

# Taxonomy and ecology of sandy beach *Eurydice* (Crustacea, Isopoda, Cirolanidae) from the West coast of South Africa

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**Abstract**: *Eurydice barnardi* sp. nov., and *Eurydice kensleyi* sp. nov., are described from intertidal sandy beaches on the West coast of South Africa. The former species appears adapted to a fossorial existence, probably feeding on nematodes, while the latter is a more active swimmer which feeds on polychaetes. *Eurydice longicornis*, a subtidal species long considered the only species of the genus in South Africa, is redescribed from the type material. The ecology and biology of the species are detailed, and a key provided to the South African species *Eurydice*.

**Résumé** : *Eurydice barnardi* sp. nov. et *Eurydice kensleyi* sp. nov. sont décrites des sables intertidaux de la côte Ouest de l'Afrique du Sud. La première espèce semble adaptée à une vie fouisseuse, se nourrissant probablement de nématodes, tandisque la seconde est une espèce plus activement nageuse qui se nourrit de polychètes. *Eurydice longicornis*, une espèce subtidale longtemps considérée comme la seule espèce du genre en Afrique du Sud, est redécrite à partir du matériel type. L'écologie et la biologie des espèces sont indiquées et une clé des espèces d'*Eurydice* d'Afrique du Sud est donnée.

Keywords : Isopoda, Cirolanidae, Eurydice, sandy beaches, zonation, South Africa.

# Introduction

South Africa has long been considered as having but a single representative species of *Eurydice* on its coasts, namely *Eurydice longicornis* (Studer, 1882). This species had been recorded from Lüderitz on the Atlantic coast to Port Elizabeth on the southeastern Indian Ocean coast (Kensley, 1978; De Ruyck et al., 1992). Collection of new material from sand beach habitats together with a re-examination of the type specimens of *Eurydice longicornis* show there to be at least three readily separable species from the southern African region, *E. longicornis* a subtidal species and the two previously undescribed intertidal species.

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# Family Cirolanidae Dana, 1852 Genus *Eurydice* Leach, 1815

Restricted synonymy: Bruce, 1986: 11.- Kensley & Schotte, 1989: 147.- Brusca, Wetzer & France, 1995: 40.

#### Remarks

Recent diagnoses to the genus have been given by Bruce (1986), Kensley & Schotte (1989) and Brusca *et al.* (1995). Species descriptions given here assume that generic characters are taken as given.

Brusca *et al.* (1995) has given the most recent listing of the world species. In addition to the new species described here the other species known from the Atlantic coasts of Africa are *Eurydice clymeneia* Monod, 1926 and *Eurydice dollfusi* Monod, 1930, both from Morocco and *Eurydice mauritanica* De Grave & Jones, 1991 from the coast of Mauritania. The northeastern Atlantic species *Eurydice*  *grimmaldii* Dollfus, 1903, a pelagic species, has been recorded from the Azores and *Eurydice spinigera* Hansen, 1890, from Morocco. The only record of the genus from the South Atlantic is of three species from the coasts of Brazil (Moreira, 1972).

*Abbreviations*: CP - circumplumose; CPS - circumplumose setae; PMS - plumose marginal setae; SAM - South African Museum, Cape Town, South Africa; ZMUC - Zoologisk Museum, University of Copenhagen, Denmark.

#### Key to the southern African species of Eurydice

1 - Pleotelson posteriorly narrow, with 2 spines, anterior dorsal surface without distinct depression; antennal flagellum of ♂ not extending beyond pereonite 4; pereopods 1 - 3 propodus with abundant long setae extending anteriorly beyond dactylus

*E. barnardi* sp. nov.
 Pleotelson not posteriorly narrow, with 4 spines, anterior dorsal surface with distinct depression; antennal flagellum of ♂ extending beyond pereonite 5; pereopods 1 - 3 propodal setae not extending anteriorly beyond dactylus 2

2 - Antennal flagellum of ♂ extending to pereonite 5; coxae posterolateral angles rounded; pereopod 7 slender; appendix masculina longer than endopod

*E. kensleyi* sp. nov. - Antennal flagellum of ♂ extending to pleonite 5; coxae posterolateral angles acute, produced; pereopod 7 wide; appendix masculina shorter than endopod

# *Eurydice longicornis* (Studer, 1882) Figures 1-3

Cirolana longicornis Studer, 1882: 28, pl 2, fig. 15a-c; 1884: 21.

*Eurydice longicornis.* - Hansen, 1890: 375; Stebbing, 1910: 421; Barnard, 1914: 350a; Kensley, 1978: 72, fig 30D; Bruce, 1986: 221; Brusca, Wetzer & France, 1995: 43. *?Eurydice longicornis.* Branch, *et al.*, 1994: 66, fig 29.1.

#### Material examined

*Lectotype* (here selected).  $\delta$  (5.1 mm), "Tafelbai, S. Afrika, Gazelle" (ZMB 4824). *Paralectotypes*. 3  $\Im$  (non-ovig 5.4, 5.5, 6.1 mm), same data and registration number as lectotype (ZMB 4824). The label accompanying the specimens is not the original label, and the station number, date, collector and depth are not recorded.

#### Type locality

Table Bay, South Africa, 50 fathoms (= c. 91 m) (Studer, 1882).

#### Description of male

Body about 2.4 times as long as greatest width; maximum width at pereonites 5 and 6. Cephalon anterior

margin rounded, with obscure minute rostral point. Eyes well developed, 5 - 7 ocelli horizontally, c. 10 ocelli vertically. Coxae 2 - 3 posterolateral angles acute, with distinctly produced posteroventral point. Pleonite 1 largely concealed by pereonite 7, posterior margins of pleonites 2 - 5 acute; pleon narrowing slightly towards posterior. Pleotelson about 85% as long as pleon in lateral view; posterior margin emarginate, rounded, with c. 14 short PMS and 4 spines; anteromedial dorsal surface with distinct depression.

Antennule peduncle article 1 without setae; articles 2 and 3 subequal in length; article 2 posterodistal angle with 2 brush tipped setae; article 3 anterodistal angle with cluster of 1 plumose and 2 short simple setae; flagellum about 1.1 times as long as peduncle, with 5 articles, article 1 of which is longest, about 3.3 times as long as article 2; flagellum just reaching pereonite 1. Antenna peduncle articles 1 and 2 short, article 1 anterodistal angle without setae, article 2 anterodistal angle with 2 slender simple setae; article 3 about 1.3 times as long as wide and about 1.8 as long as article 2, anterior margin with 13 stout acute submarginal spines; article 4 longest about 2 times as long as 3, anterior margin with 5 clusters of 1 - 3 short acute spines, posterior margin with row of single or paired simple setae; flagellum extending to anterior of pleonite 5, composed of about 20 articles.

Frontal lamina distinct; clypeus blade prominent, acute. Mandible spine row with 6 spines; molar process anterior margin with about 22 spines; palp article 1 shortest, 2 about 1.6 times as long as 1, with 4 simple setae along dorsal margin, 5 simple setae on distolateral margin, article 3 about 0.4 as long as article 2, with 5 apical simple setae. Maxillule lateral lobe with 13 spines on gnathal surface, most medial of which are serrate, medial lobe with 2 stout CP spines (third spine may be broken or missing). Maxilla lateral lobe with 3 stiff finely serrate setae, middle lobe with 4 stiff finely serrate setae, medial lobe with c.5 simple and 4 CP spines. Maxilliped palp articles all entire, palp article 1 with 3 long simple setae at distolateral margin; medial margins with stiff simple setae, setae at distal margin of article 5 long; lateral margin with setae at distal angle of articles 3 and 4; those of lateral margins being longer than those of medial margins; endite with 2 short and 1 long simple setae and 1 long CPS.

Pereopod 1 posterior margin of merus with 5 simple spines, carpus with 1 simple spine and propodus with 3 distinctly pectinate spines; dactylus about half (0.46) as long as propodus; spine opposing dactylus half as long as unguis; anterodistal angles of ischium and merus with abundant long setae, distal half of propodus with regularly spaced row of 8 stiff curved setae. Pereopods 2 and 3 similar to pereopod 1, but with additional setae on posterior margin of basis, and more and larger spines present on posterior margin merus, carpus and propodus and at anterodistal angle of merus; anterior margin of propodus *c*.7 stiff curved

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**Figure 1.** *Eurydice longicornis* (Studer). A-D lectotype, E-H paralectotype 5.5 mm. A, dorsal view; B, lateral view; C, frons; D, pleotelson posterior margin; E, antennule; F, antenna peduncle; G, right mandible; H, mandible palp. Scale line 1.0 mm.

**Figure 1.** *Eurydice longicornis* (Studer) A-D lectotype, E-H paralectotype 5,5 mm. A, vue dorsale ; B, vue latérale ; C, tête vue de face ; D, bord postérieur du pléotelson ; E, antennule ; F, pédoncule de l'antenne ; G, mandibule droite ; H, palpe mandibulaire. Echelle (A-B) : 1,0 mm.



Figure 2. Eurydice longicornis (Studer). D, E, lectotype, A-C, F paralectotype 5.5 mm. A, maxilliped; B, maxillule; C, maxilla; D, pleopod 1; E, pleopod 2, and appendix masculina apex; F, uropod.
Figure 2. Eurydice longicornis (Studer) D, E, lectotype, A-C, F, paralectotype 5,5 mm. A, maxillipède ; B, maxillule ; C, maxille ; D,

pléopode 1 ; E, pléopode 2 ; F, uropode.



**Figure 3.** *Eurydice longicornis* (Studer). Paralectotype 5.5 mm. A, pereopod 1; B, pereopod 2; C, pereopod 7. **Figure 3.** *Eurydice longicornis* (Studer). Paralectotype 5,5 mm. A, péréiopode 1 ; B, péréiopode 2 ; C, péréiopode 7.

setae, and c. 8 long simple setae. Pereopod 7 ischium 0.67 as long as basis, merus 0.7 as long as ischium and about as long as carpus, propodus 1.2 times as long as carpus; basis with 2 prominent anteroproximal clusters of simple setae, posterior margin with proximal cluster of long simple setae; ischium posterior margin with 4 clusters of 1, 1, 1, and 2 spines, distal margin with 2 and 6 spines, anterior margin with 4 clusters of 2, 5, 5, and 5 setae, and cluster of c. 9 setae at distal angle; merus posterior margin with 2 clusters of 2 setae and 2 and 3 spines, distal margin with 2 and 3 stout spines, anterior margin indented, with continuous setae and 2 clusters of 2 and 3 spines; carpus posterior margin with 2 clusters of 3 spines together with 1 - 2 setae, distal margin with cluster of 4 and 5 spines, anterior margin indented with 2 clusters of 2 small spines and 3 setae and 1 long seta; propodus posterior margin with 4 clusters of 1, 3, 3, and 3 spines, anterior margin with 2 clusters of 1 and 2 small spines and 1 seta.

Penial processes observed in situ, similar to other species.

Pleopod 1 exopod with 28 PMS, endopod with 25 PMS. Pleopod 2 exopod and endopod with 35 and 32 PMS respectively; appendix masculina straight, slightly wider distally than basally, lateral margin proximal half thickened, distally with short acuminate tip, 0.7 as long as endopod. Uropod peduncle with 10 curved stiff PS and single spine; exopod about 0.75 times as long as endopod, medial margin convex with about 12 setae and about 2 spines (could not be accurately assessed); endopod lateral margin weakly convex, with about 8 evenly spaced sensory setae (most have been rubbed off), medial margin obliquely truncate, with 2 small subapical spines and about 18 PMS.

#### Female

Similar to male, slightly larger in size; oostegites not observed.

#### Colour

The chromatophores and colour of these old specimens have long since faded.

#### Remarks

The date of publication for *Eurydice longicornis* is 16 February 1882, although it has been misquoted as 1883. Studer (1884) has also often been misquoted as 1883 (e.g., Bruce, 1986), but the date of publication is given on the cover as 1884, and facing page 1 it is stated that the printing began on 1 November 1883, and sent out 28 February 1884. Therefore 1884 is the correct date of publication.

*Eurydice longicornis* is easily separated from *Eurydice barnardi* sp. nov. by having a pleotelson with an anterior depression and a wider posterior margin with 4 spines (in *E. barnardi* very narrow and with 2 spines), less setose pereopods and far longer antennal flagellum. *Eurydice* 

*longicornis* can be distinguished from *Eurydice kensleyi* sp. nov. by having far longer antennae, the flagellum of which extends to the posterior of the pleon, acute coxae, more prominent and more closely spaced setae on the anterior margin of the propodus of percopods 1 - 3 and a shorter appendix masculina. Furthermore *Eurydice longicornis* is a subtidal species, while the other two species here recorded from the region are intertidal. A good colour photograph of a *Eurydice'' longicornis*'' has been given by Branch *et al.* (1994), but the true identity of their specimen is uncertain.

The redescription given here is based on the male specimen, and as this effectively alters the concept of this taxon from what it was, this specimen has been selected as the lectotype.

The description given here is brief owing to the fragility of the specimens, and spine and setal counts may be inaccurate (cf. uropods) owing to spines and setae having been rubbed off.

#### Distribution

Given the probability that most records of *Eurydice longicornis* are misidentifications, the only reliable record is the type locality.

# *Eurydice kensleyi*, sp. nov. Figures 4 - 8

# Material Examined

*Holotype.*  $\delta$  (3.5 mm), Silwerstroomstrand, 33°34'S, 18°22'E, 17 May 1992, intertidal sand, coll. A. G. Soares (SAM A41946). *Paratypes.* 13  $\delta$  (2.7 - 3.5 mm, mean = 3.08 mm; dissected  $\delta$  3.5 mm, appendix masculina from  $\delta$  2.9 mm), 15 $\mathfrak{P}$ (ovig 4.2, 4.4, 4.9, 5.2; 11 non-ovig 2.8-4.2, mean = 3.4 mm), same data as holotype (SAM A41947, ZMUC CRU1962).

## Description of male

Body about 2.3 times as long as greatest width; maximum width at pereonites 4 and 6. Cephalon anterior margin rounded, without rostral point. Eyes prominent, about 5 ocelli horizontally, 7 - 9 vertically. Coxae 2 - 6 posteriorly rounded, posterolateral angles of coxae 7 acute, but not produced. Pleonite 1 largely concealed by pereonite 7, ventral margins of pleonites 2 -5 acute; pleon narrowing slightly towards posterior. Pleotelson about 82% as long as pleon in lateral view; posterior margin emarginate, subtruncate, with 9 short PMS and 4 spines, dorsally with 4 submarginal simple setae; anterodorsal surface with distinct depression.

Antennule peduncle article 1 anteriorly with 2 setae; articles 2 slightly shorter (0.83) than 3; article 2 posterodistal angle with 2 simple, 1 pappose setae, anterodistal angle with 1 simple seta; article 3 anterodistal angle with cluster of short simple setae; flagellum about 0.8 times as long as peduncle, with 5 articles, article 1 of which



**Figure 4.** *Eurydice kensleyi* sp. nov. A - C, holotype, D-G & paratype 3.5 mm. A, dorsal view; B, lateral view; C, frons; D, antennule; E, antenna peduncle; F, antenna, distal flagellar articles; G, mandible. Scale 1.0 mm.

**Figure 4.** *Eurydice kensleyi* sp. nov. A-C holotype, D-G paratype & 3,5 mm. A, vue dorsale ; B, vue latérale ; C, tête vue de face ; D, antennule ; E, pédoncule de l'antenne ; F, antenne, articles distaux du flagelle ; G, mandibule. Echelle (A-B) : 1,0 mm.

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**Figure 5.** *Eurydice kensleyi* sp. nov. *d* paratype 3.5 mm. A, mandible palp; B, maxillule; C, maxilla; D, maxilliped; E, penial process; F, pleotelson posterior margin.

**Figure 5.** *Eurydice kensleyi* sp. nov. paratype & 3,5 mm. A, palpe mandibulaire ; B, maxillule ; C, maxille ; D, maxillipède ; E, processus pénial ; F, bord postérieur du pléotelson.

is longest, about 1.7 times as long as article 2; flagellum extending to pereonite 1. Antenna peduncle articles 1 and 2 short, article 1 anterodistal angle without setae, article 2 anterodistal angle with 2 slender simple setae; article 3 short and wide, about 0.9 as long as wide and about 1.5 as long as article 2, anterior margin with 15 stout acute marginal and submarginal spines, becoming progressively longer distally, posteroproximal margin with single pappose seta; article 4 longest about 2.3 times as long as 3, anterior margin with 4 clusters of 4, 4, 3 and 1 stout acute marginal and

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submarginal spines, posterior margin with 2 minute and 2 long simple setae and single brush tipped seta; flagellum extending to anterior of pereonite 6, composed of about 13 articles, articles 1 and 2 anteriorly with prominent setal cluster, remainder with cluster of small setae, articles 3 - 12 with plicate process; flagellum articles 2 - 10 posteriorly with single seta at distal angle.

Frontal lamina distinct; clypeus blade prominent. Mandible spine row with 5 spines; molar process anterior margin with about 28 spines; palp article 2 about 2.8 times



**Figure 6.** *Eurydice kensleyi* sp. nov.  $\eth$  paratype 3.5 mm. A, pereopod 1; B, pereopod 2; C, pereopod 1, dactylus. **Figure 6.** *Eurydice kensleyi* sp. nov. paratype  $\eth$  3,5 mm. A péréiopode 1; B péréiopode 2; C, dactyle du péréiopode 1.

as long as 1, with about 3 simple setae along dorsal margin, 3 simple setae on distolateral margin; article 3 less than half (0.3) as long as article 2, with 3 apical simple setae. Maxillule lateral lobe with 13 spines on gnathal surface, some of which are weakly serrate, medial lobe with 3 stout CP spines, and 2 short simple spines. Maxilla lateral lobe with 4 stiff simple setae, middle lobe with 3 stiff finely serrate setae, medial lobe with 4 simple and 4 CP spines. Maxilliped palp articles 1 and 2 coalesced with article 1 coalesced with basis; article 1 with 4 long simple setae on





**Figure 8.** *Eurydice kensleyi* sp. nov. & paratype 3.5 mm, except B, & 2.9 mm. A - D, pleopods 1-3, 5 respectively; E, uropod. **Figure 8.** *Eurydice kensleyi* sp. nov. paratype & 3,5 mm, except B, & 2,9 mm. A - D, pleopodes 1, 2, 3, 5 respectivement ; E, uropode.

distolateral margin, article 3 medial margin with 3 sets of 2 setae, lateral margin without setae; article 4 medial margin with 2 setae, lateral margin with 3; article 5 with 3 lateral, 5 distal and 1 medial long simple setae; endite with 1 short and 2 long CPS.

Pereopods 1 - 3 moderately setose. Pereopod 1 dactylus about half as long as propodus; spine opposing dactylus large, extending to accessory unguis; accessory unguis slender, 0.8 length of unguis. Pereopods 2 and 3 similar to pereopod 1, but with additional setae on posterior margin of basis, and spines present on posterior margin merus, carpus and propodus and at anterodistal angle of merus. Pereopods 5 -7 essentially similar to each other. Pereopod 6 ischium 0.85 as long as basis, merus 0.5 as long as ischium and 1.6 times as long as carpus, propodus 1.2 times as long as carpus; basis with prominent proximoanterior cluster of simple setae, 4 pappose sensory setae along anterior margin, posterior margin with group of 5 subdistal setae and prominent distal cluster of c. 8 long stiff setae; ischium posterior margin with 3 clusters of 3, 5 and 4 spines, distal margin with 6 and 6 spines, anterior margin with 2 clusters of 2 and 4 setae, and cluster of c. 4 setae at distal angle; merus posterior margin without setae, with cluster of 5 spines, distal margin with 6 and 4 spines, some biserrate, anterior margin with 2 single spines and 2 setae and distal cluster of c. 4 setae; carpus posterior margin without setae, with clusters of 1 and 5 spines, distal margin with clusters of 6 and 3 spines, some serrate, anterior margin with 2 clusters of 2 and 3 small spines and setae; propodus posterior margin with 3 clusters of 4, 4 and 3 spines, anterior margin with 3 clusters of 1 small spine and single seta. Pereopod 7 similar to percopod 6, but slightly shorter; basis with fewer setae on anterior margin, and 5 pappose sensory setae on posterior margin; with more setae and more and longer spines on posterior margin of ischium, merus and propodus.

Penial process about 1.8 times as long as basal width, maximum width 1.3 times basal width; lateral margin convex, distal margin rounded.

Pleopod 1 exopod with 22 PMS, endopod medial margin thickened, with 18 PMS. Pleopod 2 exopod and endopod with 28 and 22 PMS respectively; appendix masculina of even width, distally sinuate, distal quarter bent medially with bluntly rounded tip, 1.4 times as long as endopod, extending beyond endopod by half of its length. Pleopods 3-5 endopods each with about ~15, 11 and 0 PMS respectively. Pleopods 3-5 exopods with ~39, 41 and 58 PMS respectively, distomedially bearing dense scale patch. Uropod peduncle with 8 curved stiff PS and single spine; exopod rounded, about 0.9 times as long as length of endopod lateral margin, medial margin with about 7 PMS and 3 spines; endopod lateral margin straight, with 9 evenly spaced sensory setae and 2 PMS, medial margin obliquely truncate, with 2 small subapical spines and about 14 PMS. *Femal*e Similar to male.

Similar to mai

# Colour

Chromatophores not apparent.

Size

Males 2.7 - 3.5 mm, females 2.8 - 5.2 mm in length.

# Development

As for *Eurydice barnardi*, only smaller males possess an appendix masculina, this being lost in larger specimens which nonetheless still retain penial processes. Presumably, lacking the appendix masculina, these are no longer functional males, and this may indicate that the species is protandrously hermaphroditic.

# Remarks

The relatively wide pleotelson posterior margin, which is armed with 4 spines, the larger eyes, less setose anterior percopods and long appendix masculina readily separates *Eurydice kensleyi* from *Eurydice barnardi*, the other sympatric intertidal species. It can be separated from the subtidal *Eurydice longicornis* by having a shorter antennal flagellum, posterolaterally rounded coxae and a much longer appendix masculina.

# Etymology

Named for Brian Kensley, in recognition of his great contribution to isopod taxonomy.

# *Eurydice barnardi*, sp. nov. Figs 9 - 13

# Material Examined

*Holotype*:  $\delta$  (3.4 mm), Silwerstroomstrand, 33°34'S, 18°22'E, 17 May 1992, intertidal sand, coll. A. G. Soares (SAM A41948). *Paratypes*: 20  $\delta$  (5 with appendix masculina 2.4, 2.6, 2.7, 2.8, 2.9; 15 without appendix masculina 2.4, 2.6, 2.7, 2.7, 2.8, 3.0, 3.0, 3.0, 3.1, 3.1, 3.2, 3.3, 3.3, 3.4, 3.8 mm, mean = 3.01 mm), 7  $\mathfrak{P}$  (ovig 3.5, 3.9, non-ovig 2.5, 2.9, 3.1, 3.1, 3.2 mm, also 2 crushed), same data as holotype (SAM A41949, ZMUC CRU1960). 4  $\delta$ , 16  $\mathfrak{P}$ , unmeasured, same data as holotype (ZMUC CRU1961).

# Description of male

Body about 2.5 times as long as greatest width; maximum width at pereonites 5 and 6. Cephalon anterior median margin weakly produced, with minute rostral point. Eyes small, about 4 ocelli horizontally, 9 vertically; ocelli not close set. Coxae 2 - 3 posteriorly rounded or sub-acute, posterolateral angles of coxae 6-7 acute, but not produced. Pleonite 1 largely concealed by pereonite 7, ventral margins of pleonites 2 -5 with marginal setae ; pleon narrowing slightly towards posterior. Pleotelson about 83 % as long as pleon in lateral view; posterior margin emarginate, subtruncate but so narrow as to appear to form point, with 3



**Figure 9.** *Eurydice barnardi* sp. nov. A, B, E, holotype, C, D ovigerous 9 paratype 3.9 mm, F, G,  $\delta$  paratype 3.3 mm. A, dorsal view; B, lateral view; C, dorsal view; E lateral view; E, frons; F, antennule; G, antenna; H, cephalon anterior margin in dorsal view. Scale lines 1.0 mm.

**Figure 9.** *Eurydice barnardi* sp. nov. A, B, E, holotype, C, D,  $\varphi$  ovigère paratype 3,9 mm, F-G,  $\eth$  paratype 3,3 mm. A, vue dorsale ; B, vue latérale ; C, vue dorsale ; D, vue latérale ; E, tête vue de face ; F, antennule ; G, antenne ; H, bord antérieur de la tête, vue dorsale. Echelle (A-D) : 1,0 mm.



**Figure 10.** *Eurydice barnardi* sp. nov. A, B, δ paratype 2.7 mm, F, ovigerous φ paratype 3.5 mm, C-E δ paratype 3.3 mm. A, antennal plicate process; B, maxilliped; C, maxilla; D, maxillule; E, mandible; F, maxilliped. **Figure 10.** *Eurydice barnardi* sp. nov. A, B, δ 2,7 mm, C-E, δ 3,3 mm. F, φ ovigère paratype 3,5 mm, A, processus strié de l'anten-

ne ; B, maxillipède ; C, maxille ; D, maxillule ; E, mandibule ; F, maxillipède.



**Figure 11.** *Eurydice barnardi* sp. nov. & paratype 3.3 mm. A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 1, spines from distal merus; E, pereopod 1, dactylus; F, pleotelson posterior margin.

**Figure 11.** *Eurydice barnardi* sp. nov. paratype & 3,3 mm. A, péréiopode 1 ; B, péréiopode 2 ; C, péréiopode 3 ; D, péréiopode 1, épines du mérus distal ; E, péréiopode 1, dactyle ; F, bord postérieur du pléotelson.



Figure 12. Eurydice barnardi sp. nov. & paratype 3.3 mm. A, pereopod 6; B, pereopod 7; C, pereopod 7, spines from anterodistal angle of merus.

Figure 12. Eurydice barnardi sp. nov. & paratype 3,3 mm. A, péréiopode 6 ; B, péréiopode 7 ; C, épines de l'angle antéro-distal du mérus du péréiopode 7.

short PMS and 2 spines, dorsally with submarginal simple setae; anterodorsal surface without depression.

Antennule peduncle article 1 anteriorly with 2 setae; articles 2 and 3 subequal in length; article 2 posterodistal angle with 1 simple, 1 pappose and 2 brush tipped setae; article 3 anterodistal angle with cluster of short simple setae; flagellum about 0.7 times as long as peduncle, with 5 articles, article 1 of which is longest, about 1.8 times as long as article 2; flagellum extending to pereonite 1. Antenna peduncle articles 1 and 2 short, article 1 anterodistal angle with single simple seta, article 2 anterodistal angle with 2 slender simple setae; article 3 flattened and very wide, about



**Figure 13.** *Eurydice barnardi* sp. nov. E, & paratype 2.7 mm, remainder & paratype 3.3 mm. A, - E, pleopods 1 -5 respectively; F, apex, appendix masculina; G, uropod; H, penial process.

**Figure 13.** *Eurydice barnardi* sp. nov. A-H (sauf E) paratype & 3,3 mm, E, paratype & 2,7 mm. A-E, pléopodes 1-5 respectivement ; G, uropode ; H, processus pénial.

0.7 as long as wide and about 1.2 as long as article 2, anterior margin with 14 stout acute marginal and submarginal spines; article 4 longest about 2 times as long as 3, anterior margin with 14 stout acute marginal and submarginal spines distally clustered into groups of 3, posterior margin with 4 stiff setae and single brush tipped seta; flagellum extending to anterior of pereonite 4, composed of about 9 articles, first 2 of which are fused, articles 1 - 7 anteriorly with 1 or 2 (articles 2 and 3) stiff setae, posteriorly with cluster of simple setae; plicate process present.

Frontal lamina reduced, scarcely visible; clypeus blade weakly developed. Mandible spine row with 6 spines; molar process anterior margin with about 22 spines; palp article 2 about 2.8 times as long as 1, with about 5 simple setae along dorsal margin, 4 simple setae on distolateral margin, article 3 about one third as long as article 2, with 3 apical simple setae. Maxillule lateral lobe with 13 spines on gnathal surface, medial most which are weakly serrate, medial lobe with 3 stout CP spines, and 2 short simple spines. Maxilla lateral lobe with 10 stiff simple setae, middle lobe with 13 stiff simple setae in 2 ranks of 6 and 7, medial lobe with c. 4 simple and 6 CP spines. Maxilliped palp article 1 coalesced with basis, articles 4 and 5 coalesced, palp with 4 long simple setae on distolateral margin of article 1 and on lateral margins of articles 3 - 5; medially with long simple setae at distal angle of articles 3 and 4 and distal margin of article 5; those of lateral margins being longer than those of medial margins; endite with 1 short and 2 long CPS.

Pereopod 1 posterior margin of merus with 5 simple spines and 1 long seta, carpus with 1 simple spine and 3 setae, propodus palm with 3 distinctly pectinate spines and 4 simple setae, submarginally with 3 simple setae; dactylus less than half (0.4) as long as propodus; spine opposing dactylus more than half (0.6) as long as unguis, with slender accessory spine about 0.8 as long as unguis; anterodistal angles of ischium and merus with abundant long setae, distal half of propodus with widely spaced row of 5 curved setae. Pereopods 2 and 3 similar to pereopod 1, but with additional setae on posterior margin of basis, and more and larger spines present on posterior margin merus, carpus and propodus and at anterodistal angle of merus; anterior margin of pereopod 2 propodus with 8 stiff curved setae. Pereopods 5 -7 essentially similar to each other. Pereopod 6 ischium 0.75 as long as basis, merus 0.4 as long as ischium and 1.4 times as long as carpus, propodus 1.3 times as long as carpus; basis with prominent anteroproximal cluster of simple setae, posterior margin with 4 groups of 1, 2, 1 and 4 setae and prominent distal cluster of c. 14 long stiff setae; ischium posterior margin with 3 clusters of 4, 5 and 5 spines, distal margin with 3 and 8 spines, anterior margin with 2 clusters of 4 and 7 setae, and cluster of c. 6 setae at distal angle; merus posterior margin without setae, with cluster of 3 spines, distal margin with 6 and 4 spines, anterior margin with single spine and row of 8 setae and distal cluster of c. 4 setae; carpus posterior margin without setae, with single cluster of 4 spines, distal margin with cluster of 5 and 8 spines, some serrate, anterior margin with 2 clusters of 1 small spine and 3 setae and 3 small spines and 3 setae; propodus posterior margin with 2 clusters of 3, 5 and 4 spines, anterior margin with 2 clusters of 2 small spines and 2 setae and 2 small spines and 1 seta. Pereopod 7 similar to pereopod 6, but basis with fewer setae on anterior margin, and with more setae and more and longer spines on posterior margin of ischium, merus and propodus.

Penial process about 2.1 times as long as wide, distally rounded.

Pleopod 1 exopod with 18 PMS, endopod with 23 PMS. Pleopod 2 exopod and endopod with 17 and 26 PMS respectively; appendix masculina of even width, lateral margin proximal half thickened, curving medially with short acuminate tip, slightly shorter than endopod. Pleopods 3-5 endopods each with about ~10, 7 and 0 PMS respectively. Pleopods 3-5 exopods with ~39, 37 and 41 PMS respectively, distomedially with dense scale patch. Uropod peduncle with 9 curved stiff PS and single spine; exopod subtruncate, about 0.8 times as long as length of endopod lateral margin, medial margin with about 7 setae and about 3 spines; endopod lateral margin straight, with 8 evenly spaced sensory setae, medial margin obliquely truncate, with 2 small subapical spines and about 10 PMS.

### Female

Generally similar to male but more ovate in shape, about 2.0 times as long as greatest width; plicate process on antennal flagellum absent. Oostegites present on sternites 3, 4 and 5.

# Colour

Preserved specimens without obvious colour or chromatophores.

#### Size

Males 2.4 - 3.8 mm, ovigerous females 3.5 - 3.9 mm, non-ovigerous females 2.5 - 3.2 mm in length.

# Development

It would appear that the species is hermaphroditic, with some smaller males specimens having fully developed penes and appendix masculina, while most larger "males" have penial processes, but lack the appendix masculina. Furthermore it appears that the penes of the males without an appendix masculina lack vasa deferentia, although these specimens have no oostegites.

# Remarks

*Eurydice barnardi* differs from other southern Atlantic species, and from all other species of *Eurydice* in many details. The very distinctly triangular pleotelson with a

narrow and truncate posterior margin armed with only two spines, heavily setose anterior percopods, strongly spined antenna and antennule peduncles, antenna peduncle article 3 being rounded and the flagellar articles posteriorly each with a long seta, heavily setose maxilla, lack of a distinct frontal lamina, reduced clypeus blade and lack of any pleotelsonic depression, are all distinctive characters that serve to identify the species. The heavily setose maxilla, which has more than double the number of setae than is common for the genus (see Bruce, 1986; Brusca *et al.*, 1995 for examples, and the other species described herein) is remarkable, and apparently unique within the genus, possibly an adaptation to its suspected diet of marine nematodes.

#### Etymology

Named for Keppel H. Barnard, in recognition of his contributions to knowledge of the South African Isopoda in particular and Crustacea in general.

#### **Ecological description**

Ten beaches of the Benguela region, on the West Coast of South Africa, were surveyed during May 1991 and May-June 1992 (Table 1). On each beach, samples were collected at 15 regularly spaced stations on a transect perpendicular to the shore line, the first above the drift line and the last in the surf zone. Triplicate  $0.1\text{m}^2$  sand samples were taken at each station to 25 cm depth and sieved through 1 mm mesh. Sand samples were taken at each station for particle size analysis, together with a profile survey on each beach. Temperature and salinity were recorded in each surf zone. Breaking wave height and period were measured to characterize the morphodynamic state of each beach. Isopod dry weight biomass was obtained after drying the animals for 72 h at  $60^{\circ}$  C.

*Eurydice kensleyi* was collected in nine of ten beaches surveyed, occurring from the most northern beach, Groenrivier, to the most southern one, Bloubergstrand (Table 1). Its abundance and biomass were highest in fine sand, flat dissipative and intermediate beaches, i.e. Silwerstroomstrand and Groenrivier, and lowest in steep reflective ones, i.e. Velddrif, being absent from the coarse sand (0.600 mm) reflective Slipper Bay (Table 1). Total abundance values ranged from 34667 to 10 ind. m<sup>-1</sup> and total biomass from 23.7440 to 0.0115 g. m<sup>-1</sup> at Silwerstroomstrand and Bloubergstrand, respectively.

*Eurydice barnardi* occurred in the intertidal of only two beaches. An established population was found at Silwerstroomstrand (Table 2) while only one juvenile was collected at Slipper Bay.

Both species reached the maximum abundance and biomass in Silwestroomstrand. This beach was classified as a fully dissipative beach (sensu Wright and Short, 1984), rating 11.56 with the dimensionless fall velocity index (i.e. **Table 1.** Ecological data for *Eurydice kensleyi*, physical characteristics and location of ten beaches on the West Coast of South Africa. Mz - mean sand size; I - Intermediate; D - Dissipative; R - Reflective.

**Tableau 1.** Données écologiques sur *Eurydice kensleyi*, caractéristiques physiques et localisations des dix plages de la côte Ouest d'Afrique du Sud. Mz - diamètre moyen du sable ; I - intermédiaire ; D - dispersante ; R - réfléchissante.

| BEACHES       | Number<br>ind.m <sup>-1</sup> | Biomass<br>g.m <sup>-1</sup> | Density<br>ind.m <sup>-2</sup> | Biomass<br>g.m <sup>-2</sup> | Mz<br>(mm) | 1 /<br>slope | Dean<br>(type) | Coordi-<br>nates |
|---------------|-------------------------------|------------------------------|--------------------------------|------------------------------|------------|--------------|----------------|------------------|
| Groenrivier   | 10 889                        | 17.731 2                     | 114                            | 0.247                        | 0.25       | 33           | 4.22           | 30°51'S          |
|               |                               |                              |                                |                              |            |              | (I)            | 17°35'E          |
| Spoegrivier   | 2 794                         | 5.002                        | 35                             | 0.066                        | 0.291      | 23           | 3.43           | 30°28'S          |
|               |                               |                              |                                |                              |            |              | (I)            | 17°22'E          |
| Strandfontein | 2 880                         | 3.7074                       | 41                             | 0.052                        | 0.197      | 26           | 7.33           | 31°42'S          |
|               |                               |                              |                                |                              |            |              | (D)            | 18°11'E          |
| Dwarskersbos  | 1 460                         | 2.288                        | 35                             | 0.054                        | 0.146      | 27           | 2.41           | 32°40'S          |
|               |                               |                              |                                |                              |            |              | (I)            | 18°15'E          |
| Velddrif      | 18                            | 0.0297                       | 7                              | 0.011                        | 0.311      | 10           | 1.17           | 32°46'S          |
|               |                               |                              |                                |                              |            |              | (R)            | 18°09'E          |
| Slipper       | 0                             | 0                            | 0                              | 0                            | 0.6        | 8            | 0.43           | 32°46'S          |
| Bay           |                               |                              |                                |                              |            |              | (R)            | 18°04'E          |
| Brittania     | 5 083                         | 4.1175                       | 68                             | 0.055                        | 0.279      | 17           | 3.94           | 32°43'S          |
| Bay           |                               |                              |                                |                              |            |              | (I)            | 17°56'E          |
| Stompneus     | 1 645                         | 1.246                        | 94                             | 0.071                        | 0.202      | 11           | 1.25           | 32°42'S          |
| Bay           |                               |                              |                                |                              |            |              | (R)            | 17°58'S          |
| Silwerstroom- | 34 667                        | 23.744                       | 388                            | 0.266                        | 0.155      | 36           | 11.56          | 33°34'S          |
| strand        |                               |                              |                                |                              |            |              | (D)            | 18°22'E          |
| Blouberg-     | 10                            | 0.0115                       | 7                              | 0.008                        | 0.348      | 11           | 2.51           | 33°51'S          |
| strand        |                               |                              |                                |                              |            |              | (I)            | 18°09'E          |

Dean's morphodynamic index, Table 1). The intertidal slope was flat (1/36) with very fine sands, e.g. average grain size of 0.155 mm and uniform size composition throughout the tidal gradient (standard deviation of 0.010 mm). The surf zone was 150 m wide with spilling breaker heights of 2 m.

At Silwerstroomstrand, *Eurydice kensleyi* was distributed from 7 m below the drift line to the bottom of the swash at low spring tide with two peaks in numbers and biomass coinciding at stations 5 and 7 (Table 2). Although there was no significant difference in mean individual biomass across the transect (P > 0.05, F = 0.49, df = 11, 24), larger animals were found just below the drift line and in the swash zone, stations 3 and 13-14, respectively (Table 2).

*Eurydice barnardi* was distributed higher up than *Eurydice kensleyi*, from 7 m above the drift line to the bottom of the swash at low spring tide. It also had two peaks in numbers and biomass coinciding at stations 5 and 9 (Table 2). Total abundance and biomass were high, reaching 91410 ind. m<sup>-1</sup> and 45.1422 g. m<sup>-1</sup>, respectively. Juveniles and adults occurred together with no significant difference in mean individual biomass across the transect (P > 0.05, F = 1.998, df = 13, 28).

At Silwerstroomstrand, both *Eurydice* species formed part of a rich beach community of 19 species, with *Eurydice barnardi* accounting for most of the individuals (64% of the total) and the second highest biomass value (14% of the **Table 2.** Ecological and biological parameters of *Eurydice barnardi* (EB) and *Eurydice kensleyi* (EK) on Silwerstroomstrand beach (17/05/92).

**Tableau 2.** Paramètres écologiques et biologiques d'*Eurydice* barnardi (EB) et E. kensleyi (EK) à la plage de Silwerstroomstrand (17/05/92).

|  |                                   | PARAM         | IETERS          |                                 |       |                                    |  |
|--|-----------------------------------|---------------|-----------------|---------------------------------|-------|------------------------------------|--|
| STATIONS   | DENSITY<br>(ind.m <sup>-2</sup> ) |               | BIOM<br>(g.n    | BIOMASS<br>(g.m <sup>-2</sup> ) |       | MEAN<br>INDIVIDUAL<br>BIOMASS (mg) |  |
|  | EB                                | EK            | EB              | EK                              | EB    | EK                                 |  |
| 1  | 10                                | 0             | 0.003           | 0                               | 0.267 | 0                                  |  |
| 2 (Drift line)   | 40                                | 0             | 0.021           | 0                               | 0.533 | 0                                  |  |
| 3  | 70                                | 7             | 0.023           | 0.007                           | 0.338 | 1                                  |  |
| 4  | 736                               | 53            | 0.327           | 0.036                           | 0.444 | 0.681                              |  |
| 5  | 2 470                             | 1 653         | 1.028           | 1.164                           | 0.438 | 0.704                              |  |
| 6  | 1 337                             | 667           | 0.702           | 0.457                           | 0.525 | 0.685                              |  |
| 7  | 1 397                             | 887           | 0.755           | 0.578                           | 0.541 | 0.652                              |  |
| 8 (Glassy layer)                                       | 1 550                             | 297           | 0.796           | 0.189                           | 0.513 | 0.636                              |  |
| 9  | 1 910                             | 600           | 1.051           | 0.386                           | 0.55  | 0.644                              |  |
| 10   | 1 247                             | 210           | 0.534           | 0.121                           | 0.428 | 0.578                              |  |
| 11   | 1 213                             | 223           | 0.601           | 0.172                           | 0.495 | 0.772                              |  |
| 12 (Top of Swash)                                      | 307                               | 50            | 0.182           | 0.039                           | 0.592 | 0.78                               |  |
| 13   | 93                                | 7             | 0.035           | 0.027                           | 0.371 | 3.4                                |  |
| 14 (Bottom of Swash)                                   | 10                                | 3             | 0.005           | 0.014                           | 0.467 | 4.2                                |  |
| 15 (Surf zone)   | 0                                 | 0             | 0               | 0                               | 0     | 0                                  |  |
| AVERAGE .m <sup>-2</sup> **<br>TOTAL.m <sup>-1</sup> * | 885<br>91 410                     | 388<br>34 667 | 0.437<br>45.142 | 0.266<br>23.744                 | 0.492 | 0.971                              |  |

\* Total abundance and biomass per running meter (a one meter wide strip of the beach running from station 1 to 14, i.e. 97 m, for EB and 3 to 14, i.e. 82 m, for EJ) were estimated by integrating the area under the curve of average density and biomass per station along the transect.\*\* Average estimated for the zone.

\* L'abondance et la biomasse totales par mètre courant (une bande d'un mètre de large de la station 1 à la station 14, c.-a.-d. 97 m pour EB et de la station 3 à la station 14 c.-a.-d. 82 m pour EJ) ont été estimées en intégrant la surface sous la courbe des densités et biomasses moyennes par station, le long du transect. \*\* Moyennes estimées.

total in comparison to 48% of *Donax serra*). *Eurydice kensleyi* ranked the second highest in abundance and fifth in biomass, constituting 24 and 7% of the total, respectively. Both *Eurydice* species were grouped in the same species association as the polychaete *Scolelepis squamata*, the mysid *Gastrosaccus psammodytes* and the bivalve *Donax serra*. This association was characterized by species having distributions centered in the mid-intertidal. *Eurydice* species were found coexisting with 2 other cirolanid isopods on Silwerstroomstrand. The distribution and peak of abundance of *Eurydice barnardi* coincided with that of *Eurydice kensleyi* (Table 2) and their distribution overlapped completely with that of *Excirolana natalensis* (Vanhöffen, 1914) and *Excirolana latipes* (Barnard, 1914).

The population of *Eurydice barnardi* had a significantly higher total biomass (t = 3.78; P < 0.02, d.f. = 4) and abundance (t = 6.56, P < 0.01, d.f. = 4) than *Eurydice* 

*kensleyi* (Table 2). However, the latter had a larger mean individual biomass than the former (t = -3.59, P < 0.03, d.f. = 4; see also Table 2). A preliminary analysis of 10 stomach contents of each species from specimens of the same size range (2.6 to 5.0 mm) and both sexes collected at station 5 suggests non-overlapping feeding habits. The 20% of non-empty stomachs of *Eurydice kensleyi* were repleat with green-yellowish balls of setae, parapods and other remains of the spionid polychaete *Scolelepis squamata*. In contrast, the 50% of non-empty stomachs of *Eurydice barnardi* contained yellowish balls of remains of softbodied animals (probably interstitial nematofauna).

#### **Ecological discussion**

Eurydice kensleyi and Eurydice barnardi attained maximum densities 12 times higher than their congeneric Eurydice "longicornis" on beaches of the Southeast Cape (De Ruyck et al., 1992, De Ruyck pers. comm.; note that the identity and name of that species remain unresolved in the light of the new data presented here). Comparing with fine sand dissipative West Coast beaches, Eurydice species reached maximum densities 4 times lower than those of E. "longicornis", (Bally, 1983a; but see Table 3). On protected fine sand beaches of the West Coast, however, E. "longicornis" occurred in more modest densities (Brown, 1973, and Table 3). Despite their small individual size in comparison to filter-feeders such as Donax serra, both *Eurydice* species made a significant contribution (21%) towards the total community biomass of a high-energy dissipative beach. The total biomass of both Eurydice species in this study is considered unusually high, reaching values higher than the total macroinfaunal biomass recorded for several beaches worldwide (McLachlan, 1990;

 Table 3. Comparison of densities of *Eurydice* species from beaches of South Africa.

**Tableau 3.** Comparaison des densités des espèces d'*Eurydice* des plages d'Afrique du Sud.

| Species       | Maximum<br>Density<br>(ind.m <sup>-2</sup> ) | Beach<br>Coast     | Source          |  |
|---------------|--|--------------------|-----------------|--|
| Eurydice      | 200  | Sundays River      | De Ruyck et al. |  |
| "longicornis" |  | Southeast          | (1992)          |  |
| Eurydice      | 378  | Hout Bay           | Brown           |  |
| "longicornis" |  | West               | (1973)          |  |
| Eurydice      | 8000   | fine sand beaches  | Bally           |  |
| "longicornis  |  | West               | (1983a)         |  |
| Eurydice      | 2470   | Silwerstroomstrand | this study      |  |
| barnardi      |  | West               |                 |  |
| Eurydice      | 1653   | Silwerstroomstrand | this study      |  |
| kensleyi      |  | West               | 2               |  |

McLachlan *et al.*, 1993). This may be attributed to the upwelling process that occurs on the Benguela coast, bringing nutrient enriched waters from great depths and enhancing primary and secondary production on pelagic and neritic regions.

Since Eurydice barnardi and Eurydice kensleyi are similar to E. "longicornis" in overall morphology, they could have been overlooked in previous beach studies on the West coast of South Africa (Brown, 1973; Bally, 1983a, b). Equally, records of E. "longicornis" from the intertidal of Southeastern coast beaches (De Ruyck et al., 1991, 1992) are probably of undescribed species.

Extensive speciation has long been recognised for intertidal species of Eurvdice (Jones 1969). Species replacement along tidal (Salvat, 1966; Jones, 1971; Jaramillo, 1978; De Ruyck et al., 1992) or exposure gradients (Jones, 1971; Eleftheriou & Jones, 1976; Dexter, 1984) is common on shores where two or more cirolanid species co-occur. These patterns of spatial segregation have been suggested to be, to some extent, a result of competitive exclusion processes (Bally, 1983a) or a way to avoid such interactions (Jones, 1979). Alternatively, McLachlan (1990) suggested that patterns of faunal movement and distribution on a beach are predominantly a result of individual responses to the physical environment. The coincidence of distribution and peak abundance of Eurydice barnardi with that of E. kensleyi suggests two hypotheses: 1- physical factors maintain population levels below the carrying capacity of the beach, thus coexistence is achieved with both species exploiting the same space and food resources with weak or no competitive interactions; 2 - physical factors fail to maintain population levels below the carrying capacity of the beach, thus although both species do not partition the space resource, they do differ in food resources to allow coexistence and minimize competition. If hypothesis 1 is correct, physical factors are the most important parameters controlling community structure on sandy beaches. If hypothesis 2 is correct, biological interactions should, together with physical factors, also be considered important parameters in determining community structure on sandy beaches.

Indeed, a preliminary analysis of stomach contents of *Eurydice* species showed different feeding habits, with *E. barnardi* eating softed-bodied animals (probably nematodes) and *E. kensleyi* eating the polychaete *Scolelepis squamata*. This feeding habit, coupled with the more fossorial appendages of *Eurydice barnardi* and the larger size of *Eurydice kensleyi*, suggests a possible segregation in food niche between the two species, the former exploiting meiofauna and the latter exploiting macrofauna. Bally (1983b) observed lower densities of meiofauna in zones of high densities of *Eurydice "longicornis*" and suggested a predator- prey interaction. Analysis of stomach-contents of

both species along the tidal gradient and in different seasons could show the persistence of this niche segregation over space and time.

According to McLachlan et al.'s (1993) "Swash Exclusion Hypothesis", dissipative beaches have a benign swash climate that could support all beach species known to occur in a biogeographical area. There would be a gradual species elimination as one moves to harsher swash climates of intermediate and reflective beaches, only species adapted to these harsher conditions remaining. The fact that Eurydice kensleyi reached the highest total abundance and biomass on dissipative beaches and lowest on reflective ones, and a population of Eurydice barnardi was found to date only on a fully dissipative beach supports the "Swash Exclusion Hypothesis". The importance of biological interactions in regulating the abundance and biomass of beach isopods and the extent to which biological and physical factors interact are open questions that deserve further investigation.

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