groups for which biomass is poorly known. Therefore, biomass estimates for these two pelagic groups were cautiously examined during each iteration of the balancing process.

Since the demand remained too strong on benthic invertebrates, we assumed that *P/B* for these groups were too low, and therefore values were enhanced (approximately 70%) to be equivalent to those of other models (Arias-Gonzalez 1997; Tudman 2001). This also allowed to relieve predation on cephalopods and consecutively small pelagics (since small pelagics account for 35% of cephalopods diet), and therefore to estimate realistic biomass values, in comparison with other models of coral reef ecosystems (Table 2).

Finally, it was necessary to force predator fish to feed on imported food in order to relieve the demand on their preys. This operation was justified since these fish are highly mobile species with large home ranges. In our case, the import term indicates that a proportion of fishes censused in the shallow lagoon did not necessarily feed on autochthonous food sources, but may have obtained part of their food from the surrounding areas. Moreover, the spatial distribution of fish biomass over the shallow lagoon clearly shows that some groups are more abundant at the boundaries of the modelled area (Figs. 2a,c,d). This coincides with the proximity of richer areas in terms of biomass, i.e., the inner reefs and the deep lagoon (see also Kulbicki et al. 1994).

Ecotrophic efficiency of benthic microphytes was very low. We decided to increase *P/B* of meiofauna (+30%) for balancing the benthic microphytes group, considering that a non negligible part of meiofauna was constituted of ciliates which *P/B* is largely higher than those from nematods and benthic

Table 2. Comparison between estimated parameters of the Uvea shallow lagoon model and other Ecopath models of coral reef ecosystems.

Group	Parameter	Value	Reference
Small pelagic fish	*B*	11.0	*Present study*
	(t km^{-2})	30.0	Opitz (1993)
		3.1	Gribble (2000)
Cephalopods	*B*	2.2	*Present study*
	(t km^{-2})	8.0	Opitz (1993)
		0.7	Aliño et al. (1993)
		0.3	Gribble (2000)
		1.9	Tudman (2001)
Benthic macrophytes	*P/B*	30.6	*Present study*
	(y^{-1})	13.3	Opitz (1993)
		25	Tudman (2001)
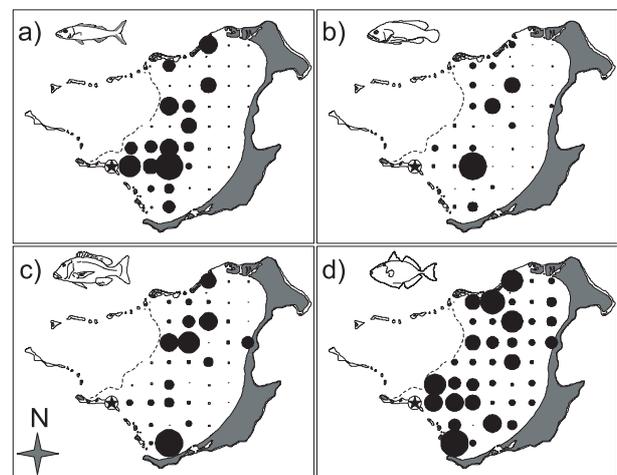
Fig. 2. Spatial distribution of fish biomass on the sampling stations (closed circles). The size of closed circles is proportional to the biomass of the following fish groups: (a) large pelagic piscivores, (b) demersal piscivores, (c) large demersal carnivores, (d) small demersal carnivores. The circled star indicates the sampling station which was removed from the calculation of the mean biomass (excessive biomass for most fish groups, see Appendix A).

copepods (Buat 1996). *P/B* estimate for benthic macrophytes was in the range of other models (Table 2).

Table 3 summarizes the input values and the output estimates for the final balanced iteration, and the final diet matrix is presented in Appendix B. All adjustments of input values had limited impact on the global distribution of biomass along the fractional trophic levels estimated by Ecopath (Fig. 3). Since the estimation of trophic levels do not account for the import terms, they had no impact on the whole trophic structure.

3.2 The trophic structure of Uvea shallow lagoon

Considering the low mean depth of the defined system (14 m), pelagic and benthic domains are very closely interrelated in the shallow lagoon. Although they can not be clearly separated, several insights on their trophic structure and

Table 3. Input and calculated (in bold) parameters for the Ecopath model of Uvea shallow lagoon.

Group name	Catch	Troph	B	P/B	Q/B	EE	P/Q	(1–AE)	P/R	R/B	Flow to detritus
PF Large piscivores	0.006	4.0	0.33	0.48	4.71	**0.969**	**0.10**	0.20	**0.15**	**3.3**	**0.3**
PF Large planktivores		2.9	0.41	0.93	8.80	**1.000**	**0.11**	0.20	**0.15**	**6.1**	**0.7**
PF Small pelagics		2.9	**1.14**	1.10	7.50	0.950	**0.15**	0.20	**0.22**	**4.9**	**1.8**
DF Sharks	0.026	4.2	0.07	0.24	4.90	**0.000**	**0.05**	0.20	**0.07**	**3.7**	**0.1**
DF Piscivores	0.006	3.6	0.34	0.39	3.99	**0.965**	**0.10**	0.20	**0.14**	**2.8**	**0.3**
DF Large carnivores	0.001	3.3	0.67	0.47	5.24	**0.999**	**0.09**	0.20	**0.13**	**3.7**	**0.7**
DF Small carnivores		3.1	0.17	1.15	9.96	**0.992**	**0.12**	0.20	**0.17**	**6.8**	**0.3**
DF Small planktivores		2.9	1.02	1.35	10.72	**0.971**	**0.13**	0.20	**0.19**	**7.2**	**2.2**
DF Large herbivores		2.0	0.41	0.68	20.42	**0.999**	**0.03**	0.35	**0.05**	**12.6**	**2.9**
DF Small herbivores		2.1	0.05	1.91	29.63	**0.969**	**0.06**	0.35	**0.11**	**17.4**	**0.5**
DF Omnivores		2.4	0.03	1.33	16.30	**0.972**	**0.08**	0.20	**0.11**	**11.7**	**0.1**
Cephalopods		3.5	**0.22**	3.10	11.70	0.950	**0.27**	0.20	**0.50**	**6.3**	**0.6**
Inv 1 carnivores		2.4	0.40	3.00	7.92	**0.992**	**0.38**	0.20	**0.90**	**3.3**	**0.6**
Inv 2 herbivores		2.0	0.04	2.30	9.42	**0.960**	**0.24**	0.40	**0.69**	**3.4**	**0.2**
Inv 3 filter-feeders		2.1	0.27	2.30	7.51	**0.998**	**0.31**	0.20	**0.62**	**3.7**	**0.4**
Inv 4 deposit-swallowers		2.1	0.08	0.86	5.57	**0.917**	**0.15**	0.30	**0.28**	**3.0**	**0.1**
Inv 5 surface deposit-feeders		2.2	0.42	2.30	7.06	**0.998**	**0.33**	0.30	**0.87**	**2.6**	**0.9**
Meiofauna	-	2.1	0.84	20.00	**153.29**	0.950	**0.13**	0.80	**1.88**	**10.7**	**104.0**
Zooplankton	-	2.0	0.08	416.10	1178.90	**0.638**	**0.35**	0.30	**1.02**	**409.1**	**42.4**
Corals/zooxanthellae	-	1.4	1.47	1.10	7.30	**0.492**	**0.15**	0.20	**0.17**	**6.5**	**3.0**
Phytoplankton	-	1.0	0.25	511.00		**0.563**	-	-	-	-	**55.3**
Benthic macrophytes	-	1.0	0.35	**30.61**		0.950	-	-	-	-	**0.5**
Benthic microphytes	-	1.0	4.24	29.87		**0.527**	-	-	-	-	**60.1**
Detritus (water column)	-	1.0	0.85	-	-	**0.358**	-	-	-	-	**68.2**
Detritus (sediment)	-	1.0	431.00	-	-	**0.229**	-	-	-	-	-

PF: pelagic fish; DF: demersal fish; Inv: benthic macroinvertebrates. Organisms assigned to the pelagic domain are in italics. Catch and flow to detritus are in g C m^{-2} y^{-1}, biomass (B) in g C m^{-2}, P/B, Q/B, and R/B (respiration/biomass) in y^{-1}, Troph (trophic level), EE (ecotrophic efficiency), AE (assimilation efficiency) and P/R (production/respiration) are dimensionless.
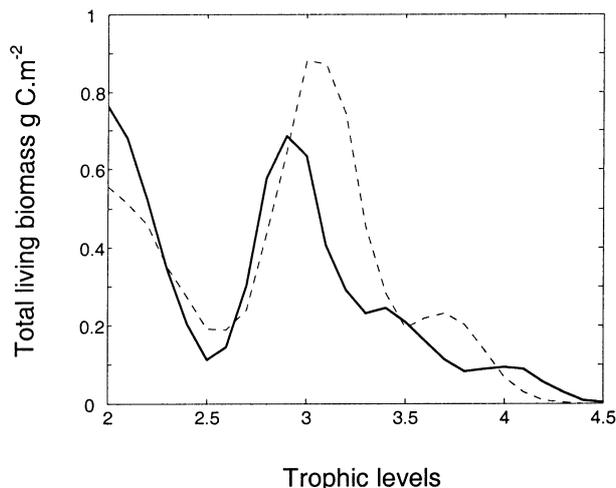
Fig. 3. Trophic spectra of the living biomass in Uvea shallow lagoon. The present trophic spectra are plots of the total living biomass along a continuous scale of trophic levels (see also Gascuel 2004; Bozec et al., in press). Such distributions reflect the diets adjustments from the first unbalanced run (dotted line) to the final balanced run (continuous line).

functioning can be summarized from the modelled trophic network (Fig. 4).

Benthic trophic groups account for more than 80% of the total living biomass in our model (Table 4). Total production is of a similar order of magnitude in the two domains, primary production accounting for 77% and 86% of total production of the pelagic and the benthic systems respectively.

Inversely, total consumption is higher in the benthic domain. Meiofauna has the greatest food intake (73% of the total benthic consumption), whereas zooplankton accounts for 86% of food intake in the pelagic system. The total benthic consumption exceeds benthic production and needs input food sources. Hence, 11% of the total benthic consumption is based upon food intake of zooplankton and water column detritus (for consumption by small demersal planktivorous fish and corals), while 4% of the consumption of demersal fishes concerns food imported from adjacent systems. Imported food accounts for 20% of total food intake of pelagic fishes and cephalopods.

As a result, the value of 3.1 calculated for the total net primary production/respiration ratio is very high. The very low assimilation efficiency ($AE = 0.2$) we imposed to meiofauna may explain this value. Since meiofauna respiration accounts for 40% of the total system respiration, the total NPP/R is very sensitive to variations in the assimilation efficiency of the meiofauna (Fig. 5).

Biomass of demersal and pelagic fishes accounts for 25% and 77% of the total biomass in their respective domain. Planktivorous fish dominate the total fish stock, estimated as 22 800 tons of fresh weight for the shallow lagoon area. Catches are low, representing less than 1% of the total fish biomass, and 2.7% of the targeted fish groups. Fish were dominated by zooplankton feeders, even when the estimated biomass of small pelagics is excluded.

The ecotrophic efficiency for some groups remains fairly low (Table 3). These groups are phytoplankton and zooplankton, benthic microphytes and corals. This may be explained by other mortality (e.g., by starvation) or export rates since we assumed that no biomass accumulation should occur in the lagoon.

4 Discussion

4.1 Model assumptions

The present study of the shallow lagoon of Uvea benefited from a large amount of data on its biological communities. The identification of the main unknown parameters arises from the mass-balanced modelling process. Balancing an Ecopath model relies on an iterative process involving manual implementations that need to be rigorously conducted. Each step of this process must be based on ecological hypotheses that are realistic. For this reason, the balancing process can be viewed as a fertile explanatory phase where ecological hypotheses are formulated in the confrontation of local knowledge and model constraints.

The model of Uvea shallow lagoon was built following an empirical but logical process. This lead to a coherent description of the food web that might be considered as the most acceptable according to our intimate knowledge in this field. The most critical point was the optimisation of realistic biomass estimates and predation demand for the two unknown stocks (i.e., cephalopods and small pelagics). The resulting food web is a possible picture of the trophic structure of Uvea shallow lagoon assuming the adjustments listed above. The solution presented here involves food imports as a minimum, since exchanges of transient species can not be formally estimated.

One limitation of the model is the probable underestimation of the microphytobenthic production, which was estimated from short-term measures whereas seasonal variations are supposed to be very high (Clavier, comm. pers.). In addition, microbial loops were neglected, as the model mainly intended to describe trophic interactions between the lagoonal fishes and their preys. However, we can reasonably assume that adding such detailed information will not modify the whole picture of this fish-oriented food web.

Concerning the high the total NPP/R ratio, it must be noticed that if the default value of 0.2 proposed by Ecopath for ($1-AE$) is applied for all groups (which is unrealistic), NPP/R reaches a value of 1.2 thus approaching more usual values observed in the field (Kinsey 1985). Since information on input value for ($1-AE$) is often missing in the published models, we decided to keep our value of 0.8 for meiofauna as recommended in the literature (Buat 1996).

4.2 Trophic functioning of Uvea shallow lagoon

The model provided valuable insights on the trophic structure in biomass, and allowed to state some hypotheses for the main structuring forces of the lagoonal food web.

Table 4. Summary statistics for the Uvea shallow lagoon model.

Parameter	Total	Pelagic	Benthic	Units
Total living biomass	13.3	2.4	10.9	g C m^{-2}
Total net primary production (NPP)	265.3	126.7	138.6	g C m^{-2} y^{-1}
Sum of all production (P)	325.4	164.2	161.3	g C m^{-2} y^{-1}
Sum of all consumption (Q)	292.1	115.3	176.8	g C m^{-2} y^{-1}
Sum of all respiratory flows (R)	85.9	44.9	41.0	g C m^{-2} y^{-1}
Sum of all flows into detritus	346.1	101.1	245.0	g C m^{-2} y^{-1}
Sum of all exports	185.0			g C m^{-2} y^{-1}
Total primary production / total respiration (NPP/R)	3.1	2.8	3.4	
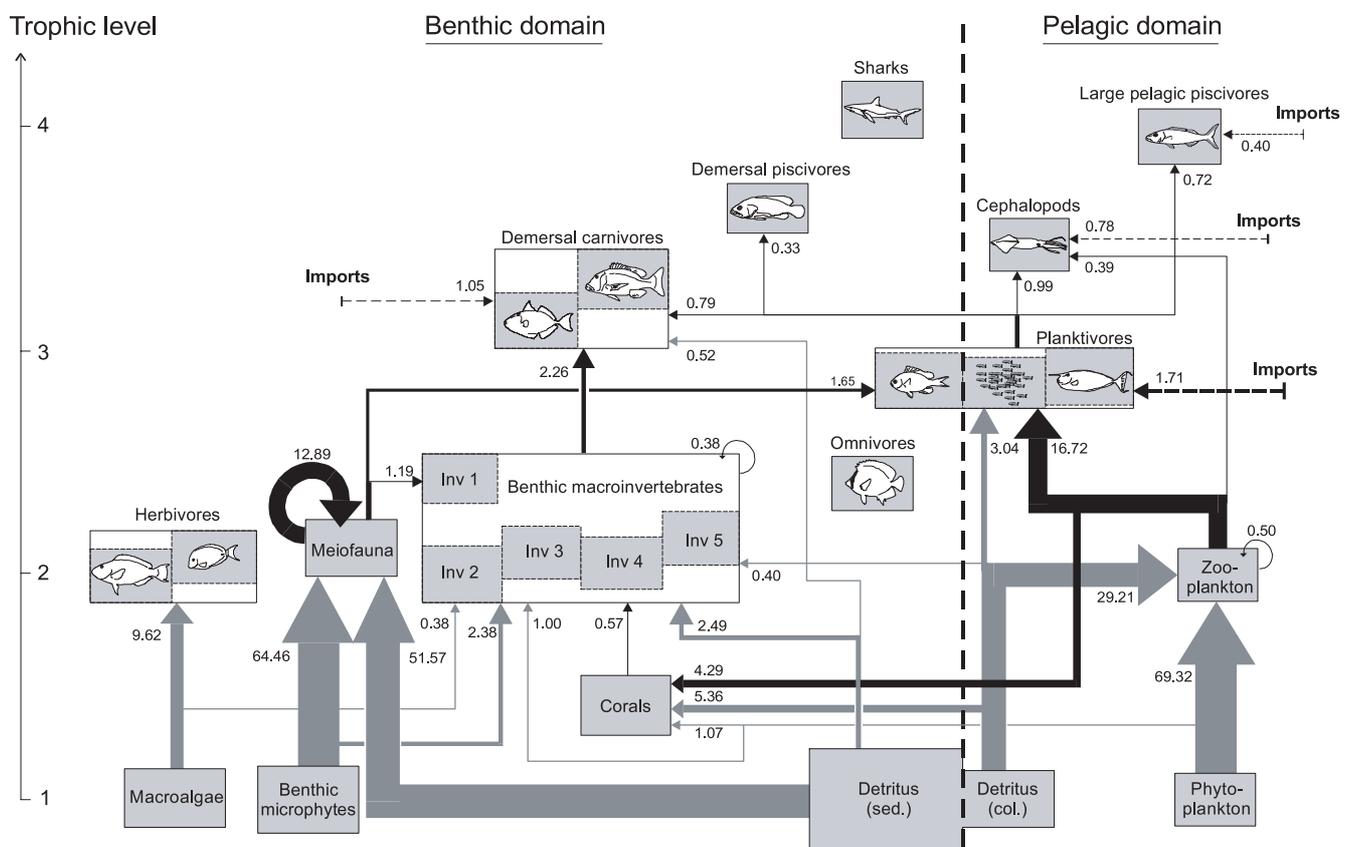
Fig. 4. Food web diagram of the Uvea shallow lagoon model. The following trophic groups were aggregated to facilitate readability: macroinvertebrates (5 groups), herbivorous fish (2 groups) planktivorous fish (3 groups) and carnivorous fish (2 groups). Box size is proportional to biomass for a given group. Main consumption flows (99% of the total food intake) from primary producer (grey arrows) and consumers (black arrows) are indicated in g C m^{-2} y^{-1}.

Firstly, there is apparently a strong predation pressure on all benthic compartments, since balancing preys of fish predators was difficult to achieve unless a fine food partitioning, independently of primary producers and detritus that were not limited. Hence, predation exerts a major structuring force on the subjacent compartments, independently from a bottom control of primary resources. The model also showed that migration due to water circulation can be integrated in the mass-balance process. Uvea lagoon is largely opened to oceanic waters, and the water flow passing over the lagoon may export phytoplankton and zooplankton biomass. Same reasoning may apply for benthic microphytes and detritus in the sediment, assuming that the high hydrodynamical conditions may induce resuspension for both living and detrital particles, and exportation towards the open ocean. The fact that part of the biomass may be exported from the system without transgressing the assumption of mass balance suggests that the model is quite realistic. Moreover, this may explain why primary resources
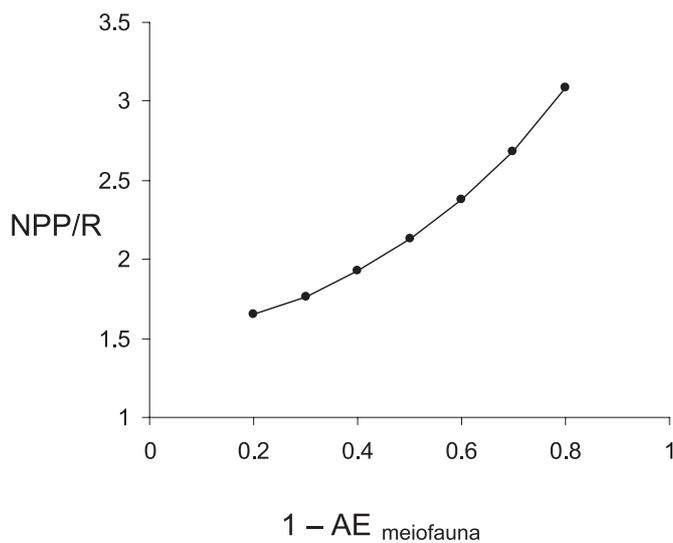
Fig. 5. Influence of variations in meiofauna assimilation efficiency (*AE*) on the estimation of the net primary production/biomass ratio (NPP/R) for the shallow lagoon.

were viewed as non limiting for consumers. Finally, the model provided a first estimation of the trophic fluxes between the shallow lagoon and its surrounding habitats. These preliminary estimates call for further investigations in adjacent areas in order to substantiate trophic interactions at a larger scale.

References

Alino P.M., McManus L.T., McManus J.W., Nanola C.L. Jr., Fortes M.D., Trono G.C. Jr. Jacinto G.S., 1993, Initial parameter estimations of a coral reef flat ecosystem in Bolinao, Pangasinan, northwestern Philippines. In: Christensen V., Pauly D. (eds.), Trophic models in aquatic ecosystems. Manila, Philippines, ICLARM 26, 252-258.

Arias-Gonzalez J.E., Delesalle B., Salvat B., Galzin R., 1997, Trophic Functioning of the Tiahura Reef Sector, Moorea Island, French Polynesia. Coral Reefs 16, 231-246.

Banse K., Mosher S., 1980, Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50, 355-379.

Bozec Y.-M., Ferraris J., Gascuel D., Kulbicki M., 2004, The trophic structure of coral reef fish assemblages: "trophic spectrum" as indicator of human disturbances. J. Recherche Océanogr, in press.

Buat P., 1996, Importance et rôle de la méiofaune dans le cycle de la matière et de l'énergie des lagons d'atoll. Thèse dr 3e cycle. Université Française du Pacifique.

Buckland S.T., Anderson D.R., Burnham K.P., Laake J.L., 1993, Distance sampling. Estimating abundance of biological populations. Chapman & Hall, London.

Charpy L., Blanchot J., 1998, Photosynthetic picoplankton in French Polynesian atoll lagoons: estimation of taxa contribution to biomass and production by flow cytometry. Mar. Ecol. Prog. Ser. 162, 57-70.

Charpy L., Charpy-Roubaud C., 1990, Trophic structure and productividy of the lagoonal communities of Tikehau Atoll (Tuamotu Archipelago, French Polynesia). Hydrobiologia 207, 43-52.

Charpy L, Charpy-Roubaud C.J., 1991, Particulate Organic Matter fluxes in a Tuamotu atoll lagoon (French Polynesia). Mar. Ecol. Progr. Ser. 71, 53-63.

Chevillon C., 1994, Sédiments récents du lagon d'Ouvéa. Évaluation des ressources en poissons du lagon d'Ouvéa : 2e partie. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM.

Christensen V., Pauly D., 1992, Ecopath II - A software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169-185.

Christensen V., Walters C.J., 2004, Ecopath with Ecosim: methods, capabilities and limitations, Ecol. Model. 172, 109-139.

Clavier J., Garrigue C., 1993, Étude du benthos de l'atoll d'Ouvéa. Évaluation des ressources en poissons du lagon d'Ouvéa : 1re partie. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM.

Clavier J., Garrigue C., 1999, Annual sediment primary production and respiration in a large coral reef lagoon (SW New Caledonia). Mar. Ecol. Prog. Ser. 191, 79-89.

Clavier J., Garrigue C., Bargibant G., Du Matteo A., Hamel P., Kulbicki M., Urbain R., 1992, Étude quantitative du benthos dans le lagon d'Ouvéa : liste taxonomique, densités et biomasses du macrobenthos, ATP, pigments photosynthétiques et matière organique dans le sédiment. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM 64.

Crisp D.J., 1971, Energy Flow Measurements. In: Holme & McIntyre, Methods for the Study of Marine Benthos.

Froese R., Pauly D., 2000, FishBase 2000: Concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines.

Garrigue C., Clavier J., Chevillon C., 1998, Investigations on the soft bottom benthos in a southwest Pacific Atoll lagoon (Uvea, New Caledonia). Atoll. Res. Bull. 450-458.

Gascuel D., 2004, Cinquante ans d'évolution des captures et biomasses dans l'Atlantique Centre-Est : analyse par les spectres trophiques de captures et de biomasses. In: Chavance P. et al. (eds.), Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest : un demi-siècle de changement. Actes du symposium Dakar (Senegal), Luxembourg, Office des publications officielles des comm. européennes.

Gribble N.A., 2000, A Model of the Ecosystem and Associated Penaeid Prawn Community, in the Far Northern Great Barrier Reef. In: Wolanski, E. (ed.), Oceanographic Process and Coral Reefs, Physical and Biological Links in the Great Barrier Reef. CRC Press, New York, pp. 189-207.

Hiatt R.W., Strasburg D.W., 1960, Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30, 65-127.

Hobson E.S., 1974, Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72, 915-1031.

Hughes T.P., 1994, Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547-1551.

Johnson C.R., Klumpp D., Field J., Bradbury R., 1995, Carbon flux on coral reefs: effects of large shifts in community structure. Mar. Ecol. Prog. Ser. 126, 123-143.

Jorgensen S.E., Nielsen S.N., Jorgensen L.A., 1991, Handbook of Ecological Parameters and Ecotoxicology. Pergamon Press, Amsterdam.

Kavanagh P., Newlands N., Christensen V., Pauly D., 2004, Automated parameter optimization for Ecopath ecosystem models. Ecol. Model. 172, 141-149.

Kinsey D.W., 1985, Metabolism, calcification and carbon production I. Systems level studies. In: Gabrie C., Salvat B. (eds.), Proc. 5th Int. Coral Reef Congress, Tahiti, 4, pp. 505-526.

Klumpp D., Polunin N., 1989, Partioning among grazers of food resources within damselfish territories on a coral reef. J. Exp. Mar. Ecol. Biol. 125, 145-169.

Kulbicki M., 1995, Estimating demersal lagoonal fish stock in Ouvea, an atoll of New Caledonia. In: Dalzell P., Adams T.J.H. (eds.), South Pacific Commission and Forum Fisheries Agency Workshop on the Management of South Pacific Inshore Fisheries, Noumea (New Caledonia). 12, 259-285.

Kulbicki, M., Barbigant, G., Menou, J.L., Mou Tham, G., 1993, Répartition du mégabenthos dans le lagon d'Ouvéa. 1re partie. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM.

Kulbicki M., Bargibant G., Menou J.L., Mou Tham G., Thollot P., Wantiez L., Williams J., 1994, Évaluation des ressources en poissons du lagon d'Ouvéa. 3e partie: les poissons. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM.

Kulbicki M., Mou Tham G., Thollot P., Wantiez. L., 1993, Length-weight relationships of fish from the lagoon of New Caledonia. Naga, ICLARM Q 16, 26-29.

Le Borgne R., 1978, Évaluation de la production secondaire planctonique en milieu océanique par la méthode des rapports C/N/P. Oceanol. Acta 1, 107-118.

Le Borgne R., Le Bouteiller A., Rodier M., Garrigue C., Richer de Forges B., 1993, Etude de l'hydrologie et du plancton du lagon d'Ouvéa (Iles Loyauté) en septembre 1992, observations sur la macrofaune benthique. Évaluation des ressources en poissons du lagon d'Ouvéa : 1re partie. Conv. Sci. Mer Biol. Mar. Nouméa, ORSTOM.

Le Borgne R., Rodier M., Le Bouteiller A., Kulbicki M., 1997, Plankton biomass and production in an open atoll lagoon: Uvea, New Caledonia. J. Exp. Mar. Biol. Ecol. 212, 187-210.

Léopold M., 2000, Évaluation de la production halieutique par la consommation en milieu insulaire – l'exemple d'Ouvéa dans le Pacifique sud. Rapp. ENSA Rennes.

Letourneur Y., Kulbicki M., Labrosse P., 1998, Length-weight relationships of fishes from coral reefs and lagoons of New Caledonia - an update. Naga 21, 39-46.

Niquil N., Arias-Gonzalez J.E., Delesalle B., Ulanowicz R.E., 1999, Characterization of the Planktonic Food Web of Takapoto Atoll Lagoon, Using Network Analysis. Oecologia 118, 232-241.

Odum H.T., Odum E.P., 1955, Trophic structure and productivity of a windward coral reef community on Enewetok atoll. Ecol. Monogr. 25, 291-320.

Opitz S., M.P., 1993, International Cent. for Living Aquatic Resources Management. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. In: Trophic models in aquatic ecosystems, Christensen, V., Pauly, D. (eds.), Manila, Philippines, ICLARM 26, pp. 259-267.

Palomares M.L.D., Pauly D., 1999, Predicting the food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar. Freshwater Res. 49, 447-453.

Pauly D., 1980, On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM 39, 175-192

Polovina J.J., 1984, Model of a coral reef ecosystem. I. The Ecopath model and its application to French Frigate Shoals. Coral Reefs 3, 1-11.

Roberts C.M., 1995, Effects of fishing on the ecosystem structure of coral reefs. Conserv. Biol. 9, 988-995.

Sano M., Shimizu M., Nose Y., 1984, Food habits of teleostean reef fishes in Okinawa Island, southern Jpn. University of Tokyo Press. Tokyo.

Sorokin Y.I., 1981, Aspects of the biomass, feeding and metabolism of common corals of the Great Barrier Reef, Australia. Proc. 4th Int. Coral Reef Symp. 2, 27-32.

Sorokin Y.I., 1990, Aspects of trophic relations, productivity and energy balance in coral-reef ecosystems. - In: Dubinsky, Z. (ed.), Ecosystems of the World - Coral Reefs. Elsevier Science Publishers, New York, pp. 401-410.

Sorokin Y.I., 1993, Coral reef ecology. Springer-Verlag, Berlin.

Steele J.H., 1974, The structure of marine ecosystems. Blackwell Scientific Publication, Oxford.

Tudman P.D., 2001, Modelling the trophic effects of fishing on a midshelf coral reef of the central Great Barrier Reef, James Cook University.

Waters T.F., 1977, Secondary production in inland waters. Adv. Ecol. Res. 10, 91-64.

Appendix A.   Source and calculations for the original input parameters

A.1.   Fish

Fish were surveyed by underwater visual census (UVC) from April 1991 to March 1992 by Kulbicki et al. (1994) on the 43 sampling stations of the shallow lagoon (Fig. 1). Two experienced SCUBA divers swam each on one side of a 100 m transect line, and counted simultaneously all fish species. Fish were individually recorded, along with body size and perpendicular distance between the fish and the transect line. Species abundance was therefore estimated from distance data following the distance sampling theory (Buckland et al. 1993). Estimates of fish size were converted into biomass using species length-weight relationships available from earlier studies in Caledonian lagoons (Kulbicki et al. 1993; Letourneur et al. 1998).

As a result, 217 fish species were identified on soft-bottoms by underwater visual census (Kulbicki et al. 1994). Fish were classified into 11 trophic groups according to feeding habits, size, and vertical position in the water column (presently defined as pelagic or demersal). Hence pelagic fish groups consist in: "large pelagic piscivores" (mainly *Aprion virescens*), "large pelagic planktivores" (body size >20 cm, mainly *Pterocaesio tile* and *Naso annulatus*), and "small pelagics" including small surface pelagic species not surveyed by underwater visual census. Demersal fish groups include: "sharks", "demersal piscivores" (26 species, including large Serranidae such as *Epinephelus cyanopodus*, large Lutjanidae and Synodontidae), "large demersal carnivores" (32 species with body size >20 cm), "small demersal carnivores" (63 species), "small planktivores" (30 species), "large herbivores" (body size >20 cm, mainly Scaridae and large Acanthuridae), "small herbivores" (16 species) and "omnivores" (17 species). Biomass of the small pelagic fish was estimated by the model, assuming an ecotrophic efficiency of 0.950. We assumed the biomass of sharks to be 0.071 g C m^{-2}

(Gribble 2000) since they are probably underestimated by the visual censuses. For all other fish groups, the biomass was estimated as a mean on 42 sampling stations, excluding one station close to the inner reefs (Fig. 2) where the total biomass was so high to be considered as realistic for lagoonal areas. Biomass values were converted to carbon assuming that dry weight is 32% of fresh weight and carbon is 40% of dry weight (Klumpp and Polunin 1989).

Annual productivity (P/B) and consumption rate (Q/B) were estimated for each species using the user interface of the FishBase (Froese and Pauly 2000) database from the following empirical relationships:

$$P/B = K^{0.65} L_{inf}^{-0.279} T^{0.463} \quad \text{(Pauly 1980)}$$

where K is the growth coefficient of the von Bertalanffy growth function, L_{inf} the asymptotic length and T the water temperature (°C), assuming that fishing mortality is null (P/B = natural mortality for unfished populations). When no estimates of K were available, instantaneous rate of natural mortality was calculated using an unpublished empirical relationship (Froese and Pauly 2000):

$$P/B = 10^{(0.566-0.718 \log L_{inf})} + 0.02T.$$

The user interface of FishBase allowed to re-estimate P/B for each species by entering regional values when available. P/B were therefore recalculated using the mean annual temperature of the south-west lagoon of New Caledonia (24.3 °C, Clavier and Garrigue 1999).

The annual consumption (Q/B) is estimated for each species from the empirical relationship of Palomares and Pauly (1999):

$$\log Q/B = 7.964 - 0.204 \log W_{inf} - 1.965T'$$
$$+ 0.083A + 0.532h + 0.398d$$

where W_{inf} is the asymptotic weight calculated from L_{inf} and length-weight relationships, T' is the water temperature (expressed as $1000 / (T + 273.15)$), A the ratio of the square of the height of the caudal fin and its surface area (aspect ratio of the caudal fin is expected to be indicative of metabolic activity), and where h and d are dummy variables indicating the feeding category of the fish species, i.e. herbivore ($h = 1$, $d = 0$), detritivore ($h = 0$, $d = 1$) or carnivore ($h = 0$, $d = 0$). Similarly to P/B, each Q/B was recalculated using the appropriate temperature. P/B and Q/B for sharks were assumed to be 0.24 and 4.9 respectively (Gribble 2000) and for the small pelagics 1.1 and 7.5 (Polovina 1984).

Diet composition was completed using dietary data from New Caledonia (Kulbicki, unpubl. data) or stomach content analysis found in the literature (e.g., Hiatt and Strasburg 1960; Hobson 1974; Sano et al. 1984). Small pelagics were assumed to be mainly zooplankton feeders. A rough annual catch ($g\,C\,m^{-2}\,y^{-1}$) was indirectly estimated from local consumption of food fishes assessed ten years after fish surveys (Léopold 2000). The following values were estimated for the shallow lagoon: 0.006 for large pelagic fishes, 0.026 for demersal piscivores, 0.006 for large demersal carnivores and 0.001 for small demersal carnivores.

A.2. Cephalopods

Biomass of cephalopods (assumed to be mainly squids) was estimated by Ecopath under the constraint of mass-balance, assuming an ecotrophic efficiency of 0.950. Input values for P/B (3.10 y^{-1}) and Q/B (11.7 y^{-1}) were taken from Opitz (1993).

A.3. Benthic macrofauna

In 1991 soft-bottom macrofauna (2 to 20 mm) was investigated using 10 grab samples per sampling station, whereas epibenthic megafauna (> 20 mm) was collected by SCUBA divers along a 50×2-m belt transect (Clavier et al. 1992; Clavier and Garrigue 1993). Density (number of individuals per m^2) and ash free dry weight were measured for 319 taxons on the 43 sampling stations of the shallow lagoon (Fig. 1). Species were classified into five trophic groups following Clavier and Garrigue (1993). For each group, the mean biomass ($n = 43$) was converted to carbon assuming that carbon is 40% of ash free dry weight (Steele 1974).

Input values for P/B and Q/B were calculated using a series of allometric relationships (see also Riddle et al. 1990). In a first step, a P/B value was estimated for each species using a direct allometric relationship between P/B and the individual body weight (Banse and Mosher 1980):

$$P/B = 0.6457 W_c^{-0.37}$$

where W_c is the individual body weight expressed in kcal, assuming that 1 g ash-free dry weight = 5 kcal (Crisp 1971). In a second step, we estimated the respiration rate for each individual from:

$$R = 7.0 W_g^{0.75}$$

where R is the respiration rate in nL O_2 (individual h)$^{-1}$, and W_g the individual body weight in μg dry weight, assuming that ash-free dry weight is 90% of dry weight (Waters 1977). Therefore, R was normalized to a yearly rate per sampling unit ($m^2\,y^{-1}$) on the basis of 365 days per year, and converted in kcal using the following conversion factor: 1 litre O_2 = 4.83 kcal (Crisp 1971). Finally, consumption rate (Q) was calculated from the previous estimates of respiration and production as:

$$Q = (R + P)/AE$$

where AE = assimilation efficiency, and Q, R, P are expressed in kcal ($m^2\,y^{-1}$). As assimilation efficiency is highly variable (Valiela 1984), we decided to assign each species a value of 80% for carnivorous (as well as predator or necrophageous species), 70% for microphages (suspension and deposit-feeders) and 60% for herbivores (Jorgensen et al. 1991).

A.4. Meiofauna

Meiofaunal biomass was estimated from a mean density of 208.5 $ind.cm^{-2}$ ($n = 15$) measured in the sediment of Uvea atoll in 1994 (Boucher, unpubl. data). Assuming that 760 animals account for 1 mg dry weight (Alongi, pers. comm.

in Johnson et al. 1995) and that carbon is 40% of dry weight (Klumpp and Polunin 1989), biomass of meiofauna was estimated at 1.097 g C m^{-2}. Assuming that hard substrate cover is 23.4% in the shallow lagoon, biomass of meiofauna becomes 0.841 g C m^{-2} in the sediment. As annual P/B varies a lot depending on faunistic composition (Boucher, pers. comm..), we decided to affect a first value of 15 y^{-1} (Johnson et al. 1995). Q/B was one of the few parameters that were estimated by Ecopath, assuming an ecotrophic efficiency of 0.950. Assimilation efficiency was 0.2 as a preliminary value (see discussion).

A.5. Zooplankton

Plankton parameters were measured in 1992 (Le Borgne et al. 1993). Zooplankton was collected by vertical hauls from the bottom to the surface in 10 sampling stations (Fig. 1). For the shallow lagoon, we estimated a mean biomass of 0.084 g C m^{-2} ($n = 6$) integrated to the depth of each sampling station and by excluding detritus. Zooplankton production has been calculated using excretion rate (measured from i*n situ* incubations) and the net growth efficiency (details in Le Borgne 1978; Le Borgne et al. 1997). This resulted in a daily P/B of 1.14 d^{-1} that we converted to a yearly rate (416.1 y^{-1}). Consumption has been deduced from excretion, production, and an assimilation efficiency of 0.7 (Le Borgne et al. 1993) that was also used for the present model. The resulting value of Q/B was 3.23 d^{-1} (Table 10 in Le Borgne et al. 1997) that we converted to the yearly rate 1178.9 y^{-1}.

A.6. Corals

Since corals contribute to the primary production through the photosynthesis of the symbiotic zooxanthellae found in the polyp tissues (Odum and Odum 1955), coral might be considered as partly autotroph. As the Ecopath model allows to specify a degree of heterotrophy for such facultative consumers (Christensen and Walters 2004), we assumed that 70% of the energy requirements of coral are provided by zooxanthellae by translocation to the animal host, 20% from zooplankton and 10% from water column detritus (Sorokin 1981).

The living coral cover was assessed visually by SCUBA divers along 5×100-m belt transects (Kulbicki et al. 1993), and estimated to be 1.5% for the shallow lagoon ($n = 43$, *s.e.* = 2.5). Considering estimations of Odum and Odum (1955) from *Lobophyllia* sp., biomass of heterotrophic tissue (polyps) and zooxanthellae in polyps are assumed to be 0.021 and 0.0038 g dry weight per cm^{-2} of coral skeletons. Therefore, we can estimate the total biomass of organic tissue

in corals (polyp + zooxanthellae) to be 3.67 g dry weight.m^{-2}. Assuming that carbon is 40% of dry weight (Klumpp and Polunin 1989), $B = 1.468$ g C m^{-2}.

We decided to use the same values of P/B (1.10 year^{-1}) and Q/B (7.3 year^{-1}) than those in the model of Tudman (2001) which were taken from Sorokin (1993).

A.7. Phytoplankton

Phytoplankton biomass was estimated from chlorophyll *a* concentrations measured by fluorimetry at various depths (Le Borgne et al. 1993) in 10 sampling stations (Fig. 1). For the shallow lagoon, we estimated a depth-integrated mean biomass of 0.248 g C m^{-2} ($n = 6$) using a C/Chl *a* ratio of 84 (Charpy and Blanchot 1998). Primary production was estimated from in situ incubations (Le Borgne et al. 1993). This resulted in a daily P/B of 1.40 d^{-1} (Table 5 in Le Borgne et al. 1997) that we converted into a yearly rate (511 y^{-1}).

A.8. Benthic macroflora

We group together all epilithic macroalgae species collected and identified by Clavier et al. (1992). This includes small filamentous algae (turf algae), fleshy macroalgae and coralline algae. In the shallow lagoon, the mean biomass of benthic macrophytes was estimated to be 0.874 g m^{-2} ash-free dry weight ($n = 42$, *s.e.* = 93.52) converted to 0.350 g C m^{-2} (carbon is 40% of ash-free dry weight, Steele 1974). P/B was estimated by the Ecopath parametrization routine.

A.9. Benthic microphytes

The mean chlorophyll *a* concentration in the sediment was estimated to be 0.11 g m^{-2}, and microphytobenthic production to be 0.45 g C m^{-2} d^{-1} (Clavier, pers. comm.). Assuming a C/Chl *a* ratio of 50 (Charpy and Charpy-Roubaud 1990), biomass is 5.54 g C m^{-2} and P/B is 29.87 y^{-1}. Considering that hard substrate cover is 23.4% in the shallow lagoon, the adjusted value of 4.24 g C m^{-2} was used for the biomass of benthic microphytes in the sediment.

A.10. Detritus

The bulk of detritus was estimated from organic matter content of the sediment (Boucher, unpubl. data). The stock of water column detritus was assessed in the different planktonic size fractions which were sampled by Le Borgne et al. (1997).

Appendix B. Diet composition matrix of the Uvea shallow lagoon model. Diet is expressed as the fraction each prey contributes to the overall diet.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 *PF Large piscivores*	0.05																			
2 *PF Large planktivores*	0.13			0.20																
3 *PF Small pelagics*	0.18			0.20								0.35								
4 DF Sharks																				
5 DF Piscivores	0.01			0.05	0.05															
6 DF Large carnivores	0.09			0.10	0.10															
7 DF Small carnivores	0.03				0.11															
8 DF Small planktivores	0.16				0.17	0.17	0.11					0.03								
9 DF Large herbivores	0.03			0.09	0.15															
10 DF Small herbivores					0.04	0.01														
11 DF Omnivores					0.02															
12 *Cephalopods*	0.06			0.06	0.08	0.05						0.10								
13 Inv 1 carnivores					0.07	0.21	0.20				0.03									
14 Inv 2 herbivores						0.04	0.04				0.04									
15 Inv 3 filter-feeders					0.02	0.10	0.05					0.01	0.04							
16 Inv 4 deposit-swallowers					0.01	0.01	0.01													
17 Inv 5 surf. deposit-feeders					0.02	0.15	0.05				0.06	0.01	0.08							
18 Meiofauna							0.14	0.15			0.02	0.02	0.20		0.05	0.05	0.15	0.10		
19 *Zooplankton*		0.85	0.70				0.10	0.70		0.05	0.05	0.15			0.05				0.01	0.40
20 Corals/zooxanthellae											0.45		0.18							
21 *Phytoplankton*															0.50				0.70	0.10
22 Macrophytes									1.00	0.85	0.35			1.00						
23 Microphytes		0.15	0.10					0.15		0.10					0.15	0.40	0.65	0.50		
24 Detritus (col.)															0.20				0.29	0.50
25 Detritus (sed.)													0.50		0.05	0.55	0.20	0.40		
Import	0.26		0.20	0.30	0.08		0.30					0.30								
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

PF: pelagic fish; DF: demersal fish; Inv: benthic macroinvertebrates. Organisms assigned to the pelagic domain are in italics.