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Comparison of, and the effects of altered freshwater inflow on, fish assemblages of two contrasting South African estuaries: the cool-temperate Olifants and the warm-temperate Breede

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This study compares the fish assemblages of the permanently open cool-temperate Olifants and warm-temperate Breede estuaries on the west and south coasts of South Africa respectively, and their responses to altered freshwater flows. Both estuaries have experienced a >35% reduction in mean annual runoff (MAR) from a historical reference condition to the present day with a >60% reduction possible under future flow scenarios. With the exception of species that have both marine and estuarine breeding populations, the Olifants Estuary fish assemblage has experienced an overall 20% decrease in abundance from reference (pristine state) to the present day and will gradually decline to 55% of reference with a predicted future 60% reduction in MAR. Consequently, future reductions in flow are likely to result in the Olifants Estuary progressing towards a low biomass, low diversity, marine-dominated system. In contrast, reduced freshwater flows in the Breede Estuary are likely to experience an overall reduction in the abundance of species that breed only in estuaries, and in freshwater and catadromous species. Collectively, entirely estuarine-dependent fish will increase in abundance, but considered individually some important exploited species such as *Argyrosomus japonicus* and *Pomadasys commersonnii* will collapse to 50% of historical numbers once there has been a 64% reduction in MAR. Overall, fish abundance in the estuary has increased by 6% from reference to the present day and is likely to increase to 115% of reference with future reductions in flow. Some species with a preference for fresh and brackish water will be all but lost from the system, but overall diversity is likely to increase with the range expansion of warm-temperate and subtropical marine species westward. In all, the fish assemblage of the Breede Estuary will experience a gradual change from a relatively high-diversity, low-abundance, freshwater-rich system under historical flow conditions to a high-diversity, high-abundance, marine-dominated system with future reductions in flow.

Keywords: abundance and diversity, ecological flow requirements, estuarine dependency, Freshwater Reserve (Environmental Flow Requirements), salinity preferences

Introduction

The range of benefits and habitats provided by estuaries is considerable, yet fish diversity in estuaries is low compared to marine and freshwater ecosystems, despite estuaries providing abundant food resources that exceed those of coral reefs, tropical forests and most other ecosystems (Whitfield 1994a, Costanza *et al*. 1997). Benefits provided by estuaries to fish are well documented and include high productivity, low predation, low salinities, and refuge from adverse conditions in the marine environment such as low temperatures or oxygen levels — thus improving body condition, growth and/or survival (de Decker and Bennett 1985, Potter *et al*. 1990, Robins *et al*. 2006).

Whitfield (1996) lists many biotic and abiotic factors influencing the abundance and diversity of estuarine-associated fish, including latitude, seasonality, catchment size, estuary size, salinity gradients, habitat diversity, mouth condition, dissolved oxygen levels, turbidity, food resources, flooding, and anthropogenic impacts. The last of these can be direct, such as pollution, dredging, bait collection and fishing; or indirect, such as upstream impoundments, water abstraction and marine fishing. Impoundments trap sediment, reduce freshwater flow and obstruct the upstream migration of catadromous species, whereas overexploitation in the marine

environment will reduce recruitment of estuarine-associated species into estuaries (Lamberth and Turpie 2003). In all, the response of estuarine fish assemblages to environmental and ecological change makes them good indicators of anthropogenic stress (Whitfield and Elliott 2002).

Despite the numerous benefits provided by estuaries, estuarine-associated fish are vulnerable because of their isolation and reliance on local conditions, which can be highly variable (Maitland 1990). Estuarine residents and obligate estuarine-dependent marine species are confined to their systems for all or part of their life cycles, resulting in many independent or discrete populations each with its own stock characteristics. This may require that juveniles of marine-spawning species return to their natal estuaries. In turn, discreteness or confinement to a single estuary makes entire populations vulnerable to factors such as disease and pollution. Therefore, for survival of a species, the number of discrete populations is more important than the number of individuals (Maitland 1990). Migrations, whether they be of diadromous fish entering or leaving the catchment or of juvenile and larval fish recruiting into the estuary, cannot take place if there are obstructions. Aggregations associated with migration are often predictable, making them susceptible to predation and fishing. Both short- and long-lived species are vulnerable to poor estuarine conditions and exploitation. Large, slow-growing, late-maturing species are attractive to fishers and at risk of being caught before they are able to spawn, whereas small, short-lived species cannot wait out the years for good spawning conditions. Consequently, estuarine fish populations may be more vulnerable to extinction than their entirely marine counterparts. However, longevity and short lifespans may both be adaptations to unstable estuarine environments including erratic freshwater flow (Blaber 2000). Longevity provides a greater chance of a successful spawning whereas brevity of life cycle allows fish to take advantage of limited windows of opportunity within a year or season.

South Africa has 255 functional estuaries along 3 200 km of coastline stretching from the Orange (Gariep) River on the West Coast to Kosi Bay in the East Coast (Turpie *et al.* 2002). The warm-temperate biogeographic region (from Cape Point to Mbhashe River) and the subtropical region (northwards of the Mbhashe River) have 125 and 121 estuaries respectively, whereas the arid cool-temperate region (Cape Point to Orange River) is estuary-poor with only nine (Lamberth and Turpie 2003). On a broad scale, southern African estuaries have been classified into estuarine lakes, estuarine bays, river mouths and permanently or temporarily open/closed systems (Whitfield 1992). Fewer than 30% are permanently open (Whitfield 2000). On a biogeographical level, low rainfall and runoff, coupled with high seawater input and evaporative loss, result in high salinities and low turbidity throughout the year in warm-temperate estuaries but only during summer in cool-temperate estuaries (Harrison 2004).

Estuarine fish diversity in southern Africa declines from south and westwards with few of the more than 100 species typical of subtropical and tropical estuaries occurring in estuaries on the cool-temperate West Coast or warm-temperate South-East Coast (Day 1981, Whitfield 1994a, Turpie *et al.* 1999, Whitfield 2005a, 2005b). Fish productivity on the other hand is highest in cool-temperate and lowest in subtropical South African estuaries. Both fish productivity and diversity are higher in permanently open than in temporarily open/closed systems (Lamberth and Turpie 2003).

National legislation requires that alterations to freshwater flows take into account the ecological needs of ecosystems (Thompson 2006). This paper focuses on alterations to freshwater flow in terms of their influences on the fish assemblages of two permanently open South African estuaries, the Breede and Olifants, which were selected because of their importance, representation of two biogeographical regions, and the fact that they are already subject to substantial water abstraction and there are future plans to further alter flows.

The philosophy adopted was to (1) assess the current species composition and abundance of fish, (2) determine their estuarine dependency, (3) measure physical conditions and how they change seasonally, (4) determine how fish respond to these changes and physical conditions, and (5) use this information to assess what fish assemblages would have been like under pristine conditions prior to the alteration of freshwater flows, and how they may change under various future scenarios.

Material and Methods

Study area

Olifants Estuary
The Olifants/Doring River system has an area of 49 000 km^2, making it the second-largest catchment in South Africa, but because it falls in an arid region it contributes only 2% of the country's mean annual runoff (MAR). The Olifants River is approximately 250 km long, and has two of South Africa's oldest large dams, the Clanwilliam and Bulshoek, in its middle reaches. The Doring River runs out of the semi-desert Ceres Karoo and joins the Olifants below the two dams. Both rivers fall within a winter rainfall area.

The Olifants Estuary flows into the Atlantic Ocean in the cool-temperate Namaqua biogeographical region on the west coast of South Africa. It is approximately 36 km long from the mouth, below the fishing village of Papendorp, to the Lutzville causeway, which inhibits tidal influence from extending any further upstream (Figure 1). The surface area of the estuary is approximately 720 ha. The upper reaches 15–36 km from the mouth are narrow, being 20–50 m in width and having water depths averaging 1–3 m. Agriculture is intensive on both banks and fields are often bulldozed to the edge and even into the estuary. The lower 15 km of the estuary widens to approximately 400 m with extensive saltmarsh on either side. About 2 km from the mouth is an approximately 2 km long backwater, which originally was a second channel that became blocked with marine sand after a severe storm in 1925 (Morant 1984). The estuary enters the sea between a rocky headland to the north and a large sandy spit to the south. The spit and beach extending 5 km to the south are diamond-mining concessions but have yet to be mined. The Hartebees Kanaal, a shallow rocky channel, bisects the northern headland. The rocky shores, beaches and subtidal areas to the north are mined for diamonds.

The lower 15 km of the estuary supports a gillnet fishery, comprised of fishers from the Ebenhaeser/Olifantsdrift and
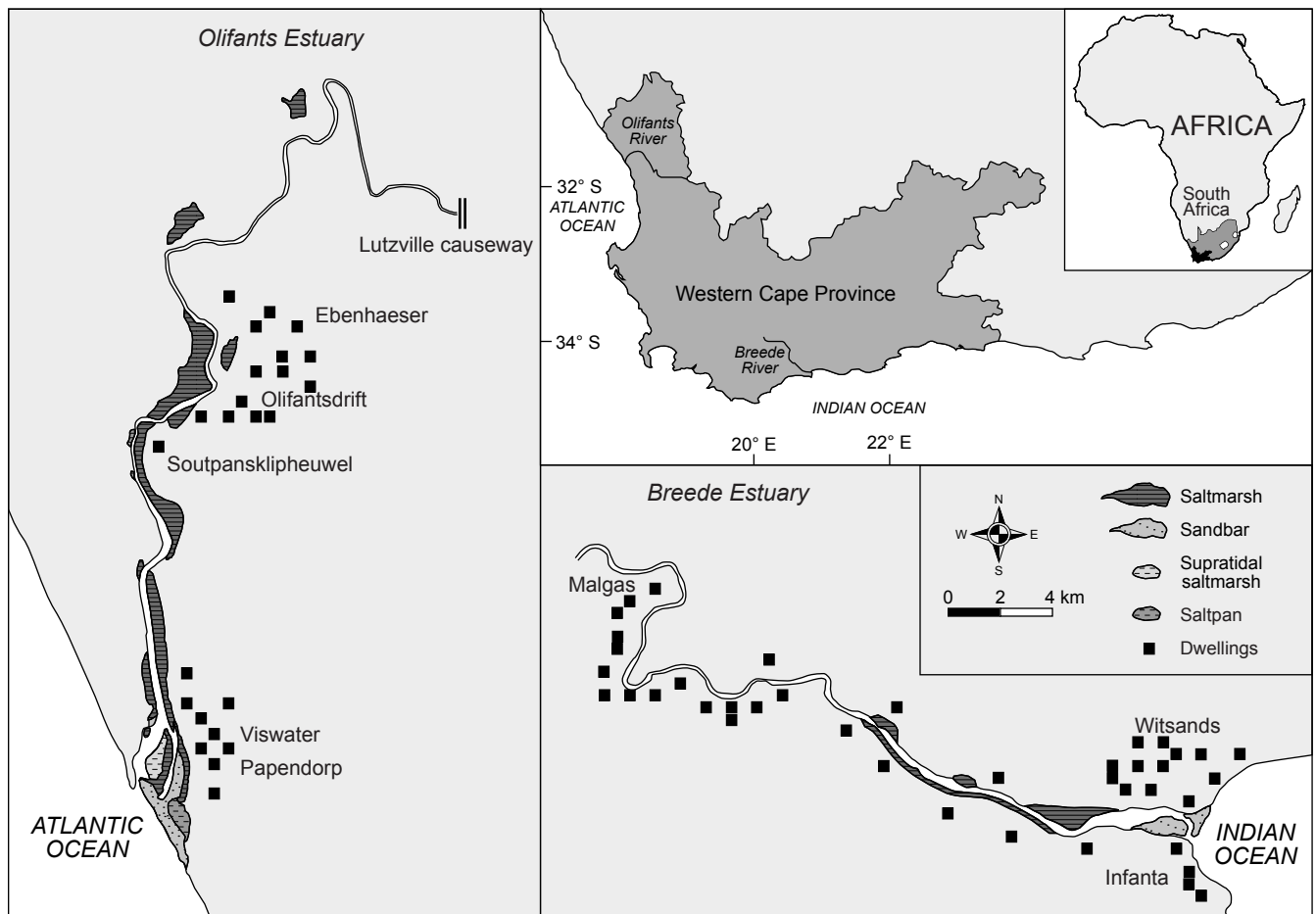
Figure 1: Maps of the Olifants and Breede River estuaries showing places mentioned in the text

Papendorp/Viswater communities. There are currently 45 operators, although there have been up to 120 in the past. Consequently, the fish fauna and assemblages are likely to have been impacted by fishing, over and above any changes arising from altered habitat or freshwater flows.

Breede Estuary
The Breede River is 322 km long from its source near Ceres to where it enters the Indian Ocean in Sebastian Bay, and falls within the warm-temperate Agulhas biogeo-graphical region. It drains a catchment of approximately 12 600 km² and its estuarine section has a total surface area of 455 ha, extending 50 km upstream to about 10 km beyond the pontoon at Malgas where tidal influence ceases (Figure 1). Three large and numerous smaller dams within the catchment have reduced the original MAR reaching the estuary by 42% to the present-day flow of 1 034 × 10⁶ m³ (Taljaard *et al.* 2001). Although the estuary falls within the winter/bimodal rainfall transition zone, most of the catchment lies in the winter rainfall area and flows are strongly seasonal with high flows and floods during winter.

The Breede Estuary is permanently open, with a mean depth of 4.6 m but there are a limited number of areas up to 17 m deep in the middle and upper reaches. In the 2 km stretch nearest the mouth, an extensive sand-spit running

from the northern bank diverts the main channel across to the southern bank where it enters the sea against a wave-cut terrace (Carter 1983). The estuary is highly responsive to freshwater inflows, and high flows of 20–95 m³ s⁻¹ are able to completely flush and reset the system during a single tidal cycle (Taljaard *et al.* 2001). The water column ranges from well mixed during spring highs to stratified during spring lows and neaps, and the river-estuarine interface (REI) zone may shift 8–10 km between tides.

Historically, prior to 1990, the estuary supported a beach-seine fishery of 40 or more participants, as well as a recreational linefishery. Nowadays, the estuary still supports a substantial recreational fishery with in excess of 100 boats recorded on the estuary during weekends and holiday periods.

Fish sampling

Gillnet sampling, which targets the adults and subadults of the larger fish species, and seine-nets, which capture juveniles and the smaller fish species, were both employed as means of sampling the fish. Quantitative data on the fish of the Olifants Estuary were obtained from (1) summer and winter seine and gillnet surveys in February and August 2004, (2) a bimonthly seine and gillnet fishery simulation exercise throughout the South-Western Cape during the

period 1997–1999, (3) a gillnet survey in March and August 1995 and (4) monthly catch returns from the commercial gillnet fishery from 2003 to 2005 (Marine and Coastal Management [MCM] Netfish System). The 2004 survey entailed sampling every 1–2 km from the mouth to the Lutzville Causeway, approximately 36 km upstream, whereas the 1997–1999 sampling was confined to the lower 8 km of the estuary (Figure 1). The 1995 survey was confined to the use of gillnets, which were used to obtain samples at 1 km intervals all the way to the Lutzville Causeway.

Quantitative data on the fish from the Breede Estuary came from (1) summer and winter seine and gillnet surveys in February and August 2000 and (2) the 1997–1999 bimonthly seine and gillnet fishery simulation exercise. The 2000 survey entailed sampling every 1–2 km from the mouth to Malgas approximately 40 km upstream whereas the 1997–1999 sampling was confined to the lower 5 km of the estuary (Figure 1). Additional information was obtained from published and unpublished material.

Gillnets used were 30 m long and 2 m deep with mesh sizes of 44 mm, 48 mm, 51 mm, 54 mm, 75 mm, 100 mm and 145 mm. During the 2000 and 2004 surveys they were deployed for approximately one hour at each site, whereas during the 1997–1999 sampling they were set and checked on an hourly basis until sufficient fish were caught. Most of the fish caught were cut from the net to prevent injury, identified, measured and released. Night sampling was avoided because of boat traffic, the possibility of net theft, and difficulty in preventing high mortalities through large catches.

The seine-net used was 30 m long and 2 m deep with a mesh size of 10 mm and hauling ropes of 50 m. Depending on the size of the catch, either all fish or subsamples were identified, measured and, if alive, released. Surface temperature, salinity (portable refractometer) and water clarity (Secchi disc) were measured at each site.

Categorisation of the ichthyofauna

To categorise fish in terms of their dependency on estuaries the five-category classification scheme originally proposed by Wallace *et al*. (1984) and refined by Whitfield (1994b), based on life-history characteristics (Table 1), was adopted.

Freshwater requirements

The Freshwater Reserve

The National Water Act (Act 36 of 1998) in South Africa recognises only two water rights: a basic human-needs reserve of 25 litres per person per day and a Freshwater Reserve which comprises the ecological water requirements necessary to sustain aquatic ecosystems in a healthy condition. The Act requires that a Freshwater Reserve be determined prior to the authorisation of water use for agriculture, urban developments and industry, among others. This stipulation led to the development of methods to determine the ecological water requirements of rivers and estuaries (Adams *et al.* 2002, DWAF 2004a).

Determining a reserve for an estuary includes delineating the geographical boundaries of the estuary and assessing estuarine health by comparing its present state with a hind-cast reference condition using an Estuarine Health Index (DWAF 2004a). This index comprises an evaluation of habitat health (abiotic variables: hydrology, hydrodynamics, mouth status, water quality, physical habitat alteration) and biological health (biotic variables: microalgae, macrophytes, invertebrates, fish, birds). Both abiotic and biotic variables are evaluated as the relationships between them are often not well understood and biotic responses to certain abiotic variables can be slow. The pristine, or reference condition, of an estuary usually refers to its ecological status at least 100 years ago, before the catchment was altered or any large-scale manipulation of the estuary mouth had taken place. Under the reference condition, it is assumed that estuaries would have received 100% of the MAR from their catchments. All hind-casting and forecasting of flow regimes and MAR are derived from modelled hydrology.

The importance of an estuary as an ecosystem is taken from a national rating system (reference condition) and, together with the present health, is used to set the future desired condition (an Ecological Reserve Category) for the estuary. Freshwater is then reserved to maintain the estuary in the desired condition. The reserve (the quantity and quality of freshwater required) is determined by assessing a number of realistic monthly river-flow scenarios, comparing these with data for the present day and evaluating the extent

Table 1: The five major categories of fish that utilise South African estuaries (after Whitfield 1994b)

Categories	Description of categories
I	Estuarine species that breed in southern African estuaries:
	Ia. Resident species that have not been recorded spawning in the marine or freshwater environment
	Ib. Resident species that also have marine or freshwater breeding populations
II	Euryhaline marine species that usually breed at sea with the juveniles showing varying degrees of dependence on southern African estuaries:
	IIa. Juveniles dependent on estuaries as nursery areas
	IIb. Juveniles occur mainly in estuaries but are also found at sea
	IIc. Juveniles occur in estuaries but are usually more abundant at sea
III	Marine species that occur in estuaries in small numbers but are not dependent on these systems
IV	Euryhaline freshwater species, whose penetration into estuaries is determined by salinity tolerance. Includes some species that may breed in both freshwater and estuarine systems
V	Catadromous species that use estuaries as transit routes between the marine and freshwater environments:
	Va. Obligate catadromous species that require a freshwater phase in their development
	Vb. Facultative catadromous species that do not require a freshwater phase in their development

to which abiotic and biotic conditions within an estuary are likely to alter with changes in river inflow. In doing so, the goal is a river flow that allows a reduction in freshwater inflow for human use while maintaining the estuary in the desired ecological condition.

Hydrology and hydrodynamics
A series of scenarios under different freshwater flows were examined for both the Olifants and Breede estuaries to explore the effects of altered flow rates. These included the reference (pristine) state, present-day conditions, and four or five future scenarios spanning both increases and further reductions for the Olifants and a series of reductions of the Breede (Table 2).

Hydrological data comprising simulated mean monthly river flows for these scenarios were provided by Ninham Shand Consulting Engineers and covered a 70-year period. Standard South African hydrological models were used to generate these simulated flows (e.g. Midgley *et al*. 1994).

A consequence of current and future catchment developments is that reductions in baseflow and an increase in the duration of low-flow periods will result in increased salinity as well as a change in salinity distribution in both estuaries. These effects were simulated using the Mike 11 mathematical modelling system, which is an advanced one-dimensional dynamic modelling system for rivers and estuaries that was developed in the 1970s at the Danish Hydraulics Institute and which has been applied locally and worldwide in various investigations (CSIR 1993, 1998, 1999, Refsgaard and Knudsen 1996, Slinger *et al*. 1997, Yan *et al*. 1998, DHI 2001). The hydrodynamic and transport dispersion modules of Mike 11 were used to model salinity distribution.

The hydrodynamic model is driven by the tidal variation at the mouth and river flow at the head of the estuary. The hydrodynamic model was calibrated by adjusting the bottom roughness until a satisfactory agreement was reached between simulated and measured water-level variations. The transport dispersion module was used to simulate the effects of the intrusion of seawater on salinities in each estuary based on tidal flows at the mouth and the inflow of freshwater upstream, and was calibrated by adjusting the dispersion coefficients until a satisfactory agreement was reached between the computed and measured salinity concentrations. The model was set up with bathymetric data collected at regular intervals of 0.5–1.0 km. Predicted water-level variations in the ocean were used as an open boundary in the marine environment. The model was calibrated using river inflow data, water-level data (4–5 stations) and salinity data (10–20 stations) collected along the length of each estuary over a neap and a spring tide using a YSI 6600 Multi-parameter Environmental Monitoring System. Evaporation was incorporated as an outflow from the model to account for evaporative losses that would have increased salinities.

Based on the measured and modelled results, four abiotic states were identified for the Olifants and Breede estuaries, ranging from freshwater-dominated through balanced to marine-dominated. These states were described in terms of typical flow patterns, tidal variations and salinity distributions. Details of these states are specified in Tables 8 and 9. In turn, the abiotic states were superimposed on monthly river-flow scenarios to evaluate changes in occurrence (frequency and duration) of the abiotic states under the simulated flow sequences. Results of the numerical modelling were also used to calculate average and maximum salinity penetration during the low-flow period for the various scenarios based on the duration and extent of different salinity regimes (<10, 10–20, 20–30, >30). These results in turn provided the platform from which biotic changes could be hind-cast (for reference conditions) or predicted (for future scenarios). All changes were evaluated in relation to the reference condition.

Abiotic states and the ichthyofauna
To predict the response of the fish assemblage in each estuary to future changes in flow, samples were grouped into five salinity ranges. For each abiotic state identified in the two estuaries, fish densities (fish m^{-2}) were multiplied by the total area of the estuary covered by each salinity range. The total number of fish under each state was the sum of the fish in all the salinity ranges. Densities of exploited fish in the Olifants Estuary were corrected for gillnet fishing effects using catch ratios of fished to non-fished estuaries obtained from Hutchings and Lamberth (2003). For each scenario, 'absolute abundance' was the average number of fish summed across all states within a 12-month period. The predicted changes are based on the assumption that overall fish abundance will correspond with the shrinking or expansion of the area covered by their preferred salinities under present-day conditions. In reality, many of the species are tolerant of a wider range of salinities and will also respond to changes in habitat availability, prey availability, turbidity and temperature (among other factors), and may therefore not conform to the calculated areas.

Results

Composition of the ichthyofauna

Olifants Estuary
In total, 38 fish species from 30 families have been recorded from the Olifants Estuary (Day 1981, Morant 1984, Harrison 1997, Hutchings and Lamberth 1999, 2002b, 2002c, this study) (Table 3). Of these, six (16%) are entirely dependent on estuaries to complete their life cycle (Categories Ia and IIa). Eight breed in estuaries (Categories Ia and Ib) and include the estuarine roundherring *Gilchristella aestuaria*, Cape silverside *Atherina breviceps*, prison goby *Caffrogobius gilchristi*, commafin goby *Caffrogobius*

Table 2: The percentage reduction in mean annual runoff (MAR) from reference (pristine) conditions under the present day and future scenarios in the Olifants and Breede estuaries. There are five and four future scenarios for the Olifants and Breede respectively

	Reduction in reference MAR (%)	
Scenario	Olifants Estuary	Breede Estuary
Present day	34	42
1	25	47
2	31	52
3	43	57
4	50	64
5	60	–

Table 3: List of all species recorded in the Olifants River and Breede River estuaries during this study and after Day (1981), Ratte (1982), Morant (1984), Coetzee and Pool (1991), Harrison (1997, 1999), Hutchings and Lamberth (1999, 2002b, 2002c) and Estuarine and Coastal Research Unit, CSIR. The species are arranged according to the five major categories of estuarine-dependence as suggested by Whitfield (1994b; Table 1)

Family	Species	Common name	Dependence category	Olifants Estuary	Breede Estuary
Osteichthyes					
Blenniidae	*Omobranchus woodii*	Kappie blenny	Ia		X
Clupeidae	*Gilchristella aestuaria*	Estuarine roundherring	Ia	X	X
Hemiramphidae	*Hyporhamphus capensis*	Cape halfbeak	Ib		X
Gobiidae	*Psammogobius knysnaensis*	Knysna sand-goby	Ia/Ib	X	X
Atherinidae	*Atherina breviceps*	Cape silverside	Ib	X	X
Clinidae	*Clinus superciliosus*	Super klipvis	Ib	X	X
Gobiidae	*Caffrogobius gilchristi*	Prison goby	Ib	X	X
Gobiidae	*Caffrogobius natalensis*	Baldy	Ib		X
Gobiidae	*Caffrogobius nudiceps*	Barehead goby	Ib	X	X
Gobiidae	*Caffrogobius saldanha*	Commafin goby	Ib	X	X
Syngnathidae	*Syngnathus temminckii*	Pipefish	Ib	X	X
Carangidae	*Lichia amia*	Leervis	IIa	X	X
Elopidae	*Elops machnata*	Ladyfish	IIa		X
Haemulidae	*Pomadasys commersonnii*	Spotted grunter	IIa		X
Monodactylidae	*Monodactylus falciformis*	Cape moony	IIa		X
Mugilidae	*Liza macrolepis*	Largescale mullet	IIa		X
Mugilidae	*Mugil cephalus*	Springer mullet	IIa/Vb	X	
Mugilidae	*Myxus capensis*	Freshwater mullet	IIa/Vb	X	X
Sciaenidae	*Argyrosomus japonicus*	Dusky kob	IIa		X
Sparidae	*Lithognathus lithognathus*	White steenbras	IIa	X	X
Sparidae	*Rhabdosargus holubi*	Cape stumpnose	IIa		X
Ariidae	*Galeichthyes feliceps*	Barbel	IIb	X	X
Monodactylidae	*Monodactylus argenteus*	Natal moony	IIb		X
Mugilidae	*Liza dumerilii*	Groovy mullet	IIb		X
Mugilidae	*Liza tricuspidens*	Striped mullet	IIb		X
Soleidae	*Heteromycteris capensis*	Cape sole	IIb	X	X
Soleidae	*Solea bleekeri*	Blackhand sole	IIb	X	X
Hemiramphidae	*Hemiramphus far*	Spotted halfbeak	IIc		X
Mugilidae	*Liza richardsonii*	Harder	IIc	X	X
Ophichthidae	*Ophisurus serpens*	Sand snake-eel	IIc	X	
Pomatomidae	*Pomatomus saltatrix*	Elf	IIc	X	X
Sparidae	*Diplodus sargus*	Dassie	IIc		X
Sparidae	*Rhabdosargus globiceps*	White stumpnose	IIc	X	X
Sparidae	*Sarpa salpa*	Strepie	IIc		X
Blenniidae	*Omobranchus banditus*	Bandit blenny	III		X
Carangidae	*Seriola lalandi*	Yellowtail	III		X
Carangidae	*Trachurus trachurus*	Maasbanker	III	X	
Clupeidae	*Sardinops sagax*	Pilchard	III	X	
Dichistiidae	*Dichistius capensis*	Galjoen	III		X
Haemulidae	*Pomadasys olivaceum*	Piggy	III		X
Rachycentridae	*Rachycentron canadum*	Prodigal son	III		X
Sciaenidae	*Argyrosomus coronus*	West Coast kob	III	X	
Sciaenidae	*Argyrosomus inodorus*	Silver kob	III	X	
Sciaenidae	*Atractoscion aequidens*	Geelbek	III		X
Sciaenidae	*Otolithes ruber*	Snapper kob	III		X
Sciaenidae	*Umbrina* spp.	Belman	III		X
Siganidae	*Siganus sutor*	Whitespotted rabbitfish	III		X
Soleidae	*Austroglossus microlepis*	West Coast sole	III	X	
Sparidae	*Diplodus cervinus*	Wildeperd	III		X
Sparidae	*Lithognathus aureti*	West Coast steenbras	III	X	
Sparidae	*Lithognathus mormyrus*	Sand steenbras	III		X
Sparidae	*Sparodon durbanensis*	White musselcracker	III		X
Sparidae	*Spondyliosoma emarginatum*	Steentjie	III		X
Stromateoidae	*Stromateus fiatola*	Blue butterfish	III		X
Tetraodontidae	*Amblyrhynchotes honckenii*	Blaasop	III		X
Tetraodontidae	*Chelondon patoca*	Milkspotted blaasop	III		X
Triglidae	*Chelidonichthys capensis*	Cape gurnard	III	X	X

Table 3: (cont.)

Family	Species	Common name	Dependence category	Olifants Estuary	Breede Estuary
Centrarchidae	*Lepomis macrochirus*	Bluegill sunfish	IV	X	X
Centrarchidae	*Micropterus dolomieu*	Smallmouth bass	IV	X	X
Cichlidae	*Oreochromis mossambicus*	Moçambique tilapia	IV	X	X
Cichlidae	*Tilapia sparrmanii*	Banded tilapia	IV	X	X
Cyprinidae	*Barbus serra*	Sawfin	IV	X	
Cyprinidae	*Cyprinus carpio*	Carp	IV		X
Cyprinidae	*Labeobarbus capensis*	Clanwilliam yellowfish	IV	X	
Galaxiidae	*Galaxias zebratus*	Cape galaxias	IV	X	
Anguillidae	*Anguilla bengalensis*	African mottled eel	Va		X
Anguillidae	*Anguilla marmorata*	Madagascar mottled eel	Va		X
Anguillidae	*Anguilla mossambica*	Longfin eel	Va		X
Chondrichthyes					
Carcharhinidae	*Carcharhinus leucus*	Zambezi shark	IIc		X
Dasyatidae	*Dasyatis chrysonota*	Blue stingray	III	X	X
Dasyatidae	*Gymnura natalensis*	Butterfly ray	III		X
Myliobatidae	*Myliobatis aquila*	Eagle ray	III	X	X
Myliobatidae	*Pteromylaeus bovinus*	Duckbill ray	III		X
Rhinobatidae	*Rhinobatos annulatus*	Lesser guitarfish	III	X	X
Rhinobatidae	*Rhinobatos blochi*	Bluntnose guitarfish	III	X	
Scyliorhinidae	*Haploblepharus pictus*	Dark shyshark	III	X	

saldanha and longsnout pipefish *Syngnathus temminckii*. Four species, white steenbras *Lithognathus lithognathus*, leervis *Lichia amia,* freshwater mullet *Myxus capensis* and flathead mullet *Mugil cephalus*, are entirely dependent on estuaries as nursery areas for at least their first year of life (Category IIa). The latter two species may also fall in the facultative catadromous category (Vb).

Another seven species (18%) are at least partially dependent on estuaries (Categories IIb and IIc), e.g. harder *Liza richardsonii*, elf *Pomatomus saltatrix,* blackhand sole *Solea bleekeri* and white stumpnose *Rhabdosargus globiceps*. In all, 50% of the fish species recorded from the Olifants Estuary can be regarded as either partially or completely dependent on estuaries for their survival. Most of the remaining taxa (32%) are marine species, e.g. silver kob *Argyrosomus inodorus*, sardine *Sardinops sagax*, bluntnose guitarfish *Rhinobatos blochi* and eagle ray *Myliobatis aquila*, which occur in estuaries but are not dependent on them (Category III). Finally, the Olifants Estuary supports seven euryhaline freshwater species (Category IV), whose penetration into estuaries is determined by salinity tolerance. These include the endemic Red Data Clanwilliam yellowfish *Labeobarbus capensis*, sawfin *Barbus serra* and Cape galaxias *Galaxias zebratus*, as well as the introduced smallmouth bass *Micropterus dolomieu*, bluegill sunfish *Lepomis macrochirus*, banded tilapia *Tilapia sparrmanii* and Moçambique tilapia *Oreochromis mossambicus*. No obligate catadromous species (Category V) have been recorded from the Olifants Estuary.

Breede Estuary
An overall total of 59 fish species from 30 families has been recorded from the Breede Estuary (Day 1981, Ratte 1982, Carter 1983, Coetzee and Pool 1990, Harrison 1999, Hutchings and Lamberth 1999, 2002b, 2002c, this study)

(Table 3). Of these, 23 (39%) are entirely dependent on estuaries to complete their life cycle (Categories Ia and IIa), of which 10 are estuarine breeders and include *G. aestuaria*, kappie blennie *Omobranchus woodii*, Cape halfbeak *Hyporhamphus capensis* and *A. breviceps* (Categories Ia and Ib). Nine, including dusky kob *Argyrosomus japonicus*, *L. lithognathus*, leervis *Lichia amia* and spotted grunter *Pomadasys commersonnii* are dependent on estuaries as nursery areas for at least their first year (Category IIa). A further four require estuaries as transit routes between the marine and freshwater environment, namely the obligate catadromous African mottled eel *Anguilla bengalensis labiata*, Madagascan mottled eel *A. marmorata* and longfin eel *A. mossambica*, and the facultative catadromous freshwater mullet *Myxus capensis* (Categories Va and Vb). Another 13 species (22%) are at least partially dependent on estuaries, e.g. *L. richardsonii*, groovy mullet *Liza dumerilii*, *P. saltatrix* and spotted halfbeak *Hemiramphus far* (Categories IIb and IIc). In all, 61% of the fish species recorded from the Breede Estuary are either partially or completely dependent on estuaries for their survival. Most of the remaining species (36%) were marine species, e.g. geelbek *Atractoscion aequidens*, bullray *Myliobatis aquila*, piggy *Pomadasys olivaceum* and musselcracker *Sparodon durbanensis*, which occur in estuaries, but are not dependent on estuaries (Category III); two are alien euryhaline freshwater species whose penetration into estuaries is determined by salinity tolerance, namely carp *Cyprinus carpio* and *M. dolomieu* (Category IV).

Abundance

Olifants Estuary
A total of 247 048 fish, representing 21 species from 14 families, was caught in 64 seine hauls in the Olifants Estuary during the period 1997–1998 and February and August 2004 (Table 4). A

further 567 630 fish, representing 13 species from 10 families, were recorded in gillnet catches during 1997–1998 and 2004 sampling periods and from 2 700 net-days reported in the 2003–2004 catch returns from the commercial gillnet fishery.

The 64 seine hauls yielded 247 048 fish or 3 860 fish haul⁻¹ (Table 4). *L. richardsonii* (55%) and *G. aestuaria* (42%) dominated numerically, together constituting 97% of the total catch. Only two other taxa, *Caffrogobius* spp. and *A. breviceps*, provided at least 1% each to the total catch. *L. richardsonii* occurred in 92% of hauls and *G. aestuaria* in 68%, *Caffrogobius* spp. (57%), pipefish *Syngnathus temminckii* (53%) and Knysna sand-goby *Psammogobius knysnaensis* (43%) occurred in more than 40% of the hauls. *Caffrogobius* spp. were not identified to species level in the field but through otolith characteristics of a selected subsample (Smale *et al.* 1995). Barehead goby *Caffrogobius nudiceps*, *C. saldanha* and *C. gilchristii* respectively contributed 90%, 7% and 3% of the genus.

Gillnet sampling caught a total of 105 fish set-hour⁻¹, at an average catch rate of 14 and 5 fish set-hour⁻¹ in summer and winter respectively. Because sampling was limited and catches were low and not considered representative of adult fish in the system, these data were not analysed further and we relied instead on the commercial catch-return data as they were continuous and comprised 2 700 net-days over a two-year period. Commercial gillnet catches were dominated by *L. richardsonii*, which constituted over 98% of the total catch (Table 5). *P. saltatrix* provided 1% whereas all other species (e.g. *M. cephalus* and *L. amia*) provided <1% of the catch. *L. richardsonii* occurred in 97% of the catches whereas *P. saltatrix*, *M. cephalus*, *S. sagax*, *A. inodorus* and *L. lithognathus* occurred in 1–10%. Catch size and occurrence of species other than *L. richardsonii* are likely to be under-reported, largely due to the fishery targeting

L. richardsonii and the fact that the landing of species such as *P. saltatrix* is prohibited.

Breede Estuary
In total, 10 995 fish, representing 34 species from 20 families, were caught during seine and gillnet sampling in the Breede Estuary from September 1997 to August 2000.

The 78 seine hauls yielded 9 492 fish or 122 fish haul⁻¹ (Table 6). *L. richardsonii* (28%), *Caffrogobius* spp. (25%) and *A. breviceps* (21%) dominated numerically, comprised 74% of the total catch. A further six species, *R. holubi* (9%), *G. aestuaria* (6%), Cape sole *Heteromycteris capensis* (2%), groovy mullet *Liza dumerilii* (2%), *P. knysnaensis* (1.5%) and *S. bleekeri* (1.5%) together contributed 22% towards the remainder of the catch. *L. richardsonii* and *Caffrogobius* spp. occurred in 68–69% of the hauls whereas *A. breviceps* comprised a few large catches in 4% of the hauls. Again, *Caffrogobius* spp. were not identified to species level in the field but from otolith identification of a subsample, which comprised 74% *C. gilchristi*, 15% *C. nudiceps*, 8% *C. natalensis* and 3% *C. saldanha* and *C. agulhensis*.

Gillnet sampling caught a total of 1 503 fish at an average catch rate of 32 fish set-hour⁻¹ (Table 7). Catches were dominated by *L. richardsonii* (62%) and to a lesser extent *L. dumerilii* (21%), which together with *P. commersonnii* (4%), striped mullet *Liza tricuspidens* (3%), *L. amia* (2%) and *R. holubi* (2%), provided 94% of the total catch. *L. richardsonii* appeared in 64% of the sets whereas *L. dumerilii* and *P. commersonnii* each occurred in 33%.

Abiotic variables

Olifants Estuary
With the exception of the mouth region, there was a marked

Table 4: Species composition and abundance (catch per haul) in 64 seine-net samples from the Olifants Estuary during 1997–1998 and 2004. Shading indicates months in which new recruits were recorded

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total catch	Occurrence (%)
Liza richardsonii	–	753.1	–	–	2 282.5	42	–	90.6	–	4 445.0	9 046.4	–	135 854	92
Gilchristella aestuaria	–	3 757.8	–	–	230.0	1.0	–	456.9	–	1 970.0	678.7	–	103 224	68
Caffrogobius spp.	–	43.3	–	–	77.5	0.3	–	4.9	–	205.0	122.4	–	3 109	57
Atherina breviceps	–	60.7	–	–	6.3		–	8.7	–	157.5	35.3	–	2 221	36
Psammogobius knysnaensis	–	22.3	–	–	10.0	7.7	–	3.7	–			–	620	43
Lepomis macrochirus	–	23.3	–	–			–	2.2	–			–	552	15
Syngnathus temminckii	–	10.1	–	–	0.5	10.0	–	2.8	–	0.5	7.7	–	391	53
Clinus superciliosus	–	1.4	–	–	0.3		–	0.8	–	105.0	11.7	–	385	23
Micropterus dolomieu	–	14.9	–	–			–		–			–	328	7
Tilapia sparrmanii	–	7.1	–	–			–	0.2	–			–	159	10
Mugil cephalus	–	7.0	–	–			–		–			–	155	3
Pomatomus saltatrix	–	1.4	–	–			–		–			–	30	13
Rhinobatos blochi	–	0.4	–	–			–		–			–	9	5
Haploblepharus pictus	–	0.1	–	–			–		–	0.5		–	3	5
Chelidonichthys capensis	–	0.1	–	–			–		–			–	2	2
Solea bleekeri	–	0.1	–	–			–	0.1	–			–	2	3
Rhabdosargus globiceps	–		–	–			–		–		0.2	–	2	2
Oreochromis mossambicus	–	0.1	–	–			–		–			–	1	2
Lithognathus lithognathus	–		–	–			–		–		0.1	–	1	2
Total per haul	–	4 703	–	–	2 607	61	–	571	–	6 884	9 902	–	247 048	
Number of species	–	17	–	–	7	5	–	10	–	7	6	–	19	

difference in surface salinities at each sampling site between the summer and winter 2004 surveys (Figure 2). During summer, salinity from the mouth to 4 km upstream ranged from 30 to 35, whereas in winter from 20 to 25. In summer, the 10–20 salinity zone spanned 5–15 km upstream but in winter it was confined to 3–4 km from the mouth. In summer,

Table 5: Species composition and abundance (catch per net-day) in the Olifants Estuary during 2003–2004. The data represents the reported catch of 2 700 net-days from the commercial gillnet fishery

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total catch	Occurrence (%)
Liza richardsonii	203.68	183.51	189.73	249.42	235.98	177.84	227.50	195.73	226.90	214.46	144.17	259.78	563 162	97.0
Pomatomus saltatrix	6.57	2.53	2.06	0.67	0.31	0.20	0.184	0.39	1.41	0.64	1.22	2.90	3 557	10.6
Mugil cephalus	0.17	0.17	0.04	0.04	0.02	0.02	0.01	0.39	0.24	0.04	0.33	0.27	410	1.9
Sardinops sagax	0.08	0.06	0.09	0.17		0.01	0.02	0.01	0.09	0.03	0.16	0.06	177	1.5
Argyrosomus inodorus	0.06	0.04	0.05	0.03				0.01	0.04	0.02	0.12	0.05	95	0.7
Rhabdosargus globiceps			0.11	0.12	0.01			0.01			0.04	0.04	68	0.3
Galeichthys feliceps	0.10								0.03	0.07	0.01	0.03	52	0.4
Chelidonichthys capensis	0.06		0.07	0.07	0.02								40	0.2
Lithognathus lithognathus		0.01		0.02	0.01	0.02	0.01	0.02	0.04	0.01			36	0.5
Micropterus dolomieu	0.01		0.01	0.02		0.01	0.01		0.01	0.01	0.01	0.02	22	0.4
Trachurus trachurus				0.01	0.01					0.01			5	0.1
Sole spp.												0.02	4	0.1
Lichia amia				0.01									2	0.1
Total per net-day	207	186	192	251	236	178	228	197	229	215	146	263	567 630	
Number of species	8	6	8	11	7	6	6	7	8	9	8	9	13	
Number of net-days	115	183	172	233	214	215	190	249	311	327	296	199	2 700	

Table 6: Species composition and abundance (catch per haul) in bimonthly seine-net samples from the Breede Estuary during 1997–2000. Shading indicates months in which new recruits were recorded

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total catch	Occurrence (%)
Liza richardsonii	14.0	34.4	35.0	–	38.8	–	15.6	30.4	37.1	161.0	60.0	–	2 627	69
Caffrogobius spp.	15.3	21.1	62.3	–	3.2	–	9.2	46.7	5.6	86.0	184.0	–	2 382	68
Atherina breviceps	103.3			–	225.0	–	60.2					–	1 961	4
Gilchristella aestuaria		7.6		–	5.5	–		9.4	1.1	63.0	5.0	–	536	37
Rhabdosargus holubi	39.0	9.3	2.3	–	14.3	–	0.6	11.2	0.9	44.0	28.0	–	808	38
Heteromycteris capensis	6.3	0.7	5.8	–	5.2	–	10.6	1.2	4.4	6.0		–	213	26
Liza dumerilii		1.5		–		–		6.0			8.0	–	198	15
Psammogobius knysnaensis	1.3	0.7	1.8	–	2.0	–	2.6	2.2	4.6			–	147	26
Solea bleekeri	1.0	4.0	1.8	–	0.2	–	2.6	0.3	0.9	1.0	6.0	–	140	35
Syngnathus temminckii		0.3	1.3	–	0.5	–	0.6	1.6	0.1	2.0	2.0	–	65	17
Rhabdosargus globiceps	0.3	0.1	1.5	–	2.0	–	2.0	0.2			22.0	–	57	21
Diplodus sargus	0.3	1.9	1.8	–	0.2	–						–	55	10
Galeichthyes feliceps		1.8	1.3	–	0.5	–						–	52	6
Pomadasys olivaceum		1.5	0.5	–	0.2	–		0.4				–	50	9
Lithognathus lithognathus	7.0	0.4	0.3	–		–		0.1	0.6	1.0	2.0	–	41	14
Mugil cephalus		0.5		–		–		0.7	0.4			–	31	8
Argyrosomus japonicus		0.7		–	1.0	–						–	22	5
Omobranchus woodii	4.0	0.1		–		–				2.0		–	15	4
Monodactylus falciformis		0.4		–		–						–	14	8
Amblyrhynchotes honckenii		0.1		–	0.5	–	0.8	0.1				–	11	8
Hyporhamphus capensis		0.2		–		–		0.1	0.6			–	11	6
Pomatomus saltatrix	0.3	0.2		–	0.3	–	0.2	0.1			1.0	–	11	9
Lichia amia		0.4		–		–						–	9	6
Lithognathus mormyrus	1.0			–	0.7	–						–	7	5
Spondyliosoma emarginatum		0.2		–		–			0.1			–	5	3
Myxus capensis		0.1		–		–		0.1				–	4	3
Pomadasys commersonnii		0.1		–	0.5	–						–	4	3
Clinus superciliosus		0.1		–		–						–	3	1
Myliobatis aquila	0.7	0.1		–		–						–	3	3
Total per haul	194	88	115	–	301	–	105	111	57	366	318	–	9 492	
Number of species	14	27	12	–	18	–	11	18	12	9	10	–	29	

Table 7: Species composition and abundance (catch per set-hour) in bimonthly gillnet samples from the Breede Estuary during 1997–2000

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total catch	Occurrence (%)
Liza richardsonii	11.5	4.5	33.8	–	29.9	–	11.5	20.6	12.8	41.2	20.0	–	938	64
Liza dumerilii	0.3	6.0	2.5	–	27.6	–	5.6	1.4		1.6		–	319	33
Pomadasys commersonnii		0.1	0.4	–	1.7	–	4.3	0.6		1.6	0.7	–	63	33
Liza tricuspidens	0.3	0.1	0.3	–	0.6	–	3.3	1.8	0.8	1.6		–	45	21
Lichia amia	1.2	1.8	0.6	–		–			0.8	0.1	1.3	–	32	24
Rhabdosargus holubi		0.8	1.0	–	2.6	–		0.1		0.4	0.3	–	26	21
Argyrosomus japonicus	0.3	0.3		–	1.3	–				0.1	1.7	–	18	12
Mugil cephalus		0.4		–	0.3	–		0.5				–	13	9
Myliobatis aquila	0.5		0.4	–		–	1.0					–	10	10
Galeichthys feliceps				–	1.5	–						–	9	3
Lithognathus lithognathus				–	0.7	–		0.2			0.3	–	7	7
Sarpa salpa			0.5	–		–			0.8			–	5	3
Pomatomus saltatrix				–	0.2	–				1.2		–	4	3
Diplodus sargus			0.2	–	0.5	–						–	4	5
Myxus capensis		0.2		–		–		0.1				–	3	3
Diplodus cervinus	0.3			–	0.1	–						–	2	3
Pteromyleus bovinus	0.2			–		–					0.3	–	2	3
Monodactylus falciformis		0.1		–		–						–	1	2
Dasyatis chrysonota			0.2	–		–						–	1	2
Amblyrhynchotes honckenii				–		–		0.1				–	1	2
Total per set-hour	14	14	40	–	67	–	26	25	15	48	25	–	1 503	
Number of species	8	10	10	–	12	–	5	9	4	8	7	–	20	

the River Estuarine Interface (REI) zone (0–10) extended from 15 km upstream all the way to the Lutzville Causeway where salinity was 2.6. In winter, the REI started 4 km from the mouth and salinities dropped to zero approximately 10 km upstream.

Water clarity (Secchi disc visibility) at the mouth ranged from more than 200 cm in summer to approximately 100 cm in winter. In both seasons, water clarity dropped approximately 3 km from the mouth, largely due to wind-mixing of fine sediments in the shallow old channel backwater. In summer, water clarity remained fairly constant at 80 cm until 15 km upstream, beyond which it fluctuated according to the presence or absence of dense beds of the pondweed *Potamogeton pectinatus*. During winter, water clarity remained at 40 cm from 5 km to 30 km upstream. Water temperature in summer ranged from 15 °C at the mouth to 26 °C at the Lutzville Causeway 36 km upstream. In winter, water temperature ranged from 12 °C at the mouth to 14 °C upstream, the exception being the shallow blind arm near the mouth where it reached 16 °C (Figure 2).

Breede Estuary
Surface salinities did not differ much between the summer (February 2000) and winter (August 2000) sampling periods (Figure 2). During winter, salinity from the mouth to 2 km upstream was 35, compared with 30 at 0.5 km in summer. In both seasons, the 20 and 10 salinity boundaries occurred at approximately 6 km and 10 km respectively. In summer, salinity dropped to 0 at 20 km from the mouth, compared with 28 km in winter (Figure 2). This is contrary to normal winter-rainfall seasonal patterns where the extent of saline intrusion shrinks in response to high winter river flows. Water clarity at the mouth ranged from approximately 500 cm in winter to 200 cm in summer. In both seasons,

water clarity dropped to below 100 cm approximately 5 km from the mouth. In winter, water clarity increased beyond the 20 km mark whereas in summer it remained <100 cm throughout. Average water temperature in summer was 24.4 °C (range = 21°–27 °C) compared to 15.6 °C in winter (range = 14°–17 °C) (Figure 2). In both seasons, temperatures increased gradually from the mouth to the middle reaches, followed by a slight decrease 20–40 km upstream.

Seasonality of the ichthyofauna

Olifants Estuary
Catches in the Olifants Estuary were strongly seasonal (Tables 4 and 5). The highest and lowest seine catches (9 902 fish haul⁻¹ and 61 fish haul⁻¹) were in spring/early summer (October) and winter (June) respectively (Table 4). The greatest number of species caught (17) was in February and the lowest (5) in June. *L. richardsonii* appeared to recruit throughout the year with the highest number of new recruits recorded in the late winter and spring (August and October). Overall, in terms of species, the highest number of new recruits was recorded in summer (February, 8 species) and the lowest in winter (June, 1 species) (Table 4).

Commercial gillnet catches were moderately to strongly seasonal, the highest catch per unit effort (CPUE) values of 229–263 fish net-day⁻¹ and 236–251 fish net-day⁻¹ being recorded in spring/early summer and autumn respectively (Table 5). The number of species caught was highest in autumn (April, 11 species) and lowest in winter (June/July, 6 species).

Breede Estuary
Catches in the Breede Estuary were not strongly seasonal (Tables 6 and 7). The highest and lowest seine catches (366
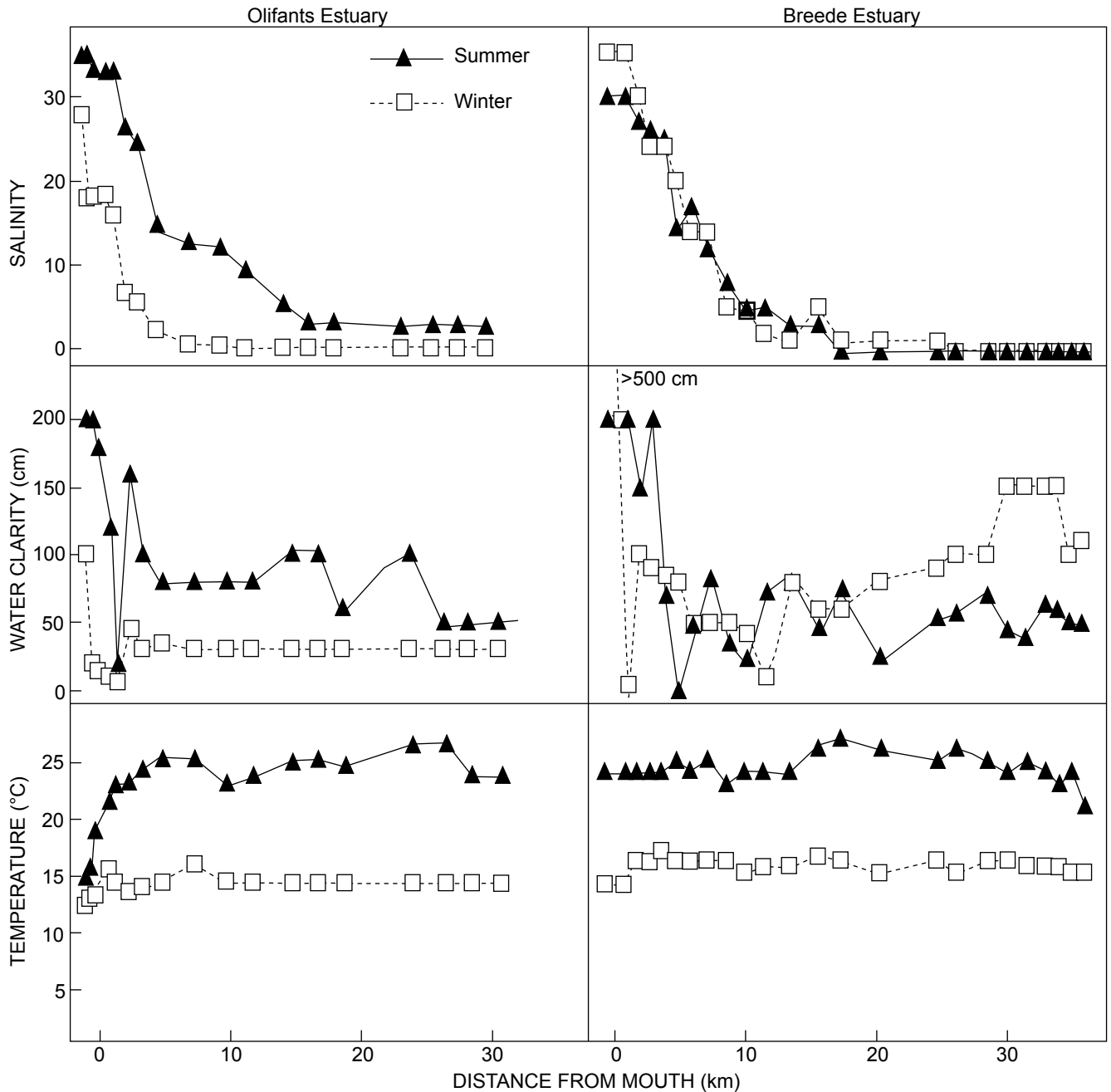
Figure 2: Salinity, water clarity and temperature measured at each sampling site during summer (February) and winter (August) on the Olifants Estuary (2004) and Breede Estuary (2000)

fish haul⁻¹ and 57 fish haul⁻¹) were in the spring — October and September respectively (Table 6). The greatest number of species caught (27) was in February and the lowest (9) in October. The number of new recruits recorded was highest in the summer (January–March) with seven species recruiting and then lowest in the winter (July–August) with three species (Table 6). Gillnet catches were just as erratic with the highest CPUE (67 fish set-hour⁻¹) and lowest CPUE (14 fish set-hour⁻¹) being recorded in May and January–February respectively (Table 7). The number of species caught was highest in May (12) and lowest in September (4). Averaging seine catches over the seasons indicated that

the highest catches were in spring (September–November) and autumn (March–May) at 247 fish haul⁻¹ and 208 fish haul⁻¹ respectively. Seasonal gillnet catches were similar, with highest CPUE in autumn (54 fish set-hour⁻¹) and spring (29 fish set-hour⁻¹).

Along-stream distribution of fish

Olifants Estuary
Upstream distribution of the species caught by the gillnet fishery and during the summer and winter seine surveys was largely a reflection of the estuarine-dependence category to

which they belong. *G. aestuaria*, a Category Ia estuarine-breeding species, with a preference for the river estuarine interface (REI) zone, showed a downstream shift in distribution and decreased in numbers during winter (Figure 3a). This downstream shift corresponded with the REI zone starting 4–5 km from the mouth during winter as opposed to 15 km during summer. In summer, Category Ib species that have marine and estuarine breeding populations, i.e. *Caffrogobius* spp., *P. knysnaensis*, *Syngnathus temminckii*, klipvis *Clinus superciliosus* and *A. breviceps*, were largely confined to the lower 12 km of the estuary in salinities of 5–35. During winter, there was a distinct downstream shift and a drop in abundance of nearly all these species (Figure 3a).

Category IIa species, which are entirely dependent on estuaries as a juvenile habitat, showed various responses between summer and winter. *L. lithognathus* shifted slightly downstream and increased in abundance during winter (Figure 3b). *L. amia* was found up to 20 km from the mouth in summer but only 10 km upstream in winter, and in lower numbers. *M. cephalus* was distributed throughout the estuary in summer with the highest densities 20–35 km upstream as opposed to winter when juveniles were completely absent and the entire population was confined to the lower 20 km (Figure 3a, b).

Of the partially estuarine-dependent species (Categories IIb and IIc), *S. bleekeri* (Figure 3a), *R. globiceps* and the barbel/seacatfish *Galeichthyes feliceps* (Figure 3b) were distributed in the lower 15 km during summer and winter, but in much lower numbers in winter. *L. richardsonii* (Category IIc) was spread throughout the estuary during summer but concentrated in the lower 20 km during winter. This species had two peaks of abundance during summer, one in the lower 5–10 km and one 30–35 km upstream, but the latter peak disappeared in winter (Figure 3a, b). *P. saltatrix* (Category IIc) occurred from the mouth to 24 km upstream in summer, up to 20 km upstream in winter, but was more abundant in summer with densities gradually increasing upstream (Figure 3b).

Marine species that are not estuarine-dependent (Category III), such as *R. blochi* (Figure 3a), *S. sagax, A. inodorus* and *C. capensis* (Figure 3b) were confined to the lower 12 km in winter and summer. With the exception of *A. inodorus*, which peaked at 8–12 km in winter and summer, they all decreased in abundance from the mouth upstream. Euryhaline freshwater species (Category IV) such as *T. sparrmanii* (Figure 3a) and *M. dolomieu* (Figure 3b) were either confined to the upper reaches with low salinities or reached their greatest abundance there, and their modal peak of abundance shifted downstream in winter.

In summary, the majority of completely and partially estuarine-dependent species were most abundant 5–20 km from the mouth in salinities spanning 0–20 and water clarity <100 cm. With the exception of *A. inodorus*, marine species that are independent of estuaries occurred mostly in the lower 5 km at salinities >20, whereas most freshwater-tolerant species were situated further than 15 km from the mouth in salinities of 0–10.

Breede Estuary

The estuary breeder *G. aestuaria* (Category Ia) was largely confined to the REI zone and showed a shift from 25–40 km upstream during summer to 5–15 km during winter (Figure 4a). Category Ib species, which have marine and estuarine breeding populations, i.e. *H. capensis*, *S. temminckii*, *P. knysnaensis* and *C. superciliosus* were largely confined to the lower reaches of the estuary in salinities of 20–35. The exception in this group was *Caffrogobius* spp., which ranged throughout the estuary during both seasons, but with the bulk of the population showing a distinct downstream shift from 10–20 km to 0–10 km from the mouth during winter (Figure 4a).

Category IIa species, which are entirely dependent on estuaries as a juvenile habitat, showed various responses between summer and winter. *R. holubi* and *L. lithognathus* showed a downstream shift of approximately 10 km during winter (Figure 4a). *A. japonicus* and *L. amia* were spread throughout much of the estuary during summer, but disappeared from catches during winter, probably a reflection of their overall low abundance rather than an absence from the system (Figure 4a, b). *M. cephalus* and Cape moony *Monodactylus falciformis* were mostly found further than 15 km from the mouth in salinities close to 0 (Figure 4a, b).

Partially estuarine-dependent species (Categories IIb and IIc), such as *L. richardsonii*, *L. dumerilii* and *S. bleekeri* were spread throughout the estuary during summer, but were concentrated in the lower 10 km or absent during winter (Figure 4a, b). Similar to the situation in the Olifants Estuary, *L. richardsonii* had two abundance peaks during summer, one in the lower 5 km and the other 30–40 km upstream, but the latter peak again disappeared during the winter (Figure 4a). With the exception of *P. olivaceum*, which was found 15 km upstream in salinities of <10, all marine species not dependent on estuaries (Category III) were confined to the lower 5 km and salinities >20 (Figure 4a). The facultative catadromous *M. capensis* (Category Vb) was found above 20 km in zero salinity during both seasons (Figure 4a, b) and has also been recorded 100 km upstream shoaling with *M. cephalus* (SJL unpublished data).

The majority of completely and partially estuarine-dependent species were most abundant from 5 km to 20 km from the mouth in salinities ranging from 0 to 20 and water clarity <100 cm. Marine species that are not dependent on estuaries were recorded most often in the lower 5 km at salinities >20, whereas most freshwater tolerant and catadromous species occurred farther than 20 km from the mouth in salinities of 0–1.

Effects of altered freshwater flows on abiotic states

Olifants Estuary

In all, four abiotic states, ranging from marine- to freshwater-dominated, were identified in the Olifants Estuary (Table 8). State 1 was marine-dominated with flow <2 m^3 s^{-1} and a REI zone comprising <26% of the estuarine area. States 2 and 3 had saline penetration limited to the middle and lower reaches respectively, whereas under the freshwater-dominated State 4, the REI zone covered 60–100% of the total estuarine area.

Under reference conditions, the Olifants Estuary would have been more river-dominated than at present: the marine-dominant State 1 never occurred, and freshwater-dominated
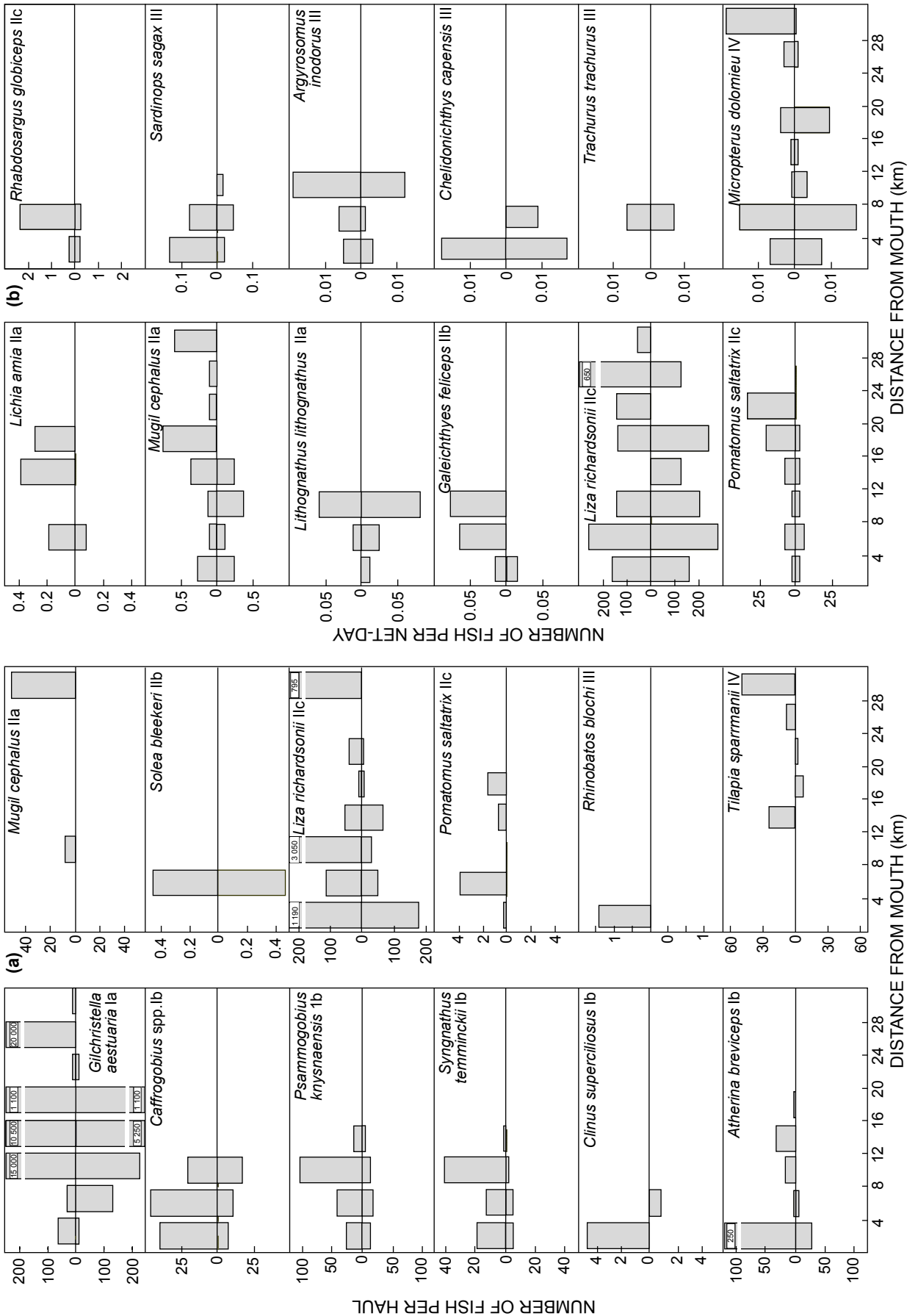
Figure 3: (a) Catch per seine haul from the mouth of the Olifants Estuary to 36 km upstream during summer (February) and winter (August) 2004 and (b) commercial gillnet catch per net-day from the mouth of the Olifants Estuary to 36 km upstream during 2003–2004. Summer catches are shown above, and winter catches below, each axis. Species are arranged in order of their estuarine dependence category (see Table 1)
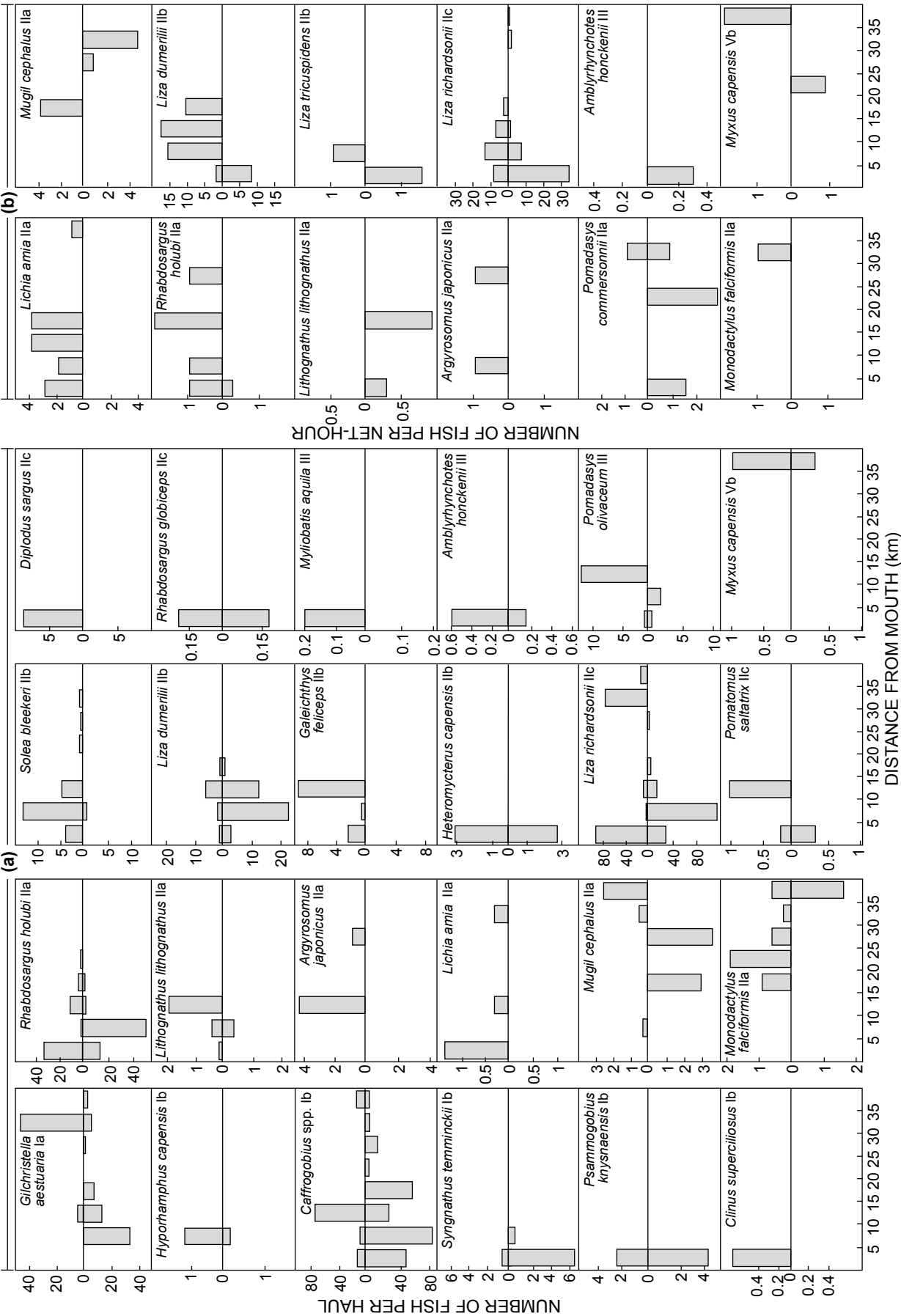
Figure 4: (a) Catch per seine haul from the mouth of the Breede Estuary to 40 km upstream during summer (February) and winter (August) 2000 and (b) catch per gillnet-hour from the mouth of the Breede Estuary to 40 km upstream during summer (February) and winter (August) 2000. Summer catches are shown above, and winter catches below, each axis. Species arranged in order of their estuarine dependence category (see Table 1)

Table 8: Summary of the characteristics of the four possible abiotic states, their monthly occurrence and percentage mean annual runoff (MAR) remaining, for the reference, present day and five future flow scenarios in the Olifants River Estuary

	State 1	State 2	State 3	State 4
General description	Marine dominated	Saline penetration extended to middle reaches	Saline penetration limited to lower reaches	Freshwater dominated
Typical flow	<2 m³ s⁻¹, usually in summer (zero occurrence under reference)	2–5 m³ s⁻¹ (summer under reference)	5–20 m³ s⁻¹ (autumn and spring under reference)	>20 m³ s⁻¹ (winter under reference)
Mouth condition	Open, slightly constricted	Open	Open	Wide open
Tidal amplitude (m)	0.3–1.3	0.3–1.3	0.3–1.3	0.3–1.3
REI zone begins (spring tides) (km)	13–20	9	1–6	0–5.4
REI area (maximum) (ha)	110–64	141	201	417–252
REI area as percentage total of surface area	26–15	34	48	100–60

Scenario	MAR (%)	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Reference	100	2	2	2	3	3	4	4	4	4	3	3	2
Present	66	1	1	1	1	2	4	4	4	4	3	1	1
1	75	1	1	1	2	3	4	4	4	4	3	2	1
2	69	1	1	1	2	3	4	4	4	3	3	2	1
3	57	1	1	1	1	2	3	4	4	3	2	1	1
4	50	1	1	1	1	1	3	4	4	3	1	1	1
5	40	1	1	1	1	1	2	2	3	3	1	1	1

State 4 conditions with average flows >20 m³ s⁻¹ would have persisted for at least four months (June–September) every year (Table 8). Under those conditions, the REI zone of 0–10 began 0–5.4 km from the mouth during spring tidal cycles and extended 36 km upstream. State 2 conditions (2–5 m³ s⁻¹) would have dominated during summer (December–March) and State 3 would have occurred during autumn (April–May) and spring (November–December). Under drought conditions, the REI zone would have persisted from 9 km upstream and constituted approximately 140 ha, or 34%, of the water surface area.

Under present-day conditions, the estuary has switched from a freshwater-rich to a marine-dominated system for much of the year. Marine-dominated State 1 conditions, which never occurred under reference conditions, with average flows <2 m³ s⁻¹, persist for six months of the year (November–April). High-flow State 4 conditions (>20 m³ s⁻¹) still occur for four months during the winter (June–September), but State 3 conditions (5–20 m³ s⁻¹), once characteristic of spring and autumn, now occur only for one month during spring. Under these conditions, the winter REI zone of 0–10 salinity still begins at 0–5.4 km from the mouth. However, under spring tidal cycles, the summer REI begins at 13–20 km as opposed to a maximum of 9 km under reference conditions. Overall, the summer REI may be 55% smaller in extent than it was under reference conditions.

Scenarios 1 and 2 represent a slight increase in flow from the present day; all future scenarios constitute a progressive increase in the duration and extent of marine-dominated relative to reference conditions (Table 8).

Breede Estuary
Four abiotic states were identified for the Breede Estuary (Table 9). Under reference conditions, the estuary was more river-dominated than present, with freshwater-dominated

State 3 and 4 conditions (>10 m³ s⁻¹) persisting for at least nine months (April–December) every year, whereas marine-dominated State 1 conditions would have been absent (Table 9). Under those conditions, the REI zone of <10 began 2–10 km from the mouth during spring tidal cycles and extended 40–50 km upstream. State 2 (3–10 m³ s⁻¹) conditions with balanced marine and freshwater influence would have dominated during summer (January–March). Under drought conditions, the REI zone would have persisted from 32 km upstream and be approximately 20 km in extent.

Under present-day conditions, the estuary is less river-dominated than under pristine conditions but State 3 and 4 conditions with average flows >10 m³ s⁻¹ still persist for at least seven months (May–November) every year (Table 9). Under those conditions, the REI zone of <10 begins 12–18 km from the mouth during spring tidal cycles and extends approximately 40 km upstream. State 2 conditions (3–10 m³ s⁻¹) are confined to mostly autumn and December, whereas State 1 conditions dominated in summer (January–February). Overall, present-day conditions represent a 42% reduction in MAR.

The future scenarios represent a further reduction in MAR ranging from 47% under the limited development Scenario 1 to 64% under the Le Chasseur Scenario 4 (DWAF 2004b). This will progressively increase marine domination and curtail freshwater domination.

The effects of altered freshwater flow on fish

Present-day conditions represent 34% and 42% reductions in MAR reaching the Olifants and Breede estuaries respectively. In the Olifants, the first two scenarios will increase freshwater flow from the present circumstance, but still represent a 25–31% reduction in flow from reference conditions. Reductions of 43% can be expected under

Table 9: Summary of the characteristics of the four possible abiotic states, their monthly occurrence and percentage mean annual runoff (MAR) remaining, for the reference, present day and four future flow scenarios in the Breede River Estuary

	State 1	State 2	State 3	State 4
General description	Marine dominated	Balanced marine and freshwater influence	Freshwater dominated with significant saline intrusion in lower reaches	Strongly freshwater dominated
Typical flow	0.5–3 m³ s⁻¹; <0.5 m³ s⁻¹ may occur in summer (November–April)	3–10 m³ s⁻¹	10–20 m³ s⁻¹, common in autumn and winter	>20 m³ s⁻¹, usually in winter
Mouth condition	Open	Open	Wide open	Wide open
Tidal amplitude (m)	0.9–1.5	0.9–1.5	0.9–1.5	0.9–1.5
REI zone begins (spring tides) (km)	32–>50	18–32	12–18	2–10
REI area (maximum) (ha)	247–0	475–247	661–475	1 168–754
REI area as percentage total of surface area	18–0	35–18	48–35	85–55

Scenario	MAR (%)	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Reference	100	2	2	2	3	4	4	4	4	4	4	4	3
Present	58	1	1	2	2	3	4	4	4	4	4	3	2
1	53	1	1	2	2	2	3	4	4	4	4	3	2
2	48	1	1	1	2	2	3	4	4	4	4	3	2
3	43	1	1	1	1	2	2	3	4	4	4	3	2
4	36	1	1	1	1	1	2	3	4	4	3	2	2

Scenario 3 and 60% under Scenario 5 with the construction of a large dam. In contrast, there are numerous proposals for the Breede catchment so that increases in freshwater flow are unrealistic and all four future scenarios examined represent a decline in flow, the largest of which would result in reductions of 57% and 64% of the MAR reaching the estuary respectively (Table 2).

Under reference conditions, the fish assemblage of the Olifants Estuary would have been dominated by Category Ia estuarine breeders (37%) and partially estuarine-dependent Category IIc species (61%), whereas that of the Breede Estuary would have been dominated by Category Ib marine and estuarine breeders (50%) and Category IIc species (28%) (Figure 5a, b). Even though overall absolute abundance has changed, the relative contribution of these categories to the fish assemblages of the two estuaries has changed little from reference conditions to the present day. Even under the worst-case scenario with 60% reductions in MAR, relative proportions will change only by 3%.

In the Olifants and Breede, species that breed only in estuaries (Category Ia, e.g. *G. aestuaria*) have undergone 20% and 15% reductions in numbers from the reference to present day, whereas those that have estuarine and marine breeding populations (Category Ib, e.g. *A. breviceps*) have increased by 74% and 9% respectively (Figure 5c, d). In the Olifants, Category Ia estuarine-breeders will increase slightly to 86% of reference with an increase in MAR under the first two future scenarios, but will decline to 59% of reference abundance if flow is reduced by 60% relatively to the historical MAR (Figure 5c). Similarly, in the Breede, Category Ia fish will decline to 61% of reference abundance once MAR declines by 64% (Figure 5d).

Under present conditions, Category IIa obligate estuarine-dependent species such as *M. cephalus* and *L. lithognathus* have declined in abundance to 17% of reference conditions

in the Olifants Estuary and are likely to decline to 8% under the maximum 60% reduction in MAR of Scenario 5 (Figure 5c). Specifically, *L. lithognathus* and *M. cephalus* have experienced an 80% and 91% decrease from reference conditions to present day and will decline to 17% and 6% under Scenario 5 (Figure 6). In contrast to the Olifants Estuary, obligate estuarine-dependent fish (Category IIa) in the Breede Estuary are 4% more abundant under present day than reference conditions (Figure 5d). Under future scenarios, they will experience a 13% increase from reference conditions. However, this is not entirely true for all species within that category. Four of the seven species will experience a drastic decline from reference conditions to the Le Chasseur scenario with a maximum 64% reduction in MAR (Figure 6). Declines will occur for *M. falciformis* (62%), *M. cephalus* (54%), *A. japonicus* (49%) and *P. commersonnii* (34%). Conversely, in this same category, *L. lithognathus*, *R. holubi* and *L. amia* will experience increases in abundance of 20–25% with decreasing flows (Figure 6).

Partially estuarine-dependent Category IIb species in the Olifants Estuary, represented only by *S. bleekeri*, have declined to 19% of reference conditions in the present day but, irrespective of increases or decreases in future flows, will not undergo any really discernable changes in abundance (Figures 5c, 6). Category IIb species in the Breede have undergone a 7% increase from reference conditions to the present with a maximum 17% increase predicted for the maximum 64% reduction in MAR (Figure 5d). The increase in abundance of this group is driven by *H. capensis* and *L. dumerilii*; barbell *Galeichthys feliceps* will decline by 13% with a future maximum reduction in MAR, whereas *S. bleekeri* will undergo no real change for any of the future scenarios (Figure 6).

In the Olifants Estuary, partially estuarine-dependent Category IIc fish, dominated by *L. richardsonii*, have
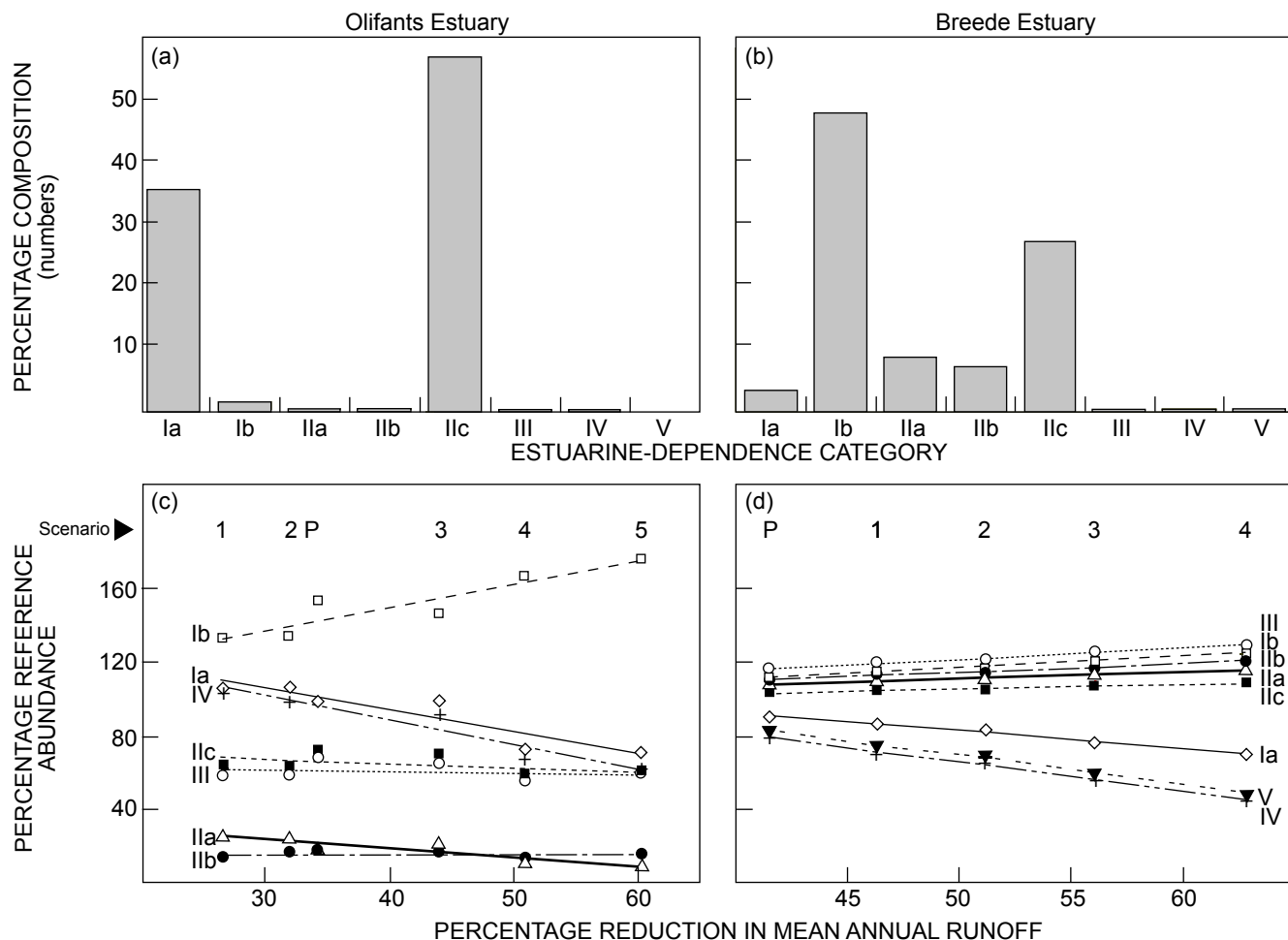
Figure 5: Percentage composition of the different estuarine-dependence categories under reference (pristine) conditions (a, b) and the responses of the fish in different estuarine dependence categories to various reductions of mean annual runoff from reference conditions under the different flow scenarios (c, d) in the Olifants River and Breede River estuaries. Responses are measured as the percentage change relative to pristine abundance. The scenarios are numbered 1–5 and P is the present day. Dependence categories after Whitfield (1994b; Table 1)

populations that are 60% of those under reference conditions (Figure 5c). Increased flows in Scenarios 1 and 2 will bring minor improvements, but all three species in that category (*L. richardsonii*, *P. saltatrix* and *R. globiceps*) will undergo a further 10% decline from present day under the worst-case Scenario 5, which will bring a 60% reduction in MAR (Figure 6). In the Breede Estuary, Category IIc species have experienced a small (3%) increase to the present day and are expected to increase to 9% more than reference by Scenario 4 (Figure 5d). Without exception, all four fish in that category (*D. sargus*, *L. richardsonii*, *P. saltatrix* and *R. globiceps*) in the Breede Estuary will increase in abundance with future reductions in flow (Figure 6).

In the Olifants Estuary, marine species that are not estuarine-dependent (Category III) have presently been reduced to 57% of their reference condition abundance (Figure 5c). However, all three species in that category (Cape gurnard *Chelidonichthys capensis*, dark shyshark *Haploblepharus pictus* and *R. blochii*) will undergo a 5–7% increase in abundance from present day to Scenario 5 involving a 60% reduction in MAR (Figure 6). In the Breede,

non-estuarine-dependent marine species will undergo the greatest increase in abundance with decreasing flows (Figure 6). At present they are 9% greater in numbers than during reference conditions and are likely to increase to 123% if the 64% reduction in MAR associated with the Le Chasseur scenario is implemented. The exception in that category is *P. olivaceum*, which is likely to decline to 74% of reference condition in the event of the worst-case scenario.

Category IV freshwater species in the Olifants Estuary, which are dominated by alien species, are likely to decline by 48% with a 60% reduction in MAR (Figures 5c, 6). Category IV freshwater fish in the Breede Estuary are also almost entirely introduced species, such as carp *Cyprinus carpio*, and may decline by 62% with the maximum 64% reduction in MAR (Figures 5d, 6). However, the facultative catadromous freshwater mullet *M. capensis* (Category V) has decreased by 25% from reference conditions to present day and forecast to drop to 38% under the Le Chasseur scenario (Figures 5d, 6).

Overall abundance in the Olifants Estuary has decreased by 20% from reference conditions to the present day and
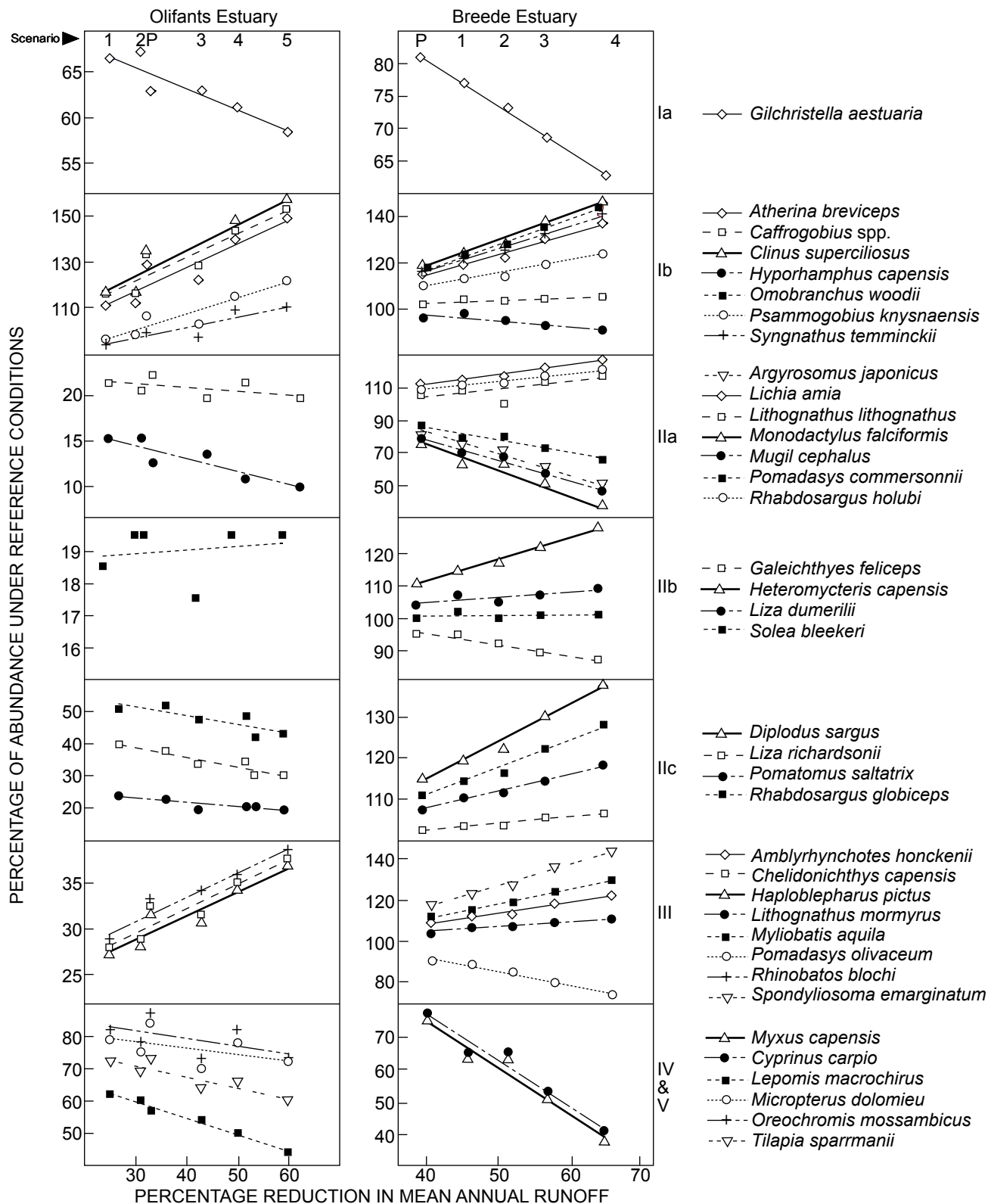
Figure 6: Estuarine fish abundance as a percentage of reference (pristine) relative to the reduction in mean annual runoff under present day conditions and for each of the future flow scenarios in the Olifants River and Breede River estuaries. The scenarios are numbered 1–5 and P is the present day. Dependence categories after Whitfield (1994b; Table 1)

will decline to 55% with the 60% reduction in MAR under Scenario 5. Overall, abundance in the Breede Estuary has increased to 106% of the reference level and is likely to increase to 115% with future reductions in flow.

Discussion

Importance of the two estuaries to fish

Species that breed in estuaries and/or estuarine residents comprise 21% and 17% of the Olifants and Breede estuary fish fauna compared to 22–26% for the West Coast Orange and Olifants estuaries combined, 25% for all South Coast estuaries (Cape Agulhas–Cape St Blaize) and 4–18% for those on the South-East and KwaZulu-Natal coasts (Bennett 1994, Harrison 1999, Lamberth 2003). Including all estuarine breeders, entirely estuarine-dependent species comprise 32% and 39% of the Olifants and Breede estuaries fish fauna respectively, which is similar to the 26–33% for all West Coast estuaries, low compared to 54% for all South Coast estuaries but high compared to the 22% and 9% for estuaries on the South-East and KwaZulu-Natal coasts respectively (Bennett 1994, Harrison 1999, Lamberth 2003). Partially estuarine-dependent species comprise 16% of the Olifants and 22% of the Breede fish fauna, within the 7–29% range of all West Coast estuaries and 18–27% for all estuaries from Cape Point to KwaZulu-Natal (Bennett 1994, Harrison 1997, 1999, Lamberth 2003).

The degree of estuarine dependency may vary within a species among biogeographical regions (Elliott *et al*. 2007). Two species of kob, silver kob *A. inodorus* and Angolan kob *A. coronus*, are known from the Berg, Olifants and Orange estuaries, but *A. coronus* has only been caught by anglers in the mouth regions (Lamberth 2003). On the south and east coasts of South Africa, the dusky kob *A. japonicus* is dependent on estuarine nursery areas whereas *A. inodorus* seldom, if ever, ventures into estuaries (Griffiths 1996). On the West Coast, however, *A. inodorus* frequently (and predictably) occurs in the Berg, Olifants and Orange estuaries, whereas *A. coronus* is predominantly caught on the beaches immediately adjacent to the mouths of these estuaries, only being recorded in estuaries during low-oxygen conditions in the sea (Lamberth 2003). Thus, *A. inodorus* may show some degree of estuarine dependence on the west coast of South Africa but not on the South and East coasts. In turn, once outside the north-western limit of *A. inodorus* in Namibia, *A. coronus* becomes abundant in predominantly open estuaries throughout Angola from the Kunene River to at least the Kwanza River in the north (Griffiths and Heemstra 1995, SJL unpublished data,)

Marine species that are independent of estuaries comprise a relatively high proportion of the fish recorded in the Olifants (32%) and Breede (36%) estuaries. However, most marine species recorded in the Breede Estuary (e.g. galjoen *Dichistius capensis*, prodigal son *Rachycentron canadum* and geelbek *Atractoscion aequidens*) or in the Olifants Estuary (e.g. *S. sagax*) can be construed as rare vagrants that seldom enter estuaries, their occurrence largely being a result of a strong marine influence in the mouth region of these permanently open systems. However, in the Olifants Estuary, *A. inodorus* and West Coast steenbras *Lithognathus*

aureti do occur in a predictable pattern depending on season and weather conditions, i.e. they are not vagrants that occur there incidentally (Lamberth 2003). Overall, although the proportion (and occurrence) of non-estuarine-dependent marine species in the Olifants Estuary is high, this is not surprising given that that estuary is permanently open and one of the few available warm-water refuges when sea temperatures drop during the summer upwelling season on the West Coast.

Catadromous anguillid eel species do not occur in the Olifants or other estuaries on the western seaboard of sub-Saharan Africa, whereas four occur on the South-East Coast, with three in the Breede system (Whitfield 2005a). These comprise one southern African endemic (*Anguilla mossambica*) and three closely related Indo-Pacific species (Tsukamoto and Aoyama 1998). Although the Indo-Pacific species are distributed throughout the eastern seaboard of Africa, no West African ancestors have dispersed to or speciated on the southern West Coast, probably on account of being inhibited by the development of the Benguela upwelling system, equatorial currents and 'poor' climatic conditions, as well as lack of rivers in the eastern Atlantic (Tesch 2003, Whitfield 2005a).

Based on distributional ranges given by Smith and Heemstra (1986), 21 (55%) of the fish recorded in the Olifants Estuary and 25 (42%) of those in the Breede Estuary are southern African endemic species. At least 12 of those are South African endemics. In terms of the fish importance score outlined in the resource directed measures methods for the allocation of freshwater resources, the Olifants and Breede estuaries have biodiversity and overall importance scores of 99 and 90 respectively, which places both systems within the top quintile of all estuaries in South Africa (Taljaard *et al*. 2005). The Olifants is one of only three predominantly open estuaries on the cool-temperate West Coast whereas the Breede is one of five permanently open out of a total of eight estuaries from Cape Agulhas to Mossel Bay on the warm-temperate South-East Coast (Harrison 1999). The importance of the Olifants lies in its rarity and the fact that it comprises more than 25% of the available estuarine habitat in the cool-temperate region. The Breede is the largest of the estuaries on the warm-temperate South Coast and accounts for 43% of the total estuarine area within that region (Turpie *et al*. 2002). Its importance lies in its size and its situation in a region of high endemicity close to the warm-temperate/cool-temperate transition zone between Cape Agulhas and Cape Point (Harrison 1999).

Seasonal patterns

Both the Olifants and Breede samples exhibited high spring and autumn CPUE values and low winter values, which could be due to a number of factors. False Bay commercial beach-seine catches show a similar pattern, which has been attributed to the shoaling of *L. richardsonii* and other species during the spring and autumn, rather than an overall change in abundance (Lamberth *et al*. 1995). However, even though many species may leave the Olifants and Breede estuaries during the winter, it is unlikely that pre-migration shoaling is entirely the cause of the higher CPUE values. It is more likely that the higher CPUE reflects

a small change in the total number of fish in the estuary in addition to distributional changes in response to flow or other variables that concentrate fish in certain areas and increase catchability. During autumn and spring, increased flows move fish downstream whereas cool marine waters force fish upstream, with the net result that they become more concentrated in the mid to lower reaches of each estuary. The higher number of species at that time can be attributed to marine species that have entered from the sea in combination with freshwater species that have moved downstream into the estuary.

The Olifants River catchment falls entirely within the winter rainfall zone. Consequently, fish catches and (by inference) abundance in the Olifants Estuary are strongly seasonal. However, it is unlikely that seasonal fluctuations in catches in the estuary are as pronounced as they were historically. Reduced flows and the prolonged summer low-flow period, as well as the effect of dams on the mainstream, will have blurred a once abrupt switch between summer and winter in abundance, along-stream distribution and catchability of different species. In contrast, seasonal fluctuations in catches in the Breede Estuary are not (and probably never were) as pronounced as for the Olifants and other estuaries on the West and South-West coasts (Bennett 1989, 1994, Lamberth 2003). Reasons include the high physical variability of the system coupled with the fact that the lower Breede falls within a winter/bimodal rainfall transition zone. The intermingling of the rainfall zones adds to the physical variability, ultimately accounting for the relatively high diversity and low abundance of the fish fauna in the Breede compared with estuaries farther to the west (Harrison 1999).

Along-stream distribution

Along-stream distribution of the species in the Olifants and Breede estuaries during the summer and winter surveys was largely predictable on the basis of their salinity preferences and the estuarine-dependence categories to which they belong. Category Ia estuary-breeders such as *G. aestuaria* were most abundant in the REI zone of 0–10 and extended well beyond the estuary into the freshwater reaches in the summer. During winter, higher flows and the downstream shift in the REI zone resulted in this fish becoming more abundant in the middle and lower reaches. Facultative catadromous species in Category Vb such as *M. cephalus* extended well into the freshwater reaches of both rivers with this species as well as *M. falciformis* and *M. capensis* being found up to 100 km upstream in the Breede River (SJL unpublished data). In Category IIa, *P. commersonnii*, a species that occurs in the Breede but not on the West Coast, displayed a seasonal response to higher flow, contrary to that expected, because most of the population remaining within the estuary during the winter appeared to move upstream to 20–40 km from the mouth. In all, many species, especially the larger obligate estuarine-dependent species (Category IIa) such as *A. japonicus* and *L. amia* ventured far into freshwater, and have been recorded more than 50 km from the mouth of the Breede Estuary (Coetzee and Pool 1991, SJL unpublished data). *L. richardsonii*, the numerically dominant species in both the Olifants and Breede estuaries, displayed a similar along-stream

distribution in both systems, having two peaks of abundance during summer, one in the lower 5–10 km and the other 25–35 km upstream, with the latter disappearing in winter when the populations shifted downstream.

Links between adjacent estuaries and the sea

Bennett (1994) argued that the high degree of estuarine-dependence of the fish in the Berg River indicates that estuaries on the West Coast are more important as nursery areas and refugia than those on the south and east coasts of South Africa. The author further suggests that there is a high reliance of 'local' marine fish on the Berg Estuary, implying that any degradation of the estuarine habitat will have worse consequences for fish on the West Coast than elsewhere in South Africa. A similar argument can be made for the Olifants Estuary where 48% of the species caught show some degree of estuarine dependency compared with 54% and 39% in the Berg and Orange respectively. The Olifants Estuary is thus of equal importance to the Berg and Orange estuaries as an estuarine habitat for fish. Moreover, the Olifants Estuary is one of only three permanently open estuaries on the west coast of South Africa, together with the Berg Estuary 125 km to the south and the Orange Estuary 380 km to the north. The loss or degradation of the Olifants as an estuarine habitat could, in a worst-case scenario, see a reduction in the range of the estuarine-dependent species by 125 km or more if the Olifants represents the western extremity of their distribution. For those fish whose range extends to the Orange River, the loss of the Olifants estuarine habitat could result in stock separation. Either of these two scenarios will ultimately depend on the movement patterns of the species concerned.

In addition, the Olifants is an important nursery area for exploited marine and estuarine species before they recruit into the marine fisheries. This is illustrated by the declines in the *L. richardsonii* stock and marine gillnet fishery catches on the West Coast, which have been directly attributed to recruitment overfishing in the Olifants and Berg estuary gillnet fisheries (Hutchings and Lamberth 2003). Closure of the Berg Estuary gillnet fishery has since seen a dramatic recovery of the populations of the target *L. richardsonii* and bycatch species such as *P. saltatrix* (Hutchings *et al*. in press).

In the long term, migration of marine and estuarine species up and down the West Coast may be facilitated by the Orange, Olifants and Berg estuaries. Throughout the year, but especially during the summer upwelling months, species such as *P. saltatrix*, *A. inodorus*, *L. lithognathus* and *L. aureti* tend to be distributed within the warm-water areas along the West Coast (Lamberth 2003). These areas are limited and tend to be in shallow bays, estuaries or warm-water plumes in the vicinity of estuary mouths. Hypothetically, the southward distribution of Angolan dusky kob *A. coronus* and West Coast steenbras *L. aureti*, both non-estuarine marine species, to as far as Langebaan Lagoon, may depend on the availability of warm-water refugia offered by estuary mouths and plumes. Southward movement is most likely during anomalous years when the barrier presented by the Lüderitz upwelling cell breaks down or when there is a southwards intrusion of warm water during Benguela *Niño* years — the net result being warmer

coastal waters (van der Lingen *et al.* 2006). Once upwelling resumes, populations of those species that have penetrated south will be confined to the limited warm-water areas provided by estuaries and shallow bays. Consequently, a reduction in estuarine flow may influence the distribution of these species by reducing the extent and availability of these refugia. A similar process could facilitate exchange between South African, Namibian and Angolan stocks of *A. inodorus, P. saltatrix* and *L. amia*. All three of these species, as well as *L. lithognathus* and *L. aureti*, are important commercial and/or recreational fish in the region.

The Breede Estuary cannot be considered independent of other estuaries in the warm-temperate South Coast region, because it comprises only one component of the complexities surrounding the interactions between estuaries and the sea. Besides larval or juvenile recruitment, many species migrate into and out of the estuary as adults, some on a daily basis. Three species, *A. japonicus*, *P. commersonnii* and *L. amia*, which are obliged to spend at least their first year of life in the estuary, are among the most important species in the nearshore and estuarine recreational fisheries (Griffiths and Lamberth 2002). The accessibility of the Breede Estuary and the high catchability of juveniles and subadults in the estuary make these species extremely vulnerable to overexploitation.

Juveniles of *P. commersonnii* recruit into estuaries, where they remain until they reach a length of at least 20 cm (Fennessy 2000). Interestingly, although adults are abundant in the Breede Estuary, few 0+ juveniles of this species have been found there or in adjacent estuaries on the South Coast (SJL unpublished data). There has been a gradual south-west range expansion of this species over the last 30 years or so, with catches changing from rare to frequent in the Breede Estuary. This range expansion may be part of a long-term cycle and/or a response to climatic change. This parallels south-easterly expansions of the ranges of several marine species such as the West Coast rock lobster *Jasus lalandi* (Tarr *et al.* 1996, Cockcroft *et al.* 2008), anchovy *Engraulis encrasicolus* (Roy *et al.* 2007) and sardine *Sardinops sagax* (van der Lingen *et al.* 2005, Fairweather *et al.* 2006), also probably attributable to climate change. Information from tagged and recaptured fish indicates that most *P. commersonnii* remain resident within a particular estuary and adjacent surf-zone and move between the two habitats on a regular basis. The longest time at liberty for a fish released in the Breede is five years, and it was recaptured in the same estuary (Fennessy 2000). There are, however, exceptions to the rule, with one *P. commersonnii* being caught and released in the Breede but recaptured in the Swartkops Estuary 563 km to the east.

In all, 10% of the recaptures of *A. japonicus* caught and released at Lekkerwater and Koppie Alleen in De Hoop Marine Reserve immediately adjacent to the Breede Estuary have been recaptured in that estuary (Griffiths and Attwood 2005). Time at liberty ranged from one to five years. One fish tagged in the Breede as a juvenile was caught seven years later as an adult off Struisbaai (M Griffiths unpublished data). In turn, one fish tagged at Stilbaai 50 km away was recaptured 1.5 years later in the Breede Estuary, 4 km upstream (van der Elst and Bullen 1991). The fish recaptured in the estuary tend to be the larger individuals of

100 cm or more in length, which indicates a degree of adult movement from the adjacent surf-zone into the estuary.

L. amia recruits into estuaries as juveniles of 20–40 mm in length and large adults are present in both permanently open and temporarily closed systems (Bennett 1989). One subadult tagged in the Breede was caught five years later 1 200 km away on the KwaZulu-Natal coast (BQ Mann, Oceanographic Research Institute, pers. comm.). On the whole, tagging studies indicate a strong link between the Breede and adjacent estuaries, and their surf-zones, emphasising the importance of these estuaries as juvenile as well as adult habitat regionally and countrywide.

Responses to altered freshwater flows

Reference conditions

Historically, the Olifants and Breede estuaries would both have been freshwater-rich systems with extensive REI zones, and turbidity would have been higher over a greater stretch of each estuary than at present. This would have favoured species such as *A. inodorus*, *A. japonicus* and *G. feliceps*, which prefer turbid waters, and *G. aestuaria* which adapts easily to either turbid or clear conditions. High turbidity would have excluded *A. breviceps*, which is a visual feeder that prefers clear water (Hecht and van der Lingen 1992). Low salinity conditions throughout much of these estuaries would have favoured freshwater-tolerant species such as *M. cephalus*, *M. capensis* and *M. falciformis*, although the latter two would have been rare or absent in the Olifants as it is at the edge of their distribution range.

Lower phytoplankton, benthic diatom and zooplankton production would have favoured *G. aestuaria*, which can rapidly switch feeding behaviour from filter- to selective-feeding (White and Bruton 1983, Talbot and Baird 1985). An abundant supply of detritus from *Phragmites* reed beds in the middle and upper reaches of both systems would have been ideal for partial detritivores such as the mullet species *M. cephalus* and *L. richardsonii*. Benthic burrowers such as the mudprawn *Upogebia africana* and sandprawn *Callianassa kraussi* would have been restricted to the lower reaches if there was suitable habitat present, but densities and productivity would have been lower due to the lower salinities (Teske and Wooldridge 2001). Consequently, adult benthic feeders preying on these two species, such as *L. lithognathus* and *R. globiceps*, would probably have occurred further downstream and in lower densities. In the lower reaches, beds of seagrass *Zostera capensis* would, in the absence of anthropogenic disturbance such as trampling and boat activity, have facilitated a much higher abundance of associated fish such as *S. temminckii* and *Caffrogobius* spp.

Overall, the fish assemblages of both estuaries would historically have been dominated by estuarine-resident (Categories Ia and Ib) or estuarine-dependent species (Categories IIa, IIb or IIc) that are tolerant of, or prefer, lower salinities (Figure 5). These would have included the estuarine resident *G. aestuaria*, and the detritivorous Mugilidae such as *M. cephalus* and *L. richardsonii*. Small individuals of the above species would have been preyed on by adults and juveniles of the large piscivorous *L. amia*, *P. saltatrix*, *A. inodorus* and *A. japonicus,* which are likely to have been the dominant predators in the system. Juveniles

of most estuarine-dependent benthic feeders such as *L. lithognathus* and *R. globiceps* would have been abundant, but the adults are likely to have had a shorter residence time within the system. Indigenous freshwater species such as *Barbus serra* and *L. capensis* would be expected to have been abundant in the Olifants Estuary during the winter and to frequent the upper reaches of the estuary throughout the year. In the Breede Estuary, at least two of the catadromous anguillid eels, *A. marmorata* and *A. bengalensis labiata*, would have been the dominant predators in the upper reaches (SJL unpublished data). In both estuaries, marine species that are not estuarine-dependent are likely to have been rare and confined almost entirely to the lower reaches of the estuary. In the Olifants, the abundance of these species would probably have been related to the frequency of upwelling events in the sea, similar to the present day. Overall, the fish assemblages of both estuaries would have been characterised by low diversity and high abundance typical of freshwater-rich systems. The two estuaries would have differed under reference conditions in that the fish assemblage of the Olifants would have been orders of magnitude larger than the Breede whereas the latter would have had a higher diversity. These differences reflect the fact that the Olifants falls within the productive but low-diversity, cool-temperate West Coast biogeographical region whereas the Breede lies in a warm-temperate region (Emanuel *et al*. 1992, Turpie *et al*. 1999, Whitfield 2005a).

Present day and the future

Decision-making surrounding future developments in the Olifants catchment is largely confined to research and debates concerning the sites for a large dam or the raising of the existing Clanwilliam Dam by at least 5 m (Taljaard *et al*. 2005). Adherence to the Freshwater Reserve and committed environmental flow releases from the raised dam should ensure that two of the future scenarios represent a slight increase in the MAR reaching the estuary compared to the present day (Table 1). Nevertheless, these two scenarios still represent a 25–31% reduction in flow from reference conditions. Construction of a large dam will result in a 60% reduction in flow. In contrast, in excess of 100 water abstraction and/or storage alternatives, ranging from pipelines to large in-channel and off-channel dams, have been proposed for the Breede catchment, the largest of these being the Bromberg and Le Chasseur schemes, which would result in reductions of 57% and 64% of the MAR reaching the estuary respectively (Table 1). However, even though the two estuaries differ in terms of their likely future development, the net result will be similar, with both systems experiencing up to a 60% reduction in MAR relative to the reference condition. The existing and proposed reductions in MAR have resulted, or will result in, both estuaries gradually changing from freshwater-rich to marine-dominated systems. The REI zones will shrink and may even come close to disappearing under drought conditions. In turn, depending on their salinity preferences, the ranges of different species of fish will either shrink or expand. Depending on the persistence of the different states and the life-history characteristics of the species concerned, changes in species composition and abundance may be either short-term or permanent. Ultimately, in each estuary, there is likely to be an irreversible shift away from

the fish assemblage as it existed under reference conditions and away from the present-day composition.

Category Ia estuarine breeders were represented solely by *G. aestuaria* in the Olifants and Breede estuaries. In both systems, their declines will be of similar magnitude and will correspond with the shrinking of the REI zone and their preferred salinity range of 0–10 that will accompany a reduction in flow. Category Ib species will increase on account of them being well adapted to the estuarine or marine environment, mostly confined to the middle and lower reaches of the estuary, and having a preference for, or tolerance of, low turbidity. The response of Category Ia species to lower flows will be entirely due to the decline in *G. aestuaria* whereas the increase in Category Ib species will be due to range expansion by Cape silverside *A. breviceps*, *Caffrogobius* spp. and *C. superciliosus* (Figure 6). Their range expansion would be enhanced by an increase in water clarity and the expansion of eelgrass beds. *G. aestuaria* will respond negatively to a loss of habitat or preferred salinity in the upper reaches of the estuary whereas *A. breviceps*, a visual feeder, will respond positively to a decrease in turbidity and an increase in area covered by their preferred salinity range (20–35) in the middle and lower reaches.

Obligate estuarine-dependent (Category IIa) species in the Olifants Estuary were represented by *L. lithognathus* and *M. cephalus*, which have declined to <20% of reference levels in the present day and could approach extinction in the system with the maximum 60% reduction in flow. In contrast, Category IIa species in the Breede Estuary will display a small but positive response to flow reduction. However, the positive response will be largely due to that of a single abundant species, *R. holubi*, and four of the seven species in this category will respond negatively to flow reduction. More importantly, the increases displayed by *L. lithognathus*, *L. amia* and *R. holubi* will be approximately half the magnitude of the declines experienced by *A. japonicus*, *P. commersonii* and other Category IIa species.

The response of *L. lithognathus* to declining flow is contradictory, being negative in the Olifants and positive in the Breede. In both systems, the benthic-feeding *L. lithognathus* is likely to respond positively to an upstream expansion of the mud and sandflats and an increase in the burrowing mudprawn *U. africana* and sandprawn *C. kraussi*. *L. amia*, a visual piscivorous predator, will respond positively to reduced turbidity (Cyrus and Blaber 1987, Hecht and van der Lingen 1992) brought about by the reduction in river flow. Consequently, in the Olifants Estuary, and in the absence of a gillnet fishery that is currently overexploiting resources, *L. lithognathus* and possibly *L. amia* could have responded in the same way as populations in the Breede by showing a small increase from reference to present day.

The 40% decline in partially estuarine-dependent Category IIc fish, dominated by *L. richardsonii* in the Olifants, is largely due to fishing effects, in the absence of which they could have been more than twice as abundant than under reference conditions. Under the future reductions in MAR reaching the estuary, Category IIc fish will continue to decline to 50% of their reference abundance. *L. richardsonii* is the mainstay of the inshore beach-seine and gillnet fisheries along the West Coast, including the Olifants gillnet fishery (Lamberth *et al.* 1997, Hutchings and Lamberth

2002a). Although lower flows from reference to the present have had a positive effect on this species, and may to some extent have compensated for the decline due to fishing, future responses to flow reduction are likely to be negative. In addition, they are regarded as overexploited and the local fishers are already struggling to maintain a viable catch (Sowman *et al*. 1997). Should this species decline in numbers under the future scenarios, it may result in many of the current fishers being forced out of the fishery, even before its planned phasing out within the next 10 years (DEAT 2006). *L. richardsonii* also dominated the partially estuarine-dependent Category IIc in the Breede Estuary, which underwent a slight increase in abundance from reference to present day and is expected to increase to 109% of reference condition with future flow reductions and an expansion of their preferred 20–35 salinity range.

The 80% decline from reference abundance and the absence of any discernable recovery of *P. saltatrix* (Category IIc) and *L. lithognathus* (Category IIa) in the Olifants under any of the future scenarios is an area of concern, as the stocks of these two species are already overexploited and/or collapsed, being at 34% and 6% of pristine respectively (Griffiths and Lamberth 2002). Fortunately the piscivorous *P. saltatrix* and invertebrate feeders *D. sargus* and *R. globiceps* in the Breede Estuary would have benefited from an increase in water clarity. However, the increase in partially estuarine-dependent species in the Breede from the reference to present day probably falls within natural variability and is slight compared with the reduction in abundance experienced by those same species in the Olifants.

In the Olifants Estuary, estuarine-independent marine species (Category III) have undergone a 43% decrease in abundance from reference conditions, but may show a slight 5% recovery with the 60% reduction in freshwater flow and stronger marine influence under Scenario 5. As with the Category IIc *L. richardsonii*, in the absence of fishing, they could have been 77% more abundant in the present day. Slightly contradictory, freshwater may also have played a role with a decline in flow, resulting in a reduction in the warm-water plume entering the sea, and a corresponding decline in the number of marine fish encountering it. Similarly, shrinkage of the plume and reduction in the magnitude of olfactory and temperature cues reaching the marine environment are likely to be the main causes of juvenile obligate estuarine-dependent species failing to locate and recruit to the estuary. In the Breede Estuary, estuarine-independent marine species will undergo the greatest increase in abundance with decreasing flows, and are likely to increase to 123% of reference conditions with a 64% reduction in MAR and the increasingly marine dominated nature of the system (Figures 5, 6).

Category IV freshwater species in the Olifants and Breede estuaries may decline by 60% or more with a 60% reduction in MAR, but as they are at present solely represented by introduced fish such as *M. dolomieu* and *L. macrochirus*, this can be regarded as a positive consequence of reduced flows. However, reduced flows, narrowing of the stream channel and increased salinity will prevent the success of any future initiatives to re-establish indigenous species, such as *L. capensis*, to the upper reaches of the Olifants Estuary.

Facultative catadromous (Category V) species display a similar response to the freshwater species with *M. capensis* collapsing to <60% of reference with a 60% reduction in MAR. This species is regarded as Vulnerable and in decline throughout its range, largely due to water abstraction and weirs and other obstacles impeding its migration into the freshwater reaches of rivers (Skelton 1993).

Conclusions

Overall, reduced freshwater flows in the Olifants Estuary are likely to result in a reduction in the abundance of species that breed only in estuaries, those that are entirely estuarine-dependent, most of those that are partially estuarine-dependent, as well as endemic freshwater species. With the addition of fishing effects, numbers may decline to such an extent that some of these species may completely disappear from the Olifants Estuary. In the absence of fishing, partially estuarine-dependent and marine species would have increased from reference conditions to the present day with the encroachment of higher salinity farther upstream and expansion of available habitat. However, they will decrease in abundance under the future scenarios that are accompanied by shrinkage of the warm-water plume entering the sea, narrowing of the stream channel, and an overall reduction in available habitat. Overall, and assuming an absence of fishing, the Olifants fish community would have experienced a gradual change from a high biomass, low diversity, freshwater-rich system under reference conditions to a high biomass, medium diversity, marine-dominated system under the present day. Overall abundance has decreased by 20% from reference conditions to present day and will decline to 55% with the 60% reduction in MAR under Scenario 5. Consequently, future reductions in flow are likely to see the Olifants Estuary progressing towards a low biomass, low diversity, marine-dominated system. Furthermore, the shrinking of the REI zone and other estuarine habitat, as well as the decline in abundance and diversity of estuarine-dependent fish in the estuary, suggests that the refuge offered by the Olifants, as well as its diverse nursery function, have been severely compromised. Consequently, line and net fisheries inside and outside the estuary will continue to suffer from falling production, and the coastal distribution of some species, especially those endemic to the region, may either split or shrink.

In contrast, reduced freshwater flows in the Breede Estuary are likely to result in an overall reduction in the abundance of species that breed only in estuaries, and in freshwater and catadromous species. Partially estuarine-dependent and marine species are likely to increase with encroachment of higher-salinity water farther upstream and an expansion of available habitat. Overall, fish abundance in the estuary has increased to 106% of the reference condition and is likely to increase to 115% with future reductions in flow. Losses of some species with a preference for fresh and brackish water are probable, but overall diversity is equally likely to increase with a range expansion of warm-temperate and subtropical marine species westward. In all, the fish assemblage will experience a gradual change from a relatively high diversity, low abundance, freshwater-rich system under historical flow conditions to a high diversity,

high abundance, marine-dominated system with future reductions in flow. Collectively, entirely estuarine-dependent fish will increase in abundance but some individual important exploited species such as *A. japonicus* and *P. commersonnii* will collapse to 50% of historical numbers with a 64% reduction in MAR. These two species comprise 74% of the total estuarine catch and *A. japonicus*, prior to its collapse to 4% of pristine spawner biomass, once dominated commercial linefish catches in the region.

The severity of past and future flow reduction is much higher for the Olifants than the Breede Estuary. Whereas the fish assemblage of the Olifants Estuary is likely to almost halve in abundance with future reductions in flow, that of the Breede Estuary will undergo an incremental increase. Fish diversity displays a similar pattern, declining in the Olifants and increasing in the Breede. However, the increase in diversity in the Breede is largely on account of the intrusion of seawater and more marine species treating the estuary as an arm of the sea rather than an increase in the number of estuarine-dependent species in the system. Overall, whilst both estuaries have undergone similar reductions in flow from the reference conditions to the present day, and in the long term may have to function with <40% of historical MAR, the Olifants Estuary is likely to lose much of its estuarine function whereas the Breede Estuary and its fish assemblage appear to be more resilient and likely to persist. However, the decline in key regionally exploited species in both estuaries will result in a concomitant decline in their estuarine contribution to the productivity of the commercial and recreational fisheries in the adjacent marine environment. Faced with declining catches or loss of estuarine function, management action and mitigatory measures should entail regulating fishers as well as freshwater flow. Singularly addressing either one of these aspects without considering the other is unlikely to lead to any significant recovery or maintenance of estuarine fish assemblages.

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