Life cycle and kelp consumption of *Paractora dreuxi mirabilis* (Diptera: Helcomyzidae): A primary decomposer of stranded kelp on Marion Island

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Wrack beds of the intertidal kelp Durvillea antarctica *(Cham.) Har. on Marion Island (46°54′S, 37°45′E) sustain large kelp fly populations.* Paractora dreuxi mirabilis *(Séguy) is a primary decomposer of stranded* Durvillea *with larvae reaching a biomass of 2 g per kg of decomposing kelp (wet mass). At 10°C* Paractora *completes its life cycle in 80-120 days. Egg, larval and pupal stages last 4, 60 and 40 days respectively. Larvae eat 0,5 times their own dry mass in kelp per day. They attain an individual live mass of up to 100 mg. The feeding and burrowing activity of larvae probably enhance microbial decay of beached kelp.* Paractora *larvae are preyed on by vertebrate insectivores and probably form an important link in nutrient and energy chains in the littoral zone on Marion Island.*

Beddings uitgespoelde kelp op Marion-eiland (46°54′S, 37°45′O) onderhou groot kelpvlieg bevolkings. Die kelpvlieg Paractora dreuxi mirabilis *(Séguy) is 'n primêre afbreker van uitgespoelde* Durvillea antarctica *(Cham.) Har.* Paractora *larwes bereik 'n biomassa van 2 g per kg verrottende* Durvillea *(nat massa). By 10°C word die lewensiklus van* Paractora *in 80-120 dae voltooi. Die eier-, larf- en papiestadiums duur 4, 60 en 40 dae onderskeidelik. Larwes eet 0,5 keer hul eie droë massa in kelp per dag en bereik 'n lewende massa van tot 100 mg. Die afbraak van kelp deur mikrobes word bevorder deur die vreet- en tonnelaksie van* Paractora *larwes. Die larwes word deur verskeie vertebraat insektivore gevreet en vorm waarskynlik 'n belangrike skakel in voedsel- en energiekettings in die litorale gebied op Marion-eiland.*

Introduction

Sub-Antarctic Marion Island (46°54′S, 37°45′E) is approximately 300 km^2 in area and rises to peaks of 1200 m. It is the largest of the two islands comprising the Prince Edward archipelago, smaller Prince Edward Island lying 20 km to the northeast. Their volcanic origin and strict isolation from other land masses make the Prince Edwards "truly oceanic islands" (Verwoerd 1971). The two islands form a distinct biogeographical unit with other islands of the Kerguelen province (Séguy 1971). Marion Island experiences an isothermal tundra climate with a mean temperature of 5,5 °C, monthly means ranging from 3,6 in February to 7,8 °C in August. Annual total precipitation exceeds 2 500 mm with precipitation recorded on an average of 311 days per year (Van Zinderen Bakker *et al.* 1971).

Séguy (1971) remarked on the paucity of Diptera on Marion Island compared with the neighbouring archipelagos of Crozet and Kerguelen. Of the seven species known from the island four are cosmopolitan and only three endemic: *Listriomastax litorea, Apetenus litoralis* (both Coelopidae) and *Paractora dreuxi mirabilis* (Helcomyzidae). At least two species, *Apetenus litoralis* and *Paractora dreuxi mirabilis*, are closely associated with wrack beds and decomposing kelp.

Little is known about the nutrient and energy pathways operative in the littoral zone on Marion Island (Smith 1977). Fronds of *Durvillea antarctica*, an epilitic phaeophyte abounding in the intertidal zone, continuously wash up on beaches around the island. After heavy seas fronds frequently pile up into large and dense wrack beds. *Paractora* larvae are the major decomposers of beached *Durvillea*, representing by far the greatest biomass of decomposers in beached kelp (Crafford, unpublished) and constituting an easily exploitable localised food resource for secondary consumers such as the feral house mouse (*Mus musculus*), and lesser sheathbill (*Chionis minor*) and possibly terns (*Sterna* spp.). Debris of *Macrocystis pyrifera*, a giant kelp species forming massive off-shore beds, occasionally washes up after heavy storms but is never colonised extensively by invertebrate decomposers; breakdown seems to proceed mainly by trampling and wave action.

Various studies on the biology of kelp flies in wrack have been undertaken elsewhere (Egglishaw 1960, Dobson 1974, Stenton-Dozey & Griffiths 1980 and others). The dipteran fauna of Île Crozet and Kerguelen has also been studied (Trehen 1981, Trehen & Vernon 1982). Except for early descriptive studies (Enderlein 1908, Jeannel 1953, Séguy 1971 and others) no information on the basic biology of any insect species on Marion Island exists. This study represents a first step in quantifying the effect of decomposers in the Marion Island ecosystem and is part of a larger investigation into the role of insects as decomposers on the island.

Material and Methods

A pebbled shore (Trypot Beach) on the northeastern coast close to the meteorological station was chosen as the study area because of its proximity to the base and because of regular deposits of kelp which maintain the fly population. A fresh wrack bed was monitored for two months and daily observations resulted in the field data on life cycle and feeding ecology. Life cycle and detailed food consumption were determined in the laboratory.

Life cycle

Adult *Paractora* were collected with an aspirator on Trypot Beach. Males and females are readily distinguishable and pairs were placed in petri dishes containing discs cut from fresh kelp frond (*Durvillea antarctica*). The petri dishes were then placed in an incubator at 10°C and 80-100% RH to simulate average conditions to which they are normally subjected in the field.

Eggs were counted and removed as soon as they were laid, placed on strips of fresh kelp frond and checked hourly during the day for signs of hatching larvae. Larvae were weighed as soon as they emerged and thereafter four-hourly during the

first four days and eight-hourly during the rest of their development. Duration of the various instars was deduced from rapid decreases in mass accompanied by reduced activity and signs of exuviae. Duration of the pupal stage was determined using both pupae from the laboratory colony and pupating larvae from Trypot Beach. Newly emerged adult flies were kept in small gauze cages and provided with discs of decomposing kelp frond for food to determine adult lifespan. Colonies were kept at 10°C and 80-100% RH throughout.

Kelp consumption

Larvae were size-matched, individually weighed and placed on weighed amounts of decomposing kelp scraped from the surface of moderately decomposed fronds. Kelp from the same frond was used during each experiment. Thirty, 20 and 10 individuals of first, second and third instar larvae respectively were used during each experiment. Larvae were reared from eggs and, for the second and third instar larvae the instar was determined by regular weighing. A rapid decrease in mass signified a moult. Kelp and larvae were placed in small muslin-covered glass vials and kept at 10°C and 100% RH in an enclosed waterbath. The kelp was placed against the sides of the vials to allow drainage of the watery faeces produced by the larvae. After 48 hours kelp and larvae were reweighed and the kelp dried to constant mass (four days at 60°C).

Four vials containing weighed amounts of kelp scraped from the same frond served as controls to account for microbial decomposition during the feeding period. To obtain initial wet mass/dry mass ratios for the kelp being used as food, kelp was scraped from the same frond, weighed immediately, dried to constant mass and reweighed. All masses were determined on a Sauter AR 100 microbalance (to one-hundredth of a gramme). Consumption data were entered into a Kontron Mop computer to fit a linear regression and calculate the equation.

Sampling of a wrack bed provided an estimate of larval biomass and kelp consumption in the field. Five samples were taken at random with a 0,1 m^2 box corer in a wrack bed

Table 1
Duration, size and mass of the life stages of *Paractora dreuxi mirabilis* at 10°C and 80-100% RH.

Stage	Duration (d)	Size (mm)	Wet mass (mg)	(n)
Egg	3 – 5	1,0 – 1,5	0,20 – 0,30	30
First instar	2 – 3	1,0 – 2,0	0,15 – 0,45	20
Second instar	4 – 6	2,1 – 4,0	0,40 – 1,00	20
Third instar	40 – 50	4,1 – 15,0	0,95 – 80,00	20
Pupa	30 – 60	9,0 – 12,0	45,00 – 80,00	20
Adult	14 – 21	5,0 – 10,0	15,00 – 40,00	30

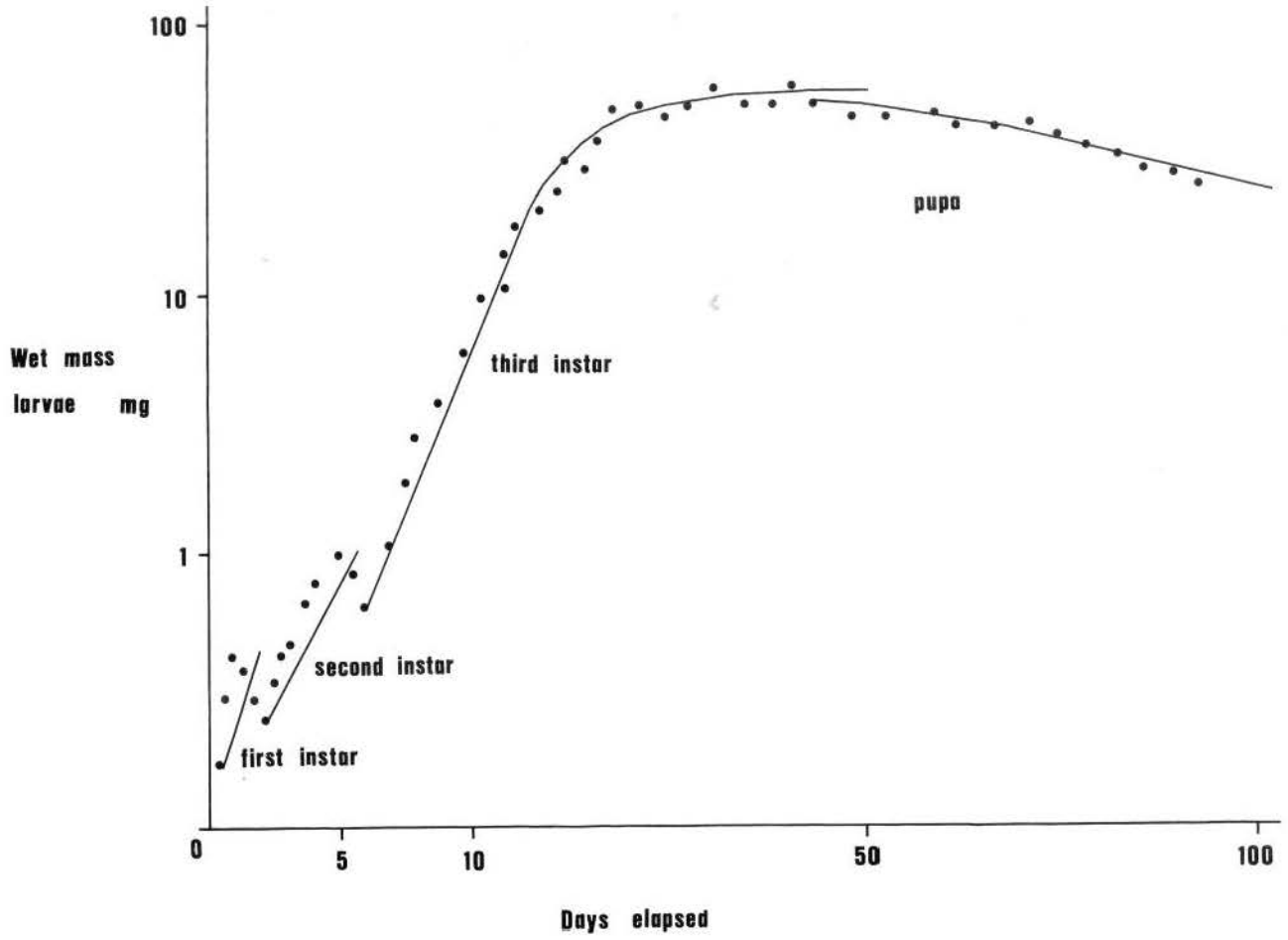

Fig. 1. Growth of *Paractora dreuxi mirabilis* larvae at 10°C and 100% RH.

approximately 5 m^2 in area and 0,3 m deep, ten days after the wrack bed formed. The kelp obtained from each sample was weighed wet. Larvae were floated out of the kelp by washing samples in lukewarm water. Because first and second instar larvae contribute very little to overall biomass and consumption, only third instar larvae were counted and weighed.

Results

Life cycle

Females laid 150-200 eggs singly and in groups on the kelp discs and against the sides of the petri dishes in the laboratory colonies, whereafter they died. Table 1 gives the duration, size and mass of each life stage at 10°C. Eggs hatched within five days, and first and second instars were completed within three and six days, respectively.

Third instar larvae grew rapidly and attained a live mass of up to 100 mg within a month, although the mass of most individuals in the laboratory colony did not exceed 80 mg. Their mass remained constant for a further 10 to 20 days; the duration of third instar was 40-50 days. Growth of *Paractora* larvae at 10°C is illustrated in Figure 1.

Most larvae in the laboratory colonies started pupating within 50 days of hatching. Duration of the pupal stage varied between individuals from the laboratory and field colonies. Most adults emerged about 30 days after pupation in the laboratory, although some individuals emerged after 80 days. Adult life span never exceeded 21 days in the laboratory. A third instar larva, a puparium and an adult male are illustrated in Figure 2.

Consumption

Figure 3 illustrates the relationship between larval wet mass and kelp consumption rate. The parameters are related by the equation y (consumption: mg dry kelp consumed) = 0,44 (wet mass of larva) $x^{2,32}$ giving an average consumption of 0,15 mg dry kelp per mg larva (wet) per day. Given the wet mass to dry

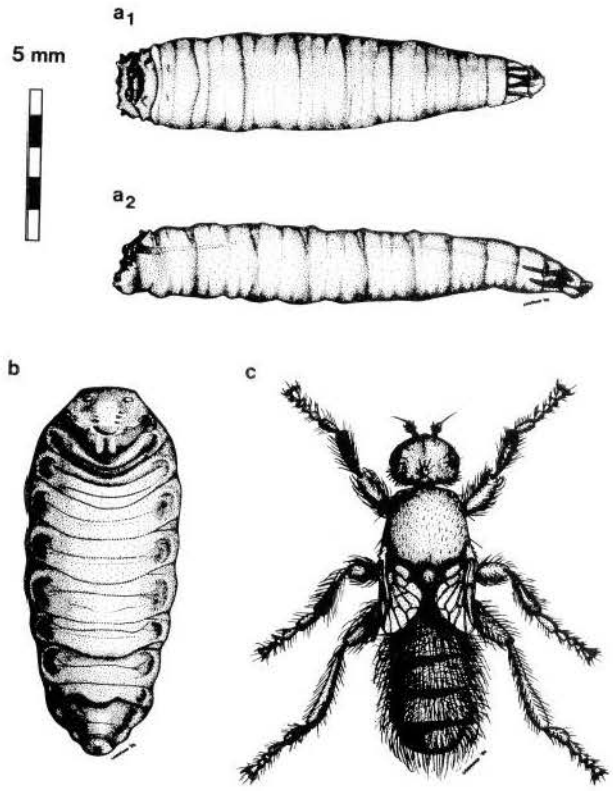

Fig. 2. *Paractora dreuxi mirabilis*. (a) Larva; (a1) Dorsal view; (a2) Lateral view with mouthparts extended; (b) Puparium; (c) Adult.

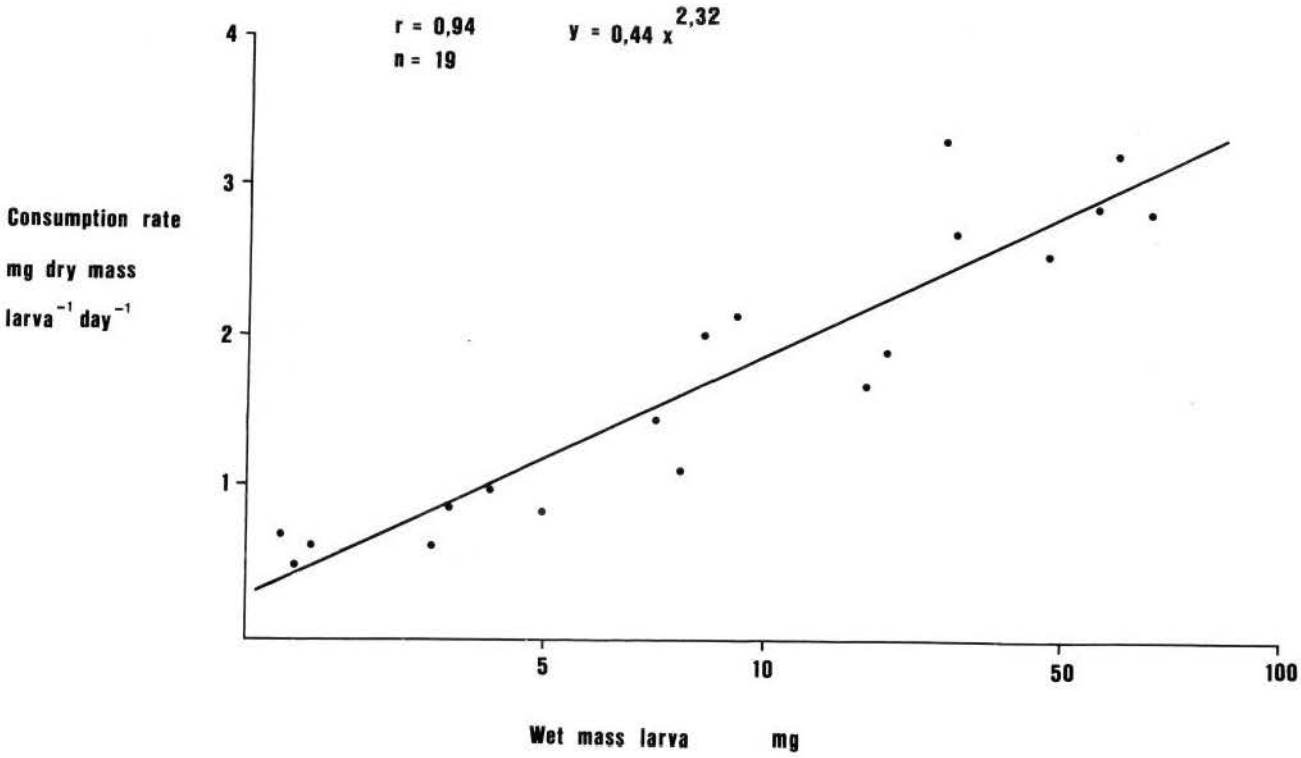

Fig. 3. Consumption of kelp by *Paractora dreuxi mirabilis* larvae at 10°C and 100% RH.

mass ratio of *Paractora* larvae (4 : 1 after 4 days at 60°C) this amounts to 0,5 mg dry kelp mg^{-1} dry larva day^{-1}. Over the average development period of 40 days the total mass of kelp consumed by a larva, based on mean daily mass, is 226 mg wet or 44 mg dry kelp (wet/dry mass ratio is 6:1). The third instar accounts for 98 % of total kelp consumption; the first instar for only 0,1 %. Adults were observed to feed on the mucus formed by decomposing kelp; in the laboratory they readily took to a mixture of sugar and milk powder, but their diet was not quantified.

Third instar larvae occur in densities of up to 20 individuals kg^{-1} of decomposing kelp. This represents a biomass of approximately 2 g wet (or 0,5 g dry) kg^{-1} of kelp. Given the consumption figures obtained in the laboratory, consumption by larvae in a natural wrack bed would amount to approximately 1 g kg^{-1} of beached kelp (wet masses) day^{-1}.

Discussion

The undersides of fresh *Durvillea* fronds are usually covered by *Paractora* eggs within two to three days of being beached at Marion Island. The thick, tough epidermis decomposes slowly and does not allow burrowing by newly hatched larvae. First, second and early third instar larvae feed mainly on the surface layer of mucus and the decomposing epidermis on the underside and between layers and folds of fronds. The rapid increase in growth of third instar larvae (Fig. 1) occurs when the kelp has decomposed sufficiently to allow burrowing into individual fronds.

Backlund (1945) distinguished between "wrack strings" (individual fronds) and wrack beds. Decomposition proceeds in different ways and at varying rates in the two types of wrack (Griffiths & Stenton-Dozey 1981). On Marion Island only wrack beds sustain kelp fly populations. Wrack strings are also colonised but are invariably subject to desiccation and are broken down mainly through trampling by penguins and seals. A wrack bed provides a warm and humid microclimate which is relatively independent of environmental conditions (Dobson 1976). On Marion Island temperatures inside wrack beds rise to well above ambient and remain constant at around 10°C (Crafford, unpublished). Temperatures may well rise much higher in deep, undisturbed wrack beds on sunny days.

Decomposing kelp is gradually trampled and washed in amongst the pebbles on the beaches, a sizeable wrack bed often disappearing within two months. This results in the build-up of a considerable reservoir of sub-surface kelp detritus which constitutes the "true interstitial biotope" described by Trehen & Vernon (1982) on pebbled beaches on île Crozet. At Marion Island this biotope is utilised by a guild of kelp detritivores (collembolans, oligochaetes and at least three other species of Diptera). *Paractora* larvae complete their development in this sub-surface detritus reservoir, gradually moving further down and eventually pupating as deep as 50 cm beneath the pebbles.

Trehen & Vernon (1982) stressed that *Paractora dreuxi* on île Crozet shows three distinct stages in its development: a first stage in stranded kelp, a second in the underlying pebbles and a third higher up on beaches and even in vegetated saltspray areas. The last stage is possibly associated with a change in diet, and mature larvae are thought to become predators of smaller fly larvae or oligochaetes. On Marion Island third instar larvae migrate higher up on the beaches but were never found as far as the adjacent vegetation. Larvae of all three instars were found simultaneously in both decomposing kelp and the underlying pebbles, although first and third instar larvae predominated in the former and the latter respectively. The fact that *P. dreuxi mirabilis* only completed its development in kelp in the laboratory suggests that they are at most facultative carnivores. It also illustrates to some extent the unusual plasticity in habits, morphology and physiology that characterises the endemic insect fauna as remarked on by Kuschel (1971) and Séguy (1971).

The long larval development of *P. dreuxi mirabilis* on sub-Antarctic Marion Island reflects a trend among holometabolous insects in the Arctic and sub-Antarctic (Downes 1965). Table 2 compares the duration of life cycles of Diptera species associated with beached kelp in Britain, South Africa and some sub-Antarctic islands.

Anatalanta aptera on île Kerguelen varies in its rate of development with temperature and life cycles being completed in 40 and 62 days at 8,6 and 4,8°C in February and May respectively (Trehen 1981). This may account for the discrepancy in duration of life stages shown in the laboratory and field colonies of *P. dreuxi mirabilis* on Marion Island where the duration of both larval and pupal stages was shorter in the laboratory than in the field.

As with *Coelopa frigida* (Dobson 1974), *Paractora* populations in the field show no temporal pattern of successive generations. On Marion Island the beaching of kelp also occurs randomly after storms and is not correlated with the lunar cycle. In South Africa the life cycle of *Fucellia capensis*, for instance, is perfectly correlated with the beaching of kelp at spring tide (Stenton-Dozey & Griffiths 1980).

During the summer, beaches on Marion Island abound with carcasses of seals and penguins that have died whilst visiting the island to breed. The glut of carrion is in excess of what the scavengers on the island (giant petrels, lesser sheathbills,

Table 2
Comparison of the duration of life stages of kelp fly species under laboratory conditions.

Species	Family	Location	Egg (h)	Larva (d)	Pupa (d)
Fucellia maritima (Egglishaw 1960)	Muscidae	Britain	40 – 60	16 – 22	18 – 21
Fucellia capensis (Stenton-Dozey *et al.*)	Muscidae	South Africa	24 – 32	10 – 12	8 – 14
Coelopa frigida (Dobson 1976)	Collopidae	Britain	22,6	6	6
*Anatalanta aptera** (Trehen 1981)	Sphaeroceridae	Île Kerguelen	—	40 – 62	18 – 30
*P. dreuxi mirabilis** (present study)	Helcomyzidae	Marion Island	96 – 120	46 – 59	30 – 60

*Subantarctic

skuas and southern black-backed gulls) can consume. Individual carcasses on the beaches are often heavily infested with *Paractora* maggots (Smith 1977, and Crafford unpublished). This suggests an opportunistic utilisation of a high protein food source when wrack is less abundant than it is during the stormy winter season. According to Egglishaw (1960) *Fucellia maritima* in Britain is also attracted to decomposing organic material other than kelp, although this is characteristic of the Family Muscidae to which this species belongs.

The decay of beached kelp is enhanced by the burrowing and feeding activity of kelp fly larvae. This is possibly due to the transfer and spread of micro-organisms by the larvae (Stenton-Dozey & Griffiths 1980). *Paractora* larvae are not rapid feeders, consuming only half their own dry mass in kelp per day. *Fucellia capensis* larvae consume as much as twice their own dry weight in kelp per day (Stenton-Dozey & Griffiths 1980). However, as a result of the high standing stock of larvae in wrack beds on Marion Island and the long larval duration, *Paractora* larvae would account for the direct consumption of relatively large amounts of kelp. This, coupled to their enhancement of bacterial decay and their availability as prey to vertebrate insectivores establish them as important links in nutrient and energy chains in the littoral zone on Marion Island. Further investigations into the ecological energetics and the effects of *Paractora* larvae on the decomposition processes in kelp are underway.

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