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TRANSLITTORAL TALITRIDAE (CRUSTACEA: AMPHIPODA) AND THE NEED TO RESERVE TRANSITIONAL HABITATS: EXAMPLES FROM TASMANIAN SALTMARSHES AND OTHER COASTAL SITES

Alastair M.M. Richardson, Roy Swain and Vera Wong[1]

Department of Zoology, University of Tasmania, GPO Box 252C, Hobart, Tas. 7001, Australia.
[1]Present address: 8 Cedex Ct, Glen Waverley, Vic. 3150, Australia.

Abstract

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Transitional habitats, e.g., those that lie between sea and land, are often ignored because of the different backgrounds of marine and terrestrial biologists, but they are important for the series of species which span the boundary. The amphipod family Talitridae has perhaps the widest translittoral range and so provides evidence from which the evolutionary process of land colonisation can be deduced. The talitrids found on two sea-land transitions in Tasmania, a sandy-beach to rainforest and a saltmarsh to dry woodland, are described, and the significance of their distributions is discussed. The need to reserve the full range of such translittoral series is noted. This will not necessarily be achieved by establishing reserve boundaries on the basis of vegetation associations.

Introduction

Transitional habitats, that is those lying between major habitats (land and sea, freshwater and land) tend to fall through the net of biological investigations (Little, 1990). Marine biologists and terrestrial biologists develop from such different backgrounds that they have little to do with each other and so the zones of interaction between their spheres of operation tend to be ignored. While marine biologists often work in the intertidal zone, their studies tend to be concentrated well below the high water mark, while few terrestrial biologists approach the high water mark from the other direction. Thus the amount of study on the intermediate zone is small, and this is particularly obvious when the transitional zone is extensive, as it is in the most sheltered sea-land interfaces, in saltmarshes and mangroves.

And yet the interface between the two major habitats is in many ways more important than the sea or land alone. The colonisation of land was one of the greatest evolutionary events in the history of those seven phyla that have achieved terrestriality. Although most of the colonisation events happened a long time ago, the habitats in which they occurred are still there, and in some cases species can be found filling many of the intermediate stages. In a few taxa, which might be called translittoral (Chester, 1992), series of species can be found with distributions spanning the entire range from fully marine to fully terrestrial. The best examples are the amphipod crustacean family Talitridae and the pulmonate mollusc family Ellobiidae. Translittoral groups of this type provide very valuable opportunities to reconstruct the evolutionary events leading to life on land (Little, 1989, 1990), and they become more valuable still when the species involved are relatively closely-related, as in the two families mentioned above.

In this contribution we will present evidence of translittoral distributions in the Talitridae and demonstrate that such distributions require a broader approach to reserve design than has been adopted hitherto.

Talitridae

The Talitridae include the only fully terrestrial members of the Amphipoda, one of only two crustacean groups (the other is the Isopoda) which have members that are fully terrestrial, ie. independent of free water for all of their life stages. The Talitridae have been loosely classified by Bousfield (1984) into four groups, the palustral talitrids (marsh-hoppers), the beach-fleas, the sandhoppers and the landhoppers. The marsh-hoppers include the most plesiomorphic forms and they are found in the lower levels of saltmarshes and mangroves, where they have an amphibious lifestyle, entering and swimming efficiently in seawater even at low tide. In some places (Tasmania: Chester, 1992, South Africa:

Griffiths, 1976) their distributions extend into fully freshwater streams. In south east Australia the genus *Eorchestia* is widespread in saltmarshes and the lower reaches of associated streams (Richardson, 1993). The beachfleas and sandhoppers are the typical talitrids of the intertidal zone, distinguished by the adaptations of sandhoppers for their particular habitat, ie loose sand. Thus the sandhoppers are large, robust and spiny talitrids, sometimes with unusual morphological adaptations for life in sand. They are efficient burrowers. The beachfleas, in contrast, are not well-developed for burrowing, preferring to seek refuge under cast seaweed or stones (non substrate modifiers: Macintyre, 1963, or nestlers: Griffiths, 1976); they are generally more lightly built and weakly spined. Beachfleas are usually found on rocky or muddy shores, but there is at least one undescribed species in Tasmania which has become convergent with the sandhoppers and forages on midtidal wet sand during low tide, taking refuge in a shallow burrow during high tide.

The landhoppers are found in a range of terrestrial habitats in the Southern Hemisphere, Japan, the Phillipines, Central America, the Caribbean and many oceanic islands. In Tasmania they are found throughout the island, but where they have colonised continents (Australia, southern Africa) they are confined to the higher rainfall zones around the continental margins. Bousfield (1984) recognises two subgroups, the plesiomorphic simplidactylate genera, which seem to be descended from a marsh-hopper like ancestor, and the cuspidactylate genera which apparently arose from the beachfleas. The simplidactylate forms are confined to Australia and southern Africa.

Thus the Talitridae show a truly translittoral range from the semi-aquatic marsh-hoppers to the landhoppers. The sister family to the Talitridae is the Hyalidae, and it is widely- accepted that talitrids descended from a hyalid-like ancestor (Bousfield, 1984). Aquatic hyalids may be found adjacent to intertidal talitrids in fully marine and brackish waters, providing a valid extension to the translittoral series.

It seems likely that the talitrid amphipods colonised land relatively recently compared to other terrestrial arthropods. Little (1990) noted that the fossil record of the amphipods is only from the Quaternary, but Bousfield (1984) and Bousfield and Poinar (1995) suggests a mid-Cretaceous origin for the simplidactylate landhoppers of the Southern Hemisphere continents, contemporary with an extensive radiation of the angiosperm flora in Gondwana.

Tasmania has a remarkably rich talitrid fauna (Richardson, 1993, 1996) which includes representatives of all Bousfield's groupings. The taxonomy of the landhoppers is well-known (Friend, 1987) and the diverse intertidal fauna is currently being described by the senior author. Friend (1987) divided the Tasmanian landhopper fauna into three ecological groupings, one of which he called the coastal group. Five or six species in three genera make up this group and they have distributions which are strongly restricted to a narrow zone, less than 100 m wide, immediately behind the high tide mark.

Tasmania also retains some places, especially in the west, where transitions from land to sea remain undisturbed, and clothed with native vegetation. These provide important opportunities to study the natural distributions of talitrid amphipods, isopods and other groups across the transition. We will consider two cases, a sandy beach to wet sclerophyll forest at South Cape Bay and a saltmarsh to dry woodland transition at Lutregala Marsh on Bruny Island. Details of these studies are described elsewhere (South Cape Bay: Richardson et al., 1991; Lutregala Marsh: Richardson and Mulcahy, in press).

Study areas and methods

South Cape Bay

South Cape Bay is in the extreme south of Tasmania (Fig 1). It faces almost due south, but is sheltered from the prevailing south westerly and westerly winds by promontories to the west. Because of strong wave action, the sand above the highwater mark is colonised by few foredune plants, so that low coastal scrub and forest appears within a few metres of high water. Closest to the shore the shrubs *Correa backhousiana, Cyathodes abietina, Westringia brevifolia* and *Olearia phlogopappa* form a low dense cover, five to ten metres deep, which gives way to low forest with emergent trees of *Eucalyptus nitida,* sassafras, *Atherosperma moschatum,* celery top pine, *Phyllocladus aspleniifolius,* and southern beech, *Nothofagus cunninghamii.* This coastal forest has an understorey of native laurel, *Anopterus glandulosus,* and often cutting grass, *Gahnia grandis.* The ground layer is mostly absent, apart from a few mosses and herbs. The vegetation becomes lower and more wind-pruned from the western to the eastern end of the bay.

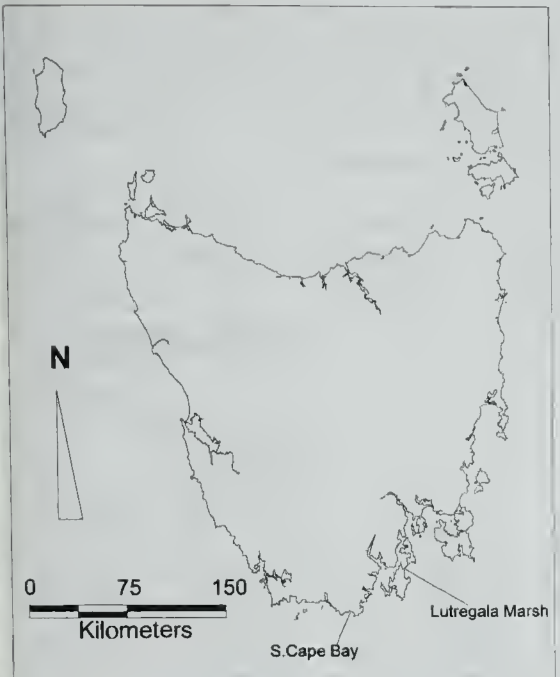

Figure 1. Tasmania, showing the locations of the two study sites mentioned in the text.

The topography immediately inland from the beach consists of a series of two or three low ridges, apparently stabilised dunes, separated by damper swales. The most landward ridge becomes higher from west to east, but at the eastern end of the bay erosion has cut into these structures, eliminating the lower seaward ridges and forming a sand cliff approximately 8 metres high. The soils are sandy, but at the eastern end of the bay waterlogged clayey soils appear within 30m inland of the top of the sand cliff.

Two transect lines were set up in February 1989, at right angles to the high water mark, from below the extreme high water mark of spring tides (EHWS) to between 40 and 70 m inland. At each meter mark along these transects a pitfall trap was set. The traps consisted of a plastic container of 5 cm diameter and 10 cm depth, let into the soil so that the lip of the trap was flush with the surface of the sand, soil or leaf litter. Saturated picric acid solution (5–10 ml) was placed in the traps as a non-volatile preservative and Petri dish lids were supported on twigs over the traps to prevent rainwater from entering them. Traps were set for one series of ten nights in February and another of 14 days in July 1989.

Lutregala Marsh

Lutregala Marsh is situated on the west coast of Bruny Island, which is just off the south east coast of Tasmania (Fig. 1). The marsh has a diverse talitrid fauna, and, importantly, a relatively undisturbed transition from saltbush saltmarsh through saline tussock grassland to native terrestrial vegetation, despite some grazing by cattle on the higher levels. The marsh occupies approximately 10 ha.

Two sampling methods were employed to determine the distribution of amphipods. Firstly, two transects of pitfall traps, more or less at right angles to the high water mark, were placed across the marsh, and extended into terrestrial vegetation up to 50 m beyond the extreme high water mark. Pitfalls were constructed in the same way as at South Cape Bay. Transect A was set and retrieved three times between March and October 1990 during overnight low spring tides, but Transect B was only used once because of persistent flooding.

In the second approach to sampling, collections were made extensively over the marsh. From a recent, colour aerial photograph, collection sites were chosen that could easily be identified on the ground, and which represented the range of vegetation types present. At each sampling site, at least 20 amphipods were collected with an aspirator, and the same environmental variables that were collected at each pitfall site were measured. These collections were also made between March and October 1990. This period covers both the non-breeding (winter) and early breeding season of the species present.

Results

South Cape Bay

Twelve species, three of which were supralittoral sandhoppers, are listed in Table 1. Two undescribed species of *Tasmanorchestia* Friend were identified, and none of the sandhoppers has been placed in a specific taxon because of the poor taxonomic knowledge of this group.

The catches from the pitfall traps (Figure 2a-d) show distinct zonations in the distribution of species. Among the sandhoppers, there is a clear series, with 'Talorchestia' species 1 found closest to the sea, followed by 'Talorchestia' species 2, which in turn is replaced by 'Talorchestia' species 3. The replacement of sandhoppers ('Talorchestia' species 3) by landhoppers (*Austrotroides maritimus* Friend) is very sharp. The overlap was never more than 2 traps (= 2m), and on several nights there was no overlap at all.

Table 1. Talitrid amphipods collected at South Cape Bay and Lutregala Marsh, with their phylogenetic affinities, ecological groupings and abundance. Bousfield's (1984) groupings are as follows. I:i: palustral talitrids. II:iii: cuspidactylate beachfleas having a 4-dentate lacinia mobilis on the left mandible. III:i: sandhoppers having a 4-dentate lacinia mobilis on the left mandible; III:ii: sandhoppers having a 5-dentate lacinia mobilis on the left mandible. IV:i: simplidactylate landhoppers. IV:ii: cuspidactylate landhoppers.

Taxon	Bousfield Group (Bousfield 1984)	Landhopper Ecological Group (Friend 1987)	Abundance at South Cape Bay	Abundance at Lutregala
Eorchestia palustris Richardson	I:i		—	Common
Beachflea	II:iii		—	Common
Talorchestia sp. 3	III:i		Common	—
Talorchestia sp. 1	III:ii		Common	—
Talorchestia sp. 2	III:ii		Common	—
Austrotroides maritimus Friend	IV:i	Coastal	Common	Common
A. longicornis Friend	IV:i	Western forest	Rare	—
Keratroides rex Friend	IV:i	Coastal	Scarce	Scarce
Mysticotalitrus tasmaniae (Ruffo)	IV:i	Eastern forest	Common	Common
M. cryptus Friend	IV:i	Eastern forest	Scarce	Scarce
K. vulgaris (Friend)	IV:i	Eastern forest	Common	Scarce
K. angulosus (Friend)	IV:i	Eastern forest	Common	—
Neorchestia plicibrancha Friend	IV:i	Western forest	Common	—
Tasmanorchestia Friend sp.1	IV:ii	Coastal	Rare	—
Tasmanorchestia Friend sp.2	IV:ii	Coastal	Rare	Rare

On transect A there was a complete replacement of sandhoppers by *A. maritimus* from trap 9 to trap 10, with no sandhoppers in trap 10 and no *A. maritimus* in trap 9 after 14 nights of catching. Once beyond the landward range of the sandhoppers, the catch at S. Cape was dominated by *A. maritimus* for the next 20–30 m inland. *Tasmanorchestia* sp. and *Keratroides rex* also appeared, but in very low numbers, and only on transect B in the summer series.

Samples collected by hand, during the day, (Table 2) from the four swales on S. Cape Bay transect B did not contain the same proportions of species as the pitfall traps at all sites. At the seaward end, hand samples failed to catch sandhoppers but caught a much higher number of *A. maritimus* and *K. vulgaris*. Further landward, most species were much less likely to be trapped than caught by hand, and only *A. maritimus* and *M. tasmaniae* were over-represented in the traps.

Further inland, beyond the traplines, the landhopper community in forest litter changes, with no trace of the coastal group species or *Mysticotalitrus tasmaniae*. *K. angulosus* and *Neorchestia plicibrancha* become the dominants, with *Austrotroides longicornis* Friend appearing at a drier site about 1 km from the beach. Further inland still, *N. plicibrancha* was the only species collected in rainforest several kilometers from the coast.

Lutregala Marsh

Eight species of talitrid amphipods were identified at Lutregala Marsh. These included one species from each of the palustral and beachflea groups, three coastal species and three forest species (Table 3). One of the coastal species was an apparently undescribed species of *Tasmanorchestia* Friend.

Profiles of the transects, the distributions of amphipods and the levels of the environmental parameters are shown in Figs 3a and 3b. Both transects cross a slight rise at their seaward ends, but Transect B is clearly much lower than Transect A and liable to tidal flooding over most of its length. At their landward ends both transects rise slightly and pass into terrestrial vegetation. The most striking contrast in the amphipod fauna is the absence of *Eorchestia palustris* on the drier Transect A, where it is replaced in the lower sites by the beachflea. On Transect B the beachflea is mostly confined to the upper levels of the transect, beyond the range of *E. palustris*.

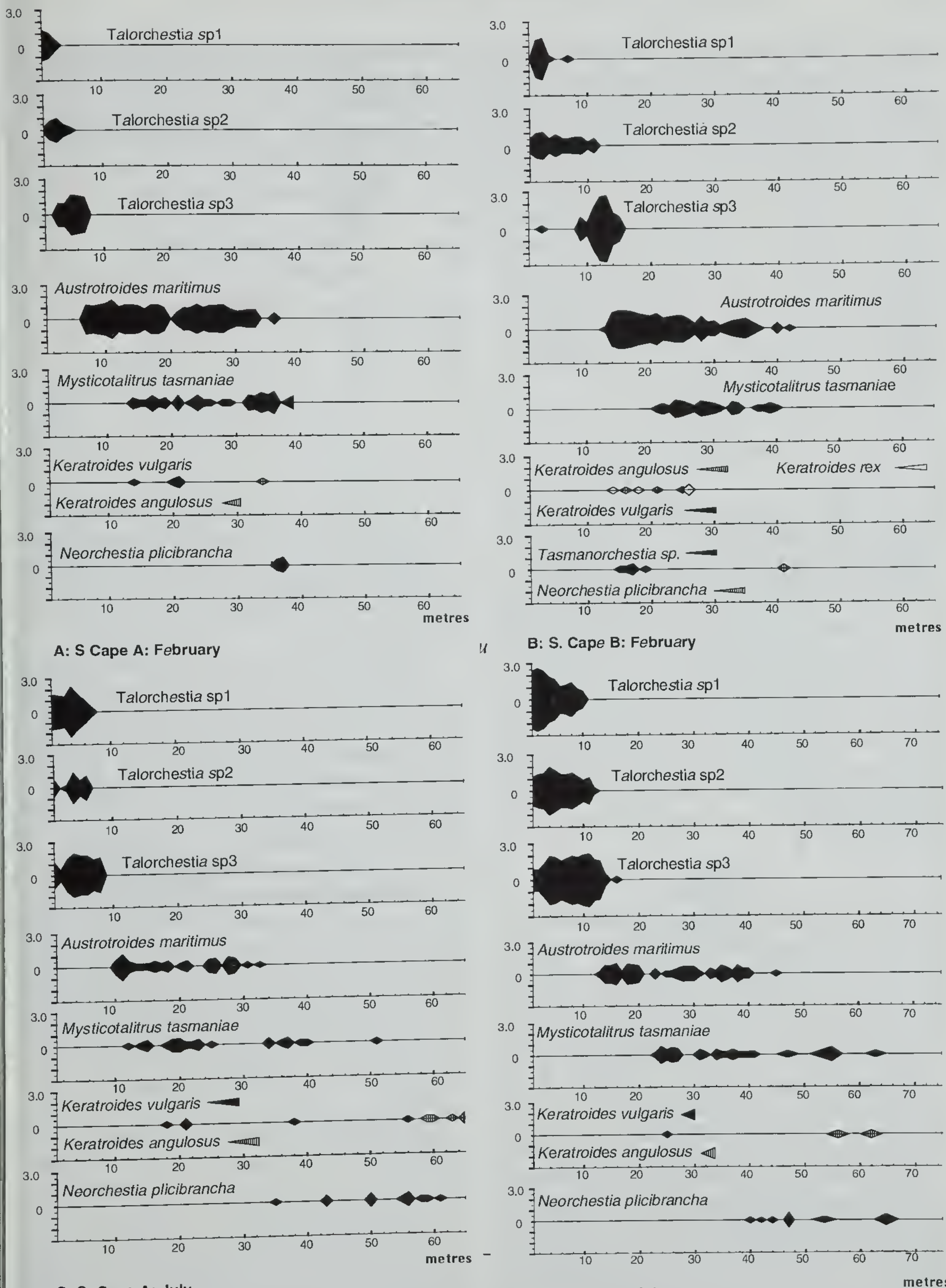

Figure 2a-d. Catches of talitrid amphipods in pitfall traps at South Cape Bay, Tasmania. The horizontal axis is in metres from Trap 1 which was set at the seaward edge of the strandline vegetation; the vertical axis is $\log_{10}(X + 1)$, where X is the average daily catch of each species in each pitfall. The transects extended 40 m (A) or 45m (B) inland during the February series, but were extended to 70 m in the July series.

Table 2. Catches of talitrid amphipods by hand (first figure) or pitfall (second figure) at or near South Cape Bay (no pitfalls were set inland of the 4th swale). Species abbreviations are as follows. Tal 2: Talorchestia sp. 2; Tal 3: Talorchestia sp. 3; Austr mar: *Austrotroides maritimus;* Kera vulg: *Keratroides vulgaris;* Kera angu: *Keratroides angulosus;* Myst tas: *Mysticotalitrus tasmaniae;* Myst cryp: *Mysticotalitrus crytpus;* Neor plic: *Neorchestia plicibrancha;* Austr long: *Austrotroides longicornis.*

	Tal 2	Tal 3	Austr mar	Kera vulg	Kera angu	Myst tas	Myst cryp	Neor plic	Austr long
Swale 1	0/1	3/96	125/1	20/0	—	—	—	—	—
Swale 2	—	0/3	125/4	78/0	6/0	30/0	—	3/0	—
Swale 3	—	—	2/4	128/1	11/0	9/8	—	8/0	—
Swale 4	—	—	—	40/0	75/2	4/4	—	35/6	—
70 m	—	—	—	1	14	—	—	6	—
1 km	—	—	—	—	—	—	14	14	6
5 km	—	—	—	—	—	—	—	8	—

On both transects there is considerable overlap between the distributions of the beachflea, coastal landhoppers, and forest landhoppers.

Fig 4 shows the distribution of species from the four ecological groups of amphipods that were present (marsh-hoppers, beachfleas, coastal and forest landhoppers) over the marsh and the major vegetation types. *Eorchestia palustris* is restricted to the wet marsh vegetation where it is regularly inundated, while the beachflea extends more deeply into the upper marsh and terrestrial vegetation. The forest landhoppers are restricted to the terrestrial scrub, but the coastal landhoppers are found both there and in the upper marsh.

Discussion

At South Cape Bay the interface between the beach and the adjacent forest is quite sharp. There was complete replacement of sandhoppers by landhoppers within 4 metres, at the point where woody vegetation formed a closed canopy and substantial amounts of organic matter began to appear in the sandy soil. The coastal landhoppers extend inland for another 50 m, beyond which the landhopper community becomes much less diverse than in the coastal zone. Further work at South Cape Bay and elsewhere in the west of Tasmania (Richardson, 1993, in prep.) shows that the distance that the coastal species penetrate inland is related to exposure to wind, perhaps because this increases the amount of salt spray deposited behind the shore.

At Lutregala Marsh, in contrast, there is no obvious point where intertidal talitrids (in this case beachfleas) are replaced by landhoppers, since there are substantial overlaps both between the distributions of the beachflea and the coastal landhoppers and between the beachflea and the marsh-hoppers which occupy a zone closer to the sea.

The numbers of talitrid species present at both sites is high, 11 species at South Cape Bay and eight at Lutregala Marsh, and phylogenetically diverse. Although the phylogeny of the Talitridae is not clearly understood, it is generally accepted (Bousfield, 1984, Moore et al., 1993) that sandhoppers form a distinct, specialised group that is unlikely to have produced any forms ancestral to the landhoppers. This, combined with the absence of beachfleas and the abrupt transition from beach fauna to forest fauna, suggests that sandy beaches were unlikely to have been the site where the colonisation of land by talitrids began. On the saltmarshes, both of the likely ancestral groups are present (marsh-hoppers and beachfleas), the transition to land is gradual, distributions overlap substantially and the saltmarsh habitat foreshadows land in the structure and nutritional nature of its vegetation.

In both these examples there are reasons why the phenomena of interest cover a wider range than "shore" or "land", however they might be defined. Certainly vegetation patterns do not give any indication of the inland limits of coastal landhoppers in either location. There has been some interest in the reservation of saltmarsh vegetation in Tasmania (Kirkpatrick & Glasby 1981), but by definition that has referred to saltmarsh plants. There are many records of beach-

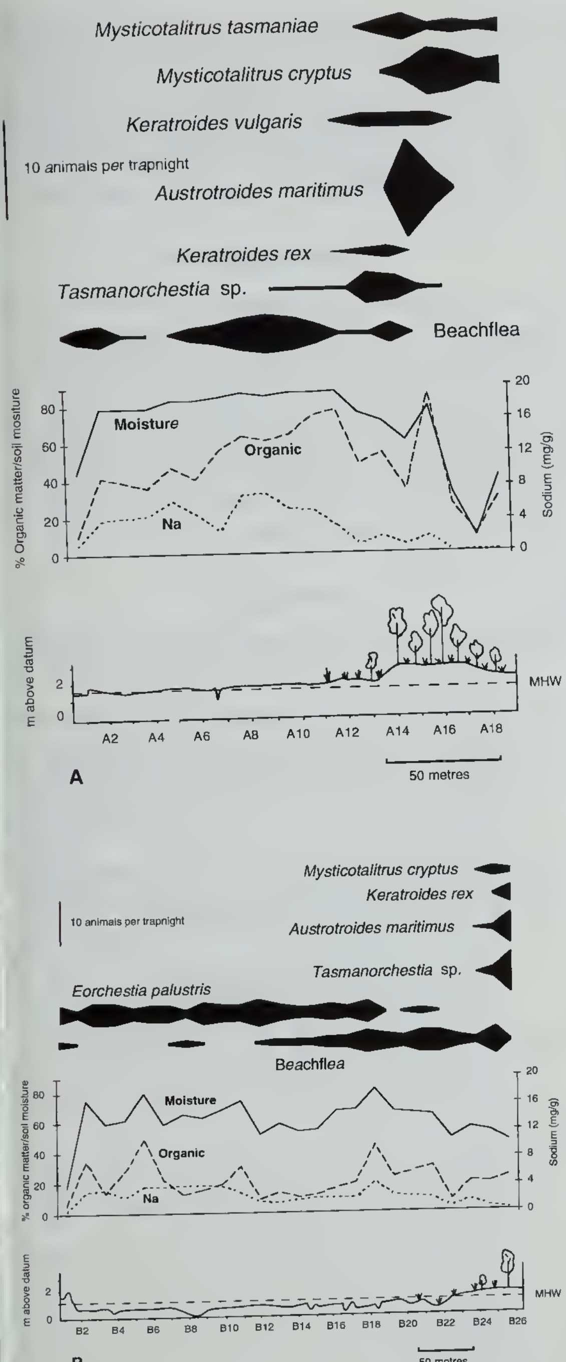

Figure 3a, b. Profile of two transects on Lutregala Marsh, showing the levels of soil moisture, soil organic content and soil salinity at each trapping position, and the relative abundance of amphipods trapped in pitfalls. MHW: mean high water level.

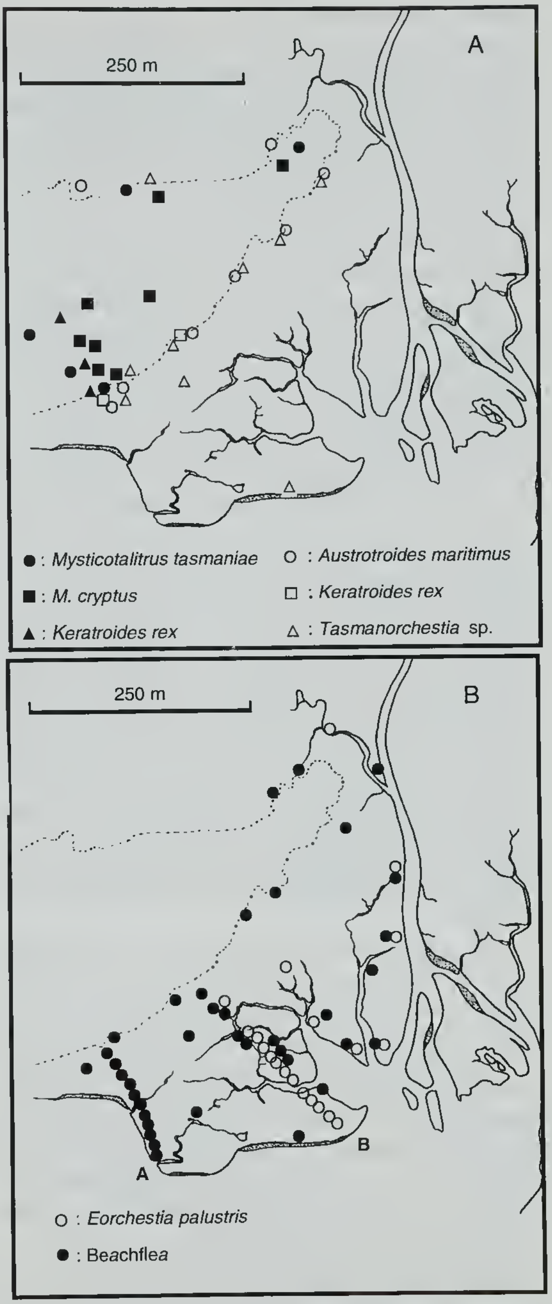

Figure 4a, b. Maps of Lutregala Marsh, showing the distributions of the four ecological groups of talitrid amphipods. A: marsh-hoppers and beachfleas; B: coastal and forest landhoppers. The dashed line represents the approximate boundary of woodland. Samples were collected by hand, and from the pitfall transects (A: start of transect A: B: start of transect B). Filled symbols refer to species of the forest landhopper group, or the beachflea, open symbols to the coastal landhopper group or to the palustral group (*Eorchestia palustris*).

fleas extending their range into terrestrial vegetation, usually in situations where there is considerable salt spray (eg Reid 1947, Bagenal 1957, Kuhnelt 1976, Bousfield 1982), and the coastal landhoppers, which are part of the translittoral series, extend beyond the landward limit of the recognised saltmarsh plants.

In a survey of the crustacean and mollusc fauna of Tasmanian saltmarshes, Wong et al. (1993) recorded the factors causing disturbance at 52 saltmarshes and 11 other brackish marshes around the Tasmanian coast. As well as grazing, invasion by exotic species, landfill, catchment modification, fire and off-road vehicles, all noted by Kirkpatrick and Glasby (1981), they also recorded the condition of the vegetation immediately behind the marshes. Very few of the marshes retained intact backing vegetation, since land clearance for grazing behind the marshes is very common (indeed, grazing in the marshes is one of the most common disturbance factors). Wong et al. (1993) recommended nine marshes for listing on the Register of the National Estate and added another three marshes of high conservation value, but even amongst this group, only five were recorded as having intact backing vegetation. Thus while it may be relatively easy to select saltmarshes for reservation on the basis of values within the marsh as defined by the vegetation, there are very few opportunities to reserve the complete series of distributions of the translittoral talitrids.

Fortunately, the situation with sandy beaches and their backing vegetation is not so bad, at least in the western half of the island, where much of the coast lies within the Western Tasmania World Heritage Area. Elsewhere, in lower rainfall areas the dunes that back the beaches are often colonised by the introduced marram grass, *Ammophila arenaria*, but in another survey (Richardson et al., in prep.), a few beaches on the east coast have been identified where the coastal vegetation remains undisturbed.

It is regrettable, though pragmatic, that reservation decisions so often have to be made on the basis of vegetation patterns, without any reference to animal distributions. While it is not surprising that there is often no clear correlation between animal distributions and plant associations, in some cases, such as the translittoral groups discussed here, defining reserves in vegetational terms can lead to the failure to protect significant zoological phenomena. There is considerable interest in the ecophysiology of land colonisation in talitrid amphipods (e.g., Moore et al., 1993, Morritt, 1987, 1988, 1989; Spicer et al., 1987; Spicer and Taylor, 1987, 1994), and Tasmania provides perhaps the best opportunity in the world to combine ecophysiology with studies of distributions and other aspects of the biology of a translittoral series, provided that places where that can be done remain intact.

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