Primary vegetation development on the sand spit of Shallow Inlet, Wilsons Promontory, southern Victoria

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Abstract: The sand spit that separates Shallow Inlet from Waratah Bay (38º52′ S, 146º13′ E), near Wilsons Promontory in southern Victoria, has developed since the previous spit was washed out in 1901. Initially without vegetation, the spit was colonised in the 1960s by the exotic grasses **Thinopyrum junceiforme* and to a lesser extent **Ammophila arenaria*. These species are native to the coast of western Europe, where they fulfil a key role in dune establishment. Being able to grow through sand accumulating among the culms, these grasses formed mounds where seeds or rhizome fragments were washed up during king tides. Where somewhat sheltered from the strongest impact of the westerlies, mounds gradually coalesced and formed short ridges at the landward side of the spit, and 'dune fields' towards its distal end. Circumstances favourable for dune field formation were enhanced by episodic processes in spit growth due to channel shifting in the tidal delta and the gradual lengthening of the main outlet channel.

Austrofestuca littoralis and *Spinifex sericeus* joined the two foreign grasses in their pioneering role. The herbaceous *Actites megalocarpa* and the shrub *Ozothamnus turbinatus* established in the lee of the grasses, but conditions on mounds, dune crests and windward slopes are too severe for other species. Only at more sheltered sites is further development of vegetation possible. In the lee of the dune fields it has progressed into an open shrubland, initially of *Ozothamnus turbinatus*, *Olearia axillaris* and *Olearia glutinosa*, later enriched by *Acacia longifolia* var. *sophorae*, *Leptospermum laevigatum* and *Leucopogon parviflorus*. Wind-dispersed taxa form the dominant component of the vegetation, but several animal-dispersed species became established as well. The complement of woody species begins to resemble that of the dune scrub found elsewhere along this part of the Victorian coast, but several wind-dispersed species, notably *Banksia integrifolia*, are still lacking and it would appear that dispersal is still a limiting factor in vegetation development. It is pointed out that dune development on the sand spit was initiated by exotic grasses and that without their presence, it is doubtful whether any vegetation would have established there.

Many photos support the text- *the narrative will say what words can say but words can never say it all* (Love 1999).

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Introduction

Shallow Inlet forms an embayment in the northeastern corner of Waratah Bay from which it is separated by a sand spit (38º52′ S, 146º13′ E; Fig. 1). It is one of the South Gippsland Marine and Coastal Parks and is contiguous with Wilsons Promontory National Park. In the terrestrial zoning for recreational activities in the Shallow Inlet Marine and Coastal Park the sand spit is classified as a Reference Zone, and no human activity of any kind, including passive recreation, is allowed there (Anon 1986, 1990).

In the late 1970s I began investigating the sand-collecting abilities of indigenous and introduced coastal plant species (Heyligers 1985) and used the spit as one of the study sites. As it was still accreting, it provided an opportunity to observe sand-interception by individual plants as well as dune formation and vegetation development. I expected that succession would demonstrate what is usually inferred from toposequences: a steady progression from pioneering grasses through a shrubby phase to taller woody vegetation (e.g. Barson & Calder 1976). However, developments on the spit did not follow such an orderly pattern and in this paper I report what actually happened.

Geomorphological setting

The largely sandy shore of Waratah Bay extends from Cape Liptrap to the mouth of the Darby River (Fig. 1a). Shallow bottom sediments are gradually transported inshore by the south-westerly swell generated in the Southern Ocean and moved to the northeastern side of the bay by longshore currents. The gently sloping beach, more than 200 m wide at low tide, and a series of offshore bars as well as the formation of additional foredune ridges, are the result of this depositional environment (Bird 1977, 1993).

Shallow Inlet has only a small catchment; hence the water regime is predominantly tidal. During ebb, large areas fall dry, leaving a meandering channel that shoals into a tidal delta at the entrance. Tidal amplitudes in Waratah Bay are about 1.9 m, with only a small difference between neap and spring tides. Strong to gale-force winds may increase tidal height by 0.5 m, sufficient to inundate low-lying areas of the spit. On occasions, in the lowest sections, overwash reaches the channel shore. Fresh to strong westerly and southwesterly winds are predominant; those from the northwest and northeast are less frequent and usually light to moderate. Rainfall is about 850 mm/yr; monthly totals vary from about 40 mm during the summer months to more than double that amount during late autumn and winter (Smith 1969).

The entrance to Shallow Inlet has a chequered history (Smith 1969, Cecil 1983, Bird 1993). A spit was present in the middle of the nineteenth century, but broke through in 1901 and the entrance shifted towards Sandy Point (Fig. 2). The old entrance sanded up, thus joining what was left of the spit with the opposite shore. However, sand conveyed by longshore currents began to block the channels in the northwest part of the delta, forcing the main channel to shift to the southeast. Thus, another spit began to form, a process that is still continuing. Smith (1969) was the first to broadly analyse it, while Cecil (1983) provided a detailed explanation of the channel dynamics of the ebb tidal delta. They concluded that the erosional and depositional effects of the tidal currents in combination with the easterly longshore drift lead to a gradual extension of the spit. While both authors concentrated on erosional aspects, less attention was paid to accretional ones. The latter, however, are critically important for understanding later dune formation.

The role of plants in dune formation

The sand-collecting capacity of plants, and consequent mound building have been reported from both coastal and desert environments (e.g. Hesp 1981, Rundle *et al.* 1991, Hesp & McLachlan 2000). The result of the interactions between wind, sand and plants depends on the growth form of the colonising species (Hesp 1982, Heyligers 1985, Danin

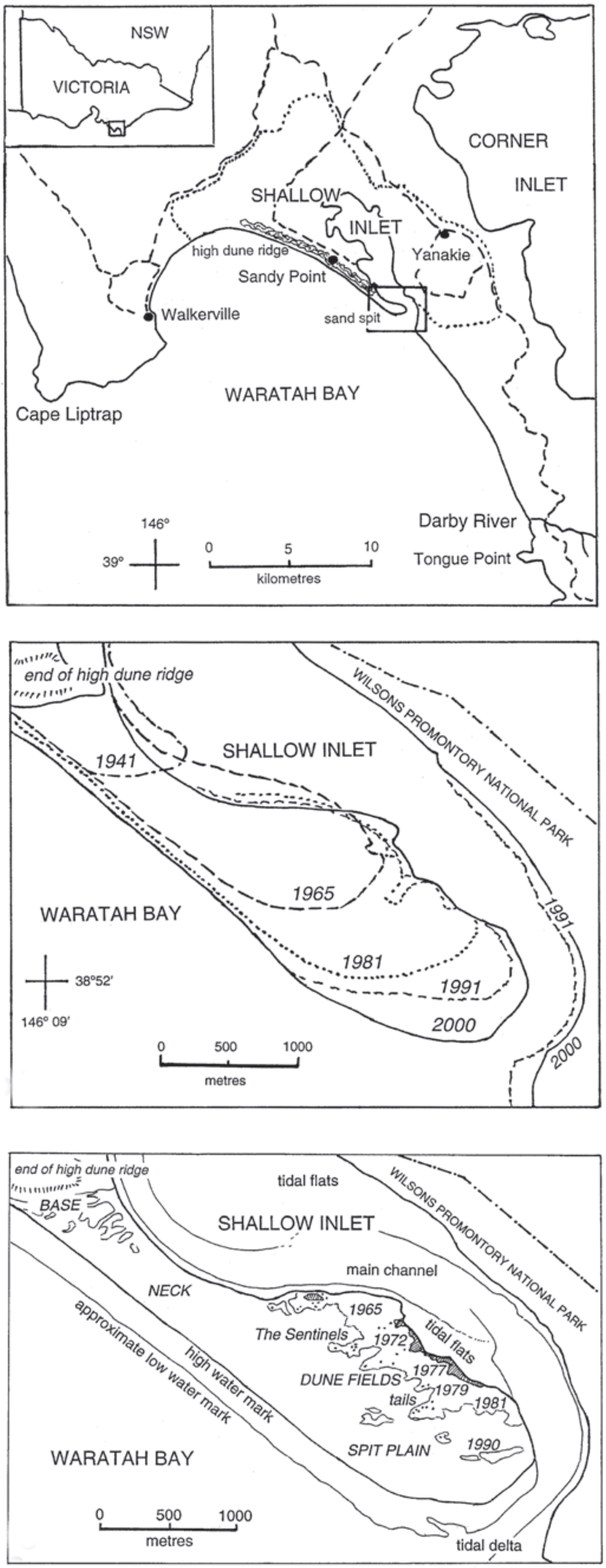
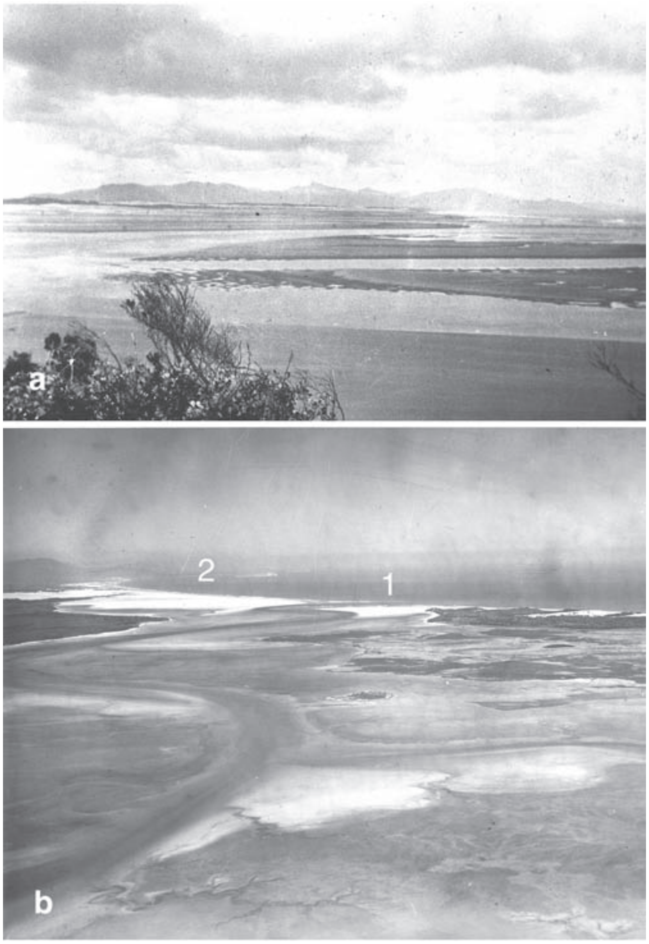


Fig. 1. Location, history and features of the sand spit at the mouth of Shallow Inlet. (a) Position along the northeast shore of Waratah Bay. Roads are indicated with broken lines, the watershed boundary of Shallow Inlet is outlined with a stipple line. (b) Growth of the sand spit since 1941; erosion of the opposite shore has only been mapped for 1991 and 2000; earlier shore outlines would overlap the position of the spit (see Figs. 2 and 4). (c) Features of the spit mapped from the 2001 airphoto. Names used to facilitate description are in italics, as are the dates approximately indicating when the first mounds appeared which lead to the formation of that section of the dune fields. The dots represent some of the more prominent mounds. The hatched area along the inlet shore indicates the *Thinopyrum* flats, that at the west end of the 1965 section the densely vegetated hollow.

1996). Sand-bearing winds leave a ridge in the lee of tussocks and bushy plants (Fig. 3). Height and width of the ridge are mainly determined by plant shape, but length depends on the strength of the airflow around the sides: stronger winds and variable wind directions leave shorter ridges. Turbulence created behind the top of a plant causes the highest point of the ridge often to be located behind the plant, rather than in it. Low, horizontally spreading plants enlarge surface drag rather than split the airflow vertically. The resultant turbulence causes sand to precipitate in the small wake areas amidst leafy branches and runners, resulting in the formation of lower, wider mounds.



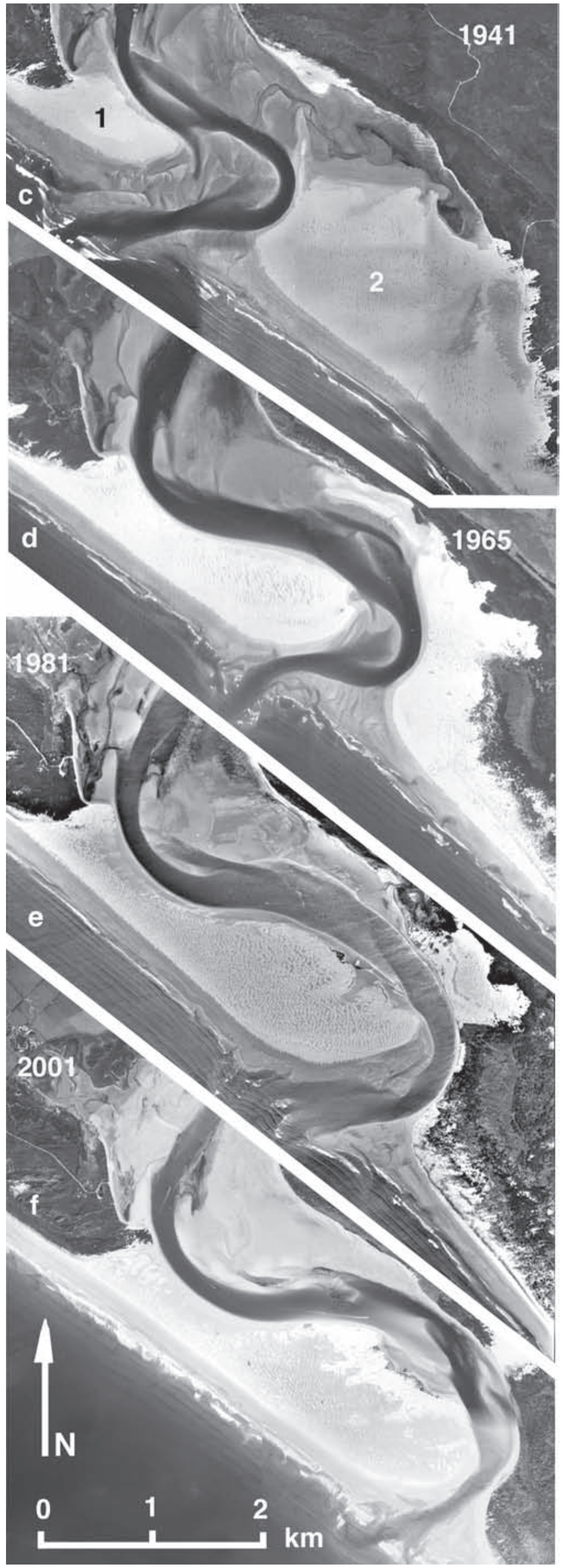


Fig. 2. Overview of the history of spit growth. (a) A 1927 view over the tidal delta from the end of the high dune ridge along Waratah Bay showing several channels at the mouth of Shallow Inlet. (b) The 1937 aerial view over the mud and sand flats of the inlet towards the mouth, where the young spit is visible at the right (1) and the sand plain, the remnant of the former spit, at the left (2). (c) The earliest vertical aerial photograph of this area, taken in April 1941. (d), (e) and (f) show the outlet channel cutting into the sand plain, shifting the tidal delta and extending the sand spit. (Picture (a) taken by C.D.H. Pilkington, courtesy of Miss V. Pilkington; (b) taken by S. Fowler (negative A2/556), used with permission of CSIRO Archives; (c) Copyright © Royal Australian Air Force; (d) Copyright © Commonwealth of Australia, Geoscience Australia; (e) Copyright © Crown (State of Victoria) 1981; (f) Copyright © Parks Victoria.)

Cooper (1958) was the first author to draw attention to the fact that an alien species could change the morphology of local dune landscapes. He reported that **Ammophila arenaria*, indigenous to western Europe and the Mediterranean and introduced to California in 1869, had formed prominent foredunes where none existed before. In Australia, this species was introduced in 1883 to stabilise the drifting dunes near Port Fairy, Victoria, and was widely used along temperate shores (Molineux 1902). On Wilsons Promontory it was first used in 1915 (Garnet 1971, Crawford 1984) and in the 1950s the Soil Conservation Authority tested this and another foreign species, **Thinopyrum junceiforme*, together with *Spinifex sericeus* and two other native species, for their sand-binding characteristics, at Tongue Point at the southern end of Waratah Bay (SCA 1960). However, only **Ammophila arenaria* was used during dune restoration work in the 1960s and 1970s at Sandy Point and the parking area at the inlet (SCA, pers. comm. 1983).

Methods

Between November 1980 and October 2003, I visited the spit 15 times. Fieldwork initially focused on general description and mound formation, and later on assessing dune and vegetation development. Observation sites were marked on airphotos or sketch maps and documented with photos from approximately standard positions. For ease of identification I gave names to features on the spit, often inspired by location or based on their age (Fig. 1c).

Mounds formed by the wind resistance of a single plant are sometimes called 'nebkas' or 'biogenic mounds' (e.g. Danin 1996, Hesp and McLachlan 2000), but I just use 'mounds.' 'Dune ridge' and 'dune field' refer to land forms where such mounds have coalesced. Botanical nomenclature follows Walsh and Entwisle (1994–1999) except in the case of *Senecio lautus*, which name has been replaced by *Senecio pinnatifolius* (Belcher 1994). Specific epithets have been used for all species except for *Acacia longifolia* var. *sophorae*, for which the varietal name has been substituted. Scientific names for mammals follow Triggs (1996), those for birds Christides and Boles (1994). Asterisks precede the names of introduced species.

After I became aware of the history of the spit, I obtained copies of maps and airphotos, spoke to local inhabitants and searched in libraries and archives for information on early vegetation development. The oldest useful picture, taken in 1927, shows a view over the mouth of Shallow Inlet from a high dune (Fig. 2). The oldest aerial photo is an oblique view

Fig. 3. Examples of mound and ridge formation by pioneer grasses. (a) Start of a **Thinopyrum junceiforme* mound around a piece of flotsam. (b) A mound established in *Spinifex sericeus*, with the highest point behind the plant. (c) Wind-shadow ridges formed behind *Austrofestuca littoralis* tussocks. (d) A low ridge formed in *Austrofestuca littoralis* tussocks along a flotsam line at the foot of the dune field.

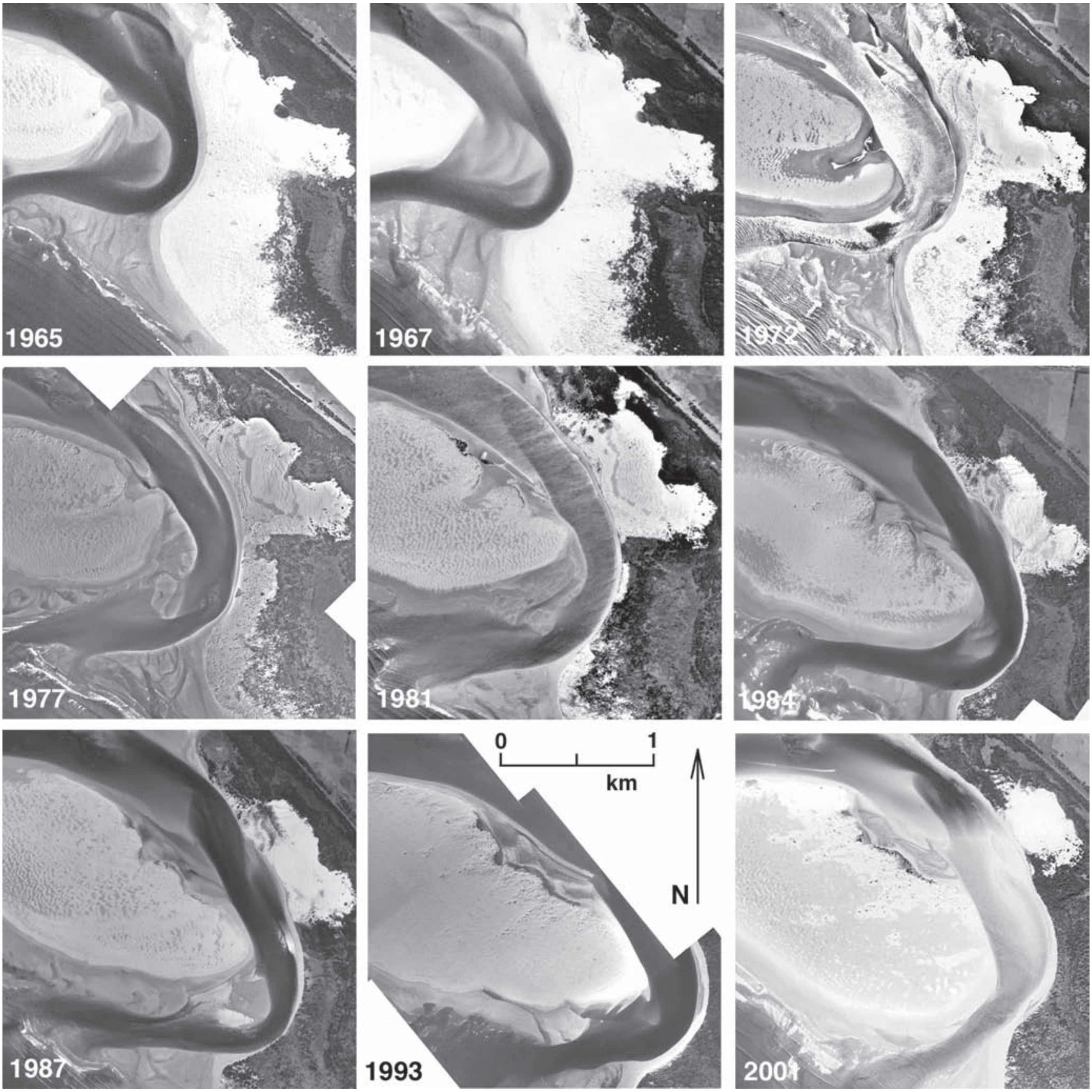


Fig. 4. Growth of the sand spit between 1965 and 2001. Nine sections from airphotos have been chosen to illustrate the successive phases of this process. The first, from 1965 to 1972, is one of substantial growth with the formation of a 'mini-spit' and a tidal 'mini-bay.' During the following years sand was mainly deposited towards the tip of this mini-spit. The mini-spit tip-growth cycle was repeated several times during the 1970s and early 1980s, although much narrower corridors were left between the newer and older parts. Later in the 1980s and during the 1990s deposition increased towards the mouth of Shallow Inlet as currents began to erode the north-east side of the spit tip. The total area added to the spit since 1965 is about 1.77 km^2. (1965 photograph Copyright © Commonwealth of Australia, Geoscience Australia; 1967 photograph courtessy of W.G. Tuddenham; 1972, 1977, 1981, 1984, 1987 and 1993 photographs Copyright © Crown (State of Victoria); 2001 photograph Copyright © Parks Victoria.)

Table 1. Vegetation of the dunes along Waratah Bay.

The table is a combination of transect and time sequences to show the general vegetation pattern from the upper beach to the rear of the high dune. Data obtained in 1983 along a track across the dunes (now named 'Access Point 6') form the basis for the table and are in bold. Data from the 1990s have been added in normal font. Observations made at the spit end of the high dune are indicated by italics. Where they were made as a transect sequence, the year of observation has been added. Without a year they refer to occasional records. - Species names are followed by a letter coding the mode of dispersal: a: wind, h: water, z: birds, mammals, ants, ?: unsure. - Abbreviations in the other columns indicate commonness: f: few; s: some, several, scattered; r: rather common; c: common; d: (co)dominant; p: in poor condition.

		YOUNGER DUNE RIDGES							OLDER DUNE RIDGE											HIGH OLD DUNE RIDGE					
		outer ridge	*2003 outer ridge*	**seaward slope (Cs)**	seaward slope	new ridge (D)	**outer ridge (C)**	*1980 foredune ridge*	**outer ridge (C) swale**	*2003 middle ridge*	*young ridge of mounds*	*1980 foredune swale*	**middle ridge (B)**	*2003 inner ridge*	former seaw. slope (Cs)	former outer ridge (C)	**inner ridge (A)**	*2003 inner lee slope*	**irregular inner zone**	**lower frontal slope**	**upper frontal slope**	*wind-shorn scrub margin*	**crest area**	**lee slope**	*open patches in scrub*
Herbaceous component																									
**Cakile maritima*	h	s	r	s	s		s		p		s		p		s										
**Thinopyrum junceiforme*	h	d	d	d	d	d	d	d	p	p	p	p	p	p	r										
Spinifex sericeus	a,h			s	r	d	r	s	c	s		s	d	s	d	d	r								s
Austrofestuca littoralis	h			s			s	s	s	s	s	s		s		s		s							
Actites megalocarpa	a							s		s	s	s	s	r	r	s									s
Carpobrotus rossii	z								s						s	s	s	s	s	s				s	s
**Senecio elegans*	a								s			s			s	s	s	s	s	s					
**Euphorbia paralias*	h									s	s			c	c			c							
Stackhousia spathulata	a									s	r	s				s									s
**Lagurus ovatus*	a								s							r	s		c	s	s				r
**Hypochoeris radicata*	a													c	r	s	s								
Isolepis nodosa	a,h													s	s	r	s		c	c					
Poa poiformis	a												s			r	s		c	c					
Agrostis avenacea	a								s				s												
Epilobium billardierianum	a														s	s									
Senecio pinnatifolius	a														s					s					
Lepidosperma gladiatum	?																				c				s
Bryophytes	a																		r	c	s				
Woody component																									
Ozothamnus turbinatus	a								s	s	s	s	s	r	s	c	s	s	s	p		s			
Olearia axillaris	a								s			s	s	s	s	s	s	s	p	f	s	s	s		
Acacia sophorae	z													s	s	r	s	r	s	c		s	s	s	
Olearia glutinosa	a														s	s		s	s	f		s			
Leptospermum laevigatum	a,z														s	s		f	r	c	d	c	d	d	
Leucopogon parviflorus	z															r	s		p	c		s	d	d	
Exocarpos strictus	z															s			s			s	s	s	
Olearia phlogopappa	a														s					f	c		s	f	
Correa alba	z?																			r	s	s			
Banksia integrifolia	a																						s	s	
Clematis decipiens	a																						f	s	
Allocasuarina verticillata	a																				s				
Myoporum insulare	z																				s				
Pomaderris oraria	z?																				c				
Rhagodia candolleana	z																				c				
Tetragonia implexicoma	z																				s				
Number of species		2	2	4	3	2	4	4	10	7	7	8	8	10	17	18	11	9	13	15	12	8	8	7	6

Fig. 5. Dune ridges along the high dune ridge of Waratah Bay. (a) The view in September 1990 from the frontal slope of the high ridge along the dune ridges formed since the 1950s. (b) A 1996 view over the rear slope of the youngest ridge which was formed after 1983 and is dominated by *Spinifex sericeus* with scattered **Thinopyrum junceiforme, Actites megalocarpa, *Euphorbia paralias,* and young shrubs of *Ozothamnus turbinatus* and *Olearia axillaris*. The shrubs in the swale are older; *Ozothamnus turbinatus*, up to 1.2 m tall, is the most common one. Young individuals of *Leptospermum laevigatum, Leucopogon parviflorus* and *Exocarpus strictus* are present, too. On the seaward side, the irregular crest of the youngest ridge is dominated by **Thinopyrum junceiforme*. (c) A southwesterly view in 2003 over the dune ridges at the end of the high dune ridge. The young, 'moundy' ridges are dominated by **Thinopyrum junceiforme*, the scrub on the older ones by *Acacia sophorae*. This species is also the more common coloniser of the swales behind the younger ridges.

of the entrance taken in 1937; the earliest vertical photographs date from 1941. Since 1965 the spit and its environs appear on airphotos of a variety of scales. 23 sets of photos were available, the latest dated 14 April 2001 but unfortunately, although they are informative about geomorphological development, recognition of vegetation is hampered by its sparse cover and overexposure of the sandy substrate.

Results – Geomorphological dynamics

Sand spit growth

The shoals in the mouth of Shallow Inlet are formed through the interacting forces of ebb and flow on the sandy sediments. Just before and after high water the eroding power of the currents in the main channel impinges most strongly on the outer bend of the meander and is often increased by wave action in the west-facing exit channel. The shore here has been eroding at an average rate of about 50 m/y (J. Whelan, pers. comm.; author's obs.). The sand thus removed largely remains in circulation in the lower reaches of the delta and is augmented with sand brought in by longshore currents. Until the early 1990s major sedimentation was predominantly along the northeastern side of the spit, but then gradually shifted to the southeastern shore. This process is described in the caption of Fig. 4. In summary, spit growth has been episodic and, as will be discussed later, this is still recognisable in the present dune landscape.

Initiation of mound building

The spit is exposed to the full force of the wind and sand is constantly moving, even under moderately windy conditions (see Bourman 1986). Although the shallow groundwater table keeps large areas near saturation point, the wind still dislodges sand grains and concentrates these into phalanxes of shallow ridges. These ridges slowly advance over the

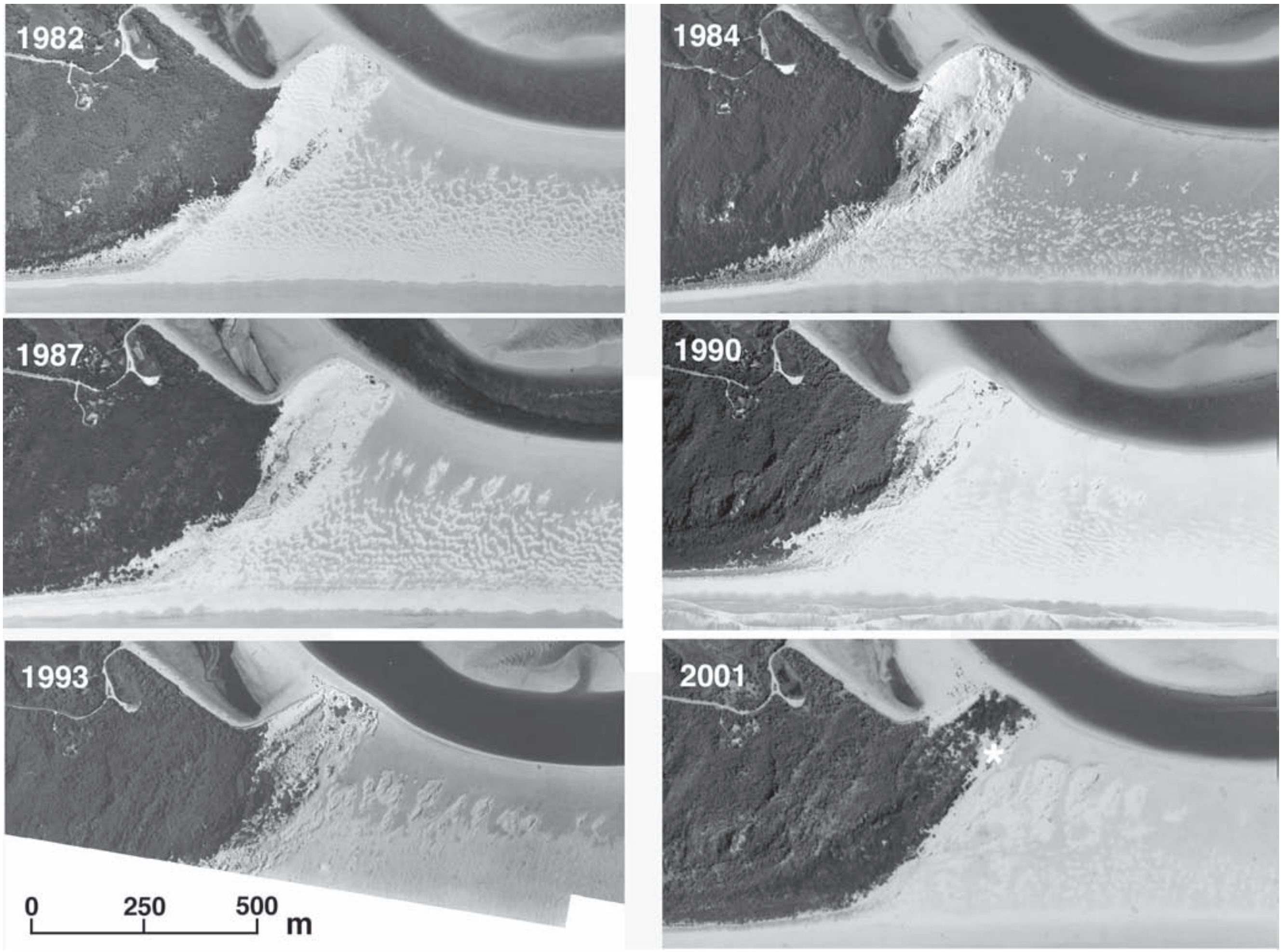


Fig. 6. The development of a series of ridges along the inlet side at the base of the spit as shown by aerial photographs. The photos also show the formation of and succession on the ridges at the southern end of the high dune ridge. The area to the east of the densily vegetated high dune was successfully stabilised by the Soil Conservation Authority with **Ammophila arenaria* in the 1970s. It provided a vantage point (marked *) for the views shown in Fig. 7. (1982, 1984, 1987 and 1993 photographs Copyright © Crown (State of Victoria); 1990 and 2001 photographs Copyright © Parks Victoria.)

moist surface and change according to variations in wind speed and direction. They form the intricate patterns often seen on airphotos. Flooding high tides, which inundate low-lying areas and on occasions even flow across the spit, erase lower ridges and their build-up begins anew.

Few species are able to cope with these harsh conditions. In order of decreasing significance they are the grasses **Thinopyrum junceiforme*, *Austrofestuca littoralis*, **Ammophila arenaria* and *Spinifex sericeus* and the sea rocket **Cakile maritima*. Seeds and rhizome fragments arrive in flotsam carried onto the spit by spring and storm tides. Here they face an uncertain future. Once germinated or sprouted, young plants may be dislodged through wind erosion or buried under sand for too long to survive. When they begin to grow, they interrupt the surface flow and sand begins to accumulate among and around the shoots. In contrast to pioneer species growing in strand lines on beaches backed by dunes, on the spit plants are sparsely spread.

Due to strong winds, the mounds accumulating in the grasses attain a more or less conical shape. Wind gullies form at the foot of the windward slope and along the sides of the mounds, while some of the eroded sand accumulates at the rear. Erosion at the windward side often exposes roots with the result that growth is usually limited to the crest and upper part of the lee slope. The inlet shore lies somewhat sheltered from the strongest impact of the westerlies and only there low wind-shadow ridges are formed (Fig. 3c). Their shape is partly determined by the wind regime and partly by the growth-form of the species: compact for *Austrofestuca littoralis*, **Ammophila arenaria* and **Cakile maritima* and spreading for **Thinopyrum junceiforme* and *Spinifex sericeus* (Heyligers 1985).

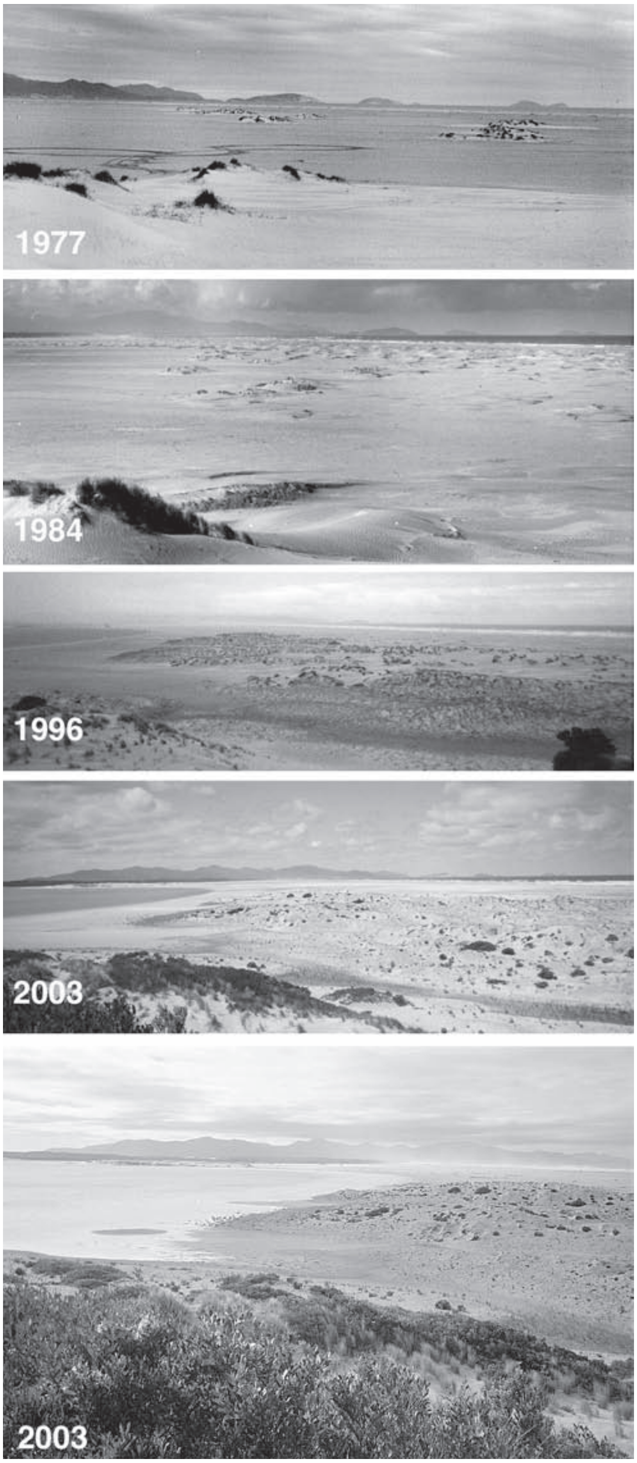


Fig. 7. The development of the ridges at the base of the spit as shown by pictures taken from a high ridge at the base of the spit (see asterisk on 2001 photo, Fig. 6). These pictures show the growth and coalescence of the **Thinopyrum junceiforme* mounds along the inlet shore. The 'dark spots' are mostly patches of *Actites megalocarpa*, others young *Ozothamnus turbinatus* bushes. The mounds in the background of the 1984 view are bare sand ripples which move over the spit at the mercy of changes in wind direction. The second 2003 view shows the scene at incoming tide, with a young **Thinopyrum junceiforme* patch still above water and the *Thinopyrum* fringe along the tips of the older ridges. (The 1977 picture taken by and courtesy of J. Whelan.)

Influence of episodic spit growth

During phases of slow spit growth the position of the upper beach changes little, while in periods of more rapid growth it gradually shifts in tandem with the progressing shoreline (Fig. 4). Consequently, sand deposition on the upper beach is also subject to variation. When the upper beach remains relatively stationary for a few years, more sand is deposited on it than when it gradually shifts, resulting in slight variations in relief. This is crucially important for mound and dune formation. Firstly, higher sections have a greater probability of 'catching' flotsam and propagules; secondly, stranded objects are more or less aligned with the shape of the former upper beach and, thirdly, a slightly higher elevation enhances the survival rate of seedlings. Hence, the resulting mounds and ridges mark episodes of little progress in spit growth and provide a means for assigning approximate formation dates for the dune fields (Fig. 1c).

Vegetation

Vegetation succession on the dune ridges adjoining the high dune of Waratah Bay has followed a 'classical' pattern and provides a context for the discussion of this process on the spit. This is followed by a short section on the formation of ridges on the base of the spit near the inlet, before I deal with the various aspects of vegetation colonisation and dune development on the spit plain.

Dune ridges near the eastern end of the Waratah Bay high dune

Along the shore of Waratah Bay, after a period of erosion along the foot of the old, 20 m high dune ridge, progradation took over and new foredunes were formed. This process was well under way in the 1960s (Smith 1968) and by the early 1980s three ridges and a zone of a rather less distinct topography separated the high dune from the upper beach (Fig. 5a).

The woody vegetation on the high dune is windshorn and only 2–3 m high on the crest and seaward slope, but increases in height to 4–6 m on the back slope. *Leptospermum laevigatum* and *Leucopogon parviflorus* are dominant in the fairly well closed canopy (Table 1). *Banksia integrifolia*, *Exocarpos strictus* and *Acacia sophorae* are of lesser importance but *Clematis decipiens* is locally common. *Lepidosperma gladiatum* is the only species regularly present in the ground cover. More species occur at the seaward side, where *Acacia sophorae* is more common.

In 1983 the outer dune ridge (C) was 10 m wide with the crest 2 m above upper beach level. It was covered by **Thinopyrum junceiforme* and some *Spinifex sericeus* (Table 1). In the depression at the rear were *Ozothamnus turbinatus* and *Olearia axillaris* shrubs up to 0.3 m tall. *Spinifex sericeus* was dominant on the next ridge (B), also 10 m wide but half a metre higher. Apart from some spindly

Fig. 8. Pictures, taken in 2003, of the oldest ridge at the base of the spit, (a) over the highest crest of the three amalgamated ridges; (b) from the side, showing the very irregular relief and the pronounced banding of **Thinopyrum junceiforme*; (c) of the *Thinopyrum* fringe formed in flotsam lines with scattered *Suaeda australis* plants on the highest ones. Scattered young *Ozothamnus turbinatus* bushes and, higher up, a sprawling young *Acacia sophorae* grow among *Carpobrotus rossii, *Euphorbia paralias*, *Stackhousia spathulata* and *Actites megalocarpa* on the sheltered lower slope of the ridge.

**Thinopyrum junceiforme* and scattered young *Ozothamnus turbinatus* and *Olearia axillaris*, few other species were present. In the next 1 m deep swale *Ozothamnus turbinatus* was common, about 2 m tall, with tops more or less level with the wind profile over the adjoining ridges. The crest of the inner ridge (A) was 3 m above upper beach level and in width similar to the other ridges. There was no **Thinopyrum junceiforme*, the *Spinifex sericeus* cover was more open and some *Isolepis nodosa* had come in; there were scattered *Ozothamnus turbinatus* and *Olearia axillaris*, 0.8 m tall, and an occasional young *Leptospermum laevigatum*, 0.3 m tall, while low *Acacia sophorae* was spreading from the shrubbery on the back slope.

The zone of irregular topography between ridge A and the high dune probably represents an older ridge and swale topography, more or less obliterated by blowout erosion. It was covered with rather impenetrable shrubbery, 2 m high, in which *Acacia sophorae*, *Leptospermum laevigatum* and *Leucopogon parviflorus* were codominant. *Ozothamnus turbinatus* and *Olearia axillaris* were still common at the seaward side, but further in their vigour strongly declined, indicative of an age gradient in the formation of this zone.

By 1993 a new ridge (D) had accumulated in **Thinopyrum junceiforme* and some *Spinifex sericeus* (Table 1; Fig 5b). It extended the foredune zone by 20 m and was still lower than ridge C. On the crest and back slope **Thinopyrum junceiforme* had already lost much of its vigour due to dwindling nutrient availability, but not so on the seaward slope, where it merged into a zone of **Cakile maritima* mounds on the upper beach, together forming a 14 m wide scree slope. The narrow depression behind ridge D was obliterated in places by sand from partial 'blow-throughs.' There the first shrubs of *Ozothamnus turbinatus, Olearia axillaris* and *Olearia glutinosa* appeared and there was more *Spinifex sericeus* than on the crest. These young shrubs were also present on the 10 m wide frontal slope and crest of ridge C (Fig. 5b). On this ridge **Thinopyrum junceiforme* was now in a poor condition, but the cover of *Spinifex sericeus* had increased. The vegetation on the back slope and in the swale had been taken over by *Ozothamnus turbinatus* and *Olearia axillaris*. A dense, 2.2 m high shrubbery of *Ozothamnus turbinatus, Olearia axillaris, Acacia sophorae*, *Leucopogon parviflorus* and *Olearia glutinosa* covered ridge B, continued over ridge A and joined the scrub in the zone with irregular topography. In summary, over a period of about ten years succession had shifted the vegetation communities of the ridges one ridge seaward.

At the southeast corner of the high dune the orientation of the ridges changes to west-east (Fig. 6). Exposed to a larger fetch and therefore increased sand supply, their topography becomes rather irregular. The newer

Thinopyrum ridges here began as strings of mounds formed by plants that successfully established in flotsam deposits aligned on high tide marks. Later, the mounds gradually merged into ridges (Fig. 5c). On the older ones some *Spinifex sericeus* and *Austrofestuca littoralis* occurred among the **Thinopyrum junceiforme*, especially on lee slopes, and were joined by *Actites megalocarpa*, *Stackhousia spathulata* and young *Ozothamnus turbinatus*, *Olearia axillaris* and *Acacia sophorae* in the swales (Table 1).

Dune ridges on the base of the spit near the inlet shore

During the 1970s, at the base of the spit, several **Thinopyrum junceiforme* patches became established along the upper shoreline of the inlet. By the early 1980s they had formed eight small mound complexes, separated by groundwater-saturated sand flats (Figs. 6 and 7). Over time, the complexes increased in size and gradually built into a series of irregular ridges. Initially they were kept apart by wind channelling over the intervening flats, but as their height and width increased the channels began to fill in. Thus the three ridges closest to the base of the spit merged and by 2003 sand accumulation between the next three ridges had raised the surface of the flats well above groundwater level. In 1993 ridge height varied from 2.5 m to 4.0 m, in 2003 from 4.8 to 7.2 m with the highest parts usually at the windward side.

**Thinopyrum junceiforme* has been the major ridge builder and forms bands across the crests and down the sides of the ridges (Fig. 8). Species other than the hardy *Actites megalocarpa* only got a chance to establish on the somewhat less exposed ridges closest to the high dune (Table 2). *Stackhousia spathulata*, *Ozothamnus turbinatus* and *Olearia axillaris* were the first to come in, followed by *Austrofestuca littoralis*, *Isolepis nodosa* and a few others, including a single *Acacia sophorae*. As yet, no *Spinifex sericeus* has been seen. Plant cover remained open, but widespread spindly **Thinopyrum junceiforme* shoots show that their rhizomes are still the main stabiliser of the dune surface. In 2003 the number of young *Ozothamnus turbinatus* shrubs had noticeably increased and the oldest shrub was now 3 m tall, had a spread of 6 m and was much sanded up in its centre.

Table 2. Vegetation of the ridges at the inlet side of the base of the spit

Ridges have been numbered (in bold) starting with the ridge closest to the high dune.

Species names are followed by a letter coding the mode of dispersal: a: wind, h: water, z: birds, mammals, ants.

Abbreviations in the other columns indicate commonness: 1: 1 plant, 2, 3: 2 or 3 plants, f: few; s: some, several, scattered; r: rather common; c: common; d: (co)dominant; j: juvenile; p: plants in poor condition.

RIDGE NUMBER AND SAMPLE YEAR

	Mode of dispersal	**4** 1993	**4** 2000	**3** 1993	**4** 2003	**3** 2000	**3** 2003	**2** 1993	**2** 2000	**1** 1993	**1** 2000	**2** 2003	**1** 2003
Herbs, including grasses													
**Thinopyrum junceiforme*	h	d	d	d	d	d	d	d	d	d	c,p	c,p	c,p
Actites megalocarpa	a			1	f	s	f	f	s	f	rc	c	c
Stackhousia spathulata	a							s	s	2	c	rc	rc
Austrofestuca littoralis	h							s	s	1	s	s	s
**Hypochoeris radicata*	a									3	1	f	f
**Cakile maritima*	h							s,j		s	s		
Epilobium billardierianum	a										1, j	f,j	f
**Euphorbia paralias*	h										1, j	f	f
Isolepis nodosa	a,h										1	1	1
Carpobrotus rossii	z											s	s
Agrostis avenacea	a									1			
**Sonchus oleraceus*	a										1		
Shrubs													
Olearia axillaris	a					1		f,j	f,j	s,j			
Ozothamnus turbinatus	a						2,j	2	4	1	s	3	c
Acacia sophorae	z										1		f
Atriplex cinerea	h												1
Number of species		1	1	2	2	3	3	7	6	9	12	10	13

Table 3. Vegetation of the dune field fringes along the margin of Shallow Inlet: species presence.
Species names are followed by a code for mode of dispersal: a: wind, h: water, z: birds, mammals, ants, ?: unsure.
Species presence is listed on a 10 – 1 scale; 10: always present; 1: occasionally present. Values of 8 and higher are in bold. Overall presence in the last column shows in how many of the ten groups the species is present.

Group number		**1**	**2a**	**2b**	**2c**	**2d**	**3a**	**3b**	**4a**	**4b**	**5**	
	mode of dispersal	*Thinopyrum* fringes	Youngest *Thinopyrum* vegetation	Young *Thinopyrum* vegetation	Older *Thinopyrum* vegetation	Oldest *Thinopyrum* vegetation	*Isolepis* vegetation, some shrubs	*Isolepis* vegetation, more shrubs	*Spinifex-Isolepis* vegetation	*Spinifex-Isolepis* veg. with older shrubs	*Ozothamnus-Olearia* vegetation	**Overall presence**
Shrubs												
Ozothamnus turbinatus	a	1	3	5	7	**10**	4	**9**	**9**	**10**	**10**	10
Olearia axillaris	a	1	4	6	**9**	**9**	5	**9**	**10**	**10**	**8**	10
Olearia glutinosa	a		4	4	**10**	**9**	5	**8**	**9**	**10**	7	9
Acacia sophorae	z		1	1	4	1		**8**	**8**	**8**	2	8
Leptospermum laevigatum	a,z							1	4	**10**		3
Leucopogon parviflorum	z							2	3	4		3
Exocarpos strictus	z							1	1	1		3
Rhagodia candolleana	z									3		1
Olearia phlogopappa	a									1		1
Grasses												
**Thinopyrum junceiforme*	h	**10**	**10**	**10**	**10**	**10**	1	3	4	5	4	10
Austrofestuca littoralis	h	2		7		7	4	3	5	5	6	8
Spinifex sericeus	a,h	1		6		**10**	5	6	**10**	**9**	6	8
**Ammophila arenaria*	h			1		1		6	5	4		5
**Lagurus ovatus*	a		2	1	**9**	3	5	**9**	6	6	2	9
Agrostis aemula	a		3	1	**9**		4	4	4	6	2	8
Poa poiformis	a				1		4		3			3
Herbs with high overall presence												
Isolepis nodosa	a,h	1	6	6	7	**9**	**10**	**10**	**10**	**10**	6	10
Carpobrotus rossii	z	1	1	4	4	7	6	**8**	8	**9**	2	10
Actites megalocarpa	a		5	7	**9**	7	5	**8**	6	6	9	9
**Melilotus indica*	?		**8**	7	**9**	**9**	6	**9**	**9**	**8**	6	9
Stackhousia spathulata	a		3	4	3	**9**	4	3	4	6	**9**	9
**Sonchus oleraceus*	a		7	7	7	**9**	4	4	1	6	2	9
Clematis decipiens	a		3	1	6	6	3	**9**	6	**10**	1	9
**Senecio elegans*	a		6	4	6	7	5	7	6	6	1	9
Epilobium billardierianum	a		4	3	4	7	5	4	3	1	3	9
**Conyza bonariensis*	a		3	1	3	6	4	1	3	6	1	9
**Hypochoeris radicata*	a		1	4	3	4	4	2	5	5	1	9
**Cakile maritima*	h,z	7	3	3	1	4	1	1			2	8
**Pseudognaphalium luteoalbum*	a		2	6	3	4		2	1	1	1	8
Senecio pinnatifolius	a		3		4	4	3	2	3	5	1	8
**Euphorbia paralias*	h		1	3	1	1	3	3	6	1		8
Other herbs												
Comesperma volubile	a		1		4	4	1	7		4	1	7
Senecio biserratus	a		5	1	3	6	3	2		1		7
Sonchus hydrophilus	a		3	3	3		1	1	1	1		7
**Cirsium vulgare*	a			3	1	4	1			1	2	6
**Hypochoeris glabra*	a			1		3		1	1	1	1	6

Group number		**1**	**2a**	**2b**	**2c**	**2d**	**3a**	**3b**	**4a**	**4b**	**5**	
	mode of dispersal	*Thinopyrum* fringes	Youngest *Thinopyrum* vegetation	Young *Thinopyrum* vegetation	Older *Thinopyrum* vegetation	Oldest *Thinopyrum* vegetation	*Isolepis* vegetation, some shrubs	*Isolepis* vegetation, more shrubs	*Spinifex-Isolepis* vegetation	*Spinifex-Isolepis* veg. with older shrubs	*Ozothamnus-Olearia* vegetation	**Overall presence**
Acaena novae-zelandiae	z					1	4	2	3	3		5
Microtis uniflora	a				1		3	4	1	1		5
**Leontodon taraxacoides*	a			1	1	1		1		1		5
Apium prostratum	h?			1	1	4		3				4
Chrysocephalum apiculatum	a			1		1				3	1	4
Centaurium* spp	a?						1	1	1		1	4
Apalochlamys spectabilis	a		1			1	1			1		4
Suaeda australis	h	4	1									2
Sarcocornia quinqueflora	h	3	1									2
Galium australe	z					1		2	1			2
Scaevola calendulacea	z						1			1		2
Bryophytes	a		1	1	1		3		1	1		6
Number of samples		11	10	7	7	7	8	9	8	8	9	

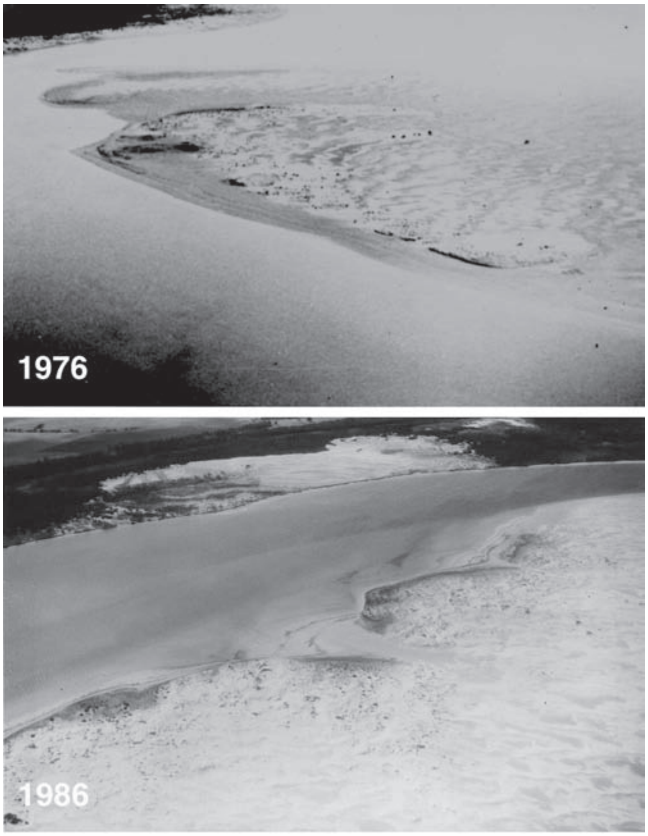
The following species, found only once, have been left out: *Limonium australe* (h,1), *Atriplex billardieri* (h,1), *Carex pumila* (h, 2d), *Paspalum vaginatum* (h, 3a), *Oxalis corniculata* (?, 4a),**Taraxacum officinale* (a, 4a), **Anagallis arvensis* (?, 4b), **Arcthotheca calendulacea* (a,z, 4b) and *Crassula decurrens* (?, 4b).
**These *Centaurium* species are **C. erythraea* and **C. tenuiflorum*.

Dune and vegetation development on the spit plain

The formation of dune fields at the inlet side of the spit plain began during the early 1960s and ended in the 1980s (Figs. 1c and 9). It happened in phases as a consequence of the episodic expansion of the spit (Fig. 4). During times of slow spit extension the increasing height of the upper beach along the inlet shore provided favourable conditions for mound building. Following the curve of the beach, the mounds formed an arc-shaped configuration, broadest at the northern end, thinning to a narrow row at the other. **Thinopyrum junceiforme* was the major mound and subsequent dune builder in the broad part, **Ammophila arenaria* was prevalent in the narrower 'tail.' During periods of more rapid spit growth conditions for mound formation ceased and only reoccurred when spit growth slowed again. Thus a series of five dune fields developed, separated by low corridors, before currents in the main channel washed out the next incipient field and diverted the main accretion of the spit towards the mouth of Shallow Inlet. This lead in the 1990s to the formation of an almost linear east-west oriented dune ridge about 450 m away form the dune fields. **Austrofestuca littoralis* and **Thinopyrum junceiforme* were the main dune builders. A repeat of this process began in 2003 with an incipient ridge on a slight, irregular rise with groups of low *Thinopyrum* mounds and one small *Austrofestuca* mound about 120 m from and parallel to the previous ridge.

With a long fetch over the spit and hence an ample supply of sand, the dune fields increased in height and volume and, starting at the plain side, the corridors between the fields were gradually filled in. After 30–40 years dune crests of older sections were 10–13 m high and the fields had become one continuous nearly 2 km long, broad ridge from which tail ridges extended onto the plain (Figs. 10 & 11). Initially, **Thinopyrum junceiforme* was the dominant coloniser, but later was joined by the other pioneer grasses. The prominence of **Ammophila arenaria* in the tail ridges is likely due to increased availability of fresh groundwater as these sections are situated towards the somewhat higher centre of the spit (Fig. 11). For the same reason **Ammophila arenaria* also established at several spots along the foot on the plain side of the dune fields and thus became part of the fields.

The crests and windward slopes of the fields have a very irregular relief due to the wind resistance of the grass-covered mounds. Apart from the grasses, *Actites megalocarpa* is the only other species that manages to grow on the windward side of the dunes, but in the lee of the mounds suitable niches occur for the establishment of *Stackhousia spathulata*, *Olearia axillaris* and *Ozothamnus turbinatus*. The latter proves to be especially hardy and is able to cope with sand burial by quick-growing shoots. Thus, it contributes to dune building and occurs on some of the highest crests (Fig. 10a). Because the vegetation on the crests and windward slopes remains very open, the dune fields are at best semi-stabilised and, locally in the older fields, erosion has deflated mounds and flattened relief.



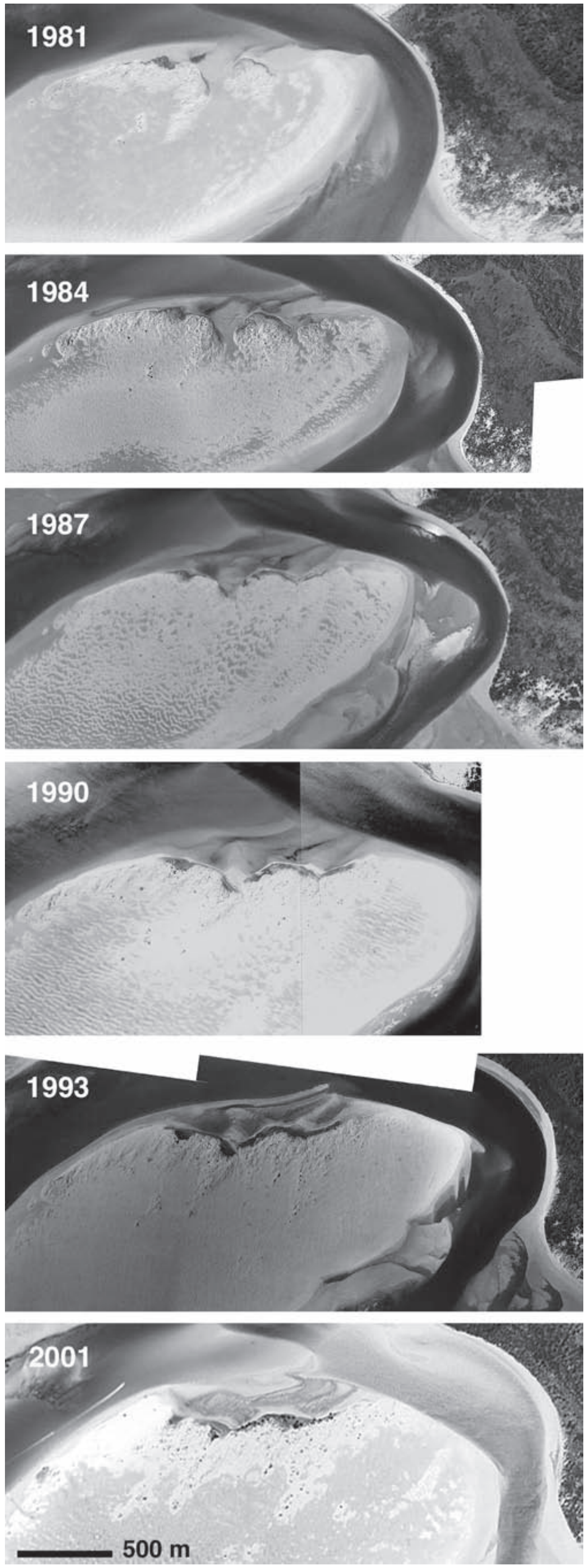


Fig. 9. The development of the dune fields at the inlet side along the spit plain since 1976. The 1976 oblique airphoto shows the 1965 and 1972 fields with beyond the wide corridor the beginnings of the 1977 field (see Fig. 1c). A wide *Thinopyrum* flat fringes the 1965 field with the strandlines clearly visible. In the background at the right the mounds of the 'The Sentinels' stand out. On the 1986 oblique photo the *Thinopyrum* fringes along the 1965 and 1972 fields appear in the foreground left and center, followed by the fringes of the 1997 and the 1979 fields. The picture also shows the sanding-up of the corridor between the 1972 and 1977 field. The series of vertical aerial photographs documents the closing-up of the corridors and the expansion of the vegetation along the somewhat sheltered inlet shore between 1981 and 2001. Also, it shows the development of 'tails,' a legacy from the episodic enlargement of the spit (see Fig. 4). The dune ridge formed in the 1990s is located close to the tip of the spit. (Oblique pictures courtesy M. Tarrant; 1981, 1984, 1987 and 1993 vertical photographs Copyright © Crown (State of Victoria); 1990 and 2001 photographs Copyright © Parks Victoria.)

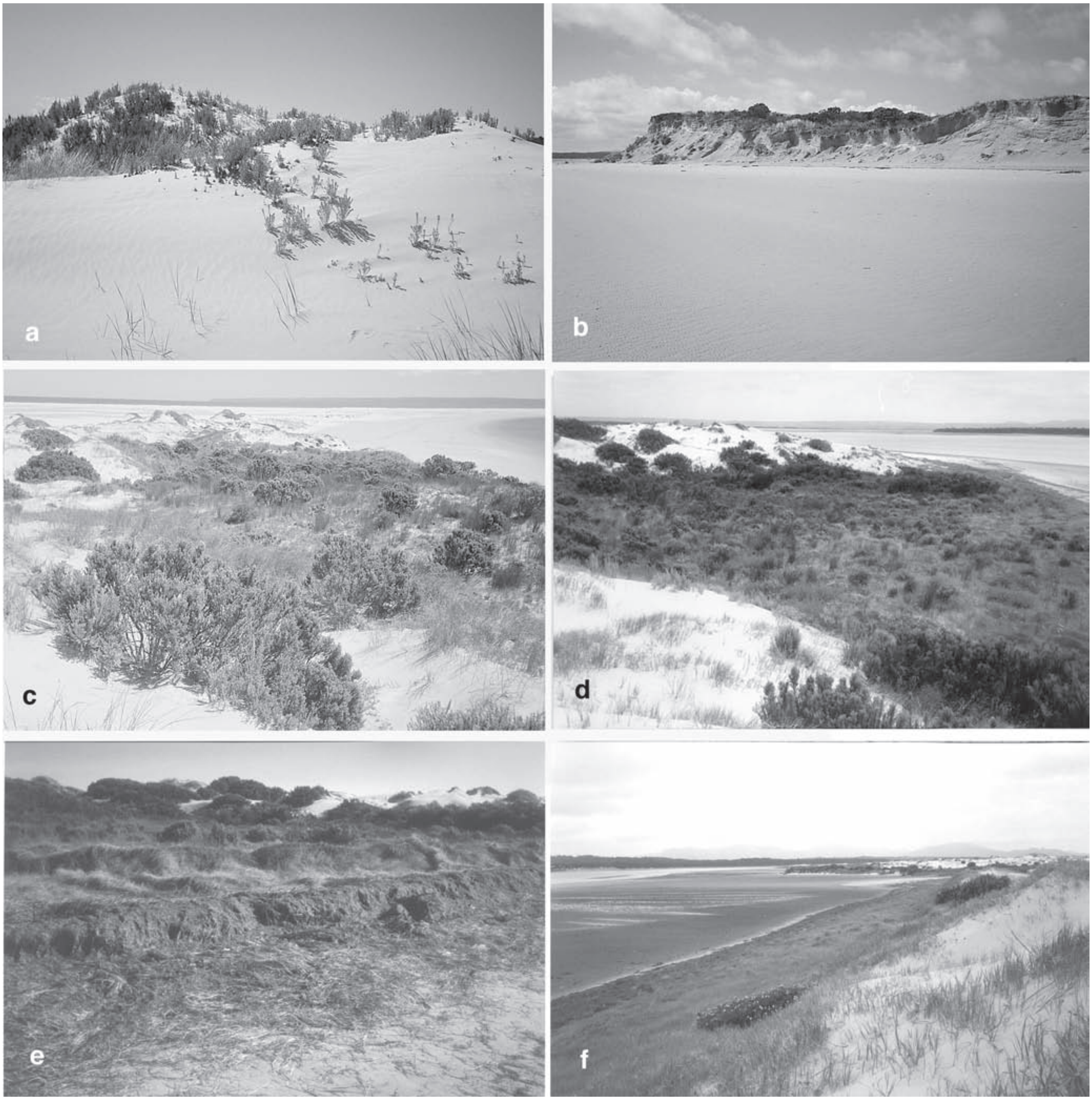


Fig. 10. Views of the vegetation of the older part of the dune field. (a) Crest dominated by *Ozothamnus turbinatus*; (b) eroded north-east side of the 1965 field, with slip slopes up to 8 m high, at low tide; (c) dune hollow above this section seen from a crest, with *Spinifex sericeus*, *Isolepis nodosa* and *Actites megalocarpa* common in the groundcover and up to 2 m tall *Ozothamnus turbinatus* shrubs (vegetation group 4a); (d) the flat between the 1965–1972 sections with **Thinopyrum junceiforme* and *Isolepis nodosa* ground cover and scattered young shrubs of *Ozothamnus turbinatus* and *Olearia axillaris* up to 0.5 m tall (vegetation group 2d); (e) the inlet side of the flat with a large amount of dead seagrass deposited in the outer margin of the flat during the last king tide; the ridge further in, with the vigorous **Thinopyrum junceiforme* growth, resulted from a similar previous event (vegetation group 1) (see also the 1976 view in Fig. 9); (f) *Thinopyrum* fringe of the 1972 field with the fringe of the 1977 field in the background; outgoing tide has exposed the wide tidal flat. **Thinopyrum junceiforme* declines in vigour towards the slope, which is lightly covered by *Spinifex sericeus*; the patch in the foreground is a flowering *Actites megalocarpa* 'tussock' (vegetation group 2c) [(a), (b) and (c) taken in 2003, (d) and (f) in 1993 and (e) in 1994].

Table 4. Vegetation of the dune field fringes along the margin of Shallow Inlet: species commonness and condition.
Species names are followed by a letter coding the mode of dispersal: a: wind, h: water, z: birds, mammals, ants; ?: unsure. Commonness and/or condition is coded as follows: do: (co)dominant, vc: very common, co: common, rc: rather common, lc: locally common, s: several, scattered or some, f: few, 1: one plant, 2, 3: two, three plants; j: juvenile, v: vigorous,
p: (very) poor condition, d: dead. Overall presence shows in how many of the ten groups the species is present.

Group number		1	2a	2b	2c	2d	3a	3b	4a	4b	5	
	mode of dispersal	*Thinopyrum* **fringes**	**Youngest** *Thinopyrum* **vegetation**	**Young** *Thinopyrum* **vegetation**	**Older** *Thinopyrum* **vegetation**	**Oldest** *Thinopyrum* **vegetation**	*Isolepis* **vegetation, some shrubs**	*Isolepis* **vegetation, more shrubs**	*Spinifex-Isolepis* **vegetation**	*Spinifex-Isolepis* **vegetation with older shrubs**	*Ozothamnus-Olearia* **vegetation**	**Overall presence**
Shrubs												
Ozothamnus turbinatus	a	f, j	s, j	s, j	s j–1 m	1–s <1.0 m	s j	s–co 1.0–2.2 m	1–s p	f–vc <2.5 m	s–co 0.5–2 m	10
Olearia axillaris	a	1, j	s, j	s, j	s j	s–rc <0.6 m	s–co j	s–co 0.6–1.7 m	1–s <1.7m	s–co <1.9 m	s–co 1.0–2.0 m	10
Olearia glutinosa	a		s, j	s, j	1–co j–1.2 m	1–s <0.7 m	rc–co j	1–co 0.4–1.8 m	f–co <2 m	s–co <1.9 m	s–co 1.0–2.0 m	9
Acacia sophorae	z		1, j	1, j	1, j	1, 0.5		1–s 0.6–2.5 m	1–f low–3 m	s–co 1.6–4.0 m	1 or 2 0.6 m	8
Leptospermum laevigatum	a,z							1, 1.2 m	1, j	1–s,<2.5 m		3
Leucopogon parviflorum	z							1–s, 1.5 m	f, <1.9 m	1, 1.7 m		3
Exocarpos strictus	z							1, 1.2 m	1, 0.5 m	1, 0.7 m		3
Rhagodia candolleana	z									1, < 0.5 m		1
Olearia phlogopappa	a									1, 0.7 m		1
Grasses												
**Thinopyrum junceiforme*	h	do, v	do, v–p	do, p	do, p	do, v–p	p	p	v p	p	s, p	10
Austrofestuca littoralis	h	s		f–s		f–rc	1–f	s	s	f	s	8
Spinifex sericeus	a,h	s		s–rc		f–s	s	s–rc	s–do	f–co	s–do	8
**Ammophila arenaria*	h			s		1		s	s–co	f		5
**Lagurus ovatus*	a		1, s	f	s–vc	lc, co	s–rc	s–lc	co	co–vc	co	9
Agrostis aemula	a		f	f	f–rc		1–f	s	s	s–co	s	8
Poa poiformis	a				1		s		s–rc			3
Herbs with high overall presence												
Isolepis nodosa	a,h	2	s–co	f–rc	f–lc	f–rc	co–do	co–do	lc–co	rc–co	s–co	10
Carpobrotus rossii	z	1, v	s, j	f–s	1–s	f	s	s	s	f–lc	f	10
Actites megalocarpa	a		s–co	rc	f–rc	rc	f–rc	s–rc	s	s	s	9
**Melilotus indica*	?		s–co	s–co	f–co	s–vc	s–co	s–co	s–do	s–co	co–vc	9
Stackhousia spathulata	a		s–co	s–co	s	s–co	s–lc	rc	co	f	s–co	9
**Sonchus oleraceus*	a		f–co	s–co	1–vc	f–co	s–co	s	co	f	f, vc	9
Clematis decipiens	a		lc	s	f	s	1, rc	s–do	f–co	s–lc	f	9
**Senecio elegans*	a		s	1–f	s	s–co	s–rc	s	s–co	f–lc	1	9
Epilobium billardierianum	a		s	lc	s–vc	s	s	s	f	s	s	9
**Conyza bonariensis*	a		s	s, co	s, co	s	s	f	s	f–s	1	9
**Hypochoeris radicata*	a		s	f	f	f	s	f	f–s	f–vc	f	9
**Cakile maritima*	h,z	s	f	1	f	1–f	s	f			1–f	8
**Pseudognaphalium luteoalbum*	a		f	f	s	s		f	f	f	f	8
Senecio pinnatifolius	a		s–lc		f	f	s	f	s,co	s–co	f	8
**Euphorbia paralias*	h		rc	1–s	1	1, p	f	s–lc	s–lc	1		8

Group number	**1**	**2a**	**2b**	**2c**	**2d**	**3a**	**3b**	**4a**	**4b**	**5**		
	mode of dispersal	***Thinopyrum* fringes**	**Youngest *Thinopyrum* vegetation**	**Young *Thinopyrum* vegetation**	**Older *Thinopyrum* vegetation**	**Oldest *Thinopyrum* vegetation**	***Isolepis* vegetation, some shrubs**	***Isolepis* vegetation, more shrubs**	***Spinifex-Isolepis* vegetation**	***Spinifex-Isolepis* vegetation with older shrubs**	***Ozothamnus-Olearia* vegetation**	Overall presence
Other herbs												
Comesperma volubile	a		1		1–s	f	3	s–co		f	co	7
Senecio biserratus	a		s	f	f	s	1, f	f		s		7
Sonchus hydrophilus	a		f–rc	s, co	f		f	co	f	co		7
**Cirsium vulgare*	a			1, f	f	1–f	1			f	f	6
**Hypochoeris glabra*	a			f		f		f	f	s	f	6
Acaena novae-zelandiae	z					f	s–co	s	s–lc	s		5
Microtis uniflora	a				lc		s	1–s	s	s		5
**Leontodon taraxacoides*	a			f	f	f		f		f		5
Apium prostratum	h?			f	1	f		f				4
Chrysocephalum apiculatum	a			f		f				f	f	4
**Centaurium* spp.	a?						f	f	f		1	4
Apalochlamys spectabilis	a		2			2	d			d		4
Suaeda australis	h	s	p									2
Sarcocornia quinqueflora	h	s	p									2
Galium australe	z					s		lc	f			2
Scaevola calendulacea	z						1			1		2
Bryophytes	a		f	f	s		s		lc	lc		6
Average number of species/sample		3	9	12	15	20	12	17	16	20	10	
Range of number of species/sample		1–6	7–15	10–18	11–18	14–29	10–15	12–24	14–21	13–26	6–18	

In 1981 the most striking element on the spit plain was an isolated group of *Ammophila* mounds, hence named 'The Sentinels,' together with a nearby 'Outlying Sentinel' (Fig. 12a). They represent the oldest tail ridge. Over the years the mounds of the group gradually coalesced notwithstanding a great deal of wind-gullying retarding this process. By 2003 they had formed a short ridge, 165 m long 50 m wide and 7.5 m high, with a 30 m wide footslope. The Outlying Sentinel, a metre or so lower, 38 m long and 30 m wide, was connected to the main group by a low, bare rise, 60–70 m wide and 1.5 m high. Some wind-borne propagules of *Ozothamnus turbinatus*, *Actites megalocarpa* and *Stackhousia spathulata* had found suitable niches among the **Ammophila arenaria* leaves, but no other species had become established.

Ten years after its formation started in the 1990s, the incipient ridge near the end of the spit had developed into a 400 m long dune with a 35 m gap between a section dominated by *Austrofestuca littoralis* and one where **Thinopyrum junceiforme* was dominant (Fig. 13). In 2003 the crests in the *Austrofestuca littoralis* part were up to 5 m high, but much lower in the **Thinopyrum junceiforme* section, except for a 3.6 m high **Ammophila arenaria* mound and some *Spinifex sericeus* mounds up to 4 m high. Strong wind-gullying caused the ridge to be very 'moundy' and apart from the four grass species and an odd **Cakile maritima* plant along the foot, no other species were present.

The vegetation of the sheltered areas along the inlet side of the dune field

Flotsam, mainly dead seagrass from the inlet shallows, washes up on the beach along the dune fields, either as strandlines or covering wider areas in sheltered nooks resulting from the filling in of corridors. In these deposits **Thinopyrum junceiforme* forms a dense sward of lush fertile shoots (Figs. 10 and 11). Over time, as sand and more flotsam gets caught along the margin, a low ridge develops, a process that is repeated when another band of flotsam is deposited on the beach. In time, low-lying '*Thinopyrum* flats' are formed on which the former strand lines are still traceable as low ridges (Fig. 10e).


a
b
c
d
e
f
g

Although the flats are sheltered from direct impact of westerly winds, they are affected in various ways by sand carried beyond the dune fields. If the dunes are high, sand precipitates as slip slopes, which encroach on the flats and choke the vegetation in their progress. When the dunes are lower, sand tends to accumulate along the inner margin of the flat thus creating a transition zone of irregular relief between dune and flat (Fig. 11e). The flats are the least exposed habitat on the spit; consequently, their vegetation is richer in species than elsewhere. The only other sheltered habitat occurs in a hollow on the highest area of the oldest dune field (Fig. 10c). Its vegetation is similar to that of the flats.

I have sorted my vegetation records of the sheltered sites into ten groups (Tables 3 & 4). Criteria have been dominance of **Thinopyrum junceiforme* and *Isolepis nodosa*, presence of *Spinifex sericeus* and *Austrofestuca littoralis*, and number and age of shrubs. Many of the other species are wind-dispersed annuals or biennials. They form a large random element and contribute little to criteria for classification. Presence of mosses adds to surface stablisation and accretion (Moore & Scott 1979, Danin 1996, Danin *et al.* 1998), but I have not been consistent in recording moss occurrence and the tables give an incomplete picture of their importance. Two common species are *Tortula princes,* known to be tolerant to saltspray (Moore & Scott 1979) and *Bryum caespiticium*.

Group 1, *Thinopyrum* fringes, comprises the pioneer vegetation on the upper beach. These fringes may be only a metre or so wide along slopes but are usually wider, especially near and in the nooks of closed-up corridors. **Thinopyrum junceiforme* is very vigorous and, in contrast to elsewhere on the spit, flowers profusely. **Cakile maritima* and some saltflat species may occur too, while *Spinifex sericeus* stolons may spread from adjacent dunes (Figs. 8c, 10e, 11a and b).

Groups 2a to 2d, *Thinopyrum* vegetation, represent areas where **Thinopyrum junceiforme* is still an important component of the ground cover, although in 2a it is already less vigorous and its condition in the other groups is often 'spindly' or poor. This provides an opportunity for other species to establish, longer-lived ones such as *Isolepis nodosa* and *Actites megalocarpa*, and annuals such as *Agrostis aemula*, **Lagurus ovatus*, **Melilotus indica* and **Senecio elegans*. *Sonchus hydrophylus* is a characteristic species for this vegetation group. The main criteria for recognising four groups have been the occurrences of *Spinifex sericeus*, *Austrofestuca littoralis* and the annual grasses together with the increasing presence and size of *Olearia glutinosa*, *Olearia axillaris* and *Ozothamnus turbinatus*. *Acacia sophorae* is the only other woody species that is becoming established. *Isolepis nodosa* and *Actites megalocarpa* are frequently present in the ground cover. Species richness increases from an average of 9 species per sample in 2a to 20 in 2d (Figs. 10d, 10e and 11a).

Groups 3a and 3b, *Isolepis* vegetation, are characterised by the prevalence of *Isolepis nodosa*, while **Thinopyrum junceiforme* is usually absent. In most samples of group 3a one or two shrub species are present, but their occurrence in group 3b is much more pronounced as shrubs are generally larger and more numerous. *Acacia sophorae* is often present and, in a few samples, *Leucopogon parviflorus* too. Group 3a has on average 12 species per sample, 3b 17. Noteworthy among these is *Clematis decipiens*, which is often found as patches on the ground. *Carpobrotus rossii* is another common member of the group.

Groups 4a and 4b, *Spinifex-Isolepis* vegetation, can be regarded as a parallel of groups 3a and 3b. The main differences are the common occurrence of *Spinifex sericeus* and an increase in the number of shrub species, with *Leptospermum laevigatum* being the most important one. The difference between 4a and 4b is a reflection of the increasing richness of the shrub component although the vegetation structure is still open shrubland. *Olearia axillaris* and *Olearia glutinosa* are generally less than 2 m tall, while *Ozothamnus turbinatus* may grow to 2.5 m, before they begin to decline in vigour. Many *Leptospermum laevigatum* shrubs were still small, but the oldest ones were up to 2.5 m high. The oldest *Acacia sophorae* was 4 m tall and had grown out to a width of 20 m. *Leucopogon parviflorus* remains more localised. *Isolepis nodosa*, *Clematis decipiens* and *Carpobrotus rossii* are important components in the ground cover. Group 4a has on average 16 species per sample, 4b 20 (Figs. 10c, 11c and e).

Fig. 11. The later dune fields. (a) A 1984 view of the corridor between the 1972 and the 1977 field, of which the *Thinopyrum* fringe occupies the foreground, with *Stackhousia spathulata* where the grass cover thins out (vegetation groups 1 and 2a). On the slope of the 1972 field a large area with about 2 m tall *Ozothamnus turbinatus* shrubbery with some *Olearia glutinosa* (vegetation group 5). (b) The same view in 2000; in the foreground the lee slope of the 1977 field with vegetation dominated by *Spinifex sericeus* and *Isolepis nodosa* and a terrace in the middleground with *Isolepis* vegetation (vegetation groups 4a and 3a, respectively). Along the inlet margin some *Acacia sophorae* and *Ozothamnus turbinatus*, about 2 m tall. (c) A 1993 view of the flat between the 1977 and the 1979 fields with, in the foreground *Spinifex-Isolepis* vegetation with scattered, about 1.2 m tall shrubs of *Ozothamnus turbinatus*, *Olearia axillaris*, and *Olearia glutinosa* (vegetation group 4b). (d) By 2003 erosion was destroying the terrace along the 1979 field thus undermining the low-growing, but wide *Acacia sophorae* bushes. (e) The irregular lee slope of the younger section of the fields in 1993, with an open vegetation of *Spinifex sericeus*, *Austrofestuca littoralis*, *Isolepis nodosa* and *Stackhousia spathulata* (vegetation group 4a), and the adjacent terrace with *Acacia sophorae*. (f) The last mounds of the younger fields; the *Spinifex sericeus* mound at the left is 5.5 m high, the **Ammophila arenaria* mound at the right 6 m. (g) View over the end of the younger fields, showing the very pronounced relief resulting from wind action on the **Thinopyrum junceiforme* mounds; in the background the dune ridge formed in the 1990s ((f) and (g) taken in 2003).

Fig. 12. Dune field tail ridges. (a) 'The Sentinels,' tail ridge of the 1965 field, accumulated in **Ammophila arenaria* over a period of 40 years; the tail ridge of the 1972 field is located further away at the left (picture taken in 2003). (b) and (c) Two aspects of the tail ridge of the 1979 field photographed in 1993; (b) seen from the dune field, showing **Ammophila arenaria* mounds and lower **Thinopyrum junceiforme* mounds, (c) the **Thinopyrum junceiforme* mounds at the end of the tail with an eroded, sanded-up flotsam deposit in front.

Group 5, *Ozothamnus-Olearia* vegetation, represents the transition from the vegetation of the dune field crests to that of the older flats (Fig. 11a). *Ozothamnus turbinatus*, *Olearia axillaris* and *Olearia glutinosa* are the species that determine the aspect as the ground layer is usually sparse. *Actites megalocarpa* and *Stackhousia spathulata* are its prominent members, species which are also present on the exposed aspects of the dunes, thus pointing to the ecotonal nature of group 5. On average there are 10 species per sample.

In general, the groups represent increasing age and complexity of the vegetation but this does not necessarily imply that topographically or over time the groups follow sequentially. The best examples of succession are to be found at the large corridor nooks between the three older dune field sections (Fig. 11 a and b). There the relief shows the position of former *Thinopyrum* fringes (Group 1) indicative of the gradual expansion of the vegetated area, thus creating zones of older vegetation and increasing species richness (Groups 2a–2d). Over this gradient the vigour of **Thinopyrum junceiforme* decreases and with an increasing importance of *Isolepis nodosa* the succession leads to the vegetation classified as Groups 3a and 3b. Where *Isolepis* vegetation with some shrubs (Group 3a) developed along the younger dune field sections it may be transformed into *Spinifex-Isolepis* vegetation (Groups 4a and 4b) where sand accumulates as irregular 'tongues' over areas with *Isolepis* vegetation. Such 'edaphic succession' does not occur along the margins of higher older sections, where spillover slopes advance over the flats. There, succession proceeds to *Isolepis* vegetation with more shrubs (Group 3b) if not cut short in the mean time through burial by the encroaching avalanche of sand.

Fig. 13. The new dune ridges, (a) to (d) show the 1990 dune ridge, (e) the incipient latest ridge; (a), taken in 1993, shows the ridge from the west, where **Thinopyrum junceiforme* is dominant; (b), taken in 2000, shows it from the highest point near its eastern end, in the section dominated by *Austrofestuca littoralis*; (c) and (d), taken in 2003, show the eastern and western sections, (c) seen from **Thinopyrum junceiforme* mounds near the inlet shore, (d) from the spit plain; (e) is the view over the 2003 incipient ridge from the western end, showing groups of low mounds, mainly accumulated in **Thinopyrum junceiforme*.

Discussion

A comparison of the dunes on the spit with the dune ridges along Waratah Bay

The *Leptospermum laevigatum-Leucopogon parviflorus* scrub of the high dune ridge along Waratah Bay is typical of other calcareous dunes along the Victorian coast ((e. g. Parsons (1966), Hazard and Parsons (1977), Barson and Calder (1981), Conn (1993), Kirkpatrick (1993) and Ashton and van Gameren (2002)). Progradation of the shore has enabled the development of a sequence of new ridges along the foot of this high ridge. Each of these ridges went through a succession from grass-dominated vegetation to a closed scrub, in species composition similar to the scrub on the high dune. Although the spit is exposed to the same strong westerlies and south-westerlies, events there have followed a different pattern. Along the spit, in the absence of a foredune, flotsam only formed diffuse strand lines and during king tides washed up all over the spit. The scattered mounds established by the pioneer grasses bear witness to this process. The situation at the end of the high dune shows the transition from 'orderly' ridge formation along existing foredunes to scattered single mounds further out on the spit.

In the 20 years after their formation the vegetation on the ridges near the inlet at the base of the spit has hardly progressed beyond the pioneering stage. During the same period the vegetation succession on the ridges along the high dune had replaced the **Thinopyrum junceiforme* vegetation on ridge C with shrubbery of *Ozothamnus turbinatus* and *Olearia axillaris*. Only when the ridges along the inlet begin to link up with those at the southwest corner of the high dune, conditions may ameliorate sufficiently to provide the opportunity for further colonisation. This shows that ridges, open to wind from all directions, are too exposed to provide suitable conditions for further vegetation development.

Similar harsh conditions prevail at the windward side of the dune fields, where the vegetation has remained equally scanty and in addition to the grasses, only the most hardy of species, *Ozothamnus turbinatus* and *Actites megalocarpa*, grow there. However, the shore-parallel dune fields have provided a relatively sheltered environment along the inlet margin. Protected from the direct impact of fierce westerlies, new species have been able to establish. The process started with **Thinopyrum junceiforme* colonising the upper beach and higher-lying tidal flats. This provided a 'rough' surface in which sand and wind-dispersed propagules were caught. Over time, an open shrubland dominated by *Ozothamnus turbinatus*, *Olearia axillaris* and *Olearia glutinosa* was formed with *Isolepis nodosa* and various Asteraceous species common among the **Thinopyrum junceiforme* ground cover. Other species, not necessarily dispersed by wind, apppeared as well, for instance *Acacia sophorae*, *Leptospermum laevigatum* and *Leucopogon parviflorus* and herbs such as *Carpobrotus rossii*, **Melilotus indica* and *Acaena novae-zelandiae*. However, nowhere in this sheltered zone has the vegetation yet reached a stage that would indicate further succession to a closed woody vegetation as present on the older ridges along the Waratah Bay high dune. One reason may be that due to the isolated location this process has stalled because of an insufficient supply of woody plant propagules.

Propagule dispersal

For development of the spit beyond the bare sand plain stage, initial dispersal by water of propagules of the four pioneer grasses was crucial. Once plants thrived, wind contributed to further spread and the arrival of other species. Wind is also crucial for bringing in propagules of species that are only found on sheltered sites. At least half of the species presently occurring there are primarily dispersed by wind (Table 3). Species with small seeds, i.e. comparable in size to sand grains, also appear to fall into this category. Wind-dispersal is a random process; in principle any seed dispersed this way may germinate and grow if conditions are favourable. However, propagules will have to be carried either across the inlet or from the Waratah Bay high dune and hence, nearest seed sources are a kilometre or more away. This may explain why there are so few *Leptospermum laevigatum* present as it has a limited effective dispersal range (Hazard & Parsons 1977). *Banksia integrifolia* and *Allocasuarina verticillata* are still missing among the wind-dispersed woody species on the flats.

About 20 per cent of the species are animal-dispersed, local potential agents being birds and mammals. Red-necked Stints (*Calidris ruficollis*) and other small waders forage along the shoreline and on the tidal flats and hundreds of birds may shelter in the flotsam on the upper shore during high tide. They may be carriers of small seeds, e.g. those of *Isolepis nodosa*, but their role in dispersal is likely to be limited. This is also true for Cape Barren Geese (*Cereopsis novaehollandiae*) which rest occasionally on the spit and could have brought in propagules from the paddocks across the inlet. Once *Ozothamnus turbinatus* and other shrubs have established, White-fronted Chats (*Epthianura albifrons*) are quick to follow, but they forage for insects, as do most of the rare visitors, possibly migrants, such as Grey Fantail (*Rhipidura fuliginosa*) and Restless Flycatcher (*Myiagra inquieta*). The only seedeaters I have seen on the spit were a flock of European Goldfinches (**Carduelis carduelis*) actively feeding on ripe **Ammophila arenaria* heads in April 1994.

A more likely dispersal agent is the Red Fox (**Vulpes vulpes*) which regularly patrol the spit for carcasses and other food. For a while the latter must have included rabbits (**Oryctolagus cuniculus*), first noticed in 1990 and last seen in 1994. Rabbits like *Carpobrotus* fruits and could have brought in *Carpobrotus rossii* seeds. Although mostly carnivorous, foxes also eat berries and could have carried in seeds of *Leucopogon parviflorus* and *Exocarpos strictus* from the Waratah Bay dunes vegetation. In 2003 a Shortbeaked Echidna (*Tachyglossus aculeatus*) was present on the 1977–1979 flat and I have occasionally seen kangaroo prints on the inlet shore along the dune fields and once those of Hog Deer (**Axis porcinus*). Seeds could come in via the coat or dung of these animals.

In whatever way species have arrived at the sheltered side of the dune fields, seed dispersal could be still a limiting factor in advancing succession from the present open shrubland to a more closed woody vegetation. However, it could also be that the environment, although relatively benign compared with that prevailing elsewhere on the spit, is still too extreme to sustain succession.

*The new arrival: *Euphorbia paralias*

**Euphorbia paralias*, indigenous to the shores of southern Europe and northern Africa, was first found in Albany, Western Australia, in 1927 and has since spread to Geraldton in the west and southern New South Wales in the east. In several coastal dune areas it has established large populations and has been subjected to local attempts at eradication (Heyligers 2002).

When I started my investigations, **Euphorbia paralias* was not yet present in the Sandy Point area, but in the mid 1980s I found a few plants on the foredune along Waratah Bay and on the shore of Shallow Inlet across from the spit. It spread along the bay and over several stretches became co-dominant with **Thinopyrum junceiforme* on the youngest foredune. It was in October 1990 that I saw the first, already well-established plant on the spit, on the northwest corner of the 'Old Field.' During following visits I noticed the spread of **Euphorbia paralias* to other areas but, as shown on Tables 3 and 4, it rarely occurs in large numbers and is just another component of the heterogeneous flora of the more sheltered areas of the spit.

What would have happened without the foreign grasses?

The pioneering capacity of **Thinopyrum junceiforme* very much outweighs that of the native *Austrofestuca littoralis* and *Spinifex sericeus*. Most of the mounds on the spit have formed as a result of the presence of this species; the spit provides a niche similar to that of its habitat on the Waddenzee Barrier Islands along the south-eastern coast of the North Sea (Heyligers 1985). **Thinopyrum junceiforme* and **Ammophila arenaria* have been crucial for the formation of the dune fields along the shore of Shallow Inlet, again similar to the situation on the North Sea Islands. I surmise that these two species created opportunities for *Spinifex sericeus* and *Austrofestuca littoralis* to establish as well, and providing a seed source for further dispersal over the spit. *Austrofestuca littoralis* especially, can now be found in situations where at first only **Thinopyrum junceiforme* took hold, for instance along the inlet shore of the neck and at the far end of the spit. I seriously doubt that if *Austrofestuca littoralis* and *Spinifex sericeus* had formed incipient dune areas, these would have been sufficiently substantial to withstand the eroding forces of gales and overwash by king tides.

The development of *Thinopyrum* flats along the inlet shore appears to be solely due to the presence of **Thinopyrum junceiforme*. I do not know of any native species in the Shallow Inlet environs that could effectively replace it in this role. Admittedly, *Sarcocornia quinqueflora* and *Suaeda australis* occur among the **Thinopyrum junceiforme*, but never in such numbers to be effective as ridge builders. *Atriplex cinerea*, an important pioneer in ridge building along the outlet shore of Corner Inlet (Heyligers 1998), could be a candidate, but the only plant I have seen on the spit occurred on a ridge at the base. Hence, the *Thinopyrum* flats are a unique feature, intimately linked with the formation of the dune fields.

Conclusion

The sand spit of Shallow Inlet exists at the mercy of currents and winds. Longshore and tidal currents supply the sand, and westerly and southwesterly winds spread it over the spit. It accumulates in mobile ridges, incessantly resculptured by shifts in wind direction. Most likely this would still be the case were it not that, in the 1950s and 1960s, **Thinopyrum junceiforme* spread along the shores of Waratah Bay. This grass is native to the northwestern shores of Europe, where it is a primary coloniser of the upper beach. Being tolerant to salty groundwater, it thrived on the spit, under conditions too harsh for native dune grasses, and accumulated mounds where propagules took hold. These mounds, when close enough, developed into dune ridges and dune fields. This provided the opportunity for other hardy species to establish; foremost among these are *Austrofestuca littoralis,* **Ammophila arenaria* and *Spinifex sericeus*. However, the impressive dune landscape near the farther end of the spit exists in a state of uneasy balance between accretion and erosion, a condition that is too severe for any further vegetation development. Only on the somewhat sheltered slopes and flats along the inlet side of these dunes could more species establish, and although there is a successional trend in the composition of this vegetation, the area is relatively small and isolated; this appears to retard the arrival of species not adapted to dispersal by water or wind.

It is doubtful that any substantial dunes existed on the spit before it broke through in 1901 close to the high dune ridge as at that time neither **Thinopyrum junceiforme* nor **Ammophila arenaria* was present in the local area. Sooner or later another king tide is expected to break through the spit at its narrowest part, but I surmise that, at least initially, the dune fields will become an island. Over time, further erosion could undermine this island and lead to its demise. However, it is a sobering thought that two foreign grasses have had such a dominant influence on the formation of the landscape of the sand spit at Shallow Inlet.

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