



Small-scale distribution and variability of demersal zooplankton in a shallow, temperate estuary: tidal and depth effects on species-specific heterogeneity.

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Abstract: The way and extent water-depth, tidal-currents and species-specific migratory behaviour affect plankton distribution were quantified in the benthic-pelagic zooplankton community of the upper Gamtoos estuary, South Africa. To compare tidal and non-tidal waters, nocturnal plankton densities were also recorded in the temporarily closed Kabeljous estuary. Most species aggregated near the sediment, especially during ebb-tides when plankters avoided faster seaward currents in surface waters. Tidal current direction modified vertical plankton stratification in even very shallow waters (ca. 1 m) by changing the amplitude of vertical migration - probably promoting retention of estuarine populations. Amphipods, and to a lesser degree cumaceans, became planktonic mainly during flood-tides, giving rise to marked differences in community structure between tidal phases and significantly increasing species diversity. In non-tidal waters, temporal density fluctuations were a function of differences in species-specific migratory behaviours. Under tidal conditions, temporal variability increased significantly with the degree plankters were axially displaced by tidal-currents. Thus, in tidal estuaries, temporal variations in plankton abundance at any given station are the combined outcome of pulses in active vertical migration and passive tidal dispersal. Consequently, multilevel sampling during both ebb- and flood-tides is seen as a minimum prerequisite for density estimation of estuarine zooplankton.

Résumé : Les effets de la profondeur de l'eau, des courants de marée et du comportement migratoire spécifique sur la distribution du plancton ont été étudiés dans la communauté zooplanctonique benthic-pélagique de la partie haute de l'estuaire Gamtoos, Afrique du Sud. Pour comparer les eaux influencées ou non par la marée, des densités de plancton nocturne ont également été enregistrées dans l'estuaire Kabeljous, temporairement clos. La plupart des espèces se concentrent près du sédiment en particulier pendant les marées descendantes où les organismes planctoniques évitent les courants de surface rapides vers la mer. La direction des courants de marée modifie la stratification verticale du plancton, même dans des eaux très peu profondes (environ 1 m), en changeant l'amplitude de la migration verticale, ce qui favorise probablement la rétention de populations estuariennes. Les amphipodes et à un moindre degré les cumacés deviennent planctoniques principalement durant les marées hautes, donnant lieu à des différences marquées dans la structure des communautés au cours du cycle de marée et augmentant significativement la diversité spécifique. Dans les eaux qui ne sont pas influencées par la marée, les fluctuations de densité temporelle sont fonction des comportements migratoires différents selon les espèces. Dans celles influencées par la marée, la variabilité temporelle s'accroît avec le déplacement axial dû aux courants de marée. Ainsi dans de tels estuaires, les variations temporelles de l'abondance du plancton à chaque station sont le résultat de migrations verticales actives et de dispersions passives dues à la marée. En conséquence, des prélèvements à différents niveaux, à la fois pendant les marées descendantes et montantes, sont des préalables indispensables à l'estimation des populations zooplanctoniques estuariennes.

Keywords: Plankton, Estuaries, Distribution, Variance, Sampling.

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Introduction

Accounting for spatial distribution of individuals is of fundamental importance in ecology and quantitative information pertaining to spatial and temporal population variability is the prerequisite to extract patterns of species dynamics and behaviour (Pimm, 1984; McArdle *et al.*, 1990).

For zooplankton the classical view that individuals are randomly distributed, acting as passively drifting particles, has over the last few decades shifted to a concept of spatial and temporal heterogeneity similar to that of terrestrial and other aquatic organisms (Downing *et al.*, 1987; Pinel-Alloul *et al.*, 1988). Such spatial and temporal heterogeneity in natural zooplankton communities may arise from both physical forces (e.g. aggregation by wind-driven water motion) and behavioural processes (e.g. social swarming behaviour). Among the active behavioural patterns displayed by zooplankton, vertical migration is the most striking and pervasive, significantly changing distributions in space and time (Stich & Lambert, 1981; Dill, 1987; Bollens & Frost, 1991). Vertical migration is also a potentially important mechanism by which planktonic organisms regulate horizontal position (Hill, 1991). This has fundamental significance for estuarine plankton, aiding in the retention of populations within the estuary given the prevailing net seaward flow of water (e.g. Weinstein *et al.*, 1980; Wooldridge & Erasmus, 1980; Schlacher & Wooldridge, 1994).

This paper focuses on spatial and temporal heterogeneity in demersal estuarine zooplankton and specifically aims to: a) determine the influence of tide and water-depth on taxon specificity of small-scale spatial distribution patterns, b) to quantify short-term, species-specific temporal variability, and c) to identify migratory behavioural patterns that result in observed density fluctuations and to assess their functional significance.

Methods

Sampling

Study sites

Plankton samples were collected in the Gamtoos and Kabeljous estuaries, situated on the south-east Cape coast of South Africa (Fig. 1). The Gamtoos is a microtidal, shallow, and turbid system, with a highly dynamic but permanently open tidal inlet. Its tributaries drain a catchment area of 34450 km² with a mean annual runoff of 501 10⁶ m³, and the tidal waters of the estuary extend over c. 20 km. The main channel of the estuary is narrow (< 50 m) and shallow (< 1.5 m) at the tidal inlet, but widens to 100 to 250 m in the lower reaches where average water depth is around 3 m. Up-estuary of 10 km from the inlet, the channel becomes progressively narrower (< 100 m) and shallower (< 2.5 m) towards the tidal head. (Heinecken, 1981; Reddering & Scarr, 1990).

The Kabeljous is a considerably smaller estuary (Fig. 1). Its tidal inlet closes temporarily during periods of low freshwater inflow when a 100 to 200 m wide sandbar forms across the mouth (Fig. 1). Its tributaries receive 16 10⁶ m³ run-off per year from a watershed area of 262 km². When the estuary is open to the sea, the tidal influence extends for c. 2.25 km upstream. A shallow lagoon with an average depth of 0.5 m forms the lower estuary and leads further upstream to a 1.7 km long channel of 1.6 to 2.3 m water depth (Reddering & Esterhuysen, 1984; Bickerton & Pierce, 1988).

The climate in the region is predominantly semi-arid with a mean annual rainfall of less than 500 mm, and periods of severe drought are often punctuated by heavy floods. Thus, rainfall is extremely unevenly distributed both in time and space. During times of reduced freshwater input, longshore and flood-tidal transport of marine sand closes the tidal inlet of small estuaries, such as the Kabeljous, often resulting in the development of hypersaline conditions. Subsequent floods scour accumulated sediments from the estuaries and completely flush the estuarine reaches with fresh water. Amplitudes and patterns of freshwater input are also significantly altered by large water storage reservoirs in the catchment basins. As a consequence of the highly erratic river flow regimes, and in contrast to many temperate estuaries of the Northern Hemisphere, salinity regimes in South African estuaries are generally not the outcome of seasonal differences in rainfall, but of the drought-flood cycle and of water release management from dams.

Field sampling

Pilot sampling over the diel cycle on both the ebb- and the flood-tide showed that most species of the estuarine zooplankton are nycthemeral, ascending into the water column only after sunset and returning to the sediment or benthic boundary layer before dawn. Since for most species of this category no clear distinction can be drawn between planktonic species *s.str.* and benthic species *s.str.*, here mesozooplankton is simply defined as all free-swimming and free-floating, heterotrophic organisms present in the water column and collected with standard WP2-plankton nets of 0.2 mm mesh aperture size.

For the present study, we collected seven series of nocturnal plankton samples in the upper reaches of the tidal Gamtoos estuary and one series in the non-tidal Kabeljous. A total of 226 samples was collected (Fig. 1, Table 1). Sampling usually commenced 30 min after sunset and the last sample was taken 30 min before sunrise. In series 6 to 8 a control sample was taken one hour before dusk and one hour after dawn to check the adequacy of the night-sampling regime: densities in these daylight samples were one to two orders of magnitude lower compared with samples collected at night. To assess the nature and magnitude

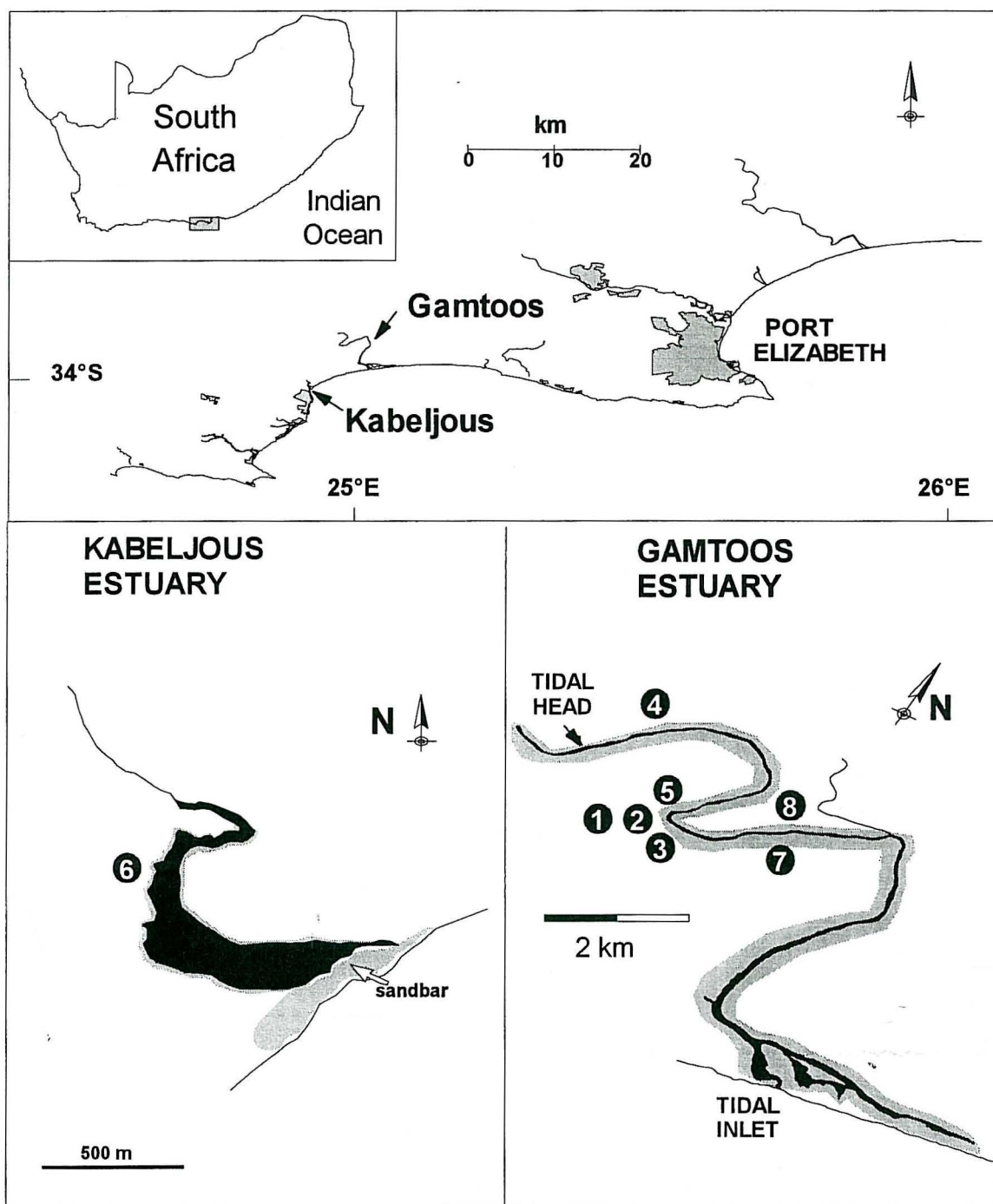


Figure 1. Location of Gamtoos and Kabeljous estuary and position of sampling sites. Site numbers correspond to sample series mentioned in the text (*cf.* Table 1).

Figure 1. Localisation des estuaires de Gamtoos et Kabeljous et emplacement des sites d'échantillonnages. Les numéros des sites correspondent aux séries d'échantillonnage mentionnées dans le texte (*cf.* Tableau 1).

of axial tidal drift, hauls were also made over a full tidal cycle at neap- and at spring-tides at three stations positioned at c. 250 m intervals along the longitudinal axis of the estuary; these samples comprised series 1 and 2 (Table 1). A detailed description of the site topography and the sampling

regime for series 1 to 3 is given in Schlacher & Wooldridge (1994). In sample series 4 to 8, a time series of samples was collected at a single, fixed anchor-station, to determine short-term temporal patterns in plankton abundance.

Table 1. Summary of site characteristics, sampling protocol and physical parameters for sample series 1 - 8 analysed in this study.**Tableau 1.** Caractéristiques des sites, protocoles d'échantillonnage et paramètres physiques pour les séries 1 - 8 analysées dans cette étude.

	Sample Series								
	1	2	3	4	5	6	7	8	
Sampling date	23/05/90	19/06/90	23/06/90	25/02/91	11/06/91	04/02/92	14/06/93	19/06/93	
Estuary	Gamt.	Gamt.	Gamt.	Gamt.	Gamt.	Kabel.	Gamt.	Gamt.	
State of tidal inlet	open	open	open	open	open	closed	open	open	
Distance of sampling site from sea (km)	14.4	14.4	14.3	19.0	14.4	1.5	11.9	11.9	
Number of stations sampled	3	3	3	1	1	1	1	1	
Distance between stations (m)	250	250	50	—	—	—	—	—	
Max. water depth (m)	2	2	2	1	2	1.5	2	2	
Number of samples taken	21	28	41	20	34	22	30	30	
Sample interval (min)	120	120	90	60	45	60	60	60	
Salinity	Surface	11.2	14.2	13.0	ca. 10	19.6	55.3	2.8	1.8
(mean psu)	Bottom	14.7	18.9	15.7	ca. 10	25.4	55.3	19.1	31.3
Temperature	Surface	13.8	13.0	12.0	23.6	15.9	28.5	15.0	13.1
(mean °C)	Bottom	13.7	14.7	13.4	25.2	17.0	28.5	16.5	16.1

Zooplankton was sampled with WP2-nets (mouth diameter 57 cm, mesh aperture size 0.2 mm). Two nets were attached to booms protruding laterally from the bow of a 4.5 m long skiboat; this arrangement ensured that the nets sampled water not disturbed by the hull of the boat. One net sampled 5 to 10 cm below the water surface and the other net was lowered to c. 25 cm above the bottom. Both nets were fitted with Kahlisco 005 WA 130 flowmeters and towed simultaneously at 1 to 2 knots for c. 2 min. The average water volume filtered per haul was 13.3 m³. The catch from each haul was immediately preserved in c. 5 % formalin in the field.

Prior to each plankton haul, depth profiles of temperature and salinity were recorded at 0.5 m intervals with a YSI model 33 S.C.T. or with a Valeport CTD meter. Current profiles were measured with a hand-held Oceanic Flowmeter model 2035 Mk III or with custom-built VACMs (Vector Averaging Current Meters). The ocean tide off this part of the coast is mainly semi-diurnal with a mean tidal range of 0.51 m and 1.61 m at neap- and spring-tides respectively. Mean tidal range in the Gamtoos estuary, c. 14 km upstream from the mouth was 0.32 to 0.41 m at neap-tides, and 0.55 to 0.63 m at spring-tides. These data were obtained during the present study, where continuous water level recorders were deployed adjacent to plankton sampling sites.

Data analysis

Temporal variability in planktonic density

To compare variability in density over time between plankton species, both Wolda's (1978) measure of temporal variation (AV) and the coefficient of variation (CV) were

computed from abundance data of each individual species in each individual samples series (*cf.* Table 1). Wolda (1978) introduced his index of temporal variation in population size under the term "annual variability" (AV): for any species in a given area the change in abundance between consecutive years is expressed by the difference (log R) of their logarithmic densities from one year to next: $\log R = \log N_i - \log N_{i-1}$, where N_i is density at time i . For a set of species these values of log R then form a frequency distribution and AV is simply the variance of this distribution: $s^2(\log R)$. Annual variability (AV) essentially describes the range of density increases and decreases which occurred among the taxa of an assemblage (Wolda, 1978). Here an important distinction of terms must be drawn between the original application of this index and its use adopted here. Wolda (1978) measured variability within a set of species, whereas we measured temporal variability within individual species. Thus, in the present situation, the AV of a particular species is the variance of all its log R-values calculated from its densities in consecutive samples. Consequently, it measures the range of density changes which occurred within a particular species from one sample to the next. Because sampling intervals in this study were in the range of hours instead of years, the original term "annual variability" AV is in the present context modified to "hourly variability" HV. Because any transformation of zero data introduces a large bias in the estimation of population variability - save the coefficient of variation (McArdle *et al.*, 1990) - all pairs of sequential samples which included zero-densities were excluded from the computation of hourly variability. To determine intertaxonomic differences in hourly variability,

the equality of variances of log R was tested among species by Levene's test (Van Valen, 1978).

Whereas AV looks at variability about trends in densities, the coefficient of variation (CV) estimates variability about the mean density in a given data set. It outperforms all other classic univariate measures of variability in being a) a scale-free measurement, b) independent of sample size, and c) not affected by zero data (McArdle *et al.*, 1990). In this study, temporal variability about the mean was compared among species by Taylor power plots of log (CV) versus log (mean density). Only species which were recorded in at least 6 of the 8 data sets were included in these regressions. If species-specific CV-values were not independent of their respective mean densities, and if the range of CVs overlapped with other taxa, the species was excluded from subsequent comparison of mean CVs by Anova; this data elimination is necessary, because in the above cases no general statement about relative variability is possible (McArdle *et al.*, 1990).

Downing *et al.* (1987) present an empirically derived algorithm, which predicts the interreplicate variance (s^2) of zooplankton samples from mean density and sampler size: $s^2 = 0.745 m^{1.622} V^{-0.267}$, where m is density of organisms per litre and V the sample volume in litres. To test if temporal heterogeneity of estuarine plankton observed in the present sampling situations follows the predictions of this general relationship, we calculated interreplicate variances from data sets 1 to 8 and compared them with predictions of s^2 obtained from Downing *et al.*'s (1987) equation.

Precision (D), which measures variation about the sample estimate itself and not the actual variation in temporal or spatial density observed in the field, is expressed by the ratio of the standard error (se) to the sample mean (m): $D = se/m$ (Downing, 1984); a high value of D denotes low precision of the sample estimate and *vice versa*.

Tidal shift

For data sets comprising samples taken simultaneously at the three stations spaced c. 250 m apart along the axis of the estuary, the centre of abundance of the planktonic population was estimated by the index of weighted mean position: $WMP = \frac{\sum_{i=1}^3 (n_i S_i)}{\sum_{i=1}^3 n_i}$, where n_i is abundance (ind. m^{-3}) at station S_i (Schlacher & Wooldridge, 1994). This index is conceptually analogous to the weighted mean depth (WMD) of Bollens & Frost (1991) and the depth-centre of mass (Z_{cm}) of Fortier & Legget (1983), but it measures the horizontal and not the vertical position of the population centre. Fluctuations of the centre of abundance over a full tidal cycle were used to assess the amplitude of axial tidal displacement.

Dispersion of a planktonic species between the three axially positioned stations at a given sampling time was measured by the Index of Dispersion Id. The Index is simply the population variance of proportional abundances at

stations 1 to 3: $\frac{1}{3} \sum_{i=1}^3 (p_i - \bar{p})^2$, where p_i is the percentage of individuals found at station i , and \bar{p} is the average percentage of individuals per station. Id reaches zero when organisms are equally abundant at all stations (i.e. maximum dispersion) and is maximum when all individuals are found at a single station (i.e. minimum dispersion). Again, the index is essentially the same as Fortier & Legget's (1983) "index of vertical dissemination" (s), but in the present study it is expressed by Id to avoid confusion with the sample standard deviation which is conventionally denoted by s .

All correlations were computed using Spearman's rank correlation and the combined probability method of Fisher. Applications of this correlation method to distribution data of plankton and explanations on computational procedures are given in detail by McCleave *et al.* (1987).

Results

Effects of depth on sample estimates

Density

The majority of species were significantly more abundant in bottom waters in about half of the eight series sampled (Table 2). On all other sampling dates, most species showed no significant difference in density between levels in the water column. Only the amphipod *Grandidierella lignorum* was found in a single sample series to be more abundant in surface waters (Table 2). Likewise, 89% of all species never occurred in significantly higher densities near the water surface. Densities of zoea larvae did not differ between depths on any sampling date (Table 2). Total planktonic density was significantly higher near the sediment in 62% of sample series, equal between depths in 25% of series, and significantly higher in surface waters on only 13% of dates sampled (Table 2).

Depth-distribution of plankton was, however, strongly affected by the phase of the tidal cycle. On ebb-tides, total density of all species combined was significantly higher in bottom waters. By contrast, on flood-tides when zooplankton was distributed throughout the water column, densities were equal between depths (Fig. 2). Similarly, half of all species were concentrated near the bottom during ebb-tides, compared with only 17% of species during flood-tides (Table 3). Again, no single species was significantly more abundant in surface waters during any tidal phase (Table 3).

Community composition

Community structure differed significantly between samples taken near the sediment and samples taken close to the water surface (Fig. 3A; 5x2-contingency table, $\chi^2 = 958$, $p < 0.0001$). Marked shifts in community composition between depths resulted mainly from a) the higher proportional densities of the copepods *Acartia* spp. in near-bottom waters, and b) an increase in relative densities of amphipods from deep to shallow strata (Fig. 3A). Numerical dominance of all other taxa changed little with water depth (Fig. 3A).

Table 2. Comparison of plankton density between surface- and bottom waters. Both depth levels were sampled simultaneously in eight sample series (refer to Fig. 1 & Table 1). Median densities per depth were compared for individual sample-series and species by Wilcoxon paired sample tests.

Tableau 2. Comparaison des densités de plancton entre les eaux de surface et celles du fond. Les deux profondeurs ont été échantillonnées simultanément dans 8 séries (voir Fig. 1 & Tableau 1). Les densités moyennes à chaque profondeur ont été comparées pour chaque série et par espèce par le test de Wilcoxon.

Species	Higher Taxon	Percentage of sample-series having		
		A - significantly higher density at level:	B - no difference in density between depths.	
		Surface	Bottom	
<i>Pseudodiaptomus hessei</i> Mrazek	Copepoda	0%	57%	43%
<i>Acartia natalensis</i> Conell & Grindley	Copepoda	0%	57%	43%
<i>Harpacticoid</i> Copepods	Copepoda	0%	29%	71%
<i>Zoea</i> Larvae	Brachyura	0%	0%	100%
<i>Rhopalophthalmus terranatalis</i> Tattersall	Mysidacea	0%	67%	33%
<i>Mesopodopsis wooldridgei</i> Wittmann	Mysidacea	0%	50%	50%
<i>Gastrosaccus brevifissura</i> Tattersall	Mysidacea	0%	40%	60%
<i>Iphinoe truncata</i> Hale	Cumacea	0%	50%	50%
<i>Cirolana fluviatilis</i> Stebbing	Isopoda	0%	43%	57%
<i>Grandidierella lignorum</i> Barnard	Amphipoda	13%	25%	62%
Total density		13%	62%	25%

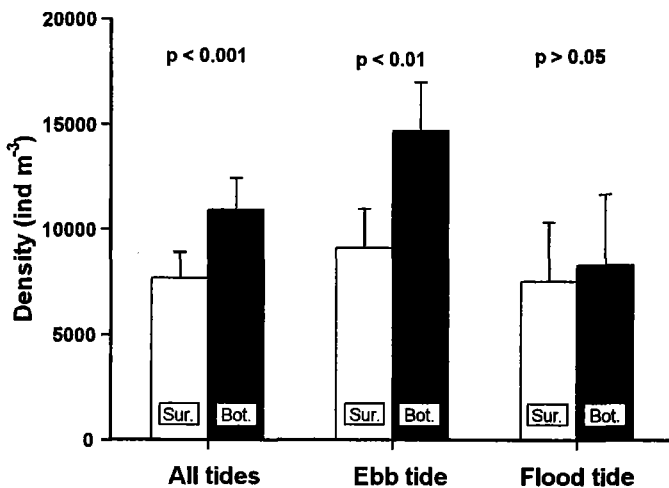


Figure 2. Comparison of total planktonic density between surface (open bars) and bottom waters (solid bars) at different phases of the tidal cycle. Error bars are one se with $n = 91$ for all tides, $n = 43$ for ebb tides, and $n = 24$ for flood tides. Median densities between depth levels compared by Wilcoxon paired sample test.

Figure 2. Comparaison des densités planctoniques totales des eaux de surface (en blanc) et des eaux du fond (en noir) à différentes phases du cycle de marée. Les écarts types sont calculés sur $n = 91$ pour toutes les marées, $n = 43$ pour les marées descendantes et $n = 24$ pour les marées montantes. Les densités moyennes à différentes profondeurs sont comparées par le test de Wilcoxon.

Table 3. Percentage of species which were significantly ($p < 0.05$) more abundant at a certain depth or showed no difference ($p > 0.05$) in density between surface and bottom waters. Data for comparison of median density between depths levels are pooled from all data series where paired surface and bottom samples were obtained. All Tides denotes data pooled from both ebb- and flood-tides.

Tableau 3. Pourcentage des espèces qui étaient significativement ($p < 0,05$) plus abondantes à une certaine profondeur ou ne montraient pas de différence ($p > 0,05$) en densité entre les eaux de surface et celles de profondeur. Les données pour la comparaison des densités moyennes à différentes profondeurs sont regroupées à partir de toutes les séries où des couples de données (surface et profondeur) ont été obtenues. "All tides" indique toutes les données regroupées pour les marées descendantes et montantes.

	All Tides	Ebb Tide	Flood Tide
Higher Abundance in:			
a) Surface Waters	0%	0%	0%
b) Bottom Waters	58%	50%	17%
No Difference between depths	42%	50%	83%

Although more species were on average recorded in deeper waters, all other diversity indices and comparison of K-dominance curves point to a more diverse plankton community in surface waters (Table 4, Fig. 4A). This can mainly be ascribed to the higher proportional density of

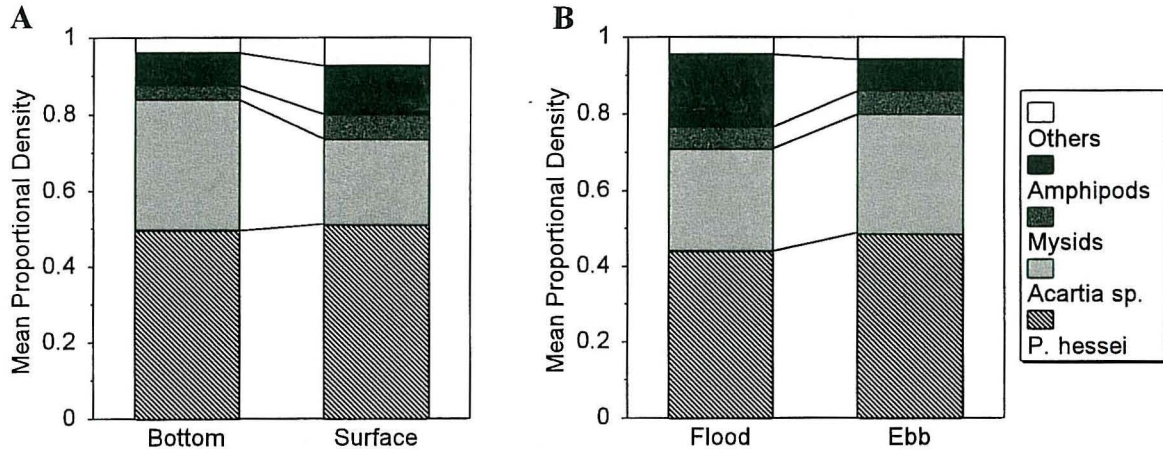


Figure 3. Composition of the zooplankton assemblage at A - two depth-levels and B - at flood- and ebb-tide. Community structure is depicted as the mean proportional numerical abundance of dominant species and higher taxa.

Figure 3. Composition des ensembles zooplanctoniques, en A - deux niveaux de profondeur, en B - à marées montante et descendante. La structure de la communauté est décrite comme l'abondance numérique proportionnelle moyenne des espèces dominantes et des taxons de rang élevé.

rarer taxa in surface samples (Fig. 3A), which primarily included fish-larvae, isopods, cumaceans, cladocerans, and amphipods other than the generally abundant *Grandidierella lignorum*. Evenness of species abundances did not differ between depths (Table 4).

Effects of tide on sample estimates

Density

The amphipod *Grandidierella lignorum* and the cumacean *Iphinoe truncata*, both peracarid crustaceans, are endo-

Table 4. Comparisons of biotic diversity between plankton in surface- and in bottom waters, and between flood- and ebb-tides. H' = Shannon's index, λ = Simpson's index.

Tableau 4. Comparaison de la diversité biotique du plancton des eaux de surface et de fond lors des marées montantes et descendantes. H' index de Shannon, λ = index de Simpson.

Indices	Depth			Tide		
	Surface	Bottom	p^1	Flood	Ebb	p^2
Richness						
Hill's N0	$N0 = S$	8.01	8.59	**	9.05	8.39 *
Diversity						
Hill's N1	$N1 = e^{H'}$	2.53	2.35	n.s.	2.98	2.52 *
Hill's N2	$N2 = \frac{1}{\lambda}$	2.12	1.90	n.s.	2.37	2.05 *
Evenness						
Hill's E5	$E5 = \frac{N2-1}{N1-1}$	0.68	0.64	n.s.	0.67	0.66 n.s.

1 Wilcoxon paired sample test, $n = 90$.

2 Mann-Whitney-U-test; ebb: $n = 104$, flood: $n = 64$.

* $p < 0.05$, ** $p < 0.01$, n.s. : no significant difference ($p > 0.05$)

benthic during the day. At night they attained significantly higher densities in the plankton on flood- compared with ebb-tides. Median pelagic abundance of all other species as well as total planktonic density did not differ significantly between tidal phases (Table 5).

Community composition

Composition of the planktonic community, depicted as proportional abundance of major taxa, changed markedly between phases of the tidal cycle (Fig. 3B; 5×2 -contingency table, $\chi^2 = 599$, $p < 0.0001$). The calanoid copepod *Pseudodiaptomus hessei* was numerically dominant on both tides, but its relative density did not vary greatly over the tidal cycle, the species accounting for 44% and 49% of the total catch during floods and ebbs respectively (Fig. 3B). Similarly, numbers of the second most abundant taxon, *Acartia* spp., increased only slightly on the ebb-tides. By contrast, relative planktonic density of the amphipod *Grandidierella lignorum* rose steeply from 8% during ebbs to 19% during floods (Fig. 3B).

More species were present in the water column during flood- compared with ebb-tides, both in terms of mean species richness and the mean number of abundant (Hill's N1) and very abundant (Hill's N2) planktonic species (Table 4, Fig. 4B). This increase in species diversity from ebb- to flood-tides coincided with a steep rise in planktonic density of the amphipod *Grandidierella lignorum* and to a lesser extent of the cumacean *Iphinoe truncata* (Table 5). When both species are removed from the original data set, calculated species richness and diversity did not differ significantly between tidal phases (U-test, max. $Z = 1.63$, min. $p > 0.10$).

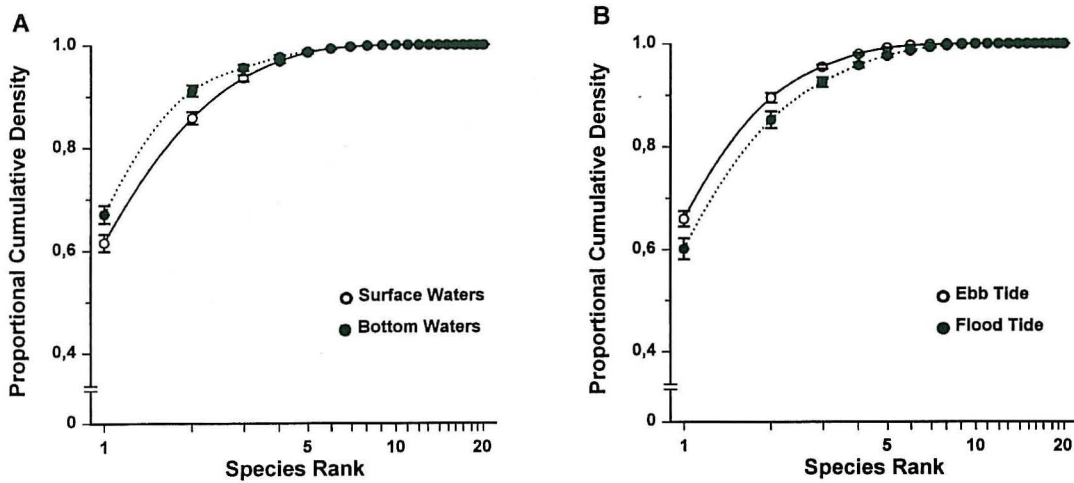


Figure 4. K-dominance curves for zooplankton assemblage in A surface - (○) and bottom-waters (●), and B - at ebb- (○) and flood-tide (●). Error bars represent one standard error of mean proportional cumulative density.

Figure 4. Courbes de dominance K pour des ensembles zooplanctoniques, en A - eaux de surface (○) et (●) de fond, en B - à marée descendante (○) et marée montante (●). Les écarts types représentent l'erreur standard de la densité proportionnelle moyenne cumulée.

Temporal variability in planktonic density

Compared with all other taxa, density of the corophiid amphipod *Grandidierella lignorum* in the plankton was most variable over time, both in terms of density changes between consecutive samples, as well as variation about mean density at a given site and date. The species showed

both marked increases as well as steep declines in abundance from one sample to the next. This is reflected by the significantly highest value of hourly variability and the shape of the actual frequency distributions of log R values (Fig. 5D, Table 6). In comparison, the calanoid copepods *Pseudodiaptomus hessei* and *Acartia natalensis* fluctuated

Table 5. Comparison of plankton density (ind m⁻³) between ebb- and flood-tides. Median densities per tidal phase were compared by Mann-Whitney-U-tests.

Tableau 5. Comparaison des densités de plancton (ind m⁻³) au cours des marées descendantes et montantes. Les densités moyennes par phase de marée ont été comparées par le test U de Mann-Whitney.

Taxon	Ebb Tide n = 104		Flood Tide n = 64		Mann Whitney U-test	
	Mean	se	Mean	se	Z	p
<i>Pseudodiaptomus hessei</i>	4791.0	794.9	3769.4	1216.5	-0.925	0.355
<i>Acartia natalensis</i>	4101.2	714.6	2376.1	570.7	-1.641	0.101
<i>Harpacticoid Copepods</i>	24.2	3.6	26.6	4.8	0.343	0.732
<i>Zoea Larvae</i>	21.1	7.2	13.1	2.7	-0.126	0.100
<i>Rhopalophthalmus terranatalis</i>	4.8	1.6	5.0	0.9	1.035	0.301
<i>Mesopodopsis wooldridgei</i>	39.1	9.2	31.1	7.3	0.937	0.349
<i>Gastrosaccus brevifissura</i>	131.1	20.9	73.0	11.2	-0.824	0.410
<i>Iphinoe truncata</i>	29.8	5.8	73.3	18.2	2.473	0.013
<i>Cirolana fluviatilis</i>	2.0	0.5	1.5	0.3	-0.930	0.352
<i>Grandidierella lignorum</i>	533.8	229.8	1182.5	391.3	5.671	1.425 10 ⁻⁸
Total density	9663.9	1292.4	7541.4	1734.7	-0.559	0.576

least over time. (Fig. 5 A, B, Table 6). These species were also the two most abundant taxa, comprising on average over 75% of total plankton numbers. Although the density of harpacticoids changed relatively little between sequential samples, the CV of temporal density was high in this group. This points to relatively consistent temporal trends but large fluctuations about mean density (Table 6). All other taxa were generally intermediate in temporal variability.

Apart from intertaxonomic differences in temporal variability, sample variances of individual species at a given site were markedly higher than those predicted by Downing's (1987) general zooplankton variance function (Fig. 6). Out of 160 variance estimates for individual species obtained in this study, 152 or 95% of observations lay above the values predicted by the general variance algorithm. This difference between actual and predicted sample variance was especially pronounced for species occurring at higher densities. Similarly, at half of all sites sampled, temporal variance of

total planktonic density was higher than that calculated from Downing's *et al.* (1987) general variance relationship.

This comparatively high interreplicate variances gave rise to a relatively low precision of sample estimates. This even held at for plankton studies relatively high replication levels ($n = 15$) and in the non-tidal, hydrodynamically stable waters of the Kabeljous estuary. Consequently, only 13% of all density estimates for individual species had standard errors which equalled or were smaller than 20% of the sample mean (i.e. $d \leq 0.2$, Fig. 7). A precision level (d) of roughly 0.2, however, is required if a halving or doubling of the population is to be demonstrated by inferential statistics (Downing, 1984). In the present data set more than half of all density estimates for individual species could only be obtained with a precision lower than 0.4 (Fig. 7). Total density measures showed better repeatability with 50 % of all samples having precision values smaller than 0.2 and no single estimate lying above $d = 0.3$.

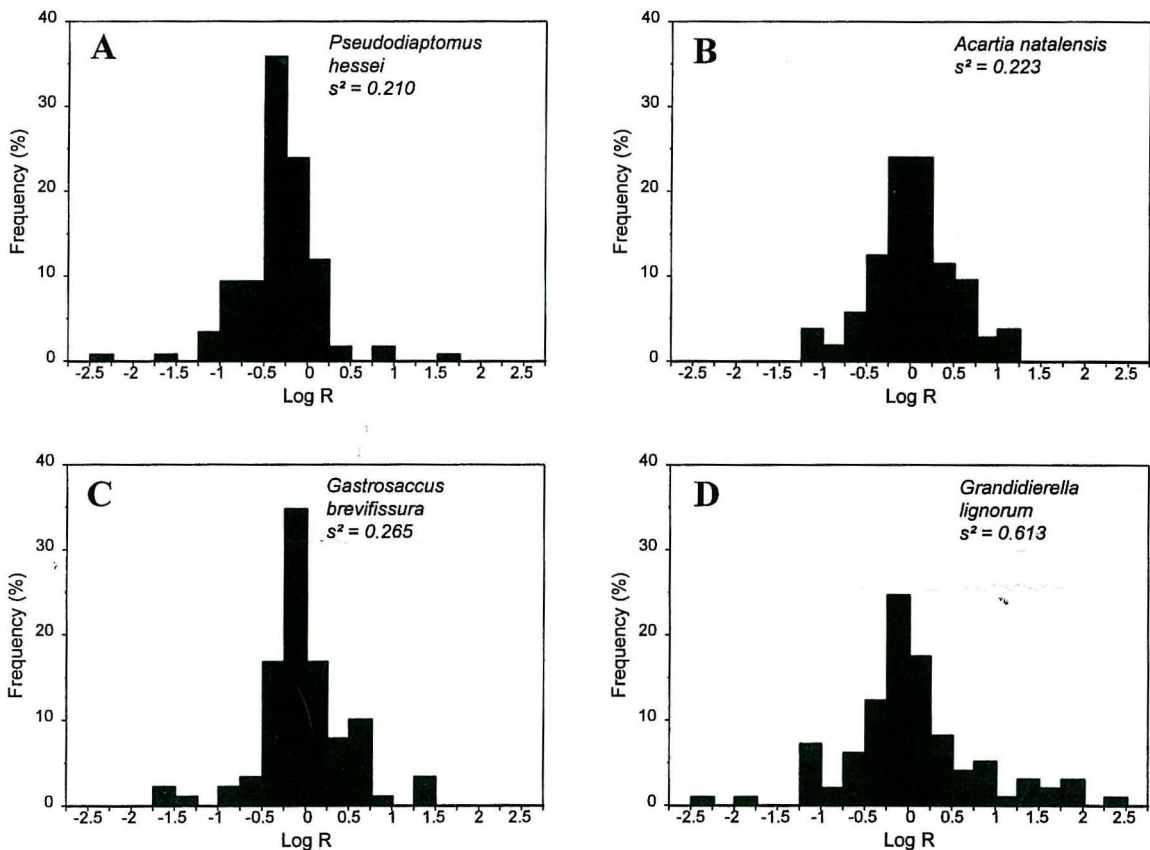


Figure 5. Frequency distribution of log R values for some selected zooplankton species ; log R is the difference in \log_{10} densities between consecutive samples, i.e. $\log R = (\log N_{i-1} - \log N_i)$, where N_i is density of species x at time i. A - *Pseudodiaptomus hessei* (copepod), B - *Acartia natalensis* (copepod), C - *Gastrosaccus brevifissura* (opossum shrimp), and D - *Grandidierella lignorum* (amphipod).

Figure 5. Distribution des fréquences des valeurs de log R pour quelques espèces du zooplancton; log R est la différence des densités en \log_{10} entre échantillons successifs, c.-à.-d. $\log R = (\log N_{i-1} - \log N_i)$ où N_i est la densité de l'espèce x à l'instant i. A - *Pseudodiaptomus hessei* (copépode), B - *Acartia natalensis* (copépode), C - *Gastrosaccus brevifissura* (mysidacé), et D - *Grandidierella lignorum* (amphipode).

Table 6. Comparison of temporal variability in planktonic density between species. Hourly variability (variance of Log R) calculated from all differences in log-densities between consecutive samples in data series 1-8, i.e. $\log R = (\log N_{i-1} - \log N_i)$, where N_i is density of species x at time i . Coefficients of variation calculated per individual data set. Only taxa which were recorded in at least 75% of all sample series are included in the analysis.

Tableau 6. Comparaison de la variabilité temporelle de la densité planctonique entre espèces. Variabilité horaire (variance de $\log R$) calculée à partir de toutes les différences transformées en \log des densités entre les échantillons consécutifs des séries 1-8, c.-à.-d. $\log R = (\log N_{i-1} - \log N_i)$ où N_i est la densité de l'espèce x à l'instant i . Les coefficients de variation sont calculés par séries de données individuelles. Seuls les taxons récoltés dans au moins 75 % de toutes les séries d'échantillonnages sont pris en compte dans l'analyse.

Taxon	Hourly Variability			Coefficient of variation	
	Mean	Variance	SNK -test ¹	CV = 100 (s/m)	se
<i>Pseudodiaptomus hessei</i>	-0.056	0.210	o	63.4	6.02
<i>Acartia natalensis</i>	0.026	0.223	o	82.9	19.22
<i>Harpacticoid Copepods</i>	0.020	0.239	o	123.3	31.56
<i>Zoea Larvae</i>	-0.017	0.396	o +	105.5	11.79
<i>Rhopalophthalmus terranatalis</i>	0.012	0.390	o +	122.6	25.79
<i>Mesopodopsis woodridgei</i>	0.01	0.467	o +	107.9	13.34
<i>Gastrosaccus brevifissura</i>	-0.025	0.265	o	96.1	30.01
<i>Iphinoe truncata</i>	0.034	0.325	o +	88.8	9.14
<i>Cirolana fluviatilis</i>	-0.036	0.328	o +	127.3	28.59
<i>Grandidiarella lignorum</i>	0.035	0.613	+	133.4	16.94

ANOVA ¹	d.f. = 9, 849	d.f. = 9, 63
	F = 3.852 p = 0.001	F = 1.603 p = 0.134

¹ Equality of variances ($s^2(\log R)$) among species tested by Levene's test and post-hoc multiple comparison by Student-Newman-Keuls test: homogenous groups denoted by o and +. Mean coefficients of variations (CV) compared among species by Fixed-Effects-Anova.

Regression analysis of Taylor power plots of $\log(CV)$ versus $\log(\text{mean density})$ showed that temporal population variability was generally independent of mean density (max. $\beta_t = -0.294$; max. $t = -2.36$; min. d.f. = 5; min. $p = 0.08$). This indicates that variability of a species measured over time did generally not differ significantly among sites. Only harpacticoid copepods were significantly more variable at sites where they occurred at low densities ($\beta_t = -0.329$; $t = -2.59$; d.f. = 7; $p = 0.04$).

Axial Tidal Drift

Amplitude of tidal drift

Axial tidal transport was of roughly the same magnitude for all species on both the neap- and spring-tides, as indicated by the equality of the coefficients of variation of WMP and Id (Table 7). When the amplitude of tidal transport is measured by the range of WMP, the centre of abundance of

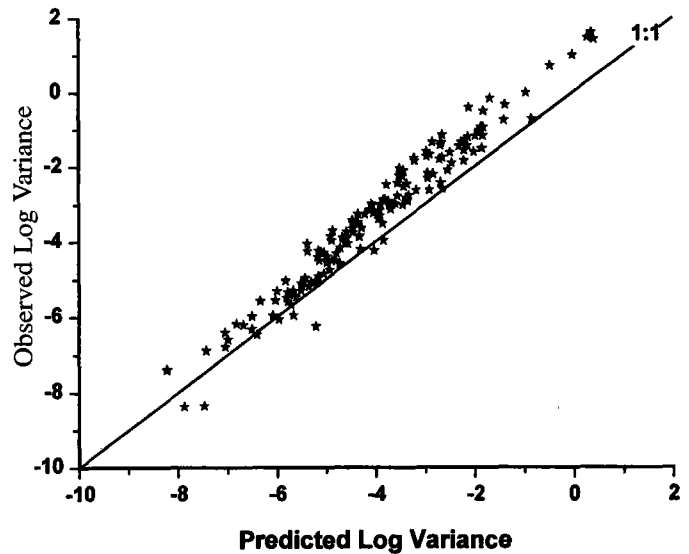


Figure 6. Comparison between interreplicate variances of individual species predicted by the general variance function published for zooplankton by Downing *et al.* (1987) and variance estimates obtained for estuarine zooplankton in this study (*). The solid line indicates a 1:1 relationship between predictions and independent observations. Number of replicate sets: 160.

Figure 6. Comparaison entre les variances des espèces individuelles estimées par la fonction de variance générale publiée pour le zooplancton par Downing *et al.* (1987) et les valeurs des variances obtenues pour le zooplancton estuarien dans cette étude (*). Le trait plein indique une relation 1:1 entre les valeurs théoriques et observées. Nombre de séries observées : 160.

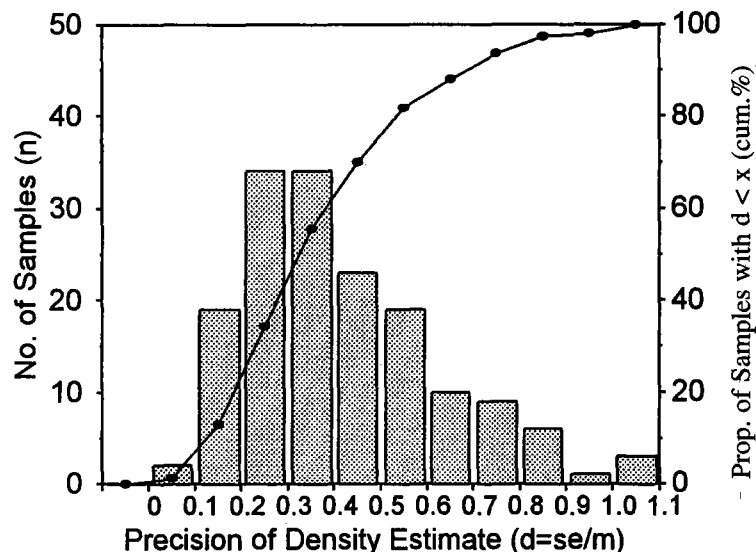


Figure 7. Distribution of precision values for density estimates obtained for individual species at fixed anchor stations (bars \square) and the cumulative percentage of sample estimates whose precision d equals or is better than x (line $- \bullet -$). Sample size $n = 160$. Precision (d) is defined as the ratio of the standard error (se) to the sample mean (m): $d = se/m$.

Figure 7. Distribution des valeurs obtenues pour les estimations de densité d'espèces individuelles à des stations fixes (\square) et les pourcentages cumulés des estimations des échantillons dont la densité estimée d , est égale ou supérieure à x (ligne $- \bullet -$). Taille de l'échantillon : 160. La précision (d) est définie comme le rapport de l'écart type (se) sur la moyenne de l'échantillon (m): $d = se/m$.

Table 7. Comparison of tidal transport between species sampled over a full tidal cycle at three axially located stations at spring- and neap-tide. Amplitude of tidal shift is estimated by a) the range of weighted mean position (WMP), b) the coefficient of variation (CV) of weighted mean position (WMP), and c) the coefficient of variation of the index of dispersion CV (Id).

Tableau 7. Comparaison du transport, dû aux courants de marée, des espèces échantillonnées au cours d'un cycle de marée, à trois stations localisées dans l'axe de l'estuaire lors de marées de vive eau et de morte eau. L'amplitude de la dérive est estimée par a) l'étendue de la position moyenne pondérée (WMP), b) son coefficient de variation (CV) et c) le coefficient de variation de l'index de dispersion CV (Id).

Taxon	Spring Tide			Neap Tide		
	WMP		Id	WMP		Id
	Range	CV	CV	Range	CV	CV
<i>Pseudodiaptomus heissei</i>	0.60	9.36	70.36	1.18	19.42	78.04
<i>Acartia natalensis</i>	0.79	15.48	86.59	1.40	23.61	91.54
<i>Rhopalophthalmus terranatalis</i>	1.71	31.54	93.10	0.36	6.41	98.99
<i>Mesopodopsis wooldridgei</i>	1.21	29.04	83.08	0.94	18.81	116.44
<i>Gastrosaccus brevifissura</i>	1.04	23.50	87.03	0.81	15.91	76.46
<i>Iphinoe truncata</i>	1.67	28.67	65.87	1.40	24.24	87.19
<i>Cirolana fluviatilis</i>	1.00	18.80	64.76	1.06	18.81	95.04
<i>Grandidierella lignorum</i>	1.18	22.04	101.25	1.22	24.27	140.75
ANOVA ¹	d.f.	7.40	7.40	7.48	7.48	
	F	1.560	0.242	1.329	0.394	
	P	0.174	0.972	0.258	0.901	

¹ Levene's test to compare equality of coefficients of variation (CVs).

copepods appeared to shift less over a tidal cycle compared with all other taxa on the neap-tide. This trend was reversed on the spring-tide, when mysids showed the smallest degree of tidal transport (Table 7).

Distribution in relation to tidal currents

During ebb-tides current velocities were significantly slower in near-bottom waters, the mean difference between depths being 13 cm s⁻¹ (Wilcoxon paired sample test, $Z = 2.712$, $n = 11$, $p = 0.007$). Under such stratified conditions the planktonic density of most species was significantly higher at deeper levels where slower ebb-currents prevailed (Table 8). Only the copepod *Acartia natalensis*, the cumacean *Iphinoe truncata* and the amphipod *Grandidierella lignorum* were equally abundant in both fast- and slow-flowing downstream currents (Table 8).

During flood-tides, the water column became well-mixed and tidal current speeds did not differ significantly between near-surface and near-bottom waters (mean difference = 4 cm s⁻¹; Wilcoxon paired sample test, $Z = 1.268$, $n = 7$, $p = 0.205$). Under such flow regimes, abundance of no individual species was correlated with tidal current speed at the corresponding sampling depth (Table 8).

The centre of abundance of the calanoid copepod *Acartia natalensis* and the opossum shrimp *Gastrosaccus brevifissura*

Table 8 Relationship between plankton density and water-current speed. Analysis used Fisher's combined probability method on Spearman's rank correlation coefficients.

Critical $\chi^2_{0.05, 6 \text{ d.f.}} = 12.592$ for both tides.

Tableau 8. Relation entre la densité du plancton et la vitesse du courant. L'analyse utilise la méthode de probabilité de Fischer à partir des coefficients de corrélation de rang de Spearman.

$\chi^2_{0.05, 6 \text{ d.f.}} = 12,592$ pour les deux marées.

Taxon	Ebb Tide		Flood Tide	
	Density is <i>not negatively</i> correlated with current speed	Density is <i>not positively</i> correlated with current speed	Density is <i>not negatively</i> correlated with current speed	Density is <i>not positively</i> correlated with current speed
	$-2 \sum \ln p_i$	p^1	$-2 \sum \ln p_i$	p^1
<i>Pseudodiaptomus heissei</i>	12.613	*	7.026	n.s.
<i>Acartia natalensis</i>	4.178	n.s.	2.536	n.s.
<i>Rhopalophthalmus terranatalis</i>	16.819	**	5.636	n.s.
<i>Mesopodopsis wooldridgei</i>	13.558	*	3.718	n.s.
<i>Gastrosaccus brevifissura</i>	19.128	**	9.899	n.s.
<i>Iphinoe truncata</i>	1.560	n.s.	3.944	n.s.
<i>Cirolana fluviatilis</i>	12.922	*	8.041	n.s.
<i>Grandidierella lignorum</i>	3.313	n.s.	9.365	n.s.

¹ Probability of no negative correlation at ebb tides and of no positive correlation at flood tides, with n.s. denoting $p > 0.05$, * $p < 0.05$, and ** $p < 0.01$.

p_i is the one-tailed probability of $r_s < 0$ (ebb) or $r_s > 0$ (flood), associated with the i -th sample series.

co-varied positively with tidal height (Table 9). This relationship points to a limited axial distribution of these species during the sampling period, where a patch drifted through the sampling area in synchrony with the tidal cycle. On the other hand, for species whose distribution extended over a wider axial range, tidal currents would have transported individuals from sections further downstream and upstream into the sampling area. Consequently, observed axial shifts of these populations from station to station within the sampling area were less distinct and did not closely follow the tidal cycle (Table 9).

Tidal drift and vertical migration as co-determinants of temporal variability

Planktonic density of any benthic-pelagic species at a given time and station is essentially the outcome of a) temporal patterns between upward vertical migration into the water column and descent to the sediment, and b) tidal introduction of individuals into a sampling area from regions of higher abundance, and, conversely, current-driven export of individuals from the sampling area.

From this follow two hypotheses: 1) at sites without tidal influence, temporal variability in abundance is higher for species who enter the water column only for short periods or have several bouts of vertical migration during a sampling series, or both, and 2) at sites with current-driven transport of planktonic organisms, temporal variability is higher for species who show a greater extent of tidal drift.

Table 9. Correlation analysis between weighted mean position (WMP) and height of water level (mm above low water in estuary), using Fisher's combined probability method on Spearman's rank correlation coefficients.

Critical $\chi^2_{0.05, 4 \text{ d.f.}} = 9.488$ for pooled data from neap- and spring tide.

Tableau 9. Analyse de corrélation entre la position moyenne pondérée et le niveau de l'eau (mm au-dessus de la marée basse en estuaire), utilisant la méthode de probabilité de Fischer à partir des coefficients de corrélation de rang de Spearman.

$\chi^2_{0.05, 4 \text{ d.f.}} = 9,488$ pour des données regroupées lors des mortes eaux et des vives eaux.

Null hypothesis Ho:

WMP is *not positively* correlated with tidal height

Taxon	$-2 \sum_i \ln p_i$	p^1
<i>Pseudodiaptomus hessei</i>	1.356	n.s.
<i>Acartia natalensis</i>	11.046	*
<i>Rhopalophthalmus terranatalis</i>	3.431	n.s.
<i>Mesopodopsis wooldridgei</i>	5.452	n.s.
<i>Gastrosaccus brevifissura</i>	10.226	*
<i>Iphinoe truncata</i>	1.009	n.s.
<i>Cirolana fluviatilis</i>	5.016	n.s.
<i>Grandidierella lignorum</i>	2.533	n.s.

¹ Probability of no positive correlation, with n.s. denoting $p > 0.05$, and * $p < 0.05$. p_i is the one-tailed probability of $r_s < 0$, associated with the i -th sample series.

The first hypothesis, of higher temporal variability in species with more variable vertical migration patterns, was tested by comparing short-term fluctuations in planktonic abundance between species recorded at a fixed anchor station in the non-tidal Kabeljous estuary. In this estuary, the tidal inlet was blocked off from the sea by the formation of sandbar across the mouth. There was no freshwater inflow into the system at the time of sampling and wind-speed was zero during sample collection. Consequently, no tidal- or wind-driven water-currents were present to horizontally displace plankton. The copepod *Pseudodiaptomus hessei* and the mysid *Rhopalophthalmus terranatalis* showed only one distinct bout of upward vertical migration after sunset, and were then found in relatively even numbers throughout the night (Fig. 8 A, C). In comparison, the amphipod *Grandidierella lignorum* showed a clearly defined abundance peak shortly after sunset, after which numbers declined progressively throughout the night (Fig. 8D). Harpacticoid copepods had a bimodal density distribution over time, with an early peak in vertical migratory activity after sunset and a smaller peak around midnight (Fig. 8B). Densities of the isopod *Cirolana fluviatilis* were the most variable over time, indicating a vertical migration pattern initially similar to amphipods but fluctuating markedly more after the first ascent into the water column (Fig. 8E)

Measures of temporal variability in non-tidal waters are summarised for these species in Table 10 and show that 1) densities of species which ascended the water column at nightfall and remained pelagic thereafter (i.e. *Pseudodiaptomus hessei* and *Rhopalophthalmus terranatalis*) or displayed a continuum of ascents and descents throughout the night were significantly less variable over time compared with species which became planktonic for shorter periods (i.e. *Grandidierella lignorum* and *Cirolana fluviatilis*), and 2) species who showed sharp but varying bouts of vertical migratory activity (i.e. *C. fluviatilis*) were significantly more variable (Table 10).

Tableau 10. Comparison of temporal variability in planktonic density between species recorded in the non-tidal Kabeljous estuary at hourly intervals.

Tableau 10. Comparaison de la variabilité horaire de la densité planctonique des espèces récoltées dans l'estuaire Kabeljous, qui est sans marée.

Taxon	Hourly Variability $s^2 (\log N_{i-1} - \log N_i)$		Coefficient of variation CV = 100 (s/m)		
	$s^2 * 100$	SNK -test ¹	CV	S_{CV}	SNK -test ¹
<i>Pseudodiaptomus hessei</i>	0.141	+	21.9	5.85	+
<i>Rhopalophthalmus terranatalis</i>	1.440	+	20.3	5.41	+
<i>Harpacticoid</i>	1.972	+	45.6	13.72	+ o
<i>Copepods</i>	26.495	o	83.9	32.32	o
<i>Cirolana fluviatilis</i>	3.381	+	85.5	33.31	o
<i>Grandidierella lignorum</i>					
ANOVA ¹	d.f. = 4, 35		d.f. = 4, 40		
	F = 7.041, p = 0.0003		F = 3.804, p = 0.0103		

¹ Equality of variances ($s^2 (\log N_{i-1} - \log N_i)$), where N_i is density at time i , and of coefficients of variation was tested among species by Levene's test and post-hoc multiple comparison using Student-Newman-Keuls test. Homogenous groups from SNK-tests are denoted by o and +.

In order to test the second hypothesis, i.e. that tidal drift increases temporal variability measured at a fixed anchorage station, the amplitude of horizontal displacement, which individual species showed between axially located stations, was correlated to their CVs of density and to their hourly variability at each station (Table 11). Temporal variability in planktonic density was positively correlated with all three measures of tidal drift entered in the analysis (Table 11). Thus, species whose axial distribution was more strongly affected by tidal drift, displayed wider fluctuations in density at a given station.

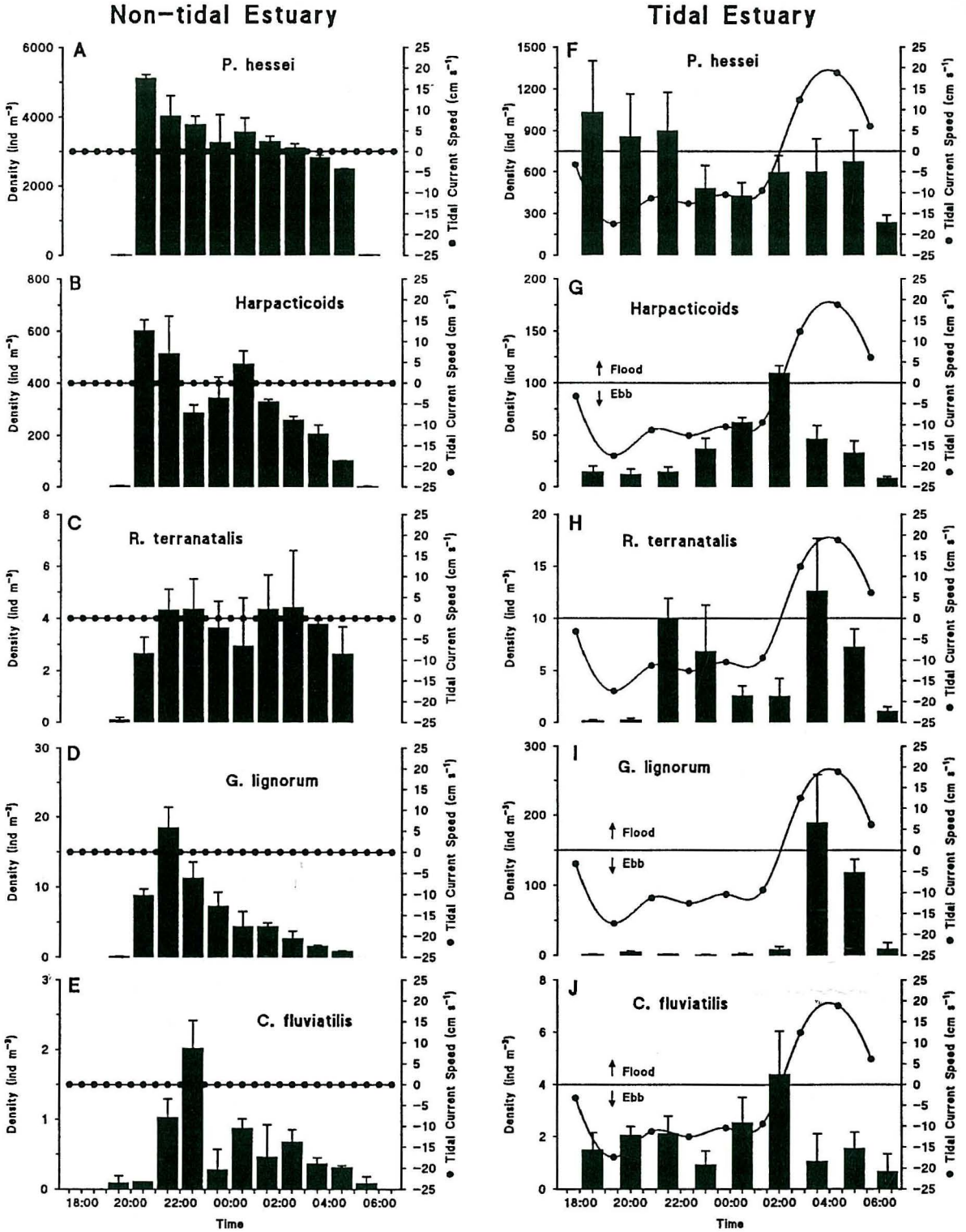


Figure 8. Temporal variation in nocturnal planktonic density recorded in the Kabeljous estuary which was blocked off from the sea by a sandbar across the mouth (non-tidal estuary, A to E) and the Gamtoos estuary which had a free tidal connection to the sea (tidal estuary, F to J).

Figure 8. Variation temporelle de la densité planctonique nocturne enregistrée dans l'estuaire Kabeljous qui est séparé de la mer par un banc de sable en travers de son embouchure (estuaire sans marée A - E) et l'estuaire de Gamtoos qui a une libre communication avec la mer (estuaire à marée, F - J).

Table 11. Relationship between short-term fluctuations in plankton density and tidal drift between axially located stations. Plankton variability measured over time at each of three stations is expressed by the coefficient of variation and by "hourly variability". Amplitude of tidal drift is estimated by the range and CV of weighted mean position, WMP, and by the CV of the index of dispersion, Id. Correlation analysis used Spearman's rank correlation (r_s) and Fisher's combined probabilities.

Tableau 11. Relation entre les fluctuations à court terme de la densité du plancton et la dérive due à la marée, au niveau des stations localisées dans l'axe de l'estuaire. La variabilité du plancton, mesurée au cours du temps à chacune des trois stations, est exprimée par le coefficient de variation et par la "variabilité horaire". L'amplitude de la dérive due à la marée est estimée par le coefficient de variation (CV) et l'étendue de la position moyenne pondérée (WMP) et par le coefficient de variation de l'index de dispersion, Id. L'analyse de corrélation utilise la méthode de probabilité de Fischer à partir des coefficients de corrélation de rang de Spearman.

	Coefficient of variation (s/m)			Hourly Variability s^2 ($\log N_{i-1} - \log N_i$)		
	Spearman's r_s			Spearman's r_s		
	Springs n = 27	Neaps n = 33	$-2 \sum_i \ln_i p_i^A$	Springs n = 18	Neaps n = 17	$-2 \sum_i \ln_i p_i^A$
WMP Range	0.46	0.17	12.646 *	0.48	0.22	10.65 *
WMP CV	0.36	0.41	15.779 **	0.44	0.29	10.93 *
Id CV	0.15	0.47	12.730 *	0.12	0.53	10.47 *

^A p_i is the one-tailed probability of $r_s < 0$, associated with the i -th sample series.

Critical $\chi^2_{0.05, 4 \text{ d.f.}} = 9.488$ for combined probabilities. * denotes $p < 0.05$, and ** $p < 0.01$.

Discussion

Depth and tidal effects on zooplankton distribution

The general trend towards aggregation in near-bottom waters observed in the present study underscores the essentially demersal nature and benthic affinity of many of the zooplankton species in South African estuaries (Grindley, 1981). Whereas higher planktonic abundance near the bottom appears self-evident for species that are truly benthic during the day (e.g. amphipods, cumaceans), it also appears to hold for many species that are classically regarded as pelagic forms (e.g. calanoid copepods). By contrast, other taxa that are entirely endobenthic during the day (e.g. corophoid amphipods) do at night migrate throughout the water column into surface waters. Such benthopelagic taxa comprised at times the numerically dominant group in the nocturnal plankton, accounting for as much as 82 % of total plankton density in surface waters. These findings suggest that the estuarine zooplankton displays a behavioural spectrum that encompasses a range from wholly benthic to wholly planktonic forms. They also support the wider notion of Alldredge & King (1980) that "demersal zooplankton" represents an ecological category for which no clear operational definition may be possible.

Vertical distribution was, however, strongly modified by the phase of the tidal cycle: while the vast bulk of the zooplankton was concentrated in slower flowing near-bottom waters on ebb-tides, a significantly higher proportion of spe-

cies and individuals migrated into surface waters on flood-tides. All zooplankton species in the Gamtoos were potentially subjected to considerable tidal displacement and at least two species (i.e. *Acartia natalensis* and *Gastrosaccus brevifissura*) are likely to have a limited axial range. Yet, the above tidally-modified migration patterns concur with the widely observed behavioural mechanisms which have evolved in estuarine species to maximise retention in estuarine waters in face of the prevailing net seaward flow. Generally, these behavioural adaptations mainly match vertical migration patterns to vertically sheared, oscillatory tidal currents (Weinstein *et al.*, 1980; Wooldridge & Erasmus, 1980; Hill, 1991; Schlacher & Wooldridge, 1994). Thus, the displayed behavioural adaptations of the "estuarine-retention-type" may explain much of the variability in vertical zooplankton density.

Temporal density variation

Three patterns stand out from the data on temporal zooplankton variability:

a) considerable intertaxonomic differences, b) higher variability than published values which aim to predict inter-replicate variance of zooplankton, and c) tidal displacement significantly increases temporal variation.

Differences in short-term fluctuations in planktonic density between species are probably the outcome of differential migratory patterns and responses to hydrological forces. While these factors may vary from one habitat to the next,

data from this study stress the need to analyse distributional data on the lowest practical taxonomic level. Clumping of species into broad categories can effectively mask biologically relevant patterns. By way of example, the opossum shrimp *Gastrosaccus brevifissura* often exhibited markedly different distributional trends than other mysids in the same habitat.

Downing *et al.*'s (1987) calculations of the general variance algorithm include few data on interreplicate variance of estuarine zooplankton. By contrast, all data from our study pertain to estuarine populations. Consequently, comparison of variance data obtained in this study with published values can only be made with prudence. Bearing these reservations in mind, the hypothesis might nevertheless be advanced that estuarine zooplankton may in general be more variable than marine forms, especially in tidal waters - both aspects which merit future, detailed comparative studies over a much wider range of estuarine species and habitats. The premise of higher variability could in particular be valid for demersal forms and for spatial heterogeneity in estuaries, where strong axial salinity gradients are developed and distributions of individual species tend to cluster around regions of particular salinity ranges.

The strong influence tidal dispersal had on temporal fluctuations of zooplankton at a given site reflects the prominent role physical forces can play in creating plankton heterogeneity. Although there is conflicting evidence about the exact way hydrodynamic factors influence zooplankton distributions, ranging from randomising to aggregating effects (see references in Pinel-Alloul *et al.*, 1988), findings from this study favour the conclusion that water movement increases dispersion and density variations in tidal estuaries. These results concur with Lee & McAlice (1979) who showed tide to be the dominant factor in determining sampling variability of estuarine zooplankton.

Implications for sampling designs

The lessons to be learnt from this study for effectively sampling estuarine zooplankton are rather dispiriting and frustrating ones. First, the high interreplicate variance obtained in the present study rendered the majority of density estimates very imprecise (i.e. $d > 0.2$); this is likely the reason why so few planktologists report measures of dispersion and often restrict analyses largely to descriptive techniques (e.g. Wooldridge & Bailey, 1982; Jerling, 1994). Secondly, even replication levels (i.e. $n = 15$) which are usually considered adequate in plankton studies did not result in acceptable precision; this effect persisted even in calm (i.e. non-tidal) waters. Thirdly, proper choice of sample number requires *a priori* estimates of interreplicate variance, which is usually calculated from estimates of expected mean density (Downing *et al.*, 1987). This approach can, however, be problematic in our sampling situation because densities at

any given station can vary by orders of magnitude over short time intervals: for example, on 14 June 1993 the calanoid copepod *Acartia natalensis* was found at a mean density of 456 ind m^{-3} and the amphipod *Grandidierella lignorum* at 4485 ind m^{-3} . Five days later, numbers of *A. natalensis* had risen sharply to 7430 ind m^{-3} , while densities of *G. lignorum* dropped to 79 ind m^{-3} . Moreover, variance of density estimates increases significantly with the range over which samples are allocated in space (e.g. Pinel-Alloul *et al.*, 1988). Since different species cluster in regions of different salinities, the question of spatial scale becomes especially critical when zooplankton is sampled across the full axial salinity gradient in estuaries (e.g. Wooldridge & Bailey, 1982). Nevertheless, variance estimation from expected mean densities presents the best - and perhaps only practical - solution to plan the number of replicates for zooplankton sampling.

Besides achieving precision requirements, sampling schemes should truly reflect actual densities and community structure - a requirement often referred to as "representative samples". At any given site two basic decisions must be made: a) at which depth, and b) at which time of the tidal cycle to sample. In this study, demersal zooplankton was generally strongly stratified even in shallow waters (c. 1 m water depth). This data combined with earlier findings on sampling methodology (Wooldridge & Bailey, 1982) stress the need for multilevel sampling, particularly under conditions of hydrological stratification.

Amphipods and to a lesser degree cumaceans were found to largely restrict their nocturnal planktonic phase to flood-tides. Consequently, ebb-tide samples need not necessarily reflect the actual density and community structure of the estuarine zooplankton. In the present situation, sampling during outgoing tides would have seriously underestimated planktonic densities of *Grandidierella lignorum* and *Iphinoe truncata* as well as species richness and diversity in general. The necessity to incorporate tidal variations into sampling schemes was stressed by Sameoto (1975) and Lee & McAlice (1979) - both studies recommending a minimum of one low- and one high-water sample. This aspect has, however, largely been overlooked in studies of zooplankton in South African estuaries (e.g. Wooldridge & Bailey, 1982; Jerling, 1994). These authors tend to argue that sampling focused on the truly endemic estuarine component and, consequently, ebb-tide sampling avoided marine species imported by flood currents. However, amphipods and cumaceans, which are clearly part of the estuarine zooplankton community, are likely to have been seriously underestimated by such approaches.

A further source of variability in density estimates can be introduced by inefficient sampling gear. One possibility to reduce apparent density variations in the vertical dimension would be the use of nets with wider mouth diameters, that

would effectively integrate plankton over greater depths than the WP2-nets used in this study. This approach would, however, lead us to loose information about vertical plankton stratification and underlying migration patterns, thereby lowering ecological resolution. Moreover, the shallow nature of the estuaries sampled necessitate the use of small boats which makes employment of nets larger than the WP2 impractical. In the horizontal dimension, the question arises as to whether integrate samples over a specified distance by towing nets or whether to consider the mean from a series of point samples - using pumps or traps - more representative. Both should give similar density values if the same area is covered, but a series of pump samples significantly increases sampling time - a critical problem if a series of sites is to be sampled at a similar tidal phase. Besides thus constraining spatial sampling coverage, we found that the larger zooplankton forms (e.g. mysids) are not effectively captured by pumps. We therefore consider WP2-nets as a suitable compromise between practicability, temporal and spatial sampling coverage, and precision requirements in this specific sampling situation.

Each study will be centred around different objectives, undertaken under different sets of environmental factors, and constrained by different logistical capacities. To extrapolate our sampling approach as a general guideline for estuarine sampling designs seems therefore inappropriate. If logistics limit the number of replicates and precision is to be sacrificed for greater spatial coverage, we do, however, generally recommend a minimum of duplicate plankton hauls, made from at least two depth-levels during both the flood- and ebb-tide at any given site in tidal estuaries.

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