Summer and winter differences in zooplankton biomass, distribution and size composition in the KwaZulu-Natal Bight, South Africa

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Abstract

Zooplankton biomass and distribution in the KwaZulu-Natal Bight were investigated in relation to environmental parameters during summer (January–February 2010) and winter (July–August 2010). Mean zooplankton biomass was significantly higher in winter (17.1 mg dry weight [DW] m−3) than in summer (9.5 mg DW m−3). In summer, total biomass was evenly distributed within the central bight, low off the Thukela River mouth and peaked near Durban. In winter, highest biomass was found offshore between Richards Bay and Cape St Lucia. Zooplankton biomass in each size class was significantly, negatively related to sea surface temperature and integrated nitrate, but positively related to surface chlorophyll *a* and dissolved oxygen. Zooplankton biomass was significantly related to bottom depth, with greatest total biomass located inshore (<50 m). Distribution across the shelf varied with zooplankton size. Seasonal differences in copepod size composition suggest that a smaller, younger community occupied the cool, chlorophyll-rich waters offshore from the St Lucia upwelling cell in winter, and a larger, older community occurred within the relatively warm and chlorophyll-poor central bight in summer. Nutrient enrichment from quasi-permanent upwelling off Durban and Richards Bay appears to have a greater influence on zooplankton biomass and distribution in the bight than the strongly seasonal nutrient input from the Thukela River.

Introduction

The east coast of South Africa is characterised by a narrow (c. 11 km) continental shelf with a steep slope that provides stability to the northern Agulhas Current (Schumann 1988; de Ruijter et al. 1999). The KwaZulu-Natal (KZN) Bight is a 160 km-long widening of the shelf between Cape St Lucia to the north and Durban to the south (Lutjeharms et al. 2000a; Figure 1). The shelf is approximately 50 km wide at its broadest part off the mouth of the Thukela (formerly Tugela) River, the largest river in the KZN province. Early oceanographic studies in this region focused mainly around Richards Bay (Gründlingh 1974; Pearce 1978; Pearce et al. 1978) or Durban (Pearce 1977; Schumann 1981, 1982; Anderson et al. 1988), with little research conducted over the bight itself. Nutrient concentrations off the KZN coast were first investigated by Oliff (1973) but the study was limited to the Richards Bay area. The first extensive hydrographic survey off the East Coast to include the KZN Bight was conducted in July 1989 (Lutjeharms et al. 2000a; Meyer et al. 2002). The St Lucia upwelling

cell was identified as the main source of nutrients for the bight, with additional upwelling of nutrients in the core of a recurrent lee eddy, known as the Durban Eddy, at the southern end of the bight, off Durban (Meyer et al. 2002). Lutjeharms et al. (1989) showed that the St Lucia upwelling cell, located where the shelf widens along the path of the current at the northern end of the bight, occurs year round and brings cold nutrient-rich waters from the central water depths onto the shelf, influencing the physical water characteristics of the whole bight (Lutjeharms et al. 2000b). Nutrient-rich upwelled water between Cape St Lucia and Richards Bay has been shown to have a substantial influence on phytoplankton productivity over the whole bight, with chlorophyll *a* concentration in the bight ranging from 0.03 to 3.88 mg m−3 (Carter and Schleyer 1988). Chlorophyll *a* concentrations closest to the Cape St Lucia upwelling cell were recorded at 1.2 mg m−3 by Lutjeharms et al. (2000a), increasing to 1.5 mg m−3 to the south, then decreasing further south (<0.5 mg m−3). Barlow et al. (2008) found that, in the bight, chlorophyll *a* concentrations peaked offshore to the north of Durban (2.8 mg m−3) and just south of Richards Bay (3.2 mg m−3), with lower concentrations near the coast ranging from c. 0.9 to 1.3 mg m−3. Most knowledge of East Coast zooplankton communities, in particular copepods, stems from a small number of once-off or widely spaced surveys conducted between the 1960s and 1980s, using a wide variety of sampling gear (De Decker 1964, 1984; De Decker and Mombeck 1964; Carter 1977; Schleyer 1985; Carter and Schleyer 1988). Zooplankton biomass on the continental shelf was up to an order of magnitude higher than in the Agulhas Current but was highly variable (mean 0.29 ml m−3; range 0.02–1.68 ml m−3), and with no evident seasonality (Carter and Schleyer 1988).

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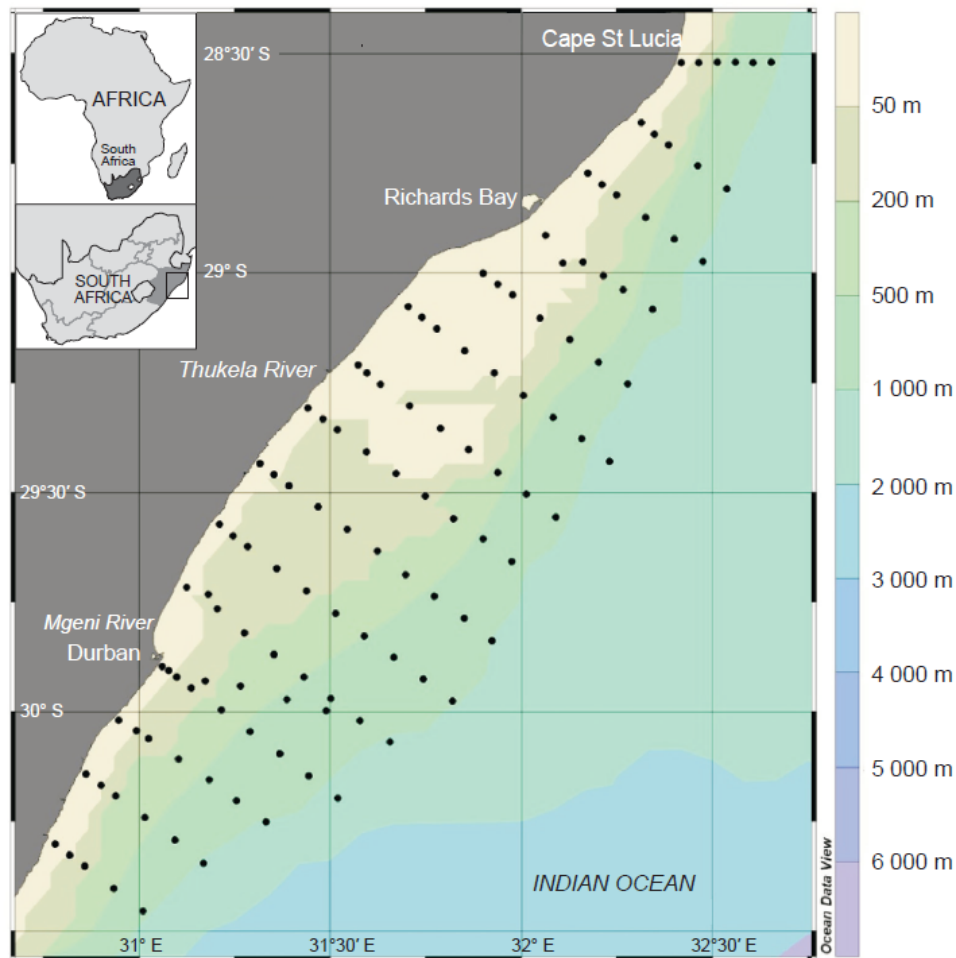
Figure 1: Locations of all the hydrographic stations sampled during the summer survey, January–February 2010. The synoptic survey began at Durban and ended at Cape St Lucia. There were 16 transects running perpendicular to the coast, and a total of 119 stations. Zooplankton were sampled at alternate stations along each transect

The bulk (c. 70%) of the biomass was concentrated in the upper 100 m. Carter (1977) identified distinct neritic and oceanic copepod communities between Port Edward (160 km south of Durban) and St Lucia, and also noted the development of large populations of *Calanoides carinatus*, an upwelling species, in association with eddy centre upwelling off Durban. Carter and Schleyer (1988) found that copepod species assemblages varied seasonally, with communities dominated by *Calanoides carinatus* and *Centropages chierchiae* during winter/spring, when primary production was elevated, and by the smaller *Paracalanus parvus* during the other seasons, with a general increase in both copepod and chaetognath abundance during summer. Copepod diversity was highest within the core of the Agulhas Current and decreased to either side of it, with lowest diversity within the bight (De Decker 1984). Although Schleyer (1985) failed to observe any distinct communities of chaetognaths off Durban, Thibault-Botha et al. (2004) observed two aseasonal assemblages of siphonophores along the east coast of South Africa: one associated with the nearshore waters of the Port Alfred upwelling cell (characterised by low overall diversity) and the second with the inshore waters north of East London, which showed some evidence of alongshore and crossshelf structure. During the KZN sardine run each winter, large schools

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of sardine *Sardinops sagax* move east and northwards along the Transkei and KZN continental shelf, using cool-water conditions adjacent to the East Coast (O'Donoghue et al. 2010; van der Lingen et al. 2010). Beckley and Hewitson (1994) also found that larvae of sardine, round herring *Etrumeus whiteheadi* (probably *E. teres* [Connell 2001], now *E. wongratanai*) and anchovy *Engraulis encrasicolu*s extended as far north as the mouth of the Thukela River. These authors observed that high larval abundance coincided with an upwelling node off Algoa Bay (near Port Elizabeth), and speculated that the same may be the case for Cape St Lucia. Understanding variability in zooplankton abundance is of general ecological interest as there has been very little zooplankton research in the KZN Bight, but also given the relevance of zooplankton in the diets of juvenile pelagic fish species such as sardine, which contribute to a commercially important fishery in South Africa. This study tests the hypotheses that (a) zooplankton biomass is elevated in (or downstream from) the three areas of local nutrient enrichment: (i) topographically-driven upwelling at Cape St Lucia; (ii) upwelling associated with the persistent cyclonic gyre off Durban (Schumann 1988; Lutjeharms et al. 2000a); and (iii) riverine inputs from the Thukela River (Schumann 1988), (b) zooplankton biomass varies seasonally, and is higher during summer (the wet season) due to higher chlorophyll *a* concentrations anticipated during this season as a result of nutrient run-off, and (c) zooplankton biomass varies with depth, being greatest inshore due to greater nutrient and chlorophyll *a* concentrations anticipated in that region, and declines offshore.

Material and methods

This study forms one component of an African Coelacanth Ecosystem Programme (ACEP) project, entitled Ecosystem Processes in the KwaZulu-Natal Bight, which was developed to investigate physical, geological and biological processes that drive the marine ecosystem in the bight, with a particular focus on the nutrient sources. Zooplankton samples were collected during two research surveys in the bight, in January/February 2010 (during the summer wet season) and July/August 2010 (during the winter dry season). Surveys of zooplankton biomass in the bight were conducted during a synoptic leg at the beginning of each research survey, and consisted of 16 transects, 15 of which extended perpendicular to the coast, from half a degree south of Durban to Cape St Lucia in the north (Figure 1). Hydrographic parameters were sampled at all 119 stations, whereas zooplankton samples were collected at alternate stations (c. 60 stations). At hydrographic stations, temperature, salinity and oxygen were profiled during CTD deployments, and seawater samples were collected at selected depths, according to the fluorescence profile, for analysis of chlorophyll *a* and nutrients (nitrite, nitrate, silicate and phosphate). Water samples for chlorophyll *a* analysis (500 ml) were filtered on board onto Whatman GF/F filters, which were then frozen and analysed later according to the fluorometric technique of Welschmeyer (1994). Nutrient samples were frozen on board and analysed ashore by standard auto analyser techniques (Mostert 1983). Integrated values of chlorophyll *a* and nutrients were calculated for the zooplankton sampling depth (upper 200 m) as well as for the whole water column beyond the continental shelf. During both research surveys, zooplankton samples were collected using bongo nets (200 μm mesh), which were hauled vertically from a maximum depth of 200 m, or several metres above the bottom. Samples were collected while on station during

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the day and night and were split in half at sea using a Folsom splitter. The first half was fractionated into four different size classes, 200–500 µm, 500–750 µm, 750–1 600 µm and >1 600 µm, and frozen for later dry-weight analysis. The second half was preserved in 5% formalin and seawater for later species identification. To obtain dry weights, samples were filtered onto preweighed GF/F filter papers and excess water was removed using a vacuum pump. Samples were then dried in an oven at 60 °C for 24 h and reweighed (Lovegrove 1962, 1966). Dry biomasses (mg m−3) were determined by dividing the sample weights by the volume filtered. Values were doubled to correct for splitting of the samples, and the proportional size composition of each sample was calculated. Contour plots of zooplankton biomass and selected environmental variables were plotted in Ocean Data View 4 (Schlitzer 2013) using variational data interpolation (DIVA), which allows data to be analysed and interpolated in an optimal way, comparable to optimal interpolation (OI). Unlike OI, DIVA also takes into account coastlines and bathymetric features to structure and subdivide the domain on which the estimation is performed. Student's *t*-tests were used to investigate seasonal differences in the environmental data and zooplankton biomass. Analysis of variance (ANOVA) was used to test the effect of season and depth on zooplankton size composition. Patterns related to season (summer and winter) and bottom depth (<50 m, 50–200 m, 200–500 m and >500 m) in the multivariate data were also tested using various software routines within PRIMER 6.1.12 (Clarke and Warwick 2001). Patterns within the environmental data were first explored using principal components analysis (PCA), following their log10(*x*+1) transformation and normalisation. A similarity matrix between samples was generated using Euclidean distance, which was used to test for seasonal (fixed), depth (fixed) and season × depth differences in the multivariate datasets (*a priori*) using PERMANOVA+ 1.0.2 (Anderson et al. 2008). PERMANOVA tests the simultaneous response of variables to one or more factors in an ANOVA experimental design on the basis of a resemblance measure, using permutation methods (Anderson et al. 2008). The routine partitions the total sum of squares according to the specified experimental design, including appropriate treatment of factors that are fixed or random, crossed or nested, and all interaction terms. A distance-based pseudo-*F*-statistic is computed (analogous to the *F*-statistic for multifactorial ANOVA models) and *p*-values are subsequently obtained by permutation. A similarity percentages routine (SIMPER) decomposes the average Bray–Curtis dissimilarities between all pairs of samples, one from each group (or decomposes all similarities among samples within a group), into percentage contributions from each variable, listing the variables in decreasing order of such contributions. The similarity between samples in terms of their zooplankton biomass size structure was determined using the Bray–Curtis index (Clarke and Gorley 2001), following square-root transformation. Three separate matrices were computed: all data, and summer and winter seasons separately. Similarity matrices were visualised using a combination of cluster analysis (group average) and/or multidimensional scaling (MDS) routines, and as with the environmental data, SIMPER was then used to determine which size classes of zooplankton accounted for the differences observed. All test results have been considered significant at the 95% level. Multivariate patterns were explored using the distancebased linear model (DistLM) which conducts a marginal test, which determines the proportion of the variance in the zooplankton biomass distribution pattern that can be explained by each environmental variable (Anderson et al. 2008). The model

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then partitions the variation in data distribution according to a multiple regression model (based on predictor variables), as selected by the user, (e.g. forward, stepwise, best fit), which provides a best solution for a combination of available abiotic variables. In this study, the selection criterion that was used was the adjusted $R2$ and the selection procedure used was the 'best fit' option. The best-fit multiple regression model showed the portion of the variation in the data, and the adjusted $R2$ criteria were chosen to exclude predictor variables in the model if they added no more to the explained sum of squares than would be expected by adding some random variable. The distance-based redundancy analysis (dbRDA) was used as a visualisation tool to model the DistLM in a multidimensional space using vector overlays and eigen analysis of the fitted data cloud (Anderson et al. 2008). Statistica 6.1 (StatSoft Inc. 2002) was used to test for significant differences between the biomass size fractions and the environmental data. Correlations were run between the size-fractionated zooplankton biomass and the environmental variables, and multiple-effects ANOVA was used to explore the effects of categorical variables such as time of day (day or night), season (summer or winter) and bottom depth (<50 m, 50–200 m, 200–500 m, >500 m).

Results
Description of the environment
In general, there was good agreement between environmental data measured at the biological stations only and those from the entire sampling grid (Table 1). Mean sea surface temperature (SST) was significantly warmer in summer than in winter ($t = 20.45$, df = 117, $p < 0.05$; Table 1), with cooler water inshore and warmer water offshore in both seasons (Figure 2a, 2b). Mean sea surface salinity was slightly but significantly higher in winter ($t = -3.35$, df = 117, $p = 0.001$; Table 1) with localised low salinity around the Thukela River in summer (34.5; Figure 2c, 2d). Mean surface and integrated chlorophyll *a* concentrations were also significantly higher during winter than summer ($t = -7.98$ and -3.66 respectively, df = 117, $p < 0.05$; Table 1; Figure 2e and 2f), but integrated nitrate concentrations in winter (mean = 15.48 mmol N m–2) were significantly lower ($t = 7.12$, df = 117, $p < 0.001$) than in summer (mean = 378.87 mmol N m–2). Integrated concentrations of silicate, phosphate and nitrite were all higher during winter than summer surveys, but not significantly so ($p > 0.05$). During the summer survey, the edge of the Agulhas Current may have been sampled offshore of the bight, whereas during winter, cooler waters were sampled, and hence there are strongly contrasting temperature regimes and water-column structures. In summer there were strong temperature gradients and the vertical nutrient profiles indicate there were high nitrate concentrations in the upper 200 m, whereas in winter the conditions were more homogeneous. The PCA of all environmental variables generated three axes with eigen values >1.0 (Figure 3), the first two of which accounted for 64.6% of total variation. PC1 separated samples on the basis of depth and integrated nitrate (coefficients >0.4), PC2 separated samples on the basis of integrated chlorophyll *a* (coefficients >0.4), and PC3 separated samples on the basis of salinity (coefficient >0.7) and integrated silicate concentration (coefficient>0.4). Figure 3 shows a clear separation of the samples by season, which is supported by the results of the PERMANOVA test (Table 2), and the key differences between seasons are depicted by the SIMPER analyses (Table 3). The average similarity between the two seasons was 24.62%, with four variables (SST, integrated nitrate, surface chlorophyll *a*

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concentration and dissolved oxygen) together contributing almost 50% of the dissimilarity within each site between summer and winter (Table 3). In the PCA (Figure 3), bathymetry influences the data as evidenced by the results of the PERMANOVA tests (Table 2).

Distribution of the biota

Total zooplankton biomass was evenly spread throughout the bight in summer (Figure 4a), with a mean of 9.5 mg DW m−3. Biomass was generally higher at depths shallower than 200 m, with highest concentrations off Durban (max. = 42.60 mg DW m−3) and a broad patch of moderate biomass (c. 20 mg DW m−3) extending northwards from Durban over much of the bight. Biomass was low in the vicinity of the Thukela Mouth, probably on account of the lower salinities in this area as a result of the influx of fresh water from the river. Mean zooplankton biomass was significantly higher during winter (17.1 mg DW m−3; $t = -4.81$, df = 117, $p < 0.001$), with patches of high concentration located in the far south of the bight, inshore at Richards Bay and in a very dense patch offshore and north of Richards Bay (max. = 117.8 mg DW m−3; Figure 4b).

Table 1: Environmental parameters recorded during the summer and winter surveys over the sampling depth (0–200 m depth) at the zooplankton stations and at the surface (0–8 m depth) at all stations in the KwaZulu-Natal Bight; Int = integrated

Parameter	Summer mean and (range)		Winter mean and (range)	
	0–200 m depth ($n = 59$)	0–8 m depth ($n = 119$)	0–200 m depth ($n = 60$)	0–8 m depth ($n = 119$)
SST (°C)	26.21 (23.55–28.77)	26.17 (22.68–28.76)	21.55 (19.98–23.23)	21.54 (19.97–23.22)
Salinity	35.30 (33.33–35.56)	35.15 (25.29–35.55)	35.43 (35.37–35.49)	35.42 (35.36–35.48)
Surface Chl a (mg m^{-3})	0.20 (0.04–1.09)	0.18 (0.03–1.08)	0.57 (0.15–1.43)	0.56 (0.15–1.50)
Dissolved oxygen (ml l^{-1})	4.32 (4.11–4.68)	4.33 (4.11–4.67)	4.49 (4.15–4.74)	4.48 (3.64–4.74)
Int Chl a (mmol Chl a m^{-2})	22.83 (4.23–68.23)		34.03 (7.60–143.18)	
Int SiO$_4$ (mmol Si m^{-2})	294.60 (0.00–1 083.47)		403.23 (19.33–1 077.05)	
Int PO$_4$ (mmol P m^{-2})	41.37 (0.19–146.51)		53.26 (3.49–163.91)	
Int NO$_3$ (mmol N m^{-2})	378.87 (0.81–1 545.15)		15.48 (2.30–39.47)	
Int NO$_2$ (mmol N m^{-2})	8.26 (0.00–65.78)		8.33 (0.53–43.30)	
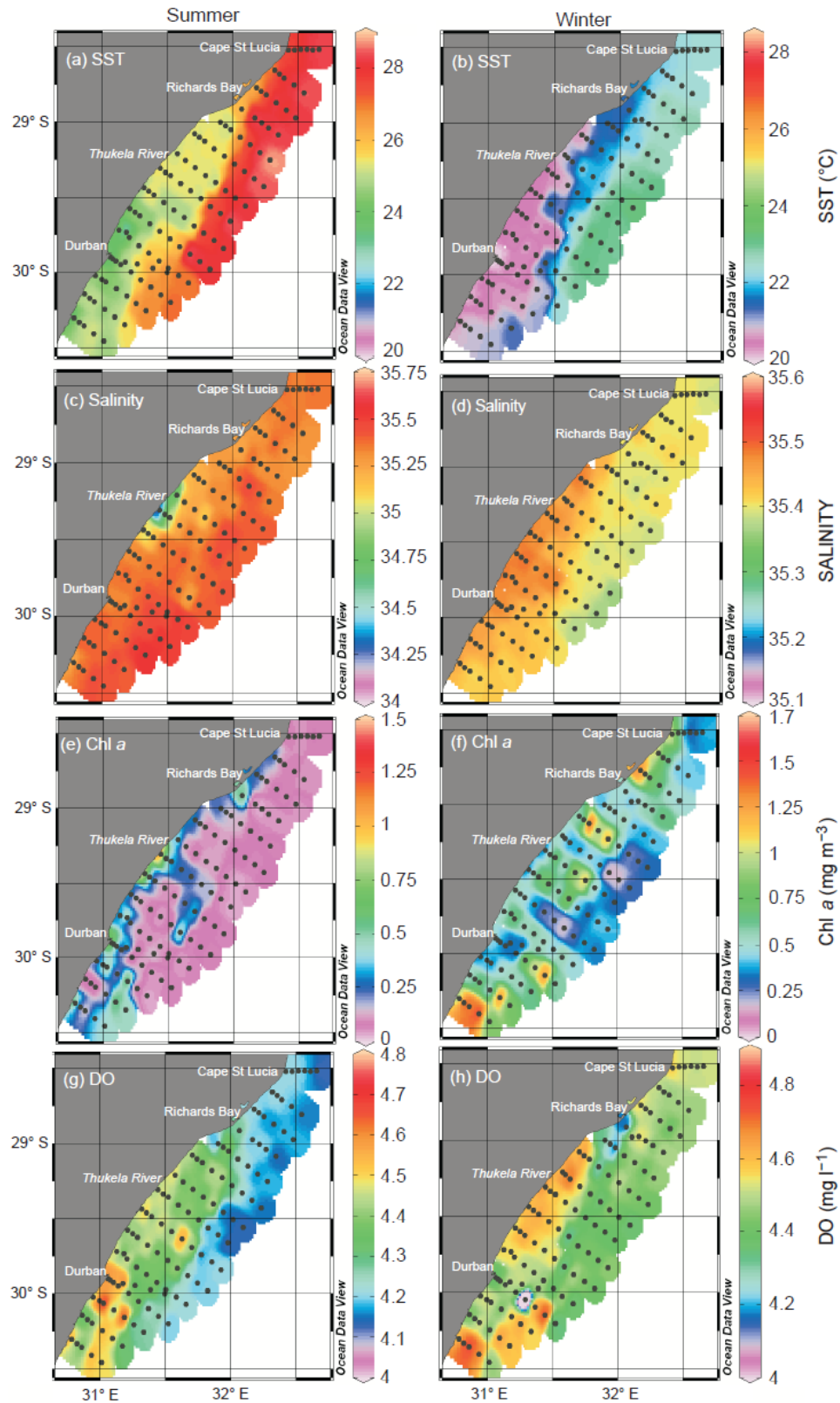
Figure 2: Surface environmental data from surveys of the KZN Bight in summer and winter 2010: (a) and (b) sea surface temperature, (c) and (d) salinity, (e) and (f) chlorophyll *a*, and (g) and (h) dissolved oxygen. Note that the scales are different for most pairs of plots

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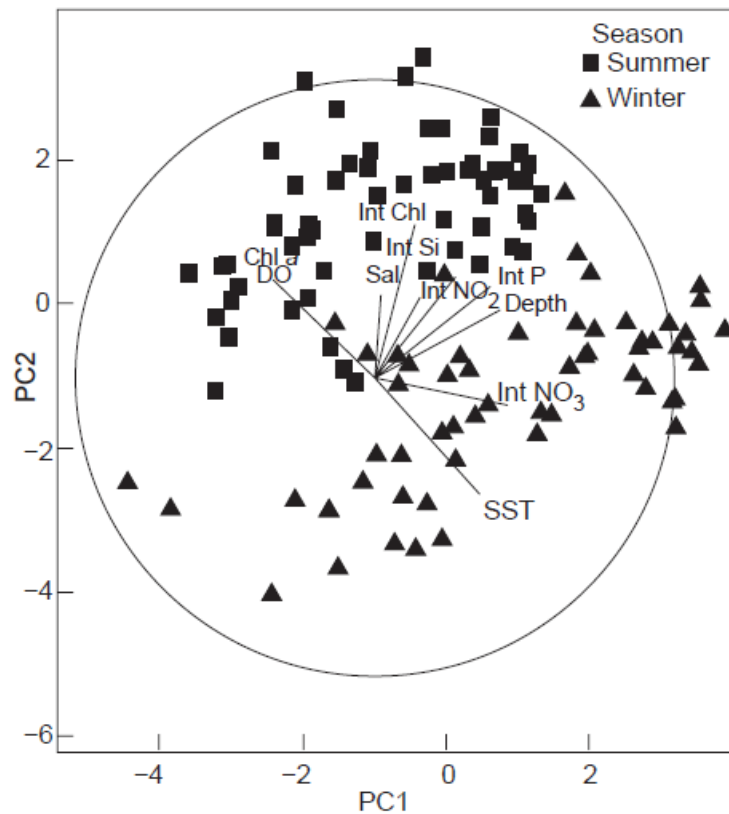
Figure 3: Principle component plot of the summer and winter samples based on measured environmental variables. Vectors showing strength and direction of the different environmental measures also shown: depth, SST (sea surface temperature), Sal (sea surface salinity), DO (dissolved oxygen concentration), Chl a (surface chlorophyll a), Int Chl (integrated chlorophyll a), Int Si (integrated silicate), Int P (integrated phosphate), Int NO_3 (integrated nitrate) and Int NO_2 (integrated nitrite). PC1 has an eigenvalue of 3.64 and represents 36.4% of the variation, PC2 has an eigenvalue of 2.82 and contributes 28.2% of the variation, and together PC1 and PC2 contribute 64.6% of the total variation

Biomass within the bight was relatively low, and more patchily distributed during winter than summer. Microscopic analysis of the four size fractions showed that the 200–500 μm fraction comprised mainly small copepods, the 500–750 μm fraction mainly mediumsized copepods, the 750–1 600 μm fraction mainly large copepods, and the >1 600 μm fraction a mix of chaetognaths, euphausiids, salps and jellyfish (henceforth referred to as 'large zooplankton'). During summer, the patch of high biomass off Durban was observed for all size fractions (Figure 5a, 5c, 5e, 5g), whereas the broad patch extending over the bight north of Durban was dominated by the large-copepod fraction (Figure 5e). During winter, all size fractions, except the large copepods, showed highest biomass in the north of the bight, particularly in the dense patch offshore and north of Richards Bay (Figure 5b, 5d, 5f, 5h). The small-copepod fraction had secondary biomass peaks off the Thukela River mouth and south of Durban (Figure 5b), whereas the large-copepod biomass was greatest inshore to the north of Durban and to the south of the bight (Figure 5f). SIMPER results showed that the 750–1 600 μm size class accounted for 27.61% of the differences observed between the seasons.

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There was greater biomass overall during winter for each size class (Figure 6), but the average percentage contribution of the zooplankton size fractions varied seasonally. The proportions of small and medium-sized copepods were significantly greater in winter (ANOVA, $F = 11.82$, $p < 0.001$ and $F = 5.65$, $p < 0.05$ respectively), the proportion of large copepods was significantly greater in summer ($F = 17.35$, $p < 0.001$) and the proportion of large zooplankton did not vary significantly between seasons ($F = 0.21$, $p > 0.1$, $n = 117$ stations for all). Considering the zooplankton population as a whole, biomass varied significantly with depth ($F = 6.40$, $p < 0.05$). A *post hoc* Tukey test showed that total biomass was greatest inshore (<50 m), and significantly greater in depths shallower than 200 m than at deeper depths ($p < 0.05$). The proportion of each zooplankton size fraction also varied with depth (Figure 7). The percentage contribution of the small and medium-sized copepods did not vary significantly with depth ($F = 1.09$, $p > 0.1$ and $F = 0.95$, $p > 0.1$ respectively), but the proportion of large copepods was significantly higher inshore (<50 m) than farther offshore ($F = 7.81$, $p < 0.001$), and the proportion of large zooplankton was significantly lower inshore (<50 m) than farther offshore ($F = 8.97$, $p < 0.001$, $n = 115$ stations for all). When MDS ordination was applied to each season separately, the summer and winter samples separated into three groups (Figure 8a, b), one dominated by shallow-water stations of <50 m (Category A), a mixed group and the other by deeper-water stations (>200 m, Categories C and D). The MDS plot for the pooled data (Figure 8c) suggests a broad depth gradient in sample distribution, with greater overlap of the depth categories in winter. Thus, depth clearly has an impact on the size structure and biomass of the zooplankton communities observed along the East Coast. Although this was more obvious when data were analysed separately by season (Figure 8a, b), the depth gradient was clear when data from both seasons were combined (Figure 8c). Indeed, the overlap in the seasonal data suggests that there is a stronger depth than seasonal impact on the size structure and biomass of zooplankton communities (Figure 8c). This observation is supported by the results of the PERMANOVA (Table 2), which show that only depth or a variable related to depth, such as distance from shore or proximity to the Agulhas Current, had an impact on the biotic data ($F = 18.42$, $p < 0.001$).

Biota and the environment

Using the DistLM, marginal tests showed that, with the exception of integrated chlorophyll *a* and nitrite concentrations, all environmental variables could explain some of the variation observed in the biotic data when considered alone and ignoring all other variables. Integrated nitrate and phosphate, depth and SST all explained >17%, whereas the balance explained >10% each (Table 4). The sequential test determines whether adding a particular variable contributes significantly to the explained variation. The variation in the resemblance matrix of zooplankton biomass showed significant differences at the $p < 0.001$ level for the 200–500 µm and the 750–1 600 µm size fractions ($F = 68.0$ and 23.5, respectively).

**Table 2:** Results of the PERMANOVA test for the environmental data and the biota data

Source	Degrees of freedom	Sum of squares	Mean squares	Pseudo-F	p (permutations)	Unique permutations
			Environmental data			
Season	1	244.4	244.4	14.90	0.027	975
Depth	3	355.2	118.4	26.76	0.001	998
Season vs Depth	3	52.7	17.6	3.97	0.001	998
Resemblance	111	491.0	4.4			
Total	118	1 180.0				
			Biota data			
Season	1	4 943.2	4 943.2	7.80	0.073	965
Depth	3	17 997.0	5 999.2	18.42	0.001	997
Season vs Depth	3	1 989.2	663.1	2.04	0.056	998
Resemblance	111	36 156.0	325.7			
Total	118	61 501.0				

Table 3: SIMPER results showing the average dissimilarity between the summer and winter environmental data (average squared distance = 24.62; Int = integrated)

Variable	Average value (summer)	Average value (winter)	Average square distance	Square distance	Contribution (%)	Cumulative (%)
SST	0.893	−0.878	3.55	1.51	14.42	14.42
Int NO_3	0.648	−0.638	2.82	1.14	11.44	25.87
Chl a	−0.643	0.633	2.80	0.88	11.36	37.22
Dissolved oxygen	−0.578	0.568	2.64	0.92	10.73	47.96
Salinity	−0.446	0.439	2.39	0.39	9.69	57.65
Int Chl a	−0.367	0.360	2.25	0.65	9.13	66.78
Int SiO_4	−0.273	0.269	2.14	0.60	8.68	75.47
Int NO_2	−0.166	0.164	2.04	0.80	8.30	83.76
Int PO_4	−0.125	0.123	2.01	0.80	8.18	91.95
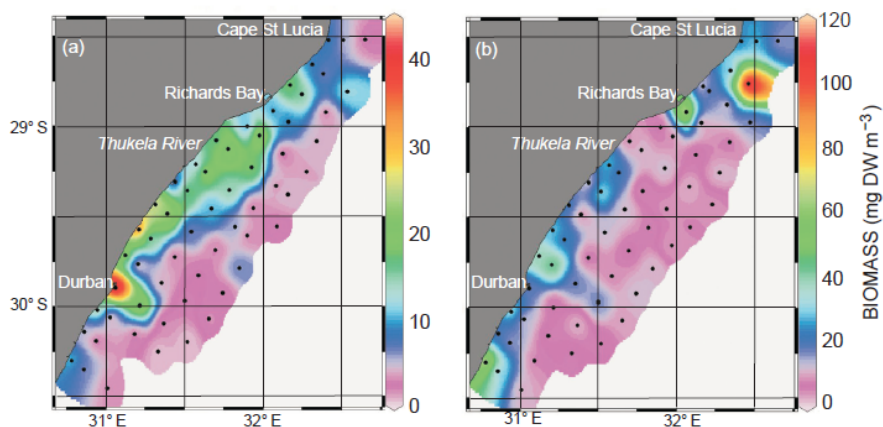
Figure 4: Total zooplankton biomass during (a) the summer survey and (b) the winter survey. Note the scales are different

The full model is visualised on the dbRDA plot (Figure 9), the first axis of which captures 93% of the fitted variability and 40.2% of the total variation (depth and integrated nitrate). There were significant positive correlations between all the zooplankton biomass size classes and chlorophyll a and dissolved oxygen, whereas there were negative correlations for integrated nitrate and temperature. Multiple effects ANOVA showed that only depth-related differences were significant ($F = 2.05$, df = 12, $p < 0.05$).

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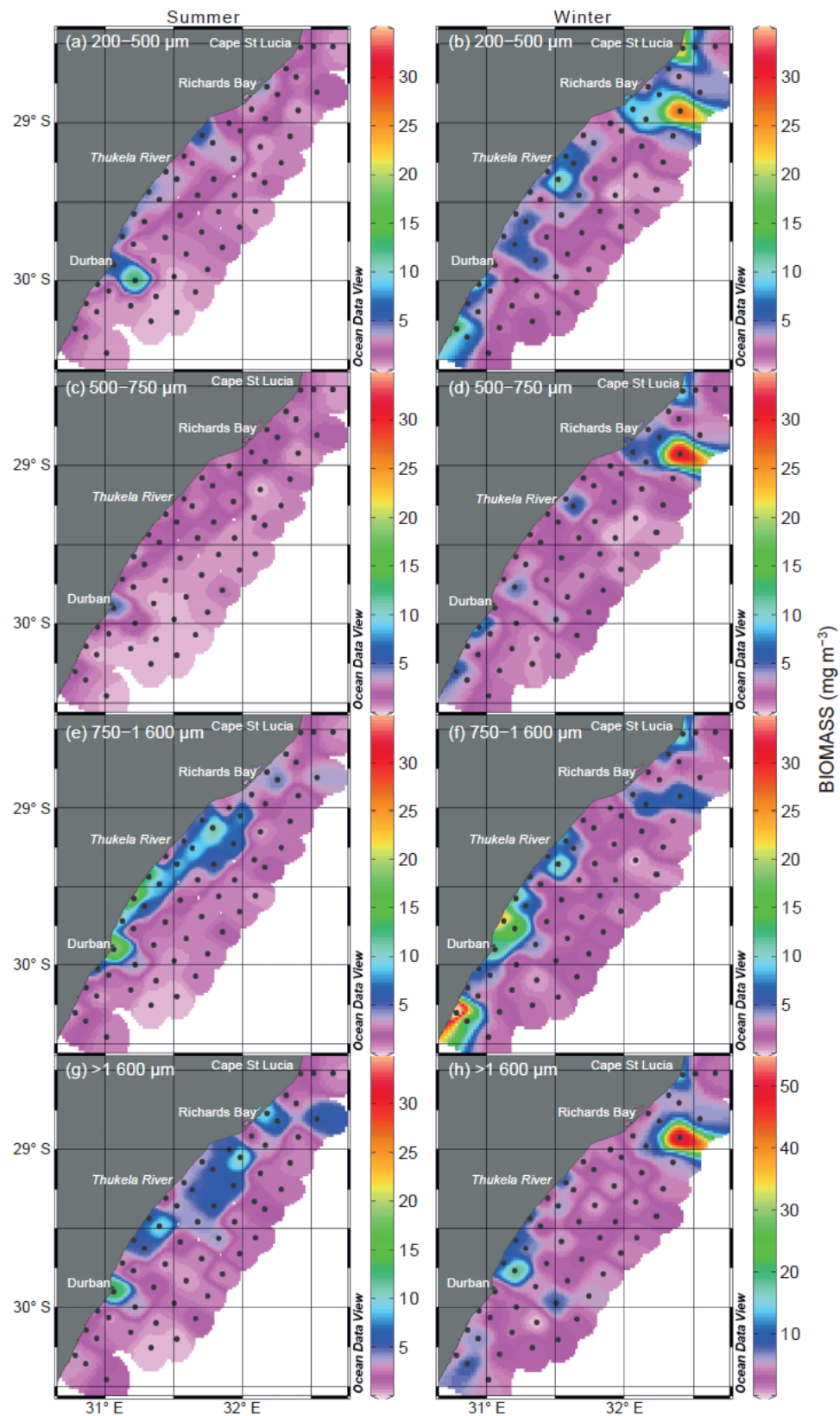
Figure 5: Zooplankton biomass during the summer and winter surveys for four size fractions: (a) and (b) 200–500 μm, (c) and (d) 500–750 μm, (e) and (f) 750–1 600 μm, and (g) and (h) >1 600 μm. Note the scales are not the same for all plots
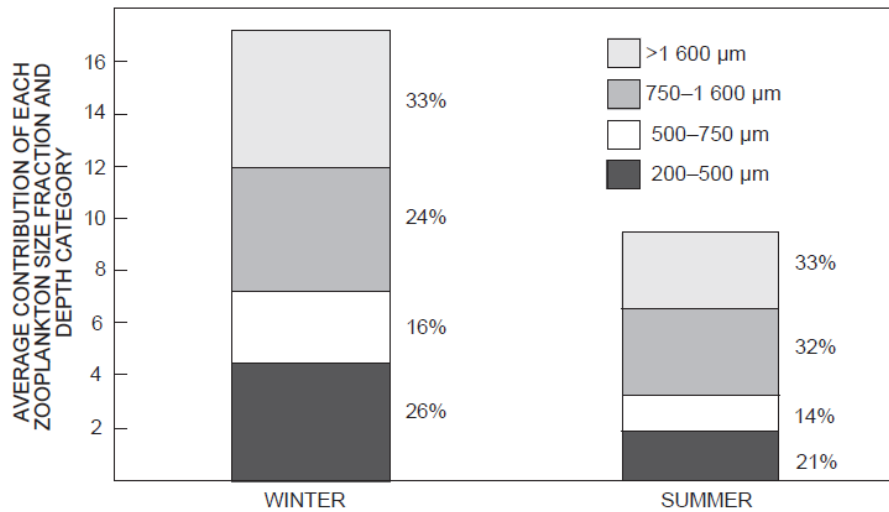
Figure 6: Mean zooplankton biomass (mg DW m⁻³) during the winter and summer seasons of four size fractions, pooled across depth classes. The average percentage contribution is indicated alongside each size fraction
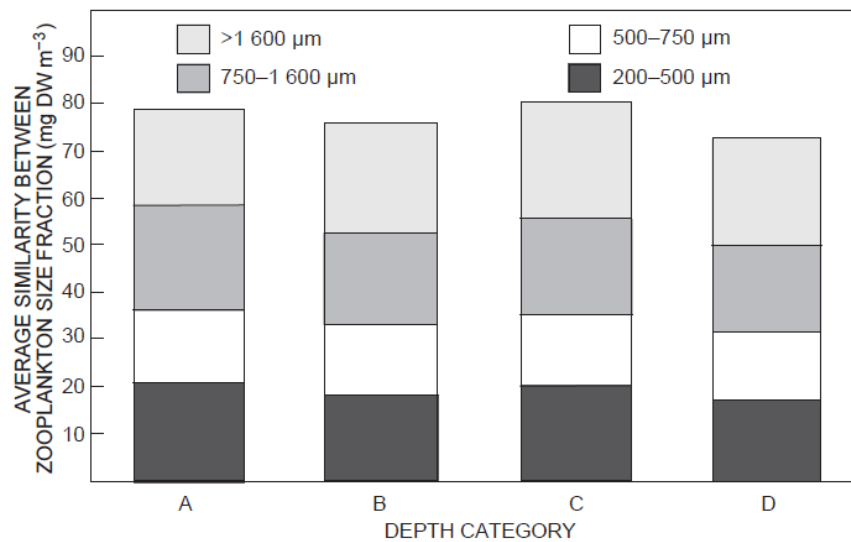

Figure 7: Average similarity between the four zooplankton size fractions and the depth categories sampled in both seasons. Depth categories: A = <50 m, B = 50–200 m, C = 200–500 m, D = >500 m

Discussion

The KZN Bight appears capable of supporting greater zooplankton biomass than other areas within the greater Agulhas Current system. The Delagoa Bight in southern Mozambique, about 500 km north of the KZN Bight, provides a useful comparison with the KZN Bight as both are situated in areas on the east coast of Africa where the continental shelf widens. The zooplankton community in the Delagoa Bight was sampled during three surveys from 2004 to 2006 and biomass was greatest inshore over the continental shelf, with maximum zooplankton concentrations corresponding to areas of maximum surface chlorophyll *a* (JAH unpublished data). In contrast to the present study, there was no clear seasonal variability in zooplankton biomass. Mean zooplankton biomass during the three surveys was c. 8 mg DW m−3, which was similar to the mean zooplankton biomass during summer in the current

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study (9.5 mg DW m−3) but only half that found during winter (17 mg DW m−3), indicating that the KZN Bight may be more productive for zooplankton, or possibly more retentive, than the Delagoa Bight.
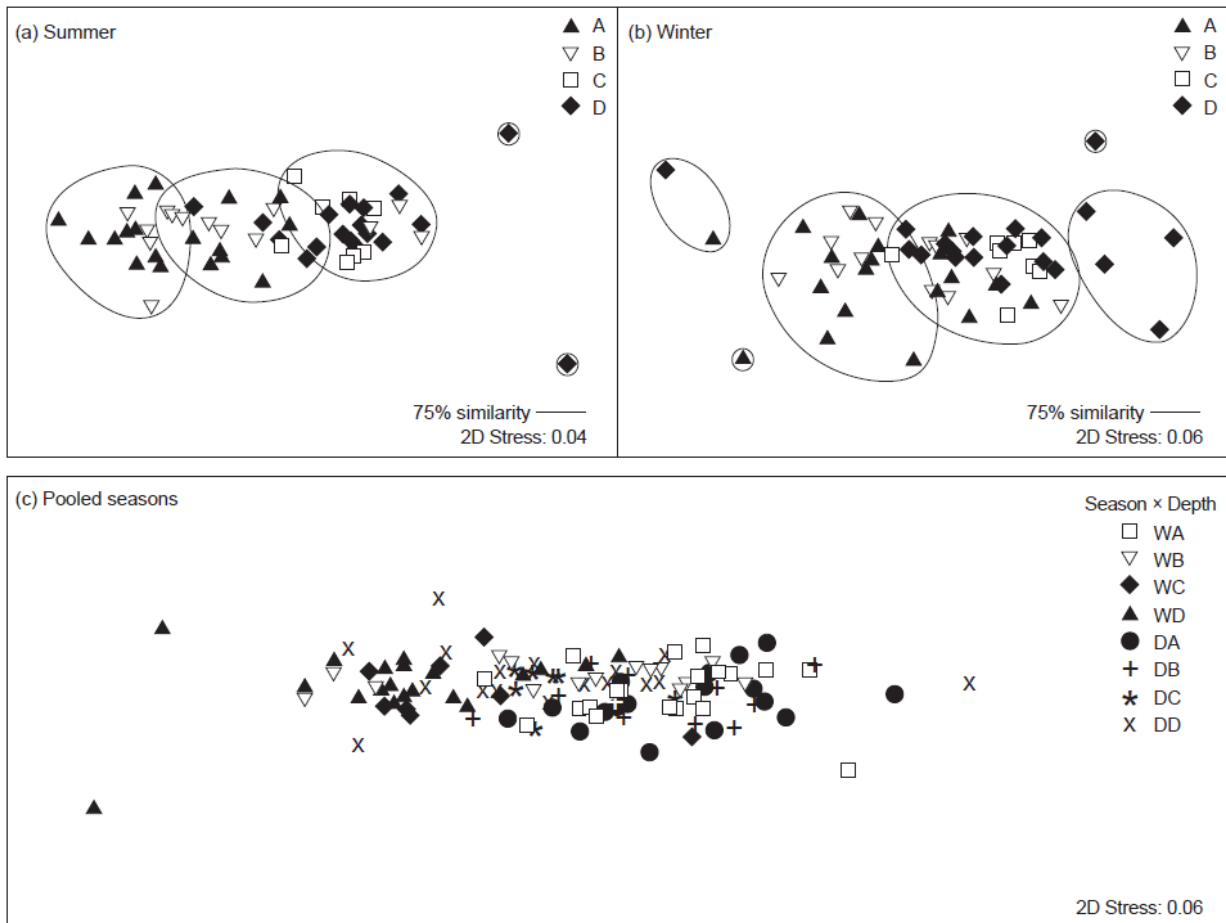

Figure 8: Multidimensional scaling (MDS) plot of zooplankton biomass for (a) summer and (b) winter showing the depth groupings at the 75% similarity level (square root transformation, Bray–Curtis similarity), (c) MDS between pooled seasons and depth categories of the stations. W = wet/summer season and D = dry/winter season. Depth categories: A = <50 m, B = 50–200 m, C = 200–500 m, D = >500 m

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Table 4: DistLM results (marginal test) for the relationship between the zooplankton biomass concentrations and the environmental variables; Int = integrated

Variable	Sum of squares (trace)	Pseudo-F	p	Proportion
Depth	12 581.0	30.089	0.001	0.20
SST	10 591.0	24.339	0.001	0.17
Salinity	2 124.6	4.187	0.025	0.03
Chl a	8 078.0	17.691	0.001	0.13
Dissolved oxygen	8 565.3	18.931	0.001	0.14
Int Chl a	472.7	0.906	0.342	0.01
Int SiO_4	6 389.5	13.565	0.001	0.10
Int PO_4	10 646.0	24.494	0.001	0.17
Int NO_3	13 072.0	31.580	0.001	0.21
Int NO_2	752.8	1.450	0.230	0.01

Zooplankton biomass in the KZN Bight was also greater than that in the Mozambique Channel. Four surveys were conducted between 2007 and 2010 to investigate the abundance, distribution and community composition of mesozooplankton associated with mesoscale eddies in the channel (Huggett 2014). Biovolume in the upper 200 m was greatest at shelf stations (4.4 mg DW m−3) compared to the mid-channel cold-core cyclonic eddies (3.7 mg DW m−3) and warm-core anticyclonic eddies (2.2 mg DW m−3), and was also greater during night-time than during the day. Mean biomass over all four surveys and seasons was 5.0 mg DW m−3, which was 50% and 25%, respectively, of that found during summer and winter in the KZN Bight. Measurements of zooplankton biomass downstream from the KZN Bight on the Agulhas Bank (between Port Elizabeth and Cape Point) are quite variable, and generally refer only to the copepod component (see Table 5 for the values).
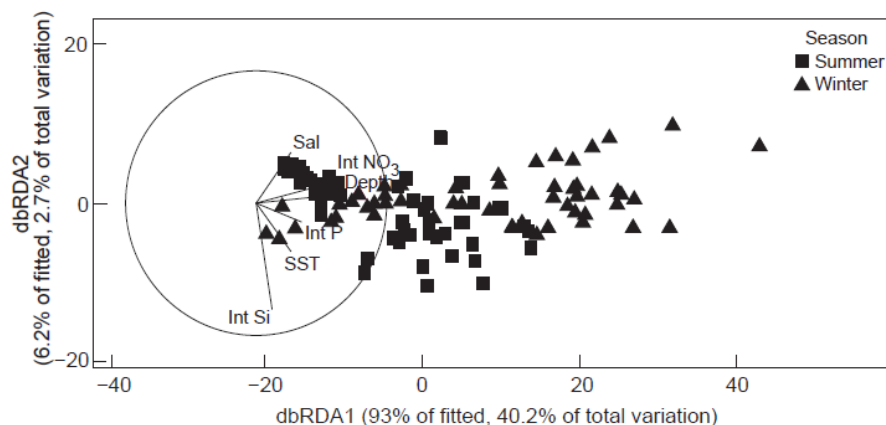
Figure 9: dbRDA plot of zooplankton biomass overlaid with the environmental variables

Table 5: Estimates of mean zooplankton standing stock/biomass for various ecosystems recorded in different studies in southern Africa. Maximum depth of sampling in all cases was upper 200 m. Data are expressed in mg DW m^{-3} and a factor of 2.5 was used to convert carbon weight to dry weight (after Peterson et al. 1990)

Date of sampling	Study area	Gear and mesh size	Mean biomass (mg DW m^{-3})	Source and comments
November 1988	Agulhas Bank	Vertical bongo net (200 µm mesh)	15	Peterson et al. (1992) Copepods only
November 1989			22	
July 1984	Northern Benguela	Oblique bongo net (300 µm mesh, 40 cm mouth)	1.76	Barange (1989) Mesozooplankton
1958/1959	Northern Benguela	N7OV (200–460 µm mesh)	31.5	Kollmer (1963) Mesozooplankton
Winter (May/June) and summer (October/November) 1988–2003	Southern Benguela	Vertical bongo net (200 µm mesh)	30.9	Huggett et al. (2009) Copepods only
2004–2006	Delogoa Bight	Vertical bongo net (200 µm mesh)	7.9 (biovolume 0.62 ml m^{-3})	JAH (unpublished data) Mesozooplankton
2007	Mozambique Channel	Vertical Hydrobios MultiNet (200 µm mesh)	0.005 g DW m^{-3}	(Huggett 2014) Mesozooplankton
2008–2010		Oblique Hydrobios MultiNet (200 µm mesh)	5	
January–February 2010	KZN Bight	Vertical bongo net (200 µm mesh)	Summer 9.5	Current study Mesozooplankton
July–August 2010			Winter 17	

Peterson et al. (1992) measured relatively high mean copepod biomass (15 and 22 mg DW m−3) over the whole Agulhas Bank in November 1988 and 1989 respectively, whereas Verheye et al. 1992 measured 4.5 and 7.6 mg DW m−3 on the western and eastern Agulhas Bank, respectively, in November 1983. Mesozooplankton biomass on the Agulhas Bank was generally higher in the eastern region (Cape Agulhas to Port Elizabeth) than the west, which was thought to be a result of higher chlorophyll *a* concentrations on the eastern Bank and the presence of a semi-closed cyclonic circulation (Peterson et al. 1992; Verheye et al. 1992). In contrast, consistently higher zooplankton biomass has been recorded off the west coast of South Africa compared to the KZN Bight (Table 5). The maximum biomass recorded for the Northern Benguela by Kollmer (1963) was double that recorded in the KZN Bight. Mean copepod biomass in the southern Benguela during annual autumn and summer surveys over a 16-year time-series was similarly higher (Huggett et al. 2009). There are very few data available on zooplankton biomass in other western boundary current systems. On the southern Brazilian shelf, biomass of zooplankton associated with upwelling areas can exceed

200 mg DW m−3 during an upwelling phase and 50 mg DW m−3 during a non-upwelling phase during summer (Valentin and Moreira 1978, cited in Lopes et al. 2006). In the Kuroshio Current region in the Pacific Ocean, Kawarada et al. (1966) recorded very little seasonal change in the distribution of copepods, with biomass generally <3.15 mg DW m−3 on the oceanic side of the current and 3.15–11.34 mg DW m−3 on the neritic (inshore) side (values estimated from wet weight, using conversion equations in Huggett [2014]). Many of these as well as other studies indicate elevated zooplankton biomass associated with upwelling events or seasons, as well as changes in community structure in response to upwelling events (e.g. Pillar 1986; Verheye et al. 1992; Huggett et al. 2009). Depending on when these seasonal events occur, the biomass reacts accordingly, in response to nutrients concentrated in deep water that are brought up onto the shelf by various processes. For the KZN Bight, these upwelling processes seem to be driven mainly by interactions between the Agulhas Current and the shelf topography, although nutrients may also be introduced by rivers, such as silicate by the Thukela River. In terms of potential zooplankton productivity, the areas of highest zooplankton biomass during the present study were the Durban area in the summer wet season and the Richards Bay/Cape St Lucia area in the winter dry season.

Durban Eddy
According to Guastella and Roberts (2016) the cyclonic 'Durban Eddy' is generally situated between Durban in the north and Sezela in the south (70 km away), although there was no evidence of this feature during either the summer or winter surveys in the current study. Despite not being present all the time, however, the eddy seems to have a strong influence on the surrounding water masses. Lutjeharms (2006) stated that nitrates within the Durban Eddy averaged 3.33 µmol l−1, reaching a maximum of 16 µmol l−1. Our study supports these findings, with nitrates of 3.5 µmol l−1 recorded off Durban during the summer survey. This suggests recent upwelling in the area, bringing nutrient-rich water close to the surface. Lutjeharms (2006) also stated that the Durban Eddy, although recurrent but not always present, shows very little local biological impact as the eddy is not enduring. However, our study showed high total zooplankton biomass off Durban, as well as relatively high biomass of large copepods farther north within the central bight, which might suggest a more mature population in this region. This might have been an effect of the Durban Eddy or of possible riverine inputs from the Mgeni River. A subsurface chlorophyll *a* maximum (indicated by elevated fluorescence) and doming of nutrients offshore of Durban was noted during the summer survey despite the Durban Eddy not being present (Guastella and Roberts 2016, their Figure 4c and e). These authors reported four eddy occurrences, based on moored current meters and satellite imagery, up to 8 weeks prior to the summer survey. Given that a period of 3–8 weeks is required for copepods to respond to growth in phytoplankton and thus increase their biomass (Postel et al. 1995 as cited in Hansen et al. 2005), it seems feasible that there was sufficient time for the phytoplankton to respond to the nutrient-rich water, promoting zooplankton production and the resultant elevated zooplankton biomass. This could explain the dominance of larger, and presumably older, copepods within the central bight. Alternatively, it is possible that summer rainfall prior to the synoptic survey could have transported nutrients from the catchments inland and deposited them into the ocean via the Mgeni River, which, in turn, could have resulted in higher chlorophyll *a*

concentrations off Durban. Season may not be a contributing factor *per se* to changes in zooplankton biomass observed in the KZN Bight, but may rather by chance be associated with varied physical oceanographic conditions at the time of sampling. Carter and d'Aubrey (1988) showed that nutrient distributions on the continental shelf were dominated more by event-scale processes than by longer-term cyclical processes. During the winter survey, a Natal Pulse, as observed by Guastella and Roberts (2016), likely contributed to the relatively low zooplankton biomass measured off Durban, as it may have masked the 'normal' winter season conditions to some extent by interrupting the flow and occurrence of the Durban Eddy. The Natal Pulse is evident in the inshore ADCP mooring data off Durban as a prolonged period of light south-westward currents, while farther offshore (position DO in their Figure 1) the ADCP mooring data reflect the passage of a Natal Pulse as an interruption to the Agulhas Current flow through a prolonged period of light northeastward currents (Guastella and Roberts 2016).

Richards Bay/Cape St Lucia upwelling cell

High zooplankton biomass was recorded during winter off Richards Bay, coincident with cooler mean SST, higher chlorophyll *a* and higher dissolved oxygen concentrations. These conditions are suggestive of upwelling off Cape St Lucia, which is driven by the interaction between the Agulhas Current and the adjacent shelf topography (Gill and Schumann 1979; Lutjeharms et al. 1989). Oliff (1973) observed a positive response in phytoplankton to an upwelling event at Richards Bay, and the high zooplankton biomass recorded may then be a direct result of a phytoplankton bloom. The shelf topography forces a distinctive upwelling cell near Cape St Lucia, which has characteristic low temperatures and high chlorophyll *a* and nutrient concentrations (Carter and d'Aubrey 1988; Carter and Schleyer 1988). Lutjeharms et al. (2000a) and Meyer et al. (2002) demonstrated that the Cape St Lucia upwelling cell is a point source of nutrients for the entire shelf, and this is further supported by the findings of Roberts and Nieuwenhuys (2016). This nutrient-rich water is then carried southwards at depth over the northern part of the bight. Surface nutrient-rich water upwelled from depth supplies the phytoplankton with a food source and thus encourages high chlorophyll *a* concentrations (Meyer et al. 2002). As a result, the KZN Bight has the highest primary production on the East Coast. Oliff (1973) and Pearce (1977) demonstrated that nutrients in deeper waters decrease with distance offshore, and the same was found in our study. Acoustic Doppler current profilers (ADCPs) were deployed off Richards Bay between September 2009 and September 2010 as a part of the ACEP project (Roberts and Nieuwenhuys 2016), but only the summer survey data had been analysed at the time of writing. These authors reported no upwelling event within the 8-week period prior to the summer survey, which could explain why there was low zooplankton biomass in this region during the summer survey. Significant seasonal effects on the size structure of the zooplankton biomass communities were observed, with small and medium-sized copepods proportionally more abundant in winter and large copepods proportionally more abundant in summer. For the two smaller groups, most of the biomass in winter was concentrated offshore between Richards Bay and Cape St Lucia, and was associated with cooler, chlorophyll-rich water. This suggests that the smaller and younger community (microscope analysis indicated most were younger individuals, as opposed to smaller species) may have

developed quite recently, following upwelling and suitable growth conditions associated with the Cape St Lucia upwelling cell, and this would also account for the low biomass of larger copepods in this region. In contrast, larger copepods dominated the zooplankton within the bight and off Durban during summer, suggesting an older and more mature community inhabited the warmer, chlorophyll-poor conditions found at this time of year. Without knowledge of recent circulation patterns within the bight, the origin of the biomass in the central bight is unclear, with possible origins including productivity associated with an earlier Durban Eddy to the south, the Cape St Lucia upwelling cell to the north, or nutrient-rich bottom waters advected onto the shelf through interaction with the Agulhas Current. The high zooplankton biomass found off Durban in the summer survey and off Richards Bay and Cape St Lucia during the winter survey could be a consequence of circulation patterns that favour retention, resulting in conditions under which phytoplankton develop and translate into high zooplankton biomass. Depth within the bight, i.e. distance from shore and proximity to the Agulhas Current, could also account for the biomass variation. In conclusion, zooplankton biomass was not evenly distributed within the bight, but was elevated off Durban and the Richards Bay/Cape St Lucia region, where nutrient enrichment from quasi-permanent upwelling may have contributed to the increase in biomass. There was no evidence of raised biomass associated with riverine input from the Thukela River during summer (the wet season). Patterns of zooplankton biomass showed clear differences between the summer and winter surveys, with significantly higher biomass during winter (the dry season). Zooplankton biomass varied with depth, being greatest inshore (<50 m), and declining offshore, although this was mainly driven by the large-copepod component, with other large zooplankton taxa being more abundant offshore. The present study provides two 'snap shots' of zooplankton biomass during summer and winter in relation to hydrographic conditions within the bight. Further studies during all seasons are required to fully assess seasonal variability in zooplankton biomass in relation to the sources of productivity in the KZN Bight system.

References

Anderson FP, Gründlingh ML, Stravropoulos CC. 1988. Kinematics of the southern Natal coastal circulation: some historic measurements 1962–63. *South African Journal of Science* 84: 857–860.

Anderson MJ, Gorley RN, Clarke KR. 2008. *PERMANOVA+ for PRIMER: guide to software and statistical methods.* Plymouth: PRIMER-E.

Barange M. 1989. Zooplankton size structure off Namibia in July 1983 and 1984. *Collection of Scientific Papers. International Commission for the Southeast Atlantic Fisheries* 16: 31–41.

Barlow R, Kyewalyanga M, Sessions H, van den Berg M, Morris T. 2008. Phytoplankton pigments, functional types, and absorption properties in the Delagoa and Natal Bights of the Agulhas ecosystem. *Estuarine, Coastal and Shelf Science* 80: 201–211.

Beckley LE, Hewitson JD. 1994. Distribution and abundance of clupeoid larvae along the east coast of South Africa in 1990/1. *South African Journal of Marine Science* 14: 205–212.

Carter RA. 1977. The distribution of calanoid Copepoda in the Agulhas Current system off Natal, South Africa. MSc thesis, University of Natal, South Africa.

Carter RA, d'Aubrey J. 1988. Inorganic nutrients in Natal continental shelf waters. In: Schumann EH (ed.), *Coastal ocean studies off Natal, South Africa.* Lecture Notes on Coastal and Estuarine Studies 26. New York: Springer-Verlag. pp 131–151.

Carter RA, Schleyer MH. 1988. Plankton distributions in Natal coastal water. In: Schumann EH (ed.), *Coastal ocean studies off Natal, South Africa.* Lecture Notes on Coastal and Estuarine Studies 26. New York: Springer-Verlag. pp 152–177.

Clarke KR, Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation* (2nd edn). Plymouth: PRIMER-E.

Clarke KR, Gorley RN. 2001. *Primer v5: user manual/tutorial.* Plymouth: PRIMER-E.

Connell AD. 2001. Pelagic eggs of marine fishes from Park Rynie, KwaZulu-Natal, South Africa: seasonal spawning patterns of the three most common species. *African Zoology* 36: 197–204.

De Decker AHB. 1964. Observations on the ecology and distribution of Copepoda in the marine plankton of South Africa. *Investigational Report, Division of Sea Fisheries, South Africa* 49: 7–33.

De Decker AHB. 1984. Near-surface copepod distribution in the south-western Indian and south-eastern Atlantic Ocean. *Annals of the South African Museum* 93: 303–370.

De Decker AHB, Mombeck FJ. 1964. South African contributions to the International Indian Ocean expedition. Preliminary report on planktonic copepods. *Investigational Report, Division of Sea Fisheries, South Africa* 51: 1–67.

de Ruijter WPM, van Leeuwen PJ, Lutjeharms JRE. 1999. Generation and evolution of Natal pulses: solitary meanders in the Agulhas Current. *Journal of Physical Oceanography* 29: 3043–3055.

Gill AE, Schumann EH. 1979. Topographically induced changes in the structure of an inertial coastal jet: application to the Agulhas Current. *Journal of Physical Oceanography* 9: 975–991.

Gründlingh ML. 1974. A description of inshore current reversals off Richards Bay based on airborne radiation thermometry. *Deep-Sea Research* 21: 47–55.

Guastella LA, Roberts MJ. 2016. Dynamics and role of the Durban cyclonic eddy in the KwaZulu-Natal Bight ecosystem. In: Roberts MJ, Fennessy ST, Barlow RG (eds), *Ecosystem processes in the KwaZulu-Natal Bight. African Journal of Marine Science* 38(Supplement): S7–S21.

Hansen FC, Cloete RR, Verheye HM. 2005. Seasonal and spatial variability of dominant copepods along a transect off Walvis Bay (23°S), Namibia. *African Journal of Marine Science* 27: 55–63.

Huggett JA. 2014. Mesoscale distribution and community composition of zooplankton in the Mozambique Channel. *Deep-Sea Research II* 100: 119–135.

Huggett JA, Verheye HM, Escribano R, Fairweather T. 2009. Copepod biomass, size composition and production in the Southern Benguela: spatio-temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Progress in Oceanography* 83: 197–207.

Kawarada Y, Kitou M, Furuhashi K, Sona A, Karohji K, Kuroda K et al. 1966. Distribution of plankton collected on board the research vessels of J.M.A. in 1965 (CSK). *Oceanographical Magazine* 18: 91–112.

Kollmer WE. 1963. The pilchard of South West Africa (*Sardinops ocellata*). Notes on zooplankton and phytoplankton collections made off Walvis Bay. *Investigational Report of the Marine Research Laboratory South West Africa* 8: 1–78.

Lopes RM, Katsuragawa M, Dias JF, Montú MA, Muelbert JH, Gorri C, Brandini FP. 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. *Scientia Marina* 70: 189–202.

Lovegrove T. 1962. The effect of various factors on dry weight values. *Rapports et Procés Verbeaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer* 153: 89–91.

Lovegrove T. 1966. The determination of the dry weight of plankton and the effect of various factors on the values obtained. In: Barnes H (ed.), *Some contemporary studies in marine science*. London: George Allen & Unwin. pp 429–467.

Lutjeharms JRE. 2006. The coastal ocean of south-eastern Africa. In: Robinson AR, Brink KH (eds),*The sea*, Vol. 14B. Cambridge, Massachusetts: Harvard University Press. pp 783 834.

Lutjeharms JRE, Cooper J, Roberts M. 2000b. Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737–761.

Lutjeharms JRE, Gründlingh ML, Carter RA. 1989. Topographically induced upwelling in the Natal Bight. *South African Journal of Science* 85: 310–316.

Lutjeharms JRE, Valentine HR, van Ballegooyen RC. 2000a. The hydrography and water masses of the Natal Bight, South Africa. *Continental Shelf Research* 20: 1907–1939.

Meyer AA, Lutjeharms JRE, de Villiers S. 2002. The nutrient characteristics of the Natal Bight, South Africa. *Journal of Marine Systems* 35: 11–37.

Mostert S. 1983. Procedures used in South Africa for the automatic photometric determination of micro nutrients in seawater. *South African Journal of Marine Science* 1: 189–198.

O'Donoghue SH, Drapeau L, Dudley SFJ, Peddemors VM. 2010. The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *African Journal of Marine Science* 32: 293–307.

Oliff WD. 1973. Chemistry and productivity at Richards Bay. NPRL Oceanography Division Contract Report CFIS 37B, Durban.

Pearce AF. 1977. The shelf circulation off the east coast of South Africa. CSIR Research Report No. 361. Council for Scientific and Industrial Research, Stellenbosch.

Pearce AF. 1978. Seasonal variations of temperature and salinity on the northern Natal continental shelf. *South African Geography Journal* 60: 135–143.

Pearce AF, Schumann EH, Lundie GSH. 1978. Features of the shelf circulation off the Natal coast. *South African Journal of Science* 74: 328–331.

Peterson WT, Hutchings L, Huggett JA, Largier JL. 1992. Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the Western Agulhas Bank. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning. South African Journal of Marine Science* 12: 487–500.

Peterson WT, Painting SJ, Hutchings L. 1990. Diel variations in gut pigment content, diel vertical migration and estimates of grazing impact for copepods in the southern Benguela upwelling region in October 1987. *Journal of Plankton Research* 12: 259–281.

Pillar SC. 1986. Temporal and spatial variations in copepod and euphausiid biomass off the southern and south-western coasts of South Africa in 1977/78. *South African Journal of Marine Science* 4: 219–229.

Roberts MJ, Nieuwenhuys C. 2016. Observations and mechanisms of upwelling in the northern KwaZulu-Natal Bight, South Africa. In: Roberts MJ, Fennessy ST, Barlow RG (eds), *Ecosystem processes in the KwaZulu-Natal Bight. African Journal of Marine Science* 38(Supplement): S43–S63.

Schleyer MH. 1985. *Chaetognaths as indicators of water masses in the Agulhas Current system. Investigational Report* No. 61. Durban: Oceanographic Research Institute.

Schlitzer R. 2013. Ocean Data View 4. Available at http://odv.awi. de [accessed 2013].

Schumann EH. 1981. Low frequency fluctuations off the Natal coast. *Journal of Geophysical Research* 86: 6499–6508.

Schumann EH. 1982. Inshore circulation of the Agulhas Current off Natal. *Journal of Marine Research* 40: 43–55.

Schumann EH. 1988. Physical oceanography off Natal. In: Schumann EH (ed.), *Coastal ocean studies off Natal, South Africa*. Lecture Notes on Coastal and Estuarine Studies 26. New York: Springer-Verlag. pp. 101–130.

StatSoft Inc. 2002. STATISTICA (data analysis software system), version 6. Available at www.statsoft.com [accessed 2013].

Thibault-Botha D, Lutjeharms JRE, Gibbons MJ. 2004. Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. *Journal of Plankton Research* 26: 1115–1128.

van der Lingen CD, Coetzee JC, Hutchings L. 2010. Overview of the KwaZulu-Natal sardine run. *African Journal of Marine Science* 32: 271–277.

Verheye HM, Hutchings L, Huggett JA, Painting SJ. 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. In Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning. South African Journal of Marine Science* 12: 561–584.

Welschmeyer N. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and phaeopigments. *Limnology and Oceanography* 39: 1985–1992.