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PATTERNS OF ENERGY FLOW IN POPULATIONS OF THE DOMINANT INSECT CONSUMERS ON MARION ISLAND

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Patterns of energy flow in populations of the dominant insect consumers on Marion Island

by

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PART I: THE CONTEXT

"We seek patterns in nature; for it is pattern, not bulk of data, that leads to understanding."

Calder (1984)

CHAPTER 1: INTRODUCTION

"The acquisition and utilization of energy in accordance with the laws of thermodynamics remains the best place to start ... to understand the higher intricacies of any ecological system."

Brown (1981)

1.1 Background, rationale and objectives of research described in this thesis

Insects dominate the sub-Antarctic terrestrial mesofauna, in terms of their abundance, total biomass, and their role in energy flow and nutrient cycling in sub-Antarctic terrestrial ecosystems. Between 1983 and 1988 I studied the energetics of five macro-insect species that dominate, both in terms of biomass and energy flow, the four major terrestrial invertebrate consumer guilds (*sensu* Root 1967) on Marion Island. These guilds are: the herbivore (angiosperm-folivore) guild, the bryophage (moss-feeding) guild, the plant-litter detritivore guild, and the kelp-decomposer guild in the island's littoral zone. The insects are, respectively, a host-specific folivore (*Embryonopsis halticella* Eaton, Lepidoptera: Yponomeutidae); two polyphagous, moss- and angiosperm-feeding weevils (*Ectemnorhinus similis* C.O. Waterhouse and *E. marioni* (Jeannel), Coleoptera: Curculionidae); a polyphagous detritivore (*Pringleophaga marioni* Viette, Lepidoptera: Tineidae) and a kelp-feeding saprophage (*Paractora dreuxi* Seguy, Diptera: Helcomyzidae). This study formed part of a long-term, multi-disciplinary investigation of ecosystem processes at the Prince Edward Islands, the ultimate aim of which was the construction of a whole-island accounting model of nutrient and energy flow. The underlying assumption was that the youth and paucity of the sub-Antarctic terrestrial biota, and hence its "simplicity," made such an ambitious approach feasible. Biotic diversity and the concomitant scope for ecological interactions are indeed less overwhelming in the sub-Antarctic than in temperate or tropical ecosystems; however, sub-Antarctic ecosystems are far more complexly and profoundly shaped by the effects of past geological events and climatological processes. The "whole island accounting model" has thus not yet been realized, but quantification of energy flow through the major primary consumers (the primary motivation for this study) has allowed the closest approximation yet of energy relations between producers and consumers in the Marion Island terrestrial ecosystem.

A study of energy flow through consumer populations presupposes knowledge of energy flow *within* such populations (i.e through their constituent individuals). Living systems on all hierarchial levels - from individuals to populations to ecosystems - are "far-from-equilibrium dissipative structures," that require a continuous input of free energy in order to maintain themselves in a steady state (Brooks and Wiley 1988). Through differentiation and growth, an organism builds itself, using materials actively acquired from its surroundings and a blueprint of instructional information contained within it. This instructional information is not only directly related to structural organization (form), but it also determines how energy will flow through the organism (function) in a particular environment (Brooks and Wiley 1988). Information and environment together limit and determine the "options" (of life histories or "ecological strategies") available to the organism.

The insect consumers on Marion Island, like all living organisms, indeed respond to their environment with a rather limited number of recognizable "ecological strategies" (Holm 1988). Such strategies evolve on a "templet" of characteristics - both spatial and temporal - of the environment (e.g. Southwood 1988). Chapleau *et al.* (1988) have objected to the "obscure, not directly testable, but omnipresent allusion of purposefulness" of the term "strategy," and advocate the use of "pattern" instead. Semantically, both "pattern" and "strategy" describe a reliable sample of traits, acts or other observable features. In ecology, the fundamental issue addressed either as "pattern" or "strategy" is the way in which food energy is acquired and proportionally allocated to different life stages and physiological processes throughout the life history of an organism. This "pattern of energy flow" in an individual or population of a species, constructed on an informational blueprint, encompasses not only all epiphenomena of its life history, but also says something about the evolutionary history and mechanisms that underly them. For instance, of the total energy flow which constitutes this "pattern," that proportion which has to be dissipated (respired) to maintain an individual or a population at non-equilibrium with its particular environment, is an indication of its "adaptation" to that environment.

The *leitmotif* of this thesis is that selection of the ways in which insects on Marion Island acquire, utilize and allocate food energy, is the major cause of the evolution of their particular life history/energy flow patterns. If the latter are occasionally called "ecological strategies," no choice or purpose on the part of the organism is implied.

Food energy "ultimately limits" (Odum 1971) heterotrophic organisms, although for insect herbivores food nitrogen is more "proximally limiting" (Mattson 1980) and food water content is "fundamentally limiting" (Scriber 1978). On the sub-Antarctic islands, plant productivity is relatively high, and a vast amount of energy is contained in the big dead and live standing crops of plant communities (both vascular and cryptogam). The low-temperature regime on the islands limits the accessibility of this energy to poikilotherm consumers (e.g. Remmert 1980), and for this reason, cold - rather than isolation and geological youth - has, at least historically, been the primary obstacle to colonisation of the sub-Antarctic islands, and the primary cause of their low biotic diversity. The "success" of dominant primary consumers can be expected to depend largely on the extent to which they are able to circumvent the limitations, imposed by low temperatures, on the acquisition and assimilation of energy. In most primary consumers on Marion Island - whether herbivores feeding on angiosperms and cryptogams, or detritivores feeding on plant litter - microhabitat selection plays an equally important role as physiological adaptation in the circumvention of the effects of low temperatures.

Temperature has been described as being, next to light, the most potent environmental component with regard to life on earth (Cossins and Bowler 1987). The impact of temperature on ectotherms is of two kinds: first, as a direct factor affecting the physiological performance of individuals, it has major ecological implications for species. Secondly, temperature can be a factor in evolution, acting as a selective force in speciation (see Cossins and Bowler (1987); but see also Endler (1986) for justified criticism of the use of the terms "selective force" and "evolutionary pressure"). A study of temperature regimes in the respective microhabitats of the five dominant insect species on Marion Island was consequently undertaken, to show how the energetics ("patterns of energy flow") of these species relate to the "templet" of their habitats, and how abiotic factors contribute to shaping their life histories and ecological attributes.

Following from the above, the objectives of the study described in this thesis can be summarized as follows:

1. To describe the patterns of energy flow in individuals ("life strategies") and populations (population energetics) of the five dominant macro-insect species on Marion Island, against the templet of their microhabitats.

2. To compare these patterns against a background of past and present geological, climatological, evolutional and ecological processes in the sub-Antarctic.

3. To use energy flow through populations of the five species as the basis for a quantitative description of energy flow through the primary consumer component of the terrestrial ecosystem on Marion Island.

This thesis is a collation of research findings already published or being prepared for publication in the scientific literature. The prolonged introduction (Chapter 2) sketches the physical and biological environment of Marion Island, in which the studies reported here find their context. This thesis also houses the results of research not directly related, but supplementary to that described in the thesis title; however, these results form an integral part of the thesis.

1.2 Marion Island in the context of the sub-Antarctic

Oceanographic, climatological and biological definitions of the sub-Antarctic differ. In oceanographic terms, the sub-Antarctic is the zone of waters between the Antarctic and the subtropical convergence (Deacon 1960). Holdgate (1965) defined the sub-Antarctic, in climatological terms, as that region of the southern ocean characterized by the absence of temperatures warmer than 8.5 °C, considered to preclude the occurrence of trees. Biologically, the sub-Antarctic has traditionally been defined only in botanical terms. Wace (1969) regarded the sub-Antarctic as the area south of the southern limit of woody-shrub growth (to distinguish it from the cool temperate zone, which includes e.g. Gough, Amsterdam and the Falkland Islands) and north of the southern limit of closed phanerogamic vegetation (distinguishing it from the maritime or low Antarctic in the south, which includes the Antarctic peninsula and islands such as Signey and the South Orkneys). According to the biological classification, the "true" sub-Antarctic islands are the Crozets (46°S), Marion and Prince Edward, Macquarie (54°S), Kerguelen (49°S), South Georgia (°S) and Heard (53°S) (Fig. 1).

The different sub-Antarctic islands share many elements of an endemic terrestrial sub-Antarctic biota. Because of their closer proximity to continental land masses (New Zealand and South America respectively), Macquarie and South Georgia also share elements of their native biota with these land masses. Heard Island, Îles Kerguelen, Îles Crozet, and Marion and Prince Edward Islands form a distinct biogeographical province, based on the high within-province endemicity and the close relationships between within-island endemics. Kerguelen Island is regarded as the source area for the biotas of the other islands in the province, being both the oldest (40 - 100 million years) and the largest in the group (Nougier 1972). Previously called the Kerguelen Biogeographical Province by e.g. Van Zinderen Bakker *et al.* (1971), the designation "South Indian Ocean Province" (SIP) (Lewis Smith 1984) is now more commonly used. The composition, diversity and characteristics of the biotas of the SIP islands are shaped, overwhelmingly, by three factors: their isolation from the continents, their youth and geological history, and the overriding influence of the surrounding ocean. The ocean has an ameliorating effect on temperatures at the islands, preventing both short- and long-term fluctuations in temperature and, because of the high water content of air masses above the islands, maintaining relatively favourable ambient temperatures. Furthermore, the host of sea-going birds and mammals that use these islands as moulting and breeding sites, play an important role in the functioning of the islands' terrestrial ecosystems, by importing vast quantities of nutrients into these ecosystems each year (Smith 1987a).

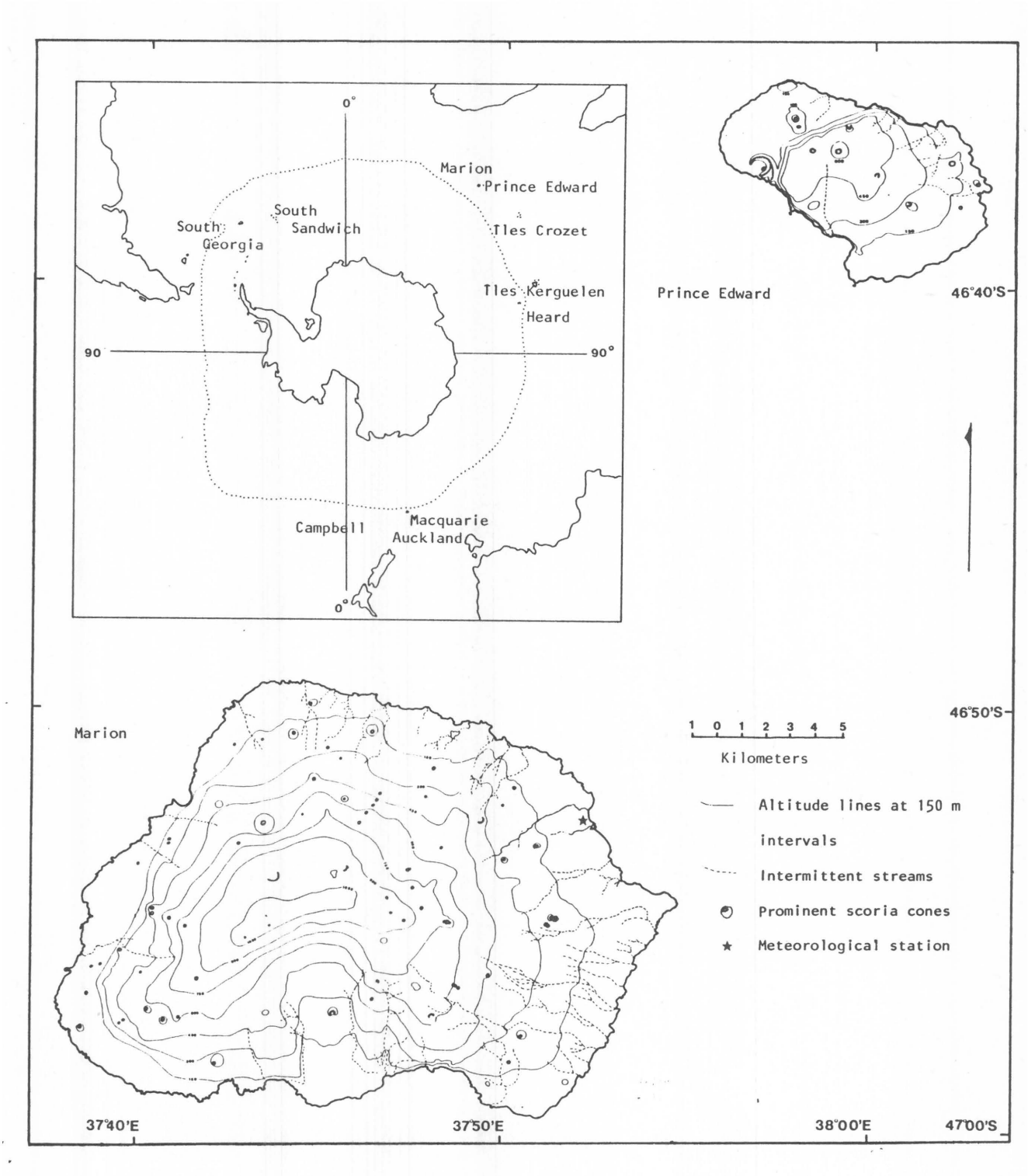

Figure 1. Marion Island in relation to the other sub-Antarctic islands of the South Indian Ocean Province.

The Prince Edward and Crozet Archipelagos, both situated north of the Antarctic Convergence, have a mean annual air temperature range of < 5°C, with mean winter temperatures of <3°C and mean summer temperatures of >7°C. Kerguelen is marginally colder and Heard Island is the coldest of the SIP Islands, with a temperature range of only -2°C - 4°C. Only Kerguelen and Heard Islands are permanently snow- and ice-covered to any significant extent. Kerguelen is about 20% snow-covered, while Heard Island is almost completely covered by glaciers and has only about 15% snow-free ground (Walton 1984).

Various authors (Gressitt 1970, Carlquist 1974, Trehen and Vernon 1982) have pointed out that the classical MacArthur-Wilson model of island biogeography (MacArthur and Wilson 1963) does not appear to fit the isolated sub-Antarctic islands of the SIP. There is indeed a poor correlation between island surface area and species richness on these islands (Table 1), but Chown (1989b) has provided a thoughtful explanation why this should be the case, pointing out *inter alia* that ice-free, and not total island area, should be used in the model.

The ages (in millions of years), surface areas, and the ranges of mean monthly temperatures of the SIP Islands, are shown in Table 1. In addition, the numbers of free-living insect species, with the percentage endemism, and the percentage occurrence of flightlessness (of insects belonging to normally winged groups) on each island group of the SIP are shown. The data were gleaned from Gressitt (1970), Chevallier *et al.* (1982), Crafford *et al.* (1986) and Laws (1984).

A striking feature of the insect faunas of the SIP Islands is the high incidence of flightlessness (either because of aptery, microptery or brachyptery) in insects that belong to normally winged orders (e.g. Lepidoptera, Coleoptera and Diptera). The four insect species that are the subject of this thesis are all secondarily flightless. The evolutionary causes and mechanisms of flightlessness have been the subject of perennial analysis and speculation, which will be added to in Chapter 8 of this thesis.

Table 1. Comparative ages, surface areas, and temperature ranges of the SIP Islands, with the sizes (species number), endemism and percentage occurrence of flightlessness (within normally winged insect groups) of their insect faunas.

Island	Age (myr)	Area (km^2)	Temp. (°C)	Insects (no of species)	Endemism	Flightlessness
Îles Kerguelen	22 - 40	7 200	2 - 7.8	36	34%	80%
*Îles Crozet	0.4 - 5.5	233	3 - 8	38	50%	84%
Heard	>10 ?	375	3 - 7.9	9	3%	100%
Marion	0.25 - 2	290	-2 - 4	27	35%	86%

* Île de la Possession only.

CHAPTER 2: THE MARION ISLAND ENVIRONMENT

"Some reasons why islands have been well suited to provoking or testing theoretical ideas are that they have definite boundaries, come in many different sizes and heights and remotenesses, often have relatively simple communities of plants and animals, and serve as ready made evolutionary laboratories offering replicate "natural experiments" in community assembly."

Diamond and May (1981)

2.1 Geological history and topography

Marion Island and its small neighbour, Prince Edward Island (Fig. 1), are the twin peaks of closely related, coalescing shield volcanoes. They arose c. 2 million years ago in a series of volcanic events, near the centre and just off the crest of the West Indian Ocean Ridge. Although similar to Marion Island in geological features and general topography, Prince Edward Island is only about one-seventh its area and about half its elevation, and as a result may have a slightly different climatic regime. Because of its smaller size and lower elevation, it also appears to have escaped glaciation during the glacial periods of the Pleistocene (Verwoerd 1971, Smith 1987a).

The total surface area of Marion Island is 290 km^{-2}, of which about half (138 km^{-2}) is below 200 m altitude. Its highest peak is 1 230 m a.s.l.. Permanent ice, in the form of a static, scree-covered glacier, covers an area of about 10 km^{-2} above 1 000 m elevation. The island was extensively glaciated throughout the Quaternary, and during the last 300 000 years was subjected to three glacial episodes, each comprising a series of stades and interstades. Volcanic activity during interglacials is thought to have been an isostatic response to the removal of the weight of the ice. The ice cover of the last glacial began to disappear rapidly about 12 000 years ago, and extensive lava flows dated to 15 000 ± 8 000 years BP may likewise have occurred as a response to this disappearance. Many lava flows are much younger, however, and a small volcanic eruption occurred as recently as September 1980 on the west coast of Marion Island. The centres of post-glacial eruptions, of which the uneroded, jagged black lava flows cover most of the coastal lowland, are c. 170 volcanic cones scattered over the island. The grey pre-glacial lava formations (dated at 276 000 + 30 000 years BP) are exposed chiefly at high altitudes, and have a smooth topography with single large, scattered boulders that were deposited as glacier debris (Verwoerd 1971, Smith 1987a).

2.2 Climate

All climate data from Marion Island refer to the macroclimate at the meteorological station, c. 10 m a.s.l. on the sheltered east coast. Little is known of microclimates in the different vegetation types, and of the climatic regime at higher altitudes or on the island's exposed west coast. The outstanding features of the island's major climatic variables (as measured at the meteorological station, and summarized from the continuous record kept since 1948) are the following (Schulze 1971, Smith 1987a):

1. The mean annual air temperature is low (c. 5°C, measured in a Stevenson Screen 1.5 m above ground) and remarkably constant. The seasonal temperature range is 4.1 °C (mean air temperature of the coldest and warmest months are 3.2 °C and 7.3 °C, respectively). Mean diurnal temperature range is 1.9°C. Absolute minimum temperatures are below zero in every month, and there are on average 16 days with absolute maximum temperatures above 15 °C during the year. The average temperature lapse rate at Marion Island is about 4.5 °C and 4.0 °C per 1 000 m altitude in winter and in summer respectively.

2. Very high precipitation (>2 500 mm per annum), mainly in the form of rain, is distributed evenly throughout the year, although the late winter months (August to October) are marginally drier. Snow may occur in any month of the year, but heavy snowfalls and snow cover extending to the coast are restricted to short periods during winter.

3. A high degree of cloudiness is prevalent on Marion Island. Annual sunshine duration is only c. 30 % of the maximum possible.

4. Constantly high relative humidity (annual mean screen RH value 83 ± 2%).

5. Strong, predominantly westerly, wind, with an average of 107 days per annum experiencing gale force (>55 km h^{-1}) wind blowing for at least one hour. The "chill factor" or freezing potential is a combined effect of strong wind and low temperature, which may reduce a "measured" temperature of 5 °C to an "effective" temperature of several degrees below zero for an organism exposed to the wind.

Marion Island is presently 2 ° of latitude north of the Antarctic Convergence, which makes it (with Îles Crozet) one of the more "temperate" sub-Antarctic Islands. Past falls in world temperature, such as occurred during the major and minor ice ages, would have had the effect of shifting the Convergence closer to, or even north of, the island, with important implications for the island's climate and biota. A temperature drop of at least 3.5 °C during the glaciations at Marion Island is indicated from the evidence of periglacial, palynological and ocean-floor sediment studies (Scott 1985; Scott and Hall 1983). At such times, Marion Island probably had a climate similar to that of Heard Island today.

Global temperature increases, especially at mid to high latitudes and linked directly to the "greenhouse effect" of an increased carbon dioxide quantity in the atmosphere, are increasingly well documented (e.g. Raper *et al* 1983). The mean annual surface temperature of Macquarie Island (54°S) shows an upward trend of about 1°C since annual records started in 1949 (Adamson *et al.* 1988). Recent evidence points to a similar trend on Marion Island, where mean summer temperatures may have risen by as much as 2 °C over the past four decades (V. R. Smith, unpublished data).

2.3 The terrestrial biota

The first descriptive studies of the terrestrial vegetation and fauna of Marion Island were undertaken during the "golden age" of scientific exploration, in the nineteenth century, but only since 1965 have scientists undertaken full-time biological (mainly autecological) studies at the island. Only during the past decade have such studies been put in a proper ecological context, and has there been an attempt to understand ecosystem processes (such as nutrient and energy flow), rather than the functioning of single components. Entomological studies have only been undertaken since 1983.

Marion Island is influenced by three major factors which have a dramatic effect on the composition of its terrestrial biota. First, its geographic isolation, by great expanses of ocean, from sources of colonization (Africa, the nearest continent, is almost 2 000 km distant; the nearest land mass is Îles Crozet, 900 km to the east). Secondly, it is geologically one of the youngest sub-Antarctic islands, and has experienced a relatively short period of physical conditions favourable for colonization. Thirdly, its macroclimate is characterized by virtual aseasonality in its (low) temperature and (high) rainfall regimes, which considerably reduce the survival potential of those propagules or disseminules that succeed in reaching the island. Consequently, the terrestrial biota are impoverished, disharmonious and poorly integrated, and are generally adapted to the

physical rather than to the biotic environment of the island. Poor adaptation to the biotic environment is reflected, inter alia, in the lack of defense mechanisms and poor competetive ability of the majority of the native biota, which render them exceptionally vulnerable to invasive predators and competitors.

2.3.1 Primary producers

Only 38 vascular plant species, of which 14 are aliens introduced by man, form part of the vegetation of Marion Island. Closed vascular plant communities occur only in areas below 500 m a.s.l., chiefly in coastal areas, and cover at least 50% of the surface area of the island. Mosses (72 species) and liverworts (35 species) contribute about 25% of total lowland plant biomass on Marion Island, but whole-island standing crop of bryophytes may rival or exceed that of vascular plants. Approximately 100 lichen species have been recorded. These are mainly crustose, epilithic forms that dominate the vegetation at high altitudes, but which also occur abundantly on the lowland plains. Most of the indigenous plant species have a wide ecological amplitude and occur over much of the range of habitats available on the island.

Gremmen (1981) distinguished 41 plant communities at the association or sub-association level, and grouped these communities into six complexes, based on their species composition and on structural and ecological considerations. These complexes are:

1. The salt-spray complex, restricted to shore-zone areas strongly affected by wind-blown sea spray. The dominant vascular plant is a small succulent, *Crassula moschata* (Crassulaceae).

2. The "biotic" complex, which is heavily influenced by trampling and manuring by animals. This complex consists of a wide range of communities, most of which occur on the coastal zone near colonies of seals and penguins. Inland, the influence of surface-nesting and burrowing birds also causes the presence of communities belonging to this complex. Dominant vascular plants are the tussock-forming grass, *Poa cookii* (Poaceae), *Callitriche antarctica* (Callitrichaceae) and *Cotula plumosa* (Asteraceae).

3. The drainage line complex, which forms at mire and lowland slope sites where there is pronounced lateral subsurface water movement. Communities of springs and flushes belong to this complex. It is dominated by the small, woody forb *Acaeana magellanica* (Rosaceae) and dense growths of filamentous mosses (*Brachythecium* spp.).

4. The mire and bog complex, dominated by bryophytes and graminoids and occurring on saturated peat. It is dominated by the grass *Agrostis magellanica* (Poaceae), the sedge *Juncus scheuchzerioides* (Juncaceae) and the liverwort *Blepharidophyllum densifolium* (Scapaniaceae).

5. The slope complex, which consists of closed and open fernbrake (*Blechnum penna-marina*) communities and dominates the vegetation of well-drained lowland slopes.

6. The fjaeldmark or wind-desert complex, which forms on rocky areas strongly exposed to wind. This complex, consisting of communities of the cushion-forming dicot *Azorella selago* (Apiaceae), bryophytes and lichens, dominates the vegetation above 300 m altitude. Fjaeldmark communities also occur at lower altitudes where they exhibit fairly high (up to 60%) aerial vegetation cover.

Chown (1989a) has made a useful, broad distinction between the "epilithic biotope" (areas dominated by cryptogams, e.g. high-altitude *fjaeldmark*, vertical rockfaces, rocky shores, and lava outcrops) and the "vegetated biotope" (areas supporting vascular plant communities, i.e. chiefly coastal plains, sheltered slopes, and low-altitude *fjaeldmark*).

Closed plant communities on Marion Island support a higher phytomass than those in many temperate or tropical areas. The development of the high phytomass can be ascribed chiefly to the long growing season (about 300 days for vascular plants and 365 days for many of the bryophytes), but also to prolonged leaf longevity in some species, and to the absence of large herbivores and the paucity of invertebrate grazers. Primary productivity (in g m^{-2} day^{-1}), however, is low compared with most vegetation types in other regions. As it is, the high phytomass is deposited as large quantities of litter, and primary production on the island is channeled ultimately through a detritus chain.

The dominant primary producer in the intertidal zone at Marion Island is the bull-kelp, *Durvillaea antarctica*. Estimated total standing crop of this kelp is 3 300 t (wet mass), which is situated in varying proportions along different shore types of the island's c. 72 km coastline. The shores consist mainly of steep cliffs and large-boulder and block beaches, and only 2 % (c. 1.5 km) consists of pebble and small-boulder beaches (De Villiers 1976, Haxen and Grindley 1985). During the frequent storms and rough seas at the island, kelp is cast ashore either as single wrack strings or in large quantities as wrack beds, although extensive wrack beds form only on the few gently sloping pebbled shores. In this ecotone between the terrestrial and marine ecosystems of Marion Island, both marine and terrestrial fauna contribute to the degradation of kelp, with resultant nutrient input for both the near-shore terrestrial and the marine littoral zones.

2.3.2 Fauna

The terrestrial ecosystem of Marion Island is profoundly influenced by the activities of marine birds and mammals, during their terrestrial phases of breeding and moulting. The total breeding avifauna of Marion Island has been put at more than 2 million pairs, belonging to 28 species. These birds, chiefly populations of four penguin and 18 Procellariiformes (albatrosses and smaller petrels) species, markedly influence the structure and functioning of the terrestrial ecosystem, by transferring energy and nutrients from the surrounding ocean to the island, or by causing erosion through trampling and burrowing (Frost 1979). The total annual guano production by populations of 14 surface nesting bird species amounts to about 4 000 tonnes (dry mass), 98% of which is voided by penguins on the coastal plain (Siegfried 1978). Nutrient input in inland areas, by populations of the 12 small burrowing petrel and prion species (Procellariidae and Pelecanoididae) has not been quantified, but is probably substantial.

Only one bird species, the lesser sheathbill *Chionis minor*, does not forage at sea and resides permanently on land, where it is the major native, vertebrate insectivore. It forages extensively for soil invertebrates inland, and may have a significant localized impact on invertebrate populations in certain habitats. Kelp gulls (*Larus dominicanus*), and possibly Antarctic terns (*Sterna vittata*) also rely on terrestrial invertebrates for part of their diets (Burger 1978a, 1978b).

On the coast, three seal species (the southern elephant seal, *Mirounga leonina*, and the fur seals *Arctocephalus tropicalis* and *A. gazella*) destruct or cause changes in vegetation, and modify local topography, in their haul-out areas (Panagis 1985). Elephant seals have been identified as important agents in both the mechanical and microbial breakdown of wrack, since they haul out chiefly on pebbled beaches, where they invariably repose and void their faeces on wrack beds (Crafford and Scholtz 1987b).

As in the rest of the sub-Antarctic, no indigenous land mammals occur at Marion Island. House mice (*Mus musculus*) were already established on the island 170 years ago, probably having arrived with the very early sealers or with shipwrecks (Watkins and Cooper 1986). They have successfully colonized the entire island and occupy most habitats, from the beaches to about 600 m altitude (Gleeson 1981). They are almost exclusively insectivorous, and have been shown to have a detrimental effect on populations of their chief

prey, the larvae of the endemic flightless moth, *Pringleophaga marioni* (Crafford and Scholtz 1987a, Rowe-Rowe *et al* 1989). These larvae are important detritivores, and their feeding activity has been shown to considerably enhance bacterial populations and hence also nutrient mineralization from plant litter. Reduction of *P. marioni* larval populations by mice therefore has implications for the rate and process of nutrient cycling in the island's vegetation and soils (Crafford in press; see also Chapter 6).

Domestic cats (*Felis catus*) were introduced to the island in 1949. They quickly turned feral, and by 1975 a breeding population of about 2 000 cats were killing an estimated 450 000 small burrowing birds annually (Van Aarde 1979, 1980; Van Aarde and Skinner 1982). Crafford and Scholtz (1987a) estimated that in one specific year (1982), cat predation, on their six major prey species, resulted in a c. 9 500 kg (dry mass) loss of guano input to inland vegetation on Marion Island. The cats have caused the local extinction of at least one of their prey species (Watkins and Cooper 1986), but the indirect effect of cat depredations, in the form of reduced nutrient input to inland vegetation, may be equally detrimental.

Prince Edward Island, with Heard and MacDonald Islands, is one of the last pristine sub-Antarctic Islands, having escaped most of the effects of human presence. It harbours no introduced mammals, and only two alien plant species and four alien invertebrate species have been recorded on Prince Edward Island. Although the native biotas of Marion and Prince Edward Islands are qualitatively similar, Crafford and Scholtz (1987a) have described quantitative differences that can be ascribed to the detrimental effects of cats and mice on ecosystem functioning at Marion Island. Its undisturbed state makes Prince Edward Island an ideal "control" site for the monitoring of long-term effects of the human impact on Marion Island's ecosystems (e.g. Cooper and Condy 1989).

Only 68 free-living invertebrate species have been recorded on Marion Island, the majority (27) of which are insects (Table 2). Only 17 of the insects are indigenous to the sub-Antarctic, the remainder being cosmopolitan synanthropes presumably introduced by man. The paucity of species is offset by high invertebrate densities and biomass in most vegetated, lowland habitats, and particularly in plant communities of the biotic complex (Fig. 2; Burger 1978a; Crafford and Scholtz 1987a).

At least five cosmopolitan insect species are intermittently recorded as vagrants at Marion Island; they are regarded as "transient aliens" (Crafford *et al.* 1986). One of these, the cosmopolitan "painted lady" butterfly (*Vanessa cardui*) may occasionally breed on the island, given the regular sightings of individuals in pristine condition (pers. obs.). Alien species have been recorded with greater frequency over the past few years, and in 1986 an established, permanent population of the cosmopolitan cabbage pest *Plutella xylostella* (Lepidoptera, Plutellidae) was discovered on the protected south-eastern coast of Marion Island (Crafford and Chown 1987). *P. xylostella* is host-specific on the Brassicaceae (Cruciferae), and on Marion Island heavily infests the native Kerguelen Cabbage, *Pringlea antiscorbutica*.

Crafford and Chown (in press) have argued that increased human activity in the Antarctic and sub-Antarctic, coupled with global warming (which is generally expected to be more pronounced at the higher latitudes), should see increased colonization of the sub-Antarctic by cosmopolitan, herbivorous insects with good dispersal ability.

Table 2. The free-living invertebrates of Marion Island.

Taxon	Number of species
Phylum Arthropoda	
Class Insecta	
Order Coleoptera	8
Order Lepidoptera	3
Order Diptera	9
Order Hymenoptera	1
Order Hemiptera	4
Order Psocoptera	1
Order Thysanoptera	1
Class Collembola	13
Class Arachnida	
Order Araneae	4
Order Acarina	19
Phylum Annelida	
Class Oligochaeta	3
Phylum Mollusca	
Class Gastropoda	2
Total	68

2.3.3. The role of insects in the terrestrial ecosystem

The "simplicity" of sub-Antarctic terrestrial ecosystems (e.g. Van Zinderen Bakker 1978) which is usually inferred from the low diversity of species and habitats in such ecosystems, is deceptive. Danks (1981) pointed out that there are numerous cross-links of interactions within similar "simplified," low-diversity ecosystems in the Arctic. At Marion Island single consumer species, because of extraordinary plasticity in behaviour and physiology, may enter the system at different trophic levels and utilize the gamut of available habitats and resources. Important grazing chains also exist in the soil at the microscopic and sub-microscopic level, while nutrient- and energy cycling on the vegetated coastal plains of Marion Island is driven, to a large extent, by marine input. The result is an intricate cross-web of interactions within and between different trophic levels, and across the boundaries of the marine and terrestrial biomes.

Insect herbivory, previously thought to be non-existent at Marion Island (e.g. Huntley 1971), probably does not account for more than about 3% of energy flow from producers to consumers (Crafford *et al.* 1986). With virtually all of plant productivity thus becoming dead organic matter (Smith 1977b), the emphasis of energy flow and nutrient circulation shifts to the below-ground, soil subsystem. At Marion Island, the litter/soil system houses a simple guild of invertebrate litter-feeders, which is dominated by only three macro-invertebrate species: the earthworm *Microscolex kerguelarum* (Lumbricidae), and the larvae of *Pringleophaga marioni* and the *Ectemnorhinus similis* species complex. Together, these three macro-invertebrates at any time account for c. 90 % of soil-invertebrate biomass in most vegetation types at

Marion Island (Burger 1978). Despite the paucity of species, soil invertebrates attain higher densities and biomass at Marion Island than in Arctic and temperate areas. Figure 2 compares the biomass of terrestrial macro-invertebrates on the coastal lowlands of Marion Island, with that of macro- and meso-invertebrates at IBP tundra biome study sites (after Burger 1985).

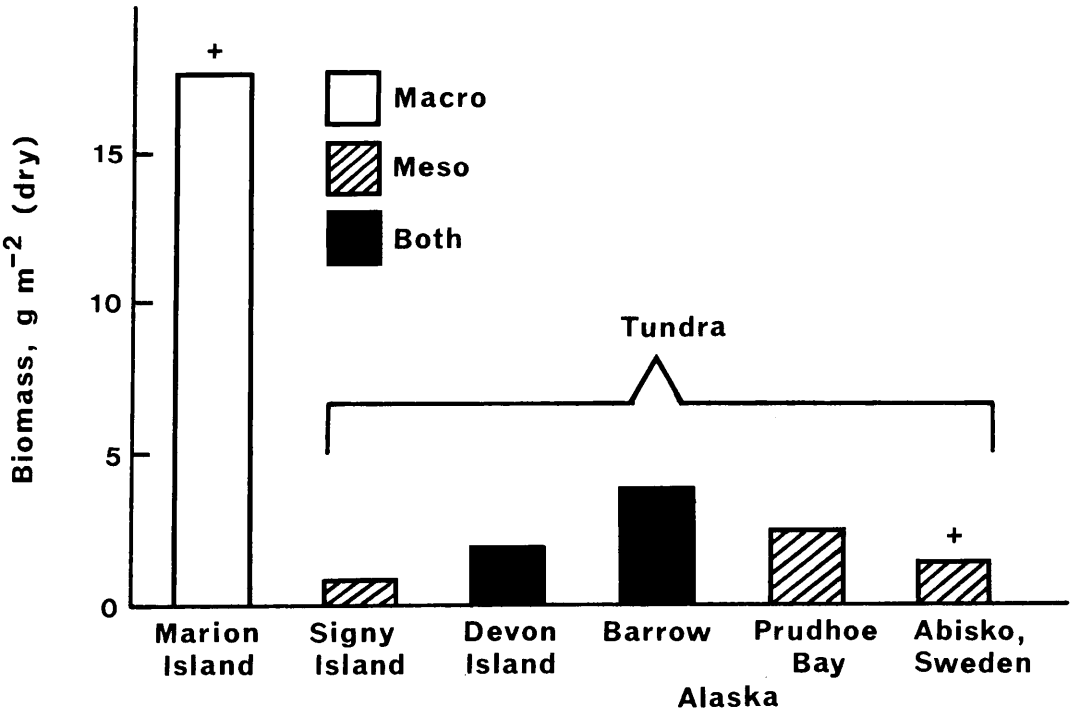

Figure 2. The biomass of terrestrial macro-invertebrates (earthworms, *P. marioni* and *Ectemnorhinus* spp. larvae, and spiders) on the coastal lowland of Marion Island, compared to that of macro- and meso-invertebrates at IBP tundra biome study sites (after Burger 1985).

It has not yet been established whether there are any nutrient limitations to primary production at Marion Island, but available pools of nitrogen at sites where Smith (1987a, 1987b, 1987c, 1988) determined the annual net production (ANP) of several plant communities, were amongst the lowest measured for any ecosystem. Available nitrogen at these sites would have to be turned over 36 to 2 180 times in the course of the growing season to supply the needs of the vegetation. Considering the large reserves of nutrients in soil organic matter (soils at Marion Island are about 90 % organic, and contain very low concentrations of "free" nutrients), and the low external nutrient input in inland areas, it appears that decomposition by invertebrate detritivores is the main "bottleneck" in nutrient recycling at the island (Smith 1985). Recent studies (Crafford in press; Steenkamp *in litt.*) have emphasized the cardinal role of insects (particularly *Pringleophaga marioni* larvae) in facilitating the release of nutrients contained in the vast dead standing crop of vegetation at Marion Island. Soil invertebrates, through sheer high biomass, process large quantities of litter, but in the process also speed up nutrient mineralization by (a) fragmenting litter, thus increasing the surface area available for microbial action, and (b) ingesting bacteria, thus stimulating bacterial growth and metabolic activity in the gut, and subsequently voiding into the environment faeces highly enriched by microbial activity. Block (1985) postulated that an understanding of the interactions of soil invertebrates and microbes is fundamental to ecosystem analysis in the sub-Antarctic, and the recent studies referred to above bear this out.

PART II: THE WORK

"Experiments on intake of natural diets usually involve gravimetric measurements, and are probably among the most tedious in the repertory of experimental entomologists, even with the advent of modern electronic microbalances. Apparently there is no way around this, and the irksomeness of the data-collecting process is probably one reason for the relatively scant work in this area ..."

Klein and Kogan (1974)

CHAPTER 3: MICROCLIMATE

"One of the major lessons of ecological physiology is that the influence of temperature on energy exchange and behaviour in natural environments is liable to be large and cannot be neglected."

Bennett (1987)

3.1 Vegetated microhabitats

3.1.1 Methodology

Three terrestrial microhabitats were selected for measurement of daily temperature regimes inside them, during the Marion Island summer (September - March) of 1987/1988. The microhabitats were:

1. The interior of a *Poa cookii* grass tussock.
2. The interior of an *Azorella selago* cushion plant.
3. The litter/soil interface.

These microhabitats are respectively occupied, either permanently or during feeding, by *Embryonopsis halticella* larvae and *Ectemnorhinus similis* adults (1); *E. similis*, *E. marioni* and *Pringleophaga marioni* larvae (2), and *P. marioni* larvae and *E. similis* and *E. marioni* larvae and adults (3). A site was selected close to the biological laboratory on Marion Island, where examples of the three microhabitats occurred in close proximity to each other. The site was an exposed slope crest, approximately 20 m a.s.l. Vegetation at the site consisted of "slope crest community" (Smith 1978c) and was dominated by single *Poa cookii* tussocks and *Azorella selago* cushions. Temperatures were measured inside each of the microhabitats, in the following manner: A Type K (chromal-alumel) thermocouple was inserted
1. Amongst the inner leaf folds of a *Poa cookii* tiller, about 50 mm above ground inside a tussock;
2. Inside, about 20 mm below the upper surface, of an *A. selago* cushion, and
3. About 20 mm deep inside the litter layer, in an exposed, well-drained mire between (1) and (2).

The three thermocouples were secured in position either with tape or with small pegs, and connected to a Kane-May digital thermometer. The thermometer was housed in a waterproof container, which was placed under a protective cover, centrally situated between the three microsites. The distance from the end of each thermocouple to the thermometer did not exceed two metres. For five months (November to March) during the 1987/1988 summer season, temperatures in each of the three microhabitats were measured daily at

08:00, 12:00, 14:00, 17:00 and 20:00 (South African Standard Time, which is Greenwhich +2). These times coincided with weather observations at the meteorological station, 80 m distant. The relevant macroclimate data were subsequently obtained from the Central Weather Bureau, Pretoria, South Africa.

3.1.2 Results

Tables 3.1 - 3.8 summarize the microclimate data collected during the study period.

Table 3.1. Hourly and daily mean, minimum and maximum temperatures for the *Poa cookii* tiller site.

Month	08	12	14	17	20	Mean daily, and lowest and highest mean daily temperatures
Mean Nov	10.58	16.79	12.46	7.31	5.28	10.62
Min Nov	4.90	4.80	8.50	2.40	0.50	6.90
Max Nov	18.20	33.80	21.20	10.90	9.90	18.53
Mean Dec	8.22	14.61	11.63	7.77	4.26	9.35
Min Dec	0.60	5.80	5.10	3.60	1.50	3.37
Max Dec	15.90	27.50	24.60	13.40	9.20	16.66
Mean Jan	9.21	12.56	11.00	8.33	5.70	9.34
Min Jan	1.10	6.30	6.40	4.40	1.40	4.28
Max Jan	18.70	28.00	22.00	13.50	10.60	15.92
Mean Feb	8.09	13.45	11.65	8.81	6.70	9.74
Min Feb	1.40	8.20	4.70	4.50	3.40	5.08
Max Feb	17.60	25.50	19.00	15.40	12.60	14.58
Mean Mar	7.03	10.55	9.80	7.21	6.07	8.18
Min Mar	-0.20	5.50	5.10	1.50	1.20	4.54
Max Mar	14.20	17.40	15.00	12.20	10.80	13.62

Table 3.2. Hourly and daily mean, minimum and maximum temperatures for the *Azorella selago* cushion site.

Month	08	12	14	17	20	Mean daily, and lowest and highest mean daily temperatures
Mean Nov	7.37	13.95	11.57	8.65	6.14	9.67
Min Nov	0.70	6.80	7.80	4.40	2.00	4.08
Max Nov	13.50	25.60	18.40	13.70	9.50	15.97
Mean Dec	5.40	11.93	11.45	9.18	5.40	8.63
Min Dec	-1.20	6.30	5.70	4.20	1.10	3.98
Max Dec	11.50	20.10	22.40	16.20	9.50	15.38
Mean Jan	8.22	13.24	11.75	9.39	6.39	9.78
Min Jan	3.10	6.80	7.80	4.80	2.50	5.92
Max Jan	18.20	23.00	21.60	14.00	11.20	15.54
Mean Feb	6.99	13.71	12.44	9.66	6.68	9.88
Min Feb	-0.80	8.00	6.80	4.70	2.60	5.04
Max Feb	13.20	23.30	19.80	16.60	12.00	15.04
Mean Mar	5.77	11.10	10.30	7.59	5.91	8.14
Min Mar	-0.70	6.00	5.00	2.30	0.00	4.20
Max Mar	13.20	16.60	14.90	12.20	10.80	13.54

Table 3.3. Hourly and daily mean, maximum and minimum temperatures for the soil site.

Month	08	12	14	17	20	Mean daily, and lowest and highest mean daily temperatures
Mean Nov	3.64	10.48	9.86	8.56	7.02	8.14
Min Nov	-3.70	4.60	6.40	5.70	4.50	3.48
Max Nov	8.50	19.20	14.50	12.00	9.70	12.37
Mean Dec	2.40	8.91	9.75	9.00	7.42	7.35
Min Dec	-3.60	5.70	6.80	6.50	4.40	4.52
Max Dec	7.00	17.80	18.20	14.50	10.50	12.44
Mean Jan	5.15	10.39	10.75	9.64	8.00	8.77
Min Jan	0.00	7.10	7.50	6.10	4.40	6.16
Max Jan	9.20	16.70	16.10	12.90	11.40	12.14
Mean Feb	5.19	10.05	11.47	9.87	7.96	8.88
Min Feb	-2.00	6.20	7.50	5.50	4.50	4.98
Max Feb	11.30	14.40	17.00	14.10	11.10	13.14
Mean Mar	4.77	8.16	8.97	8.12	7.26	7.46
Min Mar	-0.60	4.60	5.60	4.60	4.00	4.46
Max Mar	10.00	12.30	12.80	11.30	10.70	11.38

Table 3.4. Mean minumum and mean maximum temperatures, and mean, minimum and maximum daily temperature ranges at the *Poa cookii* site.

Month	Mean minimum	Mean maximum	Mean, and minimum and maximum daily ranges	
November	5.27	17.49	12.22	Mean
			1.20	Min
			26.90	Max
December	4.44	15.05	10.61	Mean
			1.30	Min
			26.00	Max
January	5.55	13.17	7.63	Mean
			1.10	Min
			25.30	Max
February	5.60	13.93	8.33	Mean
			3.20	Min
			19.10	Max
March	5.37	11.37	5.99	Mean
			0.90	Min
			11.60	Max

Table 3.5. Mean minumum and mean maximum temperatures, and mean, minimum and maximum daily temperature ranges at the *Azorella selago* site.

Month	Mean minimum	Mean maximum	Mean, and minimum and maximum daily ranges	
November	5.71	14.08	8.37	Mean
			1.20	Min
			17.30	Max
December	4.55	12.58	8.03	Mean
			0.70	Min
			14.40	Max
January	6.05	13.65	7.60	Mean
			1.40	Min
			18.00	Max
February	5.46	14.03	8.57	Mean
			3.10	Min
			16.50	Max
March	4.66	11.59	6.93	Mean
			1.60	Min
			13.60	Max

Table 3.6. Mean minumum and mean maximum temperatures, and mean, minimum and maximum daily temperature ranges at the soil site.

Month	Mean minimum	Mean maximum	Mean, and minimum and maximum daily ranges	
November	4.12	11.14	7.03	Mean
			1.50	Min
			12.80	Max
December	2.48	9.87	7.39	Mean
			1.10	Min
			14.10	Max
January	5.12	11.12	6.00	Mean
			1.60	Min
			16.10	Max
February	4.84	11.61	6.77	Mean
			1.90	Min
			13.90	Max
March	4.72	9.14	4.42	Mean
			0.90	Min
			9.10	Max

Table 3.7. Comparison of the mean daily temperature and the mean daily temperature range at each site for each month.

Month	Means			Ranges		
Site	*Poa*	*Azorella*	Soil	*Poa*	*Azorella*	Soil
November	10.62	9.67	8.14	12.22	8.37	7.03
December	9.35	8.63	7.35	10.61	8.03	7.39
January	9.34	9.78	8.77	7.63	7.60	6.00
February	9.74	9.88	8.88	8.33	8.57	6.77
March	8.18	8.14	7.46	5.99	6.93	4.42

Table 3.8. Comparison of the absolute maximum and minimum temperatures at each site during each month.

Month	Minima			Maxima		
Site	*Poa*	*Azorella*	Soil	*Poa*	*Azorella*	Soil
November	0.50	0.70	-3.70	33.80	25.60	19.20
December	0.60	-1.20	-3.60	27.50	22.40	18.20
January	1.10	2.50	0.00	28.00	23.00	16.70
February	1.40	-0.80	-2.00	25.50	23.30	17.00
March	-0.20	-0.70	-0.60	17.40	16.60	12.80

The mean daily temperatures at each of the three microhabitat sites were consistently about 3-4 °C higher than the mean daily Stevenson screen temperatures recorded at the weather station during the same period. Temperatures 2 cm below the soil surface (Table 3.4) were closer to ambient temperatures, while mean temperatures at all three sites were considerably higher than the grass minima recorded at the weather station during the same period. The temperature range in each of the three microhabitats was greater than the range in ambient temperature, as recorded by the Stevenson screen instruments, with the *P. cookii* (Table 3.5) site showing the largest and the soil site (Table 3.6) the smallest temperature range. The highest absolute temperatures at the microhabitat sites were invariably recorded at mid-day, during periods of full sunshine and very little or no wind.

To illustrate the relation between microhabitat and ambient temperatures, Fig. 3.1 compares the actual temperatures measured at the *P. cookii* site with ambient air (Stevenson screen) temperatures measured simultaneously, on the two days during the summer of 1987/1988 which had the lowest (Fig 3.1a) and highest (Fig 3.1b) mean air temperatures. Similarly, Fig. 3.2 compares simultaneous temperature measurements at the *P. cookii* site and in the Stevenson screen, on the two days on which, respectively, the absolute minimum (Fig 3.2a) and the absolute maximum (Fig 3.2b) temperatures were recorded at the *P. cookii* site.

It is interesting that the months with the highest mean daily microhabitat temperatures were those which have the highest percentage of possible sunshine (Schulze 1971), rather than those in which the highest Stevenson screen temperatures are recorded (Schulze 1971). The relationship between sunshine and microclimate at Marion Island has been documented by Huntley (1971), in his study of the daily temperature regimes inside similar microhabitats to those sampled during this study.

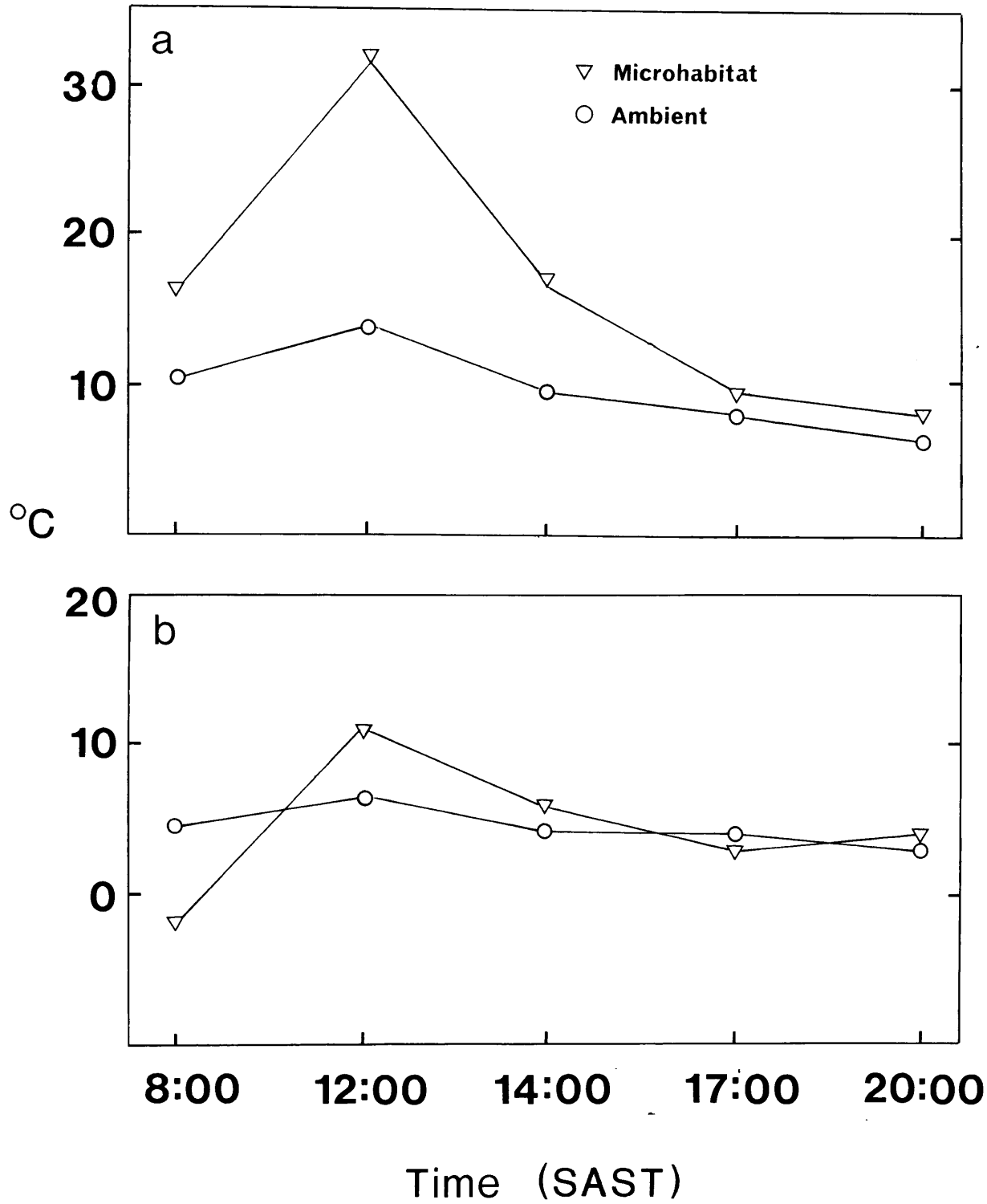

Figure 3.1. Simultaneous measurements of microhabitat and ambient air temperatures on the days on which lowest (3.1a) and highest (3.1b) ambient temperatures were recorded.

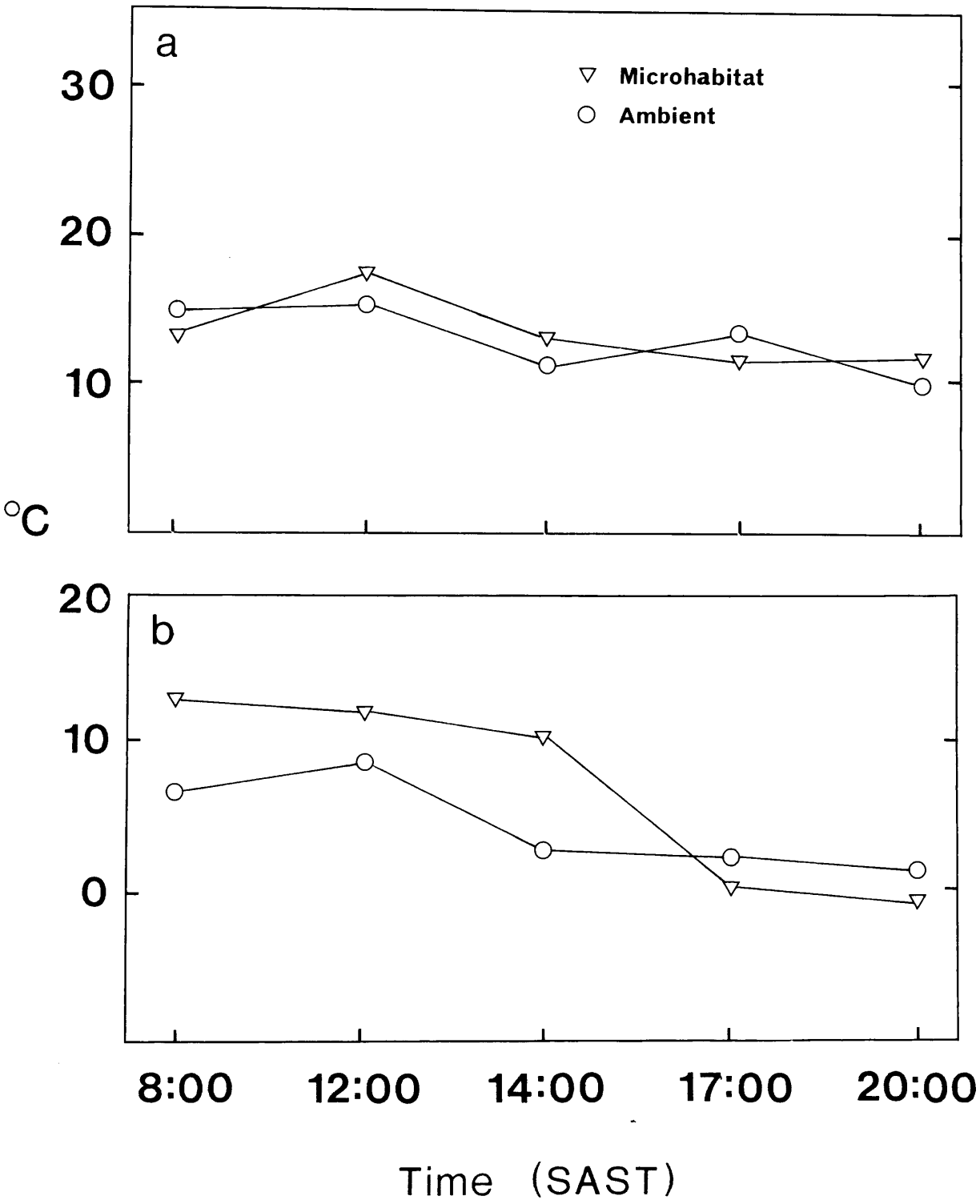

Figure 3.2. Simultaneous measurements of microhabitat and ambient air temperatures on the days on whicl the absolute minimum (3.2a) and absolute maximum (3.2b) temperatures were recorded in any microhabitat.

3.1.3 Discussion

The chief objective of this study was to determine realistic parameters for experimental studies of the life processes (particularly food consumption and utilization, and respiration) of the five dominant macro-insects under investigation in this thesis. The temperature regimes under which feeding experiments and oxygen consumption measurements were carried out in the laboratory were consequently based on the results of the microhabitat temperature recordings shown in Tables 3.1 - 3.6. However, terrestrial habitats are thermally extremely complex and varied. Vegetation has a profound influence on microclimate through the creation of boundary layers of air and by the absorption of sunlight, and vegetated microhabitats, in particular, consequently form complex thermal mosaics. Terrestrial invertebrates can take advantage of this mosaic to avoid stressful temperatures (Cossins and Bowler 1987). Unfortunately, the type of microclimatological study reported here can give no indication of the exact nature, complexity and variability of the thermal mosaic. Mean temperatures, at any rate, have little biological relevance, as has frequently been stressed. In spite of this, very few experimental studies in invertebrate ecophysiology have actually been carried out under "field conditions," mostly as a result of problems with experimental technique and procedure. The present study is no exception. The temperature means and ranges reported in Tables 3.1 - 3.6 merely served as guidelines, and care was taken not to interpret biological phenomena exclusively in terms of these thermal quantities.

It should further be borne in mind that the temperature data presented here are limited, with daily means referring only to the period between 08:00 and 20:00, and not the full 24 h period. Comparison with Stevenson screen data (those collected during the same period, and those summarized by Schulze (1971) for the period 1950 - 1965) as well as comparison with continuous recordings made in sub-Antarctic microhabitats elsewhere, may therefore be misleading. However, the microhabitat temperatures recorded during this study are remarkably similar to those recorded by Walton (1984) in and around a grass tussock (*Poa flabellata*) on South Georgia. *P. flabellata* on this island, like *P. cookii* on Marion Island, houses the dominant herbivores (the perimylopid beetles *Hydromedion sparsutum* and *Perimylops antarcticus*; Block (1981)).

Temperature represents only one, but in the sub-Antarctic perhaps the dominant, aspect of the "microhabitat templet" on which the ecological strategies of sub-Antarctic insects are constructed. Remmert (1986) has postulated that there should be a lower temperature threshold for herbivory, and on the basis of experimental data proposed that herbivory is viable only where mean summer temperatures exceed 6 °C. The temperatures recorded in the *P. cookii* tussock and the *A. selago* cushion mostly exceed this hypothetical threshold, and *E. halticella* is indeed the only indigenous insect which completes its development on live angiosperm material (Chapter 4). Significantly, it mines the leaves and stems of its host, since frost action would presumably severely limit herbivores with exposed feeding habits (Chown 1989a). Several other vascular plants in the sub-Antarctic appear suitable for herbivory both in terms of nutritional quality and temperature regimes (this study; also Smith 1978c, 1985). However, the dearth of herbivores can probably be ascribed not only to the geographic isolation and the (cold) climatic history of the islands, but also to the *constancy* of the low-temperature regimes that herbivore colonizers are exposed to. The maximum temperature ranges recorded during this study were 26.9 °C at the *P. cookii* site, 18.0 °C at the *A. selago* site, and 16.1 °C at the soil site (Tables 3.4 - 3.6). However, mean ranges were usually less than 10 °C. The high degree of cloudiness, constant high windspeed and invariably high humidity are important causes of the aseasonality of the macroclimate on Marion Island, and cause the same constancy (interspersed with short, irregular and unpredictable periods of "favourableness") in microclimates on the island. This is one of the major differences between the continental Arctic and the sub-Antarctic islands. During the short, predictable Arctic summer, temperatures may be very high as a result of the high incidence of sunshine and low windspeed (e.g. Remmert 1980), and this contrast between "predictable" and "unpredictable" favourableness causes pronounced differences in the ecological attributes and life strategies of Arctic and sub-Antarctic insects, respectively.

The drastic influence of sunshine on microclimate temperatures, especially on windstill days, was very apparent in this study and has also been documented elsewhere (Remmert 1986, Walton 1984). Such sharp increases in temperature are probably as important to the sub-Antarctic herbivores as they are to those in Arctic regions, but in either situation temperature *fluctuations* may have a more profound effect than high *absolute* temperature values. The importance of fluctuating temperatures to the nutrition and development of herbivorous insects has often been stressed (e.g. Scriber and Slansky 1981). It is significant that *P. marioni*, which inhabits the microhabitat showing the smallest range and the lowest mean temperature (Tables 3.3, 3.6) also has the longest developmental time, and poor food assimilation efficiency (Chapter 7).

It is not known to what extent the sub-Antarctic insects regulate their body temperatures through behaviour. Clustering has occasionally been observed in adult Ectemnorhine weevils, but basking either does not occur or is of limited importance (pers. obs.). This may have to do with the fact that high windspeeds tend to reduce body temperature and body moisture (Chown and Crafford in prep.). Detritivorous insect larvae (*P. marioni*, *Ectemnorhinus* species) may exhibit thermoregulatory behaviour when soil temperatures drop below the developmental null point (Chown 1989c).

3.2 Wrack bed microclimate

3.2.1 Methodology

During the summer of 1984/1985, temperatures inside a *Durvillaea antarctica* wrack bed colonized by *Paractora dreuxi mirabilis* larvae, were monitored for the duration of a study of the degradation of wrack by the larvae (see Crafford and Scholtz 1987b). The study site was a 60 m stretch of pebbled beach (Trypot Beach), 800 m from the meteorological station. An artificial wrack bed was constructed on the beach, inside a wooden frame, to a uniform depth of 20 cm. The bed was covered with a wire grid to prevent interference by resident seals and penguins. During the first two weeks after construction, the temperature inside the wrack bed was measured daily at mid-day (12:00), by inserting a thermocouple into the centre of the bed, about 10 cm down. A simultaneous reading of ambient temperature at the beach was taken from a thermometer tied to the top of a 1 m wooden stake planted into the beach, 10 m inland.

3.2.2 Results and discussion

Table 3.9 compares the temperatures recorded inside the enclosed wrack with ambient air temperatures on the first 15 days of the existence of the wrack bed. Wrack temperature increased rapidly by the fifth day, and remained on average 6.9 °C higher than ambient for the next ten days.

Dobson (1976) pointed out that wrack beds provide a warm and humid microclimate relatively independent of external environmental conditions. Strenzke (1963) recorded temperatures up to 20 °C above ambient inside wrack beds on a North Sea beach, during the early stages of decomposition of the kelp. The rapid and sustained increase in temperature over the first ten days in the wrack bed constructed for this study (Table 3.9), was probably caused by a peak period of bacterial activity and resultant "fermentation" of the kelp. The peak in wrack temperature on day seven (20 °C, 9 ° above ambient) was accompanied by a peak in the biomass of kelp fly larvae (see Fig. 7.2).

Table 3.9. Temperatures inside a protected wrack bed (T kelp) compared to ambient air temperature (Ta) over the first 15 days after deposition of the kelp. Temperature readings were taken daily at mid-day.

Day 1	Ta (°C) 2	T kelp (°C)	2-1
1	8.0	9.2	1.2
2	8.7	11.0	2.3
3	9.0	10.0	1.0
4	7.8	9.5	1.7
5	8.0	13.2	5.2
6	9.5	17.5	8.0
7	11.0	20.0	9.0
8	8.3	18.5	10.2
9	10.0	16.5	6.5
10	10.0	16.8	6.8
11	6.2	11.5	5.3
12	3.5	11.0	7.5
13	6.9	14.0	7.1
14	7.7	10.8	3.1
15	8.6	9.0	0.4

CHAPTER 4: *Embryonopsis halticella* Eaton (Lepidoptera: Yponomeutidae)

"Whether it is more advantageous to be polyphagous or monophagous may be no more fruitful a question than whether it is more advantageous to be a grass feeder or a dicot feeder, a leafminer or a leaf galler. That is, each lifestyle may be a specific response to a specific set of selective forces."

Barbosa (1988)

4.1 Introduction

The type locality of the monotypic genus *Embryonopsis* is Îles Kerguelen, from where it was described by Eaton (1875), who also reported that the larvae "fed on grasses." Later Eaton (1879) stated that they fed on *Festuca* [=*Poa*] *cookii* and *F. erecta*, sheltering in the ensheathing leaves and in the shoots. Brown (1964) observed that at Heard Island the larvae fed on the grass *Poa*, eating the lower leaves and roots. Crafford and Scholtz (1986) confirmed that the species is indeed strictly host-specific on *Poa cookii*, at least at the Prince Edward Islands. Information about the biology of *E. halticella* at Heard Island was given by Common (1970), at Îles Kerguelen by Chauvin and Vernon (1981), and at Marion Island by Vari (1971) and Crafford *et al.* (1986).

There has been much uncertainty about the family in which *Embryonopsis* should be placed. It was described in the Gelechiidae by Eaton, while Enderlein (1905) followed him and proposed the subfamily Embryonopsinae for it. It was subsequently also placed in the Glyphipterygidae (Zerny and Beier 1936), until Viette (1948) and Vari (1971) confirmed its position in the Yponomeutidae. The phylogeny of the genus is obscure. It occurs on all the SIP islands, with the exception of Iles Crozet, and has no obvious relationships inside or outside the sub-Antarctic. Its close association with *P. cookii* may indicate a relatively recent (late Pleistocene?) origin in the sub-Antarctic, since graminoid pollen appears in the palynological record of Marion Island at only about 8 000 yrs BP (Scott 1985).

Adult moths are small (4 - 7 mm long) with reduced wings (forewing length 1.5 - 2.5 mm), and well developed legs (see Appendix A for habitus). Live larvae are pale pink with two darker longitudinal dorsal stripes. The head capsule and the dorsal sclerites on the prothoracic, penultimate and last abdominal segment are very darkly sclerotized (black). Mature larvae are 8 - 10 mm long and attain live mass of up to 12 mg. The pupae are typically lepidopteran, and are encased in strong silk cocoons spun against the dead outer leaves of *P. cookii* tussocks.

4.2 Life history and phenology

4.2.1 Methodology

Life history

The life history and phenology of *E. halticella* were studied in the field, chiefly through monthly sampling of larvae in different *P. cookii* communities, but also through field observations in the different communities. Because of their specialized food and habitat requirements, attempts to rear the species in the laboratory

were unsuccessful. To determine the number of larval instars, the head capsules of larvae harvested each month from a single population in *P. cookii* tussock grassland (see below), were measured, using an ocular micrometer. The duration of only the first instar was determined in the lab; that of the other instars was deduced from population trends in the field. Mature larvae collected in the field were kept in cages outside the laboratory on Marion Island until pupation, and pupal duration under ambient conditions was subsequently determined. Freshly hatched adults were paired in the laboratory, and females were presented with fresh *P. cookii* leaves on which to oviposit. Several females were dissected immediately prior to egg-laying, to determine reproductive biomass (as a percentage of total female body mass) and fecundity (the average number of eggs per female). Fertility (percentage of eggs hatched) and the duration of the egg stage were determined under ambient conditions, in small gauze cages outside the laboratory.

Phenology

Poa cookii tussock grassland, an *Azorella selago/Poa cookii* slope crest community (Smith 1976), and an isolated, luxuriant stand of *P. cookii* surrounding a wandering albatross nest, were sampled at monthly intervals for *E. halticella* larvae. The tussock grassland site represented a virtually pure stand of *Poa cookii* against a well-drained, steep slope, undermined by numerous bird burrows. The isolated tussocks of the slope crest community were straggly by comparison, not being subjected to the same input of bird manure as the albatross nest and slope communities.

Four 25 m^2 quadrats were selected at random in the three sites - two in the tussock grassland and one each in the slope crest and albatross nest sites. Each tussock within a quadrat was numbered. Once a month, ten tussocks were selected at random and five tillers from each were cut off at ground level. Living leaves were examined for larvae, and the dead outer leaves of tillers were examined for pupae, which were removed and counted. All the larvae were removed from the ensheathing inner leaves, counted, dried to constant mass (four days at 60 °C) and weighed dry. Dry mass of the live *P. cookii* leaves was also determined. Biomass of larvae was expressed as g larvae kg^{-1} live foliage (dry mass) at each site. The monthly harvest of larvae from tussock grassland, which constituted the largest sample, was sorted into five size classes (I - V), based on head capsule measurements. These size classes were presumed to correspond to five larval instars. The mass of larvae in each size class was expressed as a percentage of the total monthly larval biomass in tussock grassland.

4.2.2 Results and discussion

Life history

A histogram of head capsule measurements of *E. halticella* larvae shows five distinct peaks, or size classes, which are presumed to represent five larval instars (Fig. 4.1). The head capsule widths of each instar are given in Table 4.1. The growth increments between the different instars, based on the increments in head capsule measurements (Table 4.1), conform to Dyar's "law" which states that the linear dimensions of sclerotized parts of Lepidoptera larvae increase by a constant ratio of about 1.4 at each moult (Wigglesworth 1974).

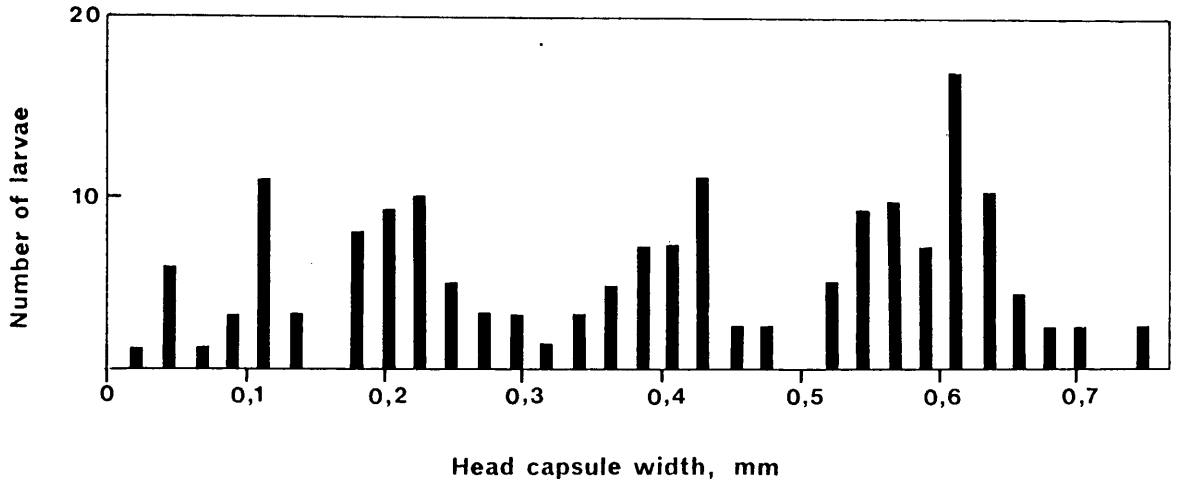

Figure 4.1. Frequency histogram of measurements of head capsules of *E. halticella* larvae from a *P. cookii* tussock grassland site.

Table 4.1. Head capsule widths (mm) of the larval instars of *E. halticella*.

Instar	n	Range	Means ± STD	Increment
I	8	0.20 - 0.24	0.22 ± 0.011	-
II	17	0.26 - 0.30	0.28 ± 0.012	1.27
III	35	0.34 - 0.44	0.38 ± 0.030	1.35
IV	31	0.46 - 0.62	0.53 ± 0.034	1.39
V	65	0.64 - 0.84	0.73 ± 0.046	1.37

E. halticella is present in all its major life stages throughout the year, although, as on Îles Kerguelen, the adults tend to peak in numbers during the height of the austral summer (December), and are absent or extremely rare during most of the winter (May to July) (Chauvin and Vernon 1981). The seasonal occurrence of adults, and the small size of the species, probably means that generations are completed in not more than one year. Only egg, first instar, pupal and adult duration were actually determined. The duration of second to fifth instars was estimated on the basis of a hypothetical generation time of one year. The duration and mean live mass of the different life stages of *E. halticella* are given in Table 4.2.

Table 4.2. Live mass (mg) and duration (in days) of the different life stages of *E. halticella*. Quantities in brackets are estimates (see text).

Stage	n	Live mass		Duration	
		Range	Means ± STD	Range	Means ± STD
Egg	63	0.082 - 0.084	0.082 ± 0.003	8 - 20	10.46 ± 3.12
Instar I	20	0.073 - 0.917	0.079 ± 0.054	4 - 8	5.27 ± 0.89
II	17	1.132 - 3.581	1.985 ± 0.934	(± 20)	
III	13	3.760 - 5.004	4.082 ± 0.062	(± 50)	
IV	21	6.432 - 10.650	8.637 ± 0.241	(± 90)	
V	25	8.301 - 15.146	12.069 ± 1.684	(± 130)	
Prepupa	14	12.185 - 18.379	13.842 ± 2.298	(± 20)	
Pupa	9	6.219 - 12.011	8.631 ± 2.010	21 - 40	32.56 ± 4.87
Adult	12	3.715 - 9.865	5.873 ± 2.684	7 - 15	10.04 ± 1.65

Adults hatched in the laboratory copulated immediately upon eclosion, and females started ovipositing within the first day of hatching. No evidence was found of chemical attraction between the sexes, but high densities and synchronized eclosion probably obviate the need for such attraction. The adults have vestigial mouthparts and do not feed (although Chauvin and Vernon (1981) speculated that the galeae could still be functional). Newly eclosed adult females kept on *P. cookii* blades in the laboratory laid between 36 and 87 eggs (mean 58, n = 8), over a period ranging from two to ten days. In the field, eggs are laid singly or in small batches against the outer leaves of *P. cookii* tussocks. Upon hatching, the larvae "mine" the tough outer leaves, and only in later instars migrate to the softer inner leaves of tillers in which they complete their life cycle. Females kept in the laboratory did not lay their entire complement of eggs, although this may be different in the field. Unlike *Pringleophaga marioni* (see Chapter 6), egg formation and development may continue after eclosion. Eggs at different stages of development were observed in the follicles of newly hatched females, although the majority of eggs in their ovaria were ripe (pers. obs.). Virtually all eggs in every batch monitored in the laboratory hatched; fertility ranged between 94 and 100%. The reproductive biomass (i.e. eggs and ovaries) of newly emerged females accounted for between 65 and 70% of total dry body mass (mean 67.36%; n = 7).

Phenology

Figure 4.2 illustrates the monthly biomass of *E. halticella* larvae at each of the three sampling sites. The contributions of the five size classes to the monthly biomass of larvae from the tussock grassland site are shown in Fig. 4.3.

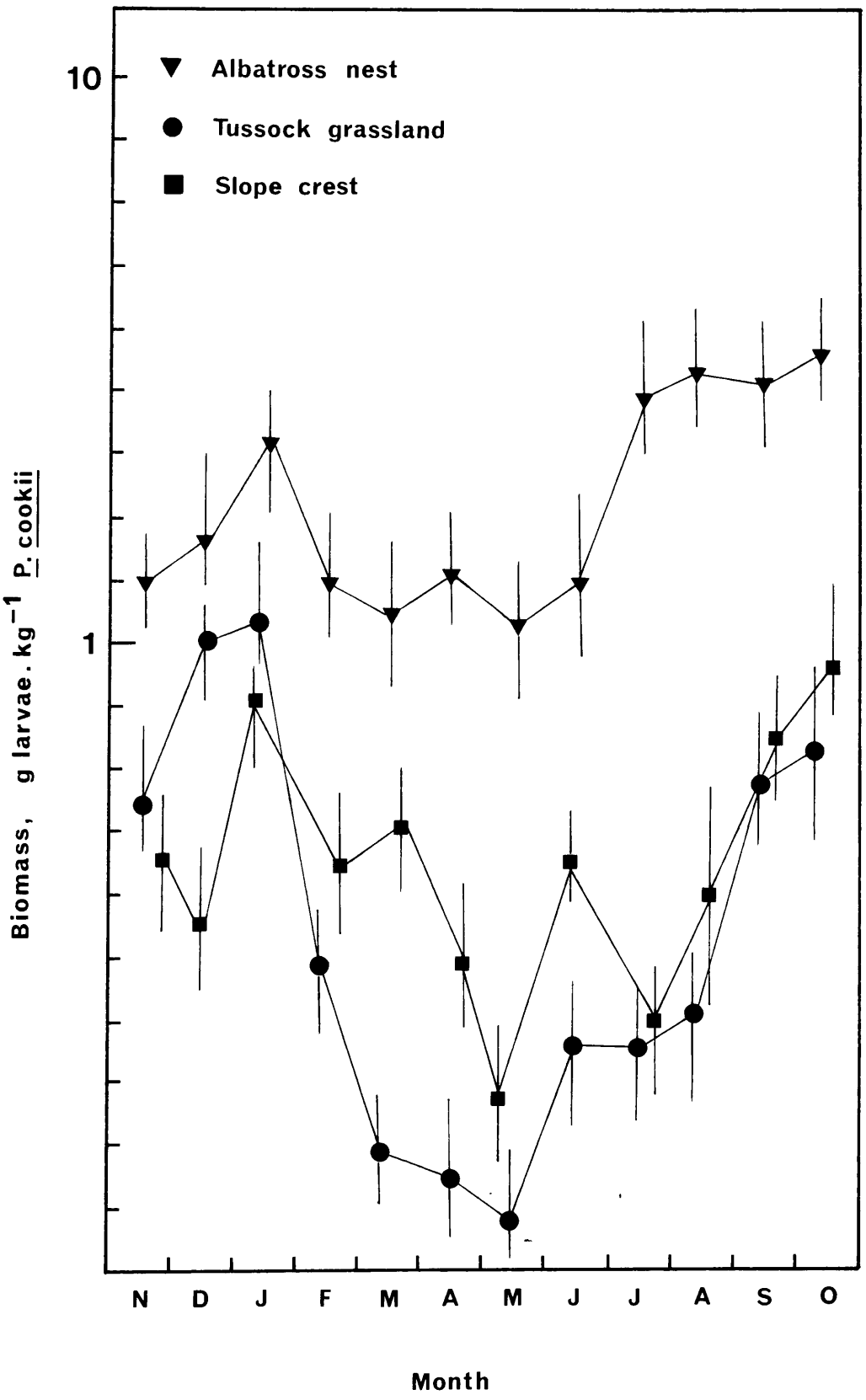

Figure 4.2. Monthly biomass of *E. halticella* larvae in three different *P. cookii* communities on Marion Island. Means with standard error bars are shown.

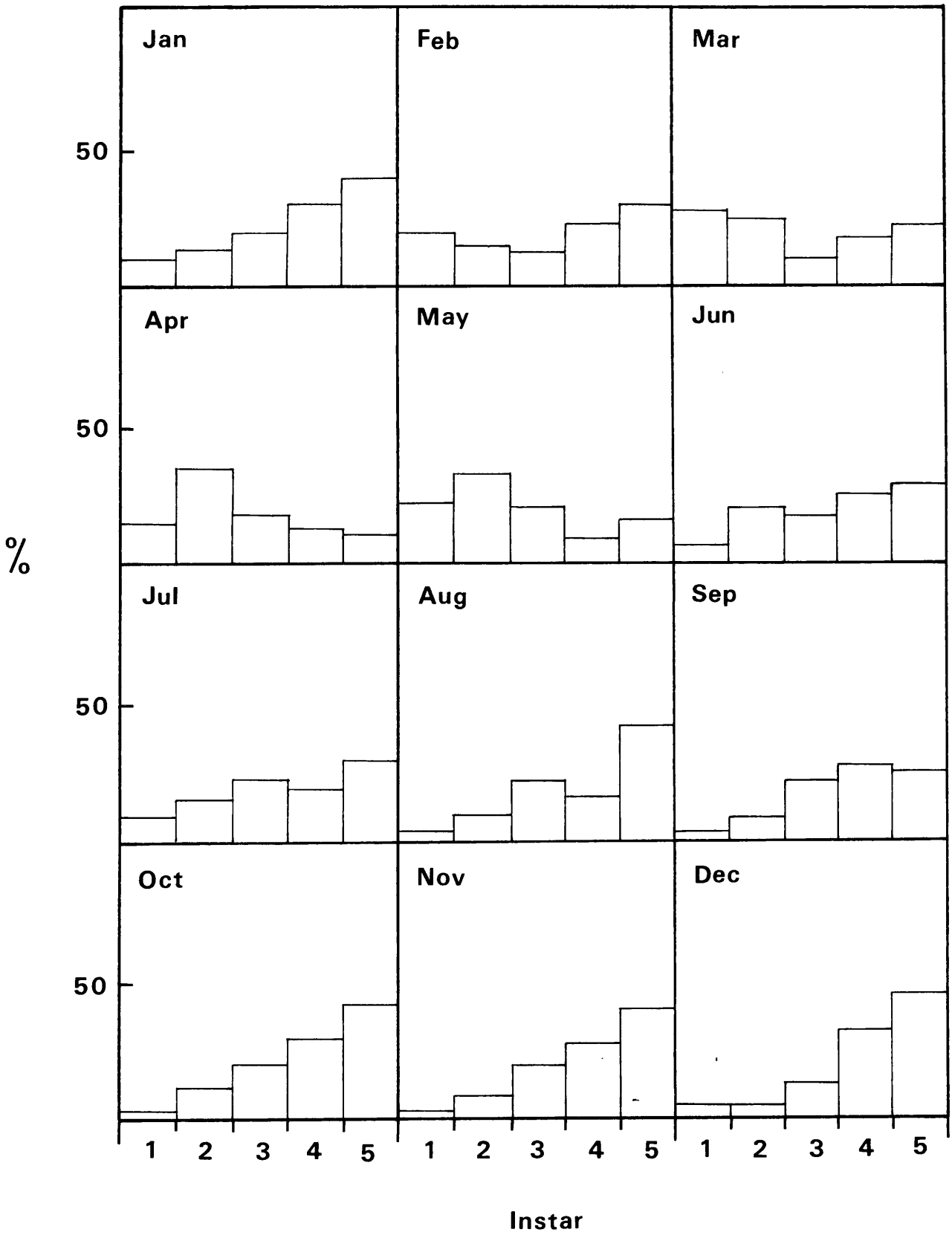

Figure 4.3. Percentage contribution of each larval instar of *E. halticella* to the total monthly biomass of larvae in a *P. cookii* tussock grassland.

Differences in *E. halticella* biomass clearly reflect the differences in nutrient status of their food plants. The larval population in the relatively "poor" slope crest community appears less stable, although generally the three populations show similar trends in production over time. *E. halticella* larval biomass peaks in summer (Fig. 4.2). In tussock grassland the peak coincides with a predominance of final instar larvae (Fig. 4.3).

The high biomass of larvae at albatross nest sites is dependent on the continuous nutrient input from resident albatrosses, which maintains the luxuriant growth of their food plants. *E. halticella* larvae have no significant predators on the island and neither the larvae nor the adults are vagile. The nest at the sampling site had been abandoned for at least three breeding seasons. The decline in plant biomass through loss of manuring and the leaching of remaining nutrients from the soil, possibly caused some "concentration" in the biomass of the isolated, sedentary larval population of the albatross nest site. This would contribute to a high larval biomass when the latter is expressed as a fraction of plant biomass, as in Fig. 4.3.

The damage caused to tussock leaves by the feeding activity of *E. halticella* larvae was observed during early investigations of the Marion Island vegetation. Smith (1977b) speculated on the origin of the damage, but erroneously ascribed it to the feeding of adult weevils (*Ectemnorhinus similis*). Thorough sampling of *P. cookii* - dominated vegetation during this study showed that only two other insect species are consistently and closely associated with grass tussocks: adult *E. similis* feed on the leaves, pollen and inflorescences, and possibly the seeds, of *P. cookii* during spring and early summer, and throughout the year can be found hiding in the bases of tussocks (see Chown and Scholtz 1989b). Aphids (the cosmopolitan *Rhopalosiphum padi*, and possibly others), heavily infest grass fronds, especially during summer (see also Smith 1977a). An unidentified mite also occurs at high densities in *P. cookii* tussocks, and has been observed (pers. obs.) preying on *E. halticella* eggs.

4.3 Feeding ecology

4.3.1 Methodology

Consumption of *P. cookii* foliage by individual *E. halticella* larvae was determined gravimetrically. Larvae were removed from *P. cookii* tillers harvested from a tussock grassland close to the biological laboratory on Marion Island. For convenience, the larvae were grouped into three size classes, loosely based on instar: Class I - first and second instars; Class II - third and fourth instars; Class III - fifth (final) instar. Segments 30 - 40 mm long were cut from the inner leaves of fresh *P. cookii* tillers and weighed immediately. Depending on size, one (late instar to mature) to five (early instar) larvae were weighed and placed inside the fold of a leaf segment. Each leaf segment with its larva(e) was placed inside a lightly stoppered 5 ml glass vial, with the proximal end of the leaf segment in damp cotton wool to maintain water content of the leaf. The vials with the leaves and larvae were kept in an incubator for five days, at constant humidity (90-100 % RH) and temperature (5, 10 or 15 °C; i.e. three replicates at three constant temperatures). A light regime similar to the one prevailing outside at the time, was established inside the incubator during each feeding experiment.

A similar feeding experiment, using the same methods, was later carried out at cycling temperatures of 5 °C (12 h), 10 °C (6 h) and 15 °C (6 h).

Leaf segments of equal size, similar to the segments used in the feeding experiments, were cut from the same leaves, weighed, and kept under the same conditions. These served as controls to compensate for changes in leaf mass through transpiration and leaf metabolism during the feeding period. Further segments cut from the same leaves were weighed immediately, dried to constant mass (4 days at 60 °C), weighed dry and used for measurement of energy content and wet:dry mass ratios of fresh leaf material.

After five days (the long duration of the feeding experiment was dictated by the extremely slow feeding rates of the larvae) the larvae and the leaf segments they had fed on were weighed, dried to constant mass, reweighed, and thereafter pulverized separately in a porcelain mortar. All the frass in each vial was carefully collected and weighed. The pulverized material, and the frass, were pressed into small (5 mm diameter) pills. The pills were weighed (the mass range was 12-30 mg) and bombed in an electronic micro-bomb calorimeter (Newham Electronics, Royston, United Kingdom) to determine their energy content. The ratio of food ingested to frass produced by larvae was also determined, by dividing the dry mass of food consumed by an individual during the feeding period, by the dry mass of egesta produced by the individual during the same period.

Larval food consumption was expressed both as absolute rate of feeding (dry mass of food consumed per day), and as mass-specific rate of feeding (i.e. feeding rate scaled with body mass, and expressed as dry mass of food consumed per live mass of larva per day).

The Q_{10} values for mass-specific feeding rates of each of the three larval size classes, were determined over the temperature ranges 5-10, 10-15 and 5-15 °C. The following equation (Schmidt-Nielsen 1979) was used to determine Q_{10}:

$$\log Q_{10} = (\log R_2 - \log R_1) \cdot 10/(T_2 - T_1)$$

The following indices of larval food utilization efficiency were calculated for each of the four temperature regimes:

Approximate digestibility (AD) (%) = 100 (C-F)/C
Efficiency of conversion of ingested food (ECI) (%) = 100 P/C
Efficiency of conversion of digested food (ECD) (%) = 100 P/(C-F)
Relative growth rate (RGR) = P/(B X T)
Relative consumption rate (RCR) = C/(B X T)

where C = food eaten, F = frass produced, P = production (biomass gain) of the insect over the feeding period, and B = mean mass of insect during the time (T) over which food consumption and growth were measured.

4.3.2 Results

Food consumption

Absolute amounts of food consumed (mg dry *P. cookii* day^{-1}) by the three size classes of larvae at constant 5, 10 and 15 °C, together with the mean live mass of the larvae, are given in Table 4.3.

Table 4.3. The mean (±SD) absolute food consumption rates of *E. halticella* larvae in each size class at 5, 10 and 15 °C, with the mean (±STD) live mass of the larvae in each size class. Number of replicates given in parentheses. Symbols between rows indicate significance levels of differences between values at different temperatures (**: $p < 0.01$; *: $p < 0.05$; n.s.: not significant; Mann-Whitney U test).

	5°C		10°C		15°C
Size class I:					
Live mass (mg)	3.58 ± 1.15		2.68 ± 0.91		3.19 ± 0.61
mg dry *P.cookii* day^{-1}	0.33 ± 0.13	**	0.59 ± 0.32	n.s.	0.42 ± 0.22
	(13)		(10)		(10)
Size class II:					
Live mass (mg)	7.28 ± 1.29		5.44 ± 0.85		6.28 ± 1.86
mg dry *P. cookii* day^{-1}	0.49 ± 0.11	**	0.84 ± 0.41	*	0.46 ± 0.26
	(8)		(12)		(5)
Size class III:					
Live mass (mg)	13.28 ± 2.37		10.74 ± 2.58		13.30 ± 4.12
mg dry *P. cookii* day^{-1}	0.47 ± 0.14	**	0.81 ± 0.48	*	0.48 ± 0.40
	(9)		(8)		(6)

The consumption rate was significantly higher at 10 °C than at either 5 or 10°C. Consumption rates under the cycling temperature regime were not significantly ($p < 0.01$) different from rates at 10 °C, and are not shown (for discussion of this apparent anomaly, see 4.3.3.).

When absolute consumption rate was plotted against live mass on a double log scale, there was either a poor or no correlation between consumption and body mass at 5, 10 and 15 °C, or under the cycling temperature regime (correlation coefficients in the linear regression equations of $\log_{10}$ consumption rate on $\log_{10}$ larval live mass, ranged from 0.35 at 5 °C to 0.06 at 15 °C). Larval live mass, in other words, accounted for only 13 % of the variation in feeding rate at 5 °C, and for virtually none (0.8 %) of the variation at 15 °C.

A better correlation existed between consumption rate and live larval mass when consumption was scaled with body mass, and expressed as dry mass of food eaten per equal unit live mass of larva. Mean (±SD) mass-specific consumption rates (dry mass of food consumed, expressed as a fraction of live body mass) of *E. halticella* larvae at 5, 10 and 15 °C are given in Table 4.4. The effect of temperature on mass-specific consumption rates is shown graphically in Fig. 4.4. Both the fitted regression line (that of $\log_{10}$ mass-specific consumption rate on $\log_{10}$ live mass) and individual data points are given for each temperature.

Table 4.4. Mean (± SD) mass-specific consumption rates (g dry mass *P. cookii* g live mass larva^{-1} day^{-1}) of the three size classes of *E. halticella* larvae at 5, 10 and 15 °C. Number of replicates (n) in parentheses. See Table 4.3 for explanation of significance levels.

	5°C			10°C			15°C	
Size class I	0.104 ± 0.044	*	(13)	0.268 ± 0.189	*	(10)	0.137 ± 0.074	(10)
Size class II	0.073 ± 0.023	*	(8)	0.159 ± 0.084	*	(12)	0.084 ± 0.059	(5)
Size class III	0.036 ± 0.012	*	(9)	0.082 ± 0.059	*	(8)	0.033 ± 0.024	(6)

The Q_{10} values for changes in the mass-specific consumption rates (Table 4.2) of each of the three size classes of larvae, over the temperature ranges 5-10, 10-15 and 5-15 °C, are given in Table 4.5.

Table 4.5. Q_{10} values for the mass-specific consumption rates of three size classes of *E. halticella* larvae.

	Q_{10}		
	5-10 °C	10-15 °C	5-15 °C
Size class I	6.64	3.83	1.32
Size class II	5.12	0.28	1.19
Size class III	5.19	0.16	0.92

The ratio of food ingested to frass produced by *E. halticella* larvae at the different temperatures, and in the different size classes, is shown in Table 4.6.

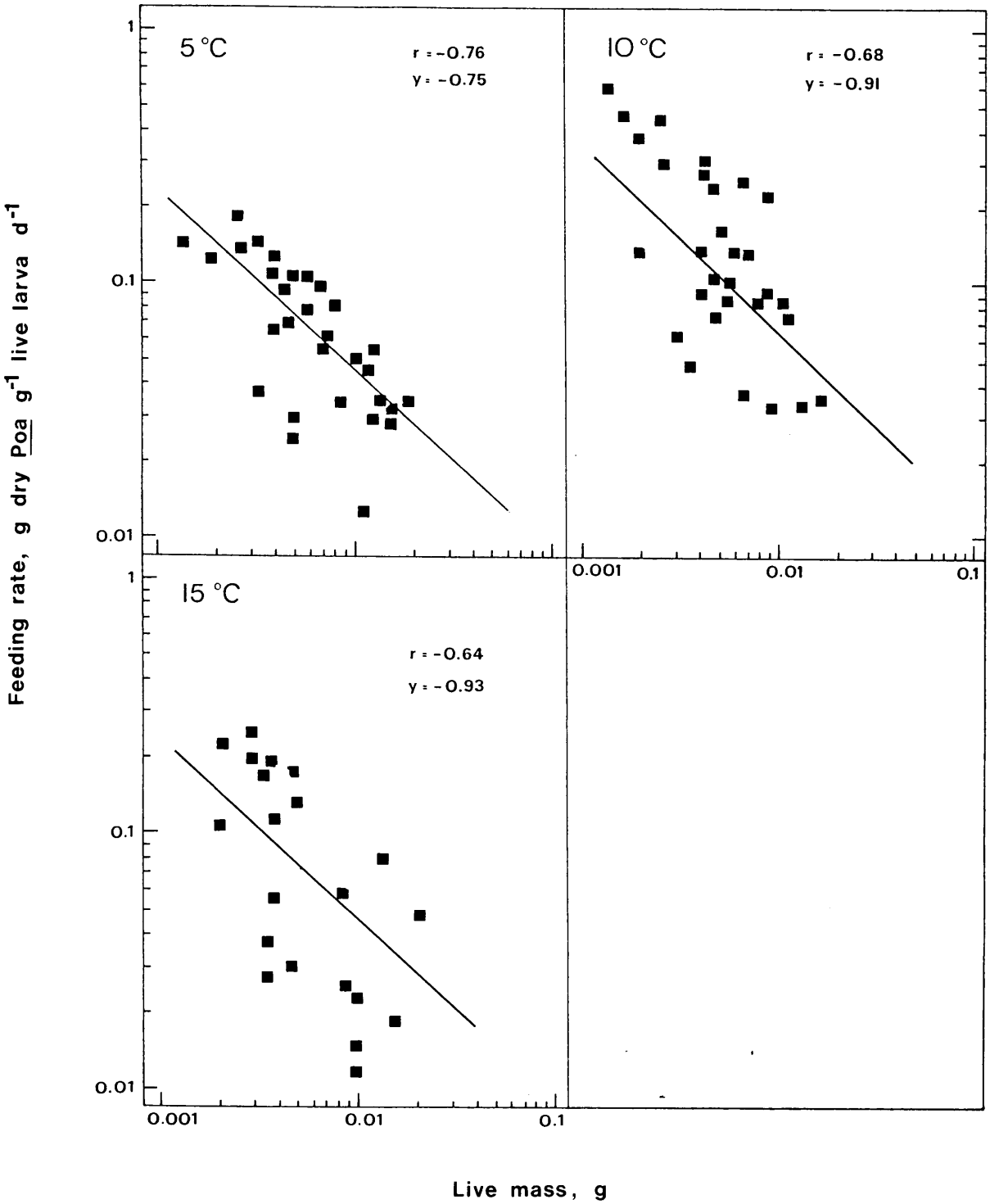

Figure 4.4. The effect of temperature on food consumption rates of *E. halticella* larvae.

Table 4.6. Mean (± STD) daily ratio of food consumed to frass produced (dry mass) by *E. halticella* larvae fed *P. cookii* leaves.

Temperature	Size class	Ingestion/egestion	n
5°C	I	2.94 ± 0.09	13
	II	2.22 ± 0.14	9
	III	2.63 ± 0.15	9
10°C	I	4.55 ± 0.18	10
	II	4.35 ± 0.09	12
	III	2.56 ± 0.15	8
15°C	I	3.85 ± 0.06	10
	II	2.56 ± 0.05	5
	III	3.23 ± 0.18	6

Energy values and ecological efficiencies

The energy and water content of *E. halticella* larvae and fresh *P. cookii* leaves, and the energy content of frass, are given in Table 4.7.

Table 4.7 Mean (± SD) water and energy content of three size classes of *E. halticella* larvae and their food, and energy content of their frass. Number of replicates (n) given in brackets. n.d.: not determined.

	Energy (kJ g^{-1})		Water (%)	
*E. halticella*larvae				
Size class I	21.71	(2)	62.50 ± 10.27	(14)
Size class II	22.70	(2)	64.30 ± 13.57	(14)
Size class III	24.72	(4)	62.66 ± 2.96	(15)
Prepupa	25.29	(3)	63.45 ± 9.76	(10)
P. cookii leaves	18.66	(5)	66.23 ± 3.12	(9)
Frass	18.04	(4)	n.d.	

The median values for AD, ECI, ECD, RCR and RGR of *E. halticella* larvae fed *P. cookii* leaves at constant temperatures of 5, 10 and 15 °, are given in Table 4.8. The AD, ECI and ECD are given both in terms of dry mass (w) and energy (e). Once again, values obtained in feeding experiments carried out under a cycling temperature regime did not differ significantly from those obtained at constant 10 °C, and are not shown.

Table 4.8 Indices of food utilization for *E. halticella* larvae fed *P. cookii* leaves at 5, 10 and 15 °C (see text). AD, ECI and ECD are given both in terms of food dry mass (w) and food energy (e). Number of replicates in parentheses. Size classes correspond to first and second instars (size class I), third and fourth instars (size class II) and fifth/final instar (size class III). Asterisks **within** a row indicate significant differences between median values at 5 and 10 °C, and between 10 and 15 °C. Asterisks **beneath** a row indicate significantly different values at 5 and 15 °C. (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: not significant; Mann-Whitney U test).

	Size class I			Size class II			Size class III		
AD (%) w	37.38 ***	86.61 ns ***	74.03	39.24 ***	80.61 ** ns	58.14	36.00 *	64.27 ns **	66.74
e	62.46 ns	86.55 ns *	73.92	60.59 **	80.53 ** ns	57.96	63.85 ns	64.11 ns ns	66.59
ECI (%)w	13.18 ns	7.37 ns ns	11.45	20.17 *	7.38 ns ns	24.48	22.75 *	13.12 ns ns	11.56
e	15.80 ns	8.84 ns ns	13.74	24.19 *	8.85 ns ns	29.35	27.29 *	15.73 ns ns	13.86
ECD(%)w	20.62 ns	10.60ns ns	15.70	36.89 **	11.19 ns ns	44.30	33.55 *	21.20 ns ns	20.72
e	24.79 ns	12.73 ns ns	18.86	44.36 **	13.45 ns ns	33.32	40.44 *	25.56 ns ns	24.94
RCR	0.42 ns	0.61 * ns	0.34	0.21 **	0.45 * ns	0.17	0.10 *	0.24 * ns	0.06
RGR	0.05 ns	0.06ns ns	0.05	0.05 ns	0.04 ns ns	0.02	0.02 ns	0.03 ns ns	0.02
	(13)	(10)	(10)	(8)	(12)	(7)	(9)	(8)	(6)

4.3.3 Discussion

Consumption rates

E. halticella larvae are slow and erratic feeders, which accounts for the poor correlation between larval mass and feeding rate. In every laboratory feeding experiment, between 30 and 50 % of the larvae used in the experiment did not consume any leaf material at all. Those that did feed, did not feed every day. The slow and erratic feeding by larvae in the laboratory made quantification of the diet extremely difficult, and it is doubtful if gravimetric measurements of food consumption can give precise results when such small quantities of food and random feeding bouts are involved. Extrapolation of consumption in the field from laboratory experiments is accompanied by a manyfold increase in error; the data presented here should simply be seen as best estimates. Ryan and Hergert (1977) encountered similar problems during feeding experiments with *Gynaephora groenlandica* (Lepidoptera, Lymantriidae) larvae at high arctic Devon Island, and state that apparently healthy larvae intermittently ceased feeding altogether and became inactive during feeding experiments. *G. groenlandica* larvae kept without food all summer appeared healthy and had lost little mass at the end of summer. Slow feeding would be the exception to lepidopteran rule in temperate areas, but reflects a general trend in the Arctic and sub-Antarctic (e.g. Downes 1965, Remmert 1980).

Lepidoptera larvae are known to eat up to 99% of their total intake during the last three instars (Waldbauer 1968). The combined biomass of the last three instars of *E. halticella* larvae constitutes the greatest percentage of total larval biomass in all but three months, while final instar larvae constitute the greatest percentage of larval biomass in all but four months (Fig. 4.4). The performance of mature larvae (class III, Table 4.7) is therefore singled out for discussion.

The CR of all larvae was significantly higher at 10 °C than at 5 °C (Table 4.4), but generally declined again at 15 °C. RCR varied less than CR between temperatures (Table 4.8), and was exceptionally low (0.06 - 0.61) compared to that of other leaf-feeding Lepidoptera, in which RCR may range from 0.5 - 5 (Scriber and Slansky 1981). A low RCR may, however, increase AD because of prolonged retention of food in the gut (Sibly and Calow 1986).

Approximate digestibility

Larvae were about equally efficient in absorbing energy from their food at all three temperatures, in spite of the significant differences in CR. AD of food biomass, however, was significantly higher at 10 and 15 °C than at 5 °C. Mature larvae had energy and mass AD values between 36 and 67 %, which are slightly higher than those recorded for mature larvae of five other species of graminivorous Lepidoptera (32 - 59%) and within the range recorded for 14 grass-specialist Orthoptera (range 17 - 71%; both data ranges cited in Bernays and Barbehenn (1987)). High AD values could result from the prolonged retention of food in the gut, from the high activity of intestinal symbionts, from the re-ingestion of faeces, or from any combination of the three. Frass accumulates behind the sedentary larvae within the enfolding grass sheaths, and its undigested appearance suggests that it may be re-ingested by the larvae - a strategy employed by various other lepidopteran larvae. Frass (and possibly exuviae, since no signs of cast larval skins were ever found) may therefore constitute a fraction of the larval diet. Feeding by *E. halticella* larvae is difficult to observe in the laboratory and impossible to observe in the field, given their crypsis, small size and exceedingly slow feeding rates, and actual coprophagy was never observed. Examination of larval gut contents also did not yield any sign of microbial symbionts.

Growth performance

ECI and ECD values for mature larvae decreased significantly from 5 to 10 °C, but were similar at 10 and 15 °C. However, at 15 °C the variance in individual performance increased dramatically (standard deviations approach the means of ECI and ECD values at this temperature), probably as a result of metabolic stress accompanying prolonged exposure to relatively high temperature. The generally high variance in the growth performance values of mature larvae can be ascribed to variation in energy expenditure between larvae of different sex or at different stages of gonadal development (e.g. Carne 1966), which in *E. halticella* is well advanced at pupation. Table 4.9 compares the mean ECD values for (a) mature *E. halticella* larvae, (b) *Oporinia autumnata* (Geometridae) larvae mining leaves of birch (*Betula tortuosa*) in northern tundra (66 °N), and (c-d) two cosmopolitan, graminivorous Lepidoptera species.

Table 4.9 Efficiency of conversion of digested food biomass (ECD) of mature *E. halticella* larvae (a), compared to ECD of larvae of (b) a northern tundra birch leaf-miner and (c) two cosmopolitan, lepidopteran graminivores.

Species	Mean daily temperature °C	ECD %	Food	Reference
(a) *E. halticella*	5	34	*P. cookii*	a
(Yponomeutidae)	10	21		a
	15	21		a
(b)*Oporinia autumnata*	12.0	28	*Betula tortuosa*	b
(Geometridae)	18.5	20	(birch leaves)	b
	22.0	23		b
(c) *Spodoptera exempta*	-	39	seedling wheat	c
Agrotis orthogonia	-	43	seedling wheat	d

a This study
b Bogacheva (1981)
c Bernays and Barbehenn (1987)
d Kasting and McGinnis (1959), cited in Bernays and Barbehenn (1987).

RGR values obtained for *E. halticella* larvae (0.02 - 0.06) are amongst the lowest recorded for leaf-feeding Lepidoptera (range 0.03 - 1.5, representing data for 26 species) and more similar to the data range recorded for detritivores, keratinophages, and tree-foliage-chewing Coleoptera (0.001 - 0.11, representing data for 78 species; both data ranges cited in Scriber and Slansky (1981)).

The effect of food nutrient quality on performance

Energy may be the "ultimate factor" limiting life (Odum 1976), but more proximate factors limit herbivores on plants. Nutrients are important regulators of energy flow at all levels (Scriber and Slansky 1981), the two most important regulators in herbivory being the nitrogen- and water content of food plants (Mattson 1980;

Strong *et al.* 1984). RGR of herbivorous insects is closely correlated with nutrient and water content of their food (e.g. Timmins *et al.* 1988), lowest RGR (<0.1) having been recorded for cecropia moth on Black Cherry leaves with a water content of c. 50 %, and nitrogen content of only c. 1 % of dry mass (Scriber 1977). Smith (1987a) described the seasonal variation of the nitrogen content of living shoots of *P. cookii* in closed and open fernbrake at Marion Island. From December to April the nitrogen content of the living shoots was constant, varying only between 1.2 and 1.4 % of dry mass. Mature-leaf water content of grasses generally ranges from 60 to 75 % (Bernays and Barbehenn, 1987); the water content of the tender inner leaves of *P. cookii* tillers fed to *E. halticella* during this study, was 66 % (Table 4.7). Scriber and Slansky (1981) plotted RGR of several species of foliage-feeding Lepidoptera larvae against the water and nitrogen content of their food, on a graph which predicts the low RGR of *E. halticella* larvae actually measured during this study (Table 4.8).

The effect of temperature on performance

"Mean temperatures" have limited relevance to biological processes that occur under a varying or cycling temperature regime, which frequently stimulates performance relative to constant temperature (Scriber and Slansky 1981; Remmert 1986). The fact that the performance of *E. halticella* larvae feeding under a cycling temperature regime in the laboratory did not differ significantly from their performance at 10 °C, which appears to constitute their temperature preferendum, is anomalous at first sight. However, it should be seen in the context of the virtual aseasonality of the sub-Antarctic macroclimate. Sunshine - and concomitant sharp increases in temperature within the larval microhabitat - are unpredictable and rare occurrences at Marion Island (see Chapter 3). I submit that the "ecological strategy" of *E. halticella* larvae does not revolve around, but merely accommodates, opportunistic responses to such temperature increases. This contention is further explored in section 4.6.

The fact that not a single performance index increased significantly at 15 °C over 10 °C (Table 4.8) suggests that the temperature optimum for *E. halticella* larvae is below 15 °C, and that they are truly cold-adapted herbivores (see also respiration data, Table 4.10). Growth performance (ECD and ECI) was consistently *better* at 5 than at 10 °C - possibly because of extremely long retention time in the gut, of food obtained during "feeding sprees" at higher temperatures (Table 4.8). Feeding is metabolically costly (e.g. McEvoy 1984). Added to the increased metabolism of larvae at higher (>10 °C) temperatures (Fig. 4.6), higher metabolic costs due to both increased feeding and faster metabolism would be reflected in lowered efficiency of food utilization at the higher temperatures.

P. cookii flowers in September/October and the seed heads remain on the plant until March or April (Smith 1985). On temperate days during early summer, *E. halticella* larvae were observed emerging to feed on flowers and young seeds (Crafford and Scholtz 1986), which have higher nitrogen content (1.5 - 2.2 % of dry mass) than leaves (Smith 1985). Such a shift in diet, short-lived and opportunistic as it is in the case of *E. halticella*, may be important in enhancing gonad growth and larval maturation prior to pupation, which follows towards the end of summer. The interaction between food nitrogen levels and food utilization efficiencies of herbivores is not well understood, but what has been well documented is the effect of host nitrogen level on population abundance (Strong *et al.* 1984). The population biomass of *E. halticella* larvae in the *P. cookii* "biotic community" around the albatross nest was up to ten times higher than population biomass in the *P. cookii* "slope crest community" (Fig. 4.3). Smith (1978) found the nitrogen content of *P. cookii* leaves to be up to twice as high (2.42% of dry mass) in biotic as in non-biotic *P. cookii* communities.

4.4 Respiration

4.4.1 Methodology

Respiration studies are time-consuming, and to obtain an adequate sample for each of the five species under consideration in this thesis, two different experimental techniques were used to measure oxygen consumption. Where both techniques were applied to the same species, the results were lumped, unless they differed significantly. Oxygen consumption rate of each species was determined over a temperature range of 20 °C (between 0 and 20°C). Insects used for respirometry were acclimated at the desired temperature for at least 48 h beforehand. Since the same methods were used to determine the oxygen consumption of each of the five species, the description of methodology which follows here will not be repeated in subsequent chapters.

The following two techniques were used:

A. Crude, direct measurements of the amount of oxygen consumed by individual *Embryonopsis halticella*, *Pringleophaga marioni* and *Paractora dreuxi* larvae, and *Ectemnorhinus marioni* adults, were obtained with the simple but efficient respirometers described by Welsh and Smith (1960). The respirometer consisted of a chamber (20 ml glass "Polytop" vials were used), fitted with a rubber stopper through which a 1 ml graduated pipette projected. A small muslin satchel filled with non-deliquescent NaOH was placed at the bottom of the chamber to absorb CO_2, and a gauze screen prevented the insect from coming into contact with the NaOH. The entire respirometer, containing one or more (depending on size) insects of known live mass, was submerged in a water bath set at the desired temperature, and was held in place horizontally, at the bottom of the water bath. The water in the bath entered the pipette, serving as manometer fluid, and as oxygen was consumed by the insect in the chamber, the position of the moving meniscus was recorded every 15 minutes over a two hour period.

Prior to total submergence, the chambers only were immersed in the water for at least 10 minutes to allow air temperature inside the chamber to equilibrate. After submergence a further 10 minutes were allowed for temperature equilibration of the entire respirometer, before observations were recorded. Since the functioning of the respirometer is influenced by pressure changes, which at Marion Island can be large and rapid, fluctuations due to pressure changes were corrected for by control respirometers containing no larvae.

B. Individual insects were placed inside 3 ml cuvettes ("Venoject" tubes were used) fitted with tight-sealing rubber stoppers, which were then immersed in a water bath set at the desired temperature. A whole series of cuvettes, each containing a different individual of the same species, and of known live mass, was prepared for each replicate. Depending on the size of the insect and the temperature at which respiration was measured, the oxygen content of the air inside each cuvette was determined after either one, two or three hours. A vacuum was drawn inside the cell of a portable oxygen analyzer (Servomex 570A), after which a needle was inserted through the rubber septum of the cuvette and the entire air content of the cuvette drawn into the vacuum. A reading of the oxygen content (% O_2) of the air in the cuvette was converted to ml O_2, after compensating for the displacement of air inside the cuvette by the volume of the insect. The oxygen analyzer had previously been calibrated at 21 % O_2 (the oxygen content of ambient air at the island). The difference between the oxygen content (in millilitres) of the cuvette before and after respiration by the insect was determined, and oxygen consumption was finally expressed as ul O_2 ind^{-1} hr^{-1}.

E. halticella larvae used for respiration experiments were collected in the field and acclimated for 48 h at the desired temperature (either 5, 10, 15 or 20 °C). The larvae were grouped into the same three size classes as for the feeding experiments (see 4.3.1).

4.4.2 Results

Effect of live mass on oxygen uptake

Mean live mass, and the mean respiration and metabolic rates at 5, 10, 15 and 20 °C of three size classes of *E. halticella* larvae, are given in Table 4.10.

Table 4.10. Mean (± SD) metabolic rates: ul O_2 g^{-1} hr^{-1} (M), respiration rates: ul O_2 ind^{-1} hr^{-1} (R), live mass: mg (W) and number of replicates (n) for three size classes of *E. halticella* larvae at 5, 10, 15 and 20 °C.

	5°C	10°C	15°C	20°C
Class I				
M	6010.78 ± 1033.84	3745.76 ± 1859.33	4213.79 ± 2134.85	2312.26 ± 792.15
R	4.77 ± 1.35	0.69 ± 0.37	1.31 ± 0.87	1.87 ± 1.36
W	0.80 ± 0.13	0.24 ± 0.12	0.53 ± 0.41	0.94 ± 0.67
n	6	4	6	4
Class II				
M	2947.81 ± 659.29	849.39 ± 164.24	1326.67 ± 161.98	1610.57 ± 97.73
R	5.26 ± 1.40	3.49 ± 1.21	5.45 ± 0.71	8.83 ± 2.67
W	1.83 ± 0.41	4.04 ± 0.83	4.20 ± 0.94	5.41 ± 1.32
n	17	8	4	8
Class III				
M	1243.94 ± 373.26	709.70 ± 137.06	1263.40 ± 237.66	1625.61 ± 275.54
R	5.35 ± 0.63	6.32 ± 2.22	15.18 ± 3.78	19.05 ± 7.56
W	4.83 ± 2.04	8.71 ± 1.60	12.42 ± 3.51	11.34 ± 3.16
n	5	7	7	7

Regression equations relating (a) respiration rate (ul O_2 ind^{-1} hr^{-1}) and (b) metabolic rate (ul O_2 g^{-1} hr^{-1}) to live mass are given in Table 4.11. Double $\log_{10}$ plots of individual respiration rate on live mass across the entire size range of larvae revealed significant differences in the relation between the two variables at 5 and 10, and at 15 and 20°C, with the slopes of the lines relating the two variables differing substantially at these temperatures (Fig. 4.5; Table 4.11). At 10 and 15 °C, however, the slopes of the regression lines were similar. At 5 °C, the slope of the regression line did not differ significantly ($p < 0.05$) from zero (Table 4.11), indicating that at this temperature live mass did not influence respiration rate and indeed explained only 6% of the measured variation in respiration rate.

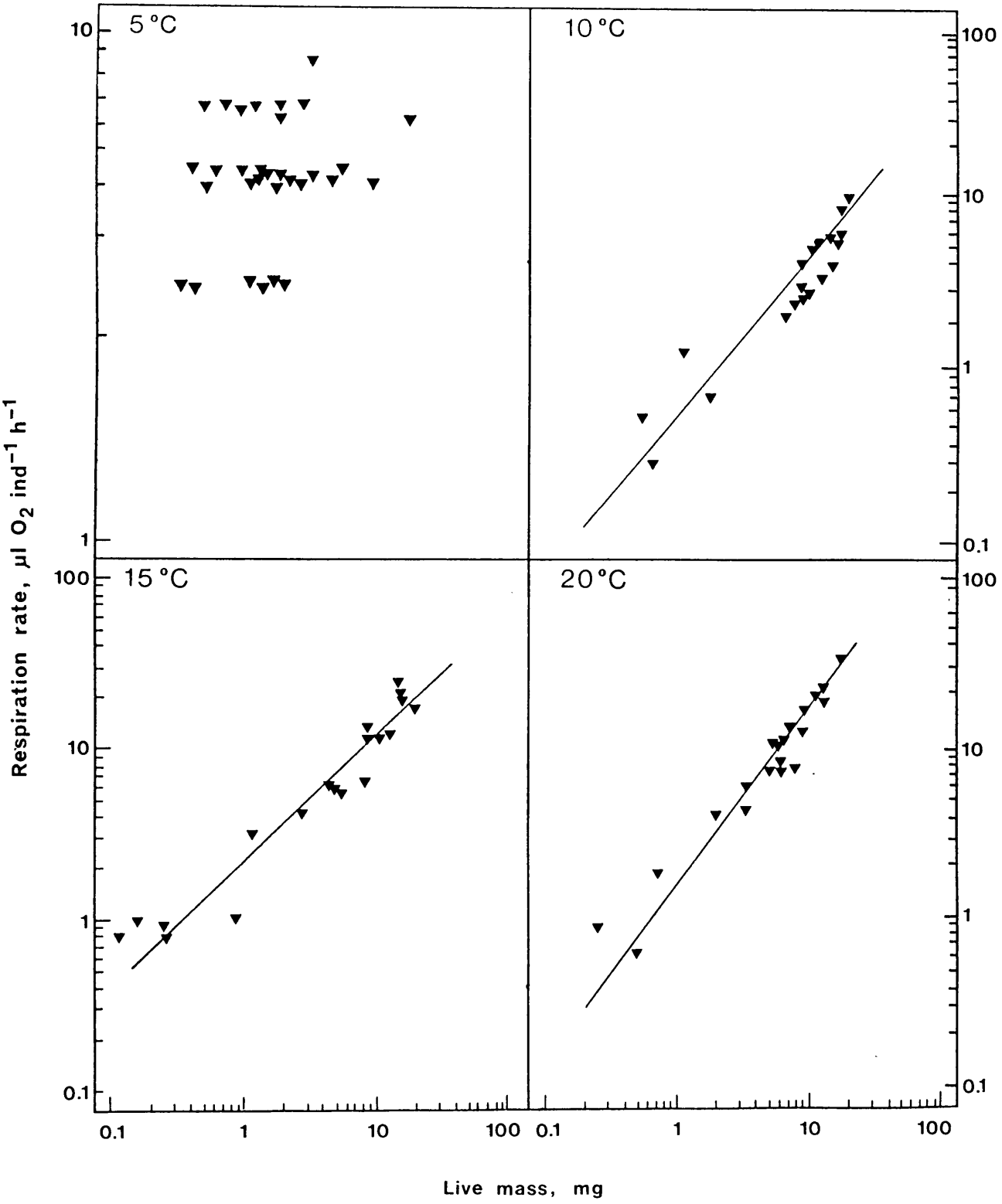

Figure 4.5. Effect of live mass on respiration rate of three size classes of *E. halticella* larvae at 5, 10, 15 and 20 °C.

A far better correlation exists between metabolic rate and live mass at 5, 10, and 15 °C (Fig. 4.6, Table 4.11). Once again, the slopes of the regression lines relating live mass to metabolic rate were similar at 10 and 15 °C. At 20 °C, however, there was a poor correlation between live mass and metabolic rate - the opposite trend to that of respiration rate at this temperature (Table 4.11).

Table 4.11. Linear regression equations of (a) $\log_{10}$ respiration rate on $\log_{10}$ live mass and (b) $\log_{10}$ metabolic rate on $\log_{10}$ live mass at 5, 10, 15 and 20 °C for *E. halticella* larvae.

	Temperature	n	a	b ± SEM	r	r^2
(a)	5	28	10.24	0.11 ± 0.09	0.22	4.66
	10	19	102.88	0.62 ± 0.06	0.92	85.18
	15	17	243.13	0.68 ± 0.07	0.91	82.93
	20	19	1,217.84	0.95 ± 0.06	0.96	92.51
(b)	5	28	10,242.80	-0.89 ± 0.09	-0.88	76.74
	10	19	10,287.50	-0.38 ± 0.06	-0.83	69.07
	15	17	2,431.31	-0.32 ± 0.07	-0.73	52.82
	20	19	1,217.84	-0.05 ± 0.06	-0.19	3.83

At 10 °C, respiration rate and larval live mass were related by the equation

$$R = 4.57\, W^{0.62} \quad \text{.....(1)}$$

where R = respiration rate and W = larval live mass. This equation was later used to determine cumulative respiration in the construction of individual and population energy budgets (section 4.5).

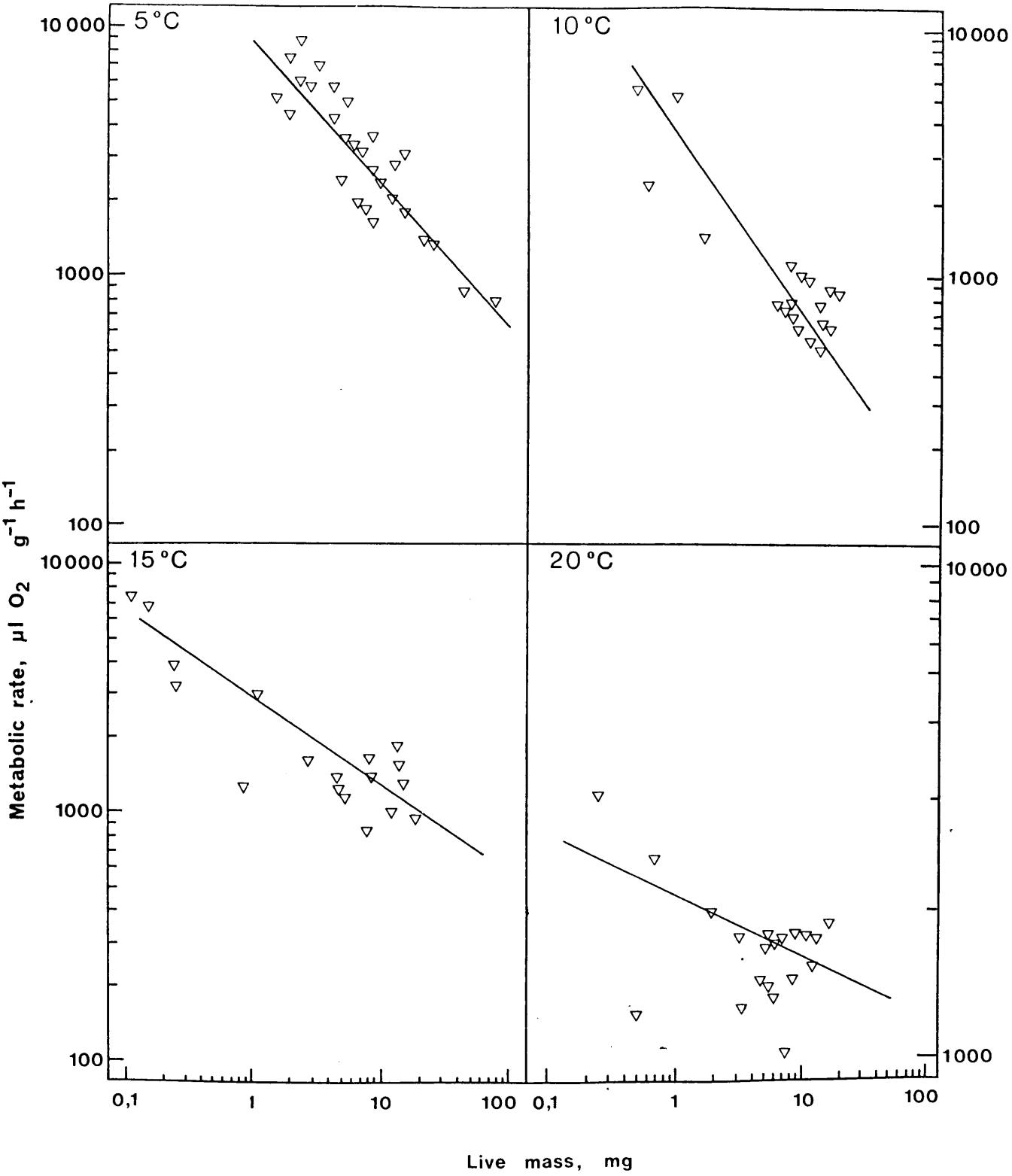

Figure 4.6. Effect of live mass on metabolic rates of three size classes of *E. halticella* larvae at 5, 10, 15 and 20 °C.

Effect of temperature on oxygen uptake

The mean respiration rates and mean metabolic rates of each of the three size classes of *E. halticella* larvae are plotted against temperature in Fig. 4.7. The respiration rates of each size class of larvae increases steadily from 10 to 20 °C, although in size classes I and II it is higher at 5 than at 10 °C, and in size class III does not increase significantly ($p<0.01$) from 5 to 10 °C (Fig.4.7a). Metabolic rates actually decrease from 5 to 10°C in each size class, but then increase with an increase in temperature from 10 to 20 °C in size classes II and III, although it continues to decrease in size class I (Fig. 4.7b). Larvae used for respiration studies at 5 °C were collected at a different time of year, when few large larvae were available, and the mean live mass of each of the three size classes differs from that of the size classes used for studies at the other temperatures (see Table 4.10). The results at 5 °C therefore in part reflect a mass effect, but the difference is so pronounced that it may indicate a real trend (see discussion).

Of various equations relating arthropod metabolism (M) to temperature (T), only the Arrhenius equation is based on thermodynamic considerations (the frequency of molecular collisions as a function of temperature). The Arrhenius equation ($M = a.e^{-u/RT}$, where T is temperature in Kelvin, a is a constant related to the frequency of molecular collisions, u is the activation energy and R is the gas constant) has the added advantage of yielding a value u (activation energy) that does not change with temperature, and generating thermodynamically correct (i.e. temperature dependent) Q_{10} values (Young 1979).

The data showing the effect of temperature on the metabolic rates of each of the three size classes of *E. halticella* larvae are presented as Arrhenius plots in Fig. 4.8. The fitted regression lines in Fig 4.8 are, for convenience, those of $\log_{10}M$ against $1/T^{\circ}K \times 10^{3}$. The corresponding regression equations (derived on a natural log basis) are given in Table 4.12.

Table 4.12. Linear regression equations of $\log_e$ metabolic rate on 1/T (°K) for Arrhenius plots of each of three size classes of *E. halticella* larvae.

Size class	n	a	b ± SEM	r
I	20	1.65×10^{3}	4.47 ± 1.55	0.89
II	37	1.28×10^{11}	-5.32 ± 1.15	-0.98
III	26	2.79×10^{13}	-6.89 ± 1.49	-0.98

Multiplying the coefficient b (Table 4.11) by the gas constant (1.98 cal $mol^{-1}K^{-1}$) gives the values for the activation energies (u values; Precht *et al.* (1973)) of larvae in each of the three larval size classes. Q_{10} values were calculated both from the equation $\log_{10} Q_{10} = 2.187\ u/T_1.T_2$ (Precht *et al.* 1973), which gives the thermodynamically correct values linked to activation energy, and from mean metabolic rates, using the equation $\log Q_{10} = (\log R_2 - \log R_1) \times 10/T_2 - T_1$ (Schmidt-Nielsen 1979).

The activation energies, and Q_{10} values over the range 10 - 20 °C, for each of the three larval size classes, are given in Table 4.13.

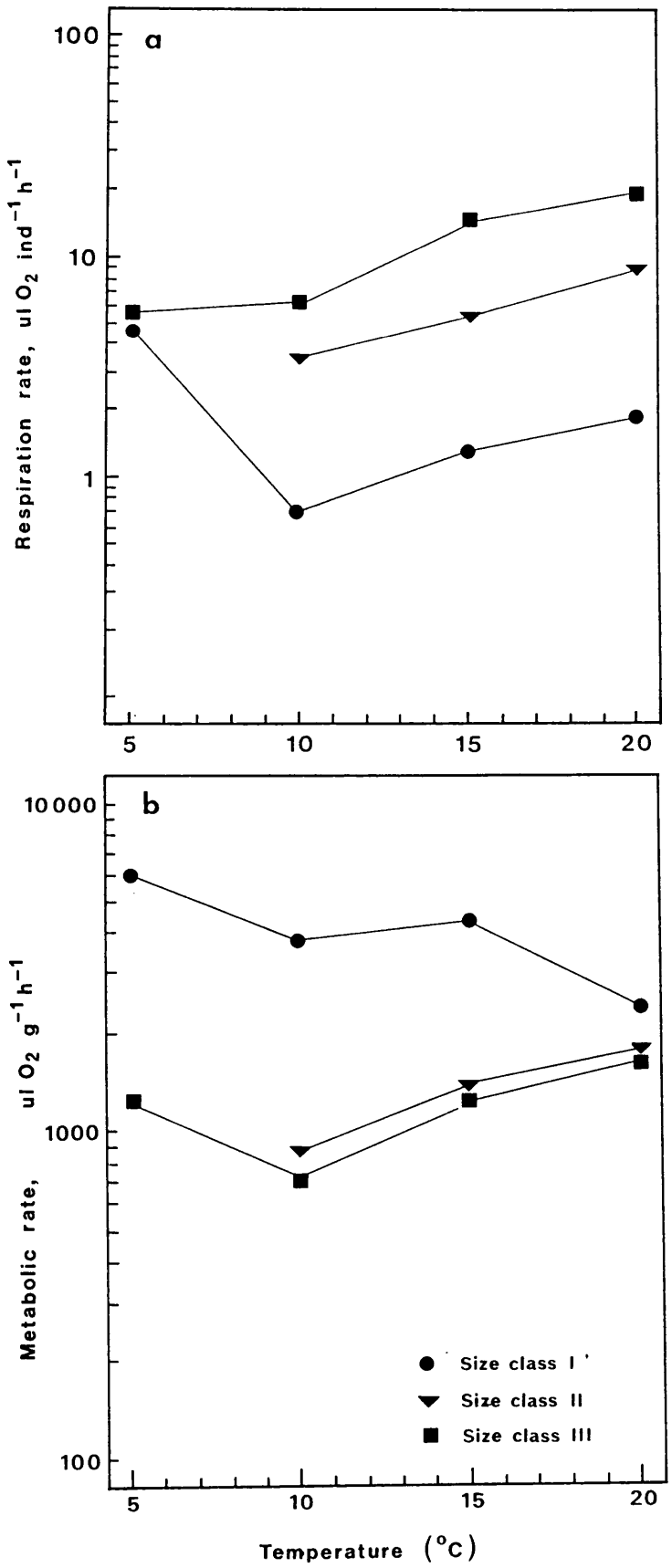

Figure 4.7. Effect of temperature on (a) mean (± SEM) respiration rate and (b) mean (± SEM) metabolic rate of three size classes of *E. halticella* larvae.

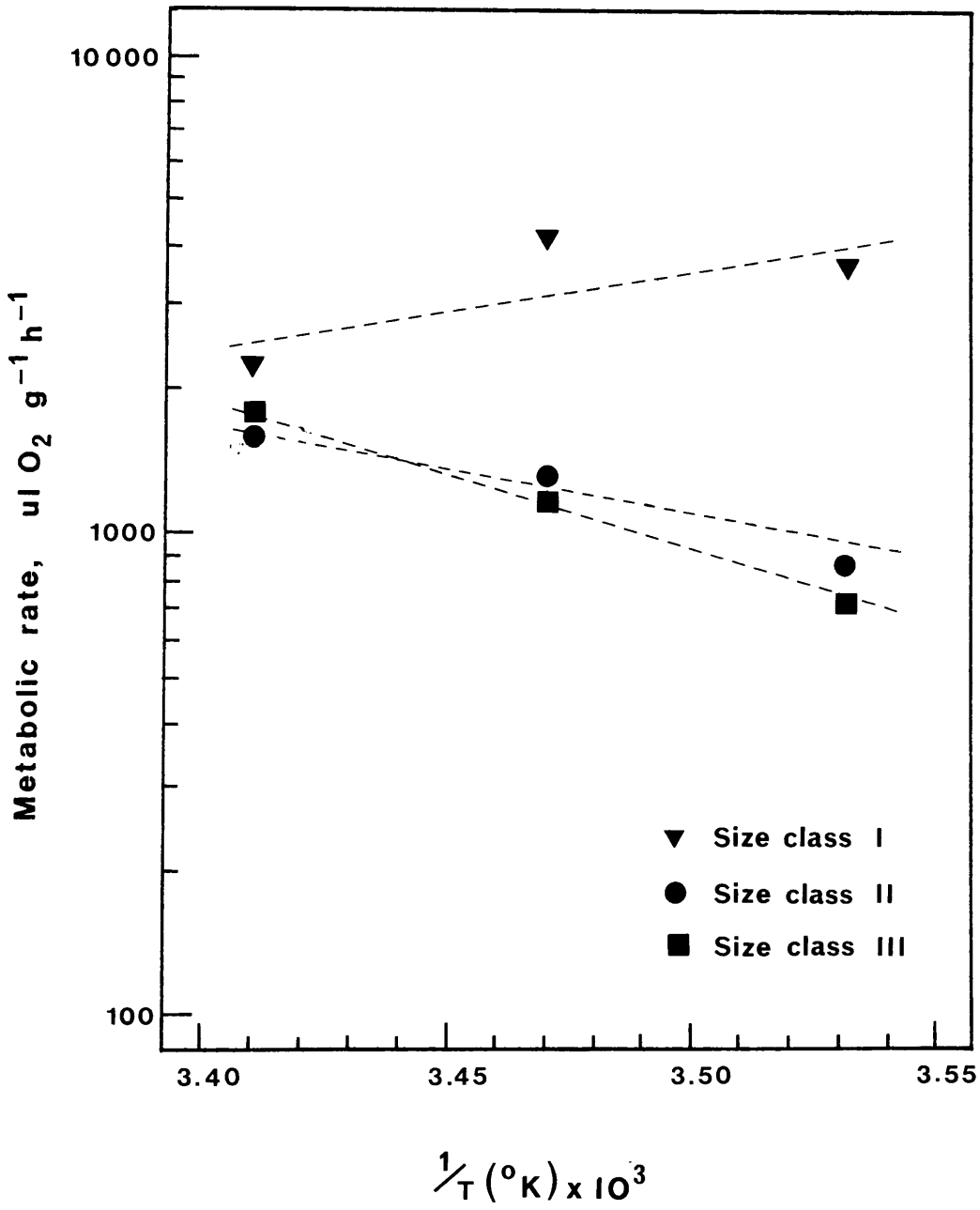

Figure 4.8. Arrhenius plots of metabolic rate (M) on temperature (T) for three size classes of *E. halticella* larvae. The fitted regression lines of $\log_e M = a.e^b$, with a and b of each size class taken from Table 4.11, are shown.

Table 4.13 Activation energies and Q_{10} values for the ranges 10-15, 15-20 and 10-20 °C of mature *E. halticella* larvae (Size classes II and III). Q_{10} values in brackets were calculated from mean metabolic rates.

Size class	Activation energy	Q_{10}		
	(kcal/mol)	10-15 °C	15-20 °C	10-20 °C
II	10.54	1.41 (2.43)	1.20 (1.47)	1.29 (1.89)
III	13.64	1.58 (3.17)	1.26 (1.65)	1.41 (2.29)

4.4.3 Discussion

There is overwhelming evidence in the literature (summarized and reviewed by Peters (1983)) that oxygen consumption scales allometrically to between 0.6 and 0.8 the power of body mass. For *E. halticella* larvae, the rate of increase in respiration rate is 0.62 the power of body mass at 10°C (equation (1)), but this ratio - as most other over-confirmed ratios in biology - has descriptive rather than analytical value. Of more importance, and more likely to reflect a real trend, is the evidence that respiration rate is independent of body mass at 5 °C, while metabolic rate is independent of body mass at 20°C (see r values in Table 4.11). It has often been confirmed that insects can "shut down" respiration without incurring an appreciable oxygen debt (Keister and Buck 1964). At 5 °C, this is most likely what *E. halticella* larvae at different stages of development do, to different extents, leading to the poor correlation between mass and respiration shown in Table 4.11. At the same time, however, the metabolism of individuals would be unaffected, and would proceed in direct proportion to their amount of metabolizing tissue (reflected in body mass). Conversely, the lack of correlation between body mass and metabolism at 20°C indicates that 20°C (and especially prolonged exposure to this temperature) is stressful, and causes a "breakdown" of metabolism (see also Young 1979).

Respiration often either fails to increase with temperature, or actually decreases over part of the range. Usually, such an irregularity (at 10 °C, as evidenced in Fig. 4.7) occurs at temperatures immediately above and below the "rearing temperature" (Keister and Buck 1964). Based on thermodynamic considerations, one would intuitively expect a temperature at which total oxygen uptake is minimal to represent the temperature optimum, since at that temperature the minimum amount of internal entropy has to be "pumped out" (Odum 1978) through respiration, in order to maintain the organism at thermodynamic non-equilibrium. The temperature optimum for *E. halticella* larvae should therefore lie close to 10 °C, as is borne out by the results from the feeding studies and the measured efficiencies at different temperatures (Table 4.8).

In spite of their capacity to compensate for changes in temperature, either in the short term through acclimatization, or over evolutionary time, through adaptation (see section 5.4.3), insects in general are considered to have little ability to compensate for environmental temperature. Scholander *et al.* (1953), in a seminal work, compared similar species of terrestrial arctic and tropical insects, and concluded that there

was little or no respiratory adaptation to temperature. More recently, however, Block and Young (1978) have claimed that cold adaptation by means of metabolic rate elevation is one of the ways in which an Antarctic mite (*Alaskozetes antarcticus*) copes with extremely low ambient temperatures. Subsequent studies (e.g. Young 1979) have provided support for the metabolic rate elevation hypothesis. The underlying mechanisms are still not entirely clear, but most likely involve changes in enzyme concentration, changes in the types of enzymes present, and modulation of the activities of pre-existing enzymes (see Chapter 8 for a discussion of the relevance of activation energies in this regard).

4.5 Energy flow

Ideally, the construction of individual and population energy budgets should be preceded by the drawing up of age- and time-specific life tables, and the detailed analysis of life history phenomena such as natality, mortality, and annual recruitment which is required for such life tables. Practical difficulties - such as the widely overlapping generations of *E. halticella*, the cryptic life style of the larvae, and the constraints on field work in the sub-Antarctic - precluded such detailed analysis. Energy relations in individuals and populations of *E. halticella* presented here are "best estimates" based on the available information, and may take extrapolation rather close to the limits of acceptability.

Since neither oxygen nor food consumption of *E. halticella* larvae differed significantly between 10 and 15 ^{o}C, and since the temperature range 10 - 15 ^{o}C closely reflects the temperature regime to which the larvae are exposed to in their microhabitat (Tables 3.1, 3.4), rates at 10 ^{o}C were used to calculate energy flow through *E. halticella* individuals and populations.

Individual energy budget

The energy equation for an individual or a population may be expressed, in its simplest form, as

$$I = P + R + E \quad \text{.....(2),}$$

where I = ingestion (consumption), P = production (growth), R = respiration, and E = egestion (faeces and urine).

The amount of energy assimilated (A) is equivalent to the sum of production (P) and the respiratory loss (R), or to the difference between ingestion (I) and egestion (E) (Southwood 1978).

The mass and energy budget for an *E. halticella* larva, from hatching to pupation, is given in Table 4.14. Total ingestion over the larval lifetime was calculated from actual mean consumption rates (dry mass *P. cookii* larva^{-1}day^{-1}) of larvae in each size class, rather than from a general equation relating consumption rate to body mass, because of the poor correlation between these parameters. Total oxygen consumption was calculated from equation (1). The mean live mass and duration of the different larval stages were taken from Table 4.2. Egestion was calculated from the ingestion:egestion ratios given in Table 4.6. Assimilation was calculated both from the AD values given in Table 4.8, and from the equation A = C - F (values derived the latter way are given in brackets). An energy equivalent of 20.50 kJ liter^{-1} O_2 was used throughout to convert respiration to energy output. This assumes a respiratory quotient (RQ) of 0.9, meaning that carbohydrates constitute at least 66 % of the dry mass of food utilized (Odum 1979, Southwood 1978). All other energy equivalents are from Table 4.7.

Table 4.14. Individual mass and energy budget for an *E. halticella* larva. See text for explanation of the sources of calculations.

Life stage	Ingestion (I) g	Egestion (E) g	Respiration (R) ml	Assimilation (A) g
Instar I	0.0030	0.0007	0.1196	0.0026 (0.0023)
Instar II	0.0118	0.0027	3.3099	0.0103 (0.0091)
InstarIII	0.0415	0.0162	12.7533	0.0336 (0.0253)
InstarIV	0.0747	0.0291	35.9905	0.0478 (0.0456)
Instar V	0.1079	0.0421	63.5439	0.0691 (0.0658)
Total g	0.2389	0.0908	115.7172 (ml)	0.1634 (0.1481)
kJ	4.4579	1.7012	2.3724	3.0490 (2.7635)

From Table 4.14 it can be seen that the final three instars accounted for 94 % of food consumed and 97 % of energy respired during larval development.

E. halticella larvae grow, on average, to a maximum live mass of 0.014 g (0.004 g dry mass), or to an energy equivalent of 0.1012 kJ. Larval skins cast during moults usually represent about 5 % of post-moult body mass (e.g. Schroeder 1973). Total exuviae produced during the development of *E. halticella* larvae would add about 0.3 g (dry) or 0.007 kJ to the production figure, bringing it to 0.1082 kJ. When production is calculated from equation (2), the figure arrived at is 0.3843 kJ. There is, however, a very good agreement between actual measurement of respiration (2.3724 kJ; Table 4.14) and the value for respiration calculated from the energy equation R = A-P (2.6553 kJ).

One reason why production calculated from equation (2) is so much higher than measured production is that egestion is probably underestimated in Table 4.14. Larvae produce relatively large quantities of silk throughout their development, spinning dense cocoons in which they moult. Silk production was not quantified, but would probably add substantially to total production, and to the energy value of egesta.

The energy relations of an *E. halticella* larva are shown graphically, in the form of an energy flow diagram, in Fig. 4.9a.

Population energetics

Because adults of *E. halticella* do not contribute to energy flow, only the energetics of larval populations are considered.

The standing crop of *P. cookii* in tussock grassland is 449g m^{-2} (dry mass) for a site similar to the one sampled during this study (Huntley 1972). This figure was used to convert the monthly standing crop of *E. halticella* larvae in tussock grassland to biomass per surface area, taking into account that only one third of the *P. cookii* biomass in tussock grassland is contained in live, productive material (Huntley 1972; Smith

1976). Since the final three instars dominate larval biomass for the greater part of the year (Fig. 4.3), and account for over 90% of energy flow (Table 4.14), the first two instars were left out of the calculation of population energy flow. Monthly food consumption by the *E. halticella* larval population in the tussock grassland sampled during this study was calculated as follows:

1. Monthly larval biomass (Fig. 4.2) was converted to g m^{-2} (see above).
2. Monthly collective biomass of the three final instars was calculated from Fig. 4.3.
3. Monthly food consumption by the three final instars was calculated from the mass-specific rate of feeding by final instar larvae at 10 °C (Table 4.4). From experience with laboratory feeding studies, it was assumed that larvae actively feed only half the time (see section 4.3.2).
4. The dry mass of food consumed was converted to an energy equivalent using the energy values in Table 4.7.

Monthly oxygen consumption by the larvae was calculated by substituting the larval biomass (see 2 above) for the mass component in the respiration equation (1). An AD (assimilation efficiency) value of 81 % (Table 4.8) was used to calculate assimilation.

The energy budget of the tussock grassland larval population is summarized in Table 4.16.

Table 4.16. Energy budget of an *E. halticella* population in *P. cookii* tussock grassland. Larval biomass is that of the last three instars only. See text for explanation of calculations.

Month	Larval biomass g m^{-2} (dry wt)	I kJ m^{-2}	R kJ m^{-2}	A kJ m^{-2}	E kJ m^{-2}	P(I-R-E) kJ m^{-2}
N	0.106	2.433	1.107	1.946	0.729	0.597
D	0.156	3.581	1.396	2.865	1.074	1.111
J	0.195	4.476	1.596	3.581	1.343	1.537
F	0.058	1.331	0.771	1.065	0.399	0.161
M	0.014	0.321	0.329	0.257	0.096	-0.104
A	0.011	0.253	0.284	0.202	0.076	-0.107
M	0.007	0.161	0.217	0.129	0.048	-0.104
J	0.039	0.895	0.608	0.716	0.269	0.018
J	0.040	0.918	0.617	0.734	0.275	0.026
A	0.059	1.354	0.779	1.083	0.406	0.169
S	0.109	2.502	1.126	2.002	0.751	0.625
O	0.156	3.581	1.396	2.865	1.074	1.111
Year		21.804	10.226	17.445	6.540	5.040

Population production is notoriously difficult to calculate for populations consisting of overlapping generations and several different cohorts, as is the case with *E. halticella* populations on Marion Island. A good estimate of production is the peak biomass reached by the "synthetic cohort" (which lumps individuals

of all generations; Ryan and Hergert (1977)) during one season. The *E. halticella* larval population at the tussock grassland site reached a peak biomass of 0.195 g m^{-2} in summer (Table 4.16). Converted to an energy equivalent, this amounts to 4.82 kJ, which is close to the calculated production (Table 4.16) of 5.04 kJ $m^{-2}yr^{-1}$.

Total annual consumption of leaf material in tussock grassland (deduced from Table 4.16) amounts to 1.17 g m^{-2} (dry mass), or 11.70 kg ha^{-1} (dry mass). The peak in consumption in summer is accompanied by the predominance of final instar larvae. During summer, however, many larvae were found feeding on *P. cookii* seeds, and single glumes of seed were often infested with as many as six large larvae. A shift in feeding pattern is likely to occur during this temporary abundance of an easily accessible, high protein food source. The extrapolated monthly consumption rate is based on leaf consumption only, and does not take this possibly significant shift in diet into account.

Smith (1978b) estimated that net primary production in Marion Island tussock grassland was approximately 352 g $m^{-2}y^{-1}$, or 3 520 kg $ha^{-1}y^{-1}$ (dry mass). This would amount to 6 568 kJ m^{-2}, using an energy equivalent for *P. cookii* of 18.66 kJ g^{-1} (Table 4.7). *E. halticella*, according to the calculations represented in Table 4.16, consume only 0.33 % of primary productivity, and account for only 0.26 % of energy flow, in tussock grassland (using an assimilation efficiency of 80 %). These figures may be an order of magnitude higher in *P. cookii* communities of high nutrient status, such as those surrounding albatross nests, given the fact that larval biomass in such communities is up to ten times higher than in other *P. cookii* communities (Fig. 4.2). It is not known what percentages of total *P. cookii* standing crop are contained in the different communities, neither whether primary productivity differs substantially between communities. It would be safe to state, however, that *E. halticella* larvae assimilate 1 - 3 % of *P. cookii* production annually. Few studies are available for comparison: at a high Arctic site (Truelove Lowland, Devon Island, Canada) it was estimated that invertebrates assimilated 5 % of the total net primary production. Severe localized feeding damage by *E. halticella* larvae causes tussock leaves to become detached and incorporated in the litter layer; at the same time accumulations of frass represent an ideal substrate for microbial action and reproduction. The contribution of *E. halticella* larvae to energy flow in the below-ground detritus chain probably exceeds their contribution to above ground energy-flow, but above-ground herbivory by the larvae is certainly of far greater magnitude than previously realized.

An energy flow diagram for a tussock grassland population of *E. halticella* larvae is shown in Fig. 4.9. The widths of the bars are scaled with the actual percentages of total energy expended on the different life processes.

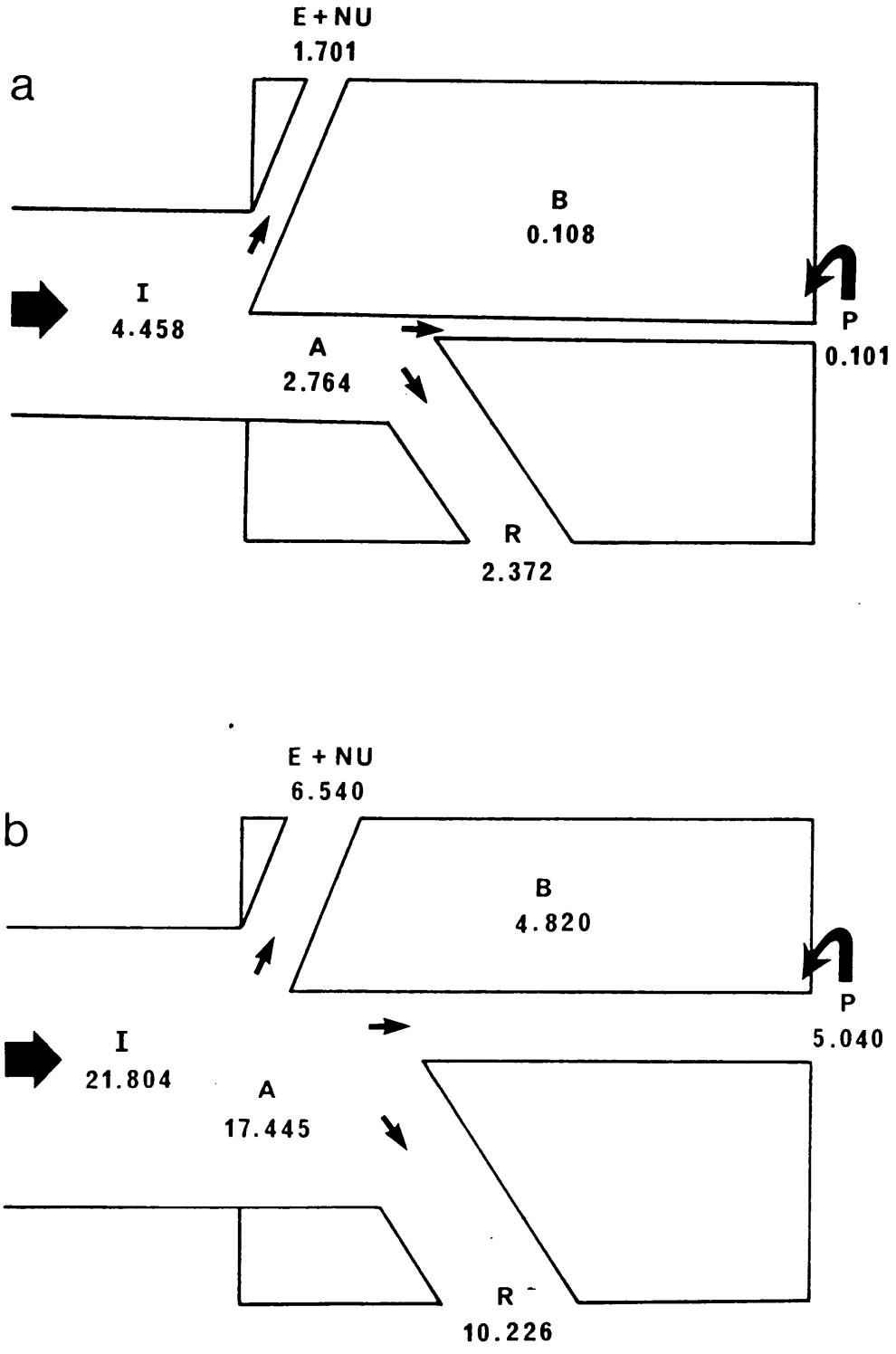

Figure 4.9. Energy flow diagram for (a) an individual *E. halticella* larva (in kJ) and for (b) a population of *E. halticella* larvae in a *P. cookii* tussock grassland (in kJ m^{-2} y^{-1}). Energy values were taken from Table 4.15.

4.6 Evolutionary perspectives

Although graminoid pollen appears in the palynological record of Marion Island at only about 8 000 yrs BP (Van Zinderen Bakker 1978), pollen similar to that of *P. cookii*, of an exotic or extinct grass, was recently found in undated interglacial peat lenses from the south-east coast of the island (Scott 1985). It is therefore quite possible that *P. cookii* (and presumably also *E. halticella*) may have been present in ice-free refugia (e.g. Van Zinderen Bakker 1978) on Iles Kerguelen and Iles Crozet, and even during interglacials on the Prince Edward Islands (specifically on Prince Edward Island, which appears to have escaped glaciation completely because of features of its size, topography and elevation). Both the periglacial (Hall 1978) and palynological (Van Zinderen Bakker 1978) evidence indicates that temperatures on Marion Island were at least 3.5 ^{o}C colder during glaciations, the last of which ended only about 12 000 yrs BP (Smith 1987b). The Antarctic convergence (presently 2 ^{o} latitude north of the island) then lay south of the island, which would then have had a climate similar to that of Heard Island today (see Chapter 1, Section 1.2). *E. halticella* larvae are prevalent throughout the range of *P. cookii* at Heard Island (Jenny Scott, pers. comm.).

The evolution of insect host range is the subject of perennial, and currently intense, debate (e.g. Bernays and Graham 1988, Schulz 1988, Rausher 1988, Thompson 1988). It is now generally agreed that factors other than secondary plant chemistry determine host plant range, "...because insects are not exposed to secondary chemicals alone, but to whole plants in distinct microenvironments characterized by certain biotic and abiotic forces, i.e., a multitude of selective forces." (Barbosa 1988). The selective advantages of host-specificity in *E. halticella* are numerous. The canopy formed by dense *P. cookii* tussocks in closed grassland communities creates a temperate microenvironment, with a temperature regime different from that of the macroclimate of Marion Island (compare Table 3.1). Such *P. cookii* communities are heavily fertilized by thousands of procellariiform seabirds, which preferentially burrow and breed amongst the tussocks, and significantly increase the nitrogen content of *P. cookii* plants (Smith 1978). *E. halticella* was pre-adapted for its present mode of life, since the Yponomeutidae characteristically tunnel in shoots or mine the leaves of their host plants (Henning 1985). In the sub-Antarctic, species diversity is low and biological factors of the environment are regarded as less important selective agents than its abiotic constraints (e.g. Crafford *et al.* 1986, Holm 1988). Climate may therefore have been the major selective cause of host-specificity in *E. halticella*, which was subsequently reinforced by the physical and chemical attributes of the host, and the biological attributes of *E. halticella* itself.

The possible evolutionary mechanisms which underlie the life history and energetics of *E. halticella* will be further discussed in Chapter 8.

CHAPTER 5: *Ectemnorhinus similis* C.O. Waterhouse and *E. marioni* (Jeannel) (Coleoptera: Curculionidae)

"Size may be an important difference between two species in one genus and have consequences which permeate into its ecology, its reproductive activities, its evolutionary progress, its development, its physiological activities. In fact, size is as important as morphology."

Bonner (1965)

5.1 Introduction

The *Ectemnorhinus similis* species complex on Marion Island comprises two species, the larger *E. similis* C.O. Waterhouse and the much smaller *E. marioni* (Jeannel). The two species are extremely close, and their larvae are morphologically indistinguishable (Chown and Scholtz 1989a). The adults are also similar, and this has led to controversy concerning the status of the two species (Chown and Scholtz 1989b). They were synonymized by Kuschel (1971) under the name *Ectemnorhinus similis*, and this treatment was followed by most subsequent workers (e.g. Smith 1977a, Burger 1978a, Crafford *et al.* 1986) Kuschel (1971) did remark, however, on the extreme variability of the species, and Crafford *et al.* (1986) subsequently recognized three different "morphs" or ecotypes, each associated with a particular vascular plant community on Marion Island. Dreux and Voisin (1986) recognized two distinct species, placing them both in the genus *Dusmoecetes*. A recent, detailed morphological and ecological study of the species complex has shown that the two species are indeed distinct, having different phenologies, habitat preferences and exhibiting marked dietary divergence (Chown and Scholtz 1989a, 1989b, 1989c). Chown (1989c) has synonymized *Ectemnorhinus* and *Dusmoecetes*, the former name enjoying priority.

Ectemnorhininine weevils form the bulk of the indigenous Coleoptera on the SIP islands, where they constitute an important part of the terrestrial arthropod fauna. Smith (1977a) first identified *E. similis* as an important member of the herbivore (adults) and detritivore (larvae) guilds on Marion Island. Chown (1989a) drew attention to the fact that the majority of the Ectemnorhinini on the SIP islands are cryptogam feeders, often associated exclusively with bryophytes, and that angiosperm herbivory in this tribe is the exception rather than the rule. Cryptogam herbivory - especially feeding on bryophytes - in turn is rare within the Curculionidae and indeed in the Insecta, and Chown (1989a) and Chown and Scholtz (1989c) have suggested that the latter strategy evolved in response to adverse conditions during the Pleistocene glaciations of the SIP islands. On Marion Island, five of the six native ectemnorhininine weevil species are cryptogam feeders; of these, *E. marioni* is the only species exclusively associated with bryophytes (both mosses and liverworts). Although *E. similis* and *E. marioni* participate in two distinctly different feeding guilds (angiosperm- and bryophyte-feeding, respectively), I shall treat them together in view of their propinquity in all other respects.

The ecological energetics of adults only were studied, partly because of experimental difficulties with the larvae and the fact that larvae of the two species are indistinguishable, but also because this investigation was aimed at describing energy flow through the guilds of which the adults - but not the larvae - are dominant members.

5.2 Life history and phenology

The basic biology and ecology of the two *Ectemnorhinus* species were studied and described in detail by Chown and Scholtz (1989b). The most important aspects of the life history and phenology of each species are summarized and compared below (after Chown and Scholtz (1989a, 1989b, 1989c)):

E. similis:

The mean live mass (mg) and duration (days, at 10 °C) of each stage in the life cycle of *E. similis* are given in Table 5.1. Developmental time of the immature stages was considerably longer at 5 than at 10 °C (up to 1 098 days at 5 compared to a maximum of 775 days at 10 °C), but in the light of recorded microhabitat temperatures (Tables 3.1 - 3.8), the latter temperature is probably of greater biological relevance. The developmental Q_{10}, theoretical null point of development and thermal constant for the immature stages (larvae and pupae, combined) of *E. similis* are 3.57, -0.62 and 3 980, respectively. Adult females kept in the laboratory lay up to 173 eggs each, and in the field are uniseasonal-iteroparous, laying eggs chiefly in *Azorella selago* leaf axils and litter, from November to April. The fecundity of *E. similis* females is within, but towards the lower end of the range estimated for adelognathous weevils. Generations overlap in the field, with both mature larvae and adults occurring throughout the year. There is a marked seasonal trend, however, with mature (seventh instar) larvae dominating larval biomass in late winter (August - September), and adults emerging in early summer and being most abundant during mid- to late summer. The larvae feed on both angiosperm and bryophyte detritus. Adults are extremely polyphagous, feeding on both bryophytes and angiosperms, but predominantly on the leaves and flowers of *Azorella selago* (Apiaceae). Known food plants (i.e. those positively identified from gut contents of adults) are listed in Table 5.2.

Table 5.1. Mean (±S.E.) live mass and duration (at 10 °C) of each stage in the life cycle of of *E. similis* (after Chown and Scholtz (1989b)). Number of replicates are given in brackets after means.

Life stage		Duration (days)		Live mass (mg)	
Egg		56.48 ± 0.93	(n = 63)	0.20 ± 0.002	(n = 30)
Instar	I	35.17 ± 1.14	(n = 60)	0.18 ± 0.002	(n = 14)
	II	36.91 ± 1.43	(n = 44)	0.59 ± 0.005	(n = 30)
	III	49.56 ± 4.59	(n = 9)	1.61 ± 0.041	(n = 17)
	IV	52.40 ± 3.75	(n = 10)	2.94 ± 0.045	(n = 21)
	V	69.63 ± 5.61	(n = 8)	6.20 ± 0.054	(n = 20)
	VI	62.00 ± 5.37	(n = 5)	11.89 ± 0.197	(n = 21)
	VII	41.53 ± 17.85	(n = 6)	19.51 ± 0.218	(n = 21)
Pupa		27.61 ± 1.31	(n = 18)	Prepupa37.33 ±0.376	(n = 6)
Adult		(up to one year)		24.81 ± 0.294	(n = 19)

Table 5.2. Food plants of *E. similis*

Bryophytes

Andreaea acutifolia (Andreaeaceae)
Ditrichum strictum (Ditrichaceae)
Brachythecium rutabulum (Brachytheciaceae)

Angiosperms

Acaena magellanica (Rosaceae)
Azorella selago (Apiaceae)
Callitriche antarctica (Callitrichaceae)
Poa cookii (Poaceae)
Pringlea antiscorbutica (Brassicaceae)
Ranunculus biternatus (Ranunculaceae)
Agrostis magellanica (Poaceae) (Rarely)

E. marioni:

The duration of the immature stages of *E. marioni* is similar to that of *E. similis* (Table 5.1), although the number of instars appears to be more flexible in the former species. *E. marioni* adults reared in the laboratory were not as long lived as *E. similis* adults, usually dying after about six months and probably sooner in the field. Both adults and larvae are associated with, and exclusively feed on bryophytes, including at least 11 liverwort (Hepaticae) and four moss species in their diet (Chown and Scholtz 1989b, 1989c). As in the case of *E. similis*, generations overlap widely in the field. Adults occur abundantly throughout the year, although numbers peak slightly during the austral summer months. They are particularly abundant in *Agrostis magellanica* mire communities which have a well-developed understory of bryophytes, dominated by the hepatic *Blepharidophyllum densifolium*. In these communities, larvae may attain densities of up to 1 000/m^2. The two *Ectemnorhinus* species co-exist in *A. selago* communities, where adults of both species can be found together in great numbers on the surface of *A. selago* "cushions," during summer. Larval mass at pupation, and resultant adult size and mass of *E. marioni*, differ between populations from different plant communities, with adults from mire communities generally being larger than those from the *A. selago* communities. Adult females lay a maximum of 11 small (compared to those of *E. similis*) eggs in the laboratory, usually amongst bryophyte fronds. The mean live mass of final instar larvae, pupae and adults of *E. marioni* is given in Table 5.3.

Table 5.3. Mean mass (±S.E.) of the final instar larvae, pupae and newly eclosed adults of *E. marioni* from *Azorella selago* (after Chown and Scholtz (1989b)).

Life stage	Live mass (mg)	n
Final instar	5.06 ± 0.075	18
Pupa	7.99 ± 0.064	19
Adult	7.77 ± 0.069	17

5.3 Feeding ecology

5.3.1 Methodology

All field and laboratory studies on the nutritional ecology and energetics of the two weevil species were carried out at and in the immediate vicinity of the research station on Marion Island, during the austral summer of 1987/1988. Adult weevils were hand-collected on their major food plants during daytime, while they were actually feeding: *E. similis* on *Azorella selago* (Apiaceae) cushions and on *Acaena magellanica* (Rosaceae) leaves in "open fernbrake" (Smith 1985) communities, and *E. marioni* on *Blepharidophyllum densifolium* (Hepaticae) "carpets" in *Agrostis magellanica* (Poaceae) communities. In the laboratory, the weevils were starved and acclimated for 48 h, in incubators in which a light:dark regime similar to that prevailing outside at the time was established. Live *B. densifolium* filaments collected in the field were placed on cottonwool in centrifuge tubes, and centrifuged at high revolution for two minutes to remove water droplets adhering in leaf axils and between filaments. The filaments were then weighed. Individual filaments were re-hydrated and placed, with a single *E. marioni* adult of known fresh mass, in 10 ml glass vials stoppered with wet cottonwool. The vials were placed in an incubator for 48 h at either constant 5 or 10 °C and 100% RH. Vials containing only fresh, weighed filaments were kept in the incubator under identical conditions for 48 h, to serve as controls for the dry mass loss of filaments through factors other than feeding by the weevil adults. Fresh filaments, dried (four days at 60 °C) immediately after they were weighed fresh, were used to determine the fresh:dry mass ratio of *B. densifolium* filaments. After 48 h, the weevils, their faeces, the filaments they had fed on, and the control filaments were weighed, dried, and weighed dry. Food consumption rates were expressed as percentage of fresh body mass eaten in food (dry mass) daily. The energy values of the frass, and of freshly dried *B. densifolium* filaments, were determined using an electronic micro-bomb calorimeter (Newham Electronics). The approximate digestibility (AD) of food energy and food mass was expressed as a percentage, and calculated using the formula

$$AD = (C - F)/C$$

where C = food eaten and F = faeces produced over the feeding period.

The same methods were used to determine the consumption rates, and the AD of food mass and energy, of *E. similis* adults feeding on fresh *Azorella selago* leaves and flower bodies (i.e. the fleshy stalk, ovary and style), and on young, unfolding *Acaena magellanica* leaves.

The AD and feeding rate values obtained on each food type, at each of the two temperatures, and for each weevil species, were ranked, and the median values of each data set were compared using the Mann-Whitney U test.

5.3.2 Results

The energy and water content of the four food types fed to adult *Ectemnorhinus* weevils during this study are compared in in Table 5.4. Comparative feeding rates (CR) and AD values at 5 and 10 °C, for *E. marioni* adults fed *B. densifolium* filaments, and *E. similis* adults fed *Acaena magellanica* leaves and *A. selago* leaves and flowers, are given in Table 5.5.

Table 5.4. Comparative energy and water content (means ± SD) of food utilized by adult weevils of the *Dusmoecetes* species complex during summer on Marion Island (n = number of determinations).

Food	Energy (kJ g^{-1} dry mass)		Water (%)	
Blepharidophyllum densifolium filaments (Hepaticae)	16.82 ± 0.49	(n=6)	66 ± 2.16	(n=11)
Azorella selago leaves (Apiaceae)	20.36 ± 0.75	(n=5)	76 ± 0.95	(n=10)
A. selago flowers	19.43 ± 0.47	(n=4)	70 ± 1.43	(n=10)
Acaena magellanica leaves (Rosaceae)	17.48 ± 0.22	(n=4)	69 ± 0.63	(n=10)

Table 5.5. Approximate digestibility of food energy (AD1) and food mass (AD2), and consumption rate (CR, expressed as % of fresh body mass day^{-1}) of food eaten by *Ectemnorhinus* adults at 5 and 10 °C. Standard deviations in brackets after means. Symbols next to values at 5 °C indicate significant differences with values at 10 °C; symbols between rows indicate significant differences between values obtained for different food types (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, no symbol: not significant; Mann-Whitney U test).

Food	5°C				10°C			
	n	CR %	AD1 %	AD2 %	n	CR %	AD1 %	AD2 %
B. densifolium fronds	19	4 (3) *	39(16)	38(16)	24	6(5)	35(15)	34(15)
		***	***	**		***	***	**
A. selago leaves	14	13(5)	65(8)	59(9)	11	13(6)	57(10)	56(11)
		***	*			***	***	***
A. selago flowers	15	7 (3) ***	44(17) ***	46(17)	12	20(11)	75(6)	75(46)
						***	***	***
A. magellanica leaves		-	-	-	23	8(2)	22(16)	26(15)

5.3.3 Discussion

The variance in performance on each food type, and at each temperature, was high, although at 10 °C the difference between arithmetic means and median values was less than at 5 °C. Median values more clearly show better performance of *E. marioni* fed *B. densifolium* filaments at 5°C than at 10°C (49% and 38%, respectively, for AD of food energy), but the difference is not statistically significant. At 5 °C, *E. similis* adults would not feed on *Acaena magellanica* leaves. At 10 °C they consumed *A. magellanica* leaves at slightly lower rates than recorded by Smith (1977a) at ambient temperatures during summer, but at rates similar to those recorded here for *E. marioni* fed *B. densifolium* filaments.

The structural, biochemical and nutritional qualities of sub-Antarctic plants have not yet been investigated in terms of their potential role in plant-herbivore interactions, mainly because the latter were long considered to be either absent or unimportant in the transfer of energy to consumer levels (e.g. Huntley 1971). Smith (1987a, 1987b, 1988) described the seasonal dynamics of phytomass and plant nutrient standing stocks in the major vascular plant communities on Marion Island; the data relevant to this study (seasonal trends in biomass and nitrogen content of bryophytes (chiefly *B. densifolium*) in a mire-grassland community, and of *A. selago* and *Acaena magellanica* in open fernbrake communities) are summarized in Fig. 5.1.

A. selago is a ubiquitous, cushion-forming plant, and is the primary vascular plant colonizer of high-altitude fjaeldmark areas. The even, hard, cushion exterior is formed by masses of small, closely compressed green leaves covered with a thick, waxy cuticle. *E. similis* larvae occur in the cushion interiors, which consist of accumulations of old leaves and leaf detritus on which the larvae feed. *E. marioni* adults occur throughout the year on cushion exteriors, where they feed on "epiphytic" bryophytes; during summer they co-occur with *E. similis* adults feeding on fresh *A. selago* leaves and flowers (Chown and Scholtz 1989b). *A. selago* flower and fruit biomass does not exceed 1 g m^{-2} (dry) during the short period of its occurrence during the austral summer (Smith 1985), when it is fed on by *E. similis* adults, and as a result no nutrient analysis of reproductive biomass was done by Smith (1985).

The energy and nitrogen content of plants increases with latitude and altitude, and is generally highest in plants adapted to "stressful environments" (White 1984). Energy, water (Table 5.4) and peak season nitrogen content (Fig. 5.1) of *A. selago* leaves are the highest of all the vascular plants eaten by insect herbivores on Marion Island (compare e.g. the nutritional qualities of *Poa cookii* eaten by *Embryonopsis halticella*; Chapter 4). The AD of *A. selago* leaf energy and dry matter was equally high for *E. similis* at both 5 and 10 °C, possibly as a result of long retention time in the gut, implied by the low ingestion rate (Table 5.5). Comparable data on weevil nutrition are few and scattered in the literature: by comparison, *Odontopus calceatus* (Curculionidae) adults fed *Liriodendron tulipifera* (yellow-poplar, Salicaceae) leaves at 27 °C had similar energy and dry mass AD (50 %) but a daily consumption rate of 97 % of dry body mass (Van Hook and Dodson 1974). At 10 °C, *E. similis* adults consumed flower bodies at the highest rate recorded during this study for any food at either 5 or 10 °C, and were able to assimilate almost twice as much food mass and energy (75 %) from the flowers as at 5 °C (Table 2). Equally high AD (79% - 81%) was recorded for rice weevil (*Sitophilus oryzae*) adults consuming similar high-energy food (wheat kernels) at 30 °C (Singh *et al.* 1976).

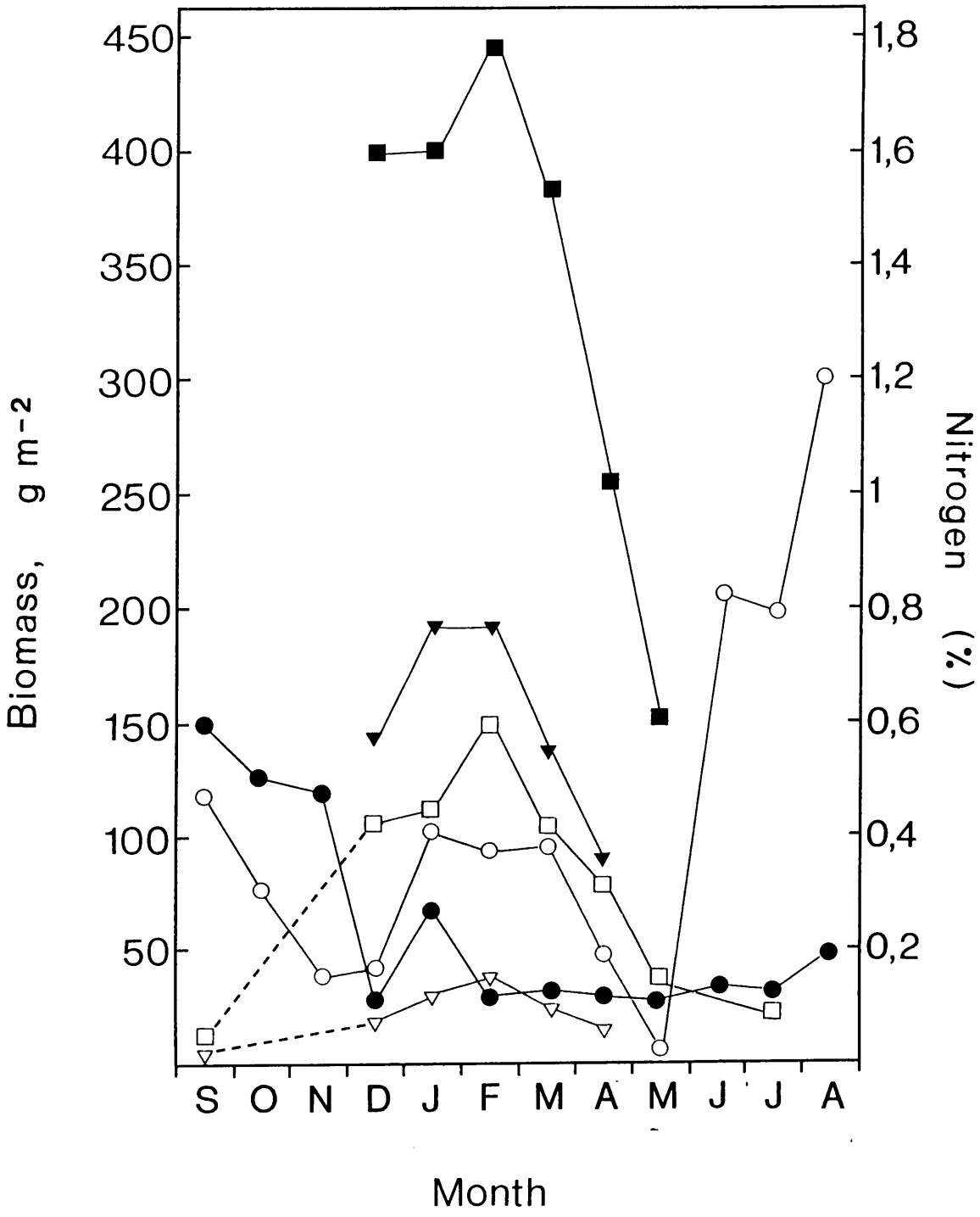

Figure 5.1. Seasonal biomass of *A. selago* leaves (□) in a fjaeldmark community, current season *Acaena magellanica* leaf shoots (▽) in an open fernbrake community and bryophytes (○) in a closed stand of mire vegetation on Marion Island. Closed symbols are for seasonal nitrogen standing stocks in the same biomass of *A. selago* and *Acaena megellanica* leaves, but for bryomass in an open stand of mire vegetation (after Smith (1985, 1987a, 1987b, 1988)).

Aceana magellanica leaves have low fibre (Walton 1985) and relatively low N (Fig. 5.1), P and K content (Smith 1985, Walton 1985). *A. magellanica* grows only at sites well protected from wind, generally against slopes or in the lee of rocks. The poor performance of *E. similis* adults collected from and fed *A. magellanica* may be due mainly to the low water content of the leaves (Table 5.4) but may also be related to the presence of tannins or other polyphenols - a surmise based on the tea-like colour of leachates from microcosms containing *A. magellanica* litter (M. Smith, pers. comm.). Increased tannin levels in leaves are indeed commonly associated with reduced water content and poor nutritional status (Bernays 1981; Scriber and Feeny 1979).

Leaf water content is the "most fundamental limiting nutrient" (Scriber 1978), and plant feeders would presumably maximize their efficiency of utilizing leaf water. *B. densifolium* filaments, apart from being tough and likely to contain polyphenols, have the lowest water content of all the major *Ectemnorhinus* food plants (Table 5.4). A film of water permanently adheres to filaments, however, and is presumably ingested with their food by adult weevils, which forage most actively on moist days, and appear so to be able to compensate for low dietary water. Apart from containing high cellulose fractions and high concentrations of ligninlike polyphenolic compounds, bryophytes actually have nutritional qualities essentially similar to vascular plants (Lawrey 1987). Bryophyte polyphenols have long been known to have antibiotic properties, which would presumably inhibit the micro-organisms required for the breakdown of dietary cellulose in the guts of moss-feeders. The activity of internal symbionts - like the feeding- and growth rates of hosts - is likely to be further depressed by constant low temperatures (Remmert 1980), such as those prevalent on the sub-Antarctic islands. At 10 °C, *E. marioni* consumed *B. densifolium* filaments at a higher rate than at 5 °C, although the AD of neither food mass nor energy changed significantly (Table 5.5). At both temperatures, however, both AD and consumption rates were significantly lower than those for *E. similis* on *A. selago* leaves, but not significantly different from those for *E. similis* feeding on *Acaena magellanica* leaves.

According to Prins (1981), moss-feeding may be adaptive in cold climates, since a highly unsaturated fatty acid produced by mosses (arachidonic acid), when ingested by moss-feeders, may afford protection to cell membranes against very low temperatures. This has been the only plausible hypothesis so far put forward to explain the predominance of moss-feeding in cold-temperate areas and its virtual absence in warm climates. The micro-climate study (Chapter 3) shows that temperatures under plant canopies (Table 3.1) and in *A. selago* cushions (Table 3.2) mostly remain at about 5 °C above ambient air temperatures, with means of about 10 °C in these two microhabitats. Mean temperatures, of course, have little ecological relevance, and the importance to development, foraging strategies and energetic performance of insect herbivores, of even short periods of high temperature, has often been stressed (e.g. Scriber and Slansky 1981; Remmert 1986). The macroclimate at Marion Island, however, because of its extreme oceanicity, is remarkably constant, having little diurnal and seasonal temperature fluctuations and low incidence of sunshine (Schulze 1971). It has been argued elsewhere (Crafford *et al.* 1986; this study, Chapter 8) that abiotic constancy has been a major cause of the evolution of the life history characteristics of Marion Island insects. In the same context, the concept of present "climatic adversity" needs to be re-examined: it appears increasingly anthropocentric in the light of the success (i.e. survival and reproduction) of organisms living under "adverse" conditions. Under present climatic conditions in the sub-Antarctic, moss-feeding probably represents phylogenetic and ecological constraints on food utilization, rather than being adaptive *sensu* Prins (1981).

Size and nutrient status of *E. similis* and *E. marioni* adults upon eclosion depend on larval nutrition and size upon pupation, but the nutritional ecology of *Ectemnorhinus* larvae is poorly known. *E. marioni* larvae are polyphagous bryophages, feeding on several species of mosses and liverworts in the bryophyte understory of *Agrostis magellanica* mire-grasslands (Chown and Scholtz 1989a, 1989b), but also in *Azorella selago* herbfields, where they co-occur with *E. similis* larvae in *A. selago* cushions. *E. similis* larvae are detritivores, feeding mainly on *A. selago* leaf litter but, in other plant communities, also on other vascular plant litter

(Chown and Scholtz 1989a, 1989b). In *A. selago* communities, *E. similis* larvae attain a prepupal mass of up to 37 mg as opposed to only 12 mg for *E. marioni* (Chown and Scholtz 1989b). There are advantages for consumers of detritus, or other plant tissue high in fiber and low in nutrients, in evolving a larger body size, partly because it allows wide-scale foraging for high-volume harvesting (Calow 1977; Mattson 1980). *A. selago* detritus is poor food for the larvae of *Pringleophaga marioni* (see Chapter 7); these larvae are also the largest of any Tineid moth.

E. marioni larvae occur throughout the year in similar numbers and biomass in mire grasslands, with a peak in numbers only in late winter. Generations overlap widely, with adults and larvae of all stages present throughout the year. *E. similis* is more seasonal, with a marked peak during late winter in larval biomass, accounted for by the predominance of final instar larvae, and a peak in early summer in adult numbers and occurrence. The latter peak coincides with the first flushes of vascular plant growth, which are known to have high water and nitrogen content. *E. marioni* is more flexible in its life cycle, having a varying number of instars and varying life cycle length, although both species generally appear to complete their life cycles in a year (Chown and Scholtz 1989b; section 5.2).

In mixed bryophyte/vascular plant communities on Marion Island, bryophyte production is suppressed during summer, when vascular plants grow most actively (Smith 1987a). Bryomass, bryophyte productivity, and bryophyte nutrient content in these communities are therefore highest during winter - a trend particularly noticable in the bryophyte understory of mire grasslands (Fig. 5.1), but also in *Acaena magellanica* communities, where the moss (*Brachythecium rutabulum*) understory "flushes" in winter after the deciduous *A. magellanica* has shed all its leaves (Smith 1985; personal observation). During winter, *E. similis* adults in the latter communities rely primarily on *B. rutabulum* for food.

5.4 Respiration

5.4.1 Methodology

Adult *E. marioni* were collected in the field, mostly on *B. densifolium* in mire grassland communities, during an early spring (September/October) visit to Marion Island in 1989. At this time of year, few *E. similis* adults can be found, and respiration studies were accordingly carried out on *E. marioni* only. The beetles were taken to the laboratory on the island, where they were provided with food and acclimatized for 48 hours at the desired temperature. Males and females were lumped. Oxygen consumption of adult beetles was determined at constant 5, 10, 15 and 20 °C, using an Oxygen analyzer and the same methods described in section 4.4.1. Individual live mass were determined on a Sautter Microbalance accurate to 0.5 mg. Respiration rates (ul O_2 individual^{-1} hr^{-1}) were converted to metabolic rates (ul O_2 g live mass^{-1} hr^{-1}) using the live mass obtained immediately prior to respirometry, since the difference in live mass before and after respirometry was negligible on the scale of resolution offered by the microbalance used.

5.4.2 Results

Effect of live mass on oxygen uptake

Mean live mass, and the respiration and metabolic rates at 5, 10, 15 and 20 °C, of adult *E. marioni*, are given in Table 5.6.

Table 5.6. Mean (± SD) metabolic rates: ul O_2 g^{-1} hr^{-1} (M), respiration rates: ul O_2 ind^{-1} hr^{-1} (R), live mass: mg (W) and number of replicates (n) for *Ectemnorhinus* adults at 5, 10, 15 and 20 °C.

	5°C	10°C	15°C	20°C
M	533.81 ± 126.68	755.05 ± 138.09	705.47 ± 157.07	876.95 ± 144.39
R	4.51 ± 1.19	5.95 ± 0.67	5.64 ± 1.35	7.02 ± 1.16
W	8.50 ± 2.10	8.10 ± 1.60	8.20 ± 2.30	7.30 ± 1.40
n	16	9	17	14

Double $\log_{10}$ plots of the data for individual respiration rate (ul O_2 ind^{-1} hr^{-1}) on live mass revealed no significant differences in the relation between the two variables at 5, 10 15 or 20 °C. Regression equations relating the two variables were calculated for each temperature (Table 5.7). Both the correlation coefficients and the coefficients of variation (r^2) were low, indicating that live mass has a minor influence on individual respiration rate. This was particularly the case at 10 °C, where the fitted respiration - mass regression accounts for only 8% of the variation (Table 5.7).

Table 5.7 Linear regression equations of $\log_{10}$ respiration rate on $\log_{10}$ live mass of *E. marioni* adults at 5, 10, 15 and 20 °C.

Temperature	n	a	b ± SEM	r	r^2
5	15	1.839	0.578 ± 0.268	0.499	0.249
10	8	1.190	0.199 ± 0.244	0.295	0.087
15	16	1.891	0.549 ± 0.216	0.549	0.301
20	13	1.856	0.474 ± 0.209	0.548	0.299

Regression equations relating metabolic rate (ul O_2 g^{-1} hr^{-1}) to live mass at 5, 10, 15 and 20 °C are given in Table 5.8.

Table 5.8 Linear regression equations of $\log_{10}$ metabolic rate on $\log_{10}$ live mass of *E. marioni* adults at 5, 10, 15 and 20 °C.

Temperature	n	a	b ± SEM	r	r^2
5	15	69.024	-0.422 ± 0.268	-0.387	0.150
10	8	15.488	-0.801 ± 0.244	-0.779	0.607
15	16	77.721	-0.451 ± 0.216	-0.475	0.225
20	13	8,966.233	0.474 ± 0.209	0.548	0.230

Metabolic rate generally appears to be even less affected by mass variations than is respiration rate (Table 5.8), with the exception of the results obtained at 10 °C, where a good correlation existed between live mass and metabolism and 60 % of the variation was explained by the fitted regression. The positive mass exponent (b) for *E. marioni* adults at 20 °C (Table 5.8) is difficult to explain. If it is not an artefact of experimental design or technique, it may demonstrate a high-temperature stress effect.

Effect of temperature on oxygen uptake

Mean respiration and metabolic rates of *E. marioni* adults are plotted against temperature in Fig. 5.2. Both individual and mass-specific oxygen consumption increase with an increase in temperature from 5 to 10, and from 15 to 20 °C, but both show a depression at 15 °C relative to 10 °C. However, the difference between rates at 10 and 15 °C is not statistically significant (Mann-Whitney U-test). This indicates that the optimum temperature for metabolic processes in *E. similis* adults lies somewhere between these two temperatures, since there is "complete compensation" (*sensu* Schmidt-Nielsen 1979) for a temperature increase within this range.

The data showing the effect of temperature on the metabolic rate of *E. marioni* adults are presented as a Arrhenius plot in Fig. 5.3. The fitted regression line, for convenience, is the one of $\log_{10}M$ against $1/T^{\circ}K \times 10^3$. The corresponding regression equations (derived on a natural log basis) are given in Table 5.9, where they are compared with those pertaining to the temperature-related metabolism of three other sub-Antarctic Coleoptera species (after Block (1981)).

Multiplying the coefficient b (Table 5.8) by the gas constant (1.98 cal $mol^{-1}K^{-1}$) provided a value for the activation energy of *E. marioni* adults. Q_{10} values were then calculated for the temperature range T_1 - T_2 (K) from the equation $\log_{10}Q_{10} = 2.187\ u/T_1.T_2$ (Precht *et al.* 1973). Q_{10} values were also determined from mean metabolic rates, using the equation $\log Q_{10} = (\log R_2 - \log R_1) \times 10/T_2 - T_1$ (Schmidt-Nielsen 1979).

The mean live mass, activation energies, and Q_{10} values over the temperature range 5 - 20 °C, of the adults of *E. marioni* and three other sub-Antarctic Coleoptera species (Block 1981) are compared in Table 5.10.

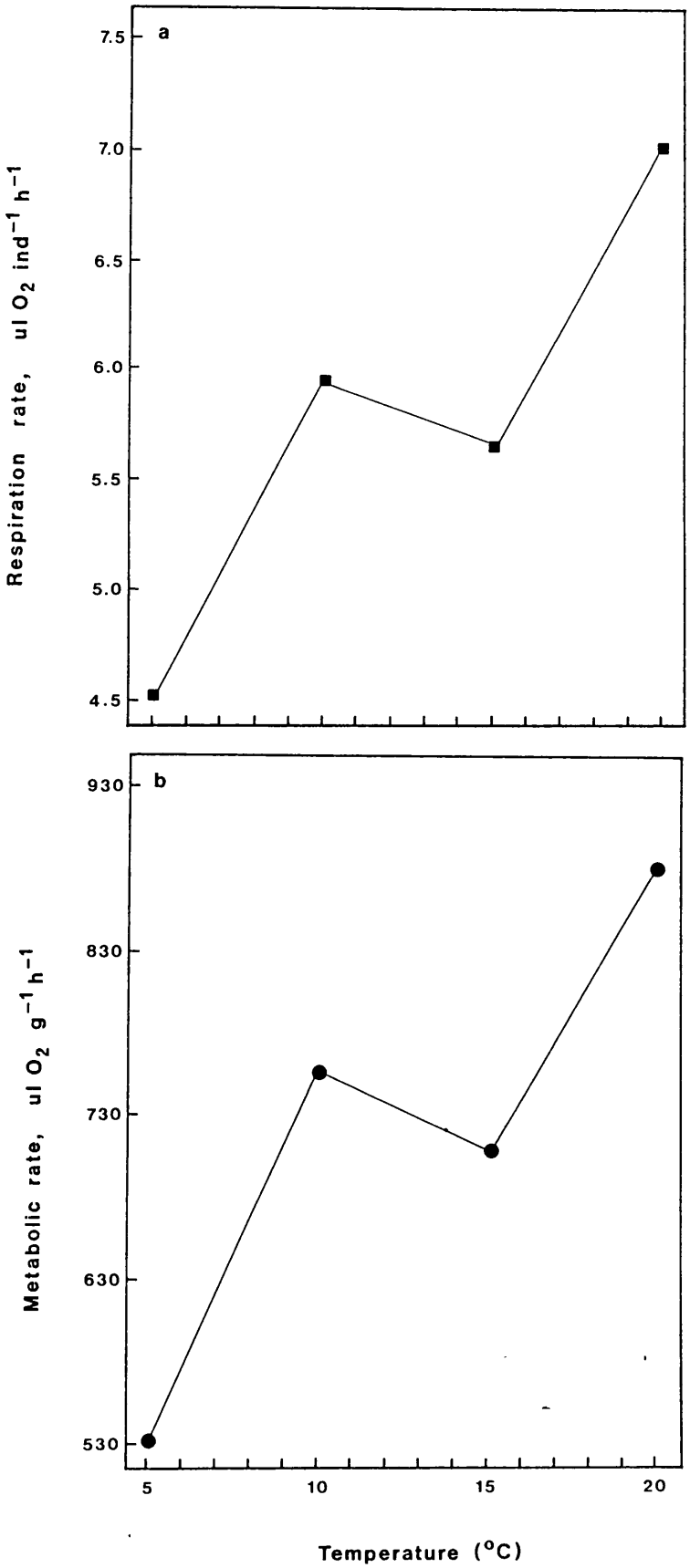

Figure 5.2 Relation of mean oxygen uptake (■) and mean metabolic rate (●) to temperature in adult *Ectemnorhinus*.

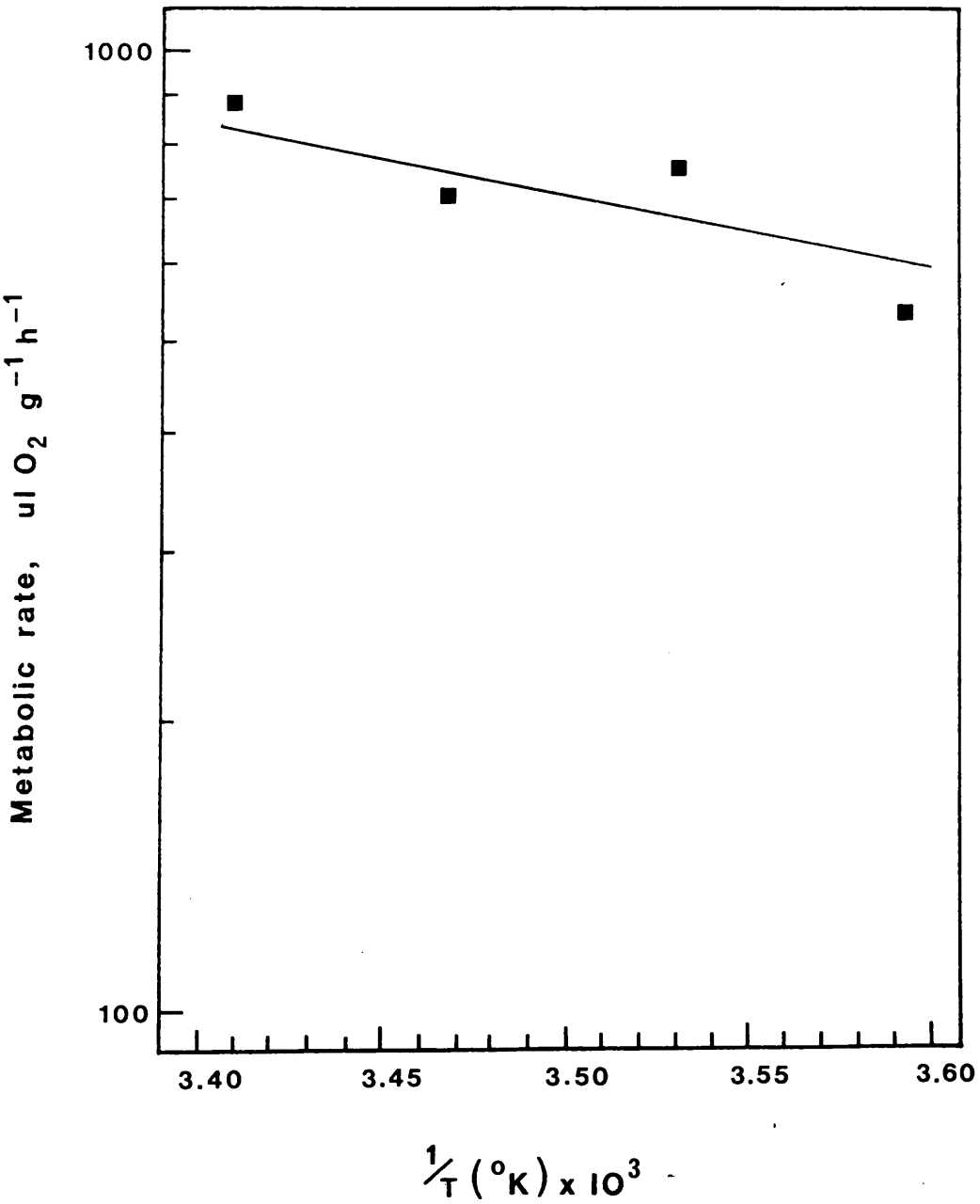

Figure 5.3 Arrhenius plot of metabolic rate (M) on temperature (T) for *Ectemnorhinus marioni* adults on Marion Island. The fitted regression line is shown of $\log_e M = 2.429 \times 10^6 . e^{-2.325 \times 10 / T}$

Table 5.9 Linear regression equations of $\log_e$ metabolic rate on $1/T \times 10^3$ (K) for Arrhenius plots of *Ectemnorhinus* adults (this study), and of the adults of three other sub-Antarctic Coleoptera species of comparable size and mass (after Block (1981)). n : number of observations, r^2 : coefficient of determination, a and b : constants in the equation $M = a.e^{b \times 10 / T}$ where M : metabolic rate (ul O_2/g/hr) and T : temperature (K).

Species	n	a	b	r	r^2
Ectemnorhinus marioni (Curculionidae)	6	2.429×10^6	-2.325	-0.883	0.779
Hydromedion sparsutum (Perimylopidae)	9	8.919×10^8	-4.372	-0.754	0.568
Perimylops antarcticus (Perimylopidae)	7	5.138×10^6	-2.901	-0.498	0.248
Merizodus soledadinus (Carabidae)	3	8.241×10^{11}	-6.275	-0.769	0.591

Table 5.10 Mean adult live mass (males and females combined), activation energies, and Q_{10} values (derived from mean metabolic rates) for the ranges 5-10, 10-15, 15-20 and 5-20 °C for adults of *Ectemnorhinus* and three other sub-Antarctic Coleoptera species (the latter after Block (1981)). Number of determinations (n) in parentheses. The Q_{10} values given in parentheses for the range 5-20 °C are those determined from the equation given by Precht *et al.* (1973). n.d: not determined. See text for explanation.

Species	Live mass (mg)	Activation energy (kcal mol^{-1})	Q_{10} 5-10	10-15	15-20	5-20	
E. marioni	8.03 ± 0.34 (56)	4.603	2.0	0.8	1.5	1.4	(1.2)
H. sparsutum	19.54 ± 0.74 (148)	8.658	-	-	-	1.7	(1.7)
P. antarcticus	12.98 ± 0.47 (104)	5.745	-	-	-	1.4	(1.1)
M. soledadinus	9.20 ± 1.34 (6)	12.426	-	-	-	2.2	(n.d)

5.4.3 Discussion

The study of the oxygen consumption of adult *E. marioni*, of which the results are reported above, suffers several defects: firstly, adults of a holometabolous species cannot be studied in isolation from their immature stages, which in this instance had to be done because of various constraints. Secondly, although *E. similis* and *E. marioni* are extremely closely related, the results obtained with *E. marioni* may not be applicable to *E. similis*, especially in the light of the size difference between the two species (the quote from Bonner (1965), which heads this chapter, is pertinent). Thirdly, the possible effect(s) of sex-related differences in metabolism was not taken into account. However, certain trends are apparent, and in the light of the similarities of these trends to those which emerged from comparable studies on other sub-Antarctic Coleoptera, they possibly reflect features both real and of wider application. The salient features of the respiratory metabolism of *E. marioni* adults appear to be the following:

1. The metabolic rate of *E. marioni* adults (Table 5.4) is higher than that of similar-sized Coleoptera from South Georgia (Block 1981), but lower than that of similar-sized temperate beetles, which typically have metabolic rates in excess of 1 000 ul g^{-1} hr^{-1} (Keister and Buck 1964).

2. The activation energy and Q_{10} values of *E. marioni* adults are comparable to those of the three Coleoptera species studied by Block (1981) on South Georgia. It is interesting, and probably not merely coincidental, that the activation energy and $Q_{10(5\text{-}20\ C)}$ of *E. marioni* is identical to that of the perimylopid beetle *Perimylopus antarcticus*, which is of similar size and has the same life-style (Table 5.9).

3. *E. marioni* exhibits "complete compensation" (*sensu* Schmidt-Nielsen (1979)) for an increase in temperature from 10 - 15 °C, which is within the range of its microhabitat temperature (Table 3.2). Hazel and Prosser (1974) distinguish between three types of temperature compensation: firstly, "instantaneous compensation," as a response to direct temperature effects; secondly, "acclimation compensation," and thirdly, "evolutionary compensation" (which can be equated with adaptation). Biochemical evidence indicates a correlation between habitat temperature and activation energy for particular enzyme systems (Young 1979). This provides a clue to the mechanism of evolutionary compensation, since the low activation energy of *E. marioni* adults (and of other sub-Antarctic arthropods) indicates that they have evolved enzymes which confer lower activation energies on the reactions they mediate.

4. Q_{10} values are closely related to activation energies and vary according to habitat temperature; Rao and Bullock (1954) found Q_{10} values to be lower in animals inhabiting low temperature enviroments. This is certainly the case with *E. marioni*, and provides further evidence that this species shows "evolutionary compensation" for the temperature range to which it is exposed in its microhabitat (or that it is "low-temperature adapted.").

5.5 Energy flow

E. similis:

If it is assumed that *E. similis* adults require daily food intake for maintenance and for the production of reproductive biomass, a single adult in an *A. selago* community would, during a maximum adult duration of one year, consume a total of 1.186 g (dry mass) or 24.147 kJ in *A. selago* leaves, of which it would assimilate 65% or 15.696 kJ (deduced from Tables 5.4 and 5.5). The annual net primary production of *A. selago* leaves

is between 100 and 200 g m^{-2} y^{-1} (2 036 - 4 072 kJ m^{-2} y^{-1}; Table 5.4) in all plant communities of which it forms a component (Smith 1985). Annual densities of *E. similis* adults in *A. selago* communities are not known, but 20 adults m^{-2} would be a realistic estimate in the light of the densities determined for *E. marioni* adults in mire grasslands (Table 5.10). However, because the adults emerge seasonally to feed on new *A. selago* growth, and because they feed also on *A. selago* flowers and on various other angiosperms, their total contribution to energy flow in *A. selago* communities can be expected to be very small. The detritivorous *E. similis* larvae would presumably process much larger quantities of food than the adults, although their role in energy flow is likely also to be minimal (see Chapter 6, though, for discussion of the important role of detritivores at Marion Island).

E. marioni:

During a sampling programme to determine the monthly biomass of *Pringleophaga marioni* larvae in different plant communities at Marion Island, core samples were taken at random along a transect on the coastal plain near the weather station (see section 6.2.1 for methodology). All *E. marioni* adults obtained from core samples that were taken in mire grasslands were removed and counted. Adult densities in *Agrostis magellanica/Blepharidophyllum densifolium* mire communities were extrapolated from these counts, and expressed as number m^{-2} (Table 5.11). Based on the mean live mass (Table 5.3) and food consumption rate (Table 5.5) of *P. marioni* adults, the energy content of *E. marioni* adults and their food (Table 5.4), and the AD of *B. densifolium* fronds (Table 5.5), an annual energy budget for a population of *E. marioni* adults in a *A. magellanica/B. densifolium* mire was constructed (Table 5.10).

Table 5.11 Annual energy flow through a population of *E. marioni* adults in a *A. magellanica/B. densifolium* mire. See text for explanation.

Month	*E. marioni* adults		I		A
	no. m^{-2}	g (live wt) m^{-2}	g (dry) m^{-2}	kJ m^{-2}	kJ m^{-2}
J	38	0.295	0.354	5.954	2.322
F	38	0.295	0.354	5.954	2.322
M	15	0.117	0.140	2.355	0.919
A	20	0.155	0.186	3.129	1.220
M	6	0.047	0.056	0.942	0.367
J	9	0.070	0.084	1.413	0.551
J	9	0.070	0.084	1.413	0.551
A	12	0.093	0.112	1.884	0.735
S	15	0.117	0.140	2.355	0.919
O	9	0.070	0.084	1.413	0.551
N	20	0.155	0.186	3.129	1.220
D	41	0.319	0.383	6.442	2.512
Year			2.163	36.383	14.189

Annual shoot production of *B. densifolium* in mire grassland was estimated at 326 g m^{-2} dry mass (Russel 1985), which appears excessive when compared to Smith's (1987d) estimate of 307 g m^{-2} total annual bryophyte production in an *A. magellanica* mire. Using Smith's (1987d) estimate, total annual production of bryophytes in *A. magellanica* mire grassland amounts to 5 716 kJ m^{-2} (energy content of live *B. densifolium* shoots is 16.82 kJ g^{-1}; Table 5.4). Of this, *E. marioni* adults annually consume and assimilate approximately 0.7% and 0.3%, respectively (Table 5.11). However, annual consumption and assimilation of *B. densifolium* production by *E. marioni* larvae is probably considerably higher, given the relatively high biomass of these larvae (up to 0.8 g m^{-2} (dry mass) in late winter; Chown and Scholtz (1989b)).

5.6 Evolutionary perspectives

In view of the evolutionary propinquity of the two *Ectemnorhinus* species, and the recency of their divergence, this evolutionary perspective will focus both on the possible *causes* of radiation in the genus, and on the *effects* of the radiation in both an organismic and an ecological context.

Since *E. marioni* and *E. similis* adults are relatively long-lived (see 5.2) and iteroparous, mating and reproducing throughout their lives, they require an adequate, constant source of food energy throughout the year. Bryophytes in the epilithic biotope are largely aseasonal in growth and nutrient status (Russell 1985), and in spite of their "reverse" trend in vascular plant communities, still represent a more continuous food resource than vascular plants, both in space and in time. This must particularly have been the case before the advent of vascular plants during the early tenure of *Ectemnorhinus* on Marion Island.

Although Prins' (1981) hypothesis may explain moss-feeding in the context of present ecological interactions, little attention has been given to what could be regarded as the "historical necessity" of moss-feeding. Moss-feeding occurs in cold-temperate areas where cryptogams presently constitute an important fraction of the vegetation, but where, during the last glaciations, they may have constituted the dominant or at times the only vegetation. Unlike northern hemisphere continental species, the insects of the SIP islands were prevented by ocean barriers from tracking the climate latitudinally (see Coope 1979), so that cryptogam feeding was presumably the only alternative to extinction (Chown and Scholtz 1989c). Geological and palynological evidence indicates that temperatures at Marion Island dropped 3-4 °C during the last glacial maximum, 16 000 - 18 000 years ago (Schalke and Van Zinderen Bakker 1971; Hall 1978). More recent palynological evidence (Scott 1985) indicates that pure stands of *Azorella* dominated vegetation on the island from about 16 000 to 14 500 B.P., after which temperatures gradually rose and *Acaena* and some pteridophytes evidently occurred. The final important recorded climatic change was c. 12 500 B.P, when mire vegetation developed.

The structural and physiological attributes that pre-adapted *A. selago* for colonization of Marion Island (e.g. the cushion growth form, with its interior microclimate and detritus accumulation) and those attributes that are consequences of its adaptation (high energy and nitrogen content) predisposed it for herbivory. (Furanocoumarins occur almost universally in the Apiaceae, but lack toxicity and may even stimulate feeding or enhance growth in insects that feed exclusively on Apiaciae (Berenbaum 1981). Nothing is known of the presence or absence of furanocoumarins in *A. selago*.) Various other vascular plants grow epiphytically on *A. selago* cushions, often at high altitudes, above their "normal" range or in areas where the substrate between cushions is unfavourable (Huntley 1972b); *A. selago* so mediates plant succession both spatially (altitudinally) and temporally.

The following least-assumption sequence of events is proposed as a mechanism for radiation in *Ectemnorhinus*, based on the results of this study and the corroborative evidence recounted above:

1. Widespread post-glacial colonization of Marion Island by *A. selago*.
2. Colonization of *A. selago* cushions by host bryophytes of ancestral *Ectemnorhinus*.
3. Oviposition on host bryophytes and on *A. selago*.
4. Favourable larval microhabitat in *A. selago* cushion interiors allows incorporation of *A. selago* detritus in the larval diet.
5. Dietary divergence in *Ectemnorhinus* larval populations.
6. Low nutritional diet selects for larger body size in *A. selago* larval populations (larger gut for high-volume consumption).
7. Resultant larger adult size in *A. selago* populations demands more (or better) nutrition for maintenance and reproduction.
8. Continuing temperature amelioration allows economical exploitation of high-nutrient *A. selago* leaves and reproductive organs; selection for synchronization of *Ectemnorhinus* life cycle with seasonal growth and reproduction of host.
9. Colonization of coastal lowlands by other vascular plants; mediated by *A. selago*.
10. Parallel colonization of increasingly vegetated coastal lowlands by *A. selago*-feeding *Ectemnorhinus* populations.
11. Recent (last 10 000 years) dietary niche expansion of *A. selago*-feeding *Ectemnorhinus* populations, to include other vascular plants (*Acaena*).

Shifts in preference for particular host plants can be very rapid (e.g. Fox and Morrow (1981), see also Bush (1975) on the tephritid fly *Rhagoletis pomonella* which developed "sibling species" on introduced plants within a few generations). If *Acaena magellanica* is indeed a "novel" food for *E. similis*, which appears likely, its poor performance on this plant can be ascribed to the documented phenomenon of insects utilizing novel food plants less efficiently than those to which they have been exposed for a long time (Schoonhoven and Meerman 1978). Poor performance in this case, however, may be traded off against smaller body size in *E. similis* from *Acaena magellanica* communities (Chown and Scholtz 1989b). *A. magellanica* flowers are probably utilized more efficiently than leaves, and are indeed fed on throughout the period when both young leaves and flowers are available (personal observation).

The synchronization of the life cycle of *E. similis* with the seasonal growth, reproduction and nutrient status of its angiosperm hosts (Chown and Scholtz 1989b), reinforced by a temperature regime that allows efficient utilization of energy and nutrients from flowers and fruits precisely when they occur, represents a likely mechanism for adaptive radiation in an ancestral population of bryophyte- and angiosperm-feeding *Ectemnorhinus* on Marion Island. Such a scenario (Chown, in press) fulfils the requirements of the recent sympatric speciation models proposed by Rice (1984, 1985).

Whatever the causes of radiation in *Ectemnorhinus* on Marion Island may be, the most important effect is the difference in body size between the two constituent species, with all its ecophysiological ramifications. On the organismic level, a difference in body size causes differences in all physiological processes that scale allometrically with body mass. On the ecological level, ecophysiological differences translate into differences in the quantity of energy (see section 5.5) and nutrients turned over by each species.

CHAPTER 6: *Pringleophaga marioni* Viette (Lepidoptera: Tineidae)

"Die Energieeinsparung durch Reduktion weitgehend funktionslos gewordener Körperanhänge reicht alleine nicht aus, um die damit verbundenen Nachteile zu überkompensieren. Das Ausweichen auf die extremen Jahreszeiten mit verringertem Feinddruck war wohl die wesentlichere Komponente in der Evolution dieser Anpassung."

Dierl and Reichholf (1977)

6.1 Introduction

P. marioni is one of three species in the genus *Pringleophaga* which, like *Embryonopsis*, is confined to the SIP islands, with no obvious phylogenetic relationships outside the sub-Antarctic. Crafford *et al.* (1986) considered these two genera to be of African/Antarctic Eocene origin, with speciation in *Pringleophaga* having occurred on various islands subsequently. *P. kerguelensis* occurs on Îles Kerguelen and on Îles Crozet, and according to Vari (1971) also on Prince Edward Island but not on Marion Island. *P. crozetensis*, confined to Îles Crozet, is very distinct from *P. kerguelensis* (Chauvin and Vernon 1981). Brown (1964) described a *P. heardensis* from Heard Island, but was subsequently shown to have merely redescribed *Embryonopsis halticella* (Common 1970). *Pringleophaga* does not occur on Heard Island. Vari (1971) states that "In most characters [*P. kerguelensis*] is exactly the same as *P. marioni* except that it is much larger. The [wing] venation is the only distinct character on which the species can be separated." Furthermore, the genitalia of the two species are extremely similar. Viette (1948), in his original description of *P. marioni*, mentioned only minor differences in the male genitalia and suggested that *P. marioni* be considered a subspecies of *P. kerguelensis*. Larvae of the two species are impossible to distinguish whereas *P. crozetensis* larvae are again distinct from either (Chauvin and Vernon 1981; pers. obs.). The taxonomic position of the genus in the Prince Edward archipelago therefore remains uncertain. It does appear strange that *P. kerguelensis* should occur on Îles Kerguelen and, 1 500 km distant, on Prince Edward Island, but not on Marion Island 20 km further.

P. kerguelensis is extremely variable in size at Îles Kerguelen (Chauvin and Vernon 1981), size being correlated with larval nutrition, which differs between larvae from different habitats. *P. marioni* at Marion Island may also be genotypically variable (see Chapter 8), with adults collected within the same habitat often exhibiting marked size variation (pers. obs.). The differences in the wing venation of the two "species" (Vari 1971) may be an allometric effect of increased body size within the same species; it certainly does not appear to be of sufficient significance for the designation of two species. Crafford (in press) showed that feral house mice prey size-selectively on *P. marioni* larvae at Marion Island, and Crafford and Scholtz 1987a) postulated that mice may even have caused the demise of *P. kerguelensis* on this island. In the light of the slow growth and reproduction of *P. marioni* populations, and the heavy predation by mice (Rowe-Rowe *et al.* 1989), such a scenario is not far-fetched. It is conceivable, at least, that mice may cause directional selection in *Pringleophaga* on Marion Island, and that the absence of size-extremes at this island may be an artefact of mouse predation. In spite of the present uncertainty about the exact taxonomic status of *Pringleophaga* on Marion Island, individuals used for experiments during this study were all regarded as *P. marioni*.

The body size of adult moths is sex-linked, females being larger than males. Male forewing length varies from about 4.5 - 6.5 mm and that of the females from about 5.5 - 7.0 mm; total body length varies between 7 - 12 mm and 10-20 mm, respectively. Larvae are heavily sclerotized, with isolated long setae evenly distributed over the body. Mature larvae grow up to 35 mm in length and may attain a live mass of up to 500 mg. The pupae are typically lepidopteran and may be formed in a cocoon, or they may lie naked in a cell. Habitus drawings of the different life stages of *P. marioni* are shown in Appendix A.

6.2 Life history and phenology

6.2.1. Methodology

Life history

P. marioni larvae live for several years, which precludes their successful rearing in the laboratory. To get an indication of the number of instars indirectly, through morphometry, the head capsule of each larva from the monthly "harvest" of larvae in an *Agrostis magellanica* mire community (see below) was measured, using an ocular micrometer. A histogram of head capsule measurements of larvae from this population was drawn up, to see if distinct peaks separated by discrete and regular increments could be discerned.

Sixty larvae across the entire size range were collected in the field and kept in petri dishes containing litter; 20 each were maintained, respectively, under ambient conditions outside the laboratory, at constant 5 ^{o}C, and at constant 10 ^{0}C in incubators. These larvae were weighed, and the litter changed, every week. Each time, the old litter was examined for signs of exuviae; if intact head capsules were found, both these and the "new" head capsules of the live larvae were measured. Fresh exuviae were removed, weighed and dried to determine what percentage of body mass they represented.

Pupae obtained from the colonies referred to above were monitored to determine pupal duration. Adults hatched from these, as well as from pupae collected in the field, were maintained in the laboratory to determine adult duration and reproductive behaviour. In addition, 11 females hatched from laboratory colonies were dissected upon eclosion, and the eggs counted and weighed; live prepupal, pupal and adult mass of these females were also determined.

Larvae collected from a wide range of habitats in the field were dissected in the laboratory, and their gut contents analysed to determine larval diet. Life history data obtained in the laboratory were supplemented by continuous field observations, during the entire period spent on field work at Marion Island.

Phenology

A transect of 100 m X 10 m, stretching inland from within the spray zone on the coast, was laid out in the Nellie Humps area near the meteorological base on Marion Island. The transect included the three plant complexes previously known (Burger 1978a) to sustain the largest numbers of soil invertebrates, viz. the saltspray, biotic and mire complexes (see 2.3.1). The percentage surface area of the transect occupied by each of the three plant complexes was approximately 10%, 30% and 60% respectively, which is similar to the vegetation composition of the coastal plain (Smith 1978a). The transect was divided into ten 10m X 10m plots. Ten samples were taken at random from each plot with a core sampler (a soil auger) 80 mm in diameter, which gave an individual sample surface area of 250 cm^2. The samples were taken to a depth of 100 mm, since most *P. marioni* larvae were found to occur in the top 50 mm of soil and litter. Cores were

sorted by hand in the laboratory. The *P. marioni* larvae (and all other macro-invertebrates) were removed, counted, dried to constant mass (four days at 60 °C) and weighed dry. Larval biomass in each plant complex was extrapolated and expressed as g m^{-2}. The head capsule of each *P. marioni* larva collected from a *A. magellanica* mire community in the "mire complex" portion of the transect, was first measured under a stereo microscope, using an ocular micrometer, to determine the size-class composition of each larval "harvest" from this community. Sampling was repeated at monthly intervals, for one year (May 1983 - April 1984).

During two short, five day visits to Prince Edward Island (May 1983 and April 1984), the density and biomass of *Pringleophaga* larvae in corresponding vegetation types were determined, to compare with those at Marion Island. *Agrostis magellanica* mire and biotically influenced *P. cookii* communities were sampled at sites both on the eastern (Cave Bay) and western (Kent Crater) sides of Prince Edward Island (see Fig. 1). Within each community, a large, reasonably pure stand of the dominant vegetation was selected. Core samples were taken at one metre intervals along a 50 m transect line of random origin and direction within each stand, using the same soil auger and similar techniques as on Marion Island. Sampling was carried out at the same site during each visit. *Pringleophaga* larvae were removed from the cores, counted, and dried for four days at 60 °C. Results from the eastern and western sites were pooled, since numbers did not appear to be significantly different at the two sites. Larval biomass was calculated and expressed as g m^{-2}, and the results compared with those obtained on Marion Island.

6.2.2 Results and discussion

Life history

P. marioni is ubiquitous at Marion Island, occurring in virtually every habitat and at elevations of up to 800 m. On the coastal lowland, larvae occur primarily in *P. cookii* communities within the biotic complex, and are particularly abundant in albatross (*Diomedea exulans*) and giant petrel (*Macronectes* spp.) nests, which are constructed chiefly out of pÎles of dead *P. cookii* leaves. The larvae are primarily detritivores, but are extremely polyphagous. They include virtually the entire range of vascular plants and bryophytes - seemingly everything in their immediate surroundings - in their diet, both as detritus and, occasionally, as live leaf material. After *P. cookii*, however, *A. selago* detritus is a major dietary item, especially in fjaeldmark areas where the larvae are confined to the interiors of *A. selago* cushions. In the laboratory, larvae kept on damp filter paper in petri dishes survived for several weeks on a diet of damp filter paper. Larvae in laboratory colonies were occasionally observed to eat both each other and other invertebrates (chiefly sedentary types such as earthworms and weevil larvae and pupae). Such occasional and facultative carnivory was also observed by French and Smith (1983), but it is doubtful if it occurs regularly outside the confines of polytops and petri dishes. At high altitudes (> 500 m) on both Marion and Prince Edward Islands, *P. marioni* larvae were often found in areas where no visible vegetation occurs, such as against the bare scree slopes of volcanic cones. Here they were found to subsist on detritus and a scraggly *Brachythecium* species (Bryophyta), a few centimetres under the loose scoria. Adults were occasionally found on large expanses of snow in bare fjaeldmark areas at high elevation. What has been confirmed beyond doubt is that *Pringleophaga* at Marion Island is in no way associated with *Pringlea antiscorbutica*; the nomenclature reflects a flight of fancy by Enderlein (1905). Chauvin and Vernon (1981) recorded a similar wide habitat range for *P. kerguelensis* at Îles Kerguelen and Îles Crozet, and for *P. crozetensis* at Îles Crozet.

A histogram of the head capsule widths of 250 *P. marioni* larvae across the entire size range (Fig. 6.1) illustrated no clear breakdown into discrete classes, as did a similar histogram for *Embryonopsis halticella* (Fig. 4.1). It is unlikely, in retrospect, that an extremely long-lived and morphologically variable lepidopteran

such as *P. marioni* should conform to any of the "laws" or "ratios" of incremental growth formulated for more conventional (i.e. short-lived, temperate) species (Wigglesworth 1974). Using the smallest head capsule width measured (0.25 mm; Fig. 6.1) and adding increments of 1.4 X (Dyar's law) until a width commensurate with the largest head capsule measured (3.68 mm) is found, gives a hypothetical number of 8 instars (based on the number of increments). However, the number of instars, as well as developmental time, is likely to be extremely variable in *P. marioni* larvae.

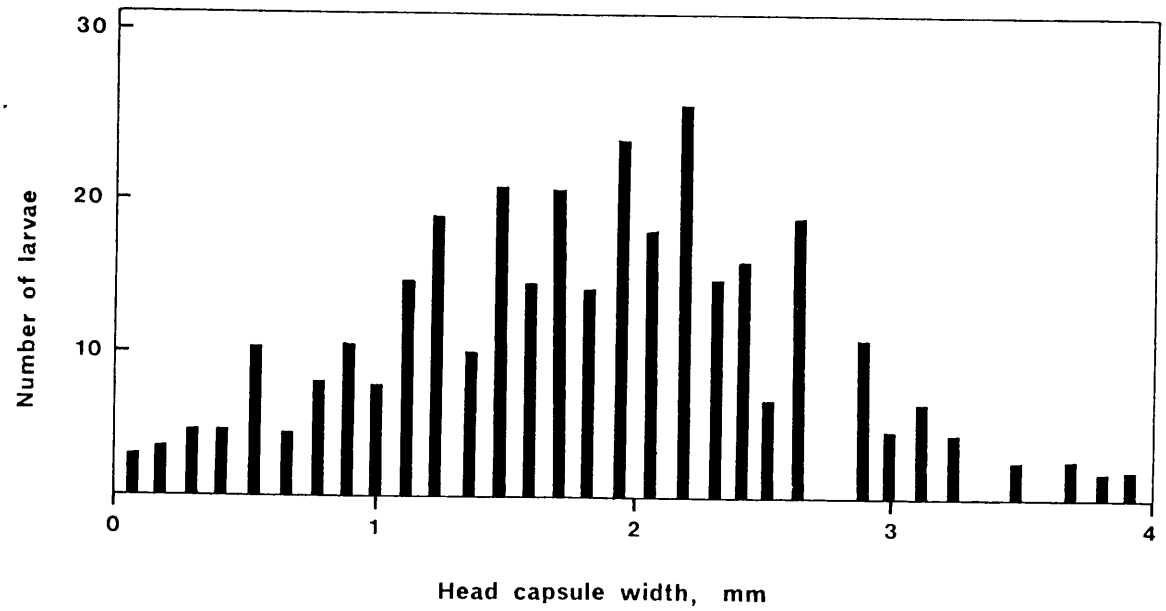

Figure 6.1. Frequency histogram of head capsule widths of *P. marioni* larvae from a Marion Island mire grassland.

Although larvae were maintained successfully in laboratory colonies for up to one year, and although adults were successfully reared from larvae collected in the field, the larval duration is still unknown. A similar-sized lepidopteran from the Arctic (*Gynaephora groenlandica*, Lymantriidae) was estimated to have a generation time of ten years (Ryan and Hergert 1977). H. V. Danks (pers. comm. to C. H. Scholtz) suggested that *Pringleophaga* spp. may have a developmental time of between five and ten years. Paulian (1953) merely stated that the larvae live "for several years."

Larvae maintained either under ambient conditions, or at constant 5 and 10 °C in the laboratory at Marion Island, moulted irregularly, and head capsule widths were frequently *smaller* after a moult than before, probably as a result of poor nutrition. Exuviae (cast integument and head capsule) weighed between 1.8 and 3.3% of the total dry body mass of the pre-moult larva (mean 2.5%; n = 24) for larvae accross the entire size range. Larvae were arbitrarily divided into five size classes (Table 6.1), chiefly in order to be able to determine larval food consumption and respiration for discrete groups. From the weekly mass determinations of these larvae, it was clear that the larvae conform at least in having relatively rapid exponential growth up to a certain size, which the larvae then maintain for an indefinite and prolonged period. It is thus the final or "mature" (i.e. maximum size) larval stage which is extended, rather than each of the instars.

A total of 20 adults was obtained from larvae collected in the field and reared through in the laboratory. Of these, nine were male and 11 female. Vari (1971) recorded a 5:1 male to female ratio in adults collected at Marion Island. However, females eclose gravid, with all eggs already ripe, and are rather sedentary. Males are active "walkers" and are consequently more conspicuous in the field, which would explain the anomalous sex ratio in field collections. Female prepupae and pupae were generally, but not always, larger and heavier than males, but pupal duration in the laboratory was similar for both sexes (52 - 67 days). Laboratory-reared adults copulated within two days after hatching. Within hours after copulation, females lay up to 203 relatively large (mean 1.1 x 0.7 mm; n = 60) eggs at random in plant litter in the laboratory, although in the field they were observed to use their long, telescopic ovipositors to lay eggs singly in the leaf axils of *A. selago*. Only one of the laboratory-reared females laid its entire egg load (203 eggs); others laid as few as 30 % of the eggs in the ovaries. Few females lived longer than a week in the laboratory (Table 6.1), but even in the field, dead and disintegrating females were observed with large retained egg loads. Presumably such eggs, if fertilized, will still hatch. The mean number of eggs per female was 173 (range 140 - 216, n = 11). Chauvin and Vernon (1981) recorded up to 180 and 220 eggs per female in *P. kerguelensis* and *P. crozetensis*, respectively. Total egg mass of newly hatched *P. marioni* females accounted for between 67 and 74% of total dry body mass (mean 68.53%; n = 11), which is similar to the figure of 67.36% for *E. halticella*.

Table 6.1 depicts the duration, where known, and mean live mass of different life stages of *P. marioni*. Adult live mass were determined upon eclosion.

Table 6.1. Mean live mass (mg) and duration (days) of the different life stages of *P. marioni*; size classes I - V are arbitrary divisions. n.d.: not determined. Estimated ranges given in brackets. See text for explanation.

Stage	n	Live mass (mg)		Duration (days)	
		Range	Means ± STD	Range	Means
Egg	60	0.42- 0.58	0.50 ± 0.01	n.d.	(30 - 50)
Larvae					
Size class I	12	10 - 30	n.d.	n.d.	
Size class II	16	30 - 50	n.d.	n.d.	
Size class III	9	50 - 100	n.d.	n.d.	
Size class IV	21	100 - 200	n.d.	n.d.	
Size class V	14	200 - 500	n.d.	n.d. Total: 1000+?	
Prepupa	20	287.35 - 511.60	409.47 ± 21.43	12 - 20	15
Pupa: female	11	113.70 - 176.70	151.30 ± 9.74	52 - 67	60
male	9	57.80 - 84.80	75.00 ± 4.23	54 - 65	59
Adult: female	11	81.10 - 102.40	93.46 ± 2.01	7 - 11	10
male	9	31.93 - 63.30	51.84 ± 6.49	12 - 18	15

Phenology

The mean monthly biomass (in g m^{-2}; all vegetation types pooled) of *P. marioni* larvae in the study site at Marion Island, is shown in Fig. 6.2. There is little seasonal variation in biomass (184 % coefficient of variation). Mean annual biomass is 0.93 g m^{-2}, or 9.3 kg ha^{-1}, which is higher than the 6.2 kg ha^{-1} obtained by Burger (1978a) in a sampling programme which also included fjaeldmark areas, in which *P. marioni* larvae are less abundant and aggregated chiefly in *A. selago* cushions. The larval biomass in each of the different plant complexes represented at the site sampled during this study, is shown in Fig. 6.3.

Although adults and pupae occur throughout the year at Marion Island, adults are more prevalent during summer and autumn (October - April). The peak in adult occurrence is preceded by the slight peak in larval biomass (Fig 6.2), which coincides with a preponderance of "large" larvae (Fig. 6.4). The size composition (based on head capsule width) of larvae harvested each month from an *A. magellanica* mire which was included in the transect, is shown in Fig. 6.4. Although Fig. 6.4 shows that larvae at all stages of development are present throughout the year, the clear seasonal trend in size class composition probably reflects the development of a single cohort, which formed the majority of the particular population sampled in the *A. magellanica* mire community. The majority of the larval population (or at least the majority of larval biomass) is always made up of a single, large size class (head capsule widths 2 - 3 mm; Fig. 6.4).

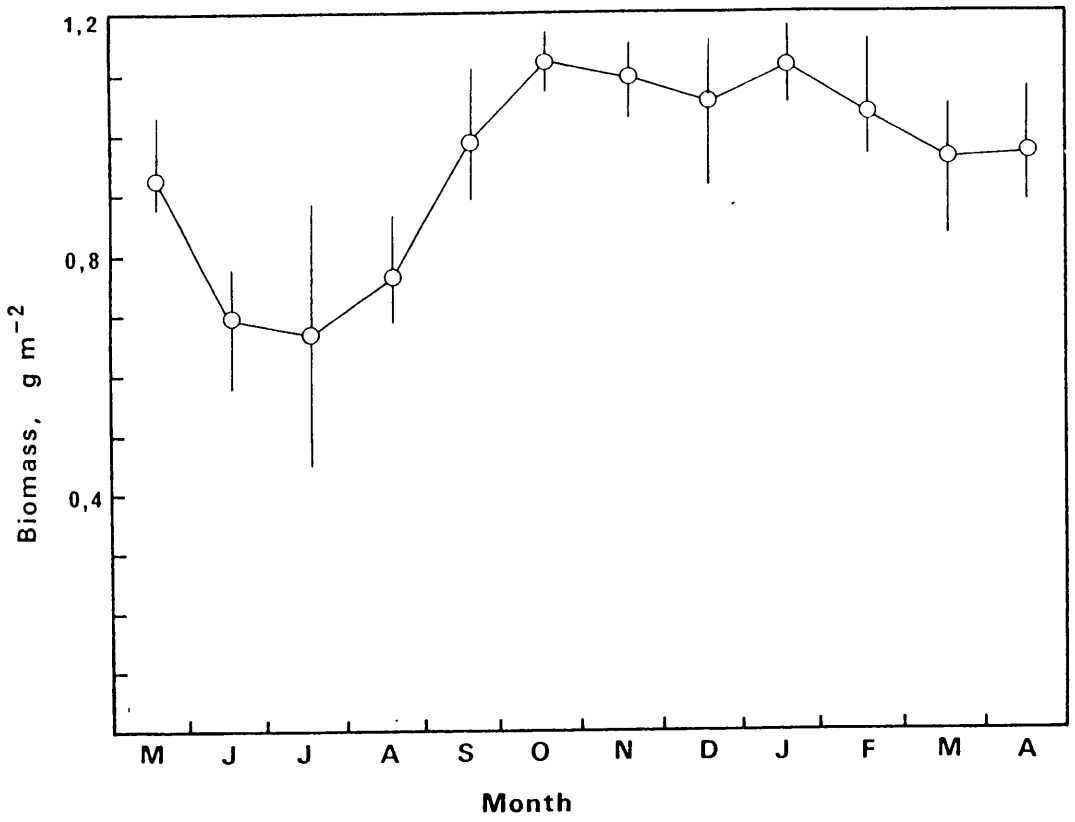

Figure 6.2. Mean monthly biomass of *P. marioni* larvae at the Marion Island study site (see text). Standard errors of means are shown.

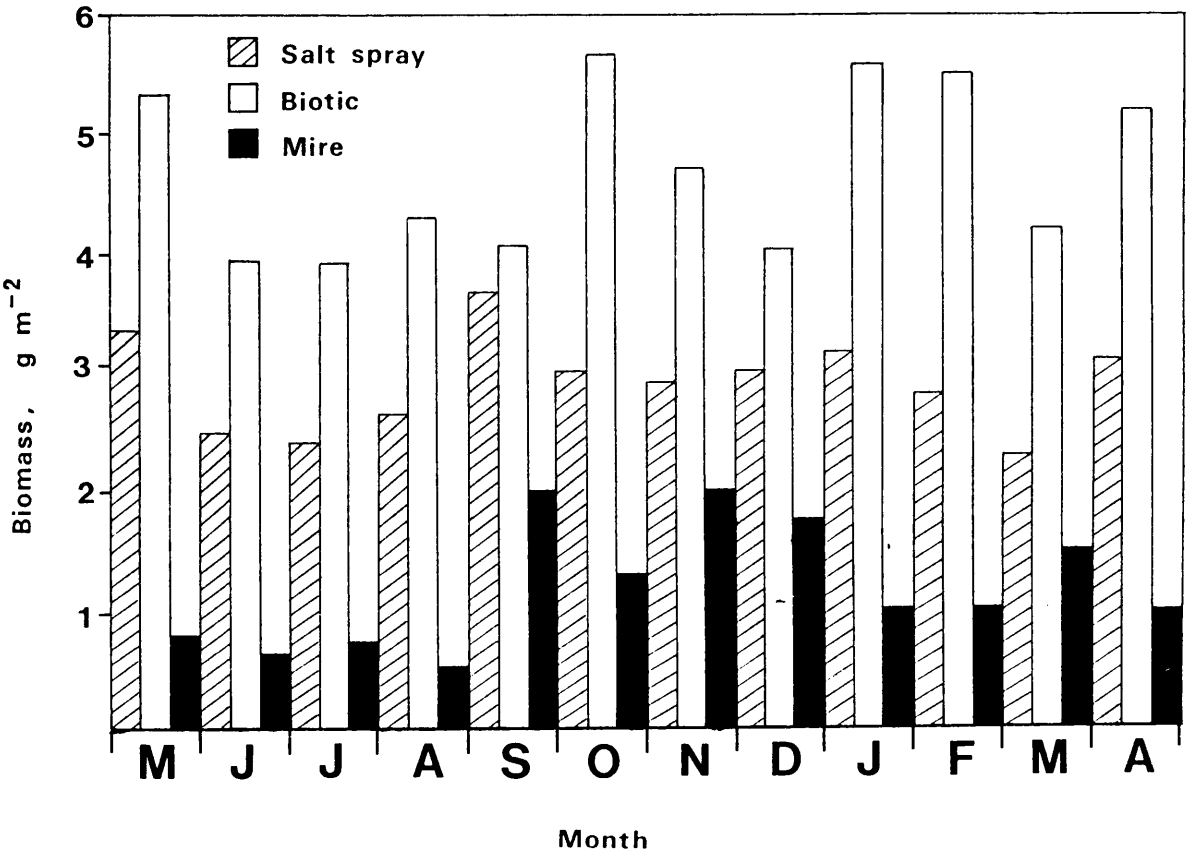

Figure 6.3. Mean monthly biomass of *P. marioni* larvae in each plant complex represented in the Marion Island study site.

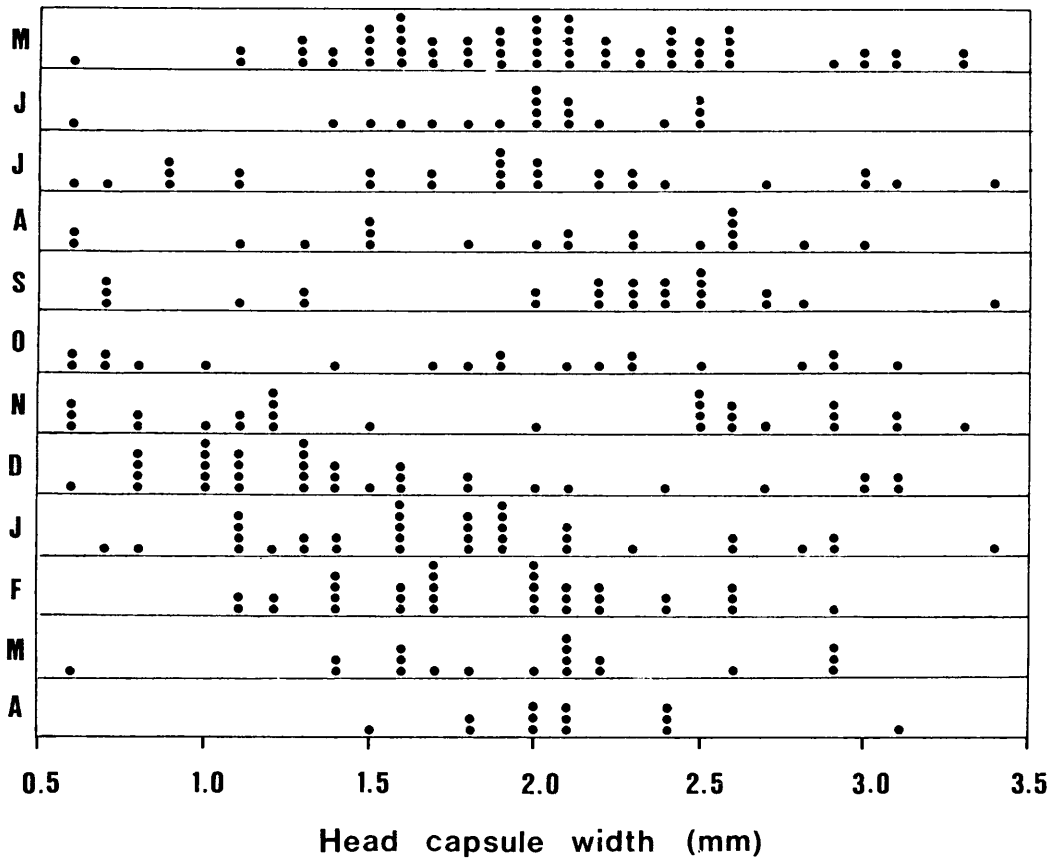

Figure 6.4. Monthly size-class composition of *P. marioni* larvae from an *A. magellanica* mire on Marion Island, based on head capsule widths. Each dot represents one individual.

The daily and yearly consumption of *P. marioni* larvae by feral house mice at Marion Island, was calculated by Rowe-Rowe *et al.* (1989) to be 65 g (dry mass) ha^{-1} day^{-1}, and 23.7 kg ha^{-1} yr^{-1}, respectively. This amounts to a daily removal by mice of 0.7 % of the standing crop of *P. marioni* larvae, and annual removal of approximately 2.5 times the mean annual larval standing crop. Crafford (in press) calculated the mean and range of sizes of larvae eaten by mice, from an analysis of the stomach contents of 50 mice trapped at random, throughout the year, in the same area where the *P. marioni* larval population was studied. The mice were found to be size-selective in their depredations of *P. marioni* larvae. In Fig. 6.5, the mean and range of the sizes of 88 *P. marioni* larvae obtained from the 50 mouse stomachs, are superimposed on the monthly size-class composition of larvae shown in Fig. 6.4.

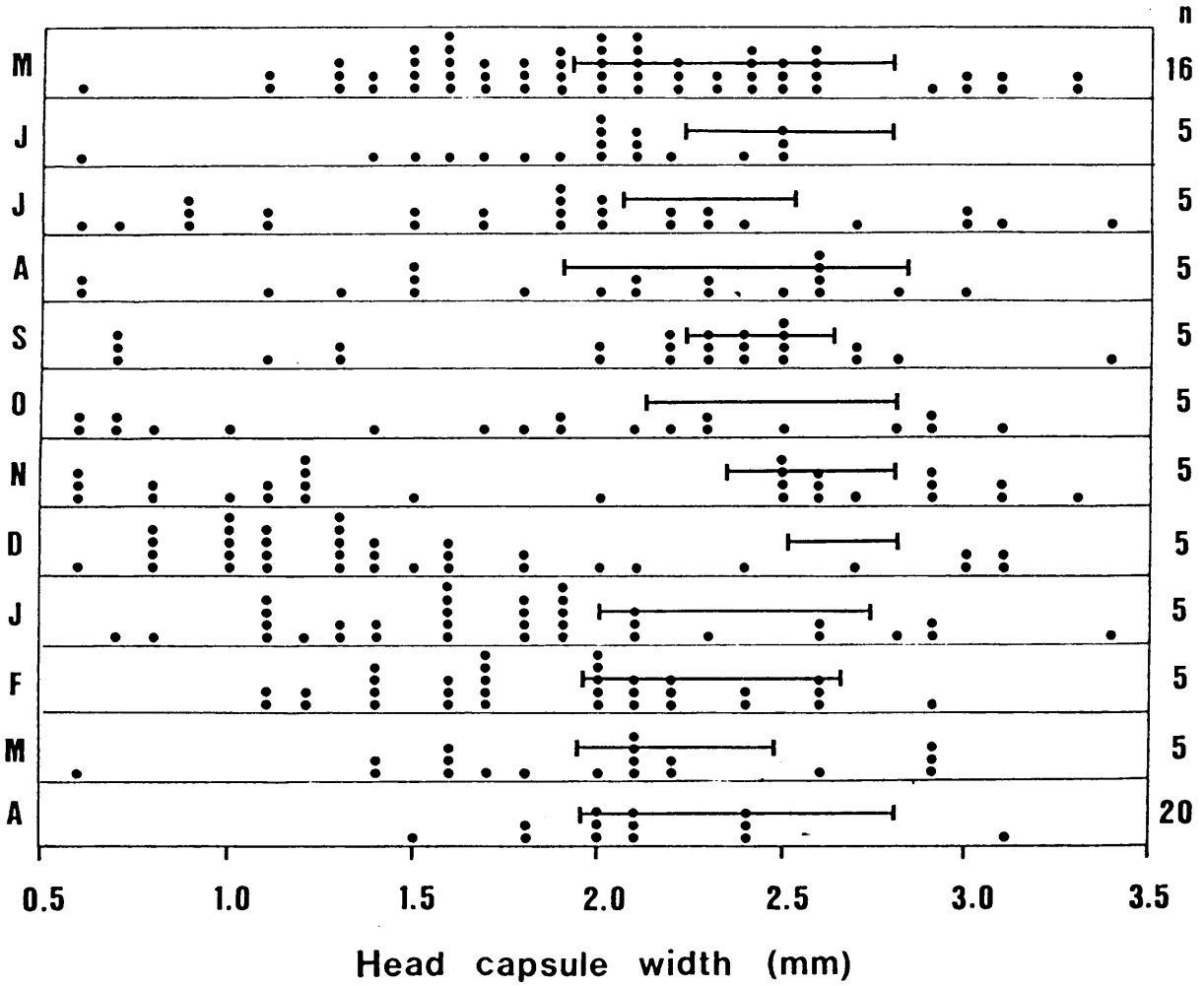

Figure 6.5. The means and range of sizes of *P. marioni* larvae obtained from mouse stomachs, superimposed on monthly size class composition of larvae. See text for explanation.

Heaviest predation can be seen to occur in the size class that predominates throughout the year, and which probably consists of many mature larvae and prepupae. Because individuals of different cohorts co-exist, and larvae of similar size may belong to different generations at different stages of development, size-selective predation is not necessarily age-selective. Constant and severe predation would cumulatively have an age-specific effect, however, and ultimately also affect recruitment to the population. If mice remove more than twice the standing crop of *P. marioni* larvae annually, the P/B ratio (production : biomass) of *P. marioni* populations has to exceed 2.5 to ensure the survival of the population.

At Prince Edward Island, *Pringleophaga* larval biomass in *Agrostis magellanica* mire and biotically influenced *P. cookii* grassland communities was significantly ($p<0.05$; Student's t test) higher than in corresponding communities at Marion Island (Table 6.2).

Table 6.2 Mean (± SD) biomass (g m^{-2}) of *Pringleophaga* larvae in *Agrostis magellanica* mire and biotically influenced *P. cookii* grassland communities at Marion and Prince Edward Islands. n: number of repetitions (X 50 samples at both Marion and Prince Edward Islands).

	A. magellanica mire	*P. cookii* grassland
Marion Island	0.58 ± 0.72(n = 8)	1.19 ± 0.27 (n = 8)
Prince Edward Island	1.12 ± 0.43(n = 6)	12.86 ± 16.23 (n = 6)

Crafford and Scholtz (1987a) speculated on reasons for this decrepancy, and concluded that mouse predation is the primary cause of the lower population densities and biomass of *Pringleophaga* larvae at Marion Island. Because of the uncertainty regarding the status of *P. marioni* and *P. kerguelensis* at the Prince Edward Islands, it is impossible to say whether the substantial quantitative differences between *Pringleophaga* populations at the two islands are due to the respective presence or absence of *P. kerguelensis* at Prince Edward and Marion Islands. Should the population differences be due to a difference in species composition (which is biogeographically unlikely), the possibility that mice could have caused the severe depletion (or even the extermination) of *P. kerguelensis* at Marion Island cannot be discounted.

6.3 Feeding ecology

6.3.1 Methodology

P. marioni larvae across the entire size range were collected in the field, weighed and placed individually in petri dishes. Fresh *Azorella selago* and *Poa cookii* litter collected in the field was oven-dried to constant mass (four days at 60°C). Weighed quantities of dried litter (from 10 - 100g, depending on the size of the larva) were added to each petri dish containing a larva. The litter was rehydrated with water in which fresh litter had been shaken up, in order to restore bacterial populations which had presumably been destroyed during oven-drying. Petri dishes containing only rehydrated litter and no larvae served as controls to compensate for mass loss of food litter due to bacterial decomposition. After 2-5 days (depending on the observed rate

of larval feeding) the larvae were removed, weighed, oven-dried and weighed dry. Their faeces, which is excreted as discrete and easily discernible pellets even in the case of small larvae, was seperated from the litter, and the faeces and the food litter were oven-dried and weighed.

Food consumption and utilization of *P. marioni* larvae were determined in incubators at constant 2, 5 and 10 °C and 100 % RH in the case of *P. cookii* litter, and at 5 and 10 °C and 100 % RH in the case of *A. selago* litter. In an attempt to determine the role of bacteria in the nutrition of *P. marioni* larvae, similar feeding experiments were conducted, at constant 5 and 10 °C and 100 % RH, using sterilized (autoclaved) *P. cookii* litter. Since such litter is rapidly recolonized by bacteria voided in the larval faeces, litter was treated with a bactericide (0.2% Streptomycin solution) after each day during the entire feeding period.

Larvae used in the feeding experiments were divided into the same size classes (Class I - V) as shown in Table 6.1. Food consumption was expressed both as absolute amounts of food eaten (mg dry litter larva^{-1} day^{-1}) and as a percentage of larval mass (mg dry litter mg larval live mass^{-1} day^{-1}). Q_{10} values for mass specific consumption rates were determined over the temperature range 5 - 10°C, using the equation

$$\log Q_{10} = (\log R_2 - \log R_1) \cdot 10/(T_2 - T_1) \text{ (Schmidt-Nielsen 1979).}$$

Since very few of the larvae used in feeding experiments actually gained mass over the feeding period, it was impossible to determine larval growth efficiencies. Only approximate digestibility (AD) of food mass and energy was consequently determined for each of the different food types (see 4.3.1 for the calculation of AD).

6.3.2 Results

Food consumption

As was the case with *E. halticella* larvae, many *P. marioni* larvae did not consume any food during the feeding experiments, and the eventual sample size was consequently much reduced. Larvae in size classes I - III, and those in size classes IV and V, were therefore lumped and shall be referred to as size groups 1 and 2, respectively. Size group 1 comprises all larvae of less than 100 mg live mass, and size group 2 includes those size classes (> 100 mg live mass) which account for the major part of larval duration. Size group 2 larvae can therefore be expected to account for the majority of food consumed during the larval stage, and the results obtained with these larvae are singled out for discussion.

Since the live mass of larvae, and the absolute amounts of dry leaf litter they consumed (mg ind^{-1} day^{-1}) varied considerably within the two size groups, only the ranges of live mass and consumption rates at constant 2, 5 and 10°C are shown in Table 6.3. The mean (± STD) mass-specific rates at which *P. marioni* larvae consumed the two food types, at the three temperatures, are given in Table 6.4.

When absolute consumption rate was plotted against larval live mass on a double log scale, there was poor or no correlation between the two parameters, except in the case of larvae fed *A. selago* litter at constant 5 °C (r=0.91, in this instance). As with *E. halticella* larvae, there was generally a better correlation between mass-specific consumption rates and live mass (Fig. 6.6).

Table 6.3 The ranges of live mass (mg: w) and food consumption rates (mg ind^{-1} day^{-1}: r), and the number of replicates (n) of *P. marioni* larvae fed *P. cookii* and *A. selago* leaf litter at 2, 5 and 10 °C.

Food type	Size group		2°C	5°C	10°C
P. cookii litter	1	w	57.90 - 101.30	21.10 - 80.70	45.90 - 89.40
		r	1.44 - 3.28	1.46 - 5.38	3.16 - 7.84
		n	5	12	3
	2	w	120.80 - 362.90	114.60 - 363.00	103.40 - 348.70
		r	2.62 - 10.58	2.16 - 10.44	3.86 - 11.64
		n	7	17	6
Sterile *P. cookii* litter	1	w	-	65.90 - 97.50	41.70 - 77.50
		r	-	3.26 - 5.64	2.42 - 5.08
		n	-	5	6
	2	w	-	102.00 - 354.80	103.70 - 251.40
		r	-	1.32 - 6.38	3.18 - 8.76
		n	-	10	7
A. selago litter	1	w	-	33.70 - 100.00	12.80 - 90.60
		r	-	2.16 - 8.16	1.50 - 6.50
		n	-	8	8
	2	w	-	112.80 - 252.90	126.90 - 300.80
		r	-	4.38 - 10.50	2.90 - 9.20
		n	-	9	6

Table 6.4. Mean (± SD) mass-specific consumption rates (g dry mass of food g live mass $larva^{-1}$ day^{-1}) of two size groups of *P. marioni* larvae at 2, 5 and 10 °C. Number of replicates the same as in Table 6.3.

Food type	Size group	2°C	5°C	10°C
P.cookii litter	1	0.027 ± 0.007	0.062 ± 0.023	0.076 ± 0.015
	2	0.021 ± 0.009	0.033 ± 0.014	0.062 ± 0.028
Sterile *P. cookii*	1	-	0.050 ± 0.016	0.063 ± 0.021
	2	-	0.027 ± 0.017	0.043 ± 0.023
A. selago litter	1	-	0.061 ± 0.013	0.080 ± 0.022
	2	-	0.043 ± 0.009	0.030 ± 0.012

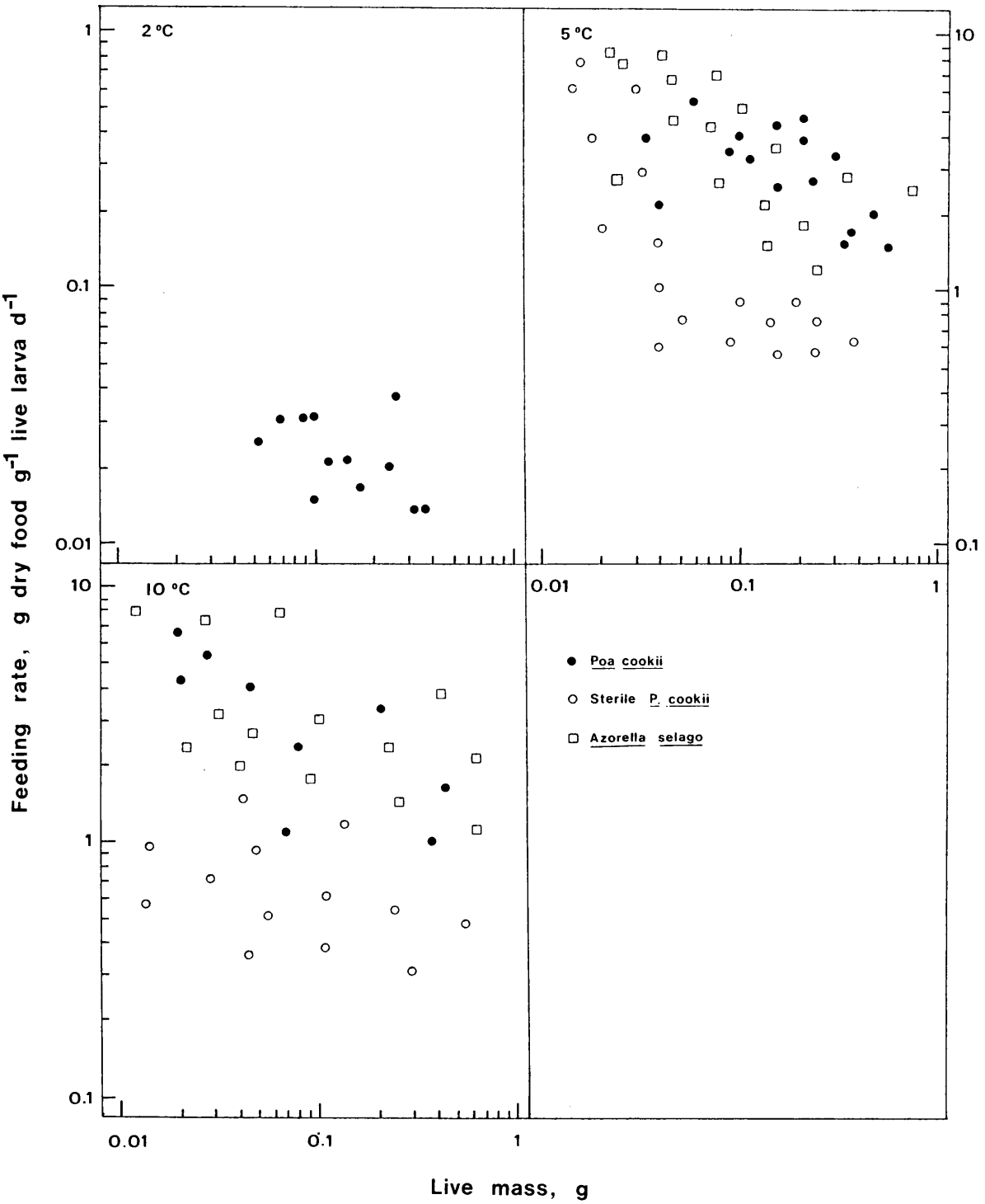

Figure 6.6. The effect of temperature on mass-specific food consumption of *P. marioni* larvae. Symbols represent individual data points.

Mass-specific larval consumption rates determined at constant 5 °C in the laboratory, were used to extrapolate monthly and annual larval consumption in the field (see section 6.5). Since the larvae feed and are active throughout the year, 5 °C appears to be the most "ecologically relevant" temperature (see Table 3.3), although temperatures during summer may exceed 10 °C in most microhabitats in which *P. marioni* larvae occur (Tables 3.2 and 3.3).

The Q_{10} values for changes in the mass-specific consumption rates (Table 6.4) of the two larval size groups, over the temperature range 2-10°C, are given in Table 6.5.

Table 6.5. Q_{10} values for the mass-specific food consumption rates of the two size groups of *P. marioni* larvae.

Food type	Size group	2-5 °C	5-10 °C	2-10 °C
P. cookii litter	1	15.97	1.50	3.65
	2	4.51	3.53	3.87
Sterile *P. cookii*	1	-	1.59	-
	2	-	2.54	-
A. selago litter	1	-	1.72	-
	2	-	0.49	-

In most Lepidoptera, there is a near perfectly linear relationship between faecal mass and the mass of food consumed, so that the former can be used as an indicator of the latter wherever gravimetric measurement of food intake is difficult or impossible. Mathavan and Pandian (1974) found ingestion/egestion ratios of Lepidoptera larvae reared at constant temperatures, on their conventional host plants, to range between 1.4 and 1.6 for moths and between 1.8 and 2.1 for butterflies. The ingestion/egestion ratio for large (size group 2) *P. marioni* larvae ranged from 1.01 to 1.54 (Table 6.6), compared to the relatively high ratios of 2.56 to 3.23 obtained with mature *E. halticella* larvae (Table 4.6).

Table 6.6. Mean (± SD) daily ratio of frass produced to food consumed (E/I) by *P. marioni* larvae fed different food items.

Temperature	Food type	Size group	Ingestion/Egestion	n
2°C	*P. cookii* litter	1	0.98 ± 0.15	5
		2	1.01 ± 0.14	7
5°C	*P. cookii* litter	1	2.17 ± 0.24	12
		2	1.41 ± 0.13	17
	sterile	1	1.16 ± 0.05	5
		2	1.15 ± 0.04	10
	A. selago litter	1	1.39 ± 0.11	8
		2	1.27 ± 0.03	9
10°C	*P. cookii* litter	1	1.28 ± 0.19	3
		2	1.37 ± 0.04	6
	sterile	1	1.49 ± 0.09	6
		2	1.54 ± 0.07	7
	A. selago litter	1	1.28 ± 0.10	8
		2	1.12 ± 0.05	6

Energy values and ecological efficiencies

The energy content of *P. marioni* larvae, *P. cookii* and *A. selago* leaf litter, and the frass of larvae fed the two food types, is shown in Table 6.7. *P. cookii* and *A. selago* leaf litter had a slightly higher energy content than fresh leaves (Tables 4.7 and 5.4), possibly because of bacteria adhering to the litter surface.

Table 6.7. Mean (± SD) energy content of *P. marioni* larvae, *P. cookii* and *A. selago* leaf litter, and the frass of *P. marioni* larvae fed the two different food items. n: number of determinations.

	Energy (kJ g^{-1})	n
P. marioni larvae	21.07 ± 0.08	4
P. cookii leaf litter	19.06 ± 1.01	4
frass	20.40 ± 0.03	4
A. selago leaf litter	21.34 ± 0.02	4
frass	19.77 ± 0.03	4

The approximate digestibility (AD) of the different food types fed to *P. marioni* larvae is shown in Table 6.8. Means and standard deviations from the means are given.

Table 6.8. Approximate digestibility (AD) of food mass (w) and food energy (e) for *P. marioni* larvae fed *P. cookii* and *A. selago* leaf litter at different temperatures. Mean values (± SD) are shown. Number of replicates in parentheses. Symbols between values indicate significance levels of differences between rates at different temperatures (**: $p<0.01$; *: $p<0.05$; otherwise not significant; Mann-Whitney U test).

Food type	Index	Size group 1		Size group 2	
		5°C	10°C	5°C	10°C
P. cookii litter	AD(%) e	50.72±25.20 **	16.11± 6.63	24.04±14.41	21.45± 3.84
	AD(%) w	53.95±23.54 *	21.62± 6.19	29.03±13.46	26.61± 3.58
Sterile *P. cookii*	AD(%) e	8.42± 5.28 **	28.37± 9.14	7.15± 4.36 **	30.29± 7.14
	AD(%) w	14.44± 4.93 *	33.08± 8.54	13.25± 4.07 *	34.87± 6.67
A. selago litter	AD(%) e	33.18± 9.82	27.57± 9.03	27.27± 2.97 **	17.30± 4.37
	AD(%) w	27.87±10.60	21.82± 9.74	21.49± 3.21 *	10.73± 4.71

6.3.3 Discussion

Food consumption and assimilation

Ingestion is the largest term in the balanced energy equation and sets an upper limit to all other variables (Peters 1983). Increases in temperature enhanced the ingestion rate of *P. marioni* larvae (Table 6.4; Fig. 6.6), but in most animals, the relationship between the amount of food required to attain a certain size or stage in development appears to remain the same at a variety of temperatures (Cossins and Bowler 1987). This means that, although the amount of food consumed per unit time is generally higher at higher temperatures, the duration of the growth period is correspondingly shorter, so that the total amount of food consumed is independent of temperature. It might therefore be expected that rearing temperatures would have little effect on final body size (Cossins and Bowler 1987).

Feeding experiments with *P. marioni* larvae were carried out at constant temperatures only, and the possible effects of fluctuating temperatures on food utilization efficiences remain unknown. Such effects are likely to be manifested particularly in growth performances, and these were not determined for *P. marioni* larvae. However, the larvae are rather sedentary and seldom leave the protective environment of the litter layer. Their micro-environment is characterized by an equable temperature (Table 3.3) and humidity regime, and is well buffered against short-term fluctuations in ambient conditions. This is true for most litter

microhabitats: in temperate pine woodland, conditions under 2-3 cm of needles and debris showed only a 3 °C and 17% RH range over a 24 hour cycle in which ambient conditions varied by 13 °C and 45% RH (Willmer 1982). Litter inhabitants in general, and *P. marioni* larvae in particular, can therefore be expected to have life strategies less markedly geared to utilizing short-term changes in ambient conditions, compared to insects whose entire life strategy revolve around physiological and behavioural responses to changes in environmental "favourableness" (e.g. Remmert's (1985) crickets in sunshine).

Although the Q_{10} values for food consumption rate were variable over the "normal" range of temperatures at which the larvae are active, they were generally low (Table 6.5). The high Q_{10} values from 2 to 5°C may reflect an "activity threshold" for the commencement of feeding, particularly for smaller larvae. The rate at which mature *P. marioni* consumed "conditioned" *P. cookii* litter did increase markedly (X 3.5) from 5 to 10 °C, while their consumption of sterile *P. cookii* more than doubled (Table 6.5). However, the AD of conditioned litter declined (although not significantly) from 5 to 10 °C, while the AD of sterile litter *increased* threefold at the higher temperature. In contrast, larval consumption of *A. selago* litter did not change from 5 to 10 °C (Table 6.5), although the AD of *A. selago* litter declined significantly at 10 °C. The AD values recorded (7 - 35% for size group 2 larvae; Table 6.8) are within the range of the low values generally recorded for terrestrial detritivores (e.g. Scriber and Slansky 1981; Werner and Dindal 1987).

The temperature-related differences in AD values shown in Table 6.8 are intriguing, and almost certainly reflect complex relationships between *P. marioni* larvae and a host of "microorganism detritivores" (Brafield and Llewellyn 1982) which they either utilize as food, or compete with for food nutrients. The most important effect of an increase in temperature on the nutritional ecology of *P. marioni* larvae appears to be a behaviourally passive switch to a different mode of food utilization (from deposit feeding to throughput feeding). Such a switch is likely to be manifested in changes in AD (see below).

The role of bacteria in larval nutrition

Most terrestrial detritus feeders also rely on external microorganisms to supplement their diets, but this association (ectosymbiosis) generally appears to be facultative rather than obligatory (Mattson 1980). Most plant parts, especially leaves, are rapidly invaded by various phylloplane microorganisms soon after their emergence from buds. As tissues age and senesce they are occupied by a succession of microorganisms, and by the time they are incorporated in the litter layer, decay organisms are abundant (Swift *et al.* 1979). The "conditioning" of plant tissues by microorganisms is important in the nutrition of terrestrial detritivores, and Cummins (1974) has likened the microbial biomass on plant litter to "peanut butter" on litter-tissue "crackers." Anderson and Sedell (1979) suggested that the increased protein value of conditioned plant litter is of primary importance, although microorganisms also have the ability to break down cellulose and lignin and so, in addition to being a protein food source, render plant litter easier for detritivores to digest and utilize.

It is not clear whether *P. marioni* larvae merely utilize the products of bacterial action, or whether they utilize microbial biomass itself, or whether they do both, but the latter possibility seems most likely. Bacteria (and possibly other microbes) are obviously important in their nutrition, especially at low temperatures. As Table 6.8 shows, the AD of sterile *P. cookii* litter was significantly lower than that of normal ("conditioned") *P. cookii* litter at 5°C, while at 10 °C the AD of sterile litter was higher than that of normal litter. The most likely explanation (and testable hypothesis) seems to be that, at low temperatures, the digestive enzyme system of *P. marioni* larvae cannot deal with cellulose food, and that bacterial biomass is digested and utilized instead. At higher temperatures bacterial action is presumably enhanced, so that the larvae and their gut bacteria (facultative (?) endosymbionts, in this instance) would compete for available nutrients. Sterile litter would then be advantagous for larval nutrition at higher temperatures (10 °C; Table

6.8). At the same time, however, digestive enzymes involved in the breakdown of cellulose appear to have a threshold temperature > 5°C, so that at 10 °C the larvae would begin to be able to actually utilize litter as food. Schramm (1972) found a sharp cut-off point at 13 ° for the ability of Lepidoptera and Coleoptera larvae from high arctic tundra to utilize food in which cellulose was the only source of carbohydrates. Evidence for a similar scenario at Marion Island remains circumstantial, but if borne out by the results of experimental testing, it would go a long way to explaining the predominance of detritivory in the Marion Island terrestrial ecosystem (and in cold climates generally). It would also support Remmert's (1986) contention that the threshold for herbivory is a mean summer temperature of at least 6 °C, and at least partially solve his "paradox of the tundra" (Remmert 1986).

6.4 Respiration

6.4.1 Methodology

P. marioni larvae across the "medium to large" size range were collected in the field. In the laboratory, they were sorted into the size classes shown in Table 6.1. Only size classes III ("size group 1") and IV and V ("size group 2"; see 6.3.2) were used for the measurement of oxygen consumption. Individual larvae were placed in petri dishes, and starved and acclimated in incubators for at least 5 days at the temperature at which oxygen consumption was to be measured. The oxygen consumption of individual larvae was measured using the two techniques described in section 4.4.1. The long starvation period was deemed particularly important in the case of *P. marioni* larvae, because of the large percentage of live body mass accounted for by gut contents. However, most larvae had retained much food in their guts after the starvation period. Gut contents were not compensated for in the results.

6.4.2 Results

Effect of live mass on oxygen uptake

The mean live mass, and mean respiration and metabolic rates of three size classes of *P. marioni* larvae at 0, 5, 10 and 15°C, are shown in Table 6.9.

Table 6.9. Mean (± STD) metabolic rates: ul O_2 g^{-1} hr^{-1} (M), respiration rates:ul O_2 ind^{-1} hr^{-1} (R), live mass: mg (W) and number of replicates (n) for three size classes of *P. marioni* larvae at 0, 5, 10 and 15 °C.

	0°C	5°C	10°C	15°C
Size class III				
M	180.83 ± 70.06	139.30 ± 31.86	220.93 ± 97.81	224.10 ± 95.93
R	14.14 ± 3.13	10.51 ± 1.62	17.25 ± 7.14	23.41 ± 10.23
W	84.50 ± 21.20	78.30 ± 15.40	78.40 ± 13.80	94.80 ± 7.40
n	7	8	11	4
Size class IV				
M	71.66 ± 14.29	102.47 ± 25.79	166.78 ± 72.05	269.04 ± 47.75
R	11.25 ± 2.66	15.21 ± 2.95	24.92 ± 9.50	44.55 ± 7.63
W	157.20 ± 20.10	152.60 ± 26.10	154.40 ± 33.50	167.00 ± 19.60
n	5	23	13	10
Size class V				
M	60.09 ± 4.25	83.28 ± 13.00	159.79 ± 35.25	206.91 ± 46.29
R	13.44 ± 1.24	21.50 ± 3.99	47.38 ± 16.21	50.24 ± 10.11
W	232.40 ± 36.80	259.10 ± 33.90	298.00 ± 85.00	246.20 ± 27.10
n	4	9	20	4

Regression equations relating (a) respiration rate (ul O_2 $ind^{-1}hr^{-1}$) and (b) metabolic rate (ul O_2 $g^{-1}hr^{-1}$) to live mass are given in Table 6.10.

Table 6.10.. Linear regression equations of (a) $\log_{10}$ respiration rate on $\log_{10}$ live mass and (b) $\log_{10}$ metabolic rate on $\log_{10}$ live mass at 0, 5, 10 and 15 °C for *P. marioni* larvae.

Temperature		n	a	b ± SEM	r	r^2
(a)	0	15	1.056	-0.056 ± 0.126	-0.118	1.39
	5	39	0.568	0.518 ± 0.074	0.749	56.05
	10	53	0.668	0.738 ± 0.055	0.846	71.63
	15	17	0.722	0.889 ± 0.219	0.711	50.58
(b)	0	15	11.997	-1.033 ± 0.128	-0.907	82.29
	5	39	40.312	-0.482 ± 0.074	-0.725	52.55
	10	53	105.456	-0.262 ± 0.055	-0.308	9.51
	15	17	195.767	-0.110 ± 0.219	-0.124	1.54

Double $\log_{10}$ plots of individual respiration rate on larval live mass (Fig. 6.7), for larvae across the entire size range sampled, showed that live mass had no effect on respiration rate at 0 °C (Table 6.10: r not significantly different from 0; $p < 0.001$). Only at 10 °C did respiration rate scale conventionally (see Peters 1983) with body mass: at this temperature the two parameters were related by the equation $R = 0.668\ W^{0.74}$, where R = respiration rate and W = larval live mass. The slopes of the lines relating respiration rate to body mass at 5 and 15 °C did not differ substantially from that at 10 °C (Fig. 6.7). The opposite trend emerged when metabolic rate was plotted against live mass on a double log scale (Fig. 6.8): at 0 °C, the two parameters were almost linearly related (r = 0.917, Table 6.10), with differences in live mass explaining 82 % of the variation in metabolic rate. At 15 °C, however, there was no correlation between the two parameters (Table 6.10: r not significantly different from 0; $p < 0.001$). The slope of the line relating the two parameters was similar at 5 and 10 °C (Fig. 6.8).

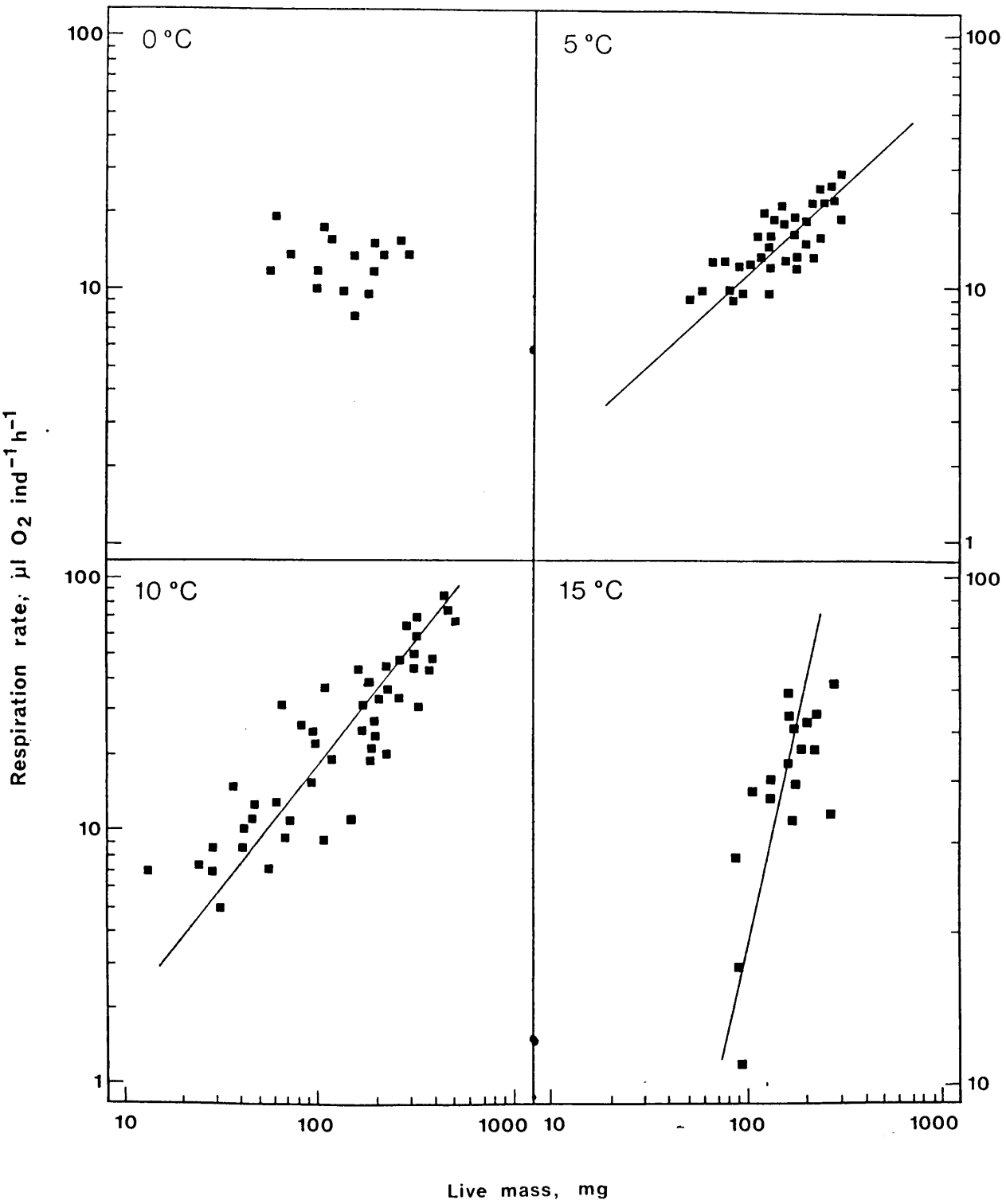

Figure 6.7. Effect of live mass on respiration rate at 0, 5, 10 and 15 °C of three size classes of *P. marioni* larvae. Individual points are shown together with the fitted regression line at each temperature.

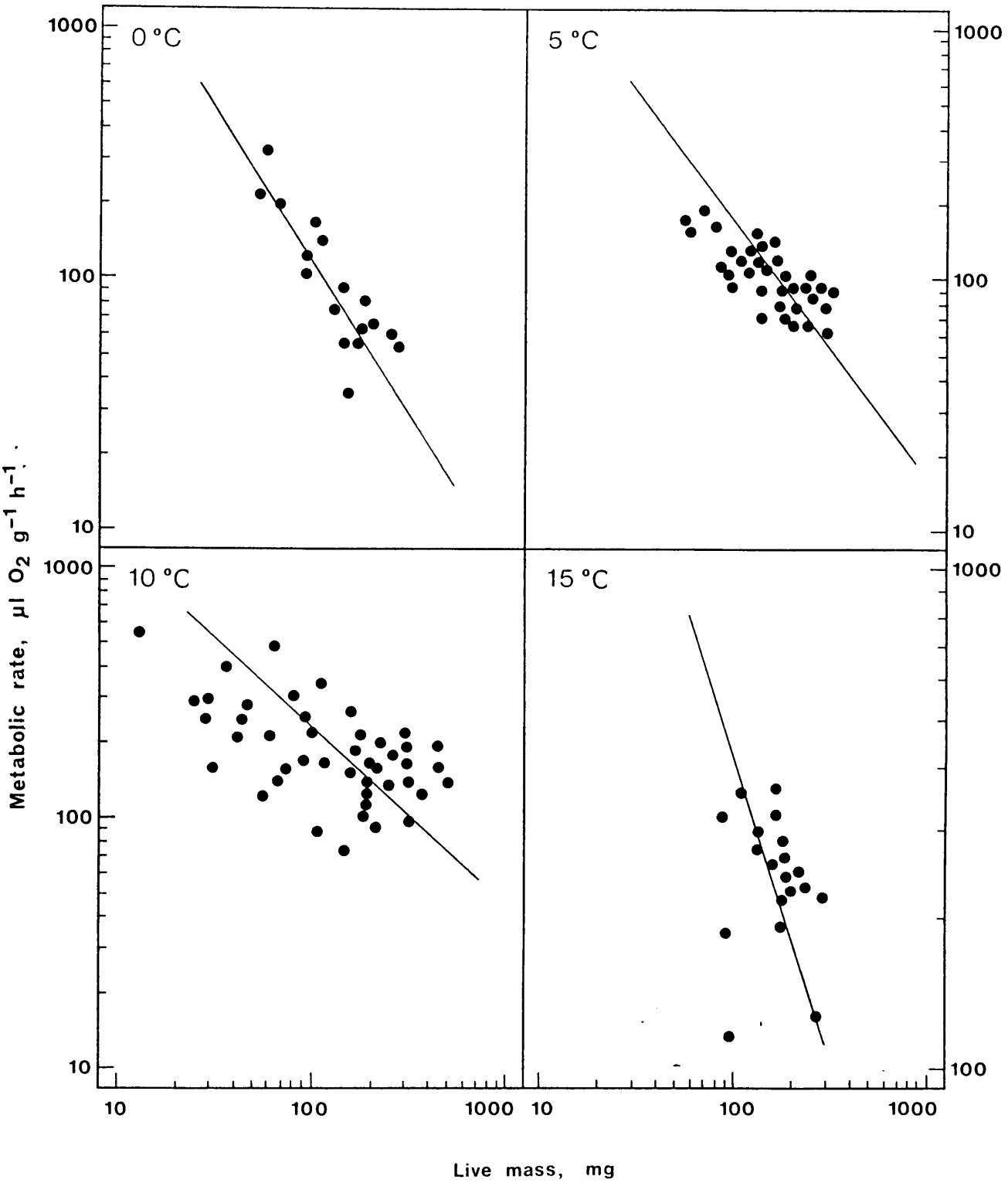

Figure 6.8. Effect of live mass on metabolic rate at 0, 5, 10 and 15°C of three size classes of *P. marioni* larvae. Individual data points are shown together with the fitted regression line at each temperature.

Effect of temperature on oxygen uptake

The mean respiration rates and mean metabolic rates of each of the three size classes of *P. marioni* larvae are plotted against temperature in Fig. 6.9.

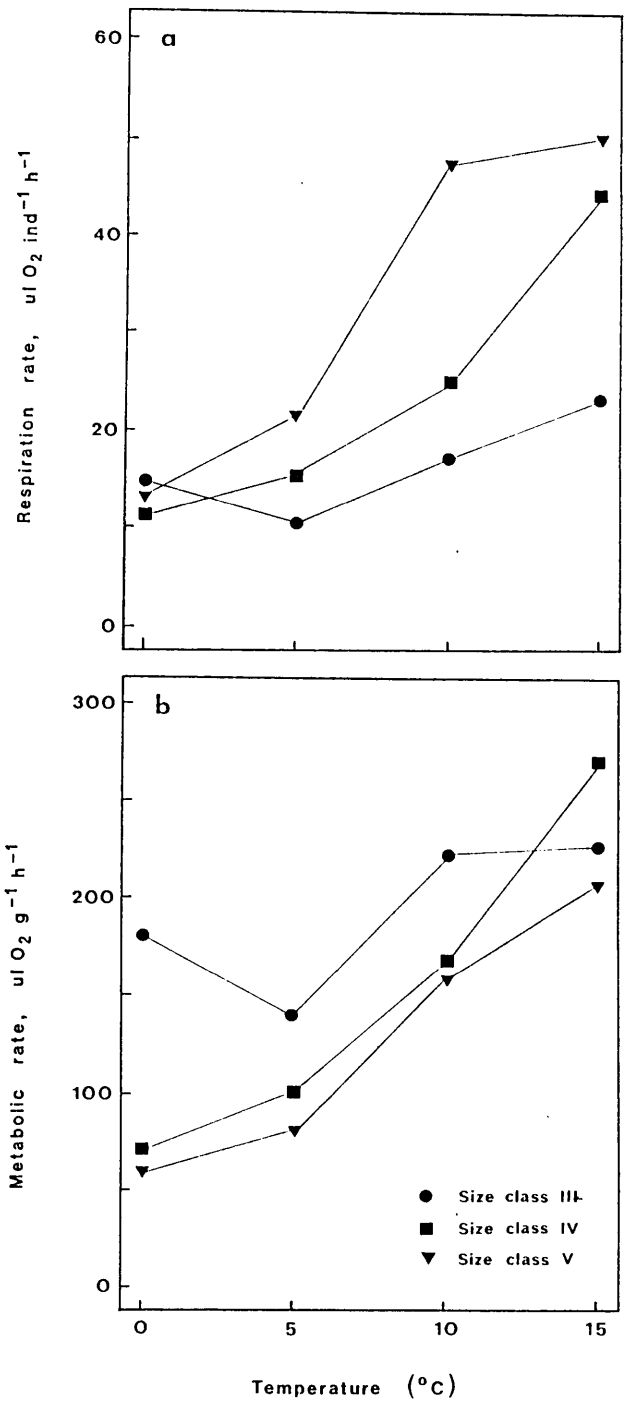

Figure 6.9. Effect of temperature on (a) mean respiration rate and (b) mean metabolic rate of three size classes of *P. marioni* larvae.

Respiration and metabolic rates of size class III larvae declined slightly from 0 to 5 °C, while the rates of size classes IV and V increased only slightly (Fig. 6.9). The greatest increase in rates, for all three size classes, ocurred from 5 to 10 °C, over which range the metabolic and respiration rates of size class V larvae increased more than threefold (Table 6.12). The data showing the effect of temperature on the metabolic rates of each of the three size classes of *P. marioni* larvae are presented as Arrhenius plots in Fig. 6.10. The Arrhenius equations (see section 4.4.2 for explanation) are given in Table 6.11.

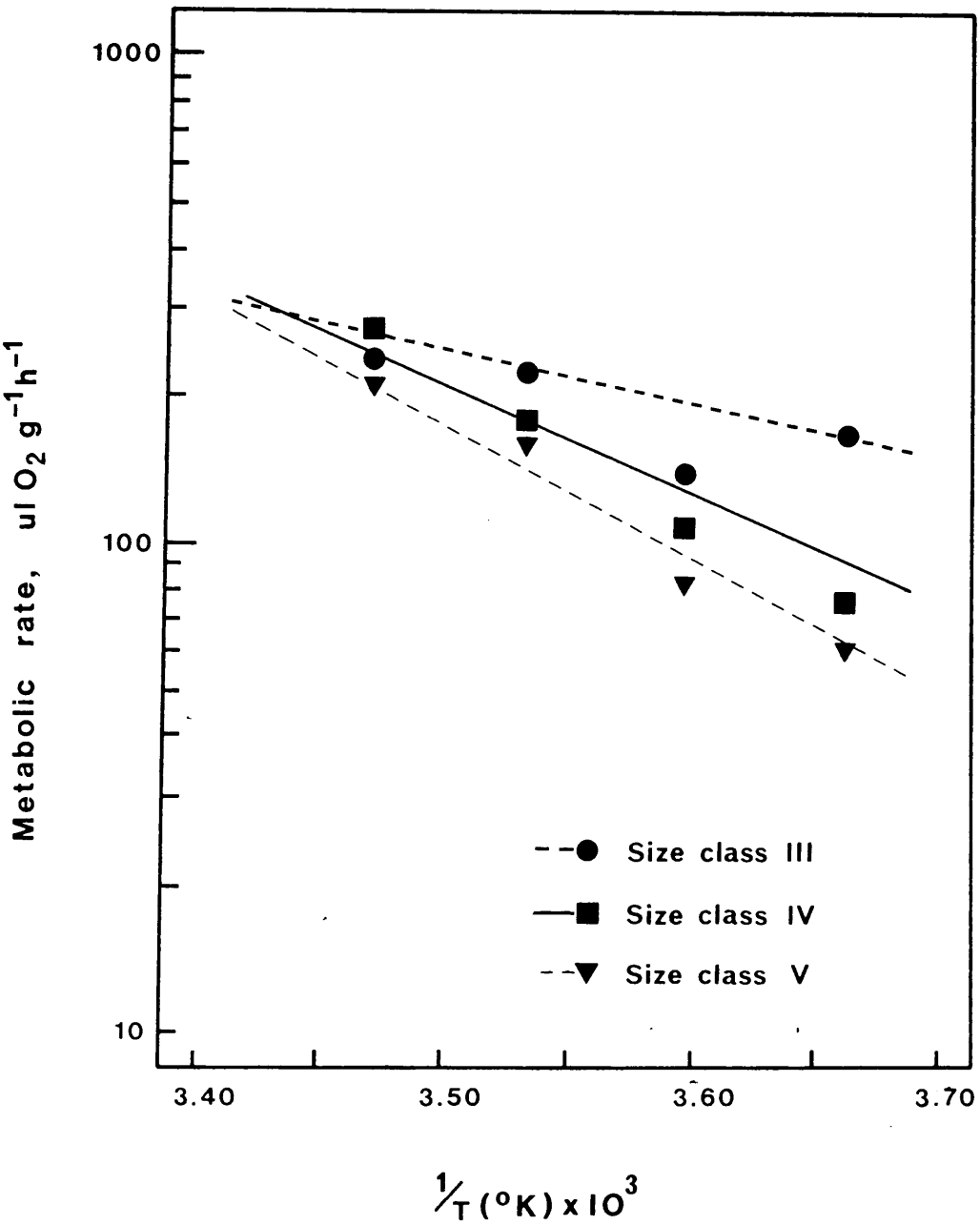

Figure 6.10. Arrhenius plots of metabolic rate (M) on temperature (T) for three size classes of *P. marioni* larvae. The fitted regression lines are shown of $\log_e M = a.e^b$, with a and b values for each size class taken from Table 6.11.

Table 6.11. Linear regression equations of $\log_e$ metabolic rate on 1/T (°K) for each of three size classes of *P. marioni* larvae.

Size class	n	a	b ± SEM	r
III	30	8.735×10^4	-1.723 ± 1.479	-0.636
IV	51	9.428×10^{12}	-7.010 ± 0.409	-0.997
V	37	4.832×10^{12}	-6.866 ± 0.806	-0.987

Activation energies, and Q_{10} values for larval metabolic rate, were calculated from the Arrhenius equations in Table 6.11. Q_{10} values were also determined from mean metabolic rates, using the equation $\log Q_{10} = (\log R_2 - \log R_1) \times 10/T_2 - T_1$ (Schmidt-Nielsen 1979). Activation energies and Q_{10} values for the three size classes of *P. marioni* larvae are shown in Table 6.12.

Table 6.12. Activation energies and Q_{10} values for the ranges 0-5, 5-10, 10-15 and 0-15 °C, and mean live mass, of each of three size classes of *P. marioni* larvae. Q_{10} values in brackets were calculated from mean metabolic rates.

Size class	Activation energy (kcal/mol)	Q_{10} 0-5	5-10	10-15	0-15	Mean live mass (g)
III	3.412	(0.59)	1.17 (2.52)	1.12 (1.03)	(1.15)	0.084
IV	13.871	(2.05)	4.04 (2.65)	1.59 (2.60)	(2.42)	0.158
V	13.595	(1.92)	3.93 (3.68)	1.58 (1.68)	(2.28)	0.259

6.4.3 Discussion

Few studies have been undertaken of the metabolism of polar or sub-polar macro-invertebrates; from the studies available (e.g. Ryan and Hergert 1976, Block 1981) it has been concluded that there exists no real adaptation of metabolism to low temperatures (Remmert 1980). The respiration rates of arctic Lepidoptera at low temperatures, at least, appear to be similar to those of temperate Lepidoptera at similar temperatures (Bogacheva 1983). However, at comparable temperatures, the respiration rate, metabolic rate and Q_{10} of late instar *P. marioni* larvae are demonstrably lower than those of *Gynaephora rossi* (Lymantriidae) larvae from the arctic (Table 6.13).

Table 6.13 Respiration rate, metabolic rate and Q_{10} of late instar *P. marioni* and *Gynaephora rossi* (Lymantriidae) larvae (the latter after Bliss (1977)). Only mean values are shown; Q_{10} derived from mean values (see Table 6.12).

Species	°C	Live mass mg	Oxygen consumption ul O_2 $ind^{-1}hr^{-1}$	ul O_2 $g^{-1}hr^{-1}$	Q_{10}
P. marioni	5	259.10	21.50	83.28	-
	10	298.00	47.38	159.79	3.68
	15	246.20	50.24	206.91	1.68
Gynaephora rossi	2	840.00	71.40	88.40	-
(Lymantriidae)	7	724.00	150.60	207.98	5.54
	12	734.80	425.00	579.43	7.76

The validity of Q_{10} comparisons between different species has been questioned, because a given temperature interval may fall in quite different portions of their respective rate-temperature curves (Cossins and Bowler 1987). The marked difference between $Q_{10(10\text{-}15\ C)}$ of *P. marioni* and $Q_{10(7\text{-}12\ C)}$ of *G. rossi* does imply vastly different temperature responses in the two species, however. The latter species is considered cold stenothermic; its high Q_{10} would therefore imply metabolic collapse at slightly higher temperatures (Remmert 1980). Unlike *G. rossi*, *P. marioni* does not, as far as could be ascertained, undergo diapause of any description. This, and its relatively low Q_{10}, would appear to confirm the contention underlying much of this chapter, namely that the constancy of the narrow temperature regime to which *P. marioni* larvae are exposed, present little selective advantage for rapid and pronounced responses to temperature increases.

6.5 Energy flow and nutrient cycling

Since herbivores account for very little energy flow from primary to secondary producers at Marion Island, virtually all of annual net primary production (ANP) becomes dead organic matter. ANP at Marion Island is generally low (see 2.3.1), but may be very high locally in certain plant communities: ANP of *A. magellanica* mire grassland, for instance, is higher than that of many grasslands in more temperate areas (Smith 1987b, 1987c). With the slow rate of microbial decomposition in the cold and waterlogged soils of the island, dead organic matter in productive plant communities such as mire grasslands accumulate to form peat deposits of great depth. The vast dead standing crop of vegetation (necromass) contains large reserves of nutrients that are "unavailable" or inaccessible for primary production. Considering the relatively low external input of nutrients, it is likely that decomposition (i.e. both fragmentation and digestion by detritivores, and microbial decomposition) is the main "bottleneck" in nutrient recycling at the island (Smith 1985). Earthworm biomass at Marion Island may be up to an order of magnitude higher than that of *P. marioni* larvae (Burger 1978a), but in terms of actual fragmentation of litter, the latter are the major detritivores. In fact, *P. marioni* larvae appear to facilitate the feeding of earthworms by fragmenting and egesting tough and fibrous plant

material such as *P. cookii* leaves. This leads to a certain degree of temporal succession and resource partitioning in habitats where *P. marioni* larvae and earthworms occur together and utilize the same food source (pers. obs.). Although the high standing crop of invertebrate decomposers represents a major energy "reservoir" available to secondary consumers, decomposers themselves contribute minimally to energy flow (Remmert 1980). Instead, their ecological role - in terms of the functioning of the terrestrial ecosystem - is primarily that of facilitating nutrient recycling.

Brafield and Llewellyn (1982) stated that detritivores have a unique role (in enhancing the cycling of inorganic plant nutrients in ecosystems) not because they are physiologically special but because of the magnitude of their activity. At a mean annual biomass of 9.3 kg ha^{-1} (dry mass) on Marion Island's coastal plain, and an individual daily consumption rate of 3 % of live body mass in litter (Table 6.4), *P. marioni* larvae are estimated to process about 100 kg ha^{-1} of litter annually. Turnover of litter in productive habitats may be an order of magnitude higher. Werner and Dindal (1987) reported that gut passage through millipedes increases the bacterial count of organic matter by at least ten times, and Steenkamp (pers. comm.) has reported similar increases in bacterial populations on litter that passed through the guts of *P. marioni* larvae. Nutrient mineralization from food litter is due as much to its fragmentation, digestion and excretion by detritivores, as by the consequent enhancement of bacterial action.

The role of *P. marioni* larve in releasing nutrients from the plant litter they feed on has been quantified (Steenkamp, in prep.), by maintaining larvae in perspex microcosms containing *P. cookii* and *A. selago* litter, and leaching the litter with doubly distilled water at weekly intervals. The amount of free nitrogen (ammonia ions) in the leachates was determined by the phenol-hypochlorite method (Solorzano 1969), and free phosphate content was determined using the method described by Murphy and Riley (1962). The amount of free N and P in the leachates was compared with that of leachates from control microcosms containing litter only. *P. marioni* larvae had a substantial effect on nutrient release from litter in the microcosms, and nutrient levels were consistently higher in the leachates from microcosms containing larvae than from the controls. Figure 6.11 shows the effect of larval feeding on N and P release from their food litter (Steenkamp, in litt.). Feral mouse predation on *P. marioni* larvae thus has implications greater than the depletion of larval populations at Marion Island, and the mice probably play a more significant role in the functioning of the terrestrial ecosystem than previously realized (Crafford in press). At the same time, the contribution of *P. marioni* larvae to energy flow in the decomposer subsystem of the island's terrestrial ecosystem is clearly of less significance than their contribution to nutrient cycling.

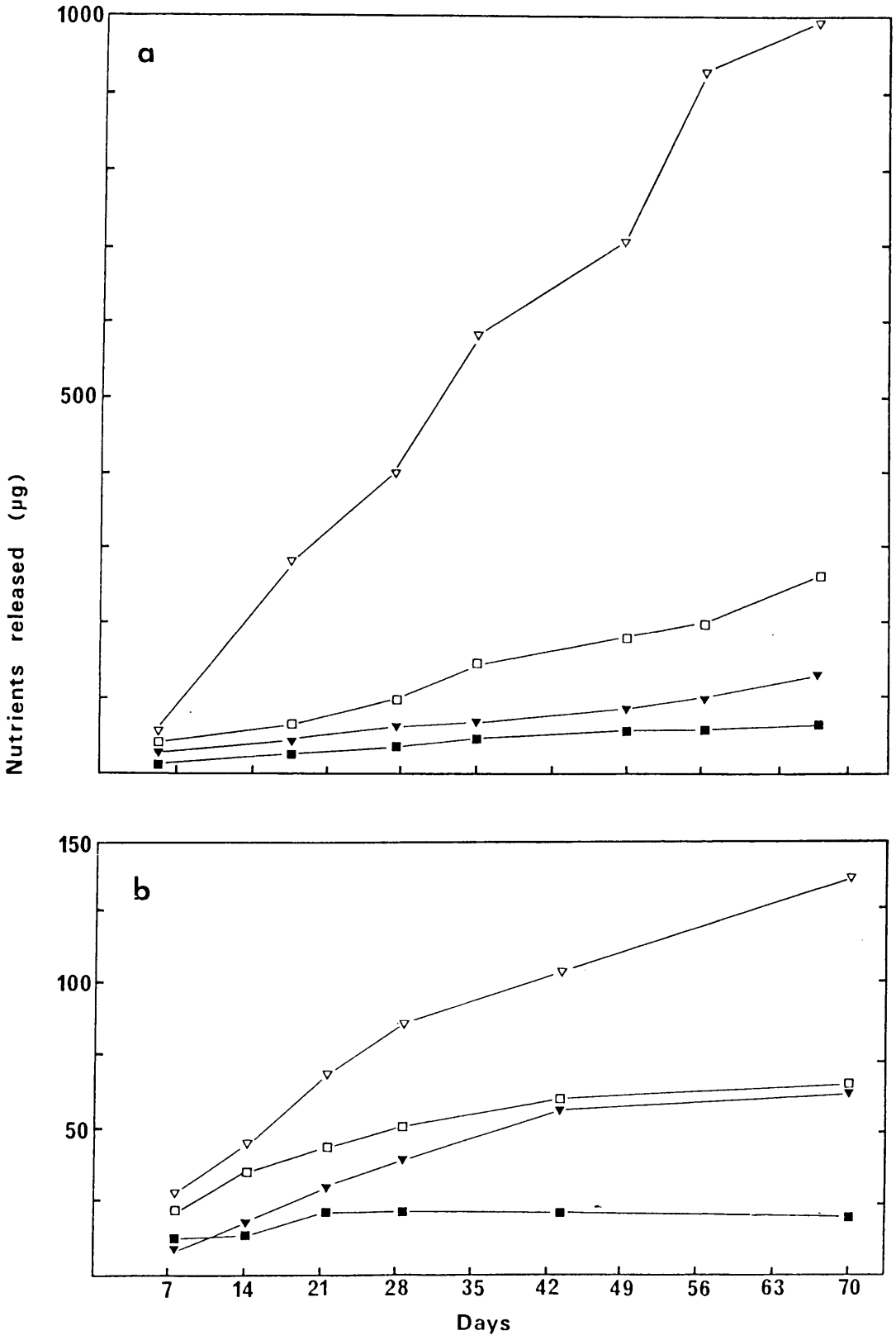

Figure 6.11 The effect of feeding by *P. marioni* larvae on the release of N (▽) and P (□) from *P. cookii* (Fig. 6.12b) and *A. selago* (Fig. 6.12a) litter in microcosms. Closed symbols show the amounts of N and P released from controls containing only litter (see text).

6.6 Evolutionary perspectives

P. marioni larvae, as far as could be ascertained, attain the largest size of any tineid larva. Several causes of the evolution of large body size in *P. marioni* suggest themselves, but these reduce, in the final instance, to selection pressures on their means of food acquisition and utilization (Slansky and Rodriguez 1987). Large body size is of selective advantage to detritivores, or other feeders on food high in fibre and low in nutrients, because it offers mechanical advantages for removing and macerating food. It also allows for high volume harvesting, because of increased gut size. Many Hesperiidae butterfly larvae have unusually large heads and associated mouth parts, probably as an adaptive response to their diet of fibrous, siliceous grasses (Mattson 1980). *P. marioni* larvae also have exceptionally large heads (Appendix A), which house the strong muscles and large processes to which the mandibles are attached (pers. obs.). The power to cut and masticate fibrous tissues increases as the square of body size (Mattson and Scriber 1987). In addition, *P. marioni* larvae have large, sack-like guts which may occupy as much as 60% of the volume and 50% of the live mass of large larvae (pers. obs.). The selective advantage of large body size in *P. marioni* is further reinforced by the thermodynamic implications of a reduced surface-to-volume ratio, which results in decreased metabolic rates (Table 6.9). Larger animals need to extract less energy per unit of ingesta than do smaller animals, because the latter have higher respiration losses (Mattson (1980); compare also the metabolic rates of *E. halticella* (Table 4.10)).

Of equal evolutionary interest as large body size, is the extreme length of the life cycle and inferred large number of instars of *P. marioni*. Complex trade-offs are likely to be involved in this combination of life history features: for instance, Sehnal (1985) has shown that holometabolous insects have more instars under "unfavourable" conditions and with poor nutrition, while Bernays and Barbehenn (1987) have pointed out that a greater number of instars may be required to replace mandibles worn down by chewing on grass foliage. All these requirements would necessitate a longer larval stage. Since the ultimate goal of the larval stage is ".. to produce an adult whose quality matches its genetically determined potential reproductive output" (Slansky and Rodriguez 1987), all larval life history characteristics can legitimately (and non-teleologically) be regarded as serving the ultimate aim of adult reproduction. In this view, growing larger and living longer are the best means by which *P. marioni* can accumulate and allocate the necessary energy resources for reproduction, while operating under the constraints imposed both by their own genome and their living and non-living environment. The loss of wings and of the necessity for long-distance dispersal; and the short-lived and non-feeding adult stage, allow *P. marioni* larvae to allocate the majority of energy to reproduction, so that adults are virtually reduced to mobile gonads. This would have been impossible in a biologically interactive ecosystem, where predation would have selected against such adult characteristics (Dierl and Reichholf 1977). The lack of biological interaction, and the predictable constancy of the abiotic environment, are probably the primary causes of the evolution of these characteristics, which would have been strongly reinforced (and genetically fixed) as a result of the energy savings they represent. This view will be further explored in Chapter 8.

CHAPTER 7: *Paractora dreuxi mirabilis* Seguy (Diptera: Helcomyzidae)

"Dass man sie als [Fliegen] zunächst nicht anspricht, ist begreiflich: fehlt ihnen doch eines der wichtigsten Attribute der Fliegen, nämlich die Flügel. Eine wundervolle Anpassung an das Leben in einer sturmdurchbrausten Region..."

Chun (1900)

7.1 Introduction

The Diptera constitute the majority of insect species on the South Indian Ocean Province Islands. The nine Diptera species recorded from Marion Island represent two suborders and seven diverse families. Two of the species are cosmopolitan, while the rest have a widespread distribution in the sub-Antarctic. Only the subspecies *P. dreuxi mirabilis* is endemic to the Prince Edward Islands. *Paractora dreuxi* occurs on Îles Crozet, while the genus *Paractora* also occurs on South Georgia, the Falklands, and in South America, but is absent from Îles Kerguelen and other islands to the west of Îles Crozet. The four native dipteran species on Marion Island (i.e. those restricted to the SIP islands) are all associated with coastal areas, and two of these (*P. dreuxi mirabilis*, and *Listriomastax litorea* (Tethinidae)) are decomposers of beached kelp.

Durvillea antarctica (Cham.) Har. (bull-kelp) is the dominant intertidal primary producer at Marion Island. The estimated total standing crop of this massive phaeophyte is 3 300 t (wet mass), which is situated in varying proportions along different shore types of the island's 72 km coastline (De Villiers 1978, Haxen and Grindley 1985). The shores consist mainly of steep cliffs and large-boulder beaches, and only about 2 % (1.5 km) consists of pebble and small-boulder (10-20 cm diameter) beaches. Heavy seas which accompany the frequent storms at Marion Island cause high mortality in the *D. antarctica* phytomass, with detached plants and broken-off fronds subsequently forming extensive "wrack beds" or "wrack strings" (*sensu* Backlund 1945), chiefly on the few gently sloping pebbled beaches. On these beaches, the stranded kelp is degraded through a combination of bacterial action and kelp consumption by a guild of macro-invertebrate kelp detritivores, dominated by *P. dreuxi mirabilis* larvae. Backlund (1945) stressed that wrack strings and wrack beds generally have different assemblages of decomposer populations and that decomposition proceeds in a different manner and at different rates in the two types of wrack. The products of degradation of both are recognized as an important source of nutrients in both the littoral zone and adjoining beaches (Smith 1977b).

Adult *P. dreuxi mirabilis* are large (body length 9-13 mm), black, micropterous and hairy. The larvae are large (up to 100 mg live mass) and fleshy with darkly sclerotized mouth-hooks and prominent spiracles. The pupae are typically Dipteran and are enclosed in a strong puparium (Appendix A, Fig. 3). The larvae, and to a lesser extent the adults, are important prey for lesser sheathbills (*Chionis minor*) and feral house mice (Burger 1978a, Gleeson 1982).

7.2 Life history and phenology

7.2.1 Methodology

Life history

A pebbled beach (Trypot Beach) on the north-eastern coast of Marion Island, 800 m south of the weather station, was chosen as the study area because of its accessibility and proximity to the laboratory. The beach is approximately 60 m wide with a gentle landward slope. It consists of small boulders and pebbles, receives regular kelp deposits and maintains permanent *P. dreuxi mirabilis* populations.

Adult *P. dreuxi mirabilis* 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 (*Durvillea antarctica*) fronds. The petri dishes were then placed in an incubator at 10 °C and 80-100 % RH. These conditions were assumed to simulate most closely those which the larvae are normally exposed to in the field (see Table 3.9). Eggs were counted as soon as they were laid, placed on strips of fresh kelp 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 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 moulting. Duration of the pupal stage was determined using both pupae from the laboratory colony and pupating larvae collected on 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.

Phenology

Durvillea antarctica plants were cast ashore in large quantities on Trypot Beach after heavy seas accompanying a summer storm in December 1984. Sixty freshly beached fronds were collected and trimmed to 1 kg (wet mass) each, and pegged out at 1 m intervals, 10 m from and parallel to the shore. Portions of fresh frond were weighed wet, dried and reweighed, to determine the initial wet mass/dry mass ratio of the kelp. For a month thereafter, two of the pegged-out fronds were collected daily at random, dried to constant mass (four days at 60 °C) and reweighed. All fronds were examined daily for signs of kelp fly activity.

Kelp fronds cast up during the same period referred to above (November 1984) were used to construct two 2 m^2 wrack beds on level sites, 10 m from the shore on Trypot beach. The laminas of the fronds were removed from the petioles and holdfasts, and deposited evenly and uniformly to a depth of 20 cm on the sites. One bed was left exposed to trampling by seals and penguins resident on the beach during the study period; the other was enclosed in a 20 cm deep wooden box frame and covered with a grid. The initial dry mass of kelp (kg m^{-2}) in the protected bed was measured by removing, drying and weighing five cores randomly taken from each bed with a 30 cm deep, 0.01 m^2 box corer. Both beds were subsequently sampled in a similar manner - daily for a week, and every alternate day thereafter. All animals exposed on the surface of pebbles or boulders, when the kelp cores were lifted, were included in the samples. The kelp samples were "washed" in warm (>60 °C) water, which successfully floated out all sizes of *P. dreuxi mirabilis* larvae. The kelp fraction of the samples was collected in a sieve, dried (four days at 60 °C) and weighed, as was the separate harvest of *P. dreuxi mirabilis* larvae. The decline in the dry mass of the kelp over the sampling period, was expressed as the percentage loss of original dry mass per unit area.

The biomass of the kelp fly larvae was expressed as their dry mass. kg^{-1} original dry mass of kelp. The decline in the dry mass of kelp in the protected bed was correlated with the extrapolated kelp consumption (see below) by larvae in the bed.

Five weeks after the deposition of the kelp, when both the protected and the natural wrack beds had disappeared, the spatial distribution and abundance of both kelp fly larvae and amphipods (the other major kelp decomposers) were determined along a 10 m transect perpendicular to, and starting from, the shore, at the sites of the two wrack beds. At 1 m intervals along the transect, a 30 cm deep, 0.1 m^2 box corer was worked into the pebbles to a depth of about 20 cm. The contents (pebbles and kelp detritus) were removed and all invertebrates floated out in warm water. The invertebrates were sorted, dried and weighed. Abundance was extrapolated from the results, and expressed as g (dry mass). m^{-2} of beach. The transect was sampled every alternate day for a week, after which rough seas caused the first subsequent deposition of *D. antarctica* wrack on Trypot Beach.

7.2.2 Results and discussion

Life history

Adult *P. dreuxi mirabilis* females laid 150-200 eggs singly and in groups on kelp and against the sides of petri dishes in the laboratory colonies, whereafter they died. 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 mature larvae in the laboratory colony generally did not exceed 80 mg. Their mass remained constant for a further 10 - 20 days; the duration of the third instar was 40-50 days (Table 7.1). The growth of *P. dreuxi mirabilis* larvae in a laboratory colony maintained at 10 °C and 100 % RH, is illustrated in Fig. 7.1.

Most larvae in laboratory colonies started pupating within 50 days of hatching. Duration of the pupal stage varied between laboratory and field populations. In the laboratory, most adults eclosed after 30 days, although some individuals only eclosed 80 days after pupation. Pupae obtained from mature larvae collected in the field, and maintained under ambient conditions outside the laboratory, generally hatched after 50 days only. On Trypot Beach, mature larvae migrate downward, from the kelp on the beach surface, to about 50 cm deep amongst the boulders, where they pupate against boulders and pebbles. Adults hatch in this "interstitial biotope" (see below), and migrate upward to colonize new kelp deposits. Adult life span never exceeded 21 days in the laboratory, and is probably even shorter in the field.

Deposition of wrack occurs sporadically and irregularly at Marion Island, but particulate kelp detritus accumulates amongst the rocks and pebbles on beaches, forming the "interstitial biotope" described by Trehen and Vernon (1982) on Îles Crozet. The interstitial biotope constitutes a stable and permanent reservoir of food for kelp-feeders, and supports a permanent stock of late-instar *P. dreuxi mirabilis* larvae and pupae available for the colonization of new wrack deposits. Coupled to its long and flexible life cycle, *P. dreuxi mirabilis* can thus react opportunistically to the deposition of kelp. The rapid, mass colonization of fresh wrack by *P. dreuxi mirabilis* adults appears to be the result of mass eclosion of pharate adults from underneath and amongst pebbles in the immediate vicinity of the fresh wrack, as much as of the migration of "existing" adults from old deposits. Mass eclosions could be a response to osmotic changes or olfactory stimuli that accompany the deposition of fresh kelp during heavy surf.

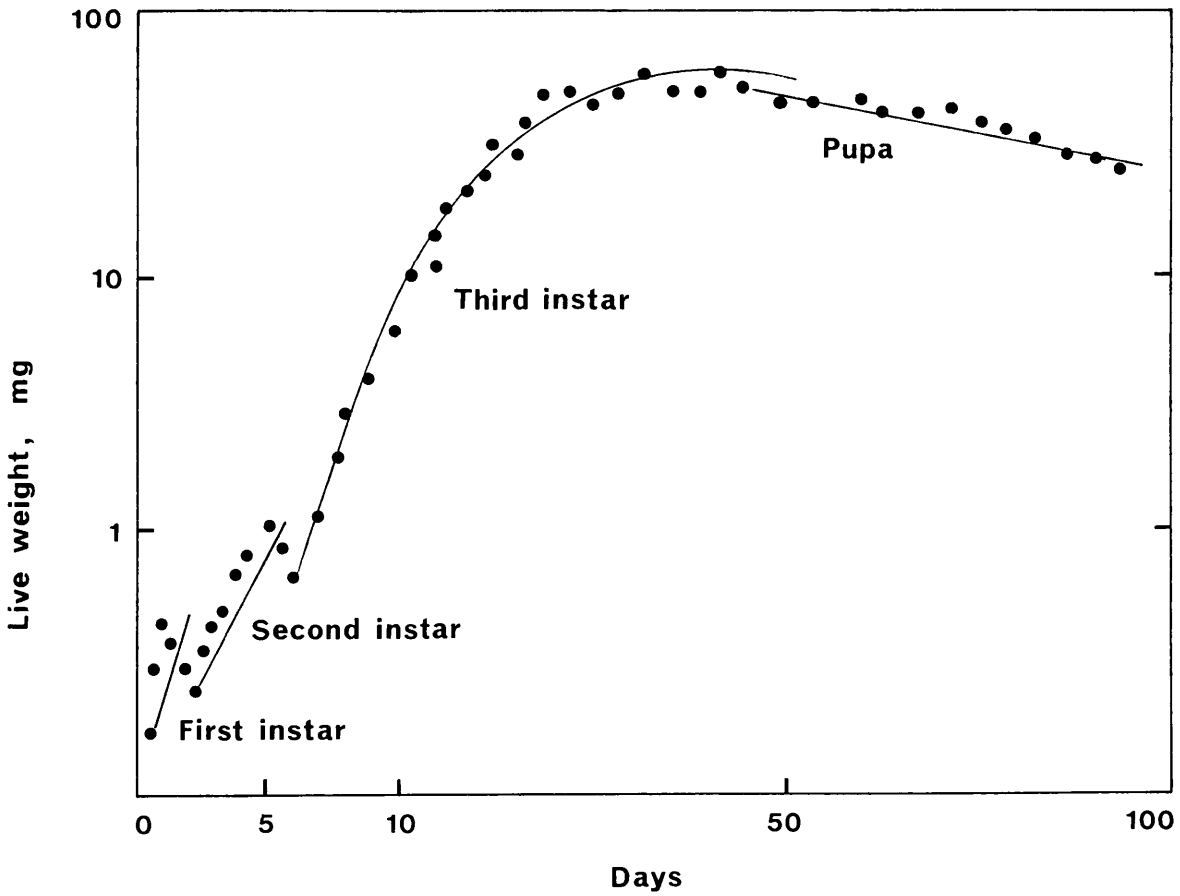

Figure 7.1. Growth of *P. dreuxi mirabilis* larvae at 10 °C and 100% RH.

Table 7.1 gives the mean (± SD) size, live mass and duration of each life stage of *P. dreux mirabilis*, at 10 °C.

Table 7.1. The mean (± SD) size, live mass and duration, at 10 °C, of the different life stages of *P. dreuxi mirabilis*.

Stage	n	Size (mm)	Live mass (mg)	Duration (days)
Egg	30	1.08 ± 0.02	0.23 ± 0.03	4.20 ± 0.92
Instar I	20	1.54 ± 0.67	0.38 ± 0.16	2.57 ± 0.08
Instar II	20	3.01 ± 1.05	0.83 ± 0.27	5.20 ± 1.94
Instar III	20	12.38 ± 4.49	20.48 ± 17.73	48.31 ± 5.02
Pupa	20	10.92 ± 0.86	60.39 ± 20.04	36.62 ± 18.60
Adult	30	8.50 ± 4.31	38.15 ± 13.27	15.96 ± 4.21

Phenology

All the wrack strings were found to shelter *P. dreuxi mirabilis* adults on the second day; one day later most of the fronds were covered with eggs. After deposition, wrack strings desiccated rapidly on days with little or no rain. Desiccation caused mortality of eggs and desertion of wrack strings by kelp fly larvae. Sustained precipitation softened the extremely tough and leathery fronds, and facilitated both their bacterial decay and temporary colonization by kelp fly larvae from surrounding wrack. When heavy surf extended the splash zone and inundated the wrack with seawater, several wrack strings were temporarily colonized by dense aggregates of amphipods.

In the wrack beds, larvae of all three instars were present throughout the sampling period, although third instar larvae dominated the larval biomass from the first day. The biomass of *P. dreuxi mirabilis* larvae in the protected wrack bed reached a peak of 27 g kg^{-1} kelp (dry mass) on day eight, declined to 8 g kg^{-1} on day 22 and remained fairly constant for the rest of the period (Fig. 7.2). The sharp decline in biomass after ten days can be explained by the dispersal of mature larvae to pupate up to 50 cm below the surface of the beach, but may also represent mortality in the artificial confines of the protected bed. The peak in larval biomass (Fig. 7.2) coincided with the peak in kelp temperature (Table 3.9), both occurring within a period of rapid decline in the dry mass of kelp. Stabilization of both kelp temperature and larval biomass concurred with the slower, constant decline in the dry mass of kelp.

The high larval biomass and resulting high consumption figure (see below) in the experimental wrack bed may partially be an artefact of the protective frame and grid, since the major predators of the larvae (feral house mice, *Mus musculus* and the lesser sheathbill, *Chionis minor*) were excluded. Flotation of kelp samples in warm water was an effective, and virtually the only practicable method, to extract the larvae from decomposed kelp, but it probably resulted in some water-soluble kelp detritus being lost. This may also have caused artificially high figures for larval biomass, since the latter was always expressed as a fraction of kelp biomass.

The decline in mass of the three kelp deposits (wrack strings, exposed and protected wrack beds) is shown in Fig. 7.3. The original dry mass of kelp in the exposed and protected wrack beds was 7.5 and 6 kg m^{-2}, respectively.

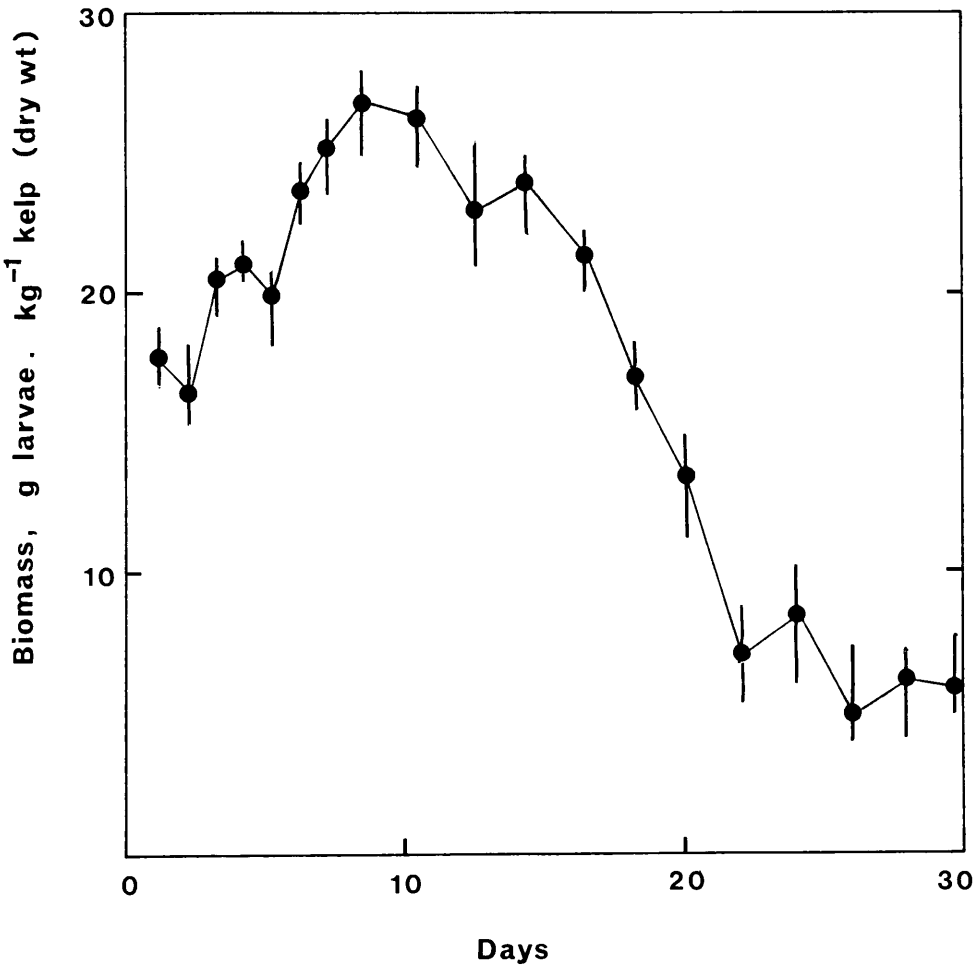

Figure 7.2. Temporal change in biomass of *P. dreuxi mirabilis* larvae in a protected, artificial wrack bed on Trypot Beach. Means and standard errors of means are shown; n = 5 cores in each sample.

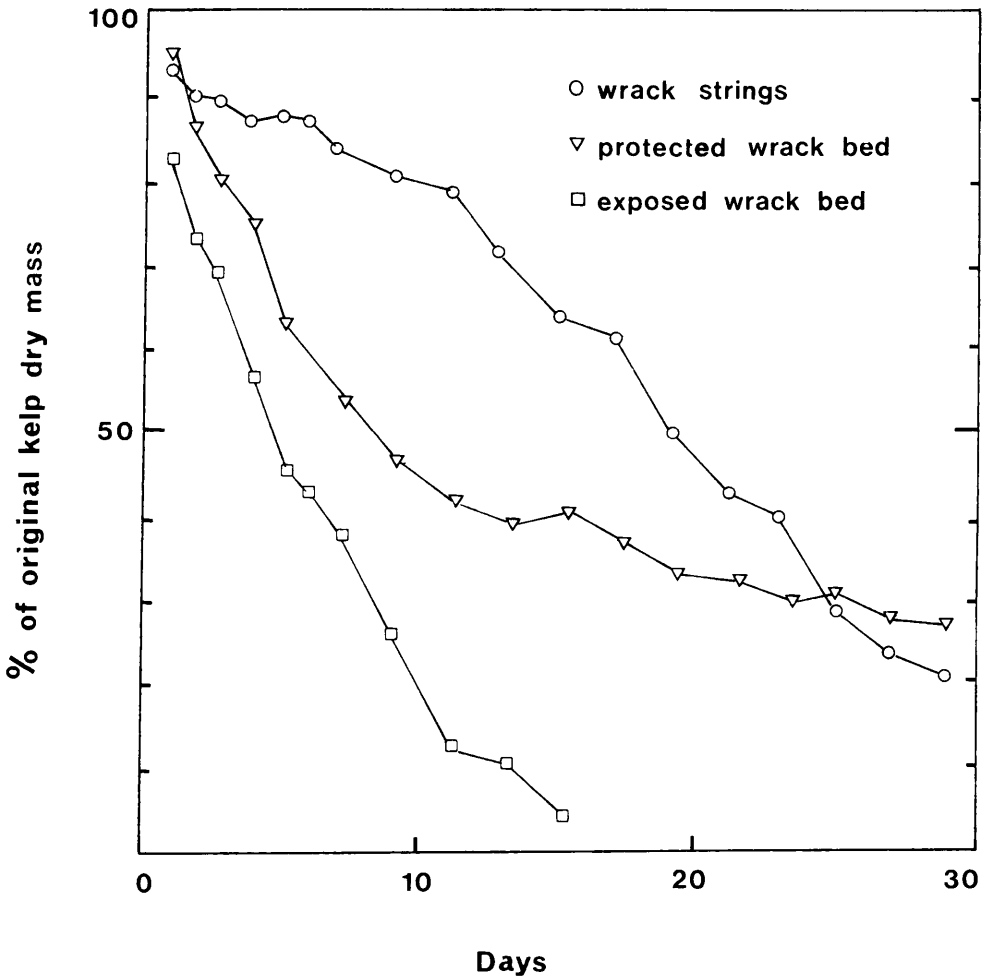

Figure 7.3. Decline in dry mass of kelp in three artificial kelp deposits on Trypot Beach.

The protected wrack bed had lost 65 % of its dry mass after 17 days. The subsequent slow rate of decline in the dry mass of this bed was probably also an artefact of the protective wooden frame which prevented scattering of kelp by vertebrates (seals and penguins) or wind.

The distribution and spatial abundance of amphipods and kelp fly larvae along a 10 m beach transect is represented schematically in Fig. 7.4. By this time (five weeks after the deposition of masses of kelp) only particulate kelp detritus remained between pebbles and boulders.

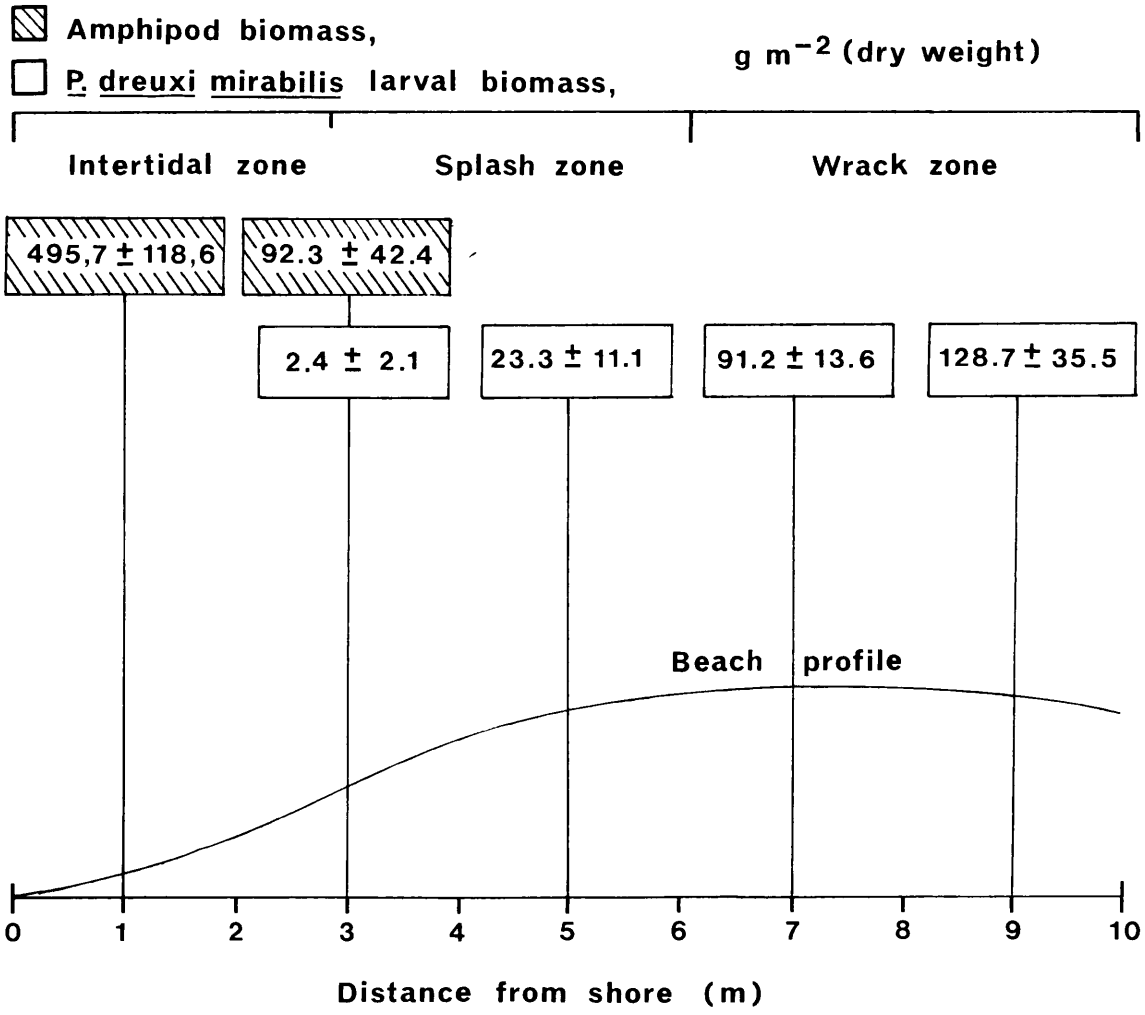

Figure 7.4. Biomass of amphipods and *P. dreuxi mirabilis* larvae in the interstitial biotope on Trypot Beach. Samples taken at 2 m intervals along a 10 m transect perpendicular to the shore.

7.3 Feeding ecology

7.3.1 Methodology

P. dreuxi mirabilis larvae were collected from decomposing kelp on Trypot Beach and taken to the laboratory, where they were sorted into instars. Individual larvae were weighed, and depending on their mass, 20 (first instar) to single (final instar) larvae were placed on weighed amounts of decomposing kelp scraped from the surface of a single, moderately decomposed frond. The kelp and larva(e) were placed in muslin-covered, 10 ml glass vials, and kept at 10 ^{o}C and 100% RH in an enclosed water bath. The kelp was placed against the sides of the upright vials to allow drainage of the watery faeces produced by the larvae. After 48 h the larvae and the kelp they had fed on were weighed, dried, and reweighed. During each feeding experiment, five vials containing only weighed amounts of kelp scraped from the same fronds, served as controls to correct for microbial decomposition of kelp during the feeding period. To obtain initial wet:dry mass ratios for the kelp being used as food, kelp scraped from the same frond was weighed immediately, dried to constant mass, and reweighed. All mass were determined on a Sauter AR 100 electronic microbalance, to 0.01 g.

Third instar *P. dreuxi mirabilis* larvae, and the kelp they had fed on during feeding experiments, were dried for 48 h at 60^{o}C, and the energy content of both the larvae and the kelp was determined using micro-bomb calorimetry (methods described in preceding chapters). In addition, the energy content of fresh kelp was determined to compare with that of the decomposed kelp actually utilized as food.

7.3.2 Results

Food consumption

Kelp consumption rate is plotted against larval live mass in Fig. 7.5. The parameters are related by the equation

$$y = 0.44\, x^{0.45} \quad \text{.....(1)}$$

where y = consumption rate (mg kelp (dry mass) larva^{-1} day^{-1}) and x = larval live mass.

Table 7.2 correlates the calculated consumption of *P. dreuxi mirabilis* larvae in the protected wrack bed with the decline in dry mass of the kelp in the bed, over a sampling period of 30 days. Total larval consumption in the wrack bed accounted for 35 % of the measured loss of dry mass of kelp over this period. Since 98 % of the total food intake of an individual *P. dreuxi mirabilis* larva is consumed during the third instar, and since third instar larvae dominated larval biomass from the first day, the effect of first and second instar larvae on the consumption figure would be negligible.

The wet:dry mass ratio of third instar larvae was 4:1, and that of the decomposed kelp used for feeding experiments was 6:1. The energy content of third instar *P. dreuxi mirabilis* larvae, and of fresh and decomposing *D. antarctica* fronds, is given in Table 7.3.

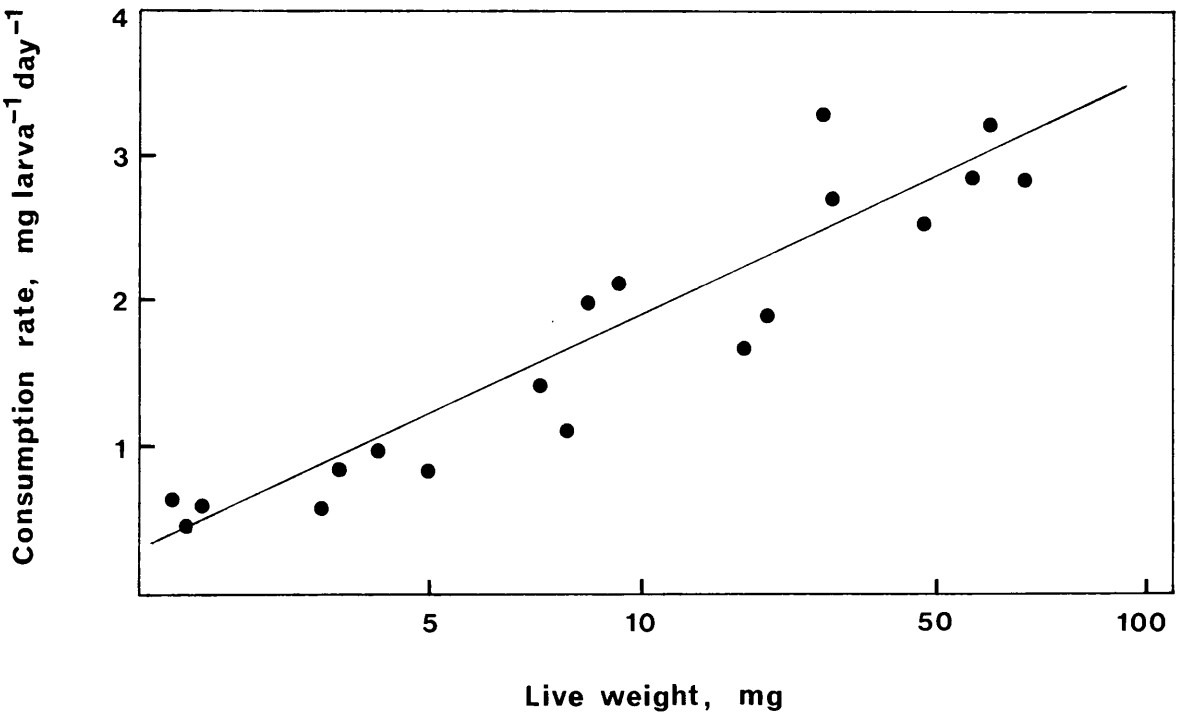

Figure 7.5. Absolute consumption of kelp (mg dry kelp larva^{-1} day^{-1}) by *P. dreuxi mirabilis larvae* at 10 °C and 100% RH.

Table 7.2. Consumption of kelp by *P. dreuxi mirabilis* larvae, compared to the actual decline in the dry mass of kelp in a *D. antarctica* wrack bed, over a period of 30 days. Larval consumption based on absolute feeding rate (Fig. 7.6); larval biomass (Fig. 7.3) and measured dry mass loss of kelp (Fig 7.4).

Day	Larval kelp consumption in wrack bed (kg)	Measured dry mass loss of kelp (kg)
1 - 10	0.78	3.18
10 - 20	0.45	0.60
20 - 30	0.21	0.30
Total	1.44	4.08

Table 7.3. Energy content of third instar *P. dreuxi* larvae and of fresh and decomposing *D. antarctica* fronds. n = number of determinations.

	kJ g^{-1}	n
Mature *P. dreuxi* larvae	22.30	5
Fresh *D. antarctica*	12.46	4
Decomposing *D. antarctica*	15.08	4

7.3.3 Discussion

The rate of kelp consumption by *P. dreuxi mirabilis* larvae was slow (0.15 mg kelp (dry mass) $larva^{-1}$ day^{-1}), compared to rates determined for other kelp-feeding Diptera of much smaller size. *Fucellia capensis* (Anthomyiidae) larvae grow to only about 10 mg compared to the 80± mg (live mass) of *P. dreuxi mirabilis* larvae, yet they daily consume almost twice as much kelp (up to 0.25 mg kelp (dry mass) $larva^{-1}$; Stenton-Dozey and Griffiths (1980)). Fresh kelp has very low energy (Table 7.3), and presumably also low nutrient content. Organisms that feed exclusively, or primarily, on nutrient or energy deficient food, have either a rapid feeding rate or prolonged development (e.g. Mattson 1980). *F. capensis* complete their larval stage within 12 days (Stenton-Dozey and Griffiths 1980) compared to the 50± days of *P. dreuxi mirabilis* (Table 7.1).

Haxen and Grindley (1985) stated that kelp thrown beyond the spray zone is decomposed by "a succession of bacteria," but gave no quantitative results. Bacterial populations on decomposing kelp fronds probably add substantially to the energy and nutrient intake of *P. dreuxi mirabilis* larvae, and the energy content of decomposed kelp was indeed substantially higher than that of fresh kelp (Table 7.3). It has often been shown

that the decay of kelp is more rapid, and of a different type, in wrack containing kelp fly larvae than in wrack without larvae, possibly because the larvae transfer and spread micro-organisms through their feeding activity (Stenton-Dozey and Griffiths 1980). It is clear that, as with the detritivorous *Pringleophaga* larvae, there exists a complex relationship between *P. dreuxi mirabilis* larvae, their food, and the decomposer micro-organisms they ingest during feeding. It appears likely that *P. dreuxi mirabilis* larvae directly utilize kelp microbes as food, since third instar larvae seldom burrow into kelp fronds, but feed mainly on and in the mucilaginous surface layers of kelp fronds.

The moisture content and salinity of freshly beached *D. antarctica* appear to be the major limiting factors in its colonization by primary decomposers (amphipods and kelp flies). Amphipods occur at much higher densities, and attain much higher biomass, than the *P. dreuxi mirabilis* larvae (Fig. 7.4) with which they co-exist. The amphipods occupy a different niche (*sensu* Arthur 1987), and attack mainly fresh wrack or wrack stranded in the surf zone. *P. dreuxi mirabilis* larvae tolerate immersion in sea water, and adult females may oviposit even on fresh wrack within the surf zone. However, the tough, leathery epidermis of fresh *D. antarctica* fronds precludes attack by kelp fly larvae, which can only burrow into partially decomposed fronds (i.e. after four to five days). Amphipods, on the other hand, graze and scarify the surface of fresh fronds. In the process, they "set off" bacterial decomposition and facilitate burrowing and feeding by early instar kelp fly larvae. A clear succession ensues, which ensures partitioning of the single resource between the two dominant, specialized kelp decomposers. This appears to be in contrast to the situation with *P. dreuxi* at Îles Crozet. Trehen and Vernon (1982) stated that *P. dreuxi* at Possession Island shows three distinct stages in its development: a first stage in stranded kelp, a second in the underlying pebbles, and a third stage 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. At Marion Island, larvae of all three instars were found simultaneously in both decomposing kelp and amongst the underlying pebbles. Mature *P. dreuxi mirabilis* larvae do migrate higher up on the beaches, but were seldom found as far as the adjacent vegetation, and no instance of cannibalism or predation was observed. Since larvae successfully completed their development in kelp only at Marion Island, predation in the field, if it occurs, is at most facultative or incidental. It is to be expected, however, that *P. dreuxi* populations at the two island groups should exhibit different life history traits, since they belong to different assemblages of invertebrates in the respective kelp decomposer guilds of the two islands (see Trehen *et al.* 1985).

P. dreuxi mirabilis larvae occasionally colonize and feed on seal and penguin carcasses on Marion Island's beaches (personal observation). However, this usually happens only during the height of summer, when the glut of carrion is in excess of what the vertebrate carrion feeders on the island can consume. At Possession Island, penguin and other bird carcasses are colonized not by *P. dreuxi*, but by three other Diptera species, none of which occurs at Marion Island: *Anatalanta crozetensis* and *Siphlopteryx antarctica* (Sphaeroceridae), and *Amalopteryx maritima* (Ephydridae) (Trehen *et al.* 1985). Not one of the three Possession species is confined to the island's beaches; all three occur in inland areas where there is organic enrichment of the vegetation by birds and seals. Since carcasses represent a spatially random and unpredictable resource, *P. dreuxi mirabilis* at Marion Island can be regarded at most as facultative, opportunistic necrophages.

7.4 Respiration

7.4.1 Methodology

P. dreuxi mirabilis larvae across the entire size range were collected in a wrack bed on Trypot Beach. The larvae were provided with food, and acclimated for 48 h in incubators set at the desired temperatures (5, 10, 15 and 20 °C). Before being put in cuvettes for the determination of oxygen consumption, the larvae were cleaned of mucus and faeces to prevent fouling of the needle of the oxygen analyzer. Up to five small (second instar) larvae, and single large (third instar) larvae were placed in a cuvette; the oxygen consumption of first instar larvae was not determined. The cuvettes were floated in a water bath set at the desired temperature, and the oxygen content of the air in each cuvette was determined after one hour (see 4.4.1 for detailed description of materials and methods).

7.4.2 Results

Effect of live mass on oxygen uptake

The mean live mass, and the oxygen consumption and metabolic rates of second and third instar *P. dreuxi mirabilis* larvae at 5, 10, 15 and 20 °C, are given in Table 7.4. The effect of live mass on the oxygen consumption and metabolic rates of *P. dreuxi mirabilis* larvae is shown in Figures 7.6 and 7.7, respectively.

Table 7.4. Mean (± SD) metabolic rates: ul O_2 g^{-1} hr^{-1} (M), respiration rates: ul O_2 ind^{-1} hr^{-1} (R), live mass: mg (W) and number of replicates (n) for second and third instar *P. dreuxi mirabilis* larvae at 5, 10, 15 and 20°C.

	5°C	10°C	15°C	20°C
Instar 2				
M	440.08 ± 244.21	1589.22 ±214.04	1303.26 ±333.72	23035.71 ±6006.56
R	1.61 ± 0.99	4.49 ± 1.40	3.97 ± 1.15	62.66 ± 18.12
W	3.60 ± 0.50	2.80 ± 0.80	3.20 ± 0.90	3.10 ± 1.50
n	5	6	7	6
Instar 3				
M	412.71 ± 126.03	1038.52 ±337.51	994.79 ±182.97	2012.86 ±958.24
R	11.25 ± 7.45	28.61 ± 11.11	22.23 ± 18.48	70.38 ± 15.17
W	25.70 ± 10.70	30.60 ± 14.10	20.80 ± 13.50	40.10 ± 15.16
n	22	10	14	18

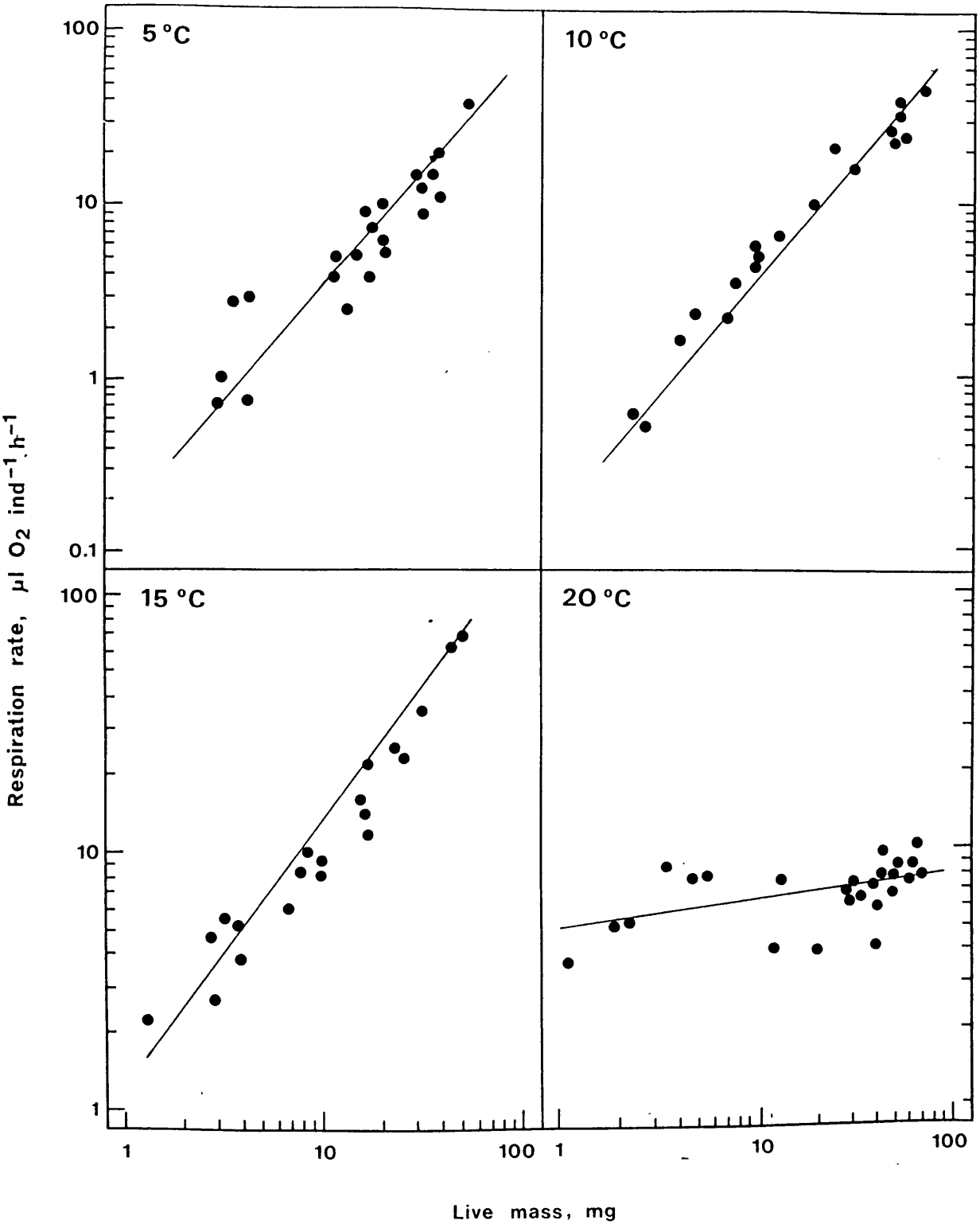

Figure 7.6. Effect of live mass on respiration rate of *P. dreuxi mirabilis* larvae at 5, 10, 15 and 20 °C. Individual points are shown together with the fitted regression line at each temperature.

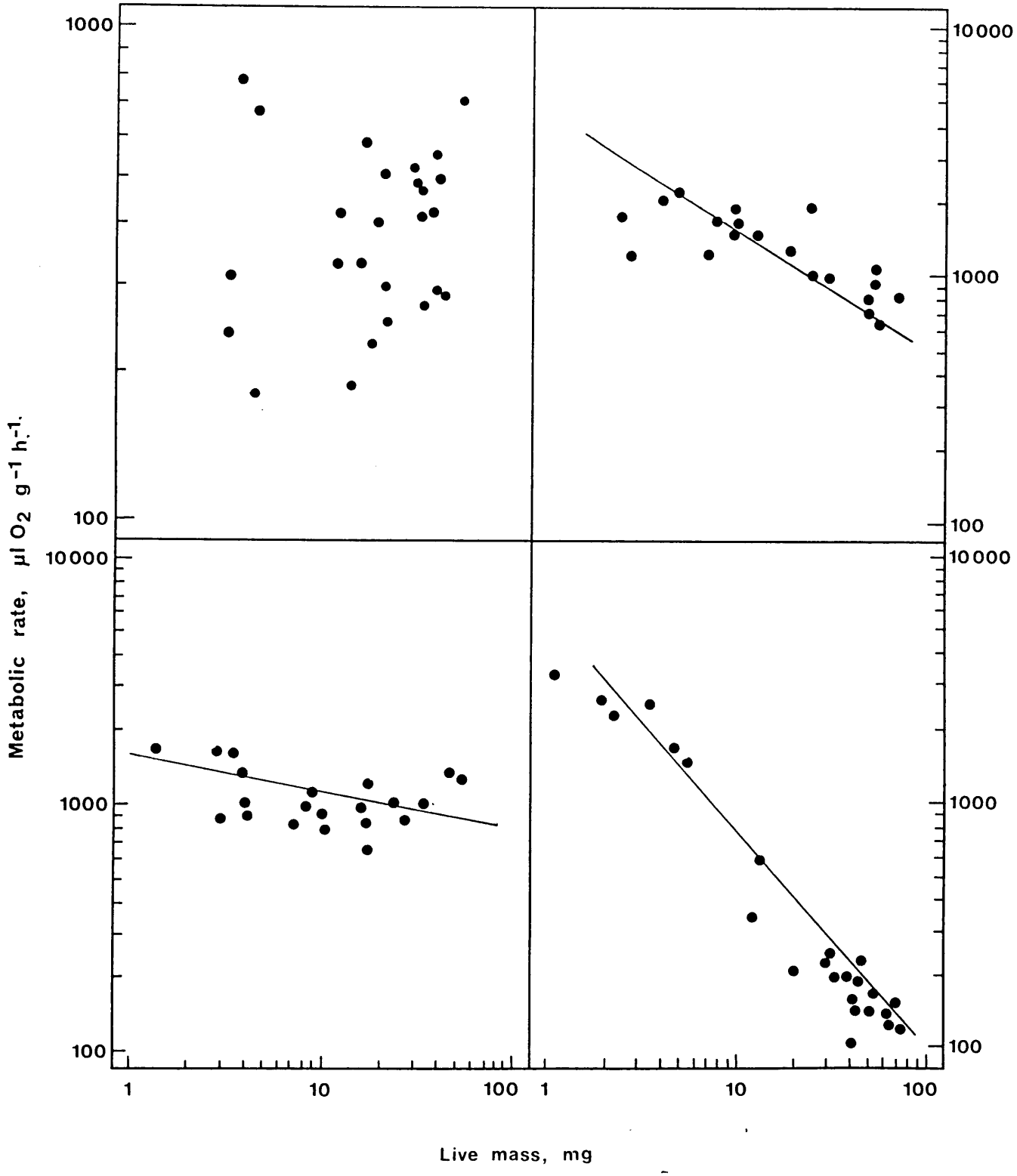

Figure 7.7. Effect of live mass on metabolic rate of *P. dreuxi mirabilis* larvae at 5, 10, 15 and 20 °C. Individual points are shown together with the fitted regression line at each temperature.

Regression equations of the double $\log_{10}$ plots relating (a) respiration rate (ul O_2 ind^{-1} hr^{-1}) and (b) metabolic rate (ul O_2 g^{-1} hr^{-1}) to larval live mass are given in Table 7.5.

Table 7.5. Linear regression equations of (a) $\log_{10}$ respiration rate on $\log_{10}$ live mass and (b) $\log_{10}$ metabolic rate on $\log_{10}$ live mass at 5, 10, 15 and 20 °C for *P. dreuxi mirabilis* larvae (second and third instars).

	Temperature (°C)	n	a	b ± SEM	r	r^2
(a)	5	26	0.441	1.094 ± 0.090	0.924	0.854
	10	19	0.438	0.834 ± 0.034	0.986	0.972
	15	20	0.457	0.919 ± 0.055	0.968	0.937
	20	29	0.301	0.107 ± 0.038	0.469	0.220
(b)	5	26	440.600	0.094 ± 0.090	0.205	0.042
	10	19	438.000	-0.166 ± 0.034	-0.757	0.573
	15	20	457.000	-0.081 ± 0.055	-0.320	0.102
	20	29	301.400	-0.893 ± 0.038	-0.976	0.953

At 10 °C, respiration rate and larval live mass were related by the equation

$$R = 0.44\, W^{0.83} \quad \text{.....(2)}$$

where R = respiration rate and W = larval live mass. This equation was later used to determine cumulative respiration in the construction of an individual energy budget (section 7.5).

Effect of temperature on oxygen uptake

The mean respiration and mean metabolic rates of second and third instar *P. dreuxi mirabilis* larvae are plotted against temperature in Fig. 7.8. The effect of temperature on the metabolic rates of second and third instar *P. dreuxi mirabilis* larvae is shown as Arrhenius plots in Fig. 7.9. The regression lines fitted to the Arrhenius plots in Fig. 7.9 are those of $\log_{10}M$ against $1/T^{\circ}K \times 10^3$. The corresponding regression equations (derived on a natural log basis) are given in Table 7.6.

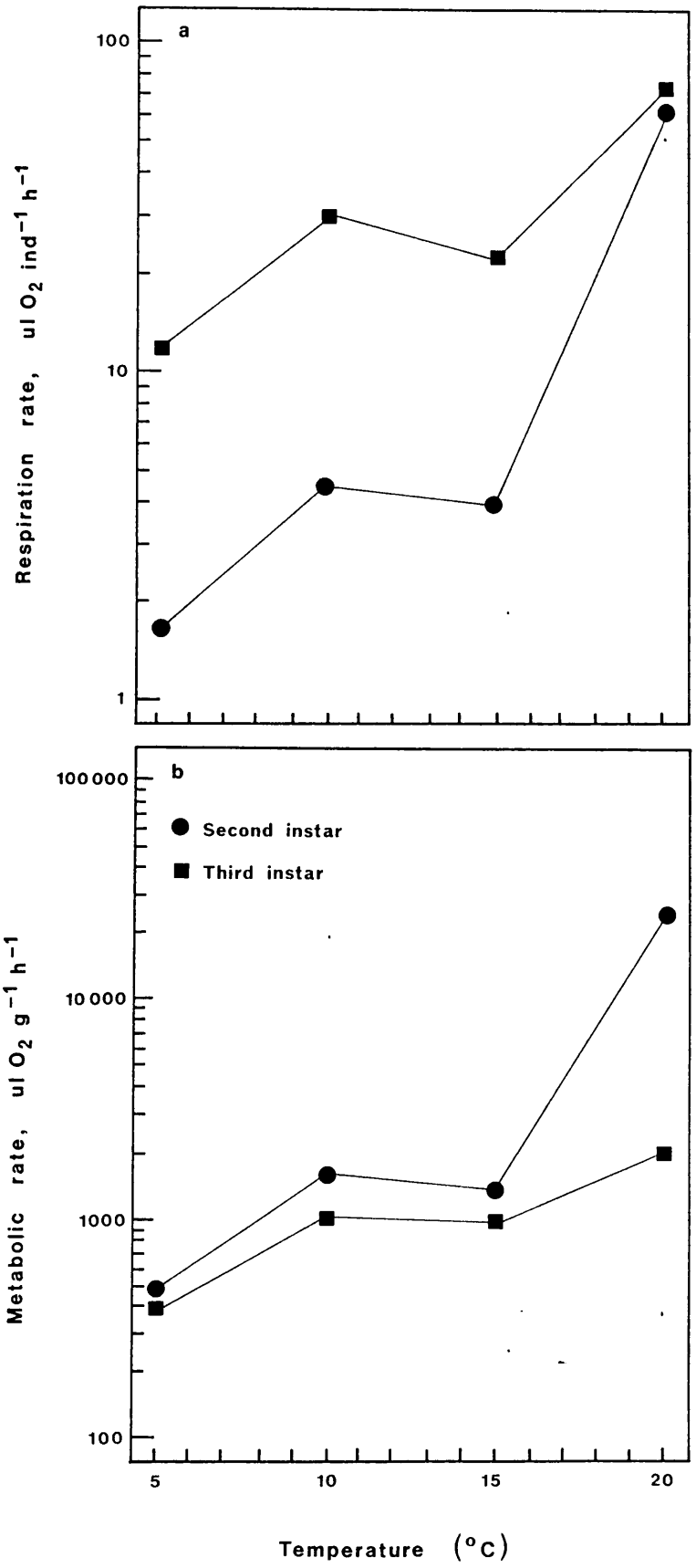

Figure 7.8. Effect of temperature on (a) mean respiration rate and (b) mean metabolic rate of second and third instar *P. dreuxi mirabilis* larvae.

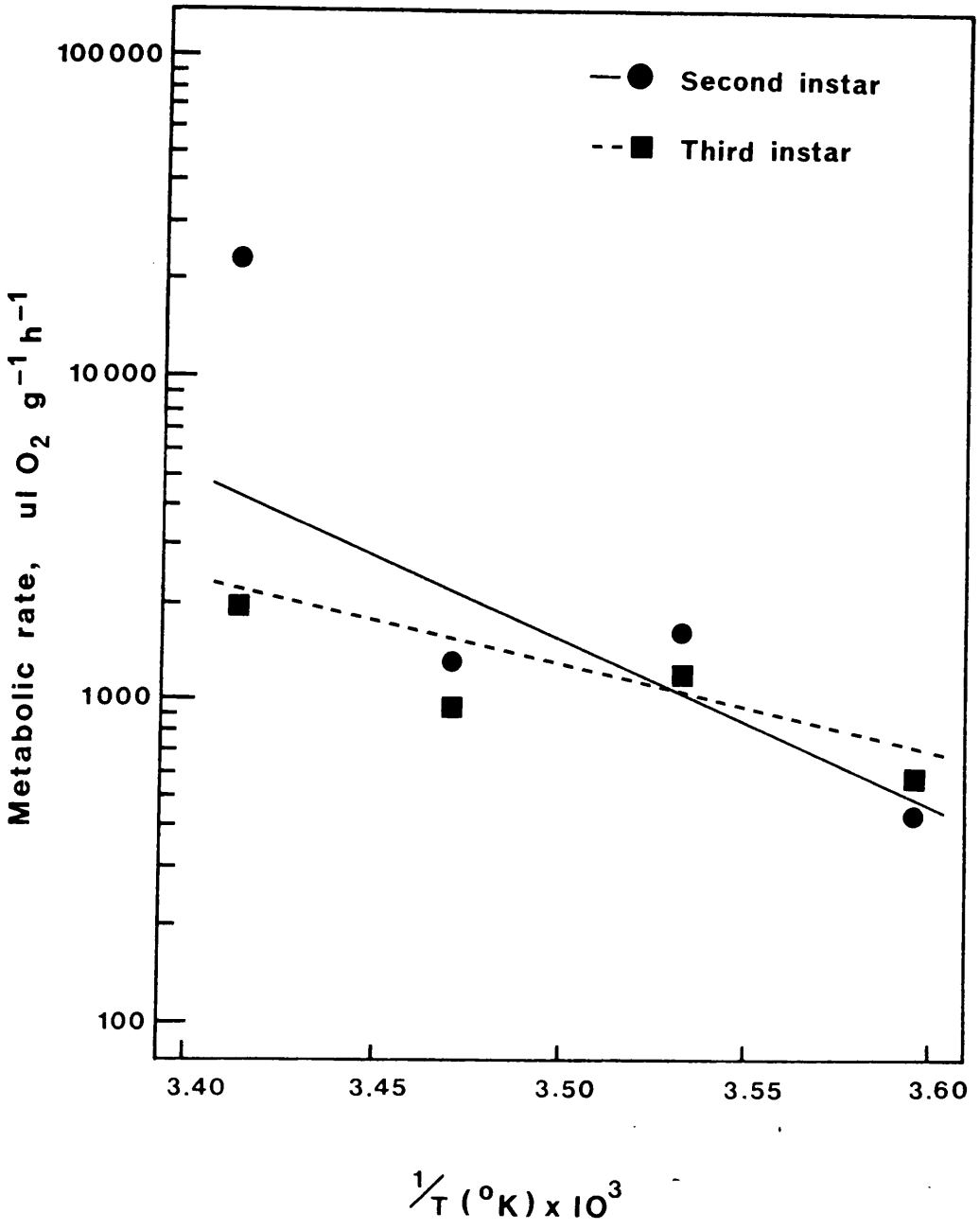

Figure 7.9. Arrhenius plots of metabolic rate (M) on temperature (T) for second and third instar *P. dreuxi mirabilis* larvae. The fitted regression lines are shown of $\log_e M = a.e^b$, with a and b of each size class taken from Table 7.6.

Table 7.6. Linear regression equations of $\log_e$ metabolic rate on 1/T (°K) for Arrhenius plots of second and third instar *P. dreuxi mirabilis* larvae.

Instar	n	a	b ± SEM	r
II	24	2.934×10^5	-8.433 ± 2.659	-0.913
III	70	9.592×10^2	-3.945 ± 1.127	-0.927

The activation energies for second and third instar *P. dreuxi mirabilis* larvae were derived from the values of b in Table 7.5 (Precht *et al* 1973; see 4.4.2). Metabolic Q_{10} values were calculated from mean metabolic rates. The Q_{10} and activation energies of second and third instar *P. dreuxi mirabilis* larvae are given in Table 7.7.

Table 7.7. Activation energies and Q_{10} values for the ranges 5-10, 10-15, 15-20 and 5-20 °C, for second and third instar *P. dreuxi mirabilis* larvae.

Instar	Activation energy (kcal mol^{-1})	Q_{10} 5-10	10-15	15-20	5-20	Mean live mass (mg)
II	16.697	13.040	0.711	29.542	14.011	3.206
III	7.811	6.333	0.864	4.350	2.878	29.313

7.4.3 Discussion

Like the insect species described in the preceding chapters, *P. dreuxi mirabilis* larvae had relatively slow rates of oxygen consumption, although respiration of small (second instar) larvae at 10 and 15 °C (Table 7.4) was comparable to that of similar-sized *Fucellia capensis* kelp fly larvae at 18 °C (Stenton-Dozey and Griffiths 1980). Respiration rates of *P. dreuxi mirabilis* larvae were similar at 10 and 15 °C, where the coefficient b (scaling respiration with live mass) was 0.83 and 0.92, respectively (Table 7.5). At these two temperatures, differences in live mass explained virtually all (97% and 94%, respectively) the variation in respiration rates, and the optimum temperature for the species once again appears to lie between these two temperatures. This contention is borne out by the low Q_{10} from 10 to 15 °C (Table 7.7).

There was no correlation between live mass and metabolic rate of *P. dreuxi mirabilis* larvae at 5 °C, which temperature may approach the lower limit of tolerance for the larvae. Metabolic rates, like oxygen consumption, did not differ significantly between 10 and 15 °C (Table 7.4). There were massive increases in metabolic rate from 5 - 10 and from 15 - 20 °C, however (Table 7.7). This implies a threshold for metabolic activity at a temperature greater than 5 °C, and metabolic breakdown at temperatures in excess of 15 °C. *P. dreuxi mirabilis* thus appears to be the most stenothermic of the four species described in this thesis,

which is not surprising in view of the extremely stable temperature regime it is exposed to (see Table 8.1). Daily ranges in temperature inside a wrack bed are not available, but it is unlikely that temperatures inside the wrack would show large short-term fluctuations similar to those recorded in *P. cookii* tussocks, for instance (Table 3.1). In addition, the oceanic influence on the macroclimate of the island is more pronounced on the coast, so that ambient temperatures are buffered from fluctuations that may occur in inland habitats.

P. dreuxi mirabilis has the fastest developmental rate of all the species studied, attaining comparable biomass at a fraction of the time required in other species. It is therefore not surprising that it should have metabolic rates substantially higher than that of any of the other species studied (e.g. 1 038 ul O_2 g^{-1} h^{-1} for mature larvae at 10°C, compared to only 159 ul O_2 g^{-1} h^{-1} for mature *P. marioni* larvae at the same temperature; see Table 8.3).

7.5 Energy flow

Individual larval energy budget

The mass and energy budget for a *P. dreuxi mirabilis* larva, from hatching to pupation, is shown in Table 7.8. Total ingestion over the larval lifetime was calculated from the general equation relating food consumption rate to larval live mass at 10 °C (equation (1)). Total larval oxygen consumption was calculated from equation (2). The watery faeces produced by the larvae, which was difficult to distinguish from kelp mucus, made quantification and direct calculation of egestion - and hence assimilation - impossible. Assimilation was therefore calculated indirectly, as the sum of production (P) and respiration (R). Production was taken as the mean maximum live mass attained by *P. dreuxi* larvae in each of the three instars (Table 7.1). An energy equivalent of 20.50 kJ $liter^{-1}$ O_2 was used throughout to convert respiration to energy output. Energy equivalents for *P. dreuxi mirabilis* larvae and decomposing *D. antarctica* were taken from Table 7.3.

Table 7.8. Individual mass and energy budget for a *P. dreuxi mirabilis* larva. See text for explanation of calculations.

Life stage		Ingestion (I) g	Production (P) g	Respiration (R) ml	Assimilation (A) g
Instar	I	0.001		0.008	
Instar	II	0.002	0.0002	0.047	
Instar	III	0.083	0.0204	5.393	
Total	g	0.086	0.0206	5.448 (ml)	
	kJ	1.918	0.4680	0.111	0.579

Table 7.8 shows that the first and second instars contribute minimally to the total amount of energy turned over during the larval lifetime: the third instar accounts for 96.51% of the total amount of food consumed, and 98.99% of the total amount of energy respired. Food energy assimilated during larval development represents 30% of the energy ingested, according to indirect calculation (A = (P ± R)/I) from the energy equation. This is identical to the assimilation efficiency recorded for *Fucellia capensis* larvae feeding on the kelp *Ecklonia maxima* on the South African coast (Stenton-Dozey and Griffiths 1980). The 24 % efficiency of conversion of ingested food (ECI, or gross growth efficiency; P/C) for *P. dreuxi mirabilis* larvae is higher, however, than the 17% recorded for *F. capensis* (Stenton-Dozey and Griffiths 1980).

The energy relations of a *P. dreuxi mirabilis* larva are shown graphically, in the form of an energy flow diagram, in Fig. 7.10.

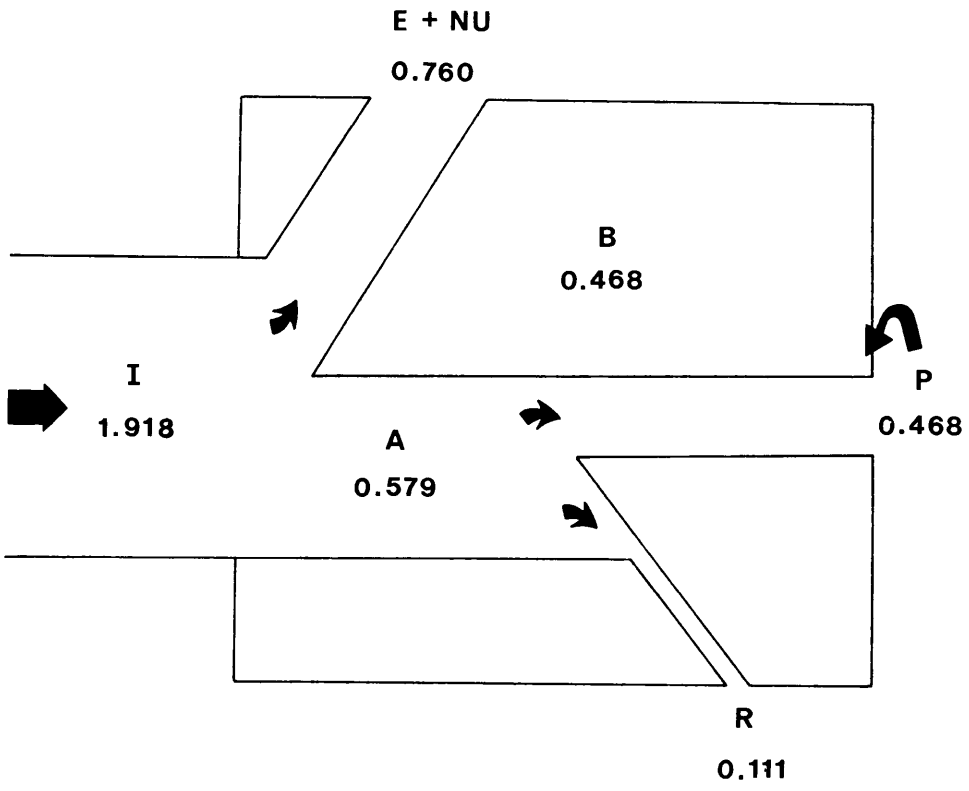

Figure 7.10. Energy budget for a *P. dreuxi mirabilis* larva. Units are kilojoules.

Larval population energetics

Because *P. dreuxi mirabilis* larval populations fluctuate randomly both in space and in time, with kelp deposition, energy flow per unit of time and area (kJ m^{-2} yr^{-1}) is difficult to calculate. From Table 7.2, however, it can be seen that larvae may consume as much as 35 % of the total dry mass of a wrack deposit. With an assimilation efficiency of 30 %, *P. dreuxi mirabilis* larvae would then account for approximately 10.5 % of energy flow in a wrack bed. This figure is probably unrealistically high, since it was derived from results obtained with an artificially constructed, protected wrack bed. The majority of energy flow may also be accounted for by microbes involved in the feeding, digestive and assimilation processes of *P. dreuxi mirabilis* larvae, rather than by the larvae themselves.

The high population densities, and the resultant large population biomass reached by *P. dreuxi mirabilis* larvae in kelp deposits, represent a substantial energy resource for secondary consumers such as feral house mice and sheathbills (*Chionis minor*). The contribution of kelp fly larvae to the nutrition and energy intake of these predators, and the role of the latter in energy flow in the littoral biotope, have probably been underestimated in the past.

7.6 Evolutionary perspectives

P. dreuxi mirabilis is clearly of South American origin (Seguy 1971), probably having been dispersed westwards by the westerly drift. As such, it is the only endemic species which does not have its closest zoogeographical affinities within the South Indian Island Province of the sub-Antarctic. Speciation in the genus *Paractora* has occurred in each of its disparate areas of distribution (Seguy 1971).

The arthropod decomposer guilds of stranded kelp usually have high species richness and diversity (e.g. Strenzke 1963, Dobson 1976). The kelp decomposer guild at Marion Island is indeed also more diverse than any of the terrestrial consumer guilds that have been examined for the purpose of this study. Because of the relatively favourable (or at least very stable) temperature regime inside a wrack bed (Table 3.9), and the relatively high species richness of the kelp decomposer guild, it may be expected that biotic interactions are more important than physical factors in shaping the ecological strategies and life history traits of the guild members. Such a scenario was predicted by Hairston *et al.* (1960), who stated that "Interspecific competition must necessarily exist" among populations of decomposers.

Using the example of Darwin's finches, Arthur (1987) has argued that *lack* of interspecific competition is an important cause of evolutionary shifts. Compared to the evolutionary conservatism of endemic (to the SIP) species such as *Embryonopsis halticella*, *Paractora* species indeed show a greater propensity for undergoing evolutionary shifts. The idea that, in spite of the relatively high biotic diversity of kelp decomposer guilds, lack of interspecific interactions has been the major factor in evolution in the sub-Antarctic, will be more fully explored in Chapter 8.

PART III: THE UPSHOT

"...it is to be emphasized that although patterns may underlie the rich and varied tapestry of the natural world, there is no single simple pattern. Theories must be pluralistic."

May (1974)

CHAPTER 8: SYNTHESIS

The organism is a compromise. The result of natural selection is adequacy and not perfection.

Bennett (1987)

8.1 Introduction

Holm (1989) pointed out that, in spite of advances in our knowledge of the genetic mechanisms of adaptation in animals, we still know surprisingly little about what animals adapt *to*. Southwood's (1977) "habitat templet" did focus attention on the pervasive influence of habitat on the life history traits and "ecological strategies" of organisms, but recently E. O. Wilson still stated that "The key remaining questions of evolutionary biology are more ecological than genetic in nature" (Wilson 1987). Ecological situations in which organisms find themselves, and which form the templet on which their life strategies are constructed (to which they adapt, *sensu* Holm 1989), are staggeringly complex and unstable. Even apparently uniform and predictable habitats may conceal a spatial and temporal mosaic of microhabitats, which defy any construct of pattern. The fact is, however, that the biota respond to a complex environment with a limited number of recognizable strategies (Holm 1989). These strategies have traditionally been assigned "positions" along the r-K continuum, the extremes of which are usually equated with "generalization" and "specialization", respectively (Holm 1985). Greenslade (1983) added the A (adversity selection) vector to the r-K gradient, which provided an explanation for the combination of r- and K-selected attributes in insects occurring in marginal or "adverse" situations (Greenslade 1983; Block 1985; Crafford *et al.* 1986). Many combinations of life history attributes can still not be explained satisfactorily, however (Holm 1989), chiefly because not all the trade-offs involved can be identified. The importance of trade-offs in modelling life histories has often been emphasized (e.g. Sibly and Calow 1986, Karlsson and Wickman 1989). Trade-offs occur between the environment, the ecological and evolutionary history, present ecological situation, physiological constraints and genetic potential of a species. A combination of such trade-offs ("adaptations," but see criticism such as that of Brooks and Wiley (1987) of "adaptationism") confers fitness on the individuals of a species to survive and reproduce in a given selective situation. The selective situation at issue here is, superficially, the terrestrial sub-Antarctic. The five insect species described in the previous chapters all inhabit the same macro-environment, but even phylogenetically close species such as the two Lepidoptera (*E. halticella* and *P. marioni*) have dissimilar life histories and ecological strategies. This appears to be the result, to a large extent, of differences in the restraints exercised upon them by the living and non-living components of their respective environments, although the differing restraints of their respective histories (both evolutional and ecological) are probably paramount.

The most important trade-off in any ecological situation appears to be that between current and future reproduction (shortened or prolonged life; Karlsson and Wickman (1989)). Timing of reproduction is determined by the adversity/favourability and predictability/unpredictability aspects of habitat (Southwood 1977). The evolutionary mechanisms which underly changes in developmental timing (heterochrony) have been explored by, amongst others, Holm (1985).

In this chapter, the environmental restraints (after Holm's (1989) categorization) that operate on each of the five species will be identified and compared, through qualitative and quantitative analysis of the respective micro-environments of the five species. The life histories and ecological energetics (patterns of energy flow) of the five species will then be compared. The combination of life history traits shown by each species will be tested against Holm's (1989) interaction matrix of environmental restraints and life history traits. Possible evolutionary mechanisms for the development of the particular life strategies of the five species will be discussed.

8.2 Environmental restraints

8.2.1 Biotic restraints

MacNally (1983) defined interaction between species as the active (e.g. interference or territoriality) or passive (e.g. exploitation) denial of access to resources by one species to another. The detection of interaction requires that the pattern of usage of resources by one or both of the species is altered as a result of the other species. Interaction *per se*, however, does not necessarily lead to competition (MacNally 1983). Any interspecific interaction, and competition in particular, is notoriously difficult to detect and often impossible to prove (e.g. Arthur 1987), yet the "classical view" (after Gause (1934)) is still that competition is an important cause of evolutionary change. Arthur (1987) has argued convincingly that *lack* of competition has significance in evolution, and I have previously applied this argument to the situation on sub-Antarctic islands (Crafford *et al.* (1986); see also Chown (1989c). Davies (1987) did provide evidence for interspecific competition between two *Amblystogenium* species (Coleoptera: Carabidae) co-existing on Ile de la Possession, and Trehen *et al.* (1985) have referred to the "strong competitive ability" of *Phreodrilus crozetensis*, which co-exists with the kelp fly *Paractora dreuxi* in kelp deposits at Ile de la Possession. It is generally not doubted that interspecific competition determines guild, and ultimately community, structure (Hairston *et al.* 1960; Arthur 1987).

The paucity of the Marion Island biota severely limits the opportunities for any type of interspecific interaction. (Predation by feral house mice is excluded from this discussion, since it may be of too recent origin to have been met by an evolutionary response in prey species; but see Chapter 6, section 6.1). The guilds most likely to be shaped by interspecific competition are the decomposer guilds to which *P. dreuxi mirabilis* and *P. marioni* larvae belong (see Hairston *et al.* 1960). Lack of evidence for competition between species of these (and the other) guilds does not mean that the possibility of its occurrence is discounted. The consumer guilds dominated by the four species treated in this thesis seldom include more than one or two other species, however. For this reason, and because of the extremely high densities reached by populations in favourable habitats, intraspecific interactions may exercise more important biotic restraints than interspecific interactions. Cannibalism has been observed in *P. marioni* larvae (pers. obs.). *E. halticella* larvae are usually evenly spaced within a tiller of grass, which suggests intraspecific competition for food and/or space. In general, however, biotic interactions can be stated with some certainty not to be a major environmental restraint. This is borne out by the lack of specialized structures and biotic adaptations

in each of the species under review. The Curculionidae (Ectemnorhinini) complex on the island may be an exception, and it is conceivable that interspecific competition could have contributed to character displacement and radiation in ancestral species of the present species complex (see Chown 1989b).

8.2.2 Abiotic restraints

Holm (1989) distinguished between qualitative and quantitative aspects of the abiotic environment which may restrict life. Environments that are *physically* (qualitatively) restrictive, are usually so because they limit the accessibility and/or utilization of resources (energy or nutrients). *Resource restraints* can therefore be said to operate in such environments.

Table 8.1 compares the mean daily temperature, and the mean and maximum daily temperature range, in the microhabitats of each of the four dominant insects described in this thesis. Although it should be emphasized once again that "means" do not necessarily have ecological significance, Table 8.1 may serve as a guideline for determining how microhabitat temperature quantitatively (stable/predictably or fluctuating/randomly) acts as an environmental restraint.

All environmental restraints are, by definition, "adverse," in that they limit the options of the biota. The notion of temperature adversity is rather anthropocentric; the question arises whether a temperature regime under which an organism still functions and reproduces can justifiably be termed "adverse" to the organism. The only objective criterion is that resources should be available to life at an expenditure less than the resource gained (Holm 1989). If an organism in an "adverse" environment manages to maintain its resource gain at a level above its resource expenditure (and they all obviously do), environmental adversity becomes a murky concept. In the present context, adversity may perhaps best be regarded as the "absence of favourability." Although the temperatures shown in Table 8.1 are very similar, it is clear (and probably not insignificant) that the two herbivores experience the greatest temperature range in their microhabitats, which presumably increases the "amount of favourability" (i.e. the incidence of favourable periods). The criterion for favourability, in this context, would be the temperature range at which enzymes involved in the digestion of green foliage can function.

Table 8.1. The mean daily temperatures, and the mean and maximum daily temperature ranges in the microhabitats of each of the four dominant insect consumers at Marion Island (from Chapter 3). n.d.: not determined.

Species	Mean daily microhabitat temperature (°C)	Mean daily range (°C)	Maximum daily range (°C)
E. halticella	9.45	8.96	26.90
E. similis	9.22	7.90	18.00
P. marioni	8.12	6.32	16.10
P. dreuxi mirabilis	8.23	n.d.	11.00

Quantitative aspects of the abiotic environment which restrict life may be of greater evolutionary significance than purely physically restrictive aspects. Holm (1989) distinguished between randomness and cyclicity of niche (*sensu* Arthur 1987) favourability ("entropical" and "continuity" restraints, respectively). Entropical restraints are caused by spatial and temporal *unpredictability* of niche favourability, while any *discontinuity* in the environment in time or space poses continuity restraints (Holm 1989).

Species invariably have "packages" of life history traits and ecological strategies, the composition of which reflect the differing extents to which they are subjected to the four basic environmental restraints (biotic, continuity, entropical and resource: Holm (1989)). For purely operational purposes, the predominant restraint on each of the four species is identified below; its correspondance (or non-correspondance) with expected life history trait "packages" will be explored in section 8.3.

E. halticella, in spite of seasonal fluctuations in nutrient content of its host and random diurnal fluctuations in microhabitat temperature, lives in an essentially predictable and continuous environment, as does *P. marioni*. These two species can thus be regarded as operating primarily under resource restraints. *E. similis*, with its life cycle linked to the seasonal occurrence of high-nutrient food, in addition operates under continuity restraints. *P. dreuxi mirabilis*, which depends on random deposition of wrack to support its populations, operates to some extent under entropical restraints. Entropic environments inevitably include the restraint of discontinuity, and entropic restraints may be represented as an extension of discontinuity restraints (Holm 1989). All else being equal, the latter two species may therefore be predicted to share certain life history traits in spite of their markedly different life styles.

Table 8.2 (modified from Holm (1989)) lists expected life strategies under the different environmental restraints:

Table 8.2. Expected life strategies under different environmental restraints (after Holm (1989).

	Restraints		
Biotic	*Continuity*	*Entropical*	*Resource*
specialization	paedogenesis	generalism	variabilty
competitiveness	cyclic migration	high vagility	retarded growth
ecological efficiency	nesting	episodic migration	long life cycle
defensive/aggressive adaptations	storage	search behaviour	neoteny
	rythmic behaviour	opportunistic life cycles	parthenogenesis
investment in information	modulated life cycles	high fecundity/ quiescence	loss of vagility
	high fecundity/ dormancy		reduced fecundity
			adaptations to physical environment

8.3 Comparative life histories and ecological energetics

A comparison of the life history traits of the four species under discussion has to take into account the inherent differences between taxa. Each species is therefore measured against other, temperate species in the same higher taxon (family or order). Salient features of the life histories of the four species are summarized and compared in Table 8.3.

Table 8.3. Comparative life history characteristics of the four dominant insect consumer species at Marion Island.

	E. halticella	*E. similis*	*P. marioni*	*P. dreuxi*
Life history traits:				
Habitat tolerance	specialist	generalist	generalist	specialist
Feeding	specialist	generalist	generalist	specialist
Body size	intermediate	large	large	large
Vagility	low	low	low	low
Life cycle	intermediate	intermediate	long	long
Fecundity	high	low	low	high
Maturity	delayed	intermediate	delayed	delayed
Developmental rate	intermediate	intermediate	slow	slow
Seasonality	intermediate	pronounced	none	none
Phenotypical variability	low	high	high	low
Adaptation to biota	poor	intermediate	poor	poor
Adaptation to physical conditions	good	good	good	good

Important aspects of the ecological energetics of the four species are summarized and compared in Table 8.4. The metabolic rates of the four species (Table 8.4) correspond exactly with their developmental rates and life cycle lengths when the four species are compared with one another. *P marioni* and *P. dreuxi mirabilis* represent the slow/long and rapid/short extremes, respectively, while *E. halticella* and *E. similis*

have intermediate life cycle lengths and developmental rates. As is to be expected, the assimilation efficiencies of the two detritus feeders are low, while those of the two herbivores are extremely low compared to other folivores.

Table 8.4. A comparison of important aspects of the energetic ecology of the four dominant insect consumer species on Marion Island. Data pertain only to mature larvae in the case of *E. halticella*, *P. marioni* and *P. dreuxi*; and to adults in the case of *E. similis*. For polyphagous species, ecological efficiencies on their major food plants are given. n.d.: not determined.

	E. halticella	*E. similis*	*P. marioni*	*P. dreuxi*
Mean metabolic rate at 10^0C ($ulO_2\ g^{-1}h^{-1}$)	709.70	755.05	159.79	1038.52
Energy assimilation efficiency at 10^0C (%)	61.01	57.00	16.11	30.00
P/C (gross growth efficiency or ECI; %)	15.14	n.d.	n.d.	24.00

Tables 8.3 and 8.4 clearly show that each species exhibits a combination of traits which conform neither to the "packages" of traits that characterize the extremes of the r-K-A continuum, nor exactly to the life strategies predicted by Holm (1989; Table 8.2) for the four basic environmental restraints. However, the majority of traits conform, overwhelmingly, to those predicted by Holm (1989) for resource restraints (Table 8.2). The operational value of Holm's predictive table (Table 8.2) is shown by the fact that the two species postulated to operate partially under continuity and entropical restraints (*E. similis* and *P. dreuxi mirabilis*, respectively), each exhibit some of the strategies predicted under such restraints in Table 8.2 (e.g. cyclic migration and opportunistic life cycles, respectively).

8.4. Matrix of environmental restraints and life histories

In Fig. 8.1, the life history trait "packages" of the four species are plotted on a "restraint matrix." The X and Y axes respectively represent the quantitative (stability/ unpredictability) and qualitative (adversity/ favourability) aspects of the environment.

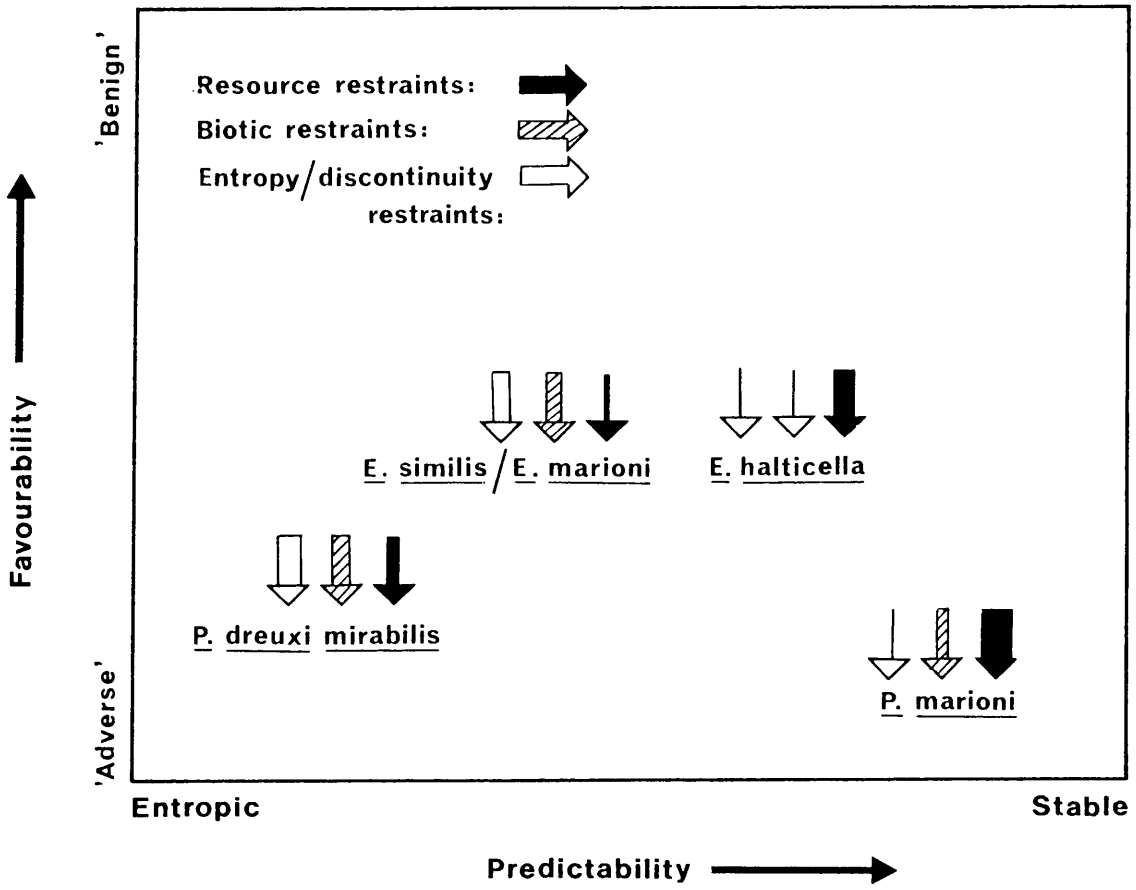

Figure 8.1. The "packages" of life history attributes of the four dominant insect consumers at Marion Island, plotted against qualitative and quantitative restraints of the environment. The width of the arrows reflect the surmised intensity of the restraints on each of the four species.

8.5 Evolutionary modes and mechanisms

If it is accepted that insect species at Marion Island are subjected chiefly to resource restraints, as the preceding sections indicate, it can be assumed that physiological economy should be at a premium, especially during development. Physiological economy requires reduction of "burdenless" structures (i.e. low-information "adult" structures; Holm (1985)). Under environmental conditions in the sub-Antarctic, there will be continuous "pressure" to achieve an adequate phenotype with the least expenditure of energy. Cossins and Bowler (1987) remarked that Antarctic species have evolved a particular suite of adaptive characteristics which include slow growth rates, reduced reproductive output, deferred maturity, and a low rate of standard metabolism. This general reduction in individual energy requirements allows a greatly increased standing biomass for a given energy input, without the high rate of energy turnover observed in warmer climates. It also paves the way for the reduction or omission of specialized (adult) structures, and of "energy intensive" (in terms of biomass maintained per unit energy flow) adult stages. Holm (1985) pointed out that, since pressure to economize remains throughout development, it will tend to reduce development itself to what is adequate for a given niche. Neoteny and/or paedomorphosis should logically result from such a scenario. It is quite clear, however, that this scenario can only be realized in a situation where selection by the biotic environment is weak or absent. Deferred adulthood is caused by heterochrony (shifts in the rate and timing of ontogenetic development), and circumstantial evidence suggests that heterochronic shifts occur precisely as a result of lack of selection: for instance, paedomorphosis occurs commonly in eusocial animals and parasites, which all live in supremely protective environments (Holm 1985). Corroborating evidence is provided by Arthur (1987), who argued convincingly that lack of interspecific competition tends to be associated with evolutionary shifts, and that this applies particularly to colonizers of biotically poor and disharmonious situations.

Delayed maturity and neotenic traits such as the strong wing reduction (see Appendix A) and poor vagility of all four species, are likely to similarly be precipitated by the paucity of biotic interactions, and the resultant weak selection by the biota. (In *E. halticella*, *P. marioni* and *P. dreuxi mirabilis*, but in *E. halticella* specifically, protective microhabitats may prevent even potential biotic interactions.) Neoteny would be strongly reinforced by its adaptiveness under the abiotic selective regime in the sub-Antarctic (e.g. wing reduction would be strongly reinforced by the constant high winds, while poor vagility and the lack of "adult" structures will be reinforced by the energy savings they represent). Long life cycles and overlapping generations would also reduce the opportunity for genetic change, since selection will act not from generation to generation but through a running mean of generations (Downes 1965). This would contribute to the "fixing" of neotenic phenotypes.

CHAPTER 9: CONCLUSIONS AND PROSPECTUS

"Bald 'conclusions,' which are not really conclusions, can...creep insidiously into...concluding sections... In order to avoid [this] syndrome... I have called [this section] 'concluding speculations.'"

Arthur (1987)

The conclusions which follow are not presented in any particular order, and pertain to disparate aspects of the thesis. However, they at least appear to warrant the status of "conclusions" rather than of "speculations."

1. It has become clear that insect consumers do not contribute significantly to energy flow in the Marion Island terrestrial ecosystem. This is a "negative result" in terms of the original objectives of the study which cumulated in this thesis. However, the study uncovered the primary role played by insects in nutrient mineralization and recycling at Marion Island, which opens up exciting and important new avenues of research.

2. It has become abundantly clear that a lack of microbiological and biochemical information seriously hampers our understanding of ecological processes in the terrestrial sub-Antarctic. A clearer understanding of the biochemistry of detritivore/ detritus/ microbe interactions, and better understanding of the restraints on herbivory in cold climates, may finally explain the "paradox of tundra" (Remmert 1986). Bacteria obviously play a cardinal role in the nutrition of detritivores, and possibly of folivores, in the sub-Antarctic. The enhancement of bacterial activity through the feeding action of detritivores and folivores is likely to be the primary mechanism of nutrient recycling in sub-Antarctic terrestrial ecosystems. In the light of the above, an integrated, multi-disciplinary research programme aimed at investigating these ecological interactions, against the background of the abiotic regime in the sub-Antarctic, is long overdue. In spite of many years of lip-service to the importance and necessity of interdisciplinary research, such a programme has not yet materialized at Marion Island.

3. Of all the nutrients that limit the growth and reproduction of insect herbivores and saprovores, energy (or rather the success with which it is acquired and utilized) remains "ultimately limiting" (Odum 1971). The evolution of the life histories and ecological attributes of sub-Antarctic insects can therefore be expected to reflect, in the first instance, the mechanisms by which they maximize their efficiency of energy *acquisition*. Put differently, the life histories and ecological strategies of insects in the sub-Antarctic are shaped, overwhelmingly, by resource restraints. In spite of this, autecological studies of insects in the sub-Antarctic have been concerned mainly with the *effects* of energy acquisition, emphasizing energy *allocation* (growth, development and reproduction) and energy *conservation* (metabolic and behavioural adaptations to low temperatures). However, it is the complex interactions between these nutritional parameters, and selection pressures on them, that "...are undoubtedly the most common *causes of* the evolution of different life styles" (Slansky & Rodriguez 1987), which in turn is one of the prime initiators of speciation (Vrba 1985; Arthur 1987).

4. A lack of interspecific competition, and the general lack of biotic selection in the poorly integrated terrestrial biota of Marion Island, are as important causes of evolution here as their presence are elsewhere.

PART IV: ACKNOWLEDGEMENTS

Be thou familiar, but by no means vulgar; the friends thou hast, and their adoption tried, grapple them to thy soul with hoops of steel...take each man's censure, but reserve thy judgement.

William Shakespeare - Hamlet

Prof. Clarke Scholtz initiated entomological research at Marion Island, which enabled me to spend, in total, almost three years in the sub-Antarctic. I am indebted to him for many things: for an experience which has enhanced my life; for his supervision of my work; for his forbearance with my English syntax; for his quiet but unfailing support and friendship; and for not censuring me too harshly for my persistent inability to meet deadlines.

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PART V: SUMMARY/SAMEVATTING

Five insect species were identified as important primary consumers or decomposers in the terrestrial ecosystem of sub-Antarctic Marion Island. Patterns of energy flow in individuals ("life strategies") and populations (population energetics) of the five species were studied against the evolutionary templet of their respective microhabitats. Energy flow through populations of the five species was used for a quantitative description of energy flow through the primary consumer component of the Marion Island terrestrial ecosystem, while the life history and ecological attributes of the five species were compared against the background of past and present geological, climatological, evolutional and ecological processes in the sub-Antarctic. The insects are *Embryonopsis halticella* Eaton (Lepidoptera: Yponomeutidae); *Ectemnorhinus similis* (C. O. Waterhouse) and *E. marioni* Jeannel (Coleoptera: Curculionidae); *Pringleophaga marioni* Viette (Lepidoptera: Tineidae) and *Paractora dreuxi mirabilis* Seguy (Diptera: Helcomyzidae). *E. halticella* is a host-specific folivore of the tussock grass *Poa cookii*, and dominates the herbivore guild on the island, while *E. similis* and *E. marioni* are polyphagous feeders of both angiosperms and bryophytes. *P. marioni* is a polyphagous detritivore and an important decomposer of plant litter. The kelp fly *P. dreuxi mirabilis* is the dominant decomposer of stranded kelp in the island's littoral zone. Herbivore populations (of *E. halticella* larvae and *E. similis* adults) assimilate less than 5 % of the annual net primary production at Marion Island. *P. dreuxi mirabilis* larval populations may assimilate up to 10 % of stranded kelp, and play an important role in enhancing the microbial decay of wrack. The predominantly moss-feeding (*E. marioni* adults) and litter-feeding (*P. marioni* larvae) terrestrial insects do not contribute significantly to energy flow, but the latter species is the primary agent of nutrient mineralization and recycling in the terrestrial ecosystem. Each of the five species exhibits a combination of life history and ecological traits which is not satisfactorily explained by the r-K-A selection continuum, chiefly because of the intensity of resource restraints. Physiological economy is at a premium, and each species has evolved a distinct suite of adaptive characteristics which include slow growth, low metabolic rates, long life cycles, and deferred maturity. The lack of interspecific competition, and the general paucity of biotic restraints inherent in the sub-Antarctic island situation, may be important factors in the evolution of the energy flow patterns exhibited by individuals and populations of sub-Antarctic insects.

Vyf insekspecies is geïdentifiseer as belangrike primêre verbruikers en afbrekers in die terrestriële ekostelsel van Marioneiland (sub-Antarkties). Energievloei deur individue ("lewensstrategieë") en bevolkings van die vyf species is bestudeer teen die agtergrond van die biotiese en abiotiese aard van hulle onderskeie mikrohabitatte. Energievloei deur bevolkings van die vyf species is gebruik vir 'n kwantitatiewe analise van energievloei tussen produseerders en verbruikers in die terrestriële ekostelsel. Biologiese en ekologiese eienskappe van die vyf species is vergelyk teen die agtergrond van vorige en huidige geologiese, klimatologiese, evolusionêre en ekologiese prosesse in die sub-Antarktiese gebied. Die vyf insekspecies is *Embryonopsis halticella* Eaton (Lepidoptera: Yponomeutidae); *Ectemnorhinus similis* C.O. Waterhouse en *E. marioni* (Jeannel) (Coleoptera: Curculionidae); *Pringleophaga marioni* Viette (Lepidoptera: Tineidae) en *Paractora dreuxi mirabilis* Seguy (Diptera: Helcomyzidae). *E. halticella* is 'n gasheerspesifieke stam- en blaarmyner van die polgras *P. cookii*, en domineer die herbivoorgilde op die eiland. *E. similis* en *E. marioni* is polifage herbivore wat op 'n verskeidenheid mosse en vaatplante voed. *P. marioni* is 'n polifage detritivoor, en 'n belangrike afbreker van plantreste. Die kelpvlieg *P. dreuxi mirabilis* is die dominante afbreker van gestrande seebamboes op die eiland se strande. Herbivoorbevolkings (*E. halticella* larwes en *E. similis* volwassenes) assimileer minder as 5 % van die netto primêre produksie op die eiland. *P. dreuxi mirabilis*

larfbevolkings kan tot 10 % van die energie van gestrande seebamboesbeddings assimileer, terwyl hulle mikrobiese afbraak aansienlik bevorder. Mosvoeders (*E. marioni* volwassenes) en terrestriële afbrekers (*P. marioni* larwes) dra nie noemenswaardig by tot energievloei nie, maar lg. species is die primêre agent verantwoordelik vir die mineralisasie en hersirkulering van nutriente in die terrestriële ekostelsel. Die vyf species vertoon unieke kombinasies van ekologiese eienskappe wat nie bevredigend deur die r-K-A seleksie kontinuum verklaar word nie, hoofsaaklik a.g.v. die uiters beperkende effek van die abiotiese omgewing. Die noodsaak vir "fisiologiese ekonomie" het by elke species gelei tot 'n kenmerkende stel aanpassings wat lae metabolisme, lang lewenssiklusse, en vertraagde volwassenheid insluit. Die oënskynlike afwesigheid van interspesifieke kompetisie, en die lae vlak van biotiese interaksies in die sub-Antarktiese eilandopset, mag die belangrikste faktor wees in die evolusie van energievloeipatrone deur individue en bevolkings van sub-Antarktiese insekte.

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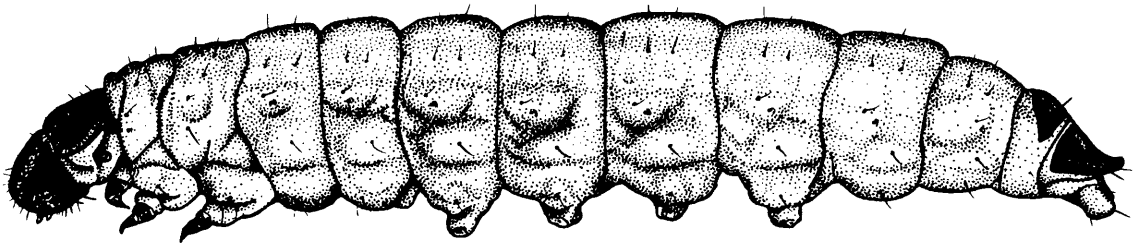
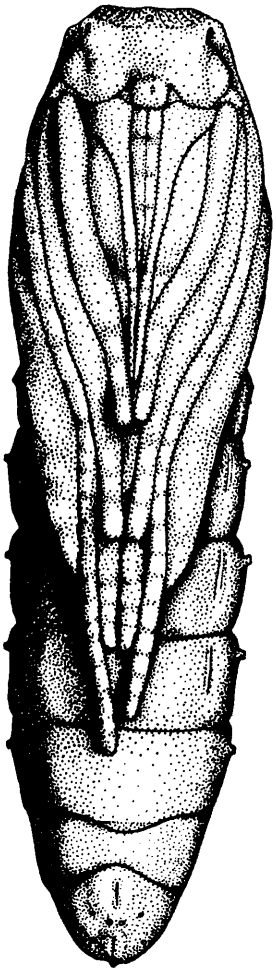
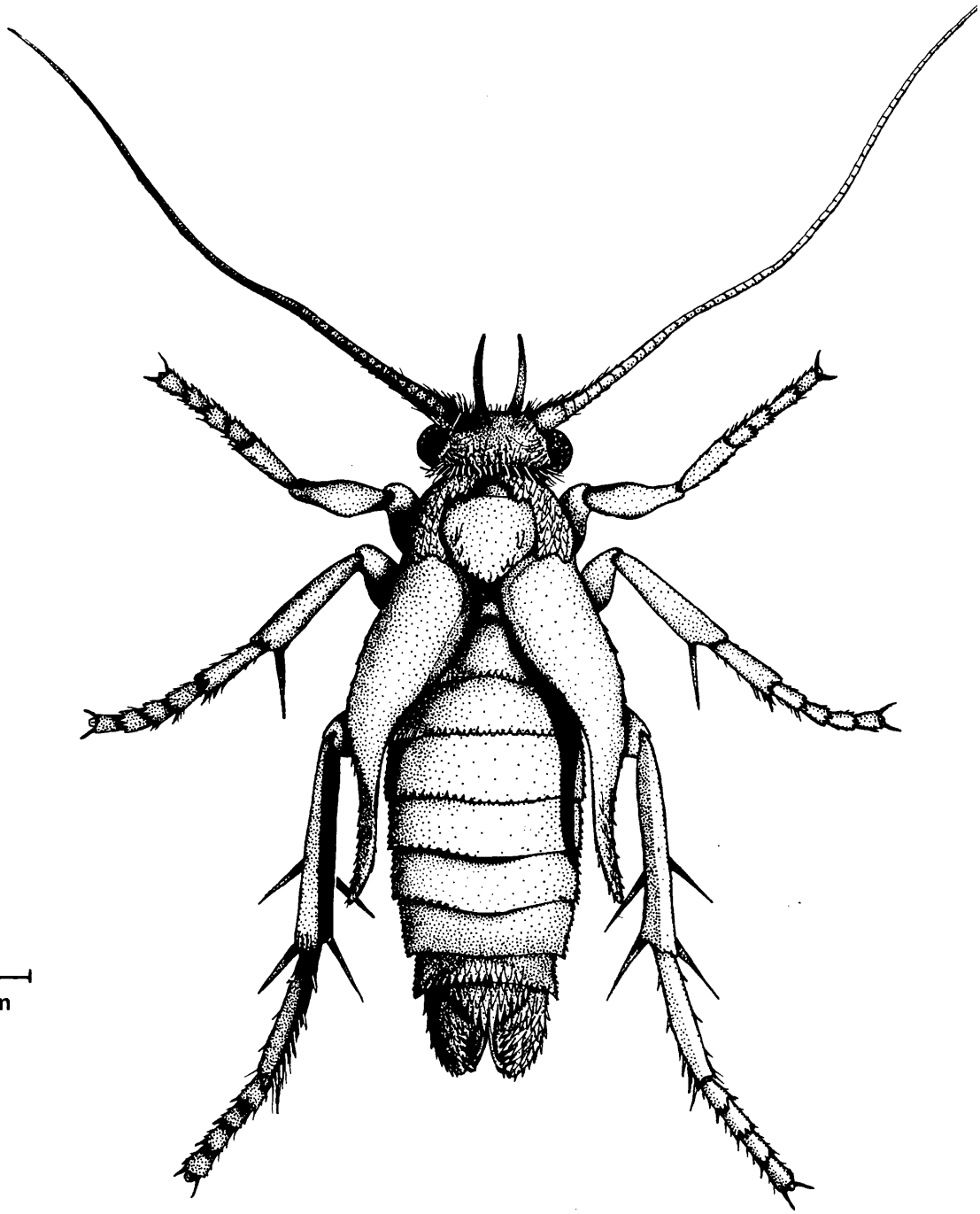
PART VII: APPENDIX

Habitus drawings







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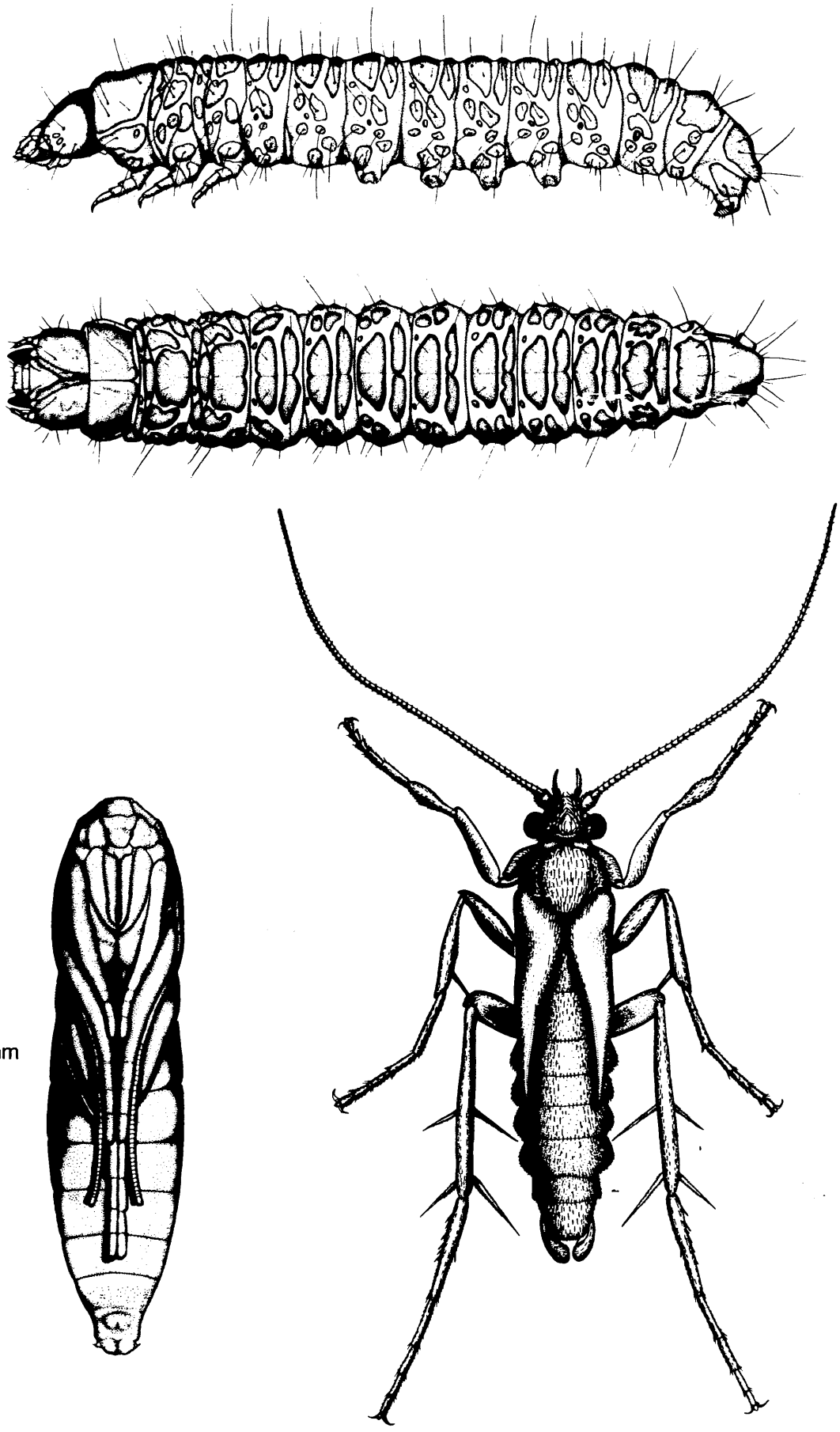
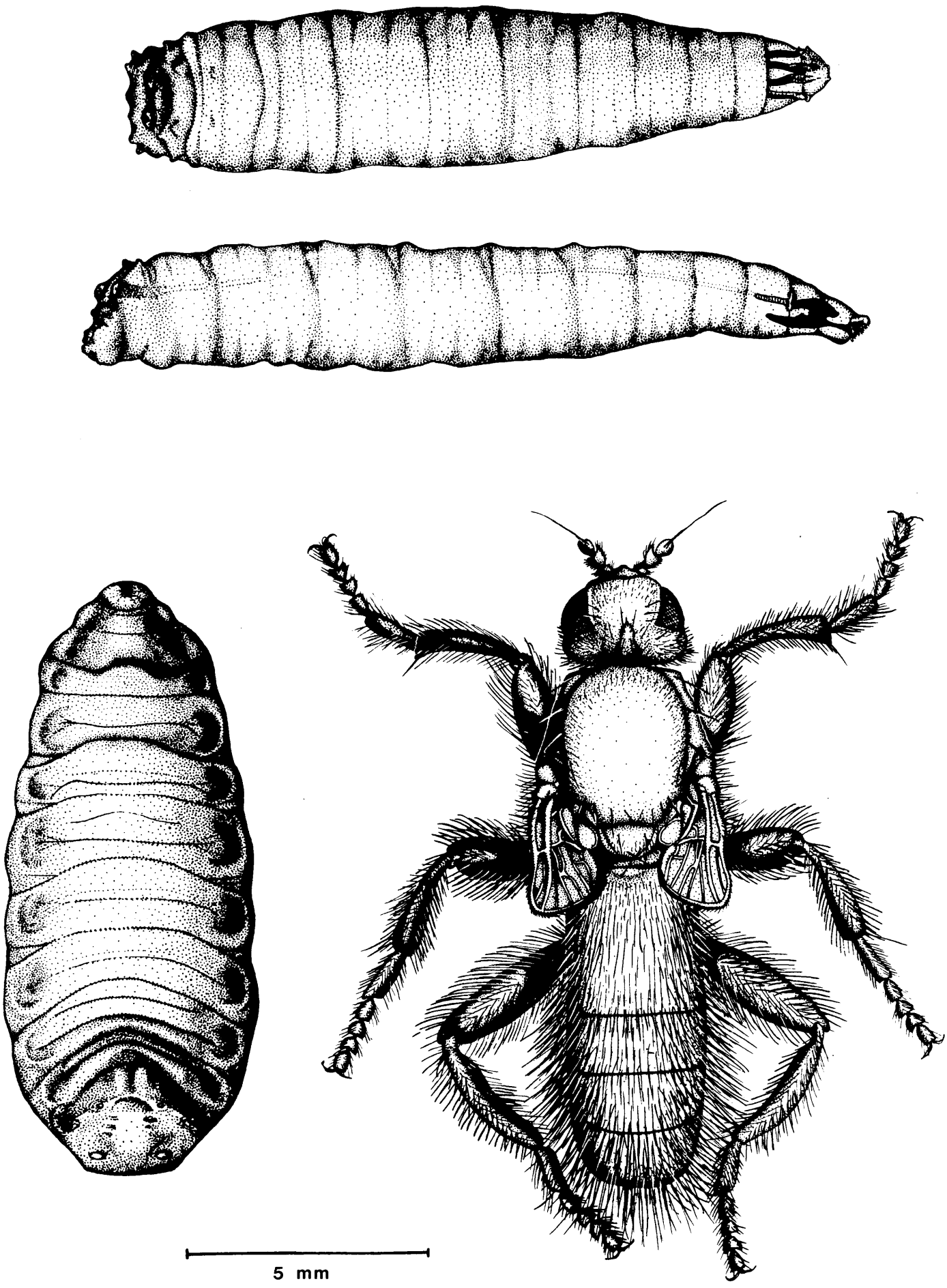
Embryonopsis halticella Eaton



Pringleophaga marioni Viette



Paractora dreuxi mirabilis Seguy