The response of *Grandidierella lignorum* (Barnard) (Crustacea: Amphipoda) to episodic flooding in three eastern Cape estuaries

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The response of the euryhaline amphipod *Grandidierella lignorum* to changing freshwater inflow was investigated in three estuaries with differing river discharges. In the Kariega and Keiskamma estuaries an increase in the density of *G. lignorum* was correlated with an increase in river inflow. The sharp reduction in salinity during flooding is suggested as a possible trigger which stimulates *G. lignorum* to rise into the water column. The position of stations along the Kariega and Keiskamma estuaries, together with seasonal effects, also influenced *G. lignorum* abundance. In the Great Fish estuary, which has a continuous large freshwater input, changes in the abundance of *G. lignorum* were not correlated with inflow. Possible reasons for this anomalous situation, as well as the biological implications of becoming part of the zooplankton during flooding, are discussed.

Die reaksie van die eurihaliene amphipod *Grandidierella lignorum* tot wisselende vloei van varswater in drie riviermondinge met verskillende vloeikoerse is ondersoek. In die Kariega- en Keiskamma-riviermonde was 'n toename in die digtheid van *G. lignorum* gekorreleer met 'n toename in vloeikoers. Die skerp daling in soutgehalte gedurende vloedtoestande word voorgestel as 'n moontlike meganisme wat die opstyging van *G. lignorum* in die waterkolom stimuleer. Die ligging van stasies langs die Kariega- en Keiskamma-riviermondinge, tesame met seisoenale effekte, het ook die volopheid van *G. lignorum* beïnvloed. In die Grootvisgetyrivier, wat 'n standhoudende groot varswatertoevoeging ondervind, was veranderinge in die digtheid van *G. lignorum* nie met toevloeivariasies gekorreleer nie. Moontlike redes vir hierdie afwykende toestand, sowel as die biologiese implikasies van 'n soöplanktonleefwyse gedurende vloedtoestande, word bespreek.

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South Africa is an arid country and as the demand for freshwater by industry, agriculture and domestic consumers increases, less will be available for the management of aquatic habitats, of which estuaries comprise a significant component (Roberts 1983; Turek, Goodger, Bigford & Nichols 1987). If the volume of freshwater entering an estuary is to be restricted (e.g. dam construction), the question arises as to whether a reasonable level of ecological functioning can be maintained by a continuous low flow release or whether periodic simulated flooding should occur.

As part of an ongoing national programme to investigate the freshwater requirements of estuaries (see Allanson & Reid 1987 for more details) we report on the response of the normally benthic amphipod *Grandidierella lignorum* to increased river discharge in the Kariega, Great Fish and Keiskamma estuaries. These three systems were investigated because of their differing freshwater inputs. The Great Fish estuary receives a constant artificial inflow diverted from the Orange River and is consequently dominated by freshwater. In contrast the Kariega estuary, with several dams in a relatively small catchment area, receives a minimal freshwater inflow and is marine dominated. Freshwater discharge into the Keiskamma estuary is intermediate between the Great Fish and Kariega systems.

Study area

Figure 1(a) shows the relative positions of the Kariega (33°41'S / 26°41'E), Great Fish (33°30'S / 27°08'E) and Keiskamma (33°17'S / 27°29'E) estuaries on the eastern Cape coast. The length of the Kariega estuary is 26 km, Keiskamma estuary 18 km and Great Fish estuary approximately 11 km. Estuary channel water depths at mean sea level normally range between 1 and 3,5 m in the Keiskamma, 2–3 m in the Kariega and 1–2 m in the Great Fish.

The pattern of river inflow into the Kariega, Great Fish and Keiskamma estuaries is largely determined by catchment size and the extent of river regulation. The Kariega estuary has the smallest catchment (686 km^2) and is highly regulated by the Settlers, Howiesons Poort and Moss dams. The catchment of the Keiskamma system is 2350 km^2 in extent and the Sandile Dam regulates river flow in the upper reaches. The Great Fish River has the largest catchment (30 427 km^2) and water abstraction for irrigation is offset by translocated turbid water from the Orange River.

The mean monthly discharge of river water into the Kariega, Keiskamma and Great Fish estuaries during the study period was 0,3; 1,9 and 16,1 $\times$ 10^6 m^3 respectively. Inflow into the Great Fish estuary is continuous whereas in the Kariega it falls to zero for long periods (Allanson & Read 1987). In the Keiskamma estuary periods of no river discharge are followed by intermittent flow or flood events (Read 1983). Suspended silt levels are low in the Kariega estuary, variable in the Keiskamma estuary depending on catchment run-off, and permanently high in the Great Fish estuary.

The Kariega estuary is a homogeneous well-mixed estuary with a salinity gradient increasing from the head to the mouth. During severe droughts a reverse salinity gradient has been recorded with salinities as high as 40‰ in the upper reaches (Allanson & Read 1987). The sustained inflow of freshwater into the Great Fish estuary results in a persistent low salinity environment in the middle and upper reaches. Only during extreme tidal incursions does seawater penetrate this region (Allanson & Read 1987). Salinities within the Keiskamma estuary are highly variable depending on river inflow e.g. at Station I salinities fluctuate between freshwater and 35‰ depending on the magnitude of the freshwater inflow and severity of the drought (Read 1983). Water temperatures in all three systems fluctuate between 11°C during winter and 29°C in summer.

Methods

Three stations in the middle and upper reaches of the Keiskamma estuary and four in the Kariega and Great Fish estuaries (Figure 1) were sampled at night (21h00–02h00) just below the water surface using a 012WA300 Clarke Bumpus (12,5 cm diameter, 160 μm mesh) zooplankton sampler. Between three and five replicate zooplankton trawls were conducted at each station. The Kariega and Great Fish estuaries were sampled at approximately two-month intervals from April 1983 – June 1984; in the Keiskamma estuary sampling extended from September 1982 – December 1984 at approximately monthly intervals. Whenever possible sampling occurred during or immediately after a river flood event.

The numbers of *G. lignorum* were normally small enough to permit enumeration of the entire sample. In those cases where subsampling was necessary, samples were made up to a known volume, uniformly agitated and subsampled using a wide-mouthed graduated pipette. Results were expressed as number of *G. lignorum* per m^3 of water filtered. The percentage frequency of abundance within different salinity ranges was calculated by dividing the number of occasions that a particular density occurred in that salinity range by the total number of samples in the data base. Replicate samples at each station were pooled for the above calculations.

Salinities > 5‰ were recorded in the field using a Goldberg refractometer and those < 5‰ were determined in the laboratory using a chloride titrator (Radiometer, Copenhagen) and converted to salinity (Harvey 1955). Surface water temperature (°C) was recorded using a standard mercury thermometer. Monthly river discharge ($m^3 \times 10^6$) data were obtained from gauging weirs P3M01, Q9M18 and R1M15 situated immediately above the Kariega, Great Fish and Keiskamma estuaries respectively.

Statistical analyses were carried out using SPSS (Statistical Package for the Social Sciences) programs. Where necessary *G. lignorum* abundance (number m^{-3}) and inflow values were log and square root transformed respectively to normalize distributions.

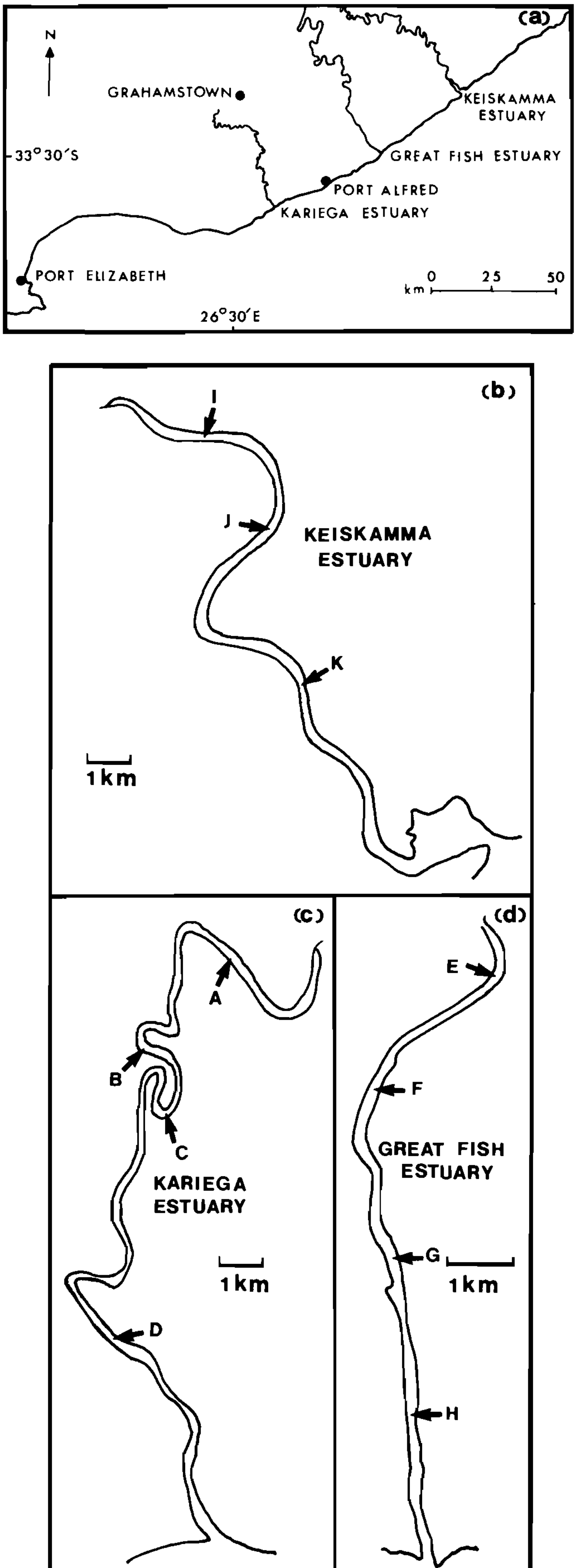

Figure 1 (a) Geographical locality of the Kariega, Great Fish and Keiskamma estuaries; (b–d) Sampling stations on the Keiskamma, Kariega and Great Fish estuaries.

Results

Kariega estuary

A two-way ANOVA revealed that both the station location and month of sampling had a significant effect ($p<0,05$) on *G. lignorum* abundance, and for this reason the stations were not pooled. The mean abundance (individuals m^{-3}) of *G. lignorum* over the study period decreased progressively down the estuary: 398 (*S.E.* = 174) at A, 200 (*S.E.* = 88) at B, 109 (*S.E.* = 49) at C and 16 (*S.E.* = 6) at D.

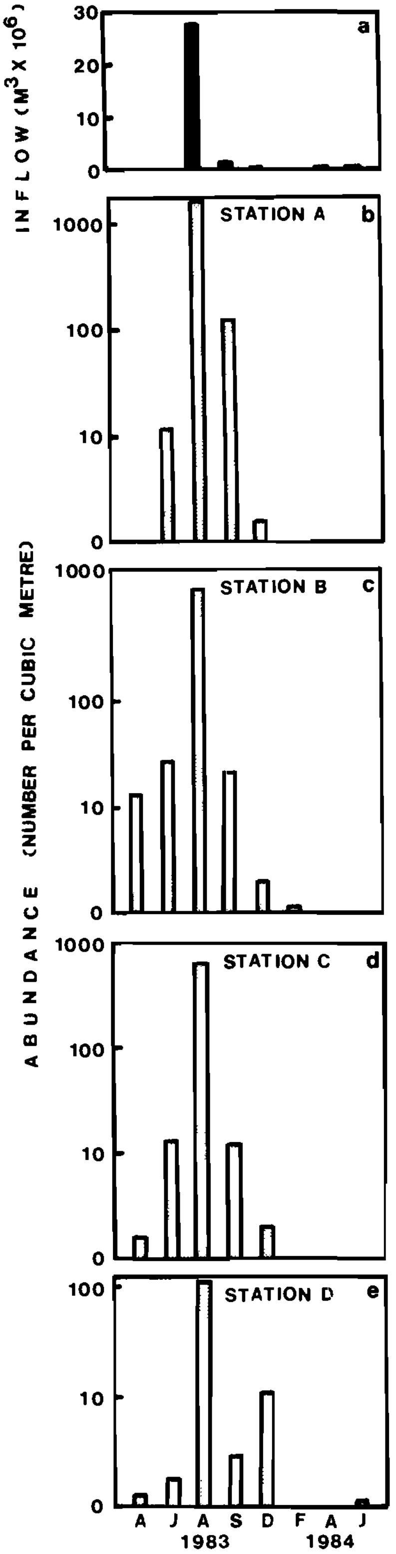

Figure 2 Monthly river discharge (a) and abundance of *G. lignorum* (b–e) at four stations in the Kariega estuary.

Figure 2 shows the correlation between *G. lignorum* and freshwater input at four stations in the Kariega estuary. There was a clear increase in abundance of *G. lignorum* at all four stations following flooding in August 1983, with localities closest to the source of freshwater input showing the largest increases (Figure 2). Correlation coefficients (*r*) of *G. lignorum* abundance with monthly inflow were 0,96; 0,98; 0,98 and 0,80 at Stations A, B, C and D respectively. An analysis of covariance (Table 1) also demonstrated that freshwater inflow was an important factor influencing the abundance of *G. lignorum* in the water column of this estuary.

Salinities following the August 1983 flood showed a progressive increase until by February 1984 all four stations registered 35‰. This coincided with a steady decline in planktonic *G. lignorum* abundance which reached zero in February 1984. Analysis of covariance (Table 1) revealed that salinity was a major factor linked to the abundance of *G. lignorum* in the Kariega estuary and this is reinforced by Table 2 which shows the pattern of distribution and abundance of the amphipod in relation to a range of salinities. The greatest densities oc-

Table 1 Covariance analysis of factors affecting the abundance of *G. lignorum* in the Kariega estuary

Source of variation	Sum of squares	*d.f.*	Mean square	F	Significance
Inflow*	1,52	1	1,52	6,10	$p = 0,015$
Salinity	4,04	1	4,04	16,22	$p < 0,001$
Temperature	4,14	1	4,14	16,60	$p < 0,001$
Station	3,35	3	1,11	4,47	$p = 0,005$
Month	7,42	3	2,47	9,91	$p < 0,001$
Two way interactions:					
Station/Season	8,16	9	0,90	3,63	$p < 0,001$
Explained	107,71	18	5,98	23,97	$p < 0,001$
Residual	27,21	109	0,25		
Total	134,92	127	1,06		

*Square root of inflow.

Table 2 The percentage frequency of abundance of *G. lignorum* over a range of salinities in the Kariega estuary from April 1983 to June 1984

Abundance (no. m^{-3})	Salinity range (‰) 0,5 – 5	20 – 30	31 – 42
0 – 10	0	9,4	59,3
11 – 100	0	6,3	6,3
101 – 500	0	3,1	6,3
501 – 1000	3,1	0	0
1001 +	6,3	0	0

curred in the salinity range 0,5–5‰, while in the higher range (31–42‰) abundance was normally < 10 m^{-3}.

Water temperature also appeared to play a significant role in the abundance of *G. lignorum* (Table 1), but this may be linked to the high winter and low summer freshwater inflow (Figure 2) together with the associated salinity effects, rather than temperature *per se*.

Great Fish estuary

A two-way ANOVA indicated that both station location and month had a significant effect on the abundance of *G. lignorum*. The four stations were therefore treated individually. The mean abundances (individuals m^{-3}) at Stations E, F, G and H were 19 (*S.E.* ± 4), 42 (*S.E.* ± 8), 55 (*S.E.* ± 19) and 32 (*S.E.* ± 7) respectively. No pattern is evident and densities are considerably lower than those obtained in the Kariega estuary.

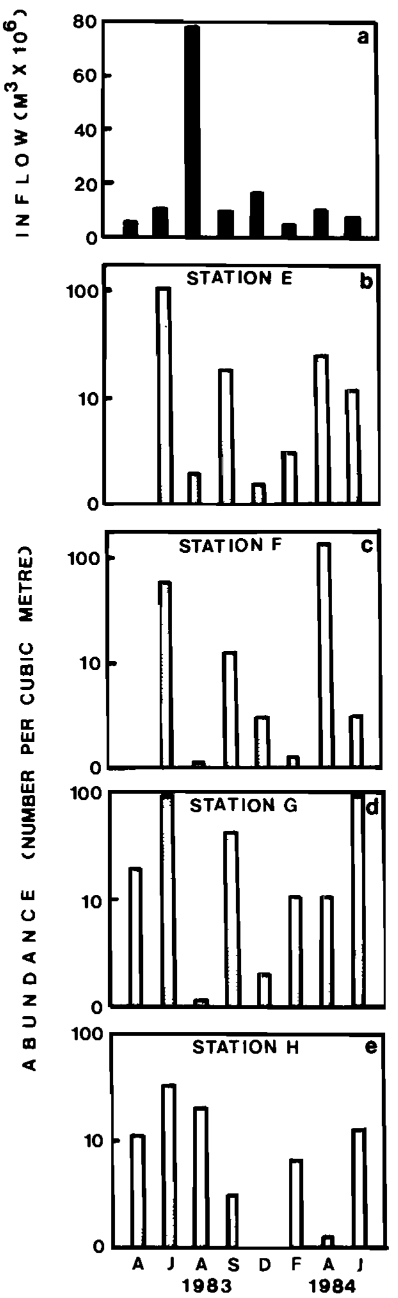

Figure 3 Monthly river discharge (a) and abundance of *G. lignorum* (b–e) at four stations in the Great Fish estuary.

No relationship exists between increased abundance and increased river flow (Figure 3), which is probably related to differences in the magnitude and regularity of freshwater discharge in the Great Fish estuary. A correlation analysis between inflow and *G. lignorum* abundance for Stations E to H gave (*r*) values of 0,06; –0,61; –0,29 and 0,37 respectively. These results indicate that in the Great Fish estuary high inflows correlated, if anything, with a decrease in *G. lignorum* abundance. Not surprisingly, the pattern of distribution and abundance of *G. lignorum* in relation to salinity (Table 3) is not as obvious as that obtained for the Kariega estuary. Low abundance (0–10 m^{-3}) was recorded at both high (31–35‰) and low (0,1–10‰) salinity ranges (Table 3) whereas in the Kariega estuary greater abundance was correlated with lower salinity. Nevertheless the highest densities were recorded in the 0,1–10‰ salinity range.

Keiskamma estuary

Figure 4 shows the relationship between inflow and the abundance of *G. lignorum* at three stations in the middle and upper reaches of the Keiskamma estuary. A two-way ANOVA indicated that both the time of sampling and station location had a significant effect on the abundance of *G. lignorum*. The three stations were therefore treated separately.

Figure 4 shows an apparent correlation between an increase in *G. lignorum* abundance and monthly river discharge. For instance in July 1983, after a prolonged period of no inflow and a steady reduction in *G. lignorum* abundance from January to June, density increased at Stations J, K, and I from zero to 5000, 3400, and 1700 m^{-3} respectively. A slight increase in river flow during October 1983 correlated with increased amphipod abundance at Stations I and J but did not extend to downstream Station K (Figure 4). Flooding during the following month (November 1983) had a major influence on the entire estuary and densities of *G. lignorum* at Station K increased dramatically.

Figure 5 shows the relationship between mean *G. lignorum* abundance from all three stations and inflow during the entire sampling period. Despite the scatter, there is a pronounced trend towards an increase in abundance with stronger river inflow. This relationship

Table 3 The percentage frequency of abundance of *G. lignorum* over a range of salinities in the Great Fish estuary from April 1983 to June 1984

Abundance	Salinity range (‰)			
(no. m^{-3})	0,1 – 10	11 – 20	21 – 30	31 – 35
0 – 10	19,2	3,9	0	15,4
11 – 50	19,2	11,5	7,7	0
51 – 100	0	7,7	7,7	0
101 – 500	7,7	0	0	0

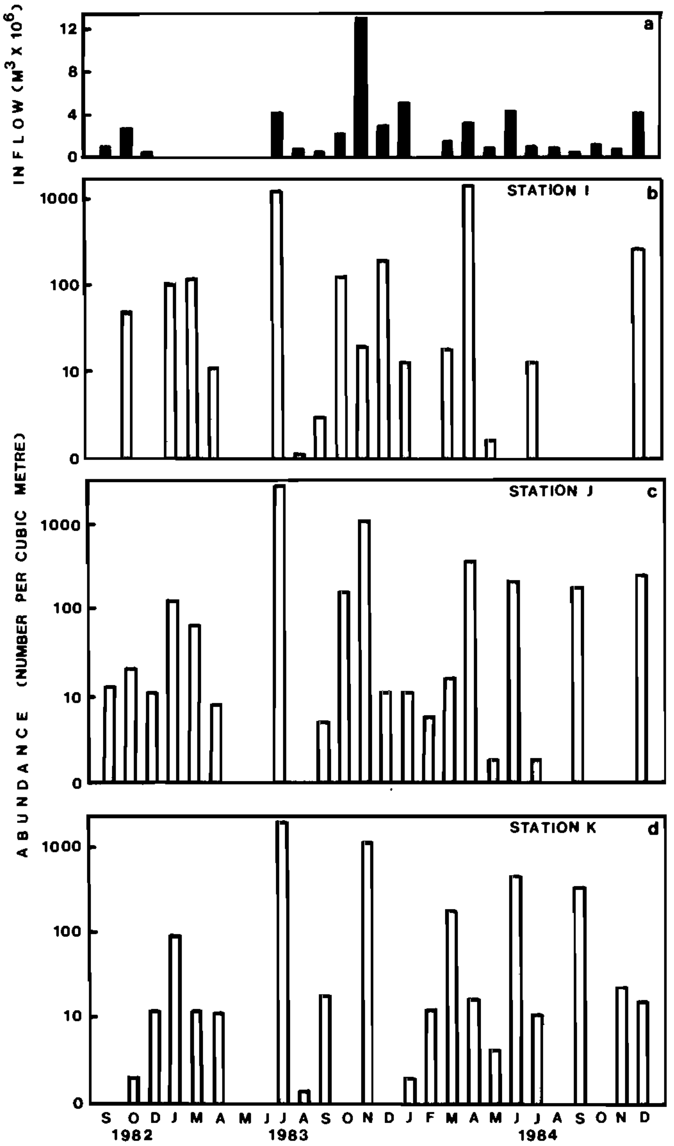

Figure 4 Monthly river discharge (a) and abundance of *G. lignorum* (b–d) at three stations in the Keiskamma estuary.

is again evident from Table 4 which shows the correlation (*r*) between mean monthly changes in *G. lignorum* abundance and inflow. Some anomalies (i.e. negative correlations) are apparent, suggesting that river inflow is not the only variable that determines *G. lignorum* abundance. Nevertheless it appears that high correlation (*r*) values are often associated with large inflows.

River discharge also alters the salinity structure of the Keiskamma estuary (Read 1983). During the study period the salinity at all three stations ranged from 0,1–35‰ and Table 5 shows that the highest percentage frequency of abundance of *G. lignorum* was associated with the lower salinity range (0,1–5‰). At salinities > 20‰ the numbers of *G. lignorum* did not exceed 500 m^{-3}. This pattern of distribution with salinity is similar to that obtained in the Kariega estuary (Table 2). An analysis of covariance (Table 6) indicated that after correcting for the main effects of station and month, inflow *per se* played a significant role in accounting for the changes in *G. lignorum* abundance.

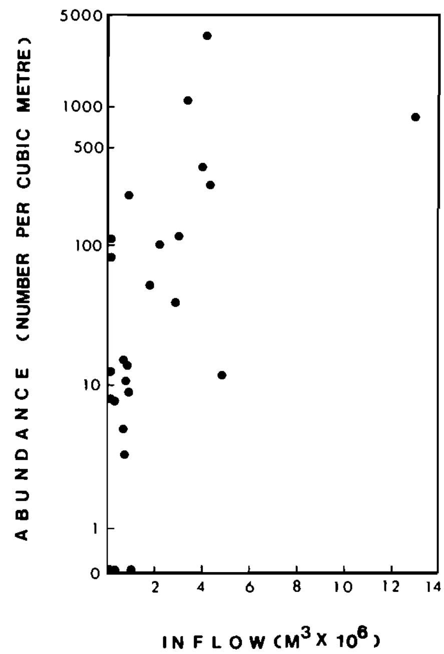

Figure 5 Relationship between freshwater inflow and mean *G. lignorum* abundance at three stations in the Keiskamma estuary.

Table 4 Correlation coefficients (*r*) of the mean monthly change in abundance of *G. lignorum* with river discharge into the Keiskamma estuary

Month	Mean abundance (no. m^{-3})	*n*	Mean inflow ($m^3 \times 10^6$)	Correlation coefficient (*r*)	Significance
January	64	27	2,19	–0,70	$p < 0,001$
February	8	12	0,12	*	–
March	73	27	0,79	–0,28	$p > 0,1$
April	561	24	1,60	0,55	$p < 0,01$
May	2	27	0,30	0,58	$p < 0,01$
June	128	27	1,95	0,70	$p < 0,001$
July	1843	24	2,45	0,82	$p < 0,001$
August	1	24	0,73	–0,42	$p < 0,1$
September	102	30	0,46	–0,64	$p < 0,001$
October	49	30	1,70	0,45	$p < 0,1$
November	433	24	7,00	0,61	$p < 0,01$
December	191	30	2,90	0,40	$p < 0,1$

* A coefficient could not be calculated since this month was not replicated.

Discussion

Although station position influenced the abundance of *G. lignorum* in all three estuaries, increased river discharge, especially in the Keiskamma and Kariega estuaries was also of prime importance. Evidence to suggest that rainfall and reduced salinities may influence the planktonic abundance of *G. lignorum* is also provided by Coetzee (1983). He found that densities of the amphipod in the Rondevlei water column increased dramatically during September and October 1976, which

Table 5 The percentage frequency of abundance of *G. lignorum* over a range of salinities in the Keiskamma estuary from October 1982 to December 1984

Abundance (no. m^{-3})	Salinity range (‰)			
	0,1 – 5	10 – 15	20 – 25	30 – 35
0 – 10	3,8	14,1	10,3	11,5
11 – 100	9,0	6,4	3,8	6,4
101 – 500	7,7	11,5	3,8	1,3
501 – 1000	1,3	1,3	0	0
1001 +	6,4	1,3	0	0

Table 6 Covariance analysis of factors affecting the abundance of *G. lignorum* in the Keiskamma estuary

Source of variation	Sum of squares	*d.f.*	Mean square	F	Significance
Inflow*	18,51	1	18,51	30,48	$p < 0{,}001$
Salinity	1,16	1	1,16	1,92	$p = 0{,}167$
Temperature	4,93	1	4,93	8,12	$p = 0{,}005$
Station	4,30	2	2,15	3,54	$p = 0{,}030$
Month	84,65	11	7,69	12,66	$p < 0{,}001$
Two-way interactions:					
Station/Season	49,09	22	2,23	3,67	$p < 0{,}001$
Explained	215,58	38	5,67	9,34	$p < 0{,}001$
Residual	162,12	267	0,60		
Total	377,77	305	1,23		

*Square root of inflow.

coincided with increased rainfall and declining salinities within the lake.

Covariance analyses also implicated temperature as an important variable governing the density of planktonic *G. lignorum,* but this may be coincidental owing to the seasonality of rainfall during the sampling period. High abundance of the amphipod in the Kariega estuary tended to be associated with low water temperature since the strongest inflows occurred in winter. *G. lignorum* is most abundant in warmer east coast estuaries (Grindley 1981; Blaber, Kure, Jackson & Cyrus 1983) and therefore unlikely to respond positively to low temperatures. The steady decrease in abundance from January – June 1983 in the Keiskamma estuary (Figure 4) and a similar decline in the Kariega estuary from April – June 1984 (Figure 2) in association with decreasing temperatures supports this hypothesis. In the Keiskamma estuary the increase in abundance is often associated with an elevated inflow and is independent of the temperature regime. For instance, the increased abundance that correlated with elevated inflows in July and November of 1983 and April, June, September and December 1984 occurred at temperatures of 15,4; 22,2; 19,7; 15,2; 20,6 and 24,6°C respectively.

No seasonal patterns of maximum and minimum abundance are evident in the Keiskamma estuary (Figure 4), possibly a result of unseasonal elevated freshwater inflows. Wooldridge & Melville-Smith (1979) and Wooldridge & Bailey (1982) reported that an increase in river discharge also leads to an increase in the population density of the copepod *Pseudodiaptomus hessei.* Although Grindley (1970) observed seasonal changes in the abundance of *P. hessei,* these were not evident in the Sundays estuary (Wooldridge & Melville-Smith 1979) owing to unseasonal increased river inflows to which *P. hessei* responded.

The almost simultaneous population density increase of *G. lignorum* associated with higher inflows, suggests that factors such as reduced predation or increased reproductive activity are unlikely to be responsible for the rapid planktonic population increases. *G. lignorum* forms part of the benthic invertebrate community (Davies 1982) with the ability to burrow into sand and mud substrata of estuaries and coastal lakes (Blaber *et al.* 1983). The fact that no *G. lignorum* were present in the water column of the Keiskamma estuary during May and June 1983 but suddenly appeared in large numbers during July 1983 (Figure 4), suggests that high densities of benthic *G. lignorum* were present prior to increased river flow in July. The environmental stimulus which triggers the behavioural change from a benthic to a pelagic existence is probably the drop in salinity which accompanies higher river discharge. *G. lignorum* is a euryhaline organism capable of surviving in freshwater (Boltt 1969) and salinities of 45‰ (Blaber *et al.* 1983).

What is the biological significance of this change, since the animals do not remain in the water column indefinitely and numbers soon decrease with rising salinity? The short-term benefits of a planktonic existence could be to exploit suspended fluvial resources and, if water currents are strong enough, resuspended estuarine food material. Read (unpublished data) has shown that high concentrations of total and particulate organic carbon are associated with increased river discharge in the Keiskamma estuary. Coupled with the increased food availability, the long-term effect could be an increase in population density and colonization of new areas when settlement occurs. In addition, rising into the water column will increase the contact between individuals from different areas and prevent genetic isolation of populations.

Pseudodiaptomus hessei, which also reacts to strong freshwater inflow, is equally tolerant of low salinities since both *P. hessei* and *G. lignorum* occur in the freshwater Lake Sibaya (Allanson, Hill, Boltt & Schultz 1966). Low salinity areas occupied by *G. lignorum* and *P. hessei* are unfavourable for major predators such as *Mesopodopis slabberi* and *Rhopalopthalamus terranatalis* (Wooldridge & Bailey 1982). Thus during periods of increased river discharge, *P. hessei* and *G. lignorum* which are physiologically adapted to low salinity, could exploit planktonic food resources in the absence of invertebrate predators.

The population density of *G. lignorum* in the water column of the Great Fish estuary (36 individuals ± *S.E.* 7) is considerably lower than in the Keiskamma (280 individuals ± *S.E.* 54) or Kariega (178 individuals ± *S.E.* 26) estuaries. Any attempt to account for these differences purely in terms of differing freshwater inputs would be speculative, since the low population densities in the Great Fish estuary may be associated with a fluctuating benthic environment, which is linked to the artificially high river discharge carrying large sediment loads. Estuarine *G. lignorum* populations do, however, appear to be well adapted to alternating conditions of zero or low flow during droughts, and high discharge during periodic flood events, both of which are features of most southern African systems. It would appear therefore that should the freshwater inflow to an estuary be artificially arrested, periodic releases of water to simulate flooding conditions, may be necessary to accommodate the long term ecological requirements of certain members of the estuarine community.

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References

ALLANSON, B.R., HILL, B.J., BOLTT, R.E. & SCHULTZ, V. 1966. An estuarine fauna in a freshwater lake in South Africa. *Nature, Lond.* 209: 532–533.

ALLANSON, B.R. & READ, G.H.L. 1987. The response of estuaries along the south-eastern coast of southern Africa to marked variation in freshwater inflow. Institute for Freshwater Studies, Rhodes University, Special Report No. 2/87: 42 pp.

BLABER, S.J.M., KURE, N.F., JACKSON, S. & CYRUS, D.P. 1983. The benthos of South Lake, St Lucia following a period of stable salinities. *S. Afr. J. Zool.* 18: 311–319.

BOLTT, R.E. 1969. The benthos of some southern African lakes. Part II: The epifauna and infauna of the benthos of Lake Sibaya. *Trans. roy. Soc. S. Afr.* 38: 249–269.

COETZEE, D.J. 1983. Zooplankton and environmental conditions in a southern Cape coastal lake system. *J. Limnol. Soc. sth. Afr.* 9: 1–11.

DAVIES, B.R. 1982. Studies on the zoobenthos of some southern Cape coastal lakes. Spatial and temporal changes in the benthos of Swartvlei, South Africa, in relation to changes in the submerged littoral macrophyte community. *J. Limnol. Soc. sth. Afr.* 8: 33–45.

GRINDLEY, J.R. 1970. The plankton of South African estuaries. In: Oceanography in South Africa, H1: 1–16, CSIR, Pretoria.

GRINDLEY, J.R. 1981. Estuarine plankton. In: Estuarine ecology with particular reference to southern Africa, (ed.) Day, J.H., Ch. 8. Balkema, Cape Town.

HARVEY, H.W. 1955. The chemistry and fertility of sea waters. Cambridge University Press, Cambridge.

READ, G.H.L. 1983. The effect of a dry and wet summer on the thermal and salinity structure of the middle and upper reaches of the Keiskamma estuary, Ciskei. *Trans. roy. Soc. S. Afr.* 45: 45–62.

ROBERTS, C.P.R. 1983. Environmental constraints in water resource development. Proceedings Seventh Quinquennial Convention of the South African Institution of Civil Engineers 1: 16–22.

TUREK, J.G., GOODGER, T.E., BIGFORD, T.E. & NICHOLS, J.S. 1987. Influence of freshwater inflows on estuarine productivity. NOAA Technical Memorandum NMFS-F/NEC-46: 26 pp.

WOOLDRIDGE, T. & BAILEY, C. 1982. Euryhaline zooplankton of the Sundays estuary and notes on trophic relationships. *S. Afr. J. Zool.* 17: 151–163.

WOOLDRIDGE, T. & MELVILLE-SMITH, R. 1979. Copepod succession in two South African estuaries. *J. Plank. Res.* 1: 329–342.