SHRIMP FAUNA (CRUSTACEA: DECAPODA) OF THE NORTH ATLANTIC SUBTROPICAL CONVERGENCE

RUDOLF N. BURUKOVSKY


Pelagic shrimps were sampled by R/V "Professor Siedlecki" cruise during August-September 1984 in the region of the North Atlantic subtropical convergence between latitudes 43°-46°N (western), 37°-46°N (eastern) and at longitudes 14°-30°W. Hauls were made from the surface down to 1200 m. Twenty nine species were identified (excluding those of the family Sergestidae). The results confirmed the existence of a transition zone where omni-ocean shrimp fauna is dominant and where mixing of northern and central Atlantic pelagic species occurs. A boundary between these two faunas occurs at approximately 42°N and is marked by a change of species diversity northwards and southwards of this boundary.


Os camarões pelágicos foram amostrado, durante um cruzeiro abordo do N/I "Professor Siedlecki", entre Agosto e Setembro de 1984 na região de convergência subtropical do Atlântico Norte entre as latitudes de 43°-46° N (Oeste), e 37°-46 N (Este) e as longitudes de 14°-30° W. Foram efectuados arrastos desde a superfície até aos 1200 m de profundidade. Identificaram-se vinte e cinco espécies (excluindo as pertencentes à família Sergestidae). Os resultados confirmam a existência de uma zona de transição, onde a fauna cosmopolita de camarão é dominante, e onde as espécies ocorrentes no Atlântico Norte e central se misturam. Uma fronteira entre estes dois tipos de fauna ocorre, aproximadamente, nos 42°N e é marcada pela mudança da diversidade de espécies a norte e a sul deste ponto.

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INTRODUCTION

During 1984 the author participated in an international research cruise conducted as part of the Open Atlantic research programme. The object was to study species composition, distribution and biology of shrimp faunas between the Azores archipelago and Portugal. This region is affected almost entirely by the eastern extremity of the North Atlantic subtropical convergence.

Previously Foxton (1972) and Fasham & Foxton (1979), describing species distribution along a 20°W transect in the North Atlantic, used principal component analysis to typify zoogeographic distribution of shrimps from 11°N to 60°N and showed that various zoogeographic boundaries exist in the North Atlantic Ocean including one at approximately 42°N, 20°W. However, although various other studies have been made, the shrimp fauna of the area of the open North Atlantic Ocean between 43°N and 46°N is rather less known than for other regions, for example, the Bay of Biscay, W. Portugal and Spain (Abbes & Casanova 1973; Le Gall &

This present study provides further information on species composition and distributions of the pelagic shrimps from the region of approximately 37°N to 46°N, 14°W to 30°W.

RESULTS AND DISCUSSION

MATERIAL AND METHODS

Hauls were made in regions previously designated for a study of mesopelagic fishes along 17 transects following the meridians separated by one degree of latitude (Fig. 1). The commercial pelagic trawl used was fitted with a small cod-end frame. A total of 83 hauls were made: 26 at depths from 330 m to 100 m, 29 from 100-500 m to 700-1200 m and 28 between 500-700 m. Fifty-six night hauls were made between 20.00 h and 24.00 h at 500-700 m. During these hauls the net was trawled horizontally for 30 or 60 minutes.

Species diversity was assessed using Glisson's coefficient (see ODUM 1975), and all catches were standardised to 60 minutes duration in order to provided comparative quantitative catch and biomass data for each species. Shrimps assigned to the family Sergestidae were not identified further because adequate taxonomic information was not available.

Shrimps occurred in all hauls except for two daytime near-surface hauls; night hauls were always successful. A total of 29 species (excluding Sergestids) were identified (Table I) representing nine natant shrimp families. Only juveniles of the epibenthic species Nematocarcinus gracilipes were caught in a few hauls over North Atlantic sea mounts since these young shrimp do not adopt the truly benthic lifestyle of the adults. Shrimp of the family Oplophoridae of which there were 12 species belonging to 6 genera, predominated.

Fig. 1. Scheme of hauls location in the investigation area. 1- hauls location.
Of the total number of species collected during the cruise, at least 24 had been previously reported from adjacent regions (Zariquiey Alvarez 1968; Abbes & Casanova 1973; Fasham & Foxton 1979; Hargreaves 1985; Burukovsky & Romensky 1991). Of the remaining 5 species, *Kirnasia nesisi* and *K. siedlecki* (Burukovsky 1988) are not known outside of the study area. *Nematocarcinus gracilipes* was collected northwards of the Azores continental slope from where it was previously recorded by Crosnier & Forest (1973), suggesting it may have a northward extension. *Meningodora compsa* was taken eastward of the Azores at 36°18’ N, 19°50’ W at a depth of 874 m thus extending its previously known north-eastward distribution; the species was previously known to occur between Senegal and Bermuda (Chace 1940; Crosnier & Forest 1973; Kikuchi 1991). *Benthisicymus iridescens*,

Table 1: Species composition and quantitative characteristic of shrimps distribution in the North-Atlantic Subtropical convergence area.

<table>
<thead>
<tr>
<th>Species</th>
<th>% FO</th>
<th>Proportion in catch, %</th>
<th>Specific number, %</th>
<th>Specific biomass, %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>by number</td>
<td>by biomass</td>
<td>range</td>
<td>mean</td>
</tr>
<tr>
<td><strong>Group 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Systellaspis debilis</em></td>
<td>71.5</td>
<td>36.8</td>
<td>27.3</td>
<td>1-235</td>
</tr>
<tr>
<td><em>Funchalia villosa</em></td>
<td>61.9</td>
<td>3.3</td>
<td>4.2</td>
<td>1-128</td>
</tr>
<tr>
<td><em>Acanthephyra purpurea</em></td>
<td>58.3</td>
<td>17.8</td>
<td>29.0</td>
<td>3-160</td>
</tr>
<tr>
<td><em>Gennadas valens</em></td>
<td>51.2</td>
<td>17.2</td>
<td>6.6</td>
<td>3-14</td>
</tr>
<tr>
<td><em>Oplophorus spinosus</em></td>
<td>46.4</td>
<td>2.7</td>
<td>1.7</td>
<td>1-32</td>
</tr>
<tr>
<td><em>Acanthephyra pelagica</em></td>
<td>35.7</td>
<td>11.8</td>
<td>15.7</td>
<td>7-240</td>
</tr>
<tr>
<td><strong>Group 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stylopandalus richardi</em></td>
<td>26.2</td>
<td>0.3</td>
<td>0.1</td>
<td>1-6</td>
</tr>
<tr>
<td><em>Ephyrina figuerata</em></td>
<td>25.0</td>
<td>2.0</td>
<td>5.0</td>
<td>1-37</td>
</tr>
<tr>
<td><em>Paraputapheia sulcatifrons</em></td>
<td>23.8</td>
<td>5.3</td>
<td>4.1</td>
<td>1-144</td>
</tr>
<tr>
<td><em>Pasiphae hophilcercus</em></td>
<td>21.4</td>
<td>0.6</td>
<td>0.7</td>
<td>1-17</td>
</tr>
<tr>
<td><em>Euphasia gileti</em></td>
<td>20.2</td>
<td>0.5</td>
<td>1.7</td>
<td>1-11</td>
</tr>
<tr>
<td><em>Meningordora vexsa</em></td>
<td>20.2</td>
<td>0.5</td>
<td>0.3</td>
<td>1-30</td>
</tr>
<tr>
<td><strong>Group 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Funchalia woodwardi</em></td>
<td>16.7</td>
<td>0.1</td>
<td>1.1</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Benthisicymus iridescens</em></td>
<td>11.9</td>
<td>0.1</td>
<td>0.3</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Gennadas tinnyrei</em></td>
<td>10.7</td>
<td>0.3</td>
<td>0.1</td>
<td>1-12</td>
</tr>
<tr>
<td><em>Gennadas elegans</em></td>
<td>8.3</td>
<td>0.3</td>
<td>0.1</td>
<td>2-8</td>
</tr>
<tr>
<td><em>Noctiluxim elegans</em></td>
<td>7.1</td>
<td>0.3</td>
<td>0.7</td>
<td>1-8</td>
</tr>
<tr>
<td><em>Nematocarcinus gracilipes</em></td>
<td>7.1</td>
<td>+</td>
<td>+</td>
<td>1-2</td>
</tr>
<tr>
<td><strong>Group 4</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Meningodora mollis</em></td>
<td>4.8</td>
<td>+</td>
<td>0.1</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Meningodora micryla</em></td>
<td>3.6</td>
<td>+</td>
<td>+</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Systellaspis cristata</em></td>
<td>2.4</td>
<td>+</td>
<td>+</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Pasiphaeae multidentata</em></td>
<td>2.4</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Meningodora compsa</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td><em>Pasiphaea sivado</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Ligur ensiferus</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Kiransia nesisi</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Kiransia siedlecki</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Hymenodora gracilis</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td><em>Physocomeis microcephala</em></td>
<td>1.2</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
</tbody>
</table>

where: *- common North Atlantic mesoplagic species as derived from other previous data; E- endemic; K- cosmopolitan; NA- North Atlantic/Mediterranean; ML- Mediterranean Lusitanian; BA- central Atlantic; AI- Atlantic and Indian Oceans; AIWP- Atlantic, Indian and West Pacific Oceans.
reported previously mainly between Tristan da Cunha and Madeira (BURNENROTH 1936) was also collected in this cruise east and north east of the Azores between 45°52'-36°59'N; 25°59'-19°01'W at depths between 550-1075 m.

Because closing nets were not used the catch frequency estimates for mesopelagic species are over-estimated. For similar reasons they may be under-estimated for bathypelagic forms. The various groupings of the shrimp are examined below in terms of the following:

a. The frequency occurrence (%FO) of each species in the total number of hauls.

b. The proportion of species in the catches in terms of number and biomass.

The species captured (Table 1) can be assigned to four groups with respect to their frequency of occurrence (shown as percentages).

1. **Background species**: a total of 6 species (>35% frequency). The most frequently occurring were *Systellaspis debilis* (71.5%) and *Furculalia villosa* (61.9%).

2. **Typical species** for the area comprising 6 species occurring at a frequency of 20-30%.

3. **Sporadically occurring species** which comprises 6 species all with a low frequency of occurrence of 5-16%.

4. **Randomly occurring species** comprising 11 species with a frequency of occurrence of less than 5%.

Estimates of the proportion of species in the catches confirmed the above division into four groups:

Group 1. Background species comprised 6 species with an average proportion in hauls of >15% by number and biomass i.e. *Systellaspis debilis*, *Acanthephyra purpurea*, *Acanthephyra pelagica* and *Gennadas valens*. The latter were numerically dominant but small in size and so low in biomass. *Furculalia villosa* and *Oplophorus spinosus* were found only in insignificant numbers and may be considered as secondary background species (2-4% by number and biomass).

The relatively small species *Systellaspis debilis* was numerically dominant while *Acanthephyra purpurea* was less numerous but had the highest biovolume.

The data also show that there is considerable pelagic dispersion of species. Shoals of *A. pelagica* could measure 50 m (calculated by vessel speed of 10km/hr/haul).

Group 2. Of the typical species for the area the proportion of the six species in the catches were relatively low (Table 1) except for *Parapasiphaea sulcatifrons* of which there were 5% by number and 4% by biomass. *Ephyrina figurata* was also relatively important (2% by number and 5% by biomass).

Group 3. The proportion in the catches of sporadically occurring species each amounted to <0.3% by number and <1.1% by biomass.

Group 4. Randomly occurring species were found in low proportions in the catches.

**ZOOGEOGRAPHY**

Species in the study area can be assigned to six groups with respect to their zoogeographic distributions.

1. **Endemic** (E in Fig. 3): *Kirnasia nesii* and *K. siedlecki* (about 7% of total shrimp fauna).

2. **Boreal** (NA-North Atlantic/Mediterranean): composed of 7 species and representing 21% of the total fauna, e.g. *A. purpurea* and *P. hoplocerca*. Some species e.g. *Pasiphaea multidentata* occur in the eastern Atlantic and during the winter may extend from the north as far southwards as the Guinea-Bissau region (12°N) via the Canarian current (BURUKOVSKY 1989).

3. **Mediterranean/Lusitanian species** (ML): comprising 3.5% of the total shrimp fauna was represented by *Pasiphaea sipada*, captured only once in the easternmost periphery of the area. *Nematocarcinus gracilipes* has a distribution very similar to many Lusitanian/Mediterranean species. It is common on the Moroccan continental slope (BURUKOVSKY 1980) and Azores, Cape Verde and Ascension regions (CROSNIER & FOREST 1973). Its capture on the mid-Atlantic ridge north of the Azores confirms that the species prefers regions of submerged sea mounts.

4. **Central Atlantic species** (BA): species of this group inhabit both boreal and midwater regions. An example is *Gennadas valens*,
distributed from 37°S to 51°N and also in the Mediterranean.

5. **Boreal-tropical distributed species (AI):**
the two species assigned to this group, *Gennadas tinayrei* and *Ligur ensiferus* which occur both in Atlantic and Indian Oceans.

6. **Widely distributed species** comprising two sub-groups 6a and 6b:
The 6a group occurs in the Atlantic, Indian and West Pacific Oceans (AIWP) and includes 10 species (at least 36% of total fauna). The 6b group are cosmopolitan deep-mesopelagic or near-surface species (K) which include *Parapasiphae sulcatifrons*, *Eupasiphae gilesii* and *Hymenodora glacialis* (BURUKOVSKY 1987, 1993; CHACE 1937, 1940), *F. villosa*, a temperate zone species, and *F. woodwardi*, a subtropical zone species from both hemispheres (BURUKOVSKY & ROMENSKY 1991). These five species represent 17.5% by abundance of the total shrimp fauna.

Thus, a mixed pelagic shrimp population inhabits the region of the North Atlantic subtropical convergence where the dominant species are common to both Atlantic, Indian and Pacific Oceans. They represent in excess of 60% of the shrimps caught in the study area.

A second feature is the simultaneous occurrence of boreal and subtropical species within the same area i.e. the boundary area where mixing occurs between waters of boreal and subtropical origin.

Furthermore a feature of the area is the relationship between mid-Atlantic fauna with that of the Mediterranean-Lusitanian zoogeographic region (at least with the Mediterranean part) as seen with the occurrence of Mediterranean-Lusitanian species such as *Pasiphaea sivado* in the eastern margin of the area and of *Lysmata nilita* and *Plesionika gigliolii* Lusitanian/Mediterranean species off the Azores (MARTINS & HARGREAVES 1991; WIRZ & MARTINS 1993). The relationship of these fauna to the mid-Atlantic ridge fauna is suggested by the presence of young forms of *Nematocarcinus gracilipes* in such catches.

A final feature characterising the mixing of these shrimp faunas within the study area is the change in species diversity as measured by Glissons coefficient (Fig. 2). In applying this coefficient the data from shallow-water hauls are excluded because of the low number of species in catches which would result in a significant over estimation of the coefficient. This varied from 0.4-0.6 to 3.25 and showed an increase from north to south for the taxa distributed from 800m downwards.

However, diel migration may affect slightly the pattern shown in fig. 2 above 100 m.

Two groups are represented in the mesopelagic element (100-400 m depth). A northern group with a coefficient of less than 1.5 and a southern group with more than 1.5. The boundary of the northern mixing of these taxa occurs at approx. 42°N. The mixing of the extremities of these shrimp faunas is confirmed by noting their areas of distribution as shown in the right-hand column of table I. Two-thirds of the 'background' species are represented by the two sub-groups designated as 6a and 6b (AIWP and K respectively). For example, the study area includes the northernmost limit of the southern *Gennadas valens*.

These relationships also obtain for the group 2 typical species discussed previously. Throughout, the quantitative indices remain constant because the widely distributed species predominate along with the secondary faunal representatives.

It can be concluded therefore, that the shrimp fauna of the North Atlantic subtropical convergence is ecotonal, whereas that of the northern and central Atlantic faunas mix as background species which represents widely distributed pelagic fauna. The influence of the adjacent Lusitanian/Mediterranean faunas is of less importance and was noted only in the eastern region of the study area. Also the relationship of these ecotonal species to those of the mid-Atlantic ridge were apparent only in pelagic hauls obtained over sea mounts north of the Azores.
Fig. 2. Variation of species diversity coefficient of shrimp taxocenosis in relation to latitude and depth of distribution.

A - Variability of species diversity from the north southwards. 1 - 100-800 m; 2- 800 m and more.

B - Variability of species diversity by depth. 1- Northwards of 42°N; 2- Southwards 42°N.

**BATHYMETRIC DISTRIBUTION**

The majority of hauls were taken by night and thus Fig. 3 shows chiefly the upper limits of vertical distributions as a result of the diel vertical migration of some species. Because non-closing nets were used it has not been possible to provide exact data on the depth distribution of each species. Nevertheless, with these limitations in mind it is possible to recognise three groups of shrimps with respect to their bathymetric occurrences:

1. **Near-surface species**: these occurred by night within the upper 100m. Four species were represented with *Funchalia* as the predominant genus of which *F. villosa* was the most common occurring in nearly every haul. Below 100m the abundance of this species rapidly decreased.

2. **Mesopelagic species**: occurring mainly between 100-700 m. *Oplophorus spinosus* and *Systellaspis debilis* occurred only very occasionally in depth less than 100 m, thought it is known to occur at shallow depths at 42°N (HARGREAVES 1985). *Acanthephyra purpurea* also predominated in the mesopelagic region.

3. **Bathypelagic species**: occurred chiefly below 700 m depth, some downwards to 1000 m. Predominant species in this zone were *Acanthephyra pelagica* and *Parapasiphaea sulcatifrons*.

The boundaries of these adjacent bathymetric zones are not necessarily definitive or always related to physical vertical zonations of water layers (STEPANOV 1974). This situation was noted by BURUKOVSKY (1978, 1980, 1981) for bottom and near-bottom dwelling species. Natural boundaries can be affected by destruction of stratified water layers and this typically occurs in the boreal parts of the North Atlantic subtropical convergence. Species habitually cross natural boundaries during vertical migrations within the water column. Furthermore migratory patterns of species composition vary. For example, *Parapasiphaea sulcatifrons* migrates during different periods depending on life stages and sex (BURUKOVSKY 1993). By comparison, entire
populations of *Acanthephyra purpurea* migrate vertically (Burukovsky in press). Such differences in behaviour can result in variations of vertical distributions, even for the species that have a more or less precise vertical range; ecological factors may be also involved.

The depth related species diversity revealed for truly benthic shrimp populations (Burukovsky 1981) is also valid for pelagic populations. Diversity increases with depth to about 700-800 m and then decreases at greater depths e.g. >1500 m (Fig. 2B). Species diversity also decreases northwards of 42°N and increases southward.

Both background and predominating species within the study area are not associated with specific depths. The cosmopolitan species *Funchalia villosa* is predominant near-surface while other species are scarce there.

North Atlantic (i.e. boreal group B) e.g. *A. purpurea* and *P. hoplocera* or Central Atlantic (group D) e.g. *Gennadas valens* are background species which do not occur near-surface.

*Systellaspis debilis* and *Acanthephyra purpurea* are the dominant mesopelagic species, although the values for each differ in depth, biomass and abundance. Of the mesopelagic populations only half of the total number of species belong to group 6 (ignoring *P. sivado*).

Finally, 10 of the 18 bathypelagic species are represented by those belonging to the widely distributed zoogeographic group F, including the dominant background species *A. pelagica*. Five bathypelagic species belong to the boreal North Atlantic/Mediterranean group B. *Kinsasia spp.* and *Nematocarcinus gracilipes* may be considered as facultative pelagic species.

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REFERENCES


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