

REVIEW

Nitrogen budget for a high-energy ecosystem

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ABSTRACT: A nitrogen budget is compiled for an exposed beach and surf zone ecosystem in South Africa. Phytoplankton (particularly diatoms) are the major users of nitrogen in this system as macrophytes are absent. Inputs of nitrogen occur via groundwater inflow and from an estuary with rain and airborne detritus being of minor importance. Loss of nitrogen to the sediment as a result of beach accretion or to the atmosphere by denitrification is considered negligible because of sediment reworking and the highly oxidised state of this high-energy surf zone. Nitrogen budgets for the major zooplankton, benthos and fish components are presented and the amounts of nitrogen recycled by the total macrofauna ($5735 \text{ g N m}^{-1} \text{ yr}^{-1}$), interstitial fauna ($5200 \text{ g N m}^{-1} \text{ yr}^{-1}$) and microbial loop ($4607 \text{ g N m}^{-1} \text{ yr}^{-1}$) trophic assemblages are estimated for a 1 m wide transect across the system (500 m long). The budget indicates that: (1) inorganic nitrogen inputs (groundwater, rain, estuarine) into the surf zone supply 13% of phytoplankton requirements for primary production; (2) the 3 trophic assemblages together recycle 99% of the nitrogen required for total phytoplankton primary production, all 3 being important in this, and (3) the dissolved and particulate organic nitrogen recycled by the macrofauna can supply 24% of the nitrogen requirements estimated for the microbial loop. The observation that fauna regenerate almost all the nitrogen required for phytoplankton primary production supports the concept of the surf zone as a self-sustaining, semi-closed ecosystem.

INTRODUCTION

Nitrogen is the nutrient most often limiting for biological production in both phytoplankton- and macrophyte-dominated coastal ecosystems (Ryther & Dunstan 1971, Smayda 1974, Goldman 1976, Teal & Valiela 1978). Nitrogen may be available in either new or regenerated forms, new production thus resulting from utilization of allochthonous inputs of nitrogen (e.g. nitrate from upwelling) and regenerated production resulting from the utilization of nitrogen regenerated *in situ* (usually ammonium and urea) (Dugdale & Goering 1967).

The importance of regenerated nitrogen for primary production has been highlighted for many marine systems (Dugdale 1976, Harrison 1980, Nixon 1981, Fogg 1982, Chapman 1986, Lucas 1986). A nutrient

budget provides a quantitative framework which tests our understanding of the system and provides a broad perspective from which a more objective assessment of the importance of various processes can be derived (Nixon 1981). Despite the great power of the nutrient budget as a tool in ecosystem analysis and management, there are few coastal marine systems for which complete nutrient budgets have been published. Exceptions include a salt marsh ecosystem (Teal & Valiela 1978), the Gulf of Maine/Georges Bank area (Schiltz & Cohen 1984), the New York Bight (Walsh et al. 1978) and Carmarthen Bay (Mantoura et al. 1988).

We use nitrogen as the currency for a budget compiled here in the form of a review of a high-energy ecosystem. Over the past decade a multidisciplinary team has investigated the physical and biological functioning of a high-energy beach/surf zone ecosystem on the southeast coast of Africa (McLachlan 1980, 1983, McLachlan et al. 1981a, b, McLachlan & Bate 1984, Bate et al. 1990, Du Preez et al. 1990, McLachlan & Romer

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1990, Talbot et al. 1990). Studies on nitrogen cycling in these beaches and beaches elsewhere have centered around benthic meiofauna (McLachlan 1982, Pugh 1983, McLachlan & McGwynne 1986) and macrofauna (Lewin et al. 1979, Prosch & McLachlan 1984, Cockcroft & McLachlan 1987, 1990, Cockcroft et al. 1988, Du Preez & Cockcroft 1988a, b, 1990, Cockcroft & Du Preez 1989, 1990, Cockcroft 1990, 1991). This paper aims to synthesize all data available into a nitrogen budget and to compare key features of this system with other coastal marine systems in terms of nitrogen inputs, outputs and recycling.

STUDY AREA

The study area is an exposed 40 km beach/surf zone at Sundays River on the northern shores of Algoa Bay (25° 40' E, 34° 00' S), South Africa (Fig. 1a). This beach is backed by extensive dunes and is typical of Eastern Cape beaches in terms of sand particle size, wave action and faunal biomass (McLachlan & Bate 1984). Tides are semi-diurnal subequal with a maximum spring tide range of 2.1 m (Beckley 1977, McLachlan et al. 1979). Water temperatures range from 11 to 25 °C (Beckley & McLachlan 1979), the lowest values occurring during small localised upwellings after easterly winds in summer (Schumann et al. 1982).

The surf zone is of the high-energy intermediate type and varies between a modal low-energy state (or transverse bar-rip configuration of Short & Wright 1983) and a modal high-energy state (longshore bar-trough state of Short & Wright 1983) with the latter predominant (70% of the time). This longshore bar-trough

configuration is characterised by an inner terrace, a deep trough and an outer bar with surf-zone width 250 m and breakers 2 to 3 m in height. During calm conditions the outer bar fuses with the beach, forming the transverse bar-rip configuration characterised by well-defined rip channels and a surf zone 150 to 250 m wide (Fig. 1b). The surf zone can become dissipative during storms or strong southwesterly winds. Rip currents are the main mechanism for the return flow of surf-zone water to the nearshore in all beach/surf zone configurations and discharge outside the breakers (Talbot & Bate 1987). The surf and rip head zones together form the ecosystem under discussion and extend 500 m offshore (McLachlan et al. 1981a). Replacement time of the inner surf-zone water is estimated at approximately 1 to 10 h while the half-turnover time for the complete surf and riphead zone may be several days (Talbot & Bate 1987).

There are no attached macrophytes in this system. The inner surf zone is characterised by accumulations of the diatom *Anaulus australis*, with *Aulocodiscus kittoni* and *Asterionella* spp. of lesser importance (Talbot et al. 1990). During the day these diatoms accumulate in the surface foam associated with rip currents (Sloff et al. 1984), resulting in distinct brown discolorations in the surf. The accumulation of *A. australis* cells is not a 'blooming' phenomenon but a direct consequence of accumulation and concentration by surf-zone circulation patterns (Talbot & Bate 1987). In the afternoon the *A. australis* cells sink and are carried to behind the breaker line by rip currents, where they accumulate near the bottom or in the sediments (Talbot 1986). The formation of a mucus sheath (to which clay particles adhere) in the afternoon aids sinking and entry into the sediments (Talbot 1986). The cells shed this mucus sheath, rise to the surface in the morning and are transported into the inner surf zone by wave action. During storms large volumes of sediments are reworked, releasing increased numbers of diatoms into the water column with richest accumulations occurring during and just after storm events. Surf-zone diatom accumulations are therefore a function of the diel vertical and horizontal migrations coupled to the storm/calm cycle.

Phytoplankton production fuels 3 distinct trophic assemblages in the surf zone: the interstitial faunal system, the macroscopic food chain, and the water column microbial loop. Of the total phytoplankton production 11% has been estimated to enter the macroscopic food chain, 18% the interstitial system and 53% the microbial loop (McLachlan & Romer 1990; Fig. 2).

Because the surf-zone environment is very dynamic, expanding and contracting rapidly in response to storm and calm conditions, the use of 1 m² as the

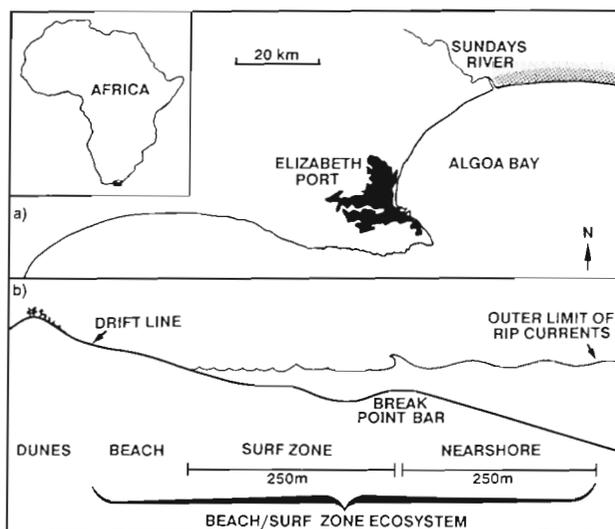


Fig. 1 (a) Study area. (b) Modal energy state for the Sundays River beach/surf zone ecosystem

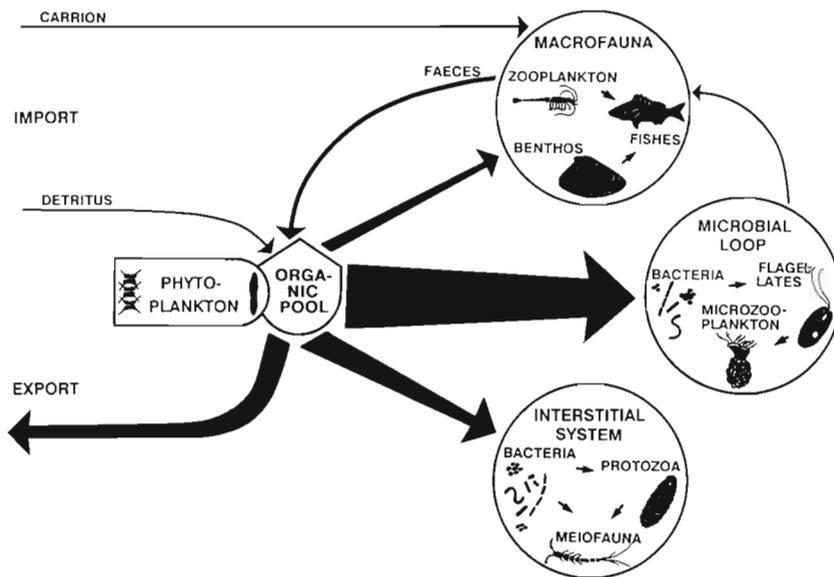


Fig. 2. The 3 trophic assemblages fueled by phytoplankton production in the Sundays River beach/surf zone ecosystem. Arrows indicate carbon flow

standard unit of area is not feasible. A 1 m strip through the whole system will always encompass all fauna regardless how the latter may concentrate or scatter during different conditions (McLachlan & Bate 1984). The inner boundary at the drift line represents a marked transition from intertidal to terrestrial conditions while the outer boundary is taken as the average position of the outer limit of surf circulation cells. The outer boundary, at an average distance of 500 m from the drift line (water depth ca 10 m), is usually visible as the outer limit of rip current plumes. The unit area in this study therefore consists of a 1 m wide strip from the drift line out to 10 m depth, a distance of 500 m, i.e. 500 m² with an overlying water volume of 2500 m³. The unit area used is similar to that used in the reviews by McLachlan & Bate (1984), McLachlan & Romer (1990) and Du Preez et al. (1990). This area exhibits weak seasonality and we summarise fluxes on an annual basis.

NITROGEN BUDGET

Requirements

The nitrogen requirements of the inner surf zone were calculated directly from the estimates of phytoplankton primary production. Primary production in the inner surf zone was measured using ¹⁴C (light and dark bottle) uptake and O₂ evolution (Campbell 1987). A mathematical model (Campbell 1987) which incorporated temperature, light, beach state and photoinhibition was used to

estimate the annual primary production of the surf zone at 1.2×10^5 g C m⁻¹ yr⁻¹ (Campbell 1987). The nitrogen requirements of the inner surf zone were obtained by calculating the portion of assimilated carbon involved in cell doubling and dividing by the C:N ratio (6.8 for *Anaulus australis*; Campbell 1987). *A. australis* (standing stock 14 mg chlorophyll m⁻³) doubles once a day and by using a carbon:chlorophyll ratio of 27 (Campbell 1987) the amount of carbon required for doubling could be calculated for a 1 m strip of surf zone. Using this method the nitrogen requirements of the surf zone are 10.1×10^3 g N m⁻¹ yr⁻¹.

Applying the same primary production model, Campbell (1987) obtained a primary production estimate of 1.1×10^5 g C m⁻¹ yr⁻¹ for

the riphead zone. The phytoplankton species composition of the riphead zone immediately outside the surf zone (Fig. 1b) differs markedly from that of the inner surf zone, with *Anaulus australis* virtually absent. The species composition in this outer zone varies widely under different physical conditions, important species including *Chaetoceros* spp. and *Navicula* spp. (Talbot 1986). Doubling rates of 0.5 to 1 d⁻¹ have been recorded for other marine diatoms (Smayda 1980) and the lower value is considered to be applicable to the outer surf zone (M. M. B. Talbot pers. comm.). Using a standing stock of 2.3 mg chlorophyll m⁻³ (Talbot 1986) and carbon to chlorophyll and C:N ratios as above, the phytoplankton nitrogen requirements for the outer surf zone are estimated at 3.1×10^3 g N m⁻¹ yr⁻¹.

The total phytoplankton nitrogen requirement for the surf and riphead zone (i.e. the beach/surf zone ecosystem) is therefore considered to average approximately 13.2×10^3 g N m⁻¹ yr⁻¹. This amount must be available annually to sustain primary production.

Inputs

The distinction between new and regenerated nitrogen (Eppley & Peterson 1979) can no longer be upheld when the sediment and water harbouring growing phytoplankton are in direct contact (Paasche 1988). Nitrogen not regenerated locally (Nixon 1981, Nixon & Pilson 1983) represents new nitrogen in these nearshore environments (Paasche 1988), and its sources are listed here as nitrogen inputs.

Groundwater. The amount of nitrogen entering the Sundays River surf zone via groundwater seepage through the dunefield system has been estimated by McLachlan & Illenberger (1986). Groundwater has an approximate mean flow of $1000 \text{ l m}^{-1} \text{ d}^{-1}$ with an average inorganic nitrogen content of 2.13 mg l^{-1} . Groundwater therefore supplies an annual input of 777 g N m^{-1} to the surf zone, mainly in the form of nitrate.

Estuarine input. Using the data currently available on nutrient levels and water flux in the Sundays River estuary an estimate of the annual flux of nitrogen out of this estuary was calculated as: (net difference in nitrogen content of ebb and flood tide waters) \times (total volume of average tidal prism) \times (number of tidal exchanges per annum). This gave a net export of 33 t N per annum, the bulk of which is in dissolved inorganic form (D. A. Lord pers. comm.). The input of this nitrogen into the surf-zone system was calculated by assuming that 80% of the net annual export is trapped in the surf cell-circulation patterns and by dividing this value by the length of the Sundays River surf zone (40 km), resulting in an input of $600 \text{ g N m}^{-1} \text{ yr}^{-1}$ over the entire stretch of beach.

Rain. The Sundays River area receives an annual rainfall of 400 to 800 mm. An average rainfall of 600 mm per annum multiplied by the area of a 1 m strip of surf zone gives a rainfall input of $3 \times 10^5 \text{ l m}^{-1} \text{ yr}^{-1}$. Using a mean value for the nitrogen content of rainwater ($1 \mu\text{g ml}^{-1}$; M. Wells pers. comm.) an input of $300 \text{ g N m}^{-1} \text{ yr}^{-1}$ was calculated for this source.

Airborne detritus. The input of particulate organic nitrogen entering the Sundays River surf zone (including plant material and insects) from the adjacent dunefield and dune slacks is considered negligible as the area is mostly unvegetated and predominant winds are onshore.

Other inputs. Other possible sources of nitrogen to the Sundays River surf zone are nitrogen fixation, guano from St. Croix island and sewage input into

Algoa Bay. Capone (1988) found nitrogen fixation to be a minor component of the nitrogen cycle in unvegetated sediments. Inputs of nitrogen from St. Croix island and sewage outfalls in Algoa Bay (10 and 20 km from the study site respectively) are considered insignificant due to the dilution effect.

Losses

Losses of nitrogen to the sediment as a result of beach accretion or to the atmosphere by denitrification are negligible because of sediment reworking and the highly oxidised state of this high-energy surf zone (Malan & McLachlan 1985, McLachlan & Romer 1990).

Recycling

Nitrogen recycling by the 3 trophic assemblages is examined in this section. Population nitrogen budgets for the major macrofaunal components (zooplankton, benthos and fish) are presented using the formula (modified from Ricker 1968): $C = P + M + F$ where C = consumption; P = production; F = faeces; and M = nitrogen loss via excretion or leakage. This differs only slightly from the formula proposed by Dagg (1976) who separated the nitrogen loss into metabolically useless material lost by excretion and metabolically useful material lost by leakage from the body. No attempt was made to separate excretion and leakage in this study. Production was calculated by difference in all cases.

Macrofauna

Zooplankton. The values used in the population nitrogen budgets for the major zooplankton components

Table 1. Summary of budget parameters and data sources used in the compilation of nitrogen budgets for the major zooplankton components of the Sundays River surf zone. All values except biomass in $\text{g N m}^{-1} \text{ yr}^{-1}$. TDN: total dissolved nitrogen

Species or group	Biomass (g N m^{-1})	Consumption	Assimilation	Faeces	Excretion TDN	Production by difference
<i>Macropetasma africanus</i>	70 ^a	2555 ^b	85% ^c	383	1832 ^h	340
<i>Mesopodopsis slabberi</i>	44 ^d	1853 ^d	70% ^e	555	1007 ⁱ	290
<i>Gastrosaccus psammodytes</i>	6 ^d	270 ^d	70% ^e	81	141 ⁱ	48
Other benthopelagic forms	0.5 ^f	20 ^f	70% ^e	6	12 ⁱ	2
Other pelagic forms	2 ^g	170 ^f	70% ^e	51	97 ^j	22

^a Cockcroft (1982); ^b Cockcroft & McLachlan (1986); ^c Forster & Gabbot (1971), Wickens (1976); ^d Webb (1986); ^e Ikeda & Matoda (1978); ^f McLachlan & Bate (1984); ^g Romer (1986); ^h Cockcroft & McLachlan (1987); ⁱ Cockcroft et al. (1988); ^j Ikeda et al. (1982)

of the Sundays River surf zone are summarised in Table 1. The component 'Other benthic-pelagic forms' includes the isopods *Eurydice longicornis*, *Pontogeloides latipes* and *Excirrolana natalensis* and 3 amphipod species. The species comprising 'Other pelagic forms' are listed in Romer (1986) together with mean abundance and mean individual biomass values. Consumption values for *Macropetasma africanus*, *Mesopodopsis slabberi* and *Gastrosaccus psammodytes* were obtained from measured consumption rates using a C:N ratio of 6.8 for phytoplankton *Anaulus australis* (Campbell 1987) and a body nitrogen content of 10% for zooplankton (Corner & Davies 1971). Consumption values for the other 2 components were derived from McLachlan & Bate (1984) using similar C:N ratios. Assimilation efficiencies for all components were derived from literature estimates. The amounts of nitrogen lost via excretion in the 3 major zooplankton species were obtained from measured excretion rates. The excretion value for the group 'Other benthic-pelagic forms' was calculated using the same excretion rate as measured for the benthic-pelagic mysid *G. psammodytes* (Cockcroft et al. 1988). The amount of nitrogen lost via excretion in 'Other pelagic forms' was obtained from the abundance and mean individual dry mass values of Romer (1986), using 3 regression equations which describe the effect of body mass on ammonia excretion rates of small zooplankton forms. The regression equations used were those of Mullin et al. (1975), Ikeda & Motoda (1978) and Ikeda et al. (1982).

Ammonia was the major form of nitrogen excreted by the zooplankton component, constituting a mean of 85% of the total dissolved nitrogen (TDN) excreted. Nitrate formed <1% and amino acids 14% of TDN excreted by zooplankton (Cockcroft & McLachlan 1987, Cockcroft et al. 1988).

Benthos. The values used in the population nitrogen budgets for the major benthic components of the Sundays River surf zone are summarised in Table 2. The component 'Other filter feeders' includes the bivalves *Macoma crawfordi*, *Phaxas decipiens*, *Mel-*

literyx capensis and *Macra glabrata*. The species comprising the group 'Others' are listed in McLachlan et al. (1984). Consumption values for *Ovalipes punctatus* and *Donax* spp. were obtained from measured consumption rates while those of the other groups were derived from McLachlan & Bate (1984). Assimilation efficiencies for all components (except *O. punctatus*) were derived from literature estimates. The excretion rates used in the calculation of nitrogen loss in *Donax* spp. (Cockcroft 1990) and *Bullia* spp. (Cockcroft & McLachlan 1990) were used in the determination of nitrogen loss in 'Other filter feeders' and 'Others' respectively. The nitrogen lost via excretion by *Donax* spp. was calculated taking into account times of inundation and exposure (Cockcroft 1990). Ammonia and amino acids constituted 75 and 25% of TDN excreted by the benthos respectively (Cockcroft 1990, Cockcroft & McLachlan 1990).

Fishes. The values used in the proposed population nitrogen budgets for the major fish feeding groups are summarised in Table 3. All biomass estimates were calculated from McLachlan & Bate (1984) using a body nitrogen content of 11% (Du Preez 1987). The consumption estimates were derived from Du Preez et al. (1990) using a C:N ratio of 6.8 for phytoplankton and mean nitrogen contents of 9.6 and 11% for *Donax serra* and zooplankton as food respectively. The assimilation efficiency used for *Liza richardsonii* was the only one not determined directly and was obtained using the equation proposed by Pandian & Marian (1985). The nitrogen lost via excretion was calculated from measured excretion rates in all cases. Ammonia constituted a mean of 80% of TDN excreted with amino acids and urea contributing 16 and 4% respectively.

Summary of macrofauna nitrogen budget. The total amount of nitrogen recycled (Table 4) by the macrofauna (5.735×10^3 g N m⁻¹ yr⁻¹) consists of dissolved inorganic nitrogen (58%), dissolved organic nitrogen (11%) and particulate organic nitrogen (31%). Ammonia constituted >95% of the dissolved inorganic

Table 2. Summary of budget parameters and data sources used in the compilation of nitrogen budgets for the major benthic faunal components of the Sundays River surf zone. All values except biomass in g N m⁻¹ yr⁻¹. TDN: total dissolved nitrogen

Species or group	Biomass (g N m ⁻¹)	Consumption	Assimilation	Faeces	Excretion TDN	Production by difference
<i>Donax</i> spp.	144 ^a	735 ^b	60% ^c	294	307 ^b	134
Other filter feeders	8 ^d	86 ^d	60% ^c	34	32 ⁱ	20
<i>Bullia</i> spp.	3 ^d	30 ^d	65% ^e	10	15 ^j	5
<i>Ovalipes punctatus</i>	1 ^c	50 ^g	70% ^f	4	33 ^g	2
Others	24 ^d	241 ^d	65% ^e	84	98 ^j	71

^aDonn (1987); ^bT. E. Donn pers. comm; ^cJordan & Valiela (1982); ^dHeubner & Edwards (1981); ^eMcLachlan & Bate (1984); ^fDu Preez & McLachlan (1983); ^gDu Preez (1983); ^hCockcroft (1990); ⁱCockcroft (1987); ^jCockcroft & McLachlan (1990)

Table 3. Summary of budget parameters and data sources used in the compilation of nitrogen budgets for the major ichthyofauna feeding groups of the Sundays River surf zone. All values except biomass in $\text{g N m}^{-1} \text{yr}^{-1}$. TDN: total dissolved nitrogen

Species or group	Biomass (g N m^{-1})	Consumption	Assimilation	Faeces	Excretion TDN	Production by difference
Benthic feeders	17 ^a	320 ^b	70% ^{c,e,f}	96	159 ^{c,e,f}	65
Zooplankton feeders	13 ^a	304 ^b	70% ^f	91	134 ^t	79
Omnivores	3 ^d	40 ^b	70% ^{c,d,e,f}	12	21 ^{c,d,e,f}	7
Piscivores	3 ^a	44 ^b	64% ^d	16	19 ^d	9
<i>Liza richardsonii</i>	6 ^a	105 ^b	60% ^g	42	44 ^e	19
<i>Rhinobatus annulatus</i>	6 ^a	55 ^b	70% ^h	17	8 ^h	30

^aMcLachlan & Bate (1984), Du Preez (1987); ^bDu Preez (1987); ^cDu Preez & Cockcroft (1988a); ^dDu Preez & Cockcroft (1988b); ^eCockcroft & Du Preez (1989); ^fCockcroft & Du Preez (1990); ^gPandian & Marian (1985); ^hDu Preez & Cockcroft (1990)

nitrogen recycled by the macrofauna with amino acids (96%) and urea (4%) the major components of the dissolved organic nitrogen recycled.

Zooplankton are calculated to recycle 79% of the dissolved inorganic nitrogen, 72% of the dissolved organic nitrogen and 60% of the particulate organic nitrogen excreted by surf-zone macrofauna, with crustaceans (mainly large motile forms) supplying the bulk of the recycled nitrogen (Cockcroft 1991). Zooplankton is thus the most important of the macrofaunal components in the recycling of nitrogen in the surf zone.

Benthos recycle 11% of the dissolved inorganic nitrogen fraction, 19% of the dissolved organic nitrogen fraction and 24% of the particulate organic component. The importance of the benthic macrofauna in nitrogen cycling is indicated not only by the amount recycled but also by the fact that benthic populations are less subject to physical disturbance than the other components, and do not migrate outside the surf zone.

Fishes recycle 10% of dissolved inorganic nitrogen, 8% of the dissolved organic nitrogen and 16% of the particulate organic nitrogen. This component is considered the least important in surf zone nitrogen recycling due to their opportunistic utilization of the surf zone and frequent migrations in and out of this zone.

Table 4. Summary of the amount of nitrogen recycled by the major macrofaunal components of the Sundays River surf zone as excretion and faeces. All units in $\text{g N m}^{-1} \text{yr}^{-1}$

Component	Dissolved inorganic	Dissolved organic	Particulate organic (faeces)	Total
Zooplankton	2626	463	1076	4165
Benthos	364	121	426	911
Fish	323	62	274	659
Total	3313	646	1776	5735

Interstitial fauna

The interstitial system is fueled by organic materials flushed into the sand by wave action. Mucus sloughed off by diatoms buried in the sand may also be an important source of organics. This system is quite distinct from the macrofauna by virtue of its entirely interstitial nature and deep vertical penetration into the sediment (McLachlan 1977). Unlike other sediments, beach and surf-zone sand is not a sink for carbon or other materials and is continually being turned over (McLachlan & McGwynne 1986).

Intertidal interstitial fauna. The amount of nitrogen recycled by the intertidal interstitial fauna was derived from the model proposed by McLachlan (1982) which estimated water filtration and nutrient regeneration by exposed sandy beaches. This model predicts the volume of water filtered daily by a beach as a function of tidal range, beach slope and sand particle size and gives a mean volume of ca $10^4 \text{ l m}^{-1} \text{d}^{-1}$ filtered in the Sundays River intertidal area. Using an equation relating the degree of mineralisation of organic matter in the filtered seawater to the distance filtered through the sand and the sand particle size, enables the calculation of the amount of inorganic nitrogen regeneration. Using this model the intertidal interstitial fauna of the Sundays River surf zone has been estimated to recycle $590 \text{ g N m}^{-1} \text{yr}^{-1}$ (McLachlan 1982).

Subtidal interstitial fauna. Surf-zone sediments out to 500 m filter nearly 10 times as much water as the intertidal sediments. Wave 'pumping' is the driving force. The flux of nitrogen from the sediment has been shown to be important in the nitrogen budgets of overlying waters in the North Sea (Billen 1978), the New York Bight (USA) (Rowe et al. 1975) and in Narragansett Bay (Rhode Island, USA) (Nixon et al. 1975). Flux measurements may be made on cores (Blackburn &

Henriksen 1983) or by chambers placed on the sediment surface which measure whole community activity (Smith et al. 1972, Hartwig 1976, Klump & Martens 1983). The oxygen consumption and nutrient fluxes of surf-zone sediments in the Sundays River surf zone were investigated using benthic incubation chambers with flexible membrane tops (Malan 1991, Malan & McLachlan 1991). This allowed the transference of wave energy into the sediment and closely simulated natural conditions. The amount of nitrogen released from subtidal sediments of the Sundays River surf zone using this method was measured at $4660 \text{ g N m}^{-1} \text{ yr}^{-1}$, the bulk (83%) in the form of ammonia, with nitrate (17%) constituting the remainder (Malan 1991).

Microbial loop

Nitrogen recycled by the microbial loop was calculated both directly from a published carbon budget (McLachlan & Romer 1990) using literature C:N ratios and from a Lotka-Volterra predator-prey model (McGwynne 1991) applied to data generated in a laboratory microcosm and extrapolated to field data. The biomass, consumption and production estimates in Table 5 are based on the carbon budget of McLachlan & Romer (1990) using a C:N ratio of 4 for bacteria and flagellates and 5 for microzooplankton (Newell & Linley 1984, Fenchel 1988). The nitrogen regenerated was calculated by difference (consumption minus production).

Despite high quantities of detritus, the surf zone bacterial populations are dominated by freely suspended forms and bacterial production appears to be coupled to phytoplankton exudates. Extracellular release of soluble organics by *Anaulus australis* could provide 50% of total bacterial carbon requirements in the ecosystem (McLachlan & Romer 1990, McGwynne 1991). The C:N ratio of *A. australis* exudate (mainly in the form of a mucous envelope (Campbell 1987) is high (C:N ratio = 20; D. R. Du Preez pers. comm.). Using the carbon consumption

estimate of McLachlan & Romer (1990) and a C:N ratio of 15 (mean C:N ratio for exudates and phytoplankton cell contents and detritus) for bacterial substrate results in a net regeneration of $502 \text{ g N m}^{-1} \text{ yr}^{-1}$ via bacteria. The amounts of nitrogen regenerated by the flagellate and microzooplankton components are calculated at 3034 and $423 \text{ g N m}^{-1} \text{ yr}^{-1}$ respectively. Using this method the microbial loop is estimated to recycle $3959 \text{ g N m}^{-1} \text{ yr}^{-1}$.

The application of the Lotka-Volterra predator-prey model (McGwynne 1991) closely followed the modified version of Lucas et al. (1987) and allowed the estimation of the predation rate and assimilation efficiency of flagellate grazing and the quantification of nitrogen regeneration due to predation. Using a value of 4 for the C:N ratios of bacteria and flagellates, the calculated values for nitrogen regenerated (per unit flagellate biomass) by flagellate predation on bacteria ranged from 0.8 to 1.0 (McGwynne 1991). Using a mean value of 0.9 and the flagellate biomass estimate of McLachlan & Romer (1990) gives an estimate of $5256 \text{ g N m}^{-1} \text{ yr}^{-1}$ being regenerated by this component.

Lucas (1986), in his review on decomposition in pelagic marine ecosystems, highlighted the problems of using models which couple carbon and nitrogen fluxes directly (as done by Newell & Linley 1984 and the present study). This approach is sensitive to the estimates of production and net growth yield (in carbon terms) as well as to the C:N ratio of the substrate. The validity of extrapolating predator-prey model results from microcosm data to field conditions is also a potential source of error. The value of $4607 \text{ g N m}^{-1} \text{ yr}^{-1}$ used in this budget represents the mean of the 2 approaches.

Budget summary

The nitrogen budget is summarised in Table 6 and Fig. 3. Several points emerge: (1) Total available nitrogen (DIN, DON and PON), i.e. inputs plus that recycled in the surf zone ($17.222 \times 10^3 \text{ g N m}^{-1} \text{ yr}^{-1}$),

Table 5. Estimated nitrogen consumption and regeneration by the micro-heterotrophic plankton community of the Sundays River surf zone. Values of nitrogen consumption and production are derived from carbon budgets proposed by McLachlan & Romer (1990) and C:N ratios described in the text

Trophic category	Biomass (g N m^{-1})	Consumption ($\text{g N m}^{-1} \text{ yr}^{-1}$)	Production ($\text{g N m}^{-1} \text{ yr}^{-1}$)	Losses ($\text{g N m}^{-1} \text{ yr}^{-1}$)
Bacteria	16.2	8043	7541	502
Heterotrophic flagellates	3.2	5110	2076	3034
Microzooplankton	3.6	630	364	423
Total		13783	9981	3959

Table 6. Nitrogen budget for the Sundays River surf zone. All values in $g\ N\ m^{-1}\ yr^{-1}$. DIN: dissolved inorganic nitrogen; DON: dissolved organic nitrogen; PON: particulate organic nitrogen

	DIN	Total DIN	DON + PON
Phytoplankton requirements			
Inner surf zone	10 100		
Outer surf zone	3 100		
Total requirements		13 200	
Inputs			
Groundwater	780		
Rain	300		
Estuarine	600		
Total inputs		1 680	
Recycled			
Interstitial fauna (intertidal)	590		
Interstitial fauna (subtidal)	4 610		
Macrobenthos	364		547
Zooplankton	2 626		1 539
Fishes	323		336
Microbial loop	4 607		
Total recycled		13 120	2 422
Net excess			
[(total inputs + recycled) - requirements]		1 600	

exceeds phytoplankton primary production requirements by $4.022 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$. However, this includes excreted particulate and dissolved organic nitrogen ($2.422 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$) not available to phytoplankton. Total inorganic nitrogen available in the surf zone (inputs plus recycled) exceeds

phytoplankton requirements by $1.60 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$. (2) Total inorganic nitrogen inputs (groundwater, rain, estuarine) into the surf zone ($1.68 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$) supply 13% of phytoplankton primary production requirements. (3) Of the total organic and inorganic nitrogen recycled by the fauna in the surf zone ($15.542 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$), 33% is supplied by interstitial fauna (sub- and intertidal) with 37 and 30% supplied by the macroscopic trophic assemblage and microbial loop respectively. (4) The faunal components of the 3 trophic assemblages (macroscopic, interstitial and microbial) together recycle 99% of the nitrogen required for total phytoplankton primary production, assuming that phytoplankton utilize only the dissolved inorganic fraction. The interstitial fauna recycle 40% of the total nitrogen required for phytoplankton primary production with the macrofauna and microbial loop components recycling 25 and 35% respectively.

(5) The dissolved and particulate organic nitrogen recycled by the macrofauna ($2.422 \times 10^3\ g\ N\ m^{-1}\ yr^{-1}$) is sufficient to supply 24% of the total nitrogen requirements estimated for the microbial loop (McGwynne 1991, G. S. Romer pers. comm.).

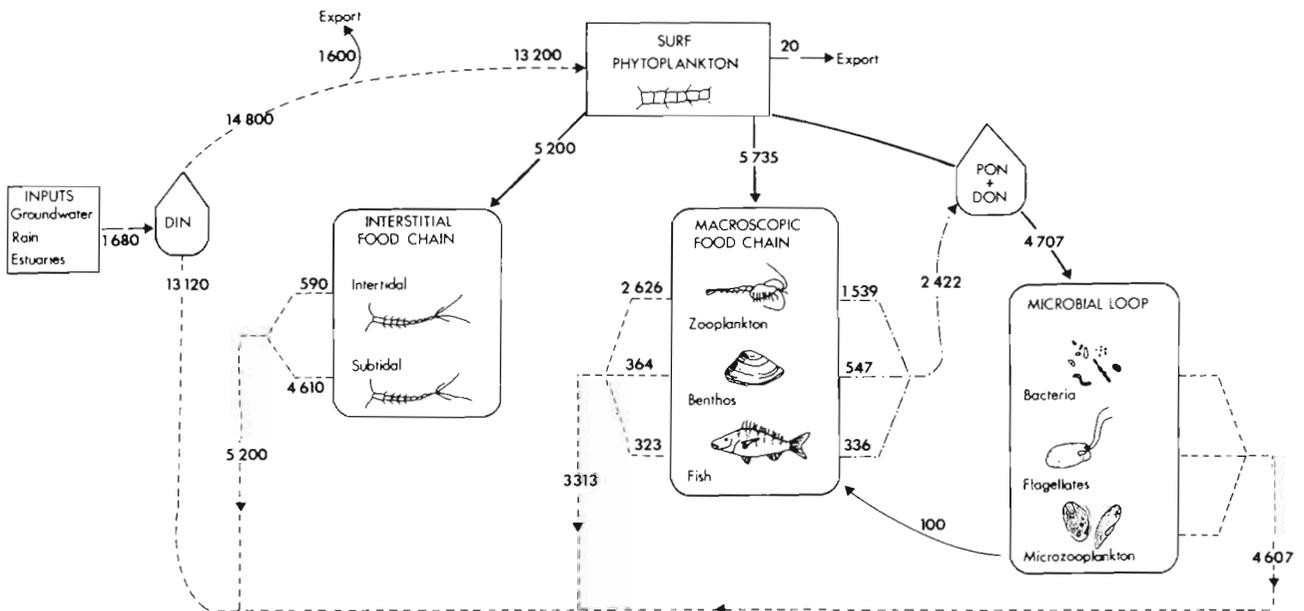


Fig. 3. Nitrogen budget and recycling in the Sundays River beach/surf zone ecosystem. Solid lines indicate grazing, broken lines recycling or nutrient flux. All values in $g\ N\ m^{-1}\ yr^{-1}$

DISCUSSION

The relative importance of regenerated versus new nitrogen for surf-zone phytoplankton production is clearly illustrated in our budget. Inputs of new nitrogen could provide 13% of total phytoplankton nitrogen requirements, with regenerated nitrogen sufficient for 99% of annual phytoplankton production. The small excess of DIN (12% of annual requirements) is considered well within the expected error of this study, but may also indicate a surplus available for export. The degree of phytoplankton dependence on new or regenerated nitrogen depends on the availability of a particular nitrogen substrate, the degree to which phytoplankton may discriminate between various forms of nitrogen available and on the physiological or nutritional status of the cells (Glibert 1988). The availability of reduced nitrogen (mainly in the form of ammonium), the rapid uptake of ammonium by marine phytoplankton (Glibert & Goldman 1981, Goldman & Glibert 1982, Glibert & McCarthy 1984) and the fact that ammonium concentrations greater than about 1 μM (a concentration often exceeded in surf-zone water; Cockcroft 1987) have been found to inhibit nitrate uptake at certain inshore localities (McCarthy et al. 1977, Garside 1981), suggests that surf zone phytoplankton production is fueled largely by regenerated NH_4^+ . The presence of nitrate reductase activity in field collected *Anaulus australis* (D. R. Du Preez pers. comm.) indicates that the diatom has the ability to use new nitrogen when available. Since urea constituted a minor fraction of both new and recycled nitrogen in this study, it is not considered significant for surf-zone phytoplankton production. Urea has, however, been shown to be an important nutrient source for coastal phytoplankton in some semi-enclosed coastal areas (McCarthy et al. 1977, Kristiansen 1983).

The role of all 3 trophic assemblages in surf-zone nitrogen recycling is highlighted in this study with macrofauna, interstitial fauna and the microbial loop regenerating 25, 40 and 35% of phytoplankton requirements respectively. Walsh et al. (1978), in their annual nitrogen budget for the Atlantic continental shelf, found that approximately 46% of primary production was supported by nutrient recycling: zooplankton were responsible for 38% of the regenerated nitrogen, benthos 38% and bacteria 24%. Harrison et al. (1983) found 50 to 80% of the nitrogen productivity (as the sum of NH_4^+ and NO_3^- uptake) was attributable to NH_4^+ regeneration in the Middle Atlantic Bight during summer: macrozooplankton excretion contributed 30%, bacterial and microzooplankton regeneration 63% and benthic flux 7% of this regenerated nitrogen. In Narragansett Bay (a phytoplankton-dominated

system), zooplankton excreted 40% and the benthic community (macrofauna and microbes) 50% of the nitrogen required by the phytoplankton (Kremer & Nixon 1978, cited in Field 1983).

Zooplankton (mainly large motile forms) are the most important macrofaunal component in surf zone nitrogen regeneration with benthic macrofauna and fishes of lesser importance in our study. The importance of nitrogen excreted by zooplankton (see review by Bidigare 1983), benthos (Lewin et al. 1979, Kautsky & Wallentinus 1980) and fishes (Whitledge & Packard 1971, McCarthy & Whitledge 1972, Durbin & Durbin 1981) for phytoplankton requirements has been highlighted for various marine systems. The observation that beach and surf-zone interstitial fauna regenerates 40% of phytoplankton nitrogen requirements is in agreement with other studies which have shown that nitrogen regeneration by marine sediments can account for about 30 to 80% of the nitrogen requirements for phytoplankton growth in water columns of 5 to 50 m (Nixon 1981, Blackburn & Henriksen 1983, Hendricksen & Kemp 1988).

The significance of the microheterotrophic community in the regeneration of nutrients necessary to support primary production in marine systems is well recognised (Harrison 1978, Glibert 1982, Taylor 1982, Newell & Lindley 1984, Lucas 1986). The surf-zone microbial loop is estimated to recycle 35% of annual phytoplankton nitrogen requirements with protozoan flagellates supplying the bulk of this regenerated nitrogen. This is consistent with recent evidence from experiments including bacterivory by flagellates, ciliates and other protozoans. The greatest nutrient regeneration rates are mediated by protozoan bacterivory rather than directly by bacteria, with remineralization enhanced with increasing complexity of the microbial food web (Fenchel 1982, Davis & Sieburth 1984, Lucas 1986).

The dissolved particulate and organic nitrogen recycled by the macroscopic trophic assemblage is considered a possible nitrogen source for the microbial loop in our system. Bacteria are able to utilize both dissolved organic and inorganic nitrogen; amino acids, in particular, may be rapidly and efficiently (74 to 86%) incorporated by pelagic bacterioplankton (see review by Lucas 1986). Although the surf-zone microbial loop has been considered a carbon sink (McLachlan & Romer 1990), a possible coupling of the macrofaunal food chain and the microbial loop via recycled organic nitrogen is suggested by this study.

Estimates of the relative importance of microheterotrophs and larger consumers in nutrient regeneration, as well as the absolute requirements of the phytoplankton, are mainly dependent on the phase of a phytoplankton bloom (Newell et al. 1988), which may vary on a short-term scale in upwelling areas, season-

ally in temperate seas, or on a longer time scale in stratified tropical waters (Wulff & Field 1983, Newell et al. 1985). A simulation model by Moloney et al. (1986) showed that following an initial pulse of new nitrogen, remineralization by bacteria and protozoa was important in sustaining the middle phase of a phytoplankton bloom, but that regeneration by crustacean zooplankton was increasingly important towards the end of the bloom. This contrasts markedly with the situation in our surf zone. Here inputs of new nitrogen (largely groundwater inflow and estuarine input) occur at a low but more or less constant level. Rather regenerated nitrogen is in plentiful supply. Furthermore, high production is a result of diatom accumulations not blooms, and there is no resultant cell senescence and bloom decay (Campbell 1987). The relative importance of new nitrogen and the nitrogen recycled by the 3 trophic assemblages in the surf zone is likely to vary more on a diel, tidal or storm/calm cycle than on a seasonal or longer term basis.

Exposed beach/surf zones are physically controlled systems driven by wave energy. The 3 trophic assemblages we have described have previously been considered to have little interaction in carbon or energy terms (McLachlan & Romer 1990). However, as bacteria are able to utilize both dissolved organic and inorganic nitrogen regenerated in the surf zone, a closer coupling between the 3 trophic assemblages in terms nitrogen is suggested by our study. McLachlan & Romer (1990) postulated a model relating the importance (in terms of energy or carbon) of the 3 trophic assemblages to the energy state of the surf zone. In their scheme, high-energy surf zones characterised by surf diatom accumulations are considered self-sustaining ecosystems, whereas low-energy surf zones, devoid of such primary production, are dependent on allochthonous inputs. Our nitrogen budget indicates that the 3 trophic assemblages regenerate sufficient nitrogen for phytoplankton primary production and thus supports the concept of high-energy surf zones as self-sustaining and semi-closed ecosystems.

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