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Comparative analysis of trophic structure and interactions of two tropical lagoons

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Abstract

A comparative study of the Ébrié lagoon (Ivory Coast) and Lake Nokoué (Benin) was made based on ecotrophic model outputs that describe each system's structure and functioning. Two models were constructed using the Ecopath software to differentiate main biomass flows in the systems.

Results indicate that biomasses and productions in both ecosystems are concentrated in trophic levels (TL) 2 and 3. Higher TL biomasses and productions in Lake Nokoué compared to Ébrié lagoon may be explained by the presence of acadjas. High production per biomass (*P*/*B*) and food consumption per biomass (*Q*/*B*) values indicate the high productivity of these systems and the abundance of juveniles in most groups which utilize these systems as refuge zones and nurseries. The difference, however, lies between the principal source of energy and how it is incorporated in the food web of each ecosystem. Lake Nokoué is a detritus-driven ecosystem while Ébrié lagoon is dominated by the phytoplankton pathway. System indicators suggest different levels of ecosystem stability and maturity. Relevance of other observations on ecosystem functioning and indicators in relation to perturbation is discussed.

Keywords: Tropical lagoons; West Africa; Transfer efficiency; System maturity; Ecopath

Introduction

Coastal lagoons are considered as some of the most productive aquatic ecosystems due to high levels of primary production, intense reserve of organic matter and habitat diversity that offer optimal niches for numerous aquatic species which utilize these areas as refuge and/or breeding grounds (Yáñez-Arancibia et al., 1994; Silvestre and Pauly, 1997; Baran and Hambrey, 1998; Berger et al., 1999; Baran, 2000; Blaber, 2002; Krause and Glaser, 2003; Lalèyè et al., 2003c; Glaser and da Silva Oliveira, 2004). According to Duarte (1995), productions in coastal lagoons are 10-15 times higher than those of other continental shelves.

On the West African coastline, these ecosystems are generally shallow with highly varying gradients. As transitional areas with intense fluctuations of environmental conditions, these ecosystems influence complex multi-species dynamics and impose physiological constraints on biota (Baran, 2000). The ecosystem structure has been observed to depend on freshwater bio-geographic regions, as well as on river discharges and hydrological regimes (Écoutin, 1992; Winemiller, 1995; Baran and Hambrey, 1998; Guiral, 1999; Welcomme, 1999; Baran, 2000). The occurrence and production of the system's living resources are seasonally variable in relation to the marine and/or continental water flows into these 'intermediate' systems. Regional climate trends seem to influence the species diversity of the lagoon community where communities of estuarine species decrease as the species of salt marshes increase.

The establishment of increasing human populations near lagoons, gulfs and bays has resulted in significant degradation and loss of coastal wetlands (Adingra and Arfi, 1998; Entsua-Mensah, 2002; Ibe and Sherman, 2002; Scheren et al., 2002; Glaser, 2003). Construction and practice of traditional forms of low-technology aquaculture, such as brush-parks or acadjas, in coastal lagoons and brackish waters in many areas of the world were to alleviate fish production to meet increasing demand for national consumption and export (Beardmore et al., 1997; Welcomme, 2002; Lalèyè, 2000; Lalèyè et al., 2003c). Changes in environmental conditions generally provoke diverse biological processes or responses (i.e. competition or food depletion) leaving more tolerant species to persist while less tolerant species are eliminated (Berger et al., 1999; Baran and Hambrey, 1998; Laegdsgaard and Johnson, 2001; Glaser, 2003).

For this study, two West African lagoons, Ébrié lagoon and Lake Nokoué, are considered. Previous ecological and biological information on these ecosystems exist such as Durand et al (1994), Adité and Winemiller (1997) and Lalèyè et al (2003c). However, as far as we know, no broad general synthesis of a multi-specific analysis and the combined influence of their characteristics (i.e. production, mortality, trophic interactions, adaptations) following environmental changes has yet been published to date.

This study attempts to summarize and integrate existing data and to depict a larger picture of interactions among biological components and how abiotic conditions mould their structure, metabolism and function in the ecosystem using a mass-balanced modelling software, Ecopath (Christensen et al., 2000). Focus is attributed on quantification of biomass flows and transfer efficiencies among trophic levels (TLs) and identification of significant trophodynamic links occurring between groups (Christensen, 1998). Modelling ecological systems can be useful in describing how an ecosystem is organized and assessing species relationship stability and diversity through complex but tractable depictions of energy transfers, trophic fluxes, assimilation efficiencies and dissipation. Results can provide critical insights that can be further utilized to evaluate the impacts of changes in abundance of a particular group on other groups (Arreguín-Sánchez, 2000) and verify multi-species management decisions and conservation (Baird and Ulanowicz, 1993; Beck et al., 2001; Glaser and da Silva Oliveira, 2004).

Research approach

Study sites

Ébrié lagoon (Ivory Coast) (Fig. 1, left) is a complex, elongated, open coastal lagoon system located between longitudes 3°47’W and 5°29 W and latitudes, 5°02’ N and 5°42’N. It has a total area of 566 km² and the lagoon stretches to about 130 km and a maximum width of 7 km. Annual precipitation in Abidjan is about 1 800 mm. The average water depth is 4.8 meters though depths of 20 m can be observed near Abidjan. The average water temperature is 28°C. Water from the Atlantic Ocean penetrates the lagoon through the Vridi canal (300 m) and mixes with freshwater discharges from three connecting rivers: Comoé, Agnéby and Mé (Laë, 1997a; Pagano et al., 2003).

Lake Nokoué (Fig. 1, right) is a shallow, sub-tropical coastal lagoon (6°25’N, 1°56’E) with a surface of 150 km² and stretches 20 km in its east-west direction by 11 km in the north-south direction. Lake Nokoué opens directly into the Atlantic Ocean by a channel at Cotonou (4.5 km) and it is connected with the Porto-Novo lagoon to its East by the 5 km Totché channel. Saltwater and marine organisms gain access into the lake through the Cotonou channel. Annual precipitation in Cotonou was recorded at 1 300 mm. The average depth of the lake varies from 1 m (dry season) to 3 m (rainy season). The average water temperature is 29°C. Spatial and temporal variations of hydrological parameters were studied in detail by Adité (1996) and recently by Adounvo et al. (2003) and by Lalèyè et al. (2003a).

Model construction

The Ecopath software is a model based on a set of simultaneous linear equations for each group considered in an ecosystem and assumes a mass balance where the production of the group is equal to the sum of all predations, non predatory loses and exports (Christensen et al., 2000). Integration of different ecological levels (i.e. individual, population and community) is pertinent in ecosystem modelling. In order to minimize information loss and taxonomic biases, biological components are pooled according to similarities of species trophic properties (i.e. diets, predators and metabolic activity) and distribution (Yodzis and Winemiller, 1999). Each trophic group has an energy balance expressed as:

$$B_i\left(\frac{P}{B_i}\right) = \sum_{j=1}^{n} B_j\left(\frac{Q}{B_i}\right) - DC_{ji} + \left(B_i\right)\left(\frac{P}{B_i}\right)\left(1 - EE_i\right) + EX_i \qquad (1)$$

where B_i is the biomass of group i; P/B_i is the production rate of i equal to the total mortality coefficient (Z) (Allen, 1971); Q/B_i is the relative consumption rate; B_j is the biomass of the predating group j; DC_{ji}, the proportion of the predated group i in the diet of the predating group j; EE_i is the ecotrophic efficiency representing the part of the total production transferred to higher TLs through predation or captured in the fisheries; EX_i export or catch in fisheries of group i, assumed exploited in fisheries.

Mass-balanced models used here were those previously developed by Villanueva (2004). A total of 42 and 31 functional groups were considered for Ébrié and Nokoué, respectively (Tables 1 and 2). For these models, input data used were mainly from primary data collected and complemented by existing literatures (Niyonkuru et al., 2003; Simier et al., 2003) from specific study sites and considering the same period to achieve proper model synchronization. The choice of the study period was based on the availability and abundance of data for each ecosystem considered, as well as on periods marked by considerable fishing and hydrologic variations. For trophic groups with several species, estimates were derived from properties of the dominant species summarized in table 1.

Biomasses were expressed and standardized as annual average in tons of wet weight (ww)$\cdot$km^{-2}. Production and consumption rates were compiled from a variety of sources and detailed in tables 1 and 2. Flows between compartments are given in tons of wet weight km^{-2} yr^{-1}.

Diet composition of functional groups considered for each models was compiled by Villanueva (2004) and are summarized in tables 3 and 4. It should be highlighted that most of these data were based on biological and ecological studies made in each ecosystem. The landings data used for the Ébrié and Nokoué models were taken from Écoutin *et al*. (1994) and the Department of Fisheries in Cotonou surveys, respectively.

The Ecoranger routine was used to test the sensitivity of each models constructed. This routine limits possible technical errors as it adjusts accordingly possible input parameters that can be modified depending on the data source and calculates the impact on the resulting estimates. This is useful in refining less accurate data, such as in the case of the Ébrié model where most qualitative data on diet composition were modified accordingly to decrease uncertainties or to achieve an ecotrophic efficiency (*EE*) value of less than 1.

Network description analysis

A. structural analyses

Group omnivory index (*OI*) is a concept introduced by Pauly et al (1993) which incorporates the TL variations of different preys consumed by a predator. *OI* values near 0 indicate a highly specialized predator while 1 indicates groups with considerable versatility.

Lindeman (1942) introduced the concept of describing food webs based on grouped taxa and quantified energetic flows of organic matters by TLs which allow assessment of energy transfer efficiency. TL is a dimensionless index that identifies what kinds of food an organism uses. This is a simplification of the food-web to determine the distribution of net input and output flows in each group that has contributed to the next TL. This concept is a useful abstraction to clarify and organize understanding of energy transfer in ecosystems and overcome bias in differing number of biological components when comparing ecosystem state and functioning. In Ecopath, group aggregations into discrete TLs (Ulanowicz, 1986) were carried out based on approach suggested by Ulanowicz (1995). TLs are represented as fractions (Odum & Heald, 1975) rather than integers (1, 2, 3...) as initially proposed by Lindeman.

B. Network analyses

The fishery gross efficiency is computed as the ratio between the total catch (landings and discards) and the total primary production in the system. The value is higher for systems with a fishery harvesting mainly in low TLs than for systems whose fisheries concentrate on high TLs. This index may increase with fisheries 'development' as indicated by Pauly et al. (1998).

The total system throughput (TST) is defined as the sum of all flows in a system. It represents the "size of the entire system in terms of flow" (Ulanowicz, 1986). As such, it is an important parameter for comparisons of flow networks.

The ratio of total system biomass to the total system throughput (*B*/TST) (Christensen, 1995) is directly proportional to system maturity where estimated value tends to be low during ecosystem development phase and increases as a function of maturity. Energy is conserved through component energy stocking (Odum, 1971; Ulanowicz, 1986).

The ratio of Net Primary Production to Total Respiration (PP/TR) is another system maturity index (Odum, 1969; Pérez-España and Arreguín-Sánchez, 1999) where values of this ratio close to 1 indicate mature ecosystems.

The net production of the system (NPP-TR) is another index of system maturity (Odum, 1969) and should be zero out in a truly balanced ecosystem.

The system omnivory index (*SOI*) is computed as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake (Christensen et al., 2000).

The connectance index (*CI*) for a given food web is the ratio of the number of actual links between groups to the number of theoretically possible links. Feeding on detritus (by detritivores) is included in the count, but the opposite links (i.e., detritus 'feeding' on other groups) are disregarded. This index is correlated with the maturity of the ecosystem because a food chain structure changes from linear to web-like as a system matures (Odum, 1969; 1971).

Initially considered by Finn (1976), the Finn's cycling index is the proportion of the total system throughput (TST) recycled in the system. According to Monaco and Ulanowicz (1997), cycling is considered to be an important indicator of an ecosystem's ability to maintain its structure and integrity through positive feedback and can be used as an indicator of stress (Ulanowicz, 1986) or system maturity (Christensen, 1995; Vasconcellos et al., 1997). This is similar to the predatory cycling index, which is calculated by excluding the cycling through detritus. Disturbed systems are characterized by short and fast cycles while complex trophic structures have long and slow ones (Odum, 1969; Kay et al., 1989; Christensen, 1995). A manner of quantifying the length of each cycle is through the Finn's mean path length which accounts for the number of groups involved in a flow. Finn's straight-through path length (excluding detritus) is another indicator of ecosystem health wherein a low value translates a stressed ecosystem and a short food chain controlled by bottom-up forces.

Macro-descriptors are typically applied for large and complex ecosystems whose aim is to present ecosystem growth and development (Ulanowicz, 1997). Ascendancy, *A*, (Ulanowicz, 1986) and mutual information, *I*, (Hirata, 1995) are examples of quantitative descriptors that differ from those used in classical food webs. Ascendancy is a measure of system growth (i.e. age, size) and development (i.e. organization) of network links. The fraction of a system's capacity not considered as ascendancy is considered as the systems overhead, which is the energy in reserve of an ecosystem (Monaco and Ulanowicz, 1997), especially in case of perturbations (Ulanowicz, 1986). The relative ascendancy (A/C) is the fraction of possible organization that is actually realized (Ulanowicz, 1986) and it is negatively correlated with maturity (Christensen, 1995).

Results

After integrating all the basic inputs, both models were balanced. Basic parameterization results for the Ébrié and Nokoué models are shown in tables 1 and 2, respectively, whereas the feeding matrices are displayed in tables 3 and 4.

Model sensitivity

Pedigree indices of 0.79 and 0.75 for Nokoué and Ébrié models, respectively were obtained from the model. Both values conform to the gauge of the overall quality of an Ecopath model as discussed by Christensen et al. (2000). The Ecoranger routine was then used for each model in order to assess their viability. For the Ébrié model, 33 acceptable runs out 10 000 were obtained with a least sum of deviation equal to 16.06. A higher number of acceptable runs (158/10 000) were obtained for Lake Nokoué with a least sum of deviation equal to 11.27. These values indicated that both models are tightly-fitted. The initial inputs and outputs based on our field data were very close to the mean values generated by Ecoranger. Ratios of respiration to assimilation (*R/A*), production to respiration (*P/R*) and estimated *EE*s for all considered group are less than 1.

Structural analyses

The TL of each group varied between 3.9 and 1.0 in Ébrié with the higher values corresponding to groups 1, 4 and 5 and with most fish groups (75 %) at TL3 (Table 1). In Nokoué, individual TL varied between 3.5 and 1.0 with the highest value corresponding to group 5 followed by groups 2, 4, 13 and 15 (Table 2).

The cumulative biomass of major fish groups was lower in Ébrié lagoon (9.48 $t \cdot km^{-2}$) than in Lake Nokoué (132.43 $t \cdot km^{-2}$). The obvious reason is the development of acadjas which are artificial fish aggregating devices built using branches that act both as a insatiable food source for detritivores (such as tilapias and benthic organisms), as well as lowering predation and competition pressure by limiting access of carnivores or piscivores (Welcomme, 1999).

Group *OI* values obtained are quite low and may be due to the specialization and predation rates of some groups depending on the environmental conditions and availability of preys in each ecosystem (Tables 1 and 2). Higher group *OI* values in Lake Nokoué may be due to possible feeding of non- or less-detritivorous groups on detritus because of eutrophication and limited access to other prey types due to acadjas installations, covering most of the lake's surface. It is interesting to note that eight groups in Ébrié lagoon occupy higher TLs and have *OI* values greater than 0.25, compared to only 5 groups in Lake Nokoué. Among these are the mobile epibenthos, such as the blue swimming crab (*Callinectes latimanus*) and pink shrimps (*Penaeus duorarum*), which consume plankton, benthos, crustaceans and organic materials.

Trophic network analysis

It is important to note that, in terms of fish and crustacean, biomasses and ecological production in TL3 are higher than in TL2 for the Ébrié lagoon model, whereas, the opposite is observed in Lake Nokoué (Table 5 and Figure 2). The proportions of species of these various groups are quite similar in both systems and fish assemblages seem to have common patterns even if their relative importance, in terms of biomass, is highly variable. In the Ébrié model, 71.5 % of the fish biomass is at TL3 or higher such as *Sardinella maderensis* (6.0 %), *Gerres* spp (3.0 %), *Chrysichthys nigrodigitatus* (11.0 %), *Dasyatis* spp (3.0 %) and *Tylochromis jentinki* (4.0 %). In Lake Nokoué, on the other hand, only 38.0 % of the total fish biomass belongs to TL3 or higher. The key groups are below TL2.5: the tilapiine fish (55.0 %), Gobiids (12.0 %) and *E. fimbriata* (32.0 %).

Transfer efficiencies decline at higher TLs in both ecosystems considered (Figure 3) which is similar to observations of Manickchand-Heileman et al. (1998) and Zetina-Rejón et al. (2003). The transfer efficiency is higher in Ébrié than in Nokoué for TL2, 3 and 4. This is in relation to the difference of structure of the fish community in both ecosystems as noted in table 5 and figure 3. The geometric mean transfer efficiency was

15.5 and 10.3 % for Ébrié lagoon and Lake Nokoué, respectively. Proportion of total flow originating from detritus is 44 % in Ébrié lagoon compared to 72.0 % in Lake Nokoué.

Trophic interspecific reactions for Ébrié lagoon and Lake Nokoué are shown in figures 3a and b, respectively. For the Ébrié model, the total consumption is estimated at 1,207.68 t·km^{-2}yr^{-1} (Table 6) where 71.5 % (740.4 t·km^{-2}yr^{-1}) of the flow from TL1 to TL2 originates from the producers whereas dead decaying materials contribute only 28.5 % (294.6 t·km^{-2}yr^{-1}) (Figure 3a). It results in a detrivory: herbivory ratio (D:H) of 1:2.5 (Figure 3a). Most phytoplanktonic production is incorporated into the food web by zooplankton and zoobenthos.

In Lake Nokoué, the total food consumption, which is higher than in Ébrié lagoon, is estimated at 25,713.42 t·km^{-2}yr^{-1} (Table 6). Figure 3b shows that energy transferred from TL1 is accessed mainly from the detritus (19,242.1 t·km^{-2}yr^{-1}) as compared to that coming from the primary production (4,133.7 t·km^{-2}yr^{-1}). It results in a D:H ratio of 4.6 : 1 (Figure 3b).

The highest flow back to detritus was observed from the autotrophs, (TL1) 1,889.6 t·km^{-2}yr^{-1}, in the Ébrié lagoon and from primary consumers (TL2), 12,167.7 t·km^{-2}yr^{-1}, in Lake Nokoué (Figure 3a and b).

The *SOI* value and the connectance index (*CI*) are lower in Ébrié (0.145 and 0.191, respectively) than in Nokoué (0.156 and 0.266, respectively) (Table 6). These indicate that Lake Nokoué has a more web-like feature of trophic structure than in Ébrié lagoon.

The mean TL of catch is 2.88 in Ébrié lagoon and is 2.46 in Lake Nokoué (Table 6). This is mainly due to the different relative importance of key-targeted groups in the fisheries occupying different TLs in each system as can be observed from tables 1, 2, 5 and 6. This has also an influence on the gross efficiency (*GE*) of the catch: lower in Ébrié (0.004) than in Nokoué (0.009). Total system throughput for each ecosystem (Table 6) is higher in Lake Nokoué than in Ébrié lagoon.

According to Christensen et al. (2000) a system primary production/respiration (*P/R*) ratio near 1 indicates an ecosystem approaching maturity (Odum, 1969). Comparing the values obtained in each model (Table 6), Ébrié is a less mature system (5.055) than Nokoué where *P/R* is near 1 (1.126). Considering other attributes of ecosystem maturity and stability (*B*/TST, TPP/TR, PP-TR, PP/*B*), values obtained for Lake Nokoué indicates that this ecosystem is reaching a mature stage and is therefore more stable.

Energy and matter recycling is considered as an important process in ecosystem functioning (Odum, 1969) and is measured as FCI. According to Heymans and Baird (2000), value of this index is between 4.0 to 15.0 % for coastal ecosystems. Estimated FCI value (Table 6) in Lake Nokoué (34.0 %) is much higher than in Ébrié lagoon (2.7 %). It is, however, relatively low compared to that obtained by Manickchand-Heileman et al. (1998). The high value of Finn's straight-through path length (excluding detritus) in Nokoué suggests a short food chain perhaps due to shifting of diets of other groups towards detritivory.

Discussion

As in any Ecopath model, the outputs and the consequent uncertainties of results are strongly related to input parameters integrated. The viability of the Ecopath models was determined by using the sensitivity analyses, i.e. Pedigree index and Ecoranger, incorporated in the software (Christensen et al., 2000). The high viability observed for each model considered, as indicated by the high pedigree indices, was due to the consideration of input parameters estimated mostly from specific studies in the considered ecosystems (i.e. Durand et al., 1994; Adingra and Arfi, 1998; Albaret, 1999; Lalèyè et al., 2003a, b, c; Simier et al., 2003; Adounvo et al., 2005). Since most of the data were based on direct observations, results indicate that both models are tightly-fitted as simulations give allocating values which have no remarkable difference from original inputs.

Fishes and macroinvertebrates are very good environmental indicators to track environmental health and ecological changes as adaptive response to stress, especially in estuaries and lagoons (Paugy and Bénech, 1989; King, 1993; USEPA, 2000). Comparing tables 1 and 2, several taxonomic groups are similarly represented in both models. Similarities of common and endemic biological assemblages are possibly due to close geographical location though dissimilarities, especially in biodiversity, are mainly due to hydrologic dynamics (Winemiller, 1995; Guiral, 1999). However, these taxonomic species occupy differing TL in each ecosystem. Winemiller (1990) indicated that similar resources are utilized by species of comparable morphological traits. However, according to Polis et al. (1996) resource utilization and ecological interactions are highly dependent on habitat heterogeneity and may explain deviation in trophic guilds and behaviors of similar taxonomic groups in different ecosystems.

Albaret and Legendre (1986) characterized *E. fimbriata* as a zooplanktivore feeder though indicated a considerable quantity of detritus in its diet in Ébrié lagoon. Charles-Dominique (1982) explained that the presence of decaying materials in its stomach coincides mainly to strong river run-offs. Observations in Lake Nokoué, on the other hand, indicate that this species is considerably feeding on decaying materials and, to a lesser degree, on plankton.

The high versatility of *S. melanotheron*, especially with regards to diet plasticity (feeding on algae, periphyton and organic matter) has been indicated by several authors (Pauly et al., 1988; Paugy, 1990), as well as its ability to adapt in terms of growth and reproduction to varying and extreme environmental conditions, i.e. ability to grow in reefs of undergrowth, limited oxygen supply (Adité and Winemiller, 1987; Duponchelle et al., 1998; Panfili et al., 2004; Pauly 2002; Villanueva, 2004). This species has already been observed to acclimate fast in several West African brackish systems such as in Sakumo lagoon (Pauly, 2002), Ébrié lagoon (Konan-Brou and Guiral, 1994), Toho-Todougba lagoon (Adité and Winemiller, 1997) and in Sine Saloum estuary (Panfili et al., 2004). The high productivity and resilience of this species to stress may also be attributed to the presence of "acadjas" which act as an extensive aquaculture system (Konan-Brou and Guiral, 1994) that increase trophic efficiency of the lagoon, i.e. suitable places for breeding, low predation and niche competition (Adité and

Winemiller, 1997; Laë, 1997b; Welcomme, 1999; Lalèyè, 2000; Villanueva, 2004). In Ébrié lagoon, *S. melanotheron* is present though less abundant and has a higher probability of occurrence concentrated in stenohaline and euryhaline sectors of the lagoon (Villanueva, 2004). Abundance and occurrence of this species may be influenced by river discharges which increases availability of food similar to observations of Adité and Winemiller (1997).

These ecosystems are characterized by complex food webs and high eco-physiological capacities of biologic communities against extremely varying environmental conditions, in space and time (Carrada and Fresi, 1988; Albaret and Écoutin, 1990; Adité and Winemiller, 1997; Lalèyè et al., 2003b; Berlow et al., 2004; Villanueva, 2004). Levels of fish structure organizations in these ecosystems are never high (Albaret and Écoutin, 1990) though Laë (1997b) observed that re-structurization of food web occurs in the case of environmental stress. Higher structural organization is observed in Ébrié lagoon (highest TL 3.9) than in Lake Nokoué (TL 3.2) which is due to lower biodiversity in the latter ecosystem.

Numerous studies have suggested that biodiversity reduces variability in ecosystem productivity through compensatory effects (Naeem and Li, 1997; Loreau, 2000; Berlow et al., 2004), which means that a species increases in abundance in response to the reduction of another in a fluctuating environment. A high biodiversity enhances an ecosystem's reliability through increase in redundant species per functional group where some groups occupying a given TL maintain ecosystem functioning by compensating for temporary loss of other groups in the same TL. The system integrity of Lake Nokoué seems to be assured against biodiversity loss and other perturbations through further simplification of food web structure and increased recycling of organic matter. According to Loreau et al (2000), low species richness does not necessarily entail weakened ecosystem properties and services. In Ébrié lagoon, diversity and production are positively correlated where differences in distribution and eco-physiological characteristics increase efficiency of energy utilization thus maintain ecosystem integrity through function replacement of some groups by others in the same TL.

The importance of the detritus and primary production pathways in such ecosystems was noted by Albaret (1999). De Sylva (1985) indicated that estuarine nektons follow either a detritus-based or a phytoplankton-based food chain. Primary producers and detritus are energy sources that play differing roles and significance in the diet of groups of higher TLs in the two ecosystems considered here. Results showed that phytoplankton is the key food source in Ébrié lagoon that sustains mainly the zooplanktonic secondary production similar to observations of Ray et al. (2000) in the Sundarban mangrove system (India). Macrophytes, on the other hand, provide shelter for crustaceans and mollusks. Paugy and Bénéch (1989) observed that in such environments, the latter is less important. This is not the case, however, in Lake Nokoué where the detrital pathway dominates over the grazing pathway similar to Orbetello lagoon studied by Brando et al (2004) and the Terminos lagoon (Arreguín-Sánchez et al., 1993; Manickchand-Heileman et al., 1998). These dead organic materials sustain large biomasses of benthos by providing substrates for epiphytes and shelters for crustaceans and mollusks (Zetina-Rejón et al., 2003; Moore et al., 2004). The high biomass of TL1 (detritus and primary producers) and its significant role in supporting the energy utilized indicate a bottom-up control in both ecosystems.

In Lake Nokoué D:H ratio is high despite the absence of micro-organisms (i.e. bacteria) among the considered functional groups in the system. This high detritus consumption is mainly due to the high density of *S. melanotheron* in this ecosystem. Adité and Winemiller (1997) indicated that reduction of available resources in Lake Nokoué due to environmental degradation may have contributed to changes of ecological interactions and ecosystem physiography leading to a relative increase of detritivores.

The importance of detritivory in Lake Nokoué is due to dietary shifts of carnivore species such as the *C. nigrodigitatus*, *E. fimbriata, Trachinotus ovatus* and *Liza falcipinnis* to a more detritus-based feeding when other resources are limited (Adité and Winemiller, 1997) and which may compete with the true detritivores, the tilapias (*S. melanotheron* and *T. guineensis*). Other fish species in TL2, as well as epibenthos (crabs and shrimps) are directly utilizing this resource (Figure 3b).

Ecosystem functioning can be better viewed in terms of biomass fluxes between TLs. Predators and resource availability can cause direct changes of diversity from one TL to the next (Nielsen, 2001). This suggests that the flow rates between predators and preys may vary as a function of limiting conditions or variables (i.e. seasonal variations; availability of food).

In Lake Nokoué the link from TL1 to higher TLs is formed mainly by zoobenthos (i.e. bivalves), decapod crustacea and fishes (i.e. tilapias) while the zooplankton (dominated by rotifers) seems to be less important. According to Gnohossou (2001), the predominance of rotifers among zooplankton populations clearly indicates intense fishing activity in Lake Nokoué. Similar observations have been indicated by A. Duncan

(RHUL, pers. comm.) in an artificial lake in Sri Lanka. Rotifers seem to be poorly consumed and may contribute to the high flow of TL2 back to the detritus (Figure 4b). In Ébrié lagoon, the zooplankton group has a positive effect on most other groups and serves as a principal link between primary producers and higher consumers (Villanueva, 2004) similar to that was observed by Zetina-Rejón et al. (2003) in Huizache-Caimanero lagoon complex, Mexico. Other groups, such as the decapod crustacea (i.e. shrimps and crabs) and zoobenthos, feed considerably on both phytoplankton production and detritus.

According to Heymans et al (2002) the amount of energy flowing through the detrital pathway can equal or exceed that observed from grazers. The low transfer efficiencies in Lake Nokoué may be aggravated by the presence of acadjas which limits predation (biomass transfer flow from TL2 mainly from *S. melanotheron* to higher TLs is reduced) resulting significant flows back to detritus (Figure 3b) similar to indications of Moore et al (2004). Poor utilization of primary production, zooplankton and even *S. melanotheron* by other groups in higher TLs is indicated by the low trophic efficiency of phytoplankton (Table 6) and the large flows back to detritus of TL1 (primary production) and TL2 (Figure 3b). According to Gnohossou (UAC, pers. data), rotifers are rarely found in food items ingested by fish, especially in plankton-feeding species such as *E. fimbriata*. Blaber (2000) indicated that this species is a visual-filtrer and high water turbidity levels in Nokoué may decrease its feeding efficiency. Inefficient grazing by herbivores has already been observed in other ecosystems such as continental shelf area in Sierra Leone (Longhurst, 1983) and Terminos Lagoon, Mexico (Manickchand-Heileman et al., 1998).

Estimated total system throughputs (Table 6) in both ecosystems are rather high compared to that obtained by Carrer and Optiz (1999) in the Palude della Rosa lagoon, Venice. TST in Ébrié lagoon (6,240 $t\cdot km^{-2}\cdot yr^{-1}$) is comparable to that estimated by Manickchand-Heileman et al (1998) in Terminos lagoon (Mexico). For Lake Nokoué; TST value (57,967 $t\cdot km^{-2}\cdot yr^{-1}$) is high compared to the two ecosystems mentioned above and also with comparable systems for instance some coastal ecosystems reported by Christensen and Pauly (1993) though relatively lower than that obtained by Lin et al (1999) in a Chiku lagoon, Taiwan.

Estimated production levels in both ecosystems, however, are higher than those in ecosystems such as Terminos Lagoon, Mexico (Arreguín-Sánchez et al., 1993; Manickchand-Heileman et al., 1998). Recent surveys made by the Department of Fisheries in Cotonou (Benin) showed that annual yield in Lake Nokoué alone reaches about 19,500 $t\cdot yr^{-1}$ (1.5 $t\cdot ha^{-1}$) which is 10 times more than in Ébrié lagoon. *S. melanotheron* forms about 77.0 % of this catch (Lalèyè, 2000). This may explain the higher gross efficiency (*GE*) value calculated in Nokoué (0.009) compared to Ébrié (0.004) (Table 6). Écoutin et al. (1994) indicated that considerable fish and crustacean exploitations already occurred from the late 1970s to the early 1980s which resulted in a remarkable depletion of annual catch in the Ébrié lagoon (Laë, 1997a). *GE* values are, however, lower than the values obtained by Lin et al. (1999) for a sand barrier lagoon in Chiku, Taiwan. According to Jarre-Teichmann (1998), cost of fish exploitation in ecological terms is less at lower TLs than those at higher ones.

Assemblages in Lake Nokoué had shown a greater interspecific resource partitioning than in Ébrié lagoon though it is important to consider that factors influencing dietary diversity (seasonal dietary shifts, spatial variations in dietary habits, etc.) which may have influenced our analyses. According to Heymans et al. (2004), a low value of *CI* coupled with a slightly elevated *SOI* value may indicate an ecosystem less dependent on detritus as a source of energy. This is essentially the case in Ébrié lagoon (Table 6). The higher *CI* and *SOI* values estimated in Lake Nokoué indicate that it is more stable and has a higher resilience to stress than in Ébrié lagoon despite a higher biodiversity of the latter.

Coastal systems such as lagoons are characterized by complex food webs and high eco-physiological capacities of biologic communities against extremely varying environmental conditions, in space and time (Carrada and Fresi, 1988; Albaret and Écoutin, 1990; Adité and Winemiller, 1997; Lalèyè et al., 2003b; Berlow et al., 2004; Villanueva, 2004). They are dynamic rather than static systems where change and disturbance are seen as natural features of these ecosystems (Bengtsson et al., 2000) which seem paradoxal when described as stable systems. Ecosystem stability can be quantified from changes and dynamics (i.e. thermodynamics, productivity) of its components and dimensions where stability is seen as a basis against which ecosystem's responses to perturbation is measured (Christensen, 1995; Nilsson and Grelsson, 1995; Gunderson 2000), such as in mature systems (Odum, 1969). It is argued that the stability, of an ecosystem is high if the connectance (weighted number of nonzero entries in the flow matrix) of the energy flow network is high (Grimm et al., 1992; Berlow et al., 2004).

Lake Nokoué may be more stable due to the increased re mineralization of organic materials in this ecosystem compared to that in the Ébrié lagoon. High detrivory in

Nokoué may mitigate resource limitations caused by environmental change. Moore et al (2004) indicated that a detritus-based ecosystem is more stable both in terms of energy fluxes and consumer population dynamics. Detritus can alter energy and effect nutrient transfer efficiencies across trophic levels and increase persistence and food web stability. According to Hairston and Hairston (1993) detritus impinge on the trophic structure and community dynamics as well as supports a vast diversity of species supporting larger predator biomass and longer food chains compared to ecosystems supported merely by living autotrophs.

The implantation of acadjas in many Asian and African countries is mainly due to its great potential in enhancing technologies, annual yield as well as alleviating social and economic welfares by providing food, employment and livelihood rapidly to the growing population (Costa and Wijeyaratne, 1994; Wahab et al., 1999; COFAD GmbH, 2002; Lalèyè, 2000; Lorenzen et al., 2001; Ekram-Ul-Azim et al., 2002). According to Sokorin et al (1996) and Lalèyè (2000), the high productivity of coastal lagoons is due to the intense bacterial re-mineralization of organic matters and the continuous circulation of water and sediment nutrients. The presence of the acadjas contributes to the production of organic materials to support the ecosystem despite low primary production from phytoplankton and terrestrial vegetations (Konan-Brou and Guiral, 1994; Welcomme, 1999) and replicates artificially favored habitats by certain species offering shelter from predators, suitable breeding grounds (Lalèyè, 2000) aside from the high abundance of food.

While this type of periphyton-based aquaculture can be conducted in sustainable ways, increasing productivity has been achieved with considerable environmental costs, threatening many aquatic and marine ecosystems (Lalèyè et al., 2001). Nutrient addition in ecosystems which increases productivity often lead to lower species richness as more productive species outcompete less productive ones (Waide et al. 1999). Lalèyè (2000) indicated that although the number and areas covered by acadjas in Benin have increased their productivity has decreased over the years (5.625 t.ha.$^{-1}$ yr^{-1} in 1959; 3.9 t.ha.$^{-1}$ yr^{-1} in 1970; 4.1 t.ha.$^{-1}$ yr^{-1} in 1981 and 1.92 t.ha.$^{-1}$ yr^{-1}, 1998) mainly due to the decline in density and quality of branches used.

De Silva (1998) indicated that aquacultures depend on two critical environmental factors: quality and quantity of water. These factors, in turn, depend upon an ecosystem's assimilative capacity for wastes and replenishment of oxygen (Beveridge et al., 1997). It was noted by Lalèyè et al. (2003a) that in Lake Nokoué, dissolved oxygen reaches 0 during the night indicating that oxygen is totally utilized by the system (high respiration rates). High oxygen depletion in other coastal lagoons in the Gulf of Guinea has also been indicated by Scheren et al. (2002). The TPP/TR ratio in Lake Nokoué (1.126) indicates a level close to "eutrophic status" as total system respiration approaches its production, which is a common feature in highly polluted systems. Ébrié lagoon seems less eutrophic due to its higher TPP/TR ratio (5.155) which may be due to lower pollution loads during the period (early 80's) considered for this study. This may be no longer true if based on recent environmental domestic and industrial pollution loads indicated by Scheren et al. (2002) in this lagoon compared to coastal waters in Benin. According to Mann et al. (1989), system ascendancy (*A*) and TST can also be used as indicators of eutrophication in ecosystems. This is characterized by an increased value in *A,* as a function of elevated TST parallel to a fall in information (*I*) (Ulanowicz, 1986). In

Lake Nokoué, an elevated *A* (47,224 flowbits) is compensated by a low value of *I* (0.815) compared to that in Ébrié where *A* is 7,656 flowbits with an *I* of 1.147 (Table 6).

Conclusion

Coastal ecosystems function is a life support system of poor populations and their destruction is a real cause of growing poverty and deprivation relating to a whole spectrum of economic and social problems (John and Lawson, 1990; Ibe and Sherman, 2002; Scheren et al., 2002; Lalèyè et al., 2003c). The most reported detrimental impacts are conversion of wetlands, destruction of valuable habitats (i.e. mangrove forests), loss of biodiversity, pollution of local waters, biological discharge of waste nutrients, rivalry between endemic and introduced exotic species and amplified pressure on natural wild stock (Beardmore et al., 1997; Baran and Hambrey, 1998; Berger et al., 1999; Lalèyè, 2000; Laegdsgaard and Johnson, 2001; Scheren et al., 2002; Glaser, 2003). Apart from various industrialized and agricultural activities, over-fishing is responsible for a wide variety of impacts on fish communities including even modification of population composition and ecosystem adaptations to a changing environment due to stress conditions.

West African coastal ecosystems, as well as in most part of the world, have experienced both long-term trends and rapid environmental changes. Recent accelerating human impacts have brought in other elements that prevent predictions of impact resulting from change. Associated organisms have evolved under these changing environmental conditions and have responded to past natural disturbances, i.e. climate change and species interactions, with adaptation or migration while others have become extinct.

Based on the present study, phytoplanktonic production showed a positive effect in supporting groups in higher TLs in the Ébrié lagoon while detritus played a major role in Lake Nokoué. Ébrié lagoon showed a greater ecological diversification and higher structural organization of biological communities due to higher species assemblages leading to favorable patterns of reliable flows. Lake Nokoué on the other hand, is more stable and shows more signs of maturity mainly due to the abundance of tolerant species that drive the recovery processes after perturbation.

The relationship discussed between organism functions, environments and responses to stress have implications for understanding environmental perturbations on ecological communities. It is evident that ecosystem changes cause a profound restructuring of local communities which can not be predicted without a clear understanding of the mechanisms that retain species' assemblages and functions. The value of an ecosystem-based evaluation, as elucidated here, should be important not only for basic science but for anticipating the likely impacts of environmental perturbations on ecosystem functions and socio-economic challenges they may involve.

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Legends of figures:

Figure 1. The Lagoon Ébrié in Ivory Coast (left) and the Lake Nokoue in Benin (right).

Figure 2. Detailed trophic structure of biomass ($t \cdot km^{-2}$, left) and ecologic production ($t \cdot km^{-2} \cdot yr^{-1}$, right), of fish groups as summarized using Ecopath: (a) Lagoon Ébrié and (b) Lake Nokoué.

Figure 3. Simplified trophic flow models of Lagoon Ébrié (**A**) and Lake Nokoué (**B**) showing discrete trophic levels. Detritus (part of TL I) has been separated to show its significance as energy source in each ecosystem. Percentage (%) values indicate trophic efficiencies per trophic level. Numbers on arrows indicate flow of energy expressed in $t \cdot km^{-2} \cdot yr^{-1}$.

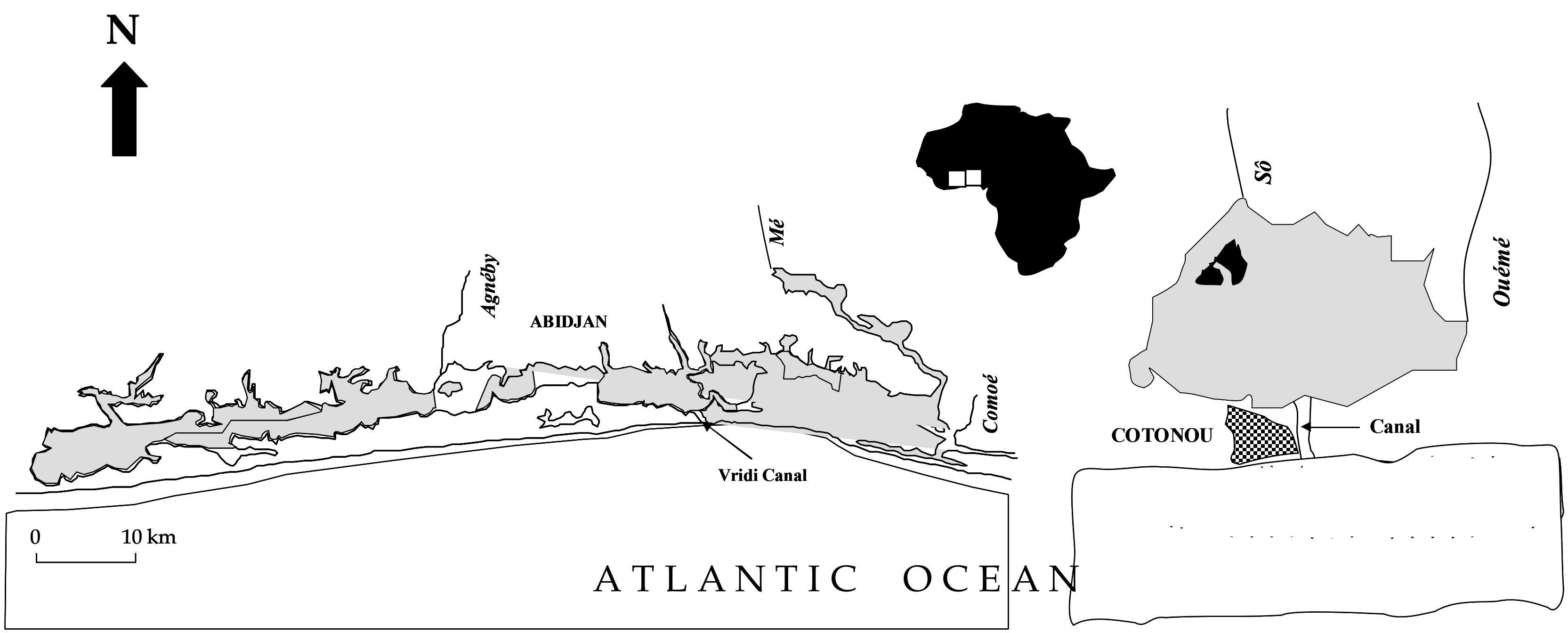

Figure 1
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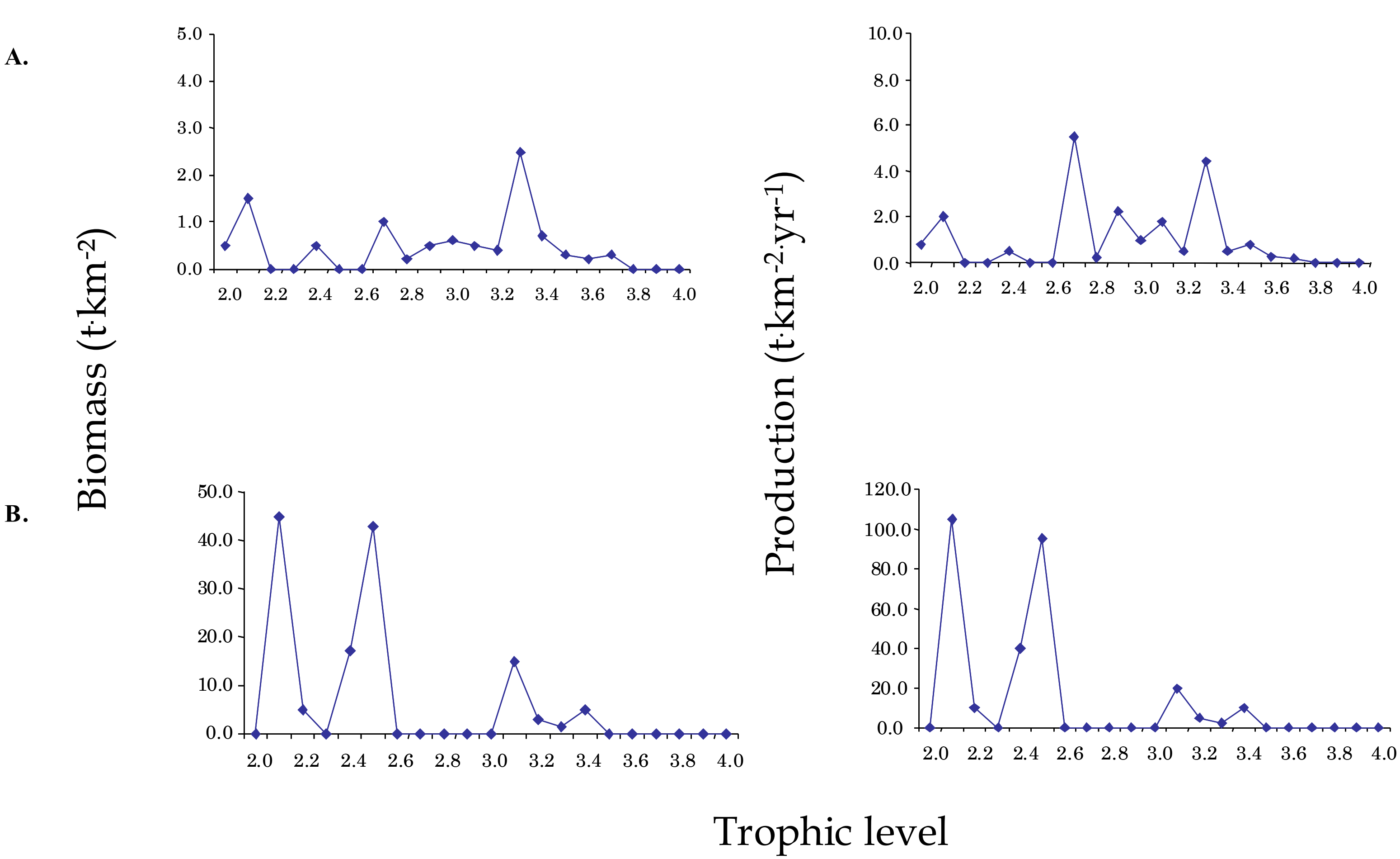

Figure 2
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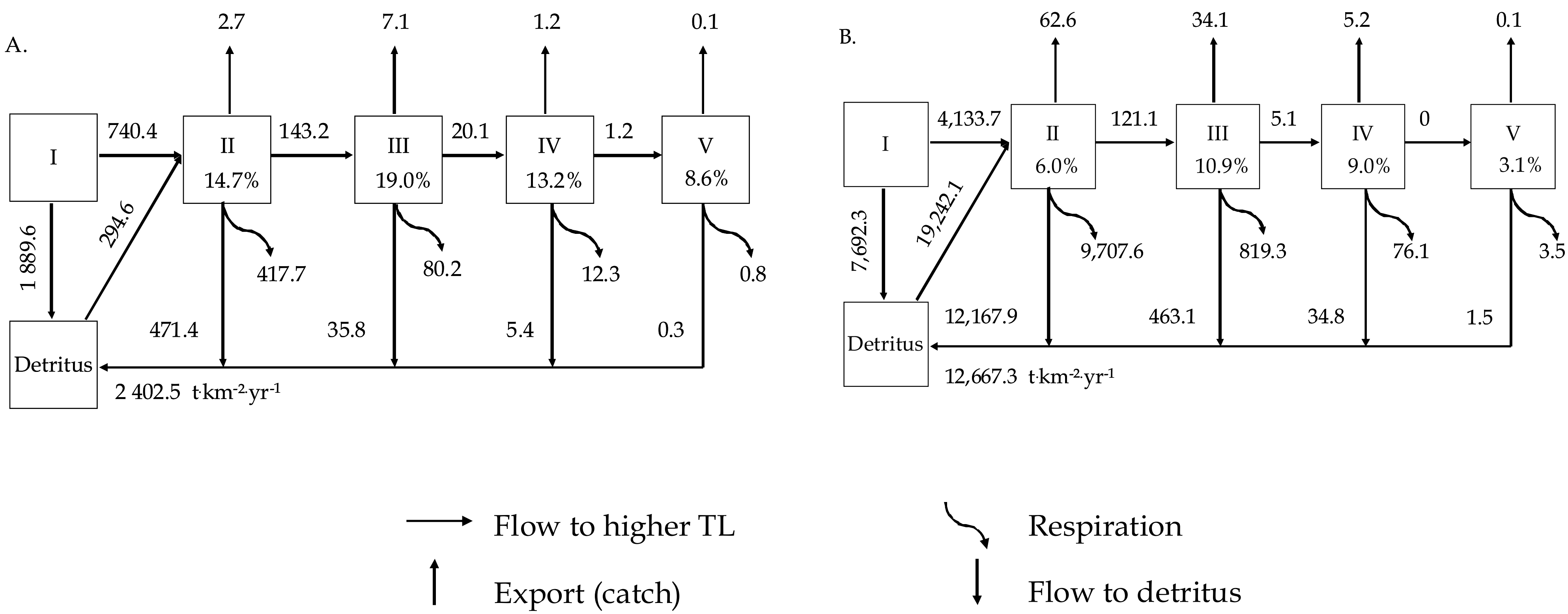

Figure 3

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Table 1. Basic inputs and estimated outputs (bold) of the Ébrié lagoon model during the early eighties.

	Group name	TL	*B*	*P/B*	*Q/B*	*Y*	*OI*
1	*Sphyraena afra**	(3.9)	0.010	2.060	8.427	0.020	**0.204**
2	*Polydactylus quadrifilis*	(3.2)	0.199	1.560	8.225	0.187	**0.142**
3	*Galeoides decadactylus**	(3.4)	0.214	1.380	15.201	0.030	**0.124**
4	*Pseudotolithus elongatus*	(3.6)	0.079	1.460	10.235	0.060	**0.214**
5	*Pseudotolithus senegalensis**	(3.7)	0.115	0.687	5.352	0.010	**0.152**
6	*Elops lacerta**	(3.3)	0.854	2.790	15.450	1.282	**0.101**
7	*Arius lastiscutatus**	(3.3)	0.160	0.430	7.290	0.004	**0.126**
8	*Pomadasys jubelini**	(3.4)	0.018	2.130	12.058	0.022	**0.076**
9	*Chloroscombrus chrysurus*	(3.1)	0.117	2.150	23.817	0.054	**0.159**
10	*Caranx hippos**	(3.5)	0.108	1.710	16.004	0.040	**0.125**
11	*Trachinotus teraia**	(3.3)	0.119	0.930	6.885	0.056	**0.364**
12	*Citharichthys stampflii*	(3.5)	0.177	3.350	17.576	0.025	**0.092**
13	*Cynoglossus senegalensis**	(3.4)	0.156	0.510	6.424	0.025	**0.201**
14	*Gerres nigri**	(3.1)	0.244	3.870	19.762	0.658	**0.138**
15	*Drepane africana**	(2.8)	0.083	0.910	8.207	0.020	**0.396**
16	*Dasyatis margarita**	(3.4)	0.250	0.530	3.726	0.020	**0.125**
17	*Ilisha africana*	(3.0)	0.217	1.559	15.071	0.030	**0.147**
18	*Brachydeuterus auritus*	(3.0)	0.022	4.220	23.047	0.050	**0.024**
19	*Hemichromis fasciatus**	(3.3)	0.014	3.680	16.315	0.030	**0.123**
20	*Schilbe intermedius**	(3.0)	0.009	4.200	20.980	0.020	**0.180**
21	*Strongylura senegalensis**	(3.2)	0.147	1.050	9.840	0.010	**0.135**
22	*Hydrocynus forskahlii**	(3.3)	0.027	1.375	12.310	0.005	**0.245**
23	*Pellonula leonensis*	(3.1)	0.047	3.560	26.022	0.070	**0.069**
24	*Eleotris senegalensis**	(3.3)	0.377	1.890	18.450	0.080	**0.144**
25	*Chrysichthys nigrodigitatus**	(3.3)	1.027	1.130	7.682	0.674	**0.037**
26	*Trichiurus lepturus*	(3.1)	0.050	0.600	5.454	0.001	**0.309**
27	*Synodontis gambiensis* *	(2.8)	0.026	1.600	12.760	0.010	**0.288**
28	*Monodactylus sebae*	(3.1)	0.129	2.240	20.021	0.056	**0.025**
29	*Ethmalosa fimbriata*	(2.7)	1.125	4.710	18.515	3.370	**0.233**
30	*Sardinella maderensis**	(2.9)	0.550	4.180	25.229	0.670	**0.105**
31	*Liza grandisquamis**	(2.4)	0.469	0.880	26.596	0.174	**0.229**
32	*Tylochromis jentinki*	(3.0)	0.386	1.400	10.508	0.354	**0.269**
33	*Sarotherodon melanotheron*	(2.1)	1.456	1.200	23.820	0.326	**0.066**
34	*Tilapia guineensis*	(2.0)	0.473	1.440	34.547	0.151	**0.020**
35	Shrimps	(2.6)	0.910	3.146	22.000	0.565	**0.322**
36	Crabs	(2.9)	(4.390)	2.228	6.285	1.956	**0.310**
37	Mollusks	(2.3)	(12.518)	3.685	10.680	-	**0.206**
38	Zoobenthos	(2.0)	(4.542)	3.965	28.000	-	-
39	Zooplankton	(2.0)	2.740	65.000	268.200	-	**0.010**
40	Phytoplankton	(1.0)	22.355	93.491	-	-	-
41	Phytobenthos	(1.0)	6.480	83.333	-	-	-
42	Detritus	(1.0)	19.20	-	-	-	**0.220**

TL: trophic level; *B*: biomass ($t \cdot km^{-2}$); *P/B*: annual production rate, *Q/B* : annual consumption rate, *Y* : catch ($t \cdot km^{-2} yr^{-1}$) and *OI* : omnivory index.

Table 2. Basic inputs and outputs (bold) of the Lake Nokoué. For fish groups with more than one species, a key species is considered and is indicated by (*).

	Group name	TL	*B*	*P/B*	*Q/B*	*Y*	*OI*
1	*Polydactylus quadrifilis*	**3.2**	0.489	2.000	17.848	0.088	**0.127**
2	*Elops lacerta*	**3.4**	3.969	1.900	17.183	1.429	**0.097**
3	*Pomadasys jubelini*	**3.3**	0.367	1.670	14.714	0.088	**0.092**
4	*Caranx hippos*	**3.4**	0.030	2.250	21.487	0.010	**0.054**
5	*Citarichthys stampflii*	**3.5**	0.070	2.670	14.477	0.088	**0.082**
6	*Cynoglossus senegalensis**	**3.2**	0.880	1.500	10.861	0.088	**0.111**
7	*Eucinostomus melanopterus**	**3.2**	1.118	3.560	26.909	0.840	**0.202**
8	*Lutjanus goreensis**	**3.3**	0.326	1.900	14.397	0.088	**0.081**
9	*Hemichromis fasciatus**	**3.3**	0.191	2.560	18.900	0.088	**0.115**
10	*Schilbe intermedius**	**3.1**	0.406	1.800	25.200	0.292	**0.164**
11	*Strongylura senegalensis**	**3.2**	0.218	2.087	20.232	0.088	**0.164**
12	*Hyporhamphus picarti**	**3.0**	0.157	3.500	28.377	0.088	**0.123**
13	*Hepsetus odoe**	**3.4**	0.048	1.500	16.013	0.011	**0.280**
14	*Pellonula leonensis*	**3.0**	0.047	5.600	37.550	0.088	**0.048**
15	*Eleotris vitatta**	**3.4**	0.293	2.390	15.770	0.088	**0.127**
16	*Gobionellus occidentalis**	**2.4**	15.501	2.500	19.887	7.797	**0.253**
17	*Chrysichthys nigrodigitatus**	**3.1**	14.492	1.590	12.364	3.681	**0.102**
18	*Synodontis schall**	**2.9**	0.105	1.700	13.257	0.048	**0.311**
19	*Monodactylus sebae*	**3.2**	0.259	2.700	21.087	0.088	**0.022**
20	*Ethmalosa fimbriata*	**2.5**	42.191	2.250	14.300	12.362	**0.303**
21	*Liza falcipinnis**	**2.2**	5.659	2.100	37.033	3.339	**0.156**
22	*Sarotherodon melanotheron*	**2.1**	38.928	2.300	32.803	30.364	**0.073**
23	*Tilapia guineensis*	**2.1**	6.673	2.300	43.800	3.003	**0.124**
24	Shrimps	**2.4**	18.267	3.100	22.000	10.595	**0.260**
25	Crabs	**2.8**	**20.439**	2.982	8.500	27.260	**0.369**
26	Mollusks	**2.3**	**47.227**	3.277	10.680	-	**0.233**
27	Zoobenthos	**2.1**	87.760	16.475	45.000	-	**0.073**
28	Zooplankton	**2.1**	147.230	39.094	120.000	-	**0.053**
29	Phytoplankton	**1.0**	29.200	270.000	-	-	**-**
30	Phytobenthos	**1.0**	14.600	270.000	-	-	**-**
31	Detritus	**1.0**	33.20	-	-	-	**0.286**

TL: trophic level; *B*: biomass ($t \cdot km^{-2}$); *P/B*: annual production rate, *Q/B*: annual consumption rate, *Y* : catch ($t \cdot km^{-2} \cdot yr^{-1}$) and *OI* : omnivory index.

Table 3. Diet matrix composition (%) of functional groups considered in the Ébrié lagoon model.

	Prey	Predator																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*Sphyraena afra**																				
2	*Polydactylus quadrifilis*	0.010																			
3	*Galeoides decadactylus**	0.100	0.005		0.020	0.020															
4	*Pseudotolithus elongatus*	0.005	0.005																		
5	*Pseudotolithus senegalensis**	0.050																			
6	*Elops lacerta**	0.030			0.002		0.005														
7	*Arius lastiscutatus**																				
8	*Pomadasys jubelini**	0.020																			
9	*Chloroscombrus chrysurus*																				
10	*Caranx hippos**	0.020																			
11	*Trachinotus teraia**																				
12	*Citharichthys stampflii*																				
13	*Cynoglossus senegalensis**	0.020																			
14	*Gerres nigri**	0.050				0.005	0.010														
15	*Drepane africana**																				
16	*Dasyatis margarita**																				
17	*Ilisha africana*	0.030						0.005			0.010	0.010							0.001		
18	*Brachydeuterus auritus*	0.010									0.010	0.005									0.010
19	*Hemichromis fasciatus**				0.001																
20	*Schilbe intermedius**					0.005															
21	*Strongylura senegalensis**	0.010			0.005																
22	*Hydrocynus forskahlii**	0.010				0.001															
23	*Pellonula leonensis*	0.010				0.005	0.005														
24	*Eleotris senegalensis**	0.030			0.050	0.039				0.005	0.010	0.010	0.010	0.005				0.010	0.004		
25	*Chrysichthys nigrodigitatus**				0.030	0.025															
26	*Trichiurus lepturus*	0.007			0.002																
27	*Synodontis gambiensis **																			0.005	
28	*Monodactylus sebae*	0.010																			
29	*Ethmalosa fimbriata*	0.100	0.005		0.100	0.115	0.030	0.030		0.005	0.100	0.020						0.010	0.005		0.010
30	*Sardinella maderensis**	0.100	0.020		0.100	0.030	0.050	0.020		0.005	0.055	0.015						0.005			0.010
31	*Liza grandisquamis**	0.020	0.005		0.010	0.005	0.005	0.005	0.010					0.010						0.005	0.010
32	*Tylochromis jentinki*	0.030	0.005			0.010	0.003														
33	*Sarotherodon melanotheron*	0.050	0.030	0.005	0.050	0.025	0.040		0.030		0.050		0.020	0.025						0.150	
34	*Tilapia guineensis*	0.050	0.010	0.005	0.060	0.020			0.030		0.025		0.020	0.030						0.010	
35	Shrimps	0.228	0.150	0.050	0.100	0.050	0.020	0.020	0.080		0.020	0.050	0.050	0.050	0.005	0.005	0.001	0.010	0.050	0.100	
36	Crabs		0.075	0.250	0.200	0.500	0.060	0.200	0.200		0.225	0.200	0.250	0.240		0.100	0.250			0.200	
37	Mollusks		0.100	0.400			0.372	0.350	0.650	0.550	0.400	0.540	0.650	0.490	0.600	0.100	0.449	0.225		0.230	0.450
38	Zoobenthos													0.100	0.100	0.150	0.300	0.150	0.450		0.130
39	Zooplankton		0.570	0.290	0.270	0.145	0.400	0.370		0.330	0.095				0.200	0.300		0.490	0.490	0.300	0.260
40	Phytoplankton															0.100					
41	Phytobenthos															0.145					
42	Detritus		0.020							0.105		0.150		0.050	0.095	0.100		0.100			0.120

Table 3. Cont.

		Predator																		
	Prey	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**
1	*Sphyraena afra**																			
2	*Polydactylus quadrifilis*																			
3	*Galeoides decadactylus**																			
4	*Pseudotolithus elongatus*																			
5	*Pseudotolithus senegalensis**						0.002													
6	*Elops lacerta**																			
7	*Arius lastiscutatus**																			
8	*Pomadasys jubelini**																			
9	*Chloroscombrus chrysurus*																			
10	*Caranx hippos**																			
11	*Trachinotus teraia**																			
12	*Citharichthys stampflii*																			
13	*Cynoglossus senegalensis**		0.010																	
14	*Gerres nigri**																0.003			
15	*Drepane africana**																			
16	*Dasyatis margarita**																			
17	*Ilisha africana*	0.050					0.008		0.002											
18	*Brachydeuterus auritus*						0.010		0.002											
19	*Hemichromis fasciatus**																			
20	*Schilbe intermedius**																			
21	*Strongylura senegalensis**		0.030																	
22	*Hydrocynus foskahlii**		0.030																	
23	*Pellonula leonensis*																			
24	*Eleotris senegalensis**	0.020	0.005																	
25	*Chrysichthys nigrodigitatus**		0.010																	
26	*Trichiurus lepturus*		0.001																	
27	*Synodontis gambiensis **		0.001																	
28	*Monodactylus sebae*																			
29	*Ethmalosa fimbriata*	0.100	0.020	0.050	0.050	0.004	0.050		0.005								0.015			
30	*Sardinella maderensis**	0.050		0.050	0.020		0.050		0.005								0.010			
31	*Liza grandisquamis**	0.005	0.010				0.005		0.005								0.001			
32	*Tylochromis jentinki*	0.005	0.005		0.005								0.006							
33	*Sarotherodon melanotheron*	0.050	0.005		0.010	0.005	0.020						0.006							
34	*Tilapia guineensis*	0.020	0.003	0.010	0.010	0.001	0.004						0.006							
35	Shrimps		0.020	0.050	0.005	0.005	0.010		0.030		0.010		0.010							
36	Crabs		0.100		0.190	0.045	0.100										0.026			
37	Mollusks		0.300	0.050	0.160	0.710	0.121	0.350	0.105	0.010	0.080		0.600			0.200	0.450			
38	Zoobenthos	0.300	0.200	0.090	0.370			0.350	0.300	0.010	0.060	0.200	0.159				0.259			
39	Zooplankton	0.400	0.200	0.700	0.180	0.230	0.490		0.546	0.635	0.750	0.150		0.070	0.020	0.300		0.280		0.010
40	Phytoplankton							0.150		0.325		0.200	0.100	0.280	0.180	0.300		0.300		0.850
41	Phytobenthos							0.050		0.010		0.150		0.050	0.200		0.031	0.150	0.150	
42	Detritus		0.050				0.130	0.100		0.010	0.100	0.300	0.114	0.600	0.600	0.200	0.205	0.270	0.850	0.140

Table 4. Diet matrix composition (%) of groups considered in Lake Nokoué model.

		Predator																											
	Prey	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
1	*Polydactylus quadrifilis*																												
2	*Elops lacerta*		0.020					0.005		0.010																			
3	*Pomadasys jubelini*																												
4	*Caranx hippos*																												
5	*Citharichthys stampflii*																												
6	*Cynoglossus senegalensis**																												
7	*Eucinostomus melanopterus**		0.010																							0.003			
8	*Lutjanus goreensis**		0.002			0.025																							
9	*Hemichromis fasciatus**									0.005																			
10	*Schilbe intermedius**													0.100															
11	*Strongylura senegalensis**											0.003																	
12	*Hyporhamphus picarti**											0.010																	
13	*Hepsetus odoe**									0.005				0.005															
14	*Pellonula leonensis*		0.001	0.001		0.005	0.001		0.005	0.005		0.002		0.005		0.005													
15	*Eleotris vitatta**			0.020							0.010																		
16	*Gobionellus occidentalis**		0.150	0.030		0.070		0.050	0.050	0.050	0.050	0.050		0.070															
17	*Chrysichthys nigrodigitatus**								0.065	0.050		0.030		0.100		0.050													
18	*Synodontis schall**										0.005			0.080															
19	*Monodactylus sebae*																												
20	*Ethmalosa fimbriata*	0.050	0.100	0.050	0.050	0.050	0.050	0.250	0.150	0.150	0.055	0.045		0.050		0.020					0.020					0.025			
21	*Liza falcipinnis**		0.050	0.040	0.050	0.030		0.060		0.020						0.005													
22	*Sarotherodon melanotheron*	0.100	0.100	0.055	0.050	0.030	0.050	0.100		0.100	0.100	0.070		0.210		0.010		0.005			0.015								
23	*Tilapia guineensis*	0.050	0.050	0.014	0.050	0.010		0.035		0.100	0.030	0.040		0.200		0.030		0.005											
24	Shrimps	0.100	0.150	0.400	0.400	0.400	0.200	0.050	0.250	0.100	0.050	0.150			0.010	0.290	0.005	0.050		0.300	0.010			0.005					
25	Crabs	0.100	0.170	0.100	0.150	0.250	0.050	0.050		0.050	0.010	0.100				0.200		0.050								0.027			
26	Mollusks	0.050	0.007	0.010	0.100	0.010	0.150	0.200	0.050	0.150	0.300	0.100	0.200		0.050	0.200		0.300	0.400	0.200	0.020	0.010		0.010		0.300			
27	Zoobenthos	0.150	0.030	0.020	0.050	0.020	0.250	0.030	0.230	0.150	0.200	0.200	0.500	0.100	0.150	0.070	0.175	0.450	0.210	0.100	0.050	0.050	0.020	0.050	0.250	0.300		0.020	
28	Zooplankton	0.350	0.160	0.250	0.100	0.100	0.200	0.070	0.200	0.045	0.100	0.150	0.200	0.030	0.750	0.100	0.150	0.090	0.100	0.400	0.350	0.100	0.050	0.050	0.100		0.300	0.050	**0.050**
29	Phytoplankton														0.040		0.100				0.250	0.150	0.150	0.300	0.010		0.150	0.010	**0.100**
30	Phytobenthos							0.050		0.010	0.015	0.050	0.050				0.150		0.100		0.050	0.250	0.150	0.300	0.040	0.030	0.050	0.100	**0.050**
31	Detritus	0.050		0.010			0.049	0.050			0.075		0.050	0.050		0.020	0.420	0.050	0.190		0.235	0.440	0.630	0.285	0.600	0.315	0.500	0.820	**0.800**

Table 5. Relative distribution of biomass ($t \cdot km^{-2}$) and catch ($t \cdot km^{-2} \cdot yr^{-1}$) among the various TLs in Ébrié Lagoon (E) and in Lake Nokoué (N). Note that biomass and/or catch of non-fish groups are not included.

TL	Biomass		Contribution per TL (%)		Catch		Contribution per TL (%)	
	E	N	E	N	E	N	E	N
VI	0.002	-	-	-	-	-	-	-
V	0.112	0.296	1.2	0.2	0.051	0.106	0.6	-
IV	1.260	5.230	13.3	4.0	0.871	1.746	10.1	2.7
III	5.400	45.000	57.0	34.0	5.668	16.200	66.0	25.3
II	2.700	82.000	28.5	62.0	2.000	46.200	23.3	72.0

Table 6. Summary statistics and network flow indices of the two ecosystems considered.

Parameter	Value	
	Ébrié	**Nokoué**
Ecosystem theory indices		
Sum of all consumption ($t \cdot km^{-2} \cdot yr^{-1}$)	1 207.682	25 731.420
Sum of all exports ($t \cdot km^{-2} \cdot yr^{-1}$)	2 119.768	1 327.479
Sum of all respiratory flows ($t \cdot km^{-2} \cdot yr^{-1}$)	510.942	10 498.570
Sum of all flows into detritus ($t \cdot km^{-2} \cdot yr^{-1}$)	2 402.998	20 410.000
Total system throughput (TST, $t \cdot km^{-2} \cdot yr^{-1}$)	6 240.000	57 967.000
Sum of all production ($t \cdot km^{-2} \cdot yr^{-1}$)	2 902.000	19 595.000
Mean trophic level of the catch	2.88	2.46
Gross efficiency (GE, catch/net p.p.)	0.004226	0.008625
Calculated total net primary production ($t \cdot km^{-2} \cdot yr^{-1}$)	2 629.989	11 826.000
Total primary production/total respiration (TPP/TR)	5.155	1.126
Net system production (PP-TR, $t \cdot km^{-2} \cdot yr^{-1}$)	2 119.047	1 327.430
Total primary production/total biomass (PP/*B*, yr^{-1})	41.596	23.788
Total biomass/total system throughput (*B*-TST, yr^{-1})	0.010	0.009
Total biomass (excluding detritus) ($t \cdot km^{-2}$)	63.304	497.141
Total catches ($t \cdot km^{-2} \cdot yr^{-1}$)	11.115	101.999
Connectance Index (*CI*)	0.191	0.266
System Omnivory Index (*SOI*)	0.145	0.156
Cycling indices		
Throughput cycled excluding detritus ($t \cdot km^{-2} \cdot yr^{-1}$)	8.16	980.57
Throughput cycled (including detritus) ($t \cdot km^{-2} \cdot yr^{-1}$)	5.09	4.98
Finn's cycling index (FCI, %)	2.57	34.00
Predatory cycling index (PCI, %)	0.57	5.72
Finn's mean path length	2.373	4.902
Finn's straight-through path length (excluding detritus)	2.733	1.525
Finn's straight-through path length (including detritus)	2.312	3.235
Information indices		
Ascendancy (*A*, flowbits)	7 656.10	47 224.00
Overhead (*Ø*, flowbits)	13 876.70	186 154.30
Capacity (*C*, flowbits)	21 032.90	233 378.30
Information (*I*)	1.147	0.815
A/C	0.340	0.202