The effects of a single freshwater release into the Kromme Estuary.
3: Estuarine zooplankton response

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Abstract

Natural patterns of zooplankton variability (temporal and spatial) in the Kromme Estuary have broken down due to persistent euhalinity (salinity values above 28‰) throughout the estuary. These conditions occur as a consequence of freshwater retention by a large reservoir. Only 2 x 10^6 m^3 (<2% of the mean annual runoff (MAR) from the catchment) is allocated to the estuary per annum, and the present study was undertaken to evaluate estuarine zooplankton response to a single release of the full reserve. The experimental release was predicted to create freshwater conditions throughout the upper half of the estuary. Instead, the water column became highly stratified for about two weeks after which salinity profiles rapidly returned to prerelease conditions. The freshwater pulse elicited no significant change in distribution or abundance in any of the dominant copepod populations. It is concluded that the <2% of MAR released in a single pulse had no direct nor indirect advantage for the endemic copepods at the population level. Similarly, no significant change was observed in zooplankton community structure after the release. Mixing of the water column and development of a permanent but dynamic longitudinal salinity gradient is a key mechanism regulating estuarine zooplankton dynamics. A regular base flow in addition to intermittent releases of freshwater pulses into the estuary is required. Because of freshwater attenuation, the Kromme Estuary is deprived of a key mechanism that regulates spatial and temporal variability of estuarine endemic copepod populations.

Introduction

River discharge into estuaries is characteristically variable under natural conditions, influencing composition and dynamics of planktonic communities in the receiving waters (Ambler et al., 1985; Cronin et al., 1962; Haertel and Osterberg, 1967; Herman et al., 1968; Hodgkin and Rippingale, 1971; Mallin et al., 1993; Miller, 1983; Nyan and Ritz, 1978). However, large storage reservoirs bring about changes in volume, quality and distribution of water flowing downstream (Davies and Day, 1998). In South Africa, reservoirs now have the capacity to retain >50% of the mean annual runoff (MAR) from catchments (Department of Water Affairs, 1986). This degree of water retention has serious implications for the structure and functioning of estuaries in a region also characterised by highly variable and unpredictable river flow patterns (Davies et al., 1993).

The warm temperate Kromme Estuary is a prime example of a South African system deprived of freshwater due to the construction of storage reservoirs in the catchment. The larger Mpofu Dam (construction completed in 1983 with a capacity 100 x 10^6 m^3) is 18 km from the coast and 4 km above the tidal head of the estuary. A second reservoir is located higher up in the catchment. The combined storage capacity of the two reservoirs is 133 x 10^6 m^3, exceeding the MAR of 106 x 10^6 m^3 from the catchment basin (Department of Water Affairs, 1986). Present management policy provides for a total annual freshwater allocation of 2 x 10^6 m^3 for the estuary, unless natural overtopping of the dam occurs. However, overtopping is infrequent, and years may pass between overspill events.

Severe drought at the end of the 1980s and early 1990s resulted in the reservoir levels falling below 30% of capacity (Jury and Levey, 1993). Freshwater was then released on a monthly basis in order to prevent hypersalinity developing in the upper estuary.

During the latter part of the drought and up to the present time, no freshwater was released for environmental purposes. Because of the severe reduction in the natural supply of freshwater, marine conditions now dominate the estuary for extended periods (years). During summer, the upper reaches become hypersaline (salinity exceeds that of seawater).

Legislation recently promulgated requires the development and implementation of resource-directed measures for the protection of the water resources in South Africa. Part of the process involves the determination of the freshwater reserve required to sustain structure and function of individual estuaries, according to specific management requirements. The Kromme Estuary has been much studied in recent years and provided an opportunity to audit the present freshwater allocation to the estuary. Thus, a multidisciplinary study was commissioned to:

- evaluate the response (magnitude and persistence) of abiotic and biotic estuarine components to a single release of freshwater (2 x 10^6 m^3) from the dam; and
- make recommendations regarding future freshwater discharges to the Kromme Estuary.

The present study reports on the estuarine zooplankton, with particular focus on the endemic copepod community.

Study site

The Kromme Estuary (Fig. 1, Table 1) has a constricted but permanently open tidal inlet. Tides are semi-diurnal with a small diurnal inequality. Mean spring tide differences outside the inlet is about 1.75 m, while neap tides average 0.57 m. A flood tidal delta extends 5 km from the mouth, but additional sand is derived from an adjacent dunefield. Aperiodic floods of sufficient magnitude scour estuarine channels, but reservoirs in the Kromme catchment dampen or filter out all floods smaller than the 1-in-30 year event

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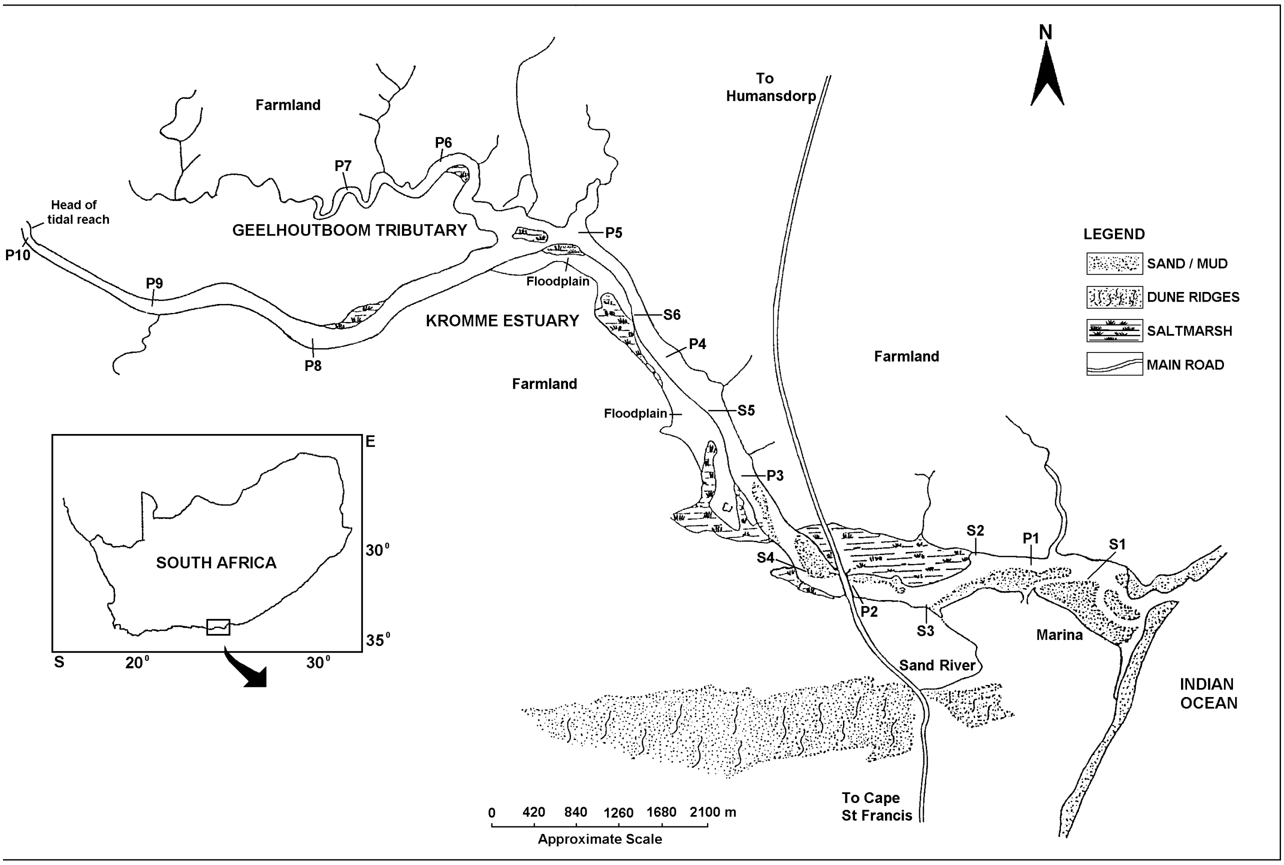

Figure 1

The Kromme Estuary showing the position of the zooplankton sampling stations (P1-P10)

TABLE 1
Physical Characterisation of the Kromme Estuary. Data From Baird and Ulanowicz (1993), Bickerton and Pierce (1988).

Length (km)	Width (m)	Depth (m)	Tidal prism
14	Maximum 175 Average 80	Maximum 7.0 Average 2.5	1.87 x 10^6 m^3

(Bickerton and Pierce, 1988). Other physical characteristics of the estuary are given in Table 1.

Materials and methods

The release of 2 x 10^6 m^3 water from the reservoir commenced on 16/11/1998, taking 7 h to reach the estuary and 36 h to complete the release. At the time, the reservoir was 87% of maximum capacity. Maximum outflow at the dam wall was 15.6 $m^3 \cdot s^{-1}$.

Four series of zooplankton samples were collected weekly at 10 stations (Fig. 1) prior to the release (25 October 1998 to 15 November 1998). A further five series were collected after the release (22 November 1998 to 20 December 1998). Samples were all collected after dark using two slightly modified WP2 plankton nets (57 cm diameter and 200 µm mesh), fitted with calibrated Kahlsico flow meters. Each net was attached to a 1 m boom extending laterally from the bow of a flat-bottomed boat (4.5 m length). Nets were towed for 2 to 3 min. at 1 to 2 knots. Except for Stations 5, 9 and 10, all samples were collected just below the water surface. When depth permitted (>2 m depth, Stations 5, 9 and 10), one net sampled below midwater. The deeper net was held at the required depth using a graduated pole.

A comparative series of salinity measurements and zooplankton samples were previously collected on a monthly basis from April 1988 to March 1991 at Stations 3 to 10 (Fig. 1) in the Kromme Estuary (Wooldridge, 1999). Data collected monthly in the Swartkops (November 1976 to October 1978)(Wooldridge and Melville-Smith, 1979) and in the Gamtoos (February 1989 to February 1991)(Wooldridge, 1999) Estuaries are also available for comparison. Sampling equipment and procedures were the same for all series.

In the laboratory, samples were diluted to predetermined volumes (up to 2 l on average) and one to three subsamples drawn off until at least 500 individuals were enumerated. Subsample volume for larger organisms (e.g. mysids) was 49 ml, while each subsample volume for smaller animals (e.g. copepods) was 8.5 ml. It was sometimes possible to process entire samples. Individuals of *Pseudodiaptomus hessei* were assigned to one of four classes (copepodids, adult males, ovigerous and non-ovigerous females). Mesh aperture size of the WP2 nets was too coarse for retention of nauplii stages. Abundance was expressed as numbers m^{-3} of water and averaged for each station. Vertical salinity and temperature profiles were determined at each station on all sampling occasions using a Valepoort CTD instrument. Measurements were taken at the surface, at 0.5 m, at 1.0 m and thereafter at 1 m depth intervals. Longitudinal salinity differences were calculated by determining the difference in surface salinity between Station 10 and Station 1.

TABLE 2
Abundance (Numbers m^{-3}) of All Zooplankton Species Collected At 10 Stations (Fig. 1) in the Kromme Estuary. Data Represent the Mean of the Four Sampling Trips Undertaken Before the Experimental Release From the Mpofu Dam.

Species	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	St. 8	St. 9	St. 10
CNIDARIA										
Hydroid medusae	0	5	0	0	0	0	0	0	0	0
CRUSTACEA										
Copepoda										
Acartia longipatella	0	3	49	1 381	2 518	3 217	4 776	6 513	2 790	3 309
Pseudodiaptomus hessei	0	3	138	2 624	3 312	5 685	1 704	1 081	2 066	19
Tortanus capensis	0	0	0	0	0	0	13	51	13	24
Mysidacea										
Gastrosaccus brevifissura	186	224	284	44	29	7	0	18	7	0
Mesopodopsis wooldridgei	4	2	8	198	178	525	109	399	10	0
Rhopalophthalmus terranatalis	0	0	2	14	6	13	6	2	0	0
Cumacea										
Iphinoe truncata	46	270	259	10	3	4	6	1	0	136
Tanaidacea										
Apseudes digitalis	0	0	0	0	0	9	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	2	0	4	5	0	0	0
Corallana africana	0	0	0	2	0	0	1	0	0	0
Cyathura carinata	0	0	0	0	0	1	0	0	0	0
Exosphaeroma hylocoetes	0	0	0	0	0	0	0	0	0	0
Sphaeromid sp.	0	0	0	0	0	0	0	0	0	0
Amphipoda										
Amphipoda spp.	14	37	104	16	12	86	81	21	2	0
Afrochiltonia capensis	0	0	0	0	0	11	0	0	0	0
Corophium triaenonyx	0	0	2	0	0	1	180	0	0	1
Grandidierella lignorum	9	35	64	5	9	68	50	1	0	0
Melita zeylanica	0	0	0	0	0	0	0	0	0	0
Urothoe sp.	3	1	0	0	0	0	0	0	0	0
Caridea										
Palaemon pacificus	0	0	0	0	0	0	0	0	0	0
Anomura										
Upogebia africana Stage 1 larvae	208	43	356	15	4	2	0	0	0	136
Brachyura										
Hymenosoma orbiculare larvae	6	43	27	32	38	85	153	260	120	98
Paratylodiplax edwardsii larvae	25	105	576	77	53	18	0	4	0	0
Sesarma catenata larvae	0	0	0	0	0	0	0	0	0	0
PISCES										
Gilchris tella aestuaria eggs	0	0	0	49	26	2	5	65	58	142

Results

Salinity

Salinity values in the Kromme Estuary over 36 consecutive months during the late 1980s and early 1990s (Fig. 2) clearly reflect marine dominance along the length of the estuary. Difference in salinity between the mouth and Station 10 in the upper estuary averaged <2‰ and during three of the four summers, the upper estuary became hypersaline. Maximum salinity exceeded 42‰ in March 1989 at Station 10. The first flood to overtop the dam wall after completion of the dam (1983) occurred in November 1989. At that time, surface salinity in the upper estuary fell to 22.4‰ while bottom-water decreased to 28.1‰. The effect was of short duration and salinity values returned to former levels within one month (Fig. 2).

Similar longitudinal salinity gradients were recorded during the experimental release period. The longitudinal salinity difference between the mouth and Station 10 at the surface was <2‰ during the four sessions prior to the release, but increased to ca 10‰ following freshwater inflow to the estuary. Bottom water in the middle and upper estuary remained unaffected for about 2 weeks, but subsequent vertical mixing (sampling session 7, Fig. 3) resulted in euhaline conditions returning to the upper estuary.

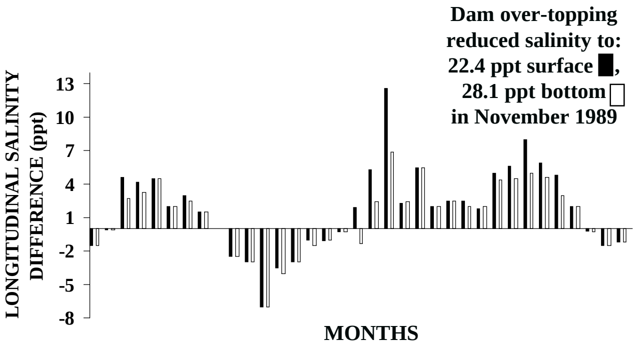
Dam over-topping reduced salinity to: 22.4 ppt surface ■, 28.1 ppt bottom □ in November 1989

Figure 2
The longitudinal salinity differences over 36 consecutive months recorded in the drought years of the late 1980s and early 1990s in the Kromme Estuary. The effect of the flood in November 1989 was of short duration. Solid bars = near-surface salinity, Open bars = near-bottom salinity.

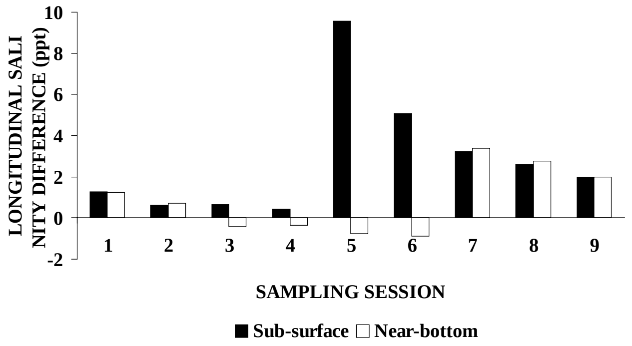

Figure 3
The longitudinal salinity differences over the experimental water release period (25 October to 20 December 1998) in the Kromme Estuary. The volume of freshwater released from the Mpofu Reservoir had limited impact on the longitudinal salinity differences in the estuary. Salinity near the tidal inlet was mixed and measured at 34.3 ‰. Salinity near the bottom at Station 10 was 35.02 ‰. Solid bars = near-surface salinity, Open bars = near-bottom salinity.

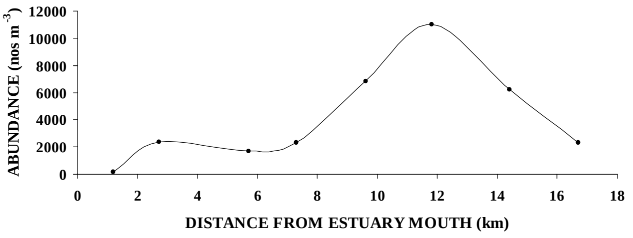

Figure 4
Spatial distribution of Pseudodiaptomus hessei *in the Gamtoos Estuary (adapted from Wooldridge, 1999). The species has a preference for mesohaline conditions that occurred in the middle and upper estuarine reaches. Data are the mean for eight stations collected over 26 consecutive months. Vertical bars represent 1 SE.*

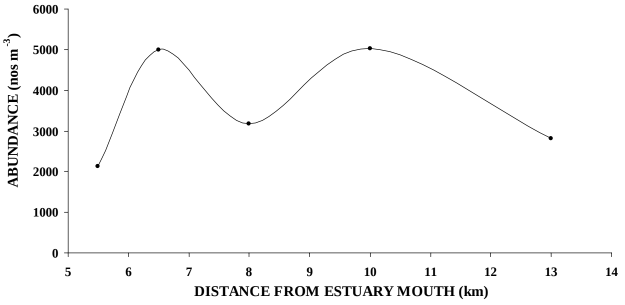

Figure 5
Salinity values remained euhaline in the upper reaches of the Kromme Estuary (see Fig. 2) and Pseudodiaptomus hessei *showed no trend in spatial distribution. Data are the mean for five stations collected over 36 consecutive months. Vertical bars represent 1 SE.*

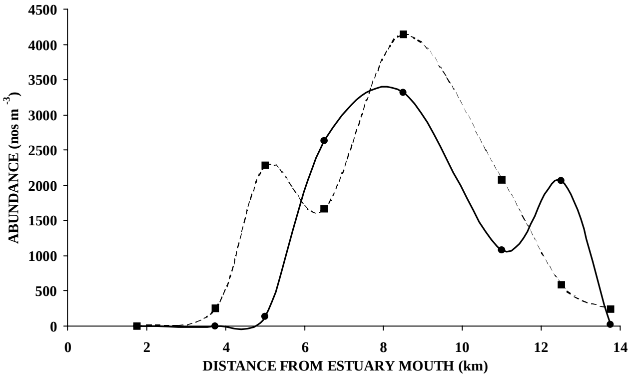

Figure 6
Distribution and abundance of Pseudodiaptomus hessei *showed no significant change following the release of freshwater from the Mpofu Dam. Data are the average of the four sessions prior to the release (solid line) and the average values for the five sessions following the release (dotted line).*

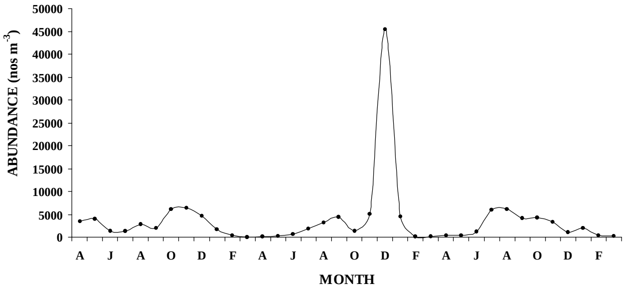

Figure 7
Mean abundance (numbers m^{-3}) of Pseudodiaptomus hessei *over 36 months in the Kromme Estuary (April 1988 to March 1991). Salinity in the estuary decreased in November 1989 (Fig. 2), followed by the peak of* P. hessei *abundance recorded in December.*

Copepod distribution

Pseudodiaptomus hessei

Pseudodiaptomus hessei reaches maximum abundance in mesohaline areas of estuaries having a strong longitudinal salinity gradient (Jerling and Wooldridge, 1991; Wooldridge, 1999) (Fig. 4). In the Kromme Estuary, a weak longitudinal salinity difference persisted over a 3-year study period (1988 to 1991) (Fig. 2) and *P. hessei* showed no trend in spatial distribution (Fig. 5).

Species abundance levels averaged for the four series collected prior to the release of water to the Kromme Estuary are given in Table 2. Table 3 provides the same information for the post-release

TABLE 3

Abundance (Numbers m^{-3}) of All Zooplankton Species Collected At 10 Stations (Fig. 1) in the Kromme Estuary. Data Represent the Mean of Five Sampling Trips Undertaken After the Experimental Release From the Mpofu Dam.

Species	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	St. 8	St. 9	St. 10
CNIDARIA										
Hydroid medusae	0	0	0	0	0	0	0	0	0	8
CRUSTACEA										
Copepoda										
Acartia longipatella	0	58	2 268	2 423	3 565	5 112	4 899	8 024	3 526	1 530
Pseudodiaptomus hessei	0	254	2 281	1 662	4 147	6 054	2 290	2 074	583	236
Tortanus capensis	0	5	6	7	11	0	0	26	8	10
Mysidacea										
Gastrosaccus brevifissura	383	261	59	65	17	2	0	14	0	0
Mesopodopsis wooldridgei	9	14	4	35	100	622	83	462	7	0
Rhopalophthalmus terranatalis	0	0	1	11	14	20	7	22	0	0
Cumacea										
Iphinoe truncata	16	37	18	4	8	10	1	1	0	0
Tanaidacea										
Apseudes digitalis	0	0	0	1	0	0	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	2	2	4	15	0	0	0
Corallana africana	0	1	1	0	2	6	8	0	0	0
Cyathura carinata	0	0	0	0	0	4	1	0	0	0
Exosphaeroma hylocoetes	0	0	0	0	10	0	0	0	0	0
Sphaeromid sp.	0	1	0	0	2	5	18	0	0	0
Amphipoda										
Amphipoda spp.	13	23	27	14	23	251	473	9	0	26
Afrochiltonia capensis	0	0	0	0	0	0	0	0	0	0
Corophium triaenonyx	0	0	0	0	0	1	6	0	0	0
Grandidierella lignorum	7	13	13	0	3	51	24	1	16	1
Melita zeylanica	0	0	0	0	0	0	0	0	0	0
Urothoe sp.	0	1	9	0	0	0	0	0	0	0
Caridea										
Palaemon pacificus juvs	0	0	0	0	1	0	0	0	0	0
Anomura										
Upogebia africana Stage 1 larvae	287	323	242	60	30	27	0	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	28	127	49	62	128	197	198	180	161	307
Paratylodiplax edwardsii larvae	867	926	3 172	1 308	1 362	1 110	51	638	16	0
Sesarma catenata larvae	115	114	87	6	772	119	0	0	0	0
PISCES										
Gilchristella aestuaria eggs	0	10	429	533	325	270	141	176	200	106

series. Copepods endemic to the estuary (*Acartia longipatella* and *Pseudodiaptomus hessei*) were the most abundant zooplankters in samples and these were used in subsequent analyses.

The distribution and abundance of *Pseudodiaptomus hessei* showed no significant change (p=0.96, Mann-Whitney test) following the release of freshwater from the Mpofu Dam (Fig. 6). This is in contrast to the population response (Fig. 7) following natural overtopping in November 1989 (Fig. 2). A comparison of population abundance levels recorded prior to the regulated release (Fig. 6) and the natural overtopping event (Fig. 7) reflects similar values (< 7 000 m^{-3} of water). However, Fig. 7 shows that average abundance increased by an order of magnitude within one month of overtopping. A maximum of 108 000 m^{-3} was recorded at a single station in the middle estuary and represents a 22-fold increase in this region (Wooldridge, 1999). By January, numbers had again decreased to former levels (Fig. 7).

Acartia longipatella and *A. natalensis*

Clear patterns of spatial and temporal succession are evident for the two acartiids endemic to local estuaries where strong salinity gradients persist. This is shown for the Gamtoos Estuary where *Acartia longipatella* occurs in water of higher salinity compared to *A. natalensis* (Wooldridge, 1999) (Fig. 8). *A. longipatella* also occurs in the plankton during the cooler months while *A. natalensis* appears in summer (Wooldridge and Melville-Smith, 1979) (Fig. 9).

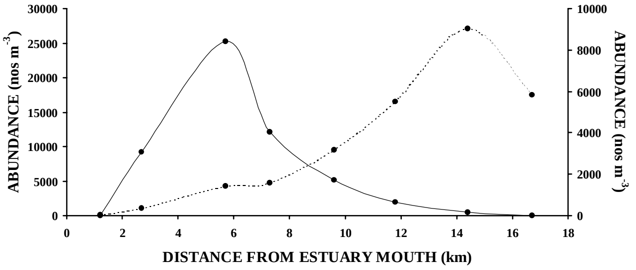

Figure 8
Spatial succession of Acartia longipatella *(solid line and Y1 axis) and* A. natalensis *(dotted line and Y2 axis) in the Gamtoos Estuary (adapted from Wooldridge, 1999). Data are the mean for eight stations collected over 26 consecutive months. Vertical bars represent 1 SE.*

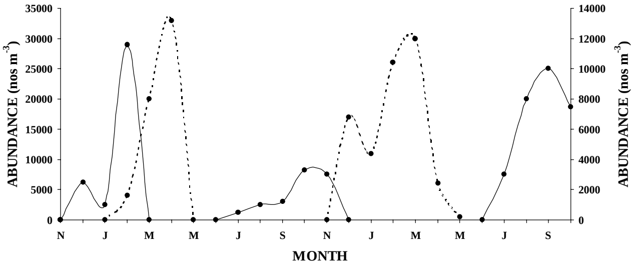

Figure 9
Temporal succession of Acartia longipatella *(solid lines and Y1 axis) and* A. natalensis *(dotted lines and Y2 axis) in the Swartkops estuary (adapted from Wooldridge & Melville-Smith, 1979). Data are the mean for 14 stations collected monthly over 24 months.*

The distribution and abundance of *Acartia longipatella* showed no significant change (p=0.37, Mann-Whitney test) following the release of freshwater from the Mpofu Dam (Fig. 10). The species was also most abundant in the upper estuary, contrary to its distribution in the Gamtoos (Fig. 8). *A. natalensis* was not recorded in the Kromme Estuary during the regulated water release study, but its presence was documented during a previous 36-month study (Wooldridge, 1999).

Zooplankton community structure – Prior- and post-release from the Mpofu Dam

Cluster analysis of the average abundance of species prior to the release (first four sampling sessions) and after the release (five sampling sessions) shows no significant change in community structure. A similar grouping of lower, middle and upper stations prior and after the water release is evident from Fig. 11. An MDS (multi-dimensional scaling) plot on the same data also shows only a slight shift. An analysis of similarity (Anosim) on the data shows that the slight shift is not significant. This is evident from the sample statistic (Global R) value of 0.047.

Discussion

Salinity and temperature are two important environmental factors influencing temporal and spatial abundance of the three endemic copepod taxa in local estuaries (Wooldridge, 1999). Inter-relationships are complex and the relative influences of these regulatory factors differ between species.

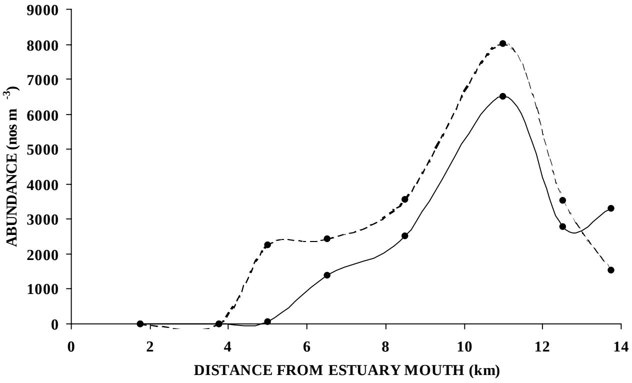

Figure 10
Distribution and abundance of Acartia longipatella *showed no significant change following the release of freshwater from the Mpofu Dam. Data are the average oo the four sessions prior to the release (solid line) and the average values for the five sessions following the release (dotted line).*

Species of *Pseudodiaptomus* occur in estuaries all around the Southern African coast, where they often dominate the zooplankton (Grindley, 1981). Wooldridge (1999) has argued that the change in season has no obvious effect on population abundance of *Pseudodiaptomus hessei*, but that in some way, river inflow regulates temporal abundance patterns. This is well illustrated in the Kromme Estuary (Fig. 7) where the strong freshwater pulse recorded in November 1989 (Fig. 2) resulted in the observed population response. Between 70 and 90% of adult females in December 1989 samples were ovigerous, on average (Wooldridge, 1999). Response was rapid (<1 month) and numbers declined rapidly to previous levels. Numbers were particularly low when the estuary was hypersaline (<500 m^{-3}, Figs. 2 and 7).

The *Pseudodiaptomus hessei* population did not respond in the expected way following the freshwater release from the Mpofu Dam. No significant change in the proportion of ovigerous females was recorded after the release. Low phytoplankton concentrations, a major food source (Jerling and Wooldridge, 1991) may have limited population growth (Snow et al. 2000). Distinct hydrodynamic regions identified by MacKay and Schumann (1990) in the Sundays Estuary also corresponded to zones of significantly different chlorophyll *a* concentrations, that ranged from $<6\ \mu g\ l^{-1}$ near the mouth of the estuary to $>100\ \mu g\ l^{-1}$ in the middle and upper reaches (Hilmer and Bate, 1990). Chlorophyll *a* in the Sundays Estuary therefore, displayed a clear salinity-related distribution. Highest chlorophyll *a* concentrations also occurred in the same hydrodynamic sector of the estuary where *Pseudodiaptomus hessei* maxima were recorded (Wooldridge and Bailey, 1982; Jerling and Wooldridge, 1991). Futher evidence is available for other estuaries along the south-east coast, where phytoplankton biomass was positively related to mean longitudinal salinity range (Schlacher and Wooldridge, 1996). Similar patterns also apply to the endemic estuarine copepods (Wooldridge, 1999; Allanson and Read, 1995) and fish (Schlacher and Wooldridge, 1996). Analogous relationships pertaining to plankton production and freshwater inflow are quoted in Skreslet (1986) and Rey et al. (1991).

The copepods, *Acartia natalensis* and *A. longipatella* demonstrate spatial and temporal succession, if a strong salinity gradient is present (Wooldridge and Melville-Smith, 1979). The former species occurs in summer in upper estuarine reaches, while *A. longipatella* appears in winter in the lower reaches of estuaries. These successional patterns are regulated by the interaction of temperature and salinity, probably through a combination of suit-

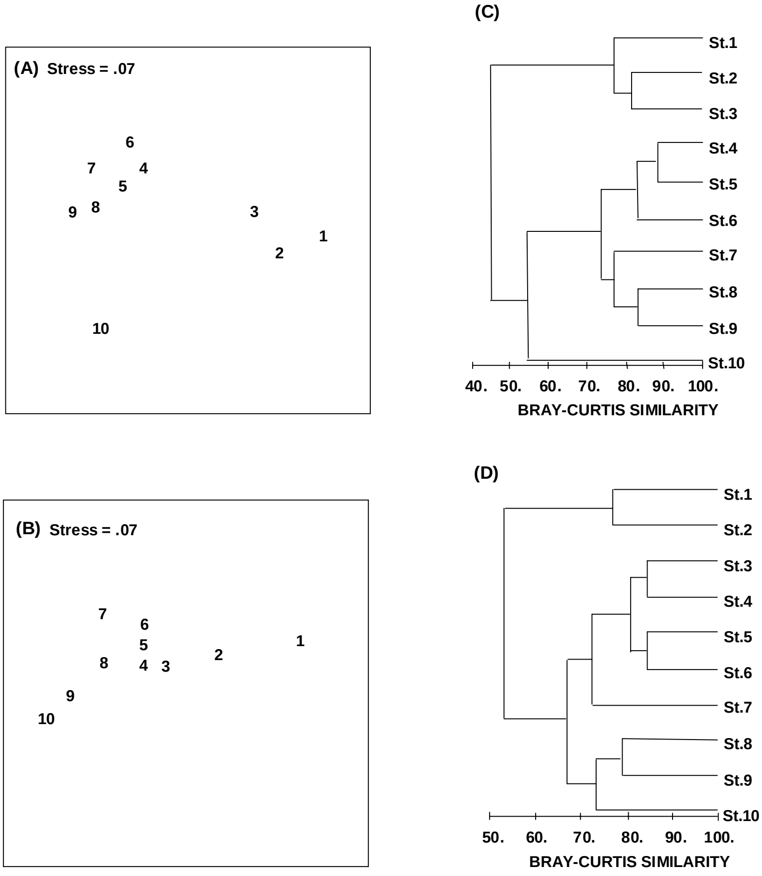

Figure 11
Analysis of Similarity (Anosim) for pre- (A) and post- release (B) of freshwater from the reservoir. Bray-Curtis Similarity of zooplankton composition shown in (C) and (D) for the same data respectively (Tables 2 and 3).

able environmental conditions (low temperature and high salinity for *A. longipatella* and low salinity and high temperature for *A. natalensis*) that enable dormant eggs present in the substrate to hatch. As environmental conditions become unfavourable, eggs do not hatch but sink to the bottom where they remain in or on the sediment until favourable conditions return. At least 24 taxa are known to produce resting eggs (*inter alia*, Greenwood, 1981; Grice and Marcus, 1981; Marcus, 1984; 1990; 1991; Uye, 1985; Sullivan and McManus, 1986; Ianora and Santella, 1991), including eight species of *Acartia* (Uye, 1985). In South Africa, acartiid eggs occur in high abundance in muddy sediments of the Swartkops Estuary and may exceed 14 x 10^6 m^{-2} (average 0.5 to 1.0 x 10^6 m^{-2}, N = 15, unpublished data). However, it has not been possible to raise nauplii hatched from these resting eggs in order to identify species.

Low abundance or absence of *Acartia natalensis* in the plankton of the Kromme Estuary is probably due to unfavourable salinity conditions. Even if water temperatures are suitable for the hatching of *A. natalensis* eggs in summer (see Fig. 9), salinity above a threshold prevents development. The salinity threshold level is unknown, but general observations suggest that it would be between 25 and 30‰. Ambler et al. (1985) obtained analogous results, concluding that the hatching of *A. clausi* eggs (a winter species) ceased at salinity values <30‰ and temperatures higher than 17.5°C. In the Kromme Estuary, the freshwater pulse did not mix into the water column. Salinity below 1 m depth remained >30‰ in the upper estuary (Fig. 3), and probably above the threshold required to induce hatching of any eggs present in the sediment.

The weak longitudinal salinity gradient in the Kromme Estuary also influenced the spatial distribution of *Acartia longipatella.* Maximum numbers occurred in the upper estuary (Fig. 10), in contrast to their distribution in estuaries having a strong salinity gradient (Fig. 8). Regulatory mechanisms controlling temporal and spatial distribution of this species are not clear, although temperature is probably the main forcing factor.

Summary

Salinity distribution impacts directly on copepod distribution and abundance in estuaries. In the Kromme Estuary, reservoir retention of river water artificially maintains euhaline conditions throughout the estuary for extended periods. As a result, spatial and temporal shifts in the natural distribution of resident copepod species may be prevented, and *A. natalensis* may not make its appearance in the plankton. The Kromme Estuary has the lowest average copepod biomass (mg dry mass m^{-3}) of six tidal estuaries for which extensive data sets are available (Wooldridge, 1999), and this is directly linked to the low average longitudinal salinity gradient. Anthropogenically induced changes in copepod distribution and abundance will have a negative ripple effect on the plankton-based foodweb within the estuary. Regulation of the river has therefore deprived the Kromme Estuary of a key mechanism that regulates temporal variability of copepod distribution and abundance. Population dynamics of the three species in Eastern Cape estuaries is primarily linked to the quality and quantity of freshwater supply (event-driven), rather than to seasonal and/or other cyclic factors (Wooldridge, 1999).

The conclusion is that the <2% of MAR released in a single pulse had no direct nor indirect advantage for the endemic copepods at the population level. Similarly, no significant change was observed in zooplankton community structure after the release. Mixing of the water column and development of a permanent but dynamic longitudinal salinity gradient is of fundamental importance in structuring the zooplankton community. For this purpose a regular base flow in addition to intermittent releases of freshwater pulses into the estuary is required. However, low nutrient levels in the reservoir are probably insufficient to promote phytoplankton production, and this may require specific attention when evaluating management options.

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