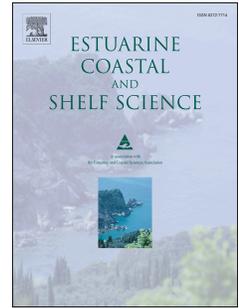


# Accepted Manuscript

Comparing the network structure and resilience of two benthic estuarine systems following the implementation of nutrient mitigation actions

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PII: S0272-7714(18)30303-2

DOI: <https://doi.org/10.1016/j.ecss.2018.12.016>

Reference: YECSS 6059

To appear in: *Estuarine, Coastal and Shelf Science*

Received Date: 9 April 2018

Revised Date: 11 November 2018

Accepted Date: 24 December 2018

Please cite this article as: Watson, S.C.L., Beaumont, N.J., Widdicombe, S., Paterson, D.M., Comparing the network structure and resilience of two benthic estuarine systems following the implementation of nutrient mitigation actions, *Estuarine, Coastal and Shelf Science* (2019), doi: <https://doi.org/10.1016/j.ecss.2018.12.016>.

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1 **Comparing the network structure and resilience of two benthic estuarine**  
2 **systems following the implementation of nutrient mitigation actions.**

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10 **Key words: Comparative studies, Ecopath with Ecosim, Estuary, Eutrophication, Network analysis.**

11 **Abstract**

12 The structure and resilience of benthic communities in coastal and estuarine ecosystems can be  
13 strongly affected by human mediated disturbances, such as nutrient enrichment, often leading to  
14 changes in a food webs function. In this study, we used the Ecopath model to examine two case  
15 studies where deliberate management actions aimed at reducing nutrient pollution and restoring  
16 ecosystems resulted in ecological recovery. Five mass-balanced models were developed to represent  
17 pre and post-management changes in the benthic food web properties of the Tamar (1990, 1992,  
18 2005) and Eden (1999, 2015) estuarine systems (UK). The network functions of interest were  
19 measures related to the cycling of carbon, nutrients and the productivity of the systems. Specific  
20 attention was given to the trophic structure and cycling pathways within the two ecosystems. The  
21 network attribute of ascendancy was also examined as a proxy for resilience and used to define safe  
22 system-level operating boundaries. The results of the resilience metrics ascendancy (A) and its  
23 derivatives capacity (C) and overhead (O) indicate that both systems were more resilient and had  
24 higher resistance to potential stressors under low nutrient conditions. The less perturbed networks  
25 also cycled material more efficiently, according to Finns cycling index (CI), and longer cycling path  
26 lengths were indications of less stressed systems. Relative Ascendancy (A/C) also proved useful for  
27 comparing estuarine systems of different sizes, suggesting the Tamar and Eden systems network  
28 structures have remained within their pre-defined “safe operating zones”. Overall, this analysis  
29 presents justification that efforts to reduce nutrient inputs into the Tamar and Eden estuaries have  
30 had a positive effect on the trophic networks of each system. Moreover, the consensus of the  
31 network indicators in both systems suggest ecological network analysis (ENA) to be a suitable  
32 methodology to compare the recovery patterns of ecosystems of different sizes and complexity.

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## 40 1 Introduction

41 There is a growing need to manage ecosystems sustainably so that they can continue to deliver the  
42 goods and services on which society depend (Beaumont *et al.*, 2007; Bennett *et al.*, 2015; Costanza  
43 *et al.*, 2017). This is particularly the case for coastal marine systems where increasing population  
44 pressure, urbanisation and nutrient run-off from the coastal zone has increased the number of large-  
45 scale impacts affecting estuarine systems (Dolbeth *et al.*, 2011; Ellis *et al.*, 2015). As a consequence,  
46 there is a growing movement towards an integrated 'Ecosystem-based' approach to management,  
47 which focuses on how individual actions affect whole ecosystems, rather than considering these  
48 impacts in a piecemeal manner (Leslie, 2018). One alternative method to considering the organisms  
49 within ecosystems as an aggregate property, is to consider the emergent properties of the whole  
50 ecological system rather than of any of its individual components. Exergy, a thermodynamic concept,  
51 has been applied in ecology since the 1970's and is defined as the amount of work a system can  
52 perform when it is brought to thermodynamic equilibrium with its environment (Jørgensen & Mejer,  
53 1977; 1979). Compatibly, ecological network analysis (ENA) can extract comprehensive information  
54 on the flow and cycling of matter from mass-balanced flowcharts, including trophic structure and  
55 transfer efficiencies, and the organisation or resilience of the food web (Field *et al.*, 1989, Gaedke,  
56 1995). Taken together, these methodologies have a long legacy in assessing ecosystem health and in  
57 analysing complex interactions within marine ecosystems (Odum, 1953; 1969; 1996; Ulanowicz,  
58 1986; 1997; 2012) with several ENA tools now available within a number of easily accessible  
59 software packages including NETWRK4 (Ulanowicz & Kay, 1991), WAND (Allesina & Bondavalli,  
60 2004), Ecopath with Ecosim (Christensen & Walters, 2004) and R (Laua *et al.*, 2015).

61 Perhaps the most commonly used and emerging example of this type of modelling approach is the  
62 Ecopath with Ecosim (EwE) modelling software (Christensen *et al.*, 2005), which has over 400  
63 models published to date (Colléter *et al.*, 2015), and is the most applied tool for modelling marine  
64 and aquatic ecosystems globally. EwE models have a number of ENA features and can be selected  
65 to: identify and quantify major energy flows in an ecosystem, interactions between species, compare  
66 coastal ecosystems of different sizes, evaluate the effects of climate induced or anthropogenic  
67 variability on ecosystems, explore management policy options. EwE models have also been applied  
68 in testing ecosystem theories on eutrophication (Patricio *et al.*, 2006; Baeta *et al.*, 2011; Vasslides *et al.*,  
69 2017), resilience, stability and regime shifts (Pérez-España & Arreguín-Sánchez, 2001; Tomczak *et al.*,  
70 2013; Arreguín-Sánchez & Ruiz-Barreiro, 2014; Heymans & Tomczak, 2016). Thus, the aim of this  
71 paper was to use the Ecopath software with ENA analysis to examine and compare the network  
72 system attributes of two temperate UK estuaries, the well-document Tamar Estuary, in south-west  
73 England and the smaller less well studied Eden Estuary, in north-east Scotland. Both systems have  
74 gone through extensive periods of ecological change over the last thirty years, as a result of a shift  
75 towards an agriculture production policy option in the Eden catchment (1999-2015) and a  
76 combination of water quality improvement initiatives in the Tamar Estuary (1990-2005), allowing the  
77 representation of eutrophic and post-eutrophic states. Therefore, five mass-balanced models were  
78 developed using the "Ecopath with Ecosim" software package for the years 1990, 1992 and 2005  
79 (Tamar) and 1999 and 2015 (Eden) to assess changes in the benthic food web properties of the  
80 Tamar and Eden estuarine systems. Field, laboratory and literature information was used to  
81 construct the models. The main study objective was to assess the effects of:

82 (1) a pre-management period of excessive anthropogenic enrichment, which led to excessive  
83 production of organic matter in the form of algal blooms and localised hypoxic symptoms (Tamar  
84 1990);

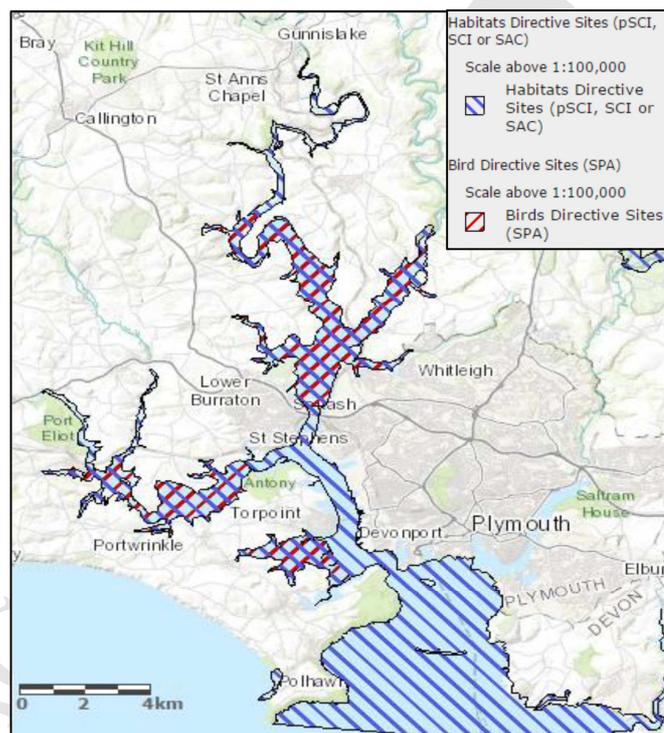
85 (2) a pre-management period with high nutrient levels (Tamar 1992; Eden 1999);

86 (3) a post-management period after the implementation of mitigation measures following long  
87 periods of hypernutrification (Tamar 2005; Eden 2015).

## 88 2.1 A brief description of the ecosystems

### 89 Tamar Estuary (50021' N, 004010' W).

90 The Tamar estuary is a medium sized (31 km-long) estuary situated on the border between Cornwall  
91 and Devon on the south-west coast of England (Figure 1). The estuary itself comprises a complex of  
92 marine inlets (rias) stretching from Gunnislake weir (upper tidal limit) to Plymouth Sound (lower  
93 tidal limit) (Money *et al.*, 2011). Together, the Tamar Estuaries Complex (encompassing the River  
94 Lynher and St John's Lake in addition to the Tamar–Tavy, and hereafter referred to as the Tamar  
95 estuary) and Plymouth Sound, are designated as a Special Area of Conservation (SAC) under the  
96 European Union's Habitats Directive (92/43/EEC) and a Special Protected Area (SPA) under the  
97 European Commission Directive on the Conservation of Wild Birds (79/409/EEC). The many different  
98 habitats within the Tamar estuary, have been studied intensively for more than a century by  
99 researchers of the Marine Biological Association (MBA), University of Plymouth (UoP) and Plymouth  
100 Marine Laboratories (PML), who have conducted numerous hydrographic, chemical and biological  
101 surveys in the Western English Channel, including Plymouth Sound and Tamar estuary (see  
102 Southward & Roberts, 1987 for historical perspective). As a result, the Tamar estuary and its  
103 surrounding waters is one of the best documented estuarine complexes in the UK and is ideally  
104 suited to conducting seascape-scale or systems-based research.



118 **Figure 1:** Map of the Tamar Estuary and Plymouth Sound European Marine Site. © Copyright European  
119 Environment Agency (EEA)

120 In common with many British estuaries, from the 1980s to the early 1990s, the Tamar experienced  
121 significant nitrogen and phosphorous enrichment due to excessive agricultural run-off due to land  
122 use changes in the upper catchment (Knox *et al.*, 1986), while sewage discharges constituted  
123 localised chronic contamination and nutrient-associated water quality problems in the lower estuary  
124 (Morris *et al.*, 1981; 1986; Readman *et al.*, 1986). As a result during these periods the system was  
125 considered eutrophic, with respect to nitrogen under criteria proposed by Dodds *et al.* (1997) (>1.5

126 mg/L<sup>-1</sup>) and the EU guideline of 9 (µg/L<sup>-1</sup>) for the protection of course freshwater fish, but not  
 127 considered polluted in terms of nitrogen according to criteria under the Nitrates Directive (>5.65  
 128 mg/L<sup>-1</sup>) for official designation as a eutrophic system (Table 1). This culminated during the period of  
 129 1990 when low river flows, high water residence times and high nutrient concentrations in the form  
 130 of phosphorous compounds, interrupted upstream communication with the upper portion of the  
 131 system, resulting in large blooms of benthic microalgae and increased biomass of macroalgae across  
 132 the estuary. The resultant conditions included widespread salmonid fish deaths caused by localized  
 133 areas of low oxygen conditions (Darbyshire, 1996; Harris, 1988; 1992), in addition to relatively low  
 134 pHs and high suspended solids (trapped in the upper estuary following spring tides), leading to  
 135 reported changes in biodiversity and functioning of the system. During this period annual reactive  
 136 phosphorous concentrations exceeded 100 (µg/L) and the Tamar was officially classed as eutrophic  
 137 using interim standards set by the Environment Agency (EA, 1998). Following a recovery period the  
 138 following year, in 1992 various management efforts such as the “New South West – Clean Sweep  
 139 and Beyond project” and the “Plymouth Urban Diffuse Pollution Project” were put in place to clean  
 140 up nutrient related issues across the estuary. As a result, much of the eutrophic symptoms  
 141 associated with the early 1990’s had subsided by the early 2000’s. For example average reactable  
 142 phosphorus concentrations were shown to decrease from 1990 levels of 110(µg/L<sup>-1</sup>) to 63(µg/L<sup>-1</sup>) for  
 143 the period of 1992 and to an even lower 47 (µg/L) by 2005 (Mankasingh, 2005).

144 **Table 1:** Summary of annual average concentrations of environmental variables for the Tamar  
 145 Estuary (1990-2005).

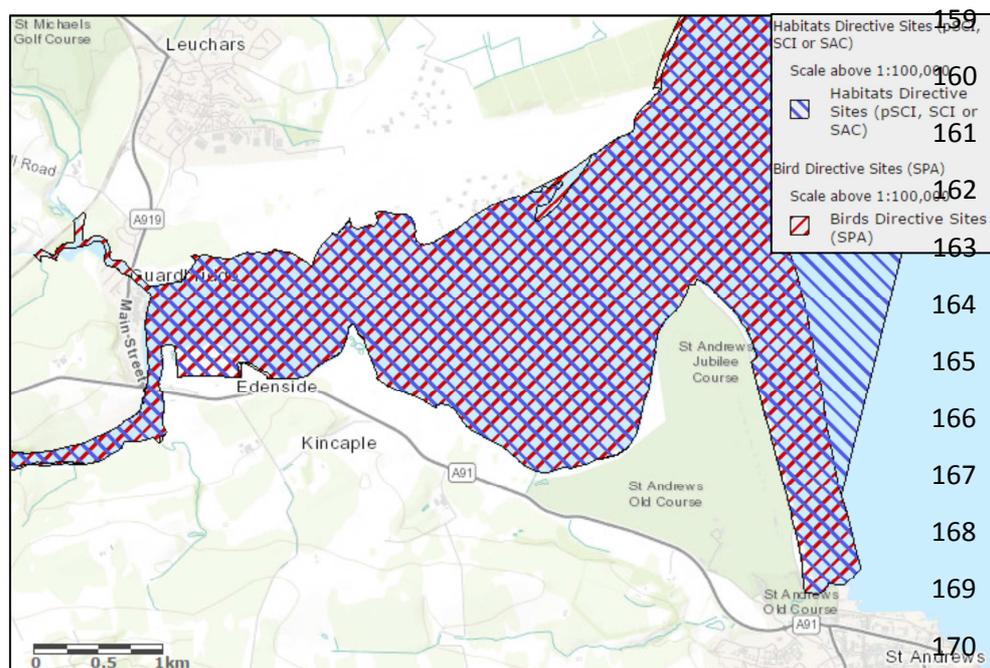
Variable/Year	1990	1992	2005	Source
Ammonium (mg l <sup>-1</sup> )	0.07	0.04	0.02	Mankasingh, (2005)
Biochemical oxygen demand (mg l <sup>-1</sup> )	2.11	1.52	1.10	Environment Agency
Chlorophyll <i>a</i> (mg l <sup>-1</sup> )	29.55	6.98	6.32	Environment Agency
Dissolved oxygen (mg l <sup>-1</sup> )	10.00	10.76	10.29	Environment Agency
Filterable reactive phosphorous (µg l <sup>-1</sup> )	110	63	47	Mankasingh, (2005)
Nitrate (mg l <sup>-1</sup> )	11.65	12.10	12.61	Mankasingh, (2005)
Nitrite (mg l <sup>-1</sup> )	0.03	0.02	0.008	Mankasingh, (2005)
pH	6.33	7.70	7.59	Environment Agency
River flow (m <sup>-3/s</sup> )	3.48	8.65	4.01	The National River Flow Archive (NRFA) Gunnislake gauging station.
Surface salinity (ppt)	17.56	16.30	16.91	Environment Agency
Temperature(°C)	12.10	11.08	11.95	Environment Agency

146

#### 147 **Eden estuary (56022' N, 2050' W)**

148 In comparison with the Tamar, the Eden Estuary is a small (11km-long) shallow bar built or ‘pocket’  
 149 estuary, located between the village of Guardbridge and the town of St Andrews on the East coast of  
 150 Scotland (Figure 2). Collectively the Eden estuary along with the Firth of Tay Estuary is designated as  
 151 a Special Area of Conservation (SAC) under the European Union’s Habitats Directive (92/43/EEC) and  
 152 a Special Protection Area (SPA) under the European Commission Directive on the Conservation of  
 153 Wild Birds (79/409/EEC). The main channel of the estuary is flanked by relatively wide intertidal  
 154 areas (8km<sup>2</sup>) that plays host to large populations of overwintering waterfowl and wading bird  
 155 species. Historically the intertidal mud and sand flats of the estuary have been sampled intensively  
 156 by researchers from the University of St Andrews, with many studies undertaken from of the Gatty

157 Marine Laboratory (Bennett & McLeod, 1998) providing a robust baseline from which to draw  
 158 comparisons.



171 **Figure 2:** Map of the Eden Estuary European Marine Site. © Copyright European Environment Agency  
 172 (EEA).

173 Anthropogenic pressure in the form of increased nutrients from arable and livestock production is  
 174 one of the most significant pressures influencing the Eden with high levels of nitrogen compounds  
 175 entering the estuary *via* the river Eden (Clelland, 1997). Historically this has led to a number of  
 176 ecological problems such as the closure of mussel beds as unfit for human consumption and  
 177 widespread fish mortalities (Defew & Paterson, 2009). As a consequence the catchment was  
 178 designated as a nitrate vulnerable zone in 2003 (SEERAD, 2003). Nutrient inputs are now in decline  
 179 (Table 2) thanks to increased legislation resulting from the Nitrates Directive (NVZ) and Sensitive  
 180 Area (UWWTD) designations (Macgregor & Warren, 2015), including an upgrade of the Guardbridge  
 181 sewage treatment works in 2008 and the closure of the Guardbridge paper mill and adjacent pig  
 182 farm with their associated effluent.

183 **Table 2:** Summary of annual average concentrations of environmental variables for the Eden Estuary  
 184 (1999-2015).

Variable /Year	1999	2015	Source
Ammonium ( $\text{mg l}^{-1}$ )	0.091	0.048	Environment Agency
Chlorophyll <i>a</i> ( $\text{mg l}^{-1}$ )	10.56	4.28	Environment Agency
Dissolved oxygen ( $\text{mg l}^{-1}$ )	11.39	10.74	Environment Agency
Filterable reactive phosphorus ( $\text{mg l}^{-1}$ )	0.23	0.098	Environment Agency
Nitrate ( $\text{mg l}^{-1}$ )	7.72	5.82	Environment Agency
Nitrite ( $\text{mg l}^{-1}$ )	0.035	0.015	Environment Agency
pH	7.92	8.11	Environment Agency
River flow ( $\text{m}^3/\text{s}$ )	2.67	2.13	The National River Flow Archive (NRFA) Kemback gauging station.
Temperature ( $^{\circ}\text{C}$ )	9.45	10.10	Environment Agency

185 **2.2 Materials & Methods**

186 Biomass flow networks ( $t/km^2/yr^{-1}$ ) were constructed for the systems outlined above, using the  
 187 “Ecopath with Ecosim” software package (v6.5) for the years 1990, 1992 and 2005 (Tamar) and 1999  
 188 and 2015 (Eden) representing eutrophic and post-eutrophic systems. Ecopath trophic models are  
 189 mass balance models that create a static snapshot of energy flows and their interactions in an  
 190 ecosystem represented by trophically linked biomass ‘pools’ or ecological guilds of species (Pauly *et*  
 191 *al.*, 2000). In a model, the energy input and output of all living groups must be balanced. Ecopath  
 192 parameterizes models based on two master equations one to describe the production term and one  
 193 for the energy balance of each group (Christensen *et al.*, 2005). The first equation divides the  
 194 production of each compartment into individual components. This is implemented with the  
 195 equation:

196 Production = total fishery catch rate + predation mortality + biomass accumulation + net migration +  
 197 other mortality

198 Or, more formally,

$$B_i \times \left(\frac{P}{B}\right)_i - \sum_j \left(B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij}\right) - Y_i - BA_i - E_i = 0 \quad \text{Equation 1}$$

199

200 Where  $B_i$  and  $B_j$  are the biomasses of prey (i) and predators (j) respectively;  $P/B_i$  the  
 201 production/biomass ratio;  $EE_i$  the ecotrophic efficiency which describes the proportion of the  
 202 production that is utilized in the system;  $Y_i$  the fisheries catch per unit area and time;  $Q/B_j$  the food  
 203 consumption per unit biomass of j;  $DC_{ij}$  the fraction of prey i in the average diet of predator j;  $BA_i$  the  
 204 biomass accumulation rate for i (the default value of zero was used to indicate no biomass  
 205 accumulation); and  $E_i$  is the net migration of i, calculated as immigration (migration into the area  
 206 covered by the model) minus emigration (migration out of the area, the default value of zero was  
 207 used). Within the model, biomass was expressed as tonnes  $km^{-2}$  and production and consumption as  
 208 tonnes  $km^{-2} yr^{-1}$ .

209 Equation two expresses how the energy balance within each compartment is ensured when  
 210 consumption by prey biomass = production + respiration + unassimilated food

211 Or, more formally,

$$B_i \left(\frac{Q}{B}\right)_i = B_i \times \left(\frac{P}{B}\right)_i + R_i + U_i \quad \text{Equation 2}$$

212

213 where  $R_i$  is the respiration rate, and  $U_i$  the unassimilated food rate. Respiration is used in Ecopath,  
 214 only for balancing the flows between groups and refers to the assimilated fraction of matter that is  
 215 not used in production. Following other estuarine Ecopath models (e.g. Baeta *et al.*, 2011), it is  
 216 assumed that autotrophs and detritus based organisms have zero respiration with all nutrients that  
 217 leave the compartment being re-utilized. For each compartment unassimilated food ( $U_i$ ) consists of  
 218 food which is egested and flows to the detritus. Following Christensen *et al.* (2000), our models used  
 219 a  $U_i$  default value of 0.20 for all groups (i.e. 20% of the consumption for all groups).

220 **2.2.1 Sampling methods and data collection**

221 Chlorophyll *a* measures provided by the Environment agency (Table 2) for each catchment were  
222 transformed into a proxy for phytoplankton biomass using a conversion factor taken from Anderson  
223 & Williams (1998). Quantitative biomass data for the main benthic primary producers  
224 (microphytobenthos, macroalgae and other macrophytes) at the estuarine scale were made using  
225 the Ecopath model based on case study specific estimates of their production, using data from small  
226 scale *in situ* measurements (e.g. Bale *et al.*, 2006) and knowledge of other trophic assemblages.  
227 Model biomass estimates were examined and compared with the existing literature to ensure the  
228 predations were plausible. For instance, there have been a number of long-term biotope and aerial  
229 surveys of saltmarsh and macroalgal extent (Webster *et al.*, 1998; EA., 2000; Widdows *et al.*, 2007;  
230 Curtis *et al.*, 2010) on various regions of the Tamar complex. The macroalgal group here is likely to  
231 comprise of locally registered species such as *Enteromorpha* and *Ulvae spp.* while the 'other'  
232 macrophyte grouping is likely to comprise a wide variety of seagrass and saltmarsh species such as  
233 by not limited to: common saltmarsh-grass (*Puccinellia maritime*), common cord-grass (*Spartina*  
234 *anglica*), common eelgrass (*Zostera marina*), red fescue (*Festuca rubra*) and sea couch (*Elymus*  
235 *pycanthus*).

236 To obtain an approximate value for microphytobenthic biomass and production in the Eden system,  
237 contact cores were taken across identical transects of each of the three main zones of the estuary in  
238 1999 and 2015 by sampling the top 2 cm of the surface sediment (see Ford & Honeywill, 2002 for full  
239 protocols). The presence of macroalgae (biomass t km<sup>2</sup>) was estimated by a survey of macroalgae  
240 within 5m radius of each sampling point (Ford & Honeywill, 2002). Macroalgae were mostly  
241 identified to be *Enteromorpha* and *Ulvae spp.* Estimates of 'other' macrophytes in the system were  
242 calculated, based on known *in situ* estimates of saltmarsh extent and production (Fife Council, 2008;  
243 Maynard, 2003; 2014; Maynard *et al.*, 2011). Common species represented by this grouping were  
244 likely to include common saltmarsh-grass (*Puccinellia maritime*), sea clubrush (*Bolboschoenus*  
245 *maritimus*) and the eelgrasses (*Zostera augustifolia*), (*Z. noltii*), and (*Z. marina*).

246 In the Tamar system, invertebrate data from three studies allowed some inter-comparisons to be  
247 made at the estuarine scale at similar times of the year, using similar sampling methodologies  
248 (Watson *et al.*, 1995; SWW Tamar Estuary sublittoral sediment survey 1992 & Sanders, 2008). In the  
249 Eden estuary, extensive surveys of invertebrate data were collected in 2015 through identical  
250 surveys to those carried out in 1999 by the BIOPTIS programme (Watson *et al.*, 2018). During this  
251 campaign three sampling grids were established across three transitional areas of the estuary  
252 (Appendix A). Invertebrate densities for both systems were converted to biomasses using case  
253 study-specific relationships (e.g., Dashfield & McNeill, 2014 Tamar & Biles *et al.*, 2002 Eden).  
254 Invertebrate species that were not naturally present in one of the years or sites or whose roles in the  
255 trophic network were unimportant (biomass < 0.01 t/km<sup>2</sup>) were not taken into account.

256 Data on demersal fish species and epibenthic crustaceans could not be collected at the estuarine  
257 level in each system for practical reasons. However, historical fisheries-independent trawl surveys  
258 mainly undertaken by Russel (1973), McHugh *et al.* (2011) & Dando (2011) reveal a relative temporal  
259 consistency in the overall numbers of flatfish and epibenthic crustaceans in the Tamar estuary  
260 between historic (1970 & 1980) and contemporary (2009) trawls. Similar observations into the  
261 autecology of the brown shrimp (*Crangon crangon*) by Henderson *et al.* (1987; 1990) and later by  
262 Campos *et al.* (2008; 2009; 2012) across several British estuaries including the Tamar suggest a  
263 consistency in the population structure and phylogeography of this species over our study period.  
264 Therefore, given that the spatial structure of the demersal fish and caridean shrimp assemblage has  
265 remained relatively constant, similar biomass values for each of these taxa were used over the time  
266 periods. Data on fish populations in the Eden were also unattainable from the literature due to a  
267 paucity of fish monitoring surveys within the estuarine complex. Demersal fish biomass estimates  
268 were therefore estimated by Ecopath, based on P/B, Q/B and EE. Data on epibenthic crustacean  
269 numbers, most specifically the brown shrimp (*Crangon crangon*) were obtained as part of the  
270 aforementioned macrobenthic invertebrate data collection.

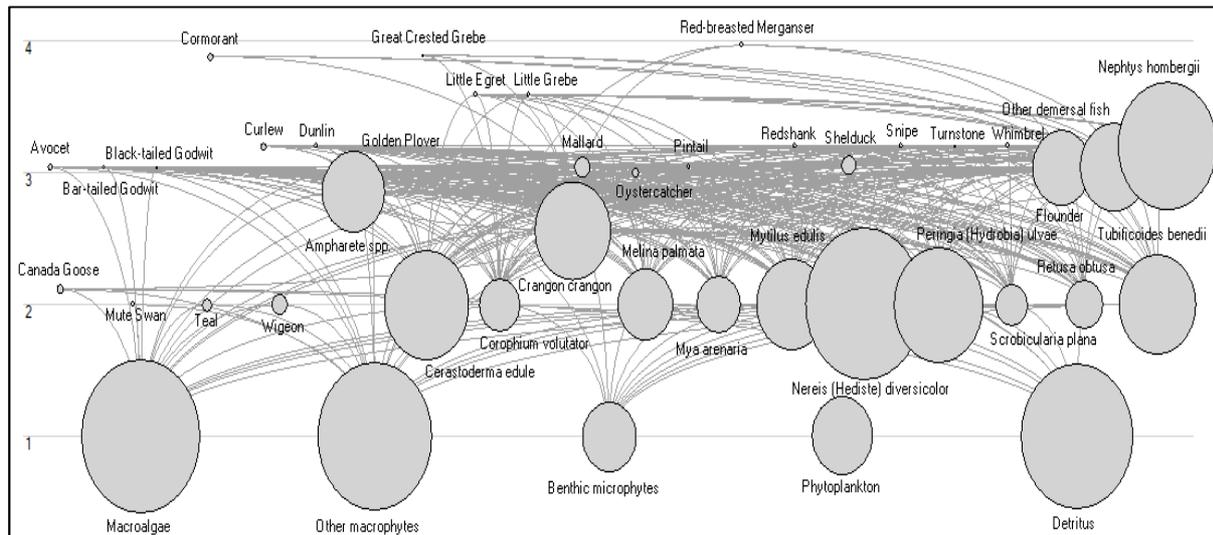
271 Population numbers for waterbirds in both systems were obtained for the period 1990-2015 from  
272 the WeBS (Wetland Birds Survey) database (Frost *et al.*, 2016). Bird counts were based on monthly  
273 observations across 15 (Tamar) & 5 sectors (Eden) covering the whole of each respective complex.  
274 Twenty-three waterbird species were selected from the Tamar system and Eighteen waterbird  
275 species from the Eden system (representing >95% of the total bird numbers in each system, with  
276 those excluded largely representing seabird species) from a list of local species known to inhabit and  
277 feed on the estuary recurrently, to increase the chance of interoperating temporal changes. Prior to  
278 analysis counts were converted to biomasses using species specific body weights outlined by Snow &  
279 Perrins (1998).

### 280 **2.2.2 Compartments**

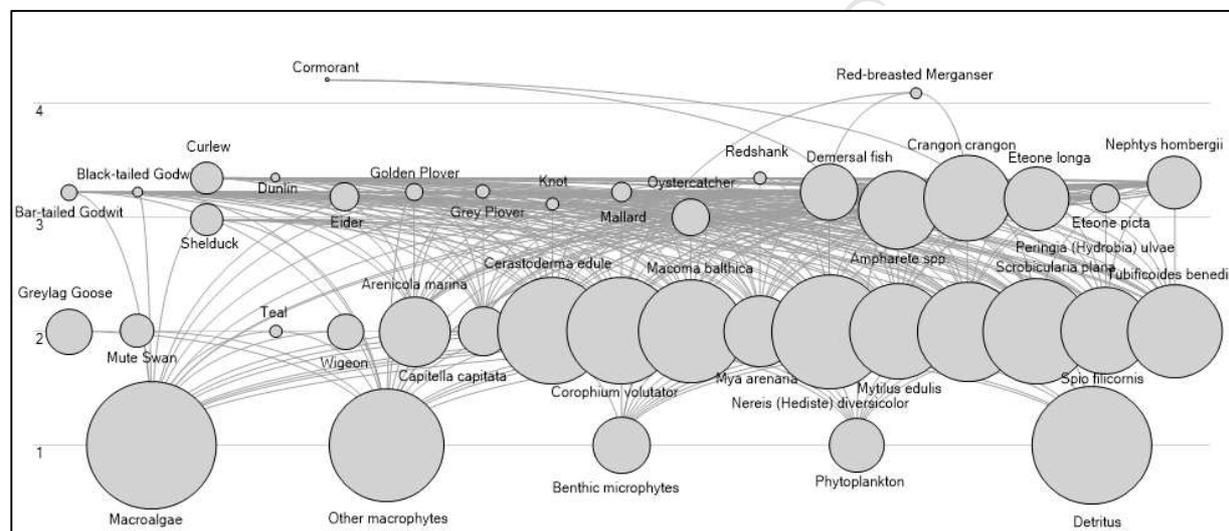
281 Some groups of species were grouped into compartments based on similar ecological niches. The  
282 benthic-microalgae group here is primarily composed of freshwater and marine diatoms with no  
283 single species dominating the community throughout the year. In the case of the Tamar, demersal  
284 fish species were amalgamated into one compartment comprising sole (*Microstomus kitt*), turbot  
285 (*Phrynorhombus norvegicus*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). In the  
286 Tamar Estuary, the flounder (*Platichthys flesus*) was considered as a separate compartment being  
287 the only ray-finned demersal fish to migrate and colonize the upper reaches of the estuary due to its  
288 considerable powers of osmoregulation (Hartley, 1940; 1947). In the Eden Estuary, the demersal fish  
289 fish identity was assumed to be a combination of all benthic fish species know to occur within the  
290 estuary. In all models, invertebrate species belonging to family Ampharetidae were grouped  
291 together, with many of these species sharing a functional role. No data were available for bacteria,  
292 therefore the benthic bacterial biomass was considered has being part of the detritus compartment,  
293 as recommended by Christensen and Pauly (1992a, b).

### 294 **2.2.3 Ecopath food webs and trophic structure**

295 The final versions of the Tamar (Figure 3) and Eden (Figure 4) food webs comprised 43 and 41 taxa  
296 respectively, distributed over four trophic levels



297 **Figure 3** 2D representation of the food web from the Tamar Estuary (1990).



298 **Figure 4** 2D representation of the food web from the Eden Estuary (1999).

299 Whilst phytoplankton and benthic-microalgae are included due to their known importance in  
 300 structuring benthic ecosystems, other water column elements (zooplankton, planktivorous fish (e.g.  
 301 shad, sand eel) and their consumers (species in the family *Salmonidae*) were not included in this  
 302 model and are considered to follow a separate pelagic trophic pathway (Hall & Raffaelli, 1991). This  
 303 is due to both planktonic and benthic networks of cycling representing independent domains of  
 304 control (Baird & Ulanowicz, 1989), with benthic-microalgae constituting a significant proportion of  
 305 benthic estuarine ecosystem functioning. This model instead centres on a detritus based pathway  
 306 with particulate organic matter passing through micro-phytobenthos to macro-invertebrates to fish  
 307 or birds (e.g. Raffaelli, 2011) and a second pathway is also used from macroalgae to macro-  
 308 invertebrates or herbivorous wildfowl (Baird & Milne, 1981). In addition, although the harbour seal  
 309 (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) are known to roam freely through the Eden  
 310 Estuary (and to a lesser extent the lower Tamar Estuary), they were not included in either modelling  
 311 framework due to their diets mainly consisting of planktivorous fish (e.g. sandeels, whiting and  
 312 species of the family *Salmonidae*) foraged out with the estuarine area in question. For instance  
 313 Sharples *et al.*, (2009), noted in a study of the diet of harbour seals in the Eden and adjacent St.  
 314 Andrews Bay to consist of 81 to 94% sandeels in winter and 63% in summer and autumn, with  
 315 salmonids making up the remaining prey captured.

#### 316 2.2.4 Production, consumption and diet composition

317 Production/Biomass ratios required for Ecopath were collected from a number of web-based  
318 databases (e.g., Fishbase (Froese & Pauly, 2016) and WeBS database (Frost *et al.*, 2016)). For all  
319 vertebrate groups this information was readily available from these databases. For avian species,  
320 production was calculated as recruitment (R) of young into the adult population in units per  
321 individual (tonnes per year; Stenseth, 2002). For the primary producer and invertebrate groups,  
322 Brey's (2001) Virtual Handbook on Population Dynamics, version 4 (Brey, 2012) was used to  
323 calculate the P/B for all species. The weight-to-energy ratios needed in order to apply the empirical  
324 method were also provided by Brey (2001). In the case of combined groups the means of each  
325 component parameters, were weighted by the relative biomass of the components. For all  
326 heterotrophic compartments, Production/ Consumption ratios were entered into the program in  
327 order to estimate the Consumption /Biomass ratio's indirectly. The only exception was in the case of  
328 demersal fish species where a holistic predictive model for Consumption/Biomass using asymptotic  
329 weight, habitat temperature, a morphological variable and food type as independent variables were  
330 calculated using Fishbase

331 Diet matrices were built for each taxa using information from a wide variety of literary sources and  
332 summed to unity. Resident invertebrate diet compositions was compiled largely from MBA data  
333 holdings including MARLIN and BIOTIC databases while shorebird and flatfish data referenced from  
334 the WeBS and Fishbase databases respectively. Complimentary diet information was also gathered  
335 from the literature (see Appendix B for all diet references). Initially all species were listed from each  
336 taxa along with their percentage contribution to the compartment. Each observed dietary item was  
337 then assigned to each individual group of species, with the final percentage of the diet assumed to  
338 be proportional to the fraction that its biomass comprised of the total biomass of the functional  
339 group.

#### 340 2.2.5 Anthropogenic exports (Yi)

341 A complete mass balanced model needs estimates of the export rates from the system, including the  
342 harvesting of economically important species. Commercial flat fishing mortality by means of landings  
343 from the Tamar was considered sufficiently small enough to be negligible, based on records of  
344 numbers of fish caught of species of 130 mm and upwards (Clark, 2012). Commercial fishing effort  
345 on the Eden Estuary was also considered to be minor, with the estuary and surrounding St Andrews  
346 Bay protected by a Scottish Inshore Fishing Order (1989) which forbids the use of all mobile fishing  
347 gears, including trawling and dredging practices within the area. Similarly the harvesting of  
348 commercial invertebrate species such as *Cerastoderma edule*, *Mytilus edulis*, *Hediste diversicolor*,  
349 *Nephtys hombergii* and *Crangon crangon* for bait fisheries or human consumption was considered  
350 insignificant in terms of overall biomass export from the system Tamar (Curtis, 2010) and Eden  
351 where bait collection is strictly controlled.

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### 360 **2.2.6 Pre-balancing analysis (PREBAL)**

361 To add rigor and validity to the models a set of pre-balance diagnostics (PREBAL) outlined by Link  
362 (2010) and recommended by Heymans *et al.* (2016) were made to assess any issues with the models  
363 structure or quality of the primary input data. First the logarithmic ratios of biomass among various  
364 taxa groups were plotted (Appendix C) as they have been repeatedly identified as a major indicator  
365 of marine ecosystem functioning (Link, 2005; Mokany *et al.*, 2016). Generally biomass  
366 decomposition generally followed a sequential decrease moving across trophic levels. While detrital  
367 groups were not used it is noted for context that detrital standing stocks were on the same order of  
368 magnitude as primary producer biomass, consistent with systems such as estuaries and benthic  
369 orientated food webs that are particularly dependent upon detrital energy. In a second step, the  
370 vital rates of all taxa, in the form of Production/Biomass ratio and Consumption/Biomass ratio were  
371 plotted (Appendix C) for comparison, as these ratios are reflective of an amalgamation of an entire  
372 suite of physiological processes. As with the biomass estimates, there was an acceptable decline in  
373 vital rates with increasing trophic level.

374

### 375 **2.2.7 Balancing the models**

376 Using the ecological and thermodynamic rules for balancing Ecopath models outlined by Darwall *et al.*,  
377 (2010) elements of the diet matrix or the values of the three inputted parameters were adjusted  
378 iteratively until all logical constraints were met. This was done starting with the lowest quality data  
379 first, preserving the most reliable data. In both the Tamar and Eden case studies, the most reliable  
380 data were the biomass and production values, and consequently these values were left largely  
381 unchanged. Diet matrices were principally unaltered but differed slightly to reflect the known  
382 trophic responses of species to different pressures. In all incidences the balancing parameter  
383 changes fell within the ranges of uncertainty associated the development of the 'pedigree'— a  
384 routine in Ecopath modelling that quantifies the quality of the input data by assigning confidence  
385 intervals based on the origin of the information. The pedigree index P calculated for the Tamar  
386 models was 0.481 and 0.593 for the Eden, with the higher latter value reflecting the use of locally  
387 collected data and trophic information used to parameterise the models. The various parameters for  
388 the balanced Ecopath models of the Tamar and Eden ecosystems are presented in (Appendix D).

### 389 **2.2.8 Summary of system statistics and indices**

390 After mass-balancing the models, a number of indices that describe the structure, function and  
391 resilience of each system as a whole were calculated using a suite of Ecological Network Analysis  
392 (ENA) algorithms incorporated into Ecopath (Christensen *et al.*, 2005). A summary of each index  
393 chosen is given in Table 3.

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402 **Table 3 Selected Ecological Network Analysis (ENA) indicators**

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System Indices	Description	Units
Sum of all consumption ( $\Sigma C$ ),	$\Sigma C$ is the sum of all consumption in a system.	$t\ km^{-2}\ yr^{-1}$
Respiratory flows ( $\Sigma R$ )	$\Sigma R$ is the sum of all respiratory flows in a system.	$t\ km^{-2}\ yr^{-1}$
Flows to detritus ( $\Sigma FtD$ )	$\Sigma FtD$ consists of what is egested (the non-assimilated food) and those elements of the groups, which die of old age, diseases, etc.	$t\ km^{-2}\ yr^{-1}$
Production ( $\Sigma P$ )	$\Sigma P$ is the sum of all production flows in a system.	$t\ km^{-2}\ yr^{-1}$
Total system throughput (TST)	TST represents the entire amount of biomass flow within the system (consumption + export + flows to detritus + respiration) and represents the size of the system (Ulanowicz, 1986). As such, it is an important parameter for comparisons of trophic flow networks	$t\ km^{-2}\ yr^{-1}$
Total biomass (excluding detritus) ( $\Sigma B$ )	Total biomass in the system excluding detritus.	$t\ km^{-2}$
Total primary production/total biomass (PP/B),	PP/B, is expected to be a function of the system's maturity (Odum, 1969).	The PP/B ratio can take any positive value and is dimensionless.
Primary production/respiration (PP/R)	PP/R, is the difference between total primary production and total respiration. It is considered by Odum (1971) to be an important ratio for description of the maturity of an ecosystem.	The PP/R ratio can take any positive value and is dimensionless.
Total throughput cycled (T cycled)	T cycled is the fraction of, an ecosystem's throughput that is recycled.	$t\ km^{-2}\ yr^{-1}$
Finn's index (CI)	CI captures the functions of carbon and nutrient cycling in the system using a proxy of (% of total throughput).	% of total throughput
Predatory cycling index (PI)	PI is a slightly modified form of the CI index, computed after cycles involving detritus groups have been removed.	% of throughput w/o detritus
Average path length (APL)	APL measures the average number of transfers a unit of medium (e.g. carbon) will experience from its entry into the system until it leaves the system (Baird <i>et al.</i> , 1991).	The APL is a positive value and is dimensionless.
The system omnivory index (SOI)	SOI specifies how consumer feeding interactions are distributed across trophic levels. A value close to 0 indicates the consumer is specialised (i.e. it feeds on one trophic level) while a higher value indicates a diet composed of prey across many trophic levels (Christensen <i>et al.</i> , 2000).	The SOI is a positive value and is dimensionless.
Ascendency (A)	A represents both the size and organisation of a system (Ulanowicz, 1986, 1997). Ascendency is a measure of a systems stability and a proxy for a systems resilience.	Flowbits or the product of flow (e.g., $t/km^2/year$ )
Development capacity (C)	C represents the upper limit for the size of the Ascendency. Both ascendency and capacity are measures of a systems stability and resilience.	Flowbits or the product of flow
System Overhead (O)	O is the difference between capacity and ascendency and is also a measure of system resilience. Higher system overheads indicate that a system has a larger amount of energy in reserve (in flowbits) with which it can use to resist impacts (Ulanowicz, 1986). Overhead is also defined as the pathway redundancy (Ulanowicz, 1997).	Flowbits or the product of flow

### 404 3 Results and discussion

#### 405 3.1 Statistics of ecological functioning and network structure

406 To quantify the difference within and between the two systems it was necessary to compare the  
407 relative magnitude of change in their various system information indices (Table 4). One clear  
408 comparison between the networks is that the Tamar is far more active than the Eden, its total  
409 system throughput ( $23464 \text{ t km}^{-2} \text{ yr}^{-1}$ , 2005, defined as the sum of all flows in the system) is almost  
410 25% larger than that of the Eden ( $17957 \text{ t km}^{-2} \text{ yr}^{-1}$ , 2015). Some of the higher activity in the Tamar  
411 can be attributed to its greater size and freshwater inputs than the Eden, but higher nutrient inputs  
412 to the Tamar are also likely to enhance its activity. Because total system throughput scales all  
413 information indices, the ascendancy and other related variables are uniformly greater for the Tamar.  
414 Despite the topological network differences of each system, in both systems, Total biomass  
415 (excluding detritus) decreased substantially between the pre and post-management periods. The  
416 impact of these changes was reflected by falls in many of the system indices including: consumption,  
417 respiratory flows, flows to detritus, and net primary production. There is also evidence that the size  
418 (TST) or 'power' of each system decreased greatly between the focal periods. These changes were  
419 almost certainly attributed to the direct bottom up-effects of nutrient reductions which altered the  
420 abundance of benthic primary producers, with cascading consequences on invertebrate and  
421 waterbird species at higher trophic levels. These changes were also responsible for changes in  
422 secondary production and a number of higher level systems metrics. The effects are believable, not  
423 because of a statistically rigorous experimental design, but because the effect sizes are very large,  
424 and the altered biodiversity and ecological functioning are clearly different relative to the post  
425 management periods.

426 Associated with TST, the network characteristics of the Tamar and Eden ascendancy (A), capacity (C)  
427 and overhead (O), all decreased considerably by the post-management periods. This is consistent  
428 with Ulanowicz's (1980;86) interpretation that nutrient perturbed systems can be defined by any  
429 increase in system ascendancy that causes a rise in total system throughput (TST), that more than  
430 compensates for any fall in the mutual information content (e.g. A, C or O) of the system. In other  
431 words, the greater nutrient inputs tend to simulate a systems growth but despite its augmented  
432 activity, its organisation or structure is degraded.

433 Relative ascendancy (A/C) was very similar between pre and post-management periods, suggesting  
434 that each system was able to accommodate (or resist) the large-scale changes in nutrient loading,  
435 primary production, and invertebrate biomass. When only the relative fluxes are concerned, the  
436 Tamar Estuary showed a decline of -1.19% in ascendancy (A/C) relative to a larger change of -3.66%  
437 in internal  $A_i/C_i$  by the 2005 period, indicating a higher dependency of this system on connections  
438 to adjacent ecological and physical systems (e.g. the Western English Channel). In contrast, internal  
439 relative ascendancy ( $A_i/C_i$ ) remained relatively similar between the periods (+0.53%) in the Eden  
440 system, indicating that this system has maintained its activity without too much dependence on  
441 external system connections. As the degree to which environmental change is likely to influence  
442 ecosystem resilience will depend on metacommunity structure and connectance (Dunne *et al.*, 2002;  
443 Fung *et al.*, 2015), the (A/C) index could therefore be a suitable indicator to compare ecosystems of  
444 different sizes (e.g. Mann *et al.*, 1989, Baird *et al.*, 1991).

445

446 **Table 4** Summary of ecological and network statistics/indices for the Tamar and Eden estuarine  
 447 systems.

Estuary	Tamar			Eden		Units
	1990	1992	2005	1999	2015	
Sum of all consumption ( $\Sigma C$ )	27416	27790	12254	26122	9386	t km <sup>-2</sup> yr <sup>-1</sup>
Sum of all respiratory flows ( $\Sigma R$ )	16474	16698	7373	15696	5648	t km <sup>-2</sup> yr <sup>-1</sup>
Sum of all flows into detritus ( $\Sigma FtD$ )	60403	6379	2982	5763	2121	t km <sup>-2</sup> yr <sup>-1</sup>
Sum of all production ( $\Sigma P$ )	11508	10863	7156	8560	3860	t km <sup>-2</sup> yr <sup>-1</sup>
Total system throughput (TST)	54675	55592	23464	50526	17957	t km <sup>-2</sup> yr <sup>-1</sup>
Total biomass (excluding detritus) ( $\Sigma B$ )	2680	2617	1703	1926	958	t km <sup>-2</sup> yr <sup>-1</sup>
Total primary production/total biomass (PP/B)	2.320	2.036	2,774	1.74	1.88	-
Total primary production/total respiration (PP/R)	0.367	0.319	0.641	0.21	0.35	-
Ascendency (A)	77715	79561	29844	68252	23523	Flowbits
Capacity (Ca)	256513	273649	127706	294697	84797	Flowbits
Overhead (O)	178798	194088	97862	226445	108320	Flowbits
Relative ascendency (A/C)%	30.02	30.68	31.21	23.16	29.21	%
Internal ascendency (IA)	47448	48099	20390	45641	15763	Flowbits
Internal capacity (IC)	175004	189876	89455	193430	75478	Flowbits
Internal overhead (IO)	127556	141777	69066	147047	59715	Flowbits
Internal relative ascendency (Ai/Ci)%	27.08	26.54	23.42	23.32	23.85	%

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### 449 3.2 Cycling structure

450 As making judgment about the trophic status of two entire ecosystems based on a few information  
 451 indices may seem precarious to some (Ulanowicz, 2004; Fath *et al.*, 2007), comparisons between the  
 452 Tamar and Eden ecosystems were supported by a broader analysis of the two networks. Support for  
 453 comparisons were made by considering the trophic structure and cycling pathways contained within  
 454 the two ecosystems. Because each trophic pathway is a series of interconnected cycles, stressors  
 455 occurring at any point will disrupt flow to higher levels (Voris *et al.*, 1980; Ulanowicz, 1983). We  
 456 would expect therefore, that systems with greater resistance to and resilience from nutrient stress  
 457 to be more complex, in the sense that they contain longer loops of connections that cycle at lower  
 458 frequencies. Conversely, systems under increased nutrient stress would possess fewer such cycles,  
 459 due to link disruptions, and each cycle would transfer less medium, particularly to higher trophic  
 460 levels (Baird & Ulanowicz, 1993). Indeed this is what the comparison shows: the cycles derived from  
 461 the Tamar and Eden systems were deficient both in number and length under high nutrient levels  
 462 consistent with hypothesis that systems with longer cycles and low proportions of cycling are  
 463 indications of less stressed systems.

464

465 Considering the magnitude of mineral and nutrient cycling within the Tamar system, Finns Index (CI)  
 466 increased between both periods by ~10 & 30% respectively (Table 5), while the Predatory cycling  
 467 index (PI) increased initially by 0.18% but then decreased by 0.59%. Together these changes point to  
 468 a general increase in the detrital cycling process, but a fall in the predatory species contribution to  
 469 these processes. Networks of cycled flows for the Tamar show that the total number of cycles in the  
 470 system is sixteen, with these cycles distributed to varying degrees though three cycling nexuses  
 471 (cycles having the same smallest transfer is called a nexus (Baird *et al.*, 1991)).

472 **Table 5** Cycle distributions of the Tamar and Eden systems

Distribution (%) of cycles per nexus	Tamar			Eden	
	1990	1992	2005	1999	2015
1	16.67	16.67	16.67	10	10
2	50	50	50	40	40
3	33.33	33.33	33.33	30	30
4	0	0	0	20	20
Number of cycles	16	16	16	10	10
Average path length (API)	2.681	2.716	2.945	2.82	2.90
Throughput cycled (including detritus) t km <sup>-2</sup> yr <sup>-1</sup>	1034	1014	984	1395	754
Throughput cycled (excluding detritus) t km <sup>-2</sup> yr <sup>-1</sup>	290	365	449.34	12.52	33.29
Throughput cycled (by detritus) %	72.76	66.06	93.4	99.02	95.52
Predatory cycling index (PI) % of throughput w/o detritus	0.68	0.86	0.27	0.03	0.24
Finn's cycling index (CI) % of total throughput	10.90	20.76	40.54	19.08	40.37

473  
 474 The API of associated cycles, and throughput of material cycled (including detritus) was fairly  
 475 consistent across the study period (2.6-2.9 and 1034-984 t km<sup>-2</sup> yr<sup>-1</sup> respectively), indicating that  
 476 flows of cycling were consistently occurring over short and fast loops. The percentage of material  
 477 specifically cycled by the detritus compartment was also proportionately high (>72%), with  
 478 increasing importance by the 2005 period (>93%).

479 In comparison with the Tamar, the cycling structure of the Eden estuary consisted of a total of ten  
 480 cycles, distributed to varying degrees though four cycling nexuses (Table 5). The API of associated  
 481 cycles, was fairly consistent between the study periods (2.8-2.9) specifying that flows of cycling were  
 482 occurring over short and fast loops. The percentage of material specifically cycled by the detritus  
 483 compartment was also proportionately very high (>95%), with around about a 4% shift towards non-  
 484 detritus based cycling during the 2015 period. Indices representing the regulating and cycling of  
 485 nutrients in a system (CI and PI) also increased during the 2015 period, suggesting greater system  
 486 retentiveness and a greater proportion of material cycled across both higher and lower trophic  
 487 levels (Odum, 1969). Both estuaries were found to recycle a large proportion of their material  
 488 though short-fast cycles, with the majority of matter (e.g. carbon) being retained for approximately  
 489 2-3 cycles. The increasingly high CI index indicates both estuaries have a relatively simple cycling  
 490 structure with both CI and API of a similar order as other estuaries with a legacy of nutrient  
 491 contamination e.g. the Ythan Scotland (Baird & Ulanowicz, 199), with a study by Raffaelli (2011) also  
 492 showing a similar increase in the CI index under a period of nutrient reduction.

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**496 3.3 A safe operational space**

497 In addition to managing stocks and flows, environmental managers often need to know if a  
498 particular model projection (or policy option) will push the system being managed into a potentially  
499 unsafe state (i.e. whether a system will cross a critical threshold or tipping point). Thus, scientists  
500 and managers invested in considering a whole-systems approach may not be interested in the  
501 marginal changes of all species (Donohue *et al.*, 2013), but instead whether the system is capable of  
502 accommodating potential changes while retaining its capacity to function while remaining within its  
503 “safe-operating” space, and hence is resilient (Raffaelli, 2016). While it should be accepted that no  
504 single descriptor can fully accommodate the multifaceted nature of ecosystem resilience (Ulanowicz,  
505 1992), one possible way to derive system-level measures of resilience, is to adopt a holistic systems  
506 approach rather than trying to measure the independent trajectories of several indicators. In  
507 particular, Ulanowicz (2011) has argued that the network metric, “ascendency,” has a restricted set  
508 of values for real-world ecosystems, where a system lacking ascendency has neither the extent of  
509 activity nor the internal organization needed to function sustainably. By contrast, systems that are  
510 so tightly constrained and honed to a particular environment appear “brittle” (in the sense of  
511 Holling (1986)) are prone to collapse in the face of even minor novel disturbances (Ulanowicz *et al.*,  
512 2009). Systems that endure lie somewhere between these extremes, with such networks falling  
513 within a “Window of Vitality” (Ulanowicz, 2005). Further, Zorach & Ulanowicz (2003) have  
514 demonstrated that such connections within the “Window of Vitality” can be adequately captured  
515 using the structural properties of networks. Thus by plotting such variables, scientists and managers  
516 can make *a priori* predictions about the preferential loss or reduction of stocks (e.g. species,  
517 populations, communities), against the effects on ecosystem functioning in relation to a “safe  
518 operating space” (Raffaelli, 2015; 2016). Such an approach also allows trade-offs between different  
519 network configurations that support different management and policy options be considered (e.g.  
520 under the impacts of different nutrient regimes). In this way different modelling scenarios or  
521 management choices can be assessed in a cost effective and canonical way, without the need to  
522 disturb natural ecosystems (Dunne & Williams, 2009).

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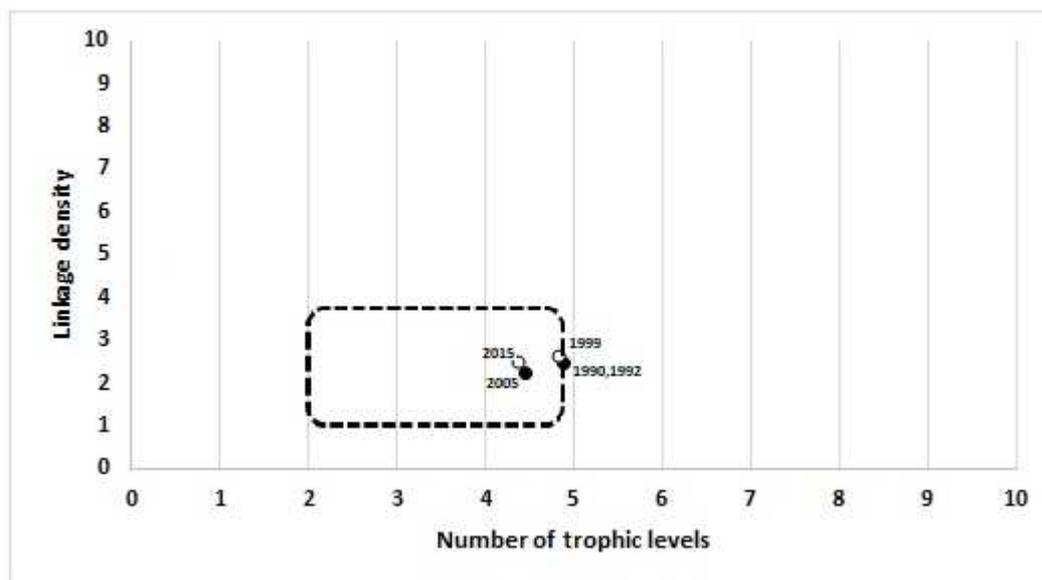
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537 **Figure 5** The “safe operating zone” (delineated by dotted lines) for the Tamar (Black circles) and  
 538 Eden (White circles) estuaries defined by ascendancy considerations and captured by two simple  
 539 topological properties of food webs: linkage density and number of trophic levels.

540 Encompassing the changes in ascendancy for the Tamar and Eden time periods within Ulanowicz’s  
 541 “Window of Vitality” (Figure 5), linkage density and number of trophic levels were shown to be very  
 542 different between the pre- and post-management periods. This would locate the post-management  
 543 Tamar and Eden periods within the right-hand boundary of the box in Figure 5. In contrast, during  
 544 the high nutrient periods in both systems graduated towards the top right area of the perimeter  
 545 space, with the Tamar effectively moving close to leaving the defined “safe operating zone”. Under  
 546 such circumstances, the results would indicate that the Eden system was able to accommodate  
 547 historic large scale effects of changes in nutrient loading over the investigated periods, while the  
 548 Tamar was operating in a relatively unsustainable state in the 1990’s and relative to its less disturbed  
 549 state in 2005. Implications for the Tamar in its high nutrient state would suggest that some trophic  
 550 pathways may have narrowed, leaving the system less resilient with insufficient reserves to resist  
 551 future disturbances (Ulanowicz, 2002). Subsequently both systems have moved closer to the  
 552 geometric centre of the window ( $c = 1.25$  and  $n = 3.25$ ) which represents the best possible  
 553 configuration for system sustainability (Ulanowicz *et al.*, 2009).

554 Overall, the system resilience measures used here suggest that large scale shifts in the nutrient  
 555 balance of each estuary did not move the systems out of their safe space, which might give grounds  
 556 for optimism of traditionally high nutrient systems such as estuaries (Leschine *et al.*, 2003; Elliott &  
 557 Whitfield, 2011). Nonetheless, both versions of the Tamar and Eden networks were close to the  
 558 “safe” operational boundary during the high nutrient periods and still remain just on the right of the  
 559 Ulanowicz’s ascendancy curve, and at the top left corner of his “Window of Vitality”. The question  
 560 remains as to whether future stressors acting additively or synergistically with changes in nutrient  
 561 loading (e.g. increased river flow or water temperatures) could push the systems out of their safe  
 562 space. By plotting the values of the three variables related to Ulanowicz’s (2005) “Window of  
 563 Vitality” for many ecosystems under different environmental pressures, it may become possible to  
 564 identify a region in perimeter space that characterises a generic healthy and robust ecosystem  
 565 (Raffaelli, 2015).

566

### 567 3.4 Model limitations

568 When interpreting the modelled outputs from this study, several assumptions and limitations of  
569 model capability must be considered. Firstly, the development of an Ecopath model strongly  
570 depends on the quality of data used to build the model (Christensen & Walters, 2004). In this study,  
571 the data for almost all groups (Biomass, P/B, Q/B) were derived from site and time specific raw  
572 databases or stock specific assessments providing a solid background for dynamic modelling.  
573 However, for groups that play an important role in the Tamar or Eden estuaries food–web but for  
574 which no or very little data was available, i.e. certain macrofauna or meiofauna, their omission from  
575 the developed ecological networks may have led to an oversimplification in the structure of all food–  
576 web components. A specific lack of long term continuous biomass monitoring data in both case  
577 study areas, particularly for invertebrates and demersal fish, was also a specific limitation in  
578 validating historic trends and improving the validity of future predicted outcomes. Moreover, due to  
579 lack of specific knowledge, several functional groups have been aggregated, e.g. demersal fish  
580 potentially masking important species interactions (Essington, 2006). Other important factors that  
581 this study did not attempt to represent included the variability of future changing climate  
582 forcing/environmental or management regimes the adaptive potential of species (e.g. by affecting  
583 refuge and breeding space, altering animal behaviour, affecting hydrodynamic transports). While  
584 some of these uncertainties could be addressed by further laboratory experiments and *in situ*  
585 monitoring of ecosystem conditions, temporal variations in species-specific habitat factors, e.g. a  
586 loss of habitat, cannot be addressed in Ecopath but instead needs a spatial model (e.g. the Ecospace  
587 component of Ecopath with Ecosim, Christensen & Walters, 2004). We also acknowledge the need to  
588 raise the standards of Ecopath models in a management context (Heymans *et al.*, 2011; 2016), with  
589 similar standards needed in exploring ecosystem theory (Pocock *et al.*, 2016). Within the last few  
590 years, a growing number of diagnostic checks, including the PREBAL checks used in this paper, have  
591 been developed to establish best practices in creating and using such models (Mackinson *et al.*,  
592 2009; Darwall *et al.*, 2010; Link, 2010; Heymans *et al.*, 2016; Scott *et al.*, 2016). These guidelines take  
593 into consideration the underlying thermodynamic and ecological rules available to users,  
594 recommend approaches to balance an Ecopath model, and how to evaluate uncertainty. In practice  
595 if these practices are upheld, it would allow not only more rigorous and consistent models, but  
596 would also aid in the acceptance of Ecopath and other mass balance models within science and  
597 management.

### 598 4 Conclusions

600 The process of constructing the Ecopath models here provides a valuable end product in itself  
601 through explicit synthesis of work from many researchers and has allowed a summarising of our  
602 current knowledge of the trophic flows, cycling structure and potential safe operational space of two  
603 estuaries with ongoing managing challenges associated with eutrophication. The models also help to  
604 highlight potential system specific data gaps (e.g. diet compositions, site-specific P/B, Q/B ratios, fish  
605 population numbers), that if collected in the future could be used to enhance and improve the  
606 knowledge of each system. The results of the mass balanced models show that the trophic structure,  
607 ecological functioning and general resilience of both the Tamer and Eden estuaries were affected  
608 similarly following distinct restoration events. This adds further evidence that reducing nutrient  
609 inputs to estuarine systems is not only beneficial to the biodiversity elements of a system (Howarth  
610 *et al.*, 2011), but also has wider positive implications on a wide range of important system properties  
611 which may only be revealed at the system level (Raffaelli, 2006). By understanding the recovery  
612 trajectory of individual systems and the metrics that can describe such responses, such information  
613 can be of direct relevance to many scientific and regulatory frameworks (Duarte *et al.*, 2015), for

614 example the European Water Framework Directive (WFD) in its pursuit to assess benthic integrity  
615 and determining good ecological status (GES). In the systems studied here, the shifts in the vast  
616 majority of the structural and functional indicators were generally consistent with recovery  
617 trajectories described for other UK and European Ecopath studies on nutrient disturbed systems  
618 (Patrício & Marques, 2006; Baeta *et al.*, 2011; Raffaelli, 2011; Selleslagh *et al.*, 2012). This supports  
619 the usefulness of ENA type approaches for assessing the recovery patterns of temperate transitional  
620 benthic systems. As scientists using the “Ecosystem Approach” are increasingly interested in how  
621 different impacts or recovery options will simultaneously change the ecological functioning of a  
622 system (Bennett, 2015) we also suggest that the comparison of information indices between  
623 networks when complemented by the inherent analysis of cycles can comprise a useful quantitative  
624 approach for inter-ecosystem comparisons (Wulff & Ulanowicz, 1989). Moreover, while the use of  
625 ENA modelling is extremely useful in establishing possible disturbance effects, one difficulty with the  
626 use of ecological models might be translating these results to stakeholders in an effective manner,  
627 (Fulton, 2011). As such, transforming process based models into simple graphical descriptions of risk  
628 may be useful to illustrate the integrity of the networks to future change. As coastal systems are  
629 host to a complex array of interactions between multiple stressors (Jackson *et al.*, 2016), a key next  
630 step will be to focus on the underlying processes and mechanisms whereby the stressors affecting  
631 these ecosystems interact.

632

## 633 **5 Acknowledgements**

634 This work [NERC Grant Ref: NE/K501244/1] was funded with support from the Biodiversity and  
635 Ecosystem Service Sustainability (BESS) programme. BESS is a six-year programme (2011-2017)  
636 funded by the UK Natural Environment Research Council (NERC) and the Biotechnology and  
637 Biological Sciences Research Council (BBSRC) as part of the UK’s Living with Environmental Change  
638 (LWEC) programme. This work presents the outcomes of independent research funded by the  
639 Natural Environment Research Council through the Biodiversity and Ecosystem Service Sustainability  
640 (BESS) programme. The views expressed are those of the author(s) and not necessarily those of the  
641 BESS Directorate or NERC. DMP also received funding from the MASTS pooling initiative (The Marine  
642 Alliance for Science and Technology for Scotland) and their support is gratefully acknowledged.  
643 MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing  
644 institutions. We are grateful to Dr Sheila Heymans (The Scottish Association for Marine Science,  
645 SAMS) and Dr Paul Somerfield (Plymouth Marine Laboratory) for their advice and for providing data  
646 for this project.

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