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Benthic-Pelagic Switching in a Coastal Subtropical Lagoon

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The structure of the ecosystem fluxes occurring in the Maspalomas coastal lagoon (Canary Islands) were investigated for three successive stages using estimates of the food webs that typify each interval. The first stage was representative of a benthic producer-dominated system and the third typified a pelagic-dominated system. The second phase was taken as the transient stage between these endpoints. The standing stocks and fluxes pertaining to each compartment and the overall trophic structure of the system were quantified as a network model. This food web budget was subjected to network analysis to assess the status of the system at each stage. The ensuing trophic analysis indicated that detritivory increases in passing from the first to the third stage (ratio of detritivory to herbivory 13·19, 7·57 and 20·32 respectively) and there is a concomitant drop in the average trophic efficiency. Cycle analysis revealed an increase in the amount of matter being cycled during the third stage (percentages of cycled matter 17·7%, 22·6% and 41·8% respectively), mostly via short, fast loops, which suggest that the third stage is representative of an immature ecosystem. Finally, the analysis of topological system-level indices reveals a dramatic increase in organization during the last stage, due primarily to the inflation of the total system throughput (TST). From a global point of view, results show a significant decline in the benthic subsystem, which represents a major perturbation to the ecosystem and renders it vulnerable to the subsequent invasion by pelagic elements. Although conditions in the third stage may seem typical of a eutrophic system, no appreciable resources are being added to the system from the outside. Therefore, the process is more accurately described as a shift in resources from one subsystem (the benthic) to another (the pelagic).

Keywords: modelling; ecosystems; eutrophication; coastal lagoons; Canary Islands

Introduction

Maspalomas lagoon is a small subtropical coastal lagoon that is subject to periodical anoxic crises (Almunia, 1998). The system is representative of shallow eutrophic lagoons characterized by high throughput rates and as a consequence, structural changes become evident over relatively short periods of time (weeks) (Llinás *et al.*, 1986; Basterretxea & Van Lenning, 1995). Inputs to the system are rapidly transferred and dissipated among its components, resulting in dramatic changes in the structure and function of the ecosystem (Almunia, 1998). One way of providing insight into the fundamental structure and behaviour of an ecosystem is to measure the energy and material fluxes taking place within the system and to estimate the efficiencies of transfer among the different compartments (Longhurst, 1984; Ulanowicz & Platt, 1985; Ulanowicz, 1986; Baird *et al.*, 1991; Baird & Ulanowicz, 1993). Accordingly, these tasks became the priorities for a research programme carried out in Maspalomas; further detail concerning sampling protocols and results can be found in Almunia (1998).

The study employed network analysis on the ecosystem to reveal several of its properties, such as its structural complexity, cycling behaviour and trophic relationships among compartments of the system. This type of analysis uses available data to quantify the material and energetic interactions within the community, which are believe to condition the self-organizing and self-regulating behaviour of the system (Odum, 1971; Ulanowicz, 1986; Ulanowicz & Norden, 1990). From a practical standpoint, the separation into distinct components allows an investigator to focus on a particular section of the network and to identify the key processes controlling the functioning of the overall system (Ulanowicz & Norden, 1990).

Self-organization of ecosystems generally occurs over an interval of decades but the changes addressed in this work transpire over the span of a single year.

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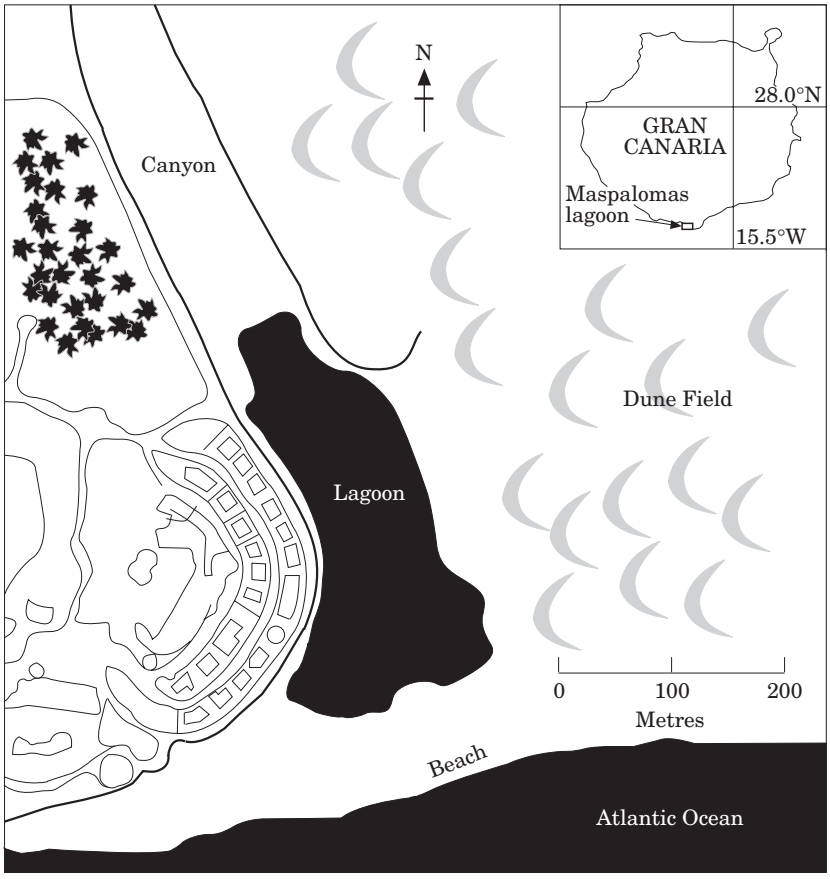


FIGURE 1. Location of Maspalomas lagoon.

Thus, it would be more appropriate to refer to any organizational behaviour as self-regulation, rather than self-organization. The differences between the dynamics of self-organization and self-regulation are discussed in some detail in Gafiychuk and Ulanowicz (1996) and Ulanowicz (in press). Whereas self-organization evolves over longer times and is mediated primarily by positive feedbacks, the much more rapid phenomenon of self-regulation involves mostly negative feedback responses by the system. Nevertheless, it remains a useful exercise to focus upon correspondences in the overall structure and function of the intra-annual stages of the system (Margalef, 1982), utilizing the same system-level indices that have proven useful for interpreting system changes over longer periods (e.g. Ulanowicz, 1984).

The aim of this work is to conceptualize, quantify and analyse the trophic schematic of the ecosystem of Maspalomas lagoon at three different stages of its transition from a benthic-dominated system, with a low, stable pelagic biomass, to a highly-variable pelagic-dominated configuration, from which benthic producers have virtually disappeared.

Study location

The ' Charca de Maspalomas ' (Figure 1) is a small (*c.* 3·5 ha), shallow 1–2 m subtropical coastal lagoon, located on the southern coast of Gran Canaria (Canary Islands). The lagoon is the result of groundwater water seepage from the landward side and infiltrations of seawater through the sand bar. The water temperature in the lagoon ranges from 30 °C in summer to 15 °C in winter. During heavy rains, water runs through the arroyo, producing very rapid increases in water level. Alternatively, seawater can enter the lagoon during spring tides or during storm surges, thereby repleting the existing fish communities, composed mainly of *Liza aurata*, *Dicentrarchus punctatus* and *Diplodus sargus* (T. Moreno, 1997). Although different species of coastal and inland birds inhabit the proximity of the lagoon (wading birds, ducks, etc.), the most representative species of waterfowl is the moorhen (*Gallinula chloropus*).

The bottom of the lagoon is muddy, with the exception of the southern end, where sand from the nearby beach and dune fields dominates. The

phanerogam *Ruppia maritima* and the algae *Cladophora* sp. and *Chara globularis* (episodically), dominate the muddy beds. The few sandy areas are practically free of bottom vegetation. As *R. maritima* is the major benthic producer in Maspalomas lagoon, its life cycle drives the major ecosystem changes. *Ruppia maritima* begins growing in early spring, reaching its maximum density in mid-summer and then decreases rapidly at the end of summer. The lagoon suffers from recurrent anoxic crises during the intervals when *R. maritima* is not visible, probably due to the lack of wind mixing in combination with high rates of community respiration. During hypoxic events water becomes extremely turbid, sharply curtailing light penetration to the bottom and promoting benthic algal decay. At these times *R. maritima* is restricted to the shallowest margins of the lagoon (Almunia, 1998).

As hypoxic conditions are related to the disappearance of the phanerogam, it was decided to study the changes induced in the ecosystem by the annual dieoff of *R. maritima*. For the purposes of this study, three stages have been selected when the Maspalomas lagoon ecosystem occurs an ecosystem with (1) low dissolved nutrients, low phytoplankton standing stocks, well-developed bottom algae and low water turbidity, (2) a transient stage with diminished benthic production and a burgeoning plankton community and finally (3) a community without benthic producers, but with high dissolved nutrients and a high density of phytoplankton; all representative of the anoxic conditions leading to fish kills.

Estimates, methods and assumptions

A carbon flow model was constructed for each of the stages described above (Figure 2, 3 and 4). In order to estimate the network model one needs the magnitude of biomass in each component, as well as the intensities of flows between compartments and exchanges between the system and its surroundings. Standing stocks are expressed in mg C m^{-2} and flows between the compartments in mg C m^{-2} d^{-1}. Due to a lack of historical studies on Maspalomas, the magnitudes of standing stocks of living and non-living constituents required by the model (Table 1) had to be obtained in most cases by direct measurement.

The food web is comprised of 17 compartments (14 in the third stage, due to the disappearance of benthic primary producers), including three non-living constituents. Living compartments were chosen to be resolved as closely to the species level as available data and sampling strategy would allow (Baird & Ulanowicz, 1989). Of course, identification to the species level occurred mainly at the higher levels of the network.

Carbon budgets were constructed for each compartment according to the balance:

$$C = P + R + E + Ex$$

where C=consumption, P=production, R=respiration, E=egestion and Ex=excretion or exudation (Crisp, 1971; Baird & Ulanowicz, 1989). Exudation by primary producers was considered to be the largest source of dissolved organic carbon (DOC) (Valiela, 1984; Baird & Ulanowicz, 1993).

The structures of trophic levels and cycling for each network were analysed and system properties were calculated using algorithms described by Ulanowicz (1983, 1986*a*) and Kay *et al.* (1989). Briefly, the relationships between any arbitrary pair of components are assessed by the total flow calculation predicated on the Leontief inverse (Leontief, 1936; 1951) as applied to ecological systems (Hannon, 1973; Szyrmer & Ulanowicz, 1987). This analysis and the ones that follow, all require the input of biomasses to each compartment, the inputs from and outputs to the surroundings, an estimation of the energy dissipation (respiration) by each component, and the matrix of fluxes between the compartments themselves.

The study is comprised of four different analyses:

(1) The input-output analysis (IOA) (Hannon, 1973), which measures the importance of each particular entity and the bilateral influences that each pair of taxa have on each other. It is in this section of the algorithm that the total contribution coefficient (TCC) and the total dependency coefficient (TDC) are calculated for each compartment (Szyrmer & Ulanowicz, 1987). The TCC is the fraction of what leaves compartment i that eventually enters compartment j, and the TDC is the fraction of the total ingestion by j which passed through compartment i along its way to j.

(2) A second analysis interprets the network according to the trophic concepts of Lindeman (1942)), but without relegating each group to a unique trophic level (Ulanowicz & Kemp, 1979; Levine, 1980; Ulanowicz, 1995). Rather, each taxon is apportioned among a series of integer trophic levels according to how much reaches the taxon in question over pathways of different lengths. Using this partitioning, an equivalent straight chain of trophic transfers can be assembled and used to track the trophic status of the ecosystem as it changes.

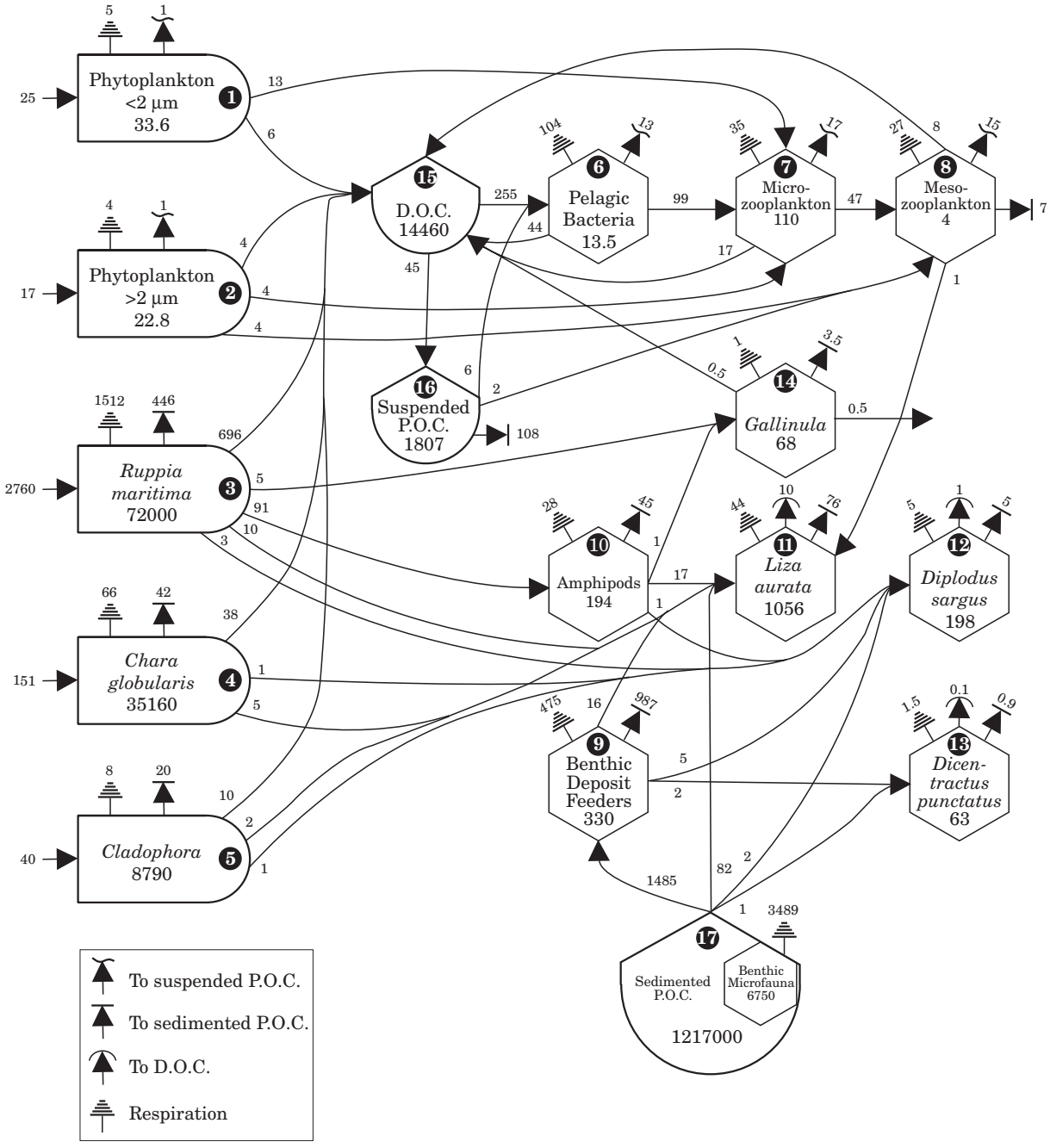


FIGURE 2. Energy flow network for stage 1 (biomass C in mg m^{-2}; carbon flows in mg m^{-2} day^{-1}; rounded rectangles—autotrophs; hexagons—heterotrophs; rounded triangles—detritus).

(3) A third segment of the algorithm enumerates the biogeochemical cycles and outlines the complexity of cycling in the system in terms of the number and length of cycles and the percentage of total system activity devoted to cycling matter (Finn, 1976). A high fraction of cycled flow could indicate a mature and less disturbed system (Odum, 1969), if the matter is cycling through long-slow cycles, but if the matter is circulating rapidly around short loops, a high fraction could be indicative of a stressed ecosystem (Ulanowicz, 1984).

(4) Finally, the topological structure of the network (Hirata & Ulanowicz, 1984; Ulanowicz, 1986; Ulanowicz & Norden, 1990) is quantified by several indices: ascendency (Ulanowicz, 1986*a*)

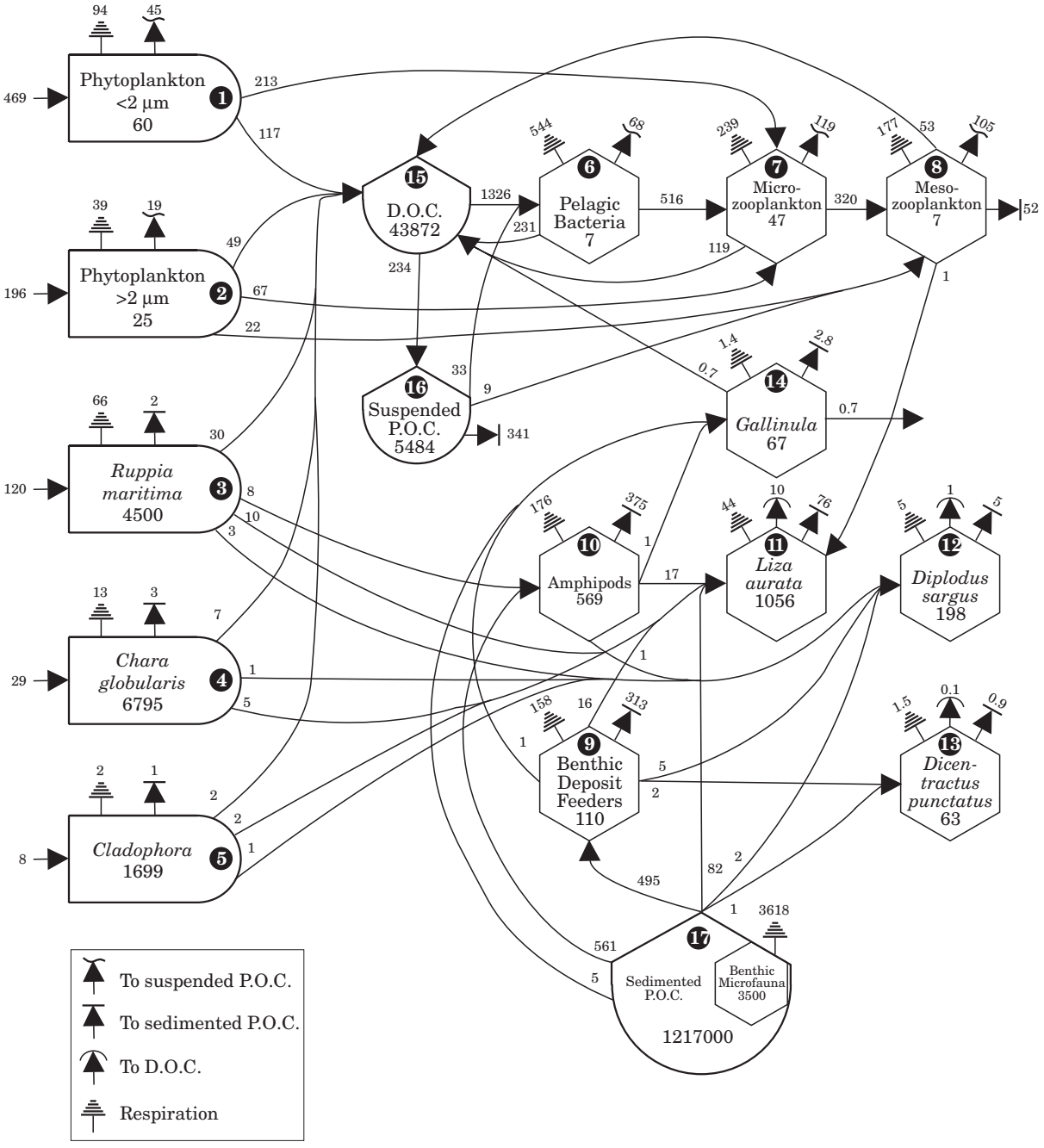


FIGURE 3. Energy flow network for stage 2 (symbols as in Figure 2).

measures in a single index both the system size and the organization inherent in its flow structure. Development capacity (Rutledge *et al.*, 1976; Ulanowicz, 1986*a*) is an upper bound on the ascendency, i.e. a measure of the network's potential for competitive advantage over other virtual network configurations. Overhead (Ulanowicz & Norden, 1990) is the difference between the magnitudes of the realized structure and its upper boundary. Whereas ascendency gauges the performance of a system in terms of how efficiently and with what definitiveness transfers are made, the overhead is complementary in that it quantifies how inefficiently and with what ambiguity the system is acting, on average. Redundancies or parallel flows in the imports, exports, dissipations and internal exchanges all contribute to the total overhead.

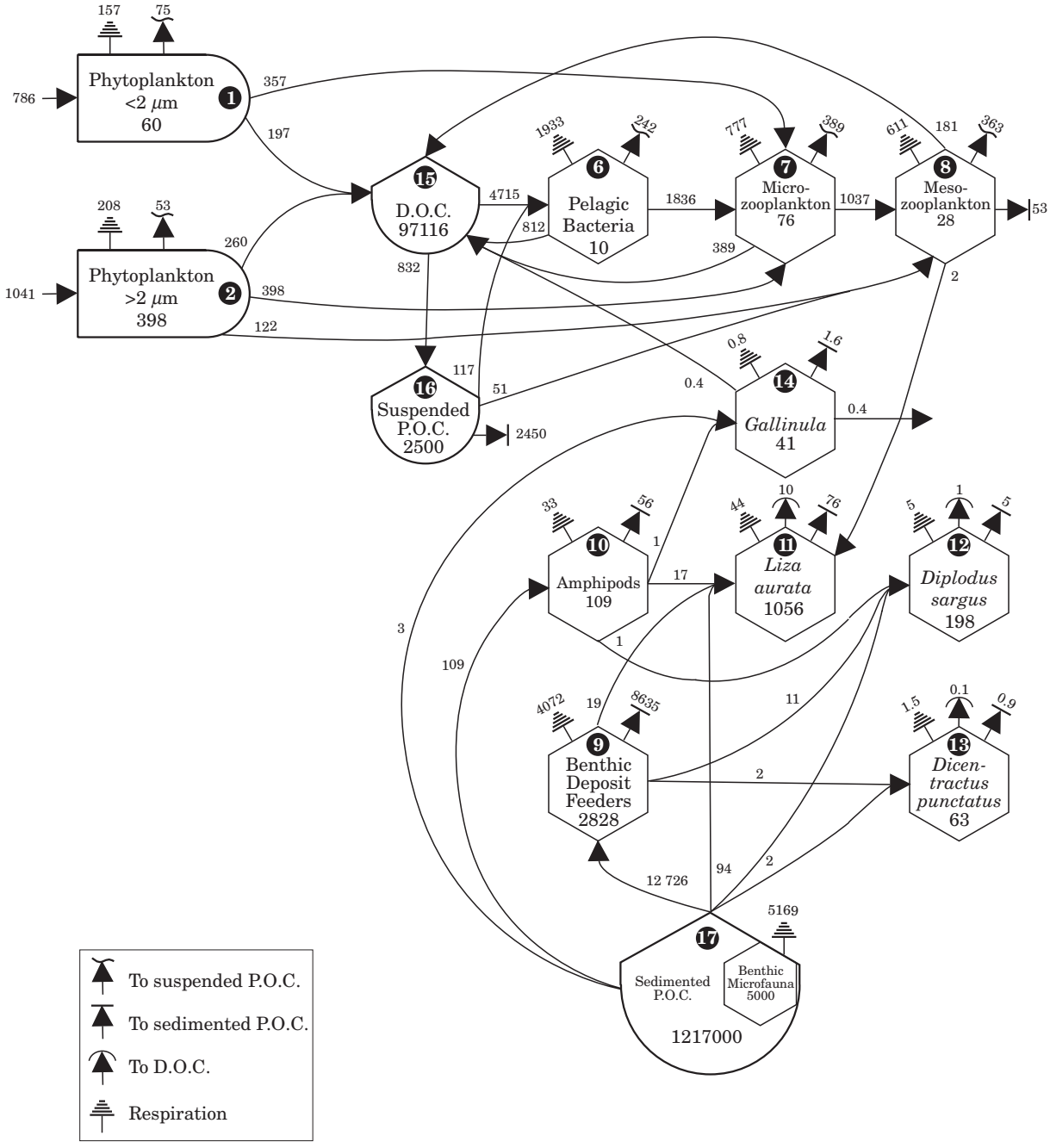


FIGURE 4. Energy flow network for stage 3 (symbols as in Figure 2).

Because the network was constructed primarily with direct measurements and supplemented with data from the literature, the final network was slightly unbalanced (by about 10% of total system throughput.) Final balance was achieved using the automated balancing routine, DATBAL (Ulanowicz, 1996). Since differences in the analyses carried out with NETWRK (Ulanowicz & Kay, 1991) for balanced and unbalanced data were minimal, the complete analysis was based on unbalanced data.

Phytoplankton

Phytoplankton was divided into two compartments, picoplankton (<2μm) and phytoplankton (>2μm). Both are grazed by microzooplankton, but

TABLE 1. Model data sources

Compartment	Parameter	Source
Pelagic primary producers	Biomass	Measurements of chlorophyll
	Production	% of net planktonic production (O2 method)
	Respiration	% of planktonic respiration (O2 method)
	Exudation	Baird and Ulanowicz (1989)
	Death	Jorgensen *et al.* (1991)
Benthic primary producers	Biomass	Direct observations and Edwards (1978), Verhoeven (1980), Harrison (1982), Flores-Verdugo *et al.* (1988) and Betancort (1993)
	Production	Congdon *et al* (1979), Pentecost (1984), Evans *et al.* (1986) and Menendez and Peñuelas (1993)
	Respiration and Exudation	Edwards (1978)
Pelagic bacteria	Biomass	Bacteria counts (epifluorescence)
	Assimilation	Calculated from planktonic respiration data
	Respiration	Hobbie and Williams (1984)
Microzooplankton	Biomass	Direct counts (epifluorescence)
	Grazing on phytoplankton, grazing on bacteria, respiration and excretion	Fenchel (1982)
Mesozooplankton	Biomass	Dry weight and CHN
	Grazing, respiration and excretion	Margalef (1983), Hobbie and Williams (1984) and Jorgensen *et al.* (1991)
Benthic microfauna	Biomass and respiration	Margalef (1983
Benthic deposit feeders	Biomass	Dry weight and CHN
	Assimilation, respiration and excretion	Moreno (1996)
Fish	Biomass	Fresh weight
	Diet, consumption and Assimilation	Moreno (1996)
	Respiration, excretion and egestion	Moreno (1996) and Wootton (1992)
Waterfowl	Biomass	Census
	Diet	Direct observation
	Respiration, excretion and egestion	Gibbons (1989)
DOC	Concentration	Total organic carbon analyzer measurements
Suspended POC	Concentration	CHN measurements
	Sedimentation and aggregation	Peterson (1984)
Sedimented POC	Concentration	CHN measurements

phytoplankton can also be eaten by mesozooplankton. Phytoplankton chlorophyll was determined fluorometrically (Holm-Hansen *et al.*, 1965) in a Turner Designs fluorometer that was calibrated with pure chlorophyll *a*. Triplicate samples were taken from the centre of the lagoon and subsamples were filtered onto Whatman GF/F filters (assumed to retain the total phytoplankton biomass) and onto Nuclepore 2μm pore size polycarbonate filters. The fraction <2μm was estimated by difference between the two measurements. A wide range of carbon to chlorophyll ratios (25 to 145) can be found in the literature (Strickland, 1960; Antia *et al.*, 1963; Parsons *et al.*, 1984; Jorgensen *et al.*, 1991) to estimate the biomass in carbon units from chlorophyll measurements. The 30 carbon/chlorophyll ratio suggested by Strickland (1960) was used, because it was closer to the values reported for healthy, actively growing phytoplankton.

Phytoplankton primary production was estimated by the differences in oxygen measurements taken in light and dark bottles, respectively. Six light and six dark bottles were incubated *in situ* at approximately 0·5 m depth from dawn to noon. The oxygen in each bottle was measured by an automated microwinkler titrator (Williams & Jenkinson, 1982); the coefficient of variation on the measures were always below 1%. Due to the lack of fractionated production measurements, estimates were divided up proportionally between the two phytoplankton compartments. Photosynthetic quotients (PQs) in the literature range from 1·1 to 1·3 (Parsons *et al.*, 1984). A PQ of 1·2 was used in this study to convert oxygen into carbon.

Literature on phytoplankton exudation showed values anywhere from 0·2 to 62% (Valiela, 1984; Baird & Ulanowicz, 1989; Jorgensen *et al.*, 1991) of primary production. The index was assumed to be

25% of primary production (Baird & Ulanowicz, 1989). The flux of phytoplankton to suspended detritus was calculated assuming a mean death rate equal to 9·6% of primary production (Jorgensen *et al.*, 1991).

Benthic primary producers

Benthic primary producers are composed mainly of the phanerogam *R. maritima* and the algae *C. globularis* and *Cladophora* sp. *Ruppia maritima* is grazed by amphipods (Verhoeven, 1980*b*), moorhens and some fishes (as deduced from stomach contents.) The algae were considered to be grazed only by herbivorous fishes.

To calculate the amount of *R. maritima* carbon per square metre, the percentage of area covered by the plant at each stage was estimated, and applied density values for *Ruppia* sp. in different reservoirs, as found in the literature (Edwards, 1978; Verhoeven, 1980*b*; Harrison, 1982; Flores-Verdugo *et al.*, 1988). Corresponding literature values were also used to calculate production (Congdon & McComb, 1979; Evans *et al.*, 1986; Menendez & Peñuelas, 1993), respiration and exudation (Edwards, 1978).

The same procedure was used to calculate algal biomass (Patronato de la Charca de Maspalomas, 1993), production, respiration (Pentecost, 1984) and exudation (25% of primary production, as in phytoplankton and *R. maritima*) for each stage.

Bacteria

Bacteria were assumed to be free-living heterotrophs suspended in the water column that use DOC and POC as their food source. They are grazed mainly by microzooplankton and occasionally by mesozooplankton.

Bacterial biomass was estimated by acridine orange staining and epifluorescence counts (Porter & Feig, 1980). A conversion factor of 2×10^{-14} g C cell^{-1} (Baird & Ulanowicz, 1989; Ballesteros, 1994) was used to estimate carbon biomass.

Although bacterial assimilation was not able to be measured directly, we were aware of the importance of estimating this parameter accurately. Therefore, planktonic respiration was calculated first, using metabolic coefficients from the literature. Then assimilation values were calculated that yielded figures for overall respiration equal to the pelagic respiration as measured in each phase using the dark bottle method.

We used ratios taken from the literature to calculate respiration, excretion and death of pelagic bacteria (Hobbie & Williams, 1984).

Respiration values by benthic bacteria were estimated from literature data for eutrophic lakes (Margalef, 1983) and were assigned to the POC compartment under the assumption that, from a trophic point of view, it is not necessary to distinguish between POC and bacterial carbon.

Microzooplankton (heterotrophic flagellates and ciliates)

The microzooplankton compartment represents the heterotrophic flagellates, which graze on pelagic bacteria and phytoplankton <2μm and are eaten by mesozooplankton.

Microzooplankton biomass was estimated by direct epifluorescence counts of heterotrophic flagellates after proflavine staining (Haas, 1982). Ratios for converting cells to carbon and rates of respiration and excretion were estimated from the literature (Fenchel, 1982).

Experiments with microzooplankton grazing on nutrient-enriched natural phytoplankton were carried out as in Landry and Hasset (1982). The grazing rate estimated in this manner was used as a maximum potential value, against which to check if microzooplankton were able to crop the existing production figures for phytoplankton and bacteria.

Mesozooplankton

The mesozooplankton compartment represents planktonic organisms >100 μm. In the second stage these consisted mainly of copepods and in the third stage, rotifers. Mesozooplankton were assumed to graze on phytoplankton >2 μm, microzooplankton and suspended POC. Due to the absence of any benthic plankton feeders or planktivorous fishes, it was considered that the mesozooplankton biomass flows primarily to the sediment POC and only a small amount is grazed by *L. aurata*.

Mesozooplankton were sampled by horizontal hauls of a WP2 (UNESCO 1968) 100 μm net. Biomass was estimated as dry weight (Lovegrove, 1966), using a 40% dry weight to carbon ratio, obtained from a CHN analysis of the dry biomass.

Grazing on phytoplankton was calculated under the same assumptions that were applied to microzooplankton and metabolic rates were taken from the literature (Margalef, 1983; Hobbie & Williams, 1984; Jorgensen, 1991).

Benthic deposit feeders

During each stage several sediment samples (1000 cm^3) were fractionated through 1000, 500 and

100 μm sieves. The results revealed that, as regards trophic habits, benthic organisms can be separated into either benthic deposit feeders (mainly worms and some chironomids) or herbivores (amphipods).

Benthic deposit feeders were separated from the sample and their dry weight was determined as in Lovegrove (1966). Biomass as carbon was calculated using an assumed carbon to dry weight ratio of 40%. Ingestion, respiration, excretion and death were calculated using indices from the literature (Moreno, 1996).

Amphipods

Amphipods have been frequently observed grazing on *Ruppia* sp. stands (Verhoeven, 1980; Menendez & Comín, 1990), so it was assumed that amphipods in Maspalomas graze exclusively on *R. maritima* and detritus, and that they are eaten by all predators that either graze on *R. maritima* or feed on detritus. Although epiphytic algae may also be part of the amphipods' diet, this item has not been considered in the present model. Amphipod biomass was calculated as for the benthic deposit feeders and the amounts of macrophytes consumed by animal populations in different seasons were taken from literature (Menendez & Comín, 1990).

Fish

The fish species found in Maspalomas exhibit different feeding behaviour. *Liza aurata* feed principally on detritus, however, mosquito larvae, benthic organisms and algae are also included in their diet. *Diplodus sargus* is an herbivorous fish feeding on the existing algal communities. Finally, *D. punctatus* is a carnivorous feeder with a high assimilation rate (Moreno, 1996).

Fish biomasses were calculated using abundance data from systematic samplings (Moreno, 1996), and carbon to freshweight indices from the literature (Parsons *et al.*, 1984). Diets were determined from an analysis of stomach contents, in conjunction with consumption to biomass indices taken from the literature (*L. aurata*: 5%, *D. punctatus*: 0·5%; and *D. sargus*: 2·75%; Wootton, 1992; Moreno, 1996). Indices from the literature also were used to calculate production, respiration, excretion and egestion for each species (Wootton, 1992).

Gallinula chloropus

The Viceconsejería de Medio Ambiente carried out visual censuses of waterfowl during recent years (R. Gallo, pers. comm.). Whereas other populations of waterfowl use Maspalomas opportunistically, *G. chloropus* appears to use this aquatic ecosystem as its primary habitat.

Unfortunately, due to the laws protecting the waterfowl, no stomach content analysis could be undertaken. The Moorhen's diet was assumed from observations on its behaviour made during each stage. Anatomic and metabolic parameters from the literature were also used (Gibbons, 1989).

POC and DOC

Both forms of organic carbon result from excretion, lysis and mortality or organisms, and become available to bacteria. Suspended POC can be filtered by mesozooplankton (no benthic filter-feeders were found in the ecosystem), whereas sedimented POC is ingested by benthic deposit feeders, fishes and moorhens.

Water samples of from 50 to 200 ml were filtered onto Whatman GF/F filters, acidified and stored frozen until measured in a Perkin-Elmer CHN Analyzer to calculate the suspended POC concentration. Phytoplanktonic carbon was subtracted from the result to calculate the concentration of detrital carbon. POC concentrations in the first 5 cm of sediment (Baird & Ulanowicz, 1989) were measured from several sediment samples taken from the muddy and sandy areas of the pond.

DOC concentrations were measured in a Shimadzu TOC Analyzer after acidification of the sample (UNESCO, 1994). Literature data were used to calculate POC sedimentation and DOC aggregation rates (Peterson, 1984).

Results

The total contribution coefficients (TCC) for each compartment do not show marked differences over the three stages (Table 2). The most relevant changes are the increments from first to second stage in almost all the contribution coefficients from pelagic bacteria, and in those from the benthic deposit feeders during the third. The total dependency coefficient (TDC) indicates overall decreased dependency on the benthic producers in successive stages (Table 3). This effect is compensated by corresponding increases in the dependencies on detritus. Both effects are to be expected from the observed development of the ecosystem; as benthic producers disappear, organisms are forced to change their diets and contributions from the detrital pool increase as a result.

The diagonal elements of the total dependency matrix indicate the amounts by which each species is

TABLE 2. Total contribution coefficients (TCC) matrix (percentage). Compartments are indicated by their number

Stage 1

	6	7	8	9	10	11	12	13	14	15	16	17
1	12	55	23	7	0	1	0	0	0	35	21	23
2	11	27	35	7	0	1	0	0	0	32	21	25
3	8	3	1	6	3	1	0	0	0	25	3	21
4	8	3	1	10	0	4	1	0	0	25	3	33
5	8	3	1	16	0	6	3	0	0	25	3	55
6	8	40	17	5	0	1	0	0	0	25	17	18
7	8	3	42	9	0	1	0	0	0	21	27	31
8	6	2	1	12	0	3	0	0	0	14	27	39
9	0	0	0	20	0	3	1	0	0	0	0	67
10	0	0	0	18	0	20	0	0	1	2	0	61
11	3	1	0	17	0	1	0	0	0	8	1	58
12	3	1	0	12	0	1	0	0	0	8	1	39
13	1	0	0	9	0	1	0	0	0	3	0	30
14	3	1	0	18	0	1	0	0	0	8	1	59
15	31	12	5	3	0	0	0	0	0	8	11	11
16	6	2	3	28	0	2	0	0	0	2	1	95
17	0	0	0	30	0	2	0	0	0	0	0	21

Stage 2

	6	7	8	9	10	11	12	13	14	15	16	17
1	31	55	24	3	4	1	0	0	0	35	24	30
2	30	45	30	3	4	1	0	0	0	34	26	31
3	22	10	4	2	9	9	3	0	0	26	7	20
4	22	10	4	3	4	18	4	0	0	26	7	29
5	24	11	5	4	5	26	13	0	0	28	8	40
6	22	45	19	2	3	1	0	0	0	25	16	2
7	18	8	43	4	4	1	0	0	0	21	17	35
8	14	6	3	4	5	1	0	0	0	14	31	38
9	0	0	0	7	8	5	1	0	0	1	0	66
10	0	0	0	7	8	5	0	0	0	0	0	68
11	7	3	1	7	7	2	0	0	0	8	2	59
12	7	3	1	5	5	1	0	0	0	8	2	41
13	3	1	1	3	4	1	0	0	0	0	1	31
14	9	4	2	5	5	1	0	0	0	10	3	43
15	86	39	17	3	4	1	0	0	0	22	29	30
16	7	3	3	8	10	2	0	0	0	2	2	75
17	0	0	0	11	12	3	0	0	0	0	0	15

Stage 3

	6	7	8	9	10	11	12	13	14	15	16	17
1	31	55	24	24	0	1	0	0	0	35	34	34
2	31	49	33	22	0	0	0	0	0	35	31	31
6	22	45	19	17	0	0	0	0	0	25	24	24
7	19	9	43	25	0	1	0	0	0	21	35	35
8	14	6	3	27	0	1	0	0	0	15	35	38
9	0	0	0	48	1	1	0	0	0	0	0	68
10	1	1	0	44	1	18	1	0	1	2	1	62
11	6	3	1	42	1	1	0	0	0	8	3	60
12	6	3	1	27	0	1	0	0	0	7	3	38
13	3	1	0	22	0	0	0	0	0	3	1	31
14	9	4	2	31	1	1	0	0	0	10	4	44
15	86	38	17	25	0	1	0	0	0	22	35	35
16	5	2	3	68	1	1	0	0	0	2	2	95
17	0	0	0	71	1	1	0	0	0	0	0	48

TABLE 3. Total dependency coefficients (TDC) matrix (percentage). Compartments are indicated by their number

Stage 1

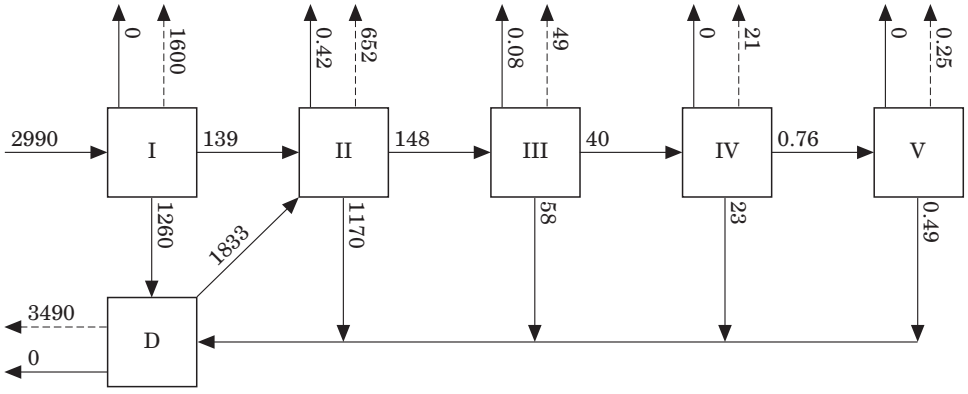
	6	7	8	9	10	11	12	13	14	15	16	17
1	1	12	10	0	0	0	0	0	0	1	5	0
2	1	4	10	0	0	0	0	0	0	1	3	0
3	90	77	65	15	99	31	39	15	100	91	65	15
4	5	4	4	1	0	5	8	1	0	5	4	1
5	1	1	1	1	0	2	8	1	0	1	1	1
6	8	85	70	1	0	1	1	1	0	8	36	1
7	4	3	82	1	0	1	0	1	0	3	27	1
8	1	1	1	1	0	1	0	1	0	1	14	1
9	0	0	0	20	0	24	42	73	0	0	0	20
10	0	0	0	1	0	14	8	1	17	0	0	1
11	1	1	1	2	0	1	1	2	0	1	1	2
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0
15	99	85	71	2	0	2	1	2	0	8	72	2
16	3	2	5	3	0	2	1	3	0	0	1	3
17	1	1	1	100	0	74	54	100	0	1	1	21

Stage 2

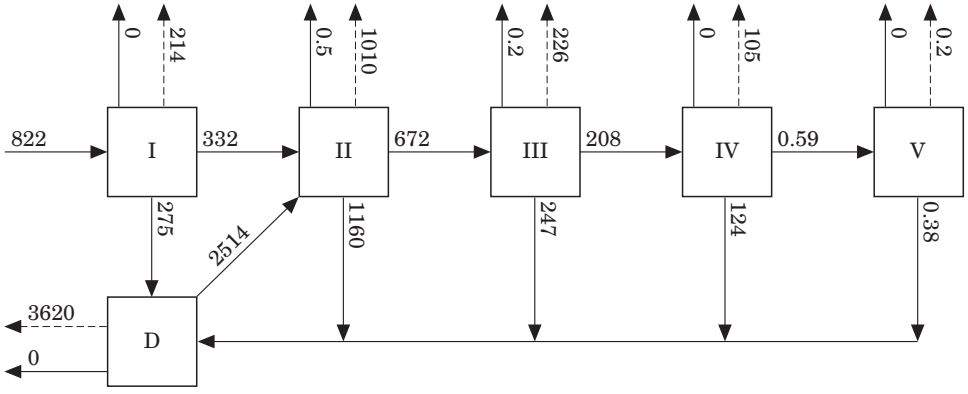
	6	7	8	9	10	11	12	13	14	15	16	17
1	14	36	30	3	3	3	2	3	3	13	25	3
2	6	12	16	1	1	14	1	1	1	5	11	1
3	3	2	14	1	2	8	24	1	1	3	2	1
4	1	0	0	0	0	4	8	0	0	1	0	0
5	0	0	0	0	0	2	8	0	0	0	0	0
6	22	65	54	6	6	5	3	6	6	22	37	6
7	13	8	83	6	6	6	4	6	6	12	27	6
8	5	3	3	3	3	4	2	3	3	4	25	3
9	0	0	0	7	7	17	40	69	20	0	0	7
10	0	0	0	9	8	19	12	9	22	0	0	9
11	1	1	0	2	2	2	1	2	2	1	1	2
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0
15	99	64	55	9	9	8	8	9	9	22	76	9
16	3	2	4	8	8	7	7	8	8	1	2	8
17	1	1	0	1	98	86	86	100	100	1	1	15

Stage 3

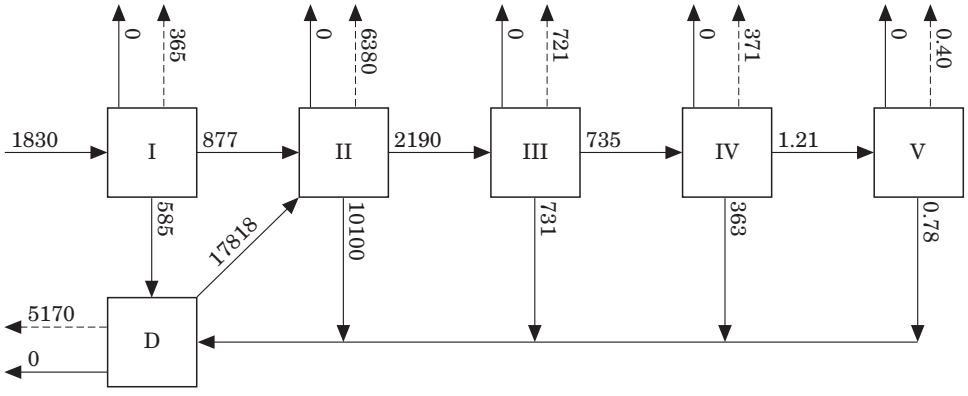
	6	7	8	9	10	11	12	13	14	15	16	17
1	6	18	16	3	3	3	3	3	3	6	10	3
2	8	21	30	3	3	4	3	3	3	8	13	3
6	22	71	62	10	10	10	10	10	10	22	35	10
7	12	9	87	9	9	10	9	9	9	12	32	9
8	4	3	3	5	5	6	5	5	5	4	16	5
9	0	0	0	48	48	55	89	83	48	0	0	48
10	0	0	0	0	1	19	8	1	26	0	0	1
11	0	0	0	0	1	1	1	1	1	0	0	1
12	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0
15	99	70	63	16	16	17	16	16	16	22	60	16
16	3	2	6	26	26	26	26	26	26	1	2	26
17	0	0	0	100	99	98	100	100	100	0	0	48



Stage 1



Stage 2



Stage 3

FIGURE 5. Aggregation of the flow web into a concatenated chain representing the discrete tropic levels and detritus (solid lines—carbon flows; broken lines—respiration; flows in mg m^{-2} day^{-1}).

dependent upon its own production via cycling pathways. These diagonal fractions generally are quite low, with only a few values equal or greater than 20% (benthic deposit feeders 20% and sedimented POC 21% in the first stage, pelagic bacteria 22%, and DOC 22% in the second and pelagic bacteria 22%, benthic deposit feeders 48%, DOC 22% and sedimented POC 48% in the third). The 48% recycling via the benthic deposit feeders and the sedimented POC is an unusually high figure. In fact, it is the largest percentage recycle of carbon ever reported. These figures provide evidence that detritivory progressively increases with each successive stages. The same evidence is provided by the successive dependencies of

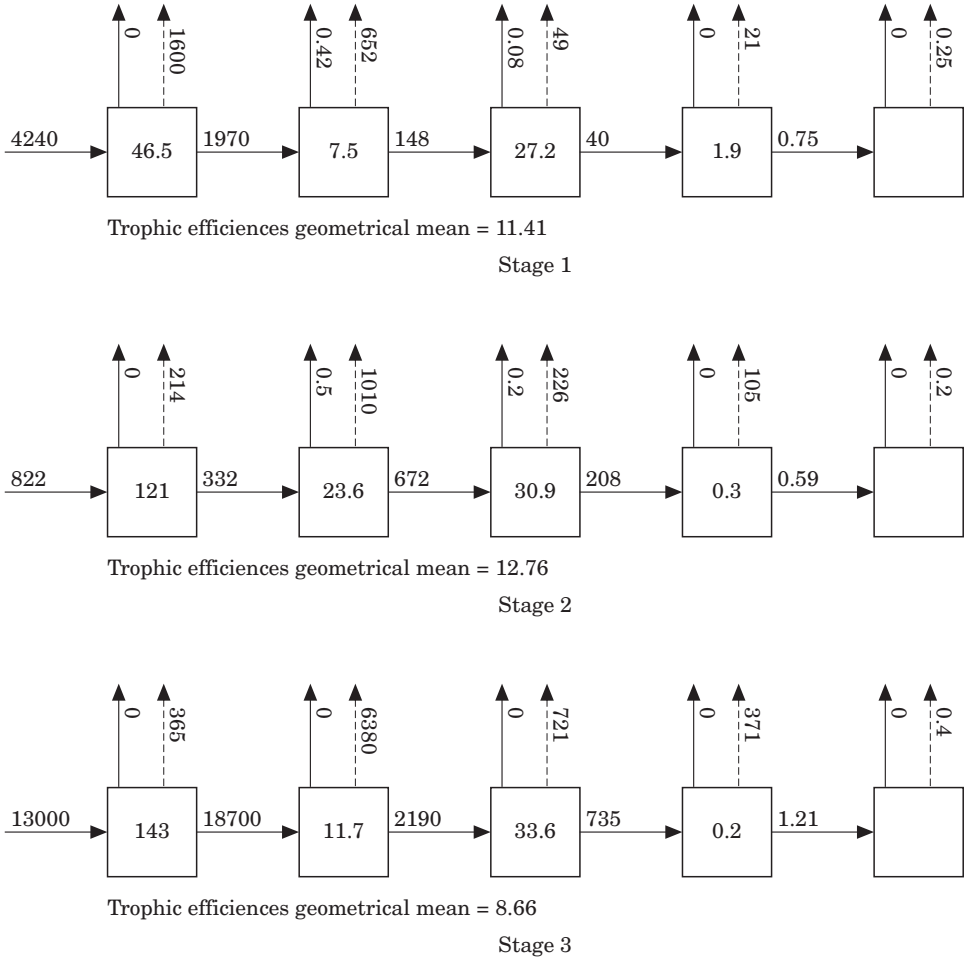


FIGURE 6. Aggregation of the flow web into a concatenated chain representing the discrete trophic levels, assuming detritus in the first level (symbols as in Figure 5).

the three detritic compartments upon themselves (DOC 2%, 9% and 16%, suspended POC 3%, 8% and 26%, and sedimented POC 21%, 15%, and 48%).

Any web of ecosystem interactions can be apportioned into a straight chain of discrete transfers (Ulanowicz, 1995) called the ‘ Lindeman spine ’. For example, if a population obtains 25% of its food from plants, 60% as a carnivore and 15% as a secondary carnivore, then its activity would be apportioned over levels 2, 3 and 4 of the Lindeman spine in the proportions 5:12:3, respectively. The Lindeman spines for the three stages all possess the same number of trophic levels (Figure 5).

Alternatively, one could weight the various pathways over which sustenance reaches a given predator by the number of trophic links in that pathway to obtain a non-integer ‘ average trophic position ’ (Levine, 1980). The predator used as an example in the last paragraph would feed at trophic level 2·9 ($=(0{\cdot}25\times 2)+(0{\cdot}60\times 3)+(0{\cdot}15\times 4)$). The highest average trophic level for any taxon is 3·64 for mesozooplankton, despite the fact that some fishes eat mesozooplankton. Fish diet is primarily based on detritus and primary producers (first trophic level) and only marginally on mesozooplankton (third trophic level). As a result, their average trophic positions fall substantially below 4.

The highest primary production values are found at the first stage, which is also when the lowest detritivory values were measured. The highest detritivory was registered in the third stage. The ratio of detritivory to herbivory was intermediate in the first stage (13·19), lowest in the second (7·57) and highest in the third (20·32). Precisely the opposite order was revealed in the geometric mean of the trophic efficiencies (Figure 6). Trophic efficiencies were moderate in the first stage (11·4), highest in the second (12·8) and lowest in the third (8·66). Trophic aggregation analysis confirms our expectation that

detritivory would be highest in the third stage, a circumstance which considerably reduces the averaged trophic efficiency at that stage.

The evolution in the pattern of recycling over the three ecosystem stages consists of an increase of the number of simple cycles from the first stage (99) to the second and third stages (159 and 155). Furthermore, the Finn Cycling Index increases as well (17·7%, 22·6% and 41·8%, respectively), indicating that the percentage of cycled matter increases as switching occurs. Odum (1969) suggested that mature ecosystems recycle a greater percentage of material and energy than do pioneer or disturbed communities. Viewed in this way, the progressive increase in the Finn Cycling Index would suggest a maturation of the ecosystem. Ulanowicz (1984), however, has remarked that perturbed systems also often exhibit greater degrees of recycling. Ulanowicz and Wulff (1991) hypothesize that such augmented cycling in disturbed systems is a homeostatic response that maintains in circulation resources that before the perturbation had been stored as biomass in the higher organisms. Looking deeper into the cycling structure, it can be seen that in all the stages, carbon cycles along short and fast loops. The average path-lengths of the system in all three stages are low (2·18, 2·42 and 2·14 respectively), and the percentage of matter cycled over loops of various trophic lengths (Table 4) reveals that in stage 3, proportionately more matter is cycling over the shortest cycles, despite the increase in the Finn Index at that stage (Table 4). This observation supports the previous indications that the system is stressed at all three stages and is not maturing.

The evolution of total system throughput (TST) begins with a smooth decrease between the first and second stage, followed by a dramatic increase in the third stage (Table 5). These changes in TST modulate the variation in development capacity (DC), the network's *potential* for competitive advantage (Ulanowicz & Norden, 1990), which increases at each stage, although the informational factor (in bits) does not change as dramatically. Much the same pattern of change can be seen in the Ascendency (a unitary measure of activity and organization), which increases markedly toward the third stage, due mostly to the precipitous rise in TST. The positive evolution of these indices, fuelled as it is by a burgeoning TST does not, however, reveal ecosystem maturation, but rather indicates what often happens after the invasion of a new spatial domain following a major perturbation (Golley, 1974; Ulanowicz, 1997), a scenario that is consistent with the previous results outlined above.

The degree to which a system realizes its potential for growth, organization and development is given by the ratio A/C (Ulanowicz & Mann, 1981). Highly organized systems exhibit the tendency to internalize most of their activity, and thereby to become relatively independent of exchanges with the external world. Hence, the ratio of the indices A_i and C_i (Internal Ascendancy and Internal Capacity, calculated using internal exchanges only) is considered to be representative of a system's developmental status (Field *et al.*, 1989; Mann *et al.*, 1989; Baird *et al.*, 1991). This ratio is almost unchanged in the two first stages and rises in the third, suggesting that the last stage is a better organized system possessing more internal stability, which makes it difficult to change its basic structure via external influences (Table 5).

TABLE 4. Cycle normalized distributions (percentage of matter cycled through different cycle length)

Cycle length	Stage 1	Stage 2	Stage 3
1	0	0	0
2	16·1	16	37
3	0·83	3·92	2·78
4	0·31	2·21	1·64
5	0·07	0·24	0·08
6	0·28	0·09	0·02
7	0·08	0·06	0·02
Total (Finn Index)	17·7	22·6	41·8

Conclusions

The ecological study of the disappearance of benthic producers from Maspalomas lagoon, describes not merely the senescence of an ecosystem, but also the development of a new pelagic structure emerges as a result of the crisis that befalls the benthos.

Part of the trophic development is an increment in overall detritivory, presumably as a homeostatic response of the system to retain the organic carbon released from the previous ecosystem structure. This large amount of matter is circulated over fast, short loops in the new structure and in combination with an increment in pelagic primary production, results in a high total system throughput. This pattern of behaviour is consistent with the hypothesis that, at the beginning, immediately after a system has undergone a major destructive perturbation, or when it is invading a new spatial domain, the initial response of the system is to augment its activities and biomass at the fastest rate possible (Golley, 1974). This increase in system activity, reflected in the significant rise in TST, also augments the development capacity and Ascendency, even though no such intense changes are

TABLE 5. Information indices. Where TST, DC, A, Overheads, R, Ci and Ai are expressed in mg C m^{-2} day^{-1}, between brackets are percentages of the development capacity, finally A/C and Ai/Ci are adimensional indices

Index	Stage 1	Stage 2	Stage 3
Total system throughput (TST)	13 626	12 264	51 544
Development capacity (DC)	47 840	52 359	192 750
Development capacity (Bits)	3·51	4·27	3·74
Ascendancy (A)	19 349 (40·4%)	19 854 (37·9%)	87·047 (45·2%)
Overhead on imports	1522 (3·2%)	1312 (2·5%)	1801 (0·9%)
Overhead on exports	2 (0%)	785 (1·5%)	6 (0%)
Dissipative overhead	13 923 (29·1%)	12 932 (24·7%)	49 389 (25·6%)
Redundancy (R)	13 044 (27·3%)	17 476 (33·4%)	54 327 (28·2%)
Internal capacity (Ci)	23 136	31 436	128 260
Internal Ascendancy (Ai)	10 091	13 960	73 935
A/C	0·404	0·379	0·452
A/TST (Bits)	1·42	1·62	1·69
Ai/Ci	0·436	0·444	0·576

evident in the normalized versions of these indices. (The ratio internal Ascendancy/internal capacity does, however, indicate an increase in the developmental status during the third stage.)

The drastic changes in the system from stage 1 to stage 3 appear outwardly to portray the process of eutrophication, but the changes in whole system indices do not confirm this conclusion. Ulanowicz (1986*b*) has defined eutrophication as ' any increase in system Ascendency due to a rise in total system throughput that more than compensates for a concomitant fall in the mutual information of the flow network. ' Although, the TST does increase drastically during phase 3, the average mutual information (A/TST) of the system does not decrease. It actually increases from 1·42 bits in stage 1 to 1·69 bits in stage 3.

The most likely explanation of this phenomenon is a shift in resources from one subsystem (the benthic) to another (the pelagic) within Maspalomas. No appreciable resources are being added to the system from the outside. If one wanted to make the case for eutrophication, one would have to confine the analysis strictly to a comparison of the pelagic subsystem between stages 1 and 3. Overall, however, resources are simply being transferred from the benthic subsystem, with its attendant redundancies, to the more streamlined pelagic subsystem. Eventually, the system reverses itself and reconstructs the more intricate benthic community.

The entire cycle is reminiscent of Holling's (1986) ' figure–8 ' scenario for ecosystem development. Holling identifies ' creative destruction ' as an element of almost all ecosystem behaviours. Although conditions in stage 3 are not aesthetically pleasing and do indicate that the process of eutrophication may have occurred over a number of decades, the transition from stages 1 to 3 is not in itself an example of eutrophication and the indices confirm this conclusion. In order to establish that the Charca is a eutrophic ecosystem, it would be necessary to compare an annual network (that could be elaborated with seasonal data presented here) with one that which existed several decades ago.

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Appendix

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
Phytoplankton<2 µm	Primary production	First	25	Primary production measured by oxygen changes (µmol $O_2 l^{-1}$ hr^{-1}) in *in situ* incubated BOD bottles (Microwinkler titration). Per unit biomass rates are multiplied by the chlorophyll in <2µm fraction. The flux is expressed as mg C m^{-2} day^{-1} considering a photosynthetic quotient of 1·2 (Parsons *et al.*, 1984), a mean depth of 1 m and the sunlight hours at each stage.
		Second	469	
		Third	785	
	Respiration	First	5	20% of primary production (Moshkina, 1961; Parsons *et al.*, 1984; Williams, 1984; Sakshaug *et al.*, 1989; and Baird & Ulanowicz, 1989).
		Second	94	
		Third	157	
	Exudation	First	6	25% of primary production (Valiela, 1984; Baird & Ulanowicz, 1989; and Jorgensen *et al.*, 1991).
	1→15	Second	117	
		Third	197	
	Death	First	1	Death rate is assumed to be 9·6% of primary production (Jorgensen *et al.*, 1991).
	1→16	Second	45	
		Third	75	
	1→7	First	13	By difference, assuming a balanced compartment.
		Second	213	
		Third	357	
Phytoplankton>2µm	Primary production	First	17	Same as for <2 µm phytoplankton, but multiplying by the chlorophyll in >2 µm fraction.
		Second	196	
		Third	1041	
	Respiration	First	4	Assumed to be 20% of primary production (Moshkina,1961; Parsons *et al.*, 1984; Williams, 1984; Sakshaug *et al.*, 1989 and Baird & Ulanowicz, 1989).
		Second	39	
		Third	208	
	Exudation	First	4	25% of primary production (Valiela, 1984; Baird & Ulanowicz, 1989, and Jorgensen *et al.*, 1991).
	2→15	Second	49	
		Third	260	
	Death	First	1	Assumed to be 9·6% of primary production (Jorgensen *et al.*, 1991).
	2→16	Second	19	
		Third	53	
	2→7	First	4	Chlorophyll consumption rate was measured by grazing experiments (Landry y Hasset, 1982) and transformed to carbon units using a C:Chl *a* ratio of 30 (Antia *et al.*, 1963; Parsons *et al.*, 1984; and Jorgensen *et al.*, 1991).
		Second	67	
		Third	398	
	2→8	First	4	By difference, assuming a balanced compartment.
		Second	22	
		Third	122	
Ruppia maritima	Primary production	First	2760	Primary production estimations (mg 0_2 g dw^{-1} h^{-1}) for different coastal lagoons were used (Congdon & McComb, 1979; Evans *et al.*, 1986; and Menendez & Peñuelas, 1993). mg C m^{-2} day^{-1} were calculated on the basis of biomass estimations, sunlight hours in each sampling and a photosynthetic quotient of 1.
		Second	120	
		Third	0	
	Respiration	First	1512	*R* is calculated using respiration rates measured for *R. maritima* (mg O_2 g dw^{-1} h^{-1}) at different production rates (Edwards, 1978). mg C m^{-2} day^{-1} were calculated from the estimated biomass, a respiratory quotient=1 and an homogeneous 24 hour respiration cycle.
		Second	66	
		Third	0	
	Exudation	First	696	Using net production data for *R. maritima* from Edwards (1978) an exudation rate of 25·2% of gross production is calculated.
	3→15	Second	30	
		Third	0	

Appendix *continued*

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
Ruppia maritima continued	3→10	First	91	Calculated from consumption to biomass indices for *Gammarus* sp. feeding on *R. maritima* (Menendez & Comín, 1990). Biomass of anphypods from direct measurements.
		Second	8	
		Third	0	
	3→11	First	10	Calculated from a 5% diel consumption to biomass index (Wootton, 1992). *Liza aurata* biomass was estimated by Moreno (1996).
		Second	10	Stomach content analysis (Moreno, 1996) showed that benthic producers were 10% of *Liza aurata* diet. Ingestion was apportioned between the benthic producers based on their abundance.
		Third	0	
	3→12	First	3	Calculated from a 2·8% diel consumption to biomass index (Wootton, 1992). Benthic producers represent 34% of *D. sargus* diet (Moreno 1996). Ingestion is apportioned between the benthic producers based on their abundance.
		Second	3	
		Third	0	
	3→4	First	5	Calculated from a 9% diel consumption to biomass index (Gibbons, 1989). Biomass estimated from visual census. *R. maritima* is considered to represent 85% of *G. chloropus* diet.
		Second	0	
		Third	0	
	Death	First	446	By difference.
	3→17	Second	2	
		Third	0	
Chara globularis	Primary production	First	151	Calculated multiplying production (μ C g dw^{-1} h^{-1}) data from the literature (Pentecost, 1984) by historical biomass data (Betancort, 1993) and sunlight hours at each sampling.
		Second	29	
		Third	0	
	Respiration	First	66	44% of primary production (Haniffa & Pandian, 1978).
		Second	13	
		Third	0	
	Exudation	First	38	25% of primary production (Valiela, 1984; Baird & Ulanowicz, 1989; and Jorgensen *et al.*, 1991).
	4→15	Second	7	
		Third	0	
	4→1	First	5	Calculated from a 5% diel consumption to biomass index (Wootton, 1992). *Liza aurata* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic producers represent 10% of *L. aurata* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	5	
		Third	0	
	4→12	First	1	Calculated from a 2·8% diel consumption to biomass index (Wootton, 1992). *Diplodus sargus* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic producers represent 34 of *D Sargus* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	1	
		Third	0	
	Death	First	42	By difference.
	4→17	Second	3	
		Third	0	
Cladophora	Primary production	First	40	Calculated multiplying production (μg C g dw^{-1} h^{-1}) data from the literature (Gordon *et al.*, 1980; Lester *et al.*, 1988 and Dodds & Gudder, 1992) by the biomass and the sunlight hours in each sampling.
		Second	8	
		Third	0	

Appendix *continued*

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
Cladophora continued	Respiration	First	8	20% of primary production (Dodds & Gudder, 1992).
		Second	2	
		Third	0	
	Exudation	First	10	25% of primary production (Valiela, 1984; Baird & Ulanowicz, 1989; and Jorgensen *et al.*, 1991).
	5→15	Second	2	
		Third	0	
	5→11	First	2	Calculated from a 5% diel consumption to biomass index (Wootton, 1992). *Liza aurata* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic producers represents 10% of *L. aurata* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	2	
		Third	0	
	5→12	First	1	Calculated from a 2·8% diel consumption to biomass index (Wootton, 1992), by *D. sargus* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic producers represent 34% of *D. sargus* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	1	
		Third	0	
	Death	First	20	By difference.
	5→17	Second	1	
		Third	0	
Pelagic Bacteria	DOC assimilation	First	255	DOC assimilation was estimated using community respiration measured in oxygen *in situ* incubations. Respiration coefficients for planktonic organisms were obtained from literature. Bacteria assimilation was adjusted to equal plankton respiration at the measured respiration rates.
		Second	1326	
		Third	4715	
	POC assimilation	First	6	Was assumed to be 2·5% of DOC assimilation.
		Second	33	
		Third	117	
Pelagic Bacteria	Respiration	First	104	Obtained from the planktonic community respiration estimations.
		Second	544	
		Third	1933	
	6→7	First	99	By difference, assuming a balanced compartment. Results were always below maximum grazing capability calculated from grazing experiments performed as in Landry and Hasset (1982). Carbon units were obtained using a C:Chl *a* ratio of 30 (Antia *et al.*, 1963; Parsons *et al.*, 1984; and Jorgensen *et al.*, 1991).
		Second	516	
		Third	1836	
	6→15	First	44	17% of assimilation (Peterson, 1984).
		Second	231	
		Third	812	
	Death	First	13	5% of assimilation (Peterson, 1984).
	6→16	Second	68	
		Third	242	
Microzooplankton	Respiration	First	35	30% of ingestion (Fenchel, 1982; Peterson, 1984).
		Second	239	
		Third	777	
	Excretion	First	17	15% of ingestion (Fenchel, 1982; Peterson, 1984).
	7→15	Second	119	
		Third	389	

Appendix *continued*

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
Microzooplankton continued	7→8	First	47	By difference, assuming a balanced prey compartment. Results were below maximum grazing capability calculated from grazing experiments performed as in Landry and Hasset (1982). Carbon units were obtained using a C:Chl *a* ratio of 30 (Antia *et al.*, 1963; Parsons *et al.*, 1984; and Jorgensen *et al.*, 1991).
		Second	320	
		Third	1037	
	Death	First	17	By difference
	7→16	Second	119	
		Third	389	
Mesozooplankton	Respiration	First	27	50·5% of ingestion (Margalef, 1983).
		Second	177	
		Third	611	
	Egestion	First	15	30% of ingestion (Jorgensen *et al.*, 1991).
	8→16	Second	105	
		Third	363	
	8+1	First	1	Due to the absence of zooplankton in the stomach contents studies (Moreno, 1996) a minimum consumption was assumed since ingestion studies were carried out during low zooplankton abundance periods.
		Second	1	
		Third	2	
Mesozooplankton	8→15	First	8	15% of ingestion (Jorgensen *et al.*, 1991).
		Second	53	
		Third	181	
	Death	First	7	By difference
	8→17	Second	52	
		Third	53	
Benthic deposit feeders	Respiration	First	475	32% of ingestion (Moreno, 1996).
		Second	158	
		Third	4072	
	9→11	First	16	Calculated from a 5% diel consumption to biomass index (Wootton 1992). *Liza aurata* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic producers represent 10% of *L. aurata* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	16	
		Third	19	
	9→12	First	5	Calculated from a 2·8% diel consumption to biomass index (Wootton 1992). Biomass estimated by Moreno (1996). Stomach contents (Moreno 1996) show that benthic producers represent 34% of *Diplodus sargus* diet. Ingestion is apportioned between the benthic producers based on their abundance.
		Second	5	
		Third	11	
	9→13	First	2	Calculated from a 0·5% diel consumption to biomass index (Wootton, 1992). *Dicentrarchus punctatus* biomass estimated by Moreno (1996). Stomach contents (Moreno, 1996) show that benthic deposit feeders represent 59% of *D. punctatus* diet.
		Second	2	
		Third	2	
	Egestion and death 9→17	First	987	By difference.
		Second	313	
		Third	8635	
Anphypods	Respiration	First	28	30% of ingestion (Verhoeven, 1980*a*).
		Second	176	
		Third	33	

Appendix *continued*

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
Anphypods continued	10→11	First	17	Calculated from a 5% diel consumption to biomass index (Wootton, 1992). Stomach contents (Moreno, 1996) show that anphypods represent 10% of *L. aurata* diet.
		Second	17	
		Third	19	
	10→12	First	1	Calculated from a 2·8% diel consumption to biomass index (Wootton, 1992). Stomach contents (Moreno, 1996) show that anphypods represent 14% of *D. sargus* diet.
		Second	1	
		Third	1	
	10→14	First	1	Calculated from a 9% diel consumption to biomass index (Gibbons, 1989). *Gallinula chloropus* biomass estimated from visual census. It is considered that anphypods represent 15% of *G. chloropus* diet.
		Second	1	
		Third	1	
	Death	First	45	By difference.
	10→17	Second	375	
		Third	56	
Liza aurata	Respiration	First	44	30% of ingestion (Wootton, 1992).
		Second	44	
		Third	44	
	Excretion	First	10	7·5% of ingestion (Wootton, 1992).
	11→15	Second	10	
		Third	10	
	Egestion	First	76	52% of ingestion (Wootton, 1992).
	11→17	Second	76	
		Third	76	
Diplodus sargus	Respiration	First	5	44% of ingestion (Wootton, 1992).
		Second	5	
		Third	5	
	Excretion	First	1	7·5% of ingestion (Wootton 1992)
	12→15	Second	1	
		Third	1	
	Egestion	First	5	38% of ingestion (Wootton, 1992).
	12→17	Second	5	
		Third	5	
Dicentrarchus punctatus	Respiration	First	1·5	37% of ingestion (Wootton, 1992).
		Second	1·5	
		Third	1·5	
	Excretion	First	0·1	7·5% of ingestion (Wootton, 1992).
	13→15	Second	0·1	
		Third	0·1	
	Egestion	First	0·9	22·5% of ingestion (Wootton, 1992).
	13→17	Second	0·9	
		Third	0·9	
Gallinula chloropus	Respiration	First	1	$0{\cdot}534\ W^{0{\cdot}723}$, where W is the *G. chloropus* biomass (Gibbons, 1989).
		Second	1·4	
		Third	0·8	
Gallinula chloropus	Excretion	First	3·5	8% of ingestion (Gibbons, 1989).
	14→5	Second	2·8	
		Third	1·1	
	Egestion	First	0·5	50% of ingestion (Gibbons, 1989).
	14→17	Second	0·7	
		Third	0·4	
	Exports	First	0·5	8% of ingestion (Gibbons, 1989).
		Second	0·7	
		Third	0·4	

Appendix *continued*

Compartment	Flux	Stage	Magnitude mg C m^{-2} day^{-1}	Source or estimation
DOC	Bacterial assimilation 15→6	First	255	DOC assimilation was estimated using community respiration measured in oxygen *in situ* incubations. Respiration coefficients for planktonic organisms were obtained from literature. Bacteria assimilation was adjusted to equal plankton respiration at the measured respiration rates.
		Second	1326	
		Third	4715	
	Aggregation 15→16	First	45	15% of the DOC concentration y^{-1} (Peterson, 1984).
		Second	234	
		Third	832	
POC	Bacterial assimilation 16→6	First	6	Was assumed to be 2·5% of DOC assimilation.
		Second	33	
		Third	117	
	16→8	First	2	Is calculated from the total zooplankton grazing and the relative abundance of POC compared to the other food resources.
		Second	9	
		Third	51	
	Sedimentation 16→7	First	108	30% of all POC inlets (Peterson, 1984; Jorgensen *et al.*, 1991).
		Second	341	
		Third	2450	
Sedimented Organic Carbon	Respiration	First	700	Calculated from subtracting to the total ecosystem respiration, which was calculated from diel oxygen cycles (Fast *et al.*, 1988), the estimated respiration for all other compartments.
		Second	700	
		Third	2661	
	17→9	First	1485	Calculated using a consumption:biomass ratio of 450% (Moreno, 1996). Benthic deposit feeder carbon concentration was obtained from sediment samples.
		Second	495	
		Third	12 726	
	17→10	First	0	Calculated from *Gammarus* sp. average consumption demand (Menendez & Comín 1990). It is assumed that *Gammarus* sp. preferably feeds on *R. maritima* and diet is compleated by sediment ingestion.
		Second	561	
		Third	109	
Sediment	17→11	First	82	Calculated from a 5% diel consumption to biomass index (Wootton, 1992). Stomach contents (Moreno, 1996) show that detritus can represent 70% of *L. aurata* diet. Only if other resources are not available the demand is compensated with detritus ingestion.
		Second	82	
		Third	94	
	17→12	First	2	Calculated from a 2·8% diel consumption to biomass index (Wootton, 1992). Stomach contents (Moreno, 1996) show that detritus may represent 18% of *D. sargus* diet. Only if other resources are not available the demand is compensated with detritus ingestion.
		Second	2	
		Third	2	
	17→13	First	1	Calculated from a 0·5% diel consumption to biomass index (Wootton, 1992). Stomach contents (Moreno, 1996) show that detritus may represent 41% of *D. punctatus*.
		Second	1	
		Third	1	
	17→14	First	0	By difference between *R. maritima* availability and *G. chloropus* consumption demand.
		Second	5	
		Third	3	