

Freshwater invertebrate fauna of the Tristan da Cunha islands (South Atlantic Ocean), with new records for Inaccessible and Nightingale Islands

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As part of a multidisciplinary floristic-faunistic study, a three week survey of the invertebrate fauna of Inaccessible Island (South Atlantic Ocean) was carried out in October/November 1989. In addition, one day of collecting was done on Nightingale Island. This paper deals only with the fauna associated with freshwater ecosystems from these islands, some of which are usually associated with marine or brackish conditions. On Inaccessible Island, five distinct types of freshwater body were identified – pH neutral streams, acidic streams (pH 5), an open pool of standing water (pH 6), areas of acidic bog, and seepages down rock faces. The survey, the most comprehensive for Inaccessible Island to date, has resulted in the discovery of 19 aquatic invertebrate species previously unrecorded on Inaccessible Island, two new to Nightingale Island, and 14 of which are new to the Tristan da Cunha archipelago. Many of the species are known from other parts of the world, indicating a low degree of endemism within the freshwater invertebrate community. Recolonisation from the source populations, preventing an isolated gene pool, may account for the low endemism. Several of the species have a degree of salinity tolerance, enabling them to withstand transportation across tracts of ocean, and others have marine origins.

INTRODUCTION

The Tristan da Cunha archipelago, situated in the South Atlantic Ocean (Figure 1), includes Tristan da Cunha Island, Inaccessible Island, Nightingale Island, and Gough Island which lies 350 km to the southeast. Inaccessible Island, the focus of this paper, lies at 37°18'S, 12°41'W. Nightingale Island lies 22 km southeast of Inaccessible Island, and has two much smaller satellite islands just to the north, known as Stoltenhoff and Middle Islands, which are not considered in this paper due to their small size and lack of collecting activity associated with them. In 1997, Inaccessible Island, as one of the least disturbed temperate islands in the world, and the surrounding ocean out to 12 nautical miles from shore, was declared a nature reserve, and a management plan has been established to protect it (Ryan & Glass, 2001).

The islands are all volcanic in origin, and lie approximately 540 km to the east of the Mid-Atlantic Ridge. They are approximately 2900 km and 3200 km from the nearest points of mainland South Africa and South America, respectively (Figure 1).

Inaccessible Island measures about 4.6 km by 5.7 km (Ryan & Glass, 2001) and is the second smallest of the islands in the Tristan da Cunha group (Figure 2). Inaccessible Island is surrounded on all sides by sheer cliffs, with the undulating summit reaching a height of 511 m (Fraser *et al.*, 1983; Siddall, 1985; Ryan & Glass, 2001), though Ollier (1984a) puts the highest point as 615 m.

Ryan & Glass (2001) give a detailed account of the climate, which is classified as cool-temperate oceanic, with frontal rain and rapid weather changes throughout the year. Few weather records exist for Inaccessible Island, but measurements for Tristan da Cunha give an average annual rainfall near sea level of 1671 mm (Ryan & Glass, 2001). The higher elevation of

Tristan da Cunha (2010 m) results in a greater annual rainfall than Inaccessible Island, which in turn has a higher rainfall than the low-lying Nightingale Island, which peaks at 335 m. The annual rainfall at sea level on Gough Island stands at around 3225 mm, and precipitation increases to about half as much again at 600 m (Holdgate, 1960). Air temperatures near sea level on Tristan da Cunha range from 3 to 24°C.

The first scientific collections from Inaccessible Island date to the visit of the HMS Challenger in 1873 (Moseley, 1879), though intermittent collections were made on the islands before this, the first being a collection of flora and fauna in 1793 by the French botanist, Aubert du Petit-Thouars (1811). Explorers in passing ships also contributed, for example Carmichael (1818), who collected on Tristan da Cunha. However, it was not until the Norwegian Scientific Expedition visited Tristan da Cunha, from December 1937 to March 1938, that any intensive studies were carried out. Based on Tristan da Cunha, this group spent three weeks on Inaccessible Island (Christopherson, 1947). The British Royal Society organised an expedition in 1962, which again concentrated on Tristan da Cunha, spending only a week on Inaccessible and Nightingale Islands together (Dickson, 1965). The Gough Island Scientific Survey of 1955–1956 made a detailed study of the flora and fauna of Gough Island, and conducted a detailed study of that island's freshwater fauna (Holdgate, 1961). The four month Denstone Expedition of 1982–1983 was the first ground-based survey of Inaccessible Island. This resulted in the first detailed map of the island (Siddall, 1985) and made some significant contributions to the knowledge about the island's freshwater diatoms and palaeoecology (Preece *et al.*, 1986). For details on the history of scientific visits to the Tristan da Cunha archipelago, refer to Holdgate (1965); for Inaccessible Island to Ryan & Glass (2001)

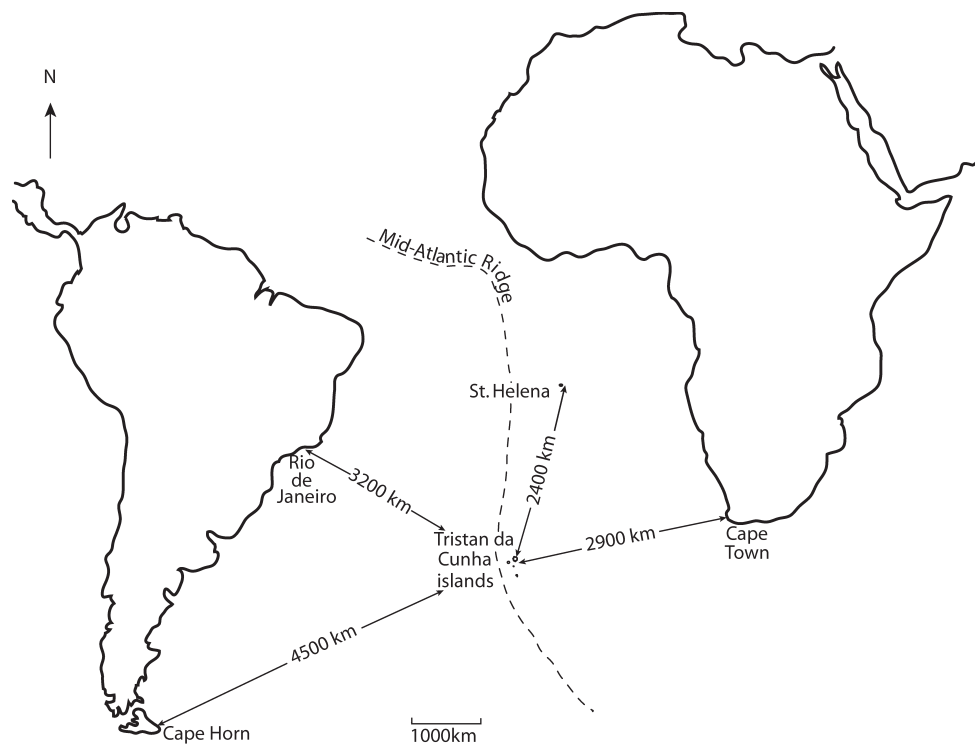


Figure 1. Location of the Tristan da Cunha group of islands (modified after Preece *et al.*, 1986).

and for Gough Island to Hänel *et al.* (2005).

In October 1989, a group of scientists from South Africa funded through the Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, spent three weeks on Inaccessible Island, and one day on Nightingale Island. This paper deals only with findings related to the aquatic or semi-aquatic organisms collected from freshwater ecosystems on the islands during this expedition. Since no further surveys have been carried out on the freshwater fauna of the islands, this is still the most recent work on the subject. A comparison is made between the freshwater fauna of Inaccessible Island and that of the neighbouring islands. This is compiled from the results of the 1989 survey reported here, as well as a synthesis from the literature on freshwater fauna from other collections (Holdgate, 1961, 1965; Jones *et al.*, 2003). The results offer some insights into the biogeographical origin of the fauna, their mainland associations and methods of dispersal to the islands.

MATERIAL AND METHODS

Description of sites studied on Inaccessible Island

There are five types of freshwater bodies on Inaccessible Island (Table 1; Figure 3). To the west, in the only flat low-lying land, is 'Skua Bog' (collecting site A). This wetland, of which a large portion is dominated by *Scirpus sulcatus* Thours, has an area of open water at one end forming a small lake, referred to as 'Skua Pond' by Ryan & Glass, 2001. The lake is about 180 m long by 70 m wide, and 1.5 m at it deepest, although dimensions vary with rainfall. The water is acidic (pH 6). A small, clear, pH-neutral, spring-fed freshwater stream (collecting site B) runs down through the lowland area (Figure 3). It is narrow and shallow (up to about 60 cm wide and about 15 cm deep), flanked with tall *Spartina arundinacea* Carmichael, which densely covers the lower parts of the island, growing closely on each bank for most of its course.

The plateau area, at around 500 m above sea level, forms most of the island. It is traversed by a number of dark brown, acidic (pH 5) streams (collectively labelled as collecting sites 'C'

(Figure 3)) draining to the southeast and two draining to the northeast. Occasionally these streams cascade as small waterfalls into pools, and finally plunge over sheer cliffs into the sea below. Bright green patches of *Sphagnum* bog, as seen at 'Dick's Bog' (collecting site D) (Figure 3), occur along the courses of these plateau streams. The plateau vegetation is very different to that found in the low-lying land. *S. arundinacea* is less common and the dominant plant is *Blechnum palmiforme* (Thouars), a dwarf tree fern. This grows densely along the water courses, interrupted by groves of *Phyllica arborea* Thouars, which dominates in places. Certain types of vegetation introduce humic substances into streams resulting in acidic, brown peat-stained water (Ødegaard *et al.*, 1986), as seen in the plateau streams.

There are numerous freshwater seeps along the cliffs bordering the coast (collecting sites E) (Figure 3), formed by the slow release of water from the ground.

Sampling

Qualitative sampling was undertaken in all the waterbody types outlined above, by use of a hand net (mesh size 80 μ m). Organisms adhering to rocks or plants or in sediments were collected in the net, then flushed into a white tray, from which they were sorted and placed into vials of 80% ethanol. In addition, a drift net of the same mesh size, with a square-framed opening (30 \times 30 cm) and tapering tail, trailing for 70 cm, was set up at site B. Due to the uncertainty of the weather and the steep ascent to the plateau, no drift sampling was undertaken in the upland streams (sites C). These upland streams were regarded as being similar in nature, and were therefore treated as one waterbody type. *Sphagnum* bog areas were sampled by trailing a net through the water around the margins of the *Sphagnum* plants.

Each waterbody exhibits several distinct biotopes, each sample representing a number of biotopes collected together. The different waterbodies and biotopes at each site are explained in Table 1. Flow, water quality and the diversity of biotopes available all affect species diversity and distribution.

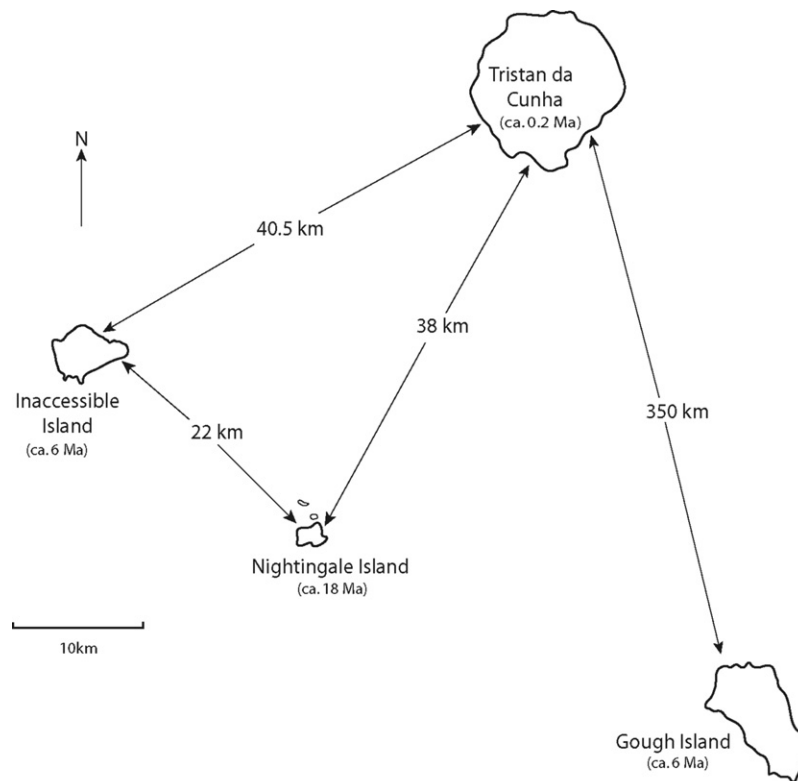


Figure 2. The relation of the four islands to each other. The distance to Gough island is not illustrated to scale. The approximate age of each island is indicated in brackets.

The term 'biotope' is used here to define the environment of a community (*sensu* Udvardy, 1959).

All pH measurements were made with Merck Universal Indicator pH 0–14 paper strips. Neither nutrients nor salinity were measured.

In an attempt to catch flying insects, in particular the aerial stages of the freshwater insects, malaise traps were set up in the *Phylica* woodland adjacent to Skua Bog and in an open area amongst *Spartina* above Blendon Hall Beach, not far from Site B.

Sampling on Nightingale Island aimed simply at collecting whatever possible in a short time. A hand net was used in water, and an aerial insect net on land. There is no running water on Nightingale Island, only somewhat acidic pools.

Analysis

For a comparison of the affinities of the fauna on the four islands, Sørensen's coefficient (SC) of biotic similarity was used to assess the strength of association between the islands. $SC = 2a/(2a + b + c)$, where a = the number of taxa common between

two regions, b = the number of taxa unique to the first region, c = the number of taxa unique to the second region (Sørensen, 1948).

RECORDS

Table 1 presents a summary of the waterbody types and biotopes in each waterbody, for the four main islands of the Tristan da Cunha group. Table 2 provides a synopsis of all the freshwater organisms recorded from the entire island group, together with the organisms collected in the 1989 survey. Collection sites are indicated, and new and known records from Inaccessible Island are indicated. Care has been taken to ensure use of current taxonomic names.

Of the 27 freshwater-associated invertebrate species collected on Inaccessible and Nightingale Islands during the 1989 survey (Table 2), 19 are new records for Inaccessible Island, two are new records for Nightingale Island and 14 are new records for the entire island group. Eight species were collected from Inaccessible Island on previous expeditions. Fifteen of Inaccessible Island's freshwater invertebrate species are known from

Table 1. Types of freshwater habitats on the Tristan da Cunha archipelago, indicating biotopes present in each (derived from personal observations; Holdgate, 1961, 1965; Jones *et al.*, 2003 and <http://www.tristandc.com/>).

Islands	Freshwater habitats present, with different biotopes indicated					Total no. of waterbody types	Total no. of different biotopes
	A Pools	B Neutral streams	C Acidic streams	D Bog	E Seeps		
Inaccessible	c,f,g*	a,b,c,f	a–g	c,f	d	5	7
Nightingale	c,f,g	none	none	c,f	d	3	4
Tristan	c,f,g,h	a–f	a–g	c,f	d	5	7
Gough	c,f,g	none	a–g	c,f	d	4	7

*a = stones-in-current; b = stones-out-of-current; c = marginal or emergent vegetation; d = hygropteretic regions; e = bedrock; f = sediment; g = surface of pool; h = man-made reservoir; 'none' indicates waterbody type not present. A–E refer to freshwater habitats indicated in Figure 3.

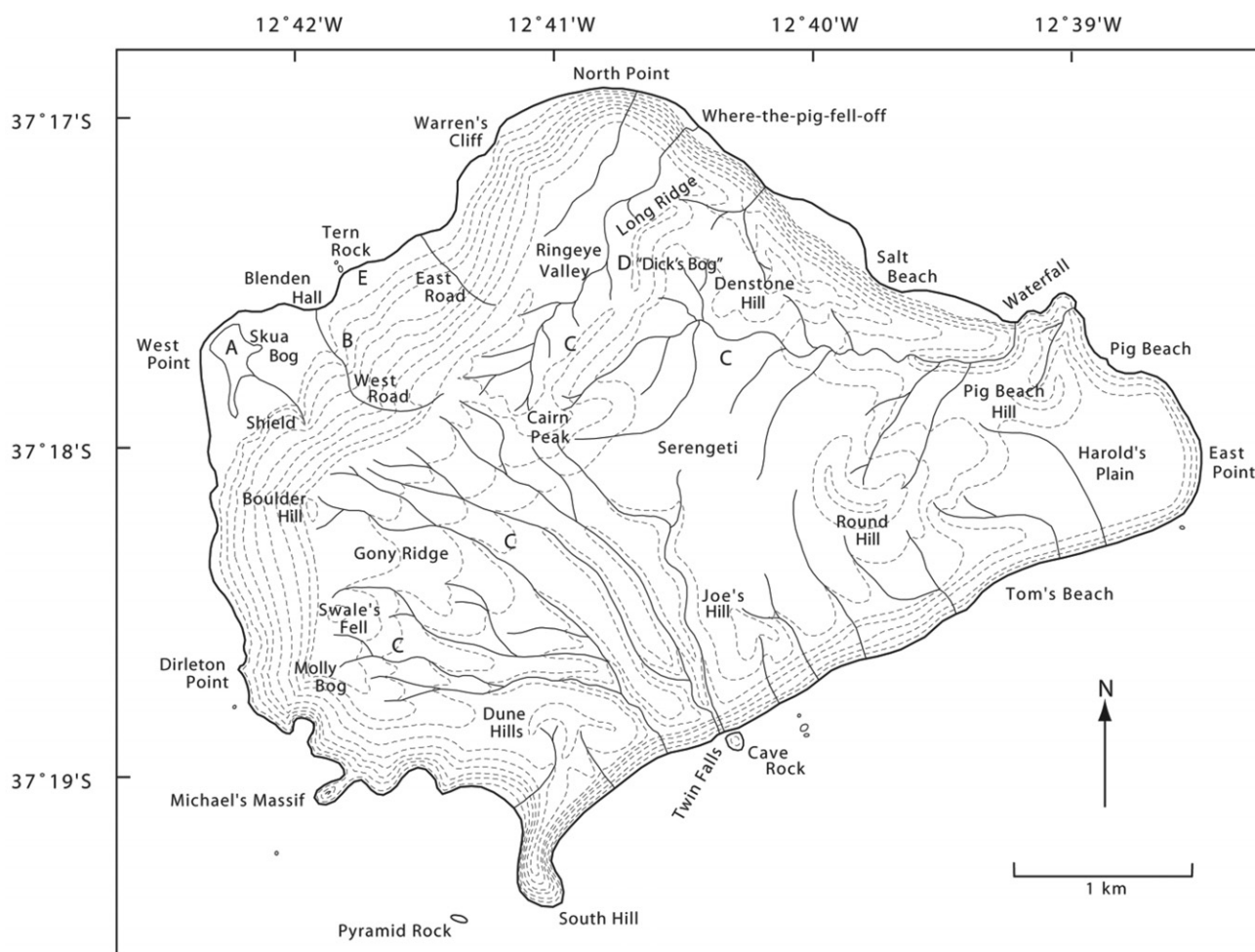


Figure 3. Details of Inaccessible Island, indicating the different freshwater ecosystems. **A**, Open pool and *Scirpus* bog – ‘Skua Bog’; **B**, clear stream, pH 7; **C**, brown-watered acidic streams, pH 5; **D**, *Sphagnum* bog; **E**, coastal seeps. Contours are at 50-m intervals. Map modified after Ryan & Glass, 2001.

other islands in the Tristan da Cunha archipelago. Two species collected during earlier surveys were not found again during the 1989 survey. Some species occurring on other islands of the Tristan da Cunha group have not been recorded to date on Inaccessible Island.

Ecology of freshwater organisms on Inaccessible Island

Each sampled waterbody type on Inaccessible Island possesses its own complement of species, with little overlap between waterbody types (Table 2), although Skua Bog (site A) and the neutral stream (site B) have a number of species in common, possibly due to their close proximity to one another (Figure 3). The acidic upland streams (sites C) exhibit a relatively depauperate fauna, while the pH-neutral, clear water stream (site B) has a higher faunal diversity than any of the other waterbodies sampled (Table 2). Salinity of all the waterbodies may be increased due to salt spray from the sea, which is frequently blown across the island, especially over sites A and B, resulting in a fauna with a tendency to be halobiontic. This is discussed later.

Each of the five freshwater ecosystems on Inaccessible Island has its own combination of biotopes (Table 1). It would be expected that the greater the number of biotopes present, the higher the species diversity. Although all biotopes are present in both the neutral stream (site B) and the acidic plateau streams (sites C), the neutral streams have a much higher faunal diversity (Table 2). Differences in food quality in the two stream types may account for this, as the quality of food

available for detritivores in an acidic stream is lower than for a neutral stream (Groom & Hildrew, 1989). The majority of species in each waterbody type are detritivores or fungivores, with the dytiscid beetles (both larvae and adults) being the only carnivores present. Thus, species diversity in the plateau streams (sites C) may be limited by their acidic nature. Although thoroughly searched by turning over stones and sweeping marginal vegetation hanging into, or growing in the streams, the plateau streams may have yielded a higher diversity if they had also been sampled with a drift net. No invertebrates were collected from the *Sphagnum* bog areas. While it is possible that some organisms may have been overlooked in this ecosystem, the anaerobic nature of the bog is probably the main reason for the absence of organisms. The lack of organisms associated with the peat bog is consistent with findings from Gough Island (Holdgate, 1965; Jones *et al.*, 2003).

Whether or not a species becomes established in a particular environment is dependent upon a combination of its own attributes, the climate, and chance events (de Moor, 1992). Once a species has colonised a particular waterbody, it may adapt to the conditions characterising that waterbody, or may already be pre-adapted to such a waterbody, if this is similar to its native habitat. An adjacent waterbody, exhibiting different characteristics, may not provide a suitable habitat. In a sense, therefore, the different types of waterbodies may be considered as islands within an island to species with specialist habitat requirements. Holdgate (1965) commented that the different organisms on Gough Island bear little taxonomic relation to

Table 2. Summary of freshwater invertebrates recorded from the Tristan da Cunha archipelago, based on the 1989 survey of Inaccessible and Nightingale Islands, and including other published records.

Taxa	Freshwater ecosystems on Inaccessible Island					New records for Nightingale Island 1989	Summary of records from Tristan Island group	Known additional distribution
	A	B	C	D	E			
Platyhelminthes								
Turbellaria								
Procerodidae								
<i>Obrimposthia ohlini</i> (Bergendal) *** #		x					I,G	Tierra del Fuego, Kerguelen
Annelida								
Oligochaeta								
Naididae								
<i>Nais elinguis</i> Müller ****			x				I	Cosmopolitan sp.
<i>Pristina aequisetata</i> Bourne ****			x				I	Cosmopolitan sp.
<i>Pristinella jenkiniae</i> (Stephenson) ****			x				I	Cosmopolitan sp.
<i>P. osborni</i> (Walton) ****			x				I	Palaeartic, Nearctic, Afrotropical, Oriental
Tubificidae								
Gen. sp. indet. ****	x	x					I	Cosmopolitan fam.
Enchytraeidae								
<i>Enchytraeus australis</i> Stephenson ⁺							G	
<i>Enchytraeus</i> sp. ⁺							G	
<i>Fridericia</i> sp. ⁺							G	
<i>Henlea</i> sp. ⁺							G	
<i>Lumbricillus</i> sp. ⁺							G	
Gen. sp. indet. ***	x	x					I	Cosmopolitan fam.
Crustacea								
Copepoda								
Cyclopidae								
<i>Paracyclops poppei</i> (Rehberg) **** #	x	x					I	Cosmopolitan sp.
Ostracoda								
Cyprididae								
<i>Cypridopsis</i> sp. ⁺							T	Cosmopolitan gen.
<i>Potamocypris</i> sp. ⁺							I	Cosmopolitan gen.
<i>Sarscypridopsis elizabethae</i> (Sars) **** #	x	x					I	Afrotropical
Isopoda								
Jaeridae								
<i>Iais elongate</i> Sivertsen & Holthuis * #			x				I	Inaccessible Island
<i>I. pubescens</i> (Dana) ⁺ #							G	S. hemisphere
Amphipoda								
Talitridae								
<i>O. platensis</i> (Kroyer) ⁺ * #							T,I,G	Neotropical
<i>O. scutigerula</i> Dana ⁺ #							I,N,G	Neotropical
<i>Orchestia</i> sp. * #	x	x	x				I	Neotropical
Acarina								
Mesostig mites								
Parasitidae								
<i>Pergamasus longicornis</i> Berlese *	x						I	Palaeartic
<i>Pergamasus</i> sp.							T,G	
Eupopidae								
<i>Linopodes</i> sp. *	x						T,I	Nearctic, Holarctic, Afrotropical
Halacarid mites								
Halacaridae								
<i>Lobohalacarus weberi tristanensis</i> Bartsch **** #			x				I	Cosmopolitan sp., endemic subsp.
Oribatid mites								
Phthiracaridae								
<i>Notophthiracarus</i> sp. ****			x				I	S. hemisphere, Palaeartic
<i>Phthiracarus</i> sp. ⁺							G	Cosmopolitan gen.
Malaconothridae								
<i>Trimalaconothrus</i> sp. ****	x	x					I	Cosmopolitan gen.
Lohmanniidae								
<i>Lohmannia (Carolohmannia)</i> sp. ****			x				I	Nearctic
Scheloribatidae								
<i>Schelorbates</i> sp. ****			x				I	Cosmopolitan gen.

Continued on p. 29

Table 2 (continued)

Taxa	Freshwater ecosystems on Inaccessible Island					New records for Nightingale Island 1989	Summary of records from Tristan Island group	Known additional distribution
	A	B	C	D	E			
Insecta								
Coleoptera								
Dytiscidae								
<i>Liodessus involucer</i> (Brinck) * **	a,l	a,l	a			a	I,N,G	Neotropical, Australian
<i>Lancetes dacunhae</i> Brinck *		l					T,I,G	Neotropical
<i>Senilites tristanicola</i> Brinck *							I,N	Endemic to I and N islands
Diptera								
Chironomidae								
Orthocladiinae								
<i>Bryophaenocladus</i> sp.†							G	Cosmopolitan
<i>Clunio africanus</i> Hesse † #							G	Afrotropical
<i>Limnophyes minimus</i> (Meigen) ****		a,l,p	a				I,G	Cosmopolitan species
<i>Thalassosmittia</i> sp. nr. <i>thalassophila</i> #							G	Nearctic, Palaearctic
Telmatogetoninae								
<i>Telmatogeton sanctipauli</i> (Schiner) **** #		a			a		T,I,G	Afrotropical, St. Paul Island
Ephydriidae								
<i>Centromeromyia eremita</i> Frey †							N	Neotropical
<i>Dimecoenia tristanensis</i> Frey #			a,l,p				T,I,N,G endemic	Tristan da Cunha archipelago
<i>Dimecoenia</i> sp. * #		l,p	a	a	l	a	I,N	Nearctic & Neotropical gen.
Limoniidae								
<i>Dicranomyia distans</i> Osten Sacken *** #		a	a		a		T,I,G	Neotropical, Nearctic
<i>Symplecta holdgatei</i> (Freeman) *** ** #			a			a	I,N,G endemic	Tristan da Cunha archipelago
<i>Symplecta</i> sp. #							G	Cosmopolitan genus
Psychodidae								
<i>Psychoda albipennis</i> Zetterstedt ***		l					I,G	Palaearctic, Afrotropical, Canary Islands, Macquarie Island
Total no of species in each waterbody type	9	23	7	1	4			
Total no. of species known on each island							8, 31, 7, 23	
Total no. of species known on all the islands							45	
Total species from Inaccessible in 1989 = 27								
New taxa recorded from Inaccessible = 19								
New taxa recorded from Nightingale = 2								
New taxa recorded for TDC archipelago = 14								

† indicates not collected during 1989 expedition.

x indicates presence on Nightingale Island or in specified water body on Inaccessible Island in 1989, with the developmental stages given for insects (a = adult, l = larva, p = pupa). A, Skua Bog and Pond; B, neutral streams; C, acidic streams; D, *Sphagnum* bog; E, coastal seeps.

Islands: T = Tristan da Cunha; I = Inaccessible; N = Nightingale; G = Gough.

****new record for whole island group; ***new record for Inaccessible Island; ** new record for Nightingale Island; *previously recorded from Inaccessible Island.

indicates marine affinities or known salinity tolerance. Other records from Holdgate, 1961, 1965, Preece *et al.*, 1986 and Jones *et al.*, 2003.

one another, implying that they colonise independently and have limited affect on each other. This also appears to be true for Inaccessible Island, with only few predators, such as the Dytiscidae, being dependent on the other organisms as a food source.

Since the early work on population ecology (e.g. by Mac Arthur & Wilson (1967) and Pianka (1974)), species have been categorised into having either r-select or K-select ecological attributes; r-selection favours a rapid rate of population increase, but with little specialisation and a high mortality; K-selection occurs in stable, predictable environments, in which a population is maintained near the carrying capacity. However, many of the species on an island exhibit 'adversity' or A-select attributes. This concept was developed by Whittaker (1975) and expanded by Greenslade (1983). A-selected characteristics, which combine characteristics of both r- and K-selected species, enable a species to survive successfully in conditions that are extreme yet predictable. Such conditions would not favour either traditionally r- or K-selected species. Crafford *et al.* (1986) found that the insects on the Prince Edward Islands mostly

exhibit this attribute. Apart from predatory aquatic beetle species, the majority of the freshwater invertebrates on the Tristan da Cunha Islands are detritivorous, with opportunistic, unspecialised life cycles adapted to a harsh environment, typical of A-select species. *Limnophyes minimus* (Meigen) is a classical example of an A-selected species (de Moor, 1992), and on Marion Island it inhabits every possible freshwater biotope (Crafford, 1986) and mires (Hänel & Chown, 1998). In contrast to this widespread distribution on Marion Island, during the 1989 Inaccessible Island survey it was collected only from the neutral stream (site B). This species is discussed further in the section on Chironomidae.

Intra-island distribution of organisms

With a total of 31 recorded taxa of freshwater organisms, Inaccessible Island has the largest diversity of all four islands in the Tristan da Cunha group (Table 2). In order to compare the strength of association of the freshwater fauna between the islands, Sørensen's coefficient of biotic similarity (Table 3) was calculated using the taxa listed in Table 2. This shows that the

Table 3. Sørensen's coefficient of similarity between the islands of the Tristan da Cunha archipelago, based on the freshwater taxa detailed in Table 2. The higher the value, the greater the similarity between the faunas.

	Tristan	Inaccessible	Nightingale	Gough
Tristan	–	0.41	0.41	0.50
Inaccessible		–	0.41	0.47
Nightingale			–	0.40
Gough				–

affinity is strongest between Tristan da Cunha and Gough Islands, followed by that between Inaccessible and Gough Islands. The associations between the remaining islands are weaker but similar, the weakest being between Nightingale and Gough Islands. The relatively strong link between Tristan da Cunha and Gough Islands may be due at least in part to the effects of human passage between these two islands, resulting in a greater man-induced interchange of fauna between these two islands.

Unequal collecting effort on each island may be partly responsible for observed differences, although several collections have been made on Tristan da Cunha Island (Christopherson, 1947; Dickson, 1965; Fraser *et al.*, 1983) and Gough Island (Holdgate, 1961; Jones *et al.*, 2003). It may have been expected that the three northern islands would be the most similar, with Gough Island, 350 km farther south, the outlier.

Holdgate (1965), however, notes that the freshwater habitats of the four islands are not as similar as might be expected, Tristan having few permanent streams and Nightingale none, while Inaccessible and Gough have several, so types and permanence of waterbodies (Table 1) would account in part for the differences in diversity apparent on the different islands.

The respective ages of the islands may be an important factor influencing species diversity and distribution. There is, however, little consensus on the exact ages of the islands, probably due to difficulties with the methods used to date the rocks (Le Maitre, 1960). Inaccessible Island has been estimated to be 6.5 Ma (Chevallier *et al.*, 1992), 6.0 Ma (Miller, 1964) or 2.9 Ma (Gass, 1967; Ollier, 1984a). Tristan is put at around 0.21 Ma (McDougall & Ollier, 1982; Ollier, 1984a), although an earlier analysis (Miller, 1964) estimated Tristan to be 1.0 Ma. Nightingale Island's oldest rock formations are around 18 Ma (Miller, 1964; Ollier, 1984a). Le Maitre (1960) maintains that, due to inaccuracies in various dating techniques, Gough Island cannot be dated more accurately than as late Tertiary, but Miller (1964) and Ollier (1984b) date Gough Island at approximately 6.0 Ma. These studies suggest that Nightingale Island is by far the oldest island, with Gough and Inaccessible Islands intermediate and of similar age, and Tristan da Cunha Island the youngest. If island age is important, Nightingale Island, being the oldest, could be expected to have the highest diversity, as it has had the longest period for colonisation and speciation. Instead, the youngest and the oldest islands have the lowest number of aquatic species (Table 2). Nightingale, however, is highly eroded, with fewer suitable ecosystems. Tristan da Cunha Island is still volcanically active, and major seismic or volcanic cataclysms in the more recent past may have eliminated previously established faunas. There is evidence of eruptions on the other islands within the past 100 000 years (Ollier, 1984a), but not since.

MacArthur & Wilson (1967) suggest a linear relationship between island surface area and the number of species present. Considering the results of the current study, island size in

terms of surface area does not appear to influence freshwater invertebrate diversity. Tristan da Cunha is the largest island of the group, with the second lowest number of species, and Nightingale Island is the smallest, with the lowest number of species. It should be remembered, however that, as only freshwater organisms are being considered here, availability and abundance of suitable biotopes is more relevant than island size. This will be further affected by rainfall, topography and porosity of the rocks, determining the type and permanence of any rivers.

Holdgate (1965), when considering the total fauna of each island as then known, concluded that island size was relevant to faunal diversity in that case. A more recent study (Chown *et al.*, 1998), examining the biogeography of the southern ocean islands, separated indigenous biota from introduced biota. They concluded that natural species richness on these islands does follow the island biogeography variables proposed by MacArthur & Wilson (1967), this being masked when including introduced species in the analysis.

When the aquatic fauna is considered alone, the types and permanence of types of freshwater bodies available on each island is more significant than the influence of island size. Inaccessible and Gough Islands share four of five possible freshwater types (acidic streams, pools, bogs and seeps), while Nightingale Island has three inland acidic ponds but no running water. Tristan da Cunha has several standing waterbodies in the form of small crater lakes, which are acidic in nature, being fed by permanent streams arising from peat bogs. There is also a summit crater which freezes over in winter. There are several small clear-water spring fed streams, the most notable being the stream known as 'Big Watron', which has been impounded near the settlement Edinburgh. The largely porous nature of the rock on Tristan da Cunha may be the reason for the lack of permanent rivers on this island (P. Ryan, pers. comm.), though the island is traversed by boulder-strewn, normally dry river beds called gulches resulting from run-off after heavy rain. The availability and duration of suitable freshwater types would affect the colonisation of freshwater fauna on each island more than any other factor. It is probable that there is at least limited dispersal of aquatic invertebrates between the islands, but the lack of suitable waterbodies prevents populations from establishing themselves.

Coope (1986) notes that climatic and geographical history should be known in order to make sense of present-day distributions. Quaternary glaciations have affected the composition of insect communities on the South Indian Ocean Province Islands (Prince Edward Islands, Îles Crozet, Îles Kerguelen and Heard and McDonald Islands) (Chown, 1990). The past history of each of those islands has influenced the species richness observed today. Unlike those islands, however, the Tristan da Cunha group of islands did not experience glaciation during the Pleistocene (Brinck, 1960; Hollin & Schilling, 1981).

Thus, successful colonisation of the freshwater ecosystems on these islands appears to be by chance and not related to island age or size. The availability of suitable waterbodies may play a role in the successful establishment of species.

Origins, biogeography and biology of the freshwater fauna of the Tristan da Cunha Islands

When considering which species arrive and establish themselves on an island, many factors must be considered. These include the dispersal abilities of organisms, distance from the mainland, prevailing direction of air and ocean currents and bird migration patterns. Further factors include the similarity

of island conditions compared to those of the mainland, the presence or absence of natural enemies, such as predators and parasites, the arrival of sufficient individuals of a species to enable reproduction and survival, propensity to parthenogenesis and more recently, human activities. As Holdgate (1986) notes, many more species disperse than succeed in establishing viable populations. Thus, the fauna of an island is largely fortuitous and the result of random successful colonisations. Recent studies (e.g. Chown *et al.*, 1998; Gaston *et al.*, 2003) have extensively covered anthropomorphic effects on southern ocean island faunas, in particular the introduction of alien species.

In the case of oceanic islands of volcanic origin, continental drift is clearly not a factor in dispersal, and in any case the Tristan da Cunha group of islands, with the oldest at 18 Ma (Miller, 1964; Ollier, 1984a), formed long after the breakup of the supercontinent Gondwanaland. Considering all four islands, the aquatic fauna bears relation to both African and American faunas (Table 2). There is, however, a stronger South American influence than sub-Saharan African influence, with 11 species clearly having a Neotropical affinity, and only seven species with an Afrotropical affinity (Table 2). This substantiates the findings of other faunal studies (e.g. Brinck, 1948, 1960; Holdgate, 1961, 1965; Jones *et al.*, 2003), who also noted a neotropical dominance in the fauna (these studies included terrestrial as well as freshwater fauna). As many species are cosmopolitan, the mainland affinities if such species remain unclear.

Of the 45 freshwater species recorded on the Tristan da Cunha archipelago, 17 have some marine affinity or known salinity tolerance (Table 2), enabling them to withstand transportation across tracts of ocean. The Turbellarian *Obrimoposthia ohlini* (Bergendal), originally described from Tierra del Fuego, is normally found in marine ecosystems. On Inaccessible Island it occurs in the lower-lying waterbodies, which, due to their proximity to the ocean, may be more saline than the plateau streams, although salinity was not measured. *Obrimoposthia ohlini* also occurs in a low altitude freshwater stream on Gough Island (Holdgate, 1961), and on the Kerguelen Islands (Sluys & Ball, 1989). Several species of Oligochaeta are present on Inaccessible Island (Table 2). The naidid oligochaete *Nais elinguis* Müller is known to be tolerant of a wide chlorinity range (‰Cl⁻) (Verdonschot *et al.*, 1982), indicating that this species would also be able to survive in sea water. The other oligochaete species are known only from freshwater (R. Grimm, pers. comm.). Many species of Naididae are cosmopolitan, although *Pristina* spp. tend to be tropical and *Nais* spp. temperate (Grimm, 1987). Many aquatic oligochaetes, especially the Naididae, are cosmopolitan in their distribution (Brinkhurst & Gelder, 1991). This is true for the Inaccessible Island species, with the exception of *Pristinella osborni* (Walton), known from southern Europe, Africa, India and North America (R. Grimm, pers. comm.). The enchytraeid oligochaetes collected were not identified beyond family level, although several genera have been determined from Gough Island (Holdgate, 1965). The family has a cosmopolitan distribution. It is possible that those collected on Inaccessible Island may have been associated with the soil litter on the banks of the stream and Skua Bog, rather than from the waterbody itself.

The cosmopolitan copepod species *Paracyclops poppei* (Rehberg) is also known to have a high salinity tolerance, having been recorded from some coastal areas in South Africa (N. Rayner, pers. comm.). The ostracod *Sarscypridopsis elizabethae* (Sars) has no direct marine affinities, but is a common ostracod in southern Africa and is known to tolerate saline conditions (K. Martens, pers. comm.). *Sarscypridopsis elizabethae*

is closely related to *Potamocypris*, collected on Inaccessible Island by Preece *et al.* (1986) but not found during this study. *S. elizabethae* occurs in bisexual populations on Inaccessible Island, implying that it is not a recent introduction (K. Martens, pers. comm.). Some species of *Sarscypridopsis*, such as *S. aculeata*, are known to be salinity tolerant, and *S. gregaria* was collected in a wetland in the Western Cape, South Africa, with a salinity between 20 and 25‰ (K. Martens, pers. comm.). The cosmopolitan ostracod genus *Cypridopsis* is known from Tristan da Cunha (Holdgate, 1965).

In Quaternary core samples from Skua Bog, Preece *et al.* (1986) report Ostracoda (*Potamocypris* sp.) from the lower part of the core (below 255 cm), and suggest that these may be the same species as the extant *Potamocypris* sp. which they collected from Skua Bog. *Potamocypris* was not, however, collected in the current survey. Instead, a second genus, *Sarscypridopsis*, previously unrecorded from the island, was collected. It was suggested that although *Potamocypris* and *Sarscypridopsis* are closely related, both genera may be present, as it is unlikely that their identification could be confused (K. Martens, pers. comm.).

The isopod *Iais elongata* Sivertsen & Holthuis, also usually a marine species (Holdgate, 1961; B. Kensley, pers. comm.), occurs only in the lowland stream (site B) on Inaccessible Island. *Iais elongata* was originally described from marine material collected near Inaccessible Island (Sivertsen & Holthuis, 1980). Kensley (1994) redescribed this species, including details of its biology, from material collected from freshwater (site B) during the current study. Most Jaeridae are marine species, although *Iais pubescence* (Dana), usually commensal on sphaerotid isopods, is free-living in freshwater streams on Gough Island (Holdgate, 1961), and in estuaries on South Island, New Zealand (Chilton, 1909), indicating that the species has a wide salinity tolerance. This species has not yet been recorded from Inaccessible Island, although it is known to have a wide Southern Hemisphere distribution.

The amphipods, *Orchestia* spp., comprise a large genus of semi-terrestrial amphipods which mostly occur in salt marshes and similar waters'-edge biotopes in many parts of the world. The Talitridae are generally a South American family of amphipods, unrelated to South African freshwater amphipods (C. Griffiths, pers. comm.). Only a few species in related genera are truly aquatic, for example, *Allorchestia recens* (Thomson) from New Zealand (Chilton, 1909). Three species of *Orchestia* are known from the Tristan da Cunha island group (Holdgate, 1965). Two of these, *O. scutigera* Dana and *O. platensis* (Kroyer), have been reported from both the coastal zone and from freshwater on Gough Island (Holdgate, 1965). The third (*O. gammarellus* Pallas) is not known to have colonised fresh water. A cosmopolitan, usually coastal marine species, it has been collected from Tristan da Cunha (Holdgate, 1965), but is not known from Inaccessible Island.

The dispersal of the Phthiracaroida mites poses an interesting question. They make galleries in decaying plant matter, usually wood, where they remain throughout their life (Niedbala, 1992). Thus, the most likely means of transportation of these mites from the mainland is in driftwood, rather than on birds' feet. The mite *Phthiracarus* sp., which has been recorded from Gough Island (Holdgate, 1965), has a cosmopolitan distribution (L. Coetzee, pers. comm.). The mesostig mite *Pergamasus longicornis* (Berlese) is confined to the Palaearctic region (Athias-Henriot, 1967), which suggests that this may have been introduced onto Inaccessible Island by humans. The mites *P. longicornis* and *Linopodes* sp. were both collected from site A (Table 2), associated with floating aquatic macrophytes.

Neither species are truly aquatic and inhabit damp, mossy substrates, where *Pergamasus* spp. prey on other small Arthropods, and *Linopodes* spp. feed on fungi (E. Lindquist, pers. comm.). *Pergamasus* has a Palaearctic distribution (Athias-Henriot, 1967), which suggests that it may have been translocated to Inaccessible Island by humans. *Linopodes* is widespread in the Nearctic, Holarctic and Afrotropics, where it is more abundant in warmer climates (P. Theron, pers. comm.). A new mite subspecies of the *Lobohalacarus weberi* (Romijn & Viets) complex, *Lobohalacarus weberi tristanensis* was recognised by Bartsch (1995). Other members of the *L. weberi* complex are known from mud and mosses at the edge of pools and springs, in ground water and the hyporeic sand in rivers (I. Bartsch, pers. comm.). The *L. weberi* complex has a global distribution. The oribatid mites (Table 2) are not all truly aquatic, with the exception of the malaconothrid, *Trimalaconothrus* sp. (R. Norton, pers. comm.). The other mites are terrestrial or perhaps semi-aquatic, being found in soil and litter, and were probably living along the edges of the stream. *Trimalaconothrus* has a worldwide distribution, as has *Scheloriabates*. *Lohmannia* is also widespread but the subgenus *Carolohmannia* was only known from southeastern USA prior to the collection of the mite on Inaccessible Island. The genus *Notophtthiracarus* is widespread in the southern hemisphere (R. Norton, pers. comm.), and is also known from a single species from the Himalayas, Nepal, (Niedbala, 1992), providing a Palaearctic record (Table 2). The occurrence of *Notophtthiracarus* on Inaccessible Island fits in with the dominantly southern distribution of this genus.

Collembola were collected from the neutral stream (Site B), but have not been identified. Holdgate (1965) listed 12 species, but none of these are aquatic. Since it is not yet known what the species are, and whether or not they are aquatic, they have been omitted from Table 2.

Three species of diving beetle (Dytiscidae) are distinctive to the islands (Table 2). *Liodessus involucer* (Brinck) belongs to a genus known exclusively from South America and Australia, being unrepresented in Africa (Brinck, 1948), *L. involucer* being endemic to the Tristan da Cunha Island group. *Lancetes dacunhae* Brinck is closely related to the South American *L. dacunhae* Fabricius, described from Patagonia. *Senilites tristanicola* Brinck is an endemic genus and species described from Inaccessible and Nightingale Islands.

Some ephydrid (Diptera) larvae are known to have a high salinity tolerance, living in coastal salt marshes (McCafferty, 1981). Frey (1954) described the endemic species *Dimecoenia tristanensis* from Tristan, Inaccessible and Nightingale Islands, and mentioned a second species from Inaccessible Island, which was not described. During this expedition, adults, larvae and pupae of *Dimecoenia* species were collected from Inaccessible Island from several different sites. Larvae and pupae were found at site B, and unnamed Ephydridae larvae were collected from the freshwater seeps (Site E) on cliffs along the beach, and similar seeps over rocks along the river courses on the plateau. Adults were collected in a malaise trap set up between these two sites in *Phyllica* woodland. Larvae, pupae and adults (tentatively identified as *D. tristanensis*) were also collected from the plateau rivers. The behaviour of the adults in these streams is of particular interest. In shallow sections of these upland streams, they were seen to dive under the surface of the water and swim down to the rock surface below, where they appeared to feed on fine detrital matter on the rocks. Individual flies were observed to remain under water from 10 to 46 minutes. A film of air could be seen trapped between the wings and the hairs of its body, and this may have been acting as a plastron gill. Of

eight specimens caught on re-emerging, two were male and six female. An additional 18 flies caught in the immediate vicinity produced 11 females and six males. Although the females of *D. tristanensis* are reported to oviposit underwater (Holdgate, 1961; Jones *et al.*, 2003), the flies observed during this study were not seen to lay eggs. The presence of both sexes underwater also suggests that these flies were feeding rather than ovipositing. *Dimecoenia* is known from Argentina, Chile and North America, indicating that the species on these islands have a neotropical affinity. *Centromeromyia eremita* Frey is an ephydrid genus and species endemic to Nightingale Island (Frey, 1954), and was not collected during this expedition.

The chironomid *Limnophyes minimus* has a global distribution and is often found associated with damp soil, which may enable it to be transported in soil particles on the feet of birds. Originally described as *L. pusillus* Eaton, this species was synonymised with *L. minimus* (Sæther, 1990). Based on the large size of eggs developing in the female, *L. minimus* appears to be parthenogenetic, as with the populations on the other sub-Antarctic islands (A. Harrison, pers. comm.). On Marion Island, where *L. minimus* larvae form the only benthic fauna in streams, all freshwater biotopes, including moist mud, have been colonised by this species (Crafford, 1986), but on Inaccessible Island larvae were found only in the lowland stream. Crafford (1986) suggests that they were introduced to Marion Island by early European explorers. Whether the same is true for Inaccessible Island, or whether birds or other agents of dispersal have brought this chironomid to these islands cannot be said with any certainty, though they are considered to be an alien species. Hänel & Chown (1998) found that on Marion Island, *L. minimus* is not restricted to freshwater bodies, but is found associated with plant populations in mires, where it at times exceeds the densities of other detritivorous macroinvertebrates, thus having a significant effect on nutrient recycling and a negative impact on indigenous fauna.

The chironomids *Clunio africanus* Hesse and *Thalassosmittia* sp. nr. *thalassophila* are known from Gough Island (Holdgate, 1965; Jones *et al.*, 2003), but have not been recorded from Inaccessible Island. *Clunio* is a marine chironomid, with a worldwide distribution, with some species occurring in the intertidal zone (Cranston *et al.*, 1983). *Telmatogeton sanctipauli* Schiner was previously recorded from Tristan da Cunha and Gough Island (Holdgate, 1965), and was collected from the coastal seeps (site E) on Inaccessible Island during this survey. Holarctic species of *Telmatogeton* are known to have marine associations, inhabiting the intertidal zone (Cranston, 1983). Like these species, *T. sanctipauli* was collected from the intertidal zone from seaweed-strewn rocks on Inaccessible Island, and from small freshwater seeps running down the cliffs near the beach. *T. sanctipauli* is also known from South Africa and St. Paul Island, mid Indian Ocean (Freeman & Cranston, 1980). The genus *Telmatogeton* has a worldwide distribution (Cranston, 1989).

The dipteran family classically known as Tipulidae has undergone considerable revision, and currently four families are recognised (Savchenko *et al.*, 1992). Those species associated with the Tristan da Cunha Island group now fall into the family Limoniidae. *Dicranomyia distans* Osten Sacken, originally described from Gough Island by Freeman (1962) as *Limonina* (*Dicranomyia*) *mediatlantica* Freeman, is a neotropical species (Hutson, 1980). It has been recorded on Tristan da Cunha and Gough Island, but this is the first record for Inaccessible Island. The flightless *Symplecta holdgatei* (Freeman) is endemic to these islands, also known previously from Tristan and Gough Island, and now from Inaccessible and Nightingale islands. *Symplecta*

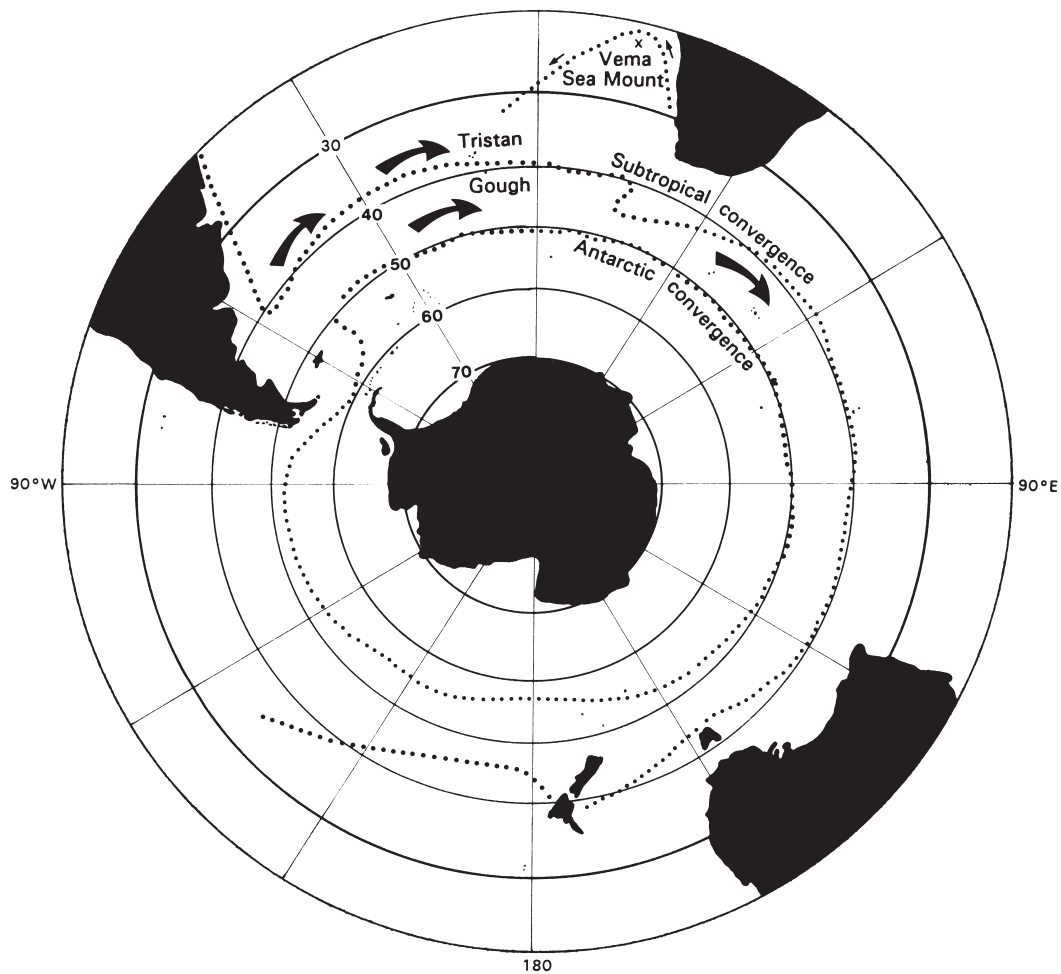


Figure 4. The southern hemisphere south of latitude 30°S, showing the positions of the Subtropical Convergence and Antarctic Convergence currents. Arrows indicate the clockwise current flow, from West to East, which may transport organisms allowing colonisation from South America. The eddy via the Vema Sea mount may carry organisms from Africa. Map based on Wace, 1961.

is endemic to the Tristan islands, and its biogeographic relationships are unclear (Jones *et al.*, 2003). Both *Dicranomyia* and *Symplecta* are reported to have tolerances to salinity (Bayly, 1972). *Psychoda albipennis* Zetterstedt is a cosmopolitan species of Psychodidae, most likely to have been introduced.

Although none of the Tristan Islands are reputed to have undergone glaciation during the last ice age (Brinck, 1960; Hollin & Schilling, 1981), they were partially submerged as a result of rising sea level during glacial periods. Nunn (1984), looking at low-level platforms and deposits on South Atlantic coasts, provides evidence that the sea-level was higher in the Holocene. This would have resulted in some of the lower parts of the islands being flooded with sea water. As the water levels fell again in post glacial times, the marine species were gradually subjected to more fresh water, some of them possibly adapting to their now freshwater environments on the islands. Preece *et al.* (1986), examining core samples from Skua Bog on Inaccessible Island, found that brackish diatom remains were dominant in the deeper (older) sediments, with freshwater species becoming prevalent in the upper (younger) sediments. This substantiates the idea of changing salinities for at least this biotope.

Two main factors which have most influenced the mainland affinities of the fauna of the Tristan Island group are wind and ocean currents. The prevailing winds are the Westerlies, while the main ocean current flowing past the islands is the Subtropical Convergence (Figure 4), which also flows from west to east. Both of these could carry organisms from South

America across to the islands, explaining the dominant South American influence in the fauna. *Nothofagus* driftwood is frequently represented on South Atlantic islands (Smith, 1985), indicating successful transportation of driftwood from South America. A small eddy flows up the west coast of Africa, past the Vema Sea Mount and recurving to the Tristan Islands (Figure 4). This current could bring organisms from Africa. Most of the vagrant land birds arriving at the Tristan islands are of South American origin, with less regular arrivals from the New World and none from Africa (J. Cooper, pers. comm.).

Endemism

Examining the freshwater fauna of the island group as a whole, eight species or subspecies are endemic. Three of these are the Dytiscidae *Liodessus involucer*, *Lancetes dacunhae* and *Senilites tristanicola*, which are endemic at specific, sub-specific and generic levels, respectively. The other endemics are the isopod *Iais elongata*, the ephydriids *Dimecoenia tristanensis* and *Centromeromyia eremita*, the crane fly, *Symplecta holdgatei*, and the subspecies of halacrid mite, *Lobohalacarus weberi tristanensis*.

Some of the non-endemic organisms may have been on the islands for a long time, and become native to the islands, without becoming separate species. Possibly speciation may be averted by additional colonisations from the mainland sources, keeping the gene pool of that species diverse. Species that have a cosmopolitan distribution must be able to disperse easily. It would be necessary to study the life histories of each species to gain a clearer understanding of the speciation pattern. Those

species with longer life cycles may change more slowly than those with a more rapid generation turn over because of reduced genetic exchange. Some of the non-endemic freshwater invertebrates are relatively sedentary, and again birds may play a role in the distribution of some of these. In some instances, organisms such as *Obrimoposthia ohlini* which have a wide salinity tolerance, may frequently recolonise from the marine habitat, keeping the population in contact with a larger gene pool and thus lessening the chance of speciation. It is possible that some of the species have colonised the island fairly recently, and have not been in isolation for long enough for speciation to have occurred.

Holdgate (1965) draws attention to the reduction in the number of species on these islands originally believed to be endemic, but subsequently being found elsewhere, although he still considers the level of endemism to be "fairly high" (Holdgate, 1969). The present study shows that about 18% of the total known freshwater fauna of the four islands is endemic. While it may be possible to calculate the percentage endemism for each individual island, this is seen as unrealistic due to the different natures of the waterbodies on each island. Inaccessible Island has the only recorded endemic aquatic invertebrate subspecies, this being *Lobohalacarus weberi tristanensis*, although it is possible that this exists on one or more of the other three islands but remains to be discovered. Two of the three dytiscids are flightless (*Liodesus involucer* and *Senilites tristanicola*), yet they occur on two or more of the islands, as does the winged *Lancetes daunhae* (Table 2). Thus, mobility does not seem to be a consideration in this case. The most likely explanation for the dispersal of the flightless Dytiscidae between the islands is the transportation of eggs on the feet of birds.

It is possible that the distribution of the ephydriids *Dimecoenia* spp. is influenced by their ability to fly, the winged adults being picked up by strong winds and blown between the islands. They are the only freshwater organisms to occur on all of the islands, having only part of their life cycle associated with water. It is therefore surprising that *Centromeromyia eremita* has only been found on Nightingale Island.

Hammer & Wallwork (1979) note that the oribatid mite fauna of the subAntarctic islands (extending from Macquarie to South Georgia) have a low degree of endemism. Most of the Inaccessible Island oribatid genera have a cosmopolitan distribution (Table 2), but the mite fauna on the other Tristan Islands is not known well enough to comment further about their level of endemism. Hammer & Wallwork (1979) suggest that dispersal between the sub-Antarctic islands has been post-Pleistocene, and they assume frequent recolonisation by wind or water from the source population. However, it has already been noted that the Tristan Islands did not experience glaciation during the Pleistocene, so it is likely that colonisation of these islands goes back further in time. One may therefore expect a higher degree of endemism of mites on the Tristan Islands than on the subAntarctic islands.

CONCLUSIONS

Each type of freshwater body on Inaccessible Island has a unique fauna, with little species overlap. This distribution is probably influenced by adaptations to differences in pH, salinity, flow and permanence of water. The distribution of the freshwater species between the four islands does not seem to be related to island size, distance from mainland, or distance of islands from each other. Rather, the intra-island distribution may be influenced by the availability of suitable aquatic biotopes on each island. Differences in extent and methods of

collecting on each island may also be relevant. Further studies on each island would without doubt reveal more invertebrate species.

This study revealed a low number of endemic aquatic invertebrate species on Inaccessible Island. Many of the species have some association with saline conditions. The influence of rising and falling sea levels during interglacial and glacial periods may have encouraged the initial colonisation of some halobiontic species. There is a stronger South American influence in the fauna than a southern African one. This is probably as a result of wind and ocean current movements and bird migration patterns.

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