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Ecosystem considerations of the KwaZulu-Natal sardine run

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The annual winter sardine run along the South African east coast impacts the KwaZulu-Natal (KZN) coastal system in a variety of ways. These include ecological impacts, such as enrichment of a largely oligotrophic environment, competition between migrant sardine *Sardinops sagax*, other migrant and resident small pelagic fish species, and interactions with predators, as well as the socio-economic impacts of the sardine run on the local people. Enrichment of KZN coastal waters with organic nitrogen contained within the sardine is compared with alternative sources of nitrogen such as upwelling, river, sewage and stormwater runoff, and groundwater discharge. The sardine run appears to contribute most nitrogen to this system — 96 000 t compared to 500–3 300 t for each of the other significant sources at trophic level 2, although upwelling estimates are extremely wide. Nonetheless, the majority of surviving sardine, their young and predators return southwards, suggesting that the nett export of nitrogen to KZN waters during the run is likely to be of a similar order of magnitude as that from other sources. Further, whereas the sardine supply of nitrogen is exclusively during winter, the bulk of the riverine input is in summer, thus ensuring that nitrogen supply in the region is maintained at fairly constant levels throughout the year. Competition for food between small pelagic fish is minimised by resource partitioning, but further dietary data are needed for resident species. Although interactions between sardine and top predators must exist, further studies are needed to confirm links between top predator life cycles and the sardine run. The estimated value of sardine as a tourist spectacle is compared to that from a seasonal beach-seine or boat-based purse-seine fishery for this species. Whereas the estimated value of the sardine as a tourist attraction appears substantially higher than could be derived from catching them, the small-scale beach-seine fishery itself draws tourists and also provides limited, seasonal employment opportunities.

Keywords: competition, nitrogen sources, predators, relative economic value, sardine run, South African east coast

Introduction

The KwaZulu-Natal (KZN) sardine run represents a major ecosystem event in which relatively high concentrations of sardine *Sardinops sagax* move seasonally to the extreme of their range in warm subtropical waters in the austral winter and then retreat back to more temperate waters as summer approaches and water temperature increases (Armstrong et al. 1991). The proximity of the shoals to the shoreline and the obvious predatory activity associated with the shoals stimulate consumptive (fishing) and non-consumptive (tourism-related) activities which provide a considerable boost to the economy of the KZN and Eastern Cape (van der Lingen et al. 2010). Small pelagic fish require moderate to high concentrations of plankton to sustain their metabolism and still provide scope for growth and reproduction (Blaxter and Hunter 1982, James et al. 1989). The costs of an apparently arduous migration, the energetic demands of extreme avoidance behaviour in response to massed predators in clear subtropical waters with low to moderate productivity and increased thermal stress imply that there must be some major return in terms of growth or reproductive success to offset the losses and allow an evolutionary stable strategy to evolve (Fréon et al. 2010). Sardine appear to remain in KZN waters after the run, indicated by the presence of sardine eggs sampled off Park Rynie between June and December (Connell 2010). They are, however, no longer observed close inshore or in near-surface waters during this time and may therefore be confined to deeper water or within the eutrophic area of the KZN Bight, until displaced southward by warming waters in summer.

The 'success' of the sardine run is qualitatively assessed by local people in terms of the quantity of fish that are close inshore and captured in the surf zone by beach-seines and sundry smaller nets. There are many anecdotal incidences of sardine schools spotted offshore yet not being available to fishers on the shore either netting sardine or catching associated predators. Pelagic fish surveys from the South African west coast to as far as Port Elizabeth or Port Alfred have been conducted each May and November since 1984 (Hampton 1987, 1992, Coetzee et al. 2008, de Moor et al. 2008). Only four hydroacoustic surveys have attempted to study sardine on the East Coast, three conducted in August 1986, June 1987 and June 1990, reported by Armstrong et al. 1991, and the June 2005 survey described by Coetzee et al. (2010). These surveys all yielded remarkably similar biomass estimates of sardine taking part in the run (c. 30 000 t), despite large variation in the total size of the sardine population. It seems therefore that there is no relationship between the number of sardine moving into KZN waters and the size of the population on the Agulhas Bank.

In contrast to the predominantly upwelling-driven Benguela ecosystem of the South African west coast, KZN coastal waters are considered oligotrophic with limited nitrogen supplies from a number of terrigenous and marine sources, including river runoff, groundwater and limited local upwelling (Lutjeharms et al. 2000, van Ballegooyen et al. 2007, Lamberth et al. 2009). Intuitively, sardine should also provide a significant input, at least during the winter months. This, coupled with the spectacular nature of the run close to the shore, growing publicity and increasing tourism surrounding the run, makes it imperative that we: (1) increase our understanding of the role of this event in ecosystem functioning; (2) improve our ability to predict the relative strength of the run; and (3), failing (2), develop techniques for early detection such as aerial spotting, satellite imagery and real-time moored temperature monitoring buoys off the Transkei coastline, to facilitate planning and execution of activities related to the run.

This paper outlines some of the major ecosystem considerations of the sardine run in terms of nitrogen input into the marine system from sardine and other sources as well as the importance of the sardine run as a food source for predators and its potential consequences for competitors. Furthermore, social and economic factors associated with the sardine run are discussed in terms of their relative importance to the KZN region.

Nitrogen inputs

Total nitrogen (N) input to ecosystems consists primarily of inorganic N (nitrite-N, nitrate-N plus total ammonia-N [NH_3-N + NH_4^+-N]) and organic N (dissolved and particulate). Inorganic N is the source of nutrients for autotrophic (primary) production whereas organic N supports heterotrophic (secondary) production. The section below (summarised in Table 1) provides details on known and potential inputs of nitrogen into the KZN coastal region and the relative contribution of each source.

The nitrogen content of sardine

Van der Lingen (1999) gives information on the conversions from sardine wet mass to organic N content. Dry weight is approximately 30% of wet weight and nitrogen content is 10.64% of dry weight, so 30 000 t of sardine (wet weight) equates to (30 000 $\times$ 0.3 $\times$ 0.1064 =) 958 t of organic N that is injected into the KZN coastal waters. This can be compared with that estimated from river runoff, upwelling, stormwater runoff, wastewater effluent, rainfall and nitrogen injection from shelf-edge upwelling or Natal Pulses. (Aeolian N was not considered due to the paucity of data, but is considered negligible.) Because sardine feed on small- and medium-sized copepods (van der Lingen 2002, van der Lingen et al. 2006), their trophic level has been estimated to be 3.0 (Shannon et al. 2003) or 2.91 (Watermeyer et al. 2008). Because sardine were also consuming large quantities of fish eggs during the June 2005 survey (Mketsu 2008), they may be considered to be between trophic levels 3 and 4. This would, however, depend on the interpretation of where ‘passive’ consumers such as fish eggs occur in the trophic spectrum (are they at the level of their parents or are they much lower as ‘non-consumers’?). At a trophic transfer efficiency of approximately 10%, the organic N in sardine at trophic level 2 would be the equivalent of 95 800 t of inorganic N (e.g. nitrate-N) or nearly a million tonnes if sardine are at trophic level 3. This assumes that the average total biomass of sardine entering KZN waters is 30 000 t, the mean value for the three acoustic estimates (Armstrong et al. 1991, Coetzee et al. 2010). However, this figure applies to the stock of sardine east of Port Alfred, which may not all enter KZN waters. It also ignores the fact that surviving fish, as well as their progeny, return southwards. There is evidence that mainly only the larger fish move farthest north (Coetzee et al. 2010, van der Lingen et al. 2010), but for the purposes of this paper the biomass east of Port Alfred will be considered an integral part of the sardine run. In addition, there is enormous mortality of sardine from catches and predators alike, and the acoustic estimate is partially dependent on the date of the survey: the first survey in 1986 was in August, near the end of the run, when considerable mortality was presumed to have occurred; the 1987 and 2005 surveys were at the peak of the run in June. These acoustic biomass estimates are therefore likely to be minimal estimates rather than overestimates, so the quantity of nitrogen is likewise an underestimate.

River runoff

There are approximately 73 catchments discharging into the sea along the KZN coastline, of which 12 provide 92% of the total runoff to the coast (Begg 1978, Jezewski et al. 1984, DWAF 2004a; Figure 1). Of these, five systems — Thukela (35%), Mzimkulu (13%), Mkomazi (9%), Mfolozi (8%) and (Mgeni 6%) — make the most significant contribution in freshwater input to the coast.

Median concentrations for inorganic N for the 12 significant catchments were derived from data collected by the former Department of Water Affairs and Forestry (DWAF) available from www.dwaf.gov.za (Table 2; no data were available on organic N input from catchments). Within each of the catchments, inorganic N concentrations measured at the most downstream monitoring station were used as these were considered most representative of the concentrations that enter the sea. De Villiers and Thiart (2007) also calculated the concentration of inorganic N for three

Table 1: Summary of sources of nitrogen to the KZN shelf and the relative importance (%) of each source to the total nitrogen input at trophic levels 2 (TL2) and 3 (TL3)

Source	Input (t N per annum)	Total estimated input (%)	Comments
Winter sardine run	30 000 t of sardine = 960 t N ~96 000 if at TL2 ~960 000 if at TL3	24 (TL2)–76 (TL3)	Mean sardine biomass estimated from three (1986, 1987 and 2005) sardine run surveys; N estimated from conversion of sardine wet mass to nitrogen content and 10% ecotrophic efficiency
River runoff	Median value = 2 333 t	0.6 (TL2)–0.18 (TL3)	Annual median runoff (estimated from nitrogen concentrations per unit catchment area multiplied by catchment size for the major rivers in KZN; see Table 2)
St Lucia upwelling	Min. = 3 066 t Max. = 576 122 t Mean = 289 154 t	2.9 (TL2)–0.3 (TL3) 84.9 (TL2)–37.3 (TL3) 73.8 (TL2)–23 (TL3)	Range of nitrogen uplift estimated from minimum and maximum values of upwelling area (200–5 200 km^2), upwelling rate (1–10 m d^{-1}), N-NO_3 concentrations (140–210 mg m^{-3}), and temporal occurrence (30–78% of the time). Mean value used for percentages of total input (column 3)
Shelf-edge upwelling/Ekman veering	Enrichment of <100 t of nitrate (N-NO_3) per annum (negligible)	<<0.01 (TL2)–<0.01 (TL3)	Ekman uplift of bottom water estimated from measurements of nitrate (N-NO_3) in upper 50 m, usually <1–2 μmol l^{-1}
Natal Pulses	Enrichment of <100 t of nitrate (N-NO_3) per annum (negligible)	<<0.03 (TL2)–<0.01 (TL3)	Estimated 1–2 pulses per annum based on frequency of observed offshore excursions of the Agulhas Current core
Municipal wastewater discharges	3 330 t	0.85 (TL2)–0.26 (TL3)	Derived from 3 066 t of offshore untreated discharge (raw sewage); 22 t and 241 t from secondary treated outflow into the surf zone and estuaries respectively (see Table 3)
Stormwater runoff and fertilisers	Unknown	Unknown	Little or no quantification, but major fluxes assumed to be carried in river flow and not isolated stormwater outlets
Groundwater discharge	224–898 t Mean = 560	0.14 (TL2)–0.04 (TL3)	Nitrogen derived from groundwater may contribute up to 95% of surf-zone phytoplankton production. Groundwater N discharge range 1.1–4.1 g N m^{-1} d^{-1}
Total	391 577 t (TL2) 1 255 577 t (TL3)		Sardine at TL2, i.e. ~96 000 t N-NO_3 or 960 000 t at TL3: assumed average upwelling at St Lucia

of these catchments (Mkomazi, Thukela and Mfolozi), but only considered nitrite-N and nitrate-N. The estimated annual inorganic N loads entering the marine environment from each of these catchments were calculated using the median inorganic N of the available data and mean annual runoff (MAR) (Table 2). The combined inorganic N contribution from the 12 large catchments is estimated at 2 333 t per year.

Average monthly flow distributions of the catchments along the KZN coast show that the freshwater inflow mainly occurs in summer (December–March), with the high runoff period being more defined in larger catchments such as the Thukela and Mhlathuze, which peak from January to February (DWAF 2004a). Smaller catchments such as the Mdloti exhibit less variability in flow, but are still dominated by significant river inflow during the summer (DWAF 2007). Figure 2 illustrates the relative monthly flow distribution along the KZN coastline, estimated as a percentage of the total annual inflow based on a 15-year dataset for 17 catchments (DWAF 2004a).

It should be noted that the above approach ignores any estuarine dynamics in terms of the N cycle wherein nitrogen may be utilised or fixed before entering the coastal waters. However, estuarine production depends on water retention time, which, during the wet season, is of short duration in the larger catchments considered here.

Spatial and temporal changes in the relative contribution or dominance of the different N sources also need to be considered. Catchment-derived inorganic N is predominantly from the summer rainfall months, whereas sardine presence is limited to the period June–December (Connell 2010, van der Lingen et al. 2010) and upwelling is sporadic throughout the year (Lutjeharms et al. 1989). During drought years, catchment-derived inorganic N will decrease and the relative contribution of the sardine run to the nitrogen budget will become more important. However, drought years and ‘failure’ of the sardine run to reach the KZN coast often coincide (DWAF 2004a, Lamberth et al. 2009, van der Lingen et al. 2010), and in those years coastal production is likely to depend more on inorganic N introduced by upwelling.

Upwelling at the St Lucia upwelling cell in the KZN Bight

This area has been the subject of numerous studies from ship and satellite observations (e.g. Pearce 1977, Lutjeharms et al. 1989, 2000, Meyer et al. 2002). Persistent upwelling has been detected in the region between Richards Bay and St Lucia, identified by the presence of cool water, higher nutrients and enhanced chlorophyll *a* concentrations, which spreads southwards over the KZN Bight at the surface and the bottom. The estimates of the active area of upwelling, the nutrient concentrations and the rate and frequency of upwelling differ widely between these studies, so we have calculated a lower and upper estimate based on some approximations:

- The area of upwelling varies between 200 km^2 (Pearce 1977) and up to 5 200 km^2, for around 24% of the time (Lutjeharms et al. 1989), with high variability between event-scale estimates. Cool water (<18 °C) is estimated to cover an area of 996 km^2 (Figure 2 from Lutjeharms et al. 1989). There is a need, however, to distinguish between the actual area of vertical uplift and the area where the effects of upwelling are advected downstream when calculating nutrient fluxes, because mixing, water column stratification and biological uptake all occur concomitantly.
- The rate of upwelling was estimated by Pearce (1977) on only one occasion from repeated daily transects and indicated a rise in isotherms of up to 30 m per day, a rate similar to those estimated by Andrews and Hutchings (1980) for the very active wind-driven Cape Peninsula upwelling site. However, wind seems to play a minor role in the upwelling process in the KZN Bight (Pearce 1977, Lutjeharms et al. 1989), which appears to be primarily driven by the flow of the Agulhas Current past a widening shelf, and induced upward flux as a consequence of changes in vorticity (Lutjeharms et al. 1989). Nonetheless, a change of winds from north-east to south-west, which accompanies the passage of coastal lows, causes an immediate sinking of isotherms as near-coastal currents reverse. Thus, upwelling appears to be frequent but

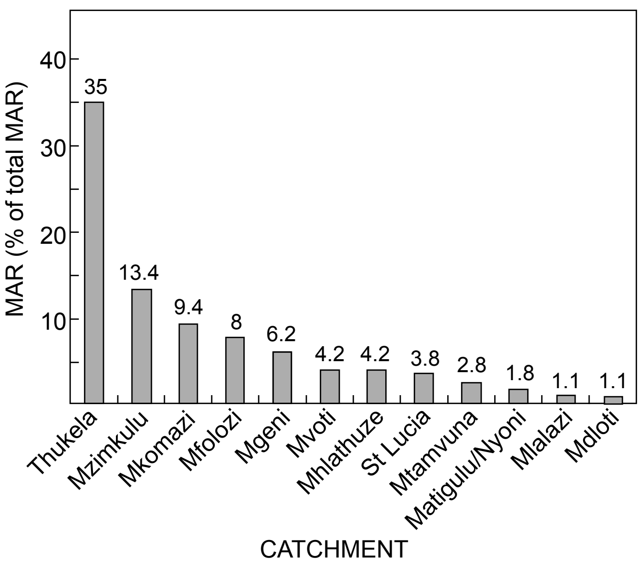

Figure 1: River catchments along the KZN coastline that contribute more than 1% to the total mean annual runoff (MAR) discharging into the sea along the KZN coast

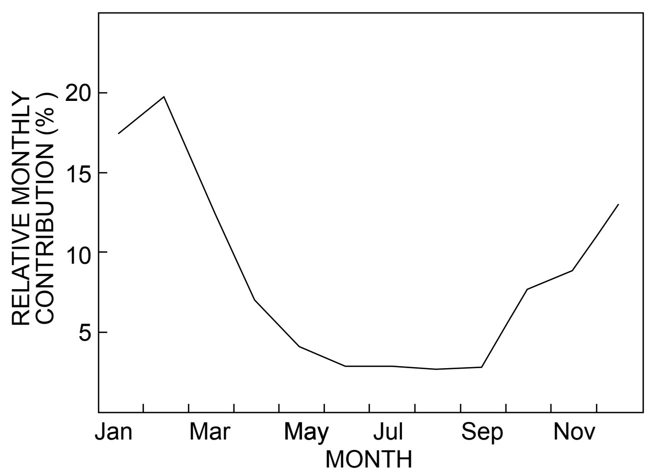

Figure 2: Relative monthly inflow distribution from rivers along the KZN coastline estimated as a percentage of the total annual inflow

Table 2: Median inorganic N concentration, marine annual runoff (MAR) and estimated annual dissolved inorganic nitrogen (DIN) loads from the 12 large catchments discharging into the sea along the KZN coast

Catchment (DWAF station)	Data record	n	Median inorganic N (µg l^{-1})	MAR (million m^3)	Estimated inorganic N load (t y^{-1})
Thukela (V5H002)	1977–2005	473	300	3 865.0	1 160
Mzimkulu (T5H007)	1980–2005	94	210	1 478.2	310
Mkomazi (U1H006)	1978–2005	341	120	1 036.2	124
Mfolozi (W2H032)	1995–2005	101	99	887.3	88
Mgeni (U2H054)	1990–1995	239	133	682.9	91
Mvoti (U4H007)	1977–1997	210	390	468.2	183
Mhlathuze (W1H009)	1977–2005	370	287	467.5	134
St Lucia (W3R002)	1973–2004	570	113	414.0	47
Mtavuna (T4H001)	1978–2005	351	290	303.8	88
Matigulu (W1H010)	1976–1992	235	146	201.1	29
Mlalazi (W1R002)	1981–2005	253	209	117.0	24
Mdloti (U3H005)	1985–1995	443	467	117.0	55
Estimated annual DIN load from 12 major catchments					2 333

DWAF = Department of Water Affairs and Forestry short-lived, so rates of 30 m per day are followed by sinking at the same rate, and realistic rates of uplift probably vary between 1 m and 10 m per day. Slight changes in the path and strength of the Agulhas Current may also influence the frequency and intensity of the upwelling events.

- Based on 86 ship-based observations, Pearce (1977) indicated the occurrence of upwelling about 30% of the time, whereas satellite and airborne radiation thermometer surveys conducted by Lutjeharms et al. (1989) indicate upwelling may be occurring up to 78% of the time. The latter seems more likely if driven by the Agulhas Current, which displays only minor seasonal variability.
- Inorganic N concentrations (in this case nitrate-N) of 140–210 µg l^{-1} (10–15 µmol l^{-1}) in the 75–100 m depth zone have been reported (Meyer et al. 2002). These concentrations can periodically also occur in the near-surface zone (<50 m), with a corresponding increase in chlorophyll *a* concentrations which advect southwards in a wedge-shaped extension.

Based on the above information, minimum and maximum values of inorganic N uplift into the euphotic zone (the upper 50 m) were calculated (Table 1).

For the minimum, area is 200 km^2, rate of upwelling 1 m d^{-1}, inorganic N concentrations of 140 µg l^{-1} (or 140 mg m^{-3}) and occurring 30% of the time (109.5 days):

$$200 \times 10^6 \times 1.0 \times 140 \times 109.5 \times 10^{-9}$$
$$= 3\ 066 \text{ t inorganic N per annum}$$

For the maximum, area is 966 km^2, rate of upwelling 10 m d^{-1}, inorganic N of 210 µg l^{-1} and occurring 78% of the time (284 days):

$$966 \times 10^6 \times 10.0 \times 210 \times 284 \times 10^{-9}$$
$$= 576\ 122 \text{ t inorganic N per annum}$$

The mean value is 289 154 t of nitrogen per annum and contributes 23–74% of total inorganic nitrogen input. The upwelling rate in the KZN Bight therefore constitutes a major source of variability in the estimates, ranging from 3% to 85% of total N input (Table 1). Although these are rough estimates, they provide insight into the relative magnitude of the supply. These values can be compared with the upward flux of inorganic N in the very active Cape Peninsula upwelling cell, which has an area of 2 033 km^2 and 2 120 t inorganic N per day (381 600 t per upwelling season of six months), with an upwelling rate that averages 4.5 m per day, over the summer upwelling season or 30 m per day in a 5 km wide strip along the Peninsula (Andrews and Hutchings 1980). Given the much higher phytoplankton abundance off the Cape Peninsula (Andrews and Hutchings 1980) compared with the KZN Bight (Meyer et al. 2002, Lutjeharms 2008), it suggests the lower (minimum estimates of nitrogen flux calculated above) from upwelling in the KZN Bight are more realistic.

Other oceanic sources of nitrogen

Ekman veering, or shelf-edge upwelling, is caused by the bottom frictional effects slowing down the rapid western boundary flow, which results in a shoreward deflection and the upward pumping of water along the shelf slope (Lutjeharms 2008). Data from numerous ship-based surveys along the east coast of South Africa show that inorganic N concentrations are mostly below 14–28 µg l^{-1} (1–2 µmol l^{-1}) in the upper 50 m, except for intermittent outcroppings at topographic discontinuities such as the KZN Bight and Waterfall Bluff (Meyer et al. 2002, TM unpublished data). The Ekman uplift of bottom water can probably be discounted along much of the sardine run domain and inorganic N enrichment is likely to be <100 t per annum. The cool patches inshore along the East Coast, interspersed with areas where warm waters from the Agulhas Current flow close inshore (Coetzee et al. 2010), also contribute inorganic N to the nearshore waters, but these patches are ephemeral and difficult to quantify.

Natal Pulses are large excursions of the main course of the Agulhas Current that propagate from the vicinity of the KZN Bight (Lutjeharms 2008). These excursions grow as they move southwards and may induce upwelling as the current diverges from the coastline, with increasing effects in the southern Agulhas Current. Offshore excursions of the core of the Agulhas Current occur about 22% of the time and with the southward movement of about 20 km per day over the northern part of the current (1 000 km), it should take about 50 days to traverse the East Coast. If they are detected 20% of the time from satellite imagery (Lutjeharms 2008), there are likely to be 1–2 pulses per annum. There is little documentation of enrichment potential of the nearshore region from these pulses, but it is likely to be small (<100 t inorganic N per annum) along the KZN coast.

Municipal wastewater discharges

In South Africa, municipal wastewater that is discharged to the offshore marine environment contains a high level of raw sewage that undergoes only limited prior treatment (e.g. coarse screening and maceration — referred to as preliminary treatment) (DWAF 2004b, RSA 2004). Municipal wastewater discharged to the surf zone and estuaries requires at least secondary treatment, which includes processes such as activated sludge treatment and/or biofiltration.

In untreated domestic wastewater (raw sewage), nitrogen is found primarily in the form of organic N and inorganic N (mainly total ammonia-N), typically consisting of about 40% organic N and 60% inorganic N (Sedlak 1991). Nitrogen concentration in secondary treated wastewater can vary greatly depending on the selected treatment process (WRC 1990, FAO 1992). In South Africa, existing municipal wastewater treatment works, discharging to the surf zone and estuaries, however, should be designed to meet general authorisation limits, which are set at 6 000 µg l^{-1} (6 mg l^{-1}) for total ammonia-N and 15 000 µg l^{-1} (15 mg l^{-1}) for nitrite-N plus nitrate-N (RSA 2004). Considering that secondary treatment processes are generally very effective in reducing suspended solids concentration and biological oxygen demand (indicative of organic content) by 85–95% (Asano et al. 2007), it is considered reasonable for the purposes of this assessment, to use inorganic N as a proxy for average total N for secondary treated municipal wastewater discharges, in this case 21 000 µg l^{-1} (sum of legal limits specified for inorganic forms of N, i.e. 6 000 µg l^{-1} for ammonia plus 15 000 µg l^{-1} for nitrite+nitrate).

Total N loading from municipal wastewater discharges entering the marine environment along the KZN coast was calculated from estimated annual volumes (DWAF 2004b, RSA 2004) and total N concentrations in domestic wastewater derived from the literature (Sedlak 1991, RSA 2004). Wastewater treatment outflow is conservatively estimated to provide 3 330 t of total N to KZN waters annually (Table 3).

Stormwater runoff and agricultural fertilisers

There is little or no quantification of stormwater runoff volume or concentrations of nitrogen from agricultural fertilisers. The only reasonable assumption is that localised concentrations from urban or intensive agricultural areas would be high relative to less developed rural areas. Nonetheless, the major fluxes are probably carried down in river flow rather than isolated stormwater outlets that open directly into the sea and are consequently already accounted for.

Groundwater discharge

The potential for a nitrogen supplement from groundwater discharge is high relative to most of the South African coast with high rainfall in summer months and high inorganic N levels of at least two orders of magnitude greater than ambient in the nearshore zone. Inorganic N is likely to be a steady source through groundwater discharge even during the dry months (April–September; van Ballegooyen et al. 2007). However, few estimates of the actual volume of groundwater discharge are available, but inorganic N from groundwater is important in surf-zone ecosystems throughout the eastern seaboard of South Africa, where it may contribute up to 95% of phytoplankton (primary) production (Campbell and Bate 1991a, 1991b). Groundwater discharge rates of inorganic N into the surf zone range from an average of 1.1 g N m^{-1} d^{-1} along the KZN coastline (Campbell and Bate 1991b) to 4.1 g N m^{-1} d^{-1} along the Alexandria dunefields in the Eastern Cape (Campbell and Bate 1991a). Based on these values, groundwater-derived inorganic N along 600 km of KZN coastline is estimated at 224–898 t per annum.

Biological interactions

Competition between species

Sardine, East Coast round herring *Etrumeus teres*, West Coast round herring *Etrumeus whiteheadi* and anchovy *Engraulis encrasicolus* all overlap in diet on the East Coast in a food-impoverished environment that is transitional between tropical and temperate environments. A feeding study by Mketsu (2008) on sardine caught during the 2005 sardine run survey showed partial partitioning between anchovy and sardine and that sardine consumed smaller prey (mainly fish eggs and small calanoid copepods) than the two round herring species, which have separate thermal optima and a limited degree of spatial overlap. Sardine penetrate farther into KZN waters than anchovy and must impact on pelagic fish that feed on similar-sized small and medium copepods, but dietary data on tropical species and chub mackerel *Scomber japonicus* and *Decapterus* spp. are lacking. Sardine formed a small portion of the pelagic fish assemblage in midwater trawl catches in warm waters of the KZN Bight, 0.53–4.98% during the August 1986 and June 1987 surveys, with East Coast round herring, Indian anchovy *Stolephorus indicus,* longjaw glassnose *Thryssa setirostris* and Indian pellona *Pellona ditchela* being relatively abundant (Armstrong et al. 1991). Farther south, sardine and anchovy constitute roughly equal quantities of 30 000–40 000 t, about one-third to one-sixth the biomass of West Coast round herring at 224 000 t (1986) and 91 000 t (1987).

Top predators

Top predators associated with the annual sardine run include cetaceans, mainly common dolphins *Delphinus capensis*, Bryde's whale *Balaenoptera edeni* and Minke whale *Balaenoptera bonaerensis* (O'Donoghue et al. 2010), sharks such as bronze whaler *Carcharhinus brachyurus* and raggedtooth *Carcharias taurus* (Dudley and Cliff 2010), and teleosts, predominantly elf *Pomatomus saltatrix* and garrick *Lichia amia* (Fennessy et al. 2010), as well as geelbek *Atractoscion aequidens* and dusky kob *Argyrosomus japonicus*. These predatory fish species breed in KZN waters in late winter/spring (Beckley and Connell 1996) and potentially utilise the sardine run food source during their upstream migration into KZN spawning grounds. Significant relationships were found between the shore-based catch rates of elf and garrick and the timing of the sardine run (Fennessy et al. 2010), whereas boat-based catches of geelbek and dusky kob seemingly also increase at this time. This migration of predators is predominantly a temperate-species movement to subtropical temperatures and it remains unclear whether it is timed to coincide with the sardine run or whether it is undertaken to ensure successful southward drift of spawning products to nursery areas located on the Cape south-east coast (Fennessy et al. 2010).

Tropical fish predators that have been shown to be associated with the sardine run include the king mackerel

Table 3: Estimated annual volumes, total N concentration and annual total N loads from municipal wastewater discharging into the marine environment along the KZN coast

Discharge location/type	Volume (m^3 y^{-1})	Average total N concentration (mg l^{-1})	Estimated total N load (t y^{-1})
Offshore (assuming raw sewage)	76 650 000	40	3 066 (60% inorganic N)
Surf zone (assuming secondary treatment)	1 058 500	21	22 (mainly inorganic N)
Estuaries (assuming secondary treatment)	11 497 500	21	241 (mainly inorganic N)
Total		82	3 329

Scomberomorus commerson and blacktip kingfish *Caranx heberi*. Fennessy et al. (2010) report significant positive correlations between shore-based angling catches of both these species and the timing of the sardine run and suggest that their occurrence in KZN waters at this time may indicate a post-spawning migration to coincide with increased availability of sardine. In general, information on reproductive cycles, weaning periods and condition factors of other top predators is surprisingly sparse. More data are needed to establish links between life cycles of top predators and the sardine run, either as specific migrations or as part of larger migrations such as that of humpback whales *Megaptera novaeangliae*, which, despite being abundant, have not been observed feeding during the sardine run (O'Donoghue et al. 2010).

Social and economic benefits

It is unclear whether tourists to KZN are simply avoiding the cold (inland) and/or wet (South-Western Cape) areas of South Africa or making the sardine run a specific tourist destination or purpose (Dicken 2010). Whereas recreational fishing is reportedly better after the run, a significant number of recreational fishers are still attracted to the south coast of KZN during the run (Fennessy et al. 2010). Diving safaris to experience predation events on sardine shoals, particularly massed predator attacks on 'baitballs', are an increasingly exciting attraction for tourists and are associated with extensive media coverage (Dicken 2010). This practice is also increasing in areas farther south such as off East London, although the higher visibility in clear waters of KZN and Pondoland make these preferred operational sites (Dicken 2010, Myeza et al. 2010). The value of foreign and domestic tourism in KZN is estimated at approximately R12 billion, which is spread evenly throughout the year, with domestic peaks in summer and winter (KZN Tourism Authority 2009). Conditional on the assumption that 10–50% of the visitors are specifically coming to view the sardine run, or that the sardine run adds another 10–50% to the attractiveness of the KZN south coast and a gross tourism income over the winter holiday period, coincident with the sardine run, of R1 billion, the value of the sardine run would equate to R10–500 million. This figure can then be compared with a number of alternative uses of sardine for direct consumption (Table 4). A study by Dicken (2010), which reflects on the economics of nine sardine run diving operators in the Pondoland Marine Protected Area, indicates a total expenditure of between R5–6 million, of which one-third is for international air fares. Because the package includes visits to other venues in southern Africa it is not possible to separate the proportion of the costs attributable to the sardine run from the total, although the main attraction to the region seemingly was the sardine run diving experience. This 'adventure tourism' is small relative to the total tourism economy in KZN, hence the wide limits on our estimates. A more focused economic survey would certainly improve this estimate. It must be noted that widespread publicity in wildlife magazines, television natural history programmes and adventure tourism have increased the profile of this natural event enormously in recent years, and expanded the tourist spectrum from only recreational fishers to a much wider sphere (van der Lingen et al. 2010).

The sardine beach-seine fishery is a tourist spectacle in its own right, but the 200–700 t of sardine caught and sold for direct human consumption and bait (van der Lingen et al. 2010) has a supply/demand inverse effect on prices. When sardine are readily available they are considerably cheaper (c. R80 per 20 kg crate) than when they are scarce (c. R200 per 20 kg crate) and there is also usually a downward trajectory of prices through the season. Using the average price of R160 per crate or R8 per kg enables comparison of the value of the beach-seine catch with that which a purse-seiner would achieve, if allowed to catch 10% of the migrating stock (3 000 t). Approximately R22 per kg is obtained for sardine destined for canning or for use as bait by the linefish sector compared to the R1–3 per kg obtained for sardine destined for fishmeal. These values result in a gross income of R6–33 million for 3 000 t of sardine, although these prices fluctuate widely in response to supply and demand and to fuel price changes. Additionally, there are high overhead costs in the form of a canning or fishmeal factory, fuel and processing costs. Some 3 000 t would therefore only be viable for one or two vessels and the inherent variability and unpredictability of the appearance of sardine on the KZN coast would add considerably to operating costs, because there is no information network available from a fleet of vessels. Another important consideration for a purse-seine fishery is the likely unacceptably high incidental mortality of top predators, particularly dolphins and sharks, associated with sardine schools.

Table 4: Estimates of the value of sardine across different sectors

Sector	Range (million rands)	Mean (million rands)	Comments
Sardine: beach-seining	0.8–6	3.4	Highly erratic availability Fluctuating prices dependent on supply Additional tourist spectacle
Sardine: purse-seining	6–33	20	Considerable land infrastructure (factory) required Unacceptable incidental mortality of predators
Tourism	10–500	255	Total tourism R12 billion per annum; domestic tourism peaks in summer and winter
Predators	Unknown	Unknown	No data on energy reserves or condition as a proxy for enhanced survival rates. Values imbedded in tourism

Summary

The sardine run brings approximately 960 t of organically bound N into KZN waters. If the nitrogen is converted back to the inorganic source, and considering the trophic efficiency of roughly 10% between trophic levels, the equivalent of up to nearly a million tonnes of nitrogen could be transported from the Agulhas Bank into KZN waters, a contribution of between 24% and 76% of the nitrogen budget of the East Coast. Some of this nitrogen is excreted directly back into the environment in the form of urea, but the bulk of the flux is likely to be directly to top predators, with little chance of sardine decaying uneaten on the seabed. This said, an undetermined biomass of sardine, including surviving adults and eggs, larvae and juveniles, as well as most of the accompanying predators, return southwards to cooler waters in the months following the run. Thus, the area is important as a transitionary one between tropical and temperate bioregions during winter, when energy fluxes are facilitated within the foodweb at the forage fish level.

The bulk of the riverine input occurs during the (more productive) summer wet season, whereas the sardine run occurs in the dry winter months. Consequently, nitrogen supply is relatively evenly spread throughout the year. Wastewater discharge is conservatively estimated to provide 3 330 t of nitrogen to KZN waters annually. Apart from a relatively small increase during the holiday seasons, this nitrogen supply is likely to remain fairly constant throughout the year. Groundwater-derived nitrogen along the KZN coastline was estimated at 224–898 t per annum, most of which would be rapidly entrained in nearshore productive processes. Upwelling is an important source of nitrogen to this coast, providing 3 000–390 000 t N from the Richards Bay area, the most consistent site for uplift on the East Coast, driven dynamically by the Agulhas Current flowing past the changing topography. Other oceanic sources such as shelf-edge upwelling and Natal Pulses probably contribute only minor quantities of nitrogen (<300 t) into the euphotic zone.

The two major priorities to address the important sources of variability are investigations into the trophic level of sardine, perhaps using stable isotope analyses, and the quantification of the upwelling in the KZN Bight. This preliminary study indicates that land-based sources of nutrients are of lesser magnitude than those of marine origin, but timing of enrichment may be crucially important for productivity of fish in the KZN coastal region.

The value of sardine for top predators is unknown and difficult to quantify, because there are few survival, condition or productivity measures or indices available for top predators on the East Coast. Large aggregations of top predators are obvious, but the benefits in terms of future generations require more focused studies.

As a tourist attraction, the sardine run could be roughly estimated at about R10–R500 million per annum, expended over the winter period. Tourism therefore generates considerably more than fishing yields, but tourism wealth is often recycled from other parts of South Africa, whereas commercial fishing generates 'new' wealth. Tourism wealth would need to be divided into foreign and local components to specify the benefits for South Africa.

Sardine from beach-seine fishing generate R0.8–6 million at point of sale on the beach, but the netting operations themselves are part of the tourism drawcard. The important point here is that a low-key, modest operation provides a number of transient employment opportunities and partially satisfies the huge demand for fresh and frozen bait from anglers and commercial fishers. Sardine from purse-seine operators could produce R6–33 million, per annum, but there are logistical and biodiversity constraints that would reduce the profitability calculations considerably.

Finally, it is acknowledged that many of the estimates given here are not accurate and some are based on makeshift assumptions but they provide some of the first attempts at assessing ecosystem and economic boundaries, or perspectives, for the sardine run.

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References

Andrews WRH, Hutchings L. 1980. Upwelling in the southern Benguela Current. *Progress in Oceanography* 9: 1–81.

Armstrong, MJ, Chapman P, Dudley SFJ, Hampton I, Malan PE. 1991. Occurrence and population structure of pilchard *Sardinops ocellatus*, round herring *Etremeus whiteheadi* and anchovy *Engraulis capensis* off the east coast of Southern Africa. *South African Journal of Marine Science* 11: 227–249.

Asano T, Burton FL, Leverenz HL, Tsuchihashi R, Tchobanoglous G (eds). 2007. *Water reuse: issues, technologies, and applications* (1st edn). New York: Metcalf and Eddy, Inc., McGraw-Hill.

Beckley L, Connell A. 1996. Early life history of elf *Pomatomus saltatrix* off the east coast of South Africa. *Australian Journal of Marine and Freshwater Research* 47: 319–322.

Begg GW. 1978. Estuaries of Natal. Natal Town and Regional Planning Report No. 41, Pietermaritzburg.

Blaxter JHR, Hunter JR. 1982. The biology of clupeoid fishes. *Advances in Marine Biology* 20: 1–223.

Campbell EE, Bate GC. 1991a. Ground water in the Alexandria dune field and its potential influence on the adjacent surf-zone. *Water SA* 17: 155–160.

Campbell EE, Bate GC. 1991b. The flora of the sandy beaches of southern Africa. IV. The east coast microflora. Report 28. Port Elizabeth: Institute for Coastal Research, University of Port Elizabeth.

Coetzee JC, Merkle D, de Moor CL, Twatwa NM, Barange M, Butterworth DS. 2008. Refined estimates of South African pelagic fish biomass from hydro-acoustic surveys: quantifying the effects of target strength, signal attenuation and receiver saturation. *African Journal of Marine Science* 30: 205–217.

Coetzee JC, Merkle D, Hutchings L, van der Lingen CD, van den Berg M, Durholtz MD. 2010. The 2005 KwaZulu-Natal sardine run survey sheds new light on the ecology of small pelagic fish off the east coast of South Africa. *African Journal of Marine Science* 32: 337–360.

Connell AD. 2010. A 21-year ichthyoplankton collection confirms sardine spawning in KwaZulu-Natal waters. *African Journal of Marine Science* 32: 331–336.

de Moor CL, Butterworth DS, Coetzee JC. 2008. Revised estimates of abundance of South African sardine and anchovy from acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine. *African Journal of Marine Science* 30: 219–232.

de Villiers S, Thiart C. 2007. The nutrient status of South African

rivers: concentrations, trends and fluxes from the 1970's to 2005. *South African Journal of Science* 103: 343–349.
Dicken ML. 2010. Socio-economic aspects of boat-based ecotourism during the sardine run within the Pondoland Marine Protected Area, South Africa. *African Journal of Marine Science* 32: 405–411.
Dudley SFJ, Cliff G. 2010. Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. *African Journal of Marine Science* 32: 383–397.
DWAF (Department of Water Affairs and Forestry). 2004a. Thukela Water Project Decision Support Phase. Reserve Determination Model. Volume 1: Appendices to Thukela Estuarine Flow Requirements. PBV000-00-10307. Directorate of National Water Resource Planning. Pretoria: DWAF.
DWAF (Department of Water Affairs and Forestry). 2004b. Water Quality Management Series Sub-Series No. MS 13.4. Operational policy for the disposal of land-derived water containing waste to the marine environment of South Africa – Appendices. Edition 1. Pretoria: DWAF. Available at http://www.dwaf.gov.za/Dir_WQM/docs/marine/MarineWasteAppendicesOct04.pdf [accessed September 2010].
DWAF (Department of Water Affairs and Forestry). 2007. Determination of the preliminary ecological reserve on a intermediate level for Mdloti Estuary. Final Report submitted to Directorate Resource Directed Measures, 2007. Pretoria: DWAF.
FAO. 1992. Wastewater treatment and use in agriculture. Prepared by MB Pescod. *FAO Irrigation and Drainage Paper* No. 47. Rome: Food and Agriculture Organization of the United Nations.
Fennessy ST, Pradervand P, de Bruyn PA. 2010. Influence of the sardine run on selected nearshore predatory teleosts in KwaZulu-Natal. *African Journal of Marine Science* 32: 375–382.
Hampton I. 1987. Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. *South African Journal of Marine Science* 5: 901–918.
Hampton I. 1992.The role of acoustic surveys in the assessment of pelagic resources on the South African continental shelf. *South African Journal of Marine Science* 12: 1031–1050.
James AG, Probyn T, Hutchings L. 1989. Laboratory-derived carbon and nitrogen budgets for the omnivorous planktivore *Engraulis capensis* Gilchrist. *Journal of Experimental Marine Biology and Ecology* 131: 124–145.
Jezewski WA, Pyke PD, Roberts CPR. 1984. Estuarine and lake freshwater requirements. Technical Report No. TR123. Pretoria: Department of Water Affairs and Forestry.
KwaZulu-Natal Tourism Authority. 2009. Catalogue of KwaZulu-Natal Tourism Authority research reports Available at http://www.zulu.org.za/index.php?investors [accessed at 10 July 2009].
Lamberth SJ, Drapeau L, Branch GM. 2009. The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore line-fishery. *Estuarine, Coastal and Shelf Science* 84: 527–538.
Lutjeharms JRE. 2008. *The Agulhas Current*. New York–Berlin–Heidelberg: Springer.
Lutjeharms JRE, Grundlingh ML, Carter RA. 1989. Topographically induced upwelling in the Natal Bight. *South African Journal of Science* 85: 310–316.
Lutjeharms JRE, Valentine HR, van Ballegooyen R. 2000. The hydrography and water masses of the Natal Bight, South Africa. *Continental Shelf Research* 20: 1907–1939.
Meyer AA, Lutjeharms JRE, de Villiers S. 2002. The nutrient characteristics of the Natal Bight, South Africa. *Journal of Marine Systems* 35: 11–37.
Mketsu QK. 2008. Comparative dietary analysis of sardine and other clupeids from presumed mixed shoals off South Africa's east coast. MSc thesis, University of Cape Town, South Africa.
Myeza J, Mason RB, Peddemors VM. 2010. Socio-economic implications of the KwaZulu-Natal sardine run for local indigenous communities. *African Journal of Marine Science* 32: 399–404.
O'Donoghue SH, Whittington PA, Dyer BM, Peddemors VM. 2010. Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. *African Journal of Marine Science* 32: 361–374.
Pearce AF. 1977. The shelf circulation off the east coast of South Africa. CSIR Research Report No. 361. Stellenbosch: Council for Scientific and Industrial Research.
RSA (Republic of South Africa). 2004. Revision of general authorisations in terms of section 39 of the National Water Act, 1998 (Act no. 36 of 1998) Requirements for the purification of waste water or effluent. *Gazette No. 26187, Government Notice* 399.
Sedlak RI (ed.). 1991. *Phosphorus and nitrogen removal from municipal wastewater. Principles and practice* (2nd edn). New York: Lewis Publishers.
Shannon LJ, Moloney C, Jarre, A, Field JG. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems* 39: 83–116.
van Ballegooyen RC, Taljaard S, van Niekerk L, Lamberth SJ, Theron AK, Weerts SP. 2007. *Freshwater flow dependency in South African marine ecosystems: a proposed assessment framework and initial assessment of South African marine ecosystems*. WRC Report No. KV 191/07. Pretoria: Water Research Commission.
van der Lingen CD. 1999. The feeding ecology of, and carbon and nitrogen budgets for, sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. PhD thesis, University of Cape Town, South Africa.
van der Lingen CD. 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African Journal of Marine Science* 24: 301–316.
van der Lingen CD, Coetzee JC, Hutchings L. 2010. Overview of the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 271–277.
van der Lingen CD, Hutchings L, Field JG. 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* 28: 465–477.
Watermeyer KE, Shannon LJ, Griffiths CL. 2008. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science* 30: 351–382.
WRC (Water Research Centre). 1990. Design guide for marine treatment schemes. Volume I: Introduction and Volume II: Environmental design and data collection. Report No. UM 1009. Swindon: Water Research Centre.