

SPECIAL ISSUE: The Dynamics and Value of Ecosystem Services: Integrating
Economic and Ecological Perspectives

Measuring contributions to economic production—use of an Index of Captured Ecosystem Value

Kent Gustavson ^{a,*}, Stephen C. Lonergan ^a, Jack Ruitenbeek ^b

^a Department of Geography, University of Victoria, PO Box 3050, Victoria, Canada, BC V8W 3P5

^b H.J. Ruitenbeek Resource Consulting Limited, RR # 2, Site 52, C21, Gabriola, Canada, BC V0R 1X0

Abstract

The production of an economic good derived from a renewable natural resource base involves the extraction of ecosystem function values as represented by the contribution made to production by the originating ecosystem. The artisanal mixed-species fisheries of Jamaica is used as a case study in the development of a biophysically based index to account for captured ecosystem values (or embodied ecosystem values) and an examination of the extent to which those values are proportionately reflected in monetary exchange values. The Index of Captured Ecosystem Value (ICEV) is developed from a basis in information theory relevant to an analysis of network flows in ecosystems. Technical coefficients, describing the production relationship between ICEV values and market values of catches associated with individual fishing efforts in Jamaican fisheries, reveal that captured ecosystem function associated with fisheries using distinct technologies (i.e. China net, trap, hand line, palanca and speargun) are valued differently by the market. This surplus value is rooted in the observation that certain fisheries target species that are more connected within the coral reef food web than those species typically captured by other fisheries. Consideration of the biophysically based contributions of coral reef ecosystems to fisheries production reveals distortions between market and supply-side values, indicating that the role of ecosystems is not being consistently treated. Comment and direction is offered regarding the development of indices of ecosystem function or value that can be applied to policy questions concerning the extraction of a renewable natural resource. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Index; Indicators; Ecosystem function; Food web; Ecosystem value; Supply-side value

1. Introduction

Economic valuation of the environment is concerned with estimating the monetary value of the

flow of ecosystem services, where ecosystem services are taken to include all goods, services or other benefits derived from natural capital. de Groot (1994) defined ecosystem functions as they relate to economic values as “the capacity of natural processes and components to provide goods and services that satisfy human needs (directly and/or indirectly)”. Services from such functions include materials, energy and informa-

* Corresponding author. Present address: Gustavson Ecological Resource Consulting, PO Box 115, Gabriola, Canada, BC V0R 1X0. Tel.: +1-250-247-9734; fax: +1-250-247-9735
E-mail address: kent@gerc.bc.ca (K. Gustavson).

tion used to contribute to human welfare (e.g. Costanza et al., 1997). There have been many attempts to place a value on ecosystem services. The list of potential services is long and varied, including: generating and maintaining soils; maintaining hydrological cycles; regulating gas; nutrient cycling and storage; assimilation and elimination of pollution and wastes; regulating disturbances; biological control; pollination of crops; food production; maintaining species and genetic resources; maintaining biogeochemical cycling; and, regulating weather and climate (Folke et al., 1994; Bingham et al., 1995; Myers, 1996; Costanza et al., 1997).

The values perceived by humans and the preferences expressed in the market system, or through other monetary valuation means, may not take into account what is necessary or relevant for ecosystem integrity for the maintenance of natural ecosystems and their associated services, nor does it necessarily take into account the co-evolutionary and complex nature of the environment-economy system (Holling et al., 1995). Yet the production of goods and services by the human economy relies on the drawing of services provided by natural capital and, thus, on the productivity of natural biotic systems. The drawing of services provided by natural capital may be described as a process that captures or ‘embodies’ function value of the originating ecosystem. It is through this involvement of natural biota in economic production processes that contributions by the originating ecosystem are made to the value of the final economic goods and services (i.e. through a value-added process of which the natural biota is a part or, alternatively, as a form of contributory value) (Ulanowicz, 1991).

Isard (1969, 1972) presents a conceptual framework for the analysis of the interactions or linkages between economic and ecological systems (Fig. 1). It is based in a traditional commodity-by-industry input-output modeling framework describing linear interactions between sectors within the economic system (e.g. Miller and Blair, 1985), but extends the matrix to include ecological commodity inputs and outputs to economic activities, economic commodity inputs and outputs to ecological processes, and ecological commodity in-

puts and outputs to ecological processes. Each cell entry in the larger matrix represents an input of a commodity into (a positive cell entry) or use of a commodity by (a negative cell entry) a process or activity. Despite drawbacks, the framework is particularly attractive in that it does allow for the “...systematic description in relationships and magnitudes as they exist at a point in time. This description in itself often provides much insight” (Isard, 1972, p. 95). Some work has been done explicitly applying input–output analysis to the study of ecosystem structure and function (e.g. Hannon, 1973; Finn, 1976).

The lower right quadrant (Fig. 1) represents interactions within the ecological system and is analogous to what an ecologist envisions through the definition of food webs, with food webs depicting the flow of ecological commodities between trophic species or groupings. Positive cell entries in the upper right quadrant represent outputs of ecological processes provided as resources or products directly as economic commodities. Negative cell entries in the lower left quadrant represent the use of ecological commodities within economic processes. Whether the product of an ecosystem process is recorded as an output of an ecological process (economic commodity, upper right quadrant) or as an input to an economic process (ecological commodity, lower left quad-

	Economic activities	Ecologic processes
Economic commodities	Economic system: intersector coefficients	Ecologic processes: input and output coefficients, re: economic commodities
Ecologic commodities	Economic sectors: input and output coefficients, re: ecologic commodities	Ecologic system: interprocess coefficients

Fig. 1. Framework for the analysis of ecological economic interactions (adapted from Isard, 1969, 1972).

rant) involves an arbitrary decision on behalf of the researcher (Isard, 1969).

The biophysical value of products of natural ecosystems as ecological commodities, expressed as some measure of ecosystem function value per unit of economic production value within a given economic sector, defines technical coefficients within the ecological economic model:

$$a_{ij} = \frac{Z_{ij}}{X_j} \quad (1)$$

where, a_{ij} , technical coefficient defining the production relationship between the ecological commodity input i (biophysical units) and the economic sector j (dollars); Z_{ij} , flow of ecological commodity input i to economic sector j (biophysical units) and, X_j , gross output value of economic sector j (dollars).

If one is concerned with the direct capture of biophysical ecosystem values as represented by technical coefficients, what may be used as an index of ecosystem function value for use in Eq. (1)? Certainly, it would be possible to rely on a simple measure of biomass for all Z_{ij} , yet it would be more advantageous to adopt a measure that more explicitly and consistently acts as a proxy for ecosystem functions that gave rise to the commodity.

There is a growing body of ecological work that continues to examine the relationship between traditional measures of biodiversity and ecosystem function (e.g. Ehrlich and Ehrlich, 1981; di Castri and Younés, 1990; Grassle et al., 1991; Schulze and Mooney, 1994; Lamont, 1995; Bengtsson et al., 1997). The evidence is often contradictory and, if anything, seems to point in the direction that the most often relied upon measures of biodiversity may not be adequate indices because the relationship is often functional process specific, ecological system specific (in space, time and scale), and dependent on the definition of biodiversity employed. About all that can be generally said about the role of biodiversity in relation to function is that it provides the "...medium for energy and material flows, which in turn provide ecosystems with their functional properties..." (Myers, 1996).

Currently, there are no widely accepted indices of ecosystem function per se. Some preliminary work in that direction, however, is evident from the literature. Indeed, there appears to be a growing movement by many ecologists towards a focus on finding general, measurable attributes that characterize the functioning of ecosystems (e.g. Friend and Rapport, 1991; Holling, 1992; Holling et al., 1995; Martinez, 1996). For example, Martinez (1996) advocates a focus on the conceptualization of biodiversity itself as "the spatial and temporal variability of the structure and function of living systems". This definition explicitly recognizes the importance of establishing proxy measures for ecosystem function.

There have been efforts to define and measure resilience (e.g. DeAngelis, 1980; Ives, 1995; Ludwig et al., 1997; Neubert and Caswell, 1997), but ecological theory has yet to advance a general predictable or supportable theoretical relationship between properties of resilience and function. Much has been debated about the possible relationships between stability and structure (e.g. MacArthur, 1955; May 1972, 1973, 1975; Pimm, 1982, 1984; Hall and Raffaelli, 1993). Indeed, a general and predictable relationship between properties of resiliency and how ecosystems function is not intuitively obvious and may not exist. Stability statements alone tend to be specific to the ecological situation under consideration and cannot be assumed to apply to the larger, more general case (Grimm and Wissel, 1997).

Where else can one turn to define an index of ecosystem function? What is ideally required for use in Eq. (1) is a general proxy measure of the functional characteristics of species within a community which is supported by theory, calculable using a limited dataset and information base, and applicable to a wide array of ecosystems. An Index of Captured Ecosystem Value (ICEV) is derived relying on relatively simple descriptions of the structure of the food web of interest and the nature of the trophic relationships between its elements. Information theory will provide the basis for the analysis.

2. Methods

It is reasonable to accept that ecological processes and ecosystem function are synonymous terms (Lawton and Brown, 1993) or that ecological functions are more generally interactions with ecological processes (Martinez, 1996). Functional diversity may be quantified from the type and number of functional groups represented in an ecosystem and the nature of their interactions. Food webs are simply depictions or models of how species in a community interact (e.g. Pimm, 1982; Lawton, 1989; Yodzis, 1989; Hall and Raffaelli, 1993), in which interactions with processes are as either consumers or resources, and thus can serve as the basis for the derivation of an index of ecosystem function.

The development of the index will be approached initially from a basis in information theory (e.g. Kullback, 1968). Ulanowicz (1986), Ulanowicz and Norden (1990) outline the theory behind measures of uncertainty and information content relevant to the analysis of network flows in ecosystems, building on the previous work of MacArthur (1955), Rutledge et al. (1976), Ulanowicz (1980), Hirata and Ulanowicz (1984).

Following Ulanowicz (1986), the uncertainty regarding a specific outcome of an event can be described by

$$H_i = -K \log(p_i) \quad (2)$$

where, H_i , the uncertainty associated with outcome i ; p_i , the probability of outcome i ; and K , a constant (imparts the physical dimensions or 'size' to the index) (Ulanowicz, 1986).

Where a suite of outcomes are possible, one can estimate the average uncertainty as

$$H = -K \sum_i p_i \log p_i \quad (3)$$

Information concerning events represents a reduction in the uncertainty associated with predicting the outcomes. Thus, one can similarly define the average gain in information concerning a suite of possible outcomes as

$$I = K \sum_i p_i \log \left(\frac{p_i}{p_i^*} \right) \quad (4)$$

where, p_i^* , the probability of outcome i based on an initial assumed distribution; and p_i , the probability of outcome i based on new information.

The linking of events is an organizational characteristic of network flows. Applying information theory principles to network flows, one can describe the information concerning the outcome of an event provided by knowledge of a linked or related event as

$$I = K \log \left[\frac{p \langle b_j | a_i \rangle}{p \langle b_j \rangle} \right] \quad (5)$$

where, $p \langle b_j | a_i \rangle$, the probability of b_j given that a_i has occurred; and $p \langle b_j \rangle$, the probability that b_j will occur.

One can then describe the average mutual information as presented by Ulanowicz (1986) as

$$A = K \sum_i \sum_j p(a_i, b_j) \log \left[\frac{p \langle b_j | a_i \rangle}{p \langle b_j \rangle} \right] \quad (6)$$

When applied to a network, Eq. (6) measures the information of the flow structure, or specifically, "...how well, on the average, the network articulates a flow event from any one node to affect any other specific locus" (Ulanowicz, 1986, p. 97). To apply this to an open ecosystem and ensure that the solution is symmetrical with respect to the consideration of either compartment inputs or outputs, one first defines the matrix describing the flows from the i th compartment to the j th compartment, T_{ij} , where i and j range from 0 to $n+1$ (0 refers to exogenous inputs to the system, while $n+1$ refers to losses or exports from the system) (Ulanowicz and Norden, 1990). The average mutual information (Ulanowicz and Norden, 1990) then becomes

$$I = \sum_{i,j=0}^{n+1} f_{ij} Q_i \log \left(\frac{f_{ij}}{\sum_k f_{kj} Q_k} \right) \quad (7)$$

where, $Q_i = \sum_k T_{ik} / \sum_{l,m} T_{lm}$, the estimated probability that flow passes through compartment i , and; $f_{ij} = T_{ij} / \sum_k T_{ik}$, the fraction of total flow through compartment i that also passes through compartment j (or the estimated conditional probability that flow will pass through j given that it has passed through i).

Ulanowicz (1980, 1986), Ulanowicz and Norden (1990) scale the measure of the average mutual information (I) by the size of the total flow through the system:

$$A = TI \tag{8}$$

where, A , ascendancy; and T , total system throughput, or $\sum_{i,j} T_{ij}$.

System ascendancy, as a measure of the magnitude of the information flow through the network structure of an ecosystem, is effectively an index of ecosystem function. Moreover, it has many useful advantages, such as the ability to be applied to open, far-from-equilibrium systems (Hirata and Ulanowicz, 1984; Ulanowicz, 1986). However, its use does demand a relatively complete description of the nature and magnitude of the interactions among all species. Furthermore, there are the additional complexities associated with providing realistic and appropriate allowances for temporal and spatial variations in such relationships (Pahl-Wostl, 1995). The development of mass-balance models (e.g. the ECO-PATH models) (Christensen and Pauly, 1992) may provide a rich information base, but do require specific assumptions regarding biomasses, rates, and food web relationships. As it is the intention of this study to derive an index of ecosystem function which can be applied with a relatively limited knowledge of the ecosystem in question, we chose to ‘back away’ from information demands associated with using the average mutual information or system ascendancy concepts strictly as described above.

Let us assume that one does not have sufficient information regarding either the size of the system throughput or the associated probabilities of interspecific interactions for a given food web, but does have knowledge regarding the species or trophic species involved and whether or not interspecific interactions may occur between any pair of species. In other words,

$$f_{ij} = \frac{1}{l_i} \tag{9}$$

$$Q_i = \frac{l_i}{L} \tag{10}$$

$$\sum_k f_{kj} Q_k = \frac{l_j}{L} \tag{11}$$

where, l_i , the total number of species i forward links with other species (i.e. the total number of species or trophic species which use species i as a resource or as prey); l_j , the total number of species j backward links with other species (i.e. the total number of species or trophic species which species j uses as a resource or as prey); and L , the total number of links between all species in the set.

Since one is assuming that we do not have sufficient information regarding the probabilities associated with any pair of interactions, all interspecific interactions are given an equal probability of occurring as long as a link is known to exist. Thus, assuming maximum uncertainty regarding the strength of interspecific interactions, Eq. (7), which defines the average mutual information, becomes

$$I = \sum_{i,j=0}^{n+1} \left(\frac{1}{l_i}\right) \left(\frac{l_i}{L}\right) \log\left(\frac{1/l_i}{l_j/L}\right) \tag{12}$$

which reduces to

$$I = - \sum_{i,j=0}^{n+1} \left(\frac{1}{L}\right) \log\left(\frac{l_i l_j}{L}\right). \tag{13}$$

Eq. (13) thus defines the average gain in information regarding the occurrence of interspecific interactions or flows through the given food web, given that one has knowledge of the interactions that do occur. This can be contrasted to the case in which there is no knowledge of the nature of the interactions, and there is simply uncertainty or complexity associated with a given set of species (e.g. Ulanowicz, 1986).

Now consider predator compartment j and prey or resource compartment i . The economic extraction of a species from compartment j is ultimately made possible through flow from the set of compartments consisting of R to which compartment j is backward linked. The mutual information concerning the flow to compartment j given knowledge of the existence of the link with any one compartment i is

$$- \log\left(\frac{l_i l_j}{L}\right). \tag{14}$$

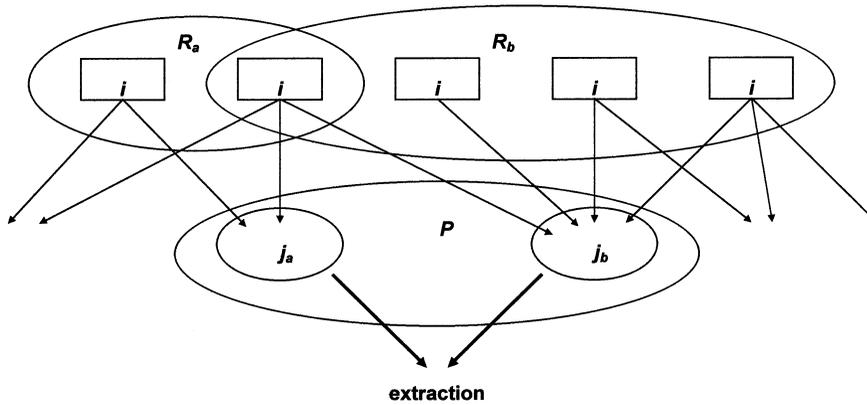


Fig. 2. Conceptual trophic interactions model. The sum of the number of all forward links from prey species i is represented by l_i . The sum of the number of all backward links from predator species j is represented by l_j . The set of all i species utilized by species j defines set R . For example, R_a is the set of all species i to which j_a is linked. The set of all j species extracted from the environment defines the set P .

One can then subsequently consider the mutual information for all pairs of compartments i and j linked, considering only the set of compartments consisting of P from which natural resources are extracted, with each compartment j within the set P having a unique set R of species which it utilizes as a resource. A conceptual example of this model is shown in Fig. 2.

In allowing the reduction of the average mutual information index to Eq. (13), however, we assumed no knowledge concerning the size of the network flows. The discussion so far similarly does not consider the magnitude of the economic extraction of the natural resource. In order to factor in the magnitude of this extraction, the total biomass (B) extracted in a given period is treated similarly to Ulanowicz (1980, 1986), Ulanowicz and Norden (1990) consideration of total system throughput. Thus, using Eq. (13), we arrive at the ICEV:

$$ICEV = -B \sum_{i,j} \left(\frac{1}{L_{ij}} \right) \log \left(\frac{l_i l_j}{L} \right) \quad (15)$$

where, L_{ij} , the total number of links between all i,j pairs considered, in which all i,j pairs are those linked within the food web structure for which compartment j is utilized or extracted as a natural resource (i.e. within set P).

To apply the index, it is necessary to develop a typology of functional species groups based on the variety of interactions with ecological processes. At the most disaggregated level, individual taxonomic species or ontogenetic stages within any one species may be distinguished as functional groups. More relevant for food web studies, however, trophic species are identified (Briand and Cohen, 1984; Pimm et al., 1991).

As a case study to illustrate application of the ICEV, the existence of surplus value within Jamaican artisanal mixed-species fisheries is investigated. Information regarding the food web structure and species composition of Caribbean coral reefs is widely scattered. Information specific to Jamaica is limited—some community composition information exists, but is focused on resolving patterns for sessile benthic species (e.g. Goreau, 1959; Goreau and Goreau, 1973; Liddell and Ohlhorst, 1981, 1987; Liddell et al., 1984). However, Opitz (1996) was able to construct a steady-state model for a generalized Caribbean coral reef ecosystem, in the process compiling a taxon interaction matrix based on assumed diet compositions derived from the numerous literature sources with an emphasis on fish species. Opitz (1996) used the comprehensive study of fish diets by Randall (1967) for the US Virgin Islands, supplemented with fish species listings provided in

Fischer (1978), as the ‘scaffold’ to develop the matrix which identified the fish taxa and key flora, invertebrate and vertebrate taxa on which they directly depend.

Trophic species were identified from the diet composition matrix presented in Opitz (1996). Before the analysis was applied, all non-zero interaction coefficients in the diet composition matrix were recoded to 1, thus recording predator–prey relationships as either ‘on’ or ‘off’. It was felt necessary to generalize the matrix in such a way because: (i) Opitz (1996) had to employ fairly rough estimation techniques to arrive at specific coefficient values, at times when only qualitative data were available regarding diet; and, (ii) the quantitative data for the matrix were based using information largely from Randall (1967) for the US Virgin Islands. It was not reasonable to maintain the precision of the interaction coefficients as presented in Opitz (1996) and apply the data to model present-day Jamaican coral reefs given the current lack of information regarding the food webs of Jamaican reefs or other regions of the Caribbean.

For five Jamaican coral reef-based artisanal fisheries (China net [gill net], trap, hand line, palanca [bottom set long-line], and speargun fishing), the capture of ecosystem function value as measured by the ICEV and the existence of surplus value were explored using data from 1996 catch and effort surveys conducted by the Fisheries Division (Ministry of Agriculture, Government of Jamaica, unpublished data). Individual survey samples were eliminated from the set if they failed to record the composition of individual catches by genus (at a minimum) and by weight. Non-fish species were ignored for the present analysis. Typical market prices are estimates of the mean price obtained for the year 1996 (Fisheries Division, Ministry of Agriculture, Government of Jamaica, unpublished data).

The technical coefficient associated with each fishery is represented as

$$a_{ij} = \frac{\text{ICEV}_{ij}}{V_j} \quad (16)$$

where, a_{ij} , technical coefficient defining the production relationship between the ecological com-

modity input i (ecosystem function value as measured by the ICEV) and the fishery j (Jamaican dollars); ICEV_{ij} , flow of ecological commodity input i to fishery j ; and V_j , market value of fishery j (Jamaican dollars).

For each finfish taxon represented in the catch and effort surveys, the market price for the year 1996 and the ICEV value (Eq. (15)) per kg, as well as the corresponding technical coefficient (Eq. (16)) associated with each individual taxon, was calculated. Subsequently, the technical coefficient (Eq. (16)) was calculated for all individual fishing efforts by fishing technology, considering the total ICEV and monetary value of each bundle of fishes. In order to explore whether or not fisheries using distinct technologies (i.e. China net, trap, hand line, palanca and speargun fishing) led to ecosystem function value as measured by the ICEV being equally valued by the market (i.e. is there surplus value?), a non-parametric Kruskal–Wallis (ANOVA by ranks) test was conducted to determine if the mean technical coefficient of individual fishing efforts within any one fishery was significantly different from any other fishery. We initially look simply for differences between the fisheries, lacking a strong a priori basis on which to justify a stronger directional test, and keeping in mind our primary goal of illustrating an application of the ICEV within the context of a production relationship defined by technical coefficients. All statistical procedures were conducted using SPSS® for Windows (Release 7.5.1, 1996) statistical software package.

3. Results

The identification of trophic species resulted in the reduction of the 250 original taxonomic groups as represented in the diet composition matrix of Opitz (1996) to 246 groups. Only four pairs of species of fishes shared both the same set of predators and prey as recorded in the matrix: (i) *Diodon holocanthus* (long-spine porcupinefish) and *D. hystrix* (spot-fin porcupinefish) from the family Diodontidae; (ii) *Grama loreto* (royal gramma) and *G. melacara* (blackcap

basslet) from the family Grammitidae; (iii) *Kyphosus incisor* (yellow sea chub) and *K. sectatrix* (Bermuda sea chub) from the family Kyphosidae; and, (iv) *Pomacanthus arcuatus* (grey angelfish) and *P. paru* (French angelfish) from the family Pomacanthidae. All other trophic species are as listed in Opitz (1996). For the complete trophic interaction matrix, the total number of links in the community (L) was 3317.

For each of the five coral reef-based fisheries technologies examined in this investigation, summary statistics of the values of the technical coefficients calculated using the results of individual fishing efforts are shown in Table 1. The results of the non-parametric Kruskal–Wallis (ANOVA by ranks) test were highly significant ($\chi^2 = 106$, $df = 4$, $P < 0.001$), indicating that fisheries based in different technologies capture different levels of ecosystem function value per dollar of catch. In other words, surplus value is created. This surplus value is rooted in the observation that certain fisheries themselves rely on species representing the capture of a greater or lesser amount of ecosystem information value—in other words, fishing species which are more or less connected within the food web than is the case with other fishing technologies, and these differences not being reflected in market prices. This interpretation is supported by an analysis of the average mutual information associated with individual species captured by each fishery (Kruskal–Wallis test, $\chi^2 = 80$, $df = 4$, $P < 0.001$), indicating that the captured ecosystem value is fundamentally different among fisheries utilizing different technologies.

4. Discussion

It is evident that Jamaican artisanal coral reef fisheries based in the use of distinct technologies capture ecosystem information values that are not, to the same extent, proportionately reflected in the market values obtained for the catch. Certain fisheries appear to exploit species that are directly and indirectly more intimately connected within the coral reef food web as measured by the ICEV, and thus rely on the capture of greater ecosystem function value for each unit of monetary value as measured by the market. Further detail regarding these patterns will require subsequent analyses, likely requiring an expanded dataset with improved representation by certain technologies (Table 1).

This study was primarily interested in deriving and exploring the application of an alternative theory of value which can be applied to the extraction of a renewable natural resource. This analysis demonstrates that if one considers biophysical values (i.e. the biophysical contribution of the coral reef ecosystem to fisheries production), distortions between market values and supply-side values become evident. What does this creation of surplus value mean? In effect, we are not valuing the ecosystem contributions to the creation of final products to the same extent within a given sector, or perhaps between sectors of the economy. We are not consistently considering ecosystem function values. But interpretations necessarily become more complicated as we examine differences across markets and over time because of changes in ecosystem functions and market supply and demand conditions. This is rightfully the subject of further research.

Table 1

Summary statistics for technical coefficients ($J\$^{-1}$) associated with China net, trap, hand line, palanca and speargun fishing in Jamaica for the year 1996

Fishery	n	Mean value	S.D.	Minimum value	Maximum value
China net	47	0.00698	0.00104	0.00529	0.01088
Trap	279	0.00887	0.00190	0.00407	0.01659
Hand line	31	0.00683	0.00137	0.00507	0.01027
Palanca	16	0.00632	0.000796	0.00464	0.00791
Speargun	20	0.00771	0.00220	0.00543	0.01511
Total	393	0.00832	0.00197	0.00407	0.01659

The theoretical development and use of indicators and indices is still very much an art rather than a hard science, with much room left for future developments and improvements. The remainder of this discussion will be devoted to providing comment and direction with that in mind.

4.1. *Future directions for index development*

The food web model used for the derivation of the ICEV is static. It does not consider or accommodate dynamic changes to the structure or functioning of the ecosystem that may occur through either human-induced or natural influences. It may indeed be possible to modify the structure of the ICEV or the method of its calculation to accommodate food web dynamics, yet to do so would require a level of scientific knowledge concerning the ecosystems in question that may not be currently sufficient.

In addition to not accounting for ecosystem dynamics, the methodology applied in this analysis did not make any explicit distinctions between the ways in which the functioning of ecosystems of different 'types' may systematically vary. In other words, it would be useful to explore the application and behavior of the ICEV as calculated for the extraction of a renewable natural resource from different ecosystems as represented by distinct food webs.

A pronounced shortcoming of the present analysis is the inability to take into account thresholds or criticality. Questions concerning the appropriate level of exploitation for sustainable use have dominated natural resource economics and biological studies of exploited populations; however, the question before us was not the level of exploitation possible or the fate of the exploited populations, but measuring the contribution to the value of the economic product. However, it may indeed be fruitful to explore the incorporation of bioeconomic principles directly into the construction and use of an index of ecosystem function.

Meredith et al. (1994) discuss thresholds of environmental criticality as both an objective construct, as is the case concerning biophysically and

economically defined standards, and a subjective construct, which may often be the case concerning socially defined standards. They emphasize the possibility of 'multiple anthropocentric assessment perspectives' as determined by the particular set of personal values. The ICEV was more objectively defined based on ecological and economic principles. However, the selection and definition of the indicator necessarily involved a value judgment concerning what was to be measured. Broadening the indicator to consider criticalities will increase the subjective content inherent in the indicator construction and use simply because the dimensionality of the indicator will be increased, requiring further value judgments to be made, often where there is a lack of scientific evidence to which one can appeal. This will not compromise the validity of the indicator per se, but will require prudent documentation and justification for the values selected.

It would also be potentially fruitful to explore the junctions between an ecosystem-based application of information theory, as done in this study, and economic information theory models. Inadequate information and risk as introduced into economic decision-making models is through consideration of either endogenously modeled market uncertainties or exogenously modeled event uncertainties (e.g. Hirshleifer and Riley, 1979, 1992). The economics of information, as relevant here, involves the process of individual economic agents attempting to gain information regarding exogenous event uncertainties in order to assist in the decision-making process. The ICEV represents a gain in information regarding the contribution of a natural ecosystem to productive value and, in essence, reduces uncertainty regarding the role of ecosystems in the economic production process (a role that is normally exogenous to neo-classical economic production models). As a more specific example of how information economics may potentially be applied, there is a significant body of work examining the effect of asymmetric information between principles and agents in the formation of contractual relationships (e.g. Feltham et al., 1988; Macho-Stadler and Pérez-Castrillo, 1997). As a specific issue of moral hazard (a gain in informa-

tion by one party after the establishment of the contract between fishers and management authorities) or adverse selection (private information held by one of the contracting bodies), the ICEV or other aspects of ecosystem information theory may be able to be applied to economic asymmetric information models as represented by conflicting objectives through knowledge gained concerning the value of ecosystem function. It would be interesting to formally pursue this information-adding angle as it relates to existing economic information theory and decision-making.

4.2. *General issues concerning food web statistics*

The ICEV requires information regarding the structure of the food web of interest, and as such is effectively a food web statistic. There are caveats and limitations associated with food web statistics, primarily stemming from the limitations of the food webs descriptions themselves. As stated by Lawton (1989), “In Pimm’s words (1982), most published webs are, therefore, ‘caricatures of nature’. My dictionary defines caricature as a representation exaggerated for comic effect, or a ludicrously inadequate or inaccurate imitation! This is a fair assessment of most of the published information on food webs.”

There has been much debate surrounding the calculation and use of food web statistics, particularly concerning connectance (e.g. Paine, 1988; Peters, 1988; Lawton, 1989; Pimm et al., 1991; Hall and Raffaelli, 1993). The calculation of the ICEV and food web connectance both rely on a description of the links between trophic species, and as such are inherently related. The critical debate concerning the calculation and use of information theory indices to describe network flows as it relates to many of the issues raised in the debate concerning the use of food web statistics has yet to develop in the literature.

4.3. *General considerations for index development for use in decision-making*

Biological indices have been developed with the primary purpose of being used as tools for scientific description and inquiry. However, use has

been extended within the arenas of government and management to help fulfill the need for ecosystem information relevant for broader matters of ecosystem management, policy and regulation. What may often be underappreciated, however, is that such use may not be appropriate given the theoretical underpinnings and design of the specific indicator or index employed.

A useful index must be developed with a specific purpose in mind. Such purpose is reflected in the range of indicator characteristics and properties, and the derived index implicitly restricts the set of appropriate applications. But generally what are the properties of a good indicator or index? What are the potential uses one should consider and how should these impact the indicator design?

The properties of a ‘good’ indicator for use in policy development and decision-making regarding the environmental management of multi-dimensional, complex systems include:

- the indicator design corresponds to the selected purpose and application;
- the value base behind the indicator is explicit;
- the indicator provides a sufficient simplification or abstraction of the system characteristics;
- the theory behind the design of the indicator is relatively robust;
- the sensitivity of the indicator to system changes has been sufficiently explored and defined, and the indicator is sufficiently sensitive to meet the design purpose; and,
- The information provided by the indicator can be understood and applied by the user.

Most indicators or indices cannot be expected to meet all of the above criteria; however, it remains the goal of indicator development to satisfy as many as is possible given shortcomings of the level of available scientific knowledge, logistical restrictions and the demanding needs of the users. It is asserted that the ICEV meets many of the criteria of a ‘good’ indicator, with the one notable exception that the sensitivity and behavior of the index to parameter changes remains to be explored further.

This present study was confronted with severe data restrictions, given our overall limited knowledge of the functioning, structure and dynamics of

most of the world's ecosystems. This can be expected to be the norm for some time to come, yet management decisions and government policy is significantly affecting how and in what ways humans are currently interacting with the environment. Science needs to begin to move closer to operational means to evaluate impacts and analyze the trade-offs involved. The ICEV is presented as one possible tool.

Acknowledgements

Sandra Grant (Data Manager/Analyst) and Andre Kong (Director) of the Fisheries Division (Ministry of Agriculture, Government of Jamaica) kindly provided access to unpublished government data for Jamaican artisanal fisheries from their Catch and Effort Data Collection Programme. Comments from anonymous reviewers were greatly appreciated and improved earlier drafts. The authors take full responsibility for the content of this paper.

References

- Bengtsson, J., Jones, H., Setälä, H., 1997. The value of biodiversity. *Trends in Ecology and Evolution* 12, 334–335.
- Bingham, G., Bishop, R., Brody, M., Bromley, D., Clark, E., Cooper, W., Costanza, R., Hale, T., Hayden, G., Kellert, S., Norgaard, R., Norton, B., Payne, J., Russell, C., Suter, G., 1995. Issues in ecosystem valuation: improving information for decision making. *Ecological Economics* 14, 73–90.
- Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. *Nature* 307, 264–267.
- Christensen, V., Pauly, D., 1992. *ECOPATH II*—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61, 169–185.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- DeAngelis, D.L., 1980. Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* 61, 764–771.
- de Groot, R.S., 1994. Environmental functions and the economic value of natural ecosystems. In: Jansson, A.M., Hammer, M., Folke, C., Costanza, R. (Eds.), *Investing in Natural Capital: The Ecological Economics Approach to Sustainability*. Island Press, Washington DC, pp. 151–168.
- di Castri, F., Younés, T., 1990. Ecosystem function of biological diversity. *Biology International, Special Issue* 22, 20 pp.
- Ehrlich, P.R., Ehrlich, A.H., 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York.
- Feltham, G.A., Amershi, A.A., Ziemba, W.T., 1988. *Economic Analysis of Information and Contracts*. Kluwer Academic Publishers, Boston.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56, 363–380.
- Fischer, W. (Ed.), 1978. *FAO Species Identification Sheets for Fishery Purposes: Western Central Atlantic (Fishing Area 31)*, vols. I–VII. Food and Agriculture Organisation of the United Nations, Rome.
- Folke, C., Hammer, M., Costanza, R., Jansson, A.M., 1994. Investing in natural capital—why, what, and how. In: Jansson, A.M., Hammer, M., Folke, C., Costanza, R. (Eds.), *Investing in Natural Capital: The Ecological Economics Approach to Sustainability*. Island Press, Washington DC, pp. 1–12.
- Friend, A., Rapport, D., 1991. Evolution of macro-information systems for sustainable development. *Ecological Economics* 3, 59–76.
- Goreau, T.F., 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. *Ecology* 40, 67–90.
- Goreau, T.F., Goreau, N.I., 1973. The ecology of Jamaican coral reefs II. Geomorphology, zonation, and sedimentary phases. *Bulletin of Marine Science* 23, 399–464.
- Grassle, J.F., Lassere, P., McIntyre, A.D., Ray, G.C., 1991. Marine biodiversity and ecosystem function. *Biology International, Special Issue* 23, 19 pp.
- Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334.
- Hall, S.L., Raffaelli, D.G., 1993. Food webs: theory and reality. *Advances in Ecological Research* 24, 187–239.
- Hannon, B., 1973. The structure of ecosystems. *Journal of Theoretical Biology* 41, 535–546.
- Hirata, H., Ulanowicz, R.E., 1984. Information theoretical analysis of ecological networks. *International Journal of Systems Science* 15, 261–270.
- Hirshleifer, J., Riley, J.G., 1979. The analytics of uncertainty and information—an expository survey. *Journal of Economic Literature* 17, 1375–1421.
- Hirshleifer, J., Riley, J.G., 1992. *The Analytics of Uncertainty and Information*. Cambridge University Press, Cambridge.
- Holling, C.S., 1992. Cross-scale morphology: geometry and dynamics of ecosystems. *Ecological Monographs* 62, 447–502.
- Holling, C.S., Schindler, D.W., Walker, B.W., Roughgarden, J., 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings, C., Mäler, K.-G., Folke, C., Holling, C.S., Jansson, B.-O. (Eds.), *Biodiversity Loss: Economic and Ecological Issues*. Cambridge University Press, Cambridge, pp. 44–83.

- Isard, W., 1969. Some notes on the linkage of the ecologic and economic systems. *Papers. Regional Science Association* 22, 85–96.
- Isard, W., 1972. *Ecologic–Economic Analysis for Regional Development*. The Free Press, New York.
- Ives, A.R., 1995. Measuring resilience in stochastic systems. *Ecological Monographs* 65, 217–233.
- Kullback, S., 1968. *Information Theory and Statistics*. Dover Publications, New York.
- Lamont, B.B., 1995. Testing the effect of ecosystem composition/structure on its functioning. *Oikos* 74, 283–295.
- Lawton, J.H., 1989. Food webs. In: Cherrett, J.M. (Ed.), *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World*. Blackwell Scientific Publications, Oxford, pp. 43–78.
- Lawton, J.H., Brown, V.K., 1993. Functional redundancy. In: Schulze, E.D., Mooney, H.A. (Eds.), *Biodiversity and Ecosystem Function*. Springer, Berlin, pp. 255–270.
- Liddell, W.D., Ohlhorst, S.L., 1981. Geomorphology and community composition of two adjacent reef areas, Discovery Bay, Jamaica. *Journal of Marine Research* 39, 791–804.
- Liddell, W.D., Ohlhorst, S.L., 1987. Patterns of reef community structure, north Jamaica. *Bulletin of Marine Science* 40, 311–329.
- Liddell, W.D., Ohlhorst, S.L., Boss, S.K., 1984. Community patterns on the Jamaican fore reef (15–56 m). *Palaeontographica Americana* 54, 385–389.
- Ludwig, D., Walker, B., Holling, C.S., 1997. Sustainability, stability, and resilience. *Conservation Ecology*, 1. <http://www.consecol.org/vol1/iss1/art7>.
- MacArthur, R., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36, 533–536.
- Macho-Stadler, I., Pérez-Castrillo, J.D., 1997. *An Introduction to the Economics of Information: Incentives and Contracts*. Oxford University Press, New York.
- Martinez, N.D., 1996. Defining and measuring functional aspects of biodiversity. In: Gaston, K.J. (Ed.), *Biodiversity: A Biology of Numbers and Difference*. Blackwell Science, Oxford, pp. 114–148.
- May, R.M., 1972. Will a large complex system be stable. *Nature* 238, 413–414.
- May, R.M., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- May, R.M., 1975. Stability in ecosystems: some comments. In: van Dobben, V.H., Lowe-McConnell, R.H. (Eds.), *Unifying Concepts in Ecology*. Dr W. Junk B.V. Publishers, The Hague, pp. 161–168.
- Miller, R., Blair, P., 1985. *Input–Output Analysis: Foundations and Extensions*. Prentice Hall, Englewood Cliffs.
- Meredith, T.C., Moore, C., Gartner, L., Smith, W., 1994. *Canadian Critical Environmental Zones: Concepts, Goals and Resources*. A report of the Critical Zones Panel of the Canadian Global Change Program. Canadian Global Change Program Technical Report Series Report 94-1. The Canadian Global Change Program Secretariat, The Royal Society of Canada, Ottawa.
- Myers, N., 1996. Environmental services of biodiversity. *Proceedings of the National Academy of Science (USA)* 93, 2764–2769.
- Neubert, M.G., Caswell, H., 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* 78, 653–665.
- Opitz, S., 1996. *Trophic Interactions in Caribbean Coral Reefs*. International Centre for Living Aquatic Resource Management, Manila.
- Pahl-Wostl, C., 1995. *The Dynamic Nature of Ecosystems: Chaos and Order Entwined*. Wiley, Toronto.
- Paine, R.T., 1988. Food webs: road maps of interactions or grist for theoretical development. *Ecology* 69, 1648–1654.
- Peters, R.H., 1988. Some general problems for ecology illustrated by food web theory. *Ecology* 69, 1673–1676.
- Pimm, S.L., 1982. *Food Webs*. Chapman and Hall, London.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food web patterns and their consequences. *Nature* 350, 669–674.
- Randall, J.E., 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5, 665–847.
- Rutledge, R.W., Basore, B.L., Mulholland, R.J., 1976. Ecological stability: an information theory viewpoint. *Journal of Theoretical Biology* 57, 355–371.
- Schulze, E.D., Mooney, H.A. (Eds.), 1994. *Biodiversity and Ecosystem Function*. Springer, Berlin.
- Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. *Journal of Theoretical Biology* 85, 223–245.
- Ulanowicz, R.E., 1986. *Growth and Development: Ecosystem Phenomenology*. Springer, New York.
- Ulanowicz, R.E., 1991. Contributory values of ecosystem resources. In: Costanza, R. (Ed.), *Ecological Economics: The Science and Management of Sustainability*. Columbia University Press, New York, pp. 253–268.
- Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overhead in flow networks. *International Journal of Systems Science* 21, 429–437.
- Yodzis, P., 1989. *Introduction to Theoretical Ecology*. Harper and Row, New York.