Ecosystem development during open and closed phases of temporarily open/closed estuaries on the subtropical east coast of South Africa

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A B S T R A C T

Temporarily open/closed estuaries, or TOCEs, are the predominant type of estuary along the South African coast. Typically cut off from the sea during parts of the year, their ecosystems feature various developmental stages due to inlet breaching and the following closure. A full cycle ranges from breaching to drainage into the sea, thereafter a short period of tidal estuary followed by closure and a closed phase until breaching occurs again. Documented differences in biomass of various biota during open and closed phases of the Mdloti and Mhlanga estuaries over a seasonal cycle were translated into ecosystem networks. From these, ecosystem indices were calculated, and several (especially A/DC, AMI) reflected the changes between open and closed phases on the ecosystem level, and changes along a gradient of number of days the estuary has been open or closed. Differences in the developmental stages of the estuaries thus not only occurred at the community level, but also at the ecosystem level in terms of flow distribution and amount of carbon processed along the various trophic links. Furthermore, the fitness, or sustainability of system configuration, of the estuaries along the seasonal cycle was estimated and showed both estuaries to have a sustainable configuration, despite the periodicity of the open and closed inlet to which they are subjected, their altered freshwater inflow regimes, and some pollution.

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1. Introduction

Estuaries provide numerous ecosystem services including high biotic productivity, while they act as natural purifiers of inflowing river water, serve as nursery area for many fish and invertebrate species, provide food sources for human consumption, and are sites for recreation. In general, estuaries are high value ecosystems on the world’s coast. In South Africa, a relatively small proportion of estuaries are permanently open to the sea, whereas the dominant type of estuary (71%) is that of temporarily open/closed estuaries, or TOCEs (Whitfield, 2000), also named intermittently closed estuaries in other parts of the world. South Africa features 258 estuaries in total, with 93 TOCEs alone in the subtropical coastal region of the east coast of South Africa, from Mbashe (32°15’5” 28°54’E) estuary in the south to Kosi Bay (26°54’5” 32°52’E) in the north (Whitfield, 2000). Only about 10% of KwaZulu-Natal (KZN) estuaries are of the permanently or predominantly open type, whereas 73 estuaries are classified as TOCEs (Begg, 1978).

Although TOCEs are generally small in size, they fulfill an important function in providing habitat for estuarine dependent species, and along the KZN coast that stretches for 590 km, these habitats occur at frequent intervals along with the few permanently open estuaries (POEs), two estuarine bays and two estuarine lakes in the far north. TOCEs provide not only a habitat for estuarine species, but fulfill the same important functions as the POEs or estuarine lake systems, however on a smaller scale in terms of productivity of the entire system. TOCEs on the KZN coast are predominantly closed during the dry winter season, but open frequently during the wet summer season. The timing of inlet opening is dependent on the amount of freshwater inflow, the inlet dimensions, and the width of the sandbar between the estuary and the sea. KZN TOCEs are in general perched, i.e. the water level during the closed phase rises well above mean sea level. Once it reaches the height of the sand berm separating it from the sea, seepage and erosion initiate mouth opening and the estuary empties into the sea. Thereafter follows a short period of tidal exchange, after which the estuary closes again (Whitfield, 1992). Closure is facilitated by sand transport of a long-shore drift in a south to north direction, and limited scouring through tidal action during the open phase.

The importance of estuaries along the KZN coast can be summarised as follows. Firstly, they provide nursery areas for fish and invertebrate species (Perissinotto et al., 2010), a large proportion of which is of commercial importance in the in- and nearshore marine systems in terms of line- (Lamberth and Turpie, 2003;
part of the eThekwini Metropolitan area. Both their catchments are demonstrated to influence the Thukela Banks (nearshore to about the 60 m isobath), mainly through transport of nutrients and detritus into the oligotrophic nearshore region (Forbes and Demetriades, 2005; Lambeth et al., 2009). Furthermore, Lambeth et al. (2009) state that a reduction in flow from KwaZulu-Natal catchments has the potential to reduce catches for e.g. Argyrosomus thorpei (squaretail cob) and Chrysoblephus puniceus (slinger) in the nearshore.

Several authors have commented on significant differences in biomass and productivity between the open and closed phases of temporarily open/closed estuaries. Examples include that of higher phytoplankton production and biomass of benthic microalgae during the closed phase in the Mdloti and Mpenjati estuaries along the KZN coast (Nozais et al., 2001; Froneman, 2002; Perissinotto et al., 2002; Thomas et al., 2005; Anandraj et al., 2007). A similar pattern was found for meiofauna by Nozais et al. (2005) and for zooplankton by Perissinotto et al. (2006). However, no definite patterns are apparent for the macrobenthos community (Perissinotto et al., 2010). Macro-benthos is disturbed, however, when sediment is displaced during opening and flushing of the estuary. Although fish can recruit to a limited extent during overtopping events, an open inlet is required to sustain their biomass. For example, in a review of previous studies on TOCEs, James et al. (2007) found a decline in fish biomass during prolonged inlet closure due to predation and lack of recruitment. Biota in TOCEs are thus clearly impacted by inlet opening and closure, and a change in ecosystem state during the successional open—closed cycle. Their states change from closed lagoon, to that of a flowing river during drainage, a tidal estuary between drainage and flow from water treatment works (proportion from effluent >50% during low flow conditions) in the Mhlanga estuary, and river water abstraction and some inflow from water treatment works in the Mdloti estuary (Stretch and Zietsman, 2004; Lawrie et al., 2010). This has led to a decrease in inlet closure from 82% to 55% in the Mhlanga estuary, and to an increase in closure from <5% to 69% in the Mdloti estuary (Stretch and Zietsman, 2004). The average breaching interval in the Mhlanga estuary was calculated at 30–40 days (Lawrie et al., 2010), and the Mdloti estuary breaches half the number of times compared the Mhlanga estuary (Stretch and Zietsman, 2004). In addition, the Mdloti estuary closes for extended periods of time during the dry season, while the Mhlanga estuary continues to breach frequently (Stretch and Zietsman, 2004). The change in freshwater inflow from natural conditions was estimated at ~8% for the Mdloti estuary, and +58% for the Mhlanga estuary (Stretch and Zietsman, 2004).

2.2. Network building

Trophic flow models with carbon as currency were built based on data gathered during March 2002—March 2003 during quarterly surveys. During these surveys, data on phytoplankton (Thomas et al., 2005) and microphytobenthos (Perissinotto et al., 2006) chlorophyll-a, zooplankton and macrobenthos abundance, fish CPUE and sediment organic matter were collected (Perissinotto et al., 2004). Networks were built according to guidelines in Fath et al. (2007). After the ecosystem was delineated, existing data were first used to establish carbon biomass and carbon trophic flow rates between compartments and across the system boundaries (river, sea) using data and methodology as described below. All mass was expressed as mg C m⁻², and all trophic flows as mg C m⁻² d⁻¹. All compartments in the network, and the networks as a whole are mass balanced, so that Consumption = Respiration + Production + Egestion (=unassimilated food). These data are incorporated into an adjacency matrix, which serves as input into ecological network analysis software (Ulanowicz and Kay, 1991; Allesina and Bondavalli, 2004).

Existing data from the quarterly surveys during 2002—2003 were converted to carbon biomass and carbon flows as follows. Chlorophyll-a was converted to carbon using a ratio of 60%, Zooplankton and macrobenthos density (no m⁻² and no m⁻² respectively) were converted to carbon biomass using data from the literature (see Table 1). Abundance data were converted to dry weight using data from the literature for the same species, or taxonomically similar species when not available. Carbon content of species was used when available in the literature, otherwise a 40% C content of dry weight was assumed. Production/biomass ratios, production/respiration ratios, and consumption/biomass ratios were used to calculate carbon flow rates from the initial carbon biomass values. CPUE of fish (in terms of g wet weight) of seine and gill nets (data and gear description in Perissinotto et al., 2004) were converted to carbon biomass in the following manner. Firstly, it was assumed that gill nets sample a length of 100 m of estuary (50 m on either side of the net). Secondly, the seine nets sample ¼ of a cylinder, since they are deployed from the shore, on a slope in a half circle. The radius of the ¼ cylinder sampled is calculated from the length of the seine net, and volume using the height of the seine net. The total area sampled by a seine net was then converted to fish abundance (number per m² for each fish species) and wet weight was converted to Joules using energy contents from Marais and Erasmus (1977), Marais (1990) and Marais and Venter (1991). Joules were converted to carbon using conversions in McLusky and Elliott (2004).

2. Materials and methods

2.1. Study sites

The Mhlanga (29°42’S, 31°06’E) and Mdloti (29°38’S; 31°08’E) estuaries are situated on the KwaZulu-Natal coast, South Africa (Fig. 1). They are semi-urban estuaries in the vicinity of Durban and part of the eThekwini Metropolitan area. Both their catchments are relatively small, with an estimated size of 80 km² and 500 km², and mean annual runoff of 13 x 10⁶ m³ and 100 x 10⁶ m³ respectively (Stretch and Zietsman, 2004). Both are temporarily open/closed estuaries (TOCEs). However, their natural opening and closing patterns have been somewhat altered through increased fresh-water inflow from water treatment works (proportion from effluent >50% during low flow conditions) in the Mhlanga estuary, and river water abstraction and some inflow from water treatment works in the Mdloti estuary (Stretch and Zietsman, 2004; Lawrie et al., 2010).
Fauna and abiotic components that have not been sampled during the period March 2002–March 2003 but were important to include in the networks were bacteria, heterotrophic microplankton, meiofauna, and suspended detritus. Bacteria, heterotrophic microplankton and suspended detritus were sampled during April 2008, in order to give an indication of the standing stocks of these groups. Bacteria were sampled in duplicate from about 50 cm depth and preserved in 3% Formalin. Bacterial cells were counted (Muir, unpub. data) using the methods of Hobbie et al. (1977) and Marais and Erasmus (1977). The software programme Nikon Element F (Nikon) was used for image capture, using a Nikon submersible (50 cm depth) water sample. For a carbon content of 5.6 gC m⁻³, samples of known volume and dilution were stained with 0.1 µg ml⁻¹ (f.c.) DAPI dilactate (Sigma) and vacuum filtered onto pre-stained, black 0.2 µM pore size isotip™ polycarbonate membrane filters (Sigma), which were mounted on glass slides and viewed under UV illumination at an excitation wavelength of 330–380 nm. The software programme NIS Elements F (Nikon) was used for image capture, using a Nikon Digital Sight DS-Fi1 digital camera. Sufficient fields were digitally captured to allow for counting of approximately 300 cells per sample. A carbon content of 5.6 × 10⁻¹–13 gC µm⁻² (Bratbak, 1985) was used to convert measured biovolume into carbon.

Heterotrophic microplankton was sampled subsurface (ca. 50 cm deep) in duplicate and 250 ml preserved in Lugol. 100 ml of each sample was concentrated using an Utermöhl chamber and fields of view counted at 400× using an inverted microscope, to about 100 cells per sample. Biovolume was measured and calculated of about 20 cells per group (ciliates, tintinnids), and carbon content was calculated using equations in Menden-Deuer and Lessard (2000). Suspended detritus was determined by filtering 500 ml of subsurface (50 cm depth) water onto pre-combusted Whatman GF/F filters and ashing the dried filters at 60 °C at 450 °C for 6 h. Total organic carbon content determined in this way was taken as a representative of carbon. Microfauna was investigated by Nozais et al. (2005). Bacteria, heterotrophic microplankton, meiofauna, and suspended detritus were included in the networks due to a lack of abundance data of the species frequently observed in the two estuaries. Observation of birds at the two estuaries (Perissinotto et al., 2004) were used to infer the presence of feeding guilds, which were a dominance of piscivorous birds, and few sightings of wading birds. In addition, Perissinotto et al. (2004) found no difference in bird abundance and diversity between open and closed mouth conditions. In the present networks it was recognised that bird consumption can constitute an important trophic pathway across the ecosystem boundary, especially for fish. A generalised export of 5% of the production of fish was used to calculate the amount exported through birds.

Ecological networks are descriptions of flows and standing stocks in an ecosystem. The standing stocks or biomasses have been determined as described above. Carbon processing of compartments were determined using metabolic rates and other ratios derived from the literature (Table 1). In this process, mass-balance was adhered to so that inputs (consumption) equals outputs (sum of production, respiration, and egestion). Imports and exports across ecosystem boundaries (river, sea) were calculated using information on freshwater inflow and tidal flows and, during periods of inlet closure, seepage of estuarine water occurring due to their perched nature through the sand berm using hydrodynamic information generated by Stretch and Zietsman (2004). Mass values for the pelagic biota and detritus were calculated by integration over depth.

Information on the diet of fish was obtained using information from Froese and Pauly (2010) and information on the feeding guilds of invertebrates was obtained from various literature sources, including Fauchald and Jumars (1979), Ross et al. (2000) and Branch et al. (2005). Feeding links were quantified using a least-inference routine as described by Ulanowicz and Scharler (2008). Here, the amount of carbon available to flow in a network is constrained by the parameters specified above, i.e. imports and exports to and from the system, consumption, production, respiration and egestion of each group. Carbon is distributed in the network such that each link is assigned a small amount of flow in an iterative fashion, until either the demand by the receiving compartment is met, or

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the resource has been exhausted. This method assures that both small and large links are preserved in the network. Thereafter the networks were balanced according to a method proposed by Allesina and Bondavalli (2003), in order to satisfy the mass-balance assumption from the conservation of energy. Overall, there were five networks for both the Mdloti and Mhlanga estuary, representing March, June, September and December 2002, and March 2003. The number of compartments in the Mdloti and Mhlanga models were 49 and 48 in March 2002, 46 and 50 in June 2002, 43 and 46 in September 2002, 44 and 47 in December 2002 and 46 and 48 in March 2003 respectively.

2.3. Biomass and ecosystem indices

The biomasses of the various components in the networks were represented for open and closed mouth conditions. The resulting mass-balanced networks of trophic exchanges were analysed using WAND (Allesina and Bondavalli, 2004) for selected ecosystem indices over open and closed mouth conditions. These indices have been used in the past to compare estuarine ecosystems on temporal (e.g. Baird et al., 1998; Schramski et al., 2007) and spatial scales (e.g. Monaco and Ulanowicz, 1997; Scharler and Baird, 2005), and they are used in this study to compare two different ecosystem states, namely the two estuaries under open and closed conditions. The indices chosen include Total System Throughput (TST), which represents the sum of flows in an ecosystem. This is theorised to be higher during closed conditions, which presents a calmer physical environment, and an increased pelagic and benthic habitat due to higher water levels.

Secondly, the ratio of detritivory to herbivory is expected to be lower during closed inlet conditions due to the higher availability of microalgae (phytoplankton and microphytobenthos) compared to open inlet conditions. Similarly, the trophic efficiency from trophic level 1 to 2 is expected to be lower during closed inlet conditions where more material is available on trophic level 1 due to higher algal biomass during closed inlet conditions. The extent of recycling of material, expressed as the Finn Cycling Index (FCI), is expected to be higher during closed inlet conditions.

Indices calculated from information theory illustrate the patterns of flow through the system, and derive their values from both the number of connections and the quantities transferred along them. In general, values of the indices are higher the fewer connections there are, and the more unequal the flows are distributed along the connections. Information theory indices describe the developmental stage of an ecosystem along a successional continuum (Ulanowicz, 1986). When flows are indeterminate (little specialisation) in early successional stages (e.g. the estuary just after inlet opening), the index values are low. However, under less frequent disturbance conditions (e.g. during calmer conditions when the inlet is closed), specialisation is thought to occur in terms of preferred feeding links having prominence over indiscriminate feeding. The average mutual information (AMI) is an index quantifying the flow specialisation. It is the difference between the probability (probability of occurrence of known inflow into a compartment) and the conditional probability of a flow event occurring (probability of occurrence of known inflow and known outflow from source compartment a timestep earlier) (Ulanowicz, 1986). It is expected to be higher during conditions of little disturbance, i.e. during closed inlet conditions in the absence of major physical disturbance such as high river flow, and the consequent opening of inlet and emptying of estuary. The counterpart to the quantification of specialised flows in terms of AMI is the unspecialised flows. These unspecialised flows occur due to parallel pathways in the network (flow redundancy R), to respiration (energy which is of no further use to the ecosystem), and imports and exports across the ecosystem boundary (Ulanowicz, 1986, 2004). AMI has an upper theoretical limit, represented by H, Shannon’s diversity index applied to flows. H characterises the flow distribution according to the number of links in an ecosystem, and is the weighting for the frequency of occurrence of each flow event, or material moving along the feeding links (Ulanowicz, 1986; Scharler, 2008). The AMI equals H if there is no difference between the probability of a flow occurring (probability of occurrence of known inflow into compartment) and the conditional probability of a flow occurring (probability of occurrence of known inflow and known outflow from source compartment a timestep earlier). If both probabilities are the same, AMI equals H, and the inflows into compartments equal outflows from the source compartments. This situation can only be achieved if every compartment has only one in- and one outflow and all compartments are joined in one large single loop (Ulanowicz, 1986; Scharler, 2008). Thus the more specialisation that occurs in an ecosystem (i.e. the smaller the difference between the probability and conditional probability of flows occurring), the higher the AMI value relative to H.

All information from unspecialised and specialised flows can be scaled to the particular system by its size, represented by the TST, where e.g. ascendancy (A) is the product of AMI and TST, and development capacity (DC) that of H and TST. However, scaling by the TST often obscures changes in the indices, since the TST always has a far greater number compared to the information index. For the present study, the unscaled indices (AMI, H, R/DC, (Overheads on exports and imports)/DC) are therefore used, removing the singular effect of TST.

Information on the flow specialisation confers knowledge on the robustness or resilience (in terms of flow redundancy), developmental stage (in terms of AMI/H) and in terms of reliance on imports and exports (as fraction of DC). The AMI/H ratio is anticipated to be higher under calmer conditions when the inlet is closed, and no physical stresses such as displacements during floods/inlet opening occur. The Redundancy/DC ratio expresses the unspecified flows due to parallel pathways as a fraction of the development capacity DC, and is expected to be lower during closed inlet conditions. The overheads with regards to imports and exports are again expressed as a fraction of DC, and are anticipated to be lower during periods of closed inlets when exports occur only via seepage through the sand berm and feeding links (e.g. exports via birds).

From the same networks, an index describing the fitness of the seasonal ecosystems indicating its sustainability and describing the position of the network in a so-called “window of vitality”, was calculated as follows. Zorach and Ulanowicz (2003) calculated limits to a “window of vitality” in which empirical networks were found to exist in comparison to randomly generated networks. The space of the “window of vitality” was calculated according to the connectivity, c, (of weighted links) and number of roles, R, in the networks. Roles have been defined as different functions in the networks according to material flow, specifically as a group of nodes or compartments receiving material from one source and passing it on to another. Since the number of nodes in ecological networks varies according to the researcher’s specifications, a more widely applicable definition of ‘role’ is that of trophic levels, which are representative of groups of nodes, or parts thereof, feeding on a certain trophic level. The connectivity of empirical, weighted networks was found to be between 1 and 3.01, whereas the number of roles between 2 and 4.5 (Zorach and Ulanowicz, 2003; Ulanowicz et al., 2005), i.e. a network has at least 2 trophic levels (e.g. primary producer and grazer, or detritus and detritivore) and at most 4.5. Ulanowicz et al. (2009) proposed the geometric centre of the connectivity and roles in the “window of vitality”, translated into A/DC, as the optimal configuration for sustainability of the network.
itself. If the network moves away from this geometric centre in any direction, its sustainability diminishes. From the A/DC values, a term describing fitness of the ecosystem was derived, where fitness describes the sustainability of an ecosystem. It is scaled between 0 and 1, and calculated from both the certainty (order) and uncertainty (disorder) of flows. The following formula (Ulanowicz et al., 2009), a product of a measure of order (as A/DC, or a) and a measure of disorder (as the Boltzmann measure — \( k \log(a) \)) was used to calculated fitness of the Mhlanga and Mdloti ecosystems:

\[
F = -\left[ \frac{e}{\log(e)} \right] a^\beta \log(a^\beta)
\]

\( \beta \) was derived as follows: the maximum fitness value of 1 is equivalent to the geometric centre of the “window of vitality”. At this geometric centre, \( c = 1.25 \) and \( R = 3.25 \), which can be calculated, according to Zorach and Ulanowicz (2003) and Ulanowicz et al. (2009), into an A/DC, or \( e_{centre} = 0.4596 \). In order for the fitness value to be 1 at the geometric centre, \( \beta = 1.288 \). The F values for the Mdloti and Mhlanga networks are calculated from the individual A/DC values of their 10 networks, using \( \beta = 1.288 \).

The above mentioned ecosystem indices (TST, Detritivory/Herbivory, AMI, H, Redundancy, FCI, Overheads for Imports and Exports, Fitness) were calculated for ten networks in total, five seasons each for the Mdloti and Mhlanga estuaries. They were compared between open and closed phases, and to the trends shown by the community biomasses of these two states. In addition, the ecosystem indices were described in terms of the theoretical behaviour during open and closed inlet conditions outlined above.

3. Results

3.1. Biomass variability between open and closed phases

Overall, five networks for 5 seasons per estuary were analysed. The inlet of the Mdloti estuary was open in March and September 2002 and closed in June, December 2002 and March 2003. In the Mhlanga estuary, open inlet conditions prevailed during June and December 2002 and closed inlet conditions occurred during March and September 2002, and March 2003. The open and closed conditions thus did not occur during the same times in the two estuaries (except during March 2003), and both open and closed conditions were found during the dry winter and wet summer months (Stretch and Zietsman, 2004).

There was a clear trend in biomass distributions in the Mdloti estuary between open and closed mouth conditions. Biomass of the groups measured during 2002–2003 in general tended to be higher during closed than open mouth conditions (Fig. 2). Differences in biomass between open and closed mouth conditions were significant for all biota except fish. In the Mhlanga estuary, biomasses of the small pelagic groups (phytoplankton and zooplankton) were higher during closed mouth conditions, similar to the Mdloti estuary (Fig. 2). However biomass of benthic groups (microphytobenthos and macrobenthos) were lower during closed mouth conditions, as was the CPUE for fish (Fig. 2). Statistically significant differences in biomass between open and closed mouth conditions in the Mhlanga estuary were apparent only for phytoplankton (\( p = 0.026 \)) and macrozoobenthos (\( p = 0.046 \)) (Fig. 2).

3.2. Ecosystem indices — differences between open and closed phases

The indices compared between open and closed phases and estuaries included TST, AMI, A/DC, R/DC, (Overheads for exports and imports)/DC, FCI, the detritivory/herbivory ratio, and the trophic efficiency from the first to the second trophic level. When comparing between open and closed phases, the fairly clear trends seen from the biomasses (Fig. 2) were somewhat, but not as clearly, reproduced in the indices (Fig. 3). In some cases, large variations in the indices (and associated 95% CI) were the results of a small sample size that made comparisons less reliable.

The TST, including all biotic and abiotic components in the system, was very variable in the Mdloti and did not reflect the trends seen in the biomasses presented for the selected biota (Fig. 3). The TST during the open phase comprised the lowest and highest values measured overall. In the Mhlanga estuary, mean TST values were similar to the Mdloti during the open phase (84 884 mgC m\(^{-2}\) d\(^{-1}\)), but about half of that during the closed phase (42 734 mgC m\(^{-2}\) d\(^{-1}\)). In both the Mdloti and Mhlanga estuaries, the TST thus does not follow the biomass pattern observed for the biota (Fig. 2).

Fig. 1. Location of the Mdloti and Mhlanga estuaries along the South African coast.
Fig. 2. Mean (±95% CI) of biomass sampled during March 2002–March 2003 in the Mdloti and Mhlanga estuaries. Differences between open and closed phases (denoted by a, b) were calculated at $p \leq 0.05$. 
Fig. 3. Mean (±95% CI) of selected ecosystem indices in the Mdloti and Mhlanga estuaries. Differences between open and closed phases (denoted by a, b) were calculated at $p < 0.05$. TST = Total System Throughput, A/C = Ascendency/Development Capacity, AMI = Average Mutual Information, FCI = Finn Cycling Index, TE = Trophic Efficiency from Trophic Level I to Trophic Level II.
Fig. 3. (continued).
A/DC (=AMI/H), the proportion of ascendency to development capacity, is higher during the closed phase in the Mdloti estuary, as expected from theory. However, it is lower in the Mhlanga estuary during the closed phase (Fig. 3). R/DC, the proportion of redundancy to development capacity, is equally higher during the closed phases of both estuaries, although they were expected to be lower because of the loss of parallel pathways which lowers the value of R. The overhead on imports and exports was predictably lower during the closed phase, and the difference is significant (p = 0.001) between the two phases in the Mdloti estuary. The index of cycling (FCI) was expected to be higher during the closed phase, which was apparent in the Mdloti estuary. The overall variability during both the open and closed phases for the FCI in the Mhlanga estuary (Fig. 3) did not reveal any trends.

Due to the higher microbial growth reported during the closed phase (Anandraj et al., 2007), it was anticipated that the detritivory/herbivory ratio be lower during the closed phase in both estuaries. However, there were no significant differences between the open and closed phases in both estuaries (Mdloti: p = 0.127; Mhlanga: p = 0.794) (Fig. 3). The trophic efficiency between trophic level 1 (TL 1) and trophic level 2 (TL 2) of ecosystems is higher when food availability at TL 1 is low compared to demands of TL 2. In both estuaries, the trophic efficiency was higher during closed phases with a statistically significant difference only for the Mdloti estuary (p = 0.006), implying that there was food shortage (at the first trophic level) during the closed phase compared to the open phase. Thus not only Trophic Level I food sources increased (e.g. microalgae showed an increased biomass), but also their consumers (zooplankton, macrozoobenthos, fish) increased in biomass (see also Fig. 2).

3.3 Continuous change of ecosystem indices over time

Open and closed phases in estuaries do not occur at regular intervals and the phases last over variable time periods. To illustrate further differences between open and closed phases, all indices were plotted against the number of days the estuary has been open (number of days closed were translated into negative number of days open). Some indices revealed interesting patterns. Firstly, the TST in the Mhlanga is lower during the closed than during the open phase (Fig. 4). In the Mdloti estuary, there seems to be a trend of a decrease in the TST with increasing time of closure, and a lower TST was apparent a few days after inlet opening compared to ca. 10 days later (Fig. 4).

The Finn Cycling index is in both estuaries lower during the open phase than during the closed phase. The magnitude of recycling seems to increase over several days during the open phase for both estuaries from breaching (Day 0) onwards (Fig. 5). The detritivory/herbivory ratio shows a similar pattern as the FCI during the open phase, is decreasing with increasing time of mouth closure, and is overall higher during the closed phase in the Mdloti, but not the Mhlanga estuary. This may reflect the higher microalgae productivity during the closed phase compared to the open phase. In the Mhlanga estuary, the detritivory/herbivory ratio shows a sharp increase between one day after mouth closure and about 9 days closed. This result implies that proportionally more microalgae become available the longer the mouth is closed (Fig. 4). The FCI and the trophic efficiency (from trophic level 1 to 2) show the same trend during open and closed conditions in both estuaries (see Fig. 4). To summarise, the extent of recycling, the trophic efficiency (from level 1 to 2), as well as the proportional usage of microalgae compared to detritus was generally lowest within one day of breaching and 1 day of closure. All three indices increase with the number of days the estuaries are open. During the closed phase however, there is an initial increase for all three indices which tapers off and decreases with prolonged closure (Fig. 4).

The information theoretical indices show a complementary pattern. The average mutual information (AMI) in the Mdloti decreases as the mouth stays open and increases with increasing number of days closed (Fig. 4). Flows are thus most constrained (or specialised, i.e. fewer links carrying proportionally higher amount of material) during periods of absence of breaching and tidal events. In the Mhlanga estuary, on the other hand, flow specialisation is fairly similar during both the open and closed phases. The A/DC and R/DC ratios show an opposite pattern, as expected from theory, in that when the proportion of organised flows increases, the proportion of flow redundancy decreases. The A/DC ratio was lowest during the open and physically more disturbed phase in the Mdloti estuary, with no clear trend apparent for the Mhlanga estuary. The proportion of redundant flows (R/DC) was lowest during the open phase in the Mhlanga estuary, increasing as days of closure increase, thus showing an opposite trend to theoretical expectations (Fig. 4). Overheads on imports and exports expectantly decrease from the open to the closed phase when exports are largely absent (Fig. 4). However, when water levels in the estuary rise, there is some export towards the sea from seepage through the sand berm (e.g. Stretch and Zietsman, 2004). In summary, the information theoretical indices behaved largely according to theory in the Mdloti estuary and to some extent in the Mhlanga estuary.

When fitness was plotted against number of days open, there was a slight decrease in fitness from the closed to the open phase (Fig. 5a). The Mdloti showed a greater variability compared to the Mhlanga estuary in terms of fitness. The lowest fitness value in the Mdloti estuary coincides with the highest A/DC value of about 60%. The connectivity and number of roles of the 10 networks were plotted with the geometric centre of the “window of vitality” in order to ascertain their position in relation to the centre and borders. All 10 values plotted within the window, and none on the edge of the window (Fig. 5b). The values for the Mhlanga estuary clustered in the lower right quarter of the window, and also showed the values that are closest to its edge (Fig. 5b).

4. Discussion

The overall aim of this study was to investigate whether the empirically derived biomass changes that are seen between open and closed phases of temporarily open/closed estuaries (TOCEs) are also manifested in changes at the ecosystem level. In particular, the question was whether ecosystem states change between the two phases, and if so, whether they change to a large enough extent to cause changes in ecosystem indices. Furthermore, estuaries open and close over intermittent time periods and patterns, which raised the question whether the number of days an estuary has been open or closed is reflected in the value of the ecosystem indices.

The ecosystem indices used here have been ascribed to the theoretical behaviour of ecosystems in terms of succession (Ulanowicz, 1986, 1997), which in this context is the recovery of the food web after breaching and ecosystem development after mouth closure. Some of the indices used here reflected these patterns, whereas others did not. Also, the two estuaries did not always show the same responses. However, their natural opening/closing regime has been altered in different ways, so that the Mdloti estuary is now closed for longer periods of time, and the Mhlanga estuary opens more frequently (see Section 2.1).

Since the biomasses for several biota were higher during the closed phase, a higher TST was expected. However, the TST is a sum of all flows in the system, including those of exchanges with the sea, which are considerably higher during the open phase. Therefore the clear biomass pattern between open and closed phases in the Mdloti was not reflected in the TST. However, other indices did show the expected pattern, including that of AMI and the A/DC
Fig. 4. Ecosystem indices in relation to days the estuary has been open after breaching. Negative days open indicate number of days closed.
ratio, as well as those of overheads on imports and exports, however more clearly in the case of the Mdloti estuary compared to the Mhlanga estuary. In addition, the higher detritivory/herbivory ratio and the higher trophic efficiency from TL1 to TL2 can be explained by the higher microalgae productivity (Anandraj et al., 2007) during closed phases for both estuaries.

The A/DC and R/DC ratios are complementary so that one can increase at the expense of the other. The R/DC ratio, although expected to be lower during calmer closed conditions, was higher during the closed phase in both estuaries. This ratio seems to compensate for the decrease in overheads on imports and exports during the closed phase. In general, the closed phase might not have lasted long enough to allow for ecosystem development towards an even higher A/DC ratio at the expense of a lower flow redundancy.

The question arose whether the Mdloti and Mhlanga estuaries operate as ecosystems in a sustainable configuration, or whether the impacts they have sustained thus far (altered flow regimes, increased pollution in terms of agricultural and human waste related runoff) have altered their functioning from their original natural functional status. Since there is no comprehensive dataset available for these estuaries under natural conditions for comparison, the ecosystem indices were compared to those of other estuaries. For instance, the A/DC ratios for 7 networks in the present study fall within the range of other estuaries in South Africa and the Eastern USA of between 32 and 49% (e.g. Baird and Ulanowicz, 1989 (Chesapeake Bay); 1993 (Kromme, Swartkops, Ems, Ythan estuaries); Monaco and Ulanowicz, 1997 (Narragansett Bay, Delaware Bay, Chesapeake Bay); Christian et al., 2005 (Neuse estuary); Scharler and Baird, 2005 (Kromme, Swartkops, Sundays estuaries)), while the A/DC ratios of three networks in the present study were calculated >49% (50–60%). The R/DC ratios ranged of the here cited literature models fall between 27 and 42%, but 19–40% in the present study. Six of the Mdloti/Mhlanga networks had an R/DC ratio smaller than 27%, implying that their redundancy, and thus resilience, is lower compared to those cited above. The Mhlanga estuary showed overall lower R/DC ratios compared to the Mdloti estuary. In terms of the A/DC and R/DC ratios, the Mhlanga and Mdloti networks thus fall within a wider range compared to other estuaries.

The placement of the 10 networks into the window of vitality (Fig. 5b) and the calculation of fitness suggest that both the Mdloti and Mhlanga estuaries possess enough resilience yet to operate in a sustainable configuration. However, there is no guarantee that they will do so in future. Current threats that might push the estuaries to lower resilience are common to those of other TOCEs in South Africa, i.e. further freshwater abstraction and prolonged inlet closure, inorganic and organic pollution and loss of riparian habitats. Any disturbance in addition to present ones may place them outside the “comfort zone”, which was for this study taken as the range of indices of other estuaries, and the “window of vitality” originally established from empirical networks. However, where the tipping point is in terms of network related indices is as yet unknown. Estuaries are by nature very dynamic ecosystems that demand resilience from their biota in terms of coping mechanisms of individual species. On the ecosystem level, resilience in this study is measured in terms of parallel trophic pathways, including imports to and exports from the system. For as long as these functionalities are maintained, and the food web does not implode to monospecific trophic levels, their current sustainability could be retained. Link losses that are caused by the loss of species, however, can only be re-established through recolonisation from other estuaries. It is therefore not only important to establish the resilience and sustainability of single ecosystems, but their status needs to be viewed as an integral part of the coast.

In summary, the hydrological characteristics of mouth opening/closure were to a fairly large extent reflected at the ecosystem level. The Mdloti and Mhlanga estuaries did not always show the same patterns, although, their flow regimes have been altered in different ways. The AMI and A/DC ratio turned out to be good ecosystem descriptors for this particular study, and have been used before to characterise ecosystem states, e.g. as indicators of environmental stress (Baird and Heymans, 1996; Patrício et al., 2006; Tobor-Kaplan et al., 2007), ecosystem succession (Holtkamp and Tobor-Kaplan, 2007), or switching of benthic-pelagic systems (Almunia et al., 1999).

In order to specify exactly how short-term changes influence ecosystem functioning, future studies to compare pristine and impacted estuaries, as well as recovery studies after a breaching event will provide more insight into the variability of ecosystem
functioning of TOCEs. Further, the time span needed for ecosystem development from one functional state to another needs further attention. Ecosystem level studies will provide a means to explore threats to estuaries in South Africa that are similar to those in other arid and semi-arid parts of the world. Freshwater abstractions from the catchment leave less river water to flow into estuaries, thereby decreasing the frequency of opening and extending the closure times. Agricultural and industrial activities and human settlements inevitably lead to an increase in nutrient loads and concentration, pollutants in estuarine habitats, and sediment loads from erosion, while prolonged closures of estuaries inlets prevent the dilution of pollutants in estuaries and recruitment of biota. Although impacts on selected biota and water quality are often documented, the impact on whole ecosystem functioning as explored in this study is rather scarce.

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