TROPHIC ECOLOGY OF CARNIVOROUS ZOOPLANKTON IN THE BENGUELA

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Carnivorous zooplankton in the Benguela system have tended to be ignored by all but early taxonomists and a handful of recent researchers. An attempt is made here to address the importance of carnivores in this system but, because the database is poor, it was necessary to apply material from outside the region. The taxa covered include ctenophores, cnidarians (Scyphozoa and Hydrozoa, including Siphonophora), chaetognaths and hyperiid amphipods as well as such minor groups as pelagic gastropods and decapods. Most groups of carnivores within the Benguela are represented by only one or two "common" species. These tend to be epiplanktonic and generally concentrated inshore of the shelf-break, where their distributions are influenced by changes in local hydrography. Their densities frequently exceed those of herbivores. The dominant carnivores share a number of attributes: wide-ranging diets, high assimilation and growth efficiencies and mostly a Type I functional response to food concentration. They fall into two categories. The first is the gelatinous species, which have short lifespans and exhibit rapid growth and often massive reproductive response to high concentrations of food. They are patchily distributed and some appear to have behavioural traits that enable them to stay within localized patches of prey on which they may be dependent because of high metabolic costs. In the second category are crustacean predators and chaetognaths which have slower response times to the food environment but may have longer lifespans, lower daily maintenance needs and an ability to store lipids. They are less dependent on high densities of food organisms and can survive throughout winter, when gelatinous predators are rare. The effect of predation on abundance of copepods is estimated on the basis of both published and unpublished data. Should swarms of predators coincide with a critical gateway of zooplankton or larvae, then there may be total depletion. This applies especially to the nearshore zone of the West Coast and to semi-enclosed bays. The role of carnivorous zooplankton in the diets of commercially important fish species is stressed, but their importance in the regeneration of nutrients may be insignificant.

Met die uitsondering van vroeëre taksonome en 'n paar onlangse navorsers was daar 'n algemene neiging om die rol van karnivore soöplankton in die Benguelastelsel te ignoreer. 'n Poging word in hierdie referaat aangewend om die belang van karnivore in die betrokke stelsel aan te spreek, maar aangesien die databasis onvoldoende is, was dit nodig om gebruik te maak van gegewens wat buite die streek verkry is. Die taksa wat oorweeg is, sluit in Ctenophora, Cnidaria (Scyphozoa en Hydrozoa, met inbegrip van Siphonophora), Chaetognatha en hiperiïede Amphipoda, sowel as sulke kleinere groepe soos pelagiese Gastropoda en Decapoda. Die meeste groepe karnivore in die Benguela word deur slegs een of twee "algemene" spesies verteenwoordig. Hierdie spesies neig om epiplanktonies te wees en is oor die algemeen op die aanlandige deel van die vastelandsplat gekonsentreer, waar hulle verspreiding deur veranderinge in die plaaslike hidrografie beïnvloed word. Hulle digthede oortref dikwels dié van herbivore. Die dominante karnivore het 'n aantal eienskappe gemeen: byvoorbeeld 'n breëspektrumdieet, hoë doeltreffendheid ten opsigte van assimilasie en groei en hoofsaaklik 'n Tipe I funksionele reaksie op voedselkonsentrasie. Hulle ressorteer onder twee kategorieë. Die eerste hiervan is die jellieagtige spesies wat 'n kort lewensduur en snelle groei vertoon en met massiewe reproduksie op hoë voedselkonsentrasies reageer. Hulle is kol-kol versprei en sommige van hulle vertoon gedragspatrone wat hulle in staat stel om binne gelokaliseerde kolle prooi te vertoef, waarvan hulle moontlik afhanklik is as gevolg van hoë metaboliese vereistes. In die tweede kategorie is krustaseë-roofdiere en chetognate wat stadiger reaksietye teenoor die voedselomgewing het, maar hulle kan 'n langer lewensduur hê en oor laer daaglikse instandhoudingsvereistes en die vermoë om lipides op te berg, beskik. Hulle is minder afhanklik van hoë digthede van voedselorganismes en kan die winter wanneer jellieagtige roofdiere skaars is, oorleef. Die uitwerking van roofbedrywighede op die talrykheid van kopepodes word bereken aan die hand van gepubliseerde en ongepubliseerde gegewens. Indien die voorkoms van swerms roofdiere saamval met a kritieke poort vir soöplankton of larwes, kan totale uitputting plaasvind. Hierdie geval het veral betrekking op die gebied naby die kus aan die Weskus en half-geslote baaie. Die rol van karnivore soöplankton in die dieet van kommersieel belangrike visspesies word benadruk, maar hulle belang in die regenerasie van voedingstowwe mag onbeduidend wees.

As a guild, carnivorous zooplankton have to date been dismissed by all but early taxonomists and a handful of more recent researchers: for instance, the review of Shannon and Pillar (1986) includes only chaetognaths and hyperiid amphipods. An attempt to redress this oversight is presented here. However, the number of taxa involved is large and the quantity of information small, so it has been necessary to apply material from outside the Benguela. The carnivorous role of such omnivorous zooplankton as euphausiids

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has been discussed by Pillar *et al.* (1992), and this paper is therefore restricted to "exclusively carnivorous" taxa. Included in that definition are ctenophores, cnidarians, chaetognaths and hyperiid amphipods, as well as minor groups such as pelagic gastropods and decapods. The focus of the paper is the responses of the different phyla to the food environment, in terms of actual consumption, growth, reproduction and distribution. Also, in some instances, estimates are made of the impact of the different groups on the mesozooplankton community. Much of this is conjecture because data are lacking in many cases, and the intent here is to stimulate further research.

CTENOPHORA

Three species of ctenophore are known from the South-East Atlantic and Benguela system (O'Sullivan 1986), but only *Pleurobrachia pileus* and *Beroe cucumis* are common (Unterüberbacher 1964, Lazarus 1974). Both species are neritic but, because *B. cucumis* preys exclusively on tentaculate ctenophores and has no direct predatory impact on mesozooplankton assemblages, only *P. pileus* will be discussed here[1].

Although local densities are unknown, *P. pileus* is frequently seen by sports divers and the population must be abundant enough to support the populations of *B. cucumis*. Because *P. pileus* is epiplanktonic (Fraser 1970), densities are likely to be influenced by advective processes and tidal currents (Hirota 1974, Schneider 1987). That may explain partly why *P. pileus* is more abundant locally in the sheltered area of Stompneus Bay than elsewhere in the St Helena Bay region (Lazarus 1974). Ctenophores are known to swarm in localized patches elsewhere (Fraser op. cit., Williams and Collins 1985, Frank 1986), and it has been postulated that they may be dependent on dense aggregations of prey to support high metabolic demands (Larson 1987a). Certainly, the abundance of *P. pileus* in the Benguela would appear to be correlated with total zooplankton density (Lazarus op. cit.) and, under these circumstances, the positive relationship between food concentration and growth rate and reproductive output (Hirota 1972, cited in Hirota 1974; Reeve *et al.* 1978, Stanlaw *et al.* 1981) may allow population maintenance. Somatic growth in ctenophores replaces reproduction in an environment lacking food (Reeve *et al.* 1989) and, although polar species may survive through winter by utilizing lipid reserves

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[1] Two lobate ctenophores resembling species of *Bolinopsis* and *Leucotheca* have been observed in Table Bay, but require further work (MJG, pers. obs.).

(Kremer 1982, Percy 1988, Larson and Harbison 1989), animals are otherwise very seasonal (Fraser op. cit.). Peaks in local abundance seem to vary with locality, but they are more noticeable in summer and autumn than at other times (Lazarus op. cit.).

Despite early observations to the contrary (Lebour 1922, 1923), ctenophores of the genus *Pleurobrachia* are strictly carnivorous. Post-larval *Mnemiopsis* readily consume zooflagellates, ciliates and copepod nauplii (Stoecker *et al.* 1987a), whereas adults essentially eat whatever zooplankton they can catch. They are passive, cruising, entangling predators (Greene 1985), whose diet is largely determined by the "speed" of the ambient prey (Greene *et al.* 1986). Copepods are dominant prey, but chaetognaths and euphausiid and fish larvae are also eaten (Fraser 1970, Hirota 1974, Lazarus 1974, Reeve and Walter 1978, Purcell 1985, Larson 1987b, c). Ingestion rates are proportional to food concentration, and clearance rates vary with animal size and experimental conditions (Greene *et al.* op. cit., Gibbons and Painting in press). In the laboratory, prey type also influences the rates of both ingestion and clearance (Green *et al.* op. cit.), prey being selected on the basis of speed and escape response, such selection criteria appear to fall away *in situ* as a result of water motion (Larson 1987c).

Tentaculate ctenophores represent a considerable destabilizing force at high densities and are known to have a severe negative impact on copepod populations (Van der Veer and Sadée 1984) and, indirectly, on fish stocks (Frank 1986). The absence of dense aggregations in the Benguela may reflect a lack of data and poor sampling techniques, but alternatively it may be explained by the rarity of enclosed bays, vigorous physical processes and the short-pulsed nature of the food supply. On the other hand, with the exception of *Beroe* and *Pleurobrachia*, ctenophores are easily damaged by even the most careful handling and can be overlooked easily.

Without quantitative data on ctenophore abundance it is difficult to speculate in any detail on their impact on planktonic communities in the Benguela, but it is likely to be small in all but enclosed bays.

SIPHONOPHORA

Of the 34 species of siphonophore reported by Pagès and Gili (1991a) from the waters off northern Namibia, only three are associated with the Benguela. Four species have been recorded in the southern Benguela (Pagès *et al.* 1991a), but only *Muggiaea atlantica* is abundant (Pagès 1992). This species is characteristic of cold neritic water of the eastern

Atlantic and is abundant in the upwelling regions off North Africa (Thiriot 1978). The siphonophore assemblage in the northern Benguela consists of three components: one associated with coastal upwelling, one typical of shelf waters and one characteristic of oceanic waters (Pagès op. cit.). The diversity of Siphonophora is greatest in oceanic waters, where calycophorans are supplemented with physonectids (Pagès and Gili 1991b, Pagès op. cit.).

Densities of siphonophores are low (Table I^2) and decrease offshore (Pagès et al. 1991a, Pagès and Gili 1991b). Most calycophoran and all cystonect species are epiplanktonic and susceptible to surface water movement, so that changes in density, distribution and community structure can occur as a result of upwelling (Pagès et al. op. cit., Pagès 1992), surface water intrusions (Pagès and Gili op. cit.) and other hydrological events (Gili et al. 1987). Dense patches have been observed elsewhere developing in response to topographic features and are more common in sheltered or enclosed areas than outside (Purcell 1981). Densities are likely to vary with cycles in zooplankton abundance (Stephens et al. 1969), as a result of the strong correlation of growth rate (Mackie et al. 1987) and reproductive output (Purcell 1982) with availability of food.

Diets are a function of the interaction between feeding behaviour, morphology and nematocyst type (Purcell 1984b, Mackie et al. 1987). Cystonects feed exclusively on soft-bodied zooplankton (Purcell op. cit.), whereas calycophorans such as *Muggiaea* and *Sphaeronectes* prey preferentially on small crustaceans (Purcell 1982, Purcell and Kremer 1983). Ingestion rates of *M. atlantica* are proportional to food concentration but are also heavily dependent on prey type; they are lower for nauplii than other copepod stages (Purcell 1982). The combination of published daily rates of ingestion and ambient food concentration provides a ready means of recalculating filtration or clearance volumes (Table II). Some of these values are very high, but it should be remembered that densities of siphonophores and prey may be taken from net collections spanning depths greater than the patch size. They therefore disrupt the vertical association of predator and prey. Nevertheless, in the absence of more-realistic data, and because most samples are collected in this way, they provide a useful baseline.

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² The estimates of abundance used in this table have been culled from a literature that spans several decades. During this period, methods for the collection of samples and estimations of densities have changed several times. Some species of crustacean are able to avoid some of the nets used (Omori 1974), whereas other nets by their very design underestimate abundance. Superimposed on these biases, however, is the fact that densities are rarely stable and naturally fluctuate over multiple scales of space and time. Caution is advised in their use.

The impact of *M. atlantica* on the copepod community of the southern Benguela (based on abundance estimates made from net collections and published clearance rates) seems to be low (Table II). Similar conclusions were drawn by Mackie et al. (1987) for other crustacean-eating siphonophores. This contrasts with the situation for cystonects and other species that prey on fish larvae (Mackie et al. op. cit.). Purcell (1984a) observed that *P. physalis* at very low densities (0,005 · m⁻²) had profound effects on the rates of survival of fish larvae. *P. physalis* is thought to accumulate on and spawn over the Agulhas Bank at the same time of year as clupeoids (Shannon and Chapman 1983) and so could consume large numbers of fish larvae drifting over the Bank. However, because the bulk of the clupeoid larvae recruiting to the West Coast fishery only begin to hatch during transport up the West Coast, they tend to be spatially segregated from dense aggregations of *Physalia*. The factors responsible for subsequent distribution of *Physalia* and fish larvae in the Benguela differ (wind and currents respectively), so that persistent patch separation up the West Coast is likely in all but enclosed bays.

SCYPHOZOA

Seven species of Scyphozoa have been described from the Benguela (Vanhöffen 1903a, b, 1908, Stiasny 1934), but only *Chrysaora hysoscella* is common. This species appears to be more abundant in the northern than in the southern Benguela, where it is confined to waters shallower than 200 m (Fearon et al. in press, Pagès 1992). Ephyrae and small individuals are found inshore and north of the adults because, as the animals increase in size, they alter their occupational depth, are swept south by deep counter-currents and transported offshore (Fearon et al. op. cit., Pagès op. cit.).

Estimates of abundance in the region are approximate and, although average values are high (Table I), they are in themselves of limited value because animals tend to extreme patchiness. Dense (>1·m⁻²) aggregations are commonly observed elsewhere as a result of Langmuir circulation (Hamner and Schneider 1986), tidal currents (Feigenbaum and Kelly 1984) and local winds (Vučetić 1983). Although the local hydrography is thought to influence the distribution of *Chrysaora* in the northern Benguela, its effect on patch size or distribution either there or in the southern Benguela is unknown. Such patches are likely to be short-lived in the absence of enclosed areas (Van der Veer and Oorthuysen 1985), but they could be maintained when food is abundant (Bailey and Batty 1983, Larson 1987d) and stable hydrological conditions prevail.

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Table I: Maximum, minimum and mean estimates of densities of carnivorous zooplankton in the Benguela system. Mean densities are averaged over the water column (depth specified if available). Maximum and minimum values are, in the case of RMT-1×6 nets, estimates for particular strata (depth is specified for maximum values). Also included are the months sampled ("all" refers to year-round), the gear used (VB, vertical Bongo; OB, oblique Bongo; OBS, personal observations; RMT, 1 m² Rectangular Midwater Trawl) and location (N, northern Benguela; S, southern Benguela; SHB, St Helena Bay; TB, Table Bay). Data expressed per m³ or per m² (latter prefixed *). "Others" refers to trachy-, limno- and narcomedusae. These antho- and leptomedusae are all shelf and neritic species, as are the calycophoran siphonophores. Calycophoran values exclude *M. atlantica*, which are presented separately

Taxon	Species	Minimum density	Maximum density	Integrated density	Water depth (m)	Month	Loca-tion	Gear	Source and comments
Siphonophora	*M. atlantica*	0,013	8,57	–	Var.	Jun.	S	RMT	Pagès *et al.* 1991a
	M. atlantica	0,138	1,28	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
	M. atlantica	0,039	2,125	0,648	3 550	Apr.	N	RMT	Pagès and Gili 1991b: Mean from upper 40 m
	Unspecified	–	0,14	0,016	250	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
	Calycophorae	0,79	1,18	–	3 550	Apr.	N	RMT	Pagès and Gili 1990: Max. above thermo-cline
	Calycophorae	0	0,0001	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
	Unspecified	–	–	48,7–88,2	45	Mar./Apr.	SHB	Pump	Verheye 1991
Scyphozoa	*Chrysaora*	*0,03	*0,5	–	Var.	Nov.,Feb.	S	OBS	Peterson unpublished
	Chrysaora	–	–	*0,06	Var.	All	N	OB	Fearon *et al.* in press
	Chrysaora	0	0,019	0,019	3 550	Apr.	N	RMT	Pagès and Gili 1991b: Mean from upper 40 m
	Chrysaora	0,009	0,059	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
Hydromedusae	*Mitrocomella*	0,015	75,08	–	Var.	Jun.	S	RMT	Pagès *et al.* 1991a
	Proboscidactyla	0,009	1,58	–	Var.	Jun.	S	RMT	Pagès *et al.* 1991a
	Unspecified	–	0,14	0,03	80	Feb.	S	RMT	Gibbons unpublished: Max. in 70–75 m
	Aequorea	–	*6,35	*0,097	Var.	All	N	OB	Fearon *et al.* in press
	Anthomedusae	0,0001	0,003	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
	Anthomedusae	0,001	0,011	0,014	3 550	Apr.	N	RMT	Pagès and Gili 1991b: Mean from upper 40 m
	Leptomedusae	0,011	0,057	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
	Leptomedusae	0,004	0,349	0,199	3 550	Apr.	N	RMT	Pagès and Gili 1991b: Mean from upper 40 m
	Others	0,018	0,049	–	Var.	Dec.–Mar.	N	RMT	Pagès 1992
	Others	0,275	0,725	0,527	3 550	Apr.	N	RMT	Pagès and Gili 1991b: Mean from upper 40 m
Chaetognatha	*S. friderici*	–	–	14,4	–	All	N	VB	Venter 1969
	S. friderici	–	–	24,3	Var.	All	S	VB	Heydorn 1959
	S. friderici	–	–	10,4	Var.	All	S	VB	Masson 1972
	S. friderici	–	364,1	35–207	45	Mar./Apr.	SHB	RMT	Stuart and Verheye 1991: Max. in 0–15 m
	S. friderici	–	393	–	Var.	All	TB	VB	Lazarus (1974): Min. not provided
	S. friderici	0,09	64	6,8–14,8	100	Oct.	SHB	RMT	Gibbons unpublished: Max. in 10–20 m
	S. friderici	0,03	5,17	0,2–1,6	180	Oct.	SHB	RMT	Gibbons unpublished: Max. in 25–50 m
	S. friderici	0,06	1 645,6	2,2–514,5	80	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
	S. friderici	0,04	3,51	0,02–0,4	250	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
	S. s. tasmanica	0,11	38,6	5,1–18,1	80	Feb.	SHB	RMT	Gibbons unpublished: Max. in 45–65 m
	S. s. tasmanica	0,02	15,35	0,1–2,16	250	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
	S. s. tasmanica	0,08	63	1,0–36,7	100	Oct.	SHB	RMT	Gibbons unpublished: Max. in 0–10 m

Table I *(continued)*

Taxon	Species	Minimum density	Maximum density	Integrated density	Water depth (m)	Month	Loca-tion	Gear	Source and comments
	S. s. tasmanica	0,25	71,3	0,7–32,9	180	Oct.	SHB	RMT	Gibbons unpublished: Max. in 100–184 m
	S. s. tasmanica	–	–	71,3	Var.	All	N	VB	Venter 1969
	Unspecified	–	–	83,6	Var.	All	SHB	VB	Hopson 1983
	Unspecified	–	*>30 000	*2 727,2	Var.	Apr.	N	RMT	Olivar and Barangé 1990: Min. not provided
Decapoda	*Pasiphaea*	–	1,03	0,56	80	Feb.	SHB	RMT	Gibbons *et al.* in prep.: Max. in 0–20 m
	Pasiphaea	0,03	1,89	*4,9–198,4	105–146	Jun.	S	VB	Gibbons *et al.* in prep.
	Pasiphaea	0,05	0,17	*6,4–34,4	84–143	May	S	VB	Gibbons *et al.* in prep.
	Pasiphaea	0,02	0,17	*4,0–61,8	85–161	Jun.	S	VB	Gibbons *et al.* in prep.
	Pasiphaea	–	*>200	*2,9	Var.	Apr.	N	RMT	Olivar and Barangé 1990: Min. not provided
Stomatopoda	Alima	–	–	1,65	Var.	All	SHB	RMT	Hopson 1983
	Alima	–	0,51	0,01–0,1	80	Feb.	SHB	RMT	Gibbons unpublished: Max. in 45–65 m
	Alima	–	2,12	0,01–0,2	250	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
Hyperiidae	*Themisto*	–	–	3,34	Var.	All	SHB	RMT	Hopson 1983
	Themisto	0,02	178,02	4,0–62,1	80	Feb.	SHB	RMT	Gibbons unpublished: Max. in 45–65 m
	Themisto	0,02	2 383	1,4–103,4	250	Feb.	SHB	RMT	Gibbons unpublished: Max. in 0–20 m
	Themisto	0,03	131,6	2,3–22,4	180	Oct.	SHB	RMT	Gibbons unpublished: Max. in 75–100 m
	Themisto	2,3	64,3	8,0–16,8	100	Oct.	SHB	RMT	Gibbons unpublished: Max. in 0–10 m
	Themisto	–	*>6 000	*33,2	Var.	Apr.	N	RMT	Olivar and Barangé 1990: Min. not provided

Growth rates (Van der Veer and Oorthuysen op. cit., Larson 1986) and strobilation are strongly correlated with the food environment (Spangenberg 1968, Chen *et al.* 1985). Strobilation could therefore coincide with peaks in zooplankton abundance (Gröndahl 1988), and encystment could occur under poor feeding conditions (Cargo and Schultz 1966, cited in Clifford and Cargo 1978, Hernroth and Gröndahl 1985). High productivity year-round in the northern Benguela may preclude seasonal changes in the density of *Chrysaora* (Fearon *et al.* in press) and, although this may be aided by the slow rate of turnover of water there (Brown *et al.* 1991), data are lacking.

A few rhizostome medusae may possess patches of zooxanthellae (Rahat and Hofmann 1987, Costello and Kremer 1989), but otherwise all scyphozoa are exclusively carnivorous. Small medusae readily consume large oligotrich ciliates and copepod nauplii (Stoecker *et al.* 1987b), whereas larger animals will eat essentially any zooplanktonic or small nektonic organisms they contact and retain. Copepods therefore constitute the dominant prey type (Möller 1978/79,

1980, Kelly 1983, cited in Feigenbaum and Kelly 1984, Fancett 1988), and these and other items tend to be selected both passively (Bailey and Batty 1983, 1984) and actively (Stoecker *et al.* 1987b, Sandrini and Avian 1989, Larson 1991). Ingestion rates are proportional to prey densities (Clifford and Cargo 1978, Bailey and Batty 1984, Gamble and Hay 1989), and asymptotic relationships are the result of laboratory artifacts (Bailey and Batty 1983, Morand *et al.* 1987). These and clearance rates are also determined by medusa and prey size, and by prey escape response (Möller 1984, De Lafonteine and Leggett 1987, Strand and Hamner 1988, Gamble and Hay op. cit., Fancett and Jenkins 1988). Reported rates of filtration by *Chrysaora* vary widely (Clifford and Cargo op. cit., Feigenbaum *et al.* 1982, cited in Feigenbaum and Kelly op. cit.), but it should be remembered that these are the products of laboratory experiments.

While the impact of scyphozomedusae on microzooplankton is likely to be insignificant (Stoecker *et al.* 1987b), their effect on copepod and other zooplankton populations could be great when medusan

Table II: Possible predatory impact of carnivorous zooplankton on copepod communities in the southern Benguela (unless indicated). The total applies to the southern region but incorporates mean *Chrysaora* data from the northern Benguela. Impact estimates for gelatinous species are calculated as the product of local predator abundance (per m³ or per m²) and published feeding rates (m³·day⁻¹). Prey densities are not considered and daily impact is presented simply as the proportion of water cleared daily. Therefore, the maximum *M. atlantica* density in the southern Benguela is 8,57·m⁻³. Each animal has a filtration rate of 0,005 m³·day⁻¹. The product of the two values is 0,0429 or 4,3 per cent·day⁻¹. The filtration rates for *Chrysaora* are half the published values because they were originally calculated for *Artemia* and are used here on naturally occurring copepods (see text). The assumption of such extrapolations is that all zooplankton are consumed non-selectively. While this is clearly not true on the basis of laboratory experiments, water movement may modify such patterns (Larson 1987c). Impacts for non-gelatinous zooplankton are calculated using predator densities and ingestion rates and published prey densities. *Physalia* is excluded from impact estimates because there is no record of it consuming copepods directly

Taxon	Species	Daily clearance rates (m³·predator⁻¹)		Daily ingestion	Density	Prey type	Daily impact (%)	Sources and comments
		Laboratory	Field					
Siphonophora	*M. atlantica*	–	0,002–0,005	–	0,013–8,57·m⁻³	Copepods	0,05–4,3	Densities (Pagès *et al.* 1991a); clearance rates (Purcell 1982)
Scyphozoa	*Chrysaora*	0,45	–	–	0,06·m⁻²	All	0,09*	Average diameter; clearance rates (Feigenbaum *et al.* 1982, in Feigenbaum and Kelly 1984)
Chaetognatha	*S. friderici*	–	–	0,48 items	35–207·m⁻³	Copepods	1,0–5,3	Stuart and Verheye 1991
	S. s. tasmanica	–	–	0,6–0,9 items	28–35·m⁻³	Copepods	0,6–2,8	Data from Gibbons 1992
Amphipoda	*Themisto*	–	–	1,5 mg	2,3–22,4·m⁻³	Copepods	4,0–38,5	Inshore (October 1987). Copepod biomass (Peterson *et al.* 1990):
		–	–	1,5 mg	8,0–16,8·m⁻³	Copepods	13,7–28,9	Midshelf (October 1987). Hyperiid density (Gibbons unpublished); hyperiid size (6 mm — Siegfried 1965); hyperiid ingestion at 13,5°C where copepods represent 48 per cent of the diet (Sheader and Evans 1975)
Total						Copepods	5,74–50,99	

* Impact integrated over the upper 30 m only, otherwise over the entire water column

populations are high (Möller 1978/79, Feigenbaum and Kelly 1984, Morand *et al.* 1987). The essentially mutually exclusive distribution of *Chrysaora* and the leptomedusa *Aequorea* in the northern Benguela (Fearon *et al.* in press) may be just such a result of predatory interaction (Gröndahl 1988, Strand and Hamner 1988, Purcell 1991). The effect of scyphozoa either directly as predators of fish larvae (Möller 1984, Bailey and Batty 1983, 1984, Gamble and Hay 1989), or indirectly as competitors for food, depends on the coincidence of larvae and predator in time and space. *Chrysaora* in the southern Benguela are found both at the shelf-break and in the nearshore waters of St Helena Bay at the same time as anchovy larvae

move through each area (Peterson 1988). Also, although seasonal densities of *Chrysaora* in the northern Benguela are not thought to change (Fearon *et al.* op. cit.), relevant estimates of density are unknown, so it is not possible to calculate their impact. Nevertheless, crude estimates for the northern and southern Benguela can be made, based on average densities, sizes and extrapolated clearance rates (Table II[3]). Should *Chrysaora* move into deep water during the day, as is

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[3] Note should be made here that the published filtration rates used in Table II were calculated in the laboratory with *Artemia* as prey. Because copepods occurring naturally have better-developed escape responses than *Artemia*, the filtration rates are halved here.

known for other species of scyphozoa (Strand and Hamner 1987), then the integrated impact over the upper 30 m would be low, even at relatively high densities. However, should animals remain in the upper 5 m, then their impact could be high.

HYDROMEDUSAE

Kramp (1957, 1959) described 18 neritic, 23 epipelagic and 15 bathypelagic species of hydromedusae from South Africa. Millard (1975) listed another 10 and Pagès *et al.* (1991b) described another four. Although further work in the area will undoubtedly reveal more species, it is clear that only *Aequorea* is common year-round (Fearon *et al.* in press, Pagès 1992). Although this species is most abundant in neritic waters, overall medusoid diversity probably increases with distance from the coast, because antho- and leptomedusae are supplemented with trachy-, narco- and limnomedusae offshore (Pagès op. cit.). Certainly, the hydromedusan assemblage in the northern Benguela was subdivided by Pagès into oceanic, neritic and upwelling components, in order of decreasing diversity.

Data on abundance of hydrozoan medusae in the southern Benguela are few, but it would appear that densities are low (Table I, Pagès *et al.* 1991a). In the northern Benguela, by contrast, biomass of *Aequorea* is high (Venter 1988, Fearon *et al.* in press) and the density of other species may be elevated as a result of advection processes (Pagès and Gili 1991b). As most hydromedusae are epiplanktonic, densities will fluctuate with changes in surface hydrology (Hamner and Schneider 1986, Gili *et al.* 1988, Sabatés *et al.* 1989), and neritic populations may be moved offshore by upwelling (Pagès *et al.* 1991a). Like other gelatinous zooplankters, hydromedusae tend to patchiness, and aggregations could persist for prolonged periods in enclosed areas (Zelickman *et al.* 1969). The seasonal distribution and abundance of *Aequorea* in the northern Benguela (Fearon *et al.* in press) appears to reflect that of fish larvae (Olivar 1987), suggesting some correlation with food availability. Growth rates (Zelickman *et al.* op. cit., Daan 1986) and medusa release (Roosen-Runge 1970) are strongly influenced by food concentration, and asexual reproduction may replace sexual reproduction in an abundant food environment (Zelickman *et al.* op. cit.), possibly to permit swarm persistence. The elevated abundances of *Mitrocomella* observed by Pagès *et al.* (1991a) in the neritic waters of the southern Benguela during upwelling may therefore be explained by trophic and thermal cues (Arai 1987).

Although hydromedusae are exclusively carnivorous, differences in nematocyst structure between sub-

orders enforce dietary segregation. Anthomedusae preferentially ingest crustacean zooplankton whereas leptomedusae prefer soft-bodied zooplankton, including other gelatinous species (Purcell and Mills 1988, Purcell 1991). Otherwise, medusae feed most on the dominant ambient prey items, which are taken both passively (Mills 1981, Fulton and Wear 1985, Purcell *et al.* 1987, Purcell 1989) and by active selection (Pennington 1990).

Hydromedusan ingestion rates are of the Type I functional response, and clearance rates vary with medusa size and prey type (Fulton and Wear 1985, Daan 1986, Costello 1988). Nevertheless, generally low numbers may mean that, even when feeding maximally, hydromedusae have a negligible effect on communities (Daan op. cit.). Although severe impacts on copepods have been noted in enclosed harbours (Huntley and Hobson 1978, Fulton and Wear op. cit.), the high degree of intraguild predation may act to reduce overall pressure on copepod standing stocks and enforce stability (Purcell 1991). While it is tempting to suggest that the seasonal impact of *Aequorea* on fish larvae in the northern Benguela may be as high as that predicted elsewhere (Arai and Hay 1982, Purcell *et al.* 1987, Purcell and Grover 1990), without information on relative densities this is not feasible.

HOLOPLANKTONIC GASTROPODA

Morton (1954) described eight cosmopolitan species from the R.R.S. *William Scoresby* surveys. The single heteropod, *Atlanta peroni*, was only present in the southernmost regions, whereas the most common of the five thecosomes, *Limacina bulimoides*, avoided the colder upwelled water towards the coast. *L. bulimoides* and, indeed, the other species are typical of oceanic waters (Bé and Gilmer 1977).

Although gastropods may dominate zooplankton communities (Sameoto 1984) and are especially common in areas of local enrichment and upwelling (Auras-Schudnagies *et al.* 1989, Le Borgne *et al.* 1989, Schalk 1990), densities in the Benguela are likely to be low throughout the year. While rings of Agulhas water may entrain individuals from the South and East coasts, where they are common (pers. obs.), these are unlikely to enter the Benguela system *per se*. Should they do so, or should oceanic water be pushed inshore, then, because reproductive output is influenced by food availability (Conover and Lalli 1972, Wormuth 1985), and growth efficiencies may be high (Conover and Lalli 1974), rapid population development is possible (Wormuth op. cit.). However, current evidence suggests that they are transient visitors. Because thecosomes are only partially carnivorous suspension-

feeders (Gilmer and Harbison 1986) or trappers (Richter 1977), and gymnosomes are genus-specific predators of thecosomes (Lalli 1970), their role in the higher trophic dynamics of the Benguela is probably small.

CHAETOGNATHA

Of the 18 species of chaetognath reported by Stone (1969) and Schleyer (1977) from the Agulhas Current, only three are routinely common in the southern Benguela (Heydorn 1959, Masson 1972) and two in the northern Benguela (Venter 1969). *Sagitta friderici* dominates the neritic waters around the coast, whereas *S. serratodentata tasmanica* and *S. minima* are typical of the midshelf and oceanic environments of the northern and southern areas respectively (Heydorn op. cit.). While *S. friderici* and *S. s. tasmanica* are epipelagic species, *S. minima* is most common at depths of 200–400 m in the southern Benguela, so that its presence nearshore may indicate recent upwelling (Stone op. cit.). *S. minima* is encountered in the nearshore waters of the northern Benguela only during quiescent upwelling there, whereas *S. enflata* is indicative of warm-water intrusions southwards from Angola (A. G. Timonin, Institute of Oceanology, Moscow, pers. comm.).

The densities of chaetognaths are considerably greater than those of any other carnivorous group (Table I) and are higher inshore than offshore over the entire region (Heydorn 1959, Venter 1969, Fearon et al. 1986, Olivar and Barangé 1990). Although high densities may be associated with the 200 m isobath and upwelling centres in the northern Benguela (Fearon et al. op. cit.), there are no clear latitudinal variations in abundance (Olivar and Barangé op. cit.). Changes in abundance associated with hydrology have not been documented in the southern sector, although neritic animals are encountered beyond the shelf-break (Heydorn op. cit.). Whereas the density of large chaetognaths (*S. friderici*) in the southern Benguela has been described as temporally stable (Hopson 1983), summer peaks in abundance may be associated with the recruitment of winter- (Lazarus 1974) or spring-spawned (Hopson op. cit.) individuals. The timing of recruitment to coincide with high zooplankton biomass has been observed elsewhere (Sameoto 1973) and, while spawning may be continuous (Lazarus op. cit., Hopson op. cit.), fecundity is thought to be correlated with food concentration (Stone 1969, but see also Sameoto 1972). Growth is determinate and somatic production is replaced by reproductive production on maturity (Reeve 1970). Growth rate and

maturity are dependent in turn on temperature and food concentration (Reeve op. cit.), and reproductive output is halted under starvation conditions (Reeve op. cit.). Chaetognaths are generally ill-equipped to cope with starvation (Feigenbaum and Maris 1984), although they are not dependent on high-density patches of prey to meet daily energy requirements. *S. s. tasmanica* is unusual in that lipids are conspicuous (Thiriot 1978), and these may allow it to survive periods of poor food concentration so typical of pulsed upwelling.

All chaetognaths are strictly carnivorous (Feigenbaum and Maris 1984). Animals eat a wide range of prey, the size of which increases with chaetognath size (Stuart and Verheye 1991). Tintinnids may be eaten by small individuals and smaller chaetognaths by large, but copepods predominate (Feigenbaum and Maris op. cit.). Indeed, they represent 86 per cent of the diet of *S. friderici* (Stuart and Verheye op. cit.) and almost 100 per cent of that of *S. s. tasmanica* (Gibbons 1992). Copepods appear to be selected on a size basis, but whether this is a reflection of size *per se*, associated mobility or specific identity is as yet unknown. Cannibalism, which may be an energetically superior strategy for large chaetognaths, is rare in the southern Benguela (Lazarus 1974, Stuart and Verheye op. cit.), but it is common elsewhere (Pearre 1982); it probably reflects the small head widths of local species (Gibbons op. cit.) and the low densities of juvenile chaetognaths (Hopson 1983).

Evidence correlating chaetognath feeding with food density is weak (Feigenbaum and Maris 1984). However, it would appear that, when both predator and prey are in close association throughout the day, then feeding may be continuous (Stuart and Verheye 1991, Gibbons 1992). Alternatively, when predators display diel vertical migration within a stratified food environment, then a diel pattern of feeding emerges (Gibbons op. cit.). These two responses are commonly seen in the nearshore and offshore waters of the Benguela respectively.

There have been few laboratory studies on feeding (Feigenbaum and Maris 1984), and most estimates are the result of *in situ* collections corrected for both gut passage time (Stuart and Verheye 1991) and codend feeding (Feigenbaum and Maris op. cit.). The impact of chaetognaths on copepod communities in the southern Benguela varies between 1 and 5 per cent of the standing stock (Table II), and these are similar to or higher than most records elsewhere (Sameoto 1973, 1987, Øresland 1990). However, very high rates of consumption have been observed in tropical waters (Reeve and Baker 1975, Szyper 1978) and in winter at high latitudes when productivity is low (Sameoto 1972, Øresland op. cit.). As copepods in the southern

Benguela undergo alternate periods of starvation and production (Attwood and Peterson 1989) in phase with environmental conditions, the accumulated impact of chaetognaths on copepods under poor environmental conditions may be significant.

HOLOPLANKTONIC DECAPODS AND STOMATOPODA

Although 39 species of natantid decapods were described from the region by Barnard (1950), only 19 occur at depths <250 fathoms. Lebour (1954) listed 12 pelagic species from the surveys of the R.R.S. *William Scoresby* and Macpherson (1991) found some 28 species in the northern Benguela. None of these can really be considered as common in the south, although *Pasiphaea semispinosa*(?) is routinely caught nearshore (Gibbons *et al.* in prep.). The decapods of the northern Benguela are split into inshore and offshore communities, with the boundary between the two approximating the shelf-break (Macpherson op. cit.). While the diversity of the offshore community is high, the neritic community is dominated almost exclusively by *P. semispinosa* (Macpherson op. cit.), which peak in abundance at the shelf-break (Olivar and Barangé 1990). The intensity of upwelling in the northern Benguela appears to determine the number of species and individuals in the nearshore community (Gibbons *et al.* op. cit.), as does the intrusion of water from the Angola Current (Macpherson op. cit.).

Similarly, densities of *Pasiphaea* in the south may be influenced by intrusions of water from Namibia. The abundance of *Pasiphaea* is high in the northern Benguela but low in the south (Table I). Such differences probably reflect differences in the stability of the upwelling environment. Dense, surface swarms of *Pasiphaea* in the Benguela have not been reported (see Dagnino *et al.* 1985), although Miller *et al.* (1983) detected a "superswarm" of *Funchalia woodwardi* in 465 m of water (beyond the shelf-break). Miller *et al.* (op. cit.) argue that *F. woodwardi* may be more common than previously considered, because it occurs outside routine sampling areas, is probably dispersed for much of the time and is frequently recorded from hake stomachs (Barnard 1950, Miller *et al.* op. cit.). Most decapods are able to avoid standard nets (Omori 1974), and therefore estimates of abundance so based may be an order of magnitude lower than those derived from acoustic techniques (Miller *et al.* op. cit.). The densities of *Pasiphaea* presented in Table I are therefore likely to be severely underestimated.

The naupliar and zoeal stages of caridean decapods

have no functional mouthparts, utilize endogenous foodstuffs before metamorphosis and then feed carnivorously as adults (Omori 1974). Most decapods are opportunistic predators whose diets vary seasonally, locally and with the ambient spectra at the depth of occupation (Omori 1969). *Pasiphaea* feeds on the benthos during the day and in the plankton at night (Relini and Relini 1990), where it preferentially eats euphausiids (Relini and Relini op. cit.), probably as a result of bioluminescent cues (Lagardère 1975). Decapod abundance and vertical and horizontal distribution appear to be strongly correlated with the quantity of available food (Omori 1974) and fluctuate with changes in supply (Blackburn *et al.* 1970). The potential impact of *Pasiphaea* on euphausiid populations in localized areas may therefore be high, especially in the perennial upwelling off Lüderitz. Unfortunately, no quantitative data pertinent to the feeding of any pelagic natantid crustaceans exist, although Go (1986) suggests they may be serious competitors of fish for food. Because of the often dramatic change in vertical habitat experienced daily, *Pasiphaea* and other species have long been recognized as important conveyors of epipelagic energy to depth. Because they are also available to a very wide range of predators, from demersal fish (Payne *et al.* 1987) to surface-feeding lariids (Relini and Relini op. cit.), they may be central to the trophic functioning of certain systems. Available evidence based on densities would suggest that planktonic decapods are unimportant in the southern Benguela, but this situation may change farther north. It is recommended, however, that their abundance, distribution and feeding ecology be addressed, because the single swarm of *F. woodwardi* reported by Miller *et al.* (1983) was estimated to have a greater biomass than the entire South African prawn catch in 1980 (only 1 029 tons).

Stomatopod larvae (alima) tend to have a prolonged planktonic life of between 2 and 9 months (Senta 1967, Pyne 1972, Morgan 1980) and may be relatively common for much of the year in enclosed bays (Table I, Hopson 1983). Abundance appears to peak in late winter and spring (Hopson op. cit.), and may be linked to environmental productivity. Alima are thought to be "rapacious" predators (Morgan op. cit.) that may have an important effect on zooplankton community structure. However, because there are no quantitative data on feeding, it is not possible to be any more specific about their impact.

AMPHIPODA

A total of 77 species of hyperiid amphipods have

been identified from the northern and southern Benguela (Barnard 1932, 1940, Siegfried 1963). Of these, five were described as common and one as abundant (*Themisto gaudichaudii*). The diversity of hyperiids appears to increase with distance from the coast (Siegfried 1965, Zeidler 1984, Sheader 1990). This is no surprise if one considers that most are associated with gelatinous zooplankton (Laval 1980), which generally increase in diversity offshore in the Benguela (Van Zyl 1960, Lazarus and Dowler 1979). However, *T. gaudichaudii* is characteristic of neritic, and shelf waters between 4 and 15°C (Siegfried 1965, Ramirez and Vinas 1985). Unlike most hyperiids, it has no clear association with gelatinous zooplankton (Sheader op. cit.) and unpublished data of the senior author suggest there is no correlation between densities of the two.

Hyperiid densities may be high in upwelling regions (Table I, Meruane 1981) and, whereas abundance does not appear to change across the shelf of the northern Benguela (Fearon *et al.* 1986, Olivar and Barangé 1990), it may peak at the shelf-break farther south (Hopson 1983, Verheye and Hutchings 1988). Patches of hyperiids were described by Olivar and Barangé (op. cit.), and dense aggregations or swarms of both sexes are commonly reported (Hardy and Gunther 1935, Gray and McHardy 1967, Sheader 1990). As *Themisto* is an epipelagic genus (Kane 1966), densities may be influenced by hydrographic features (Evans 1973, as cited by Sheader 1981). Hopson (op. cit.) and Siegfried (1965) noted spring and summer peaks in abundance of *T. gaudichaudii* in the southern Benguela, which would suggest that densities may be linked to planktonic production cycles (Siegfried op. cit.). Animals breed serially and asynchronously throughout the year (Sheader 1990), and the number of eggs increases with animal size and food availability (Sheader 1977, 1981). Although growth is indeterminate and strongly influenced by temperature (Sheader 1975, 1981), levels of nutrition also influence intermoult period and final morphology (Sheader 1981). Low concentration of food results in a long intermoult period and a long-legged, or *bispinosa* form. The appropriate conditions produce *forma compressa*.

Although hyperiids are considered exclusively carnivorous (they have a simple gut structure and the mouthparts are unsuitable for filtration — Sheader and Evans 1975), both Siegfried (1965) and Lazarus (1974) recovered diatoms from the guts of *T. gaudichaudii*. The diet of *T. japonica* changes from herbivory to carnivory with increasing age, and it has been suggested that adults may in fact be omnivorous rather than carnivorous (Sugisaki *et al.* 1991). Adult *T. compressa* have recently been observed to consume

marine snow in the North Atlantic (C. M. Turley, Plymouth Marine Laboratory, pers. comm.), and adult *Themisto* otherwise appear to be active visual predators, whose opportunistic diet varies with the ability of the food organisms to avoid capture (Sheader and Evans op. cit., Yamashita *et al.* 1985). The range of prey eaten is wide and, whereas copepods may dominate the diet numerically, animals can eat prey up to 3–4 times their body length (Sheader and Evans op. cit.). Larger items such as chaetognaths may therefore be more important as food (Sheader and Evans op. cit., Yamashita *et al.* op. cit.). Prey size is generally proportional to both body length and the morphology of the feeding appendages (Sheader and Evans op. cit., Sheader 1990), so that the *bispinosa* form eats larger prey than the *compressa*. This not only allows food partitioning under sympatry but enables animals to make the most of the range of food available. Members of the genus *Themisto* appear to be additionally adapted to fluctuations in the food environment, because they have rich oil reserves (Percy and Fife 1981), are able to survive for prolonged periods without food, and have large distendable stomachs which can be filled rapidly (Sheader op. cit.). The latter would suggest that ingestion becomes independent of food concentration at high concentrations, as demonstrated by Yamashita *et al.* (1984) for *T. japonica*.

The only data on daily ingestion from field-collected material are presented by Sheader and Evans (1975) for *T. compressa* of different sizes at various temperatures. Unfortunately, these data are based on the assumption that animals feed maximally for 24 h and ignore the effect of diel vertical migration (Hardy and Gunther 1935) and changes in the types and densities of prey (Sugisaki *et al.* 1991), although food may be retained in the gut for longer than 24 h (M. Sheader, University of Southampton, pers. comm.). The impact of *Themisto* on copepod populations in the southern Benguela is unknown, although very crude estimates (Table II) can be made on the basis of the *Themisto* size distributions of Siegfried (1965), the *Themisto* densities shown in Table I, the copepod densities presented by Peterson *et al.* (1990) and the ingestion data of Sheader and Evans (op. cit.), where copepods represent approximately 48 per cent by number of 6 mm amphipod diets. As larger components of the diet (e.g. chaetognaths) may be more important as a carbon source, and because not all the population feeds maximally (Sheader and Evans op. cit.), the data are likely to be overestimates. Faith in the results is small, but they suggest that *Themisto* may be more important than previously thought.

Both yolk-sac and post yolk-sac fish larvae are vulnerable to *Themisto* and may be seasonally important components of the diet (Siegfried 1965, Sheader and
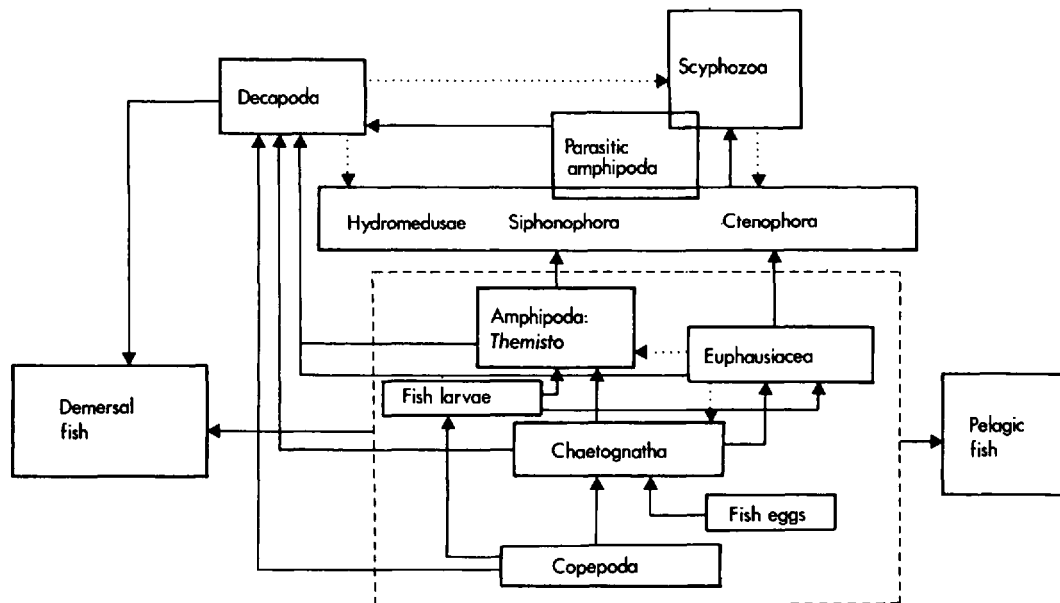
Fig. 1: Diagrammatic illustration of the possible trophic interactions between invertebrates in the Benguela ecosystem. Solid lines indicate the flow of carbon from juveniles and adults to adults, and dotted lines indicate the more complicated "reverse" flow of juveniles to adults. Animals at the same level can readily consume each other, and with the exception of parasitic hyperiids, any organism below it as well. Information used in the construction of this figure has not all been derived from the Benguela

Evans 1975, Yamashita *et al.* 1985). Indeed, as densities of both tend to be coincident in time and space, *Themisto* may have serious direct and indirect effects on clupeoid recruitment. Such has been argued by Sheader and Evans (op. cit.) for the North Sea and Yamashita *et al.* (1985) for Otsuchi Bay, Japan. Olivar and Barangé (1990) suggested that predatory pressures may be one of the factors contributing to negative correlations between the density of hyperiids and fish larvae off Namibia.

GENERAL DISCUSSION

The diversity of carnivorous zooplankton within the southern and northern Benguela is low, and most groups are represented by only one or two "common" species. These tend to be epiplanktonic and generally concentrated inshore of the shelf-break, but their distributions are influenced by changes in local hydrography. Because many of the groups reach highest diversities in "stable" equatorial or oceanic waters, the low temperatures and constantly fluctuating physical and biological environment experienced nearshore may account for the paucity observed.

Densities of "common" carnivorous species are nevertheless high, and they frequently exceed those of herbivores (Hopson 1983, Olivar and Barangé 1990, Fearon *et al.* in press). Their greater abundance in the north than in the south of the Benguela probably reflects differences in the relative stability and productivity of the two systems.

The dominant carnivorous organisms all have wide-ranging diets, feed continually and mostly have Type I functional responses to prey concentration; assimilation and growth efficiencies are also high. Otherwise, however, they fall into two categories, epitomizing two different strategies to the food environment. The gelatinous species (Cnidaria and Ctenophora) may have short lifespans and exhibit very rapid growth and often massive reproductive (sexual and asexual) responses to elevated food. Some appear to have behavioural traits enabling them to stay within localized patches of prey (Bailey and Batty 1983), on which they may be dependent because of high metabolic cost. Crustacean predators and chaetognaths, on the other hand, respond more slowly to changes in food abundance, but they may have longer lifespans, lower daily maintenance needs and the ability to store lipids. They are less dependent on high-density patches of food and can therefore survive over winter, when gelati-

nous predators are scarce.

Maximum and minimum estimates of predatory impact by invertebrate carnivores on copepod standing stocks in the southern Benguela are given in Table II. These values should be treated with caution, however, because they are mostly based on foreign laboratory measurements of dubious value, combined with largely irrelevant (by scale) estimates of local abundance. In the case of *Chrysaora*, published filtration rates were calculated using *Artemia* as prey, so extrapolations to the copepod community must be treated with caution: they have been reduced by 50 per cent accordingly.

The impacts are overestimates, especially those used to evaluate amphipod consumption, because little confidence is placed on them in the light of evidence of omnivory (Sugisaki *et al.* 1991). Nevertheless, if swarms of gelatinous zooplankton or amphipods coincide with an aggregation of zooplankton or fish larvae, then there can be total depletion. This may be of particular significance in the nearshore zone of the West Coast, which is subject to strong predation pressure from pelagic fish recruits, and in "semi-enclosed" areas such as St Helena Bay, which may allow the build-up of invertebrate populations. Swarm conditions are probably rare, and therefore the more realistic estimate of carnivorous impact is probably illustrated by the lower figure in Table II.

Estimates of predatory impact on copepod populations ignore higher trophic interactions, which may serve to stabilize carnivore populations and in turn the zooplankton community itself (Purcell 1991). Within-guild predation is very much a top-down process for adults (Fig. 1), but when larvae, juveniles or other immature stages are included, the whole series of interrelationships become more complicated (Fig. 1). Fish are also important predators: chaetognaths, amphipods and decapods are frequently found in the stomachs of demersal and pelagic species such as Cape hake *Merluccius* spp. (Payne *et al.* 1987) and anchovy *Engraulis capensis* (James 1987). Vertebrate predators of gelatinous zooplankton have yet to be identified in the region, and as the prey of fish, they are rapidly broken down on ingestion and are often only detectable as nematocysts. Elsewhere, small medusae and siphonophores are consumed by a very wide range of fish species, from tuna and mackerel to flying fish (Runge *et al.* 1987), although their importance as food is unknown. By their larger size, carnivorous zooplankton act for fish species as convenient concentrators and stores of patchily produced energy. Should the very large scyphozoa be immune to predation by all but turtles (Holland *et al.* 1990) and amphipods (Mills in press), it could be argued that they represent a considerable loss of carbon from the water column and possibly even to the system if they are transported beyond the shelf-break.

PERSPECTIVES

As noted previously, the estimates of impact presented here are mostly based on foreign laboratory measurements of dubious value, combined with largely irrelevant (by scale) estimates of local abundance. Densities are typically orders of magnitude greater inside than outside patches (Omori and Hamner 1982), so that if reliable estimates of overall density are required, it is important that patch size and distribution be determined. The factors leading to patch formation and persistence tend to influence both prey items and predators, yet with the exception of cold-core rings (Shillington *et al.* 1990), their dynamics in the region are poorly understood. The pros and cons of laboratory v. field measurements of feeding fall outside the scope of this perspective (although see Purcell and Kremer 1983), but detailed local field estimates of feeding under different regimes should be attempted, especially as they relate to gelatinous species. Ideally, behavioural studies such as those of Hamner *et al.* (1987) should be undertaken because they are conducted at relevant scales of distribution.

The horizontal association of predator and prey abundance deserves greater attention, to highlight areas of persistent presence, wherein it is suggested that predator population development, dynamics and maintenance should be investigated.

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