

SOME OBSERVATIONS ON THE PELAGIC DECAPOD *PASIPHAEA SEMISPINOSA* HOLTHUIS 1951 IN THE BENGUELA UPWELLING SYSTEM

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Information on vertical and horizontal distribution patterns, abundance and morphology of the decapod *Pasiphaea semispinosa* in the Benguela upwelling system is presented. *P. semispinosa* is the dominant pelagic decapod in the system, occurring between 19 and 32°S along the mid and inner shelf in concentrations of 10–100 · m⁻². Although it is more abundant during abated than during active upwelling in the northern Benguela, it would appear to be equally abundant during both upwelling scenarios in the southern Benguela. In the southern Benguela, reproductive females are present during winter and juveniles dominate during active upwelling, but juveniles appear to be more common during abated upwelling in the northern Benguela. The estimates of abundance of *P. semispinosa* presented in this study are subject to sampling biases attributable to their vertical migratory behaviour and net avoidance capabilities.

Inligting oor vertikale en horisontale verspreidingspatrone, talrykheid en morfologie van die dekapode *Pasiphaea semispinosa* in die Benguela-opwelstelsel word aangebied. *P. semispinosa* is die dominante pelagiese dekapode in die stelsel en kom tussen 19 en 32°S op die middel- en binneplat in konsentrasies van 10–100 · m⁻² voor. Ofskoon dit in die noordelike Benguela talryker is wanneer opwelling bedaar het as wanneer dit aktief is, is dit in die suidelike Benguela blykbaar ewe volop tydens albei opwelsenario's. In die suidelike Benguela is voortplantende wyfies in die winter aanwesig en oorheers jongdiere gedurende aktiewe opwelling, maar in die noordelike Benguela lyk dit of jongdiere volop is wanneer opwelling bedaar het. Die ramings van talrykheid vir *P. semispinosa* wat in hierdie studie aangebied word, is onderhewig aan bemonsteringsydigheid wat aan hulle vertikale migrasiegedrag en netvermydingsvermoë toegeskryf kan word.

Excluding the taxonomic and expedition literature (e.g. Lebour 1954, Barnard 1950, Macpherson 1983, 1988), little information is published on the pelagic decapods of the Benguela ecosystem. Several reasons account for this paucity: the belief that they are relatively scarce in the plankton; the knowledge that they lack commercial value; and the difficulty of assessing their abundance with traditional net sampling. As a result, they are perceived as playing a secondary trophic role in the Benguela ecosystem (Gibbons *et al.* 1992).

Two assemblages of pelagic decapods can be identified in the northern Benguela, one associated with the shelf and the other with the slope (Macpherson 1991). These two assemblages are separated by a cross-shelf barrier and are probably maintained by different circulation patterns (Barange and Pillar 1992). Although the species diversity of the slope assemblage is greater than that of the shelf community, densities tend to be higher across the shelf (Macpherson 1991). Both density and diversity of these assemblages are depressed during active upwelling, but both parameters are elevated during periods of relaxed upwelling and intrusions of warm, near-surface, Angolan water from the north

(Macpherson 1991).

While it has been suggested that *P. semispinosa* is an important component of the northern Benguela shelf assemblage (Olivar and Barangé 1990, Macpherson 1991), information on its distribution, abundance and ecology is scarce. This paper reports on collections of *P. semispinosa* taken during various cruises in both northern and southern Benguela. The main objective is to synthesize available data to facilitate a better understanding of the trophic role of the species in the Benguela system.

MATERIALS AND METHODS

Samples were collected in the northern Benguela during the two Spanish Namibian Environmental Cruises (SNEC I and II), which were conducted in September/October 1985 and April 1986 respectively. More detailed descriptions of the survey grids and sampling methodology employed during these cruises are provided by Olivar and Barangé (1990) and Macpherson

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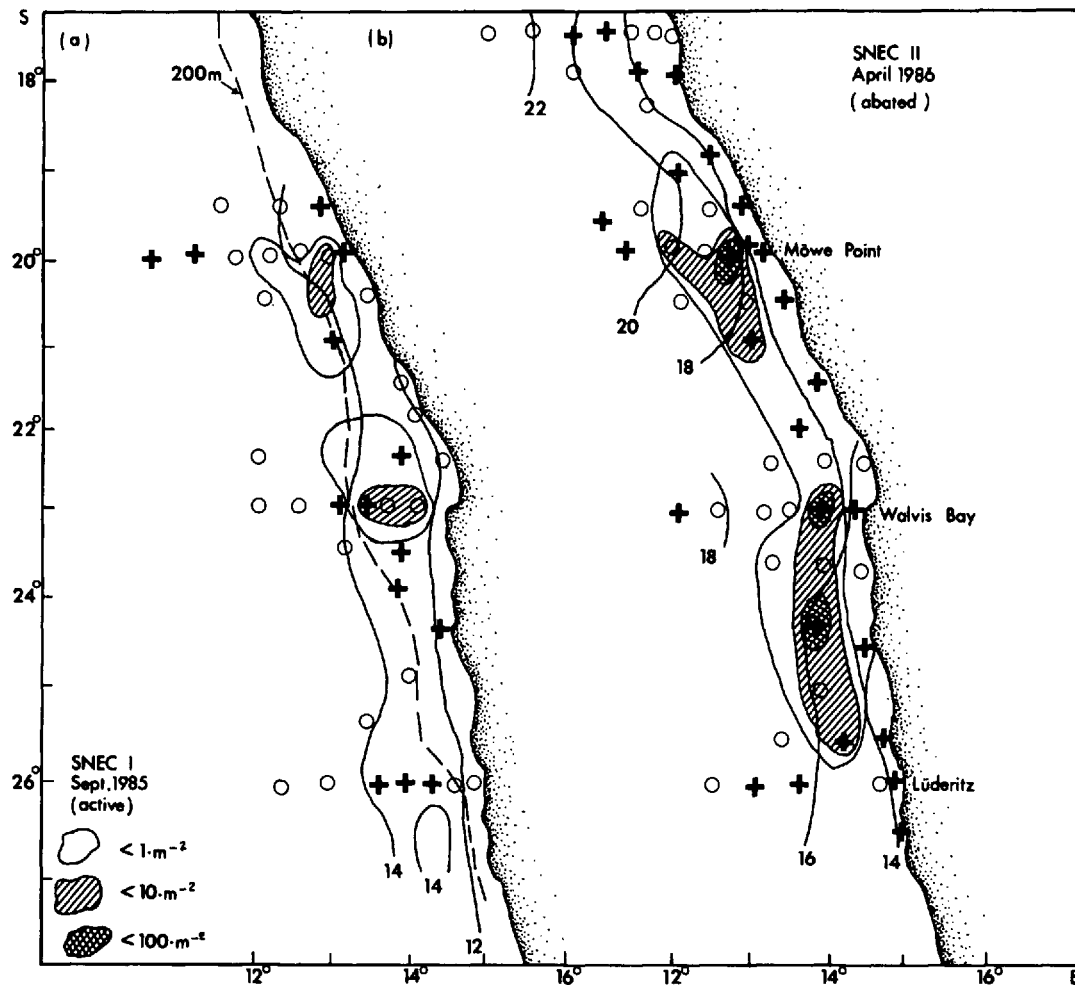


Fig. 1: Distribution and abundance of *P. semispinosa* in the northern Benguela, during periods of (a) active and (b) abated upwelling. Sea surface temperature (SST, °C) records are presented in 2°C intervals. Stations are depicted as daytime (circles) and night-time (crosses) collections

(1991). However, in summary, as shown in Figure 1, a total of 66 (SNEC I) and 54 (SNEC II) stations were sampled in an area extending from Möwe Point (19°23'S) to 26°S (SNEC I) and from the Cunene River (17°30'S) to 26°S (SNEC II). Both cruises extended from 5 miles from the coast to a maximum of approximately 135 miles offshore. CTD profiles (Masó and Manríquez 1986, Masó 1987), chlorophyll (Estrada and Marrasé 1987) and carbon and nitrogen measurements (Barange *et al.* 1991), as well as zooplankton collections (Barange 1991, Pagès 1991), were made at each station. Zooplankton samples were collected by means of a 1 m²

multiple-opening/closing rectangular midwater trawl fitted with six nets of 200- μ m mesh (RMT-1x6). The nets were towed at 1 m · s⁻¹ through four (SNEC II) or five (SNEC I) depth strata from near the bottom (or to a maximum depth of 200 m) to the surface.

Data from the southern Benguela were collected from two main sources, one from a single, dedicated cruise and the other from various routine cruises. During February 1991, a dedicated plankton dynamics cruise, lasting 16 days, sampled a number of stations along a transect running 67 miles off the mouth of the Olifants River (31°37'S). Two of these stations were studied

intensively, each over a period of 72 h, one in 65 m of water 2 miles from the coast and the other in 255 m of water 30 miles offshore. *P. semispinosa* occurred only at the innermost station of the transect. A more detailed description of sampling procedures used during this cruise is provided by Gibbons (1993). Zooplankton were collected at five depth strata from near the bottom to the surface in a manner similar to that employed during the SNEC cruises. At the 72-h stations, zooplankton were collected at 4-h intervals during the day and at 2-h intervals at night (20h00–06h00).

Unpublished records of *P. semispinosa* were examined from zooplankton samples collected during routine, spring/summer (1989, 1990) and winter (1988, 1989, 1990, 1991) Sea Fisheries Research Institute (SFRI) cruises. Samples were reinspected where necessary. Details of the survey grids and sampling methodology employed during these cruises are provided in various unpublished SFRI cruise reports. Summer cruises generally extended from Lambert's Bay on the West Coast (32°S, 18°E) to Port Elizabeth on the South Coast (35°S, 25°30'E). Winter cruises on the West Coast extended from the Orange River mouth (28°40'S, 16°30'E) to approximately Cape Agulhas (34°50'S, 20°E). Zooplankton samples were collected along transects of stations extending from near the coast to the shelf break, towing 200- μ m mesh Bongo nets vertically at a speed of 1 m·s⁻¹ from near the bottom to the surface (from a maximum depth of 200 m).

All zooplankton collections were preserved in buffered, saline, 5% formalin and, in the laboratory, *P. semispinosa* were enumerated and measured (carapace length *CL*). Females were examined for presence of eggs and the number of eggs per female was counted. Counts were standardized to numbers under 1 m² from knowledge of the volume of water filtered by the nets and the depth of the tow. When possible, the vertical distributions of *P. semispinosa* were determined from RMT-1 x 6 collections, and the weighted mean depth (WMD) was determined by means of the method of Roe et al. (1984).

As supplementary information, data on *P. semispinosa* were examined from the archives of the Marine Biology Department of the South African Museum, Cape Town. Various morphometric data were analysed from collections taken off the West Coast during a cruise in August 1989 (Appendix).

In order to examine which parameters were important in influencing the horizontal distribution of *P. semispinosa* during SNEC II, the data were subjected to ANOVA analysis. Square-root transformation was applied to normalize the data. Paucity of data precluded similar analysis of the results of other cruises.

RESULTS

Physical features

Detailed descriptions of the physical environment in the northern Benguela during the SNEC I and II cruises are given by Masó and Manriquez (1986) and Masó (1987). The essential features are that, during SNEC I, there was active upwelling along the whole Namibian coast, but during SNEC II, there was limited upwelling off Lüderitz. There was also a strong intrusion of warm Angolan water north of 21°S during SNEC II (Fig. 1).

Details of the February 1991 cruise off the mouth of the Olifants River are given by Gibbons (1993). There was no active upwelling throughout the 16-day study period, but such conditions prevailed just prior to the cruise.

Descriptions of the survey areas and sampling methodology employed during the routine SFRI pelagic cruises are provided by Hampton (1992) and various unpublished cruise reports. Salient features of the physical environment in the southern Benguela can be found in Shannon (1985). Typically, upwelling in this region is more frequent during spring and summer (September/October–March/April) than it is in winter (June–August).

Biological features

NORTHERN BENGUELA

P. semispinosa were found along the mid and outer shelf of the northern Benguela, south of 19°S, during both abated and active upwelling (Fig. 1). They were less abundant during active than during abated upwelling (Fig. 1), and numbers peaked over the mid shelf (Table I). There were no significant differences either between latitudinal sectors south of 19°S or between daytime and night-time abundances (Table II). Although data were too scattered and inconclusive to determine diel patterns of the vertical distribution of *P. semispinosa* in the northern Benguela, they suggest that the horizontal variability was greater than that associated with the diel cycle.

A wider size range of *P. semispinosa* and a greater proportion of animals >10 mm *CL* were caught during active upwelling than during abated upwelling; 29 and 5% respectively (Fig. 2). However, more animals of 4 mm were caught during abated than during active upwelling, 38 and 13% respectively, suggesting either

Table I: Mean density (number \cdot m⁻²) and standard error SE of *P. semispinosa* collected during the SNEC II survey (April 1986) in the northern Benguela, relative to sampling period, station depth and latitude (n = number of plankton tons)

Parameter	Density (number \cdot m ⁻³)		
	Mean	SE	n
Sampling period			
Day	16,8	8,7	24
Night	14,9	6,4	25
Station depth (m)			
0–100	0,8	0,6	11
100–200	61,1	17,9	11
200–1000	7,0	3,4	13
>1 000	0,4	0,3	14
Latitude			
South of 23°S	22,9	11,5	13
21–23°S	22,4	18,7	9
19–21°S	15,6	9,6	14
North of 19°S	4,6	3,2	13

a seasonal recruitment of individuals or an offshore advection of juveniles during upwelling.

SOUTHERN BENGUELA

Data are sparse, but results from routine cruises suggest that the distribution of *P. semispinosa* extends northwards from Cape Columbine along the west coast of South Africa. The species appears to be confined to water depths of <200 m (Fig. 3), but this finding may be a function of the areas surveyed. Its capture at more northerly latitudes during autumn than during summer may be a reflection of the seasonal differences in areas surveyed (Hampton 1992). There are no records of *P. semispinosa* off the South Coast. Densities from net sampling on the West Coast were generally low (between 10 and 100 \cdot m⁻²), and their abundance did not

Table II: Summary of the ANOVA analyses performed on the horizontal abundances (number \cdot m⁻²) of *P. semispinosa* recorded during the SNEC II survey. Data were square-root transformed

Parameter	Sum of squares	Degrees of freedom	F	p
Period	10,7	1	2,49	0,126
Latitude	17,6	3	1,40	0,276
Station depth	257,3	3	19,88	0,001
Period v. latitude	3,1	3	0,24	0,860
Period v. depth	21,7	3	1,67	0,190
Latitude v. depth	33,9	9	0,80	0,550
Residual	112,10	26		

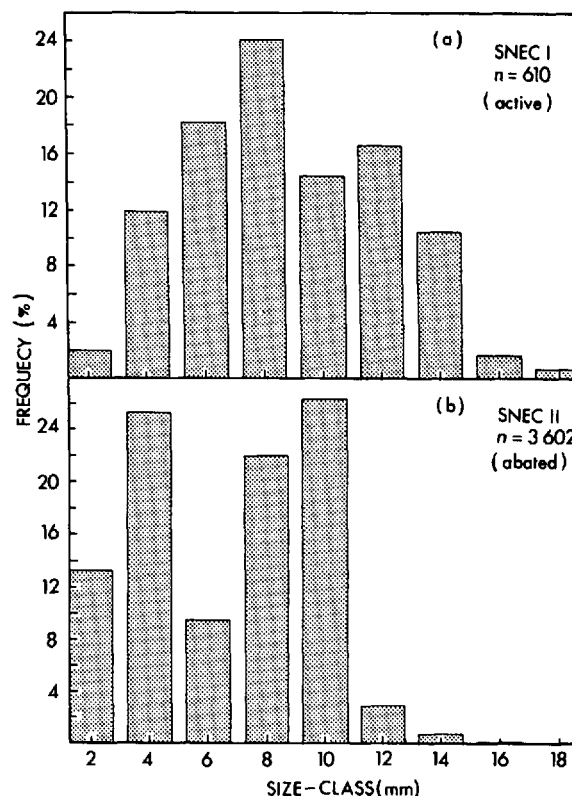


Fig. 2: Size composition of *P. semispinosa* sampled during (a) active (SNEC I) and (b) abated (SNEC II) phases of upwelling in the northern Benguela

appear to vary seasonally.

Day/night differences and the diel vertical migration of *P. semispinosa* were analysed from the collections taken at the 72-h fixed station during February 1991 (Fig. 4). Although densities were low (<10 \cdot m⁻²), individuals appeared to occupy shallower depths in the water column at night than during the day. Consequently, *P. semispinosa* could be out of the tracking range of the nets during the day, so accounting for their scarcity in the daytime collections.

Too few specimens were collected during any one routine cruise to compile a reliable length frequency distribution per cruise. The composite length frequency distribution for all the data collected during the autumn cruises (Fig. 5a) is similar to the population size structure computed for the single cruise during August 1989 (see insert in Fig. 5). There were insufficient data to make a similar study for the summer routine cruises, and therefore the material collected during the 72-h study in February 1991 was assumed to be representative of summer conditions (Fig. 5b). Contrary to observations made in the northern Benguela, individual *P.*

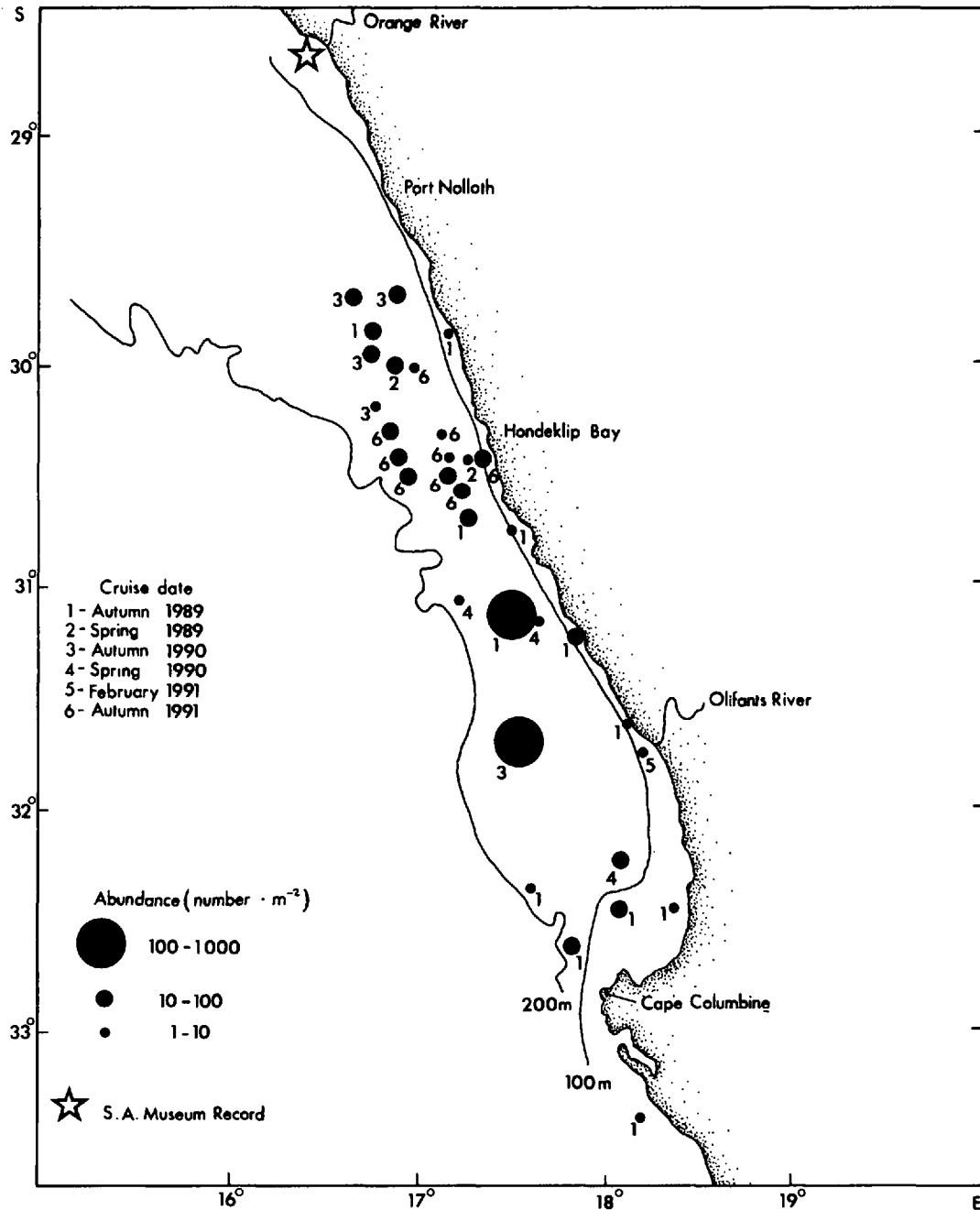


Fig. 3: Distribution and abundance of *P. semispinosa* in the southern Benguela, as determined from routine cruises of the Sea Fisheries Research Institute and other sources. The dates of sample collection are indicated

semispinosa caught during the upwelling season (summer) in the southern Benguela were mostly juveniles and subadults (4–6 mm CL), whereas adults (14–

16 mm CL) predominated the autumn (quiescent season) collections (Fig. 5).

No data are available on the spawning frequency of

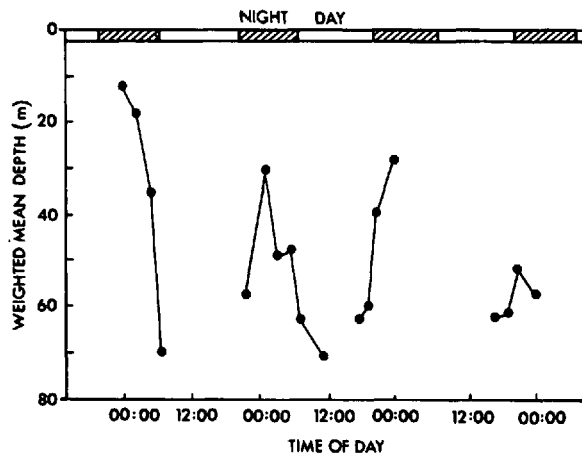


Fig. 4: Changes in the vertical distribution of *P. semispinosa*, expressed as weighted mean depth in the inshore waters off the mouth of the Olifants River during February 1991

P. semispinosa, but egg-bearing females were caught only in winter and only juveniles were caught in summer. Fecundity (E) was found to be proportional to CL (Fig. 6), according to the equation

$$E = 5,51CL - 74,57 \quad (r^2 = 0,68; n = 25).$$

DISCUSSION

Pelagic decapods are known to show pronounced net-avoidance (Omori 1974), and consequently the abundance estimates presented here should be treated cautiously. This caveat is especially applicable to vertical Bongo net collections from the southern Benguela (Pillar 1984) and to RMT-1 x 6 collections in deep water of the northern Benguela. In the latter case, because *P. semispinosa* may occur at daytime depths >200 m (Lagardère 1972), abundance estimates, especially those from the outer shelf, will be erroneous. Therefore, the present data may be considered as being minimum values. Miller *et al.* (1983) noted that density estimates of the prawn *Funchalia woodwardi* from 8-m² rectangular midwater trawl (RMT-8) collections, taken beyond the shelf in the southern Benguela, were 29 times lower than those derived by acoustic means. Those authors attributed the bias to net-avoidance. The abundance estimates of *P. semispinosa* reported in this study, as well as those recorded by Gibbons *et al.* (1992), are higher than the net-estimated densities within the large *F. woodwardi* swarm reported in Miller *et al.* (1983), suggesting that *P. semispinosa* may also swarm in local waters. High densities of

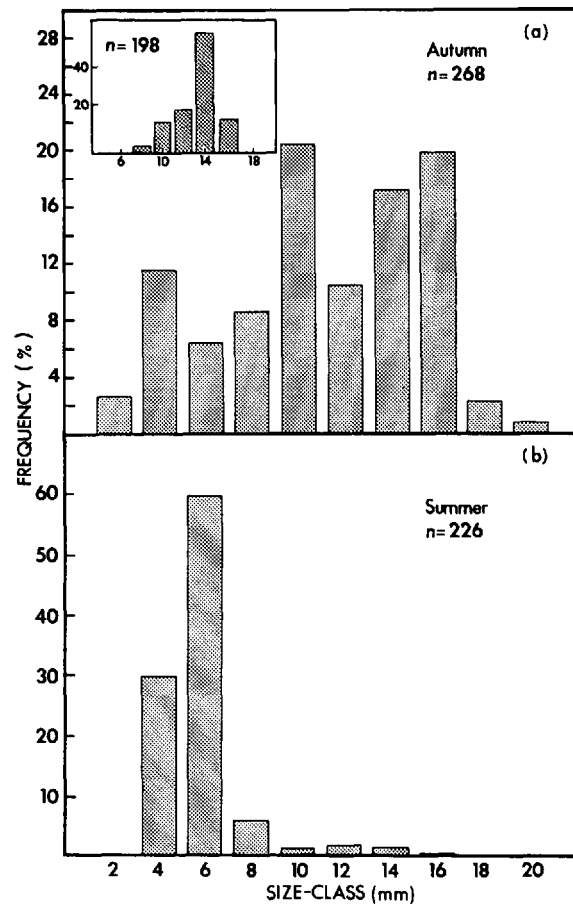


Fig. 5: Size composition of *P. semispinosa* sampled during (a) autumn (routine pelagic cruises of the Sea Fisheries Research Institute) and (b) summer (February) in the southern Benguela. The inset in (a) represents the size distribution of the population sampled during a single cruise in August 1989

Pasiphaea have been observed elsewhere (Krygier and Percy 1981, Dagnino *et al.* 1985, Relini and Relini 1990). Abundance and mean densities (and ranges) of *P. semispinosa* for the Benguela system are summarized in Table III.

The positive correlation between the size of *P. semispinosa* and upwelling conditions in the northern Benguela contrasts with the inverse situation found in the southern Benguela. However, it is consistent with observations made for a number of different zooplankton taxa in the two regions. In the southern Benguela, the euphausiid *Euphausia lucens* is largest and most reproductively active in spring (Pillar *et al.* 1989). The hyperiid amphipod *Themisto gaudichaudi* is also most reproductively active in spring, and consequently,

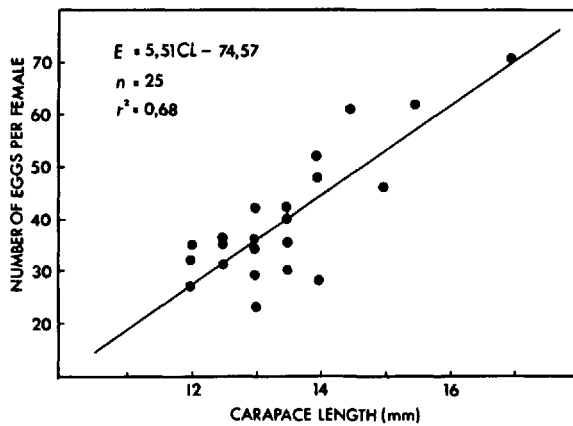


Fig. 6: Relationship between female carapace length *CL* and number of eggs *E* in *P. semispinosa*

small individuals are more common during late spring and early summer than during winter (Siegfried 1965, Hopson 1983). Hopson (1983) similarly noted small chaetognaths to be more common during spring and early summer than at other times of the year. The present observations for *P. semispinosa* may be linked to the prolonged period of maternal protection and non-feeding behaviour of caridean nauplii (Omori 1974), and to the possible synchronization of protozoal developmental with environmental productivity. In the northern Benguela, euphausiids are more numerous but small during abated upwelling, but they are larger and less common during active upwelling (Barange and Stuart 1991). Such a pattern is also displayed by gelatinous zooplankton (Pagès 1991) and copepods (M. Carola, formerly Instituto de Ciencias del Mar, Barcelona, unpublished data), as is the case in the present study. These observations suggest that seasonal reproduction in zooplankton in the Benguela is linked to upwelling conditions (Shannon 1985, Pillar et al. 1992, Verheye et al. 1992).

The distributions presented for *P. semispinosa* in

Table III: Mean density (number · m⁻²), standard deviation *SD* and range of *P. semispinosa* recorded in the northern (SNEC I and II) and southern Benguela (Olifants River transect). All samples (*n*) were collected with an RMT-1 x 6 net

Survey	Density (number · m ⁻²)			
	Mean	<i>SD</i>	Range	<i>n</i>
SNEC I	10,9	16,4	0,4– 57,2	13
SNEC II	26,8	44,9	0,2–171,3	29
Olifants River transect	4,3	9,2	0,1– 38,2	16

the Benguela must be considered as provisional for a number of reasons. First, it is likely that their absence from collections, especially daytime ones, is partly attributable to net-avoidance. Second, the distribution of *P. semispinosa* is only as complete as the area surveyed. The sampling grids in the south extended as far as the shelf edge (approximately 200 m), but in the northern Benguela they extended to beyond the shelf break, although the nets were only fished to a maximum of 200 m. Therefore, the data are constrained by the 200-m depth contour. While most other species of *Pasiphaea* have been reported to be common in inshore and shelf waters and rare offshore and in the open ocean (Omori 1974, Krygier and Pearcy 1981), members of the genus are known to occur deeper in areas where the water is deep (Lagardère 1972). It is likely, therefore, that *P. semispinosa* occurs outside the 200-m isobath in the southern Benguela, as is the case north of the Orange River, and that it is more common in deeper water in the north than the present results suggest.

The density and distribution of pelagic decapods found elsewhere is often strongly correlated with the distribution and abundance of their prey (Omori 1974, Relini and Relini 1990). For adult *P. semispinosa*, these prey are principally euphausiids, which are thought to be selected on the basis of bioluminescent cues (Lagardère 1975). The longshore distribution of *P. semispinosa* roughly overlaps areas of dense populations of euphausiids over the shelf of the Benguela (Pillar et al. 1992). Some authors have suggested that *P. sivado* forage on zooplankton in midwater at night and on the benthos during the day (e.g. Relini and Relini 1990), but there are currently no conclusive data on the diel feeding of *P. semispinosa*.

Because of its presence in the diet of many species of fish, *P. sivado* was identified as a key species in the trophic webs of the Mediterranean (Relini and Relini 1990). Using the average abundances presented in Table III and the length:mass relationship provided in the Appendix, and assuming an average length of 10 mm *CL*, a range of 6–40 mg dry mass · m⁻² is computed. This value is not an inconsequential quantity of organic matter, even without taking into account net avoidance, but it compares poorly with ranges of 0,46–3,28 and 0,35–6,3 g · m⁻² estimated for euphausiids and mesozooplankton respectively from the west coast of South Africa (Pillar et al. 1992, Verheye et al. 1992). The productivity of *P. semispinosa* in the Benguela is also likely to be lower than that of euphausiids or mesozooplankton, because these decapods are relatively large, may live for between 2½ and 3 years, brood few larvae for prolonged periods of time and probably reproduce seasonally. Although their contribution to the productivity of the Benguela ecosystem may therefore be minimal, *P. semispinosa* are frequently

preyed upon by key fish species of the region, such as Cape horse mackerel *Trachurus t. capensis* (Andronov 1975) and hake *Merluccius capensis* (Roel and Macpherson 1988). As such, they may play a more important role in transferring energy to higher trophic levels (Pearcy *et al.* 1977) than was previously thought (Gibbons *et al.* 1992).

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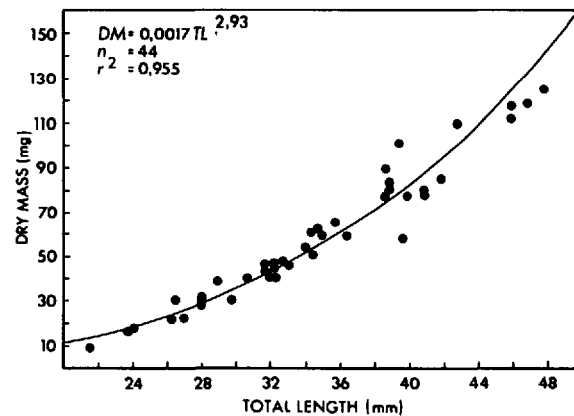
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APPENDIX

App. Table 1: Regression parameters between various morphological features of *P. semispinosa* collected during August 1989 in the southern Benguela. All measurements are in mm and expressed in the form $y = mx + c$

Morphological features		Regression parameters			
x	y	m	c	r ²	n
Total length	Carapace length	0,35	-2,24	0,98	27
Total length	Telson length	0,17	-0,67	0,99	27
Carapace length	Telson length	0,49	0,51	0,97	27



App. Fig. 1: Relationship between total length TL and dry mass DM of *P. semispinosa* collected during August 1989 in the southern Benguela