

Ecological Network Analysis Metrics:

The need for an entire ecosystem approach in management and policy

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27 **Abstract**

28 **In this paper, we identified seven ecological network analysis (ENA) metrics that, in our**
29 **opinion, have high potential to provide useful and practical information for**
30 **environmental decision-makers and stakeholders. Measurement and quantification of the**
31 **network indicators requires that an ecosystem level assessment is implemented. The ENA**
32 **metrics convey the status of the ecological system state variables, and mostly, the flows**
33 **and relations between the various nodes of the network. The seven metrics are: 1)**
34 **Average Path Length (APL), 2) Finn Cycling Index (FCI), 3) Mean Trophic level (MTL),**
35 **4) Detritivory to Herbivory ratio (D:H), 5) Keystoneness, 6) Structural Information (SI),**
36 **and 7) Flow-based Information indices. The procedure for calculating each metric is**
37 **detailed along with a short evaluation of their potential assessment of environmental**
38 **status.**

39

40 **Keywords: Ecological Network Analysis; Cycling; Trophic Length; Marine and Coastal**
41 **Environment; Food web**

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43 **1.0 Introduction**

44 Ecological network modeling and analysis is used to characterize and compare the organization
45 and functioning of ecosystems, and it is most often applied to study food webs (Ulanowicz
46 1986, Baird and Ulanowicz 1993, Fath and Patten 1999, Borrett et al. 2018). A strength of
47 Ecological Network Analysis (ENA) is the generation of multiple whole-network metrics that
48 may be useful for food web assessment and management (Niquil et al. 2012, Tomczack et al.
49 2013, Heymans et al. 2016, Heymans and Tomczack 2016, Lau et al. 2017, de Jonge et al.
50 2012, accepted). The Schleswig-Holstein Agency for Coastal Defence, National Park and
51 Marine Conservation and the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und
52 Meeresforschung Wattenmeerstation hosted a workshop on ENA from 25–27 September 2017
53 on the barrier Island of Sylt between the North Sea and the Wadden Sea. The focus of the
54 workshop was to determine how to reach a broader audience, specifically environmental
55 managers and decision-makers, with network tools and perspectives.

56 To reach this broader audience, it was evident that the managers must be amenable and
57 receptive to the ‘ecosystem approach’. We also recognized that because it is holistic and
58 comprehensive it requires an expensive and elaborate data gathering approach, which may or
59 may not have already been part of the standard monitoring. Therefore, if only quick and crude
60 answers are solicited for individual species or interactions, perhaps this is not the best approach.
61 However, history shows that fragmented solutions from reductionistic approaches that do not
62 take ecosystem effects into account tend to spawn numerous unpleasant and unintended
63 consequences (e.g., fossil fuels as energy source led to climate change, fertilizers for agriculture
64 led to eutrophication, CFC as a refrigerant led to ozone depletion, etc.). The benefits of an
65 ecosystem approach are further considered here, and we take for granted that managers
66 appreciate the advantages of such comprehensive approaches as they facilitate understanding
67 of ecosystem function. Therefore, management aims toward viable ecosystems and the
68 sustainability of ecosystem services. However, such approaches are not always easy to
69 understand or implement in management (Helsenfeld and Enserink 2008), and this prompted
70 the authors to provide information on how to use a network approach for this purpose.

71 The field of ecosystem service indicators is well developing (e.g., Layke et al. 2012, Vo et al.
72 2012, van Oudenhoven et al. 2018), partially due to their prominence in the Millennium
73 Ecosystem Assessments (MEA 2005, Acosta et al. 2016). The provisioning of such services
74 depends on functioning ecosystems, and this functionality may be indicated and explained
75 through ecosystem network metrics. Biotic and abiotic ecosystem parts, their interlinkages and
76 connectivity to other ecosystems provide the information to calculate numerous metrics, which
77 have been broadly described in the literature in terms of their descriptive capacity of ecosystem
78 functioning, health, development, or state in general. The applicability of these metrics to
79 characterize ecosystems is underpinned by theory (e.g., Odum 1969, Patten 1978, Ulanowicz
80 1986). However, to facilitate their incorporation into management, they need to fulfill certain
81 criteria to become robust indicators. This includes sensitivity to change, having a sound
82 theoretical basis, describing directional change, being easily communicable to managers and
83 policy makers, and being integrative and indicative to a known response to a disturbance (Dale
84 and Beyeler 2001).

85 The workshop was structured around framing presentations about the current state of ecological
86 network analysis in marine systems. These were followed by break-out sessions to brainstorm
87 on specific network indicators and to select the most useful and appropriate for application in
88 marine ecosystem management. We first started with a long, but not exhaustive, list of network

89 indicators (Table 1, for a more comprehensive list of network indicators see Borrett and Lau
 90 2014 or Kazanci and Ma 2015). From this break-out session emerged a short list of 7 network
 91 indicators (Table 2) that all build on the basic properties of ecosystem networks such as flow,
 92 connections, throughflow, and biomass. Another plenary session was used to discuss in depth
 93 the definition and meaning of these indicators specifically as though they would be
 94 communicated to a decision-maker. That session was organized around the following question:

95 *“The objective of this discussion is to put ENA in a management perspective and to discuss*
 96 *how, and if, (selected) ecosystem indices provide insight into ecosystem functioning and*
 97 *ecosystem services, which are collectively a function of complex interactions among species*
 98 *and their abiotic environment. Is it possible to identify an index, or a suite of indices, useful*
 99 *for management purposes? This follows from the broader question: Can the indices be*
 100 *operationalized? In other words, are the metrics responsive enough to serve as indicators of*
 101 *change and thereby inform decision-makers how to better manage their systems?”*

102 Table 1. Step one. List of network properties that emerged from workshop brainstorming
 103 session

- Number of compartments (n)
- Connectance (%)
- Mean Node degree, In degree, Out degree
- Average Path Length (APL)
- Finn Cycling Index (FCI)
- Mean Trophic Level (MTL)
- Relative Ascendency (ASC)
- Relative Overhead (Φ)
- Robustness
- Relative Redundancy (R)
- Total Systems Throughflow (TST _{flow}) and Total System Throughput (TST _{put})
- Indirect/direct relationships
- Network homogenization
- Network aggradation
- Mutualism and Synergism ratios
- Keystoneness
- Structural Information (SI)

- Flow Diversity
- Detritivory/Herbivory ratio (D:H)

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Table 2. Step two. Refined list of network indicators as having most relevance and importance for decision makers implementing an ecosystem approach, with primary reference for each – see below for more detail on each metric.

1. Average Path Length (APL)	Finn 1976
2. Finn Cycling Index (FCI)	Finn 1980
3. Mean Trophic Level (MTL)	Pauly et al. 1998
4. Detritivory Herbivory ratio (D:H)	Ulanowicz and Kay 1991
5. Keystoneness	Libralato et al. 2005
6. Structural Information (SI)	Ludovisi 2009
7. Flow-based Information indices	Ulanowicz et al. 2009

108

109 This paper is a summary of those results. The first section is an overview of the network
110 mathematics used later in the paper. This is followed by a description and application of each
111 of the indicators in the management sphere, ending with a discussion of the application of each
112 metric for environmental management, specifically, ocean and coastal management.

113

114 **2.0 Background to networks:**

115 Every system of compartments and connections can be realized as a network of nodes and arcs.
116 There are numerous papers providing an overview to the network methods described herein.
117 We refer the reader to Ulanowicz (1986), Fath and Patten (1999), and Fath et al. (2007). A
118 brief overview is given here to provide a common notation for discussion within this paper.
119 Consider a network with n compartments or nodes, which can be represented as x_i , for $i=1$ to
120 n . The flow or transaction of the energy–matter substance moving from node i to node j is
121 given by f_{ij} and can be arranged into a matrix \mathbf{F} containing all pairwise flows in the network¹.

¹ In some of the literature the flows are arranged from node j to node i for ecological reasons

122 In addition, these ecological or environmental systems are open to receive new input and thus
 123 generate also new output. Such flows that cross the system boundary are labelled z_i and y_i , for
 124 $i=1$ to n , respectively. In some ecosystem studies, y_i is divided into export (e_i) and respiration
 125 (r_i) flows because the former is usable material outside the system, whereas the latter is heat
 126 lost which is unable to do further work. Knowing the total amount of material or energy
 127 moving through each node and the entire network is an important indicator of the scale of
 128 activity within that system. From the flow matrix and input/outputs, we can find this total
 129 activity going through any node as either the sum of all the flows into the node or all the flows
 130 out of the node.

$$131 \quad T_i^{in} = z_i + \sum_{j=1}^n f_{ji} \quad (1)$$

$$132 \quad T_i^{out} = y_i + \sum_{j=1}^n f_{ij} \quad (2)$$

133 At steady state,

$$134 \quad T_i^{in} = T_i^{out} = T_i \quad (3)$$

135 The Total System Throughflow (TST_{flow}) is the sum of all the individual nodal flows, given
 136 by:

$$137 \quad TST_{flow} = \sum_{i=1}^n T_i \quad (4)$$

138 This differs from the measure of Total System Throughput (TST_{put}) which is the sum of all
 139 nodal inflows and outflows, including the boundary flows (or sum inputs):

$$140 \quad TST_{put} = \sum_{j=1}^n z_j + \sum_{i=1}^n \sum_{j=1}^n f_{ij} + \sum_{i=1}^n y_i \quad (5)$$

141 The main difference is that TST_{put} includes *both* the input and output plus the internal flows,
 142 whereas TST_{flow} is the sum of all the inflows *or* the sum of all the outflows (this avoids double
 143 counting the same flow as inflows and also as outflows). One advantage of the TST_{put} approach
 144 is that it is not required for the system to be in steady state to calculate it (but see also de Jonge
 145 et al. accepted A who demonstrate that balancing of the flows of living and non-living
 146 compartments or nodes is always preferred). Note that by definition $TST_{put} \geq TST_{flow}$.

147 As stated above, node throughflow (T_i) is the contribution of each node to the system activity.
 148 When the network model represents a food web, T_i is equivalent to the gross production of the
 149 node (Ulanowicz and Puccia 1990), and when the model currency is energy, T_i has been

150 interpreted as the node power in thermodynamic terms (Patten 1995). Further, it can be used
 151 as a global centrality metric that indicates the relative importance of each node in a system
 152 (Borrett 2013). TST_{flow} and TST_{put} are then network-level indicators of the size and activity of
 153 the system, and depending on the model specifics they indicate the amount of production or
 154 power the system contains (Finn 1976; Ulanowicz and Norden 1990).

155 The flows in the Flow matrix (\mathbf{F}) capture the direct transactions, but network analysis can be
 156 used to determine indirect flow paths and influences as well. Indirect impacts refers to flows
 157 between nodes that are not in direct exchange but that influence each other through paths of
 158 length 2 or greater. The matrix algebra of network analysis allows us to calculate these indirect
 159 contributions, accordingly when the network is at steady state. First, we calculate a non-
 160 dimensional, output oriented flow intensity matrix designated by \mathbf{B} , where $b_{ij}=f_{ij}/T_i$. A
 161 complementary input-oriented non-dimensionalized flow matrix can also be constructed,
 162 where $b'_{ij}=f_{ij}/T_j$. Ecological Network Analysis (ENA, see Fath and Patten 1999) tells us that
 163 taking powers of this matrix gives the flow intensities along path lengths commensurate with
 164 the power, i.e., \mathbf{B}^2 are two-step pathways, \mathbf{B}^3 three-step, etc. Another important discovery of
 165 ENA is that it is possible to simultaneously consider *all* powers in one term by summing the
 166 infinite series which converges to a composite matrix, we call, \mathbf{N} , such that

$$167 \quad N = \sum_{m=0}^{\infty} B^m = B^0 + B^1 + B^2 + B^3 + B^4 + \dots \quad (6)$$

168 The \mathbf{N} matrix is termed the integral flow matrix because it sums or integrates the flow along
 169 the direct and *all* indirect pathways. Due to the open and dissipative thermodynamic nature of
 170 ecosystems and food webs, the infinite series in eq (6) converges. The exact value of this
 171 convergent infinite series is given by the identity in eq (7), which highlights the similarity of
 172 the \mathbf{N} matrix to the Leontief inverse in economic input-output analysis (Hannon 1973).

$$173 \quad N = \sum_{m=0}^{\infty} B^m = (I - B)^{-1} \quad (7)$$

174 These basic network building blocks identifying direct and indirect pathways are used to
 175 develop the specific network metrics described below.

176

177 **3.0 Network Metrics**

178 3.1 Average Path Length

179 Average Path Length (APL) is defined as the total system throughflow divided by the total
180 boundary input into the system (Finn 1976):

$$181 \quad APL = \frac{TST_{flow}}{\sum_{i=1}^n z_i} \quad (8)$$

182 In Finn's original interpretation (1976), this is the average number of paths a given unit of input
183 (often carbon) will travel in the system before exiting the system. More generally, it is an
184 indicator of the amount of system activity (TST_{flow}) generated by each unit input into the
185 system. Since cycling contributes to overall system flow, a higher degree of cycling equates
186 to a larger APL. Thus, it is an indicator of the organization of the system and the system's
187 ability to do more work with given resources (the boundary input). This is why Jørgensen et
188 al. (2000) interpreted it as an indicator of system growth and development, which they renamed
189 network aggradation.

190

191 *3.1.1 Relevance for stakeholders*

192 Assuming that most resource flows are scarce, the more impact each unit of boundary flow has
193 within a system, the more the system will benefit. APL is easy to measure and calculate. It is
194 intuitively easy to understand and communicate the meaning to others. For example, in
195 ecological terms the indicator shows that the higher the boundary flows are, the more external
196 carbon is available for an ecosystem. In this situation, APL will be lower when the internal
197 TST_{flow} remains stable. In contrast, if the internal TST_{flow} increases when the boundary inputs
198 stay the same, then the system organization has developed in a way to make more or better use
199 of the initial resource input. In economic terms, this is conceptually similar to the multiplier
200 effect, which is a measure of how many times a unit of currency that enters into a market will
201 be exchanged before exiting that market. The market boundaries are akin to the network system
202 boundaries. High multiplier values indicate healthy levels of cross-scale circulation and a
203 robust internal economy. APL is expected to be higher in systems with higher diversity of flows
204 and cycling (Christensen 1995) and decrease in the face of stress as found by Tecchio et al.
205 (2015) and Schückel et al. (2015). In ecosystems, a higher APL value does not necessarily
206 indicate health, but the ability to generate flows within the system per a given boundary input.
207 Changes in this relation may indicate increased or decreased boundary flows, or changes in the
208 flow structure of the system, or both.

209

210 3.2 The Finn Cycling Index

211 Finn (1976, 1980) proposed a method to calculate precisely the fraction of the total system
212 throughflow (TST_{flow}) that is cycled in the network, in other words, how much of the flow
213 would revisit the same node multiple times before exiting the system. Cycled flow of node i
214 ($TSTc_i$) can be calculated by the following formulation:

$$215 \quad TSTc_i = ((n_{ii} - 1)/n_{ii})T_i \quad (9)$$

216 Finn Cycling Index can be calculated by the total cycling throughflow divided by total system
217 throughflow:

$$218 \quad FCI = \frac{\sum TSTc_i}{TST_{flow}} \quad (10)$$

219

220 3.2.1 Relevance for stakeholders

221 Cycling is tied to the average path length (APL) because greater cycling is one mechanism to
222 increase TST without increasing boundary inputs. Increased cycling means that the energy or
223 material stays in the system longer. For resources that have a positive impact on the system,
224 cycling indicates that the internal flow organization allows for some degree of self-reliance
225 (Ulanowicz 1983). Other cases show a stressed system also exhibits higher levels of cycling
226 (Scharler and Baird 2005, Tecchio et al. 2015). Systems with a low FCI but high throughflow
227 are dependent on boundary flows to sustain a high level of throughflow (e.g., agricultural
228 systems, systems that receive lots of waste (POC and DOC) such as Dollard in de Jonge et al.
229 accepted and de Jonge and Schückel, submitted to OCMA). Flows across the system boundary,
230 in addition to the inner system structure, are therefore important determinants of whether
231 changes in FCI are within a natural variability (stochastic impact of diurnal, seasonal, or
232 ecological parameters), or may indicate a change in system state. Although the property is
233 dimensionless, some researchers urge caution when comparing FCI across systems (Heymans
234 et al. 2014) because the chosen degree of aggregation of cycling during the network
235 construction process influences the extent of the cycling.

236

237 3.3 Mean Trophic Level (MTL), Mean Trophic Level of the Catch (MTLC)

238 The trophic level of an organism is the average position it occupies in a food chain. Food
 239 chains start at trophic level 1 with primary producers such as plants, move to herbivores at level
 240 2, and predators at level 3 and typically finish with carnivores or apex predators at level 4 or 5.
 241 The path along the chain can form a one-way food “flow” (chain), or a food "web." Highly
 242 evolved and unstressed systems often have higher abundances and biomasses of high trophic
 243 level species. Most ecosystems feature considerable levels of omnivory, where omnivores feed
 244 on different trophic levels and therefore occupy themselves a trophic level somewhere in
 245 between (Raoux et al. in press). The trophic level, TL, for any consumer species (i) is calculated
 246 as:

$$247 \quad TL_i = 1 + \sum_j (TL_j * DC_{ij}) \quad (11)$$

248 where, TL_j is the fractional trophic level of the prey j, and DC_{ij} represents the fraction of j in
 249 the diet of i.

250 The *Mean Trophic Level* of a system is calculated from the trophic positions of each system
 251 compartment and its relative contribution to the system biomass:

$$252 \quad MTL = \frac{\sum_i (B_i * TL_i)}{\sum_i B_i} \quad (12)$$

253 where B_i and TL_i are the biomasses and trophic levels of each of the contributing groups (i) of
 254 the system (Branch et al 2010, Shannon et al. 2014).

255 While we recommend the use of MTL as a holistic indicator of the ecosystem functioning, the
 256 mean trophic level is often difficult to estimate. It is often easier to calculate the *Mean Trophic*
 257 *Level of the Catch*, which is usually comprised of some species only, for which the landed
 258 biomass is, moreover, easily determined. For its calculation the yield replaces the biomass in
 259 the above formula:

$$260 \quad MTLC = \frac{\sum_i (Y_i * TL_i)}{\sum_i Y_i} \quad (13)$$

261 and Y_i and TL_i are the yields and trophic levels of the species that comprise the catches.
 262 Furthermore, the indicator is sensitive to the way the ecosystem is partitioned into functional
 263 groups (i.e., model topology), therefore the field will benefit with common and good standards
 264 in network creation (see e.g., Fath et al. 2007).

265 *3.3.1 Relevance for stakeholders*

266 This index is often (see, e.g., Pauly et al. 1998) used in the assessment of sustainability in
267 fisheries as its decrease over time this is considered to reflect the phenomenon of “fishing down
268 the food web”, since fishing pressure depletes top-predators more severely than low-trophic
269 level species. This concept, which assumes that the catch composition reflects general trends
270 in the considered ecosystem, has been adopted by the Convention of Biological Diversity
271 (CBD) to be “ready for global use” (BDI partnership 2010). However, factors that determine
272 the trophic composition of landings are complex and it may well be that a simple catch increase
273 in low-trophic level species leads to lower MTLC values, while the top predator populations
274 may still be doing well (see Essington et al. 2006). MTL estimates derived from sound
275 ecosystem surveys may provide a good picture of the ecosystem state. In this case, a higher
276 MTL of an ecosystem indicates a higher proportion of higher trophic level species, which is in
277 concordance of ecosystem succession to include comparatively more k-strategists (larger,
278 slower growing species) as part of the ecosystem. The loss of toothed whales, large carnivorous
279 sharks and fish, for instance, would decrease the MTL, and such a decrease could also be
280 achieved by eliminating carnivorous fauna within any other invertebrate or vertebrate group.

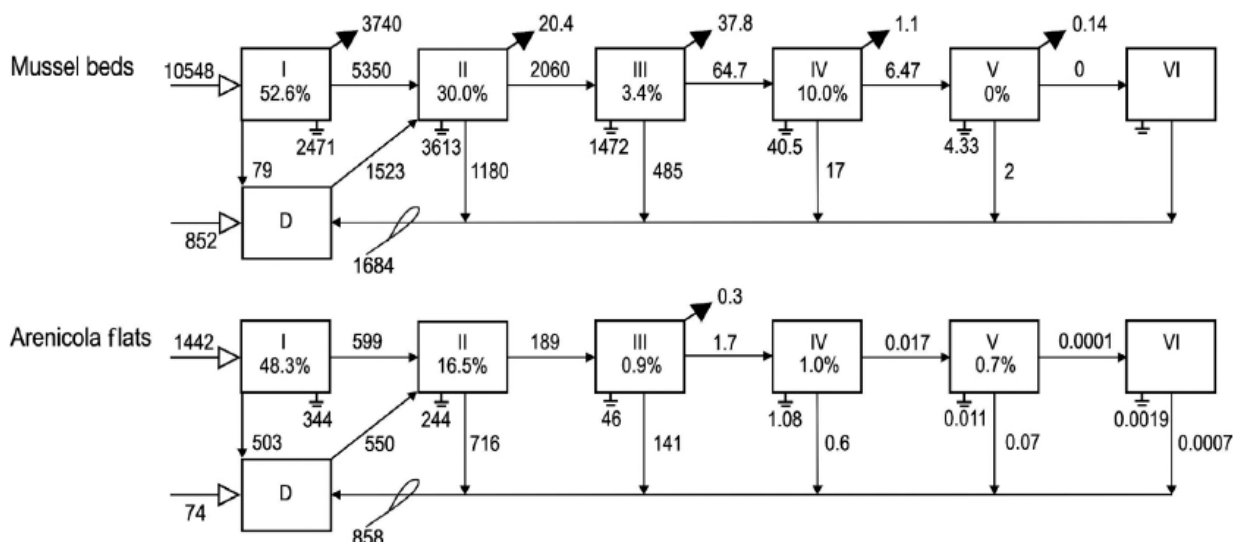
281

282 *3.4 Detritivory : Herbivory (D:H) ratio*

283 MTL describes how the consumers organize into food chains of various lengths, but does not
284 describe to what extent these chains rely on the first trophic levels for energy and nutrients.
285 The second trophic level of a food web can rely on two feeding modes, herbivory and
286 detritivory. Herbivory is the consumption of autotrophic organisms, which are responsible for
287 the carbon incorporation into the ecosystem through the process of photosynthesis, provide an
288 important link between inorganic dissolved nutrients and biomass. These autotrophic
289 organisms are in turn consumed by herbivorous consumers (grazers). Detritivory is the
290 consumption of non-living organic matter, which can be composed of locally produced matter,
291 through the processes of dejection and mortality, or it can be from allochthonous origin,
292 through the process of importation of non-living material from adjacent environments (Postma
293 1967). In most models, this non-living matter is either gathered into one compartment or
294 separated into size-based or habitat-based compartments (e.g., Allesina et al. 2005). For
295 example, to show the impact of classifying detritus, we refer to some specific studies. The
296 “particulate detritus” or “particulate organic matter” is usually composed of the matter whose

297 size is practically greater than 0.7 μm , and the “dissolved organic matter” is composed of those
 298 less than 0.7 μm (see Strickland and Parsons 1972 and Grasshoff et al. 1983). The lower size
 299 limit corresponds to the lower pore diameter of, e.g., the GFF filters, GFC filters, or Millipore
 300 filters as widely used in oceanographic research. The compartment “particulate organic matter”
 301 (POC) should be divided into “suspended” (susPOC) and “sediment” particulate organic matter
 302 (sedPOC) since POC alternately can occur as sediment or be resuspended in association with
 303 inorganic sediment (e.g., Postma 1967, de Jonge 1995) and sediment inhabiting micro-algae
 304 (de Jonge 1995, de Jonge and van Beusekom 1995).

305 To calculate the D/H ratio, the sum of all flows from non-living compartments within the
 306 system to consumers are divided by the sum of flows from all autotrophic compartments to
 307 consumers. Only internal consumers are considered (those belonging to the considered system).
 308 This can be done either using the matrix of flows directly or using the Lindeman spine (1942).
 309 A Lindeman spine is a linear chain, summarizing the food web, where each species is allocated
 310 to a discrete level (Baird and Ulanowicz, 1993). Because autotrophs and non-living detrital
 311 pools are separated at the first trophic level, the Lindeman spines identifies the flows entering
 312 the food web, originating from these 2 sources. In the example of two subsystems of the Sylt-
 313 Rømø Bight given in Figure 1 (Baird et al., 2007), the flow of detritivory is 1523 $\text{mgC m}^{-2} \text{d}^{-1}$
 314 in the mussel bed and 550 $\text{mgC m}^{-2} \text{d}^{-1}$ for the *Arenicola* flat, and herbivory is respectively
 315 5350 and 599 $\text{mgC m}^{-2} \text{d}^{-1}$ resulting in a D/H ratio of 0.28 and 0.9, respectively. For the full
 316 food webs of three main reaches (Lower, Middle, Dollard) representing the main part of the
 317 Ems estuary, de Jonge et al. (accepted) found values ranging from 3.1 (Lower) – 4.3 (Middle)
 318 – 9.0 (Dollard) from the sea in an upstream direction indicating greater reliance on detritus
 319 based resources moving inward.



320

321 Figure 1. Lindeman spine of two subsystems of the Sylt-Rømø Bight. Flows are in mgC m^{-2}
322 d^{-1} . The boxes indicated D refer to the detrital pool in each subsystem, and the Roman
323 numerals in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes
324 refer to the efficiency of energy transfer between the integer trophic levels. From Baird et al.,
325 2007.

326

327 *3.4.1 Relevance for stakeholders*

328 Wiegert and Owen (1971) were first to publish on the importance of two parallel pathways
329 fueling the food webs, one which relied on the consumption of living organisms (grazing-
330 predation base) and the other on the consumption of non-living material (detrital base). The
331 D/H ratio is a means to describe which one of these two sources dominates. Some examples
332 show that the ratio D/H reflects the availability of primary producers as a food source, with
333 higher herbivory (low D/H) being associated with higher primary production (e.g., Chrystal
334 and Scharler 2014, de Jonge et al. accepted), but this is not always the case. The example of
335 the graminoid marshes ecosystem of the South Florida Everglades (Heymans et al., 2002)
336 shows that a high D/H ratio can also be associated with a high primary production, when the
337 plant material is not consumed directly, but only after breaking down and forming detritus.
338 The measure is also high in cases when POC and DOC is transported into the system from
339 algae production elsewhere – as is the case in the Florida Everglades and North Sea estuaries
340 such as the Ems estuary. This demonstrates the need for using this index in complement to
341 flow information (e.g., primary production) to ascertain the relative importance of flows from
342 primary producers and non-living modes. Odum (1969) describes the evolution of ecosystems
343 from a linear chain to a complex web where flows do not rely only on direct primary producers
344 but also on indirect detritus consumption. For this reason, detritivory has been considered as
345 an indicator of maturity (Christensen 1995).

346

347 3.5 Keystoneness

348 There are multiple definitions of keystones in the ecological literature (Valls et al. 2005) with
349 the main concept being that certain species play a particular role that is fundamental in
350 structuring an ecosystem or exerts a strong impact on its function. Paine (1969) defined
351 keystone as species with a relatively small range of biomass that influences the community

352 structure by its predation on other species and thus has an outsized effect on diversity on
353 community structure, functioning, and function. Ecosystem engineers, on the other hand, alter
354 the abiotic environment and thus enable many other organisms to develop a community that is
355 adapted to these special conditions (Jones et al. 1994). Organisms such as reef building corals,
356 bivalves, or macrophytes often form large aggregations and dominate a community in biomass
357 or abundance attracting many organisms to settle because of offering shelter, food, and
358 substrate. In this way, the organisms provide opportunity for new organisms in a self-
359 reinforcing cycle that promotes biodiversity (Cazzolla Gatti et al. 2018). These engineers,
360 although of great relevance in terms of ecosystem structuring, are generally not considered
361 keystone species due to their high biomass.

362

363 Keystoneness has been identified on both a qualitative and a quantitative base. In experimental
364 studies, mainly qualitative criteria such as the impact of a predator on species richness and
365 species presence/absence were used to assess this special role (Paine 1994; Menge et al. 1995;
366 Power et al. 1996; Estes et al. 1998). Since keystone species for a given system may change in
367 space and time, the concept was criticized, and a general and consistent definition was
368 postulated (i.e., Mills et al. 1993; Bond 2001). To support this effort, quantitative aspects of
369 the definition were applied especially in energy flow models such as EcoPath (Ulanowicz and
370 Puccia 1990, Christensen and Pauly 1992) or Ecological Network Analysis (ENA) (Fath and
371 Patten, 1999, Jordán 2009) or some dynamic applications of these modelling tools such as
372 Ecopath with Ecosim (EwE) (Libralato et al. 2005; Heymans et al. 2014; Valls et al. 2015).

373

374 Within these models the trophic niche overlap of certain species was defined and formulated
375 as an index. While there are a few different approaches to calculate keystoneness, here, we use
376 the one by Libralato et al. (2005), which combines the indirect network relations proportional
377 to the total biomass (i.e., big effects are offset if the biomass is also big). This approach relies
378 on the network-based methods described above:

$$379 \quad KS = \log[\varepsilon_i(1 - p_i)] \quad (14)$$

380 where,

$$381 \quad \varepsilon_i = \sqrt{\sum_{i \neq j} m_{ij}^2} \quad (15)$$

382 where, m_{ij} are the elements of the mixed trophic impact matrix (Ulanowicz and Puccia 1990).

383 The parameter p_i relates to the relative biomass of species i with respect to the total biomass of
384 all the components in the food web and is calculated from the following:

$$385 \quad p_i = \frac{B_i}{\sum_{k=1}^n B_k} \quad (16)$$

386 In ENA the mixed trophic impact analysis was formulated as a special tool that compares the
387 impacts a certain species has on all food web compartments (Ulanowicz and Puccia, 1990).
388 Related to the target species the mixed trophic impact can be positive or negative. The target
389 species can be involved in both direct (such as predation) or indirect (cascading, competition)
390 processes and can thus exert bottom up or top down effects by positive and negative
391 interactions (Bondavalli and Ulanowicz 1999). This technique is usable to any “focal” species,
392 but for the identification of a keystone species further selection criteria are needed. Although
393 keystone species have been defined as those whose effect is disproportionately large relative
394 to their abundance (Power et al. 1996), it appears that a threshold of abundance and time must
395 be reached to result in strong cascading community effects (Konar, 2000).

396

397 *3.5.1 Relevance for stakeholders*

398 Food webs display the myriad interactions of different species or groups by their trophic
399 interactions. These interactions relate to direct feeding or indirect feeding via cascading effects.
400 Ranking species with the highest proportion of overlap identifies those exerting the highest
401 impact on others in the ambient food web or ecosystem. If this degree of overlapping is
402 combined with a relatively low biomass, then we can measure the interaction strength between
403 a target species and all other species and denominate this particular species as a keystone
404 species (Araújo et al. 2011). From a stakeholders’ perspective, a keystone species may be of
405 particular interest for conservation or sustainable management efforts, knowing, in fact, that
406 the ‘species oriented’ keystone emerged from an analysis of whole ecosystem interactions.

407

408 *Entropy based indicators*

409 From a thermodynamic standpoint, ecosystems can be viewed as self-organizing systems able
410 to maintain themselves in a far-from-equilibrium condition by exploiting the entropy
411 exchanges with the surrounding environment (Nicolis and Prigogine 1977; Schrödinger 1944;
412 Ulanowicz and Hannon 1987). A flow of low-entropy energy is needed in order to sustain the
413 self-organization of organisms, the trophic network and the matter cycling (Morowitz 1968).

414 Several entropy/information-based functions have been proposed as ecological indicators
 415 and/or orientors (Fath et al. 2004; Jørgensen et al. 2007) and they have been used to describe
 416 the developmental state of an ecosystem, as well as its complexity. Among them, we can
 417 mention Structural Information (Ludovisi 2009) and flow-based information indices (Average
 418 Mutual Information and related indicators such as Flow Diversity and Overhead (Ulanowicz
 419 1986).

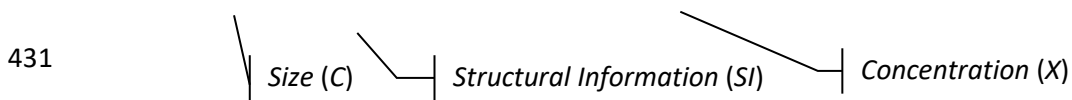
420 3.6. Structural Information

421 Structural Information (SI) refers to the food web relations and connections, such that a more
 422 complex structure (more feeding pathways and levels – see Figure 2) has more information.
 423 One approach to measure this has been derived within the framework of the exergy concept.
 424 Starting from the basic formulation of exergy for ecosystems (Mejer and Jørgensen 1979):

$$425 \quad Ex = RT \sum_{i=1}^n c_i \ln \frac{c_i}{c_{i(e)}} - (c_i - c_{i(e)}) \quad (17)$$

426 where R is the gas constant, T the absolute temperature and c_i the concentration of the i -th
 427 ecosystem component in suitable units (with the subscript e indicating the reference
 428 equilibrium state). Ludovisi (2009) proposed to express exergy as a function of three terms, as
 429 follows:

$$430 \quad Ex = RT \left[C \sum_{i=1}^n p_i \ln \frac{p_i}{p_{i(e)}} + \left(C \ln \frac{C}{C_{(e)}} - (C - C_{(e)}) \right) \right] \quad (18)$$



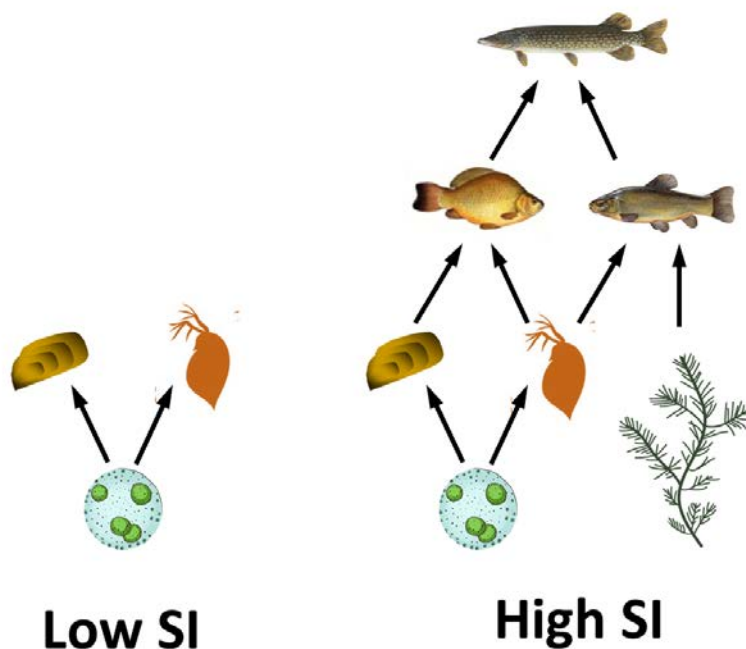
432

433 where $C = \sum_i c_i$ is the total concentration of components, $p_i = c_i / C$ is the relative abundance of the
 434 i -th component.

435 The three terms of the expression are the total concentration of components (the *size* term, C),
 436 a term accounting for the change in the total concentration of components (the *concentration*
 437 term, X), and the *Structural Information (SI)*, which expresses the relative information arising
 438 from the change in the matter apportionment between equilibrium (the reference state) and the
 439 actual state. The calculation of the terms of the equation requires that the equilibrium
 440 concentration (c_i) of all the relevant ecosystem components are estimated. The estimate of these

441 values for organisms and particulate organic matter in general represents the most troublesome
442 step of the calculation. To face this issue, Ludovisi (2009) suggested applying the condition of
443 thermodynamic equilibrium to the ultimate reaction (e.g., oxidation) which leads a system to
444 thermodynamic equilibrium. Such a calculation leads to *virtual equivalent concentration* at
445 *equilibrium (VECE)* values, which are inversely dependent on the body size of organisms. For
446 example, in a surface water environment, the *VECE* values can be estimated as 10^{-12} cells l^{-1}
447 for bacteria and 10^{-26} Ind. l^{-1} for fish.

448 Therefore, the three terms of the exergy, and particularly SI, are strongly dependent on
449 community composition, especially in terms of size spectrum, community structure, and
450 diversity (Figure 2). Since large-sized organisms typically dominate in late stages of ecological
451 succession (Odum 1969), SI is expected to increase along with ecosystem development. The
452 soundness of SI as ecological orientor has been shown in theoretical studies (Jørgensen et al.
453 2010; Ludovisi 2009; Ludovisi and Jørgensen 2009), and its effectiveness as ecological
454 indicator has been tested by application to simulated (Ludovisi 2009) and real case studies, also
455 in comparison with other thermodynamic orientors (Ludovisi 2014; Ludovisi et al. 2012).
456



457
458 Figure 2. Structural Information increases with increasing abundance of large-sized species,
459 which mostly appear at high trophic levels.

460

461

462

463 *3.6.1 Relevance for stakeholders*

464 Besides contributing to fill the gap between indication based on network composition (type and
465 importance of network compartments) and flow structure (type and importance of flows among
466 compartments), the integration of the above entropy/information measures is also suitable to
467 be implemented for the purposes of the Water Framework Directive (WFD) and the Marine
468 Strategy Framework Directive (MSFD), as the data needed for calculation are collected
469 according to the current standard protocols used for the assessment of the ecological status of
470 water bodies or habitats. In particular, the use of SI could help to overcome drawbacks entailed
471 in the methodologies currently used to assess the ecological state of ecosystems, as explained
472 further below.

473

474 *3.7.7. Flow-based Information indices*

475 There are several information based indicators that rely on the configuration of flow
476 interactions between pairs of nodes. Here, we consider Flow diversity (H), Development
477 Capacity (DC), Average Mutual Information (AMI), Ascendency (ASC or A), Overhead (Φ),
478 Redundancy (R), and Robustness. These indicators are used to assess the growth and
479 development of an ecosystem, the balance between levels of diversity and flexibility
480 (resilience), and streamlining of energy flows (efficiency). Both measures are combined into
481 one robustness metric using Ulanowicz' Window of Vitality for networks (Ulanowicz et al.
482 2009). Ulanowicz (2009) showed that the organization of flows in empirical ecosystem
483 networks exhibit a robust trade-off – hypothesized as a result of long-term adaptive and
484 evolutionary pressures – such that an extremely high efficiency, or an extremely high flow
485 redundancy is not reached. Biodiversity, in networks revealed as the number of nodes and
486 flows, and in food web (or other weighted) networks the diversity of connections between
487 nodes, are important concepts for the resilience and efficiency of ecosystems. The flow
488 diversity is calculated by applying Shannon's diversity index to flows (MacArthur 1955):

489
$$H = -k \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}}{T_{..}} \right) \quad (19)$$

490 where T_{ij} denotes a flow from source i to recipient j , $T_{..}$ a summation over flows in the system,
491 and the log is base 2. Note that in the calculation of all information based flow indices, $T_{..}$

492 equates to TSTput. Due to the skewed distribution of flow magnitudes in weighted networks,
 493 the flow distribution in ecosystem networks is such that about 20% of flows contribute 80% to
 494 H (Scharler and Fath 2012). To scale the diversity index to the size of the ecosystem, k can be
 495 replaced with $T_{..}$, which results in the metric Development Capacity (DC):

$$496 \quad DC = -\sum_{i,j} T_{ij} \log\left(\frac{T_{ij}}{T_{..}}\right). \quad (20)$$

497 Most often, $T_{..}$ is several orders larger than H, and consequently variations in the value of H
 498 may be masked by a trend in $T_{..}$. To focus on trends in the diversity of flows, it is therefore
 499 advisable to report H rather than DC.

500 A more detailed description of information generated from pairwise interactions of nodes is
 501 revealed by the Average Mutual Information (AMI) (Ulanowicz 1986). The information is
 502 generated by the joint probability of a certain flow occurring ($T_{ij}/T_{..}$), the marginal probability
 503 of a flow entering the consumer j ($T_{.j}/T_{..}$), and the conditional probability that T_{ij} leaves its
 504 source node i ($T_{ij}/T_{.i}$) (Scharler 2008). The three different parts join to the AMI index:

$$505 \quad AMI = K \sum_{i,j} \left(\frac{T_{ij}}{T_{..}}\right) \log\left(\frac{T_{ij} T_{..}}{T_{.i} T_{.j}}\right). \quad (21)$$

506 Also, this index may be scaled to the system size by replacing k with $T_{..}$, resulting in the
 507 Ascendency (ASC, or A) (Ulanowicz 1986, 1997):

$$508 \quad A = \sum_{i,j} T_{ij} \log\left(\frac{T_{ij} T_{..}}{T_{.i} T_{.j}}\right). \quad (22)$$

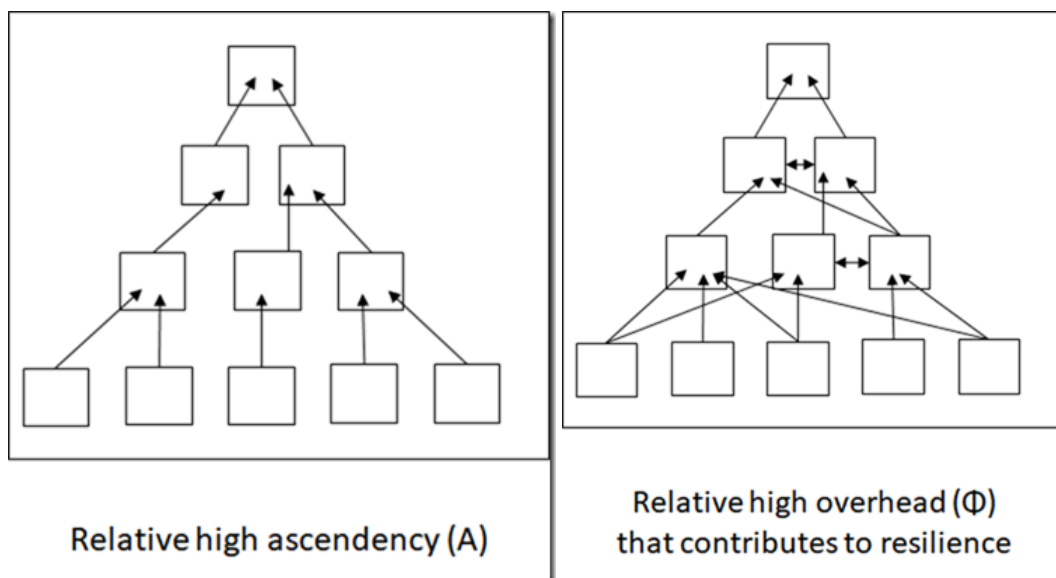
509 The same considerations apply as to the interpretation of DC, since also this metric consists of
 510 two parts with very different magnitudes (AMI and $T_{..}$).

511 The two metrics H and AMI are related such that H reflects the upper boundary to AMI in each
 512 ecosystem (Ulanowicz 1986). There is always a difference between H and AMI, or DC and
 513 ASC, and this difference is important for the resilience of ecosystems. It represents redundant
 514 flows, which are additional (parallel) pathways between nodes. These can be calculated for
 515 internal flows, respiration, and other boundary flows (imports and exports), collectively called
 516 Overhead. The unscaled and scaled version are calculated as follows:

517
$$H_c = -k \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}^2}{T_i T_j} \right), \text{ and} \quad (23)$$

518
$$\Phi = -\sum_{i,j} T_{ij} \log \left(\frac{T_{ij}^2}{T_i T_j} \right). \quad (24)$$

519 This overhead is important to the resilience of a network, as highly efficient ones (high AMI
 520 value) are perceived to be prone to disturbance. Redundancy measures the useful array of
 521 parallel pathways along which biomass may exchange between the compartments (Ulanowicz,
 522 1986). Due to the larger number of parallel pathways, greater redundancy corresponds to a
 523 system that should be able maintain stability when it is perturbed (See Figure 3 for variation in
 524 food webs that display high ascendency versus high overhead).



525
 526 Figure 3. On the left, the food web with mostly simple “food chain” connections will be more
 527 predictable than the flows on the right; and therefore, the ascendency (AMI) is higher.
 528 However, the lack of redundancy on the left makes the overhead lower. The figure on the right
 529 shows multiple pathways that lowers the proportion of ascendency (AMI) and raises that of
 530 overhead.

531
 532
 533 In fact, the ratio AMI/H, or ASC/DC has been widely used to characterize efficiency,
 534 resilience, and even health of ecosystems (Christian et al. 2005, Ulanowicz 2009), and this ratio
 535 is known to be resilient to uncertainty in model parameterization (Kaufman and Borrett 2010).
 536 The ratio has subsequently been incorporated into a single measure, a system robustness index,
 537 to capture these opposing tendencies in system organization (Ulanowicz 2009). This index has

538 previously been called fitness, but also labelled sustainability, resilience, and robustness. We
 539 prefer the name robustness which has a different connotation than the other terms already used
 540 for various other ecological concepts (Figure 4):

541 $Robustness = -a \ln a$, (25)

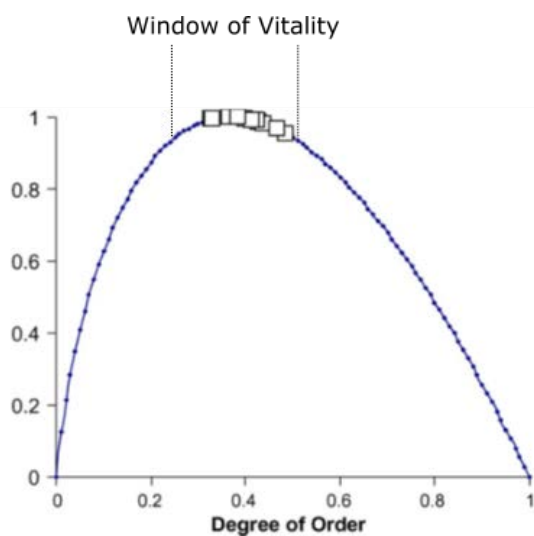
542

543 where $a = \frac{A}{DC}$ (26)

544

545 Empirical networks (see de Jonge et al. accepted B) revealed that ecosystems tend to
 546 congregate on top of the resulting curve showing highest robustness values (Figure 4). This
 547 led to an interpretation that viable ecosystems consist of different types of pathways, some of
 548 which are efficient, and others that are redundant in the sense of representing parallel, or
 549 additional, pathways. Networks with flow constraints that are on the whole intermediate, but
 550 consist of efficient and redundant pathways are therefore thought to be optimal.

551



552

553 Figure 4. Theoretical curve showing the information-based approach tradeoff between system
 554 efficiency and redundancies (Ulanowicz 2009). Evidence from empirical ecological networks
 555 cluster around the optimum range and therefore do not exhibit maximization of efficiency or
 556 redundancy.

557

558 *3.7.1 Relevance for stakeholders*

559 Such system level metrics give us additional information to species and community-level
560 indicators and allow to gauge the overall structure and functionality of ecosystems. An increase
561 or decrease in the value of AMI, H, or AMI/H is determined by the individual flows structure,
562 such that changes in large flows result in a larger change of the indices compared to changes
563 in small flows. A change in the indices therefore does not necessarily indicate a change in the
564 health of an ecosystem, unless the metric change is caused by a decrease or extinction of several
565 species producing small flows as opposed to a decrease in large flows (usually originating from
566 bacteria, phytoplankton, or detritus). However, the metrics serve to identify the changing state
567 of a system. Whether a state change is detrimental or beneficial depends on the present state
568 (e.g., natural, impacted), and on which flows caused the change in the metrics (Ludovisi and
569 Scharler 2017, de Jonge and Schückel submitted). Management actions are in general targeted
570 at the node or species level, and these metrics show the consequences of such actions on the
571 overall ecosystem robustness. For instance through exploratory studies, such actions can be
572 incorporated into the ecosystem to explore whether they will lead its robustness towards
573 efficiency or resilience (e.g., Mukherjee et al. 2015, Ludovisi and Scharler 2017).

574

575 **4.0 Discussion**

576 The definition of indicators for describing changes in the functioning of ecosystems has been
577 a central question for researchers in ecology and fisheries sciences during the last two decades.
578 A good indicator should be simple, specific, and sensitive to changes (natural and human
579 induced perturbations) in ecosystems caused by different pressures (eutrophication, dredging,
580 fisheries, etc.) to define the pressure-state change relationships as exemplified by de Jonge and
581 Schückel (submitted, their Fig. 1 and 3). There is usually a clear tension and difference
582 between what policy makers and decision makers ask for to facilitate their work process and
583 what scientists deliver. Management decisions related to ecosystem assessments are more
584 difficult compared with those related to single species assessments, but even then the decision
585 makers need preferably clear-cut suggestions and ways of implementing them. They explicitly
586 do not like to engage with the many versions, uncertainties, exceptions, pros and cons and
587 caveats that scientists are very good in delivering. The difference between the demands and the
588 offers easily leads to confusion and even friction. The crucial point is that, when asked for help,
589 scientists typically stick to their own nuanced and detailed views while the decision makers
590 (and other stakeholders) look for clear cut answers. A better bridge is needed between the two
591 worlds.

592 Ecosystem based management received a boost when its approach was woven into the
593 Convention of Biological Diversity, which was signed in 1993. There was a subsequent rise
594 in demand for indicators to assess the ‘structure’ and the ‘functioning’ of ecosystems linked
595 with the publication in 2000 of the European Water Framework Directive (WFD) and later in
596 2008 of the European Marine Framework Directive (MSFD), which settled one descriptor
597 based on the food-web and one on the species. Several actions are worth to be mentioned here.
598 Some were individual such as de Jonge et al. (2003, 2012, accepted B, submitted to this SI)
599 and de Jonge (2007) in connection to the WFD. Patricio et al. (2009) have helped advance the
600 use of indicators (particularly benthic ones) applied to estuarine water quality. Also, Baird
601 (2012; et al. 2001) promoted the use of ecological network indicators in studies of the Sylt-
602 Rømø Bight. Regarding the MSFD again, groups of researchers gathered to coordinate answers
603 to this demand and published the results in the context of EU collaborative projects (e.g.,
604 Devotes, Lynam et al. 2016, Pirrodi et al. 2016), or ICES groups (e.g., Tam et al. 2017), or
605 OSPAR groups (e.g. Rombouts et al 2013, Safi et al, submitted to this SI). One of the early
606 coordinated efforts defined a list of indicators in ecosystem-based management using food web
607 functioning of fishing activities (called EAF for Ecosystem Approach to Fisheries). From the
608 end of the 2000s, members of this consortium set up large inter-ecosystem comparisons of
609 marine exploited systems through the group IndiSeas, whose work recently led to the
610 publication of numerous articles (e.g., Fu et al. 2018, Reed et al. 2016, Coll et al. 2016, Bundy
611 et al. 2016). Among the different indicators considered, the ENA indices appeared as a new
612 way of describing the flows in the entire system (“functional” and “holistic” indicators), even
613 if more research was still considered as needed to make them operational.

614 Decision makers are looking for characteristic or SMART indicators (Doran, 1981) that at the
615 same time are also quite specific and sound (ROARS; see e.g., www.mnestudies.com), are
616 ‘simple, cheap, easy to understand’ (de Jonge et al. 2012), and thus, appealing for the short-
617 term, high pressure needs of the decision-maker (de Jonge et al. 2003). The specifications of
618 the required indicators are presented in Box #1. Some further requirements for indicators are
619 that they i) are limited in number, ii) comprise a mix of quantitative and qualitative indicators,
620 iii) are practical & simple (direct the problem and the solution), iv) are easily communicable,
621 and v) inform human society about the situation. It is not possible to meet all these requirements
622 in this paper, but a start will be made by confronting what we have available with the
623 requirements set by the users. Based on the list of suggested indicators (Table 2), we attempt
624 to test their suitability preliminarily against the presented requirements in Box #1. All of the

625 indicators presented are important, but they are at the moment not easily understandable to
 626 non-experts and thus also not all easily communicable (Table 3).

627 Box #1

Qualities of Good Indicators: ROARS	
Relevant:	It relates to an important part of an objective or output
Objective:	Based on facts, rather than feelings or impressions and thus measurable
Available:	Data should be readily available or reasonably measurable
Realistic:	It should not be too difficult or too expensive to collect the information
Specific:	The measured changes should be expressed in precise terms
Characteristics of Good indicators are also SMART:	
Specific:	Measured changes should be expressed in precise terms and suggest the direction of actions
Measurable:	Indicators should be related to things that can be measured in an unambiguous way
Achievable:	Indicators should be reasonable and possible to reach, and therefore sensitive to changes
Replicable:	Measurements should be the same when made by different people using the same method
Time-bound:	There should be a time limit within which changes are expected and measured

628

629 Table 3. Assessment of indicators for aspects critical to management and communication with
 630 managers. Table values generated from expert input of the paper authors.

Indicator	1) APL	2) FCI	3) MTL	4) D/H	5) Keystone	6) SI	7) Φ/DC A/DC
Relevant	++	++	+	+	-	+	++
Objective	++	++	+	+	+	++	++
Available	+	-/+	+	+	+	-	+/-
Realistic	+	-	-	+	-	+	+
Specific ²	+	-	-	+	+/-	+/-	+
Measurable	+	+	+	+	+	+/-	+
Achievable	+	+	+	+	+/-	+	+
Replicable	+	+	+	++	+	+	++
Communicable ³	++	+	+	++	++	+/-	+

631 Most attractive of all the Table 3 indices is the fact that they are replicable and not subjective,
 632 given that the basic data set is good (flow matrix and energetics table). However, all are affected
 633 by the degree of aggregation of the network and the flow balancing of the living and the non-
 634 living compartments.

² Specific is the last aspect of ROARS and the first of SMART, and is only presented once here

³ We have omitted the last aspect of SMART, Time-bound, which does not seem relevant here, but have instead included the characteristic if it is communicable.

635 *4.1 Average Path Length*

636 The APL index is for general purposes very useful. It basically indicates what part of the
637 boundary input is not used by the ecosystem and calculates an index based on ratio of
638 throughflow to boundary flow. The maximum of this value is reached when the boundary flow
639 approaches zero and the APL approaches infinity (∞). This occurs when there is significant
640 cycling such that a high internal flow is maintained for a small input. Thus, a high or increasing
641 APL reflects a rather developed or developing system. The index is thus dependent on good
642 estimates of ecosystem boundary input values. One weakness, similar to any of the flow-based
643 methods, is that if the study cannot provide accurate enough values for external carbon inputs
644 then users should be careful in using the index. A second weak point for decision makers is
645 that there is no generic optimum value or minimum value available, but that their magnitudes
646 are system specific.

647 *4.2 Finn Cycling Index*

648 The recycling is a property of ecosystem functioning which is central in trophic ecology
649 studies. The recycling is associated with the ability of a system to re-use material and avoid
650 loss, leading to a better efficiency. It has also been associated with a buffer reaction to human
651 induced system stress, with recycling leading to a greater resistance (Saint-Béat et al 2015).
652 Observations are numerous of observed effects of pressures on the ecosystem leading to higher
653 recycling. The concept was already proposed in Odum (1985), and was then quantified in
654 numerous applications of the FCI calculation in inter-system comparisons with differences of
655 pressures. Recently, de Jonge et al. (accepted A) demonstrated a strong increase of FCI in an
656 estuary in upstream direction where the concentrations of non-living carbon and turbidity
657 naturally increased. Tecchio et al. (2016) observed a higher FCI after the building of the
658 Port2000 extension of the harbor of Le Havre, in the Seine estuary. Higher FCI corresponds
659 to higher re-use, but as stated above this may also occur when the system is stressed so it is
660 necessary to know the context of the system which produces the FCI value. A disadvantage of
661 the indicator is that also here there is no clear reference value.

662 *4.3 Mean Trophic Level*

663 The MTL describes how the consumers organize in shorter or longer chains (Shannon et al.
664 2014, Coll et al. 2016). This is a simple and intuitive metric that gives an overall impression

665 of the complexity of the food web. A system with a higher MTL implies a more complex
666 ecosystem. While the index does not have any immediate management implication on its own,
667 it could be used for long term monitoring to indicate if there is a harmful disturbance in the
668 system, which would result in a decreasing MTL of the catch (MTLC). The “Fishing down the
669 food web” paradigm (Pauly et al. 1998) is based on the assumption that increasing fishing
670 pressure leads to a continuous reduction in MTLC since the high TL species are removed first.
671 While this reduction in MTLC has been observed in many fisheries, the mechanism behind the
672 observed decrease in MTLC may differ between systems.

673 Often fishermen increasingly target the low trophic level species because of their higher overall
674 productivity, which also results in a decrease in MTLC but does not necessarily mean
675 overfishing of the high TL species (Sethi et al. 2010, Rehren et al. 2018, Tuda et al. 2016).
676 Branch et al. (2010) show that the negative trend in global MTLC observed at the end of the
677 1990s is no longer supported by the most recent decades of data. Looking at the Swedish
678 fishery, Hornborg et al. (2012) also show that there was no correlation between landings and
679 survey data MTL and conclude that the trend in landing MTL appears to be, at most, a weak
680 measure of the ecosystem state and pressures on biodiversity in the area. Shannon et al. (2014)
681 further evaluated a number of trophic level indicators, including MTL, and conclude that they
682 can be useful, especially when a trophic level threshold (excluding lower trophic levels) is
683 used. We may conclude from the above that the use of MTLC as an indicator of the state of an
684 ecosystem can be meaningful if additional information is available on the relative contribution
685 of the different species to the MTL.

686 *4.4 D/H ratio*

687 This ratio, indicating the importance of detritus compared to that of primary production
688 products is very appealing because it can easily be explained to non-experts. However, the
689 index should preferably be used in complement to other information to provide the required
690 detail of interpretation. For example, the average path length will give valuable information on
691 the residence time of the matter within the food-web, but it will not describe if this matter
692 comes directly from primary producers or from detritus, produced locally (local recycling) or
693 imported (allochthonous recycling). This is why several articles describing food web
694 functioning in different situations have joined these indices together (e.g., Horn et al 2017, de
695 la Vega et al., in press). In their article comparing three tidal ecosystems of the Wadden Sea,
696 de la Vega et al. (in press) showed that main features of system functioning such as the D/H

697 ratio are influenced by the dominant habitat type of the studied area. Specifically, de la Vega
698 observed that the Jade Bay system, dominated by mudflats relied on detritivory pathways (D/H
699 ratio 2.44) whereas the Sylt-Rømø Bight and the Norderaue tidal basin are dominated by
700 herbivory pathways (D/H ration 0.9 and 0.87, respectively) attributed due to high standing
701 stocks of suspension feeding mussel beds. However, within any existing ecosystem, the typical
702 flow configuration is a web, rather than a chain. An increase in the D/H ratio of an ecosystem
703 between two points in time is to be interpreted as a relative change between that of natural
704 variability and that caused by extreme events including human intervention. If primary
705 productivity is low, then it also indicates that the system can sustain its activity (throughflow)
706 only by increasing detritivory, which in turn will increase the internal cycling of material (and
707 therefore the FCI). This also has implications for the detritivory as a buffering capacity as
708 indicated by de Jonge and Schückel (submitted to OCMA for this SI). If the main detritus
709 producers are plants or algae, then the extent of detritivory will decrease with a decrease in
710 primary productivity. It is therefore important to have good knowledge of the flow structure
711 between individual nodes for the interpretation of network indices.

712 *4.5 Keystoneness*

713 This index represents the overlap of trophic interactions and indicates a mutual influence
714 between species. It falls in the category ‘easy to understand and to communicate to decision
715 makers’. Sensitivity analysis regarding this parameter is an ongoing area of research. The
716 index, however, has potential when it comes to exploring effects of specific management or
717 conservation measures where the composition of species and their key role capacities come
718 into play. Some prominent examples for ecosystem changes due to man-made removal/addition
719 of keystone species have been reported from terrestrial and marine systems. These are the
720 extinction of wolves in Yellowstone Park in 1920 and its reintroduction as a management
721 measure in 1995 (i.e. Berger et al. 2008; Berger & Smith 2005), and the extirpation of sea-
722 otters at the American west coast from 1741 until 1910, its influence on the kelp beds and its
723 recovery due to protection measures in 1911 (Estes and Palmisano, 1974; Kenyon 1969). In
724 both cases the consequences of the recovery of the keystone species on the total ecosystem
725 could have been predicted by using the proposed index and combining it with an ENA- impact
726 analysis.

727 Jordán (2009) describes three options to understand networks and their central players better.
728 Aggregation of the network does not facilitate to find a keystone species because the bias of

729 the biological content is potentially large. The focus on an isolated subgraph of the network
730 leads to problems explaining how the neglected external effects are influencing members of
731 the subsystem. Another method is to consider the heterogeneity of the network, to determine
732 critical nodes and deriving indices from it. Considering the number of neighbors leads to define
733 the degree (D) as the number of neighbors of a graph node to define the positional importance
734 or the “topological importance”. Some keystone species such as the Asteroid *Pisaster*
735 *ochraceus* (Paine 1969) has only few direct partners but a rich indirect interaction system.
736 Therefore, also the neighbors of these neighbors must be included in the assessment of
737 keystone-ness.

738 Biologists are often faced to document a cascade effect in a food web after a species is removed
739 by local extirpation or extinction. Decisions on measures about the re-colonization process of
740 wolves in Europe as well as the conflict between fishermen and seals in the Wadden Sea or
741 other coastal areas could be facilitated by using this special index combined with ENA models.

742 *4.6 Structural Information*

743 This index provides information complimentary to that of other entropy-based indicators.
744 However, it also clearly adds a challenge for decision makers to fully understand them, in that
745 the information provided is less easily interpretable than that of the structural indicators
746 discussed so far. Structural Information provides an interpretation of the system’s organization
747 from the biomass distribution between smaller r- and larger K-strategists, and insofar is a
748 valuable contribution to understanding of its structure.

749 In the context of Ecological Network Analysis, SI can be of particular interest, as it provides a
750 complimentary information to that provided by other entropy-based indicators typically used
751 to measure the information embedded in the flow structure of a network, i.e. Average Mutual
752 Information (AMI) and Flow Diversity (H). Altogether, these indicators can give a
753 comprehensive picture of an ecological network, describing the information embedded in
754 network composition (SI), network connectivity and equitability (H) and network determinacy
755 (AMI). Moreover, it has been shown (Ludovisi and Scharler 2017) that their responses along a
756 putative successional pathway give rise to a pattern that conceptually agrees with the current
757 ecosystem theory. Since these indices share the common currency of entropy/information, they
758 lend themselves to be combined in order to obtain a comprehensive indicator of network
759 complexity. As shown by Scharler and Ludovisi (Sylt ENA workshop, 2017), a particular

760 combination of these indicators can represent a promising orientor of network development,
761 and thus a potential suitable indicator of ecosystem's health state.

762

763 The main focus of ecological state assessment is to reach a single, objective as possible and
764 comprehensive figure able to express the condition of an entire ecosystem. The current standard
765 protocols based on the bioindication concept use the abundance data of organisms belonging
766 to various ecological categories (macrophytes, fish, macrobenthos, diatoms, etc.) to give partial
767 judgements of ecosystem state. The partial judgements are then often weighted and averaged
768 in order to reach a unique index representative of ecosystem state. Such a procedure entails
769 several practical drawbacks for any single category, mostly dealing with the incomplete
770 knowledge of ecological optimum/tolerance by species, uncertainty in taxonomic attribution,
771 problems in extending bioindicator values to different biogeographical area. And, what if the
772 partial judgments obtained for different ecological categories are very different from one
773 another? Is it ecologically proper to average the response of different ecological categories as
774 if they were independent of one another?

775

776 Moreover, and more conceptually, is a judgement based on species tolerance of certain
777 conditions a true indicator of ecological quality? In this respect, indicators reflecting the
778 distance covered by an ecosystem away from the 'dead state' (i.e. a state without life), such as
779 SI, could represent useful and practical tools to reach a reliable assessment of ecosystem state
780 and quality. A case study showing the potential effectiveness of SI as a tool for ecosystem state
781 assessment is reported in Ludovisi (2014). The author calculated SI for three Byelorussian
782 lakes, which are adjacent, connected to each other and have similar morphology, hydrology
783 and hydro-chemical features, but very different trophic state and biocoenosis. The results
784 showed that SI, calculated on the basis of the whole biocoenosis (from algae to fish and
785 macrophytes), increased clearly from the hypereutrophic Lake Batorin to the mesotrophic Lake
786 Myastro and to the oligotrophic Lake Naroch, reflecting the marked changes in the dominance
787 of the various ecological categories. From a theoretical point of view, such results confirms the
788 thought of Odum (1969) that eutrophication pushes an ecosystem back, in successional terms,
789 to a younger or 'bloom' state". From a more practical standpoint, SI gives a measure of how
790 much an ecosystem has moved along the successional path, and thus represents one of the most
791 'objective' measures of ecological state and quality.

792

793 *4.7 Information based indicators*

794 This category consists of several indices such as the flow diversity (H), the ascendancy (A),
795 the overhead or loss of information in redundant pathways (Φ), the development capacity (DC),
796 the average mutual information (AMI), or the internal redundancy of the flows (R). Assessing
797 the system functioning and structure (e.g., by the relative overhead, flow diversity H, or
798 robustness) is something the EU Commission appreciates (EC, 2000, 2008). Apart from the
799 flow diversity also the relative ascendancy (A/DC and which is also related to the Robustness)
800 and relative overhead (Φ /DC) are very interesting for decision making because they indicate
801 the efficiency (A/DC) and the overall resilience (Φ /DC) of ecosystems. The latter two indices
802 are even more interesting since they scale between 0 and 1 because $1 = A/DC + \Phi/DC$. This
803 definite scale is something decision makers appreciate because it facilitates interpretation.
804 Further, there are indications that the relative overhead (Φ /DC) can be related to the species
805 diversity (de Jonge and Schückel in prep). Due to the work on the Robustness indicator we
806 know that Φ /DC has an optimum (0.61, the highest point on the robustness curve) (Ulanowicz
807 2009). The robustness indicator has the advantage of a known optimum value, which facilitates
808 studies related to the effects of system stress as well as foreseen measures to diminish it and
809 makes it very attractive one for decision makers. Redundancy represents only part of the Φ /DC
810 but indicates the system's potential flexibility to respond to perturbations (Heymans 2003,
811 Heymans et al. 2014, Heymans and Tomczak 2016, Tomczak et al. 2013). Both Φ /DC and
812 A/DC seem thus very suitable as an overall characterization of the resilience of any ecosystem.
813 Taken into the robustness metric, an optimum value is apparent, and a region where viable
814 ecosystems exist (Ulanowicz 2009).

815 Numerous studies have been led recently in order to test the hypothesis that such indices may
816 be sensitive to different sources of stress. In the case of the Seine Estuary, where the pressure
817 is forming a gradient from North (high pressure, close the harbor of Le Havre) to South (low
818 pressure, protected area), the system showed in the same direction a rising activity (TSTflow)
819 associated with a rising diversity of flows (H) (Tecchio et al. 2016). In neighboring Bay of
820 Seine, the simulation of the reef effect, associated with the future building of offshore wind
821 farms, was shown to increase the total activity of the system but to decrease the relative
822 ascendancy (A/DC) showing a less mature system associated to this new hard substrate
823 appearance in the middle of a soft bottom habitat (Raoux et al, 2018). Tam et al. (2017)
824 evaluated MTL, FCI, and information based indicators within a long list of proposed indicators

825 and received good marks in “availability” and “conceptual” items but low rates in
826 “communication” and “management”. Lynam et al. (2016) reviewed available modelling
827 methods applied to ecosystems and discussed ENA in the context of simulation of climate
828 change effects on the distribution of species. For example, the Bay of Biscay ecosystem was
829 studied to investigate the effect of climate change on the distribution of small pelagic fish and
830 its consequences on food web functioning (Chaalali et al. 2016). There is also a growing
831 literature to apply this information based approach to economic studies (Kharrazi et al. 2017,
832 Kharrazi et al. 2013, Goerner et al. 2015).

833 *4.8 Future Directions*

834 While we intend that this paper provide useful overview and guidance to practitioners of
835 ecosystem management, we recognize that application and implementation of these tools and
836 metrics is still progressing. There are several challenges that remain to be addressed to improve
837 the use and communication of the metrics. From a scientific perspective, future work should
838 focus on further developing the underlying theory behind the indicators to better understand
839 the causative factors that influence the values. This should only help our ability to implement
840 and communicate the metrics. Second, there is also the question of model and empirical data
841 sensitivity. This gets to the question of conceptualizing the system, setting the system
842 boundary, and selecting the nodes to be included. For example, it is known that model
843 aggregation (lower diversity of species represented in the model) can affect the metric values
844 (Fath et al. 2013, Baird et al. 2009, Allesina et al. 2005, Abarca-Arenas and Ulanowicz 2002,
845 de Jonge et al. accepted), and uncertainty in model parameterization (e.g., flow estimations)
846 can also impact ENA results (Kones et al. 2009, Kaufman and Borrett 2010, Hines et al. 2018,
847 Waspe et al. 2018). Heymans et al. (2014) demonstrate the difficulties that arise from modeler
848 bias resulting in model topology when comparing across ecosystems. While there is yet no
849 settled theory of modelling about how to construct the model, some guidance is provided in
850 Fath et al. (2007).

851 A few studies (Heymans et al. 2007, Heymans and Tomczak 2016, Tomczak et al. 2013) have
852 used network metrics to detect change of ecosystem state in terms of flipping from one regime
853 to another. However, this is an area of open research as thresholds for regime shifts are difficult
854 to discern. For example, is it possible to say that an FCI = 0.25 is healthy, yet, 0.24 is not? We
855 are doubtful that this is the case given the “grey zone” in both the ecosystems and the indicators
856 used to assess them and would warn against spending too much time looking for generic

857 thresholds. A more fruitful approach is to use them for comparative analyses across time and
858 space. Benchmarks of healthy and unhealthy ecosystems could be used as well as observations
859 of dynamic trends the ecosystem undergoes (Lau et al. 2017).

860 Lastly, we advise decision makers not to seek one magic bullet. Ecosystems are not only
861 complex but also at the same time adaptive (Levin, 1998). It is only sensible that it would take
862 multiple dimensions and methods to evaluate and interpret the high number of interactions and
863 feedbacks. Therefore, it should be recognized that not one indicator addresses all the concerns,
864 but rather that they are complementary and should be used as a toolbox of approaches. The
865 advantage is that all are calculated from the same food web monitoring and datasets, such that
866 once one has the data needed to calculate one the others will follow. Data needed for
867 calculation can be collected according to current protocols used for the assessment of the
868 ecological status of water bodies or habitats. For example, in the North Sea region, existing
869 monitoring programs imposed by MSFD and other EU Directives, such as the Habitats
870 Directive (92/43/EEC), the Birds Directive (2009/147/EC) and the Water Framework Directive
871 (WFD, Directive 2000/60/EC) or the Trilateral Monitoring Assessment Program in the Wadden
872 Sea (TMAP) are compatible with requirements to build up a network. ENA software exists
873 (Fath and Borrett 2006, Borrett and Lau 2014) to make these calculations all in one software
874 package. Therefore, a critical piece for success is continuous ecosystem-scale monitoring
875 necessary to implement the Ecological Network Analysis metrics described herein, and the
876 successful translation of scientific results to the management and policy realm.

877

878 **5.0 Conclusions**

879 There is a movement in the policy community to address the functional aspects of ecosystems
880 using holistic frameworks such as the Water Framework Directive (WFD, Directive
881 2000/60/EC), the Marine Strategy Framework Directive (MSFD), the Sustainable
882 Development Goals (SDGs), and numerous other approaches from around the world. The
883 present paper contributes to the ongoing requirements in politics and management to assess
884 and manage marine ecosystems in a holistic way specifically using food web indicators and a
885 holistic ecosystems approach (Tam et al. 2017).

886 The short list of indicators provided here contains some indicators that can be applied more or
887 less immediately as a first step to create a foundation for EBM by an unambiguous ecosystem
888 assessment as demanded by the European Union (e.g. EC, 2000, 2008). These indicators are
889 Φ /DC, A/DC, D/H, H, APL, MTL, and FCI because these can easily be communicated with
890 decision makers. Because the other indicators presented here are more complex and/or more
891 theoretical, they are seen as foundational for additional indices in future assessments.

892 The metrics described here are not a complete not a definite list of the ecological network
893 metrics, but they were singled out by experts at the workshop as metrics that have been widely
894 applied and have the greatest potential to convey meaningful and understandable information
895 to stakeholders and decision-makers. These metrics have been used in numerous studies as
896 described above and we have confidence that they provide useful and trustworthy information
897 and insight for better ecosystem management. We anticipate that with further application and
898 discussion of additional network metrics more will be incorporated in environmental
899 management. This can only be ascertained following more use of the approaches, which we
900 greatly encourage.

901

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905

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