COASTAL LAGOONS

Critical Habitats of Environmental Change

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4 Ecosystem Health Indexed through Networks of Nitrogen Cycling

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ABSTRACT

Assessing ecosystem-level status is a challenge, and several indices from information theory are used to assess the status of ecosystems. Food web networks are generally used in these assessments, but we have applied them to simpler networks of nitrogen cycling. Specifically, we indexed status in the framework of ecosystem health and three of its attributes: organization, vigor, and resilience, respectively indexed by ascendency (A), total system throughput (TST), and overhead (O). These indices were derived from seasonal networks of nitrogen cycles in two coastal lagoons: the Hog Island Bay, Virginia, and the Sacca di Goro, Emilia Romagna, Italy. The sites represent a large range of nutrient loading and subsequent trophic conditions from mesotrophic to hypereutrophic and dystrophic. As the degree of eutrophication (indexed through TN loading) increased, the cycling, efficiency of use of nitrogen, and degree of organization decreased. Indeterminacy of flows, as redundancy, increased. A problem of spurious correlations arose in the empirical analysis of ascendency vs. overhead because they share the same TST as a component. We propose that log transformations of TST can lessen the problem and might be used more generally in the empirical applications of information indices. Our results

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are encouraging but illustrate the point that, while ecosystem-level assessments with theoretical foundations are increasingly possible, there remains considerable need for validation with empirical information.

Key Words: eutrophication, coastal lagoons, Sacca di Goro, Hog Island Bay, macroalgae, ascendency, spurious correlation

4.1 INTRODUCTION

Ecosystem-based management is challenged by the need for assessments of system-level status (Dame and Christian 2006). Traditional assessments of coastal aquatic ecosystems focused on population dynamics or community structure. These have been used in numerous situations in estuaries, coastal lagoons, and coastal waters among other systems (Niemi and McDonald 2004; Jørgensen et al. 2005). Assessments of ecosystem function or structure have had a shorter and less pervasive history. This is not to say that coastal aquatic ecosystems have not been assessed. Bricker et al. (1999, 2007) provided national assessments of the impacts of eutrophication on coastal aquatic ecosystems, and the Millennium Ecosystem Assessment (2005) included coastal systems from a global perspective. These are excellent frameworks for large-scale policy making, but may lack detailed observations necessary for management of individual systems.

Ecological network analysis (ENA) has been used to assess ecosystem status of individual (Baird and Ulanowicz 1989) and multiple aquatic ecosystems (Christensen 1995). ENA begins with the formal description of ecosystem components and the interactions between them as networks. The interactions are mostly associated with feeding and trophic structure, but biogeochemical cycles (Christian et al. 1996, 1998; Bondavalli 2003) have also been studied. Analyses result in indicators of: (1) strength of direct and indirect interactions; (2) relative importance of components to overall activity; (3) amount of flow involved in cycling vs. passing through the system; and (4) overall status of development, structure, and activity. Agencies focused on fisheries management use ENA of trophic structure to characterize aquatic ecosystems and to aid decision making (Christensen and Pauly 1993; Dame and Christian 2006).

Here we explore the use of ENA of nitrogen cycles in coastal lagoons to assess ecosystem status as "ecosystem health" defined by Costanza (1992) and interpreted for ENA by Ulanowicz (1997). Healthy ecosystems function well and are structured to do so, whereas less healthy ecosystems are not performing these functions as well (Costanza 1992). The image of health for ecosystems is less clear than for individual organisms with better defined boundaries. Furthermore, the term conveys a bias that promotes normative science (Lackey 2001). However, thoughtful implications and activities have arisen from the concept (Jørgensen et al. 2005). Ecosystem health is also linked to other aspects of status. Westra (1995) used ecosystem "integrity" as a generalization and extension of "health." The chief difference is that the notion of health is good performance (at processing materials), whereas ecosystem integrity references the "wild" condition. Integrity is perceived in the broader context of human cultural, political, and socioeconomic activities.

Synthesizing a longer list, Costanza (1992) defined ecosystem health through three attributes: organization, resilience, and vigor. He gave examples for each attribute, but his examples were not meant to be all-inclusive. Organization could be represented as biodiversity or connectivity. Resilience could be represented as response to perturbation to either resist change or return to some nominal condition. In addition, vigor could be represented as productivity or rate of metabolism. His "health index" was the product of indices of these three attributes. He recognized the value of ecological network analysis in developing the indices but did not fully develop specific ENA indices. He did, however, suggest that eutrophication would increase metabolism (vigor), while decreasing organization and resilience. Ulanowicz (1997) interpreted the three aspects of ecosystem health in the context of his information theoretic ENA indices (Ulanowicz 1986, 1992; Ulanowicz and Norden 1990), including flow diversity (H), constrained flow structure or average mutual information (AMI), and unconstrained flow structure (S). The total sum of flows (i.e., total system throughput, TST) is multiplied by each index, yielding developmental capacity, ascendency, and overhead, respectively.

Information theoretic indices reflect Costanza's three components of ecosystem health quite appropriately (Ulanowicz 1992). Mutual information reflects the degree to which two variables are dependent on each other. Organization appears to be characterized by the average mutual information (AMI), as a system measure of the direct mutual influence of different compartments directly on one another. Resilience can be represented by the unconstrained flows through S. S increases with evenness of flows for both donor and recipient compartments and number of flows. These flows include imports, exports, dissipation or respiration, and interactions within the system. A major contribution to S consists of the number of parallel pathways among these flows, where resiliency and S increase, as more options exist for a unit of material or energy to pass through the system (functional redundancies). In other words, removal or reduction of a small number of links has less impact on overall flow as resiliency increases. Finally, vigor can be represented by TST, a measure of the activity of the system. Vigorous systems are expected to have higher TST. Because ascendency is the product of AMI and TST and overhead is the product of S and TST, Ulanowicz (1997) proposed a graph of ascendency vs. overhead to represent a phase plane of ecosystem health (Figure 4.1).

Coastal aquatic ecosystems are subject to numerous human impacts and stressors (Kennish 1999; Peterson et al. 2008). These include enrichment of nutrients and organic matter, alterations to sediment delivery, habitat disruption, contaminant pollution, overharvesting of resources, and now the consequences of climate change. These alter ecosystem functions and health. Of particular interest are the impacts of eutrophication. Viaroli et al. (2008) reviewed how eutrophication of shallow, coastal lagoons alters community structure and biogeochemistry. Dominant primary producer communities often shift away from rooted aquatic vegetation to macroalgae and blooming phytoplankton as nutrient loading increases. These changes alter biogeochemical cycling. To assess these changes, we construct and analyze nitrogen networks of different habitats, containing different distributions of growth forms of primary producers, of two coastal lagoons with different levels of eutrophication. We focused on nitrogen, as it is often the primary controlling nutrient to primary production and thereby the health of coastal ecosystems (Kennish 1999; Bricker et al. 1999, 2007; Viaroli et al. 2008).

Ecological network analyses of nitrogen cycles have not been conducted as extensively as those of trophic structure. Christian et al. (1996) compared the nitrogen networks of three coastal lagoons, an estuary, and a rice field. These systems represented a range of eutrophication, primary production, hydrogeomorpology, and distribution of primary production associated with phytoplankton, macroalgae, and phanerogams. Residence time of water within the systems promoted recycling, where the

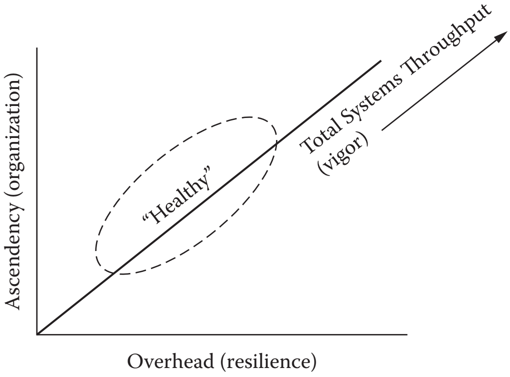

FIGURE 4.1 The three components of ecosystem health (organization, resilience, and vigor) proposed by Costanza (1992) as diagrammed, using network indices (ascendency, overhead, and total system throughput). (From Mageau, M.T., R. Costanza, and R.E. Ulanowicz, *Ecosys. Health* 1: 201–213, 1995. With permission.)

degree of recycling was also positively correlated to the proportion of primary productivity associated with phytoplankton. This was also found in a more developed analysis of 16 seasons of nitrogen cycling within the Neuse River Estuary (Christian and Thomas 2003).

Information indices were not used to evaluate these networks of nitrogen cycling. The networks of nitrogen cycling contained only five to seven compartments with highly aggregated consumer compartments, in contrast to networks focused on trophic structure with perhaps tens of compartments. Christian et al. (1996) expressed concern that small networks may not provide the flexibility to use information theory. We reevaluate this contention using networks of nitrogen cycling for two coastal lagoons that represent mesotrophic and hypereutrophic conditions. Specifically, we evaluate the ability of information indices to quantify ecosystem status within the framework of Ulanowicz (1997) based on Costanza (1992). Further, we assess other ENA indices and compare them to the information indices. This represents the first such empirical test of this ecosystem health framework.

4.2 METHODS

4.2.1 Study Sites

Two well-studied coastal lagoons with very different trophic conditions were assessed for network construction and analysis: Hog Island Bay (HIB), Virginia, USA (37º 26′ N, 75º 45′ W) and Sacca di Goro (GOR), Italy (44º 48′ N, 12º 18′ E). Hog Island Bay is a large, shallow coastal lagoon (area ≈100 km^2, depth <1–2 m at mean low water with the exception of a deep main channel) on the eastern shore of the Delmarva Peninsula and is part of the Virginia Coast Reserve (VCR) Long Term Ecological Research (LTER) Site (http://www.vcrlter.virginia.edu/). The Sacca di Goro (area ≈26 km^2, mean depth ≈1.5 m) is at the mouth of the Po River, receiving water from nutrient-rich distributaries, the Po di Volano and Po di Goro.

Large differences in nutrient loading are represented with numerous low and high rates to Hog Island Bay and the Sacca di Goro, respectively. Since no large rivers feed Hog Island Bay, nutrient inputs from the watersheds are via groundwater and atmospheric deposition (Anderson et al. unpublished data). The shallow aquifer is enriched in nitrogen primarily from agricultural activities which represent 55% of the Hog Island Bay watershed (442 km^2) (Bohlke and Denver 1995; Hamilton and Helsel 1995; Gu et al. 2008). Baseflow nutrient loading rates to Hog Island Bay are low compared to other lagoons (Chauhan and Mills 2002; Stanhope 2003; Stanhope et al. 2009), in part due to a high removal of NO_3^- from groundwater discharging to the streams by denitrification in a narrow band of sediments and bank materials (Flewelling personal communication). The Po di Volano is the major source of nutrients into the Sacca di Goro with a total loading of dissolved nitrogen from all sources exceeding demand most of the time (Christian et al. 1998; Viaroli et al. 2005; Giordani et al. 2008).

Both systems have macroalgae, microphytobenthos, and phytoplankton but their importance within the systems and among habitats differs. Hog Island Bay was formerly vegetated with seagrasses, which disappeared in the 1930s as a result of the storm disturbance of disease-weakened populations (Orth et al. 2006). Microphytobenthos and macroalgae are currently the dominant primary producers in the lagoon; however, both natural recolonization of seagrass and recent restoration efforts (since 2006) have increased seagrass areal coverage in localized areas. Benthos is generally net autotrophic except in localized, mid-lagoon areas where macroalgae accumulate and decay in mid-summer (McGlathery et al. 2001). The water column is typically net heterotrophic throughout the lagoon except following the mid-summer macroalgal collapse.

Sacca di Goro locations exhibit large amounts of primary production and standing stocks by macroalgae with mid- to late summer dystrophy (Viaroli et al. 2001; Giordani et al. 2008). *Gracilaria* and *Ulva* spp. dominate different regions of the lagoon, with the dynamics of *Ulva* spp. most significant to dystrophy (Viaroli et al. 1992). Little microphytobenthic or phytoplankton production has been noted (Christian et al. 1998; Viaroli and Christian 2003).

We consider Hog Island Bay and the Sacca di Goro to be mesotrophic and hypereutrophic lagoons, respectively, largely on the basis of nitrogen loading and general characteristics of primary production. External nutrient loading and variations in water residence time from the ocean inlet to the mainland creeks result in gradients of nutrient inputs and sediment organic matter across Hog Island Bay, with the highest concentrations of dissolved nitrogen and sediment organic matter found closest to the mainland (McGlathery et al. 2001). We captured that gradient in our sampling sites as Creek (Crk) near the mainland, Shoal (Shl), and near Hog Island (HI) (Figure 4.2a). High production rates are supported mostly by remineralization in the sediments and efficient internal nutrient cycling. Microphytobenthos control benthic–pelagic nutrient coupling (Anderson et al. 2003); in particular, nitrogen uptake by benthic algae suppresses denitrification to negligible rates and prevents the efflux of mineralized nitrogen from the sediment to the water column (Havens et al. 2001; Tyler et al. 2001, 2003; Anderson et al. 2003).

Two habitats [Gorino (Gor) and Giralda (Gir)] were assessed for the Sacca di Goro (Figure 4.2b). Dystrophy is most common in the very shallow and hydrologically isolated area of Gorino with intense growth of *Ulva* spp. (Viaroli et al. 1992). In contrast, Gir is largely devoid of macroalgae (Bartoli et al. 2001a), and microphytobenthos contribute significantly to overall primary production. One important aspect of the ecology of the Sacca di Goro is the farming of the Philippine clam, *Tapes philippinarum*. This invasive but farmed species dominates much of the benthos and can control much of the flux of oxygen and nutrients between the sediments and water column (Bartoli et al. 2001b; Nizzoli et al. 2007).

4.2.2 NETWORK CONSTRUCTION

We constructed our networks of nitrogen cycling during two periods at each habitat (three in Hog Island Bay (HIB) and two in the Sacca di Goro (GOR)). A presumably more productive period in spring and early summer (Sp; March to June) was compared to a presumably less productive period in late summer and early autumn (Su; August to October).

The generalized network (Figure 4.3), and specific modifications for period and habitat were similar to those described by Christian et al. (1996). Dimensional units of standing stock were mmol N m^{-2}, and flows were mmol N m^{-2} d^{-1}. Three compartments were used for primary producers: phytoplankton (PHY), macroalgae (MAC), and microphytobenthos (MPB). Rooted phanerogams were not present in any of the habitats. Dissolved nitrogen was divided into separate inorganic (DIN) and organic (DON) compartments. The trypton (TRP) compartment contained non-phytoplankton N in seston including any consumer organisms. Estimates of the importance of size of aquatic consumers to nitrogen cycling indicate that planktonic-sized consumers, included in seston, dominate fluxes (Christian et al. 1992). The sediment (SED) compartment contained all forms of nitrogen within sediments, including nitrogen within and outside of organisms, except MPB. Standing stocks and flows were derived from a number of sources.

We quantified both flows between compartments as well as flows connecting internal components to the outside of the system. The latter consisted of imports and two forms of outputs: exports, and dissipations. Compartments PHY, TRP, SED, DIN, and DON received nitrogen from outside the location. All compartments, except MPB, have the potential to export nitrogen from the system. Growth of MAC was represented as either export (Hog Island Bay) or dissipation (Sacca di Goro) to allow mass balancing of networks. Inadvertently each group chose a different route for growth as biomass removal, but the route did not affect our interpretations. Dissipation for both locations involved the loss of nitrogen due to denitrification from the sediment. Compartments were internally connected via feeding, biogeochemical, and detrital pathways. When a flow was considered possible but not detectable or could not be inferred from available data, it was given a minimal value of 0.001 mmol N m^{-2} d^{-1}.

Table 4.1 provides a summary of imports, exports, dissipations, and intercompartmental flows initially used for the networks. Comments on the sources, logic, or assumptions associated with

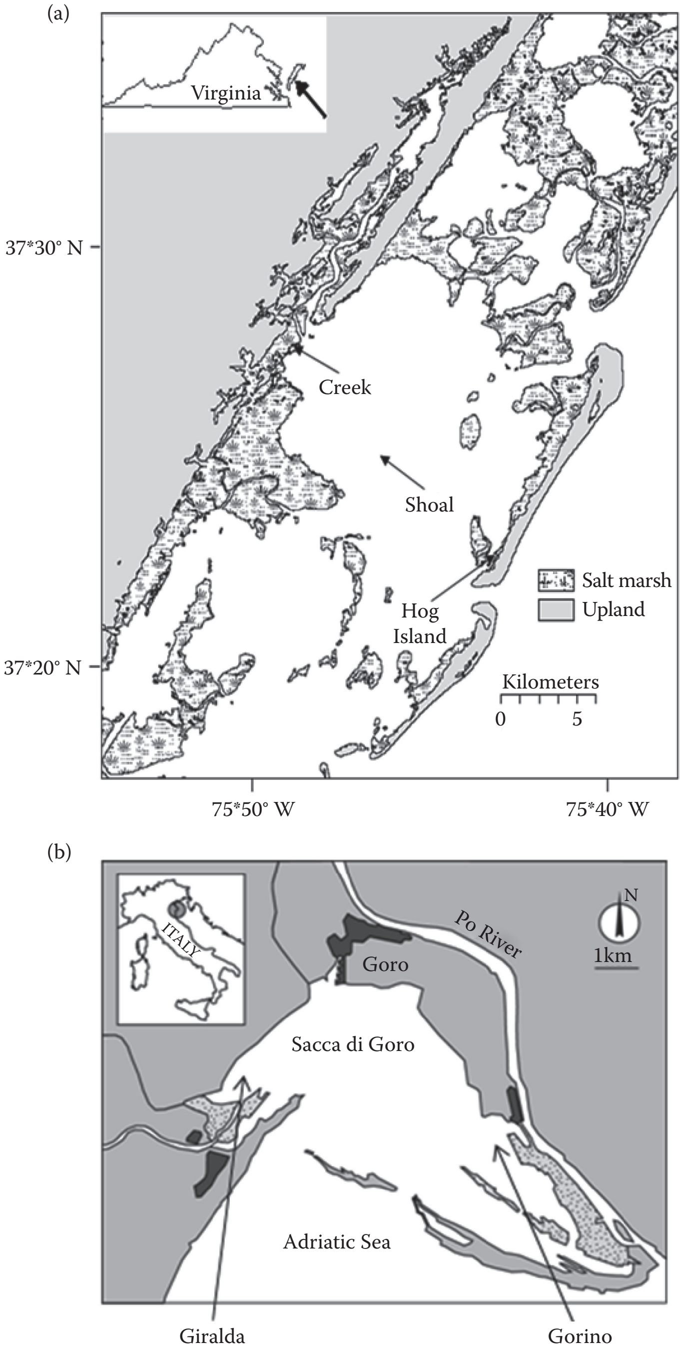

FIGURE 4.2 Maps of (a) Hog Island Bay, Virginia, and (b) Sacca di Goro, Italy. Maps show the three sampling sites in Hog Island Bay (Creek, Shoal, and Hog Island) and the two sampling sites in Sacca di Goro (Giralda and Gorino).

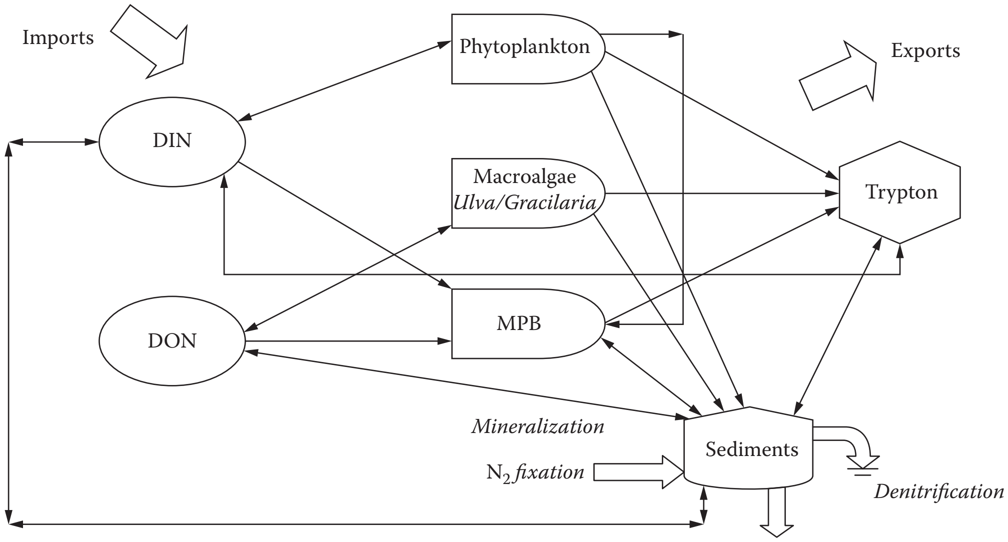

FIGURE 4.3 Generalized network of N cycling within Hog Island Bay and Sacca di Goro. Compartments include N in three primary producers: phytoplankton, macroalgae, and microphytobenthos (MPB); N in trypton (non-phytoplankton seston including any consumer organisms); dissolved organic (DON) and dissolved inorganic (DIN) nitrogen; and all forms of N within sediments (including organisms except MPB).

each flow are included. The specific reference is not given for each flow or standing stock in the interests of brevity. However, many of the flows derive from the references given in "Study Sites." Much of the information for Hog Island Bay comes from both published and unpublished research of McGlathery, Anderson, Tyler, and their colleagues (e.g., McGlathery et al. 2001; Havens et al. 2001; Tyler et al. 2001, 2003; Anderson et al. 2003). Most of this work was done in the late 1990s and early 2000s. Information for the Sacca di Goro largely came from 1997 because the available dataset was most complete from investigations under the NICE (Nitrogen Cycling in Estuaries) project (Bartoli et al. 2001a; Viaroli et al. 2001, 2006). These data were integrated with additional data from different field campaigns, laboratory studies, and literature (e.g., Naldi and Viaroli 2002).

Network analysis is more easily interpreted when flows of matter entering and leaving a given compartment, and the ecosystem as a whole, are steady state (Allesina and Bondavalli 2003). The construction of nitrogen cycle networks in coastal ecosystems required quantification of flows between different compartments measured directly (e.g., sediment–water N exchange) or indirectly (e.g., N burial, phytoplankton imports and exports) (Table 4.1). The natural variability of coastal ecosystems, the application of different flow-measuring approaches, and errors associated with measurements, among other factors, resulted in unsteady flow networks. Therefore, to construct robust N networks, rules and procedures for converting field data to flows and standing stocks were established (see details in Christian et al. 1992; Christian and Thomas 2003). Once the flow networks were constructed using initial values, flows for each compartment were balanced.

In this study, balancing was achieved by a three-step process. The first step, based on expert judgment, changed flows in such a way that: (1) it made ecological sense; (2) it went in the direction of balancing; (3) it tried to minimize the change in flows perceived to be most reliable; and (4) it promoted final closure on imports or exports. In this step and based on the degree of uncertainty in the measurements, the original flows were categorized as highly reliable (e.g., standing stocks of all compartments but trypton, denitrification, all flows from sediments), intermediately reliable (e.g., trypton standing stocks, DIN and DON consumption by macroalgae and phytoplankton), and least reliable (e.g., imports of all primary producers, DIN and DON consumption by trypton). In each case, the maximum adjustment to the flow was allowed to increase with decreased reliability.

TABLE 4.1
Compartments, Flows, and Processes Considered in Network Analysis of Nitrogen Cycling in Sacca de Goro (GOR) and Hog Island Bay (HIB)

From	To	Flow ID	Process Represented	Flow Estimation Sources
Input to	PHY	F_{01}	Loading	Chlorophyll *a* direct measurement multiplied by inflow
Input to	TRP	F_{04}	Loading	Particulate direct measurement multiplied by inflow for both and atmospheric inputs at HIB
Input to	DIN	F_{06}	Loading	DIN direct measurement multiplied by inflow for both and atmospheric inputs at HIB
Input to	DON	F_{07}	Loading	DON direct measurement multiplied by inflow for both and atmospheric inputs at HIB
Export from	PHY	F_{10}	Water flow from the lagoon to the sea	GOR = tide measurements multiplied by the average concentration determined in the lagoon HIB = by balancing and modeled residence time
Export from	MAC	F_{20}	Flow from the lagoon to the sea	GOR = quantified as 10% of the compartment total uptake HIB = growth of MAC
Export from	TRP	F_{40}	Water flow from the lagoon to the sea	GOR = tide measurements multiplied by the average concentration determined in the lagoon HIB = by balancing and modeled residence time
Export from	SED	F_{50}	Sediment burial	GOR = sedimentation rate times direct determination of N content in sediment HIB = considered insignificant
Export from	DIN	F_{60}	Water flow from the lagoon to the sea	GOR = tide measurements multiplied by the average concentration determined in the lagoon HIB = by balancing and modeled residence time
Export from	DON	F_{70}	Water flow from the lagoon to the sea	GOR = tide measurements multiplied by the average concentration determined in the lagoon HIB = by balancing and modeled residence time
Dissipation from	MAC	R_{20}	Macroalgae biomass increase	GOR = growth as 60% of the compartment total uptake HIB = considered as export
Dissipation from	SED	R_{50}	Denitrification	From experimental measurements and *in situ* estimations
PHY	MPB	F_{13}	Phytoplankton sedimentation rate	GOR = 1 turnover of stock per day HIB = 50% stock per day
PHY	TRP	F_{14}	Phytoplankton degradation and grazing	GOR = PHY mass balance difference from other processes HIB = 12.5% of donor's uptake
PHY	SED	F_{15}	Phytoplankton grazing by benthos	GOR = measured clam grazing rates HIB = 12.5% of donor's uptake
PHY	DIN	F_{16}	Phytoplankton release	GOR = considered insignificant HIB = 5% of donor's uptake
PHY	DON	F_{17}	Phytoplankton release	35% of donor's uptake for both lagoons
MAC	TRP	F_{24}	*Ulva* degradation	GOR = 10% of donor's uptake HIB = 10%–25% of donor's uptake
MAC	SED	F_{25}	*Ulva* sedimentation rate	GOR = 10% of donor's uptake HIB = 4%–7% of donor's uptake
MAC	DIN	F_{26}	Macroalgal release	GOR = considered insignificant HIB = measured directly
MAC	DON	F_{27}	Macroalgal release	GOR = 10% of donor's uptake HIB = measured directly

TABLE 4.1 (continued)
Compartments, Flows, and Processes Considered in Network Analysis of Nitrogen Cycling in Sacca de Goro (GOR) and Hog Island Bay (HIB)

From	To	Flow ID	Process Represented	Flow Estimation Sources
MPB	PHY	F_{31}	Resuspension (alive MPB)	Minimum flow (0.001 mmol N/m^2/d)
MPB	TRP	F_{34}	Resuspension (dead MPB)	GOR = 10% of donor's uptake
MPB	SED	F_{35}	MPB mortality and decomposition	GOR = MPB compartment mass balance HIB = 90% of donor's uptake
MPB	DON	F_{37}	MPB release	GOR = 35% of the compartment total uptake HIB = 0 because assumed all goes to sediment
TRP	SED	F_{45}	Trypton sedimentation rate	GOR =1 times the standing stock per day HIB = 35% of donor's uptake as sedimented fecal pellets
TRP	DIN	F_{46}	Trypton mineralization	GOR = DIN compartment mass balance HIB = 15% of donor's uptake
TRP	DON	F_{47}	Trypton excretion	GOR = considered insignificant HIB = 50% of donor's uptake
SED	MPB	F_{53}	MPB uptake	Experimental measurements and *in situ* estimations HIB = 80% uptake from sediments
SED	TRP	F_{54}	Sediment resuspension	Experimental measurements and *in situ* estimations HIB = 0%
SED	DIN	F_{56}	Sediment release to the water column	Experimental measurements and *in situ* estimations
SED	DON	F_{57}	Sediment release to the water column	Experimental measurements and *in situ* estimations
DIN	PHY	F_{61}	Phytoplankton uptake	Experimental measurements and *in situ* estimations
DIN	MAC	F_{62}	Macroalgal uptake	Experimental measurements and *in situ* estimations
DIN	MPB	F_{63}	MPB uptake	GOR = minimum flow (0.001 mmol N/m^2/d) HIB = 20% of uptake from water column
DIN	SED	F_{65}	Sediment uptake	Experimental measurements and *in situ* estimations
DON	PHY	F_{71}	Phytoplankton uptake	Experimental measurements and *in situ* estimations
DON	MAC	F_{72}	Macroalgal uptake	Experimental measurements and *in situ* estimations
DON	MPB	F_{73}	MPB uptake from water column	GOR = considered insignificant HIB = 20% of uptake from water column
DON	TRP	F_{74}	Net trypton consumption	DON compartment mass balance
DON	SED	F_{75}	Uptake by sediments	GOR = uptake fluxes undetectable HIB = *in situ* estimations
DON	DIN	F_{76}	Mineralization	GOR = considered insignificant HIB = measured experimentally

Note: PHY = phytoplankton (compartment 1), MAC = macroalgae (compartment 2), MPB = microphytobenthos (compartment 3), TRP = trypton (compartment 4), SED = sediments (compartment 5), DIN = dissolved inorganic nitrogen (compartment 6), DON = dissolved organic nitrogen (compartment 7). Much of the information for Hog Island Bay comes from both published and unpublished research of McGlathery, Anderson, Tyler and their colleagues (e.g., McGlathery et al. 2001; Havens et al. 2001; Tyler et al. 2001, 2003; Anderson et al. 2003). Most of this work was done in the late 1990s and early 2000s. Information for the Sacca di Goro largely derived from 1997 because the available dataset was most complete from investigations under the NICE project (Bartoli et al. 2001; Viaroli et al. 2001a; Viaroli et al. 2006). These data were integrated with additional data from different field campaigns, laboratory studies, and literature (e.g., Naldi and Viaroli 2002). Values for which there were no measurements on site or literature values were estimated by best professional judgment or by difference in mass balance calculations. More detail is given in the text.

Balancing proceeded until the balance between imports and exports and dissipations was within 10%, or when further flow modifications were not ecologically meaningful. In step two, we applied the Output-Input and/or the Average algorithms for balancing ecosystem networks using the WAND Balance package (see Allesina and Bondavalli 2003). In the case of Hog Island Bay, the Average balance routine resulted in a substantial distortion of the most dominant flows (i.e., from microphytobenthos to sediments and vice versa) than with the Output-Input balance. As flow distortion between these compartments was high even after balancing with the Output-Input algorithm, a third step in the balancing procedure was included for Hog Island Bay. In this step, the MPB to sediment and the sediment to MPB flows in the matrix obtained from the Output-Input balance were substituted by their original values, and an Average balance was performed on the modified matrix. This was not necessary for networks from the Sacca di Goro, where only the Average balance algorithms were used. ENA was applied on 10 balanced matrices using WAND (see Allesina and Bondavalli 2004). We have posted each of the balanced networks for input to and the results of all as separate analyses within WAND as Excel files on www.verlter.virginia.edu/cgi-bin/w3-msg12/data/query/datasets/show_data.html?Qdata_ID=VCR10171

4.2.3 NETWORK ANALYSIS AND SENSITIVITY TO UNCERTAINTY

For this chapter, we focus on information indices that could be used to indicate ecosystem health and variables that might correlate to the degree of health. We considered average mutual information (AMI), unconstrained flow diversity (S), ascendency (A), developmental capacity (C), and overhead (O), along with total system throughput (TST) (Ulanowicz 1986, 1997). Correlative variables include TST, the sum of imports (total N loading), summed N uptake by primary producers, and average path length (APL, a measure of degree of cycling) (Finn 1976).

Flow measurement uncertainty resulting from natural and/or experimental variability is a concern during the ENA estimation of indices. A simple relative sensitivity analysis was conducted using primary production variability in the network of spring Hog Island Bay Shoals as a case study to determine the robustness of selected information indices. Primary production (i.e., the flows of N from DIN, DON, and sediments to phytoplankton, macroalgae, and MPB) for each producer was varied by ±10%, ±25%, and ±40% in the previously balanced flow matrix, and the resulting matrix was balanced with the Average algorithm before running the network analysis.

At the largest variation in primary production (±40%), the resulting information indices generally showed variation of less than 10% (Table 4.2). This result is partially from the fact that the

TABLE 4.2
Sensitivity Analysis Results Showing Information Theoretic Index Values before and after an Increase by 40% in Microphytobenthos (MPB) Primary Production at Shoals Site in Hog Island Bay during Spring

Producer	% Change	O	A	C	AMI	S	H	TN Loading	APL	TST	PP
MPB	0	46.1	29.1	75.2	1.46	2.31	3.76	0.96	19.83	20.0	8.02
MPB	+40	47.9	31.8	79.6	1.45	2.05	3.50	0.96	21.81	21.9	8.92
% change in index values		3.9	9.3	5.9	–0.7	–11.3	–6.9	0.0	10.0	9.5	11.2

Note: O = overhead; A = ascendency; C = capacity; AMI= average mutual information; S = unconstrained flow structure; H = flow diversity; TN loading = total nitrogen loading; APL = average path length; TST = total system throughput; PP = primary production. % change in values = [(value with +40% in MPB – original value)/(original value)] × 100 information indices are log-transformed values and partially from the dampening effect that the balancing step had on the modified matrix. If the antilogarithms were used, then AMI, S, and H would have higher percentage variations; however, our focus is on the more commonly used log transformed indices. We explain the dampening effect of balancing as follows. We increased the primary production of MPB in the "original" (balanced) matrix from 4.7 to 6.6 mmol N m^{-2} d^{-1} (i.e., +40%). MPB primary production was one of the highest flows in the spring Hog Island Bay Shoals network. Subsequent balancing of this new matrix with the average algorithm decreased the MPB primary production to 5.7 mmol N m^{-2} d^{-1}, a value 21.2% above the original. Balancing reduced the influence of large uncertainty in the data. Furthermore, no output variable approached this percentage (Table 4.2). Therefore, integrating and log transformed indices estimated through ENA appear modulated relative to flow measurement uncertainty. This limited analysis supports similar assessments (Baird et al. 1998; Christian and Thomas 2003).

4.3 RESULTS AND DISCUSSION

4.3.1 Trophic Status

Hog Island Bay (HIB) is characterized as biologically active but with relatively low nutrient loading (McGlathery et al. 2001; Havens et al. 2001; Tyler et al. 2001, 2003; Anderson et al. 2003; Stanhope 2003), while the Sacca di Goro (GOR) has larger nutrient loading and is eutrophic or hypereutrophic with dystrophic crises (Viaroli et al. 1992, 2005; Christian et al. 1998; Giordani et al. 2008). We categorize Hog Island Bay as mesotrophic to highlight the differences in trophic status as summarized in Table 4.3. Six networks from Hog Island Bay represented three habitats, and four networks of two habitats represented the Sacca di Goro, with each habitat being modeled for two seasonal periods. We used three measures of trophic status: TN loading, N uptake for primary production (PP), and total system throughput (TST) as the sum of all flows. TN loading rates ranged from 0.52 to 1.03 mmol N m^{-2} d^{-1} for the mesotrophic Hog Island Bay, which were one to two orders of magnitude less than the 16.1 to 25.3 mmol N m^{-2} d^{-1} for the hypereutrophic Sacca di Goro. Primary production was less

TABLE 4.3
Ecosystem-Level Status Indicators Estimated through Nitrogen Network Analyses for Hog Island Bay (HIB) and Sacca di Goro (GOR) during Spring (Sp) and Summer (Su)

Ecosystem	Model	O	A	C	AMI	S	H	TN Loading	APL	TST	PP
HIB	Crk-Sp	32.5	21.7	54.2	1.36	2.03	3.39	0.99	15.16	16.0	6.23
HIB	Crk-Su	43.9	31.6	75.5	1.40	1.94	3.34	0.52	42.46	22.6	8.98
HIB	Shl-Sp	46.1	29.1	75.2	1.46	2.31	3.76	0.96	19.83	20.0	8.02
HIB	Shl-Su	77.7	51.3	129	1.44	2.18	3.62	1.03	33.56	35.6	14.8
HIB	HI-Sp	17.8	13.2	31.0	1.43	1.92	3.35	0.37	24.00	9.25	3.64
HIB	HI-Su	37.2	21.0	58.2	1.48	2.62	4.10	0.97	13.64	14.2	5.10
GOR	Gor-Sp	375	188	563	1.41	2.82	4.23	25.3	4.26	133	27.1
GOR	Gor-Su	279	125	404	1.33	2.98	4.31	19.6	3.78	93.7	14.3
GOR	Gir-Sp	249	111	360	1.28	2.88	4.16	22.1	2.92	86.6	8.39
GOR	Gir-Su	182	80.6	263	1.24	2.81	4.05	16.1	3.04	65.0	5.58

Note: HIB sites are Creek (Crk), Shoal (Shl), and Hog Island (HI) and GOR sites are Gorino (Gor) and Giralda (Gir). See site locations in Figure 4.2. O = overhead; A = ascendency; C = capacity; AMI= average mutual information; S = unconstrained flow structure; H = flow diversity; TN loading = total nitrogen loading; APL = average path length; TST = total system throughput; PP = primary production. TN loading, TST and PP are indicators of trophic status.

than 10 mmol N m^{-2} d^{-1} in five of six networks for Hog Island Bay (3.64 to 8.98 mmol N m^{-2} d^{-1}). Primary production for Giralda fell within this range. Large macroalgal standing stocks and growth in Gorino during both periods and in the Shoal site of Hog Island Bay contributed the only primary productivities greater than 10 mmol N m^{-2} d^{-1}. The high primary productivities in Gorino fostered the two highest TST values. The next most active site was Giralda. While the most active site in Hog Island Bay was where macroalgae contributed to high primary productivity (Shoal in summer), all Hog Island Bay sites had TST values less than 55% of the lowest site in the Sacca di Goro. Spring in the Sacca di Goro had higher values of PP than in summer, whereas the opposite occurred in Hog Island Bay, where summer PP had higher values than spring.

Average path length (APL) is a measure of the degree to which material remains in the system and thus may be linked to the degree of recycling. It was higher within Hog Island Bay, ranging from 13 to 42 path lengths, than in the Sacca di Goro, ranging from 3 to 4 path lengths (Table 4.3). The equation for APL calculates higher APL with higher TST and lower TN loading. As TST is lower for Hog Island Bay than for the Sacca, the longer path lengths reflected the low rates of loading in the mesotrophic lagoon.

Information indices capture both the amount of activity and degree of organization by containing the product of TST and some algorithm of probabilistic interrelationships. Not surprisingly, given the higher TST in the Sacca di Goro, its networks' ascendency (A), capacity (C), and overhead (O) are the highest (Table 4.3). The organizational components remove the direct influence of TST, but still show differences between networks of the two lagoons. H is flow diversity, reflecting the structure of both constrained and unconstrained flows. H of Hog Island Bay networks ranged from 3.34 to 4.10 bits and were generally less than those of the Sacca di Goro (4.05 to 4.31 bits). AMI, the indicator of constrained flow structure, ranged from 1.24 to 1.48 bits. The lowest values were for Giralda, while the highest generally occurred within HIB. The spring Gorino network at 1.41 bits had a value within the range of HIB networks. S indicates unconstrained flow structure and is the difference between H and AMI. S demonstrates considerably greater unconstrained flow structure in the Sacca di Goro networks (2.81 to 2.98 bits) than for Hog Island Bay networks (1.92 to 2.32 bits). Thus, the higher H values for the Sacca are a result of higher degrees of unconstrained flows or evenness of parallel flows.

Clearly, the organizational structure of nitrogen networks from the Sacca di Goro is different from that of Hog Island Bay, and the direction of differences is consistent with expectations of trophic status. However, are differences associated with geographical location within the systems also consistent with expectations? We used pair-wise correlation analysis between measures of trophic status (i.e., TN loading, primary production, and TST) with each of the information indices (i.e., AMI, S, and H). Although significant Pearson correlations ($p < 0.01$) were found for either TST or TN loading with either S ($r = 0.793$ for TST and 0.857 for TN loading) or H ($r = 0.767$ for TST and 0.804 for TN loading), graphic representation failed to show any patterns across locations within lagoons. Furthermore, when correlations of these results from locations within each lagoon were determined, no statistically significant correlation was found. Therefore, the information indices did not track trophic status within a lagoon, although they did across the two very different lagoons. This is likely because H, AMI, and S are logarithmic terms and variations are thereby muted. In addition, the simple biogeochemical networks of few compartments may limit sensitivity by limiting opportunities for differences in structure (Christian et al. 1996). Unfortunately, the statistics of these information indices remain unstudied.

4.3.2 ECOSYSTEM HEALTH FRAMEWORK

Costanza's (1992) identification of ecosystem health as organization, resilience, and vigor is represented through network analysis as average mutual information (AMI), unconstrained flow structure (S), and total system throughput (TST), respectively (Ulanowicz 1997). Ulanowicz

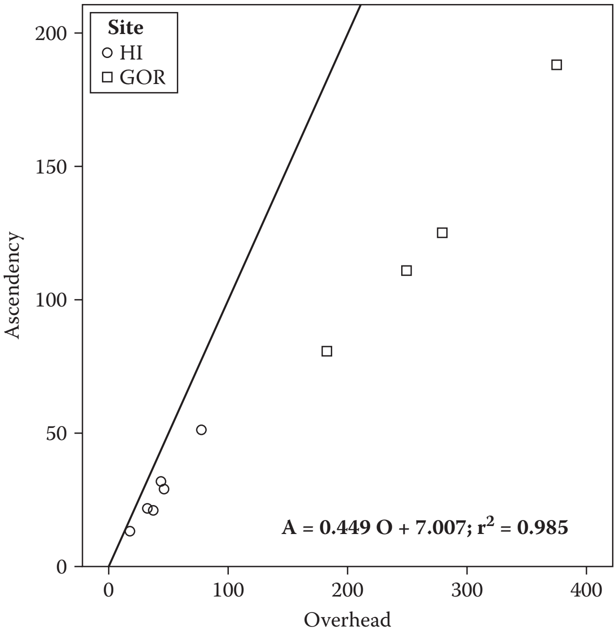

FIGURE 4.4 Position of nitrogen networks, within the framework for ecosystem health proposed by Ulanowicz (1997), for three sites in Hog Island Bay (HI) and two sites in Sacca di Goro (GOR) during two sampling periods (see Section 4.2 for details). Units for Ascendency and Overhead are mmol N m^{-2} d^{-1} bits. The line represents the 1:1 relationship and not the linear regression equation.

(1997) proposed a plot of ascendency (A) vs. overhead (O) that represents a phase plane of ecosystem health. A contains AMI, and O contains S. Both increase as TST increases, as TST is multiplied by AMI and S for A and O, respectively. The A vs. O of nitrogen networks provides the linear relationship suggested by Ulanowicz (1997) (Figure 4.4). The linear regression equation is A = 0.449 O + 7.007 with an $r^2 = 0.985$. This relationship demonstrates the relative loss of organization (lower A relative to O) with increased eutrophication. Ulanowicz (1997) previously postulated that eutrophication can be defined as increased TST with a decrease in organization (AMI or A). Our findings support this hypothesis at least in a relative sense. AMI was generally lower in the Sacca di Goro networks, although A was higher in the eutrophic system. Given that TST values in the Sacca were over 10 times those of the bay, it is not surprising that A values for the Sacca di Goro, which are the product of TST and AMI, were higher than for Hog Island Bay. Perhaps more significant, the S values in the Sacca are higher, reflecting greater disorganization or indeterminacy.

Empirical evaluation of Ulanowicz's framework (Figure 4.4) has a statistical complication—the potential for spurious correlation (Brett 2004). Spurious correlations can arise from shared variables embedded in the correlated variables. In this case, TST is shared as A = TST × AMI and O = TST × S. Such a relationship increases the value of r^2 needed to reject the null hypothesis (Brett 2004). The amount of r^2 for the null hypothesis of zero correlation increases as the coefficient of variation (CV) of TST increases above that for either AMI or S. As these latter two variables are based on logarithms and TST is not, the differences are large. The coefficients of variation of AMI, S, and TST are 5.6, 17.0, and 85.9%, respectively. The ratio of CVs of TST:AMI was therefore 15, and of TST:S, as 5. Using Monte Carlo simulations, Brett (2004) found random nonshared variables of X and Y in X × Z vs. Y × Z gave coefficients of determination over 0.9 when the CV ratios of shared to unshared variables were only 4. Thus, a high correlation and well-fit regression would be expected for the relationship of A vs. O simply through spurious correlation.

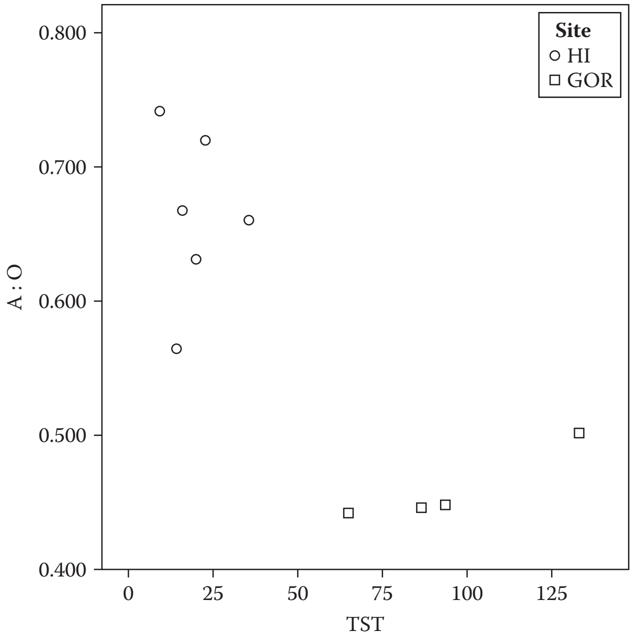

FIGURE 4.5 The ratio of Ascendency (A) to Overhead (O), representing the relationship of organization over resilience, plotted against TST, representing vigor, for three sites in Hog Island Bay (HI) and two sites in Sacca di Goro (GOR) during two sampling periods (see Section 4.2 for details). A:O is nondimensional, and TST units are mmol N m^{-2} d^{-1}.

This complication led to an evaluation of the framework in two alternate ways more appropriate for evaluating empirical information. First, A/O is equal to AMI/S and represents the relative amounts of organization to disorganization. This relative index was related to TST (Figure 4.5). The A/O values for the Sacca di Goro, where TST is higher, were lower than for Hog Island Bay, supporting our previous interpretations. Also, no trends were obvious within each lagoon. Second, we log-transformed TST to reduce its CV, making it more similar to those of AMI and S and evaluated the transformed A vs. O framework (i.e., [(log TST) × AMI] vs. [(log TST) × S]). The CV of log TST reduced to 27.0%, but still gave ratios of shared to unshared CVs of 1.6 to 4.8. The resultant r^2 of the transformed A vs. O lowered to 0.875 (Figure 4.6), which remains near values for random relationships by Brett (2004). While this did not fully equalize coefficients of variation in our study, it did reduce the differences significantly. We propose that log transformations of TST might be used more generally in the empirical applications of information indices to reduce this statistical problem.

While our recommendation provides some correction to the issue of spurious correlation, the problem of shared variables among information indices is much more complicated. H, AMI, and S are constructed on the same flows and network structure and represent different probability conditions of those flows. The flows themselves are interdependent and constrained by mass balance. Thus, shared variables occurred across hierarchical levels of calculation, and statistical inference of the interactions of ascendency, capacity, and overhead is a challenge for which we have only provided a beginning.

4.4 CONCLUSIONS

Measures and indices of the ecosystem status at the system level are necessary if ecosystem-based management is to be a reality. The Millennium Ecosystem Assessment (2005) provides the most ambitious attempt, but is focused on global and regional scale conditions. Bricker et al. (1999,

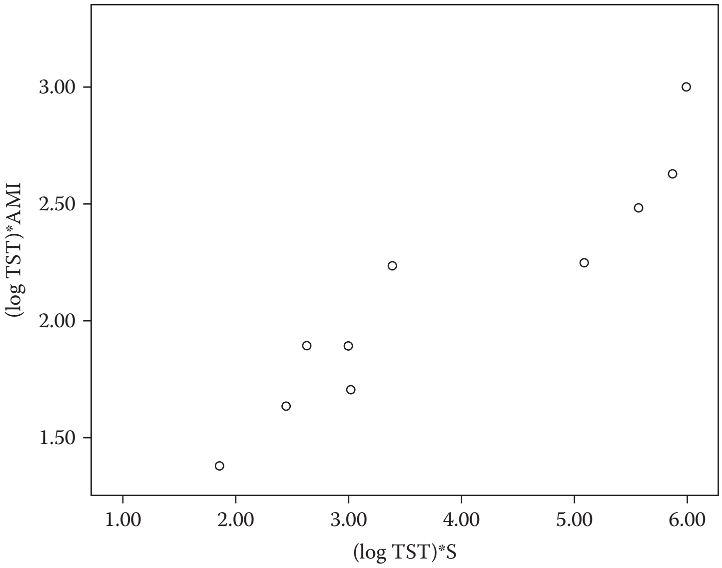

FIGURE 4.6 Position of nitrogen networks within framework for ecosystem health proposed by Ulanowicz (1997), using versions of A and O in which TST is log transformed and multiplied by AMI or S, respectively. Networks are for three sites in Hog Island Bay (HI) and two sites in Sacca di Goro (GOR) during two sampling periods (see Section 4.2 for details).

2007) developed an assessment of eutrophication of coastal systems within the United States with ecosystem-specific information. However, neither approach uses the in-depth observational and experimental information that exists for some of the better studied coastal ecosystems. ENA provides this opportunity with several system-level indices (Jørgensen et al. 2005). Our networks have tracked nitrogen as an important controlling element to lagoonal dynamics. We have not directly addressed the human causes for the differences in nitrogen loading or the consequences to humans, as in the broader assessments. Our efforts only address the consequences to the lagoon's trophic status. One might infer that lagoons with less healthy ecosystems are less valuable to humans, but this is untested. In fact, the Sacca di Goro is a highly valued ecosystem for its economically important seafood production (Bartoli et al. 2001b; Viaroli et al. 2006). Ecological network analysis can be extended to include other currencies and human dimensions directly. This is one of the next major steps for the methodology.

While most ENA studies have focused on trophic structure, we evaluated ecosystem status using nitrogen cycling of two well-studied coastal lagoons: Hog Island Bay, USA, and Sacca di Goro, Italy. The latter has much higher nutrient loading with clear signs of cultural eutrophication, while the former is minimally impacted by nutrients. The less impacted system, Hog Island Bay, demonstrated greater cycling of nitrogen (as measured by average path length) with more efficient use of the lower amount of loading compared to the highly eutrophic Sacca di Goro. This confirms the findings of Anderson et al. (2003). Previously, Christian et al. (1996) found cycling (as measured by the Finn Cycling Index) in coastal aquatic ecosystems to be largely associated with primary producer growth form, increasing with greater relative importance of phytoplankton to primary productivity. However, among the systems with rooted macrophytes and macroalgae, systems with higher loading had reduced cycling. Thus, as eutrophication alters the sources of primary production (Viaroli et al. 2008); it may also significantly retard nitrogen cycling and reduce efficiency of the element's use.

We applied information theoretical metrics to index "ecosystem health" properties (*sensu* Costanza 1992) of organization, resilience, and vigor (Ulanowicz 1997). We found ecological network analysis results reflected the trophic status of the two coastal lagoons. Ulanowicz (1997) proposed that eutrophication promoted the increase in total system throughput (TST) while decreasing average mutual information within ascendency. In a sense, eutrophication sets back ecosystem development. We found this generally to be the case in the comparisons of the two coastal lagoons. Thus, "organization" decreased with eutrophication, while TST rose. Additionally, the "resilience" component or unconstrained flow structure (S), representing indeterminacy and redundancy, increased with eutrophication. Thus, ecosystem health as portrayed in this manner does not simply improve as all of the three components increase. Rather, the ecosystem status reflects the balance of the three. Our results are consistent with the hypothesis that eutrophication disrupts organization, and less eutrophic systems may provide more determinant and efficient use of nutrients. While this hypothesis appears reasonable, extended testing and generalization remain.

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REFERENCES

Allesina, S. and C. Bondavalli. 2003. Steady state ecosystem flow networks: A comparison between balancing procedures. *Ecol. Model.* 165: 221–229.

Allesina, S. and C. Bondavalli. 2004. WAND: An ecological network analysis user-friendly tool. *Environ. Model. Software* 19: 337–340.

Anderson, I. C., K. J. McGlathery, and A. C. Tyler. 2003. Microbial mediation of "reactive" nitrogen transformations in a temperate lagoon. *Mar. Ecol. Prog. Ser*. 246: 73–84.

Baird, D. and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay. *Ecol. Monogr.* 59: 329–364.

Baird, D., J. Luczkovich, and R. R. Christian. 1998. Assessment of spatial and temporal variability in ecosystem attributes of St. Marks National Wildlife Refuge, Apalachee Bay, Florida. *Estuar. Coastal Shelf Sci.* 47: 329–349.

Bartoli, M., G. Castaldelli, D. Nizzoli, L. G. Gatti, and P. Viaroli. 2001a. Benthic fluxes of oxygen, ammonium and nitrate and coupled-uncoupled denitrification rates within communities of three different primary producer growth forms. Pp. 225–233, In: F. M. Faranda, L. Guglielmo, and G. Spezie (eds.), *Mediterranean ecosystems: Structure and processes*. Milan: Springer-Verlag.

Bartoli, M., D. Nizzoli, P. Viaroli, E. Turolla, G. Castaldelli, E. A. Fano, and R. Rossi. 2001b. Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* 455: 202–212.

Bohlke, J. K. and J. M. Denver. 1995. Combined use of groundwater dating, chemical, and isotopic analyses to resolve the history and fate of nitrate contamination in two agricultural watersheds, Atlantic coastal plain, Maryland. *Water Resour. Res.* 31: 2319–2339.

Bondavalli, C. 2003. Effect of eutrophication upon radionuclide dynamics in the Sacca di Goro lagoon (Po river delta, Italy): A combined field, experimental and modeling study. *Environ. Pollut*. 125: 433–446.

Brett, M. T. 2004. When is a correlation between non-independent variables "spurious"? *Oikos* 105: 647–656.

Bricker, S. B., C. G. Clement, D. E. Pirhalla, S. P. Orlando, and D. R. G. Farrow. 1999. *National Estuarine Eutrophication Assessment: Effects of nutrient enrichment in the nation's estuaries*. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science, Silver Spring, Maryland.

Bricker, S., B. Longstaff, W. Dennison, A. Jones, K. Boicourt, C. Wicks, and J. Woerner. 2007. *Effects of nutrient enrichment in the nation's estuaries: A decade of change*. NOAA Coastal Ocean Program Decision Analysis Series No. 26, National Centers for Coastal Ocean Science, Silver Spring, Maryland.

Chauhan, M. J. and A. L. Mills. 2002. Modeling baseflow nitrate loading on the eastern shore of Virginia. Presented at the Atlantic Estuarine Research Federation Spring Meeting, Lewes, Delaware.

Christensen, V. 1995. Ecosystem maturity: Towards quantification. *Ecol. Model.* 77: 3–32.

Christensen, V. and D. Pauly (eds.). 1993. *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings 26, Manila, the Philippines.

Christian, R. R., J. N. Boyer, D. W. Stanley, and W. M. Rizzo. 1992. *Network analysis of nitrogen cycling in an estuary*. Pp. 217–247, In: C. Hurst (ed.), Modeling the metabolic and physiologic activities of microorganisms. New York: John Wiley & Sons.

Christian, R. R., E. Forès, F. Comín, P. Viaroli, M. Naldi, and I. Ferrari. 1996. Nitrogen cycling networks of coastal ecosystems: Influence of trophic status and primary producer form. *Ecol. Model.* 87: 111–129.

Christian, R. R., M. Naldi, and P. Viaroli. 1998. Construction and analysis of static, structured models of nitrogen cycling in coastal ecosystems. Pp. 162–195. In: A. L. Koch, J. A. Robinson, and G. A. Milliken (eds.), *Mathematical modeling in microbial ecology*. New York: Chapman & Hall.

Christian, R. R. and C. R. Thomas. 2003. Network analysis of nitrogen inputs and cycling in the Neuse River Estuary, North Carolina, USA. *Estuaries* 26: 815–828.

Costanza, R. 1992. Toward an operational definition of ecosystem health. Pp. 239–256, In: R. Costanza, B. G. Norton, and B. D. Haskell (eds.), *Ecosystem health: New goals for environmental management.* Washington, D.C.: Island Press.

Dame, J. K. and R. R. Christian. 2006. Uncertainty and the use of network analysis for ecosystem-based fishery management. *Fisheries* 31: 331–341.

Finn, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol.* 56: 363–380.

Giordani G., M. Austoni, J. M. Zaldívar, D. P. Swaney, and P. Viaroli. 2008. Modelling ecosystem functions and properties at different time and spatial scales in shallow coastal lagoons: An application of the LOICZ biogeochemical model. *Estuar. Coastal Shelf Sci.* 77: 264–277.

Gu, C. H., G. M. Hornberger, J. S. Herman, and A. L. Mills. 2008. Effect of freshets on the flux of groundwater nitrate through streambed sediments. *Water Resour. Res.* 44, W05415. DOI: 10.1029/2007WR006488.

Hamilton P. A. and D. R. Helsel. 1995. Effects of agriculture on ground-water quality in five regions of the United States. *Ground Water* 33: 217–226.

Hassan, R., R. Scholes, and N. Ash (eds.). Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Current state and trends*, Vol. 1. Washington, D.C.: Island Press.

Havens, K. E., J. Hauxwell, A. C. Tyler, S. Thomas, K. J. McGlathery, J. Cebrian, I. Valiela, A. D. Steinman, and S. J. Hwang. 2001. Complex interactions between autotrophs in shallow marine and freshwater ecosystems: Implications for community responses to nutrient stress. *Environ. Pollut.* 113: 95–107.

Jørgensen, S. E., F.-L. Xu, F. Sala, and J. C. Marques. 2005. Application of indicators for the assessment of ecosystem health. Pp. 5–66, In: S. E. Jørgensen, R. Costanza, and F.-L. Xu (eds.), *Handbook of ecological indicators for the assessment of ecosystem health*. Boca Raton, Florida: CRC Press.

Kennish, M. J. 1999. *Estuary restoration and maintenance: The National Estuary Program*. Boca Raton, Florida: CRC Press.

Lackey, R. T. 2001. Values, policy, and ecosystem health. *BioScience* 51: 437–443.

Mageau, M.T., R. Costanza, and R.E. Ulanowicz. 1995. The development, testing and application of a quantitative assessment of ecosystem health. *Ecosys. Health* 1: 201–213.

McGlathery, K. J., I. C. Anderson, and A. C. Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Mar. Ecol. Prog. Ser.* 216: 1–15.

Naldi, M. and P. Viaroli. 2002. Nitrate uptake and storage in the seaweed *Ulva rigida* C. Agardh in relation to nitrate availability and thallus nitrate content in a eutrophic coastal lagoon (Po River Delta, Italy). *J. Exp. Mar. Biol. Ecol.* 269: 65–83.

Niemi, G. J. and M. E. McDonald. 2004. Applications of ecological indicators. *Annu. Rev. Ecol. Evol. Syst.* 35: 89–111.

Nizzoli, D., M. Bartoli, and P. Viaroli. 2007. Nitrogen and phosphorus budgets during a farming cycle of the bivalve *Ruditapes philippinarum*. *Hydrobiologia* 587: 25–36.

Orth, R. J., M. L. Luckenbach, S. R. Marion, K. A. Moore, and D. J. Wilcox. 2006. Seagrass recovery in the Delmarva coastal bays, USA. *Aquat. Bot*. 84: 26–36.

Peterson, C. H., R. T. Barber, K. L. Cottingham, H. K. Lotze, C. A. Simenstad, R. R. Christian, M. F. Peihler, and J. Wilson. 2008. National Estuaries. Pp. 7-1–7-108, In: S. H. Julius and J. M. West (eds.), [J. S. Baron, L. A. Joyce, P. Kareiva, B. D. Keller, M. A. Palmer, C. H. Peterson, and J. M. Scott (authors)]. CCSP. 2008: *Preliminary review of adaptation options for climate-sensitive ecosystems and resources*. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Washington, D.C.: U.S. Environmental Protection Agency.

Stanhope J. W., I. Anderson, and W. G. Reay. 2009. Base flow nutrient discharges from lower Delmarva Peninsula watersheds of Virginia, USA. *J. Environ. Qual.* 38: 2070–2083.

Stanhope, J. W. 2003. Relationships between watershed characteristics and base flow nutrient discharges to Eastern Shore coastal lagoons, Virginia. M.S. Thesis, College of William and Mary, Gloucester Point, VA.

Tyler, A. C., K. J. McGlathery, and I. C. Anderson. 2001. Macroalgae mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuar. Coastal Shelf Sci.* 53: 155–168.

Tyler, A. C., K. J. McGlathery, and I. C. Anderson. 2003. Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnol. Oceanogr.* 48: 2125–2137.

Ulanowicz, R. E. 1986. *Growth and development: Ecosystem phenomenology*. New York: Springer-Verlag.

Ulanowicz, R. E. 1992. Ecosystem health and trophic flow networks. Pp. 190–206, In: R. Constanza, B. G. Norton, and B. D. Haskell (eds.), *Ecosystem health: New goals for environmental management*. Washington, D.C.: Island Press.

Ulanowicz, R.E. 1997. *Ecology: The ascendent perspective.* New York: Columbia University Press.

Ulanowicz, R. E. and J. S. Norden, 1990. Symmetrical overhead in flow networks. *Int. J. Systems Sci.* 21: 429–437.

Viaroli, P., R. Azzoni, M. Bartoli, G. Giordani, and L. Tajè. 2001. Evolution of the trophic conditions and dystrophic outbreaks in the Sacca di Goro lagoon (Northern Adriatic Sea). Pp. 467–475, In: F. M. Faranda, L. Guglielmo, and G. Spezie (eds.), *Mediterranean ecosystems: Structure and processes*. Milan: Springer-Verlag.

Viaroli, P., M. Bartoli, R. Azzoni, G. Giordani, C. Mucchino, M. Naldi, D. Nizzoli, and L. Tajè. 2005. Nutrient and iron limitation to *Ulva* blooms in an eutrophic coastal lagoon (Sacca di Goro, Italy). *Hydrobiologia* 550: 57–71.

Viaroli, P., M. Bartoli, G. Giordani, M. Naldi, S. Orfanidis, and J. M. Zaldivar. 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: A brief overview. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 18(1):S105–S117.

Viaroli, P. and R. R. Christian. 2003. Description of trophic status, hyperautotrophy and dystrophy of a coastal lagoon through a potential oxygen production and consumption index. *Ecological Indicators* 3: 237–250.

Viaroli, P., G. Giordani, M. Bartoli, M. Naldi, R. Azzoni, D. Nizzoli, I. Ferrari, J. M. Zaldivar Comenges, S. Bencivelli, G. Castaldelli, and E. A. Fano. 2006. The Sacca di Goro Lagoon and an arm of the Po River. Pp. 197–232, In: P. J. Wangersky (ed.), *The handbook of environmental chemistry, Estuaries*, Volume 5, Part H. Berlin: Springer-Verlag.

Viaroli, P., A. Pugnetti, and I. Ferrari. 1992. *Ulva rigida* growth and decomposition processes and related effects on nitrogen and phosphorus cycles in a coastal lagoon (Sacca di Goro, Po River Delta). Pp. 77–84, In: G. Colombo, I. Ferrari, V. U. Ceccherelli, and R. Rossi (eds.), *Marine eutrophication and population dynamics*. Fredensborg, Denmark: Olsen & Olsen.

Westra, L. 1995. Ecosystem integrity and sustainability: The foundational value of the wild. Pp. 12–33, In: L. Westra and J. Lemons (eds.), *Perspectives on ecological integrity*. Dordrecht, the Netherlands: Kluwer.