S. Afr. J. mar. Sci. 11: 499–512
1991

ESTIMATES OF STANDING STOCK, PRODUCTION AND CONSUMPTION OF MESO- AND MACROZOOPLANKTON IN THE BENGUELA ECOSYSTEM

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Attempts are made to consolidate current information on estimates of standing stock, production and consumption of meso- and macrozooplankton from the shelf region of the west and south coasts of southern Africa for inclusion in a network analysis of carbon flow in the Benguela system. The meso- and macrozooplankton communities consist chiefly of copepods and euphausiids respectively. Although geographic and seasonal differences in standing stock are reasonably well described for the inner shelf (<200 m), knowledge of production and rate processes affecting standing stock is limited, and extrapolation to the whole shelf area (<500 m) provides only a crude appraisal of the real situation. Despite the uncertainties, direct measurements have improved on estimates previously inferred. It seems likely that grazing by meso- and macrozooplankton plays a minor role in phytoplankton losses in the Benguela system. However, it would appear that predation by macrozooplankton, particularly under swarming conditions, has an appreciable impact on mesozooplankton biomass.

'n Poging word aangewend om bestaande inligting oor skattings van die bestand, produksie en verbruik van meso- en makrosoöplankton in die vastelandsplatstreek van die wes- en suidkus van Suider-Afrika saam te voeg in 'n netwerkontleding van koolstofvloei in die Benguelastelsel. Die meso- en makrosoöplanktongemeenskappe bestaan grootliks uit kopepodes en eufausiïdes onderskeidelik. Ofskoon geografiese en seisoensverskille in bestand redelik goed beskryf is vir die binneste vastelandsplat (<200 m), is die kennis beperk oor produksie en prosesse wat met tempo te doen het en die bestand raak, en ekstrapolering na die hele platgebied (<500 m) verskaf maar 'n ruwe taksering van die werklike situasie. Die onsekerhede ten spyt, het regstreekse metings die vorige skattings wat deur afleidings verkry is, verbeter. Dit lyk waarskynlik dat beweiding deur meso- en makrosoöplankton 'n ondergeskikte rol in fitoplanktonverliese in die Benguelastelsel speel. Dit wil egter voorkom of roofbedrywighede deur makrosoöplankton, veral onder swermvormingstoestande, 'n aansienlike uitwerking op die biomassa van die mesosoöplankton uitoefen.

The objective of this paper is to provide more-realistic estimates of standing stock, consumption rates and production of zooplankton for inclusion in a network analysis of carbon flow through the foodweb of the Benguela system (Field *et al.* in prep.). Zooplankton covers a size range spanning several orders of magnitude, but only two size groups, meso- and macrozooplankton, are considered in the present paper. Both groups, collectively referred to as net zooplankton, are retained by a 200 μm mesh net, but only macrozooplankton are retained by a net of 1 600 μm mesh. These categories are empirically derived by the most commonly used screens and sieves employed to separate the two size fractions of zooplankton collected in the Benguela system and do not pretend to aspire to universal acceptance.

The most common organisms contributing to meso- and macrozooplankton are copepods and euphausiids respectively, which together share >90 per cent of the standing stock in terms of dry mass of net zooplankton in the Benguela system (Fearon *et al.* 1986, Pillar 1986). It must be emphasized that small-sized copepods, particularly cyclopoids and copepodite stages, pass through the plankton nets used commonly (Pillar 1984b). Therefore, estimates of standing stock of net mesozooplankton must be considered as being underestimates of the real situation. It is not the intention of this paper to give a detailed account of copepod and euphausiid ecology, because current knowledge of their community structure, life history strategies and trophodynamics have recently been reviewed comprehensively for publication by Verheye *et al.* (in press) and Pillar *et al.* (in press). This paper rather serves as a preliminary attempt at deriving estimates from direct measurements of the rate processes underlying zooplankton abundance, production and consumption, values which have previously been inferred in budget studies of the Benguela system (e.g. Bergh *et al.* 1985, Shannon and Field 1985).

DATA SOURCE AND METHODS

Study area

For the purpose of the network analysis, the area defined as the Benguela system is considered as shorewards of the 500 m isobath and extending from approximately 17°S to 27°E (Fig. 1). For comparative purposes the area is divided into northern (179 000 km²) and southern (220 000 km²) regions.

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Manuscript received: April 1991

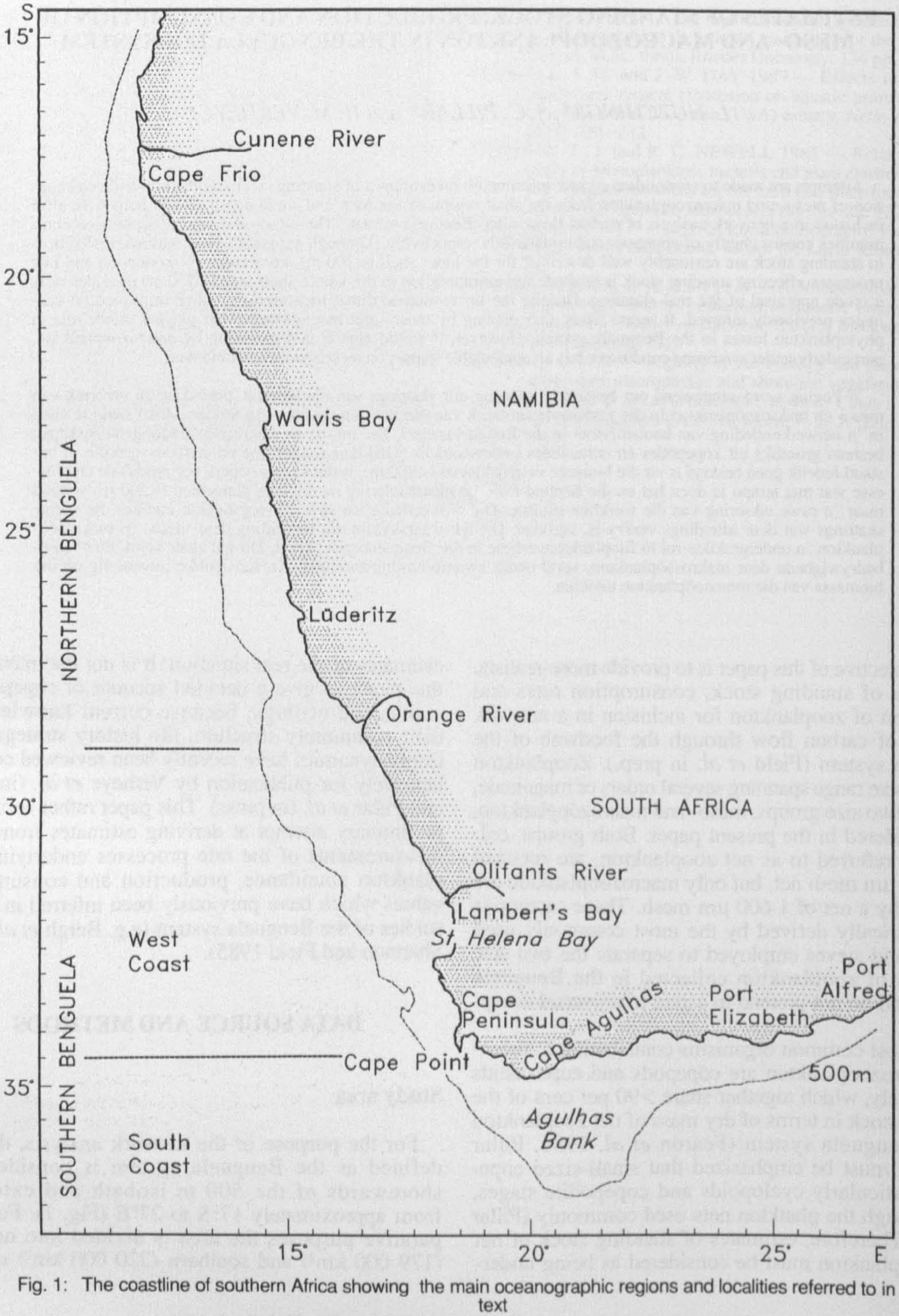

Fig. 1: The coastline of southern Africa showing the main oceanographic regions and localities referred to in text

The southern Benguela is further subdivided into West (104 000 km²) and South (116 000 km²) coasts. The South Coast encompasses the Agulhas Bank region.

Estimates of standing stock

A comprehensive account of early distributional studies of zooplankton abundance in the Benguela system is given by Shannon and Pillar (1986); it includes details of some of the sampling grids referred to in the text. The following gives an account of more-recent sources of information relevant to the assessment of zooplankton standing stock.

NORTHERN BENGUELA

During the 1970s and 1980s, plankton was sampled quantitatively with 300-μm mesh, 57-cm diameter paired Bongo nets towed obliquely in the upper 50 m. Sampling extended 65 miles offshore during the South West African Pelagic Egg and Larva Surveys (SWAPELS), which were conducted during summer (November–March). Data for one month (January 1985) were broken down into wet masses of principal groups (copepods, euphausiids, chaetognaths and amphipods) to provide size-differentiated data (Fearon *et al.* 1986). Collections from nine SWAPELS cruises between September 1982 and March 1984 formed the basis of a study of the euphausiid community structure of Namibian waters (Barange 1991, Barange and Stuart 1991, Barange and Pillar in press).

In July 1984 and 1985, 58 tows were made with 300-μm mesh Bongo nets in the upper 200 m during the Spanish Benguela V and Benguela VII cruises between Walvis Bay (23°S) and the mouth of the Orange River (28°30′S). These collections provided material for further size-differentiated studies (Barange 1991). In September 1985 and April 1986, additional data were collected at 55 and 95 stations respectively during the Spanish Namibian Environmental Cruises (SNEC) with a multiple opening-closing net of 200 μm mesh and a mouth area of 1 m² (RMT-1×6) towed obliquely in the upper 200 m. Data were categorized into major taxonomic groups by numbers of individuals (Olivar and Barangé 1990).

SOUTHERN BENGUELA

Andrews and Hutchings (1980) reported on inter-annual (1971/3), seasonal (monthly) and short-term changes in mesozooplankton standing stock (in terms of dry mass) collected with a vertically hauled WP-2 net (200 μm) off the Cape Peninsula. With a similar net, Hutchings (1988) reported on seasonal (quarterly) changes in mesozooplankton off the West Coast between Cape Point and Cape Columbine in 1974.

During the Cape Egg and Larva Programme (CELP) in 1977/8, a grid of 120 stations along the coast of the South-Western Cape was sampled monthly in the upper 100 m with an obliquely towed 57-cm diameter Bongo net with 300-μm mesh. Pillar (1986) used the night-time hauls from this data set to analyse seasonal and spatial differences in copepod and euphausiid standing stock (dry mass). A further 23 RMT-1×6 tows and 11 vertical Bongo net tows (both 200 μm mesh) were made in May 1983 between the mouth of the Orange River and Cape Agulhas (Verheye and Hutchings 1988). They provided an estimate of zooplankton abundance intermediate between the summer maximum and the winter/spring minimum. A further 20 hauls were made with the RMT-1×6 net between Cape Point and Port Elizabeth in November 1983 (HMV unpublished).

Although these RMT-1×6 data are scanty, they do provide the best estimates of meso- and macrozooplankton by combining a large mouth area (to reduce avoidance) with a fine mesh (to reduce escapement). Peterson and Hutchings (1989) used a vertically towed bridle-free Bongo net (200 μm mesh) from the bottom to the surface to estimate zooplankton abundance on the Agulhas Bank during November 1988. Verheye (1991) used similar gear during a 27-day Anchor Station time-series in St Helena Bay in 1987, as well as samples pumped from 5 or 6 different depths and filtered through 200- and 37-μm mesh nets.

Grazing and production studies

Virtually all estimates of zooplankton grazing and production have been made in a limited area on the inner shelf in newly upwelled or maturing upwelled waters between Cape Point and Lambert's Bay. The exception was the study of Peterson and Hutchings (1989), who measured copepod production across the Agulhas Bank. Olivieri (1985) made estimates of the fraction of phytoplankton grazed by copepods on four occasions in maturing upwelled waters off the Cape Peninsula. She used a Coulter counter to measure changes in total cell volume in parallel plant growth and grazing experiments. Borchers and Hutchings (1986), using data from Hutchings (1979), estimated grazing impact and production on the basis of copepod biomass, generation length and turnover times. Their assumptions on ecological efficiency and relationships between production and standing stock were derived from the literature.

Carter *et al.* (1986) estimated zooplankton consumption relative to phytoplankton production on the eastern

Table I: Estimates of standing stock of meso- and macrozooplankton in the Benguela ecosystem. All data were converted to carbon biomass using a carbon : wet mass ratio of 0,04 and dry mass : wet mass ratio of 0,10 for crustacean-dominated zooplankton (Parsons *et al.* 1984). For comparative purposes, the data were standardized for a 200 µm mesh (see Pillar 1984b)

Area	Gear and mesh (µm)	Depth sampled	Sampling date	Standing stock (gC·m^{-2})		Source and comments
				Mesozoo-plankton	Macrozoo-plankton	
						Northern Benguela
17°30′–23°30′S	Oblique Bongo 300	Upper 50 m	Jan. 1985	0,392	0,200	Fearon *et al.* 1986 – means of 48 night-time stations
17°30′–26°30′S	RMT-1x6 200	Upper 200 m	Apr. 1986	0,478 0,974 0,564	0,319 0,649 0,376	Olivar and Barangé 1990 – means for three longitudinal cross-shelf regions (inshore, shelf, slope)
23°00′–29°30′S	Oblique Bongo† 300	Upper 200 m	Jul. 1983 Jul. 1984	0,548 0,141	0,452 0,090	Barangé 1989 – means of 32 (1983) and 26 (1984) shelf-break and shelf stations
						Southern Benguela
29–31°S	RMT-1x6 200	Upper 200 m	May 1983	0,580	0,796	Verheye and Hutchings 1988 – means of nine stations between mouths of Orange and Olifants rivers
29°30′–31°00′S	RMT-1x6 200	Upper 200 m	Jun. 1986	0,475	0,397	Verheye (unpublished) – means of 19 stations between Port Nolloth and Olifants River mouth
31–33°S	RMT-1x6 200	Upper 200 m	May 1983	0,424	1,672	Verheye and Hutchings 1988 – means of 11 stations between Olifants River mouth and Cape Columbine
31–33°S	RMT-1x6 200	Upper 200 m	Jun. 1986	0,237	0,237	Verheye (unpublished) – means of 18 stations between Olifants River mouth and Cape Columbine
31°20′–33°00′S	Oblique Bongo 300	Upper 100 m	Aug. 1977– Aug. 1978	0,863	0,516	Pillar 1986 – annual means of monthly night-time sampling (n = 157) between Blinkwater Bay and Cape Columbine
32°33′S,18°05′E	Pump 200	Upper 45 m	Apr./May 1987	2,520	0,864	Verheye 1991 – means of a 27-day Anchor Station time-series at a fixed position in St Helena Bay
31°30′–34°20′S	RMT-1x6 200	Upper 200 m	Nov. 1983	0,748	0,210	Verheye (unpublished) – means of eight stations between Olifants River and Cape Point
33–34°S	Oblique Bongo 300	Upper 100 m	Aug. 1977– Aug. 1978	0,646	0,245	Pillar 1986 – annual means of monthly night-time sampling (n = 135) between Cape Columbine and Cape Point
33–34°S	RMT-1x6 200	Upper 200 m	Jun. 1986	0,443	0,079	Verheye (unpublished) – means of 12 stations between Cape Columbine and Cape Point
34°S	WP-2 200	Entire water column	Oct. 1970– Mar. 1973	0,920	*	Andrews and Hutchings 1980 – annual mean of 30 months of sampling off the Cape Peninsula. Split hauls above and below thermocline
33–35°S	Vertical Bongo 200	Upper 200 m	May 1983	0,784	*	Verheye and Hutchings 1988 – means of 11 stations between Cape Columbine and Cape Agulhas

Table I *(continued)*

Area	Gear and mesh (µm)	Depth sampled	Sampling date	Standing stock (gC·m^{-2})		Source and comments
				Mesozoo-plankton	Macrozoo-plankton	
				South Coast		
18°10′–20°00′E	RMT-1x6 200	Upper 200 m	Nov. 1983	0,360	0,058	Verheye (unpublished) – means of eight stations between Cape Point and Cape Agulhas
18°10′–21°30′E	Oblique Bongo 300	Upper 100 m	Aug. 1977–Aug. 1978	0,451	0,112	Pillar 1986 – annual means of monthly night-time sampling (*n* = 227) between Cape Point and Cape Barracouta
20–26°E	RMT-1x6 200	Upper 200 m	Nov. 1983	0,610	0,079	Verheye (unpublished) – means of 12 stations between Cape Agulhas and Cape Recife
18–27°E	Vertical Bongo 200	Upper 200 m	1988/89	0,360–2,072	–	Verheye *et al.* (in press) – range of means estimated for various parts of the Agulhas Bank

* Macrozooplankton not captured quantitatively
† 40 cm mouth diameter Bongo nets; in all other studies Bongo nets had a 57 cm mouth diameter
– No data

Agulhas Bank on the basis of relationships between respiration, production and consumption. Hutchings (1979, 1988) estimated net mesozooplankton production along a transect of stations extending across the shelf off the Cape Peninsula on the basis of copepod biomass measured over 33 months, together with literature-derived values of turnover times for copepods. Peterson *et al.* (1990b) estimated the *in situ* grazing impact of copepods on the shelf north of Cape Columbine in October 1987, using gut fluorescence and evacuation rates, together with rates of egg production for selected copepods.

Measurements of egg production and grazing rates were determined in a series of laboratory experiments on dominant copepod species by Attwood and Peterson (1989), Peterson *et al.* (1990a) and Peterson and Painting (1990). Field-based estimates of copepod biomass, egg production and moulting rates were reported by Painting and Huggett (1989) and Peterson and Hutchings (1989). Armstrong *et al.* (1991) used both direct and indirect methods to estimate rates of egg production by *Calanoides carinatus* during the Anchor Station in St Helena Bay. During the same study, Verheye (1989, 1991) derived estimates of copepod grazing and production from field data on the abundance and vertical distribution of different stages of the lifecycle of *C. carinatus* combined with laboratory-derived estimates of development time at different temperatures (Borchers and Hutchings 1986, Peterson and Painting 1990).

Quantitative estimates of growth, production and feeding of macrozooplankton are confined to those of euphausiids. From laboratory-derived growth rates documented by Pillar (1984a) and cohort analysis from field data, Stuart and Pillar (1988) estimated production and *P*/*B* ratios of *Euphausia lucens* in the southern Benguela. The data for that analysis were collected monthly at two transects extending offshore between St Helena Bay and Lambert's Bay. Measurements of grazing and trophic behaviour of euphausiids were determined from laboratory (Stuart 1986, 1989) and field-based studies (Pillar and Stuart 1988, Stuart and Pillar 1988, Gibbons *et al.* 1991a, b, Barange *et al.* 1991).

RESULTS AND DISCUSSION

Standing stock

Estimates of standing stock of meso- and macrozooplankton in the Benguela and on the South Coast are summarized in Table I. In most cases only single cruises, with a limited number of collections and usually

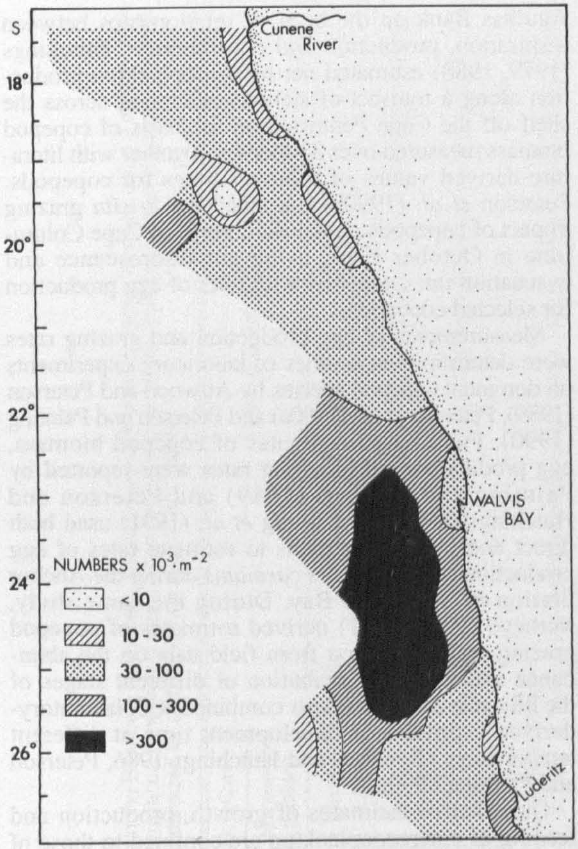

Fig. 2: Horizontal distribution of copepod abundance in the northern Benguela. Data were collected during the SNEC cruise in April 1986 by means of RMT-1×6 nets (200 μm mesh) in the upper 200 m (after Olivar and Barangé 1990)

within the 200 m isobath, have provided estimates of standing stock and, as such, extrapolation from these data to the whole shelf area should be viewed with caution. More-comprehensive temporal and spatial coverage is provided by Andrews and Hutchings (1980) and Pillar (1986), but their methods of sampling place certain limitations on the merit of these estimates. Quantitative information on macrozooplankton is lacking in Andrews and Hutchings (op. cit.) owing to net-avoidance by the more motile organisms. Also, estimates of standing stock by Pillar (op. cit.) needed adjusting to account for losses of small copepods through the meshes. Estimates of standing stock based on sampling by the RMT-1×6 net are considered to be the best available and these are supported by the more detailed data just described.

MESOZOOPLANKTON

Estimates of standing stock reported for the northern Benguela range between 0,1 and 1,0 gC · m^{-2} (Table I). Although Fearon *et al.* (1986) found biomass to be at its highest north of Walvis Bay, Olivar and Barangé (1990) noted a decrease to the north of this region. An intrusion of warm Angolan water from the north appeared to limit mesozooplankton standing stock during that study. Maximum values were in the mid-shelf region (Fig. 2), for which a mean value of 1,0 gC · m^{-2} was reported by Olivar and Barangé (op. cit.). This value represents almost the entire shelf area (80–400 m isobaths), and therefore a best estimate of 1,0 gC · m^{-2} is considered for mesozooplankton standing stock in the northern Benguela.

Estimates of mesozooplankton standing stock in the southern Benguela range between 0,2 and 2,5 gC · m^{-2}. Andrews and Hutchings (1980) estimated an annual mean of 0,9 gC · m^{-2} and showed a fourfold seasonal variation, with maximum values during the upwelling period. Considerable monthly variation is evident (Fig. 3). If the values of standing stock recorded by Pillar (1986) are adjusted to account for the losses of small copepods through the 300-μm mesh net (Pillar 1984b), a mean estimate of standing stock similar to that of Andrews and Hutchings (op. cit.) is obtained (Table I).

The distribution of mean standing stock of mesozooplankton in the southern Benguela from monthly collections taken between August 1977 and August 1978 is presented in Figure 4. Pillar (1986) showed that standing stock was higher on the West Coast than over the western Agulhas Bank and that seasonal variations were only marked between Cape Point and Cape Columbine, where there were summer maxima and winter minima. Results for the nearshore zone were highly variable, with coefficients of variation of 1,5–2,0, decreasing offshore. Verheye (1991) showed that daily fluctuations in mesozooplankton standing stock were not pronounced at a fixed station in St Helena Bay and that changes were not coupled to the upwelling cycle. A high mean standing stock of 2,5 gC · m^{-2} was recorded over the 27-day study period, which reflects typically high secondary production, a result of the benefits of the substantial phytoplankton food resource available in St Helena Bay (Brown *et al.* 1991). From the values presented in Table I, it is considered that the best estimate of mesozooplankton biomass for the shelf region of the southern Benguela is 0,8 gC · m^{-2}, within the range 0,2–2,0 gC · m^{-2}.

Peterson and Hutchings (1989) recorded copepod standing stocks of 0,2–2,0 gC · m^{-2} on the South Coast, increasing from west to east, and with an overall mean of 1,3 gC · m^{-2}. Analysis of unpublished data

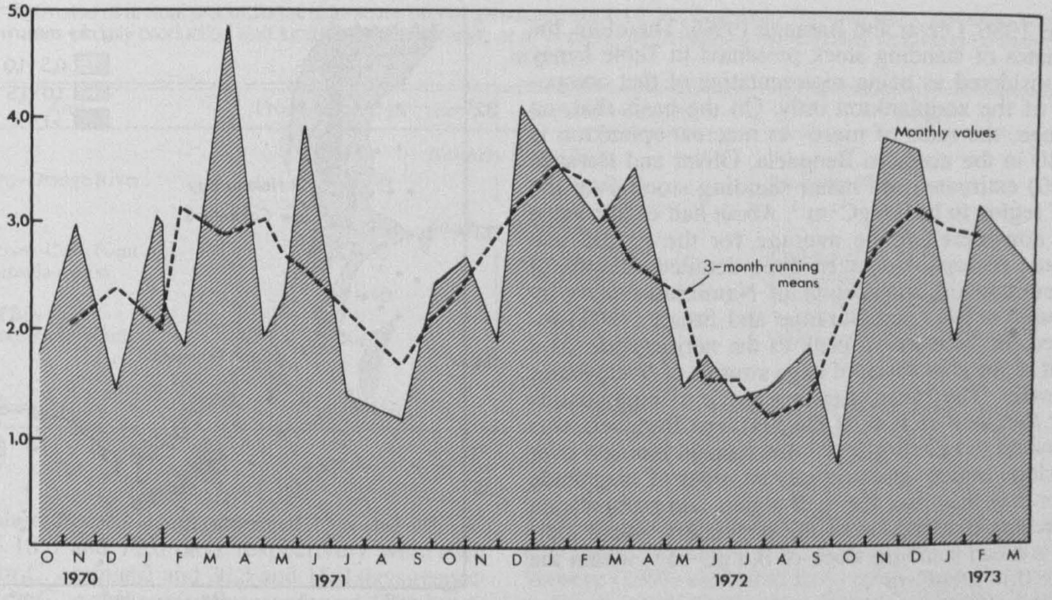

Fig. 3: Seasonal variation of the mean standing stock of mesozooplankton along an upwelling plume off the Cape Peninsula between 1970 and 1973. Data were collected with WP-2 nets (200 µm mesh) — after Andrews and Hutchings (1980)

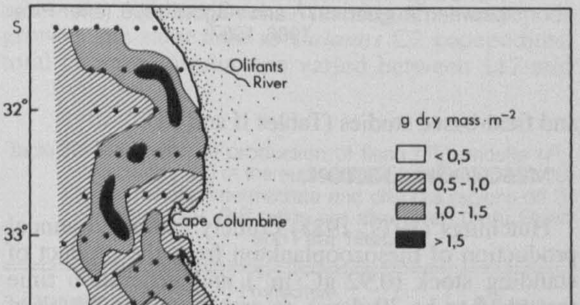

Fig. 4: Horizontal distribution of mean monthly standing stock of mesozooplankton in the southern Benguela and over the western Agulhas Bank. Data were collected with Bongo nets (300 µm mesh) during CELP surveys between August 1977 and August 1978 (after Pillar 1987)

from collections taken between Cape Point and Port Alfred supports this finding (Table I). The decrease in copepod abundance towards the western edge of the Agulhas Bank in November is thought to be due to heavy predation by spawning anchovy, which feed primarily on calanoid copepods. This group of copepods dominates the mesozooplankton community on the South Coast, constituting up to 90 per cent in terms of biomass (Peterson and Hutchings op. cit.).

Studies on seasonal changes in mesozooplankton stocks on the South Coast are restricted to the western Agulhas Bank, where Pillar (1986) found no significant inshore-offshore or seasonal differences in the standing stock. Quantitative information on temporal changes is lacking for the eastern Agulhas Bank, so the available data only give rough indications of abundance. Taking into account the dominance of large calanoid copepods on the South Coast, relative to the situation on the West Coast, it is not too unrealistic to assume a slightly higher standing stock of copepods for the South Coast. The mean standing stock for this region is considered to be 0,9 $gC \cdot m^{-2}$, within the range 0,1–2,0 $gC \cdot m^{-2}$.

MACROZOOPLANKTON

In terms of dry mass, euphausiids form the major portion of the macrozooplankton in the Benguela system

(Pillar 1986, Olivar and Barangé 1990). Therefore, the estimates of standing stock presented in Table I may be considered as being representative of that component of the zooplankton only. On the basis that, on average, the ratio of meso- to macrozooplankton is 60 : 40 in the northern Benguela, Olivar and Barangé (1990) estimated the mean standing stock over the shelf region to be 0,6 $gC \cdot m^{-2}$. About half of this value was considered to be average for the neritic and oceanic regions. However, more-detailed analysis of the euphausiid community of Namibian waters by Barange (1991) and Barange and Stuart (1991) revealed the biomass to peak in the neritic zone, as a result of the abundance of large swarms of *Nyctiphanes capensis*. The mean standing stock of euphausiids over the shelf region of the northern Benguela was estimated to be 0,8 $gC \cdot m^{-2}$. Euphausiid biomass over the slope region approximates an order of magnitude lower than in or over the shelf region, and extrapolation to include that portion of the population would indicate a mean standing stock of 0,6 $gC \cdot m^{-2}$, within the range 0,1–1,0 $gC \cdot m^{-2}$.

Pillar (1986) demonstrated that mean standing stock of macrozooplankton in the southern Benguela was significantly higher north of Cape Columbine (0,5 $gC \cdot m^{-2}$) than off the South-Western Cape (0,2 $gC \cdot m^{-2}$) and over the western Agulhas Bank (0,1 $gC \cdot m^{-2}$). This decrease in standing stock at higher latitude is clearly shown in Figure 5. Verheye and Hutchings (1988) confirmed this trend by showing that estimates of standing stock based on RMT – 1×6 net collections ranged from 0,8 $gC \cdot m^{-2}$ in the north to 0,1 $gC \cdot m^{-2}$ in the south. Despite considerable monthly variability in standing stock, especially off the West Coast, no seasonality was apparent in the southern Benguela (Pillar op. cit.). Standing stock was generally highest over the shelf off the West Coast, with a marked decrease beyond the slope. No appreciable inshore-offshore gradients of standing stock were found over the Agulhas Bank. Unfortunately, few studies on macrozooplankton are available for the eastern Agulhas Bank, but it appears that dense swarms of euphausiids are found along the East Coast (Cornew *et al.* 1992). The average standing stock off the West Coast is assumed to be 0,5 $gC \cdot m^{-2}$, within the range 0,1–1,0 $gC \cdot m^{-2}$, whereas a lower value of 0,1 $gC \cdot m^{-2}$ is considered appropriate for the Agulhas Bank.

Estimates of production and rate of turnover

Earlier attempts to calculate production and rate of turnover were based on crude estimates of abundance, growth rates and generation times. More recently, these estimates have been refined by both laboratory- and field-based studies (Tables II and III).

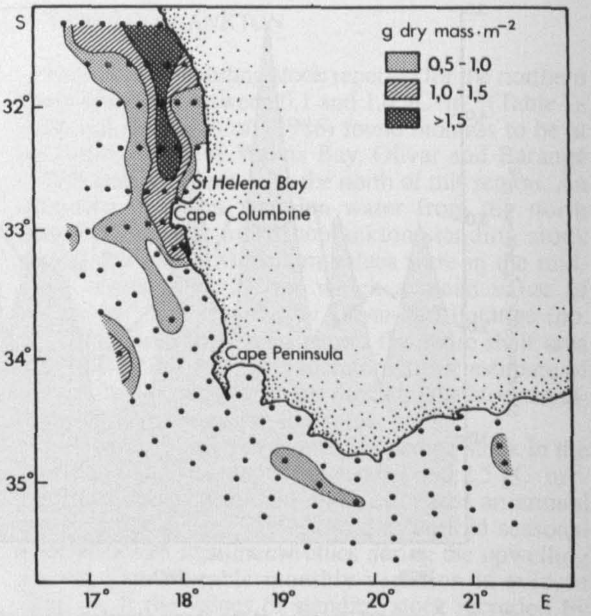

Fig. 5: Horizontal distribution of mean monthly standing stock of macrozooplankton in the southern Benguela and over the western Agulhas Bank. Data were collected with Bongo nets (300 µm mesh) during CELP surveys between August 1977 and August 1978 (after Pillar 1986, 1987)

MESOZOOPLANKTON

Hutchings (1979, 1988) crudely estimated annual production of mesozooplankton from the product of standing stock (0,92 $gC \cdot m^{-2}$) and generation time (assumed to be 30 days), to arrive at an estimate of 11 $gC \cdot m^{-2} \cdot year^{-1}$. Borchers and Hutchings (1986) determined generation times for *Calanoides carinatus* at temperatures of 7–18°C and, allowing for intermittent suboptimal feeding conditions, postulated a probable generation time of about 25 days at ambient temperatures of 13–15°C. They modified Hutchings' earlier production estimate using Steele's (1974) observation that production in a generation is 2–3 times the standing stock, which increased Hutchings' value to 30–40 $gC \cdot m^{-2} \cdot year^{-1}$. For a mean mesozooplankton standing stock of 1 $gC \cdot m^{-2}$, an annual P/B ratio of about 30–40 is implied.

Peterson and Painting (1990) estimated development rates from egg to adult of two abundant copepods, *Calanoides carinatus* and *Calanus agulhensis* (De Decker *et al.* 1991), under excess food conditions

Table II: Estimates of annual production and turnover rate of mesozooplankton in the Benguela. The data were converted from estimates of daily production and turnover rates (Verheye *et al.* in press) by multiplying by 365 days, assuming no seasonality of growth

Area	Production ($gC \cdot m^{-2} \cdot year^{-1}$)	Turnover rate ($\cdot year^{-1}$)	Source
	Northern Benguela		
Walvis Bay–Orange River	34–46	7–11	Cushing 1971
	Southern Benguela		
Orange River–Cape Point	24–33	6–8	Cushing 1971
Cape Peninsula region	11	11	Hutchings 1979, 1988
	30–40	30–40	Borchers and Hutchings 1986
St Helena Bay	79	61	Verheye 1991
Off Olifants River mouth	66–75	51–84	Walker and Peterson 1991
	South Coast		
Agulhas Bank	17–150	36–91	Peterson and Hutchings 1989

in the laboratory. At temperatures of 15,5 and 19,5°C, rates of 18,3 and 12,0 days respectively were estimated for *C. carinatus* and 20,3 and 16,0 days respectively for *C. agulhensis*. Peterson and Hutchings (1989) reported production rates of the latter species of between 22 and 770 mg dry mass$\cdot m^{-2} \cdot day^{-1}$ (3–112 $gC \cdot m^{-2} \cdot year^{-1}$, assuming carbon content is approximately 40% of dry mass; Parsons *et al.* 1984) across the Agulhas Bank. Assuming small copepods grow at the same rate as *Calanus* C2 copepodites, total copepod production varied between 117 and 1 027 mg dry mass$\cdot m^{-2} \cdot day^{-1}$ (17–150 $gC \cdot m^{-2} \cdot year^{-1}$), with daily *P*/*B* ratios of 0,10–0,25 (36–91 annually). Verheye (1991) estimated daily production of all copepodite stages of *Calanoides* during an Anchor Station time-series to be 1,7 $mgC \cdot m^{-3} \cdot day^{-1}$, with *P*/*B* ratios varying between 0,110 and 0,234$\cdot day^{-1}$ (mean = 0,167$\cdot day^{-1}$) over the 27-day period. Extrapolation to the herbivorous, crustacean-dominated mesozooplankton community gave an average daily production of 4,8 $mgC \cdot m^{-3} \cdot day^{-1}$. On an annual basis, this converts to 79 $gC \cdot m^{-2} \cdot year^{-1}$ with a *P*/*B* of 61$\cdot year^{-1}$ (range 40–85$\cdot year^{-1}$), assuming no seasonal variation in growth.

Table III: Mean annual production of flesh (P_g), moults (P_e) and eggs (P_r) of the euphausiid *Euphausia lucens* for the inshore, intermediate and offshore regions off St Helena Bay. *P*/*B* ratios are also given (from Stuart and Pillar 1988)

Parameter	Production (mg dry mass$\cdot m^{-3} \cdot year^{-1}$)	*P*/*B* ratio
	Inshore	
P_g	185,6	3,92
P_e	281,4	5,95
P_r	12,4	0,26
P(total)	479,4	10,14
	Intermediate	
P_g	77,2	7,92
P_e	60,0	6,15
P_r	5,1	0,52
P(total)	142,3	14,59
	Offshore	
P_g	92,7	8,91
P_e	64,4	6,19
P_r	9,3	0,89
P(total)	166,4	16,01

Based on *in situ* measurements of rates of egg production of dominant calanoid copepods, Painting and Huggett (1989) calculated copepod production along the inshore region of the West Coast shelf during June 1988. Generally, production ranged between 0 and 15 $mgC \cdot m^{-2} \cdot day^{-1}$ (0–6 $gC \cdot m^{-2} \cdot year^{-1}$), but in some cases, it was in excess of 20 $mgC \cdot m^{-2} \cdot day^{-1}$. Values were low in St Helena Bay because females there are subject to heavy predation by anchovy recruits. It would appear from the results of Painting and Huggett (op. cit.) that, for June 1988 at least, only about 10 per cent of the shelf was suitable for moderate to high rates (>10 $mgC \cdot m^{2} \cdot day^{-1}$) of copepod production. Therefore, in extrapolating production rates and *P*/*B* ratios of mesozooplankton to the whole shelf, it must be borne in mind that it is a matter of qualitative conjecture as to what proportion of the shelf area is suitable for maximum rate processes. Examination of the mean concentration of chlorophyll *a* (Brown *et al.* 1991) shows that only approximately 30 per cent of the West Coast shelf has sufficiently high concentrations (>2 mg chl $a \cdot m^{-3}$) to support rates of copepod egg production in excess of 50 per cent of laboratory-derived estimates. If these concentrations are further size-fractionated into <10 μm and >10 μm (Peterson and Bellantoni 1987, Painting and Huggett op. cit., Peterson and Hutchings 1989, Armstrong *et al.* 1991), perhaps even a smaller proportion of the shelf area of the southern Benguela is suitable for near-maximum production rates. In Namibian waters, the concentrations of chlorophyll *a* are about double those in the southern Benguela, and assuming no differences in the C: chlorophyll *a* ratios or the palatability of the phytoplankton, production of copepods may be higher in Namibian waters than in the southern Benguela. Tentative annual *P/B* values of 40 and 20 are adopted for the northern and southern Benguela respectively.

Estimates of production/consumption ratios, or gross growth efficiencies, are from laboratory studies documented by Peterson *et al.* (1990a). They measured *P/C* ratios of 32–37 per cent for the copepod *Calanoides carinatus*. A *P/C* ratio of about 30 per cent is widely accepted in the literature (Omori and Ikeda 1984, Parsons *et al.* 1984), and this value is adopted for mesozooplankton. Respiration losses for crustacean zooplankton are quite high, varying between 40 and 60 per cent (Omori and Ikeda op. cit., Parsons *et al.* op. cit.). A value of 50 per cent is considered appropriate.

MACROZOOPLANKTON

Pillar and Stuart (1988) demonstrated *Euphausia lucens* to be reproductively active throughout the year in St Helena Bay, with the most intense spawning between August and October. Multiple spawning by females does occur, with the largest number of euphausiids living inshore but higher proportions of gravid females being found offshore where concentrations of chlorophyll *a* are low. Stuart and Pillar (1988) estimated total production in terms of flesh, moults and eggs (Table III) for inshore, intermediate and offshore areas, which ranged from 142 to 479 mg dry mass$\cdot$m$^{-3}\cdot$year^{-1}. As only the upper 100 m were sampled in that study, these values are equivalent to 5,7–19,2 gC$\cdot$m$^{-2}\cdot$year^{-1}. Annual *P/B* ratios ranged from 10 to 16, with higher values offshore where there were large numbers of early larvae (calyptopes). These *P/B* values are relatively high compared with those reported for other euphausiids, owing in part to the consistently high food availability and mild temperatures experienced perennially in the Benguela. An annual *P/B* ratio of 13 is considered appropriate for both the northern and southern Benguela.

Little is known of local rates of production of chaetognaths, hyperiid amphipods and gelatinous predators, and literature values for *P/B* ratios are extremely scarce and highly variable. Reeve and Baker (1975) estimated the annual *P/B* ratio for the chaetognath *Sagitta hispida* in tropical waters to be 109, and Sameoto (1971) and McLaren (1969) estimated the annual *P/B* ratio for *S. elegans* in cool temperate waters of Nova Scotia to be between 1,0 and 2,1. An annual *P/B* ratio of 44 was reported by Reeve and Baker (op. cit.) for the ctenophore *Mnemiopsis mccradyi*, and Hirota (1974) estimated a daily *P/B* ratio of 0,02 for *Pleurobrachia* off California. However, as these macrozooplankton groups form only a small portion of the macrozooplankton standing stock relative to euphausiids (Pillar 1986), their role as producers is likely to be relatively minor compared to that of copepods and euphausiids.

Estimates of growth efficiency of macrozooplankton are based on those derived for *Euphausia lucens* by Stuart (1986). A value of 41 per cent is assumed on the basis that assimilation efficiency approximates 80 per cent and that 39 per cent is lost as a result of respiration.

Consumption estimates

In a system where there appears to be an excess of phytoplankton (Borchers and Hutchings 1986), herbivory is likely to be the dominant mode of feeding, particularly inshore. Most of the mesozooplankton is considered to be primarily herbivorous, whereas most of the macrozooplankton is typically omnivorous. Estimates of the impact of zooplankton grazing are few and confined to inshore areas (<200 m) of the southern Benguela. Extrapolation to the rest of the shelf of the Benguela system therefore only provides a rough estimate of the portion of the phytoplankton standing crop likely to be consumed by zooplankton.

MESOZOOPLANKTON

Olivieri (1985, recalculated by LH) estimated that copepods were removing 7 per cent (range 3–54 per cent, *SD* = 10 per cent) of the daily available phytoplankton (i.e. biomass plus production) in newly upwelled water off the Cape Peninsula. This constituted a daily ration of 13–40 per cent of body mass in terms of carbon. Peterson *et al.* (1990b) estimated that copepods inshore north of Cape Columbine were consuming 1–5 per cent of the phytoplankton crop. Because of some problems associated with the calculation of ingestion and filtration rates, this estimate could be too low by a factor of 2–4. This would, however, still indicate that copepods were not removing a large fraction of the available standing crop of phytoplankton.

Borchers and Hutchings (1986) made indirect calculations of the grazing impact of copepods. By assuming a daily ration of 40 per cent of body mass in terms of carbon, a doubling of the biomass to account for undersampling of macrozooplankton by the WP-2 net, that one-half of the zooplankton fed carnivorously, and an ecological efficiency of about 20 per cent, they estimated that, at most, 60 per cent of the primary production could be grazed in the nearshore region. Carter *et al.* (1986) estimated that zooplankton requirements were only about 5 per cent of the primary production on the eastern Agulhas Bank during April 1985.

Verheye (1989) estimated that *Calanoides carinatus*, which constituted 13 per cent of the mesozooplankton biomass in St Helena Bay, consumed 4–11 per cent of the daily primary production during a 27-day Anchor Station study. Assuming that half of the mesozooplankton was herbivorous and that other species also grazed at similar rates as *Calanoides*, an average of only 22 per cent of the phytoplankton production, or 8 per cent of the phytoplankton biomass, would be removed by grazing (Verheye 1991).

Rations of herbivorous copepods vary in the literature between 10 and 120 per cent of body mass (in terms of carbon) per day, smaller animals generally having a higher mass-specific ration (Parsons *et al.* 1969, Beers *et al.* 1971, Herbland *et al.* 1973, Parsons *et al.* 1984). Rations for copepods in the southern Benguela have only been determined directly for female *Calanoides* in the laboratory (Peterson *et al.* 1990a). At *Thalassiosira weissflogii* concentrations of 1 500–8 000 cells$\cdot\ell^{-1}$, rations varied from 59 to 128 per cent in terms of carbon. Under field conditions, rations are likely to be substantially less, probably in the vicinity of 40–50 per cent (calculated from Armstrong *et al.* 1991 and Verheye 1991).

MACROZOOPLANKTON

Stuart and Pillar (1990) estimated that 15–60 per cent of total carbon ingested by the euphausiid *Euphausia lucens* was in the form of phytoplankton and the remainder as copepod prey. Carnivory was important when chlorophyll levels were low, but it still contributed up to 40 per cent of the total ingested carbon at high concentrations of phytoplankton. The impact on phytoplankton stocks in the southern Benguela is low, however, of the order of 1,0 per cent of the available phytoplankton (Stuart and Pillar op. cit.). Rations vary between 0,7 and 8,4 per cent and between 2,5 and 5,6 per cent of body carbon per day when feeding on phytoplankton or copepods respectively. Patchiness of phytoplankton and copepods and the swarming behaviour of euphausiids make calculations of mean annual rates of consumption difficult for the whole shelf region, because selection and diet depend on the vertical migratory habits of the euphausiids and the relative abundance and size of the prey organisms encountered (Gibbons *et al.* 1991a). The potential predatory impact of euphausiids was estimated at approximately 2–7 per cent of the available copepod density, but at higher concentrations of predators, typical of swarm conditions, up to 60 per cent of the copepods could be removed per day (Stuart and Pillar op. cit.). At a nearshore station off the Olifants River mouth, which was sampled intensively for 72 h during Febuary 1991, a swarm averaging approximately 300 adult euphausiids per m^3 was capable of consuming up to 90 per cent of the copepod population per day (Sea Fisheries Research Institute unpublished data).

Other groups, such as chaetognaths, hyperiid amphipods and ctenophores form a small proportion of the

Table IV: "Best" estimates and ranges of the annual mean of various zooplankton parameters in the Benguela

Parameter	Zooplankton category	Northern Benguela	West Coast	South Coast
Standing stock ($gC\cdot m^{-2}$)	Mesozooplankton	1,0 0,1–1,0	0,8 0,2–2,0	0,9 0,1–2,0
	Macrozooplankton	0,6 0,1–1,0	0,5 0,1–1,0	0,1 0,01–0,1
P/B ratio ($\cdot year^{-1}$)	Mesozooplankton	40 10–100	20 10–100	20 10–100
	Macrozooplankton	13 10–16	13 10–16	13 10–16
P/C ratio (%)	Mesozooplankton	30 14–50	30 14–50	30 14–50
	Macrozooplankton	41 15–59	41 15–59	41 15–59
Diet (% phytoplankton)	Mesozooplankton	50 10–90	50 10–90	50 10–90
	Macrozooplankton	60 25–88	60 25–88	60 25–88

Table V: Estimates of meso- and macrozooplankton standing stock, production and consumption in the Benguela by area

Parameter		Value (tons C)					
		Northern Benguela (179 000 km²)		West Coast (104 000 km²)		South Coast (116 000 km²)	
		Mesozooplankton	Macrozooplankton	Mesozooplankton	Macrozooplankton	Mesozooplankton	Macrozooplankton
Standing stock	Best	179 000	107 400	83 200	52 000	104 400	11 600
	Lower	17 900	17 900	20 800	10 400	11 600	1 160
	Upper	179 000	179 000	208 000	104 000	232 000	11 600
Production	Best	7 160 000	1 396 200	1 664 000	676 000	2 088 000	150 800
	Lower	179 000	179 000	208 000	104 000	116 000	11 600
	Upper	17 900 000	2 864 000	20 800 000	1 664 000	23 200 000	185 600
Consumption (best only)	Phytoplankton	11 933 333	2 043 220	2 773 333	989 268	3 480 000	220 683
	Microzooplankton	11 933 333	–	2 733 333	–	3 480 000	–
	Mesozooplankton	–	1 362 146	–	659 512	–	147 122

macrozooplankton community in terms of carbon (Pillar 1986), and estimates of their predatory impact are extremely limited. Gibbons *et al.* (in press) calculated the predatory impact of the chaetognath *Sagitta serratodentata tasmanica* on medium-sized copepods as 1–3 per cent per day on the shelf region off St Helena Bay in October 1987. Stuart and Verheye (1991) estimated the grazing impact of *Sagitta friderici* to be similar (1–5%) off the Cape Peninsula. As chaetognath concentrations decline rapidly in a seaward direction, being perhaps only 10 per cent as abundant in the mid- and outer-shelf regions, predatory impact over the whole shelf is probably of the order of 1–2 per cent per day, with a selection for medium or small copepods. If copepod generation time is about 25 days, chaetognath predation could be quite severe at low rates of copepod production.

CONCLUSION

Recent information on the consumption and production of copepods and euphausiids has, in conjunction with studies on life history strategies of the dominant species and on feeding selectivity of largely zooplanktivorous pelagic fish such as anchovy, greatly improved understanding of the dynamics of zooplankton in the Benguela. Irregular pulsing of the upwelling system, combined with seasonal appearance of pelagic fish recruits along South Africa's west coast during winter, has resulted in a highly dynamic and variable balance between food availability for transfer to fish and replenishment of zooplankton following losses due to predation or advection. The values listed in Table IV are currently the most realistic estimates of the parameters discussed in this paper.

For the purpose of the network analysis (Field *et al.* in prep.), estimates of meso- and macrozooplankton biomass, production and consumption have been calculated for each region (Table V). These are very broad generalizations based on limited data and the estimates presented will be subject to future re-interpretation. We are still at a very preliminary stage in deriving measurements of dynamic processes in zooplankton and there are major gaps in the data set which require attention before better assessments can be made. In particular, the role played by gelatinous filter-feeders such as salps and doliolids, which often swarm over the Agulhas Bank and off the coast of the South-Western Cape, has been ignored. The use of dry mass or carbon as a measure of standing stock has minimized the impact of gelatinous organisms in general. Another important omission is the role of microzooplankton in the trophic scheme of the Benguela. Despite their potential significance to the standing stock, few measurements are available (Armstrong *et al.* 1987). Most of the production and consumption estimates along the West Coast are limited to the inner shelf, where phytoplankton biomass and productivity are higher than between the 200 and 500 m isobaths. Therefore, most of the measurements of dynamic processes have been made in the zone where production exceeds consumption and extrapolation to the outer shelf and shelf-break on an annual basis is likely to provide little more than a point of departure.

ACKNOWLEDGEMENTS

We thank Drs M. Barange (Instituto de Ciencias del Mar, Barcelona, Spain) and M. J. Gibbons (University of Cape Town) for their comments on the manuscript.

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