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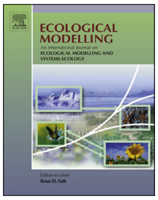

Temporal variation of keystone species and their impact on system performance in a South African estuarine ecosystem

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ABSTRACT

Anthropogenic intervention along with natural variability can both influence and compromise continued ecosystem functioning. Ecological network analysis (ENA) was used to explore ecosystem functioning following disturbances to food web networks of a South African estuary, Mdloti, under different seasons. Keystone species, in particular, play an important structural role in spite of having low levels of presence in terms of biomass. From networks of carbon exchanges, the keystone species are identified which include high trophic level carnivorous fish species like Argyrosomus japonicus, Caranx sexfasciatus and Monodactylus falciformis. It is observed that keystone species differed between seasons, according to changing conditions of the estuary. The positive and negative direct and indirect effects that the keystone species have on the different components of the system are evaluated by a Mixed Trophic Impacts (MTI) analysis and results of the direct-indirect impacts analysis are not consistent across seasons.Results reinforce the fact that the keystone species are context dependent as they show variation over the different networks following species composition change following alteration of the estuaries physical status and season. To simulate disturbance, the keystone species biomass in the initial five networks was changed by 10% in stepwise intervals up to ± 99% and it was observed that the system is somewhat resistant to the perturbation effects of the keystone species.

1. Introduction

Ecological understanding is achieved through either a reductionistic (autecology: concerned about a single species) or holistic approach (synecology: system as a whole) to find structural and functional patterns of relationships between organisms and their environment. In particular, following a holistic tradition, system level properties can be identified through the exploration of food web networks (Jørgensen, 1997). These studies are useful when ascertaining the status of an ecosystem. Studies show that ecosystems are amply complex which makes it difficult to comprehend properly their mode of functioning (Allen, 1971; Likens, 1985). To work around this difficulty, simplified models may be developed possessing relevant information from the natural system, but not making it too complex to understand. The analysis can be achieved by studying food web networks that describe the biotic exchanges occurring in any ecosystem, and by displaying the interconnected feeding relations of 'who eats whom'. A food web is like a snapshot of the trophic flows in the system (Christensen and Pauly, 1993) allowing the study of the trophic structure and importance of the various component species of that ecosystem.

Estuarine ecosystems, at the margin of land and sea, are of paramount importance as they provide different ecosystem services including high levels of biological productivity, serving as a nursery area for many different fish and other aquatic invertebrate species (Beck et al., 2001), while performing as filters for river water (Scharler and Baird, 2005). They contribute also to human food sources and have high aesthetic value and are often a source of economic dependence for a fairly large population through subsistence fishing (Forbes and Demetriades, 2005; Lamberth and Turpie, 2003). Estuaries and continental shelves consist of about 5.2% of the earth's surface and according to Lindeboom (2002) these systems are constantly under threat owing to direct and indirect

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anthropogenic activities and also due to natural causes. Anthropogenic activities including urbanization, deforestation, expansion of agriculture to support the growing population and pollutant discharge from industrial and household sources contribute to major degradation of estuarine ecosystems (Chapin et al., 2000; Karr and Chu, 1998; Myers and Knoll, 2001). Overexploitation of estuarine resources (e.g., fish) is a major factor in the disruption of the ecosystem functioning (James et al., 2007; Kennish, 2002). The present study deals with the Mdloti estuary in South Africa, which has a unique property. This estuary belongs to a group of estuaries known as temporarily open/closed estuaries (TOCEs). These estuaries in general remain open and connected to the sea during the wet season and conversely remain closed in the dry season depending on the amount of freshwater received via rivers (Whitfield, 1992). Some well-defined changes are observed in the faunal composition of these systems following open/closed states (Ortega-Cisneros et al., 2014; Perissinotto et al., 2010).

The behaviour of all species in the ecosystem is not uniform. The most abundant species in terms of biomass exert important control by maintaining, to some extent, the maximum energy flow and also by providing some resource support and shelter to the other less abundant organisms (Ashton, 1992; Dayton, 1985; Duran and Castilla, 1989; Gentry and Dodson, 1987; Paine and Suchanek, 1983; Strong, 1977). Many experiments have demonstrated that some species, though less abundant, may have strong effects on the system structure and are collectively called keystone species (Paine, 1969). The main differences separating the keystone from other species are 1) that its presence (biomass) in the system is not necessarily high as compared to the other organisms and 2) it has a disproportionally large effect on the other component species and also on the whole system (Paine, 1966; Power et al., 1996). Keystone species can be different from the dominant species present in the system, as the weighting of influence per unit of biomass generally excludes the most abundant species, but certain exceptions are also present like fig trees in a woodland ecosystem as observed by Terborgh (1986). A broad range of species has been documented by various researchers to have a keystone effect, such as: predatory starfish, snail, sea urchin, sea otter, piscivorous fish, rabbit and elephant. These are found in different ecosystems ranging from rocky intertidal and subtidal zones, soft sediments, freshwater bodies to woodlands (Carpenter et al., 1985; Estes and Palmisano, 1974; Kvitek et al., 1992; Laws, 1970; Oliver et al., 1985; Paine, 1966; Tansley and Adamson, 1925; Zaret and Paine, 1973). In cases where alterations to the system functioning and associated biodiversity losses are evident, focussing on the influence and prevalence of keystone species can serve to understand better their interactive role in the system (Sparks et al., 1990; Terborgh, 1986).

Another important and interesting fact to note is that all the species that are present in any system possess some level of “keystoneness” at a time, for a given purpose (Bond, 1994, 1993; Libralato et al., 2006; Mills et al., 1993; Power et al., 1996). Most of the existing information about keystone species shows that they are context specific, i.e., they do not necessarily show dominance as controlling agents but adapt the role of keystone species as and when required (Menge et al., 1994; Paine, 1966). For example, it was shown that a certain species that is the original keystone of a specified area (system) may have weak to negligible impacts in a different situation (Menge et al., 1994). The results obtained related to keystone species cannot be generalized for any system that may face change of state due to environmental reasons. Hence there arises the need to identify the keystone species in a system that may feature different conditions. Although the interactions of these species with the others in the system may seem negligible, they might be magnified owing to cascading effects that arise from interactions of the various functional groups (Brett and Goldman, 1996; Pace et al., 1999). The indirect pathways in a food web as recognized earlier (Higashi and Patten, 1989; Wootton, 1994, 1993; Yodzis, 1980) may influence the system so much that they can turn the beneficial direct relationships in to negative and vice versa (Bondavalli and Ulanowicz, 1999; Scharler and Fath, 2009).

Previous applications of keystone estimates show two different approaches; the first one, based upon graph theory, uses successive elimination of functional groups from a trophic web model and then evaluating their impacts on the system (Jordán, 2001; Jordán et al., 1999; Sole and Montoya, 2001). On the other hand, the second path takes a dynamic modelling approach by evaluating the changes in the biomass of the system following perturbations or extinctions (Okey et al., 2004). In this study, we concentrate on trophic networks where the keystone species are identified through their relative total impact on the system. Using the method developed by Libralato et al. (2006), our identification is done through the following steps: 1) Calculating the *MTI* matrix, 2) Using this *MTI* matrix to calculate the keystone index of each compartment. This is followed by perturbation scenarios (as described in Section 2.4) and the ensuing ENA results are next analysed to check the effect of perturbations of the keystone in the system. The extent of the changes in the system depends to some extent on the trophic position of the concerned species in the food web and also depends on the level of connectedness (Kay et al., 1989; Ray, 2008).

The present study on the trophic flow networks of the Mdloti estuary presents a unique opportunity to investigate whether the keystone species change under various conditions following the idea of “context dependency” of keystone species (Power et al., 1996). With the objective of identifying the keystone species in the system and understanding their relative importance (through *MTI* and ENA indices analysis) we try to investigate why keystone species vary in the same ecosystem. Also we explore through perturbation scenarios how much each of the keystone species is capable of affecting the system functioning and whether the effect of the different keystone species is similar on other components in the system following perturbation.

2. Materials and methods

2.1. Study site

The South African Mdloti estuary is a temporarily open/closed type estuary (TOCE) along the KwaZulu-Natal (KZN) coastline (Fig. 1), so named because it opens frequently in the wet summer season as compared to prolonged periods of closure during the drier winter months. The water level in this estuary (and in other KZN TOCEs in general) rises above sea level during the closed phases which is followed by a breach of the sand berm separating it from the sea. This is followed by a brief period of tidal exchange before the estuary is reclosed (Whitfield, 1992). About 71% of the total 258 estuaries in South Africa (Whitfield, 2000) and about 90% in KZN (Begg, 1984) are TOCEs. The Mdloti is a semi-urban estuary situated in the vicinity of Durban, in the eThekwini Metropolitan area (29°38′S, 31°08′E) and has a catchment area of about 500 km^2 with an annual runoff of about $100 \times 10^6\ \text{m}^3$ (Stretch and Zietsman, 2004).

The natural opening and closing patterns of this estuary have been altered due to the abstraction of river water and also inflow from wastewater treatment plants. This has led to an increase in the closure time of the estuary to about 69% (Stretch and Zietsman, 2004) with breaches once in about 60–80 days (Lawrie et al., 2010). In addition, the estuary also shows prolonged periods of closure during the summer seasons and a change has been observed in the freshwater inflow from natural conditions which is estimated at −8% for this system in the early 2000 s (Stretch and Zietsman, 2004).