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Occurrence of a continental slope decapod crustacean community along the edge of the minimum oxygen zone in the south eastern Gulf of California, Mexico

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ABSTRACT. Decapod crustaceans living in deep-water in the south eastern Gulf of California were collected during two research cruises in August 1991 and 2000. Benthic sledges were operated in the depth range of 550 to 2250 m. Vertical distribution of dissolved oxygen was obtained at selected stations and epibenthic oxygen content was measured at almost all sampling stations. A total of 31 species was collected, 21 strictly benthic and eight strictly pelagic. They belong to the Penaeoidea (five species), the Caridea (13 species), the Anomura (seven species), the Astacidea (one species), the Thalassinoidea (two species), the Eryonoidea (two species) and the Brachyura (one species). The oxygen minimum zone at bottom level represents a dispersal barrier for continental shelf species, including species known to have a wide bathymetric distribution. The deep-water decapod crustacean fauna (i.e., below 550 m) living along the offshore edge of this oxygen minimum zone is dominated by species of *Munidopsis*. The number of benthic species collected at the stations varied considerably, from zero to 15. The highest numbers of species were caught in the depth range of 1188-1245, where hypoxic (0.6-0.76 ml O₂/l) conditions prevailed. Stations with higher oxygen content had fewer benthic species. Factors other than oxygen content, affect the occurrence of species in the area.

KEY WORDS: Decapod crustaceans, continental slope, southeastern Gulf of California, hypoxia.

INTRODUCTION

While the northern part of the Gulf of California is relatively shallow, with the exception of the Delfin basin, the central and southern parts increase in average depth towards the mouth of the Gulf. Several deep basins are found offshore with depths reaching 3000 m or more. The southern Gulf of California opens to the Pacific, with depths greater than 3000 m at the entrance (PARKER, 1964; ALVAREZ-BORREGO & SCHWARTZLOSE, 1979). In the southern Gulf, water temperature does not show any special structure. It decreases monotonically with depth and reaches values of less than 10°C below 400-500 m. There is an orderly progression to the deepest portions of the Gulf of from 10°C to <4°C at 2000 m. The southernmost basin, from about 26° N to the mouth of the Gulf, has epibenthic water temperatures of 2°C or less, characteris-

tic of the bottom water of the equatorial Pacific (PARKER, 1964).

Epibenthic dissolved oxygen concentration has been recognized as a major limiting factor for benthic and demersal species. Although it is generally admitted that respiration in most marine invertebrates is not significantly affected until extremely low oxygen concentrations are reached, i.e. below 2.0 ml/l or even less (ROSENBERG et al. 1991; DIAZ & ROSENBERG, 1995), decreasing oxygen content near the bottom or in the water column can create an anoxic zone where no macrofauna occur (DIAZ & ROSENBERG, 1995). Species diversity at depths from 100 m to 2140 m off the coast of Southwest Africa, and at depths of 1100-1300 m in the Santa Catalina Basin, off California, has been shown to decline with reduced oxygen content of the bottom water or to be lower than adjacent areas where oxygen content is higher (JUMARS, 1976; GRASSLE, 1989).

Oxygen minimum zones have long been recognized in different parts of the world, either in fjords, coastal water

or in open ocean. The widest area where severe hypoxia has been observed is in the east Pacific (WYRTKI, 1966; KAMYKOWSKI & ZENTARA, 1990). Severe hypoxia can drastically reduce diversity and size of natural communities (see NILSSON & ROSENBERG, 1994).

Since deep water crustaceans were collected by the "Albatross" in 1891 off the coast of Mexico to Peru, almost no studies have been performed in the southern Gulf of California. The most complete study of the deep water fauna of the east Pacific slope is by PARKER (1964), based on series of 11 samples obtained on the middle continental slope (731-1799 m), and of 19 samples obtained between 1800 and 4122 m in the abyssal southern basins and outer slope of the Gulf of California. Parker's definition of assemblages, however, was based mostly on molluscs and the occurrence of decapod crustaceans must be inferred from a long data matrix (Parker, 1964: Table 7) and related to a map of sampling stations. He found 14 species of decapod crustaceans below 500 m of which only two were recorded in the Southeastern Gulf of California. WICKSTEN (1989) provided a synthesis of all species of eastern Pacific decapod crustaceans with the majority of records at 50 m or deeper (defined as "off-shore species"). A total of 183 species is included, of which 117 have records in the depth category of 500-1000 m, 96 at 1000-1500 m and 46 at depths >1500 m (WICKSTEN, 1989). An analysis of habitats and biodiversity of decapod crustaceans in the Southeastern Gulf of California (HENDRICKX, 1996a) reported that 19 deep-water species were collected between 200 and 1200 m, some of which represent new records for the area (HENDRICKX, 1996b).

An oxygen minimum zone has long been recognized in the Gulf of California. According to PARKER (1964), this zone of low oxygen concentration (ca. 0.5 ml/l) at or near the bottom forms a fringe parallel to the coast that extends, on both sides of the Gulf, from the east and west entrances to ca. 29° N. Up to 90 km wide, it mostly covers the outer continental shelf and the upper slope, roughly from 100m to 500 or 1000 m, depending on location. Recent studies, however, indicate that almost anoxic conditions are occasionally found on the shelf at 60 m (HENDRICKX et al., 1984; GARDUÑO-ARGUETA & CALDERÓN PÉREZ, 1995).

The purpose of this study is to define the deepwater decapod crustacean community that occurs on the off-shore side on the oxygen minimum, roughly in the depth range of 550 to 2200 m, in the SE Gulf of California.

METHODS

Crustaceans samples were dredged at depths of 550 to 2250 m in the SE Gulf of California. Material was obtained during two cruises aboard the R/V "El Puma" of the Universidad Nacional Autónoma de Mexico. Samples were obtained with benthic sledges at 11 stations in

August 1991 (TALUD III cruise) and at eight stations in August 2000 (TALUD IV), off the coast of Sinaloa, Mexico (Table 1). The sledges were operated at depths from 550 to 1380 m (TALUD III) and from 785 m to 2250 m (TALUD IV). Two different benthic sledges were used: a 2.5 m wide by 1.0 m high modified Agassiz sledge equipped with a collecting net of ca. 5.5 cm (2 1/4") stretch mesh lined with ca. 2.0 cm (3/4") mesh net (TALUD III) and a 2.35 m wide by 0.95 m high standard benthic sledge equipped with a collecting net of ca. 5.5 cm (2 1/4") stretch mesh lined with ca. 2.0 cm (3/4") mesh net in the mouth area (TALUD IV). At selected sampling stations of the TALUD III cruise and at all sampling stations of TALUD IV cruise, a previously calibrated CTD probe equipped with an oxygen sensor was used to obtain temperature, salinity and dissolved oxygen profiles from surface to near bottom level. During the TALUD IV cruise, an opening-closing bottle was used to obtain near bottom water samples used to measure the dissolved oxygen by the Winkler method (duplicate samples). During the TALUD III cruise, oxygen measurements were obtained from the pre-calibrated probe (a SEB Seacat Profiler) and are considered reliable for biological interpretation. The CTD probes and opening-closing bottle were not operated less than 15 m off the bottom.

TABLE 1

Sampling stations where decapod crustaceans were caught during the TALUD III and IV cruises.

Station	Date	Position	
		Lat. N	Long. W
10/III	18/Aug/1991	23.41.9	107.31.8
10A/III	18/Aug/1991	23.44.3	107.38.6
14A/III	19/Aug/1991	24.38.8	108.26.9
14B/III	19/Aug/1991	24.39.2	108.37.8
19/III	20/Aug/1991	25.12	109.07
20A/III	24/Aug/1991	25.12.6	109.06
24/III	21/Aug/1991	25.33.6	109.42.02
24A/III	24/Aug/1991	25.45.2	109.46.8
4/IV	23/Aug/2000	21.59.0	106.35.0
13/IV	24/Aug/2000	23.17.51	107.29.85
14/IV	24/Aug/2000	23.13.4	107.41.8
18/IV	25/Aug/2000	24.15.2	108.17.1
19/IV	25/Aug/2000	24.15.3	108.24.1
20/IV	25/Aug/2000	24.27.4	108.35.26
25/IV	26/Aug/2000	24.53.2	108.59.4
26/IV	26/Aug/2000	24.56.4	109.05.6
27/IV	26/Aug/2000	24.59.0	109.12.1
33/IV	27/Aug/2000	25.45.9	109.48.1
34/IV	27/Aug/2000	25.40.67	109.54.4
35/IV	27/Aug/2000	25.53.98	110.11.29

Crustaceans were sorted onboard, preserved in diluted formaldehyde or in 70% ethanol. A list of all species is tabulated with accompanying data. Body lengths were measured with vernier calipers, usually to the nearest

0.1 mm. Carapace length was measured in shrimps while total length was used with lobsters and galatheids. The identified specimens form part of the collections of the Mazatlán Marine Station, UNAM.

Only species collected during the TALUD IV cruise and of special interest were treated individually in the systematic section. Biogeographic or ecological data related to species collected during the TALUD III cruise have been reported elsewhere (see HENDRICKX, 1996b). Data on other species captured during these cruises are summarized and included in a general table with their respective collecting data.

Abbreviations used: St., sampling station; CL, carapace length; TL, total length; BS, benthic sledge.

RESULTS

Systematic section

PENAEOIDEA

Family Solenoceridae

Hymenopenaeus doris (Faxon, 1893)

Haliporus doris FAXON, 1893: 214.

Haliporus doris. – FAXON, 1895: 191, pl. 49, Figs. 1-1c.

Hymenopenaeus doris. – BURKENROAD, 1936: 104; 1938: 60. – PÉREZ-FARFANTE, 1977: 283, Figs. 9, 17a, 18a, 19-20. – MÉNDEZ, 1981: 55, Figs. 155, 156, 156a-c. – HANAMURA, 1983: 55, Fig. 2. – WICKSTEN, 1989: 311. – WICKSTEN & HENDRICKX, 1992: 4. – HENDRICKX, 1993: 305; 1995d: 529, Fig. 1b, 530, Fig. 3b, 531, Fig. 8a, 532, Fig. 9a, 534; 1996c: 119, Fig. 60. – HENDRICKX & ESTRADA-NAVARRETE, 1996: 40, Fig. 24.

Aliporus doris. – DEL SOLAR, 1972: 4.

Material examined. – St. 19-IV, 25/VIII/2000, 1 male (CL 13.5 mm) and 1 female (CL 12.0 mm), 1245-1240 m, BS.

Previously known distribution. – From Punta Chivato, Mexico to Guanape, Peru (HENDRICKX, 1996c).

Remarks. – The only records in benthic samples for the Gulf of California are off Punta Arena and Punta Chivato, along the Baja California Peninsula (HENDRICKX, 1996c). The species has also been captured in the water column (see HENDRICKX & ESTRADA-NAVARRETE, 1996) and its presence in bottom trawls might be due to incidental catch during recovery of the gear.

Family Benthesicymidae

Benthesicymus tanneri Faxon, 1893

Benthesicymus tanneri FAXON, 1893: 215.

Benthesicymus tanneri. – FAXON, 1895: 205, Fig. H. – RATHBUN, 1904: 147. – SCHMITT, 1921: 23, Fig. 10. – MÉNDEZ, 1981: 31. – RODRÍGUEZ DE LA CRUZ, 1987: 20. – WICKSTEN & HENDRICKX, 1992: 2. – HENDRICKX, 1993: 305; 1995d: 436, Fig. 4, 437; 1996c: 12, Fig. 5.

Material examined. – St. 13-IV, 24/VIII/2000, 1 male (CL 31.8 mm), 1530-1520 m, BS; St. 19-IV, 25/VIII/2000, 3 females (CL 36.5-37.3 mm), 1245-1240 m, BS; St. 26-IV, 26/VIII/2000, 1 male (CL 30.2 mm) and 2 juveniles (not measured), 1225-1240 m, BS; St. 33-IV, 27/VIII/2000, 2 males (CL 33.2 and 34.8 mm), 1040 m, BS.

Previously known distribution. – From San Diego, California, USA to Ilo, Peru. Southeastern Gulf of California; Galapagos Islands (HENDRICKX, 1996c).

Remarks. – The distribution of this species is synthesized by HENDRICKX (1996c). *Benthesicymus tanneri* is a common species in deep water of the SE Gulf of California. Material captured during this study includes the largest specimens known to date (up to 135 mm TL). Adult specimens are rather heavy (ca. 13.0-16.5 g of individual fresh weight for specimens of 110-135 mm TL) and they most probably live close to the bottom. Often captured with *Heterocarpus affinis*, a potential deep-water resource in the eastern tropical Pacific (HENDRICKX 1995d), *B. tanneri* could represent an interesting by-catch species in pandalids fishery.

CARIDEA

Family Pandalidae

Pandalus amplus (Bate, 1886)

Pandalopsis amplus BATE, 1888: 671, pl. 175, Fig. 3.

Pandalopsis ampla. – FAXON, 1895: 155. – RATHBUN, 1904: 51. – SCHMITT, 1921: 46. – WICKSTEN, 1989: 313. – WICKSTEN & HENDRICKX, 1992: 9.

Material examined. – St. 19-IV, 25/VIII/2000, 2 females, the smallest ovigerous (CL 31.6 and 32.6 mm), 1245-1240 m, BS.

Previously known distribution. – From Sea Lion Rock, Washington, USA to Acapulco, Gro., Mexico. ATL from off Montevideo, Uruguay to Argentina (WICKSTEN & HENDRICKX, 1992).

Remarks. – *Pandalus amplus* is a common species off the coast of California, where it has been reported at least in 28 localities (HENDRICKX & WICKSTEN, 1989) and from a depth range of 132-2000 m. There are only five records along the Pacific coast of Mexico, including two in the Gulf of California. The present record represents a range extension of this species along the east coast of the Gulf of California to 24°15.3' N - 108°24.1' W. The size of the largest female (165 mm TL) is close to the maximum known size (170 mm TL) for the east Pacific. Fresh weight of specimens examined are 22 and 24 g.

Family Crangonidae

Sclerocrangon atrox Faxon, 1893

Sclerocrangon atrox FAXON, 1893: 199.

Sclerocrangon atrox. – FAXON, 1895: pl. 35, Figs. 1, 1a-f. – MÉNDEZ, 1981: 121. – WICKSTEN & HENDRICKX, 1992: 6.

Material examined. – St. 13-IV, 24/VIII/2000, 1 male (CL 27.8 mm), 1530-1520 m, BS; St. 19-IV, 25/VIII/2000, 1 male (CL 25.2 mm), 1245-1240 m, BS.

Previously known distribution. – From near Tres Marias Islands, Nayarit, Mexico to off Mollendo, Peru (WICKSTEN & HENDRICKX, 1992).

Remarks. – A large (up to 162 mm TL; ca. 38 mm CL) and rather rare species of Crangonidae. The present material increases the range northwards by two degrees of latitude, from off Tres Marias Islands to 24°15.3'N - 108°24.1'W.

Family Oplophoridae

Acanthephyra brevirostris Smith, 1885

Acanthephyra brevirostris SMITH, 1885: 504.

Acanthephyra brevirostris. – SMITH, 1886(1887): 670, pl. 14, Fig. 2, pl. 15, Figs. 2, 8, pl. 16, Figs. 1, 6. – FAXON, 1895: 167. – KENSLEY, 1972: 38, Fig. 17m. – CROSNIER & FOREST, 1973: 41, Figs. 8c-d. – HANAMURA, 1983: 75. – CHACE, 1986: 8 (Key), Figs. 2e, 4e, 5e, 6d, 8d. – HENDRICKX & ESTRADA-NAVARRETE, 1989: 113; 1996: 109, Fig. 67.

Material examined. – St. 26-IV, 26/VIII/2000, 1 juvenile (CL 6.5 mm), 1225-1240 m, BS.

Previously known distribution. – From off Baja California and off Ecuador, including the SE Gulf of California; SW Indian Ocean; East and West Atlantic Ocean (HENDRICKX & ESTRADA-NAVARRETE, 1996).

Remarks. – Only two records of this species are available for the east Pacific (off Ecuador, 0.58° S - 115.15° E; Dowd Tablemount, off Baja California, Mexico) (HENDRICKX & ESTRADA NAVARRETE, 1996). The juvenile examined, although slightly damaged, shows features distinctive of this species. This deep-water pelagic species has been collected between 1280 and 5394 m, mostly in mid-water trawls. Examined material was most probably collected in the water column during recovery of the dredge.

Hymenodora gracilis Smith, 1887

Hymenodora gracilis SMITH, 1886 (1887): 680, pl. 12, Fig. 6.

Hymenodora gracilis. – SIVERTSEN & HOLTHUIS, 1956: 16, Figs. 12, 13. – CROSNIER & FOREST, 1973: 83, Fig. 25a. – WASMER, 1986: 49, Figs. 10b-c. – CHACE, 1986: 43 (clave), Figs. 21p-t. – IWASAKI & NEMOTO, 1987a: 20. – KRYGIER & WASMER, 1988: 87. – HANAMURA, 1989: 54, Fig. 2. – HENDRICKX & ESTRADA-NAVARRETE, 1989: 115; 1996: 119, Fig. 73. – ALLEN & BUTLER, 1994: 426, Fig. 5.

Material examined. – St. 35-IV, 27/VIII/2000, 1 male (CL 12.0 mm), 2016-2020 m, BS.

Previously known distribution. – From Oregon, USA to West coast of Baja California; coast of Chile and in subantarctic waters of the South Pacific Ocean (HENDRICKX & ESTRADA-NAVARRETE, 1996).

Remarks. – This is the first record outside the temperate waters of the NE and SE Pacific. A mesopelagic and bathypelagic species, *H. gracilis* is reported from ca. 300 to 5300 m (HENDRICKX & ESTRADA NAVARRETE, 1996). Some of these depth records, however, might be erroneous caused by the use of non-closing, bottom sampling devices. The material reported here was accidentally captured in the bottom sledge and there is no way to assess correctly the depth at which it was collected. *Hymenodora glacialis*, a closely related species, has been previously recorded in the central Gulf of California (HENDRICKX & ESTRADA NAVARRETE, 1996).

Family Pasiphaeidae

Pasiphaea emarginata Rathbun, 1902

Pasiphaea emarginata RATHBUN, 1902: 905.

Pasiphaea emarginata. – RATHBUN, 1904: 22, Fig. 4. – SCHMITT, 1921: 30, Fig. 15. – CHACE, 1937: 110. – WORD & CHARWAT, 1976: 205-206 (Illustration). – HENDRICKX & ESTRADA-NAVARRETE, 1989: 111; 1996: 89, Fig. 55.

Material examined. – St. 25-IV, 26/VIII/2000, 2 males (CL 35.1 and 36.0 mm) and 10 females (CL 27.3-38.3 mm), 870-835 m, BS.

Previously known distribution. – From West coast of Baja California (up to 26° N) and in the Gulf of California (up to 30°11' N); south to the Gulf of Panama and Lobos de Tierra Islands, Peru; Galapagos Islands (HENDRICKX & ESTRADA-NAVARRETE, 1996).

Remarks. – In addition to the type material taken near Concepcion Bay entrance, the only other two records of this species in the Gulf of California are over 60 years old (CHACE, 1937); all these records are from the central Gulf.

Pasiphaea magna Faxon, 1893

Pasiphaea magna FAXON, 1893: 209.

Pasiphaea magna. – FAXON, 1895: 176, pl. 45, Fig. 2. – WORD & CHARWAT, 1976: 208. – MÉNDEZ, 1981: 64, Figs. 190-192. – KRYGIER & WASMER, 1988: 77. – HENDRICKX & ESTRADA-NAVARRETE, 1989: 111; 1996: 91, Figs. 56, 57.

Material examined. – St. 19-IV, 25/VIII/2000, 1 female (CL 31.1 mm), 1245-1240 m, BS.

Previously known distribution. – From Oregon, USA, and the SE Gulf of California to the Gulf of Panama and Peru (HENDRICKX & ESTRADA-NAVARRETE, 1996).

Remarks. – This is the second record of *P. magna* in Mexican waters (see HENDRICKX & ESTRADA-NAVARRETE, 1996). Maximum recorded size is 185 mm (TL). The examined specimen is 106 mm TL.

Family Hippolytidae

Lebbeus scrippsi Wicksten & Méndez, 1982

Lebbeus scrippsi WICKSTEN & MÉNDEZ, 1982: 106.

Lebbeus scrippsi. – WICKSTEN, 1989: 312. – HENDRICKX, 1996b: 946.

Material examined. – St. 19-IV, 25/VIII/2000, 4 males (CL 6.7-8.2 mm) and 3 ovigerous females (CL 9.5-10.9 mm), 1245-1240 m, BS; St. 26-IV, 26/VIII/2000, 2 males (CL 6.7 and 10.3 mm), 1225-1240 m, BS.

Previously known distribution. – From Peru to Chile; one record in southeastern Gulf of California (WICKSTEN, 1989; HENDRICKX, 1996b).

Remarks. – This rare species is again reported in the area; two females (CL 9.0 and 9.4 mm), including one ovigerous, were reported in 1996. Among the 9 specimens reported here are 3 ovigerous females carrying 32-66 eggs each (Table 2). The largest female from station 26 (CL 10.9 mm) is 42.0 mm TL, slightly longer than the largest paratype (TL 41.2 mm).

TABLE 2

Sizes by sex, eggs number and eggs size in *Lebbeus scrippsi* from the Gulf of California continental slope (M, male; F, female).

Sex	CL/TL(mm)	Eggs Number	Size range (mm)
M	6.7/26.8	---	---
M	7.0/30.1	---	---
M	8.2/35.8	---	---
M	8.2/36.9	---	---
F	9.5/32.0	32	1.35-1.65
F	10.0/36.2	35	2.10-2.55
F	10.9/42.0	66	1.58-2.02
M	10.3/36.5	---	---
M	6.75/30.9	---	---

Family Glyphocrangonidae

***Glyphocrangon sicaria* Faxon, 1893**

Glyphocrangon sicarius Faxon, 1893: 202.

Glyphocrangon sicaria. – FAXON, 1895: pl. 39, Figs. 1, 1a-e. – WICKSTEN, 1989: 314. – WICKSTEN & HENDRICKX, 1992: 6.

Material examined. – St. 14-IV, 24/VIII/2000, 1 specimen not sexed (CL 6.5 mm), 2160-2150 m, BS; St. 26-IV, 26/VIII/00, 1 specimen not sexed (CL 9.0 mm), 1225-1240 m, BS.

Previously known distribution. – From South of Punta Guiones, Costa Rica to Gulf of Panama (WICKSTEN & HENDRICKX, 1992).

Remarks. – One of the 5 species of the genus reported for the eastern tropical Pacific, *G. sicaria* has so far been reported exclusively below ca. 1454 m (1454-3310 m; WICKSTEN, 1989).

Family Nematocarinidae

***Nematocarcinus* cf. *ensifer*
(Smith, 1882)**

Eumiersia ensifera SMITH, 1882: 77, pl. 13, Figs. 1-9.

Nematocarcinus ensiferus. – SMITH, 1884: 368, pl. 7, Fig. 1.

Nematocarcinus ensifer. – CROSNIER & FOREST, 1973: 116, Figs. 32a-c, 33a-c. – WICKSTEN & HENDRICKX, 1992: 6.

Material examined. – All specimens unsexed and unmeasured. St. 13-IV, 24/VIII/2000, 6 specimens, 1530-1520 m, BS; St. 26-IV, 26/VIII/2000, 5 specimens, 1225-1240 m, BS; St. 33-IV, 27/VIII/2000, 2 specimens, 1040 m, BS; St. 34-IV, 27/VIII/2000, 1 specimen, 1240-1250 m, BS.

Previously known distribution. – *Nematocarcinus ensifer* is known from off Acapulco, Mexico, to the Galapagos Islands; distributed worldwide (Atlantic, Pacific, Indian Ocean and Mediterranean Sea (WICKSTEN & HENDRICKX, 1992).

Remarks. – The material is assigned to *N. ensifer* with some doubts. It includes specimens with no ventral teeth on the rostrum and others with 1-3 clearly distinguishable small teeth in the distal portion. According to CROSNIER and FOREST (1973), presence of ventral teeth on some *Albatross* specimens, reported by FAXON (1895) as belonging to an atypical form of “*N. ensifer*” from the east Pacific, should be linked with the presence, in this area, of another species. A revision of W. Faxon material by R. Burukovsky (pers. comm. October 2000) prompted this author to describe a new species (forthcoming manuscript) close to *N. agassizi* Faxon, 1893, the second species of this genus previously reported in the east Pacific. Although our material features a rostrum clearly distinct from *N. agassizi*, a careful revision of the specimens collected during both TALUD cruises (see HENDRICKX, 1996b) should be undertaken. Although the dorsal process on the posterior margin of the third abdominal segment is similar in large, adult specimens, the rostrum features either long dorsal spines and a few ventral spines, or short dorsal spines on a longer rostrum and no ventral spines (Fig. 1). As noted by R. Burukovsky, species of *Nematocarcinus* are difficult to identify, mostly because they are generally damaged during sampling (loss of pereopods).

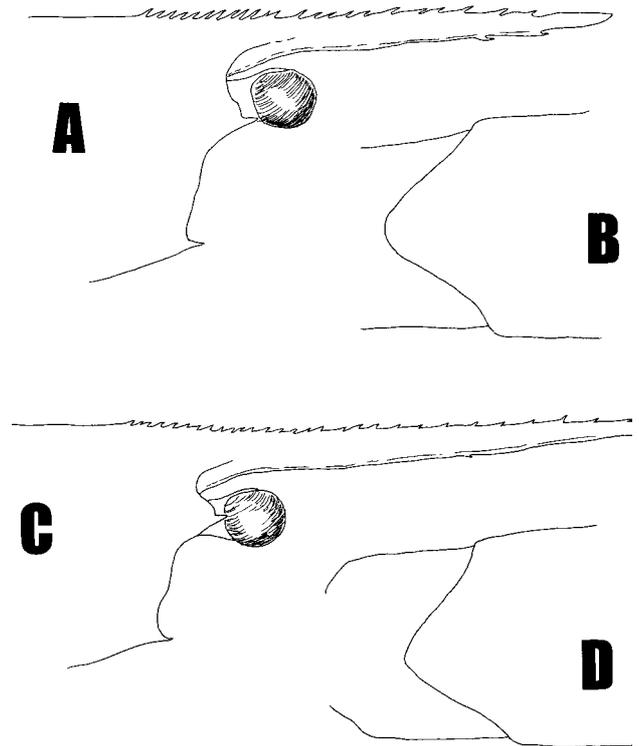


Fig. 1. – A, C) Anterior part of carapace and rostrum of *Nematocarcinus* cf. *ensifer*. B, D) Dorsal view of 3rd abdominal tergite (A, B, St. 34. CL 16.6 mm; C, D, St. 26, CL 22.2 mm).

ERYONOIDEA

Family Polychelidae

***Stereomastis pacificus* (Faxon, 1893)**

Polycheles sculptus pacificus Faxon, 1893: 196.

Polycheles sculptus pacificus. – FAXON, 1895: 122, pl. C, Fig. 1, 1a.

Eryoniscus agassizi. – SCHMITT, 1921: 105, pl. 15, Figs. 1-2.

Stereomastis sculpta pacifica. – WICKSTEN, 1981: 914, Fig. 1; 1989: 311. – HENDRICKX, 1995a: 156.

Material examined. – St. 19-IV, 25/VIII/00, 1 male (TL 118.0 mm), 2 females (CL 105.0 and 108.0 mm) and 1 ovigerous female (CL 129.0 mm), 1245-1240 m, BS.

Previously known distribution. – From San Clemente Island, California, USA, to Valparaiso, Chile. Off Tres Marias Islands (HENDRICKX, 1995a).

Remarks. – There is a total of 41 records of *S. pacificus* from the east Pacific (off the coasts of southern California, USA, Mexico, Panama, Costa Rica, Colombia, Peru and Chile) (see WICKSTEN, 1981), thus indicating that it has been frequently caught within its range. Original records by FAXON (1893) include one from the SE Gulf of California, off Tres Marias Islands; this is believed to be the only published record for this species within the Gulf of California. WICKSTEN (1981) mentioned a series of 32 adults from 20 stations in Costa Rica, Mexico and southern California, but without further details.

ANOMURA

Family Galatheidae

***Munidopsis ciliata* Wood-Mason, 1891**

Munidopsis ciliata WOOD-MASON, 1891: 200.

Munidopsis ciliata. – FAXON, 1895: 84, pl. 18, Fig. 3. – BENEDICT, 1902: 318. – AMBLER, 1980: 19, Fig. 3. – WICKSTEN, 1989: 315. – HENDRICKX & HARVEY, 1999: 376.

Munidopsis brevimana. – HENDERSON, 1885: 414; 1888: 154, pl. 17, Figs. 1, 2.

Munidopsis (Orophorhynchus) ciliata. – ALCOCK, 1901: 267.

Material examined. – St. 19-IV, 25/VIII/00, 2 males (TL 45.7 and 52.3 mm) and 1 ovigerous female (TL 58.8 mm), 1245-1240 m, BS.

Previously known distribution. – From Oregon, USA to off Panama, including the southern Gulf of California (WICKSTEN, 1989).

Remarks. – Within its geographic range, *M. ciliata* had been reported from a depth range of 2030-2075 m (WICKSTEN, 1989). The present record is from much shallower water. The ovigerous female carried 56 eggs.

***Munidopsis depressa* Faxon, 1893**

Munidopsis depressa FAXON, 1893: 189.

Munidopsis depressa. – FAXON, 1895: 96, pl. 22, figs 2, 2a, 2b. – BENEDICT, 1902: 319. – WICKSTEN, 1989: 315. – HENDRICKX, 1996b: 946. – HENDRICKX & HARVEY, 1999: 376.

Material examined. – St. 25-IV, 26/VIII/2000, 205 males (TL 8.5-37.0 mm), 64 females (TL 12.0-35.0 mm) and 4 ovigerous females (TL 27.0-33.0 mm), 870-835 m, BS; St. 26-IV, 26/VIII/2000, 33 males (TL 12.5-37.0 mm), 13 females (TL 16.0-35.0 mm) and 3 ovigerous females (TL 27.0-35.0 mm), 1225-1240 m, BS. St. 33-IV, 27/VIII/2000, 1 male (TL 36.0 mm) and 1 ovigerous female (TL 38.0 mm), 1040 m, BS.

Previously known distribution. – From off Santa Catalina Island, California, USA, to the Gulf of California, Mexico, from off Ahome Point, Sinaloa, to off Tres Marias Islands (HENDRICKX, 1996b).

Remarks. – Five samples were obtained during the previous cruise (TALUD III) at depths between 820 and 1208 m in the same area (HENDRICKX, 1996b). Considering these records and the new material obtained during this study, *M. depressa* appears to be one of the most common and abundant species of decapod crustacean on the continental slope in the SE Gulf of California.

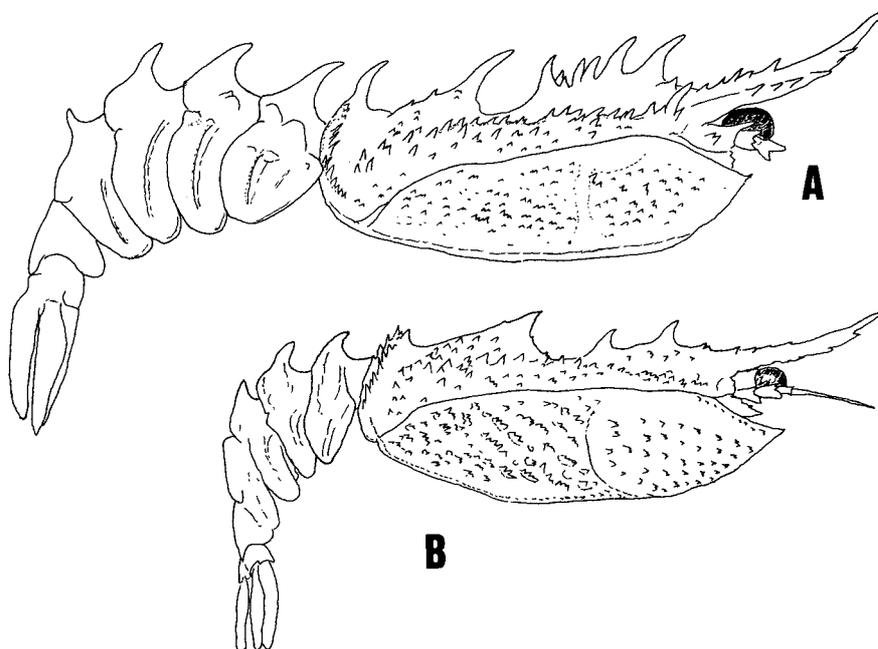


Fig. 2. – Lateral view of *Munidopsis depressa*. A) Specimen with unusually strong and long spines on carapace and a dorsal tooth on 5th abdominal segment (St. 33). B) Type material (after Faxon, 1893).

Specimens from stations 26 and 33 represent a spinose form of *M. depressa*. Spines on the carapace are much stronger and more numerous; also, the dorsal teeth on the abdominal segments are much stronger and there is one dorsal tooth on the fourth segment (Fig. 2), while material from the other stations lack this tooth, as does the type material illustrated by FAXON (1893). Close examination of these spinose specimens, including shape of the third maxilliped, the basal article of the antenna and antennula, the sternum and the chelipeds, indicates that this spinose form corresponds to an extreme variation of *M. depressa*.

Of the total (324 specimens), 239 specimens were males (74%). Only 8 ovigerous females were collected. Number of eggs varied from 21 to 29 in the smallest females (i.e., TL 27.0 to 33.0 mm) to 68 in the larger specimen collected at station 33; three hatching females had only 7 eggs retained on the pleopods.

***Munidopsis palmatus* Khodkina, 1973**

Munidopsis palmatus KHODKINA, 1973:1164-116, Figs 5-6.

Material examined. – St. 19-IV, 25/VIII/00, 1 ovigerous female (TL 22.0 mm), 1245-1240 m, BS; St. 26-IV, 26/VIII/2000, 1 ovigerous female (TL 24.0 mm), 1225-1240 m, BS.

Previously known distribution. – Known only from the type locality, off the coast of Chile, north of Valparaiso (32°11'6" S – 71°46'3" W).

Characteristics. – Rostrum triangular in dorsal view, about 1/3 carapace length. Carapace as long as wide; gastric and cardiac regions raised, strong antero-branchial protuberance, granulated, tipped with spine or blunt tubercle. Antennal spine blunt or obsolete; protuberance at antero-lateral angle tipped with strong tooth, curved inside; lateral margin posterior to cervical groove entire, granulated. Dorsal carapace roughly granulated; cervical groove poorly marked, pair of large, strong gastric tubercles and conical median tubercle beyond this pair; posterior margin raised.

Surface of sternite 4-6 smooth; sternites 5 to 7 with transverse ridges minutely granulate, not raised. Abdominal segments without spines or tubercles, punctate; transverse ridge on segments 2-4 strong.

Eyes small, without pigmentation and without spines, diameter less than 1/2 length of rostrum.

Antennular basal segment broad, bearing large ventro-internal spine with accessory spinules, sharp external spine and two distal spines, dorsal one directed upwards; outer margin granulated. Outer distal spine of basal antennal peduncle strong, sharp, not reaching distal margin of 3rd segment of antennular peduncle. Merus of third maxilliped with two strong spines on flexor margin (no distal spine); extensor margin armed with one distal spine.

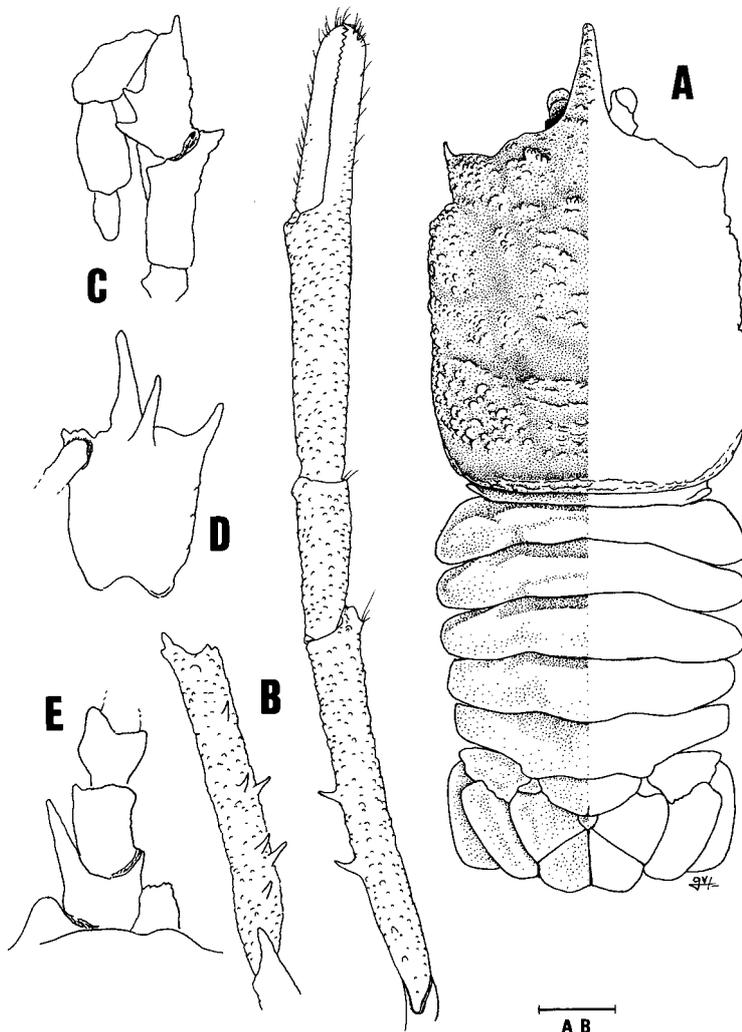


Fig. 3. – *Munidopsis palmatus*. A, Dorsal view. B) Left cheliped, dorsal view, and ventral view of merus. C) Left third maxilliped, lateral view. D) Right basal segment of antenna, dorsal view. E, Left antenna basal segments, dorsal view (scale = 2 mm).

Cheliped about three times as long as carapace, granulated; merus with 5-6 sharp spines on inner margin, one distal. Carpus without spine; chela without spines, longer than merus, flat; palm slightly longer than fingers, wider distally.

Lower and upper margin of manus spineless; fingers flattened, ventral margin of fixed finger and dorsal margin of dactylus spineless. Carpus subcylindrical, about 2/3 length of palm; dactylus shorter than palm.

Pereiopods slender, without spines. Propodus about 3/4 merus length; dactylus falciform, more than half propodus length.

Remarks. – This species, together with three other species described from off the coast of Chile by KHODKINA (1973: *M. verrucosus*, *M. cochlearis* and *M. follirostris*) was overlooked by RETAMAL (1981) and WICKSTEN (1989) in their respective review of the decapod crustaceans of Chile and analysis of the deep-water decapod crustaceans fauna of the east Pacific. The rediscovery of *M. palmatus*, previously known only from the male holotype (8.9 mm CL), in the SE Gulf of California indicates that this species is probably distributed throughout the east Pacific. The original description was in Russian, so the characteristics distinguishing this species from other *Munidopsis* present in the area are presented above.

Both specimens were ovigerous females. The specimen from station 19 carried 7 eggs but had obviously started hatching prior to capture; the female from station 26 carried 12 eggs.

Munidopsis quadrata Faxon, 1893

Munidopsis quadrata FAXON, 1893: 188.

Munidopsis quadrata. – FAXON, 1895; pl. 23, Figs. 1, 1a-c. – BENEDICT, 1902: 325. – HART, 1982: 38. – WICKSTEN, 1989: 315. – HENDRICKX & HARVEY, 1999: 376.

Material examined. – St. 26-IV, 26/VIII/2000, 1 male (TL 31.0 mm), 1225-1240 m, BS.

Previously known distribution. – From Queen Charlotte Islands, Canada to Tres Marias Islands, Gulf of California, Mexico (WICKSTEN, 1989; HENDRICKX & HARVEY, 1999).

Remarks. – The rediscovery of *M. quadrata* in the southern Gulf of California confirms the presence of this temperate species in deep water of tropical Mexico. It is the first record of this species here since it was described by FAXON (1893) from 4 specimens captured at 1220-1225 m off Tres Marias Islands, Mexico. The male specimen reported here is slightly larger than the type material.

Other collected species

In addition to the 16 species treated above in the systematic section, the material from the TALUD IV cruise included nine species (see Table 3) that are briefly treated here. Two species of the strictly pelagic Sergestidae were captured. According to HENDRICKX & ESTRADA-NAVARRETE (1996), *Sergestes halia* Faxon, 1893, is a common species in the southern Gulf of California and extend throughout the eastern tropical Pacific. *Sergia phorca* (Faxon, 1893) shows a similar distribution pattern along the Pacific coast of America, but extends much further southwards, to southern Peru. *Gennadas sordidus* Kemp, 1910, is the only species of *Gennadas* known to the Gulf of California where it occurs abundantly except in the upper Gulf (HENDRICKX & ESTRADA-NAVARRETE, 1996). Adaptation of this species to low oxygen content in the water column consists of a strong increase of branchial surface (HANAMURA, 1983). The rest of the species (*Heterocarpus affinis* Faxon, 1893; *Acantheephyra brevicarinata* Hanamura, 1984; *Glyphocrangon spinulosa* Faxon, 1893; *Munidopsis diomedea* (Faxon, 1893); *M. hystrix* Faxon, 1893; *Nephropsis occidentalis* Faxon, 1893) were also captured during the TALUD III cruise in the same area (Table 4).

TABLE 3

Species of decapod crustaceans collected during the TALUD IV cruise in the SE Gulf of California. Oxygen measured at bottom level. M = male; F = female; FF = ovigerous female; juv. = juvenile.

Species	Station	Depth	Oxygen content	Material examined (size)
Benthescymidae				
<i>Gennadas sordidus</i>	13	1530-1520	1,46	1 F (CL 9.8 mm)
<i>Gennadas sordidus</i>	18	856	1,03	2 M (CL 9.0, 9.5 mm); 1 F (CL 9.8 mm)
<i>Gennadas sordidus</i>	19	1245-1240	0,73	1 juv. (CL 8.5 mm)
<i>Benthescymus tanneri</i>	13	1530-1520	1,46	see text
<i>Benthescymus tanneri</i>	19	1245-1240	0,73	see text
<i>Benthescymus tanneri</i>	26	1225-1240	0,76	see text
<i>Benthescymus tanneri</i>	33	1040	0,51	see text
Solenoceridae				
<i>Hymenopenaeus doris</i>	19	1245-1240	0,73	see text
Sergestidae				
<i>Sergestes halia</i>	4	1260	0,84	
<i>Sergia phorca</i>	26	1225-1240	0,76	1 F (CL 16.0 mm)
Pasiphaeidae				
<i>Pasiphaea emarginata</i>	25	870-835	0,29	see text
<i>Pasiphaea magna</i>	19	1245-1240	0,73	see text

Species	Station	Depth	Oxygen content	Material examined (size)
Oplophoridae				
<i>AcanthePHYra brevicarinata</i>	19	1245-1240	0,73	1 M (CL 20.7 mm); 1 F (CL 28.1 mm)
<i>AcanthePHYra brevicarinata</i>	20	1510	1,26	1 M (CL 27.8 mm)
<i>AcanthePHYra brevicarinata</i>	26	1225-1240	0,76	2 FF (CL 22.0, 22.2 mm)
<i>AcanthePHYra brevicarinata</i>	27	1550-1546	1,32	1 juv. (TL 45.0 mm)
<i>AcanthePHYra brevicarinata</i>	33	1040	0,51	1 FF (CL 21.5 mm)
<i>AcanthePHYra brevicarinata</i>	34	1240-1250	0,79	1 M (CL 11.2 mm)
<i>AcanthePHYra brevicarinata</i>	35	2016-2020	1,68	1 F (CL 11.7 mm)
<i>AcanthePHYra brevirostris</i>	26	1225-1240	0,76	see text
<i>Hymenodora gracilis</i>	35	2016-2020	1,68	see text
Nematocarcinidae				
<i>Nematocarcinus</i> cf. <i>ensifer</i>	13	1530-1520	1,46	see text
<i>Nematocarcinus</i> cf. <i>ensifer</i>	26	1225-1240	0,76	see text
<i>Nematocarcinus</i> aff. <i>ensifer</i>	26	1225-1240	0,76	see text
<i>Nematocarcinus</i> cf. <i>ensifer</i>	33	1040	0,51	see text
Hippolytidae				
<i>Lebbeus scrippsi</i>	19	1245-1240	0,73	see text
<i>Lebbeus scrippsi</i>	26	1225-1240	0,76	see text
Pandalidae				
<i>Heterocarpus affinis</i>	25	870-835	0,29	1 F (CL. 34.8 mm)
<i>Heterocarpus affinis</i>	33	1040	0,51	14 specimens (CL 23.5-38.5 mm)
<i>Pandalus amplus</i>	19	1245-1240	0,73	see text
Crangonidae				
<i>Sclerocrangon atrox</i>	13	1530-1520	1,46	see text
<i>Sclerocrangon atrox</i>	19	1245-1240	0,73	see text
Glyphocrangonidae				
<i>Glyphocrangon sicaria</i>	14	2160-2150	2,44	see text
<i>Glyphocrangon sicaria</i>	26	1225-1240	0,76	see text
<i>Glyphocrangon spinulosa</i>	19	1245-1240	0,73	2 F (CL 22.4, 22.9 mm)
<i>Glyphocrangon spinulosa</i>	26	1225-1240	0,76	3 F (CL 17.1, 17.9 mm); 1 FF (CL 26.6 mm)
Nephropidae				
<i>Nephropsis occidentalis</i>	19	1245-1240	0,73	2 M (CL 32.3, 33.2 mm); 1 F (CL 35.5 mm)
<i>Nephropsis occidentalis</i>	26	1225-1240	0,76	1 F (CL 33.3 mm)
Polychelidae				
<i>Stereomastis pacificus</i>	19	1245-1240	0,73	see text
Paguridae				
<i>Parapagurus foraminosus</i>	14	2160-2150	2,44	1 FF (CL 7.4 mm)
Galatheidae				
<i>Munidopsis ciliata</i>	19	1245-1240	0,73	see text
<i>Munidopsis depressa</i>	25	870-835	0,29	see text
<i>Munidopsis depressa</i>	26	1225-1240	0,76	see text
<i>Munidopsis depressa</i>	33	1040	0,51	see text
<i>Munidopsis diomedea</i>	19	1245-1240	0,73	1 M (TL 65.0 mm)
<i>Munidopsis diomedea</i>	20	1510	1,26	1 FF (TL 73.0 mm)
<i>Munidopsis diomedea</i>	26	1225-1240	0,76	1 juv. (TL 19.9 mm)
<i>Munidopsis hystrix</i>	25	870-835	0,29	4 M (TL 48.4-51.5 mm)
<i>Munidopsis hystrix</i>	26	1225-1240	0,76	1 M (TL 59.0 mm)
<i>Munidopsis palmatus</i>	19	1245-1240	0,73	see text
<i>Munidopsis palmatus</i>	26	1225-1240	0,76	see text
<i>Munidopsis quadrata</i>	26	1225-1240	0,76	see text

TABLE 4

Species of decapod crustaceans collected during the TALUD III cruise in the SE Gulf of California. Species marked with an * have been reported in details elsewhere (see Hendrickx, 1996b).

Species	Station	Depth	Oxygen content (ml/l)
Benthescymidae			
<i>Benthescymus tanneri</i>	14A	1016-1020	0,40
<i>Benthescymus tanneri</i>	14B	1188-1208	0,60
<i>Benthescymus tanneri</i>	24A	1027-1060	-
Oplophoridae			
<i>AcanthePHYra brevicarinata</i>	10A	956-980	0,25
<i>AcanthePHYra brevicarinata</i>	14A	1016-1020	0,40
<i>AcanthePHYra brevicarinata</i>	20A	880-1052	-
<i>AcanthePHYra brevicarinata</i>	24A	1027-1060	-
Hippolytidae			
<i>Lebbeus scrippsi*</i>	14B	1188-1208	0,60
Nematocarcinidae			
<i>Nematocarcinus cf. ensifer*</i>	14A	1016-1020	0,40
<i>Nematocarcinus cf. ensifer*</i>	14B	1188-1208	0,60
<i>Nematocarcinus cf. ensifer*</i>	24	1224-1380	-
<i>Nematocarcinus cf. ensifer*</i>	24A	1027-1060	-
Pandalidae			
<i>Heterocarpus affinis</i>	10A	956-980	0,25
<i>Heterocarpus affinis</i>	14A	1016-1020	0,40
<i>Heterocarpus affinis</i>	20A	880-1052	-
<i>Heterocarpus affinis</i>	24	1224-1380	-
<i>Heterocarpus affinis</i>	24A	1027-1060	-
Crangonidae			
<i>Paracrangon areolata*</i>	14A	1016-1020	0,40
Glyphocrangonidae			
<i>Glyphocrangon spinulosa*</i>	10A	956-980	0,25
<i>Glyphocrangon spinulosa*</i>	24A	1027-1060	-
Nephropidae			
<i>Nephropsis occidentalis*</i>	14B	1188-1208	0,60
Ctenochelidae			
<i>Callianopsis goniophthalma*</i>	24A	1027-1060	-
Axiidae			
<i>Calocarides quinqueseriatu*</i>	10A	956-980	0,25
Polychelidae			
<i>Stereomastis nana</i>	14B	1188-1208	0,60
Galatheidae			
<i>Munidopsis depressa*</i>	10	820-826	-
<i>Munidopsis depressa*</i>	10A	956-980	0,25
<i>Munidopsis depressa*</i>	14A	1016-1020	0,40
<i>Munidopsis depressa*</i>	14B	1188-1208	0,60
<i>Munidopsis depressa*</i>	24A	1027-1060	-
<i>Munidopsis diomedae</i>	19	1188-1208	-
<i>Munidopsis hystrix*</i>	20A	880-1052	-
Atelecyclidae			
<i>Trachycarcinus corallinus*</i>	14B	1188-1208	0,60

Oxygen content in the water column

Analysis of the dissolved oxygen concentration measured close to bottom (Fig. 4) indicated critical hypoxic conditions at depths between 300 and 800 m. Values higher than 1.0 ml O₂/l are found at ca. 1300 m and there is a clear

tendency for oxygen content to increase significantly in deeper water. Values obtained during the TALUD IV cruise in August 2000 are similar, although slightly higher, to those registered at a depth range of ca. 400-1200 m during the TALUD III in August 1991 (Fig. 4). The vertical distribution of oxygen in the area (Fig. 5) indicates the presence

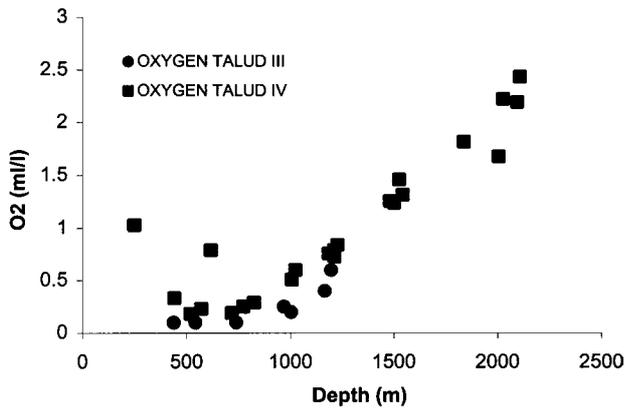


Fig. 4. – Dissolved oxygen concentration measured near bottom during TALUD III and IV cruises.

of three successive environments. The well-oxygenated epipelagic zone ranges from surface to about 80-125 m, with oxygen concentration as high or higher than 2 ml/l. Deeper into the water column, a wide hypoxic to almost anoxic mesopelagic zone is found, extending roughly from 150-200 m to 600-800 m (or to the bottom in stations shallower than 800 m). The deep water benthic-demersal environment is almost anoxic in localities shallower than 600-800 m but oxygen content is higher in deeper localities; oxygen reaches values of 0.5-1.0 ml/l in the depth range of 800-1300 m. In deeper water, there is a strong recovery of the oxygen content, which progressively reaches values above 2.0 ml/l in depths greater than 2000 m (Fig. 4).

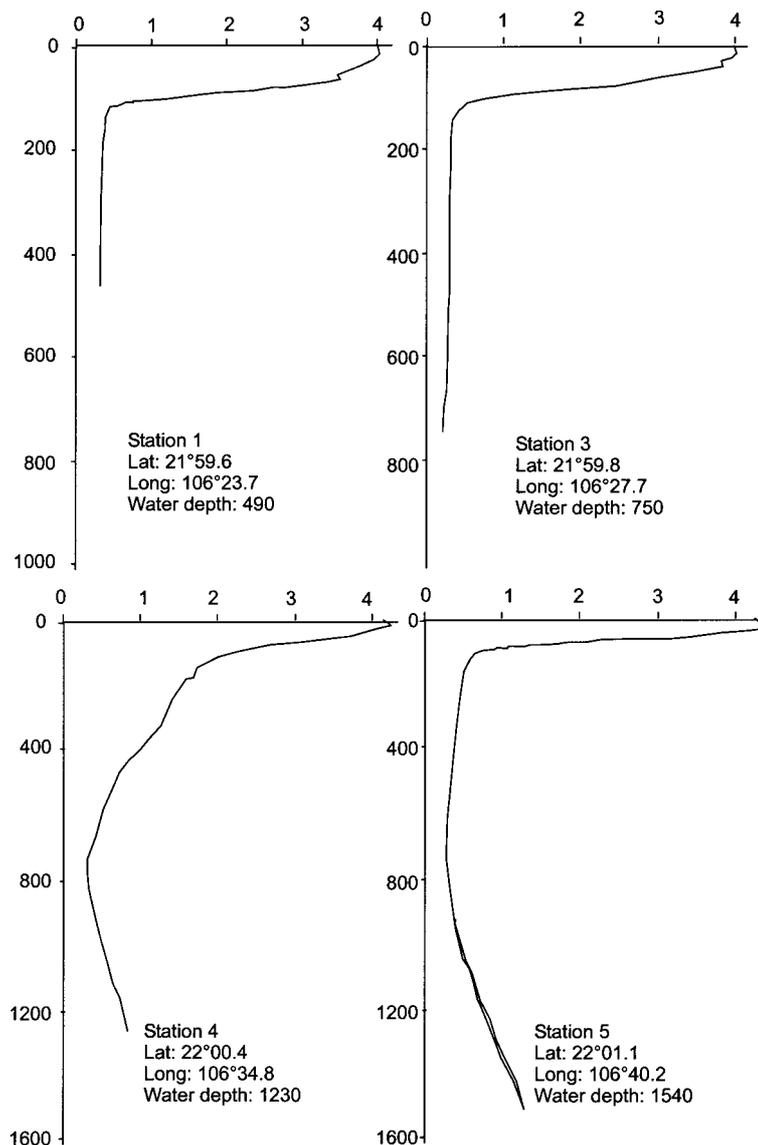


Fig. 5. – Vertical distribution of oxygen at selected stations; TALUD III (St. 9, 10A, 14, 14A, 14B and 15) and TALUD IV (St. 1, 3, 4 and 5) cruises.

Occurrence of deep-water species

A total of 31 species of decapod crustaceans living below 550 m was collected during both cruises (TALUD III, 15 species; TALUD IV, 26 species). Of these, 21 are typically benthic and eight are exclusively pelagic. Three species (*Benthescymus tanneri*, *Acantheephyra carinata* and *Nematocarcinus* cf. *ensifer*) probably have a benthopelagic habitat as they have been collected with both benthic and pelagic gear; adults of these three species are heavy, and there might be a depth or habitat segregation among juveniles and adults. Six species of the deep water galatheid *Munidopsis* were collected. Considering the number of specimens collected, *M. depressa* appears as

the dominant species (324 specimens at four stations) and no other species came near to this abundance. Four species were represented by 9-15 specimens during the entire 2000 survey (*Benthescymus tanneri*, *Nematocarcinus* cf. *ensifer*, *Heterocarpus affinis* and *Acantheephyra brevicarinata*) and the rest were even less abundant (Table 3 and text).

The number of species at each station varied considerably. During TALUD III cruise, the highest number of species obtained at one single station was eight (station depth: 1188-1208 m) and the lowest was one (Table 4). One station, at 820-826 m, yielded only one species of isopod. No strictly pelagic species were recorded. As

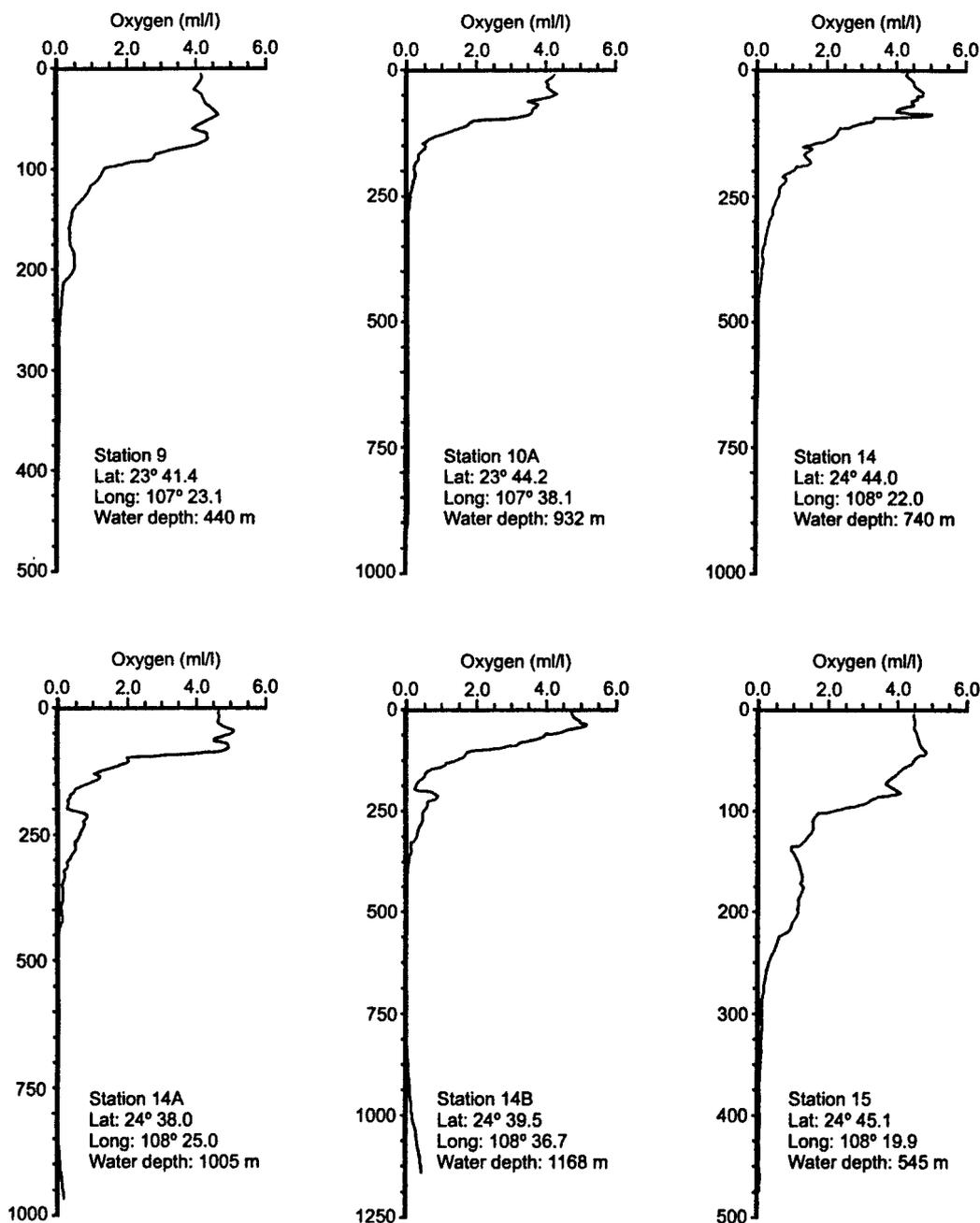


Fig. 6. – Interval of epibenthic oxygen content corresponding to species collected during the TALUD III and IV cruises.

noted previously, the second cruise (TALUD IV) yielded a considerably higher number of species. The highest number of species was obtained at station 19 (15 benthic and one pelagic species), followed by station 26 (12 benthic and one pelagic species) (Table 3). Coincidentally, both samples were obtained in the 1225-1245 m depth range and oxygen content was similar (0.73 and 0.76 ml O₂/l). The highest number of species during TALUD III cruise was obtained in similar conditions: at 1188-1208 m, with oxygen content of 0.60 ml/l. Comparatively, the other stations feature a low species occurrence (Tables 3, 4). Oxygen content at bottom level does not seem to be a critical factor; indeed, the highest oxygen content during the TALUD IV cruise was measured at station 14 (2.44 ml O₂/l) but only two benthic species were caught. The other two stations where oxygen content was above 1.0 ml/l are stations 13 (1.46 ml/l) and 35 (1.68 ml/l) only two benthic species were collected) in both stations. Two stations had four species and both feature a low oxygen content (0.29 ml/l at station 25 and 0.61 ml/l at station 33).

Results obtained during this survey allow us to determine the dissolved oxygen interval at which 21 species

occur (Fig. 6), although for some species only one oxygen value is available. These intervals indicate that all these 21 species are occasionally found in hypoxic conditions, below 1.0 ml O₂/l.

Species occurrence with depth

Combined depth occurrence of species for both cruises indicates that all species, except the Pagurid, were collected at least once within the depth range of 835-1240 m (Fig. 7). Only five species (*A. brevicarinata*, *N. cf. ensifer*, *H. affinis*, *G. sicaria* and *M. diomedae*) range to deeper water. The widest bathymetric range corresponded to *A. brevicarinata*. *Pasiphaea emarginata*, together with *P. magna*, and these were recorded in the pelagic realm. Typically benthic species *M. depressa*, *M. hystrix*, *G. spinulosa* and *H. affinis* feature a relatively wide bathymetric distribution and were rather common in samples (see Tables 3, 4 and text); they dominate the 800-1300 m decapod crustacean community.

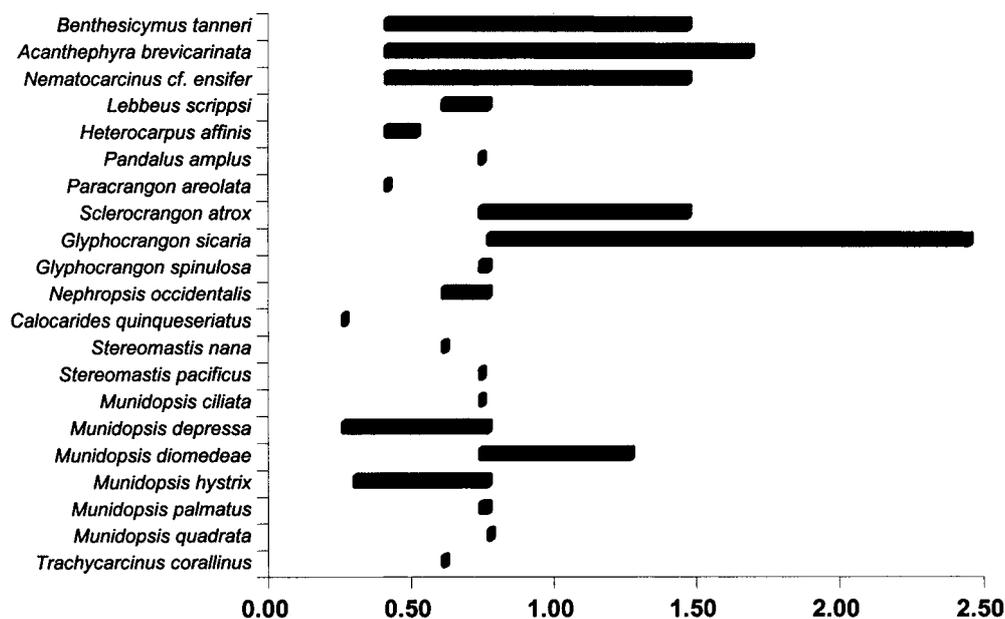


Fig. 7. – Bathymetric range observed for species collected during the TALUD III and IV cruises. (P) probably pelagic species.

DISCUSSION

The total number of species collected during both surveys is 31. Of these, 15 were described by W. FAXON on the basis of material collected by the *Albatross* in 1891. The new results indicate a higher species occurrence in the 1000-1380 m depth range, where hypoxic conditions still prevail, although measurements made near bottom level suggest a recovery in oxygen concentration at ca. 800 m. In the sampling area, oxygen content at bottom

level does not seem to be a critical factor controlling species number, as expected. Fewer species were caught at stations with oxygen content in the range of 1.46-2.44 ml/l than at stations with much lower oxygen content. It might be concluded that, although critically low oxygen content (i.e., < 0.5 ml/l) may represent an impediment for the establishment of a rich benthic fauna, a higher oxygen content does not necessarily favour the presence of a richer fauna. Other factors such as availability of food, nature of substrate or strong submarine currents could affect species occurrence.

With epibenthic values close to 0.0 ml O₂/l (see HENDRICKX, 1995b), the oxygen minimum zone that extends off the coast of the southeastern Gulf of California represented an insuperable barrier for outer-shelf species. Even species known to tolerate low oxygen content (e.g., *Squilla bififormis* Bigelow, 1891, *Solenocera mutator* Burkenroad, 1938, *Pleuroncodes planipes* Stimpson, 1860) are not found in deeper water in the area, despite the fact that there are deep water records of these species in other areas (*S. bififormis*, to 518 m; *S. mutator*, to 360-380 m; *P. planipes*, to 366 m and exceptionally to 730 m) (HENDRICKX, 1995c, 1995d, 1995e). Not a single species belonging to the southeastern Gulf of California decapod crustaceans shelf community (107 species according to HENDRICKX, 1996a) was collected.

The bathymetric fringe extending roughly from 1000 to 1380 m presents a particular interest for its species richness. Food supply and trophic relationships among these species and with large, highly mobile predators (e.g., fishes and squids) that were not sampled during this survey, probably due to the type of sampling gear that was used, are major issues to be addressed. Other major issues include the accessibility to species with fishing potential (e.g., *Heterocarpus affinis*, *Pandalus ampla*, *Benthescymus tanneri*) and the evaluation of standing stock, for which larger and faster sampling gear will have to be used.

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Feeding ecology of Konik horses and donkeys in Belgian coastal dunes and its implications for nature management

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ABSTRACT. Foraging behaviour and diet selection of Koniks and donkeys were studied in order to estimate their possible impact on vegetation development and hence their appropriateness as nature management tools.

Koniks show a larger intake rate and quantity than do donkeys. Koniks do not show significant seasonal differences in biomass intake, whereas donkeys consume significantly more in winter.

Both animal species feed mainly on graminoids. The Konik diet is composed of 86% of graminoids with an additional 12% of herbs. The donkey diet consists of 69 % of graminoids, which are mainly supplemented with browsing (18 %), e.g. twigs and leaves of *Ligustrum vulgare* and *Rubus caesius*.

Calamagrostis epigejos, *Rosa pimpinellifolia* (fruits), *Carex arenaria* and *Arrhenatherum elatius* are the most important plant species eaten by donkeys (based on number of bites and biomass). Koniks eat *Calamagrostis epigejos* significantly more, qualitatively (number of bites) as well as quantitatively (biomass intake), than any other plant species, but *Cirsium arvense*, *Calamagrostis canescens*, *Juncus subnodulosus*, *Holcus lanatus* and *Claytonia perfoliata* are also frequently consumed.

Koniks as well as donkeys do eat plant species that nature managers would like to see decline in dominance, e.g. *Calamagrostis epigejos*, but browsing on scrub species is insufficient to decrease the area occupied by shrubs.

KEY WORDS: foraging behaviour, diet selection, feeding preference, management, dunes, horse, donkey.

INTRODUCTION

During the 19th and the beginning of the 20th century grazing by domesticated livestock was a common practice in the coastal dunes (DE SMET, 1961). Sheep, cattle, donkeys and horses grazed natural vegetation. For example in 1828 the dune area of the western Flemish coast (approx. 2500 ha) was grazed by 450 sheep, 240 cows, 112 donkeys and 51 horses. Wherever they appeared, scrub species were cut down and used as firewood. As a result a semi-natural landscape developed that was largely composed of a mosaic of white dunes, marram dunes, grey dunes, moist dune slack vegetation and dry dune grassland (MASSART, 1908).

Since these agricultural practices were abandoned gradually during the middle of the 20th century shrub development increased. This led to a present-day scrub cover of about two thirds of the remaining open (not built-up) dune area. Among others the area of species-rich dune grassland decreased significantly. These trends, together with the increasing dominance of some competitive grasses e.g. *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Elymus repens*, *Holcus lanatus*, are believed to threaten the relatively large number of dune specific species (VAN DIJK, 1992; TEN HARKEL & VAN DER MEULEN 1995). In addition, part of the landscape changed from a fine-scale mosaic of different habitats to a more or less monotonous shrub vegetation, which is relatively poor in habitat and in coastal dune specific plant and spider species (PROVOOST & HOFFMANN, 1996¹; BONTE et al., 2001²).

Since the legal protection of all Belgian coastal dune areas (Vlaamse Regering, 1993³), interest is growing in the possibility of using appropriate nature management to conserve at least the remaining biodiversity.

Because large herbivores formerly played an important role in the preservation of semi-natural dune communities (WESTHOFF, 1985; HEWETT, 1985; DROST & MUIS, 1988; VAN DIJK, 1992; VAN DEURSEN et al., 1993; KOOIJMAN & VAN DER MEULEN, 1996), the Department of Nature of the Flemish Community decided to introduce cattle, horses, donkeys and sheep into some of their nature reserves.

To reach this goal, equids are considered to be interesting management "tools". Current knowledge about the feeding preferences of equids suggests that they should be very useful to control graminoids (GUDMUNDSSON & DYRMUNDSSON, 1994). They should also affect some tree species (VAN WIEREN, 1987; DUNCAN, 1992). Their impact on herbs and shrubs on the other hand is considered to be lower than that of cattle (DUNCAN, 1992).

While some knowledge is available on the feeding behaviour of domesticated horses under semi-natural conditions in European ecosystems (DUNCAN, 1983; DUNCAN, 1992; PUTMAN et al. 1987; GORDON, 1989), much less is currently known about an almost forgotten equid species, the domesticated donkey (*Equus asinus*) (VAN ASSCHE, 1993; HOFFMANN et al., 2001).

To be able to predict the possible long-term effect of the feeding ecology of these large herbivores, we started a large-scale investigation into their diet preferences and their habitat use and location selection in some coastal dune areas. Here we describe some aspects of the foraging behaviour and the botanical characteristics of the diet of the domesticated donkey and the Konik horse (*Equus caballus*), a horse that is closely related to the Tarpan (*E. ferus silvaticus*).

MATERIAL AND METHODS

Sites, animals and management

In April 1997 a small herd of six donkeys (1 stallion, 5 mares) of Romanian origin was released for year round grazing in the nature reserve Houtsaegerdunes (80 ha).

In 1998 four Konik horses (2 stallions, 2 mares), and two Scottish Highland cattle were released also for year round grazing in the northern fenced area (54 ha) of the nature reserve, the Westhoek.

By March 2000 the Konik herd had grown with one 1999-born foal and the donkey herd then numbered 12 individuals (2 stallions, 7 mares and 3 foals).

The animals received no supplementary feeding. Water was available during the whole period at different sites in the study area.

Shrubs of *Hippophae rhamnoides*, *Ligustrum vulgare* and to a lesser extent *Salix repens* occupy the largest part

of both dune areas. Before the start of the grazing project in the Westhoek 12% of the original 79 % shrub cover was cut down and removed, resulting in an area of ruderal vegetation composed of a low, grass-dominated layer and patches of tall herbs (*Eupatorium cannabinum*, *Lythrum salicaria* and *Cirsium arvense*). Old, deteriorating *Hippophae*-scrubs are generally replaced by *Calamagrostis epigejos* or *C. canescens*. Dune grasslands, moss-rich grey dunes, open sand dune and young dune slacks together occupy another substantial part of both dune areas (Table 1). A typical phenomenon of the Houtsaegerdunes is the non-indigenous plant species, introduced in the past as hedge plants along small fields or escaped from neighbouring gardens (e.g. *Syringa vulgaris*, *Fallopia aubertii*).

Methods

Each month we observed herbivore activities during 48 hours, distributed more or less evenly over 6-hourly morning (6-12 h), afternoon (12-18 h) and evening (18-24 h) sessions. Before starting a session, 1 animal was randomly chosen to be followed for the next 6 hours. Observations were conducted within a 3-m range; animals were not visibly affected by the observations (after a fortnight of habituation to an observer).

Herbivore activities e.g. grazing (food intake), defecating, moving, standing inactive, lying and social interactions were recorded simultaneously by one observer in both areas.

During those observations we used continuous time registration with sessions subdivided in periods of 15 minutes, which is the smallest unit chosen for counting bites and calculating mean bite rates and bite frequencies. All plant species and plant parts seen bitten were recorded. Plant state (dead or alive) was also noted. Mixed bites were registered as different bites of one plant species but were counted only one time for bite rate calculation.

Finally we recorded in which vegetation community and vegetation height class (<10cm, 10-50cm and >50cm) activities occurred.

To estimate mean bite mass of the more frequently consumed plant species, bite simulations were conducted after every observation session. Plants or plant parts were hand-plucked using thumb and a backward bent forefinger, simulating the animals' grazing as closely as possible at the same place where the species was frequently seen bitten (HOBBS et al., 1983; WALLIS DE VRIES, 1994). These samples, consisting of 10 times 30 bites of each plant item, were stored in paper bags, oven dried at 60 °C for 48 hours and weighed to get an estimate of bite mass. Together with the bite rate data, these bite size estimates were used to estimate intake (-rate) at the plant species level.

To investigate diet composition, diet preferences and temporal patterns in feeding ecology, we mainly used

TABLE 1

Main vegetation units of the 'Houtsaeger dunes' and the 'Westhoek noord' based on a vegetation analysis in 1998 respectively 1999 (VAN BRAECKEL unpubl. respectively DEVOLDERE & DEGEZELLE unpubl.).

Vegetation unit + code	Description	Area (ha)	Area (%)	Area (ha)	Area (%)
		Houts.	Houts.	West. N.	West. N.
White dunes (A)	Open vegetation with <i>Ammophila arenaria</i> , <i>Carex arenaria</i> , <i>Festuca juncifolia</i>	2.69	3.6	2.2	4.11
Grey dunes (T)	Moss and Lichen rich dunes				
	With scattered <i>C. arenaria</i> and therofytes.	4.67	5.87	2.8	5.24
Rough vegetations (U/C)	Grass layer (<i>Holcus lanatus</i> , <i>Poa trivialis</i> , <i>Claytonia perfoliata</i>) with scattered patches of tall herbs (e.g. <i>Eupatorium cannabinum</i> , <i>Cirsium arvense</i> , <i>Lythrum salicaria</i>)	none	5.55	10.36	
Ruderal vegetation (C5/U+R)	<i>Arrhenaterum elatius</i> dominated, with other grasses and <i>Urtica dioica</i> , <i>Rubus caesius</i> and <i>fruticosus</i>	4.78	6.01	none	
Dune grasslands (G)	Short grasslands with high plant diversity (e.g. dicotyledons)	0.93	1.17	2.19	4.09
Rose vegetation (I)	Dune grasslands dominated by <i>Rosa pimpinellifolia</i>	2.99	3.76	0.55	1.03
Dune-slack pioneer (J1/(S))	Short pioneer vegetation with <i>Carex</i> spp., <i>Juncus</i> spp. and young <i>Salix repens</i> and <i>Hippophae rhamnoides</i>	0.29	0.36	1.94	3.64
Rough dune-slack (J9/C1/C3)	Tall vegetation dominated by <i>Calamagrostis epigejos</i> , <i>C. canescens</i> and <i>Lythrum salicaria</i>	none		1.4	2.61
Reed	<i>Phragmites australis</i> dominated	0.23	0.3	none	
Deteriorating scrub (H/C1)	Dead scrub of <i>Hippophae rhamnoides</i> , grass layer dominated by <i>C. epigejos</i>	3.13	3.94	5.86	10.95
Scrub (L/H/S/P)	Scrub dominated either by <i>Ligustrum vulgare</i> , <i>H. rhamnoides</i> , <i>Salix repens</i> or mixed with other shrubs + sometimes herb layer with <i>Claytonia perfoliata</i> .	54.38	68.4	30.08	56.21
Wood (B)	<i>Populus</i> spp. or <i>Alnus glutinosa</i> dominated wood patches	4.64	5.8	0.16	0.31
paths	Pioneer vegetation of dry or wet situations	0.8	1	0.78	1.45
Total		79.53	100	53.51	100

ANOVA for testing significance of differences between means (F-test). Means were usually based on data at the 15-minute level. In case of inconsistency with the assumptions of ANOVA even after data transformation we used Kruskal-Wallis One way analysis (SOKAL & ROHLF, 1995; SIEGEL & CASTELLAN, 1988). For a test of normality and of homogeneity of variances we used respectively the Kolmogorov-Smirnov and Levenes test.

Multiple comparisons among means were carried out using an a posteriori HSD (equal variances assumed) or Games-Howel test (unequal variances) in SPSS 7.5 for Windows (NORUSIS, 1997).

To compare plant species preference we used the diet-availability ratio (COLEBROOK et al., 1987), discussed by STUTH (1991):

$$D/A = \{(\% \text{ Diet} - \% \text{ Availability}) / (\% \text{ Diet} + \% \text{ Availability})\} * 10$$

STUTH (1991) used the following expressions for three different classes: preferred species: $D:A > 0.35$; desirable

species: $-0.35 < D:A < 0.35$; undesirable, avoided or forced species: $D/A < -0.35$.

As a measure of diet we used the number of bites in summer, as a measure of availability we used the above ground biomass of every species in summer in the vegetation patches visited by the animals during the observation sessions (COSYNS & DEVOLDERE, unpubl.).

RESULTS

Bite rate and bite frequency

Bite rate (bites/min. grazing) of Koniks is significantly higher than that of donkeys. This is the case over all seasons with the greatest difference in summer and the smallest in winter (Table 2). Bite rate of both animals varies with seasons. Koniks graze substantially faster in summer than in autumn and winter ($p < .001$). Bite rate of donkeys shows the opposite trend; winter bite rate differs significantly from bite rate in summer and autumn ($p < .001$).

Bite frequency (Bites/min. observation time) of Koniks does not show any significant difference between seasons. On the contrary, donkeys reach a substantially higher bite frequency in winter than they do in the other two seasons ($p < .001$) (Table 3).

Koniks spend significantly more of their time grazing (73%) than do donkeys (52%) ($p < .001$). Neither Koniks nor donkeys show a significant seasonal variation in grazing pattern, although donkeys tend to increase grazing time from summer to winter (Fig. 1).

TABLE 2

Variation in mean bite rate (bites/ min. foraging time) of konik and donkey per season. All results are significantly different between both herbivores within seasons (columns) ($p < .001$).

(Bites/min. grazing)	Seasons		
Animal	Summer	Autumn	Winter
Konik	33.74	24.10	26.28
Donkey	10.41	12.59	18.13

TABLE 3

Bite frequency (bites/min. observation time) of konik and donkey per season. Bite frequency is used as a preliminary measure for their intake. Therefore mean bites/min. observation time is compensated for differences in mean bite rate between seasons. Significantly different results ($p < .001$) between periods are indicated (***)

(Bites/min. observ.)	Seasons		
Animal	Summer	Autumn	Winter
Konik	20.12	18.66	20.05
Donkey	6.30	6.80	8.60 (***)

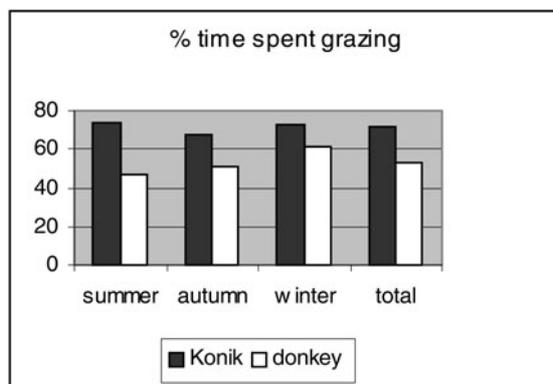


Fig. 1. – Mean grazing time of konik and donkey as % of total observation time/season. Koniks spend significantly more of their time grazing than donkeys ($p < .001$). Koniks do not show significant seasonal differences. Donkeys tend to increase foraging time from summer to winter (but $p = 0.052$, F-test).

Forage class

We observed significant differences ($p < .001$) among animal species, although they both feed mainly on grasses and grass-like species. The diet of the Konik horse is composed of 86% grasses, the remainder being mainly herbs e.g. *Cirsium arvense*, *Stellaria media* and seedlings of *Claytonia perfoliata* (12%). Woody species (mainly *Rubus caesius*) are only consumed in small amounts. Graminoids were eaten significantly more in summer than in autumn or winter ($P < .001$). Herbs (mainly *Claytonia* and *Stellaria*) were eaten substantially more in winter (Table 4).

TABLE 4

General diet composition (% of total number of bites) of konik and donkeys in two Belgian coastal dune nature reserves during summer-winter 1999-2000. Overall number of bites (compensated for differences in observations) is significantly different between both equid species ($p < .001$).

Forage class	Summer	Autumn	Winter	Total (***)
Konik				
Graminoids	93.6	87.1	80.6	86
Herbaceous plants	4.4	11.2	18	12
Woody plants (browse)	2	1.7	1.4	2
Donkey				
Graminoids	60.6	79.5	86	69
Herbaceous plants	10.4	7.4	6.6	13
Woody plants (browse)	29	13.1	7.4	18

The donkey's diet consists of 79 % graminoid species, the remainder provided mainly from browsing of woody species, e.g. twigs and leaves of *Ligustrum vulgare* and *Rubus caesius*, fruits of *Rosa pimpinellifolia* and *R. canina* (13%). Woody material was eaten more in summer and autumn than in winter ($p < .001$). Herbs were the smallest part in this diet (8%) and were mainly eaten in winter (*Claytonia perfoliata*).

Plant species

Koniks and donkeys consume a wide variety of plant species. During the whole observation period Koniks ate 89 plant species: 24 graminoid species, 54 herb species and 11 woody species.

During the same period donkeys ate 111 plant species: 18 graminoid species, 63 herb species, 27 woody, 1 fern, 1 lichen and 1 moss species.

In both cases about one third of all plant species known in the respective study areas were bitten.

With mean bites/min. foraging time as the criterion, the Konik diet over the whole period was mainly composed of grasses. *Calamagrostis epigejos*, *Poa trivialis* and

(1991), we found some similarities but also some striking differences. Koniks prefer *Holcus lanatus*, *Calamagrostis epigejos* and desire *Rubus caesius*, whereas *Eupatorium cannabinum*, *Cirsium arvense* are undesirable (Table 7). Donkeys prefer *Carex arenaria* and desire *Calamagrostis epigejos* and *Avenula pubescens*. Undesirable to donkeys were e.g. *Arrhenaterum elatius*, *Rubus caesius*, *Ammophila arenaria*, *Festuca rubra* and *Achillea millefolium*.

TABLE 7

Plant species preferences of konik and donkey expressed by the diet-availability ratio (COLEBROOK et al., 1987).

Only those Plant species of which the total available biomass exceeds 1% of the total biomass in the area are taken into account.

Preferred D/A > 0.35	
Konik	Donkey
<i>Holcus lanatus</i>	<i>Carex arenaria</i>
<i>Calamagrostis epigejos</i>	
-0.35 < Desirable D/A ≤ 0.35	
<i>Rubus caesius</i>	<i>Calamagrostis epigejos</i>
Undesirable D/A ≤ -0.35	
<i>Eupatorium cannabinum</i>	<i>Avenula pubescens</i>
<i>Rosa pimpinellifolia</i>	<i>Arrhenaterum elatius</i>
<i>Cirsium arvense</i>	<i>Ammophila arenaria</i>
	<i>Rubus caesius</i>
	<i>Achillea millefolium</i>

Plant parts and plant state

Green leaves are by far the most bitten plant parts by both herbivore species (Table 8). This is certainly true for all grass (-like) species, but not necessarily the case for herbaceous or woody plant species. For example donkeys prefer fruits of *Rosa* spp. and the inflorescences of

Hieracium umbellatum, *Melandrium album* and *Eupatorium cannabinum* above their foliage.

Koniks were seen biting inflorescence, young leaves and shrivelled plants of *Cirsium arvense*, inflorescences of *Eupatorium cannabinum* and, to a much lesser extent, fruits of *Rosa pimpinellifolia* and *Rubus caesius*. During winter Koniks not infrequently dig up and consume roots and rhizomes of *Urtica dioica* and *Epilobium hirsutum*.

DISCUSSION

Temporal feeding behaviour

As hindgut fermenters equids have to spend a lot of their time foraging (DUNCAN, 1992, ILLIUS & GORDON, 1993). Free-ranging horses devote 50-70% of their time to eating and only 20-30% to resting. Towards the autumn the time spent grazing increases (GUDMUNDSSON & DYRMUNDSSON, 1994). However, the increase in foraging time is limited. Camargue horses -although nutritionally stressed at the end of the winter show only a slight increase of 6 % in feeding time, suggesting a certain threshold above which further increase in feeding time would not outweigh the costs of sleep deprivation or fatigue (DUNCAN, 1992).

Our results with Koniks are to some extent in agreement with these conclusions, although grazing time in summer and autumn appears to be only slightly greater (3%) than time spent grazing in winter. Perhaps Koniks are at the border of feeding capacity in the winter- not being able to enlarge consumption anymore. The rather poor condition of one of the lactating mares in winter can be interpreted as a first signal for nutritional stress and the inability to increase intake for maximum nutrient assimilation. We therefore hypothesise that the feeding strategy of Koniks is based on high intake when food items are of high quality and best available (late spring, summer and early autumn) and that they rely upon their body reserves during periods of inadequate food availability.

TABLE 8

Konik and donkey diet composition at the plant part level (% of total number of bites)

Forage class	leaf	stem	Flower	fruit	seedling	root	bark
Konik							
Graminoids	73.07	0.01	0	0	0	0	0
Herbaceous plants	9.79	7.19	0.44	0.07	7.25	0.17	0
Woody plants	0.95	0.72	0.01	0.23	0.03	0	0.07
Total	83.81	7.92	0.45	0.3	7.28	0.17	0.07
Donkey							
Graminoids	71.71	0.27	0.42	0.29	0.19	0.01	0
Herbaceous plants	5.91	5.46	0.40	0.26	0.01	0.03	0
Woody plants	6.49	4.78	0.06	3.41	0.01	0	0.29
Total	84.11	10.51	0.88	3.96	0.29	0.04	0.29

Donkeys increase their intake significantly in winter and hence are able to maintain good condition. Donkeys are capable of consuming fibre at a high rate because of an efficient tooth and jaw apparatus and an ability to swallow larger feed particles (MUELLER et al., 1998). Donkeys are also known to be capable of digesting low quality food. Compared to horses, they have lower energy requirements (IZRAELY et al., 1989a; IZRAELY et al., 1989b). We suggest that a combination of these factors makes it profitable for them to feed more in winter. So donkeys seem to behave in a slightly different way when faced with decreased quality but still adequate quantities of food.

Botanical aspects of the diet

Free ranging horses consume a wide variety of plant species and are seasonally dependent in their selection. The availability of plant species has a great influence on their selection (GUDMUNDSSON & DYRMUNDSSON, 1994). Horses prefer grasses and other graminoid species above herbaceous species that have a larger amount of less favourable secondary compounds (PUTMAN et al., 1987; GORDON, 1989; DUNCAN, 1992; GROOT BRUINDERINK et al., 1997). Diet selection by Koniks and donkeys is quite similar. They seem to select first those graminoid species that are common and widespread. When it is possible, they can be very selective, consuming leaves and twigs, flowerheads or fruits of different herbaceous or woody species, which perhaps offer them some indispensable nutrients. At such times donkeys seem to prefer woody as well as herbaceous species whereas Koniks seem to select almost only herbaceous species. Reasons for that remain unclear. Nevertheless many herbaceous species are almost not or never eaten presumably because of secondary compounds or structural defences.

So far both animals can be considered as interesting nature management 'tools':

First of all Koniks as well as donkeys eat dominant plant species that nature managers would like to see decline in dominance, e.g. *Calamagrostis epigejos*, *Arrhenaterum elatius* and *Cirsium arvense*. However, browsing on scrub plants is insufficient to cause a visible decrease in their presence. Only some trimming effect and ring barking are achieved by the donkeys, while the Koniks have no foraging impact on scrub plants whatsoever. This minor impact of both equids on woody species might, however, result from the relative abundance of the more preferred graminoid species. In other areas, where graminoid presence is limited, donkeys have had considerable impact on woody species (VAN ASSCHE, 1993; VELTER, pers. comm.).

Within the given circumstances of relatively low-productive dune ecosystems, both animal species seem to perform well. Generally they cope well with periods of scarcity of food resources. However, they use different

feeding strategies, presumably based on physical and physiological differences.

Before deciding on herbivore species and densities to be used for specific management goals, the feeding ecology of other large herbivores and of the effects of increasing animal densities on animal diet selection and vegetation dynamics need further attention. Clearly further assessment of food quantity and quality is inherent within this kind of research.

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Feeding behaviour in the bumble bee *Bombus terrestris*

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ABSTRACT. Bumble bees (*Bombus terrestris*) are social insects that live in one-year colonies. Larvae are fed progressively by the workers up until the moment they pupate and transform into adults. An elaborate hypothetical scheme concerning the dynamics of feeding behaviour is presented. The central hypothesis is that larvae emit a hunger-signal that can inform workers about their nutritional status and thereby influence the feeding behaviour of the workers. In addition it is hypothesized that the receptivity of the workers for the hunger signal and their motivation also influence their decision whether or not to go and feed larvae. This contrasts with the prevalent view that workers impose a feeding regime on larvae, who passively undergo their rearing. Worker (feeding) behaviour in a number of colonies was recorded and experiments were conducted in order to elucidate several aspects of the dynamics of feeding behaviour. In the experiments presented here the strength of the hunger signal was manipulated in various ways: by starving larvae, feeding artificial food to larvae in vivo, and varying the number of larvae. The results of the experiments indicate that indeed in *B. terrestris* larvae emit a short-range hunger-signal that can be perceived by workers and that can trigger worker behaviour such as "long pollen eating" (which usually precedes feeding) and feeding larvae. This strongly suggests that a feeding regime is not simply imposed on larvae by workers. However, the motivation of workers also plays a decisive role in feeding behaviour.

KEY WORDS: *Bombus terrestris*, bumble bee, feeding behaviour, pollen eating, larvae, hunger signal, caste determination.

INTRODUCTION

Bumble bees are social insects that live in one-year colonies. The queen lays the eggs and the workers perform all necessary duties, among others foraging and feeding larvae. In *Bombus terrestris* (Latreille) larvae are fed progressively with a mixture of pollen and nectar plus some glandular secretions (PEREBOOM, 2000). At the colony level the feeding rate seems to be well regulated (PENDREL & PLOWRIGHT, 1981). At the level of individual larvae, however, regulation of the feeding rate appears relatively poor; the time between successive feedings of a larva varies considerably (PENDREL & PLOWRIGHT, 1981; RIBEIRO, 1999).

RÖSELER & RÖSELER (1974) refer to several authors who reported that in *Bombus* species some larvae are fed

more than others, e.g. because of their position in the brood clump, and that this determines their final size. The prevalent view is that the workers impose a feeding regime on the larvae who passively undergo their rearing (RÖSELER, 1970, 1991; see also PLOWRIGHT & JAY, 1977). Contrasting with this view is evidence from PEREBOOM (1997) that workers are able to perceive the nutritional status of larvae and adjust their behaviour accordingly: He showed that starved larvae are fed more often than non-starved larvae. In addition, PEREBOOM (1997) found that larvae ingest food on their own account, and are capable of refusing food. These findings suggest a more active role of the larvae.

Before being able to feed, a worker needs to drink nectar and eat pollen. DUCHATEAU (unpublished data) found that workers who fed larvae after pollen eating ate pollen significantly longer than workers that did not feed after pollen eating (workers were observed for 30 minutes after they had stopped eating pollen). She also found that workers who were going to feed larvae spent more time on the

broodnest and more time manipulating the larvae's wax envelopes than workers who were not going to feed.

The work of PEREBOOM (1997) and DUCHATEAU (unpublished data) strongly suggests that workers initiate pollen eating and feeding in response to information they perceive concerning the nutritional status of larvae. Both PEREBOOM (1997) and RIBEIRO (1997) suggested that larvae produce some kind of stimulus that elicits feeding behaviour. On the basis of their work we hypothesized that larvae emit a signal that can inform workers about their nutritional status ("hungryness"). The fact that there is considerable variation in the characteristics of the feeding behaviour of an individual worker (PENDREL &

PLOWRIGHT, 1981; RIBEIRO, 1997, 1999; PEREBOOM, 1997) is an indication that receptivity for the hunger signal and the motivation to feed of the workers also play a role in feeding behaviour. In addition, many other factors may influence the dynamics of feeding behaviour. On the basis of literature and our hypotheses we made a schematic representation of the dynamics of feeding behaviour (Fig. 1). Several experiments were conducted to test the validity of this scheme. In this paper, experiments investigating the presence of the hunger signal are presented. This was done by starving larvae, manually feeding larvae in vivo and varying the number of starved larvae.

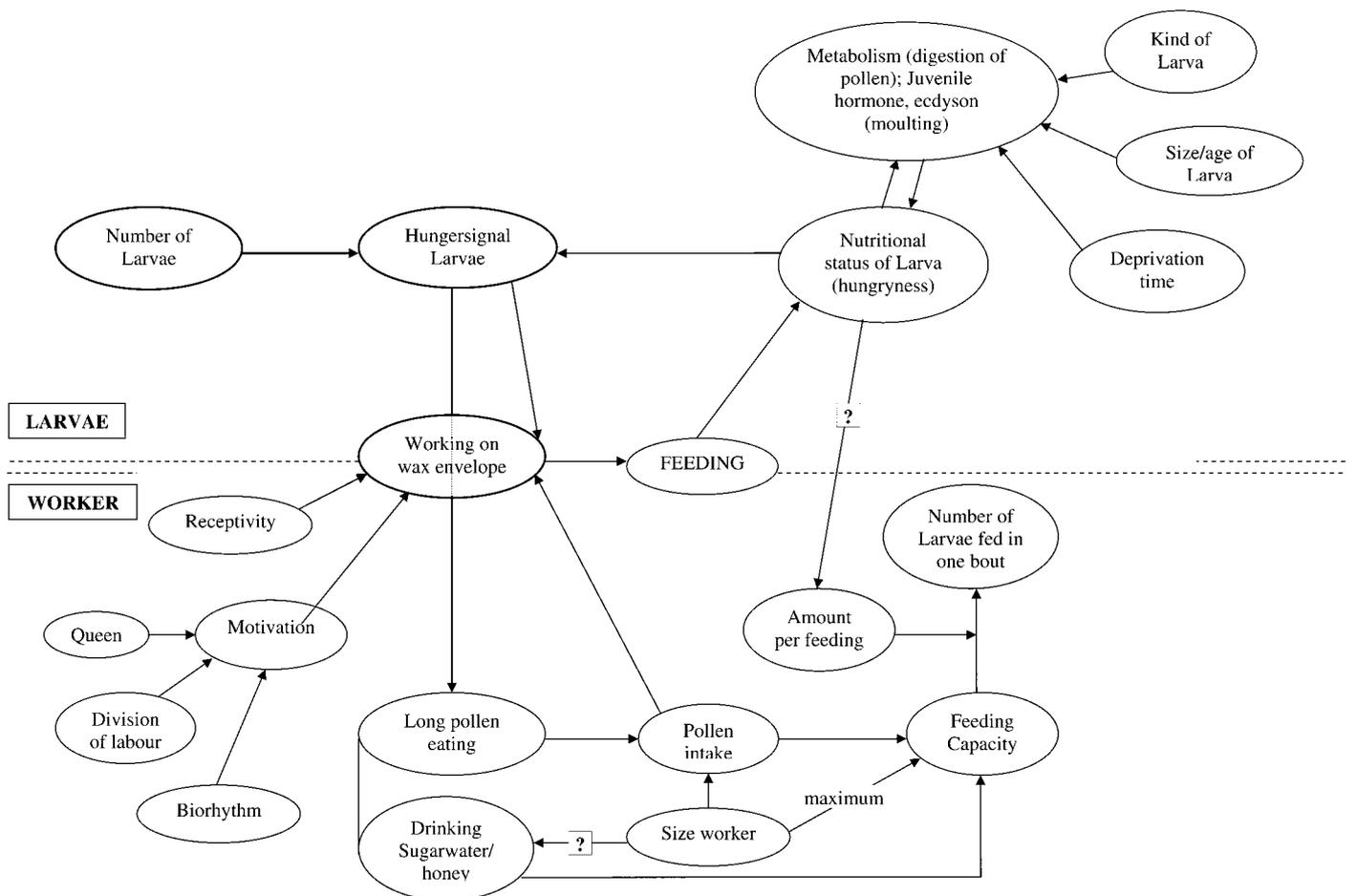


Fig. 1. – Hypothetical schematic representation of the dynamics of feeding behaviour.

MATERIAL AND METHODS

All observations and experiments were conducted under standard laboratory conditions in a climate-controlled room (28°C, 60% rH), illuminated by red light. Colonies of *Bombus terrestris* were reared and kept in the laboratory under the same conditions and provided with ad libitum pollen and sugar water (DUCHATEAU & VELTHUIS, 1988). Data were transformed and analyzed using Microsoft Excel 97 and SPSS 9.0.0 for Windows.

Observations of feeding behaviour in a colony

Young colonies were placed in an observation room (28°C, 60% RH) and connected to a small flight cage (40*50*66 cm) with a plastic tube (inner Ø 15mm). The flight cage was covered by a non-transparent cloth and illuminated by a UV-lamp (TL/05 40 Watt) from 9.30 hours till 21.30 hours. A container with sugar water (1:1) was provided in the flight cage, ad libitum pollen in the nest box. Observations started as soon as the bees had

learned to forage for the sugar water. Non-foraging workers were selected and marked by glueing a small numbered tag on their thorax. Marked workers were followed for at least 15 minutes until one of them started eating pollen. From that moment on all behaviour of this worker was continuously recorded for at least 90 minutes according to an elaborate ethogram using The Observer version 3.0 (Noldus Information Technology 1994). For the sake of simplicity, only one behavioural state was active at a time. If, at the end of 90 minutes of observation, the worker had just eaten pollen or was in the middle of a feeding bout the observation was continued up to 120 minutes. In this way 13 different workers from six colonies were observed. One worker was observed ten times, the others one, two or three times depending on whether or not they were the first of the marked workers in a colony to start eating pollen. The total number of observation sessions was 29.

From the observational data, the duration of each behavioural element was calculated. Later, several intervals related to feeding behaviour, such as the time between the end of a Pollen Eating (PE) session and the first feeding, and the time between the last feeding in a bout and the next PE-session, were calculated. If the time between two instances of pollen eating (PE) was smaller than 30 s, the durations of the two PE-sessions were lumped and counted as one PE-session. If the time between two instances of pollen eating exceeded 20 minutes (1200 s) and no larvae were fed, the two PE-sessions were considered separate sessions. If the time between two instances of PE was between 30 s and 20 minutes (1200 s) and no larvae were fed, the durations of PE were lumped but counted as two sessions (of one "pollen-eating bout").

Feeding behaviour has the following characteristics: a worker (or queen) manipulates the wax envelope surrounding (a clump of) larvae and makes a small opening with her mandibles, if necessary. Then she inserts her mandibles, antennae, and part of her head, and after 0.5 up to about 10 seconds of "positioning" she sits motionless for a short time (0.5-5 seconds) and subsequently regurgitates a droplet of food from her honey stomach onto the ventral side of the larva by contracting and/or elevating her abdomen. After that, she either closes the orifice or manipulates it for some time (see also KATAYAMA, 1973, 1975; RIBEIRO, 1999). The feeding behaviour as described above is usually repeated several times in a short period of time, comprising a feeding bout (KATAYAMA, 1973, 1975 for *B. ignitus* and *B. hypocrita*; PENDREL & PLOWRIGHT, 1981).

Choice experiment starved/non-starved larvae

A standard observation box (20x30x7 cm) was divided into three compartments by two pieces of metal grid. In one of the grids there was a small flexible piece allowing the experimenter to open and close a small door. In the

middle compartment sugar water and pollen were available.

Larvae of roughly similar size (aged 4-7 days) were taken from several colonies and placed in groups of ten to 12 in flat cups constructed from bee wax. The cups were covered with a thin layer of the larvae's own wax envelope and, if there was not enough of that, with involucreum, in order to mimic a natural group of larvae. The cups were placed two by two in boxes with five workers that were seen to manipulate wax in a colony, allowing the workers to "remodel" the wax covering of the cups. In the first trial, half of the cups were put separately in a box after several hours, starving them overnight (14-17 hours). In the second trial, sugar water and pollen were provided initially but the pollen was taken away from half of the boxes for the night to prevent the workers from feeding larvae. The next day a group of starved and a group of non-starved larvae were placed in one of the outer compartments of the observation box, alternately left and right of the small door, about 2 cm from the metal grid.

In the first trial, one worker that was observed to feed larvae was taken from a colony and put in the middle compartment. After 15 minutes of habituation the small door was opened allowing the worker to access the compartment containing the two groups of larvae. For the following 10 minutes it was recorded on which group of larvae the worker was present and for how long. Also the occurrence of feeding and the first choice (the group of larvae she walked on first) of the worker was recorded. Then the observation box was cleaned with wet tissue to remove possible scent marks. After 3-4 hours the group of non-starved larvae was replaced by a new one. This procedure was repeated 25 times in 3 days.

In the second trial a group of five workers that were observed pollen eating or sitting on the main pollen store (located in a petri dish 5 cm in diameter) were taken from a colony and placed in the main compartment of the observation box. After the small door was opened, the occurrence of feeding and the first choice of workers were recorded. This procedure was repeated 30 times in 3 days.

Manually feeding a group of larvae in vivo

Twelve queen larvae in two different colonies were used. Six randomly chosen queen larvae were manually fed artificial food during 2 hours. This was repeated three times. During the experiment feedings by workers to these larvae and six control larvae were recorded. The artificial food consisted of a mixture of 10 g glucose and 40 g fructose filled up to 100 ml with tap water plus 1/3 volume of pollen (PEREBOOM, 1997). On two days the manual feeding regime was 19 µL every 20 minutes, on one day 9 µL every 10 minutes for 1 hour and then 3.5 µL every 5 minutes for the second hour.

Varying the number of larvae

Larvae aged 5-7 days were taken from colonies and put into flat cups constructed of bee wax in groups of approximately five or approximately 15 larvae using the same procedure as in the choice experiment described before. When larvae had recuperated sufficiently, the cups were put apart from the workers and starved overnight (16-20 hours). Then, a feeding worker was obtained from a colony. Her abdomen was pressed gently so as to remove the food store in her honey stomach. Subsequently she was placed in a standard observation box with a cup of starved larvae and provided with sugar water. After 1.5-2 hours of habituation, pollen was provided and the pollen dish and the larvae were videotaped for 6-9 hours using a Euromex tablecamera. Afterwards the tapes were analyzed recording all instances of Pollen Eating and Feeding larvae. In this way 11 sessions were done with groups of about five larvae of which ten sessions were used for further data analysis (one session yielded no data). Thirteen sessions were done with groups of about 15 larvae of which 11 sessions were used for further data analysis.

RESULTS

Feeding behaviour in a colony

In order to get a detailed impression of feeding behaviour, individual workers in a colony were observed continuously for 90 minutes or longer. Here, only the duration of Pollen Eating (PE) and the number and timing of feedings will be presented.

PE not followed by Feeding (FE) consisted of one eating session in seven out of nine cases (78%). The mean frequency of PE not followed by feeding was 0.24 ± 0.51 times per hour. The mean duration of PE not followed by feeding was 72 ± 79 s.

PE followed by FE was much more frequent, on average 1.85 ± 1.53 times per hour and consisted of one eating session in 27 out of 44 cases (61%). In the other cases (39%) PE followed by FE consisted of more than one eating session. Thirteen out of these 17 "eating bouts" (76%) consisted of two sessions (30% of the total, $30\text{s} < \text{interval time} < 1200\text{s}$). The mean duration of PE followed by FE was 287 ± 187 s. This was significantly longer than the mean duration of PE not followed by feeding (Mann Whitney U test $p < 0.01$, $n=9$ and $n=48$ respectively). This confirms the finding of DUCHATEAU (unpublished data) that on average workers eat pollen significantly longer before feeding larvae.

Choice experiment starved/non-starved larvae

To investigate whether or not workers are able to discriminate between starved and non-starved larvae from a distance of 2 cm, two choice experiments were conducted. One using one worker and one using a group of five workers. Table 1 shows the first choice of workers in both experiments. Clearly, the first choice of workers is not biased. Also, the

mean time workers spent on the broods in the one worker experiment did not differ between the two broods (starved: mean 167 ± 199 s, non-starved: mean 241 ± 214 s, paired samples t-test, $n=25$, $p=0.334$). A similar result was obtained for the five worker experiment (scan sampled, paired samples t-test, $n=30$, $p=0.365$). From this it can be concluded that workers did not prefer one or the other brood. However, in the five worker experiment nine feedings were observed, all involving starved larvae. This suggests that workers were unable to distinguish between broods of starved and non-starved larvae from a distance, but that they were able to do so when they had access to the broods.

TABLE 1

First choice of workers that were alone or in a group of five and were given access to a brood of starved and a brood of non-starved larvae. First choice indicates the brood that was visited first.

Experiment	First Choice		χ^2	p-value
	starved brood	non-starved brood		
1 worker	12	13	0.040	0.841
5 worker group	24	23	0.021	0.884

Manually feeding a group of larvae in vivo

To study in vivo whether or not workers respond to the nutritional status of larvae and the corresponding strength of their hunger signal, in a colony six out of 12 queen larvae were selected and manually fed artificial food in order to saturate them. The other six larvae served as a control. The experiment lasted two hours, during which all feedings by workers were recorded.

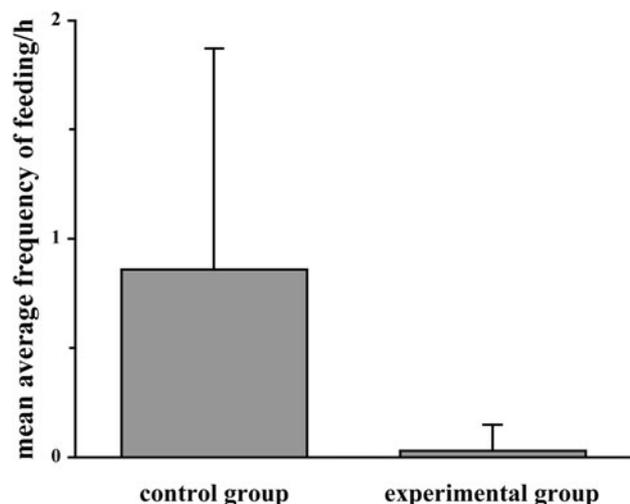


Fig. 2. – Mean average frequency/hour at which a control ($n=18$) and an experimental group of larvae ($n=18$) in a colony were fed by workers. Larvae in the experimental group were fed manually with artificial food. The frequency of feeding differs significantly between the two groups (t-test $p=0.003$).

Fig. 2 shows the mean average frequency at which larvae in the two groups were fed by workers during the experimental period. The control group was fed more by workers than the group that was fed manually ($p=0.003$). In fact, in the experimental group only one larva was fed once. Apparently, workers were able to perceive the nutritional status of larvae and they adjusted their feeding behaviour accordingly.

During the experiment a novel behaviour was observed: workers were seen to suck away the artificial food given to the larvae of the experimental group (mean frequency = 2.17 ± 1.61 times/hour/larvae, $n=18$). This “sucking away” occurred at least sometimes while larvae were still eating, which rules out the possibility that workers removed the artificial food because larvae were saturated.

Varying the number of larvae

In order to investigate the effect of the strength of the larval hunger signal on the feeding behaviour of individual workers, the pollen eating and feeding of workers confronted with broods of five or 15 starved larvae was observed. In addition, the data from the observations done in a colony were used (see before).

It was assumed that under the experimental condition a measure for the strength of the hunger signal, which triggers workers to feed larvae, is the duration of the adding pollen-first PE interval. Therefore the mean duration of this interval in the two experimental groups was compared. There was no difference between the five and 15 starved larvae groups (five starved larvae: mean 6271 ± 5303 s, 15 starved larvae: mean 4073 ± 3529 s, Mann Whitney U test, $n=10$ for both groups, $p>0.10$).

Another measure of the effect of the hunger signal on worker behaviour is the average frequency of feeding during the experimental sessions. This is shown in Fig. 3, in which the relationship between the average frequency of feeding in a session and the duration of the adding pollen-

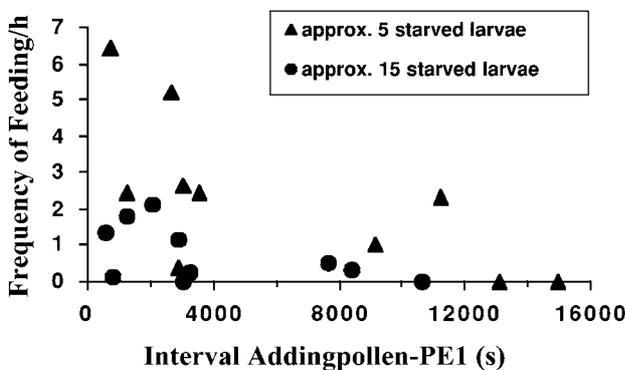


Fig. 3. – Feeding frequency after the adding pollen-PE1 interval versus the duration of the adding pollen-PE1 interval for the 5 ($n=10$) and the 15 ($n=10$) starved larvae group. For both groups there is no significant correlation (5 starved larvae $r=-0.456$, $p=0.185$, 15 starved larvae $r=-0.398$, $p=0.255$, combined ($n=20$) $r=-0.236$, $p=0.317$).

first PE interval for the two groups of workers is plotted. For both groups the correlation is not significant. However, an adding pollen-first PE interval longer than 4000s clearly corresponds with a low or zero frequency of feeding. The mean feeding frequency of the five starved larvae group tends to be higher than that of the 15 starved larvae group (Mann Whitney U test, $p=0.081$), contrary to the expectation. Interestingly, the average feeding frequency of a single worker in a colony is significantly higher than that in both experimental sessions (Kruskal Wallis $p<0.05$; Mann Whitney U test natural ($n=29$)-five starved larvae $p=0.029$, natural-15 starved larvae $p<0.001$, means \pm SD: natural 4.2 ± 2.4 , five starved larvae 2.3 ± 2.1 , 15 starved larvae 0.76 ± 0.78 times/hour). This suggests that both experimental settings had an effect on worker feeding behaviour and indicates that the motivation of workers also plays a role.

Another measure of the strength of the hunger signal is the time between PE and the first feeding following that PE. A short PE-first feeding interval is assumed to reflect that a worker is reacting on the hunger signal. In Fig. 4 the mean duration of the PE-FE1 interval is shown for the three groups. The “natural” group does not differ from the five starved larvae group (Mann Whitney U test $p=0.698$) and both these groups have a shorter mean PE-FE1 interval than the 15 starved larvae group (Mann Whitney U test 15-natural $p<0.001$, 15-5 starved larvae $p=0.001$). Again, workers in the 15 starved larvae group appear to be less motivated by the hunger signal than workers in the five starved larvae group, contrary to the expectation. Thus, measuring the strength of the hunger signal is complicated by the effect of worker motivation.

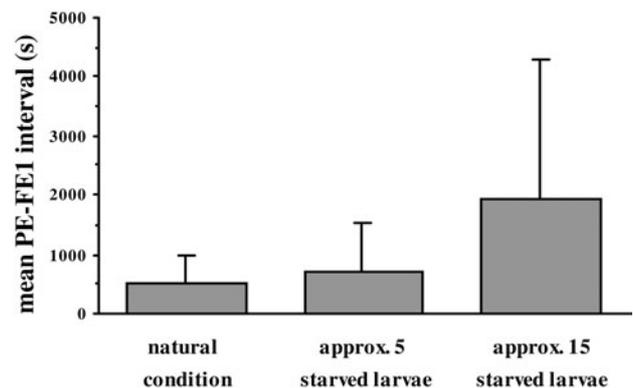


Fig. 4. – Mean time \pm SD (s) between Pollen Eating (PE) and the following (first) feeding (FE1) for workers under natural condition (in a colony, $n=48$) and single workers confronted with 5 ($n=45$) and 15 ($n=16$) starved larvae. The mean duration of the PE-FE1 interval differs significantly between the 15 starved larvae group and the other two groups (Mann Whitney U test 15 starved larvae-5 starved larvae $p=0.001$, 15 starved larvae-natural $p<0.001$, 5 starved larvae-natural $p=0.698$).

Fig. 5 shows that under a natural condition there is a low, but significant, negative correlation between the number of feedings and the PE-FE1 interval ($r=-0.373$, $p=0.019$), indicating that the duration of this interval is

indeed a possible measure of worker motivation. Interestingly, for the two experimental groups there is no significant correlation between the duration of the PE-FE1 interval and the number of feedings. This, once more, suggests that the experimental setting was too different from the natural condition, resulting in abnormal feeding behaviour of the workers.

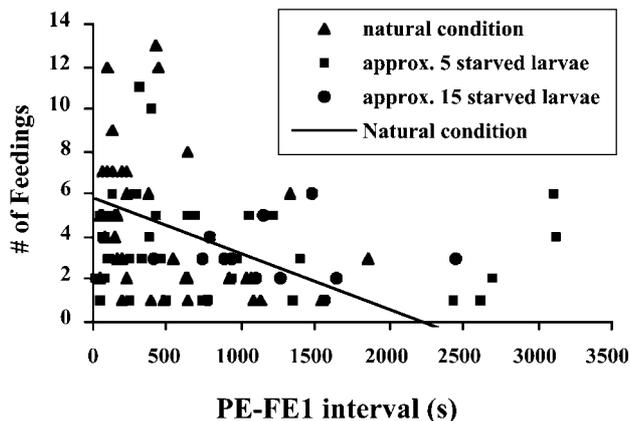


Fig. 5. – Number of feedings after Pollen Eating (PE) versus the time between PE and the first feeding for the three groups ($n=39$, $n=39$ and $n=14$ respectively). Only for the natural group there is a significant negative correlation between the PE-FE1 interval and the number of feedings after PE ($r=-0.373$, $p=0.019$. 5 starved larvae: $r=-0.170$, $p=0.300$, 15 starved larvae: $r=0.195$, $p=0.504$).

That worker motivation played a significant role in these experiments is further supported by the fact that there were big differences between the sessions of each group of experiments (using 5-15 starved larvae) in the amount of data obtained, due to differences in worker activity; some workers ate pollen and fed larvae a lot and seemed very “dedicated”. Others kept on walking around and ate pollen and fed very little, seemingly not at ease and not paying as much attention to the larvae.

DISCUSSION

Feeding behaviour in general and the presence of a larval hunger signal in particular was studied in the bumble bee *Bombus terrestris*. We replicated the finding of DUCHATEAU (unpublished data) that the duration of PE followed by feeding is on average longer than that of PE not followed by feeding. This in spite of the high degree of variation characterizing other aspects of bumble bee behaviour (PENDREL & PLOWRIGHT, 1981; PEREBOOM, 1997; RIBEIRO, 1997). We also found considerable variation in the duration and frequency of all aspects of feeding behaviour (standard deviations are usually close to the mean or even larger).

Results of the choice-experiment with a group of starved and a group of non-starved larvae show that workers are unable to perceive the difference in nutritional status between the larvae from a distance of about two

centimeters. The fact that only starved larvae were fed shows that, after given the opportunity for closer examination, workers are able to distinguish between starved and non-starved larvae, as has previously been reported by PEREBOOM (1997). Furthermore, this supports the idea that larvae somehow advertise their nutritional status to workers by emitting some kind of hunger signal.

Further evidence that workers are able to perceive the nutritional status of larvae and adjust their behaviour accordingly was provided by the experiment in which a group of larvae was manually fed in vivo: feeding by the experimenters drastically decreased the rate of feeding by workers. On two of the three days experimentally fed larvae were not fed at all, and on one day one larva was fed only once. Interestingly, workers were observed to suck away artificial food from the larvae, also when they were still eating. A possible explanation for this behaviour is that too much artificial food was provided in one “feeding” and that consequently the excess was removed. Possibly, it was also to prevent dehydration of the larvae, which might result from the high osmotic value of the food.

Comparison of the feeding behaviour of workers confronted with broods of five and 15 starved larvae yielded some unexpected results. In the case of 15 starved larvae, workers were clearly less motivated to feed than in the case of five starved larvae: the average feeding frequency was lower and the mean PE-FE1 higher for the 15 starved larvae group. In the case of 15 starved larvae, the broods that were constructed often suffered from the increased mobility of hungry larvae, requiring the workers to repair the wax envelope. Sometimes larvae were pulled from the brood cup by workers and discarded. The wax envelopes of the five starved larvae broods usually were in better “shape”. Comparison of the feeding behaviour of workers in a colony with that of workers in an experimental set up with a brood of five or 15 starved larvae yields the impression that on average in a colony workers receive a hunger signal approximately equal to or stronger than that of five starved larvae. The PE-FE1 interval and the number of feedings after PE were similar for the natural and the five starved larvae condition. However, for workers in a colony there was a significant negative correlation between the duration of the PE-FE1 interval and the number of feedings after PE. For both experimental groups this correlation was absent, indicating that not only the 15 starved larvae group but also the five starved larvae group gave rise to some extent to abnormal feeding behaviour. Therefore, it is likely that the experimental conditions of the five and 15 starved larvae were such that workers did not perform normal feeding behaviour. The results of these experiments suggest that the combination of the number of feedings after PE and the time between the end of that PE and the first feeding (PE-FE1) is a rough indicator of a worker’s motivation to feed. A worker that feeds many times shortly after eating pollen is considered more

motivated than one that feeds only once, long after pollen eating.

On the whole, the data support the hypothesis that in *Bombus terrestris* larvae emit a signal allowing the workers to perceive their nutritional status. Furthermore, this signal can trigger a worker to eat pollen for a long time, and to subsequently feed larvae. That larvae actively solicit food in relation to their level of hunger has been reported in fire ants (CASSILL & TSCHINKEL, 1995, 1996, 1999a). There, larvae are even able to regulate their exact diet (CASSILL & TSCHINKEL, 1999b). Since in bumblebees all larvae basically receive the same food (PEREBOOM, 2000), it is unlikely that food soliciting by bumble bee larvae is as sophisticated as it is in fire ants.

Our results cast doubt on the hypothesis that workers impose a feeding regime on the larvae (RÖSELER, 1970; PLOWRIGHT & JAY, 1977). RÖSELER (1970) found that in *B. terrestris* caste is determined already in the first 3.5 days of larval development. With regard to caste differentiation he states that the queen pheromonally "instructs" the workers, who in turn regulate the rearing of the larvae into either workers or queens. RÖSELER (1991) elaborates on this by stating that last instar larvae respond to quantitative changes in nutrition (imposed by workers) by modulating their endocrine activity, which in turn triggers either the worker or the queen developmental pathway. Our results suggest that it is the larvae who, once determined to become either a worker or a queen, solicit food from the workers depending on their needs (among others related to their developmental stage).

The motivation of a worker also appears to play a role in the decision to feed (see e.g. the 15 starved larvae case). LINDAUER (1952) already suggested that bees (*Apis mellifera*), while patrolling in the nest, receive numerous signals, and on the basis of this information and their "Stimmung" ("mood", influenced by age and physiological state) devote themselves to a particular task. He adds that, in addition, signals of other bees could also influence their decision to feed or not. Furthermore, Lindauer reports that feeder bees inspect the larval cells, and he suggests that on the basis of the amount of food present in the cell or some other cue, they decide to feed or not. In bumble bees, as in bees, the division of tasks is also adapted to current colony needs (FREE, 1955). However, workers do not perform inspections in order to decide to feed larvae (no such behaviour was observed during this study, see also PEREBOOM, 1997; however see RIBEIRO, 1999). We suggest that workers perceive the nutritional status of larvae (by means of the larval hunger signal) during manipulation of the wax envelope that surrounds larvae.

From the above it follows that recruitment of workers to initiate feeding behaviour somehow needs to be regulated. It is plausible that workers have some threshold above which the larval hunger signal affects their behaviour, and that this threshold differs among workers depending on their physiological state, which in turn

could depend on age, life history, food availability, temperature etc. (receptivity). If so, the signals of all larvae taken together will, through the effect they have on individual workers, eventually result in the regulation of feeding behaviour. In short, an individual worker needs to make an adaptive decision to go feeding or not depending on current larval and colony needs. The details of the interaction between larvae and workers and, more specifically, the effect of the larval hunger signal on worker behaviour require further research.

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