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Ecological responses to reductions in freshwater supply and quality in South Africa's estuaries: lessons for management and conservation

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Abstract. Fresh water, a fundamental element of all estuarine ecosystems, is South Africa's most limited natural resource. Recent projections indicate that by the year 2020 the country will be utilizing all its exploitable freshwater sources. Steeply increasing demands by a rapidly growing population on this limited commodity have already resulted in a severe reduction of water supplies to natural users such as estuaries - this trend is predicted to increase in the future. Concurrent with excessive water abstraction, poor land husbandry (e.g. soil erosion) in many catchment basins and pollution (e.g. salinization) in return flows have led to a serious deterioration in water quality. In contrast, a review of estuarine responses to varying flow regimes stresses the strong dependence of local systems on riverine fresh water inputs of adequate quantity and quality. Freshwater dependence is i.a. expressed in: flooding events that scour accumulated sediments, riverine nutrient input to drive estuarine phyto- and zooplankton production, axial salinity gradients that increase habitat and species diversity, and maintenance of open tidal inlets that prevent salinity and temperature extremes and facilitate larval exchange, fish migrations and tidal flushing of salt marshes. Thus, estuarine conservation will have to encompass management of rivers and watersheds and play an increasingly political role in decision processes concerning water allocations among 'human' and 'natural' users.

Keywords: Conservation; Ecotone; Semi-arid region; Species diversity; Watershed.

Abbreviations: MAR = Mean annual runoff; NTU = Nephelometric turbidity unit; psu = Practical salinity unit; TDS = Total dissolved solids; TL = Total length (fish).

Introduction

In estuaries – which as the major ecotones between the world's fresh water and marine ecosystems exist by virtue of seawater imported by the tides and fresh water supplied by the rivers– the balance of water inputs strongly influences their ecological milieu.

In South Africa the ecological balance, and indeed the very existence of estuaries, has become threatened by large-scale anthropogenic modifications of one of their lifelines: freshwater inflow.

Fresh water is undoubtedly South Africa's most limited natural resource and the key role it holds for the country's socio-economic development is illustrated by Lusher & Ramdsen's (1992) statement that: " … on examination, it becomes apparent that there is a steady deterioration of the water quality in rivers, availability is apparent rather than real and the price, countrywide, is set as low as possible but could become unaffordable to some sectors of the population within the foreseeable future, and in its natural state is so polluted as not to be available for use in a Third World context".

In this paper we specifically address questions of how anthropogenic modifications of the amount and quality of riverine water inflow affect the physical and biological processes in local estuaries, and discuss conservation strategies and management practices that are needed to ensure sustainable viability of South Africa's estuaries. As far as data are presently available, this is achieved by way of specific examples, which aim to illustrate both natural conditions and changes brought about by human impacts. In this context, the paper presents a broad overview of concepts and effects, rather than a comprehensive review.

Fresh water availability in Southern Africa

The sovereign position fresh water holds among South Africa's natural resources arises from natural climatic limits coupled with steeply rising human demands.

Climatic constraints

The southern African subcontinent is essentially a semi-arid region. Its mean annual precipitation of 497 mm lies well below the world average of 860 mm, with 21% of the land receiving less than 200 mm of rain per year (Anon. 1986). Rainfall and runoff are, further-more, highly variable on several spatial and temporal scales (Tyson 1986): First, humid, subtropical conditions prevail in eastern regions and dry desert conditions in the west. For example, Durban on the east coast receives on average 1070mm of rain per year, whereas the amount at Port Nolloth, which lies on the same latitude on the west coast, is a mere 58mm. Secondly, in only a few isolated areas of the country does the average annual rainfall exceed potential evaporation. As a consequence of high evaporation losses, the percentage of rainfall that becomes river flow decreases rapidly in low rainfall areas. In certain catchment areas in the dry interior, potential evaporation is about 18 × higher than precipitation, and less than 1 % of rainfall reaches the rivers as runoff (Anon. 1986). Thirdly, South Africa is periodically subjected to severe and prolonged droughts that are often terminated by heavy floods, a complete cycle spanning about 18 yr (Clarke 1991). Thus, while the climate can generally be classified as semi-arid, the regular occurrence of droughts combined with high evaporation losses necessitates excessively large water storage schemes to tide the country over the frequent and severe dry spells.

Socio-economic constraints

Spiralling population growth –South Africa will have a population of 70 million by 2025 compared with the current estimate of 43.4 million (Ministry of Population Development quoted in Sunday Times of 30 April 1995) leads to a forecast situation where by the year 2020 the country will be utilizing all its exploitable freshwater resources (Clarke 1991). With this contingency in mind, plans are under way to import water from as far afield as the Zaire river – potentially the world's largest inter-basin transfer.

Presently just over half of all available fresh water is consumed by agricultural irrigation schemes (Anon. 1986; Clarke 1991) (Fig. 1). While this might seem an obvious area from which to divert more fresh water to domestic, or even natural users such as estuaries, the political and socio-economic weight of agriculture will probably argue otherwise. This must also be viewed in the light of a policy of wealth redistribution; in this policy land allocations to the presently grossly underprivileged populace are an integral part.

All this amounts to enormous pressures on, and competition for, the available freshwater resources by domestic, agricultural, and industrial users –a situation which will undoubtedly become more severe as South Africa's population continues to expand and people improve their economic standing (Clarke 1991).

In direct competition with these socio-political heavyweights stand the fresh water requirements of 'natural users' such as wetlands, lakes, rivers and ultimately estuaries. The physical fresh water demands (evaporation and flooding) of lakes and estuaries, excluding wetlands and riverine habitats, have been estimated at 2160 millionm ^{3} per year. This quantity amounts to ca. 8% of the total exploitable water resources of South Africa (Jezewski & Roberts 1986) (Fig.1). However, the decision as to how much fresh water is in actual fact allocated to estuaries will ultimately be a political one.

Physical dependence of South African estuaries on freshwater inputs

The salient feature of estuaries along the South African coast is the alternating and dynamic pattern of sediment deposition and erosion by fluvial floods (Reddering & Rust 1990). During periods of low river discharge unconsolidated marine sediments accumulate naturally in the lower reaches of estuaries. The scouring action of fluvial floods removes these sediments from the estuaries, restoring original channel dimensions and enlarging previously constricted tidal inlets.

Opening and closing of tidal inlets is a natural occurrence in estuaries along the South African coast. Indeed, the majority of local rivers (252 or 87%) enter the sea via estuaries whose inlets close periodically due to the formation of berms across their mouths. However, owing to freshwater impoundment the scouring action of fluvial floods has been significantly reduced and many estuaries are therefore now closing more frequently and for longer periods (Whitfield & Wooldridge 1994; Wooldridge 1994). Thus, the link of estuaries to the marine environment is directly related to their link with the limnetic environment.

Water storage reservoirs in catchment areas, however, reduce the number of fluvial floods, decrease the discharge volume per flood, and lengthen the period between flooding events (Reddering 1988). Such significant modifications of the natural flooding spectrum have two consequences: first, sediment volumes in the estuary become larger than under natural flow regimes and, in the case of muddy sediments, attain a higher than natural degree of compactness. Consequently, the scouring action of subsequent river floods is less effective and channel dimensions of the estuary shrink over time. Secondly, extensive shoaling in the lower reaches impedes tidal exchange between the sea and the estuary. Such reductions in tidal action can ultimately lead to closure of the tidal inlet by marine sands which are deposited by wave action (Reddering 1988).

The effectiveness of storage reservoirs in filtering out small to medium discharge events from the natural flooding spectrum can be illustrated by population

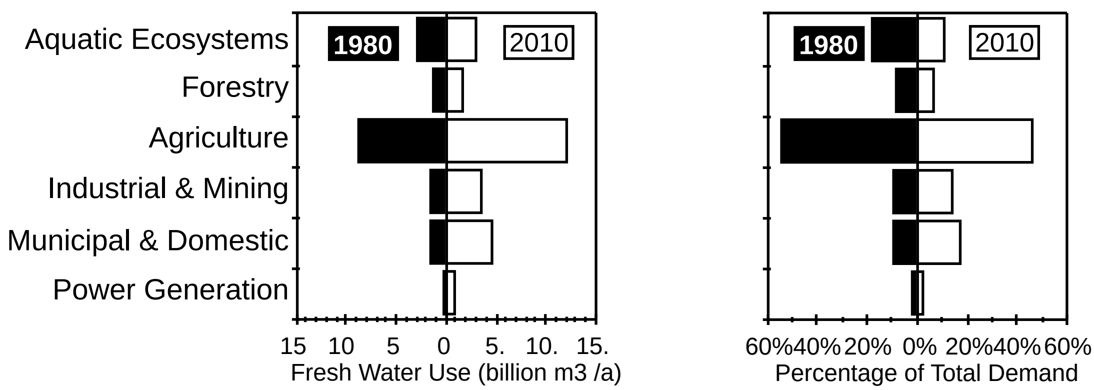

Fig. 1. Consumption of fresh water by competing users during 1980 and projected demands on available water resources by the year 2010; data from the Department of Water Affairs.

responses of the seagrass *Zostera capensis* in the Krom estuary (Fig. 2, Adams & Talbot 1992); *Z. capensis* serves as a good indicator of flooding effects because plants are highly sensitive to siltation and sediment scouring which occur during river floods (Talbot et al. 1990). Two moderate floods of similar magnitude (58.4and 30.710 ^{6}m ^{3} total discharge into dams) occurred in the catchment of the Krom estuary during August 1979 and November 1989, respectively. During 1979, when freshwater impoundment was 32 % of the mean annual runoff (MAR), fluvial flooding reduced the biomass of *Z. capensis* by ca. 50 % (Fig.2A). In contrast, following construction of a second dam in 1982, water storage exceeded mean annual runoff by 27 % and reduced the effect of all floods smaller than the 1-in-30 yr flood. Consequently, the estuarine population of *Z. capensis* was not affected by the second discharge event (Fig. 2B). For the estuary as a whole there has been a fourfold increase in the total standing biomass of *Z. capensis* after the second major dam was completed (Adams & Talbot 1992).

Although only 37 (12.8 %) of the 289 South African river mouths maintain a permanently open channel to the sea (Reddering & Rust 1990), it is the biota in those systems whose tidal inlets close for part of the year that are generally most adversely affected by reduced freshwater inflow. Over the last few decades, excessive abstraction of fresh water has led to a situation where estuarine tidal inlets now close more frequently and for longer periods (Wooldridge 1994; Whitfield & Wooldridge 1994). Thus, while river mouths which function at times as coastal lagoons and at times as true estuaries are the dominant form of a river discharging into the sea along the South African coast, adequate frequency and

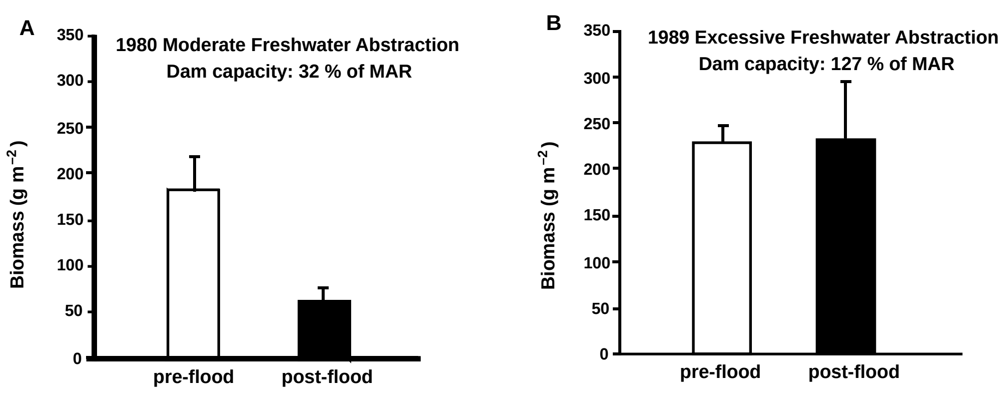

Fig. 2. Reduction in the scouring effect of river floods following excessive impoundment of runoff in the catchment basin of the Krom estuary. Flood effect is measured by the relative biomass of the seagrass *Zostera capensis* prior (□) and following a flood (■) of similar magnitude during 1980 (A) when river impoundment was moderate, and after the construction of a major dam 4 km upstream of the tidal head (B). *Z. capensis* is a good indicator of flood effects as it is highly sensitive to fluvial sediment scouring and siltation (Talbot et al. 1990); after Adams & Talbot (1992).

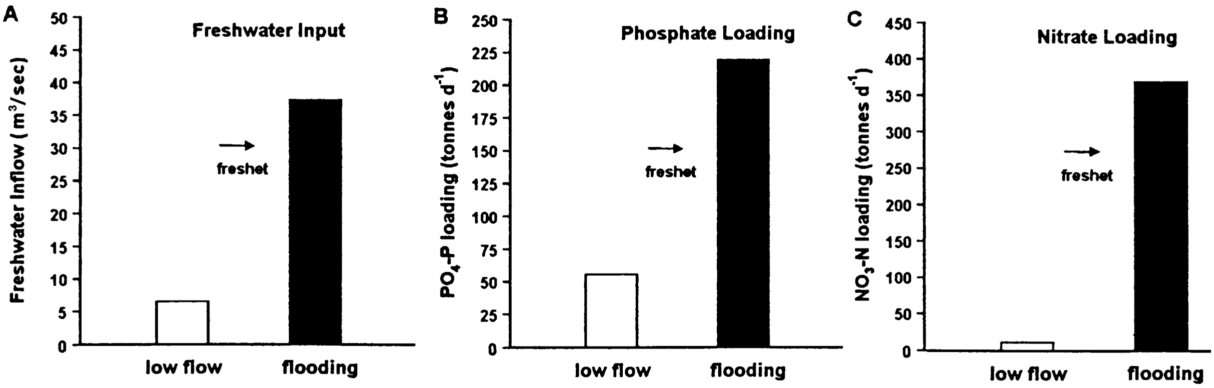

Fig. 3. Effect of a freshwater pulse (freshhet) (A) on riverine nutrient loading to the Great Fish estuary, showing dramatic increases in phosphate (B) and nitrate inputs (C) from a period of low flow (□) to the onset of freshwater flooding (■); data from Allanson & Read (1987).

magnitude of floods coupled with stable freshwater baseflows are absolute prerequisites to maintain the physical habitat integrity of all estuarine types.

Impacts of anthropogenic changes in the amount and quality of river discharge on estuaries

At present the total storage capacity of major dams in South Africa amounts to 50 % of the total mean river runoff, with only 8 % of annual runoff reaching the sea (Whitfield & Wooldridge 1994). In the dry interior, where a major part of the population is concentrated, the existing storage schemes already command virtually all the river runoff. This implies that further water development for human consumption will have to be concentrated along the coast (Anon. 1986). The magnitude of freshwater abstraction varies greatly from estuary to estuary, but in several catchment basins the storage capacity of reservoirs already exceeds the annual runoff of the rivers feeding them. In the catchment basin of the Krom estuary, for example, a Mean Annual Runoff (MAR) of 10510 ^{6}m ^{3} stands against a total dam capacity of 13310 ^{6}m ^{3}. In the watershed of the Sundays estuary (Algoa Bay, north of Port Elizabeth), reservoirs hold 7 × the runoff from tributaries (Anon. 1986; Bickerton & Pierce 1988).

A largely unknown variable in the estimation of water abstraction is the impact of numerous smaller dams build by individual farmers. At present, 59 % of irrigation schemes are in private hands and the annual growth rate of this sector between 1965 and 1978 was 3.4% –more than twice the rate of state-controlled agricultural water supplies (Anon. 1986). A paradoxical situation arises in this context, in that the long-established policy of the government to subsidize and encourage the construction of farm dams is at variance with measures by the state to check their proliferation which threatens downstream water supplies. This in turns leads to scenarios of freshwater releases from major dams that are impounded further downstream by smaller farm dams. Only minimal quantities, if any, of the released fresh water then finally reaches the estuaries. Such effects of farm dams are greatest during and after prolonged droughts and at the beginning of the rainy season (Whitfield & Wooldridge 1994).

Direct human utilization of fresh water involves essentially two processes that impact on estuaries: First, when surface water is abstracted from rivers in estuarine watersheds the amount of fresh water reaching the estuaries decreases, including flood volumes. Secondly, fresh water that eventually reaches estuaries (i.e. return flows) can have a markedly changed quality. Changes in water quality are *i.a.* caused by physico-chemical alterations during storage or by pollution in return flows after human consumption.

Indirect human effects on the flow rate and quality of river water centre on land use patterns in catchment basins, ranging from increased silt loads to reductions in runoff caused by afforestation (Anon. 1986). Regardless of whether modifications of river flow stem from direct or indirect human impacts on aquatic resources, changes occur in both the quantity and the quality of river water.

Effects of freshwater abstraction

While local estuarine ecosystems are probably well adapted to natural drought-flood-cycles – though we lack historical data to test this premise – some recent adverse effects of freshwater deprivation are well documented. For example, Whitfield & Bruton (1989) illustrated a shift in successionary trajectories of local

Table 1. Effect of medium-term increases in freshwater inflow on nutrient availability and phytoplankton biomass in two southern Cape estuaries; data from Adams (1994).

	Great Brak Estuary		Keurbooms Estuary	
	Aug. 1992	Nov. 1992	Aug. 1992	Nov. 1992
Mean salinity (‰)	18.1	3.3	14.1	11.5
Axial salinity gradient (‰)	12.2	25.8	21.2	32.8
Nitrate concentration (µg/ l)	10.6	23.4	4.3	61.1
Phytoplankton biomass (chl-*a* µg/l)	0.2	13.3	0	13.3

estuaries towards extremes of natural conditions, following reductions in river discharge, particularly floods.

Permanently open estuaries

Decline in riverine nutrient input and pelagic production. Although a host of abiotic and biotic factors (e.g. temperature, irradiance, grazing pressure, etc.) control primary productivity in estuaries, a positive correlation between phytoplankton biomass and the magnitude of freshwater inflow is a recurring one in many systems (Malone et al. 1988; Mallin et al. 1993; Harding 1994). The positive effect of freshwater inflow on phytoplankton biomass usually involves two processes; first, through the development of vertical stratification it creates hydrodynamically more stable conditions which retain phytoplankton inside the estuaries and favour the formation of blooms (e.g. Cloern 1991). Secondly, since the bulk of inorganic nutrients in estuaries is allochthonous, increases in catchment rainfall and consequent river flow increase nutrient availability to estuarine primary producers (e.g. Mallin et al. 1993). Thus, up to 40 g/kg water salinity *per se* only affects species composition of estuarine phytoplankton but not its productivity – lower productivity in euhaline waters is usually the consequence of lower nutrient loading by tidally imported seawater (Adams 1994).

These patterns are clearly evident in South African estuaries, with freshwater pulses bringing significant amounts of inorganic nutrients to estuarine waters (Allanson & Read 1987) (Fig. 3), thereby enhancing phytoplankton growth (Adams 1994) (Table 1). Thus, in estuaries along the southeastern Cape coast phytoplankton biomass is positively related to the amount of river flow (Hilmer & Bate unpubl.) (Fig. 4A). The same pattern holds for pelagic consumers: both euryhaline copepods and fish attain significantly higher biomass in estuaries having pronounced axial salinity gradients compared with estuaries of a more uniform salinity regime (Fig. 4B, C). Moreover, in individual estuaries, especially in those with normally weak salinity gradients, freshwater pulses are associated with rapid and sharp increases in copepod density (T. Wooldridge unpubl.).

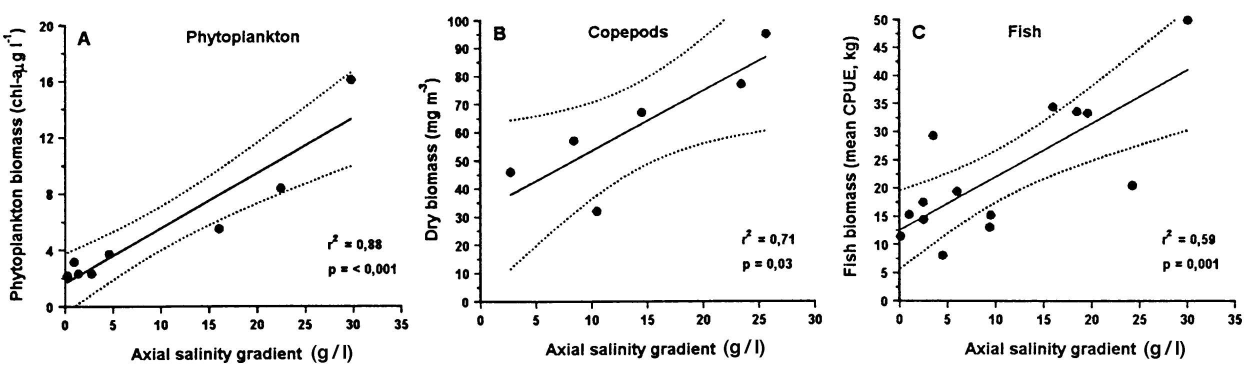

Fig. 4. Relationship between biomass of different biota and the magnitude of freshwater inflow over a range of estuaries along the southeastern Cape coast of South Africa. Measure of fresh water inflow is the difference in mean salinity between waters at the tidal head and the mouth of an estuary (i.e. axial salinity gradient). Each data point represents mean values for an estuary (i.e. eight estuaries compared in A, six estuaries in B, and 14 in C). Biomass and salinity data for phytoplankton (A) from Hilmer & Bate (unpubl.), for copepods (B) from Wooldridge (unpubl.), and for fish (C) from Marais (1988).

Changes in macrophyte community structure. Loss of axial salinity gradients, and by implications habitats, certainly has profound effects on estuarine biota. When freshwater inflow is severely curtailed, the normally oligo to mixohaline reaches become uniformly euhaline. During periods of drought, evaporation in the upper reaches exceeds dilution of seawater by riverine water inputs and hypersaline (> 35 g/kg) conditions develop. As seawater extended into the middle and upper reaches of the Krom estuary, the brackish plant communities of these regions became displaced by essentially marine species such as the seagrass *Zostera marina* (Adams & Talbot 1992; Adams et al. 1992). The result was a loss of habitat types (e.g. reeds with *Phragmites australis*) and plant diversity in the estuary as a whole declined.

Conservation of salt marshes depends on both freshwater supply, to prevent the formation of hypersaline sediments which reduce macrophyte germination and growth (Price et al. 1988), as well as tidal exchange of water to ensure flushing of the marshes. Consequently, alterations in the magnitude of either or both factors can seriously threaten the long-term viability of salt marshes. Salt marsh plants are generally associated with euhaline conditions (30 - 40 g/kg). Yet, high salinity does not seem to be physiologically optimal for growth and productivity of salt marsh plants, with production levels generally increasing with falling salinity levels and increasing freshwater input (Price et al. 1988; Adams 1994). For example, when localized freshwater pulses lowered the interstitial soil salinity in the coastal marshes of Southern California from ca. 40 g/kg to 14 g/kg for short periods (< 1 yr), the marsh grass *Spartina foliosa* increased in biomass by 40 % and *Salicornia virginica* by 160 % (Zedler 1983). By contrast, when flooding caused a severe reduction in soil salinity from hypersaline conditions to 2 - 10 g/kg, which were subsequently maintained by inflow of irrigation water, the marsh plant *Salicornia virginica* became locally extinct and was replaced by opportunistic invader species. This dramatic shift in vegetation took less than three months, but the salt marsh community did not establish itself again when salinity values returned to estuarine conditions after one year. These data stress the susceptibility of marshes to invasion by exotics and the likelihood of long-term changes in vegetation characteristics brought about by anthropogenic alterations in freshwater supply (Zedler 1983).

In addition to lowering primary productivity, elevated salinity levels in the adjacent water column can lead to salt accumulation in the intertidal marshes, ultimately causing local extinction of species. This was the case in the Krom estuary, where continuously high water column salinities (35 g/kg) have led to salt accumulation in intertidal sediments. However, even the most salt tolerant species (e.g. *Spartina* spp.) of the emergent macrophyte community in this estuary, do not persist in salinities above 45 g/kg (Adams 1994). Consequently, all vegetation in the intertidal areas of the Krom estuary died-back where sediment salinities exceeded 45 mg/g (Adams et al. 1992).

Decline in fish recruitment to estuaries. Axial salinity gradients (along the longitudinal axis of the estuary) also appear to be a principal force in determining the magnitude of fish recruitment from marine to estuarine waters. Littoral densities of larvae and 0+ juveniles of marine migrants were significantly greater in two estuaries receiving moderate to high riverine inputs compared with a system where axial salinities were relatively uniform and close to sea-water. Moreover, diversity of ichthyoplankton was markedly lower when axial salinity gradients were weakly developed and the estuarine water column differed little from adjacent marine waters in salt content and turbidity (Table 2, Whitfield 1994a). These findings are significant, since estuaries

Table 2. Comparison of recruitment of marine migrant fish species (i.e. taxa that spawn at sea, enter estuaries mainly as juveniles, and usually return to the sea prior to sexual maturity) into three estuaries which differ in riverine freshwater inflow; after Whitfield (1994a).

		Estuary		
		Kariega	Sundays	Great Fish
Physicochemical characteristics				
Mean annual river discharge (m^3)		5×10^6	13×10^6	224×10^6
Turbidity (NTU)		6.9	10.7	65.2
Mean Salinity (g/kg)		33.2	17.1	10.6
Axial salinity gradient (g/kg)		9.9	32.0	26.3
Larval and juvenile marine fish fauna				
		Ichthyoplankton[2] (WP2-nets, 0.5 mm)		
Density (Ind. $\times$ 100/m^3)		4	7	13
Richness[1]	S	7	7	8
Diversity[1]	Hill's N1	1.74	3.63	2.05
	Hill's N2	1.40	3.00	1.50
Evenness [1]	E5-ratio	0.54	0.76	0.48
		Ichthyonekton[2] (littoral seine nets, 0.5 mm)		
Density (Ind. $\times$ 100/m^3)		50	290	280
Richness[1]	S	18	20	19
Diversity[1]	Hill's N1	5,1	5,33	4,08
	Hill's N2	4,28	3,95	3,43
Evenness[1]	E5-ratio	0,8	0,68	0,79

[1] Biotic diversity indices based on individual species for nekton, but family level only for plankton;
2 All fish sampled at night with plankton nets are designated as ichtyoplankton, while those captured during daylight with seine nets are designated as ichtyonekton.

have been identified as the principal nursery area for many fish species found along the South African coast (Potter et al. 1990).

Shifts from a pelagic to benthic dominance. On an ecosystem level, freshwater input is likely to be the main physical force in setting overall system properties of many estuaries. It is generally thought that the bulk of primary production in those South African estuaries which receive adequate freshwater input is contributed by phytoplankton; such systems are therefore characterized by pelagic food webs. Conversely, when riverine discharge into an estuary is small, food webs centre around benthic primary production by macrophytes (e.g. Allanson & Read 1987). These systems often shift towards marine dominance and therefore have been labelled 'arms of the sea'. How differing riverine inputs may be reflected in estuarine system properties, can be illustrated by a comparison of the Swartkops and Krom estuary (Table 3). Both have roughly similar physical dimensions, lie in the same climatic region, but differ in the amount of riverine water input by an order of magnitude; freshwater inflow into the Swartkops averages 0.6 m^3/s, while that for the Krom is only 0.06 m^3/s –a reduction solely due to impoundment in the catchment (U. Scharler pers. comm.). The resulting shifts in ecosystem properties largely support the above notion, with a mainly benthic-based food web indicative of the fresh water-starved Krom estuary, and a significantly stronger pelagic component in the Swartkops estuary (Table 3, Baird & Ulanowicz 1993).

Table 3. Comparison of some ecosystem properties between the Swartkops estuary which receives moderate freshwater inflow and the Krom estuary where major dams in the catchment have severely reduced riverine water inflow; data from Baird & Ulanowicz (1993).

	Swartkops	Krom
Area (km^2)	4	3
Temperature range (°C)	13 - 26	13 - 28
Freshwater inflow ($m^3\ s^{-1}$)	0.6	0.06
Salinity range (‰)	10 - 35	33 - 35
Net primary production		
pelagic (mg C $m^{-2}\ d^{-1}$)	319	28
benthic (mg C $m^{-2}\ d^{-1}$)	1504	2284
pelagic : benthic	1 : 5	1 : 81
Primary consumers biomass		
suspension feeders (mg C m^{-2})	45721	21814
deposit feeders (mg C m^{-2})	8050	21556
suspension : deposit	1 : 0.28	1 : 0.99
Secondary consumers biomass		
pelagic feeders (mg C m^{-2})	5900	3
benthic feeders (mg C m^{-2})	15500	6579
pelagic : benthic	1 : 3	1 : 2193

Temporarily open estuaries: state of the tidal inlet
What is the significance of a functional tidal exchange between the estuary and the sea? Estuarine processes that are directly dependent on the state of the tidal inlet fall into three broad, but interrelated categories: (1) maintenance of typical estuarine salinity and temperature regimes; (2) migration of organisms across the estuarine mouth and (3) tidal flushing of salt marshes and regulation of water levels.

Loss of tidal influence can shift abiotic parameters to extremes. An essential element of estuaries –spatial and temporal variation in water salinity– can only be maintained by tidal mixing of sea and fresh water. If tidal inlets are blocked, the water masses trapped inside an estuary can become either hypersaline during droughts or hyposaline during rainfall pulses –both scenarios have been repeatedly recorded in South African estuaries (Whitfield & Wooldridge 1994).

The effects on the biota are, in many cases, catastrophic: large-scale fish mortalities occurred in the Seekoei estuary when water salinity reached 98 g/kg during a drought (Whitfield & Bruton 1989). Similarly, prolonged closure of the Bot estuary entrapped marine migrants and resulted in massive fish kills when salinities fell below 3 g/kg (Bennet et al. 1985). The seagrass *Zostera marina*, which forms extensive meadows in many estuaries where salinities are close to seawater, dies after a 3 month exposure to a salinity of 55 g/kg and after 1 month at 75 g/kg (Adams 1994).

Salinity in closed estuaries may reach levels which can be tolerated by adults, but exceed the threshold for reproduction. The ghost-shrimp *Callianassa kraussi*, for example, withstands salinities of <2 g/kg but its larvae require a salinity >20 g/kg to complete development (Forbes 1977). Similarly, the submerged macrophyte *Ruppia cirrhosa*, by being able to survive fresh water to hypersaline conditions (75 g/kg), is generally well adapted to the widely fluctuating salinities in local estuaries which close periodically from the sea. However, since seeds do not germinate at salinities > 55 g/kg, freshwater pulses are essential to ensure continued existence in strongly hypersaline systems (Adams 1994).

Seawater imported by the tides also serves to moderate water temperatures inside an estuary. If tidal flushing of marginal, shallow areas during summer ceases, water temperatures may rise to lethal levels; e.g. > 29 °C for the mudprawn *Ubogebia africana* (Hill 1971).

Impediment of migrations across the estuarine mouth - reduced biotic exchange. Life histories of many key estuarine organisms in South Africa comprise both an estuarine and a marine phase. In order to propagate successfully, these species actively switch between estuarine and marine waters during specific stages of their life cycle. Thus, migration through the tidal inlet is an absolutely crucial element for recruitment and population viability.

In South Africa, such exchange patterns are best known for the estuarine fish fauna. The most common life history pattern of indigenous estuarine fish comprises three stages: (1) spawning at sea, (2) immigration of larvae and juveniles into estuaries which are then utilized as nursery areas and (3) emigration of adults to sea before or after sexual maturity is attained (Whitfield 1994b) (Table 4).

Because migration through the estuarine mouth is a key element for these species (commonly labelled 'marine migrants'), closure of the tidal inlet effectively prevents recruitment to the estuary. During the closed phase of the Swartvlei estuary, the number of juvenile fish (< 50 mm TL) declined markedly, giving rise to population structures which were strongly skewed towards adults (Kok & Whitfield 1986) (Fig. 5). Moreover, prolonged mouth closure means successive recruitment failures and ultimately shifts community structure of the estuarine fish fauna towards non-migrating, resident species. After three years of inlet closure, non-migrating resident species dominated the fish fauna of

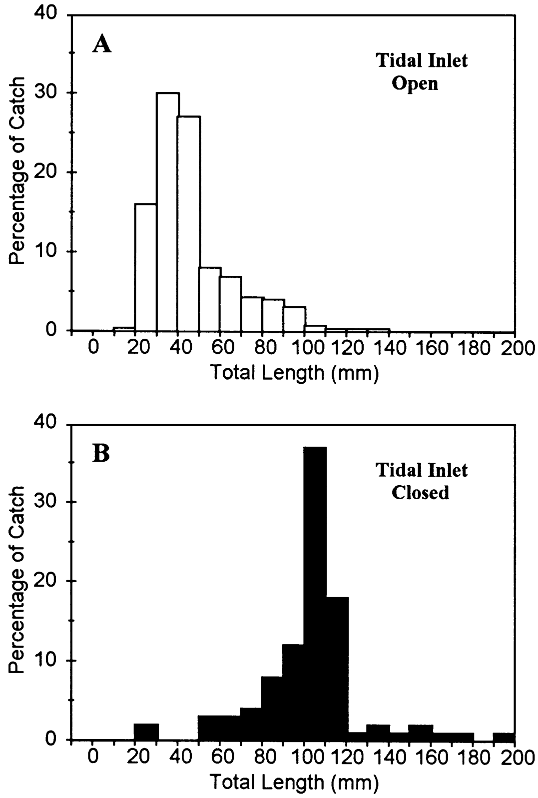

Fig. 5. Population size distribution for the fish *Diplodus sargus* (Teleostei, Sparidae) in the Swartvlei estuary during phases of an open tidal inlet (A), and when the estuary was closed off from the sea (B). Note the almost complete failure of recruitment after closure. (After Kok & Whitfield 1986.)

Table 4. Categories of fishes which utilize southern African estuaries to various degrees. Total number of estuary-associated species = 142; modified from Whitfield (1994b).

	Spawning sites			Juvenile habitat			Juveniles		
Category	Fresh	Estuar.	Sea	Fresh	Estuar.	Sea	Species	% (abs)	% (cum)
1. Estuarine residents breeding:									
1a only in estuaries		●			●		21	15	15
1b mainly in estuaries	○	●	○	○	●	○	19	13	28
2. Marine migrants whose juveniles are:									
2 a wholly estuarine dependent		●			●		16	11	39
2 b mainly estuarine dependent		●			●	○	15	11	50
2 c weakly estuarine dependent		●			○	●	30	21	71
3. Marine species without direct estuarine dependence		●				●	30	21	92
4. Euryhaline freshwater species	●	○		●	○		7	5	97
5. Obligate catadromous species		(○)	●	●	(○)		4	3	100

Full circles show strong dependence on and primary and obligate use of a particular habitat, whereas open circles indicate that species use particular habitat types facultatively. Circles in brackets indicate that estuaries represent essentially transit corridors for the catadromous species.

the Bot estuary, with marine migrants comprising 36 % of species present, but only 1 % of numbers. By contrast, in the adjacent Palmiet estuary, which maintains a permanently open mouth, marine migrants made up 73 % of species and 53 % of numbers (Bennet 1989).

Marine migrants which depend on estuaries as nursery and foraging areas comprises 61 species or 43 % of the total fish fauna associated with local estuaries (Table 4, Whitfield 1994b). Because alternative nursery areas in inshore waters of the southern African coast are largely lacking, the regional importance of estuaries to marine fish may indeed be greater than in other parts of the world (see Potter et al. 1990). Including estuarine residents and catadromous species (i.e. fish species migrating annually from fresh to salt water), 105 species of estuarine-associated fish (74% of total species) are either completely or partially dependent on estuaries for their existence (Whitfield 1994b).

According to Whitfield & Kok (1992), the open or closed condition of the tidal inlet is probably the main determinant of fish species richness and abundance in estuaries. A broad comparison of ichthyofauna data between estuaries with open and estuaries with closed inlets supports this view; all calculated indices of biotic diversity are markedly higher in estuaries having a free tidal connection to the sea (Fig. 6).

There is also increasing evidence that estuarine invertebrates show a similar dependence on tidal exchange between the estuary and the sea for completion of their life cycles as do fishes. Penaeid prawns (i.e. swimming prawns (most species commercially important) of the family Penaidae), which sustain a sizeable fishery in Natal, enter estuaries as postlarvae where they grow rapidly in these nursery areas for several months before returning to the sea where maturation and spawning takes place (Forbes & Benfield 1985). This pattern is reversed in other estuarine invertebrates: adults live inside the estuaries where they attain sexual maturity and spawn. Early larval stages then emigrate to the sea on the ebb tide. After completing larval development in marine waters, postlarvae enter the estuary on the flood tide to settle.

This life history style is exemplified by the anomuran prawn (i.e. benthic prawns of the family Callianassidae found in extensive burrow systems mostly in soft-sediment habitats) *Ubogebia africana*, which dominates the benthic fauna in many estuaries along the south coast (Wooldridge 1991, 1994). Because larvae trapped within an estuary do not develop beyond stage I, recruitment to the estuarine population is entirely by immigration of postlarvae from the sea. How strongly recruitment in *U. africana* depends on an open tidal inlet is illustrated by a population in the Great Brak estuary (Wooldridge 1994) (Fig.7). Following construction of a major dam 5 km above the estuary, the tidal inlet opened only infrequently over the next 28 months. During this time recruitment to the estuarine population was minimal (Fig. 7 A, B), with only a very small number of postlarval prawns colonising the estuary when the tidal inlet opened briefly for 30 days in November 1991 (Fig. 7B). By contrast, when the estuary remained tidal during the summer of 1992-1993, large numbers of postlarvae recruited to the resident estuarine population (Fig. 7C). However, 18 months after the last successful recruitment occurred, abundance of prawns in the Great Brak estuary (<300 burrow openings/m ^{2}) was still markedly

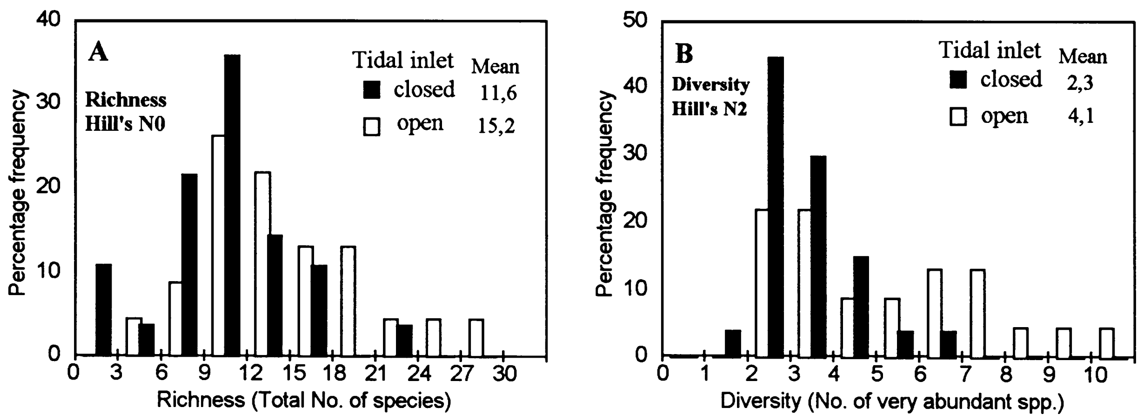

Fig. 6. Influence of tidal inlet configuration on estuarine ichthyofaunal diversity. Open bars (□) represent estuaries with permanently open tidal inlets and open phases of the tidal inlet in temporarily closed systems. Solid bars (■) denote temporarily closed systems and times when an estuary is blocked off from the sea by the formation of a sandbar across its mouth. Measure of richness is Hill's N0 (A), and of diversity Hill's N2 (B). Indices (n = 14 - 28 data sets per group) were calculated from numerical CPUE-data of Bennett et al. (1985); Kok & Whitfield (1986); Marais (1988); Bennett (1989); Whitfield & Kok (1992); Dundas (1994); Whitfield (1994a).

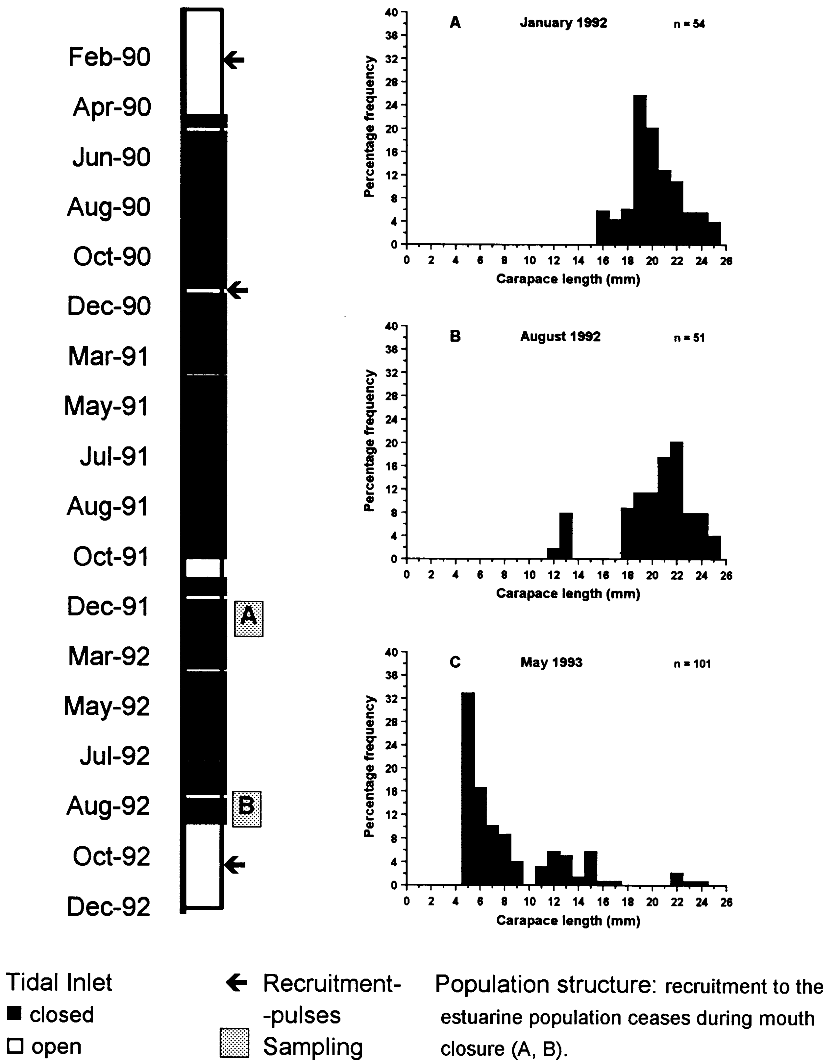

Fig. 7. Size-class distribution of the anomuran prawn *Ubogebia africana* in relation to the state of the tidal inlet (left column) in the Great Brak estuary, with filled black areas in the left-hand column indicating times with a blocked estuarine mouth and open areas showing periods when the tidal inlet was open to the sea. Recruitment pulses by immigration of postlarvae which gave rise to the cohorts evident in the histograms are indicated by arrows. Sampling dates shown by shaded rectangles; modified from Wooldridge (1994), with size-frequency data of May 1993 here supplemented.

lower compared with densities in the adjacent Klein Brak estuary (>700 holes/m ^{2}), which had a permanently open mouth. This suggests a protracted period of population recovery after tidal inlet closure, possibly because marine dispersal of larvae between estuaries is limited.

Indications are that several other decapods (e.g. saltmarsh crabs) exhibit similar exchange patterns, and thus rely on open tidal inlets for their existence. Overall, unimpeded tidal exchange appears to be the critical aspect in determining population sustainability for a wide range of estuarine organisms. Consequently, if the current trend of increasing mouth closure is allowed to continue, we predict that many species will ultimately become locally extinct in a greater number of estuarine systems along the South African coast.

Detrimental impacts of loss of tidal flushing and extreme water levels on resident plant communities. Tidal inundation of salt marshes can no longer operate in closed estuaries, resulting in significant changes in vegetation. In some local estuaries, assemblages of the marsh grass *Spartina maritima* disappeared and the typical salt marsh mosaics gave way to encroachment by brackish reeds or terrestrial invader species (Adams 1994). A similar situation is found in many coastal marshes of North America where tidal restriction, accompanied by a reduction in salinity levels, changed the structure of salt marshes dramatically. *Spartina*-dominated communities became nearly monotypic stands of the reed *Phragmites australis* (Roman et al. 1984). Overall, biotic diversity of the estuarine vegetation decreases under conditions of tidal restriction.

Closure of the tidal inlet also alters water levels within an estuary. Depending on the balance between local rainfall, freshwater inflow and evaporation, water levels either rise to flood the marshes with low salinity water or previously subtidal areas become exposed and hypersaline conditions develop.

Prolonged inundation of salt marsh plants with low salinity water causes rapid decomposition of tissue and prevents flowering and production of seeds, thereby lowering recruitment after water levels subside again (Adams & Bate 1994a).

In two periodically open estuaries, closure of the tidal inlet resulted in a significant lowering of the estuarine water level. This exposed the normally subtidal beds of *Ruppia cirrhosa* and, after 3 months, the species was locally extinct. After localized rainfall events the plants did, however, recover rapidly due to the large number of seeds (4850seeds/m ^{2}), which were produced during favourable conditions (Adams & Bate 1994b). Similarly, growth of the marsh grass *Spartina maritima* is significantly reduced when soil moisture falls below the levels normally maintained by periodic tidal flushing of the marshes (Adams 1994).

Catchment degradation and water quality

According to O'Keeffe et al. (1992) the basis for management of freshwater ecosystems follows from the fact that "the conditions, water quality and biota of any body of fresh water are the product and reflection of events and conditions in its catchment". Because estuarine ecosystems are strongly dependent on the input of fresh water they receive from the rivers, this applies equally well to estuaries. Yet, the quality of many water sources in South Africa is declining, mainly as a result of salinization and to a lesser extent because of eutrophication and pollution by trace metals and micropollutants (Anon. 1986; Lusher & Ramdsen 1992).

Salinization

Salinization (i.e., TDS, increase in the concentration of total dissolved solids in inland waters) is a common threat in semi-arid regions (Hart & Allanson 1984). Although many freshwater bodies in South Africa are naturally high in dissolved salts (O'Keeffe et al. 1992), progressive salinization by irrigation, industrialization, mining and urbanization has become a serious hazard to water quality and aquatic ecosystems (Hart & Allanson 1984; Anon. 1986). The concentration of salts in many large reservoirs (TDS 99 to 2200 mg/l) already lies above the threshold of salinity tolerance of many important crop species (e.g. potato: 660mg/l) and the recommended level for drinkwater (TDS 350 to 500mg/l).

Some estuaries receive fresh water of elevated salinity from such reservoirs. For example, in Lake Mentz, which impounds the tributaries of the Sundays estuary, the concentration of salts (TDS) exceeds 738mg/l for 90 % of time and 1470mg/l in 10 % of the sampling occasions (Anon. 1986). In the lower reaches of the Sundays river, TDS-concentrations are generally in the range of 1000 to 15000mg/l and the insect fauna of the stream appears impoverished (Forbes & Allanson 1970).

While slightly elevated salinity levels in inflowing 'fresh water' may not be detrimental to estuaries which receive moderate to high runoff, they would obviously be less effective in diluting marine waters and creating axial estuarine salinity gradients when riverine input is below average. In addition, when water is released from reservoirs to create and maintain waters of low salinity in the upper regions of an estuary, greater allocations must be made if the released water is already of a brackish nature.

Total dissolved solids give only a general indication of the overall salt concentration, but the impact of salinization on biota will often depend on the specific chemical composition of the water. A drastic example of altered soil chemistry is given by La Cock (1992); soils in areas which are bare of vegetation show increases in aluminium concentration and lowered pH-values. Al has inhibitory effects on plant growth and is toxic to plants at high concentrations. In South Africa overgrazing by small livestock (e.g. domestic goats) in many watersheds is a serious problem and reduces vegetation cover dramatically (G. Kerley pers. comm.)

It is reasonable to assume that such changes in soil chemistry will be reflected in altered water chemistry in the rivers receiving runoff from watersheds being subjected to overgrazing. If the same pattern of significant growth inhibition by elevated concentration of minerals such as Al holds for aquatic plants, it could have severe repercussions on estuarine ecosystems situated along these catchment basins. At present, we lack data on such effects –clearly a situation of considerable environmental concern.

Although nutrients in estuaries are naturally allochthonous, most being imported by the rivers, increasing human activity along water courses over the last few decades has significantly accelerated the inflow of nutrients into estuaries. Effects of eutrophication, mainly in the form of spectacular algal blooms and floating plants, are quite common in South African freshwater dams and streams (Hart & Allanson 1984; Anon. 1986; O'Keeffe et al. 1992). Local estuaries appear thus far less frequently affected and are less severely subjected to eutrophication events. However, indications are that increased nutrient loading from urban settlements and farming on the estuarine floodplains, coupled with recent reductions in freshwater input which decrease flushing and dilution of wastes, will markedly shift this situation towards more frequent and widespread algal blooms in the near future (J. Adams & P. Huizenga pers. comm.).

Soil erosion and fluvial silt loads

Soil, one of South Africa's most basic resources, is being lost to erosion at an alarming rate. On average, the rate of soil loss (3 tonnes ha^{-1} yr^{-1}) exceeds the rate of soil formation (0.31 tonnes ha^{-1} yr^{-1}) by a factor of 10 (Verster et al. 1992). South Africa is currently loosing 300 million tonnes of topsoil annually, which is equivalent to loosing 15 cm of soil over 150 000 ha (Gilliomee 1992). Yet, this average figure gives only a conservative estimate of the scale of physical soil degradation. Most cultivated lands in the region experience soil loss well in excess of 4 tonnes ha/yr, with some areas being subjected to extreme erosion in the range of 40 and 120 tonnes ha^{-1} yr^{-1}. For the country as a whole, severe soil erosion has rendered more than three million ha unproductive and over 60 % of South Africa's surface area is in poor condition with respect to soil erosion (Verster et al. 1992).

Although numerous natural causes contribute to soil erosion, relatively recent socio-economic developments are thought to have led to an exponentially accelerating rate of soil loss (Clarke 1991). On the one hand, commercial agriculture of an essentially First World nature, though frequently marked by overcropping and overgrazing, has replaced the indigenous vegetation over large areas. The result is usually a diminished plant cover and density, which significantly accelerates the rate of soil loss. On the other hand, and often in stark contrast to the former, the political abnormalities of the past have denied large parts of the populace the chance for economic advancement. Farming and pastoralism of an essentially Third-World type, often with fierce competition for land which precludes environmentally sound practices, are now the only form of subsistence available to the extremely poor in the seriously overcrowded tribal areas. Again, this has left the land bare of vegetation and the rains then rapidly wash away the unprotected topsoil (Gilliomee 1992). In parts of Tanzania, for example, a tenfold increase in erosion rates over the last 20 - 30 yr is associated with high cattle densities, flat cultivation and densely settled areas (Stocking 1984). Above all, to quote James Clarke (1991): "It seems there came a point when the 'culture' went out of agriculture among black and white farmers alike."

Land deterioration on so grand a scale obviously has tremendous implications for the rivers draining catchment basins affected in this way –the most obvious being a rise in fluvial silt loads. Martin (1987) found that modern rates of sediment supply to the Natal Valley (i.e. a prominent geomorphologic feature on the continental shelf along the east coast of South Africa) are 12 to 20 × greater than the geological average He ascribes this steep increase in fluvial sediment yields mainly to poor land-use practices in the catchments. There is some dispute among geologists about the exact values of such sedimentation and erosion rates (see McCormick et al. 1992), but a view of relatively recent increases is a prevailing one.

For the estuaries lying in this drainage region, siltation has consequently been identified as the factor having the most detrimental impact on the estuarine environment (Begg 1978). Over the last few decades siltation has generally led to a gradual infilling of many estuaries, resulting in a loss of storage capacity, smaller water area, and encroachment by reeds (Begg 1978). This view was contested as a generalization by Cooper (1989), although he based it on data from a single estuary only. Historical observations, however, illustrate the extent of sediment infilling. Within living memory some estuaries were deep enough to be used as harbours by coastal steamers; now they can be waded across and are only called 'ports' out of nostalgia (Branch & Branch 1981).

Apart from reducing physical channel dimensions, progressive fluvial siltation also raises turbidity levels of the water column. Because estuaries are generally nutrient-rich but turbid, light availability is considered the most important factor controlling primary production by phytoplankton (Cole & Cloern 1987). Excessive turbidity lowers underwater irradiance to such levels as to markedly reduce primary production in local estuaries. More significantly, high turbidity and siltation effectively preclude the growth of benthic macrophytes. In several Natal and Transkei estuaries heavy siltation and high turbidities have killed seagrass populations (Day 1981), thereby reducing the range of habitats and resource diversity available to the estuarine fauna. Effects of turbidity on estuarine fish encompass a wider range of patterns. Some indications are that ichthyofaunal densities in South African estuaries are positively correlated with turbidity (e.g. Marais 1988; Whitfield 1994a). Similarly, the majority (16 out of 20 species) of marine fish having juveniles common to estuaries were shown by Cyrus & Blaber (1987a, b) to have a preference for turbid waters. Such preferences are reflected in differential distribution patterns of fish within an estuary, where certain species are only present in consistently clear waters and others only in consistently turbid areas (Cyrus & Blaber 1987a). From this follows that estuaries with a range of turbidity levels support a greater number of species. Conversely, in estuaries with uniformly high turbidity regimes, caused by silt-laden freshwater inflow, clear-water species will not be present and thus ichthyofaunal diversity is lower –both concepts which still need quantitative testing. By contrast, impoundment of fresh water can effectively reduce estuarine turbidity levels to that of seawater thereby reducing the number of turbid-water species. It may therefore be the range of conditions rather than the absolute value of turbidity in any given estuary which is a co-determinant of biotic diversity. Both excessive freshwater abstraction and heavy sediment loads can permanently shift the turbidity regime to extremes of natural conditions and thus effectively reduce spatial and temporal habitat heterogeneity.

Some lessons for estuarine conservation

Integrating catchment and estuarine management

Hydrologists have long recognized the close links between catchment characteristics and runoff (e.g. Hart & Allanson 1984; O'Keeffe et al. 1992), borne out by Hynes' (1975) statement that: " … in every respect the valley rules the stream …". Limnological problems can therefore be essentially seen as catchment problems (Hart & Allanson 1984).

Although essentially the same concepts hold for estuaries, coastal managers have in the past realized the importance of integrated catchment conservation to a lesser degree than have freshwater ecologists. Strategies which aim to mitigate negative anthropogenic impacts on water quality and quantity in the river catchments are therefore a relatively recent development in estuarine conservation strategies. However, by their very nature as transition zones between limnetic and marine waters, estuaries are not independent ecosystems and should therefore not be managed as such (Day 1981). Indeed, the crucial dependence of estuaries on the freshwater tributaries and their associated catchment basins is a factor in most estuarine conservation problems –also the recurring theme in this paper.

Given the need for estuarine managers to "move their conservation strategies from the coast further inland" (i.e. expand the geohydrological and ecological range of conservation measures towards the interior), the question arises as to what size of catchment unit will provide the most effective conservation output. Hart & Allanson (1984) give three limnological criteria for identifying the optimum size of a catchment unit to be managed for freshwater ecosystems: (a) water yield; (b) demand for water use and (c) nature and complexity of limnological perturbations arising from the catchments. According to O'Keeffe et al. (1992), it is the quantification of environmental freshwater requirements rather than the implementation of policies which, at present, represents the main problem in the conservation of freshwater systems. Clearly, all of these criteria apply equally well to estuarine systems, and the need to assign quantitative values to each factor is an imminent one. To this end, an engineering approach which provides for 'hard figures' on estuarine fresh water demands - data that are more readily assimilated by decision makers - should in the future augment the more complex ecological arguments.

Water allocation policies

In a country that is extraordinarily rich in natural resources, fresh water is perhaps the major exception (O'Keeffe et al. 1992). Because fresh water is a limited commodity in South Africa, decisions concerning how much water different sectors may use are inevitable and pressing. Such decisions can be based on many grounds, ranging from purely economical to entirely environmental. The overriding factor will, however, always be that water is *the* fundamental element for human survival, and in South Africa "the availability of water promises to set a finite limit upon the size of population which can be supported at an acceptable standard" (Hart & Allison 1984).

While estuaries have quite recently been identified as legitimate consumers of fresh water (Anon. 1986; Jezewski & Roberts 1986), this policy is not guaranteed to continue into the future. Jezewski & Roberts (1986) hint on this development by stating: "In certain cases it might not be possible to obtain desirable ecological conditions in the estuarine system and a decision might have to be taken to 'write-off' the estuary." Yet, in the formulation of the new Water Act there have been strong inclinations to consider the natural environment (i.e. rivers, estuaries) as a resource *per se* and not solely as a competitor or user of fresh water (e.g. agriculture, mining, etc.). Water allocations might then give priority to environmental demands and all other consumers will have to compete for the remainder. Perceptions about the necessity to supply estuaries with fresh water may ultimately only hold to the point when water allocations to human users become insufficient. Given the rampant population growth, this scenario is not unlikely.

We believe that this rather pessimistic view may at the same time hold the key for successful estuarine conservation strategies. Regardless of the proximate motives, water allocations to competing users are, and will ultimately be, political ones (here we use 'political' in the sense of public policy formation not restricting its meaning to ideological preferences). If estuarine managers adopt a stronger political role they can have a more direct influence on decision making processes regarding freshwater allocation between human and 'natural users' such as estuaries. Stronger political involvement does not imply the sacrifice of environmental principles but, on the contrary, provides a means to promulgate them more effectively.

Estuarine conservation in the Southern African context: economic vs. ethical motives

Because competition for fresh water in South Africa is so fierce, each rival in this contest would gain considerable advantage if their arguments stand on some higher ground. In the context of estuarine conservation this typically translates into general statements on the importance and values of estuaries (e.g. Day 1981). While all these values may indeed be obvious to the relatively affluent conservationist, they are at least obscure, if not incomprehensible, to the desperately poor slum-dweller who does not even has access to safe drinking water. Indeed, in some instances where estuaries border slum areas, the contrast between First World aspirations for conservation and Third World economic deprivation becomes frightfully stark. Although most conservation issues are ultimately a question of ethics, such motives are likely to be of little practical significance in a Third World context where huge socio-economic needs predominate.

A common yardstick by which the 'obscure' benefits of estuarine conservation could be translated into more tangible values is money. Here we can borrow liberally from economic sciences and methods such as cost-benefit analysis and utility analysis can be routinely employed in balancing development versus conservation goals (Day 1981). These approaches, however, have the disadvantage that not all features of the environment can always be given a monetary value (e.g. aesthetic factors). The final outcome of such methods therefore represents only certain economic aspects but does not account for intrinsic values of natural assets such as an estuary. Most significantly, importance ratings and assignment of monetary values to environmental parameters depend entirely on the value judgement of the community utilising a specific natural resource. For example, protection of some rare water fowl will rank high among the ornithological fraternity, but the underprivileged majority of the population will view it as an extravagance. Thus, in a Third World context the exclusive use of economical considerations to justify intangible goals in estuarine conservation will, at best, be controversial.

An alternative approach is to ensure that all population groups derive tangible, monetary benefits from the conservation of estuaries. While the need for such a policy has been realized in the terrestrial realm and is increasingly implemented in many game reserves, it is virtually absent in the coastal areas of South Africa. Estuaries are prime sites for holiday resorts and residential areas (Begg 1978). Because the economic viability of property and resort developments relies on the continued attractiveness of estuarine watercourses, such developments can even constitute important driving forces for conservation. On the other hand, development for purely residential purposes generally serves only a privileged minority with far fewer economic spin-offs to local communities than, for example, eco-tourism can provide. Most importantly, by commanding most of the available waterfront property residential areas effectively bar future developments and lower the values of estuaries for tourism. Consequently, to actively promote the intensive use of estuaries for eco-tourism will ultimately be of greater value to conservation than purely protective measures which largely exclude direct human utilization. For many estuarine managers this might represent too radical a deviation from the much cherished practices of over-protection. However, they and we must constantly be reminded that South Africa's estuaries are a valuable natural resource which, if used wisely, can provide a way to better the economic standing of the country's people. Estuarine management must, therefore, in the future encompass measures which ensure that monetary benefits derived from the utilization of the estuarine resource are spread over a wider spectrum of the population.

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