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Organization and Dynamics of Oligochaeta and Diptera on Possession Island

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Summary. In terms of abundance and biomass, flies (Diptera) and earthworms (Acanthodrilidae) are principal organisms in the decomposition of organic matter. Their effects on decomposition processes, as compared to those of micro-organisms, vary in accordance with characteristics of the local substratum, altitude, distance from shore, origin (animal or plant) of litter, production periodicity of organic matter, etc. The organization and dynamics of these principal organisms in decomposer communities were investigated in the field and in the laboratory. The investigations included studies of their micro-distribution, demography, fecundity, growth, and trophic specificity. The co-existence of two species in the same biotope is examined. The low number of species and the nature of interspecific relationships indicates the fragility of these Sub-Antarctic decomposer communities.

1 Introduction

The organization of invertebrate populations at Possession Island is of special taxonomic interest, due to their high degree of endemism. Morphological, physiological, and behavioural adaptations to Sub-Antarctic conditions are evident. Current studies of some of these adaptations include alary polymorphism, duration of post-embryological development, longevity, fasting, reproductive behaviour and locomotor activity of Diptera (Vernon 1981; Tréhen 1982; Tréhen and Vernon 1982).

It is generally acknowledged that the diversity and abundance of many Sub-Antarctic invertebrate populations depend on seaweed deposits, which accumulate at high-water zones, and manuring by seabirds and seals. Smith (1978) demonstrated the inter-relationships between primary producers on Marion Island and exogenous manuring by animals. The invertebrate communities are organized in response to these factors, each mono-specific population revealing its own responses. Our investigations on Possession Island, where invertebrate species diversity is low, illustrate these interrelationships at various levels. Only two groups, Diptera and Oligochaeta, are considered in this study. The groups included similar numbers of species. These species show similar distribution patterns over the island but they occupy different niches. Three complementary aspects were covered by our investigations: the distribution of Diptera and Oligochaeta at Possession Island, focusing on the relationship between different species and local topographic, edaphic, and biological characteristics; animal-environment relationships, focusing on edaphic characteristics as principal factors in the micro-distribution and abundance of certain earthworm species and the role of manuring in the organization of necro-saprophagous Diptera communities; and, a trial working model of the *Durvillea*-Diptera-Oligochaeta ecosystem.

2 Material and Methods

Field work was carried out during 1980–1982. Live Diptera specimens were collected and counted by hand in sampling areas. Dispersal activity and behaviour were quantified by capturing the insects in pitfall traps distributed over these sampling areas. Earthworm communities were evaluated by manually examining ca. 4,000 cm^3 soil samples in the laboratory. The samples were removed from the upper layer of soil in the sampling areas. These areas were selected and delimited prior to quantitative estimation of population sizes. For the population estimates of *Anatalanta crozetensis*, individuals were marked with coloured metallic paints and a capture-recapture technique employed. Specimens of the sea-shore earthworm, *Phreodrilus crozetensis*, and its cocoons, were collected by washing fractions of soil taken from the sampling areas.

Dry weights (dry wt.) were obtained by drying specimens at 60 °C with their digestive tracts full. Experimental laboratory work was done at the Station Biologique de Paimpont (France), where animals were reared throughout the year and their reproductive cycles studied. Data on the distribution of the species were computed, using the map of Delettre et al. (1982). Factorial correspondence analysis was used to examine the species' specific affinities for environmental characteristics.

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Table 1. Distribution and alar development of Diptera

Family	Species	Alar development	Distribution	Code (in Fig. 1a)
Helcomyzidae	*Paractora dreuxi*	Micropterous	Marion-Crozet	PAR
Ephydridae	*Amalopteryx maritima*	Stenopterous	Crozet-Kerguelen-Heard	AMA
Coelopidae	*Apetenus litoralis*	Micropterous	Marion-Crozet-Kerguelen	
	Listriomastax litorea	Macropterous and micropterous	Marion-Crozet-Kerguelen	LIS
Sphaeroceridae	*Siphlopteryx antarctica*	Sub-apterous	Crozet	SIP
	Anatalanta aptera	Apterous	Crozet-Kerguelen-Heard	APT
	Anatalanta crozetensis	Apterous	Crozet	CRO
	Dreuxiella spinosa	Apterous	Crozet	

3 Results

3.1 Distribution of Diptera and Oligochaeta

The brachycerous Diptera of the Crozet archipelago include eight species, of which five are known from other islands of the southern Indian Ocean (Table 1). Of these, this paper does not deal with *Dreuxiella spinosa* (only one suspected specimen collected which could have been an immature stage of *Anatalanta crozetensis*) and *Apetenus litoralis* (a strictly rock-dwelling species of the sea-shore, which together with the chironomid *Halirytus amphibius* (Diptera) and the curculionid *Palirheous eatoni* (Coleoptera) comprise an original seaweed-eating community). The following morphological features were common to the six other species found among organic debris: physogastry (mainly in the genus *Anatalanta*); reduced wing size with consequent loss of flight capability (except *Listriomastax*); and, wing polymorphism (e.g., *Anatalanta* is completely wingless) which does not seem to impair colonizing ability.

Four species of earthworms (Phreodrilidae and Acanthodrilidae), previously described by Michaelsen (1905), occur on Possession Island. Both morphological (size, colour, place of nephridial pores) and ecological features led us to distinguish more forms (Table 2). Taxonomic studies of these are in process. The presence of introduced Lumbricidae is common at most Sub-Antarctic islands. We have observed *Dendrobaena rubida tenuis* on Possession Island where it is a recent colonizer around the base which was established in 1962. Studies on the colonizing process and the response of the indigenous fauna to this are in process. This species and the other earthworms are all epigeous or epiendogeous (Bouché 1972). Only *P. crozetensis* is known from South Georgia and the southern part of Tierra del Fuego (Tetry 1947). The genus *Microscolex* (except for the two nomadic species, *M. dubius* and *M. phosphoreus*) is known only from the high latitudes of the southern hemisphere (Stephenson 1930). When and how the Sub-Antarctic islands were colonized by earthworms have been discussed by Benham (1903), Michaelsen (1905), Tetry (1947), and Bouché (1982).

Data from 60 Diptera and Lumbricidae samples were processed according to factorial analysis of correspondence (Figs. 1a and 1b). The main environmental factors taken into account were: elevation above sea-level (A), distance from the sea-shore (D), cover abundance (vegetation) (V), reference to general environment, such as shore type (L), grass type (H), fell-field type (F), type (E), and nature (O) of manuring, and soil moisture (U). The analysis showed that the organization and the distribution of communities depend on two principal factors: altitude and structure of vegetation.

Several types of organic manuring occur, despite a decreasing density of vertebrates as distance from the shore increases. This includes seaweed wracks on the shore, moulting areas of Elephant Seals, *Mirounga leonina*, and Gentoo Penguin, *Pygoscelis papua*, and King Penguin, *Aptenodytes patagonicus*, rookeries and moulting areas adjacent to the shore, nests of albatrosses in the grassland zones farther inland, and finally burrows of Whitechinned Petrel, *Procellaria aequinoctialis*, and Georgian Divingpetrel, *Pelecanoides georgicus*, in both the grassland and higher-altitude fell-field zones far inshore. Decaying seaweed, guano, seabird regurgitates and carcasses, and moulted skin and feathers constitute the main trophic substratum for Diptera and probably for some species of Lumbricidae as well (Figs. 1 and 2).

Table 2. Oligochaeta of Possession Island

Family	Species	Code (in Fig. 1b)
Phreodrilidae	*Phreodrilus crozetensis*	PC
Acanthodrilidae	*Microscolex crozetensis*	C
	Microscolex luykeni var. *typique*	LT
	Microscolex enzenspergeri var. *typique*	ET
	Microscolex enzenspergeri var. *alba*	EA
	Microscolex enzenspergeri var. *nigra*	EN
	Microscolex enzenspergeri var. *bicolor*	EB
	Microscolex luykeni var. *halophila*	LH
	Microscolex luykeni var. *albinique*	LA
	Microscolex frenoti nov. sp.	F

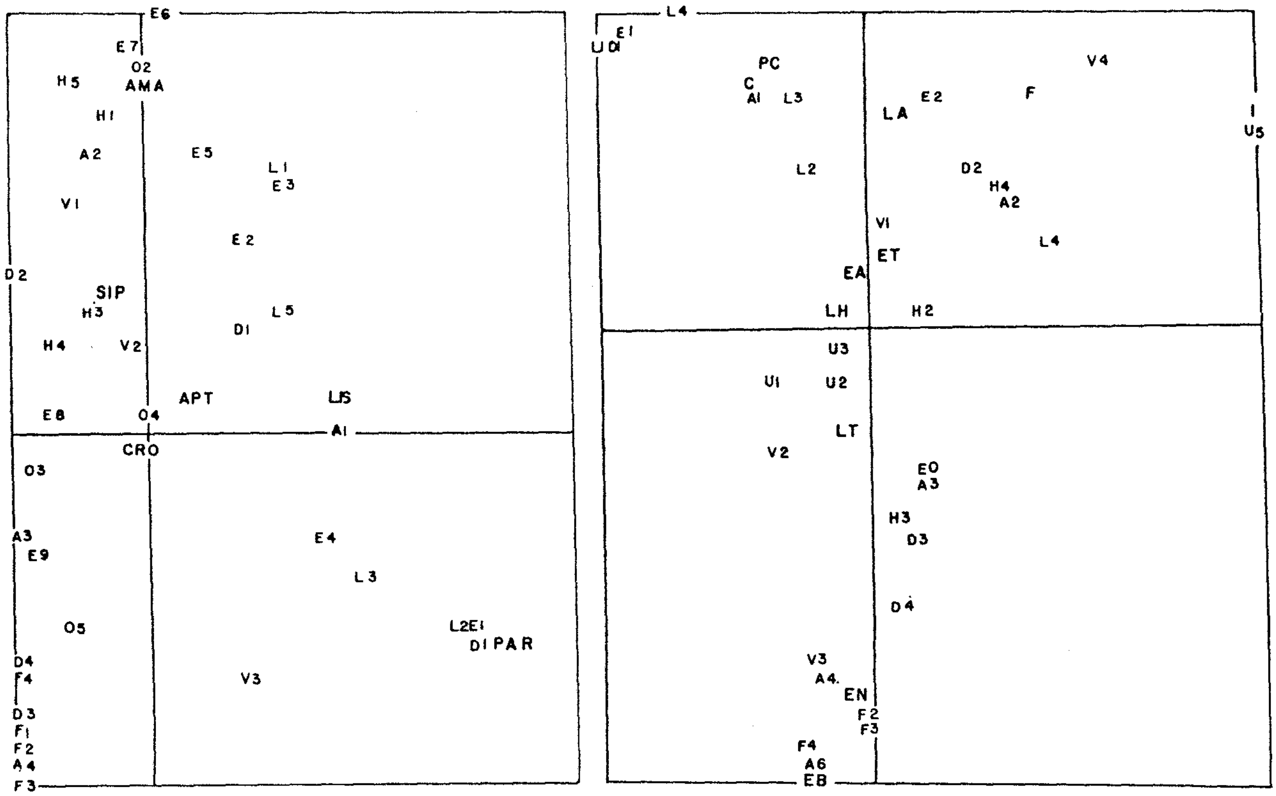

Fig. 1a,b. Graphical representation of Diptera-environment relationships (a) and Oligochaeta-environment relationships (b). Species codes are given in Tables 1 and 2 espectively. a *A1* to *A4* increasing elevation above sea-level; *D1* to *D4* increasing distance from the sea-shore; *V1* to *V3* decreasing cover abundance; *L1* to *L5* shore type; *H1* to *H5* grass type; *F1* to *F5* fell-field type; *E1* seaweed wracks; *E2* Elephant Seal wallows; *E3* King Penguin rookeries; *E4* Macaroni Penguin rookeries; *E5* Gentoo Penguin rookeries; *E6* King Penguin moulting areas; *E7* Albatross and Petrel nests; *E8* Petrel burrows; *E9* other types of organic enrichment; *O1* seaweeds; *O2* droppings; *O3* regurgitations; *O4* carcasses; *O5* other forms of organic enrichment. b *A1* to *A6* increasing elevation above sea-level; *D1* to *D4* increasing distance from sea-shore; *V1* to *V4* decreasing cover abundance; *L1* to *L4* shore type; *H2* to *H4* grass type; *F2* to *F4* fell-field type; *U1* to *U5* increasing soil moisture; *E0* no organic enrichment; *E1* rookeries; *E2* other forms of organic enrichment

4 Diptera

Paractora dreuxi is a shore-dwelling species common among pebbles and is observed exclusively at high-water marks in decaying seaweed. *Listriomastax litorea* may also occur on decaying seaweed, but it is more typical in the coastal rookeries of Gentoo Penguins, and the moulting areas of King Penguins. *Amalopteryx maritima* is found in the inland grass zone, wherever birds and mammals manure the phanerogamic vegetation. The Sphaeroceridae (*Siphlopteryx, Anatalanta*) show a wider distribution and occur wherever there is organic enrichment on Possession Island (Tréhen and Vernon 1982) and are the only Diptera able to survive on the fell-field above 400 m altitude, feeding on bird carcasses and regurgitates of Georgian Divingpetrels, and dwelling in petrel burrows. The two *Anatalanta* species occur from sea-level up to 600 m and are necrophagous, coprophagous, and phycophagous. It is therefore very difficult to discriminate between *A. aptera* and *A. crozetensis*, but they are, however, good biological indicators of the presence of any kind of manuring in Sub-Antarctic situations (Vernon 1981).

5 Oligochaeta

Two species are confined to the littoral zone. *Microscolex crozetensis* occurs in spindrift-influenced areas, on low, vegetation-covered coasts and in penguin rookeries, and also at higher altitudes (Fig. 2c) where spindrift occurs, which seems to indicate that salinity plays an important part in the distribution of this species. *Phreodrilus crozetensis* occurs on shingle beaches together with *Paractora dreuxi*, and both species feed at the high-water mark. It is also fairly common in rookeries, around wallowing areas of Elephant Seals, in grasslands surrounding the nests of albatrosses, and in the burrows of petrels. It is generally found wherever organic deposits can be observed and, like *Anatalanta, P. crozentensis* probably plays an important role in the decomposition of animal remains. *Microscolex e. nigra* and *M. e. bicolor* occur strictly in the fell-field zone, where the soil is mainly coarse and well-drained, and has a discontinuous vegetation cover. These two species are distinguished by their pigmentation pattern: *bicolor* has no ventral pigmentation and it occurs only above 300 m (Fig. 2b), usually in

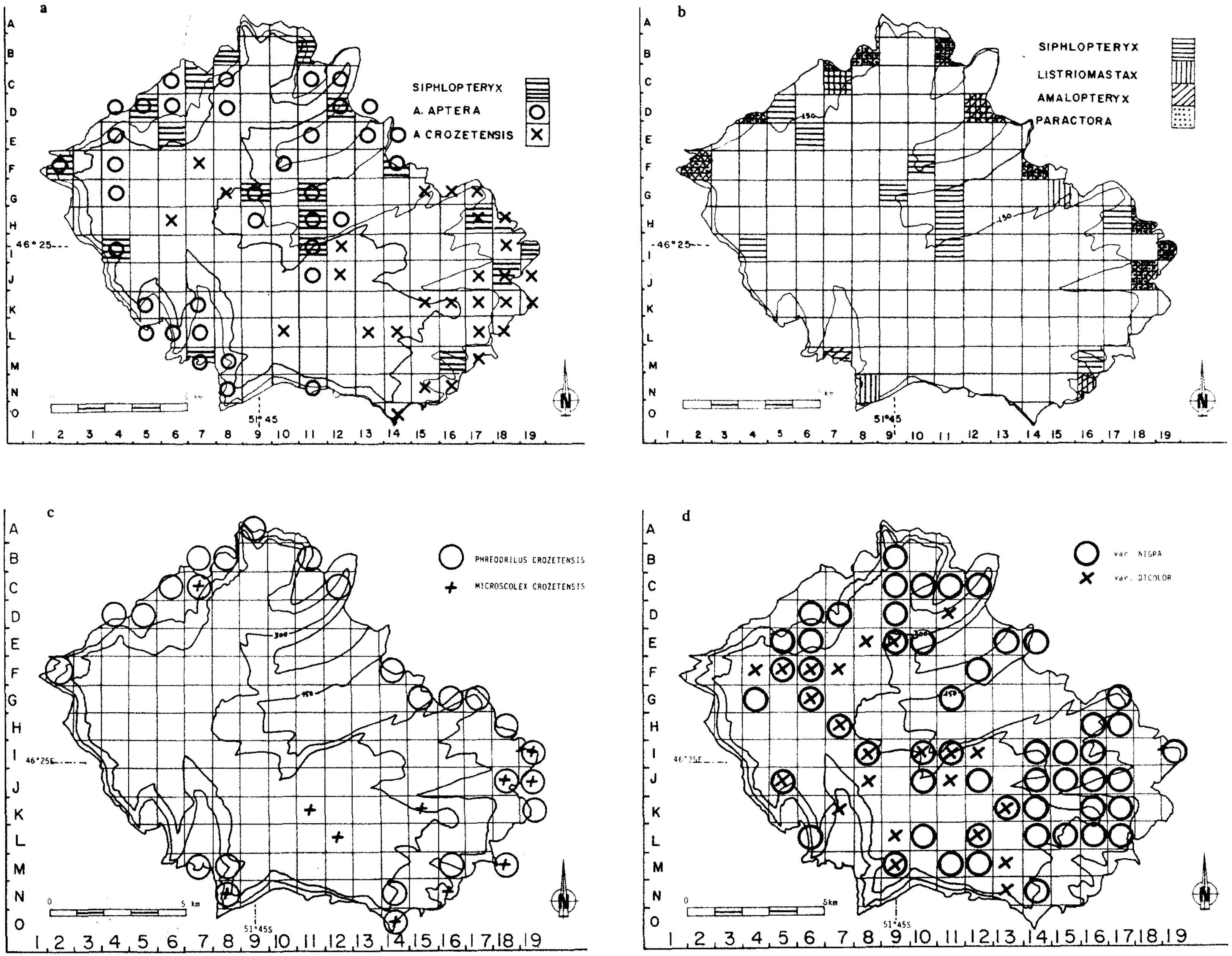

Fig. 2a–d. Distribution of Diptera brachycera and Oligochaeta on Possession Island. a Sphaeroceridae. b Other families including *Siphlopteryx antarctica*. c Sea-shore-dependent Oligochaeta. d Oligochaeta of the fell-field

Poa cookii tufts and rolling mosses, whereas *nigra* colonizes all types of fell-field. *Microscolex frenoti* is an aquatic species, occurring among weeds and mosses in lakes and rivers or in flooded grassland areas.

It is more difficult to identify the inter-relationships between the five other species of earthworms (EA, ET, LT, LH, LA in the centre of Fig. 1b), based on the ecological factors considered here. Further study of the micro-distribution of the earthworms and of the structures of these communities is necessary.

5.1 Oligochaeta-Environment Inter-Relationships

During January 1983 observations were made along a transect established over the large, peaty bottom of a glacial valley (Vallée des Branloires), and divided into nine zones according to micro-topography, water-content of the soil, and vegetation (Fig. 3). Preliminary observations on one soil extraction (200 × 200 mm) per zone were made, except for Zone III where three samples were extracted.

Two main earthworm communities were observed: (a) Zones I to VI, where *M. enzenspergeri alba* and *M. luykeni halophila* were encountered and (b) Zones VII to IX, where only *M. e. typique* and *M. frenoti nov.* sp. were present. The pH of circulating water averaged 4.10 in the first community (Zones I–VI) and 5.10 in the second community (Zones VII to IX). *Agrostis magellanica* and several species of mosses form the vegetation of the first community, except in Zone III, where *Blechnum penna-marina* is dominant and earthworms are completely absent. Zone VII includes large boulders covered with *Acaena magellanica* and liverworts. The vegetation of Zone VIII (*A. magellanica* and *Juncus pusillus*) is scattered over a sandy substratum. The level of ground-water is almost flush with the soil surface in Zone I, but the water content of the top layer of the soil, where earthworms live, decreased progressively from Zones II to IV, and increased again from Zones V to IX. This factor seems important with regard to the density and distribution of earthworms.

5.2 Colonization of a Penguin Carcass by Diptera

Carcasses may be considered as temporary habitats. Their presence in a given area is random both in time and space. Three Diptera species (*Anatalanta crozetensis, Siphlopteryx antarctica*, and *Amalopteryx maritima*), respectively apterous, sub-apterous, and stenopterous, occur in Gentoo Penguin rookeries. The colonization patterns of these three species on the decaying carcass of a Gentoo Penguin chick (body mass = 2.1 kg) were followed from 18 February to 19 March, 1980. On 18 February, the carcass was placed under a 300 × 300 mm board. Pitfall traps (θ = 60 mm) filled with diluted teepol were set around the bait. Four traps were placed in a row radiating out in a north, south, east, and west direction from the carcass. The traps of each set were numbered from 1 to 4 according to their distance from the carcass (i.e., 10, 30, 100, and 300 cm). A control set of four traps was placed 20 m from the carcass of evaluate the density and activity of Diptera without a trophic substratum. Catches were collected at 5 day intervals during 1 month (R1–R6). The results showed that colonizing activity (Heydeman 1961, in Nentwig 1982) fluctuated greatly from one species to another. Compared with the first catch (R0), the third catch (R3) was 18.5 × as great for *A. crozetensis*, 1.8 × as great for *S. Antarctica*, and 2.0 × as great for *A. maritima*. The catch patterns for *S. antarctica* and *A. crozetensis* dif-

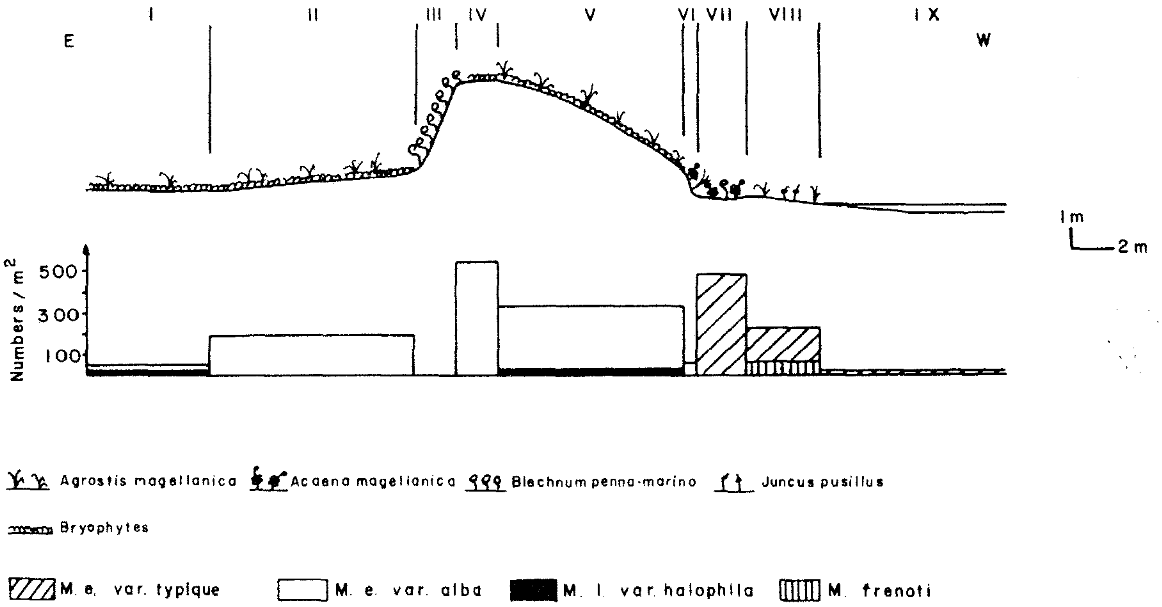

Fig. 3. Micro-distribution of Oligochaeta on a transect across Vallée des Branloires at Possession Island

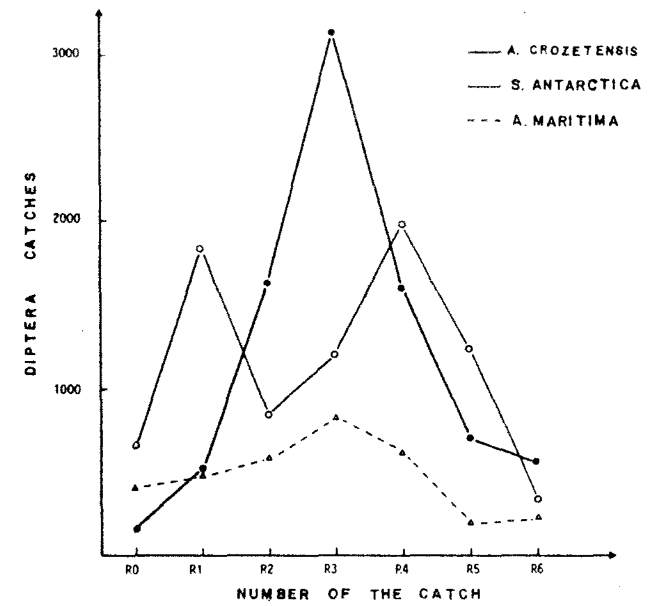

Fig. 4. Diptera catches at 5-day intervals (*R0* first catch; *R6* catch at 30 days after *R0*) in a penguin-manured study area

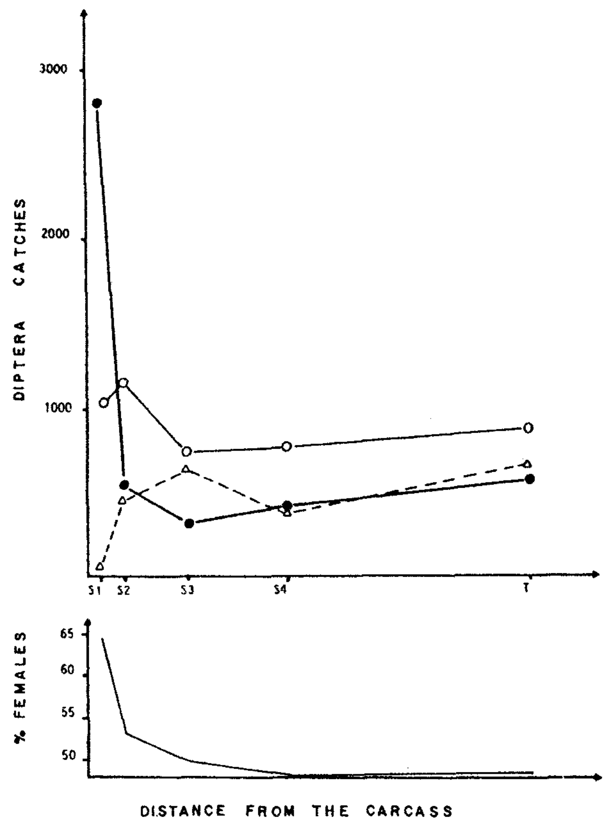

Fig. 5. Change in numbers of diptera caught at different distances from a decaying penguin carcass (*S1* 10 cm; *S2* 30 cm; *S3* 100 cm; *S4* 300 cm; *T* 20 m). *Top graph* represents total numbers, *bottom graph* represents proportion of females of *A. crozetensis*. See Fig. 4 for species' names

fered. The catch curve for adult *A. crozetensis* was symmetrical (Fig. 4), and the decrease in catches corresponded to an increased occurrence of larvae in the carcass. This kind of relationship between adults and larvae has also been found in other communities of necrophagous Diptera (Vernon 1983).

Some 9,200 Diptera were caught around the bait, but at different distances for each species. Approximately 65% of all catches (82% of all *A. crozetensis*, 59% of all *S. antarctica*, and only 39% of all *A. maritima*) were made within 300 mm of the bait (Fig. 5). Each catch peak was situated at a specific distance from the bait: S1 at 100 mm for *A. crozetensis*; S2 at 300 mm for *S. antarctica*; and S3 at 1.0 m for *A. maritima*. The latter species was never found on the carcass, and a comparison of capture frequencies showed that the attractive effect of the bait decreased for distances > 3 m, but may be different for males and females. *Anatalanta crozetensis* females were much more abundant near the bait, whereas the percentage of males increased at 1 m and at greater distances the sex-ratio tended towards parity (Fig. 5). The presence of the carcass clearly biased the spatial distribution of these species. It attracted *A. crozetensis* and *S. antarctica* and repulsed *A. maritima* during the first weeks. However, these biases may be modified by seasonal factors which influence the biological activity of these insects, as well as the probability of occurrence of vertebrate carcasses.

To examine some of these factors in greater detail, a population of *A. crozetensis* was monitored for 9 months, from February to October 1982. The study was conducted in a fenced area of 5 × 5 m, at an elevation of 126 m, in which live King Penguins were kept during February and March 1982 for physiological experiments. The pebbles used to secure the wire netting at ground level formed a suitable biotope for the insect community associated with the Penguins. This community included *A. crozetensis* and *S. antarctica* (Fig. 6). Insects among these pebbles were caught and marked with a different coloured metallic paint for each side of the enclosure where they were caught. Repeated counts were made throughout the period. The Penguins were released in April. Results for *A. crozetensis* are given in Table 3. Values are calculated from observed data according to Schumacher-Eschmeyer's formula (in Barbault 1981). The results indicate a significant decrease in numbers begining in May, and the percentage of females in the population increased during the winter months. The decrease in numbers in May is probably over-estimated, because some 335 flies (208 < N < 1,000) were attracted to a Wandering Albatross, *Diomedea exulans*, carcass 7 m away, and it is likely that many of these insects came from our enclosure.

The main factor influencing the decrease from May (Sub-Antarctic autumn) is probably related to the decrease in temperature during autumn and winter. Below 7 °C, insect emergence decreases and larval growth slows down (Tréhen 1982). The increased percentage of females during autumn and winter may be due either to a higher mortality or a higher mobility in the males. They were more widely dispersed from the shelter of the pebbles, whereas eggs, nymphs, and pupae were found only under the pebbles. Recaptures

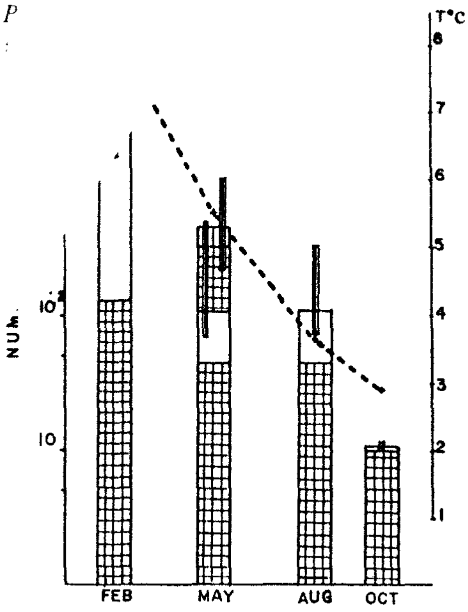

Fig. 6. Seasonal variation in numbers (*hatching* represents females, *clear* represents males) of *A. crozetensis* in relation to mean temperture (*broken line*)

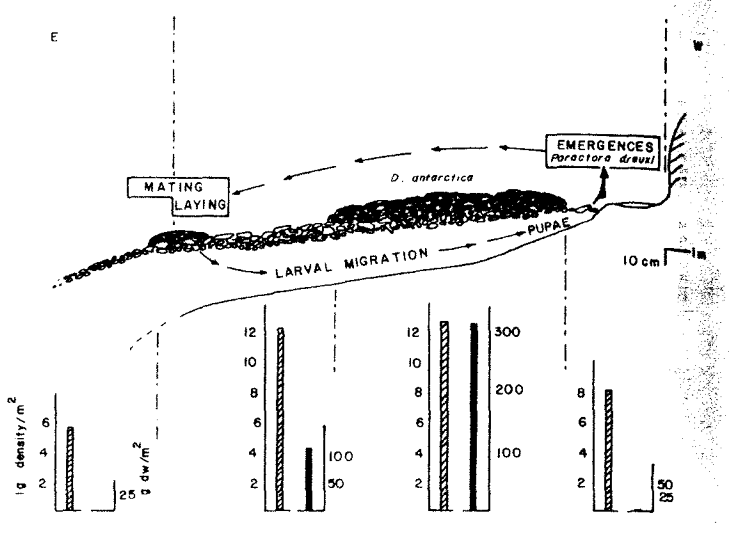

Fig. 7. Sea-weed (*Paractora* – *Phreodrilus*) transect at "Crique du Sphinx"; with earthworm density and biomass estimates at different sites on the beach

of marked individuals showed that 87% occurred at the site of marking. However, males were more frequent in catches made away from the marking sites, and formed 83% of these catches. It seems that during winter the more sedentary females are less susceptible to mortality than the more mobile males. It is possible that females move towards protected egg-laying sites while males, in search of sexual partners, disperse away from these sites where they are less protected from the elements and therefore suffer a higher mortality. Observations on *A. aptera* at Kerguelen (De Blignieres and Tréhen 1982) show that in this species males are also more mobile than females.

5.3 Model of the Durvillea-Diptera-Oligochaeta Ecosystem

The producer compartment in this model comprises seaweed wracks (*Durvillea antarctica*) decaying on pebbles just above the tidal zone on a beach called "Crique du Sphinx" (Fig. 7). The insect community, described previously by Tréhen and Vernon (1982), comprises only a small number of species. One of the Diptera, *Paractora dreuxi*, is a micropterous, mobile species able to colonize seaweed immediately after its deposition on the beach. Dead seaweed biomass can sometimes be very high (> 5 kg m^{-2}) but fluctuates very quickly and randomly. The biomass of *P. dreuxi*, the first colonizer, can reach 90 g (dry wt.) m^{-2} but also fluctuates in space and time with the fluctuations in seaweed.

The oligochaete *Phreodrilus crozetensis* does not colonize the actual seaweed deposits, but occurs in the products of its decay which flow seawards between the pebbles of the beach. Earthworm biomass is the highest ever recorded for terrestrial oligochaeta (density = 250,000 ind. m^{2}, biomass = 320 g (dry wt.) m^{-2}). Biomass fluctuates as the seaweed deposits fluctuate, but they are also controlled by the high reproductive potential of this sedentary earthworm species.

Table 3. Seasonal variation of numbers of individuals in a population of *Anatalanta crozetensis* on Possession Island

	February	May	August	October
Total number	1,457	119	122	18
Standard error 95% confidence except May: 90%	1 162 < N < 1 923	71 < N < 500	77 < N < 333	15 < N < 28
Number of females	N = 163 (11.18%)	45 (37.8%)	46 (37.7%)	12 (66%)
Standard error (95%)	66 < N < 260	26 < N < 166	35 < N < 83	10 < N < 16
T °C monthly average	8.2 °C	5.5 °C	3.7 °C	2.9 °C

Cocoon production is synchronized with arrivals of seaweed wrack, with a delay for sexual maturation. The earthworm *P. crozetensis* is a secondary colonizer and is probably also a prey species for the last instars of the fly *P. dreuxi*, and for other invertebrates (Acarina, Gamasida).

6 Conclusion

Possession Island has a poor dipteran fauna compared with continental communities. On the other hand, there is a relatively rich earthworm community on the island. This difference in species richness may be due to different colonizing strategies and to the fact that the oligochaetes occupy a more stable substratum.

Edaphic factors are dominant with regard to the distribution of Oligochaeta but altitude, vegetation type and different types of manuring play important roles in their distribution. The species present on the island occur in different biotopes ranging from the shore (*Microscolex crozetensis*) all the way up to the fell-field above 300 m (*M. enzenspergeri bicolor*). It is also shown that in the case of *M. frenoti nov.* sp., soil-water content and the pH of soil water strongly influence its occurrence.

Diptera communities on the island are generally unstable, with eight species having relatively specialized trophic forms: necrophagous, phycophagous, saprophagous, keratophagous etc. The sequential occurrence of *Anatalanta crozetensis* and *Amalopteryx maritima* on the same substratum (carcass) is influenced by these specializations as well as a difference in rate of larval development on the substratum. Males show a greater winter mortality than females. The latter lay eggs through winter and spring, so that larval development can occur in summer when temperatures and substratum availability are more favourable. Species composition of communities is determined mainly by the origin, form and periodicity of substrata.

One of the more important substrates is decaying seaweed which accumulates at high-water marks. *Paractora dreuxi* (Diptera) and *Phreodrilus crozetensis* (Oligochaeta) are the two main species associated with these. Their population sizes and dynamics are dependant on the random fluctuations of the seaweed deposits and each of these species has a specific strategy to cope with these fluctuations: *P. dreuxi* has a strong colonizing ability; *P. crozetensis* is strongly competitive. These two strategies are the two main factors influencing biological equilibrium between Oligochaeta and Diptera populations in terrestrial subantarctic regions.

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