The role of currents in the dispersal of introduced seashore plants around Australia

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Abstract: The aim of this study was to assess the role of currents in the dispersal of seashore species with buoyant propagules. Four introduced species which have now attained a wide distribution in southern and eastern Australia were used as indicators: *Cakile edentula, Cakile maritima* (Brassicaceae), *Euphorbia paralias* (Euphorbiaceae) and *Arctotheca populifolia* (Asteraceae). None arrived in Australia unaided, as all early collection localities are near ports and early long-distance dispersal within Australia was often due to shipping.

Buoyancy and viability of propagules were tested to assess dispersal and colonisation potential. Propagule spread was analysed using information from herbarium specimens and fieldwork. A progression of herbarium specimen collection dates could often be explained by regional current regimes, as revealed by stranding locations of drift bottles and drift cards. The eastward spread of *Euphorbia paralias* from King George Sound, Western Australia, correlated well with stranding patterns of drift bottles released south of the Sound. The colonisation by *Arctotheca populifolia* of the southern extremity of the Eyre Peninsula and the south-east of South Australia was achieved through fruits carried from Western Australia by the Leeuwin Current. These and other congruencies between patterns of spread and the results of drifter releases are analysed and discussed.

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We know remarkably little about long-distance transport of the propagules in water, although there are reports of strandline plants having travelled great distances (Guppy 1906; Ridley 1930). (Davy & Figueroa 1993)

Introduction

In 1979 I found a colony of the daisy *Arctotheca populifolia* in South Australia at the south-western tip of the Eyre Peninsula more than 800 km from the nearest location of this naturalised species in Western Australia. It occurred to me that introduced species, by virtue of being foreign to the native flora, could be used as markers to analyse the role of sea currents in propagule dispersal. I checked herbarium specimen collection details and found distribution patterns that correlated with the general circulation in the oceans around Australia (Heyligers 1983, 1984).

In this paper I analyse the dispersal histories of four, now widespread, introduced species and assess what these reveal about the role of near- and offshore currents for plant dispersal. *Cakile edentula* (Bigelow) Hook. and *Cakile maritima* Scop. (Brassicaceae) were accidentally introduced during the 19th century (Rodman 1974, 1986), while *Euphorbia paralias* L. (Euphorbiaceae) and *Arctotheca populifolia* (P. Bergius) Norlindh (Asteraceae) arrived during the early decades of the 20th (Heyligers 1983, 1989a) (Fig. 1).

Currents and wind are the main dispersal agents; currents because of the buoyancy of the propagules, wind because of its influence on drifting objects, as well as its capacity to move propagules over bare sandy surfaces. Before the advent of radio-tracked buoys, drift bottles and drift cards were used to study ocean currents (Russell 1894; Anon. 1968a; Marshallsay & Radok 1972). Their application in oceanography suffered the drawback that only points of release and stranding were known — no information on deeper currents was obtained. Nowadays, they are still used for specific purposes, e.g. research on dead seabird strandings (Wood 1996) or marine organisms with a buoyant phase in their development (Vaux & Olsen 1961; Anon. 1968b; Walker & Collins 1982; Collins & Walker 1985; Olsen & Shepherd 2006, Petrusevics 1990, 1991). The outcomes from drift bottle and card studies are also relevant to the dispersal of buoyant plant propagules. A significant difference between plant propagules and bottles or cards is that the latter are released from known positions, while the former first have to become sea-borne. Storm surges that erode foredunes, or breach sandbars closing off coastal lakes will carry propagules into the sea. Offshore winds can push fruits and seeds down the beach and out to sea, where rip currents may contribute to the start of the floating phase. Another important difference is that while stranded bottles or cards can be picked up and reported by any beachcomber, an inconspicuous, washed-up plant propagule first needs to establish a plant, if not a small population, before being noticed by a knowledgeable person.

Methods

Propagule buoyancy and longevity

Cakile and *Arctotheca populifolia* samples were collected in 1984–85 along the South Coast of New South Wales, with additional samples obtained in Western Australia and South Australia and from plants grown from cuttings. The main sample of *Euphorbia paralias* was collected in 1985 by Parks Victoria staff at Norman Bay on the south-west coast of Wilsons Promontory, Victoria. Other samples came from Three Mile Beach on the east coast of the Promontory, from the Sir Richard Peninsula, South Australia, and from Dalmeny, New South Wales. Tests were started shortly after samples were collected and the number of samples tested was 9 of *Cakile edentula*, 15 of *Cakile maritima*, 6 of *Euphorbia paralias* and 12 of *Arctotheca populifolia* plus 13 from plants grown from cuttings.

Samples were stored in paper envelopes at room temperature. To test buoyancy, propagules were put in jars with seawater and, initially, numbers remaining afloat were assessed daily; later, the interval between inspections lengthened until it became one or two years for truly long floaters. Viability was tested at the start of buoyancy experiments; during subsequent tests the viability of stored ('dry'), floating and sunken propagules was assessed. These tests were of an exploratory nature, sometimes done with a small number of propagules. Moreover, the number of propagules used in any one buoyancy test limits how many propagules can subsequently be used for viability testing. Ideally, I would use at least 50 propagules for a buoyancy test and 10 or 20 dry, floating and sunken propagules for viability testing. In practice, and especially in the case of long floating propagules, it became a matter of balancing the number used for viability testing against how many to leave to continue the buoyancy test. Nonetheless, the outcomes should give at least an indication of what one may expect to happen in nature.

Historical evidence of spread

The early collections of all four species were made when far fewer people lived in Australia and collecting activity was less intense, especially in remote areas. Therefore, I tested the possible influence of remoteness by checking the pre-1950 records for six common native Western Australian coastal species and found that even in the early days collecting had not been confined to centres of population but also had happened in isolated locations. This gives reasonable confidence that, if any of the introduced species dealt with in this paper had been present in an area long before it was first collected, it would have been collected earlier. Hence, my axiom has been to assume that a directional progression of early collection dates, separated by large gaps, was a true indication of dispersal by sea.

During the 1980s and 1990s I visited many Australian herbaria and the Herbarium of the Royal Botanic Gardens, Kew (U.K.), to obtain specimen data. Each species was

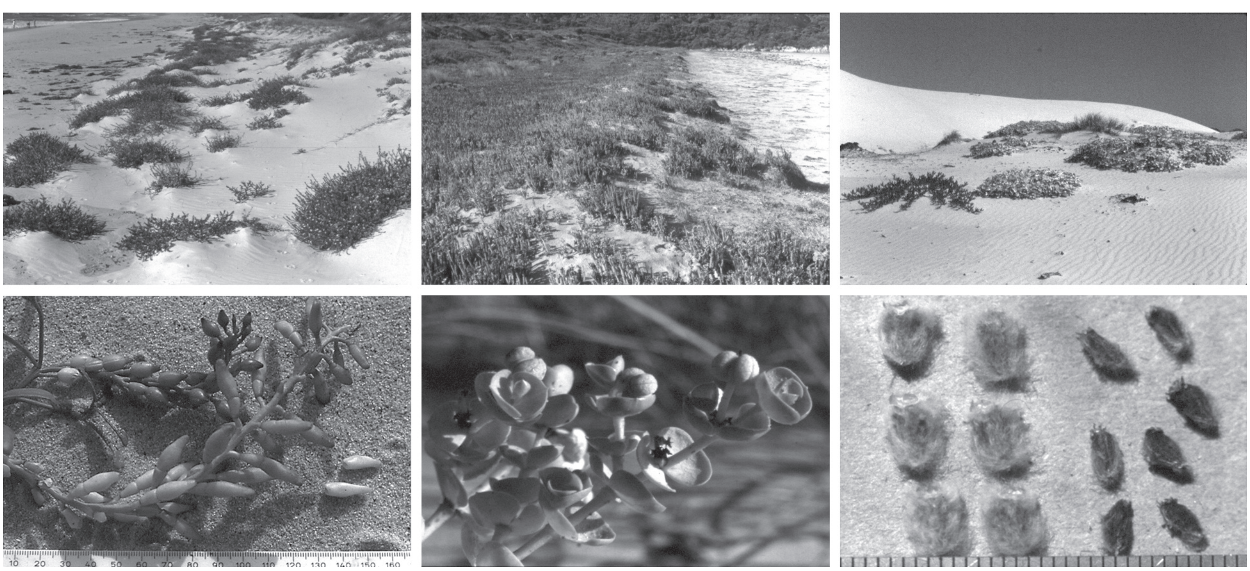

Fig. 1. Pictorial introduction to the four species discussed in this paper. **Left column**: a hummocky strandline dune in southern New South Wales formed by plants of *Cakile edentula* (left and centre) and *Cakile maritima* (right) impeding the movement of sand along the upper beach; the lower photo shows the two-segmented fruits of *Cakile edentula* (top) and *Cakile maritima*. **Centre column**: *Euphorbia paralias* on the foredune at Norman Bay, Wilsons Promontory, where it contributed to the stabilisation of the dune, and part of an inflorescence with fruits that 'explode' when mature and scatter their three round seeds. **Right column**: *Arctotheca populifolia* (centre and at right) in drift sands near Mungo Brush, where the species was first collected in New South Wales. The fruits (achenes) of the western form (left) are compared with those of the eastern form in the lower picture.

sorted by collection dates to find those collections made sufficiently distant from earlier ones to indicate a population established after long-distance dispersal, either by sea or through shipping. In the figures, the locations of the earlier collections are in bold. Collections made in the general vicinity shortly thereafter were mapped with indicative symbols, others with small circles. Coastline sections without data were then sketched in to complete the maps.

Oceanographic aspects

Oceanographic information for the seas around Australia was obtained from the literature and summarised in a map. For a detailed analysis of local currents I used retrieval reports from ballasted and empty drift bottles (Anon. 1968 a, b) and high density PVC cards (Marshallsay & Radok 1972). To assess the influence of wind on drifting objects, logbooks were inspected at the Bureau of Meteorology in Melbourne to obtain data on wind strength and direction during and after the drifter releases near Eclipse Island, Western Australia, and in Bass Strait.

Results

Species origins and propagule characteristics

Cakile edentula is indigenous to the Atlantic coast of North America, *Cakile maritima* and *Euphorbia paralias* to the shores of western Europe and the Mediterranean, and *Arctotheca populifolia* to those of southern Africa. All are strandline pioneers with buoyant propagules and play a role in foredune formation (Heyligers 1985; Fig. 1). The populations of *Arctotheca populifolia* from eastern Australia are noticeably different from those of western and southern Australia; they are less robust, have ovate leaves and

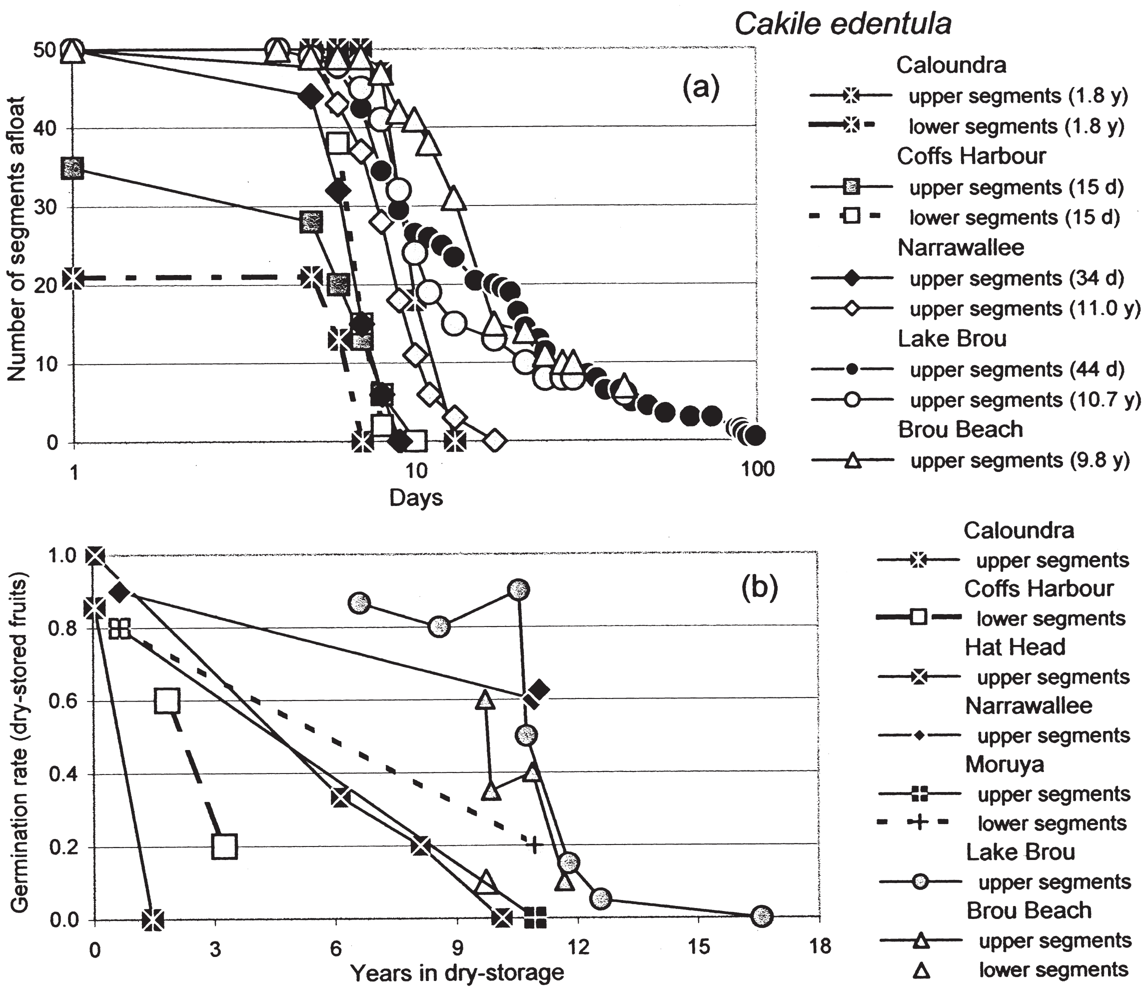

Fig. 2. Buoyancy (a) and viability (b) of dry-stored *Cakile edentula* fruit segments. Geographic names refer to sample locations. In the legend of (a) the time between collecting the fruits and starting the tests is given in parentheses. Where applicable, the number of segments afloat has been adjusted for removal of segments for viability testing. For viability testing pericarps were removed from the seeds. Data points for upper fruit segments have been connected by solid lines, those for lower segments by broken lines.

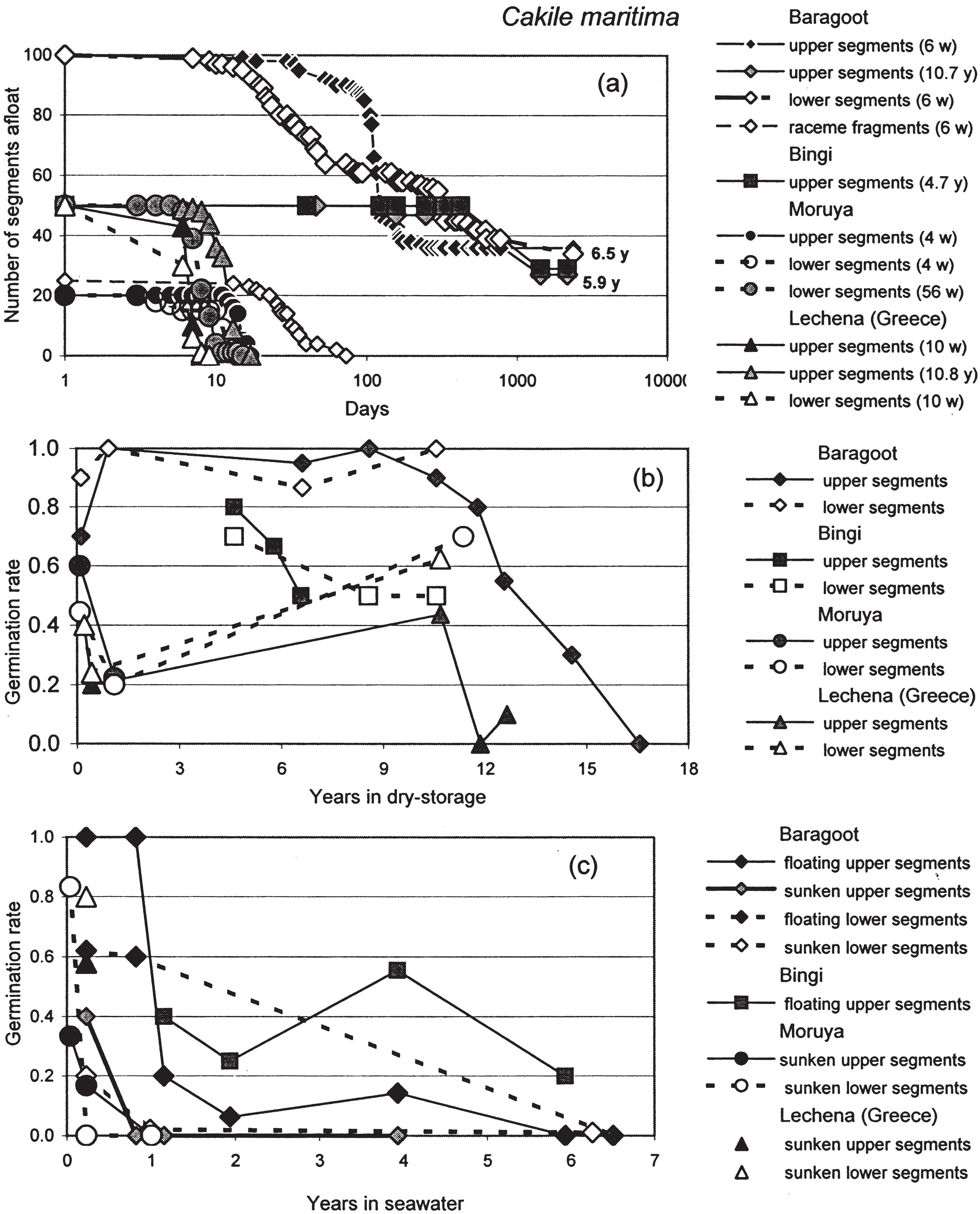

Fig. 3. Buoyancy (a) and viability of (b) dry-stored and (c) floating and sunken fruit segments of *Cakile maritima*. For comments see caption for Fig. 2.

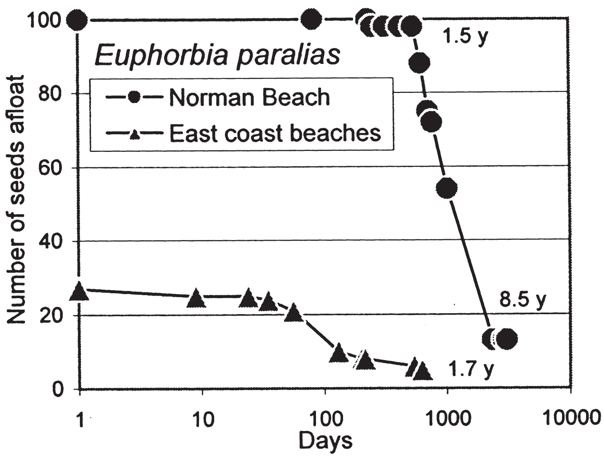

Fig. 4. Buoyancy of *Euphorbia paralias* seeds from Wilsons Promontory, Victoria.

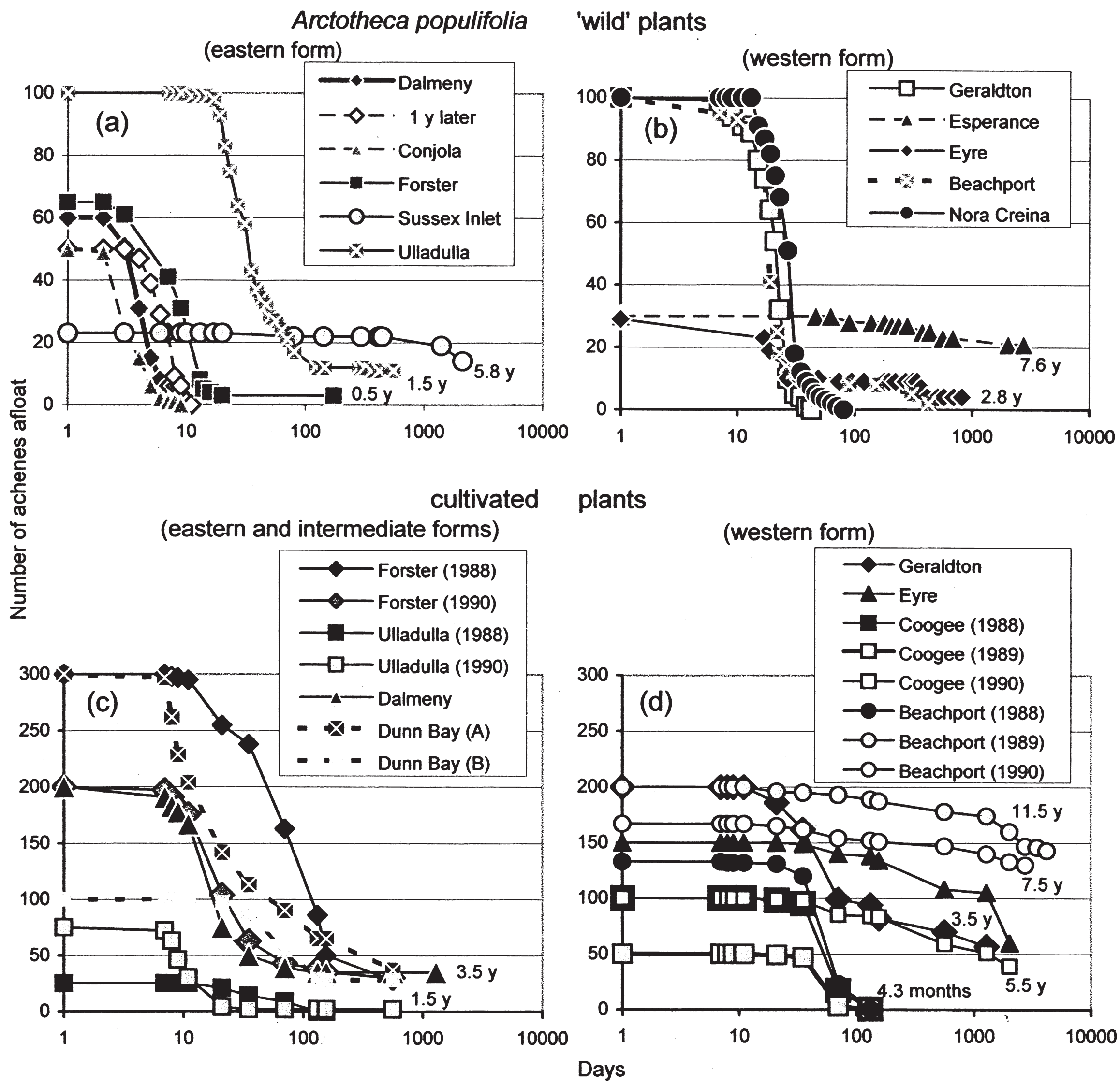

Fig. 5. Buoyancy of *Arctotheca populifolia* achenes: (a) from 'wild' plants of the eastern form, (b) from 'wild' plants of the western form, (c) from plants of eastern and intermediate forms grown from cuttings, and (d) from plants of the western form grown from cuttings. In the legend of (c) and (d) the dates in parentheses refer to the years of harvest.

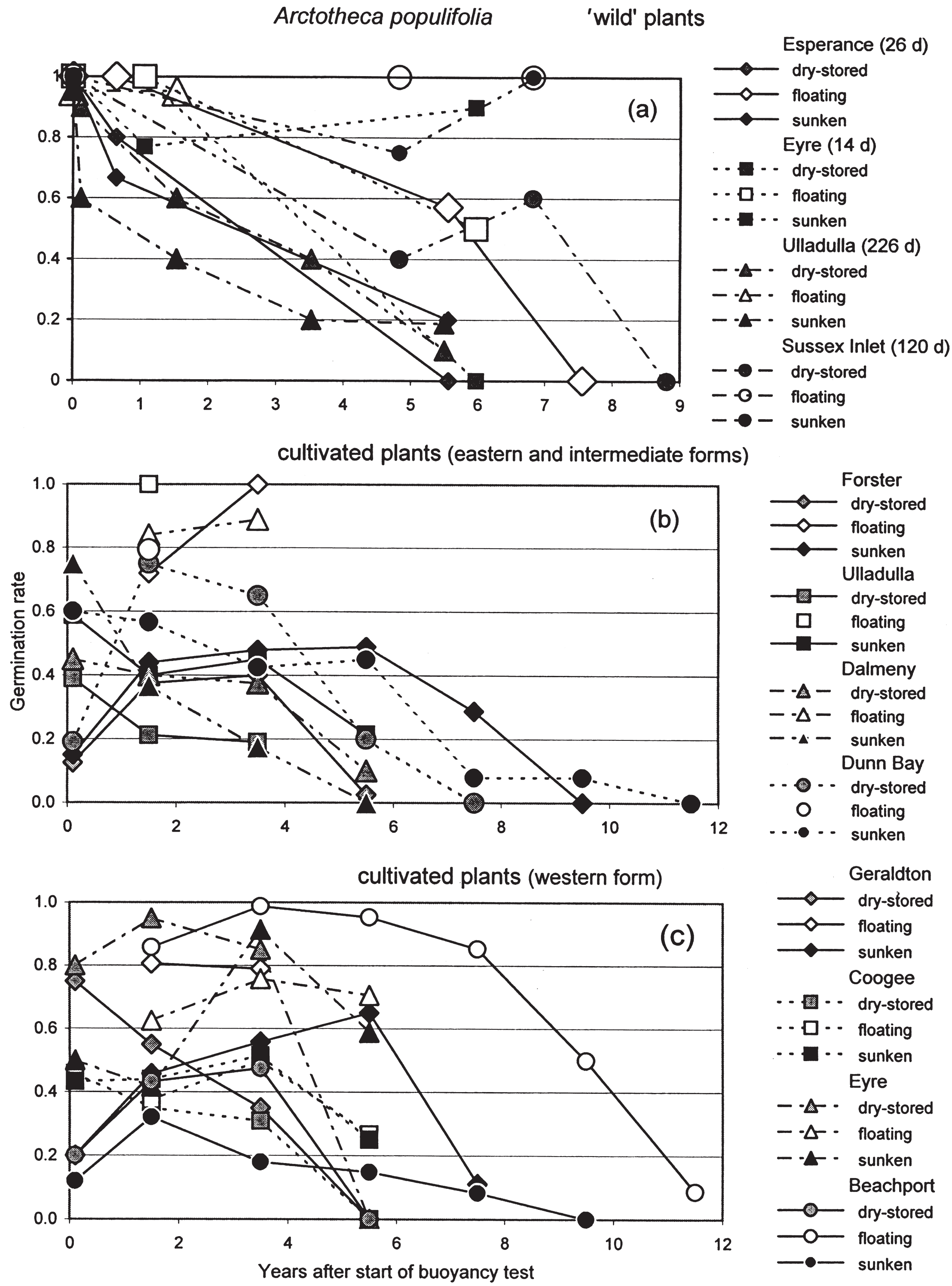

Fig. 6. Viability of *Arctotheca populifolia* achenes from plants of which at least some achenes stayed afloat for several years: (a) from 'wild' plants, (b) from plants of eastern and intermediate forms grown from cuttings, and (c) from plants of the western form grown from cuttings. In the legend of (a) number of days refers to time in storage before testing.

12–14 ray florets with well-developed ligules. The western form has leaves of an angular outline, sometimes with lobes along the transition to the petiole, and 12–19 ray florets with only short ligules. The forms have remained distinct, although some plants collected near Cape Naturaliste appeared to come close to the eastern form. The *Arctotheca populifolia* collections from South Africa in the Herbarium at Kew show a morphological variation that encompasses the forms found in Australia.

A *Cakile* fruit is c. 20 mm long and 6 mm wide, has a corky pericarp and consists of two, usually one-seeded, segments. On maturity the upper segment separates from the lower one, which remains attached to the plant. The fruit of *Euphorbia paralias* is a capsule containing three round seeds, which measure c. 3 mm across. The mature fruits open explosively, scattering the seeds up to 2 m from the plant (Heyligers 2002b). The pubescent achenes of *Arctotheca populifolia* are c. 5 mm long and 2.5 mm wide. The pubescence of the western form is consistently more luxurious than of the eastern form. The achenes drop onto the sand when the flowerheads have matured.

Propagule buoyancy and longevity

Most *Cakile edentula* and *Cakile maritima* fruit segments did not float longer than two weeks, a period marginally extended by prolonged dry storage (Figs. 2 and 3). These results are in agreement with observations of Guppy (1906), Rodman (1974) and Ignaciuk & Lee (1980). However, there were notable exceptions; from some *Cakile edentula* samples up to 25% of fruit segments stayed afloat for several months, while some of *Cakile maritima* did so for many years.

Dry fruit segments of *Cakile edentula* germinated after about 5 weeks, those of *Cakile maritima* after about 10 weeks. Exposure to seawater during one week before sowing at least halved germination times. Germination rates for *Cakile edentula* were initially better than 80% and declined slowly during storage with a few seeds still viable after 12 years. Germination rates for *Cakile maritima* were variable but some seeds remained viable for more than 15 years.

Viability of floating fruit segments of *Cakile edentula* declined rapidly and was lost after 6 weeks, with a noticeable exception of 6 seeds from a sample of 10 upper segments, which still germinated after 12 weeks. Once segments sank, seeds were no longer viable. Viability of *Cakile maritima* segments dropped sharply after a year or so, but a few seeds still germinated after segments had been afloat for 6 years. Seeds in sunken segments lost their viability rather quickly but some remained viable for 6 months. Loss of viability is likely due to seawater penetrating the fruit wall, because seeds removed from dry fruits and exposed to seawater lost their viability within a few days. The quicker deterioration of *Cakile edentula* fruits might be due to their thinner pericarp.

Most *Euphorbia paralias* seeds remained afloat for a year and a half, after which their number steadily declined for several years to stabilise at 13% (Fig. 4). After 8.5 years the experiment finished with the viability test of the last remaining seeds. Fresh seeds went through a dormancy period of about half a year after which the germination rate of dry and floating seeds was about 40%. Floating seeds maintained this rate for at least two years but none germinated after six years. The comparable figures for dry seeds were 13 and 16 years. No sunken seeds were viable.

Buoyancy periods of *Arctotheca populifolia* achenes proved highly variable (Fig. 5). Achenes from plants of the western form generally stayed afloat longer than those from the eastern form, a difference more marked in the tests with achenes from the cultivated plants. Some of the achenes collected at Sussex Inlet were still afloat after 5.8 years, some from Esperance after 7.6 years, while one in ten achenes from cuttings taken at Beachport were still afloat after 11.5 years.

Germination rates of fresh achenes varied, but usually 50% or more germinated (Fig. 6). There was no dormancy involved and while viability declined slowly during storage, some seeds remained viable for up to seven years. Germination rates of floating achenes were not uncommonly about 80% and remained high for up to eight years, while two of the 23 achenes from Beachport plants still germinated after floating for 11.5 years. Germination rates of sunken achenes were variable, but some were still viable after 7.5 years.

Currrent regimes

Currents around the southern and eastern coasts of Australia are shown in Fig. 7.

Data from drift card and drift bottle releases is given in Figures 9 to 13 with results summarised in Appendix 1. Relevant details are used in the analyses of individual plant dispersal histories.

The Leeuwin Current has its origin off north-west Australia and flows south between the Western Australian Current and the coast, narrowing and gathering speed during the process. Where it meets the Antarctic Circumpolar Current, it flows with speeds of up to 1.8 m sec^{-1} (or 150 km day^{-1}) along the upper slope of the continental shelf, but speeds closer inshore are at best 0.5 m sec^{-1}. The strength of the Leeuwin Current varies between seasons and from year to year (Cresswell 1991; Cresswell & Griffin 2004). In years of maximum flow, its influence is thought to extend to the west coast of Tasmania.

Currents off South Australia are primarily driven by the Antarctic Circumpolar Current. Already a century ago this was demonstrated by the stranding patterns of drift bottles released from vessels plying between eastern and western harbours (Russell 1894–1902; Lenehan 1904). In the Great Australian Bight, in response to the prevailing south-westerly winds, an anti-clockwise current is generated which flows most strongly along the eastern shore of the Bight (Herzfield & Tomczak 1999). In the rather isolated shallow waters of

Spencer Gulf and Gulf St Vincent currents are thought to circulate in a clockwise direction (Bullock 1975; Bye 1976). In south-eastern South Australia the easterly flow translates into a south-easterly longshore current. However, as winds turn more southerly during summer, it is displaced by the northerly flow of the Flinders Current (Bye 1983).

The Zeehan Current runs along the continental shelf edge off south-eastern South Australia, possibly originating from the outflow of high salinity water from the Gulfs and the Great Australian Bight (Cresswell 2000). It is a permanent but rather narrow c. 40 km wide current, which may reach speeds of 17.5 km day^{-1} and flows southward over the outer half of the shelf to the west coast of Tasmania. During the strong winter flow, satellite-tracked drifters were carried around the southern coast and up the east coast before coming under the influence of the East Australian Current (Fig. 7). During summer, when the Zeehan Current is weaker, drifters went only as far as the southern end of the island before being trapped by this current.

Bass Strait is a shallow coastal sea between Tasmania and the mainland. Although tidal currents dominate the circulation throughout the Strait, there is a residual mainly wind-driven current of highly variable speed and direction with easterly flows generally stronger than flows in other directions (Baines *et al.* 1991). During autumn and winter this current moves with an average speed of roughly 20 km day^{-1} (Fandry *et al.* 1985). In the northern half of the Strait it flows past East Gippsland and turns northward along the coast of New South Wales, while in the southern half it flows through the gap between Flinders Island and north-eastern Tasmania and then northward (Tomczak *et al.* 1984). During summer, when tidal flows dominate, the direction of the current off south-western Victoria reverses and reinforces the Flinders Current (Olsen & Shepherd 2006), but off south-eastern Victoria the flow is still predominantly eastward and changes to a northerly direction along the coast of New South Wales (Marshallsay & Radok 1972; Godfrey *et al.* 1980a).

The East Australian Current originates in the Coral Sea as the southward-flowing branch of the South Equatorial Current (Sokolov & Rintoul 2000; Spear & Steinberg 2001; Fig. 7). It flows most strongly along and beyond the continental shelf edge, although surface speeds, sometimes exceeding 1.5 m sec^{-1}, vary markedly in space and time. Currents nearer the coast are weaker and although generally correlated to the conditions further out to sea, on occasions reverse and flow

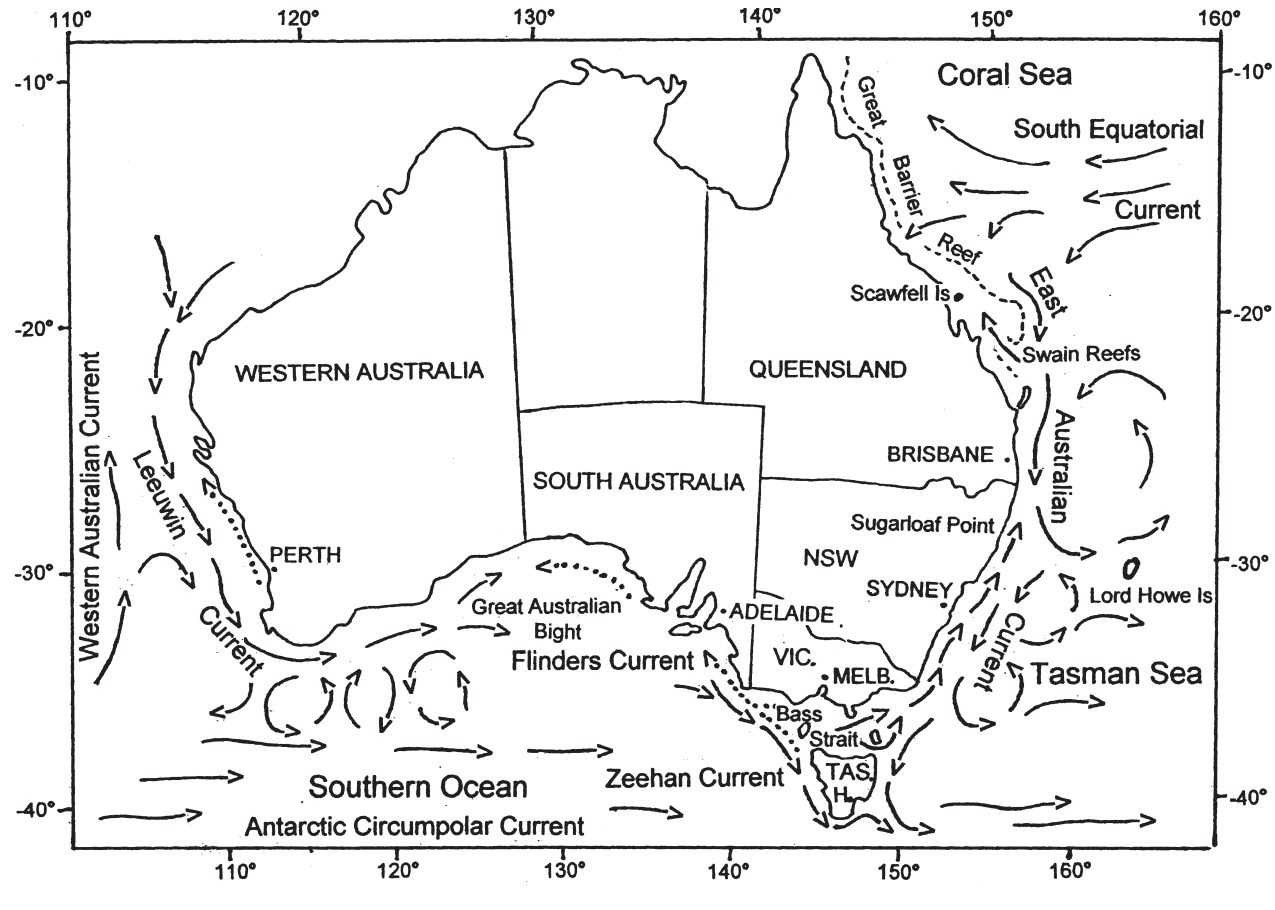

Fig. 7. Schematic of major currents operative in long-distance dispersal of strand- and foredune plants with buoyant propagules. Solid arrows represent permanent currents or currents mainly running during the winter half-year, stippled ones those running only during summer. The figure is based on papers referred to in Results: Current regimes.

northward (Cresswell *et al.* 1983). Off northern New South Wales, between Smoky Cape near South West Rocks and Sugarloaf Point near Seal Rocks, the East Australian Current veers away from the coast in a south-easterly direction (Godfrey *et al.* 1980b; Roughan & Middleton 2002).

Closer inshore, along the southern New South Wales coast, runs an intermittent and variable northerly counter-current, which originates from the easterly flow through Bass Strait. Near Sugarloaf Point it becomes to a greater or lesser degree entrained in the East Australian Current (Cresswell *et. al.* 1983). When the core of the East Australian Current is located far offshore, the northward flow is less impeded and a weak current of at best 0.4 m sec^{-1} continues along the coast north of Smoky Cape (Roughan & Middleton 2002). Near-shore currents off southern New South Wales, although variable in direction and strength (mostly < 0.5 m sec^{-1}), often have a marked onshore component (Huyer *et al.* 1988), presumably under the influence of south- to north-easterly winds.

The Great Barrier Reef occupies the continental shelf between the southern coast of Papua New Guinea and Fraser Island (Fig. 7). It consists of about 2500 individual reefs, varying in size from 0.1 to 100 km^2 (Wolanski 1994). A broken chain of outer reefs outlines the continental shelf edge. Where the South Equatorial Current meets the reef about 10% of the flow spreads onto the continental shelf, while the remainder divides into a northerly and southerly longshore current, the latter being the origin of the East Australian Current (Sokolov & Rintoul 2000; Brinkman *et al.* 2001). Two comprehensive investigations in the southern section of the reef (Griffin *et al.* 1987; Middleton *et al.* 1994) showed that the current regime is dominated by the tides, but also strongly influenced by local wind stress. Hence, due to the variable interactions between tides, wind and longer-term current phenomena, the resulting circulation is highly complex and subject to rapid change.

Also important for dispersal of drifting objects are the 'linear oceanographic features.' Expressed as 'slicks' on the surface, they are convergence zones of three-dimensional circulations resulting from interactions between water masses of different salinity, tidal currents, bottom topography and wind conditions (Kingsford 1990). Slicks vary in length from less than 100 m to many tens of kilometres. They are accumulation zones of plankton, drift algae and flotsam. Shorter slicks frequently occur in near-coastal situations, e.g. around headlands, islands, reefs or estuary entrances, and may facilitate the stranding of propagules. Longer ones, known as 'wind rows,' are aligned in the direction of the wind and their downwind speed is greater than that of their surroundings (Cresswell pers. comm.). Hence, windrows may not only concentrate drifting propagules, but also speed up their long-distance transport. Moreover, they can transfer drifting objects from one current system to another.

Dispersal of Cakile maritima

Cakile maritima was introduced into Western Australia towards the end of the nineteenth century (Fig. 8). The port of Fremantle is the likely point of entry, although another

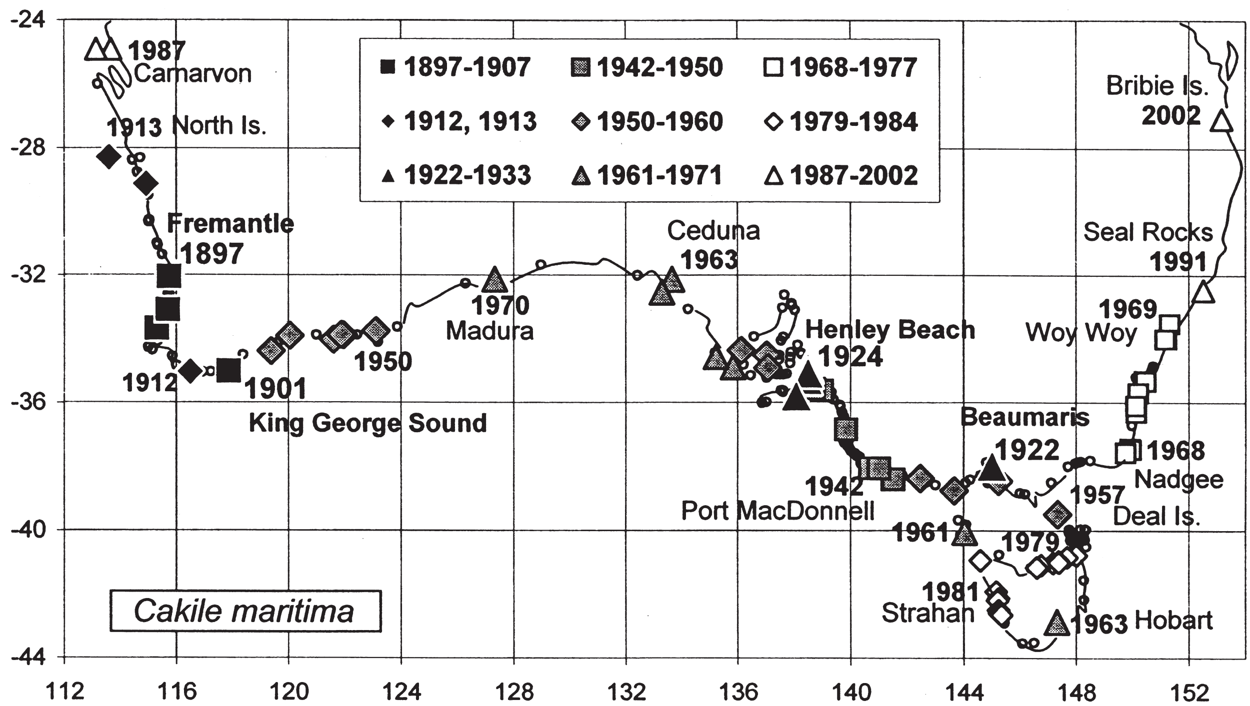

Fig. 8. Evidence for *Cakile maritima* dispersal, based on collection dates of 448 herbarium specimens. The progression of dates indicates a spread from early nodes near harbours in southern Australia to Carnarvon on the west coast and Bribie Island on the east coast.

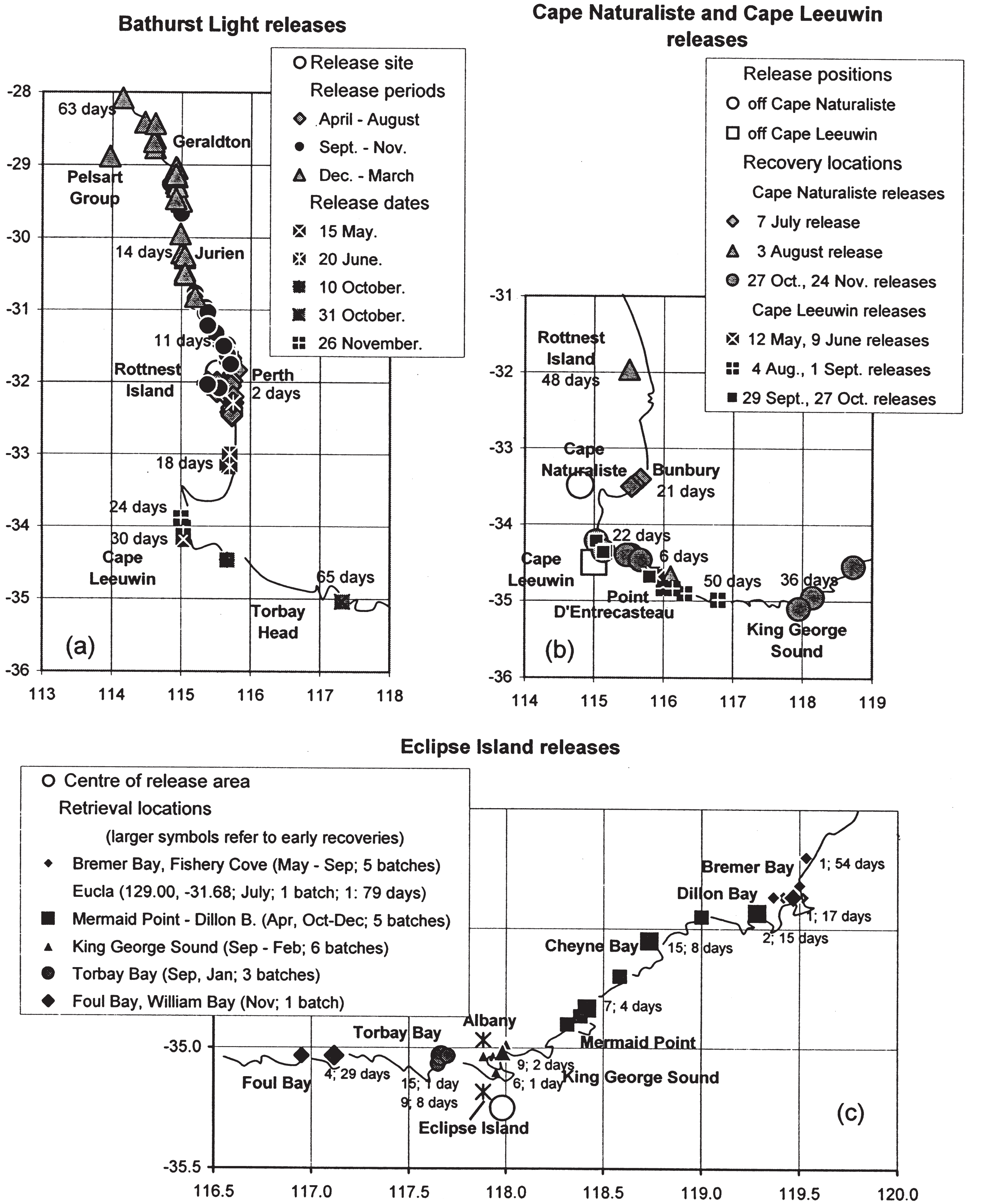

Fig. 9. Retrieval results of ballasted drift bottles, released in batches of 20, at four positions off the south-west coast of Western Australia between February 1956 and January 1957 (data from Anon. 1968b); (a) stranding locations of 136 bottles from 28 batches released 12.6 km north-west of Bathurst Light, north of Rottnest Island, (b) of 14 bottles from six batches released off Cape Naturaliste and 20 bottles from ten batches released off Cape Leeuwin, (c) of 113 bottles from 30 batches released off Eclipse Island. Locations have been grouped according to regions and dates or periods of release. Number of days refers to the time between release and recovery. The chart of (c) shows for some locations the number of bottles found and the time between release and the first bottle recovery.

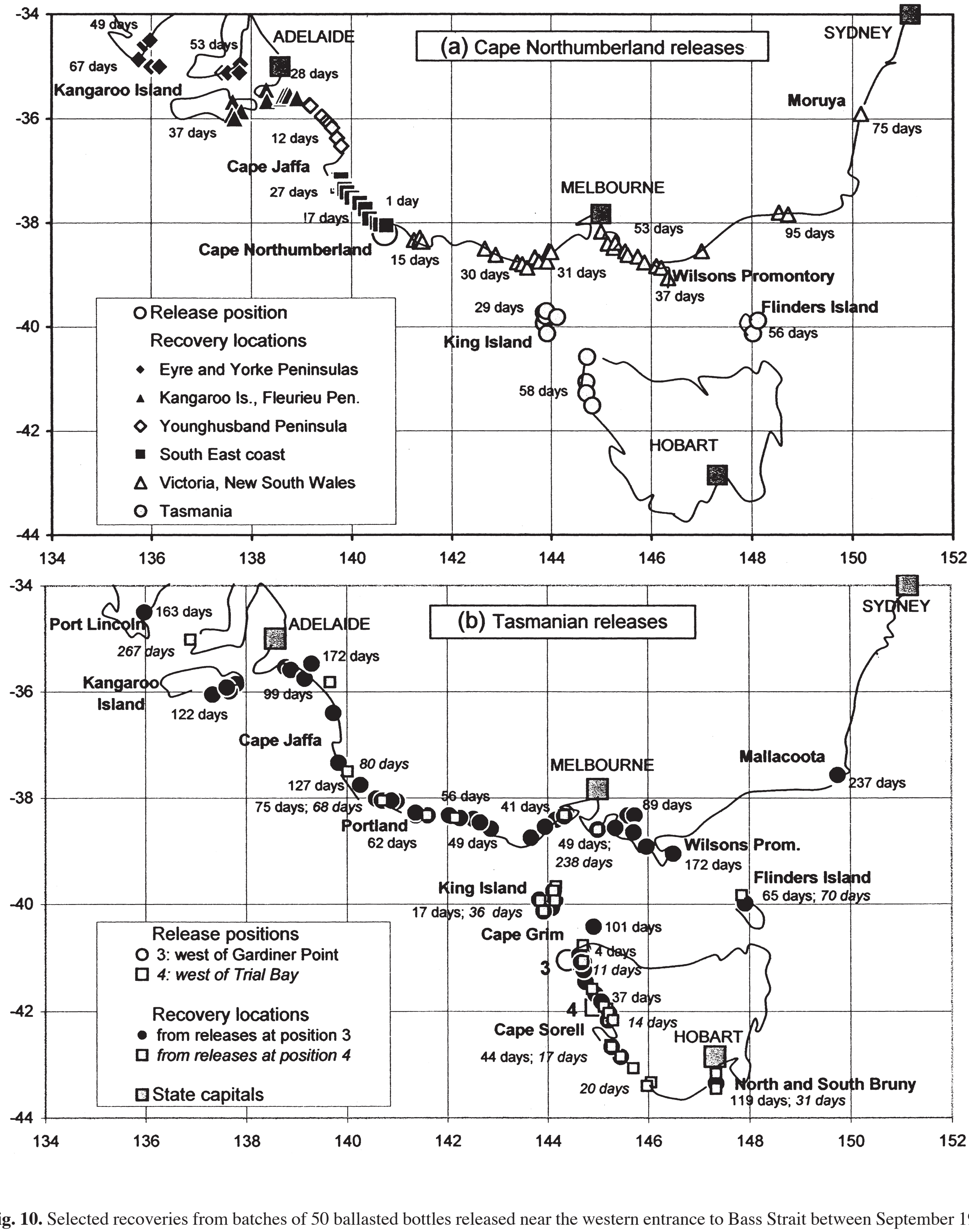

Fig. 10. Selected recoveries from batches of 50 ballasted bottles released near the western entrance to Bass Strait between September 1958 and May 1962 (data from Anon. 1968a). (a) Recoveries from 45 batches released about 14 km south of Cape Northumberland, (b) from 35 and 37 batches released at positions 3 and 4 off the north-western coast of Tasmania. Numbers of days indicate the shortest time between release and retrieval for particular locations. In (a) most strandings between the Fleurieu Peninsula and Wilsons Promontory have been left out. The strandings shown in (b) are from batches of which at least one bottle was found on a shore other than Tasmania's, together with strandings along the south-west coast from other batches. The retrieval of a bottle at Burleigh Heads, in south-eastern Queensland, after 307 days has not been mapped.

introduction at King George Sound is also a possibility. Within a decade or so it became widespread between these ports. Diels (1906) mentions that *Cakile maritima* was usually the first plant to be found on the loose sand of the flat shoreline. By 1913 it was also present at Dongara and on North Island of the Houtman Abrolhos group and by 1950 had spread to the Esperance — Israelite Bay coast and some of the islands of the Recherche Archipelago.

Drift bottles released during winter and spring north of Rottnest Island floated south and stranded not only along the west coast but also east of Cape Leeuwin as far as Torbay Bay (Fig. 9). A similar drift pattern for this time of year was also evident from releases off Cape Naturaliste and Cape Leeuwin, with strandings as far west as Cheyne Bay. Bottles were often adrift less than a month, short enough for some *Cakile maritima* fruits to remain afloat. Hence, it would appear that in addition to local dispersal processes linked to tidal and inshore currents, the Leeuwin Current provided an efficient vehicle for dispersal in south-western Western Australia.

In 1922 *Cakile maritima* was collected at Beaumaris along the shore of Port Phillip Bay, Victoria, and two years later also at Henley Beach near Adelaide, locations again close to busy harbours (Fig. 8). Whether these were new introductions from overseas or originated from populations in Western Australia cannot be determined, but I think it unlikely that propagules floated across from Western Australia. Apparently, the plants at Beaumaris failed to establish a viable

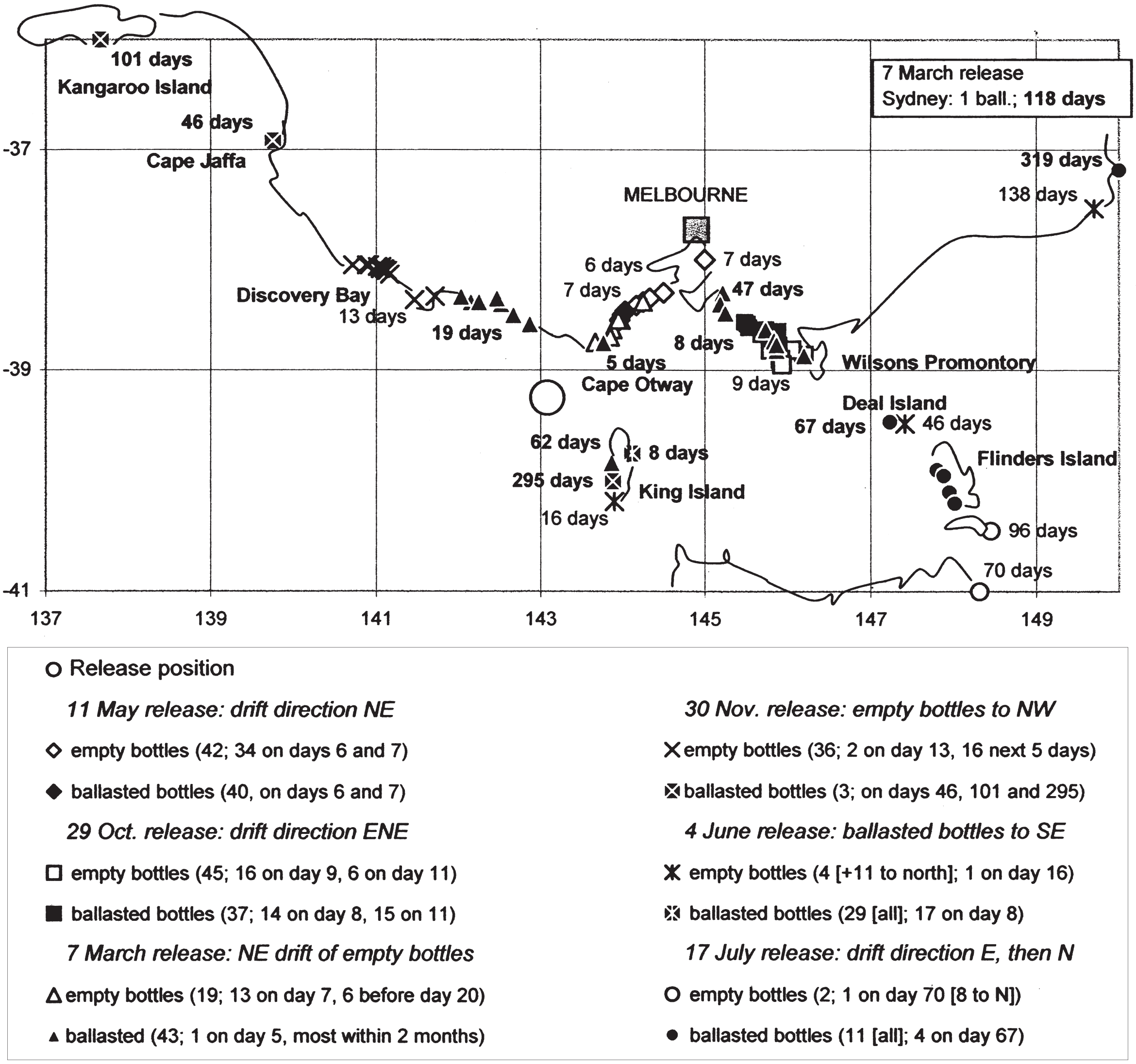

Fig. 11. Results of six releases off Cape Otway where batches of 50 non-ballasted ('empty') and 50 ballasted bottles were released at about monthly intervals in 1960 (data from Anon. 1968a). Number of days usually refers to the time between release and the first reported stranding(s), but for widely spread strandings, to later dates as well. Numbers of days in bold refer to ballasted bottles. Although large numbers of bottles beached on King Island, only the stranding site of one bottle per batch has been mapped.

population, as there were no further collections from around the Bay for another 30 years, but *Cakile maritima* became well-established along the beaches of Gulf St Vincent. In summer, when winds are mainly south-easterly, drift cards released at the entrance of the Gulf stranded at the western side of the Gulf, while those released during winter, under influence of south-westerlies, stranded on the eastern shores (Petrusevics 1990, 1991). It is likely that the predominance of the southerly winds kept fruits confined to the Gulf for many years as it was not until the 1940s that *Cakile maritima* was also collected at other locations in south-eastern South Australia. The first of those collections was made at Port MacDonnell, an indication that the fruits had come under the influence of the south-easterly longshore current once they had 'escaped' from the Gulf.

In 1950 *Cakile maritima* was collected at Cowes on Phillip Island, in 1953 at Apollo Bay on the Otway coast, and in 1957 on Deal Island, indicating that the fruit segments, like drift bottles released near Cape Northumberland and Cape Otway (Figs. 10 and 11), were spreading through the northern half of Bass Strait. It was not until the mid 1960s that *Cakile maritima* was found on King Island and much later before it was collected on the west and north coast of Tasmania. The fruits colonising King Island and the west coast are likely to have been carried from the mainland by the Zeehan Current. Drift bottles released near Cape Northumberland were found in north-west Tasmania after 58 days (Fig. 10a), a period sufficiently short for many *Cakile* fruit segments to stay afloat. *Cakile maritima* became widespread along the north coast, a reflection of efficient local distribution by the predominantly tidal currents that dominate the southern waters of Bass Strait as demonstrated by the drift card study of Marshallsay & Radok (1972; Fig. 12). An isolated find near Hobart in 1963, like four decades earlier in Phillip Bay, appeared to have failed to lead to further colonisation of the east coast.

Collections made in 1968 and 1969 were the first indication that *Cakile maritima* occurred in far East Gippsland and New South Wales. During the 1970s it was collected 14 times along the NSW South Coast, twice as often as *Cakile edentula*.

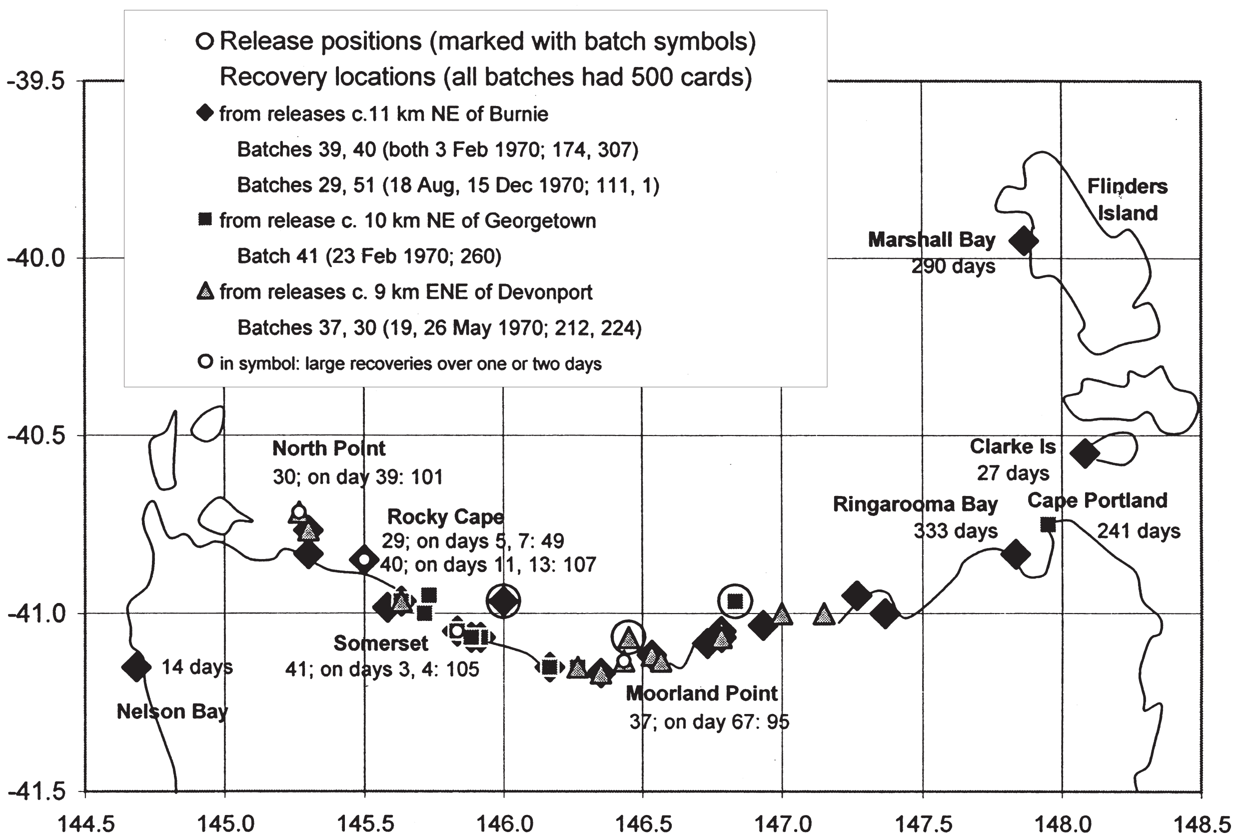

Fig. 12. Retrieval locations of drift cards released on seven occasions during 1970 in batches of 500 off the north coast of Tasmania (data from Marshallsay & Radok 1972). The legend gives release dates and total numbers of cards retrieved. Batch number(s) and retrieval data have been added to the names of early and some outlying stranding locations. If strandings happened over a long period, only the data for the first two are given. Three recoveries outside Tasmania have not been mapped.

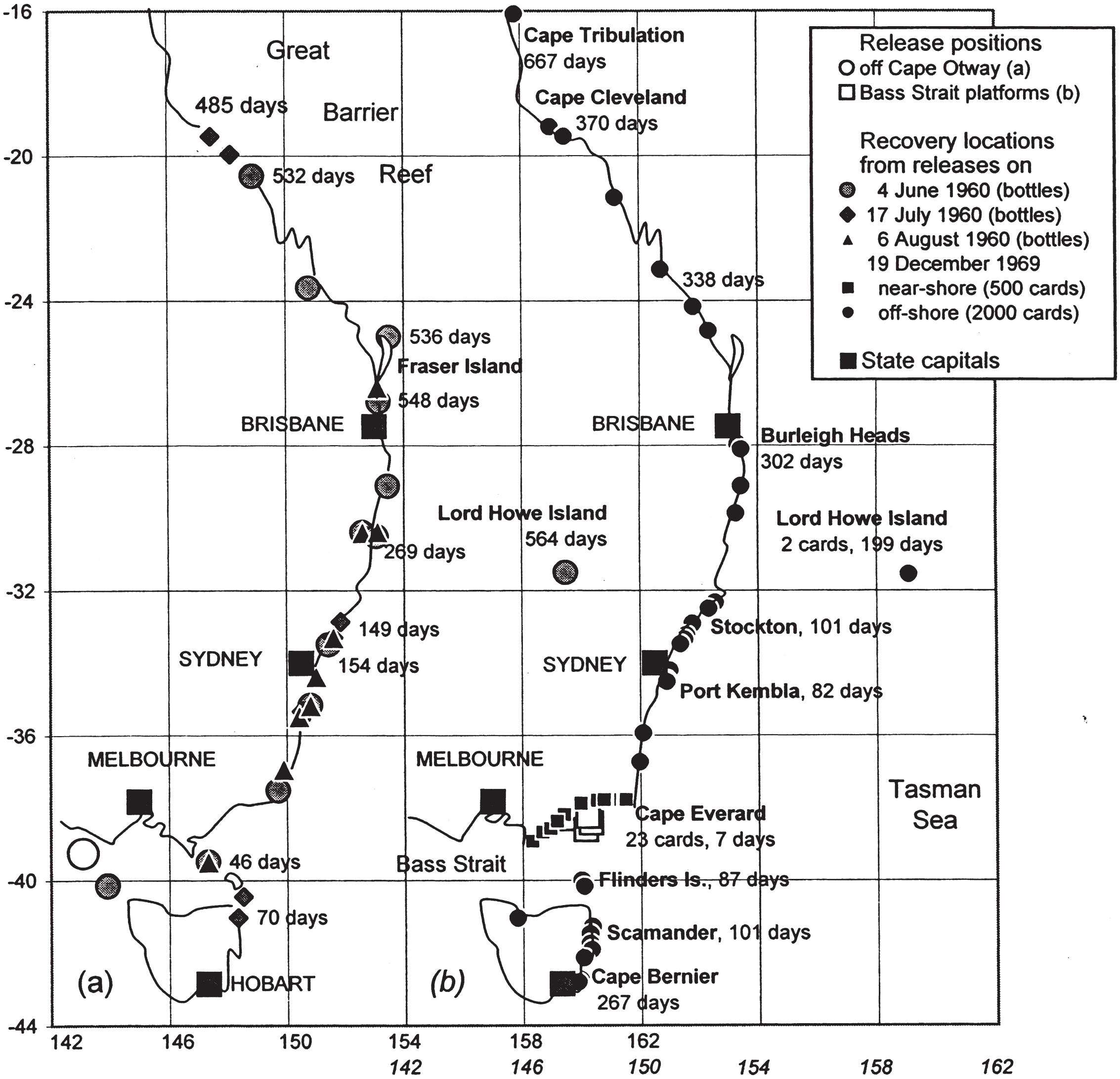

Fig. 13. East coast retrieval locations of 150 empty bottles released about 55 km south-west of Cape Otway during the winter months of 1960 (a), compared with those of the 2500 drift cards released on 19 December 1969 from oil and gas platforms at the north-eastern entrance to Bass Strait *(b)*. Numbers of days indicate time between release and retrieval. Data for (a) from Anon. (1968a), for *(b)* from Marshallsay & Radok (1972); the maps have been partly overlaid for easier comparison.

Could this mean that *Cakile maritima* had been overlooked due to its resemblance to *Cakile edentula*? Probably not. If that had been the case, it should have appeared among the 13 *Cakile edentula* collections made between 1955 and 1968. Moreover, in view of the fact that it was only in 1957 that *Cakile maritima* was collected on Deal Island, its appearance at the south-eastern corner of the mainland 11 years later seems to be 'right on target.' It is noteworthy that most of the long sandy shore of Gippsland was bypassed, indicating a propagule origin west of Wilsons Promontory in accordance with the outcomes of drifter experiments (Figs. 11 and 13). The collection at Woy Woy could indicate that fruit segments had been carried northward along the coast and, if the seeds that arrived at Woy Woy had been a few of a large propagule wash-out, the widespread occurrence of the species along the South Coast soon afterwards could have originated from the same event.

There is a large gap in time before *Cakile maritima* was collected near Forster on the NSW North Coast in 1991 and, in 2002, on Bribie Island in southeastern Queensland. Apparently, occurrences remain sporadic but further colonisation could be expected in view of the ongoing spread of *Cakile edentula* to be discussed later.

Dispersal of Euphorbia paralias

Euphorbia paralias, first found near Albany in 1927, spread eastward from King George Sound and in 1950 was collected at Esperance and in the Recherche Archipelago. In the following decades it spread further east along the western shore of the Great Australian Bight (Fig. 14). *Euphorbia paralias* was not found west of King George Sound until a 1986 survey revealed some localised occurrences between the Sound and Point D'Entrecasteaux (Heyligers 1989a). A few years later large populations were found on the west coast on the shores of Geographe Bay (Heyligers 1989a) and Garden Island (Keighery & Dodd 1997).

The results from drift bottle releases near Eclipse Island (Fig. 9c) show drift into King George Sound during spring and summer, the Bremer Bay area as the nearest long-distance destination during winter, strandings between these locations to be common in the transition periods between these seasons, and only very infrequent strandings west of Torbay Bay. It would appear that during summer, with the prevailing southerly winds, flotsam could get 'locked up' in the Sound, which then may function as a source for dispersal in an easterly direction. Its shape would impede drift in other directions, especially during periods of a strongly flowing Leeuwin Current. This may explain why 60 years elapsed before *Euphorbia paralias* was found west of King George Sound. However, it is also possible that dispersal to these areas and further north along the west coast may have been assisted by human agencies, such as transport on fishing vessels (Keighery & Dodd 1997) or by recreational vehicles (pers. obs.)

In 1934 *Euphorbia paralias* was found near Port Victoria on the east coast of the Spencer Gulf (Fig. 14). As this was only a few years after being collected at Albany, its occurrence close to a harbour points again to being introduced through shipping. Initially, *Euphorbia paralias* became common along the eastern shore of the Gulf before spreading to the western shore. However, seeds remained 'locked up' in the Gulf for several decades, as it was not before 1958 that the first collection was made outside the Gulf, on the western extremity of Kangaroo Island.

Ten years later, at Normanville, *Euphorbia paralias* was collected on the eastern shore of Gulf St Vincent close to the entrance and open to the strait between Yorke Peninsula and Kangaroo Island. An easterly current runs through the strait; so it is likely that the colonising seeds came from the population in Spencer Gulf. The species has become very common in the Normanville area, has gradually extended its range northward and is now widespread along the east coast of the Gulf.

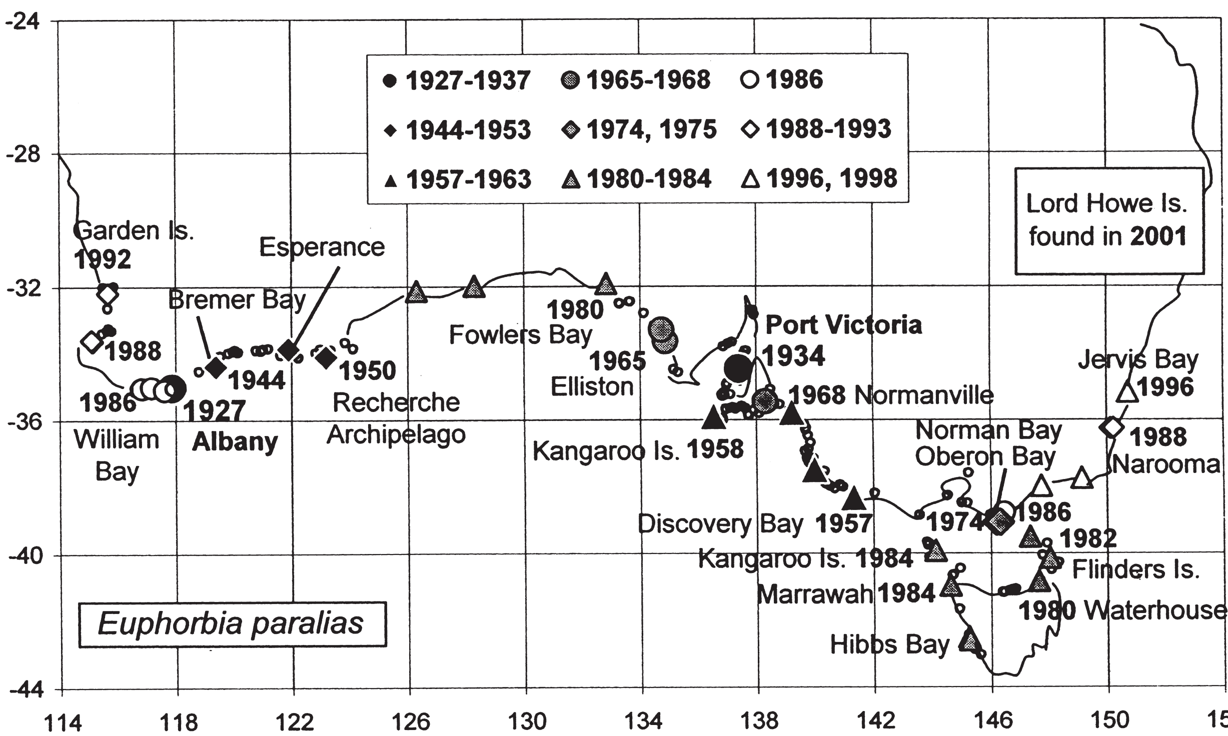

Fig. 14. Evidence for *Euphorbia paralias* dispersal, based on collection dates of 242 herbarium specimens. The progression of dates indicates a spread from early foci near Albany in King George Sound and Port Victoria on the east coast of the Spencer Gulf to the Perth region, the NSW South Coast and Lord Howe Island.

In the same period *Euphorbia paralias* also spread to Bass Strait and in the mid-1970s was found twice along bays in the south-west corner of Wilsons Promontory. The colonising seeds could have come from Western Australia as well as from the South Australian Gulfs. Apparently, this population was the result of a colonisation by seeds that had floated more than halfway through Bass Strait before making landfall as it was only in the 1980s that *Euphorbia paralias* made its appearance on the intervening coast of Victoria, on King Island and along the Tasmanian west coast, on islands in eastern Bass Strait, and on the adjacent coast of Tasmania.

In 1984, *Euphorbia paralias* was collected at three locations along the west coast of Tasmania, at one of which only one plant was seen. In 2001 a detailed survey found this species to be widespread and at many sites with populations of hundreds, if not thousands, of plants (Hilton pers. comm.). Once seeds transported by the Zeehan Current had established local populations, that rapid local dispersal was almost guaranteed as indicated by the results from drift bottle releases off the west coast (Fig. 10b). There are no *Euphorbia paralias* collections from Tasmania's east coast and in 2001 this species was only found at one of 18 locations searched in the south-east (Hilton pers. comm.). Hilton's survey also found a couple of occurrences on the central east coast, where I had seen no *Euphorbia paralias* in 1993. It is possible that the seeds were carried up the east coast during the strong winter flows of the Zeehan Current.

Euphorbia paralias turned up along the NSW South Coast in the late 1980s and at Cape Conran in East Gippsland in 1993. Soon thereafter it was seen at several other sites in the eastern part of East Gippsland, which formed foci for further local spread. In New South Wales it now occurs as far north as Jervis Bay (Heyligers 2002a, b). In 2000 a large population was found in Nadgee Nature Reserve, close to the Victorian border; its size was such that this area could have been colonised earlier than the beach south of Narooma. As, again, there was an initial bypassing of East Gippsland, the source of the seeds would have been somewhere west of Wilsons Promontory. Likewise, one may assume that the seeds for the recent colonisation at Lord Howe Island also came from this source. Strandings of drifters released in Bass Strait certainly support this assumption (Fig. 13).

Dispersal of Arctotheca populifolia

Between 1930 and 1936 *Arctotheca populifolia* was collected seven times in the far south-western corner of Western Australia, which indicates that it must have arrived several years, if not a decade or so, earlier (Fig. 15). Hence, it is difficult to be sure about where and how long ago it was introduced. Carried by the Leeuwin Current, achenes spread eastward, reaching Esperance by 1950 and the western shore of the Great Australian Bight by 1962.

During the 1970s *Arctotheca populifolia* established on the tip of the Eyre Peninsula; by the mid-1980s it had colonised beaches and sand-drifts at the Head of the Bight and in the South-East of South Australia, while in 2001 it was found near Nelson along Discovery Bay (N. Walsh pers. comm.). In the 1970s the nearest source of *Arctotheca populifolia* fruits was the southern coast of Western Australia and one may assume that the fruits that stranded on the Eyre Peninsula and in south-eastern South Australia had drifted across from Western Australia. The charts of Russell (1894–1902) and Lenehan (1904) show these coastal sections prone to receiving ocean flotsam from the Antarctic Circumpolar Current (Fig. 7). Several bottles stranded in the Head of the Bight and, given that the occurrences of *Arctotheca populifolia* there are still isolated, it is possible the colonisation of that area has also been through achenes originating in Western Australia.

At present the western form of *Arctotheca populifolia* is poised at the north-western entrance to Bass Strait for further expansion and the question is: where will it appear first? If the evidence of the spread of *Cakile maritima* and *Euphorbia paralias* is an indication, *Arctotheca populifolia* could appear along the coast of Victoria as far west as Wilsons Promontory, before spreading to King Island and, later, to islands at the eastern side of Bass Strait and to the west and north coasts of Tasmania.

Almost contemporaneous with the early collections in Western Australia, three *Arctotheca populifolia* collections were made on the east coast near Newcastle, the first one near Mungo Brush in Myall Lakes National Park. These early locations bear the hallmark of an original introduction through shipping from South Africa. The spread of the eastern form has been slow. In 1953 it was collected near Port Macquarie and field work has shown that it still does not occur beyond South West Rocks, about 60 km to the north (Clarke 1989 a, b; pers. obs.). Along the NSW South Coast *Arctotheca populifolia* was first collected at Jervis Bay in 1955 and has become fairly widespread, albeit in low numbers, as far as Mallacoota (Clarke 1989a, b; Heyligers 1989b, 1991). In 1990 it was also found on the east coast of Flinders Island, but has not yet been reported from Tasmania. It took *Cakile maritima* less than 30 years to achieve a distribution along the east coast of the mainland that virtually matches that of *Arctotheca populifolia*. Why was the spread of *Arctotheca populifolia* along the east coast apparently slow and erratic? As the fruits of these two species have fairly similar buoyancy characteristics, it is probably due to its prolific propagule production, that *Cakile maritima* has spread more rapidly than *Arctotheca populifolia*. Also, when flowerheads of *Arctotheca populifolia* mature, they bend down to the surface within the confines and along the perimeter of the procumbent parent plant, where they are prone to be covered by wind-blown sand, thus kept out of circulation until exposed by erosion.

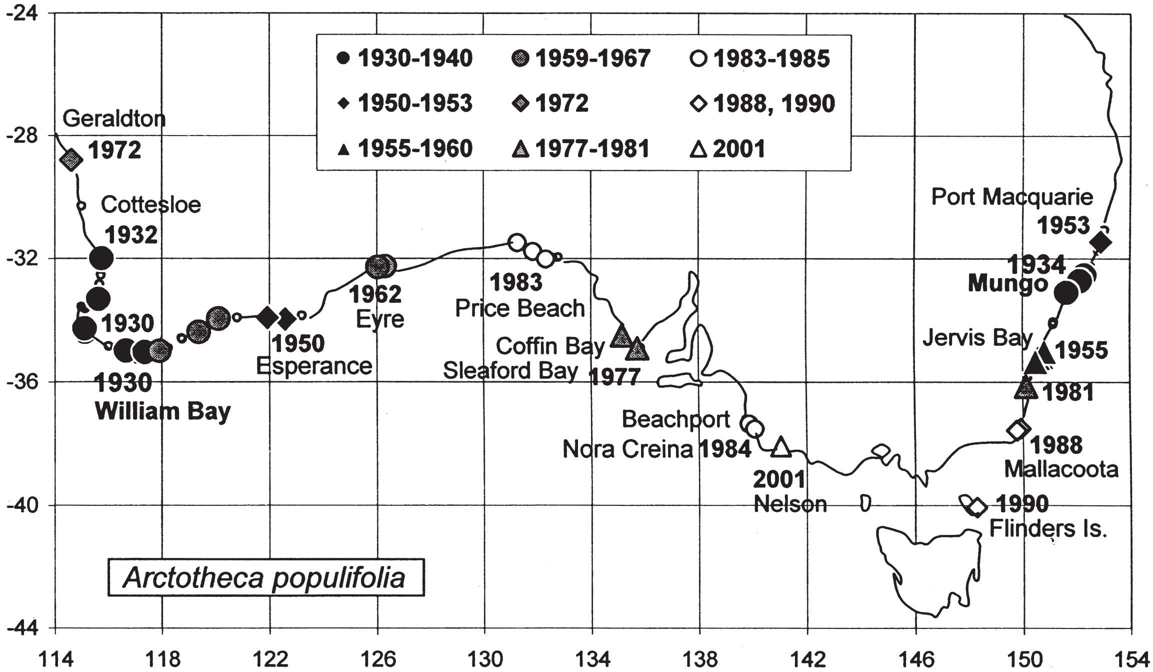

Fig. 15. Evidence for *Arctotheca populifolia* dispersal, based on collection dates of 73 herbarium specimens of the western form and 40 of the eastern form. The western form has spread from south-western West Australia along the west coast to Geraldton and along the southern coast to Nelson in western Victoria. The eastern form has spread predominantly southwards from the Newcastle area and has reached Flinders Island.

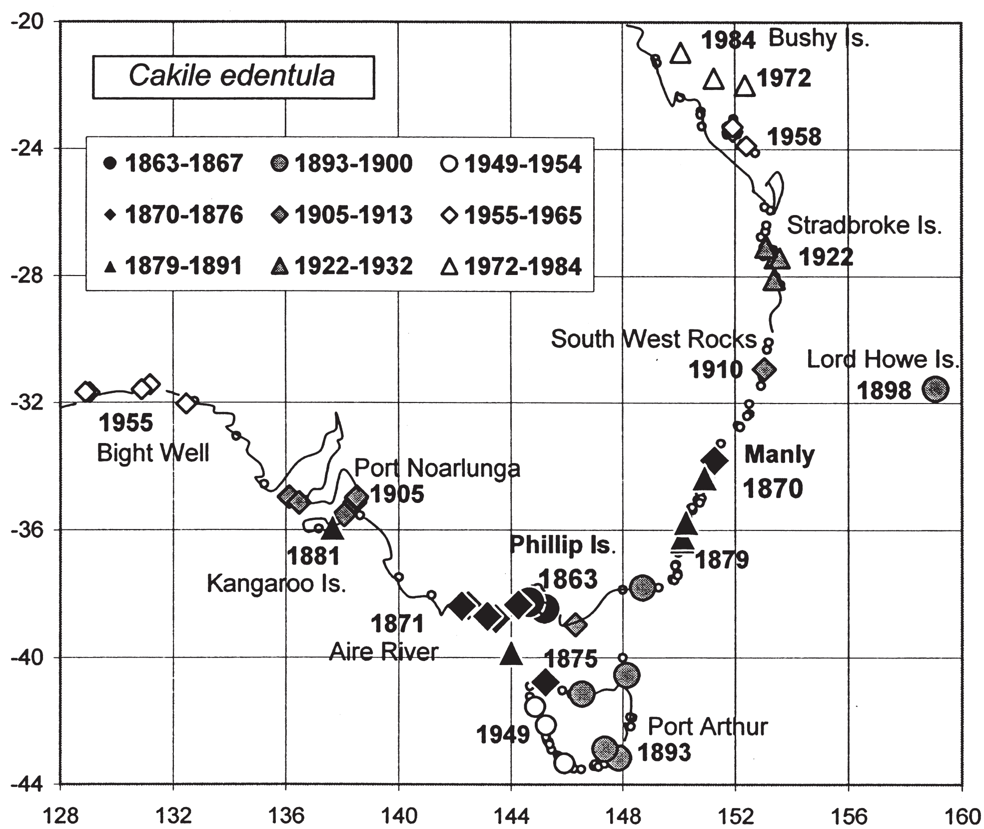

Fig. 16. Evidence for *Cakile edentula* dispersal, based on collection dates of 276 herbarium specimens. The progression of dates indicates a spread from the northern shores of Bass Strait to the Head of the Bight, southern Tasmania, Lord Howe Island, and Bushy Island of the Great Barrier Reef.

Dispersal of Cakile edentula

Cakile edentula probably arrived in Australia in ballast or gear of American sealing vessels from the New England region in the early decades of the nineteenth century (Rodman 1974). There are no collections from this period, but the situation changed during the latter half of the century. *Cakile edentula* became widespread along the shores of Bass Strait, Kangaroo Island and the southern coast of New South Wales (Fig. 16). The 1870 collection date from Manly, near Sydney, and the 1893 date from Port Arthur suggest that the occurrences there originated from secondary introductions. Be that as it may, the widespread occurrences in Bass Strait would have provided an important source for dispersal, as demonstrated by the strandings of cards and bottles (Fig. 13). In the twentieth century *Cakile edentula* spread westward as far as Eucla, southward along the west coast of Tasmania and northward along the east coast to central Queensland and several islands of the southern section of the Great Barrier Reef.

In 1922 *Cakile edentula* was collected on Stradbroke Island, south-east of Brisbane in Moreton Bay. The label of a collection made a few years later mentions that it was 'abundant on sand dunes near the sea.' In 1930 it was also collected on Bribie Island, north-east of Brisbane. The appearance of this species in the Moreton Bay region could have been due to shipping, but arrival through long-distance drifting is also a possibility.

During the 1930s *Cakile edentula* became widespread along the coast and adjacent islands of south-eastern Queensland. Early collection dates indicate a steady northward progression. The arrival of *Cakile edentula* in the southern section of the Great Barrier Reef is documented by a 1958 collection from Heron Island and soon afterwards it was also found on several other islands of the Capricorn and Bunker Groups. The northerly spread continued and in 1972 *Cakile edentula* had reached Gannet Cay, a small island of the Swain Reefs, while in 1984 and 1989 it was collected on Bushy Island and in 1986 on Scawfell Island (Batianoff 1995), both about 300 km north-west of the Capricorn Group and about 50 km distant from each other. The spread along the mainland coast went on apace; in 1993 *Cakile edentula* was collected twice near Mackay, at about the same latitude as Scawfell Island.

The gradual spread of *Cakile edentula* in a north-westerly direction is in agreement with results obtained with surface drifters released in the vicinity of the Capricorn Group, which showed that on occasions drifters stranded near or past Mackay. Later, hydrographic research confirmed that, after accounting for tidal effects and other periodic events, the remaining flow is to the north-west due to the predominance of south-easterly winds and inflow from an eddy over a bench in the continental slope (Marion Plateau) (Griffin *et al*. 1987). Is it likely that the spread of *Cakile edentula* will continue in that direction? The current regime in the central section of the Reef differs from that of the southern section. It is influenced to a greater degree by the East Australian Current due to fewer reefs in the Outer Reef and consequently, has a larger southerly component (Wolanski 1994). This could prevent, or at least delay, further expansion of *Cakile edentula*.

Repeated investigations of the flora of several Barrier Reef islands have shown that occurrences are often ephemeral (Chaloupka & Domm 1985; Flood & Heatwole 1986). By the same token, *Cakile edentula* occurrences on the mainland are often scattered and temporary and the species has virtually disappeared from the Bass Strait region, southern New South Wales and all but the far west of South Australia (Rodman 1986). In South Australia and western Victoria this happened before the arrival of *Cakile maritima* (Heyligers 1996). Although competition between these species has been advanced as a cause of the disappearance where the two species occur together (Rodman *l.c.*), lesser fecundity, an annual lifecycle and short buoyancy and viability periods of fruits could make *Cakile edentula* more vulnerable to the effects of beach erosion. Repeated erosion at short intervals could lead to the depletion of local stock and eventual disappearance from large sections of the coast. However, *Cakile edentula* is still widespread, although not necessarily common, in Tasmania and from the North Coast of New South Wales to central Queensland.

Discussion

A closer look at dispersal from Western Australia to south-eastern Australia.

The charts of Russell (1894 – 1902) and Lenehan (1904) show that much ocean flotsam washes up on the shores of south-eastern South Australia and western Victoria. For instance, a bottle released 180 km northwest of Cape Leeuwin was picked up along Encounter Bay 18 months later; its average daily progress must have been about 5 km, a moderate figure if one considers that some bottles averaged drift speeds of 14 km day^{-1}, comparable with the 17.5 km day^{-1} attained by drifter buoys (Hahn 1986). In view of their buoyancy and longevity, for *Arctotheca populifolia* achenes to survive six if not 18 months at sea appears to be quite feasible and hence, the proposition that the plants near Beachport and the large population on the Ten Mile Sandhills, to the north, (pers. obs.) originated from achenes brought in by the Leeuwin Current straight across from Western Australia to be perfectly sound. Similarly, seeds of *Euphorbia paralias* may remain afloat and viable for many years. Hence, it is certainly possible that seeds drifting across from Western Australia colonised the beaches of south-eastern South Australia, rather than propagules from the Spencer Gulf. And in view of Russell and Lenehan's results it would even appear feasible that the population at Norman Bay at Wilsons Promontory was founded by seeds of Western Australian origin that drifted into Bass Strait.

During my research in south-eastern South Australia I have found other indications for long-distance drifting from Western Australia. Some *Spinifex* (Poaceae) populations on the dunes along that coast have the appearance of hybrids between *Spinifex hirsutus* Labill., the species occurring in Western Australia and along the Great Australian Bight, and *S. sericeus* R. Br., found on the dunes of eastern Australia (Heyligers 1988). Although these species are primarily wind-dispersed, I found that mature spikelets of *Spinifex sericeus* are buoyant and stay afloat for up to three months. Typical plants of *Spinifex hirsutus* are rare in the South East; the most easterly occurrence I have seen is near the South Australian-Victorian border. Although the contact between populations of both species is likely to predate European colonisation, the scarcity of *Spinifex hirsutus* would indicate that there have only been occasional arrivals from more westerly shores.

The occurrence of the introduced succulent herb *Tetragonia decumbens* (Aizoaceae), found in 1989 at Cape Jaffa in south-eastern South Australia, could also conceivably be explained by drifting across from Western Australia (Heyligers 2002c). Indigenous to southern Africa, this species was first collected near Fremantle in 1932. It has become common in the dunes of coastal south-western Western Australia and has localised occurrences in the Adelaide region and at the NSW Central Coast, both of which are likely due to shipping. During tests some of its fruits remained buoyant for more than two years and still contained viable seed. I think it unlikely that *Tetragonia decumbens* 'escaped' from Gulf St Vincent in view of the 'locking up' phenomenon. Its occurrence at Cape Jaffa could be linked to the presence of the nearby fishing settlement of Kings Camp, but to me, the results of drift bottle and buoy releases present a compelling case for *Tetragonia decumbens* fruits drifting in on currents crossing the ocean south of the Great Australian Bight.

The influence of the Sugarloaf Point-Smoky Cape region off the northern New South Wales coast

When I was analysing the patterns of spread along the east coast, the question arose "why had *Arctotheca populifolia* and *Cakile maritima* (before being found on Bribie Island) not spread further than Smoky Cape?" Along the coast between Sugarloaf Point and Smoky Cape progress of propagules in a northerly direction appeared be impeded because the East Australian Current, as it veers away from the coast, often entrains the inshore northerly flow (Roughan & Middleton 2002). This implies that propagules would be taken further out to sea and, consequently, drifting times would become longer and chances of survival less. It may be due to the greater availability of fruits and the somewhat better chance of staying afloat longer that *Cakile maritima* fruits, rather than *Arctotheca populifolia* achenes, eventually reached southern Queensland.

The change of direction of the East Australian Current near Smoky Cape forming a barrier to northerly spread is also evident from other dispersal histories. There are few records of *Hydrocotyle bonariensis* Lam. (Apiaceae) north from this region and none of *Gladiolus gueinzii* Kunze (Iridaceae), both introduced dune plants (Heyligers 1998). The small, abundantly-produced fruits of *Hydrocotyle bonariensis* remain afloat and viable for 12 years (pers. obs.). First collected at Botany Bay in 1893 the species had become common along the NSW Central Coast by 1917 and had reached the Smoky Cape area by 1964. The first positively identified *Hydrocotyle bonariensis* collection from Queensland came from Cooloola in 1971, with two collections from Moreton Island in 1980. Some corms of *Gladiolus gueinzii* stay afloat and remain viable for seven months (Heyligers 2000). The first collection of this species was made at Stockton, north of Newcastle, in 1950. It was collected near Smoky Cape in 1964 and was still there in 1985. The history of dispersal for these two species along the east coast is similar to that of *Cakile maritima*, *Cakile edentula* and *Arctotheca populifolia*, which strongly suggests that the marked changes in the flow of the East Australian Current have a bearing on dispersal.

Although the map in Smith (1991) shows that the greatest variety of tropical disseminules is found north of Smoky Cape, the presence of fruits and seeds among stranded flotsam as far south as Mallacoota demonstrates that the blocking influence of the East Australian Current is not absolute. A few of the 1200 plastic drifters released during September–October 1966 in the southern region of the Great Barrier Reef stranded along the NSW east coast, as far south as Jervis Bay (Woodhead 1970). In contrast, drift bottles and cards released in Bass Strait have been recovered as far north as Cape Tribulation (Fig. 13) showing the potential reach of propagules moving northward. That none of the species in this paper has made a comparable big leap northward shows that propagules are even more vulnerable to the vagaries of the sea than bottles or cards.

Conclusion

Dispersal is an ongoing process. One may expect the western form of *Arctotheca populifolia* to turn up on Wilsons Promontory and, given time, along the NSW east coast where it will meet the eastern form of the species. Intermingling of populations could have interesting consequences. One may also expect *Euphorbia paralias* to continue its northerly spread along the NSW coast and, like *Cakile maritima*, into Queensland. Will these species follow *Cakile edentula* into the Great Barrier Reef region? Time will tell.

Given that *Euphorbia paralias* has already spread to Lord Howe Island, will it appear in New Zealand? The fact that several drift bottles and cards released in Bass Strait were recovered along New Zealand shores and a few plants of *Atriplex cinerea* Poiret (Chenopodiaceae), an Australian coastal species, have been found along Cook Strait (Heyligers 2001) makes this more than a hypothetical question.

These days introduced species are eyed with suspicion and some dealt with in this paper are no exception. The *Cakile* species have been too long in Australia to attract much attention and are sometimes even thought to be native! In contrast, *Euphorbia paralias*, a more recent arrival, has been subject to local eradication campaigns (Heyligers 2002a). Given the dispersal capacity of this species, it should be clear that such efforts will meet limited success as recolonisation will be ongoing. It may be of help to know, that although I do not deny that these introduced species do change the composition of the herbaceous foredune flora, all four are shade-intolerant and succession by woody species will automatically suppress and, if sufficiently dense, eliminate them.

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Appendix 1 Commentaries on the results of drift bottle and drift card releases (Figs. 9–13)

Commentary on Figure 9

Strandings from bottles released near Bathurst Light revealed the existence of a northerly longshore current, while prevailing wind directions caused the seasonality apparent in the stranding locations. Bottles released off Cape Naturaliste between August and November drifted past Cape Leeuwin and like those released off Cape Leeuwin followed an easterly course under the influence of the Leeuwin Current. Further east, this current separates from the coast and consequently, from the 15 batches released between April and September near Eclipse Island, only single bottles from six batches were recovered, near Bremer Bay and at Eucla. Bottles from batches released at other times usually floated in a northerly or north-easterly direction under the influence of southerly winds.

Commentary on Figure 10

Drift bottles released from May to early October floated mainly into Bass Strait, but those released later in October and during the following months drifted north, some as far as the southern beaches of Eyre, Yorke and Fleurieu Peninsulas and Kangaroo Island, thus demonstrating the influence of the seasonal Flinders Current.

Commentary on Figure 11

The results of simultaneous releases demonstrate the variability of currents in the Strait. Stranding locations of both types of bottles sometimes coincided, but on other occasions differed greatly, apparently mainly due to wind conditions. Coinciding strandings over a limited stretch of coast, for instance from the May and October releases, were preceded by a spell of strong winds from the quarter opposite to the drift direction. Under these conditions deeper floating ballasted bottles were transported in the same direction as empty bottles. When winds are lighter and changeable, the drift paths of ballasted bottles are more erratic due to the greater influence of tidal currents. This is demonstrated by the March release: many empty bottles were found on the Otway coast, while ballasted bottles were recovered in the Port Fairy area as well at Wilsons Promontory.

Commentary on Figure 12

There were three recoveries outside Tasmania, as follows: two cards from batch 29, one was found after 186 days 45 km south-west of Lakes Entrance, Victoria, the other one after 322 days near Sydney; and one from batch 40, found on the North Island of New Zealand after nearly 22 months.

From the strandings being largely confined to Tasmania's north coast it is apparent that there is little interaction between this southern part and the rest of Bass Strait. This suggests that the influence of tidal movements may be even stronger here than elsewhere in Bass Strait.

Commentary on Figure 13

The strandings demonstrate that the whole of Australia's east coast comes within the reach of drifting objects once they have left Bass Strait. However, at present there is no evidence that any of the propagules of the species discussed in this paper have made the journey to the Great Barrier Reef without 'stop-overs' and one may safely assume that the chances of surviving such a long journey are virtually nil.