

Nathalie Niquil · J. Ernesto Arias-González
Bruno Delesalle · Robert E. Ulanowicz

Characterization of the planktonic food web of Takapoto Atoll lagoon, using network analysis

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Abstract The planktonic food web of Takapoto Atoll lagoon was studied using network analysis. This analysis includes four types of indices dealing with bilateral interactions of compartments, the trophic structure, biochemical cycles, and the topology of the flows. We found numerous parallel carbon pathways of similar importance, indicating a highly complex system compared to other marine ecosystems. Other characteristics were trophic levels not ranked in the same order as the size classes, the domination of system activity by processes at the first trophic level (and especially by herbivory), and cycling processes that involve many pathways. This is the first use of network analysis to describe completely a planktonic food web, and also the first comprehensive description of the trophic structure of the planktonic system in an atoll lagoon.

Key words Plankton · Food web · Network analysis · Ascendency · Atoll lagoon

Introduction

During the last 20 years, ecology has evolved toward a vision of the ecosystem as a system of interactions

(Fasham 1984; Frontier and Pichod-Viale 1995), where the center of interest is no longer the state of the biomasses of the different groups of organisms, but the interactions between them, quantified by flows of matter or energy. This change in the view of the ecosystem has provoked an increasing interest in food webs, i.e., the schema gathering these flows into an ecosystem, or segregating out part of an ecosystem.

It is difficult to comprehend the nature of complex food webs through direct observation, because the number of flows of matter or energy involved can be overwhelming (Pimm 1982; Ulanowicz 1987). To define and quantify the essential processes among the many interactions, several indices have been developed that characterize properties of the food web through an overall vision of its structure and functioning (Ulanowicz 1987; Kay et al. 1989). These network methods, usually invoked in connection with entire ecosystems, were applied in this instance to the planktonic subsystem of an atoll lagoon.

The planktonic food webs of corallian atolls have become the focus of interest in recent years because of the development of pearl oyster farming. These oysters interact directly with the planktonic food web. Additionally, they have attracted attention because of the seemingly increasing frequency of mass faunal mortality events abetted by algal blooms. Thus, the lack of knowledge concerning the global functioning of the planktonic community has become apparent. So far, the planktonic system has remained poorly described in coral reef ecosystems as most studies have focused on open shallow reefs dominated by benthic metabolism (Atkinson and Grigg 1984; Kinsey 1985; Sorokin 1990; Arias-González et al. 1997). Planktonic productivity, however, becomes important and can even dominate benthic processes in particular corallian ecosystems, such as coral atoll lagoons, where coral patches are scarce and the water is often deep (Charpy-Roubaud 1988; Furnas 1988).

The planktonic food web is characterized by complex interactions between non-living organic carbon, bacte-

N. Niquil (✉) · J.E. Arias-González¹ · B. Delesalle
Ecole Pratique des Hautes Etudes, URA CNRS 1453,
Université de Perpignan, F-66860 Perpignan Cedex, France
e-mail: niquil@univ-perp.fr

N. Niquil · J.E. Arias-González · B. Delesalle
CRIOBE, BP 1013 Moorea, Polynésie française

R.E. Ulanowicz
University of Maryland, Chesapeake Biological Laboratory,
PO Box 38,
Solomons, MD 20688, USA

Present address:

¹Centro de Investigación y Estudios Avanzados del IPN,
AP 73 Cordemex,
CP 97310, Mérida, Yucatán, Mexico

ria, the phytoplankton as primary producer, and the zooplankton as consumer. The exchange between these different compartments of the food web can be quantified by the flow of carbon between them during the processes of consumption, excretion, or respiration.

The planktonic compartments in atoll lagoons have recently been the subject of several studies. The characteristics emphasized were a phytoplankton community dominated by the size class $<3\ \mu\text{m}$ (Blanchot et al. 1989; Charpy et al. 1992), a high abundance and fast turnover of zooplankton (Le Borgne et al. 1989), slow-growing bacterioplankton (Torréton et al. 1997), and large stocks of non-living particulate organic carbon that is strongly grazed by zooplankton (Gerber and Gerber 1979) and other animals (Alongi 1988; Sorokin 1990; Arias-González 1993). However, these studies focused upon individual compartments, and quantitative descriptions of the network characteristics of planktonic food webs in atoll lagoons, i.e., of the exchanges between the living and non-living non-motile compartments of the water column, have been rare. Only Wilkinson (1987) and Charpy and Charpy-Roubaud (1990) have attempted to examine the entire planktonic system in coral reefs. The food webs they built were based on direct estimations in the field. These studies remain incomplete, however, as only calculation will allow the construction of complete food webs, because field estimation of all the flows is impossible.

The aim of our study was to describe fully the functioning of the planktonic system in an atoll lagoon. A study of the Takapoto Atoll lagoon provided an ideal opportunity, since much information on its planktonic compartments has been collected over the years. This lagoon has been the focus of a multidisciplinary program and survey since 1974, and the planktonic community was studied from 1990 to 1994. Here, we intend to examine the structure of the carbon flow of this food web. A previous study (Niquil et al. 1998) has already described a complete model of the carbon flow, employing inverse analysis – a numerical approach aimed at estimating missing flow values using data from the literature. However, this description utilized only direct observation of planktonic flow and cannot analyze the full structure of all the carbon pathways involved. Therefore, we applied network analysis to the model and data. This type of analysis uses global indices to characterize the structure of the network of trophic exchanges between the compartments, and with their surroundings. This study is the first attempt to apply to planktonic food web studies these two numerical approaches, i.e., inverse analysis for building the complete model and network analysis for analyzing the structure obtained.

Network analysis involves calculating indices that yield information over four domains, each one being a way of describing the structure of the food web: (1) the relationships between planktonic compartments considered two by two (input-output analysis), (2) a picture of the underlying structure of the food web in terms of

trophic levels (trophic structure analysis), (3) the pattern for recycling (cycles analysis), and (4) overall indices that characterize the geometry of the connections (topological analysis). None of these perspectives is available through direct investigation. These characteristics can address different questions: What are the strongest links and the most important compartments in the carbon circulation? What are the dominant trophic levels and how important are herbivory and detritivory? How are the processes of carbon cycling characterized? How can the geometry of the flows be characterized? How specialized are the carbon pathways?

The sum of these analyses should allow us to describe the trophic functioning of the planktonic system of the Takapoto Atoll lagoon. Furthermore, a comparison of these results with previous descriptions of complete coral reef food webs in shallow reefs dominated by the benthic community, or with other food webs describing communities in various marine ecosystems will be possible.

Materials and methods

Study site and studied model

Takapoto Atoll ($145^{\circ}10'W$, $14^{\circ}40'S$) is located in the South Pacific, in the Tuamotu Archipelago (French Polynesia). It is a medium-sized ($81\ \text{km}^2$) atoll, in which the lagoon, of moderate depth (23 m), is isolated from the ocean by an almost continuous reef rim (Fig. 1). A few shallow channels show a generally weak current.

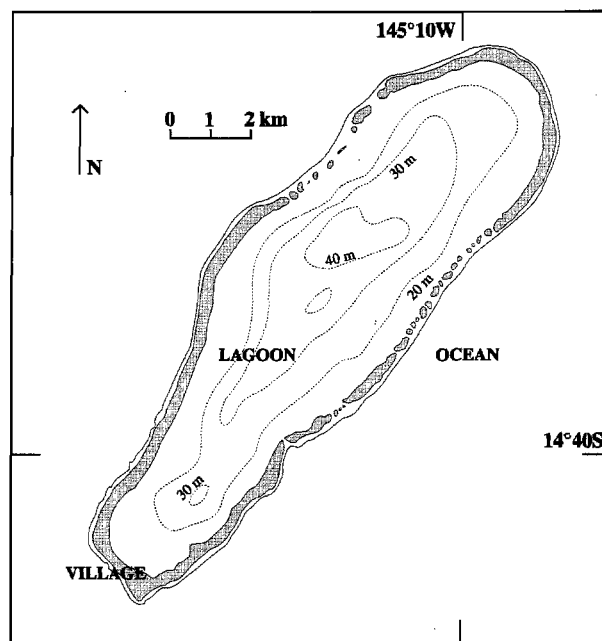


Fig. 1 Takapoto Atoll (located in the northwest of the Tuamotu Archipelago, French Polynesia). The surface area of the lagoon is $81\ \text{km}^2$ (Andrefouët 1994) and its mean depth is 23 m (Ricard et al. 1979).

This indicates that the ocean water hardly enters into the lagoon (Sournia and Ricard 1976). In this almost closed atoll, the water residence time is long: 4 years (Sournia and Ricard 1976), and the eastern trade winds are the main factor determining water motion (Rougerie 1979).

The atoll was initially studied in 1974 during the UNESCO Man And Biosphere Program (Salvat 1976, 1988), in relation to the development of pearl oyster farming (Salvat and Richard 1985), and later as part of the General Research Program on the Pearl Oyster (Programme Général de Recherche sur la Nacre, PGRN). One of the objectives of the latter program was to describe the planktonic system, which was considered to be the main food source for the oysters (Charpy et al. 1994a). For this reason, the program gathered specialists on each compartment of the planktonic community. The data were collected during several field trips that took place from 1990 to 1994. The sampling procedures varied, from one measurement per week for chlorophyll *a* determination, to a full year of monthly estimates for zooplankton (see Niquil et al. 1998 for a summary of the sampling procedure). The spatial coverage of the lagoon also varied according to the field trips (Niquil et al. 1998 and references in Table 1).

Data from the PGRN (presented in Table 1) were all averaged spatially and temporally and translated into units of carbon per square meter, where stocks were concerned, or into carbon per square meter per day, when processes, i.e., flows of carbon, were taken into account. These data were used to build a model of the carbon cycling by juxtaposing the flows of carbon from all the various processes occurring in the water column: e.g., predation, grazing, excretion, respiration (Niquil et al. 1998). This model was based on the assumption that each compartment maintains constant mass, i.e., the quantity of carbon coming into each compartment was the same as that leaving it. This assumption can be expressed by the fact that, for each compartment:

$$\text{consumption} = \text{production} + \text{respiration} + \text{excretion}$$

The planktonic organic carbon was divided into seven compartments (Fig. 2) based on function and size: (1) dissolved organic carbon (DOC); (2) non-living particulate organic matter (POC); (3) bacteria; (4) phytoplankton; (5) nanozooplankton ($\leq 35 \mu\text{m}$ that was assumed to be similar to protozoa); (6) microzooplankton (35–200 μm), and (7) mesozooplankton ($> 200 \mu\text{m}$).

The combination of information from the field and the requirement for conservation of matter within each compartment is not sufficient to estimate all the carbon flow values. Flows that could not be directly quantified from the field information were estimated using the inverse analysis technique of Vézina and Platt

(1988). The aim of this numerical analysis is to estimate realistic values for all the flows in a food web, when only some can be deduced from field data. The originality of this method lies in the use of previous knowledge on physiological rates to estimate the values of the flows that constitute the most realistic food web. The final determination of the unique solution is based on the principle of parsimony, which postulates that the best solution minimizes the sum of squares of the flows. The flow values yielded by these criteria are given in Table 2 and are represented graphically in Fig. 2. We considered that the food web obtained was

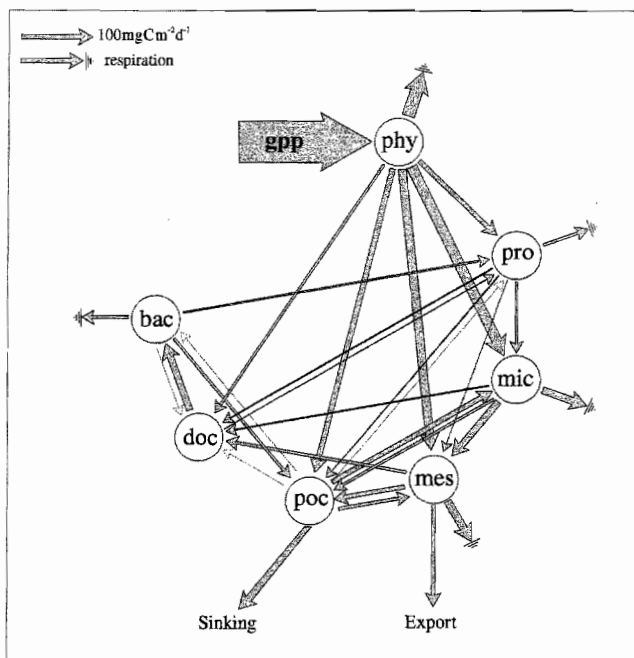


Fig. 2 Inverse solution for the planktonic food web flows in the lagoon of Takapoto Atoll. Each carbon flow is represented by an arrow whose width is proportional to the calculated value *gpp* gross primary production, *phy* phytoplankton, *pro* protozoa, *mic* microzooplankton, *mes* mesozooplankton, *poc* non-living particulate organic carbon, *doc* dissolved organic carbon, *bac* bacteria (from Niquil et al. 1998)

Table 1 Data of the PGRN and values used for the inverse analysis. Vertical water column integration was over a mean depth of 23 m (Ricard et al. 1979)

Description	Value used in the model	Published value	Reference
Stocks			
Phytoplankton	585 mgC m^{-2}	$0.31 \pm 0.01 \mu\text{g Chl } a \text{ l}^{-1}$	Charpy et al. (1992)
Bacteria	300 mgC m^{-2}	$13 \pm 2 \mu\text{gC l}^{-1}$	Torréton et al. (1997)
Protozoa	3 mgC m^{-2}	3 mgC m^{-2}	Charpy et al. (1994a)
Microzooplankton	98 mgC m^{-2}	98 mgC m^{-2}	Charpy et al. (1994a)
Mesozooplankton	47 mgC m^{-2}	47 mgC m^{-2}	Charpy et al. (1994a)
Detritus	2400 mgC m^{-2}	2400 mgC m^{-2}	Charpy et al. (1994a)
Dissolved organic carbon	33,400 mgC m^{-2}	$121 \pm 14 \mu\text{M}$	Torréton et al. (1997)
Flows			
Gross particulate primary production	820 $\text{mgC m}^{-2} \text{ day}^{-1}$	$0.82 \pm 0.1 \text{ gC m}^{-2} \text{ day}^{-1}$	Charpy et al. (1992)
Bacterial production	76 $\text{mgC m}^{-2} \text{ day}^{-1}$	$3.3 \pm 0.6 \mu\text{gC l}^{-1} \text{ day}^{-1}$	Torréton et al. (1997)
Microzooplankton production	131 $\text{mgC m}^{-2} \text{ day}^{-1}$	$131 \text{ mgC m}^{-2} \text{ day}^{-1}$	Charpy et al. (1994a)
Microzooplankton total ingestion	342 $\text{mgC m}^{-2} \text{ day}^{-1}$	$342 \text{ mgC m}^{-2} \text{ day}^{-1}$	Charpy et al. (1994a)
Microzooplankton respiration	147 $\text{mgC m}^{-2} \text{ day}^{-1}$	$30.8 \mu\text{mol O}_2 \text{ mg}^{-1} \text{ day}^{-1}$	Charpy et al. (1994b)
Mesozooplankton production	75 $\text{mgC m}^{-2} \text{ day}^{-1}$	$75 \text{ mgC m}^{-2} \text{ day}^{-1}$	Charpy et al. (1994a)
Mesozooplankton total ingestion	358 $\text{mgC m}^{-2} \text{ day}^{-1}$	$358 \text{ mgC m}^{-2} \text{ day}^{-1}$	Charpy et al. (1994a)
Mesozooplankton respiration	147 $\text{mgC m}^{-2} \text{ day}^{-1}$	$63.5 \mu\text{mol O}_2 \text{ mg}^{-1} \text{ day}^{-1}$	Charpy et al. (1994b)

Table 2 Flows of the steady-state model, with abbreviations used in Fig. 2. For each flow, the value obtained from the inverse analysis is given (from Niquil et al. 1998) (*DOC* dissolved organic carbon, *POC* particulate organic matter carbon)

Description	Flow name	Inferred value (mgC m ⁻² day ⁻¹)
Gross phytoplankton production	gpp-phy	863
Phytoplankton respiration	phy-res	250
Grazing of phytoplankton by protozoa	phy-pro	88
Grazing of phytoplankton by microzooplankton	phy-mic	205
Grazing of phytoplankton by mesozooplankton	phy-mes	167
DOC excretion by phytoplankton	phy-doc	43
Phytoplankton detrital POC production	phy-poc	109
Protozoa respiration	pro-res	51
Grazing of protozoa by microzooplankton	pro-mic	40
Grazing of protozoa by mesozooplankton	pro-mes	1.5
Protozoa egestion	pro-poc	12
DOC excretion by protozoa	pro-doc	17
Microzooplankton respiration	mic-res	147
Grazing of microzooplankton by mesozooplankton	mic-mes	131
Microzooplankton egestion	mic-poc	46
DOC excretion by microzooplankton	mic-doc	18
Mesozooplankton respiration	mes-res	147
Mesozooplankton egestion	mes-poc	82
DOC excretion by mesozooplankton	mes-doc	54
Bacterial respiration	bac-res	51
Use of bacteria by protozoa	bac-pro	28
Bacterial detrital POC production	bac-poc	48
DOC excretion by bacteria	bac-doc	0
Grazing of non-living POC by protozoa	poc-pro	0
Grazing of non-living POC by microzooplankton	poc-mic	97
Grazing of non-living POC by mesozooplankton	poc-mes	58
Use of non-living POC by bacteria	poc-bac	0
Non-living POC oxydation into DOC	poc-doc	0
DOC consumption by bacteria	poc-bac	127
DOC consumption by protozoa	poc-pro	6.4
Sedimentation of non-living POC	poc-los	142
Grazing of mesozooplankton by higher-level organisms	mes-los	75

representative of the mean state of the system during the period 1990–1994. This assumption has to be treated cautiously, however, as the period of measurement was highly variable (Niquil et al. 1998).

This method gave us a first description of the food web, which combined field information and calculations. Our interpretation of the functioning of the planktonic system was limited, however, due to the high complexity of the schema of carbon flows. That is why network analysis was applied to characterize the structure via the calculation of several informative indices.

Network analysis

Network analysis is a domain of ecology that aims at characterizing the properties of food webs, i.e., the complex flow of matter or energy between groups of organisms in an ecosystem or a community. Network analysis was applied to the planktonic food web of Takapoto Atoll using the program NETWRK 4 (Ulanowicz 1987). This program calculates a set of indices that characterize the structure of the food web. The calculations of these indices were derived from various scientific domains, ranging from economics to signal theory, in order to give a comprehensive description of the network properties in terms of processes that occur at different levels of food web organization. As described below, the indices can be classed into four groups, according to the type of structure described.

Input-output analysis

The first question asks which are the main links between the compartments of the network, or between a compartment and the surroundings? To identify these links, one employs the indices of

input-output analysis, which characterize the relationships at a particular time between any two compartments of the system or between any single compartment and the surroundings of the system (Ulanowicz 1987). The “total contribution coefficients” (see definition in the legend of Table 4) characterize the destinations of the carbon that leaves each compartment. The “total dependency coefficients” (definition in Table 5) characterize the origins of the carbon arriving at each compartment. These two sets of indices quantify three types of links between compartments: direct links, recycling, and indirect effects (Baird and Ulanowicz 1989). The total dependency coefficients can also be interpreted as the extended diets of the individual taxa (Baird and Ulanowicz 1989; Kay et al. 1989), that is, the combined information on the diet consumed and where it came from.

In this section we rank the compartments according to their activities in order to identify the most important compartments involved in the circulation of carbon. Such activity is quantified by the total quantity of carbon flowing into each compartment. This quantity is called the compartment throughput.

Trophic structure

In the second part, the program characterizes the trophic structure according to how much each population feeds at the various trophic levels. Traditionally, the ecosystem was considered as a trophic pyramid composed of successive trophic levels. This view has been criticized for two reasons: the fact that each animal can feed on various sources and therefore belongs to several trophic levels, and the difficulty of taking into account the fact that trophic chains can be based on detritus, as well as on autotrophs. In this section, network analysis combines the conventional ecological vision of the ecosystem as a pyramid of species with the more recent image of more complex interactions.

Most consumers feed on several compartments, which may belong to different trophic levels. For example, zooplankton consume autotrophic organisms like phytoplankton as well as other consumers, such as smaller zooplankton. To obtain the "average trophic position" of a compartment, the lengths of the different consumption pathways are averaged, as weighted by the quantity of carbon that passes over each (Field et al. 1989). Like the primary producers, the non-living, detrital compartments are assigned to the trophic position 1. The strict herbivores or detritivores consequently occupy a position of 2 (one plus one).

The consumer organisms can also be allocated to several discrete trophic positions, according to the amounts that reach them along feeding pathways of various lengths (Table 6). This is the idea behind the Lindeman trophic aggregation, that summarizes the complicated food web in terms of a single linear chain (Kay et al. 1989). The efficiency of the transfer from one aggregated trophic level to the next is calculated as the fraction of the total carbon input to a given level that is transmitted to the next higher level (Baird and Ulanowicz 1989). The contributions of each trophic level to respiration, imports, and exports are also evaluated (Ulanowicz 1995).

In this part, the importance of detritivory versus herbivory is also assessed. Although these two processes are both considered to occur at the same trophic level, whether one dominates the other is considered to be an important characteristic of trophic functioning.

Biochemical cycle analysis

Biochemical cycles (Kay et al. 1989) are pathways of flow whereby carbon returns to a compartment that it had exited previously. These pathways are important to the functioning of the system as they can facilitate homeostatic control over the magnitudes of the flows. The total number of cycles in the system, their size and the compartments that are most often involved in cycling are the key features that characterize cycling. The importance of cycling processes is also characterized by the Finn cycling index, i.e., the percentage of total carbon exchange that contributes to cycling (Finn 1976).

Topological analysis

The last type of analysis characterizes the geometry of the flows, i.e., the status of the network topology. The indices used are derived from information theory (Ulanowicz and Norden 1990; Ulanowicz 1997). The topology is characterized primarily by an index called the ascendancy of the system. The system ascendancy is defined as the product of the total flow of carbon in the system and the information inherent in the structure of the flows. This information is linked to the freedom that an atom of carbon has in going from one compartment to a next. The more the system is specialized in its carbon flow, the more constraint or information will be involved in guiding the flow. The more numerous the choices presented to an atom of carbon, the less information required. The maximum value for ascendancy is called the capacity for development. It corresponds to a food web with maximum specialization. It will prove useful to express the ascendancy as a percentage of this development capacity. This ratio quantifies the percentage of the maximum specialization that is actually realized in the system. The difference between this percentage and 100% corresponds to a dearth of information, that is, the freedom available to the atom of carbon because of the diversity of flows. If the freedom is expressed inside the system, that is in flows that link two compartments together, the drop in information corresponds to what is called the redundancy of the system. In other words, the redundancy quantifies the multiplicity of parallel flows between any two arbitrary compartments of the system. Ambiguities associated with exports or respiration are quantified as the overhead on exports or the dissipative overhead (the carbon respired is lost for all the organisms, i.e., it is dissipated), respectively.

Sensitivity analysis of system indices

It is important to know how robust the model is to changes in the data. Therefore, the sensitivities of the results were analyzed.

Several sensitivity analyses were performed to study the capabilities of the inverse analysis to build a complete model of the carbon flows. The results were published in Niquil et al. (1998). In summary, the resulting structure was quite robust with respect to variations of the input data. The most influential of these data in determining the flow values was primary production.

For this reason, we chose to perform a sensitivity analysis of the network indices by studying how the results from the inverse analysis vary when primary production takes on values plus or minus 10% of that estimated in the field. Network analysis was then carried out using NETWRK on the results from inverse analysis under the perturbed inputs.

Results

Input-output analysis

The exchanges between the system and the environment are portrayed by a unique entry of carbon as phytoplankton primary production ($863 \text{ mgC m}^{-2} \text{ day}^{-1}$) but with numerous outputs (respiration 75%, sedimentation of POC 16%, and consumption of mesozooplankton by external predators 9%). There was no appreciable export of carbon out of the lagoon by water advection.

The rankings of the compartments according to their activity, estimated by the compartmental throughputs (Table 3), was not related to their respective masses. Other than the phytoplankton, the compartments with the most important throughputs were the micro- and mesozooplankton, followed by the POC.

POC was the main destination for carbon leaving the six other compartments (Table 4); each one had at least 25% of its output going to POC. Micro- and mesozooplankton were also an important destination. Micro- and mesozooplankton were the main sources (Table 5) of carbon entering the bacteria (32% and 44%, respectively), POC (32% and 37%) and DOC (32% and 44%). Mesozooplankton were also strongly dependent on microzooplankton (42% of their extended diet). POC was the compartment most involved in cyclic pathways, with a diagonal value of 14% (Tables 4, 5), which means that 14% of its activity is related to recycling.

Table 3 Stocks (in mgC m^{-2}) and compartmental throughput (sum of the flows in $\text{mgC m}^{-2} \text{ day}^{-1}$) of the seven compartments. The compartments are ranked in order of decreasing throughputs

Compartment	Stock	Throughput
Phytoplankton	585	863
Mesozooplankton	47	358
Microzooplankton	98	342
POC	2,400	297
DOC	33,000	133
Bacteria pool	300	127
Protozoa	3	122

Table 4 Total contribution coefficients. Each value corresponds to the percentage of the carbon leaving the vertical compartment and entering the horizontal compartment. These include indirect path-

Sink: Source:	Protozoa	Microzooplankton	Mesozooplankton	Bacteria	POC	DOC
Phytoplankton	13	36	37	14	29	14
Protozoa	5	39	21	18	25	19
Microzooplankton	3	10	44	12	27	13
Mesozooplankton	4	11	10	16	29	17
Bacteria	23	22	18	7	44	7
POC	2	35	34	7	14	8
DOC	26	23	18	10	43	8

ways, which means that the sums of the lines can be greater than 100%. The *diagonal elements* (italicized) give the amount by which each compartment is dependent upon itself in cyclic pathways

Table 5 Total dependency coefficients. Each value corresponds to the percentage of the carbon entering the horizontal compartment coming from the vertical compartment. These include indirect pathways which means that the sums of the columns are greater

Sink: Source:	Protozoa	Microzooplankton	Mesozooplankton	Bacteria	POC	DOC
Phytoplankton	100	100	100	100	100	100
Protozoa	5	15	8	18	11	18
Microzooplankton	9	10	42	32	32	32
Mesozooplankton	12	12	10	44	37	44
Bacteria	23	8	6	7	20	7
POC	4	29	27	15	14	15
DOC	28	9	7	10	21	8

than 100%. The *diagonal elements* (italicized) give the amount by which each compartment is dependent upon itself in cyclic pathways

Trophic structure

The following characteristics of the interaction of trophic levels were observed. The mean trophic positions were not ranked in the same order as organism size. Mean trophic levels were 2.23 for protozoa, 2.14 for microzooplankton, and 2.42 for mesozooplankton. The bacteria pool, as an obligate detritivore, occupied a trophic position of 2, because the non-living compartments were summarily assigned to level 1, as were the autotrophs.

In building the Lindeman chain (Table 6), all consumer compartments were apportioned mainly to the second trophic level (i.e., they fed largely upon the first trophic level consisting of autotrophs and detritus). Protozoa and mesozooplankton were also linked strongly with the third trophic level.

The equivalent Lindeman chain consisted of five trophic levels (Fig. 3), i.e., the maximum possible for a system with four heterotrophic compartments. The flow reaching the fifth level, however, was small in value (0.4% of the gross primary production). Moreover, the fifth level was composed of a small amount of a single taxon (0.9% of the mesozooplankton).

The highest transfer efficiency (Fig. 3) occurred at the first trophic level (65.6%). This level aggregates primary producers with non-living materials. Herbivory in the system totaled $461 \text{ mgC m}^{-2} \text{ day}^{-1}$, whereas detritivory summed to $288 \text{ mgC m}^{-2} \text{ day}^{-1}$; herbivory exceeded detritivory by 60%.

Table 6 Repartition of the heterotrophic compartments into each trophic level of the Lindeman trophic aggregation. Level II corresponds to strict detritivory or herbivory and levels III–V to consumption of consumers

	Level II	Level III	Level IV	Level V
Bacteria	100%			
Protozoa	77.4%	23.6%		
Microzooplankton	88.4%	9.0%	2.6%	
Mesozooplankton	63.0%	32.7%	3.4%	0.9%

Cycling

As many as 24 cycles were counted among the different pathways of carbon flow. Of these, 17 were longer than or equal to four transfers (Fig. 4). DOC was the compartment through which most cycles flowed. It was present in 21 of the 24 existing cycles. The amount of carbon involved in cycling (Finn cycling index) equaled 17.5% of the total carbon flow.

Network topology

The topology of the network resulted in an ascendancy that comprised 37% of its maximum value, i.e., that level corresponding to a maximum specialization. The indeterminacy in the system was expressed as 4% of the overhead on export, 19% on respiration (the dissipative overhead), and 40% on internal flows (the redundancy,

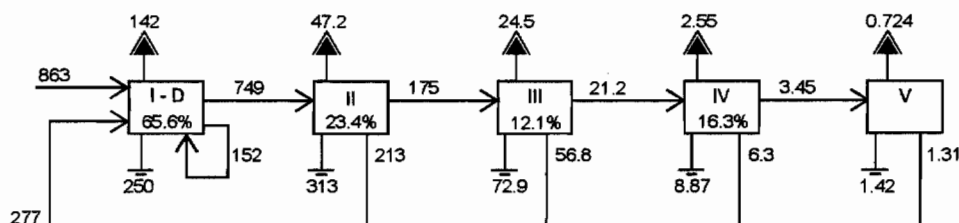


Fig. 3 Linear food chain of Takapoto planktonic food web. Flows out of the top of compartment boxes represent export ($\text{mgC m}^{-2} \text{ day}^{-1}$) and flows out of the bottom represent respiration ($\text{mgC m}^{-2} \text{ day}^{-1}$). Black doubled arrows represent exports and mass signs represent respiration. Level I-D corresponds to the association of level 1 (autotrophs) and D (detritus: non-living compartments). The heterotrophic compartments are divided in levels II-V, according to their diet

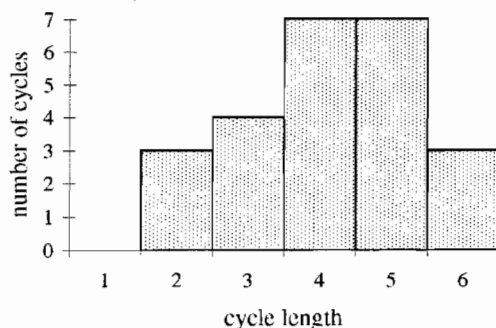


Fig. 4 Number of cycles versus cycle length, i.e., the number of compartments constituting the cycle

or the importance of parallel carbon pathways between compartments).

Sensitivity analysis

The indices that result from varying the primary productivity by plus or minus 10% are presented in Table 7. By and large, the major characteristics mentioned above still pertain to the two modified systems. The ranking of the throughput remains independent of the mass, the POC still dominates the cyclic pathways (diagonal elements of the two tables showing the coefficients of contribution and dependency), the effective trophic level is still not proportional to the size of organisms, the first trophic level remains the most efficient, herbivory continues to be superior to detritivory, and the multiplicity of the internal flows (redundancy) stays at the same level. The most sensitive indices to variation in primary production are those related to the cycling processes. A decrease in primary production requires the system to recycle more in order to meet its needs for carbon, whereas when primary production increases, recycling becomes less necessary.

Discussion

The interactions among the different compartments of a food web are quite complex, and any emerging diagram soon resembles a "spaghetti plate" (Pimm 1982; Ulanowicz 1987). This remains the case, even when only part of the ecosystem, e.g., the planktonic food web, is considered (Fig. 2). Direct observation (Niquil et al. 1998), without the use of network analysis, provides valuable clues on the functioning of the system, but this description remains limited. The directly visible characteristics included high phytoplankton primary production and low bacterial production, domination of the system by metazoan compartments (micro- and mesozooplankton) due to their high metabolism, and the central role played by the POC, which adds complexity by sustaining all the consumers (Niquil et al. 1998). Network analysis allows one to elaborate this description significantly, as described below.

The application of inverse analysis to incomplete data sets gave images of the food web that were more or less realistic (Niquil et al. 1998). The sensitivity analyses showed that the fundamental system characteristics were quite robust, as had been demonstrated using the simulation model built with the help of inverse analysis.

The first remarkable system characteristic is that the trophic levels are not ranked in the same order as the size classes. The trophic level of compartments is usually assumed to increase along with the size of the organisms, e.g., protozoa are consumed by microzooplankton, which in turn are consumed by mesozooplankton, and so on. In the planktonic system of Takapoto, however, this grazing chain involves less carbon than is transferred up the ladder by herbivory and detritivory. Moreover, the protozoa, feeding as they do on bacteria (trophic level 2), occupy a higher trophic position than the microzooplankton, which feed mainly on phytoplankton (trophic level 1.) Thus, the normal correlation of trophic position with size does not seem to pertain to our planktonic system. A similar observation was made by Baird and Ulanowicz (1993) in three of the four estuaries they studied: the smaller-sized class of zooplankton fed at a higher trophic level than did some larger-bodied zooplankton.

This absence of correlation between size and trophic level derives from the fact that herbivory and detritivory dominate over carnivory. In other words, ingestion of the first trophic level, which combines herbivory and detritivory, is by far the most important consumption.

Table 7 Results of the sensitivity analysis of the indices to a variation in the value of gross primary production (*PGRN* values obtained with the initial model, *GPP-10%* values obtained for a model constructed with a primary production decreased by 10%, *GPP+10%* with a primary production increased by 10%)

	<i>PGRN</i>	<i>GPP-10%</i>	<i>GPP+10%</i>
Input-output analysis			
Throughput			
Phytoplankton	863	777	949
Mesozooplankton	358	358	358
Microzooplankton	342	342	342
POC	297	270	317
DOC	133	133	139
Bacteria pool	127	127	138
Protozoa	122	122	122
Diagonal elements of the tables of coefficients of contribution and dependency			
Protozoa	5%	6%	2%
Microzooplankton	10%	11%	9%
Mesozooplankton	10%	12%	9%
Bacteria	7%	8%	6%
POC	14%	16%	13%
DOC	8%	9%	6%
Trophic structure			
Effective trophic level			
pro	2.23	2.26	2.20
mic	2.14	2.18	2.09
mes	2.42	2.47	2.40
Transfer efficiencies			
I-D	65.6%	69.4%	63.1%
II	23.4%	26%	21.3%
III	12.1%	15.8%	8.03%
IV	16.3%	16.6%	15%
Herbivory/detritivory	1.60	1.49	1.72
Cycling			
Number of cycles	24	24	20
Finn cycling index	17.5%	19.9%	15.3%
Topology			
Ascendency (%A max)	37%	37%	38%
Overhead on exports	4%	4%	4%
Dissipative overhead	19%	18%	19%
Redundancy	40%	41%	38%

That the initial trophic levels dominate over succeeding ones is made evident by the sharp decline in trophic efficiency after the first level and by the fact that little carbon reaches the highest levels. A similar decrease was observed in Tiahura, a shallow reef dominated by the benthic community, for which a comprehensive food web model was created (Arias-González 1993; Arias-González et al. 1997). The Takapoto planktonic system differs from the Tiahura benthic system in the degree that herbivory dominates over detritivory, i.e., in Takapoto, primary production is exploited mainly by consumers, whereas at Tiahura it is recycled directly via the detritus. One cannot neglect detritivory in Takapoto, however, as it contributes to the complexity of the system – each zooplankton compartment effectively grazes on at least one non-living compartment (POC or DOC). Moreover, the two non-living compartments play a central and critical role in cycling. POC receives most of the cycled carbon, and DOC is the compartment most frequently found in the cycles. The resulting scheme combines successively the direct exploitation of primary production by herbivores, followed by recycling through non-living compartments.

The processes that allow recycling can be characterized as very complex in the sense that they involve numerous pathways (24 cycles), although the quantity of

carbon involved in these processes is low (Finn cycling index of 17.5%). This indicates that, despite an abundance of cycles, a large amount of the total carbon flow is not being recycled. Most of the published values for the Finn cycling index in various marine systems or estuaries are higher than that of Takapoto: they vary from 23 to 58% (Baird et al. 1991; Ulanowicz and Wulff 1991; Baird and Ulanowicz 1993; Johnson et al. 1995; Arias-González et al. 1997). Lower values are found only in the Benguela (0.01%) and the Peruvian (3.2%) upwellings (Baird et al. 1991), i.e., two sites characterized by very high advection. As regards reef ecosystems, the Finn ratio in Takapoto is lower than the indices calculated for the Tiahura fringing and barrier reefs (50 and 58%, respectively; Arias-González et al. 1997) and lower than that for the Davies Reef ecosystem (26%; Johnson et al. 1995). Thus, carbon cycling presents a completely different profile, depending on whether the system of concern is a shallow, widely open reef or a deep enclosed lagoon. The difference could be related to the relative availability of nutrients to the primary producers. The Tiahura reef system is a narrow, shallow reef that is quickly flushed by very oligotrophic oceanic waters. Residence time in Tiahura is less than 1 day, whereas it reaches 4 years in the closed lagoon of Takapoto. More effective recycling is required to sustain the existing high

biomass in Tiahura, where the severe lack of available nutrients does not permit much in the way of primary production.

The geometry of the flows in the planktonic food web is characterized by the fact that carbon flows over numerous parallel pathways, i.e., the system redundancy (which quantifies the ambiguity of pathways between compartments) is high. The value reached in Takapoto (40%) is higher than values previously published for marine, estuarine, and upwelling ecosystems, which range from 22% for the Baltic sea to 36% for the Swartkops estuary (Baird et al. 1991; Baird and Ulanowicz 1993). The redundancy reaches 40.4 and 37.6% in the barrier and fringing reefs, respectively, of Tiahura, however, values similar to those obtained for the planktonic system of Takapoto (Arias-González 1993). Ulanowicz (1980, 1986, 1997) and Kay (1984) hypothesized that a mature system will be characterized by a low value for redundancy, because ecosystems are thought to evolve toward highly specialized food webs via selection for the most efficient pathways. Accordingly, the planktonic community of Takapoto Atoll lagoon appears to be an immature system. Possibly, this immaturity arises from frequent stresses which prevent the evolution of this system towards greater specialization. Because the lagoon is nearly closed, the planktonic system is left free to respond to local variations in environment that would otherwise be buffered by greater access to the relatively unchanging oceanic environment. Such lability can even lead at times to algal blooms.

Network analysis is normally considered to provide insights into the properties of whole ecosystems (Field et al. 1989). We chose, however, to apply the approach to a food web that constitutes only a part of the ecosystem: the planktonic food web of Takapoto lagoon. One must question how appropriate it is to apply NETWRK to only the planktonic part of the Takapoto lagoon ecosystem and then to compare the results to those derived from consideration of whole ecosystems. It should be obvious that applying NETWRK to Takapoto plankton yielded deeper insight into the trophic functioning of the planktonic food webs. The results must be regarded with caution, however, as the observations were not made at the usual hierarchical level, i.e., the planktonic system is part of a whole ecosystem. When only a subsystem is being examined, one expects that the exchanges with the external world will comprise a higher proportion of the total system activity. This should be reflected in the subsystem having smaller values for the internal components of ascendancy or overhead than would be the case when dealing with whole ecosystems. Here, for example, the planktonic system has obligatory links with the rest of the bioecoses, whereas a whole ecosystem is by definition more isolated. Nevertheless, in our comparison we relied mainly on the relative ascendancy and the Finn cycling index which are dimensionless quantities, and thus not as sensitive to aggregation (Field et al. 1989) or to the number of compartments.

Finally, using network analysis in combination with the inverse algorithm of Vézina and Platt (1988) proved to be an efficient tool for comparing very different systems, whatever their structures, in order to gain new insights into ecosystem functioning and to infer new principles for ecology. This combination of numerical approaches revealed the following characteristics of the planktonic food web of Takapoto Atoll lagoon: (1) trophic levels that do not correlate well with the size classes of consumers, (2) domination of the ecosystem by processes involving the first trophic level, and most especially herbivory, (3) cycling processes that consist of numerous pathways but little carbon, and (4) a structure that is not very specialized, which can be interpreted as a lack of maturity of the system. Our study indicates that coral reef food webs differ from other marine systems in their higher degree of redundancy in pathways of carbon flow. This degree of ambiguity is what makes the food web of the lagoon so complex.

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References

- Alongi DM (1988) Detritus in coral reef ecosystems: fluxes and fates. *Proc 6th Int Symp Coral Reef*, Townsville 1:29–36
- Andreouët S (1994) Caractérisation des éléments morphologiques des atolls des Tuamotu à partir des données SPOT. Mémoire de DEA, Université Française du Pacifique, Papeete
- Arias-González JE (1993) Fonctionnement trophique d'un écosystème récifal: secteur de Tiahura, Ile de Moorea, Polynésie française. PhD thesis, Ecole Pratique des Hautes Etudes, Paris
- Arias-González JE, Delesalle B, Salvat B, Galzin R (1997) Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* 16:231–246
- Atkinson MJ, Grigg RW (1984) Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii *Coral Reefs* 3:13–22
- Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol Monogr* 59:329–364
- Baird D, Ulanowicz RE (1993) Comparative study of the trophic structure, cycling and ecosystems properties of four tidal estuaries. *Mar Ecol Prog Ser* 99:221–237
- Baird D, McGlade JM, Ulanowicz RE (1991) The comparative ecology of six marine ecosystems. *Phil Trans R Soc Lond B* 333:15–29
- Blanchot J, Charpy L, Le Borgne R (1989) Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). *Mar Biol* 102:329–339
- Charpy L, Charpy-Roubaud C (1990) Trophic structure and productivity of the lagoonal communities of Tikehau atoll (Tuamotu Archipelago, French Polynesia). *Hydrobiologia* 207:43–52
- Charpy L, Blanchot J, Lo L (1992) Contribution des cyanobactéries (*Synechococcus* spp.) à la production phytoplanctonique dans un lagon d'atoll fermé (Takapoto, Tuamotu, Polynésie Française). *C R Acad Sci Paris Ser III* 314:395–401
- Charpy L, Buestel D, Pouvreau S, Cabral P (1994a) Synthèse des recherches sur l'environnement du lagon de Takapoto: résumé des actions de recherche du PGRN. IFREMER-EVAAM, Tahiti
- Charpy L, Langy S, Le Borgne R, Lo L, Rochette JP (1994b) Etude de la perte de matière organique particulaire pour la nacre par

- les compétiteurs planctoniques. Rapport de la fiche 14 du PGRN. IFREMER-EVAAM, Tahiti
- Charpy-Roubaud CJ (1988) Production primaire des fonds meubles du lagon de Tikehau (atoll des Tuamotu, Polynésie française). *Oceanol Acta* 11:241–248
- Fasham MJR (1984) Flows of energy and materials in marine ecosystems: theory and practice. NATO Conf Ser ser IV. Marine science. Plenum, New York
- Field JG, Wulff F, Mann KH (1989) The need to analyze ecological networks. In: Wulff F, Field JG, Mann KH (eds) *Network analysis in marine ecology*. Springer, Berlin Heidelberg New York, pp 3–14
- Finn TJ (1976) Measures of ecosystems structure and function derived from the analysis of flows. *J Theor Biol* 56:363–380
- Frontier S, Pichod-Viale D (1995) *Ecosystèmes: structure, fonctionnement, évolution*, 2nd edn. Masson, Paris
- Furnas MJ (1988) The behavior of nutrients in tropical aquatic ecosystems. In: Connell DW, Hawker DW (eds) *Pollution in tropical aquatic systems*. CRC, London, pp 29–65
- Gerber RP, Gerber MB (1979) Ingestion of natural particulate organic matter and subsequent assimilation, respiration and growth by tropical lagoon zooplankton. *Mar Biol* 52:33–43
- Johnson C, Klumpp D, Field J, Bradbury R (1995) Carbon flux in coral reefs: effects of large shifts in community structure. *Mar Ecol Prog Ser* 126:123–143
- Kay JJ (1984) Self-organization in living systems. PhD thesis, Department of Systems Design Engineering, University of Waterloo, Ontario, Canada
- Kay JJ, Graham LA, Ulanowicz RE (1989) A detailed guide for network analysis. In: Wulff F, Field JG, Mann KH (eds) *Network analysis in marine ecology*. Springer, Berlin Heidelberg New York, pp 15–61
- Kinsey WD (1985) Metabolism, calcification and carbon production. *Proc 5th Int Coral Reef Congr, Tahiti* 4:515–526
- Le Borgne R, Blanchot J, Charpy L (1989) Zooplankton of Tikehau atoll (Tuamotu archipelago) and its relationship to particulate matter. *Mar Biol* 102:341–353
- Niquil N, Jackson GA, Legendre L, Delesalle B (1998) Inverse model analysis of the planktonic food web of Takapoto Atoll (French Polynesia). *Mar Ecol Prog Ser* 165:17–29
- Pimm SL (1982) Food webs cell: population and community ecology. Usher MB, Rozenzweig ML (eds). Chapman & Hall, London
- Ricard M, Gueredrat JA, Magnier Y, Renon JP, Rochette JP, Rougerie F, Sournia A, Wauthy B (1979) Le plancton du lagon de Takapoto. *J Soc Océan* 35:47–57
- Rougerie F (1979) Caractéristiques générales du milieu liquide lagunaire de l'atoll de Takapoto. *J Soc Océan* 35:35–45
- Salvat B (1976) Un programme interdisciplinaire sur les écosystèmes insulaires en Polynésie française. *Cah Pac* 19:397–406
- Salvat B (1988) Bibliographie de l'atoll de Takapoto, Archipel des Tuamotu. *Bull Soc Et Océan* 243, 20:55–60
- Salvat B, Richard G (1985) Takapoto atoll, Tuamotu archipelago. *Proc 5th Int Coral Reef Congr, Tahiti* 1:323–378
- Sorokin YI (1990) Aspects of trophic relations, productivity and energy balance in coral reef ecosystems. In: Dubinsky Z (ed) *Ecosystems of the world*, no 25. Coral reefs. Elsevier, Amsterdam, pp 401–409
- Sournia A, Ricard M (1976) Données sur l'hydrologie et la productivité d'un lagon d'atoll fermé (Takapoto, Tuamotu). *Vie Milieu* 26:243–279
- Torréton JP, Pagès J, Dufour P, Cauwet G (1997) Bacterioplankton carbon growth yield and DOC turnover in some coral reef lagoons. *Proc 8th Int Symp Coral Reef, Panama* 1:947–952
- Ulanowicz RE (1980) An hypothesis on the development of natural communities. *J Theor Biol* 85:223–245
- Ulanowicz RE (1986) *Growth and development: ecosystem phenomenology*. Springer, Berlin Heidelberg New York
- Ulanowicz RE (1987) NETWORK 4, a package of computer algorithms to analyze ecological flow networks
- Ulanowicz RE (1995) Ecosystem trophic foundations: Lindeman exonerata. In: Patten BC, Jorgensen S (eds) *Complex ecology: the part-whole relation in ecosystems*. Prentice-Hall, Englewood Cliffs, NJ, pp 549–560
- Ulanowicz RE (1997) Ecology, the ascendent perspective cell: complexity in ecological systems. Allen TFH, Roberts DW (eds). Columbia University Press, New York
- Ulanowicz RE, Norden JS (1990) Symmetrical overhead in flow networks. *Int J Syst Sci* 21:429–437
- Ulanowicz RE, Wulff F (1991) Comparing ecosystem structures: the Chesapeake Bay and the Baltic Sea. In: Cole J, Lovett G, Findlay S (eds) *Comparative analyses of ecosystems: patterns, mechanisms and theories*. Springer, Berlin Heidelberg New York, pp 140–166
- Vézina AF, Platt T (1988) Food web dynamics in the oceans. 1. Best-estimates of flow networks using inverse methods. *Mar Ecol Prog Ser* 42:269–287
- Wilkinson CR (1987) Microbial ecology on a coral reef. *Search* 18:31–33