African Journal of Marine Science
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tams20

Epipelagic siphonophores off the east coast of South Africa

D Thibault-Botha & MJ Gibbons
Published online: 08 Jan 2010.

African Journal of Marine Science 2005, 27(1): 129–139
Printed in South Africa — All rights reserved

Copyright © NISC Pty Ltd
AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814–232X

Epipelagic siphonophores off the east coast of South Africa

D Thibault-Botha[1] and MJ Gibbons[2]*

[1] *Formerly Department of Zoology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa; now Laboratoire d' Oceanographie et de Biogeochenie, UMR 6535 — Centre d' Oceanologie de Marseille, Campus de Luminy — Case 901, 13288 Marseille Cedex 09, France*
[2] *University of the Western Cape, Private Bag X17, Bellville 7535, South Africa*
* *Corresponding author, e-mail: mgibbons@uwc.ac.za*

This work represents the first systematic analysis of the common Siphonophora from the Agulhas Current (South-West Indian Ocean). A total of 56 species of siphonophores was collected from a series of three largely epipelagic cruises between Algoa Bay and the Tugela River along the east coast of South Africa. Although no readily identifiable Cystonectae were observed, four families and nine species of Physonectae were collected. Calycophorae were the most common and abundant siphonophores, and five families and 47 species were recorded. Details of locations where each species was collected are given, but descriptions and illustrations are provided only for taxa that represent new records for the region.

Keywords: Agulhas Current, distribution, Siphonophora, South Africa, South-West Indian Ocean, taxonomy

Introduction

Siphonophores are often conspicuous components of oceanic plankton assemblages (Totton 1965, Pugh 1984). They are carnivorous and prey on a wide variety of zooplankton (Alvariño 1981, Purcell 1983, Mackie *et al.* 1987, Arai 1988). Owing to their rapid feeding rates (see Mackie *et al.* 1987 and references therein), siphonophores are thought to have a considerable impact on other zooplankton populations when they occur at high densities (Pugh 1999). Siphonophores in turn fall prey to a number of predators, including ctenophores and medusae, fish and turtles (Pugh 1989, Purcell 1991, Mills *et al.* 1996).

Understanding of siphonophore assemblages along the West and South-West coasts (including the Benguela Current) of southern Africa is fairly good (Pagès and Gili 1991a, 1991b, 1992a, 1992b, Pagès *et al.* 1991, Pagès 1992), largely because Pagès and Gili (1992b) have provided a basic taxonomic account of the species that are found there. However, understanding of siphonophore assemblages along the east coast of South Africa (including the Agulhas Current) is relatively poor because basic groundwork in terms of species identification is lacking.

The Agulhas Current is the major western boundary current of the South Indian Ocean (Lutjeharms 1996). It is composed of Indian Subtropical Surface Water, and Indian Tropical Surface Water is present on its landward side (Gordon *et al.* 1987). This current exhibits little seasonal variation in surface temperature (~3–4°C), with maximum temperature reaching about 28°C. It has a very stable trajectory between Durban and Port Elizabeth (Lutjeharms 1996), meandering <15km to either side (Gründlingh 1983). The core of the current follows the edge of the shelf,which is close to shore in the north, and moves gradually offshore to the south-west and along the edge of the Agulhas Bank. It retroflects off Cape Agulhas. Filaments, eddies and rings may form and be shed along the south coast of South Africa, which can make their way into the South Atlantic Ocean (Lutjeharms 1996). Other physical and chemical characteristics of this current do not display any seasonal variations (Pearce and Gründlingh 1982). Intrusions onto the shelf take place with no clear pattern. Shelf-edge upwelling on the inshore side of the Agulhas Current is a typical feature that occurs almost exclusively in the Port Alfred upwelling cell (Lutjeharms *et al.* 2000), where cooler Indian Ocean Central Water is moved onto the shelf and occasionally outcrops at the sea surface.

Although the Agulhas Current plays an influential role in global surface circulation and heat flux, apart from a few, mainly descriptive, studies on copepods (De Decker 1973, Carola 1994), chaetognaths (Stone 1969, Schleyer 1977) and fish (Beckley and van Ballegooyen 1992, Olivar and Beckley 1995), knowledge is sparse on its biota. The first account of siphonophore species from along the east coast of South Africa is presented here, including material from the Agulhas Current. The work is intended to complement that of Pagès and Gili (1992b), and it contributes a baseline that should allow increased knowledge and understanding of the general distribution of siphonophores in the region. In an effort to avoid duplication, and in the interests of brevity, illustrated descriptions are confined to new records only. This paper accompanies two others, which have used the current data to describe patterns in the distribution of

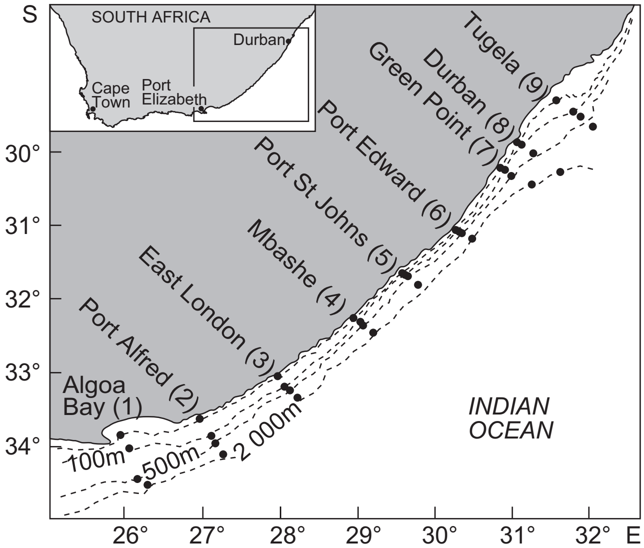

Figure 1: Map of the study area showing the position of sampling stations and underlying bathymetry

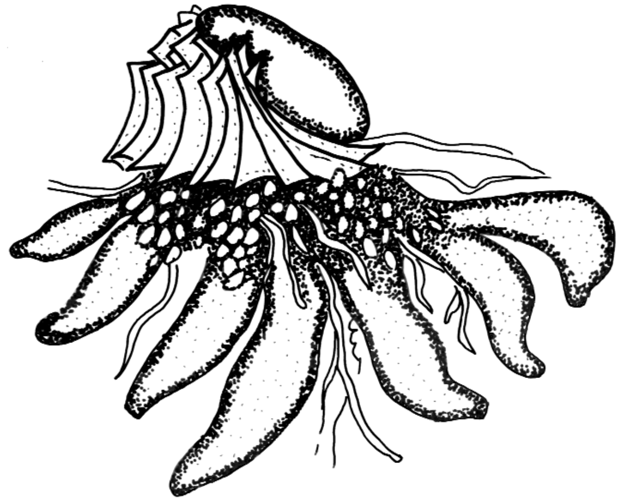

Figure 2: *Athorybia rosacea* entire animal less bracts, redrawn from Alvariño (1981)

siphonophore assemblages in the region (Gibbons and Thibault-Botha 2001, Thibault-Botha *et al.* 2004).

Material and Methods

The material examined was obtained from archived samples that were collected during three ichthyoplankton cruises conducted along the east coast of South Africa during autumn (May) and spring (October) 1990, and summer (February) 1991. Full details of the sampling programme and methods used can be found in Beckley and van Ballegooyen (1992). The surveys extended across the shelf from between Algoa Bay in the south (34°S, 26°E) to the Tugela River mouth in the north (29°S, 31°E, Figure 1). Samples were collected at four stations (located at the 50-m, 100-m, 500-m and 2 000-m isobaths) across nine transects, using Bongo nets (57-cm mouth diameter) fitted with 500-µm mesh. Nets were towed obliquely in the upper 80m (40m for the shallow stations) at 1m s^{-1}. The volume of water filtered by each net averaged 196.8m^3.

On retrieval, all samples were preserved in 5% saline formalin. A total of 105 samples was sorted and all siphonophores were counted and isolated. Only species that were not illustrated by Pagès and Gili (1992b) were considered for drawings. Well-preserved and undamaged individuals were placed under a dissecting microscope and drawn using a *camera lucida*. All drawings reflect preserved individuals directly and are neither stylised nor composites. Measurements were made using a calibrated eyepiece micrometer.

Descriptions are accompanied by information on the stations at which number of specimens recovered (indicated as nectophore — n, primary nectophore — 1n, posterior nectophore — pn, anterior nectophore — an bract — b), as well as the station location (Station number–depth, i.e. 1–500 refers to Transect 1 at the 500-m isobath); the station of maximum nectophore abundance is indicated in bold typeface. The distributions of those species that were described and illustrated by Pagès and Gili (1992b) are tabulated in Table 1. The locations corresponding to stations are shown in Figure 1. A series of selected references is provided to allow the reader to source fuller, illustrated descriptions. The regional and worldwide distributions of described species are summarised from the selected references (for each species) and from Alvariño (1971, 1981), Pagès and Gili (1992b) and Pugh (1999).

Systematic Account

Subclass Siphonophorae
Order Physonectae Haeckel 1888
Family Athorybiidae Huxley 1859
***Athorybia rosacea* (Forskål 1775)**
(Figure 2)

Stations
February (10 pneumatophores): 1–2 000, 4–100, 4–500, 5–50, 6–50, 6–500, 6–2 000, 7–100, **9–50**.

Selected references
Totton 1965: 87–89, Fig. 48, Pl. XVII, Figs 1–16; Daniel 1974: 64–68, Fig. 5a–h; Alvariño 1981: 398–399, Fig. 174–11; Pugh 1999: 483, Fig. 3.17, 3.30.

Description
Colony small, without nectophores. Pneumatophore compact, relatively large (reaching 3mm in height), with long axis orientated ventrally and apex almost completely recovered by nectostyle in a hood-shape manner; pigmentation strong at apex, slightly radiating, dark red/brown in colour; surrounded by cormidia. Material without bracts or palpons.

Remarks
This species is one of three within the Family Athorybiidae, all of which are characterised by having a reduced nectostyle,

Table 1: Distribution records of those siphonophores collected, but not described here, previously recorded by Pagès and Gili (1992b) from the west coast of southern Africa

Species	Transect and depth (m)																																			
	Algoa Bay				Port Alfred				East London				Mbashe River				Port St Johns				Port Edward				Green Point				Durban				Tugela River			
	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000
Agalma elegans			x	x		x		x	x			x	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x		x	x	x
Agalma okeni			x	x	x		x			x	x	x	x	x		x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Halistemma rubrum										x	x	x		x				x			x	x			x		x		x					x		x
Nanomia bijuga			x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Physophora hydrostatica											x			x	x	x	x	x			x				x	x	x		x						x	x
Forskalia edwardsi																	x																			
Forskalia contorta							x		x			x	x	x	x				x	x			x	x	x	x		x	x			x	x	x		
Amphicaryon acaule					x	x	x			x	x			x		x		x					x				x							x	x	
Amphicaryon ernesti				x						x		x			x	x					x	x	x	x						x	x	x		x	x	
Praya reticulata			x	x		x									x		x		x						x		x			x			x			x
Rosacea cymbiformis			x												x							x				x										
Rosacea plicata			x	x	x	x				x		x			x	x				x		x	x		x	x	x	x	x	x	x			x	x	x
Hippopodius hippopus			x			x	x			x	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x				x	x
Vogtia glabra					x	x		x		x				x	x	x																		x		
Sulculeolaria biloba			x			x				x	x		x		x	x	x	x	x		x	x	x		x	x	x		x			x	x		x	x
Sulculeolaria chuni			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Sulculeolaria monoica			x	x	x		x			x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x			x	x	x	x		x	x	x
Sulculeolaria quadrivalvis				x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Sulculeolaria turgida		x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Diphyes bojani	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Diphyes chamissonis			x	x	x	x	x	x	x		x		x		x	x	x	x			x	x	x	x	x	x		x	x	x	x		x	x	x	x
Diphyes dispar		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lensia campanella			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lensia conoidea		x				x				x															x								x			x
Lensia fowleri				x						x								x			x	x	x	x					x	x		x		x		
Lensia hardy														x		x	x	x								x		x				x				x
Lensia hotspur			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lensia meteori		x	x		x	x				x	x							x		x		x	x	x	x				x	x	x	x		x		x
Lensia multicristata		x	x			x	x			x		x	x	x		x	x	x			x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Lensia subtilis			x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lensia subtiloides	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Muggiaea atlantica	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Muggiaea kochi		x																		x											x	x				x
Dimophyes arctica															x																					
Chelophyes appendiculata			x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Chelophyes contorta	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Table 1 cont.

	Transect and depth (m)																																			
	Algoa Bay				Port Alfred				East London				Mbashe River				Port St Johns				Port Edward				Green Point				Durban				Tugela River			
	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000	50	100	500	2 000
Eudoxoides mitra	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Eudoxoides spiralis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Sphaeronectes gracilis			x					x						x	x	x	x	x		x				x	x	x			x	x		x		x	x	x
Ceratocymba dentata																x																				
Ceratocymba leuckarti																			x				x	x			x									
Abylopsis eschscholtzi	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Abylopsis tetragona	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bassia bassensis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Enneagonum hyalinum		x	x	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x

a relatively large pneumatophore and few (if any) nectophores. Despite the lack of bracts and palpons in the present material, *A. rosacea* can be readily separated from the other species in the Athorybiidae by its compact shape and its oblique and 'half-covered' pneumatophore.

Distribution
East coast of South Africa: only reported in summer. Worldwide: rare, mainly in tropical and subtropical oceanic waters of the three main oceans. Epi- and mesopelagic.

Family Forskaliidae Haeckel 1888
***Forskalia tholoides* Haeckel 1888**
(Figure 3)

Stations
May (59 1n): 2–50, 5–500, 6–2 000, **7–50**, 8–50, 8–100, 8–500, 9–50, 9–500, 9–2 000. February (25 n): 5–50.

Selected references
Haeckel 1888: 244–247, Pl. VIII; Totton 1965: 108.

Description
Nectophore flimsy, tapering and essentially triangular in overall shape; up to 4mm long. Dorso-ventrally flattened, and without enlarged wings. Large nectophores have a smooth appearance, but smaller specimens may be regularly incised immediately distal to the nectosac. Pigmentation absent. Nectosac up to one-half nectophore length, irregularly rounded (1.9mm x 1.5mm) and not laterally expanded; ostium small (0.7mm). Pedicular canal extending from the nectosac along the length of the nectophore; lateral radial canals run along the border of the nectosac and join with the ring canal basally and with the pedicular canal distally. Neither pneumatophore nor bracts recovered.

Remarks
Although the condition of the present material was not good, the nectophore conforms in all respects to previous descriptions. The nectophores of *Forskalia* are generally characterised by their simple appearance. They tend to be dorso-ventrally flattened, and to be flimsy in structure. They are mostly asymmetrical. Of the four commonly recognised species, the nectophore of *F. tholoides* is possibly the easiest to distinguish, because it is relatively long, smooth and tapering, it lacks any pigmentation and is relatively symmetrical. Although the nectophore of *F. cuneata* Chun 1888 may also taper, it is characterised by irregular incisions, and by the presence of strongly pigmented, red bands in the sub-umbrella. The nectophores of *F. contorta* Milne Edwards 1841 and *F. edwardsi* Kölliker 1853 are less tapered, and squarer in overall appearance, than those of either *F. tholoides* or *F. cuneata.* They also bear one (*F. edwardsi*) or more (*F. contorta*) deep incisions distally, and are consequently asymmetrical. The nectophore of *F. edwardsi* supports a 'lemon-yellow' pigment spot at the juncture of the upper radial and circular canals, whereas *F. contorta* has a 'fiery-red' rete along the pedicular canal.

Distribution
East coast of South Africa: most frequently seen during

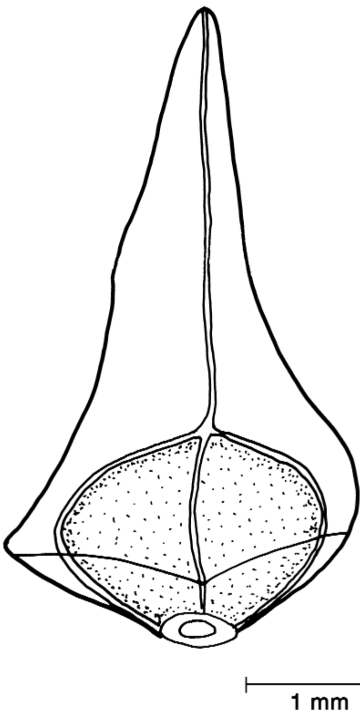

Figure 3: *Forskalia tholoides* nectophore

autumn, from the core of the Agulhas Current. Worldwide: temperate regions in all three oceans. Epipelagic.

Order Calycophorae Leuckart 1854
Family Prayinae Kölliker 1853
Subfamily Prayinae Chun 1897
***Praya dubia* (Quoy and Gaimard (1833) 1834)**
(Figure 4)

Stations
May (230 b): 2–50, 2–500, 3–500, 4–2 000, 5–50, 5–100, 5– 2 000, 6–500, **7–50**, 7–100, 7–500, 9–100, 9–500, 9–2 000. February (55 b): 2–500, 4–100, 7–100, **9–100**, 9–500.

Selected references
Totton 1965: 122–123, Fig. 70, Pl. XXIII; Daniel 1974: 87–88, Fig. 7a, b; Kirkpatrick and Pugh 1984: 58, Fig. 19; Pugh 1992: 898, Fig. 2; Pugh 1999: 485, Figs 3.36, 3.47.

Description
Bract of eudoxid large, 'kidney-shaped', maybe flattened laterally following preservation (should appear concave), with smooth dorsal surface, up to 10mm long; divided into two lobes, ventral lobe larger than hydroecial lobe. Bracteal cavity located ventrally. Bracteal canal with four main branches — ventral, dorsal, and right and left hydroecial canals. Dorsal canal projecting to apex of bract, relatively short, may bear small, short branches sub-terminally; ventral canal unbranched, extending to end of ventral lobe; left hydroecial canal less than half the length of the hydroecial lobe; right hydroecial canal extending over length of lobe, may branch sub-terminally, not re-curved. Polygastric phase not recovered.

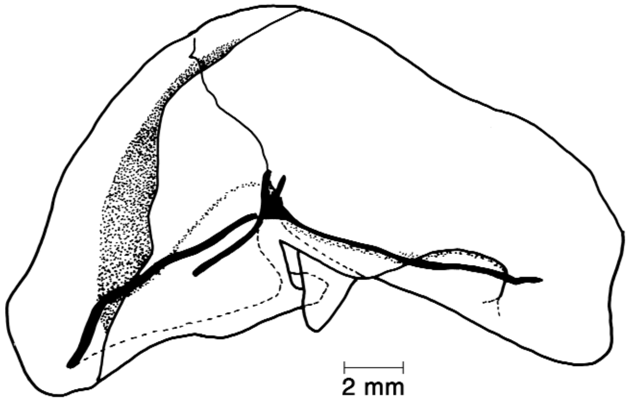

Figure 4: *Praya dubia* bract, redrawn from Pugh (1992)

Remarks
Net-caught and formalin-preserved Prayidae are among the most difficult siphonophores to identify, owing to their delicate and inherently 'blobby' nature. The bracts of *P. dubia* and *P. reticulata* (Bigelow 1911) are characteristically 'kidney-shaped'; and the two species can be separated by the relative lengths and shapes of the bracteal canals. In *P. dubia*, the dorsal canal is relatively short, the left hydroecial canal is slightly shorter than the right, and the latter is not strongly recurved ventrad, distally. In *P. reticulata*, the dorsal canal can be very long and extends into the hydroecial lobe, dorsally, whereas the left and right hydroecial canals are of approximately similar size, and the latter maybe strongly recurved ventrad, distally. It should be noted that there is some confusion in the literature about which is the left hydroecial canal and which is the right (compare Totton 1965, Pugh 1999): attention should be focussed on the one relative to the other. Pugh (1992) suggested that the diagnostic difference between bracts of these two species of *Praya* is the presence of a vertical fold located on the surface of the left hydroecial flap of *P. reticulata*.

Distribution
East coast of South Africa: common over the whole region, principally in late summer. Worldwide: widely distributed, mainly located in tropical and sub-tropical regions; not reported from the Mediterranean Sea. Mesopelagic.

Family Hippopodiidae Kölliker 1853
***Vogtia pentacantha* Kölliker 1853**
(Figure 5)

Stations
October (5 n): 4–500.

Selected references
Totton 1965: 142, Fig. 81; Daniel 1974: 99, Fig. 8c–d; Alvariño 1981: 406, Fig. 174-28; Kirkpatrick and Pugh 1984: 74, Fig. 27; Daniel 1985: 33, Fig. 40; Pugh 1999: 487, Fig. 3.57.

Description
Nectophore approximately pentagonal in shape; wider than

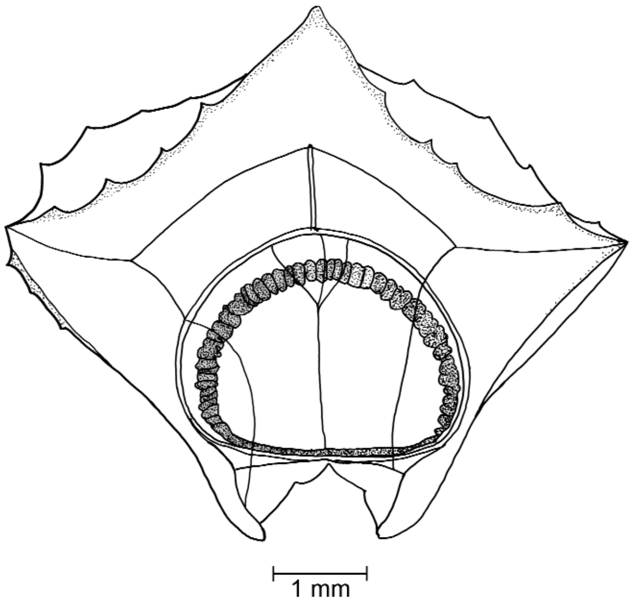

Figure 5: *Vogtia pentacantha* nectophore

long and measuring 10mm x 16mm. Small teeth (gelatinous protuberances) occasionally present on some ridges. Although facets between ridges are generally smooth, some teeth can be found at the base of the central ridge. Ostial mouth wide, and nectosac fairly small; four radial canals clearly visible, but rete mirabile on the ventral surface not obvious. Balance of polygastric stage not recovered.

Remarks
V. pentacantha can be readily differentiated from other species of the genus by the pentagonal shape of its nectophore and by the smooth, generally tubercle-free facets. Although *V. spinosa* Kefferstein and Ehlers 1861 also has a pentagonal nectophore, the facets bear numerous, obviously pointed teeth. *V. serrata* (Moser 1925) has a triangular nectophore devoid of obvious teeth, whereas *V. glabra* Bigelow 1918 has a more rounded, horseshoe-shaped nectophore with two fairly large globular prominences dorso-laterally. Younger nectophores of the latter species may be more angular in shape, but the appearance of the prominences is consistent with those of mature nectophores.

Distribution
East coast of South Africa: rare, present only at one station in autumn. Worldwide: cosmopolitan in South-West Africa, uncommon in Atlantic Ocean and Mediterranean Sea. Mesopelagic.

Family Diphyidae Quoy and Gaimard 1827
Subfamily Diphyinae
***Lensia cossack* Totton 1941**
(Figure 6)

Stations
May (44 an): 1–500, 2–50, 2–100, 2–500, 3–50, 3–500, 3–2 000, 4–100, 4–500, 4–2 000, **5–100**, 5–2 000, 6–50, **6–100**, 6–500, 7–50, 7–100, 7–500, 8–50, 8–100, 8–500, 9–100, 9–500, **9–2 000**. October (19 an): 3–100, 4–100, 4–500, **4–2 000**, 5–100, 6–50, 9–500. February (17 an): 2–500, 4–100, 6–500, 7–50, 7–500, 7–2 000, 8–100, **8–500**, 9–500, 9–1 000.

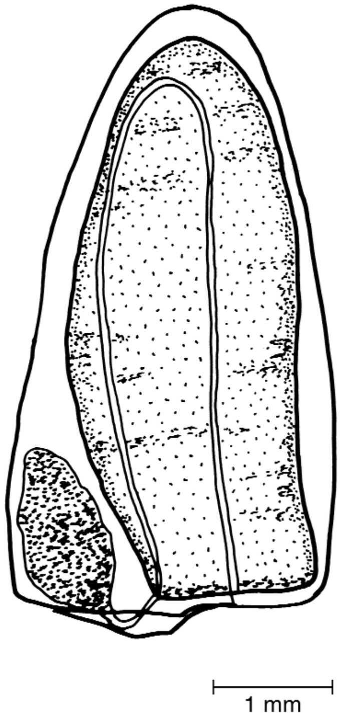

Figure 6: *Lensia cossack* anterior nectophore

Selected references
Daniel and Daniel 1963: 202, Fig. V,1; Totton 1965: 166, Fig. 101a; Daniel 1974: 143, Fig. 10t; Alvariño 1981: 410, Fig. 174–40; Daniel 1985: 239, Fig. 63; Margulis and Alekseev 1985: Fig. 3b; Pugh 1999: 490, Fig. 3.90.

Description
Anterior nectophore of polygastric phase essentially conical, rounded at apex, not twisted; up to 5.2mm in height and 2.8mm in width at ostium. Mesoglea firm. Without obvious ridges, but with four longitudinal folds. The mouthplate is reduced. Hydroecium minute, below level of ostium and open ventrally. The somatocyst is large and ovoid, ventrally slanted and extends to one-third of nectophore length; it is borne on a short stalk. Basal lamella short, oblique, without obvious lateral wings; basal facet horseshoe-shaped. Posterior nectophore not collected. Eudoxid has not been described.

Remarks
Whereas the specimens that have been previously recovered from both the Atlantic (Totton 1965) and Indian oceans (Daniel 1985) are larger than those reported here (up to 11.6mm long), this material agrees in all respects with earlier descriptions. The anterior nectophore of this species is

characterised by having a rounded, untwisted apex and by the presence of four longitudinal folds, a large, stalked and ovoid somatocyst, and a nectosac with stout musculature. In their review of the genus *Lensia*, Margulis and Alekseev (1985) considered *L. cossack* to be a subspecies of *L. campanella* (Moser 1925). Their arguments for relegation of *L. cossack* were not directly articulated, but we assume they were based on a number of shared traits (minute hydroecium, and presence of an ovoid basal facet that forms a more or less obtuse angle with ostial surface). These arguments are not strong enough to warrant relegation of the species, on their own, and it is clear that further work needs to be undertaken in order to uphold them. From an identification point of view, *L. cossack* can be readily separated from *L. campanella* using the aforementioned features in combination. Clearly, too, the views of Margulis and Alekseev (1985) are not widely held, because *L. cossack* still persists in the literature (Pugh 1999).

Distribution
East coast of South Africa: common year around. Worldwide: cosmopolitan in temperate and warm waters of the three main oceans. Epi- and mesopelagic.

Lensia gnanamuthui **Daniel and Daniel 1963**
(Figure 7)

Stations
May (1 an): 5–50. February (32 na): **1–500**, 1–2 000, 2–2 000, 3–500, 4–50, 4–2 000, 5–500, 5–2 000, 6–2 000, 7–50, 7–500, 7–2 000, 8–50, 8–500, 8–2 000, 9–100, 9–1 000.

Selected references
Daniel and Daniel 1963: 203, Fig. V,4–5; Daniel 1985: 222, Fig. 56; Margulis and Alekseev 1985: Fig. 2h.

Description
Anterior nectophore of polygastric phase conical in shape, up to 6mm in height and 2.8mm in width at ostium; with five complete, straight ridges that converge at the apex. Mesoglea delicate. Hydroecium located at and below the level of ostium, open ventrally. Somatocyst situated close to nectosac, arising at, or slightly below, level of ostium, typically minute (0.3mm) and irregular/globular in shape, borne on a short stalk; not exceeding 5% of nectophore length. Basal lamella with two short, often overlapping, wings. Posterior nectophore not collected. Eudoxid has not been described.

Remarks
Although the material described here is slightly larger than that noted previously (Daniel 1974, Daniel 1985), our specimens agree in every detail with earlier descriptions. *L. gnanamuthui* has been grouped with the other species of *Lensia* bearing five straight ridges on the anterior nectophore (Daniel 1974, Margulis and Alekseev 1985). Four of these species can be readily distinguished as having a somatocyst that lies at or below the level of the ostium (*L. subtiloides* (Lens and van Riemsdijk 1908), *L. hotspur* Totton 1941, *L. conoidea* (Kefferstein and Ehlers 1860) and *L. gnanamuthui*). The anterior nectophores of *L. subtiloides* and *L. conoidea* both have a firm consistency, and possess a somatocyst that extends at least one-third of the nectophore length (one-half in the case of *L. conoidea*). *L. gnanamuthui* can be separated from these species, and from *L. hotspur*, by the minute nature of the somatocyst, which is not ventrally slanted (as in *L. hotspur*); the hydroecium is markedly shallow and the mesoglea is relatively thin.

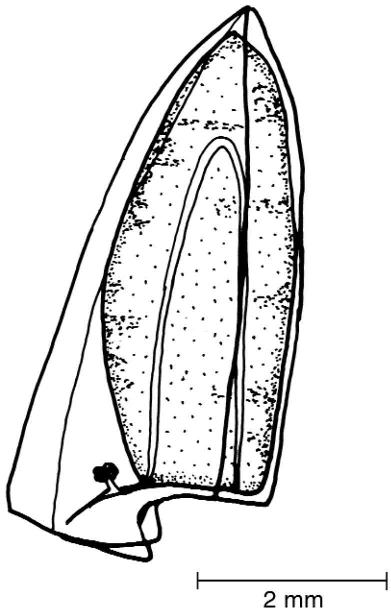

Figure 7: *Lensia gnanamuthui* anterior nectophore

Distribution
East coast of South Africa: uncommon, limited to warm seasons. Worldwide: Indian Ocean. Epipelagic.

Lensia hunter **Totton 1941**
(Figure 8)

Stations
May (1 an): 4–500. October (1 an): 2–500

Selected references
Totton 1965: 164, Fig. 101b–c; Daniel 1974: 147, Fig. 11a; Margulis and Alekseev 1985: Fig 1; Pugh 1999: 490, Fig. 3.95.

Description
Anterior nectophore of polygastric phase essentially conical, nectosac with a dorsal constriction slightly above the ostium; up to 8mm in height and 4mm in width at level of ostium. With seven ridges; the dorsal ridge and the two ventral ridges are complete; the latero-dorsal ridges do not reach the level of the ostium, whereas the latero-ventral ridges extend to form the margin of the mouthplate but fail to converge at the apex. The mesoglea is firm. Hydroecium reduced, located below level of ostium, and sloping

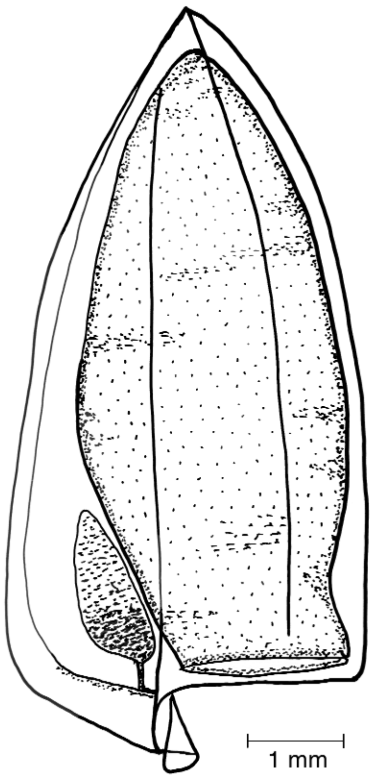

Figure 8: *Lensia hunter* anterior nectophore

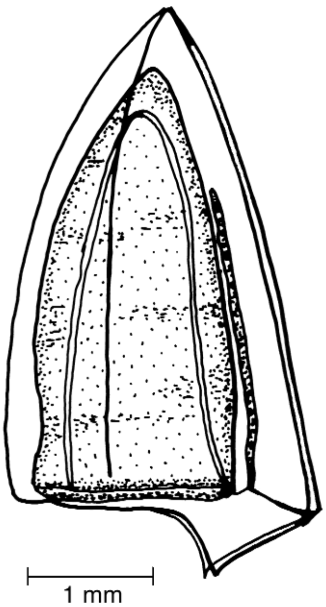

Figure 9: *Lensia panikkari* anterior nectophore

gradually to ventral facet. Somatocyst globular, asymmetrical (~2mm); borne on a short stalk (0.3mm). Basal lamella relatively large, divided into two overlapping lappets or wings that extend downwards and do not project over ostium. Neither posterior nectophore nor eudoxid has been described.

Remarks
This material agrees fully with previous descriptions. It is one of three species of *Lensia* that have anterior nectophores (of the polygastric stage) bearing seven longitudinal ridges. *L. multicristata* (Moser 1925) can be distinguished from *L. hunter* and *L. havock* Totton 1941, by its long, filiform somatocyst, and by the fact that the latero-ventral ridges neither converge at the apex nor meet the ostial margin. In the case of both *L. hunter* and *L. havock,* the latero-ventral ridges run down to form the dorso-lateral side of the mouthplate, though these ridges are complete in the latter species. *L. havock* can additionally be distinguished from *L. hunter* by its large hydroecium; the somatocyst is situated above the level of the ostium.

Distribution
East coast of South Africa: uncommon. Worldwide: tropical and sub-tropical regions of the Atlantic and Indian oceans; rare. Epipelagic.

***Lensia panikkari* Daniel 1970**
(Figure 9)

Stations
February (14 an): **4–50**, 5–50, 9–50, 9–100.

Selected references
Daniel 1974: 139, Fig. 12a; Daniel 1985: 233, Fig. 60; Margulis and Alekseev 1985: Fig. 1n.

Description
Anterior nectophore of polygastric phase conical, up to 4.5mm in height and 2.5mm in width at level of ostium; with five ridges that converge at apex, lateral ridges not reaching the level of the ostium. Mesoglea delicate. Hydroecium relatively deep, at level of ostium; open ventrally. Somatocyst narrow and filiform, without a stalk, reaching over half the length of the nectophore and up to 75% of the length of the nectosac; lies closely against the nectosac. Basal lamella large, mouthplate divided into two slightly overlapping wings. Posterior nectophore and eudoxid not known with certitude.

Remarks
Whereas other specimens collected from the Indian Ocean (Daniel 1974, Daniel 1985) have been generally larger (~9.7 x 4.5mm) than those collected here, the present material agrees in all respects with previous descriptions. This species has been grouped (Daniel 1974, Margulis and Alekseev 1985) with five other species of *Lensia* having five incomplete ridges on their anterior nectophores (*L. lebedevi* Alekseev 1984, *L. nagabhu-shanami* Daniel 1970, *L. patriti* Alekseev 1984, *L. tottoni* Daniel and Daniel 1963 and *L. leloupi* Totton 1954). It is clearly not easy to distinguish between these six species, although PR Pugh (South- hampton Oceanographic Centre, UK, pers. comm.) considers only *L. leloupi* to be valid. This species can be separated from *L. panikkari* by its relatively short somatocyst (~0.3 nectosac length).

Distribution
East coast of South Africa: uncommon, summer species. Worldwide: North Atlantic (Pugh 1984) and Indian oceans. Epipelagic.

Family Abylidae L. Agassiz 1862
Sub-family Abylinae L. Agassiz 1862
***Abyla bicarinata* Moser 1925**
(Figure 10)

Stations
May (5 an): 6–100, 6–2 000, 5–2 000, 7–2 000. October (9 na): 2–500, 3–100, 4–500, 5–50, 6–500, 7–500, 9–50, 9–500, 9–1 000. February (6 an): 1–500, 2–2 000, 7–500, 9–500.

Selected references
Sears 1953: 45, Figs 12a, 13a, 14a, 15a; Totton 1965: 211, Pl. XXXVIII, Figs 4–7; Daniel 1974: 192, Fig. 16j–l; Daniel 1985: 318, Fig. 84; Alvariño 1981: 426, Fig. 174–73; Pugh 1999: 494, Fig. 3.123.

Description
Anterior nectophore of polygastric phase wider (5.95mm) than it is high (5.6mm). Lateral ridges strongly expanded; horizontal and apico-lateral ridges rounded and neither crested nor as sharply defined as in other species of *Abyla*. Horizontal ridges located almost at the level of the apex of the hydroecium; ventral facet widest near apex. Apico-ventral facet not subdivided by a transverse ridge, and without a furrow ventrally. Somatocyst rather large. Posterior nectophore not collected in the region; eudoxid not described.

Remarks
The material examined agrees with the detailed description provided by Sears (1953). It is one of the two species of *Abyla*, which are nearly circular in dorsal or ventral view, owing to their greatly expanded lateral ridges. The other, *A. brownia* Sears 1953, can be differentiated by the crested nature of the lateral and horizontal ridges, and on the pronounced juncture between them. They can also be distinguished by the relative width of their ventral facet (with respect to the distance between the insertion of the horizontal ridges and the basal tip of the ventral facet; Sears 1953). It should be noted that *A. brownia* has been described from a single specimen, and its validity has been questioned (Pugh 1999).

Distribution
East coast of South Africa: rare. Worldwide: relatively rare, often restricted to warmer waters in every ocean. Epipelagic.

***Abyla haeckeli* Lens and van Riemsdijk 1908**
(Figure 11)

Stations
May (10 an): 1–2 000, 2–100, 4–100, 6–2 000, 6–50, 7–500, 8–500, 9–50, 9–2 000. October (5 an): 4–100, 7–2 000, 8–50. February (6 an): 3–2 000, 7–500, 7–2 000, 8–100, 9–100.

Selected references
Sears 1953: 39, Figs 11b, 12d, 13d, 14d; Totton 1965: 210, Fig. 143, Pl. XXXVI, Figs 6, 8; Daniel 1974: 191, Fig. 16g–i; Alvariño 1981: 427, Fig. 174–76; Daniel 1985: 315, Fig. 84; Pagès and Gili 1992b: 104, Fig. 48; Pugh 1999: 494, Fig. 3.124.

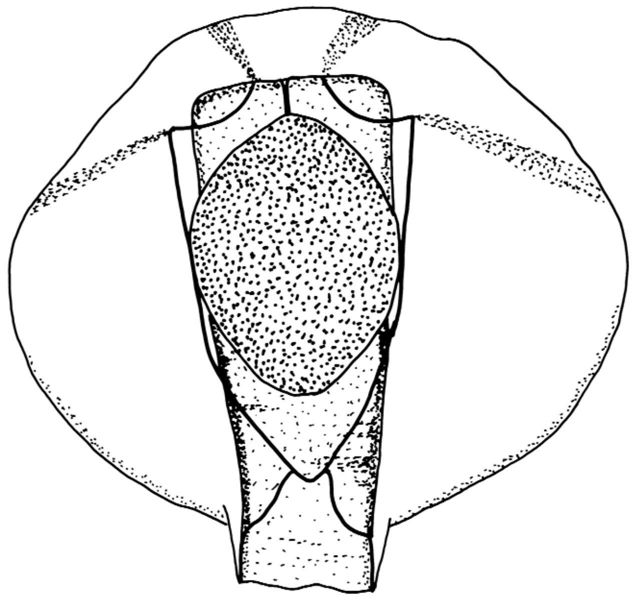

Figure 10: *Abyla bicarinata* anterior nectophore

Description
Anterior nectophore of polygastric phase as wide as long (8.2mm x 8mm). Lateral ridges not expanded, and without obvious serrations. Horizontal and apico-lateral ridges sharply defined. Apicoventral facet separated from the ventral facet by a transverse ridge; quadrangular in shape. Ventral facet describes a regular polygon, and horizontal ridges insert at or below the level of the mid-section of the somatocyst. Facets flat between the ridges. Neither posterior nectophore nor eudoxid collected in the region.

Remarks
This material examined agrees with previous descriptions. It is one of two species of *Abyla* that bears a transverse ridge, separating the apico-ventral facet from the ventral facet. The other species, *A. ingeborgae* Sears 1953, can be differentiated from *A. haeckeli* by the shape of the ventral facet — that of *A. haeckeli* describes a regular pentagon, whereas the basal sides in *A. ingeborgae* are between two and three times as long as the apical ones (Sears 1953). Although the type description of *A. ingeborgae* was based on some 23 specimens from the South Atlantic, and it has subsequently been identified from other collections in this region (Pagès and Gili 1992b), it has yet to have widespread recognition (Pugh 1999).

Distribution
East coast of South Africa: rare, offshore. Worldwide: tropical and temperate regions of Atlantic, Pacific and Indian oceans. Epipelagic.

***Abyla trigona* Quoy and Gaimard 1827**
(Figure 12)

Stations
May (20 an): 1–2 000, 2–50, 2–100, 3–2 000, 4–500, 5–100, 5–2 000, 6–50, 7–50, 7–100, 7–500, 7–2 000, 8–50,

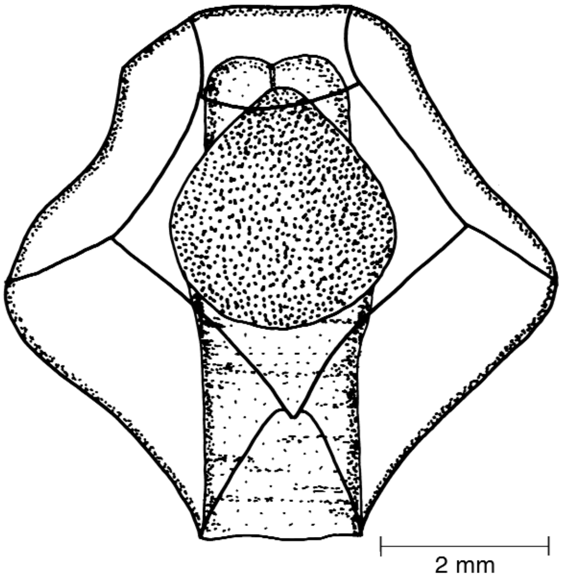

Figure 11: *Abyla haeckeli* anterior nectophore

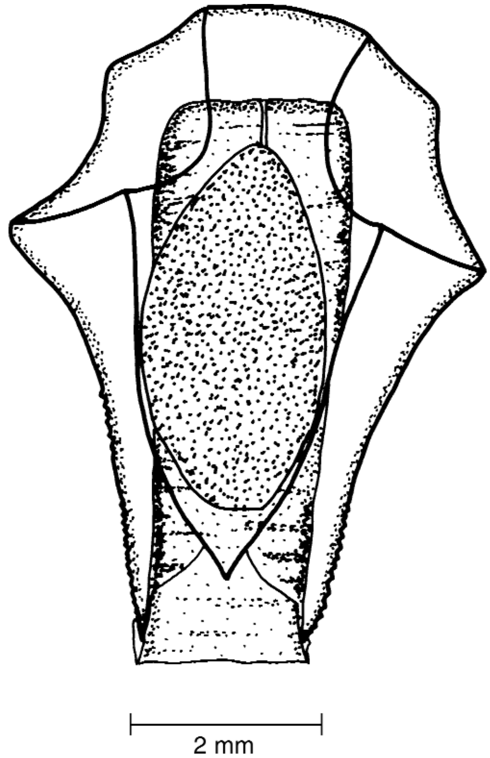

Figure 12: *Abyla trigona* anterior nectophore

9–500. February (7 an): 3–500, 4–100, 4–2 000, 5–50, 8–50, 8–100, 9–500.

Selected references
Sears 1953: 35, Figs 8b, 9b, 10b, 11a; Totton 1965: 208, Fig. 142a, Pl. XXXVI, Figs 9–10; Daniel 1974: 187, Fig. 16a–b; Alvariño 1981: 429, Fig. 174–80; Daniel 1985: 309, Fig. 82; Pugh 1999: 494, Fig. 3.125.

Description
Anterior nectophore of polygastric phase longer than wide (8mm x 5mm). Lateral ridges not expanded, strongly serrated basally. Horizontal and apico-lateral ridges sharply defined, irregularly serrated. In ventral view, horizontal ridges located almost at the level of the apex of the hydroecium, ventral facet widest near apex, basal ridges may be serrated. Apico-ventral facet not subdivided by a transverse ridge. In lateral view, lateral ridges of dorsal facet generally concave, apicodorsal facet sharply bent upward to transverse apical ridge from point of insertion of the lateral ridges; apical transverse ridge located above centre of hydroecium. Facets often depressed below the ridges surrounding them. Nematosac elongated (5.7mm long). Somatocyst egg-shaped (3.8mm x 2.3mm). Neither posterior nectophore nor eudoxid recovered from the region.

Remarks
The material examined agrees well with previous descriptions. *A. trigona* is the type species for the genus, and is one of five species of *Abyla* that have an anterior nectophore of the polygastric stage that neither possesses a transverse ridge, separating the apico-ventral facet from the ventral facet, nor has greatly enlarged lateral ridges, and so does not describe a circle in ventral or lateral view. Although this species can be separated from the other taxa using the key provided by Sears (1953), it should be noted that almost all of the distinguishing characters are subject to preservation and are fairly subjective. It is no surprise, perhaps, that some authors consider all five species to be synonyms of *A. trigona* (e.g. Pugh 1999), especially given an overall similarity in the structure and morphology of the posterior nectophore (Sears 1953).

Distribution
East coast of South Africa: rare. Worldwide: tropical and temperate waters from Equator to 35°S in the Atlantic Ocean, transported by the large oceanic circulation of the central South Atlantic Ocean, Indo-Pacific waters. Epi- and mesopelagic.

Acknowledgements — We thank the captain and crew the FRS *Sardinops* for their help in collecting the samples, as well as the Marine and Coastal Management branch of the Department of Environmental Affairs and Tourism for permission to use the samples. Phil Pugh (Southampton Oceanographic Centre, Southampton) and Francesc Pagès (Instituto de Ciencias del Mar, Barcelona) are thanked for their very helpful comments on various drafts of the manuscript. This work has been supported by the Royal Society (London) and by an National Research Foundation post-doctoral fellowship accorded to DT-B.

References

ALVARIÑO, A. 1971 — Siphonophores of the Pacific Ocean with a review of the world distribution. *Bull. Scripps Inst. Oceanogr.* **16**: 1–432.

ALVARIÑO, A. 1981 — Siphonophorae. In *Atlas del Zooplancton del Atlantico Sudoccidental*. Boltovskoy, D. (Ed.). Mar del Plata, Argentina; Publicación especial del INIDEP: 383–441.

ARAI, M. N. 1988 — Interactions of fish and pelagic coelenterates. *Can. J. Zool.* **66**: 1913–1927.

BECKLEY, L. E. and R. C. VAN BALLEGOOYEN 1992 — Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 83–93.

CAROLA, M. 1994 — Checklist of the marine planktonic Copepoda of southern Africa and their worldwide geographic distribution. *S. Afr. J. mar. Sci*. **14**: 225–253.

DANIEL, R. 1974 — Siphonophora from the Indian Ocean. *Mem. zool. Surv. India* **15**(4): 242 pp.

DANIEL, R. 1985 — *The Fauna of India and the Adjacent Countries*. Calcutta; The Director, Zoological Survey of India: 440 pp.

DANIEL, R. and A. DANIEL 1963 — On the siphonophores of the Bay of Bengal. I. Madras Coast. *J. mar. biol. Ass. India* **5**: 185–220.

DE DECKER, A. [H. B.] 1973 — Agulhas Bank plankton. In *The Biology of the Indian Ocean*. Zeitzschel, B. (Ed.). Berlin; Springer: 189–219 (also as *Ecol. Stud. Analysis Synth.* **3**).

GIBBONS, M. J. and D. THIBAULT-BOTHA 2001 — The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. *J. mar. biol. Ass., UK* **82**: 801–810.

GORDON, A. L., LUTJEHARMS, J. R. E. and M. L. GRÜNDLINGH 1987 — Stratification and circulation at the Agulhas retroflection. *Deep-Sea Res*. **34**(4A): 565–599.

GRÜNDLINGH, M. L. 1983 — On the course of the Agulhas Current. *S. Afr. geogrl J.* **65**(1): 49–57.

HAECKEL, E. 1888 — Report on the Siphonophorae. *Rept Sci. Res. H.M.S. Challenger, Zool.* **28**: 1–380.

KIRKPATRICK, P. A. and P. R. PUGH 1984 — Siphonophores and Velellids. In *Synopses of the British Fauna (New series)*. Kermack, D. M. and R. S. K. Barnes (Eds). London; Brill, E. J. and W. Backhuys: 1–151.

LUTJEHARMS, J. R. E. 1996 — The exchange of water between the South Indian and South Atlantic oceans. In *The South Atlantic: Present and Past Circulation*. Wefer, G., Berger, W. H., Siedler, G. and D. J. Webb (Eds). Berlin Heidelberg; Springer-Verlag: 123–162.

LUTJEHARMS, J. R. E., COOPER, J. and M. [J.] ROBERTS 2000 — Dynamic upwelling at the inshore edge of the Agulhas Current. *Cont. Shelf Res.* **20**: 737–761.

MACKIE, G. O., PUGH, P. R. and J. E. PURCELL 1987 — Siphonophore biology. *Adv. mar. Biol*. **24**: 97–262.

MARGULIS, R. Y. and D. O. ALEKSEEV 1985 — On the genus *Lensia* Totton, 1932 (Siphonophora, Calycophorae). *Zool. J.* **64**: 5–15.

MILLS, C. E., PUGH, P. R., HARBISON, G. R. and S. H. D. HADDOCK 1996 — Medusae, siphonophores and ctenophores of the Alboran Sea, south western Mediterranean. *Scientia Mar., Barcelona* **60**: 145–163.

OLIVAR, M-P. and L. E. BECKLEY 1995 — Early development of *Diaphus* spp. (Pisces: Myctophidae) of the Agulhas Current. *S. Afr. J. mar. Sci.* **16**: 129–139.

PAGÈS, F. 1992 — Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci*. **12**: 41–52.

PAGÈS, F. and J-M. GILI 1991a — Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser*. **75**: 205–215.

PAGÈS, F. and J-M. GILI 1991b — Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours. In *Coelenterate Biology*: *Recent Research on Cnidaria and Ctenophora*. Williams, R. B., Cornelius, P. F. S., Hughes, R. G. and E. A. Robson (Eds). *Hydrobiologia* **216**/**217**: 355–362.

PAGÈS, F. and J-M. GILI 1992a — Influence of Agulhas waters on the population structure of planktonic cnidarians in the southern Benguela Region. *Scientia Mar., Barcelona* **56** (2–3): 109–123.

PAGÈS, F. and J-M. GILI 1992b — Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). *Scientia Mar., Barcelona* **56** (Suppl. 1): 65–112.

PAGÈS, F., VERHEYE, H. M., GILI, J-M. and J. FLOS 1991 — Short-term effects of coastal upwelling and wind reversals on epiplanktonic cnidarians in the southern Benguela ecosystem. *S. Afr. J. mar. Sci*. **10**: 203–211.

PEARCE, A. F. and M. L. GRÜNDLINGH 1982 — Is there a seasonal variation in the Agulhas Current? *J. mar. Res*. **40**(1): 177–184.

PUGH, P. R. 1984 — The diel migration and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Prog. Oceanogr.* **13**: 461–489.

PUGH, P. R. 1989 — Gelatinous zooplankton – the forgotten fauna. *Prog. Underwater Sci.* **14**: 67–78.

PUGH, P. R. 1992 — The status of the genus *Prayoides* (Siphonophora: Prayidae). *J. mar. biol. Ass. U.K.* **72**: 895–909.

PUGH, P. R. 1999 — Siphonophorae. In *South Atlantic Zooplankton*. Boltovskoy, D. (Ed.). Leiden, The Netherlands; Backhuys Publishers: 467–511.

PURCELL, J. E. 1983 — Digestion rates and assimilation efficiencies of siphonophores fed zooplankton prey. *Mar. Biol.* **73**: 257–261.

PURCELL, J. E. 1991 — Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. *Mar. Ecol. Prog. Ser*. **72**(3): 255–260.

SCHLEYER, M. H. 1977 — Chaetognaths as indicators of water masses in the Agulhas Current system. M.Sc. thesis, University of Natal, Durban: 27 pp. + 36 pp. of Tables and Figures.

SEARS, M. 1953 — Notes on siphonophores. 2. A revision of the Abylinae. *Bull. Mus. comp. Zool. Harv.* **109**: 1–119.

STONE, J. H. 1969 — The chaetognath community of the Agulhas Current; its structure and related properties. *Ecol. Monogr.* **39**: 433–463.

THIBAULT-BOTHA, D., LUTJEHARMS, J. R. E. and M. J. GIBBONS 2004 — Siphonophore assemblages along the East Coast of South Africa; Mesoscale distribution and temporal variations. *J. Plankt. Res.* **26**: 1115–1128.

TOTTON, A. K. 1965 — *A Synopsis of the Siphonophora*. London; Trustees of the British Museum (Natural History): 230 pp.

Manuscript received April 2003; accepted June 2003