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.

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 rela-
tively 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 identi-
fied 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 circu-
lation 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 den-
sity 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 Barange 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 sam-
ping methodology employed during these cruises are
provided by Olivar and Baranger (1990) and Macpherson

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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.

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 Mowe 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 Manriquez 1986, Masó 1987), chlorophyll (Estrada and Marrasé 1987) and carbon and nitrogen measurements (Barange et al. 1991), as well as zooplankton collections (Barange et al. 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-μm 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...
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 Luderitz. 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 $m^{-2}$) 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)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Density (number $m^{-2}$)</th>
<th>Mean</th>
<th>SE</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>16.8</td>
<td>8.7</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Night</td>
<td>14.9</td>
<td>6.4</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Station depth (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–100</td>
<td>0.8</td>
<td>0.6</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>100–200</td>
<td>61.1</td>
<td>17.9</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>200–1000</td>
<td>7.0</td>
<td>3.4</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>&gt;1000</td>
<td>0.4</td>
<td>0.3</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Latitude</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South of 23°S</td>
<td>22.9</td>
<td>11.5</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>21–22°S</td>
<td>22.4</td>
<td>18.7</td>
<td>9</td>
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</tr>
<tr>
<td>19–21°S</td>
<td>15.6</td>
<td>9.6</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>North of 19°S</td>
<td>4.6</td>
<td>3.2</td>
<td>13</td>
<td></td>
</tr>
</tbody>
</table>

Table II: Summary of the ANOVA analyses performed on the horizontal abundances (number $m^{-2}$) of $P$. semispinosa recorded during the SNEC II survey. Data were square-root transformed

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sum of squares</th>
<th>Degrees of freedom</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period</td>
<td>10.7</td>
<td>1</td>
<td>3.49</td>
<td>0.126</td>
</tr>
<tr>
<td>Latitude</td>
<td>17.6</td>
<td>3</td>
<td>1.40</td>
<td>0.276</td>
</tr>
<tr>
<td>Station depth</td>
<td>257.3</td>
<td>3</td>
<td>19.88</td>
<td>0.001</td>
</tr>
<tr>
<td>Period v. latitude</td>
<td>3.1</td>
<td>3</td>
<td>0.24</td>
<td>0.860</td>
</tr>
<tr>
<td>Period v. depth</td>
<td>21.7</td>
<td>3</td>
<td>1.67</td>
<td>0.190</td>
</tr>
<tr>
<td>Latitude v. depth</td>
<td>33.9</td>
<td>9</td>
<td>0.80</td>
<td>0.550</td>
</tr>
<tr>
<td>Residual</td>
<td>112.10</td>
<td>26</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

SOUTHERN BENGOULA

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 the 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 $m^{-2}$), and their abundance did not 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 $m^{-2}$), 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 inset 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 $P$.
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
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 *Pasiphaea* have been observed elsewhere (Krygier and Pearcy 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,
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 protozoetal 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 1983, Pillar et al. 1992, Verheye et al. 1992).

The distributions presented for *P. semispinosa* in 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⁻³ 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 2 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

![Graph showing relationship between female carapace length and number of eggs](image_url)

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


OMORI, M. 1974 — The biology of pelagic shrimps in the ocean.

APPENDIX

App. Table I: 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 \( y = mx + c \)

<table>
<thead>
<tr>
<th>Morphological features</th>
<th>Regression parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( x )</td>
</tr>
<tr>
<td>Total length</td>
<td>Carapace length</td>
</tr>
<tr>
<td>Total length</td>
<td>Telson length</td>
</tr>
<tr>
<td>Carapace length</td>
<td>Telson length</td>
</tr>
</tbody>
</table>

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