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Assessment of environmental management effects in a shallow water basin using mass-balance models

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Abstract

Comparative analysis of trophic networks was carried out to evaluate environmental management actions aimed at countering an environmental crisis in Orbetello Lagoon, Italy. Two mass-balance models of this shallow water coastal system were constructed, for 1995 and 1996. During this period, there was an observed change in the composition of the submerged vegetation that indicated a significant improvement in the lagoon's ecology. Mass-balance models were built using the Ecopath modelling software in order to explain the energy transfer through the trophic levels (TLs) of the lagoon's ecosystem.

Comparative analysis of the two trophic networks allowed a complete description of the lagoon, and gave clear indications regarding the 'eutrophication level' sensu Nixon and the stage of system maturity sensu Odum of the ecosystem for the 2 years. The turnover rate (production/biomass ratio) of pleustophytes was proposed as an indicator of "environmental health" at the ecosystem level because it allows positioning the submerged vegetation as a whole along an axis of adaptation strategies to natural selection. All the indices of ecosystem maturity and stability examined showed that the lagoon was in a more stable condition in 1996 than in 1995, although the system was still in a condition of stress.

The effects of management actions carried out in the system were quantified by estimating the changes in primary production and accumulation of detritus in the system. Management of the lagoon as an extensive aquaculture operation was assessed by analysing the fishery catch, the transfer efficiencies at different trophic levels and the impact of cormorants, and it was found to contribute to system stability.

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1. Introduction

Coastal lagoons are ecosystems characterized by high productivity, typically 10-15 times that of conti-

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nental shelves (Carrada and Fresi, 1988; Duarte, 1995; Valiela, 1995). This is the result of intense bacterial activity which ensures ready re-mineralization of organic matter and recirculation of nutrients, including those in the sediments (Mann, 1988; Sorokin et al., 1996). Complex food webs and resilience of the communities to the changes on environmental conditions characterize these systems (Lankford, 1977; Carrada and Fresi, 1988). More than in other marine systems,

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the dynamics of primary production are linked to the role of benthic and planktonic producers (Mann, 1988; Izzo and Hull, 1991; Borum and Sand-Jensen, 1996). Coastal lagoons are "nursery" or "growing" areas for numerous valuable marine species and are areas where many species spend part of their biological cycle. Particular management activities are often necessary to maintain water exchange and migrations of fish between the sea and the lagoon, on which the productive activities of lagoons are based (Kapetsky and Lasserre, 1984; Cataudella et al., 1995). The finfish harvest from lagoons is approximately 30% by weight of total aquaculture production in Italy, as in other countries of the Mediterranean area (FAO, 2000).

Orbetello Lagoon in central western Italy is a shallow coastal environment characterized by limited exchange with the sea and a high availability of nutrients.

Between 1975 and 1993, the basin showed increasing eutrophication (Cognetti et al., 1978; Lenzi and Angelini, 1984; TEI, 1989; Bucci et al., 1991, 1992; Bombelli and Lenzi, 1995; Cartei and Innamorati, 1997). During spring and summer, algal blooms occurred with increasing frequency and often those blooms were accompanied by anoxic crisis, resulting in marked changes, notably in submerged vegetation composition, with a progressive substitution of phanerogams (Ruppia and Zostera) by pleustophytes (Ulva and Cladophora). These events were often accompanied by the death of aerobic organisms, particularly benthic fauna and finfish (Lenzi, 1992). During 1986 and 1993, 150 and 90 tonnes, respectively, of fish died during anoxic events (Lenzi, 1992; Innamorati, 1998). The last years of the 1980s were characterized by the increase of biomass of Chaetomorpha linum, until in 1995 Cladophora vagabonda dominated benthic community of primary producers of the lagoon, creating a monoxenic population (Bombelli and Lenzi, 1995).

Since 1993, a series of environmental management activities were carried out by the Government Management Authority, such as the abatement of nutrient load by reducing sewage input, increasing water circulation and selective macroalgae harvesting (Lenzi and Mattei, 1998).

The selective harvest of macroalgae and the associated nutrient reduction are management tools of which the short-term effects are understood (Cecconi and Silvestrini, 1995; Lenzi and Mattei, 1998; Lavery

et al., 1999), but the mid- and long-term effects are still subject of debate (e.g. Duarte, 1995). Algal harvesting removes a source of organic carbon and nutrients from the system, reducing the likelihood of future anoxic conditions in the basin (Lenzi and Mattei, 1998; Lavery et al., 1999). In the long-term, such management activities can facilitate the return of species that are characteristic of more stable environments (Duarte, 1995; Silvestri et al., 1999), but it is not possible to determine when and how the re-colonization, in this case of phanerogams, will occur (Cecconi and Silvestrini, 1995).

Between 1995 and 1996, the first effects of the selective algal harvest and of the environmental management were observed. After 1994, there was a gradual change in macroalgae dominance from *Cladophora* to *Gracilaria*, this latter representing up to 70% of the biomass of the community in 1996. Further, from spring 1995, significant re-growth of phanerogams (*Ruppia cirrhosa* and *Zostera noltii*) was observed, although their biomass did not reach the 10% of the total standing crop of the macrophyte community (Alberotanza et al., 1998; Lenzi and Mattei, 1998). There was also an accompanying decrease in opportunistic species in the zoobenthic community (Lardicci et al., 1997; Lardicci and Rossi, 1998).

Aside from eutrophication-related problems, there is conflict between different types of exploitation in the lagoon as fish production conflicts with the wild bird fauna. The lagoon of Orbetello is situated along one of the main bird migratory routes between Europe, Asia and Africa, and a variety of species winter there in large numbers (Baccetti and Corbi, 1988). Cormorants play a central role at Orbetello in the regulation of the marketable finfish biomass present in the ecosystem (Baccetti et al., 1997).

In the present work, a comparison between the trophic networks in 2 years, namely 1995 and 1996, was used to quantify and analyse the trophic state and development stage of the ecosystem and evaluate the effects of management activities. The network indices and the quantification of energy flows in the ecosystem structure were used to estimate energy transfer efficiency trough the trophic groups. Moreover, comparative network analysis allowed quantification of the importance of direct and indirect trophic interactions in the trophic network of this coastal environment.



Fig. 1. Map of Orbetello Lagoon, Italy.

2. Materials and methods

2.1. Site description

Orbetello Lagoon (Fig. 1) consists of two basins with a depth of about 1 m and a total area of $27 \, \mathrm{km}^2$. These shallow water basins are coastal ponds with brackish environments and no tidal influence. Thus, their morphological characteristics are different to typical lagoons systems elsewhere (Orme, 1990; Barnes, 1994). The bottom is slightly concave and there are no canals or shoal areas. The sediment structure and hydrological conditions are more typical of lacustrine systems (Brambati, 1988). Water circulation is mainly wind driven and limited exchange occurs with sea and the Albegna River via narrow channels (Fig. 1). Thus, the system acts as a sediment trap and the sediments are re-suspended only after strong wind events.

Fish barriers (*lavorieri*) in the channels linking the lagoon with sea enable Orbetello Lagoon to be used extensively for aquaculture (Cataudella, 1988; EC, 1995). As well as naturally occurring species, fingerlings of commercial species have been introduced. Harvesting is carried out by a single fishery company, Orbetello Pesca Lagunare (OPL).

2.2. Trophic network analysis and mass balance

In order to evaluate the effects of management on the whole ecosystem and to evaluate how changes in primary production might propagate through a trophic network, we used an aggregated mass-balance model in which each compartment represents a functional trophic group of the lagoon species. Such models can explain the energy transfer mechanisms between trophic levels (TLs) of the lagoon ecosystem; trophic interactions of the lagoon community are represented within the model, including fishery impact.

Mass-balance models represent a static description or a 'snapshot' of the trophic flows in the ecosystem (Christensen, 1994). Such snapshots can be readily compared and therefore, used to explore the evolution of a system through a series of stages or stable states (Christensen and Pauly, 1993a). The analysis of trophic networks consists of algorithms that describe the flows of energy, the cycles and some properties of the system through examination of the trophic food chain (Ulanowicz, 1986; Odum and Peterson, 1996). The flow structures and their dimensions contain important information on the ecosystem (Ulanowicz, 1986; Field et al., 1989; Wulff et al., 1989).

Network analysis has been widely applied as a tool in the management of coastal and lagoon environments (Mann et al., 1989; Christensen and Pauly, 1993b). Comparisons between systems or between different periods for the same system can help ecosystem managers in determining the trophic state or the development needs of the system concerned (Mann et al., 1989; Wulff and Ulanowicz, 1989; DeLos Reyes and Martens, 1994; Christian et al., 1996; Monaco and Ulanowicz, 1997). Further, trophic network analysis can be used to evaluate the 'health' of the whole system rather than only the fishery or primary producer components (Christensen, 1998).

Ecopath (Christensen and Pauly, 1992) has developed as a useful tool incorporating algorithms for the retrieval of the ecological, thermodynamic and informational indices needed for network analysis (Ulanowicz, 1993). Through a system of linear equations describing the energetic (or mass) balance for each functional component of the system, the overall ecosystem balance is obtained (Christensen and Pauly, 1992, 1993a,b; Pauly et al., 1993).

The basic equation that represents the balance for each trophic group, i, of the network is:

$$B_i \frac{P_i}{B_i} EE_i - \sum_{i=1}^n B_j \frac{Q_j}{B_j} DC_{ji} - EX_i = 0$$
 (1)

where DC is the diet matrix, which describes the relationships among groups whose elements DC ii represent the fraction of the prey i in the average diet of the predator j; B_i is the biomass of each group; P_i/B_i and Q_i/B_i are metabolic rates, i.e. production and consumption per unit of biomass, respectively; and EE_i is the Ecotrophic Efficiency, which represents the fraction of production of the group (i) used within the system as food for predators or catches of fisheries, and is also referred as the ability of a group to escape predation; while EX_i is the export of the compartment i towards other ecosystems such as net migration and harvest by fishery (Christensen and Pauly, 1993a). Since the currency of the model is energy-related, the Unassimilated/Consumption ratio (UN/Q) is used to quantify the fraction of the food (Q_i) that is not assimilated. More details on capabilities and limitations of the Ecopath suite of software are given in Christensen and Walters (2000).

2.3. The mass-balance models for Orbetello

A steady-state mass-balance model of Orbetello Lagoon was previously constructed using Ecopath II software (Christensen and Pauly, 1992) by Auteri et al. (1993) to describe the trophic interactions, particularly of exploited fish over the period 1990–1992. The food web consisted of 16 functional groups, 10 of which were fish species. We were unable to extend the trophic network of Auteri et al. (1993) to better discriminate the submerged vegetation and zoobenthic groups and their relationship with detritus since there is a considerable lack of knowledge regarding the phyto- and zoobenthic communities and their interactions with the upper trophic levels (Brando, 2000).

In order to perform network analysis of natural systems, it is often necessary to aggregate species into functional trophic groups (Carrer and Opitz, 1999; Christian and Luczkovich, 1999). To minimize the unification errors we aggregated nekton species with these characteristics: (1) similar turnover rates, (2) similar feeding habits (referred as species with

Table 1
Species identified in the Orbetello Lagoon ecosystem and their aggregation into the 12 trophic groups used as components of the mass-balance model

Trophic group	Taxa
Cormorant	Phalacrocorax carbo sinensis
Seabass	Dicentrarchus labrax
Eel	Anguilla anguilla
Seabream	Sparus aurata
Forage	Dicentrarchus labrax (juvenile), Sparus aurata (juvenile), Anguilla anguilla
	(juvenile), Solea vulgaris, Atherina boyeri,
	Aphanius fasciatus, Engraulis encrasicolus,
	Sardina pilchardus, Diplodus annularis,
	Diplodus sargus, Diplodus vulgaris
Zoobenthos	'Suspension feeders', 'deposit feeders'
Mullets (juvenile)	
Mullets	Mugil cephalus, Chelon labrosus, Liza aurata, Liza ramada, Liza saliens
Zooplankton	_
Phytoplankton	_
Pleustophytes	Cladophora vagabunda, Gracilaria verrucosa, Ulva rigida, Enteromorpha sp.,
Detritus	Chaetomorpha linum

common inputs), and (3) are exploited by the same predators and same fisheries (referred as species with common output). Thus, the trophic network was simplified by unifying in one group, "forage fish", consisting of juveniles of predator fish, sole and other small fish (*Atherina boyeri*, *Aphanius fasciatus*, *Engraulis encrasicolus*, *Sardina pilchardus*). Juvenile mullet were not included in the unified group because they had no common inputs, being largely detritivores.

The resulting simplified network comprised of 12 groups (Table 1). Biomasses are in tkm⁻² (wet weight) and the balance was computed for a whole year: thus, retrieved flows are in tkm⁻² per year.

2.3.1. Description of mass-balance parameters

Most parameters in the models developed here (Table 2) were taken directly from Auteri et al. (1993). However, some parameters estimated by Auteri et al. (1993) were updated after comparison with recent literature on Orbetello Lagoon and other temperate coastal basins.

2.3.1.1. Cormorants. Cormorants (Phalacrocorax carbo sinensis) arrive at the lagoon in October; the population reaches its maximum in January and the

Table 2 Input parameter used for 1995 and 1996 models of the Orbetello Lagoon

	B (t km ⁻²) 1995–1996	P/B (per year)	Q/B (per year)	EE	UN/Q
Cormorant	0.050-0.052	0.04	58.40		0.20
Seabass		0.57	5.13	0.369	0.20
Eel		0.39	4.00	0.840	0.20
Seabream		0.99	4.74	0.800	0.20
Forage		1.70	14.20	0.800	0.20
Zoobenthos		4.10	17.00	0.900	0.40
Mullets (juvenile)		1.74	23.45	0.900	0.50
Mullets		0.54	23.45	0.750	0.50
Zooplankton		20.00	70.00	0.980	0.50
Phytoplankton		40.00		0.722	
Pleustophytes	215–225			0.400	
Detritus	18000				

Metabolic rates such as production rate (P/B), consumption rate (Q/B), Ecotrophic Efficiency (EE) and Unassimilated ratio (UN/Q) are common to the two models, and biomasses (B) for cormorants and pleustophytes are given for each year. Missing values are estimated by Ecopath.

birds typically leave the area in March–April (Baccetti et al., 1988, 1997). Biomass of cormorants was obtained by estimating the average annual number of individuals present in the basin; an average weight of $3170 \, \mathrm{g}$ per individual was used (Auteri et al., 1993). We estimated that 430 and 450 individuals were present during the whole year for 1995 and 1996, respectively, corresponding to a biomass of 0.050 and $0.052 \, \mathrm{t \, km^{-2}}$, respectively. P/B and Q/B were set to 0.04 and 58.40 per year as in Auteri et al. (1993).

2.3.1.2. Finfish. The analysis of the fishery harvest by Auteri et al. (1993) was used as the basis for the estimation of finfish parameters. The parameters of the forage fish group, including juveniles of *Sparus aurata* and *Dicentrarchus labrax* and small fish, were estimated with a weighted average of the species-related values (Auteri et al., 1993) using as weights the harvested biomass for each species. The resulting values were P/B = 1.7 per year; Q/B = 14.2 per year; EE = 0.8; UN/Q = 0.2.

2.3.1.3. Fishery harvests. Catch data for the trophic groups are presented in Table 3. The exclusive management of fishing activities in the basin by one company allows an accurate estimation of this parameter, which for other basins is often the cause of much uncertainty (De La Cruz-Aguero, 1993; Palomares et al., 1993; Carrer and Opitz, 1999). In 1996, there was a remarkable increase in seabream (*S. aurata*) harvest,

mainly due to the introduction of seabream fingerlings beginning in 1994. Considerable declines in eel (*Anguilla anguilla*) and mullet (both adult and juvenile Mugilidae) catches followed a decade-long trend (Brando, 2000); whilst catches of seabass (*D. labrax*) remained approximately constant.

2.3.1.4. Primary and secondary producers. Phytoplankton, zooplankton and zoobenthos metabolic rates were compared with the input parameters for a similar Ecopath model of Etang de Thau (Palomares et al., 1993), a meso-mediterranean lagoon system (Bianchi, 1988). Weighted average *P/B* and *Q/B* values for crustaceans and molluscs were derived for zoobenthos, based on benthic composition reported by Morgana and Naviglio (1989) and Rossi and Lardicci (1995). For phytoplankton values similar to those of other coastal lagoon models were used (De La Cruz-Aguero, 1993; Lin et al., 1999).

Table 3 Fishery catch of commercial fish groups in Orbetello Lagoon $(t\,km^{-2}$ per year)

1995	1996	(1996 – 1995)/95
0.652	0.602	-7.6%
2.655	1.173	-55.8%
0.702	4.384	+524.6%
1.306	0.902	-30.9%
3.051	2.826	-7.4%
1.571	1.020	-35.1%
	0.652 2.655 0.702 1.306 3.051	0.652 0.602 2.655 1.173 0.702 4.384 1.306 0.902 3.051 2.826

2.3.1.5. Macroalgae. Accurate estimates of macroalgal coverage and standing crop were available for almost every month during the period of management activities. The biomass in 1995 was about 215 t km⁻² (~90% Cladophora) and 225 t km⁻² in 1996 (~70% Gracilaria and 30% Cladophora) (Brando, 2000). During the selective algal harvesting macroalgae were harvested directly by the management authority (320 t km⁻² per year in 1995 and 165 t km⁻² per year in 1996) (Lenzi and Mattei, 1998).

2.3.1.6. Detritus. The estimate of organic matter content of the sediment was obtained from core samplings carried out in the basin in 1997 and 1998 (Villa, 1999). Values of organic matter of $0.12 \,\mathrm{g}\,\mathrm{OM}\,\mathrm{g}^{-1}$ were extracted from cores 10 cm deep with a sediment density of about $1.5 \,\mathrm{kg}\,\mathrm{l}^{-1}$. This is equivalent to 18 kg OM m^{-2} , or $18,000 \text{ t km}^{-2}$. The weight of organic matter in the detritus included that of the microbial community, mostly bacteria, fungi and protozoans; because of the lack of knowledge in the local community, this community is not considered part of the model although it is clearly very important for the organic matter re-mineralization and as the source of nutrients for scavengers (Mann, 1988; Sorokin et al., 1996; Rosado-Solórzano and Guzmán Del Proo, 1998; Lin et al., 1999).

2.3.1.7. Diet composition. Diet data for the aggregated functional trophic groups were obtained from the diet compositions reported in the model of Auteri et al. (1993) (Table 4).

2.3.2. Balancing the models: trophic networks for 1995 and 1996

To depict the interactions within the trophic groups for 1995 and 1996, we used the network structure defined by the diet composition matrix (Table 4) and the values of P/B, Q/B, EE and UN/Q summarized in the input table (Table 2). Biomass values for cormorants and pleustophytes (Table 2) and fishery catch data (Table 3) for the 2 years were used to estimate the unknown biomasses and flows.

The model parameters were calibrated to obtain for all the groups EE values less than 1 and gross efficiency values (GE = P/Q) within 0.1 and 0.3 (Christensen et al., 2000).

2.4. Network description and analysis: indices used

2.4.1. Structural analysis

Trophic aggregation, effective trophic level (ETL) and the omnivory index (OI) were used to describe the structure of the networks in the Orbetello Lagoon.

"Trophic aggregation" here refers to the procedures provided by Ulanowicz (1995) for simplifying complex food webs to simple concatenated chains of trophic interactions. Such chains are useful because they provide an accurate but uncomplicated picture of the system and allocate the different dietary interactions in the systems to discrete trophic levels (*sensu* Ulanowicz, 1986). Aggregation was carried out in order to evaluate how each component of the ecosystem contributes to the trophic levels of the idealized linear food chain, i.e. primary producers to herbivores

Table 4	
Diet Composition for the Orbetello Lagoon mass-balance model (after Auteri et al., 19	993)

Prey/predators		1	2	3	4	5	6	7	8	9
1	Cormorant									
2	Seabass									
3	Eel									
4	Seabream									
5	Forage	0.650	0.410	0.300		0.015				
6	Zoobenthos		0.350	0.650	1.000	0.523	0.158	0.210	0.180	
7	Mullets (juvenile)	0.350	0.240	0.050		0.002				
8	Mullets									
9	Zooplankton					0.460	0.211	0.050		0.100
10	Phytoplankton						0.158			0.900
11	Pleustophytes						0.211	0.410	0.410	
12	Detritus						0.262	0.330	0.410	

to carnivores (Ulanowicz, 1995). Data on trophic aggregation of flows allows estimation of the sum of all flows reaching detritus and the upper trophic levels, as well as transfer efficiencies.

The ETL is based on the diet composition (weighted average trophic level of the prey organisms ingested), and represents the weighted mean number of trophic interactions that one could count in the trophic chain from the organism down to the autotrophic organisms or non-living organic matter (Christensen et al., 2000).

The OI is calculated as the variance of the trophic level of a consumer's prey groups (Christensen and Pauly, 1993b). It ranges from 0 to 1, where 0 indicates a highly specialized consumer and higher values indicate predation on many trophic levels (Christensen et al., 2000).

2.4.2. Network analyses

Some of the several parameters and indices developed for the network analysis were selected to describe the general system properties and the level of development and maturity of the Orbetello Lagoon.

The ratio of total system biomass to the Total System Throughput TST (*B*/TST) (Christensen, 1995), tends to be low in the development phase of an ecosystem and increases in value as the system matures and tends to conserve energy by storing it in its components (Odum, 1971; Ulanowicz, 1986).

The ratio of Net Primary Production to Total Respiration (NPP/TR) is also considered an important index of the system maturity (Odum, 1969; Perez-Espana and Arreguin-Sanchez, 1999). Values of this ratio close to 1 indicate mature ecosystems whereby fixed energy is balanced by the energetic cost of system maintenance.

The net production of the system, corresponding to the difference between net primary production and total respiration (NPP - TR), should be nil in a truly balanced ecosystem. This difference can also indicate the maturity of a system (Odum, 1969).

The System Omnivory Index (SOI) attempts to characterize interactions in the system as a whole through the variance in the trophic levels of all prey of predator groups (Pauly et al., 1993). A value close to 0 indicates that consumers of the system are specialized, whilst a value close to 1 indicates that consumers are more omnivorous.

Cycling is considered to be an important indicator of an ecosystem's ability to maintain its structure and integrity through positive feedback (Ulanowicz, 1986; Monaco and Ulanowicz, 1997). The cycling level can used as an index of stress (Ulanowicz, 1986; Christensen and Pauly, 1993b) or as an indicator of the maturity stage (sensu Odum) of an ecosystem (Christensen, 1995; Vasconcellos et al., 1997). The cycling level is quantified with the Finn Cycling Index (FCI), which represents the fraction of TST cycled (Finn, 1976). Similarly, the Predatory Cycling Index (PCI), is calculated by excluding the cycling through detritus. Such cycling may result from short and fast cycles, typical of disturbed systems, or long and slow ones, typical of complex trophic structures (Odum, 1969; Kay et al., 1989; Christensen, 1995). The number of groups involved in a flow is used to quantify the length of the cycles. They are expressed by Finn's mean Path Length (FPL) and the Finn's straight-through path length with and without detritus.

Ascendancy (A) is the key index that characterizes the level of development and maturity of a system, since it takes into account both the dimension (TST) and the organization (Information, I) of flows (Ulanowicz, 1986). The complement to ascendancy is system overhead, the cost to an ecosystem of circulating matter and energy (Monaco and Ulanowicz, 1997). Overhead represents the degrees of freedom a system has at its disposal to react to perturbations (Ulanowicz, 1986).

As suggested by Mann et al. (1989), the system-wide effects of eutrophication can be indexed using a combination of *A* and TST, comparing the change of flows in the whole ecosystem during and after eutrophication. Eutrophication may be defined at the ecosystem level as an increase in *A* due to a rise in TST that more than compensates for a concomitant fall in *I* (Ulanowicz, 1986).

Relative ascendancy (A/C) is the fraction of possible organization that is actually realized (Ulanowicz, 1986), and is negatively correlated with maturity (Christensen, 1995). Thus high values of this index seem related to low levels of maturity in the system and vice versa: this was demonstrated by comparison of a high number of models (Christensen, 1995).

Internal relative ascendancy (A_i/C_i) represents the balance between the efficiency of carbon flows and the system redundancy, and is most suitable for

comparing different ecosystems (Mann et al., 1989). Environments with a relatively high value of A_i/C_i have a significant internal stability (Monaco and Ulanowicz, 1997).

Due to the complexity of the input parameters, no statistical tests are available to evaluate differences in the values of the various indices across ecosystems or between different phases of the same system (Monaco and Ulanowicz, 1997). However, these indices, when taken as a whole and based on rank ordering, help to determine differences and similarities between trophic networks (Monaco and Ulanowicz, 1997).

2.4.3. Pleustophytes

Macroalgae communities are often used as indicator of ecosystem health in coastal environments (Littler and Littler, 1980; Duarte, 1995; Nielsen, 1997; Silvestri et al., 1999). The turnover rate or the maximum growth rate can be used to position the submerged vegetation as a whole along the 'axis of adaptation strategies to natural selection' described by Pianka (1970) and Grime (1979). This axis describes a continuum from fast-growing species such as *Ulva*, *Enteromorpha* and *Cladophora*, indicators of stressed and unstable environments (Littler and Littler, 1980), to slower-growing species such as phanerogams and *Gracilaria* (Nielsen, 1997) that require stable environments (Duarte, 1991).

Adaptation strategies are related to the degree of development of the ecosystem (Odum, 1969; Ulanowicz, 1986).

Values of maximum growth rate (μ_{max}) for the dominant species of the submerged vegetation in a basin, can be estimated using an allometric relation (Nielsen and Sand-Jensen, 1990) that relates their general morphology (surface area/volume ratio) to growth rate.

Pleustophytes P/B were estimated with the mass balance and represent an average of the turnover rates of all species of the submerged vegetation in the basin thus reflecting any change in composition. Therefore, pleustophytes P/B could be also a useful indicator of the environmental health of an ecosystem.

2.4.4. Conflicts between cormorants and fishery

In Orbetello Lagoon, cormorants are considered inimical to the fishery because the maximum numbers of cormorants, which occurs during December and January, coincide with the migrations of marketable fishes to the sea. The consumption by cormorants has both a direct effect on the fishery by exploitation of forage species and juvenile mullet, and an indirect one, removing prey from marketable predators (eels and seabass).

In order to evaluate the conflict between cormorants and the fishery, we separated the total consumption of common target prey among cormorants, predator fish (seabass and eels) and the fishery.

The competition between cormorants and fishery activities can be described through the ratio of consumption by cormorants to total fishery harvest (CQ/TFH). This index summarizes the direct and indirect effects of consumption by cormorants, but does not consider the variation in their diet composition. To evaluate the direct effects of cormorant predation, we introduced the ratio of consumption by cormorants to target species harvest (CQ/TSH) and for the indirect effects, we estimated the ratio of consumption by cormorants to that by nekton predators (CQ/NQ) and the ratio of consumption by cormorants to consumption by harvested nekton (CQ/NH).

3. Results

3.1. Structural analysis of the two models

The results of the aggregation of biomasses and flows into trophic levels show the presence of six levels. For each trophic group, the fractions of flows and biomasses involved in the six TLs are reported in Table 5. Since only small flows reach the highest TL and represent only a very minor fraction of the total flows, the TL VI was omitted from further analysis. Flows at the TL II largely involve the zooplankton (the dominant herbivore), zoobenthos and the two groups of mullets. At TL III involves the remaining flows from zoobenthos, mullets but also the flows from the nekton groups. Cormorants and carnivorous fish (eels and seabass) dominate the flows at TL IV, and form a portion of TL V. This lead to the values of Effective TL (ETL, also in Table 5), varying from 2.11 for zooplankton to the highest value of 3.98 for cormorants.

The zoobenthos and juvenile mullets have the most diverse diets with an OI value of 0.38. Mullets have a more diverse diet (OI = 0.32) than cormorants, seabass and eels (OI about 0.20). Seabream, forage

Table 5
Trophic aggregation of the groups in Orbetello Lagoon model (sensu Ulanowicz, 1995): breakdown of flows by discrete trophic levels (I–VI)

	Trophi	c levels		ETL	OI			
	I	II	III	IV	V	VI		
Cormorant			0.26	0.64	0.11	0.01	3.98	0.21
Seabass			0.44	0.49	0.07		3.79	0.19
Eel			0.52	0.43	0.04	0.01	3.72	0.16
Seabream			0.75	0.25			3.47	0.00
Forage			0.87	0.13			3.32	0.05
Zoobenthos		0.75	0.25	_			2.47	0.38
Mullets (juvenile)		0.74	0.21	0.05			2.36	0.38
Mullets		0.82	0.13	0.05			2.26	0.32
Zooplankton		1					2.11	0.11
Phytoplankton	1						1.00	0.00
Pleustophytes	1						1.00	0.00
Detritus	1						1.00	0.42

Effective trophic level (ETL) and omnivory index (OI) are also presented.

fish and zooplankton had low values. Since flows to detritus (natural mortality) operate at all trophic levels, the high value for detritus (0.42) was expected.

The pattern of energy flows through the network is described in terms of the number of trophic interactions of each group and the mean length of pathways (MLP) through the network (Table 6). For top predators, the number of connections was high (90–100) and with a high number of steps (MLP = 5). Mullets also belong in this category, even with a low ETL (2.26), because they are herbivores/detritivores (Table 4). For seabream, the MLP was also high (5.04), but unlike

Table 6 Flows from trophic level I (TL I) to consumers and from prey to top predators for the Orbetello Lagoon network

	TL I →	consumer	Prey →	top predators
	Total no. of paths	Mean length of pathways	Total no. of paths	Mean length of pathways
Cormorant	90	5.09		
Seabass	108	4.96		
Eel	108	4.96		
Seabream	27	5.04		
Forage	50	4.22	3	1
Zoobenthos	28	3.96	13	1.92
Mullets (juvenile)	49	4.12	6	1.5
Mullets	99	4.87		
Zooplankton	1	1	22	2.68
Phytoplankton			35	3.4
Pleustophytes			20	2.7
Detritus			20	2.7

other top predators, seabream had a low number of trophic interactions (27), due to a diet based only on zoobenthos. In the middle of the trophic chain, the forage fish, zoobenthos and juveniles mullets were both consumers (MLP = 4) and prey (MLP < 2). The groups at the base of the trophic pyramid (detritus, pleustophytes, and zooplankton), were characterized by low numbers of trophic interactions (20) and path lengths (2.7), while phytoplankton had higher values for both parameters (35 and 3.4, respectively).

3.2. Comparison between the two networks

The network diagrams of Orbetello Lagoon for 1995 and 1996 (Figs. 2 and 3, respectively) show substantial similarities, the differences being in biomass values and the dimension of the flows associated with each trophic group.

All biomass values (Table 7) were estimated by the model, except for cormorants and pleustophytes. The estimated biomass of almost all trophic groups was lower in 1996 than in 1995 by 15–35%, except for seabream and eels. Eel biomass fell by 4.52 t km⁻², or 55%, while seabass biomass increased by 4.65 t km⁻² (520%). For forage fish and juvenile mullets the changes in biomass from 1995 to 1996 (–32.2 and –15.4%, respectively) were mediated by the trophic network.

Moreover, the biomass decrease in eels and the coincident increase in seabream were approximately the same magnitude (about $4.5 \,\mathrm{t\,km^{-2}}$) and change the

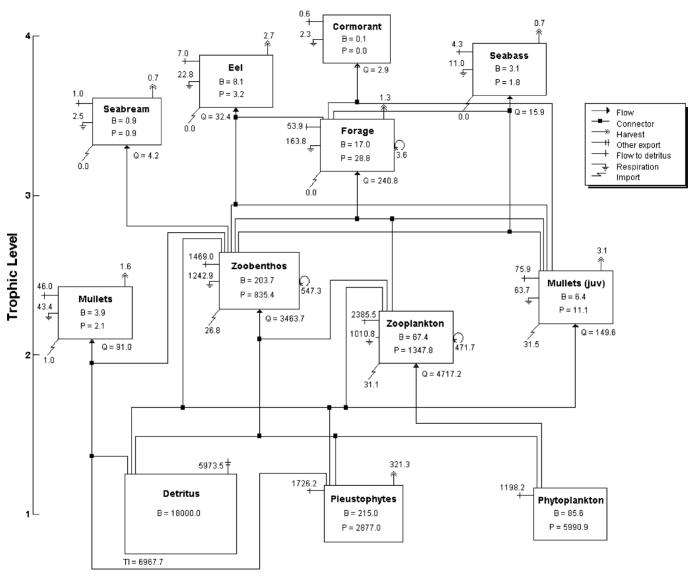


Fig. 2. Flow diagram of Orbetello Lagoon in 1995. All biomasses are in tkm⁻² and rates in tkm⁻² per year.

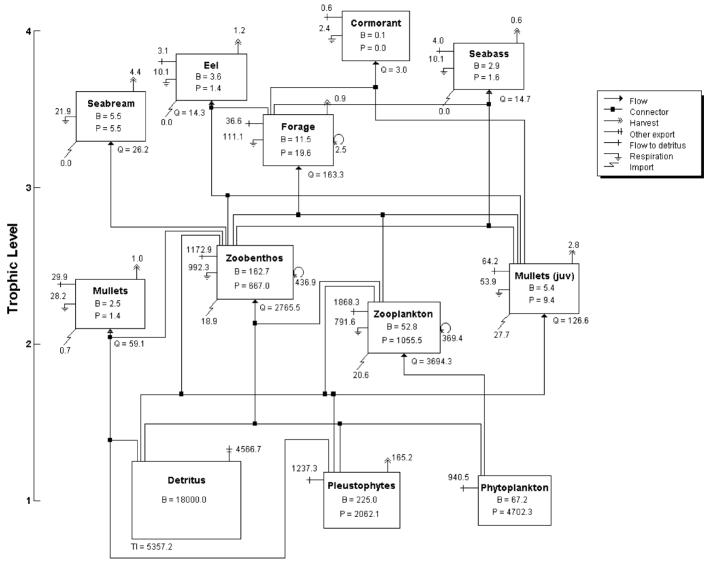


Fig. 3. Flow diagram of the Orbetello Lagoon in 1996. All biomasses are in tkm⁻² and rates in tkm⁻² per year.

Table 7 Estimated biomass $(t\,km^{-2})$ of trophic groups for the 1995 and 1996 Orbetello Lagoon networks

	1995	1996	(1996 – 1995)/95
Cormorant	0.050	0.052	4.0%
Seabass	3.10	2.86	-7.7%
Eel	8.10	3.58	-55.8%
Seabream	0.89	5.54	522.5%
Forage	16.96	11.50	-32.2%
Zoobenthos	203.75	162.68	-20.2%
Mullets (juvenile)	6.38	5.40	-15.4%
Mullets	3.88	2.52	-35.1%
Zooplankton	67.39	52.78	-21.7%
Phytoplankton	85.58	67.18	-21.5%
Pleustophytes	215	225	4.7%
Detritus	18000.00	18000.00	0.0%

The relative changes are also reported.

ETL from 3.72 to 3.47 (Table 5). Since the flows involving seabream are distributed (*sensu* Ulanowicz, 1995) between TLs III (75%) and IV (25%), while those involving eels are 52% in TL III and 43% in TL IV (Table 5), this change implies an increase in the biomass of TL III and a decrease of that in TL IV.

The 12% decrease in biomass of the network in 1996 occurred mainly in the upper trophic levels: a 37% drop in TL V. At TLs II, III and IV the decrease was about 20%, while at TL I it was only 3% (Table 8). The decrease in biomass was non-monotonic, although this should be the case for a food chain based almost entirely on primary producers.

3.3. Network analysis

The aggregation of the flow (t km⁻² per year) web into a concatenated chain of transfers trough six trophic levels (*after* Ulanowicz, 1995) is presented

Table 8
Estimated biomass (t km⁻²) at each trophic level for the 1995 and 1996 Orbetello Lagoon networks (*sensu* Ulanowicz, 1995)

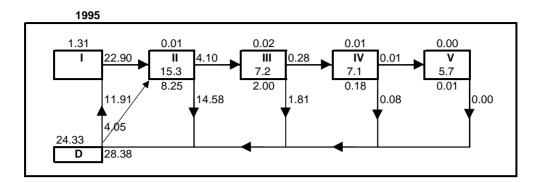
Trophic level	1995	1996	(1996 – 1995)/95
V	0.562	0.352	-37.4%
IV	8.066	6.314	-21.7%
III	73.885	59.488	-19.5%
II	227.981	180.747	-20.7%
I	300.58	292.18	-2.8%
Total (no detritus)	611.078	539.077	-11.8%

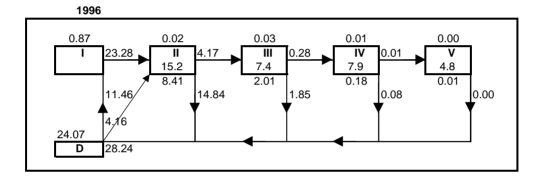
in Fig. 4. Flows from detritus and primary producers were almost the same magnitude for the 2 years (4.16 and 23.28% versus 4.05 and 22.90%). Algal harvesting (export of primary producers) for 1995 and 1996 was 1.31 and 0.87% of TST. The sum of flows reaching detritus was similar in the 2 years (28.38% versus 28.24%), and the slight decrease in the contribution by primary producers (11.46% versus 11.91%) was partly balanced by a small increase of flows from TL II (14.58% versus 14.84%). The export of detritus also decreased slightly (24.07% versus 24.33%). The energetic transfer efficiencies (TEs) at TL II were similar in the 2 years (15%). TEs at levels III and IV were slightly higher for 1996 (7.4 and 7.9%) than for 1995 (7.2 and 7.1%), while the reverse was true for trophic level V TE (5.7 and 4.8%).

There was a decrease in almost all aggregated flows in the trophic network from 1995 to 1996 (Table 9). The decrease was particularly strong in the trophic groups at TL I (2103.5 t km⁻² per year), shared between pleustophytes (-815 t km⁻² per year) and phytoplankton (-1289 t km⁻² per year). At TL II there were reduced flows for zooplankton (-1023 t km⁻² per year) and zoobenthos (-698 t km⁻² per year). Other trophic groups exhibited moderate decreases ranging between -1.2 and -77.5 t km⁻² per year. Only for seabream and cormorants were there increased flows (22.0 and 0.1 t km⁻² per year, respectively).

These changes were proportional in value to those in estimated biomass of the trophic groups in 1995 and 1996 (Table 7). For pleustophytes, the decreased flow was due to the change in P/B associated with the change of dominant algal species as discussed above. The great reduction in detritus-related flows ($-1604 \, \mathrm{t \, km^{-2}}$ per year) was a consequence of the global decrease in all the other flows.

Table 10 reports some of the indices estimated through Ecopath for the trophic networks of 1995 and 1996. A generalized decrease of the flows of the system from 1995 to 1995 is evident (reductions are estimated between -21.4 and -24.7%), and thus giving an analogous decrease on the informational indices (Ascendancy, Overhead, Capacity). However, different kind of flows show similar but not identical decrease, resulting in changes for most of the ecological indices toward values indicating higher maturity and stability. In this sense can be viewed the increase





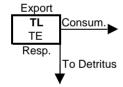


Fig. 4. The aggregation of the flows (tkm⁻² per year) into a concatenated chain of transfers trough six trophic levels (*after* Ulanowicz, 1995). Flows out of the tops of the compartment represent exports and flows out to the bottom represent respiration. Recycling of non-living material is through compartment D (detritus). The percentages in the boxes represent annual trophic efficiencies.

of *B*/TST and the decrease of Net System Production and Primary Production on Total Biomass (see Table 10). A slight decrease of –3% is also observed for Primary Production on Total Respiration index (PP/TR).

Although cycling in absolute values result as decreasing (both including and excluding detritus decrease of some between 20 and 21%), the cycling as percentage of the TST expressed through Finn's and Predatory Cycling indices, are resulting as increasing (FCI +2.8%, PCI +2.1%). A slight increase is also shown for the indices measuring the mean path length, evidencing a recycling through longer and slower paths, typical of more mature systems.

The structure of the networks for the years 1995 and 1996 was unchanged, thus no changes are observed for structure-related indices such as the Connectance Index and the Information derived from the Ulanowicz's indices (Table 10). Finally, although increase of catches was introduced with input data (and shown as an increase of +9.8%) thus did not change significantly the mean TL of the catches, changed from 4.006 to 4.1 (also reported in Table 10).

3.4. Pleustophytes

The estimated production rates (P/B) of pleustophytes for the 2 years, of 13.381 per year and 9.165

	•						
Group name	D	I	II	III	IV	V	Total
Cormorant		_	_	0.0	0.1	0.0	0.1
Seabass		_	_	-0.5	-0.6	-0.1	-1.2
Eel		_	_	-9.5	-7.8	-0.8	-18.1
Seabream		_	_	16.5	5.5	_	22.0
Forage		_	_	-67.1	-10.3	-0.0	-77.5
Zoobenthos		_	-523.3	-175.0	_	_	-698.2
Mullets (juvenile)		_	-17.0	-4.8	-1.2	_	-23.0
Mullets		_	-26.2	-4.3	-1.4	_	-31.9
Zooplankton		_	-1022.8	_	_	_	-1022.8
Phytoplankton		-1288.6	_	_	_	_	-1288.6
Pleustophytes		-814.9	_	_	_	_	-814.9
Detritus	-1604.1		_	_	_	_	-1604.1
Total	-1604.1	-2103.5	-1590.0	-244.0	-15.8	-0.9	-5558.7

Table 9
Difference between estimated flows per trophic group and per trophic level, 1996–1995 (tkm⁻² per year)

per year, indicate a decrease in turnover rate of 32% in 1996 (Table 11).

The ratio of P/B values between the 2 years did not correspond to the ratio of $\mu_{\rm max}$ values for *Cladophora* and *Gracilaria*, but taking into account the pleustophytes community structure, reported in Table 11 as the occurrence of these two main species, one could obtain weighted $\mu_{\rm max}$ for 1995 and 1996 (0.215 and 0.111, respectively) that have ratios close to that of P/B values.

3.5. Conflicts between cormorants and fishery activities

The cormorant ETL (3.98) and the average ETL of the fishery (4.006 in 1995 and 4.1 in 1996) are similar but the fishery has a wider "diet" (comparing Tables 3 and 4).

In 1995, the total consumption of target species (TSQ) was 33.05 t km⁻² of which the fishery caught 13.2%, cormorants 8.8%, and predator fish 78% (Fig. 5). In 1996, consumption was 24.1 t km⁻² of which the fishery took 15.5%, cormorants 12.6%, and predator fish 72%. The total TSQ decreased from 1995 to 1996 by 27%, with an increase in consumption by cormorants of 4%, and decreases in fishery and predator fish consumption by 14.4 and 32.8%, respectively (Fig. 5).

The ratio of consumption by cormorants to total fishery harvest (CQ/TFH) was 0.294 in 1995 and 0.278 in 1996, a slight decrease in 1996 (5.2%) due to the larger total harvest in that year (Table 12).

The ratio of consumption by cormorants to target species harvest (CQ/TSH) was 0.670 in 1995 increasing by 21.6% in 1996 to 0.815 due to the reduced fishery harvest of these species. CQ/NQ increased by nearly 55% from 0.113 in 1995 to 0.175 in 1996, while CQ/NH rose by about 94% from 0.883 in 1995 to 1.711 in 1996.

4. Discussion

The differences in estimated biomass reflect almost totally the fishery catch in the lagoon for the 2 years (Table 3).

The lower biomass of herbivores/detritivores and primary producers in 1996 than in 1995 suggest that the top-down control mediated by the fishery propagates to the lower trophic levels. Moreover, the biomass decrease in eels and the coincident increase in seabream were approximately the same magnitude (about 4.5 t km⁻²) and change the ETL from 3.72 to 3.47 (Table 5). Since the flows involving seabream are distributed (*sensu* Ulanowicz, 1995) between TLs III (75%) and IV (25%), while those involving eels are 52% in TL III and 43% in TL IV (Table 5), this change implies an increase in the biomass of TL III and a decrease of that in TL IV.

This change is propagated down in the trophic network with non-uniform changes in the TLs as reported in Table 8. The estimated decrease in biomass was non-monotonic, although a decrease in primary producer biomass should propagate monotonically

Table 10 Summary of the indices estimated for the 1995 and 1996 using the relative trophic networks built for Orbetello Lagoon

	Unit	1995	1996	Variance (1996 – 1995)/95
Ecosystem theory indices				
Total system throughput	t km ⁻² per year	24553.19	18994.94	-22.6%
Sum of all consumption	t km ⁻² per year	8717.696	6867.085	-21.2%
Sum of all exports	t km ⁻² per year	6304.715	4749.056	-24.7%
Sum of all respiratory flows	t km ⁻² per year	2563.13	2015.265	-21.4%
Sum of all flows into detritus	t km ⁻² per year	6967.649	5363.536	-23.0%
Sum of all production	t km ⁻² per year	11098.8	8525.628	-23.2%
Export from detritus	t km ⁻² per year	5973	4573	23.4%
Total biomass/total throughput (B/TST)	Year	0.025	0.028	12.0%
Total primary production/total respiration (PP/TR)		3.46	3.357	-3.0%
Net system production $(PP - TR)$	t km ⁻² per year	6304.715	4749.056	-24.7%
Total primary production/total biomass (PP/B)	Per year	14.512	12.548	-13.5%
Total catches	t km ⁻² per year	9.937	10.907	9.8%
Calculated total net primary production	t km ⁻² per year	8867.84	6764.32	-23.7%
Gross efficiency (catch/net primary production)		0.0011	0.0016	45.5%
Mean trophic level of the catch		4.006	4.1	2.3%
Connectance index		0.223	0.223	0.0%
System omnivory index		0.229	0.217	-5.2%
Cycling indices				
Throughput cycled (excluding detritus)	t km ⁻² per year	1022.6	808.8	-20.9%
Throughput cycled (including detritus)	t km ⁻² per year	1745.8	1390.5	-20.4%
Finn's cycling index	%	7.1	7.3	2.8%
Predatory cycling index	%	9.6	9.8	2.1%
Finn's mean path length		2.77	2.81	1.4%
Finn's straight-through path length (no detritus)		3.32	3.4	2.4%
Finn's straight-through path length (with detritus)		2.57	2.6	1.2%
Informational indices				
Ascendancy	Flowbits	27273.34	21158.55	-22.4%
Overhead	Flowbits	61014.11	47552.14	-22.1%
Capacity	Flowbits	90297.44	69841.34	-22.7%
Information		1.11	1.11	0.0%
A/C		0.302	0.303	0.3%
$A_{ m i}/C_{ m i}$		0.203	0.202	-0.5%

through all trophic levels in a system based almost entirely on primary producers (Odum, 1971). The non-monotonic decrease in biomass gives the evidence that a source of energy different from primary

Table 11 Estimated values of P/B and $\mu_{\rm max}$ (per day) for the 1995 and 1996 Orbetello Lagoon networks

Macroalgae community	1995	1996	1995/1996
Cladophora ($\mu_{\text{max}} = 0.232$)	90%	30%	
Gracilaria ($\mu_{\text{max}} = 0.059$)	10%	70%	
P/B (estimated by Ecopath)	13.381	9.165	1.46
μ_{max} community	0.215	0.111	1.94

The pleustophytes composition reported for the 2 years and $\mu_{\rm max}$ for each species is used to estimate the $\mu_{\rm max}$ of the community.

producer is very important for the Orbetello Lagoon: this result gives an indication of the important role played by detritus in this trophic network.

The substantial and generalized decreases in biomass of the groups produce the decrease in all flows of the system (Table 9). It should be pointed out that decrease in biomass of phytoplankton was slightly compensated by the increase of pleustophytes at TL 1 (Table 8), however, the lower production rate of this latter contribute to the generalized decrease of flows within the system (Table 9). Moreover, the P/B of pleustophytes estimated by Ecopath also showed a substantial decrease (Table 11), contributing to reduce the primary production of the system and the

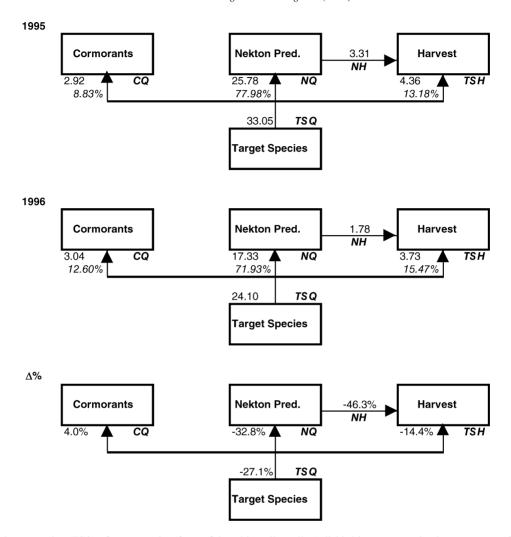


Fig. 5. Total consumption (TSQ) of target species (forage fish and juvenile mullets) divided into consumption by cormorants (CQ), nekton predators (NQ) and fishery harvest (TSH) in the 1995 and 1996 Orbetello Lagoon networks.

related indices (PP/TR, PP – TR, PP/B, shown in Table 10). The ratio of P/B values between the 2 years did not correspond to the ratio of μ_{max} values for *Cladophora* and *Gracilaria* because, while μ_{max} is species specific, P/B depends on environmental limitations (principally nutrients and temperature).

The higher transfer efficiencies at trophic levels III and IV in the 1996 model suggested better flow of the energy within this network, largely due to the increase in biomass of seabream, the fish species with the highest gross efficiency (0.21) of the fishery-related trophic groups.

Table 12
Ratios of consumption by cormorants to total fishery harvest (CQ/TFH), consumption by cormorants to target species harvest (CQ/TSH), consumption by cormorants to consumption by nekton predators (CQ/NQ), and consumption by cormorants to harvest of nekton predators (CQ/NH), estimated for the 1995 and 1996 Orbetello Lagoon networks

	CQ/TFH	CQ/TSH	CQ/NQ	CQ/NH
1995	0.294	0.670	0.113	0.883
1996	0.278	0.815	0.175	1.711
1996 - 1995	-5.2%	21.6%	54.7%	93.7%

The reduction of flows at TL I expresses the decrease in primary production in 1996, thus quantifying the effects of environmental management.

Since no changes in the water circulation were observed between 1995 and 1996, we assumed resuspension and related detritus exports had same values in the 2 years. Thus, the results that the steady-state balance of the detritus-related flows implies an export (reported in Table 10), is actually be seen as an accumulation of detritus. As shown this accumulation decreased by 23% from 5973 t km⁻² in 1995 to 4573 t km⁻² in 1996. Since eutrophication can be defined as 'an increase in the rate of supply of organic matter to an ecosystem' (Nixon, 1995) the reduction in the accumulation rate of organic matter in the Orbetello system suggests a decrease in the tendency toward eutrophication in the basin.

The gross efficiency of the system, which tends to be very low in systems where the fishery is concentrated on top predators (Christensen et al., 2000), increased from 0.0011 in 1995 to 0.0016 in 1996 (Table 10). The 45% increase in gross efficiency was mainly due to the increased catch of seabream, following the introduction of fingerlings of this species.

The 6% decrease of SOI in 1996, is related with the change from eels to seabream discussed earlier. Similar values of SOI (0.2–0.3) have been reported for estuarine environments (Monaco and Ulanowicz, 1997).

The cycled fraction of TST appears to be a similar magnitude to that reported for other lagoons (10% in Wolff, 1994) or other coastal and very productive systems (Heymans and Baird, 2000, reported in their analysis FCI between 4 and 15% for some coastal ecosystems). Moreover, Manickchand-Heileman et al. (1998) found the same value for the FCI applying Ecopath to a lagoon dominated by the detrital pathway, although they found higher number of steps in the cycling analysis.

In this environment, the cycling seems to be mainly due to the groups at the base of the trophic pyramid (detritus, pleustophytes, and zooplankton), which showed a value of 2.7 for MLP (Table 6), while the cycling through the higher portion of the network (MLP \geq 4) appear to be minimal. Moreover, both values of FPL were lower than those previously reported for brackishwater environments at low stage

of maturity (4.91, 4.1–6.0, Wolff, 1994; Monaco and Ulanowicz, 1997).

 A_i/C_i values for the Orbetello Lagoon networks in the 2 years (0.202 and 0.203) did not show remarkable difference between them, but both were lower than those reported (about 0.4) for three estuarine environments by Monaco and Ulanowicz (1997). These results, although revealing a higher maturity level of Orbetello Lagoon compared with those ecosystems, indicate that thermodynamic-informational indices do not reveal a significant difference between the 2 years. Since ecological indices based on the Odum's theory show a certain degree of improvement in 1996, this could be interpreted to indicate that the informational indices are less sensitive to such small, but still interesting differences.

The decrease of biomass of species targeted by cormorants (Table 7) produce a decrease for both nekton predators consumption and fishery harvest on this target species (Fig. 5). However, a slight increase of cormorants consumption is estimated (Fig. 5). These results, together with the increase in the three internal indices (CQ/TSH, CQ/NQ, CQ/NH) from 1995 to 1996, show the better efficiency of cormorants as predators on target species. Moreover, the changes of the ratios between 1995 and 1996 are increasing in the order CQ/TSH < CQ/NQ < CQ/NH (Table 12), showing that the competition effect with nekton is amplified through the network by the indirect competition between cormorants and the nekton fishery. The global index (CQ/TFH) was constant because it considers also the fishery harvest of seabream and mullets that do not compete directly with cormorants. This is a further validation of the extensive aquaculture management of the lagoon. These four indices can be used to analyse the exploitation of target species.

5. Conclusions

Our comparative network analysis of Orbetello Lagoon for 1995 and 1996 appears to have quantified in part the observed improvement in 'health' of the lagoon's ecosystem during this period as a result of algal harvesting and other management interventions.

The food webs had a similar structure in the 2 years but there was a decrease in biomass in all the trophic groups for 1996. The change in turnover rate (P/B) of

pleustophytes from 1995 to 1996 corresponded with observed change in the composition of the submerged vegetation of the basin during this period. Total primary production fell 20% during the 2 years.

Detritus was shown to have a key role in the system. In both years, flows to detritus were about 30% of the system throughput. Most of those flows (about 85%) were entrapped within the ecosystem acting as an organic matter and nutrient reserve. Such reserve, if available to the system, would increase the tendency to eutrophication. However, the 23% fall in TST in 1996, resulting in a proportional reduction in detritus accumulation, indicated a decrease in the tendency for eutrophication, a clear effect of environmental management activities of the basin.

The large increase in gross efficiency of the system (45%), mainly due to the increased catch of seabream and the increase in transfer efficiencies at TLs III and IV, supported the validity of introducing fingerlings in such basins. This intervention would have shown minimal effects even if no environmental management activities were carried out in the system, and indeed the seeding of the basin offset the superior efficiency of the cormorants as predators compared to the fishery.

The four attributes of ecosystem maturity and stability (*B*/TST, NPP/TR, NPP – TR, PP/*B*) indicate unequivocally that Orbetello Lagoon in 1996 was in a more stable condition than in 1995, although the system was still rather distant from values reported for other aquatic environments.

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References

- Alberotanza, L., Brando, V.E., Ferro Milone, G., Pavanati, M., Ravagnan, G., 1998. Airborne hyperspectral imagery as operational tool of the ecological status of a coastal lagoon. In: Proceedings of the Fifth International Conference on Remote Sensing and Coastal Environment. San Diego, CA, pp. 127–134.
- Auteri, R., Abella, A., Baino, R., Righini, P., Serena, F., Silvestri, R., Voliani, A., 1993. Interazioni trofiche e attività di pesca nella laguna di Orbetello. Consorzio regionale di idrobiologia e pesca, Regione Toscana. 222 p.
- Baccetti, N., Corbi, F., 1988. Lo svernamento del cormorano in Italia—Note Conclusive. In: Baccetti, N. (Ed.), Lo svernamento del cormorano in Italia. pp. 151–155.
- Baccetti, N., Cianchi, F., Mainardi, R., 1988. Lo svernamento del cormorano in Italia—Orbetello e San Rossore (Toscana). In: Baccetti, N. (Ed.), Lo svernamento del cormorano in Italia. pp. 103–127.
- Baccetti, N., Cherubini, G., Santolini, R., Serra, L., 1997. Cormorant wintering in Italy: numbers and trends. In: Baccetti, N., Cherubini, G. (Eds), IV European Conference on Cormorants. pp. 363–366.
- Barnes, R.S.K., 1994. The coastal lagoons of Europe. Coastline 3, 3–8.
- Bianchi, C.N., 1988. Tipologia ecologica delle lagune costiere italiane. In: Carrada, G.C., Cicogna, F., Fresi, E. (Eds.), Le lagune costiere: ricerca e gestione. CLEM, Massa Lubrense, pp. 57–66.
- Bombelli, V., Lenzi, M., 1995. Evoluzione del sistema lagunocostiero di Orbetello: rapporto tra eutrofizzazione, struttura dei popolamenti e produttività. Biol. Mar. Medit. 2, 31–36.
- Borum, J., Sand-Jensen, K., 1996. Is total primary production in shallow coastal marine waters stimulated by nitrogen loading? Oikos 76, 406–410.
- Brambati, A., 1988. Lagune e stagni costieri: due ambienti a confronto. In: Carrada, G.C., Cicogna, F., Fresi, E. (Eds.), Le lagune costiere: ricerca e gestione. CLEM, Massa Lubrense, pp. 9–33.
- Brando, V.E., 2000. I dati telerilevati iperspettrali e i modelli trofici quali strumenti descrittivi della condizione ecologica della laguna di Orbetello. Ph.D. Thesis, Università di Padova. 118 p.
- Bucci, M., Ghiara, E., Gorelli, V., Gragnani, R., Izzo, G., Morgana, J.G., Naviglio, L., Uccelli, R., 1991. Risanamento ambientale della laguna di Orbetello. Ricerche e risultati. L'ENEA per l'ambiente. ENEA, pp. 89–103.
- Bucci, M., Ghiara, E., Gorelli, V., Gragnani, R., Izzo, G., Morgana,
 J.G., Naviglio, L., Uccelli, R., 1992. Ecological conditions in
 the Orbetello Lagoon and suggested actions for its restoration.
 In: Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine
 Coastal Eutrophication. Elsevier, Amsterdam, pp. 1179–1188.

- Carrada, G.C., Fresi, E., 1988. Le lagune salmastre costiere. Alcune riflessioni sui problemi e sui metodi. In: Carrada, G.C., Cicogna, F., Fresi, E. (Eds.), Le lagune costiere: ricerca e gestione. CLEM, Massa Lubrense, pp. 35–56.
- Carrer, S., Opitz, S., 1999. Trophic network model of a shallow water area in the northern part of the Lagoon of Venice. Ecol. Model. 124, 193–219.
- Cartei, P., Innamorati, M., 1997. Variazioni delle condizioni trofiche della laguna di Orbetello. Biol. Mar. Medit. 4, 579–582.
- Cataudella, S., 1988. Contributi dell'acquacoltura alla gestione produttiva degli ambienti lagunari. In: Carrada, G.C., Cicogna, F., Fresi, E. (Eds.), Le lagune costiere: ricerca e gestione. CLEM, Massa Lubrense, pp. 147–156.
- Cataudella, S., Cannas, A., Donati, F., Rossi, R., 1995. Elementi per l'identificazione di un modello di gestione conservativa delle lagune costiere attraverso l'uso multiplo delle risorse. Biol. Mar. Medit. 2, 5–15.
- Cecconi, G., Silvestrini, G., 1995. Sperimentazioni per la diffusione delle fanerogame marine sui fondali della Laguna di Venezia. Quaderni Trimestrali. Consorzio Venezia Nuova, Venezia.
- Christensen, V., 1994. On the behavior of some proposed goal functions for ecosystem development. Ecol. Model. 75/76, 37– 49
- Christensen, V., 1995. Ecosystem maturity—towards quantification. Ecol. Model. 77, 3–32.
- Christensen, V., 1998. Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. J. Fish Biol. 53, 128–142.
- Christensen, V., Pauly, D., 1992. ECOPATH II—a system for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169–185.
- Christensen, V., Pauly, D., 1993a. On steady-state modelling of ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 14–19.
- Christensen, V., Pauly, D., 1993b. Flow characteristics of aquatic ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 338–352.
- Christensen, V., Walters, C.J., 2000. Ecopath with Ecosim: Methods, capabilities and limitations. In: Pauly, D., Pitcher, T.J. (Eds.), Methods for assessing the impact of fisheries on marine ecosystems of the North Atlantic. Fisheries Centre Research Reports, 8 (2) 195, pp. 79–105.
- Christensen, V., Walters, C.J., Pauly, D., 2000. Ecopath with Ecosim—A User's Guide. University of British Columbia, Fisheries Centre, Vancouver, Canada and ICLARM, Penang, Malaysia, 131 p.
- Christian, R.R., Luczkovich, J.J., 1999. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. Ecol. Model. 117, 99–124.
- Christian, R.R., Fores, E., Comin, F., Viaroli, P., Naldi, M., Ferrari, I., 1996. Nitrogen cycling networks of coastal ecosystems: influence of trophic status and primary producer form. Ecol. Model. 87, 111–129.
- Cognetti, G., De Angelis, C.M., Orlando, E., Bonvicini Pagliai, A.M., Cognetti Varriale, A.M., Crema, R., Mari, M., Mauri, M., Tongiorgi, P., Vandini Zunarelli, R., de Fraja Frangipane, E., Brambati, A., Giaccone, G., Olivotti, R., 1978. Risanamento e

- protezione dell'ambiente idrologico delle lagune di Orbetello, Comune di Orbetello, Regione Toscana.
- De La Cruz-Aguero, G., 1993. A preliminary model of Mandinga Lagoon, Veracruz, Mexico. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 193–196.
- DeLos Reyes, M., Martens, R., 1994. Philippines I. Technocommercial impact on trophic level structure of the Laguna de Bay aquatic ecosystem 1968–1980. Ecol. Model. 75/76, 497– 509.
- Duarte, C.M., 1991. Allometric scaling of seagrass form and productivity. Mar. Ecol. Progr. Ser. 77, 289–300.
- Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 87–112.
- EC (European Commission), 1995. Aquaculture and Environment in the European Commission. Luxembourg, 81 p.
- FAO FISHSTAT v. 2.3 Fishery Statistics, Aquaculture Production, 2000. Vol. 90/2.
- Field, J.G., Wulff, F., Mann, K.H., 1989. The need to analyze ecological networks. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Methods and Applications. Springer-Verlag, Berlin, pp. 3–12.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis. J. Theor. Biol. 56, 363–380.
- Grime, J.P., 1979. Evidence for the existence of three primary strategies in plant and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.
- Heymans, J.J., Baird, D., 2000. Network analysis of the northern Benguela ecosystem by means of NETWRK and Ecopath. Ecol. Model. 131, 97–119.
- Innamorati, M., 1998. La laguna di Orbetello: risanamento e gestione conservativa. Biol. Mar. Medit. 5, 1352–1361.
- Izzo, G., Hull, V., 1991. The anoxic crises in distrophic processes of coastal lagoons: an energetic explanation. In: Rossi, C., Tiezzi, E. (Eds.), Ecological Physical Chemistry. Elsevier, Amsterdam, pp. 559–572.
- Kapetsky, J.M., Lasserre, G., 1984. Management of coastal lagoon fisheries. Stud. Rev. Gen. Fish. Coun. Medit. 1 (61), 483.
- Kay, J.J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Methods and Applications. Springer-Verlag, Berlin, pp. 15–60.
- Lankford, R.R., 1977. Coastal lagoons of Mexico: their origin and classification. In: M. Wiley (Ed.), Estuarine Processes. Academic Press, New York, pp. 182–215.
- Lardicci, C., Rossi, F., 1998. Detection of stress on macrozoobenthos—evaluation of some methods in a coastal Mediterranean lagoon. Mar. Environ. Res. 45, 367–386.
- Lardicci, C., Rossi, F., Castelli, A., 1997. Analysis of macrozoobenthic community structure after severe dystrophic crises in a Mediterranean coastal lagoon. Mar. Poll. Bull. 34, 536–547.
- Lavery, P.S., Bootle, S., Vanderklift, M., 1999. Ecological effects of macroalgal harvesting on beaches in the Peel-arvey estuary, Western Australia. Estuar. Coastal Shelf Sci. 49, 295–309.
- Lenzi, M., 1992. Experiences for the management of Orbetello Lagoon: eutrophication and fishing. In: Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine Coastal Eutrophication. Elsevier, Amsterdam, pp. 1189–1198.

- Lenzi, M., Angelini, M., 1984. Indagine sulle condizioni ambientali della laguna di Orbetello. Chimico-fisica e carica microfitica. Atti Mus. Civ. Stor. Nat. Livorno 10, 3–17.
- Lenzi, M., Mattei, N., 1998. Risultati di quattro anni di gestione dell'ecosistema lagunare di Orbetello attraverso la raccolta delle biomasse algali. Biol. Ital., 7–12.
- Lin, H.J., Shao, K.T., Kuo, S.R., Hsieh, H.L., Wong, S.L., Chen, I.M., Lo, W.T., Hung, J.J., 1999. A trophic model of a sandy barrier lagoon at Chiku, in Southwestern Taiwan. Estuar. Coastal Shelf Sci. 48, 575–588.
- Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Nat. 116, 25–44.
- Manickchand-Heileman, S., Arreguinn-Sanchez, F., Lara-Dominguez, A., Soto, L.A., 1998. Energy flow and network analysis of Terminos Lagoon, SW Gulf of Mexico. J. Fish Biol. 53A, 179–197.
- Mann, K.H., 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol. Oceanogr. 33, 910–930.
- Mann, K.H., Field, J.G., Wulff, F., 1989. Network analysis in marine ecology: an assessment. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Methods and Applications. Springer-Verlag, Berlin, pp. 261–282.
- Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Mar. Ecol. Progr. Ser. 161, 239–254.
- Morgana, J.G., Naviglio, L., 1989. Risanamento ambientale della laguna di Orbetello: Indagine sulla struttura delle comunità macrobentoniche animali. In: Bucci, M., Canditelli, M., Caprioli, R. (Eds.), Risanamento ambientale della laguna di Orbetello. Relazioni delle attività svolte nel 1988. ENEA, RT/PAS/89/18, pp. 141–165.
- Nielsen, S.N., 1997. Examination and optimization of different exergy forms in macrophyte societies. Ecol. Model. 102, 115– 127.
- Nielsen, S.L., Sand-Jensen, K., 1990. Allometric scaling of maximal photosynthetic growth ratio to surface/volume ratio. Limnol. Oceanogr. 35, 177–181.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–219.
- Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
- Odum, E.P., 1971. Fundamentals of Ecology. W.B. Saunders, Philadelphia.
- Odum, H.T., Peterson, N., 1996. Simulation and evaluation with energy systems blocks. Ecol. Model. 93, 155–173.
- Orme, A.R., 1990. Wetland morphology, hydrodinamics and sedimentation. In: Williams, M. (Ed.), Wetlands. A Threatened Landscape. Blackwell, London, pp. 42–94.
- Palomares, M.L.D., Reyes-Marchant, P., Lair, N., Zainure, M., Barnabe, G., Lasserre, G., 1993. A trophic model of a Mediterranean Lagoon, Etang de Thau, France. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 224–229.

- Pauly, D., Soriano-Bartz, M.L., Palomares, M.L.D., 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 1–13.
- Perez-Espana, H., Arreguin-Sanchez, F., 1999. A measure of ecosystem maturity. Ecol. Model., 79–85.
- Pianka, E.R., 1970. On r- and K-selection. Am. Nat. 104, 592–597.
 Rosado-Solórzano, R., Guzmán Del Proo, S.A., 1998. Preliminary trophic structure model for Tampamachoco Lagoon, Veracruz, Mexico. Ecol. Model. 109, 141–154.
- Rossi, F., Lardicci, C., 1995. Evoluzioni delle comunità zoobentoniche di fondo molle della laguna di Orbetello: variazioni nella composizione specifica. Atti Soc. Tosc. Sci. Nat 102, 31–36
- Silvestri, R., Signorini, A., Giordano, P., Ottolenghi, F., Creo, C., Massini, G., Allegro, A., Izzo, G., 1999. Stabilità ecologica in lagune e laghi costieri italiani in relazione al processo di eutrofizzazione. In: Basset, A., Fedele, L. (Eds.), Proceeding of SITE 1999.
- Sorokin, Y.I., Sorokin, P., Giovanardi, O., Dalla Venezia, L., 1996.
 Study of ecosystem of the Lagoon of Venice, with emphasis on anthropogenic impact. Mar. Ecol. Progr. Ser. 141, 247–261.
- TEI Ingegneria dell'Ambiente SpA, 1989. Intervento globale di risanamento delle lagune di Orbetello dal fenomeno dell'eutrofizzazione del corpo idrico. Rapporto Finale.
- Ulanowicz, R.E., 1986. Growth and Development. Ecosystems Phenomenology. Springer-Verlag, Berlin.
- Ulanowicz, R.E., 1993. Inventing the Ecoscope. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. ix-x.
- Ulanowicz, R.E., 1995. Ecosystem trophic foundations: Lyndeman exonerata. In: Patten, B.C., Jorgensen, S.E. (Eds.), Complex Ecology: The Part-Whole Relation in Ecosystems. Prentice Hall, Englewood Cliffs, NJ, pp. 549–550.
- Valiela, I., 1995. Marine Ecological Processes. Springer, New York, 686 p.
- Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997.
 The stability of trophic mass-balance models of marine ecosystems—a comparative analysis. Ecol. Model. 100, 125–134.
- Villa, S., 1999. La stima del rischio ambientale dovuto all'utilizzazione di fitofarmaci per organismi non bersaglio. Il sistema Laguna di Orbetello. Ph.D. Thesis, Università di Milano.
- Wolff, F., 1994. A trophic model for Tongoy Bay—a system exposed to suspended scallop culture (Northern Chile). J. Exp. Mar. Biol. Ecol. 182, 149–168.
- Wulff, F., Ulanowicz, R.E., 1989. A comparative anatomy of the Baltic Sea and Chesapeake ecosystems. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Methods and Applications. Springer-Verlag, Berlin, pp. 232–256.
- Wulff, F., Field, J.G., Mann, K.H. (Eds.), 1989. Network Analysis in Marine Ecology. Methods and Applications. Springer-Verlag, Berlin