

A comparison of energy flow through the Dublin Bay and Baie de Somme intertidal ecosystems and their network analysis

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Abstract Energy (biomass) and energy flows (production, inputs, transfers and losses) were calculated for eight and twelve compartment systems (phytoplankton, benthic primary producers (macroalgae, microphytobenthos), zooplankton, benthos (meiofauna, suspensivores, depositivores and predators), fish, birds and particulate organic matter (POM) in sediment and suspended particulate matter (SPM)) both balanced and unbalanced of Dublin Bay and the Baie de Somme. The resultant models were analysed with the Scientific Committee on Oceanic Research (SCOR) network analysis package. While the two systems share many properties such as the dominant biosedimentary facies, there are fundamental differences in both structuring and responses of the systems. The network analysis suggested that the Baie de Somme was far more productive, notably in terms of water column productivity, and was the more mature system.

The high organic SPM input to Dublin Bay greatly elevated the degree of detritivory such that the analysis generated metrics indicative of a mature system but which rather reflected the degree of anthropogenic stress on the system. However, the analysis of both systems displayed varying degrees of maturity. Increasing the number of compartments greatly increased the calculated throughput (T) of the system and other associated metrics such as capacity (C), ascendancy (A) and redundancy (R). In the case of Dublin Bay, a higher number of compartments increased the various measures of system maturity, but this was much less marked for the Baie de Somme. Balancing the systems also increased T, C, A and R, and, to a lesser extent but not invariably, the system maturity metrics. The ratios of the comparative system metrics such as comparative ascendancy (A/C) were much less changed by the different methodologies and as such are recommended as robust measures for intercomparison of system performance.

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Consequences of estuarine management on
hydrodynamics and ecological functioning

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Introduction

Network analysis began with the quantitative analysis of interconnections pioneered by the

economist Leontief (1941) as input-output (I-O) analysis and was adapted for the analysis of ecological systems. The Scientific Committee on Oceanic Research (SCOR), have promoted network analysis with the aim of affording an ecosystem researcher or manager several new avenues for extracting heretofore unavailable information about the flows of material or energy in the ecosystem (Wulff et al., 1989). Clues about how an ecosystem may be reacting to a perturbation are often manifested first as changes in the relationships such as trophic transfers among the constituent taxa and these ideas have been explored more fully by Ulanowicz (1986, 1997) and Kay (1984). Under Odum's (1969) classification, systems display a range of characteristics in terms of organisation, of energy flow and of biodiversity along a gradient from immature (or developing) systems to mature, harking back to the classical models of succession to a final climax community (Clements, 1936). This has proved a useful framework within which ecological network analysis (ENA) may be evaluated, although, as with all generalisations, detailed examination has shown that there are over-simplifications. For instance, the highest biodiversity has been shown (e.g. Connell, 1978; Dial & Roughgarden, 1998) to be associated with intermediately-disturbed (i.e. prevented from attaining maturity) systems (rather than with completely undisturbed systems as Odum's (1969) scheme would predict). Various other workers, notably Gray (1981) and Warwick (Warwick, 1986; Warwick & Clarke, 2001) have explored the concept of maturity and how it might be assessed, principally in relation to benthic macrofaunal community structure, and throughout, Pearson & Rosenberg's (1978) model is universally acknowledged. Nevertheless, although there is nowhere near the same weight of evidence for his conclusions about system function as there is for community structure, Odum's (1969) ideas have received general acceptance and simple measures of biodiversity such as the Shannon-Weiner Index (H') are now in everyday use to assess maturity, degree of disturbance or pollution stress (Wilson & Jeffrey, 1994).

Opinions on the pollution status of Dublin Bay have been equivocal (Wilson et al., 1990; Wilson

& Elkaim, 1991; Wilson & Jeffrey, 1994; Roth & Wilson, 1998), but point to a range of problems in the way that the system functions, and these indications are reinforced by the pollution indices indicating considerable local problems from urban pressures (Jeffrey et al., 1985, 1991; Wilson & Parkes, 1999). Population densities of infaunal invertebrates are rather low (West et al., 1979; Wilson 1982) yet the Bay supports large numbers of overwintering wildfowl and parts are designated under both national and international (e.g. UNESCO Biosphere, RAMSAR) protection.

In contrast to Dublin Bay, the Baie de Somme is surrounded by a largely rural catchment and the major input of contaminants, both in the form of microbiological pathogens and nutrients, is the largely canalised River Somme. Secondary productivity, notably in the inner Baie de Somme is extremely high (McLusky et al., 1991, 1994) and this sustains not only an important wildfowl population again of national and international importance but also a commercial *peche à pied* for the cockle, *Cerastoderma edule*. As with Dublin Bay, pollution impacts are generally confined to localised areas (Wilson et al., 1986) but on occasion the system may overload resulting in widespread anoxia and mortalities of benthic macrofauna (Rybarczyk et al., 1996). Comparisons of the two systems are available for some parameters, such as the *C. edule* and *Macoma balthica* populations (Ducrotoy et al., 1991; Desprez et al., 1991) and for pollution status (Wilson & Elkaim, 1991).

Network analyses are now available for a range of marine and estuarine systems (Baird & Ulanowicz, 1993; Rybarczyk & Elkaim, 2003) and preliminary analyses are available for both Dublin Bay (Wilson & Parkes, 1999) and the Baie de Somme (Rybarczyk et al., 2003). In this study we extend these analyses to a direct comparison of the latter two systems.

Materials and methods

For this analysis, the Dublin Bay system was taken as being bounded by the high water mark (HWM) to the landward side (effectively up to the various structures and defences around the

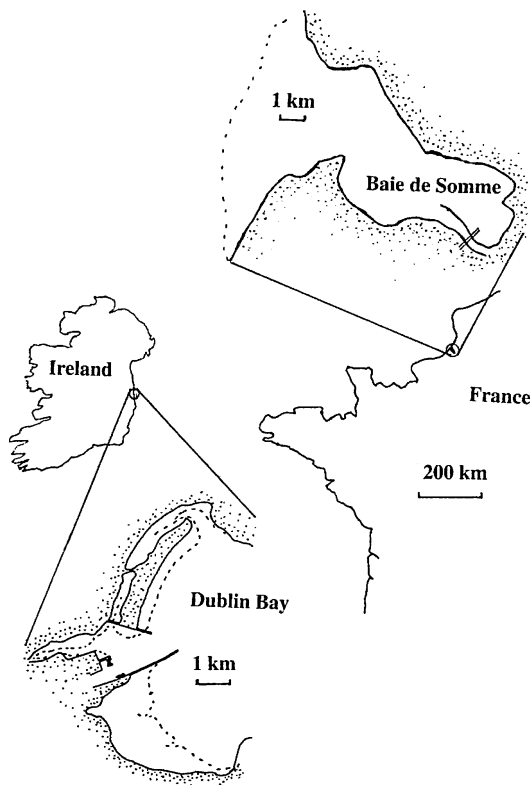


Fig. 1 Dublin Bay and Baie de Somme, showing location and extent of intertidal area (dashed line)

Bay) out to ELWS as defined by the sampling sites of Wilson (1982) (Fig. 1). The Baie de Somme is more open, and the seaward boundary was set to enclose the major intertidal biosedimentary facies in the Baie (Rybarczyk et al., 2003) with the landward boundary set in part by walls and other structures, but also by the saltmarsh to the north and east (Fig. 1). A

Table 1 Physical comparison of Dublin Bay and the Baie de Somme. See also text for discussion

Parameter	Dublin Bay	Baie de Somme
Mean tidal range (m)	2.75	7.5
Intertidal area (km ²)	18.6	50.0
Total volume (m ³)	2.6×10^7	2.0×10^8
Freshwater input (m ³ d ⁻¹)	2.3×10^6	2.85×10^6
Salinity outside bay	33.06	31.56
Mean salinity inside bay	31.25	28.86
Turnover rate (T, days)	3.57	8.0
Volume exchanged per day (m ³ d ⁻¹)	7.2×10^6	5.26×10^7

summary of the various physical parameters of the two bays is listed in Table 1.

The Somme is the larger of the two bays and in addition is a macrotidal estuary with tides of up to 11 m. Consequently the Baie de Somme has a much larger intertidal area and tidal exchange, but the riverine input to the two bays is almost the same as is the bays' turnover rate (Table 1).

For the present comparison two webs were constructed. The first was a simple web comprising just 8 compartments: benthic system (sediment OM, primary producers and macrobenthos), planktonic system (SPOM, phytoplankton, zooplankton) and top consumers (fish and birds). For the second comparison, a more complex web was constructed in which the major individual contributing elements were separated. This yielded a 12 compartment system namely phytoplankton; benthic primary producers partitioned into macroalgae and microphytobenthos; zooplankton; benthic invertebrates partitioned into suspensivores, depositivores and predators; nekton; birds (herbivores and predators); and particulate organic matter (POM) in sediments and in SPM. As with the constrained web, the latter two were the non-living compartments and accounted for the collective detritus in the food web. A distinction between living (i.e. producing) compartments and non-living compartments is necessary for the trophic analysis.

In each compartment, values must be entered for the biomass (standing stock), imports (primary productivity and input from outside the system), exports (outside the system), and dissipation (usable respiration) vectors. In addition, productivity values were calculated as part of the trophic web. Unless otherwise specified below, calculations and allocated values followed those detailed in Wilson & Parkes (1999) and Rybarczyk et al. (2003). For Dublin Bay, the data had to be altered such that the intertidal alone was considered, while for the Somme, which drains completely at low tide, the overall data could be used.

Macroalgae

Macroalgae were included with microphytobenthos in the simple (8) system, although calculated

separately by Wilson & Parkes (1999) for Dublin Bay. Macroalgae are practically absent from the Baie de Somme, although obviously locally present. To maintain consistency between the two system structures in the complex (12) web, macroalgae in the Baie de Somme were assigned nominal values of biomass of 0.01 kJ m^{-2} and of transfer to geese/widgeon of $0.001 \text{ kJ m}^{-2} \text{ y}^{-1}$.

Meiofauna

Meiofauna was introduced as a new compartment to both systems. For Dublin Bay, meiofaunal data were based on abundances as counted by Bourke (2001) with conversions to biomass and productivity rates as set out in Schwinghamer et al. (1986) for nematodes, which constituted almost 95% of the meiofauna. For the Baie de Somme, biomass and rates were based on the data of McLusky et al. (1994) for oligochaetes.

Macrobenthos

The consolidated data for Dublin bay (Wilson & Parkes, 1999) were re-allocated to suspensivore, depositivore or predator as for the Baie de Somme (Rybarczyk et al., 2003). The basic data for both systems were unchanged.

Fish

The fish data for Dublin bay refer wholly to the sublittoral, so unpublished data from Koutsogiannopoulou (Zoology Dept., TCD) were used to calculate a minimal biomass for the intertidal area. Though locally present in channels in high abundances, these fish were mainly small juveniles giving a much smaller biomass (0.02 kJ m^{-2}) than for the whole Dublin Bay system.

SPM

Data are available for marine contribution to the Baie de Somme system and this has been incorporated in to the trophic web (Rybarczyk et al., 2003). No such data are available for Dublin bay, and evidence for net import or export within the system is equivocal (Wilson et al., 2002), so a small net export, reflecting the relative volume of

the FW input over the year was calculated at $192.4 \text{ kJ m}^{-2} \text{ y}^{-1}$.

Results

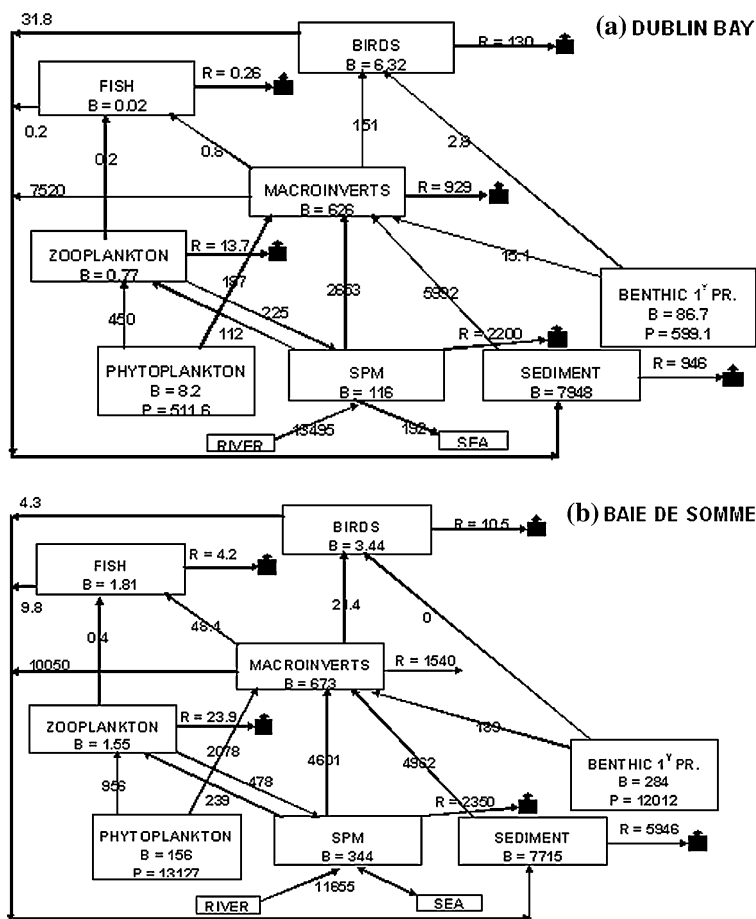
Food webs

Four food webs were produced for each system (Fig. 2a–d, 3a–d for 8-compartment and 12-compartment webs respectively). The basic webs were calculated as detailed above, and include estimates of the tidal exchanges. A great deal of water is exchanged daily in both systems, so any small change in the amount of suspended material will have radical consequences for the calculations. While neither budget studies nor flume-based calculations have produced statistically reliable data, it has been suggested that the balance (import/export) of tidal exchanges with coastal systems and estuaries varies according to a range of factors, and has been linked to the maturity of the system, to tidal amplitude (spring/neap) and to stochastic events such as rainfall (Dame & Stilwell, 1984; Dame et al., 1991) or wind strength and direction as has been shown in Dublin Bay (Wilson et al., 2002).

The two systems are remarkably similar in many respects, and indeed the major differences are in the water column, notably SPM input and primary productivity. Tidal exchange is of course much greater in the Baie de Somme, as might be expected in a macrotidal system, and although river contributions per unit area are very much more in Dublin bay, the total inputs to the two bays differ little. The concentration of SPM (including of course resuspended microphytobenthos) is almost an order of magnitude higher in the Baie de Somme, and while some of this may be due to the greater scouring of macrotidal currents, some may also be due to the much higher phytoplankton biomass and productivity (because phytoplankton cannot be separated out from the sampling and analysis of the SPM) in the Somme.

Both phytoplankton and microphytobenthos are much more productive in the Baie de Somme than in Dublin bay, and even adding in the Dublin bay macroalgal contribution still leaves total primary productivity lower in Dublin. As

Fig. 2 Energy (kJ m^{-2}) and flows ($\text{kJ m}^{-2} \text{y}^{-1}$) through 8-compartment systems: **(a)** Dublin Bay, **(b)** Baie de Somme. Arrows indicate direction of transfers between compartments; B = biomass, R = respiration



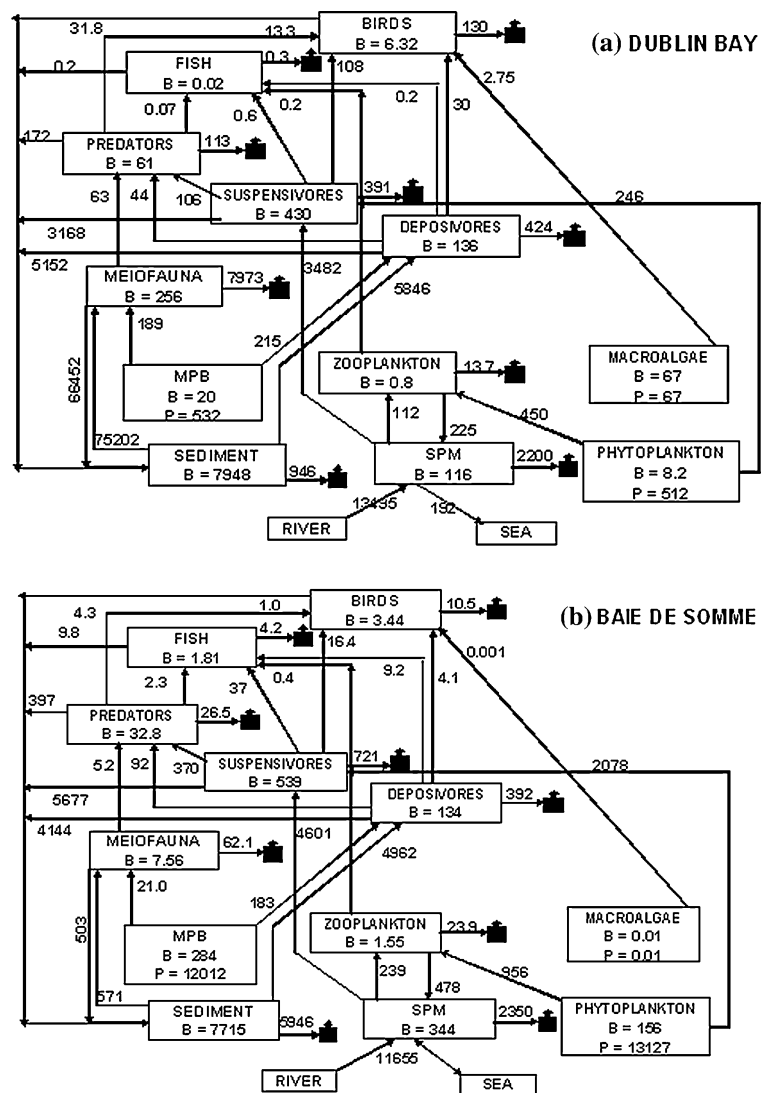
there are no striking differences between the higher levels of the two trophic systems, and that the various grazing pressures (zooplankton, invertebrates) are almost equal, it would appear therefore that primary productivity is not under top-down control. Primary production of all forms in both systems greatly exceeds consumption by secondary producers.

While both systems receive very high inputs of nutrients, in the case of Dublin bay the macroalgal growth has been strongly linked to settlement and remineralisation of nutrients in particulate form. In the higher energy system of the Baie de Somme particulate nutrients may be kept in suspension (as evidenced by the high SPM loadings) and the flushing itself may hinder attachment of macroalgae. This may explain to some extent the fact that eutrophication in Dublin Bay presents itself in the form of macroalgal mats,

while in the Baie de Somme it presents as phytoplankton blooms (Jeffrey et al., 1995; Rybarczyk et al., 1996).

As with other turbid estuarine situations, the major physical factor exerting bottom-up control may be light attenuation (McMahon et al., 1992; Heip et al., 1995), although under this scenario it might have been expected that the less turbid location (Dublin bay) would have the higher primary productivity. That this is not the case suggests another factor or factors may also be involved and one obvious influence is tidal exchange and the flushing and dilution of Dublin Bay waters with those of the adjacent coastal systems. Under these conditions, the constant exchange prevents bloom development in Dublin Bay, while offshore, the mixing depth consistently exceeds the critical depth (O'Higgins & Wilson, 2005).

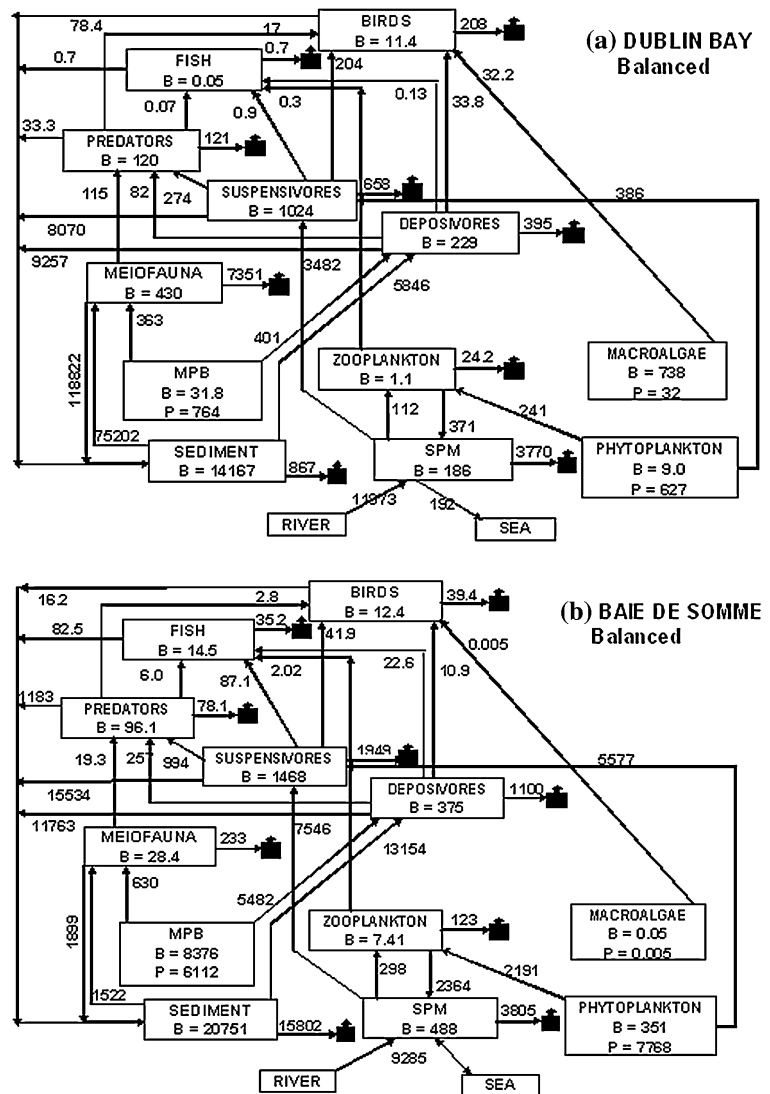
Fig. 3 Energy (kJ m^{-2}) and flows ($\text{kJ m}^{-2} \text{y}^{-1}$) through 12-compartment systems: (a) Dublin Bay, (b) Baie de Somme. Notation as Fig. 2



In both systems, the predators (invertebrates, nekton and birds) consume a considerable proportion of the secondary producers, and it may be suggested that there is some sort of feedback control between the two levels. In the rich feeding grounds of the Wadden Sea, birds consume up to 15% of the intertidal benthic biomass (Petersen & Exo, 1999). However, other mechanisms have been implicated in population regulation of secondary producers. For the cockle *C. edule* in the Somme, these include both biological and physicochemical factors. The biological factors range from internal population regulation by self-thinning, in which juvenile

recruitment is inversely related to adult density (de Montaudouin & Bachelet, 1996), to external biological regulation via inter-specific competition and habitat modification by *Pygospio filicornis* (Ducrotot et al., 1991). Stochastic climatic factors which induce anoxia are examples of physical controls (Desprez et al., 1992; Rybarczyk et al., 1996). In Dublin bay, suggestions for the observed changes in cockle densities (which never reach the densities observed in the Somme) have included climate change, eutrophication and oystercatcher (*Haematopus ostralegus*) predation pressure (Wilson, 1993, 2001, 2005).

Fig. 4 Energy (kJ m^{-2}) and flows ($\text{kJ m}^{-2} \text{y}^{-1}$) through DATBAL balanced 12-compartment systems: (a) Dublin Bay, (b) Baie de Somme. Notation as Fig. 2



Birds are important higher trophic components of both systems, from the point of view of system function and from the point of view of management and conservation. Concern has been expressed about the carrying capacity of Dublin Bay in particular, the more so since changes in sewage treatment practice will greatly reduce the allochthonous organic input to the system, with possible consequences for secondary consumers and the birds which use them as a food source (Foley, 2002). Essink (2003) has reported a decline in macrobenthos and in birds in the Dollard estuary (Netherlands) following a reduction in organic waste discharge. The data presented here

suggest that while the budgets are more-or-less in balance, the inevitable uncertainties in the process models preclude any firm conclusion about the impact of the new sewage treatment works other than that the situation should be kept under close review and more accurate data sought as a matter of some importance.

Mathematical optimisation of the two networks can be generated through the routine DATBAL which balances the overall budget such that imports, exports and losses are in steady state.

The balanced food webs for the 12-compartment systems of Dublin Bay and the Baie de

Table 2 System metrics from ENA, showing symbols, summary comments and relation to system maturity (Ulanowicz, 1986, 1997; Wulff et al., 1989; Baird et al., 1991; Baird & Ulanowicz, 1993)

Measure, Symbol	Summary comments	Mature	Immature
Total system throughput, T	Sum of all flows; indicative of size (productivity) of system	High	High or low
Mean trophic efficiency	Mean of transfer efficiencies through trophic levels	–	–
Development capacity, C	Potential of network to develop: theoretical maximum of A	–	–
Ascendancy, A	Function of both size and organisation; increases with system maturity	High	Low
Redundancy, R	Parallel (alternative) pathways in system; detracts from C .	Low	High
Relative Ascendancy, A/C	Dimensionless; measures degree of development relative to potential. System comparator	High	Low
Relative Redundancy, R/C	Dimensionless; measures degree of redundancy relative to potential. System comparator	Low	High
Internal capacity, C_i	As C but calculated on internal exchanges alone	High	Low
Internal ascendancy, A_i	As A but calculated on internal exchanges alone	High	Low
Internal relative ascendancy, A_i/C_i	As A/C but calculated on internal exchanges alone: system comparator	High	Low
Flow diversity, C/T	Maximum if all flows are equal	High	Low
Relative Detritivory, D/T	Proportion of flows through detritus pathway in relation to total.	High ^a or low ^b	Low ^a or high ^b
Finn Cycling Index, FCI	Proportion recycled in relation to total flow	High ^a or low ^b	Low ^a or high ^b

^a Odum (1969); ^b Ulanowicz (1984)

Somme are shown in Fig. 4. The balancing routine leaves the essential pathways and structure unchanged, but the overall effect has been to increase the amounts of biomass and the flows (compare Fig. 3a, b with Fig. 4a, b). For example, bird biomass (and attendant flows) in both systems was substantially increased to give a remarkably similar amount for both systems (Fig. 4a, b). Despite this similarity in the top trophic level, the Baie de Somme has still the

higher biomass and flows in the lower trophic levels.

Three major points are evident from inspection of Figs. 2–4. Firstly, the Somme system has far higher levels of primary productivity than Dublin Bay, such that autotrophic production exceeds the heterotrophic consumption in the Somme system. To that extent, the Somme estuary is rather uncharacteristic, as most estuarine systems are heterotrophic rather than

Table 3 Network analysis metrics for 8-compartment systems of (1) Dublin Bay and (2) Baie de Somme: (A) unbalanced; (B) balanced with DATBAL

Measure/index	Dublin Bay		Baie de Somme	
	A	B Balanced	A	B Balanced
Total system through-put (T , $\text{kJ m}^{-2} \text{y}^{-1} \times 10^3$)	36.4	56.7	70.3	112.0
Mean trophic efficiency (%)	8.2	11.6	3.9	5.6
Development capacity (C , $\text{kJ; bits} \times 10^3$)	99.0	158	224	380
Ascendancy (A , $\text{kJ; bits} \times 10^3$)	56.1	81.1	100	172
Redundancy (R , $\text{kJ; bits} \times 10^3$)	18.9	36.4	37.3	105
Relative Ascendancy (A/C , %)	57.4	51.2	44.8	45.3
Relative Redundancy (R/C , %)	18.9	23.0	17.0	28.0
Internal capacity (C_i , $\text{kJ; bits} \times 10^3$)	51.3	87.4	89.6	206.8
Internal ascendancy (A_i , $\text{kJ; bits} \times 10^3$)	32.6	50.9	52.3	102.2
Internal relative ascendancy (A_i/C_i , %)	63.6	58.2	58.4	49.4
Flow diversity (C/T)	2.72	2.80	3.19	3.39
Relative Detritivory (D/T , %)	24.1	34.0	13.9	18.6
Finn Cycling Index (FCI)	0.34	0.52	0.15	0.24

autotrophic (Heip et al., 1995). Moreover, the Somme primary production is internally-generated (autochthonous) energy, as opposed to the allochthonous riverine and sewage input of OM in Dublin Bay, aligning the former more with mature systems and the latter more with immature systems under Odum's (1969) classification scheme.

Secondly, the Somme system has a strong water-column based pathway, with a considerable energy flow through the zooplankton. In contrast, the zooplankton in Dublin Bay mediates a small fraction of the total primary consumer flow, and what energy there is in the water column SPM and producers is largely channeled through the benthic invertebrates.

Thirdly, the addition of extra compartments to the two systems resulted in considerable changes to the Dublin Bay trophic net, but made very little difference to the Baie de Somme. As the same compartments were added to both, the conclusion is that it is the function of the added compartments which is important rather than the system structuring. For instance the addition of a minor compartment or link (e.g. herbivorous birds in the Baie de Somme) changes little, whereas a major compartment (e.g. meiofauna, Dublin Bay) makes a correspondingly bigger change. Thus, some prior knowledge or understanding of the system to be studied would seem to be crucial to the construction of the trophic web to get a meaningful network analysis, and such webs should not be based on theoretical grounds alone.

Finally, the DATBAL routine generates larger flows than those calculated in the original budgets. Two explanations suggest themselves. The first is that the original calculation of flows was based largely on models extrapolated from short-term laboratory or similar measurements, and as such need to be viewed with caution for annual calculations. However, there is no convincing argument as to why these should be consistently low: error is likely to be random, and in that case one might expect as many models to over-estimate as to under-estimate. The second is that all components of the system need not be in equilibrium, and artificially balancing input and output need not necessarily reflect the field

situation when measurements were made. It should also be noted that a different balancing algorithm to DATBAL might generate different flows again.

Network analysis results and discussion

The input data sets, that is the biomasses, the transfers between compartments and the losses (i.e. respiration) for the network analysis are shown in the form of energy flow diagrams in Figs. 2, 3 and 4. Full versions of the outputs are available from the authors on request.

The simple system, with only 8 compartments, makes some of the network analysis package output (for example linearity of food chains, recycling) self-evident and the following discussion concentrates on the system metrics (see Table 2 and references therein for explanation). Total throughput (T) is a measure of the productivity, and is independent of system maturity, the more so since under Odum's (1969) model, both mature and immature systems can display high productivity. However, there is increasing evidence that productivity is positively related to diversity (see e.g. Grime, 1997), and, since T measures all flows, the more complex the system, the higher the value of T that might be expected. Against this argument must be weighed the fact that estuarine systems are amongst the most productive known, despite a notable lack of biodiversity (Wilson, 2002). Other metrics such as development capacity (C), ascendancy (A) (and their internal equivalents C_i and A_i) and redundancy (R) have been suggested as indicators of system maturity (Ulanowicz, 1984, 1997), while their ratios, being dimensionless, provide a good basis for system intercomparison. The diversity of the flows (C/T) provides a measure of the evenness of the trophic links (*pace* Pielou's evenness, $J = H/H_{\max}$) with the same underlying assumption: the more mature the system, the lesser dominance of any one pathway. Detritivory (D) is a measure of the importance of the detritus pathway and provides an indication of the importance of recycling, that is internalising the flows, in a system, with the D/T ratio as a system comparator. The Finn Cycling Index (FCI) again indicates the capacity of the system to retain,

through internal recycling, energy, although there is some debate as to its meaning. Odum (1969) considered a high FCI to be indicative of a mature system, although Ulanowicz (1984) argued that a high FCI was indicative of stressed systems, in which the higher trophic levels were unduly impacted and the resultant paucity of the higher consumers induced more intense recycling in the lower trophic levels. Some degree of support for Ulanowicz's (1984) views has been suggested by the comparative analysis of Baird et al. (1991) of 6 marine ecosystems.

The network analysis output for the simple systems (Table 3) show that the higher primary production in the Baie de Somme is reflected in the higher total throughput (T) of the system. However, evidence for which system is the more mature is equivocal, with Dublin bay showing the higher values for trophic efficiency, A , A/C , R/C , A_i/C_i , D/T and FCI, while the Baie de Somme showed higher values for C , R , C_i , A_i and C/T .

Balancing the systems greatly increased the absolute values of measurements (T , C , A , R) but the ratios (A/C , R/C , A_i/C_i , D/T , C/T) were far less affected. Both the FCI and trophic efficiency improved considerably, but flow diversity was much less affected.

A similar pattern was observed for the output from the 12-compartment systems (Table 4), but with the important change that Dublin bay had now a much higher total throughput (T). All

measures increased in both systems and maturity metrics also improved in both systems.

Indeed the greater changes from 8-compartment system (Table 3) to 12-compartment system (Table 4) were seen in the Dublin Bay output. Mean trophic efficiency and flow diversity (C/T) decreased in Dublin bay (compared to an increase in the Baie de Somme) but relative detritivory (D/T) and FCI increased markedly, with the latter several-fold higher than in the Baie de Somme.

The various indices of system organisation for Dublin Bay and the Baie de Somme are shown in Table 5 along with a comparison with other estuarine and marine systems.

The various arrangements of the Dublin bay and Baie de Somme systems presented here generate metrics of a similar magnitude to those from elsewhere in almost all cases. However, the major difference lies in the degree of detritivory (D/T) and recycling (FCI) in the Dublin Bay system, which attain value almost twice those reported elsewhere (Table 5). It is suggested that this may be a consequence of the high allochthonous inputs to Dublin bay, which essentially drive the system and generate abnormally high values through the detritus pathway. These results strongly support Ulanowicz's (1984) contention that detritivory and recycling are associated with a stressed system, at least as far as marine systems are concerned.

Table 4 Network analysis metrics for 12-compartment systems of (1)Dublin Bay and (2) Baie de Somme: (A) unbalanced; (B) balanced with DATBAL

Measure/Index	Dublin Bay		Baie de Somme	
	A	B Balanced	A	B Balanced
Total System through-put (T , $\text{kJ m}^{-2} \text{y}^{-1} \times 10^3$)	188	250	71.7	117
Mean trophic efficiency (%)	5.3	4.9	4.1	5.4
Development capacity (C , $\text{kJ; bits} \times 10^3$)	445	570	250	457
Ascendancy (A , $\text{kJ; bits} \times 10^3$)	274	335	117	214
Redundancy (R , $\text{kJ; bits} \times 10^3$)	106	159	46.5	137
Relative Ascendancy (A/C , %)	61.6	58.7	46.7	46.8
Relative Redundancy (R/C , %)	23.7	27.9	18.6	29.9
Internal capacity (C_i , $\text{kJ; bits} \times 10^3$)	314	423	114	279
Internal ascendancy(A_i , $\text{kJ; bits} \times 10^3$)	208	264	67.8	142
Internal relative ascendancy (A_i/C_i , %)	66.4	62.5	59.3	50.9
Flow diversity (C/T)	2.36	2.28	3.49	3.91
Relative Detritivory (D/T , %)	44.9	33.8	14.5	19.2
Finn Cycling Index (FCI)	0.76	0.65	0.14	0.24

Table 5 Indices of system organisation for Dublin Bay and Baie de Somme (Wilson & Parkes, 1999; Rybarczyk et al., 2003, this study) in comparison with other systems

(Wulff et al., 1989; Baird et al., 1991; Baird & Ulanowicz, 1993; Monaco & Ulanowicz, 1997; Rybarczyk & Elkaim, 2003)

Index	Dublin Bay	Baie de Somme	Other systems
Number of compartments	7–12	8–12	15–19
Total System through-put (T , $\text{kJ m}^{-2} \text{y}^{-1} \times 10^3$)	30–250	70–117	20–269
Mean trophic efficiency (%)	4.9–11.6	3.9–6.2	4.0–12.5
Development capacity (C , kJ ; $\text{bits} \times 10^3$)	84–570	224–457	93–960
Ascendancy (A , kJ ; $\text{bits} \times 10^3$)	36–335	100–214	36–309
Redundancy (R , kJ ; $\text{bits} \times 10^3$)	19–159	19–137	34–383
Relative Ascendancy (A/C , %)	42–62	36–47	28–56
Relative Redundancy (R/C , %)	19–28	7–30	22–36
Internal capacity (C_i , kJ ; $\text{bits} \times 10^3$)	40–423	90–279	144–3879
Internal ascendancy (A_i , kJ ; $\text{bits} \times 10^3$)	18–264	52–142	57–1757
Internal relative ascendancy (A_i/C_i , %)	44–66	49–59	29–40
Flow diversity (C/T)	2.3–2.8	3.2–3.9	2.9–4.7
Relative Detritivory (D/T , %)	18–45	14–19	6–16
Finn Cycling Index (FCI)	0.32–0.76	0.14–0.24	0.23–0.44

In terms of the outputs, manipulation of the systems by adding compartments or artificially balancing them resulted in significant changes to the various measures. However, the ratios, which can also be used as measures of system status or maturity, with all the implications for structure, processes and resilience, were much more robust, and these dimensionless figures may offer a meaningful way in which system performance may be measured and reference values established.

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