SM1
Zostera communities
Zosterion Christiansen 1934

In Britain, three species of eel-grass, *Zostera marina*, *Z. angustifolia* and *Z. noltii*, form distinctive stands in the sub-littoral and eu-littoral zones of sand and mud flats. Very few samples of this vegetation were taken and the following account relies heavily on published and unpublished material relating in particular to The Solent (C. R. & J. M. Tubbs), the Thames estuary and Essex (Wyer & Waters 1975; Charman 1975, 1977*b*, 1979), north Norfolk (Ranwell & Downing 1959, Charman & Macey 1978), Lindisfarne (D. O'Connor), the Moray Firth (Rae 1979), and the west coast of Scotland (A. Currie). There are two difficulties in making use of existing information. First, *Z. angustifolia* is not consistently distinguished from narrow-leaved forms of *Z. marina*: this partly reflects the long-standing discussion on the taxonomic status of plants variously described as *Z. marina* var. *angustifolia*, *Z. hornemanniana* or *Z. angustifolia*. Second, eu-littoral stands have often been described simply as '*Zostera*' irrespective of whether they comprise *Z. angustifolia*, *Z. noltii* or both these species. This has been particularly true of accounts of the grazing of *Zostera* spp. by wildfowl and a separate note on this important aspect of the conservation value of the vegetation has therefore been appended.

Zostera marina stands
Zosteretum marinae Harmsen 1936

Zostera marina forms stands with a cover of trailing leaves up to 1 m long. Algae, especially *Enteromorpha* spp., are usually the sole associates. *Z. marina* is essentially a sub-littoral species, extending from 1–4 m below to just above low water of spring tides, although it also occurs in lagoons. The lower salinity limit for the species is about 35 g l^{-1} (chloridity 24 g l^{-1}) but the exact limits of its distribution may be controlled by light requirement below and susceptibility to dessication above. Around The Solent, plants are exposed for only 1½ hours even at low water of spring tides.

Z. marina shows considerable morphological variation with a decrease in leaf size and density upshore. Narrow-leaved plants from the lower eu-littoral have been described as *Z. marina* var. *angustifolia* or confused with *Z. angustifolia*. There also appears to be some variation in phenology in relation to the position of the plants on the shore. *Z. marina* shows considerable leaf loss in autumn and early winter but this may be much more apparent in eu-littoral plants than in those which are permanently submerged where a dense cover is maintained throughout the winter. Regrowth occurs in all plants in spring and early summer. Flowering seems to be most frequent in eu-littoral plants and in those sheltered from wave action with larger sub-littoral plants reproducing vegetatively.

In Britain, *Z. marina* always grows on a firm substrate, usually sand or sandy mud, though sometimes with an admixture of fine gravel.

Where their ranges overlap, as in The Solent, *Z. marina* passes upshore to *Z. noltii*; elsewhere *Z. marina* stands may be separated by a considerable expanse of bare substrate from salt-marsh vegetation proper. In The Solent, *Z. marina* may have a potential competitor in the sub-littoral brown alga *Sargassum muticum*, a native of Japan which has colonised some sites once occupied by *Z. marina*.

Z. marina was much reduced in the early 1930s by a wasting disease which seems to have been a combination of attack by a protozoan and an ascomycete fungus. Butcher (1934, 1941) catalogued the most substantial decrease on the East Anglian and north Kent coasts and around The Solent. In recent years, the species has certainly reappeared in abundance in The Solent but seems to have remained rare elsewhere in the south-east. Butcher (1934) did not examine changes on the Scottish coast but *Z. marina* is now abundant down the western coast of the mainland and the Outer Hebrides and also in the Moray Firth. The map shows the distribution of the species in Perring & Walters (1962) with modifications.

Zosteretum marinae has been widely reported from throughout Europe though its exact status following the 1930s disease and subsequent erosion of substrates is uncertain. In The Netherlands, Beeftink (1962) records the association as rare; in France it appears to have recovered somewhat (Géhu 1975).

Zostera angustifolia stands

Zostera angustifolia forms stands with a cover of trailing leaves up to about 25 cm long. It may occur pure, though it is often mixed with the smaller *Z. noltii* and with a variety of algae among which species of *Ulva*, *Chaetomorpha* and *Enteromorpha* are often abundant. The table lists some samples of mixed *Zostera* vegetation from the Exe estuary, Devon. On the extensive estuarine flats of the Cromarty Firth, it occurs with *Ruppia maritima* and annual *Salicornia* spp.

Z. angustifolia can behave as a short-lived perennial. Around the Moray Firth, Rae (1979) noted that few plants lasted longer than two years and, throughout its British range, the species seems to suffer heavy leaf loss in autumn and early winter by a combination of natural shedding, storm damage and wildfowl grazing. Regrowth in spring can be largely by seedling germination (Ranwell & Downing 1959, Wyer & Waters 1975, Rae 1979) though good regeneration from existing rhizomes has also been reported.

Z. angustifolia is a plant of the lower and middle eulittoral zone, extending to well above low water of neap tides and sometimes to high water of neap tides. Its optimal salinity is about 25–34 g l^{-1} (chloridity 16–20 g l^{-1}; Proctor 1980) and, as with *Z. marina*, its exact limits seem to be controlled by light requirement below and susceptibility to desiccation above. In The Solent, it is exposed for a maximum of about 6½ hours on the spring tides. It certainly grows best in sites which are never deeply submerged at high tide nor ever fully dry at low tide and is particularly characteristic of shallow depressions on tidal flats, often with some standing water at low tide. In such situations, it may form distinctive mosaics with *Z. noltii* which prefers the drier tops of low marsh ridges (Tutin, 1942, Wyer & Waters 1975, Rae 1979). It also occurs in the wet bottoms of deep marsh creeks (Chapman 1959).

Z. angustifolia is most characteristic of muds and muddy sands. These may be quite firm and contain some fine gravel but the species is typically associated with very sloppy mud on which even duck boards are an unsuccessful aid to sampling.

Z. angustifolia may pass upshore to stands of *Z. noltii* through mosaics of the two species; elsewhere it may give way to salt-marsh vegetation proper with an expanse of bare substrate between or through *Salicornietum europaeae*. In the Exe estuary, *Z. angustifolia* is replaced upshore by *Spartinetum townsendii* (Proctor 1980).

The disease of the 1930s seems to have left *Z. angustifolia* largely untouched and, at present, the species is widespread along the south and east coasts of England and the east coast of Scotland (Perring & Walters 1962). It is all but absent from the west coast of Scotland. There are very extensive stands in the Cromarty Firth (Figure 7) and also along the Essex and north Kent coasts.

In Europe, the equivalent community *Zosteretum marinae stenophyllae* Harmsen 1936 has been recorded from The Netherlands (Beeftink 1962) and France (Géhu 1975).

Zostera noltii stands

Zosteretum noltii Harmsen 1936

Zostera noltii forms stands with a cover of delicate trailing narrow leaves up to about 20 cm long. It may occur pure or with *Z. angustifolia* (see table) and occasional plants of lower salt-marsh species such as annual *Salicornia* spp. or *Spartina anglica*. *Ruppia maritima* occurs with *Z. noltii* on the estuarine flats of the Cromarty Firth (Rae 1979).

Like *Z. angustifolia*, *Z. noltii* experiences considerable leaf loss in autumn and early winter through natural shedding, storm damage and wildfowl grazing but plants towards the lower limit may remain winter-green (Wyer & Waters 1975, Rae 1979). Unlike *Z. angustifolia*, expansion in spring seems to occur more consistently by the regrowth of existing rhizomes (Wyer & Waters 1975, Rae 1979) as well as by the germination of seed, production of which may be prolific, especially at higher levels.

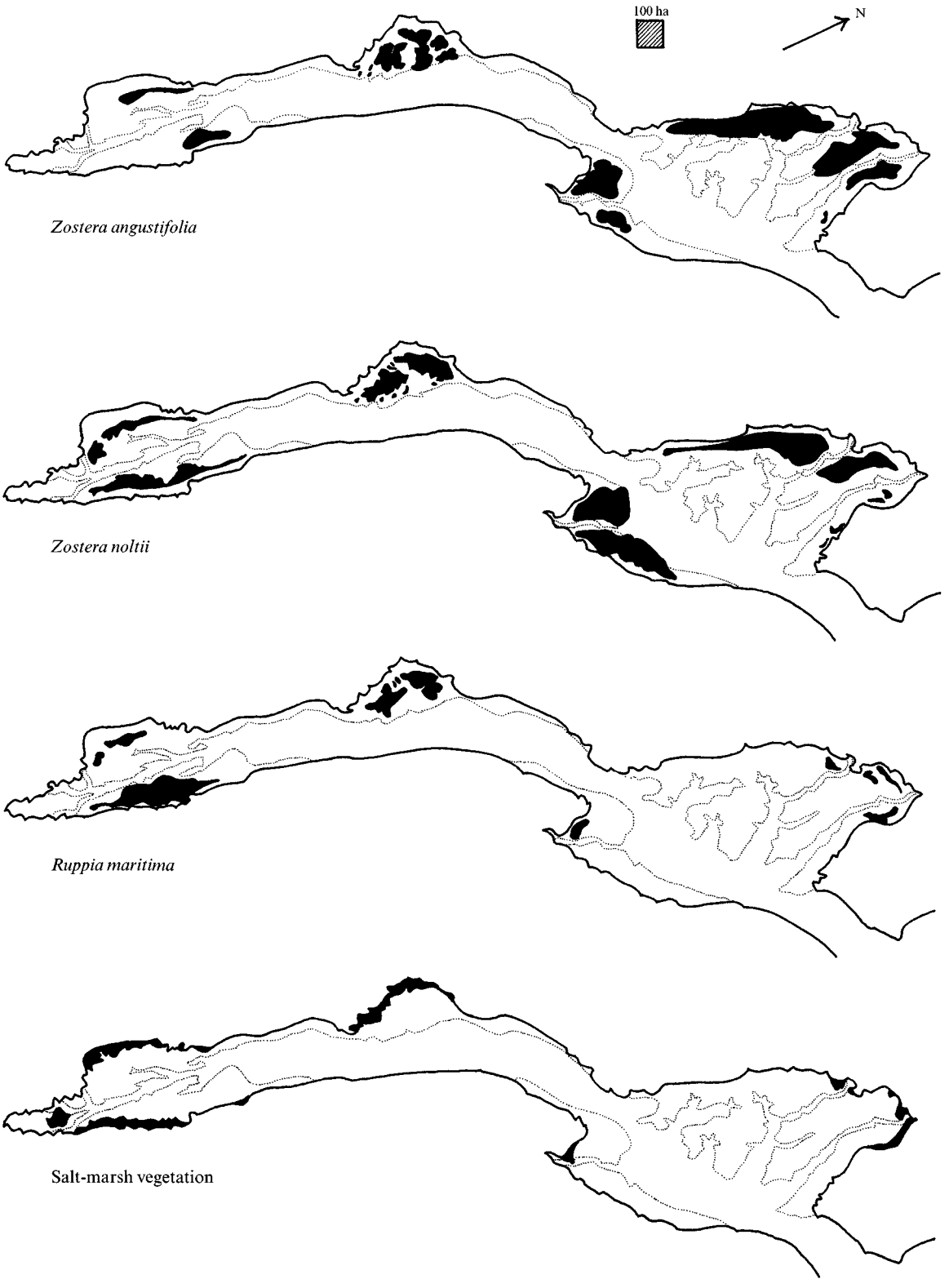
In general, *Z. noltii* is a species of the middle and upper eu-littoral zone and its lower salinity limit is about 15 g l^{-1} (chloridity 9 g l^{-1}; Mathiesen & Nielsen 1956). It occurs on mud/sand mixtures of a variety of consistencies from very soft to quite firm. It is most characteristic of situations where the substrate dries out somewhat on exposure and on flats with a gentle bar/hollow topography it forms distinctive mosaics with *Z. angustifolia*. It can also occur in shallow standing water.

Stands of *Z. noltii* pass downshore to *Z. angustifolia* and above may grade to communities of the lower salt-marsh, notably the *Salicornietum europaeae*. *Spartina anglica* is known to have invaded stands of *Z. noltii* at various sites (Chapman 1959, Goodman *et al.* 1959, Bird & Ranwell 1964, Hubbard & Stebbings 1968).

The British distribution of *Z. noltii* is similar to that of *Z. angustifolia* (Perring & Walters 1962) and there are particularly extensive stands in the Cromarty Firth (Rae 1979: Figure 7) and along the Essex and north Kent coasts (Wyer & Waters 1975).

In Europe the *Zosteretum noltii* is widespread in similar situations to those in Britain (e.g. Beeftink 1962, Géhu 1975).

Figure 7. Distribution of mud-flat and salt-marsh vegetation in the Cromarty Firth, Scotland.



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Zostera and wildfowl grazing

Zostera spp. provide an important source of food for certain wildfowl, notably in Britain for overwintering brent goose (*Branta bernicla*) and wigeon (*Anas penelope*) and, to a lesser extent, of mute swan (*Cygnus olor*) and whooper swan (*Cygnus cygnus*).

The early wildfowling literature and some recent studies (e.g. Charman 1977*a*) consider *Z. marina* to have been the species most frequently eaten by brent in the past but it seems likely that, at the present time at least, *Z. angustifolia* and *Z. noltii* account for the bulk of the *Zostera* consumed. There is some suggestion (e.g. Ranwell & Downing 1959; Charman 1977*a*, 1979) that of these *Z. noltii* is the preferred species for brent. This may reflect its generally longer periods of exposure on flats but *Z. noltii* appears to reach its standing crop maximum later in the year than *Z. angustifolia*, around September/October (Wyer & Waters 1975, Rae 1979) just when brent are beginning to gather in their winter haunts. *Z. angustifolia* may be preferentially grazed by wigeon: its standing crop peak, in July/August, coincides with the gathering of that species.

A number of studies (Ranwell & Downing 1959; Charman 1975, 1977*a*, *b*, 1979; Charman & Macey 1978) have demonstrated a distinctive sequential exploitation of flat and salt-marsh food sources by brent. The accumulating birds begin feeding on *Zostera* in September/October and only when their numbers reach a peak and the *Zostera* is largely consumed do they move on, first to *Enteromorpha*, then to salt-marsh vegetation and sometimes to arable and pasture. This timing coincides to some extent with the maximum availability of nutritious food, though Charman (1979) has suggested that, among the various foods, only *Zostera* can provide an adequate daily energy requirement for brent.

Zostera stands therefore provide what seems to be an indispensible resource for some wintering wildfowl and vast numbers of birds exploit the larger beds. The 820 ha of *Zostera* along the coasts of south Suffolk, Essex and north Kent (Wyer & Waters 1975) receive about 30000 dark-bellied brent (*Branta bernicla bernicla*) (Ogilvie 1978), the expanding stands of The Solent foreshore and harbours about 23000 (figure for 1979/80), north Norfolk about 5000 and The Wash about 6000 (Ogilvie 1978), in total about half of the world population of this race. Smaller numbers of light-bellied brent (*Branta bernicla hrota*), between 200 and 1100, winter at Lindisfarne NNR. What is probably the largest total area of *Z. noltii* and *Z. angustifolia* in Britain, the 1200 ha in the Cromarty Firth, is outside the winter range of the brent goose but the estuary is visited by enormous numbers of wigeon.

Although wildfowl sometimes uproot *Zostera* while feeding they seem mostly to eat the leaves and flowering shoots. Beds appear able to recover even from very heavy grazing and the resource to renew itself adequately from year to year by vegetative expansion and/or seed germination.

Floristic table SM1

Zostera angustifolia	V (2–8)
Zostera noltii	V (4–10)
Fucus spiralis	IV (1–4)
Enteromorpha cf. *E. marginata*	IV (1–7)
Ulva lactuca	III (1–4)
Chaetomorpha linum	II (1–6)
Polysiphonia cf. *P. insidiosa*	I (2)
Ceramium rubrum	I (1–2)
Polyneura gmelinii	I (1)
Fucus vesiculosus	I (1–2)
Cladophora sp.	I (4)
Chondria dasyphylla	I (1)
Polysiphonia cf. *P. nigrescens*	I (1)
Enteromorpha intestinalis	I (1–2)
Ectocarpus sp.	I (1)
Chaetomorpha cf. *C. tortuosa*	I (2)
Porphyra umbilicalis	I (2)
Spartina anglica	I (4)
Number of samples	15

Shells of the cockle (*Cerastoderma edule*) and common periwinkle (*Littorina littorea*) and casts of the lugworm (*Arenicola marina*) occasional to very abundant in the samples; spire shell (*Hydrobia ulvae*), mussel (*Mytilus edulis*) and shore crab (*Carcinus maenas*) recorded less frequently.

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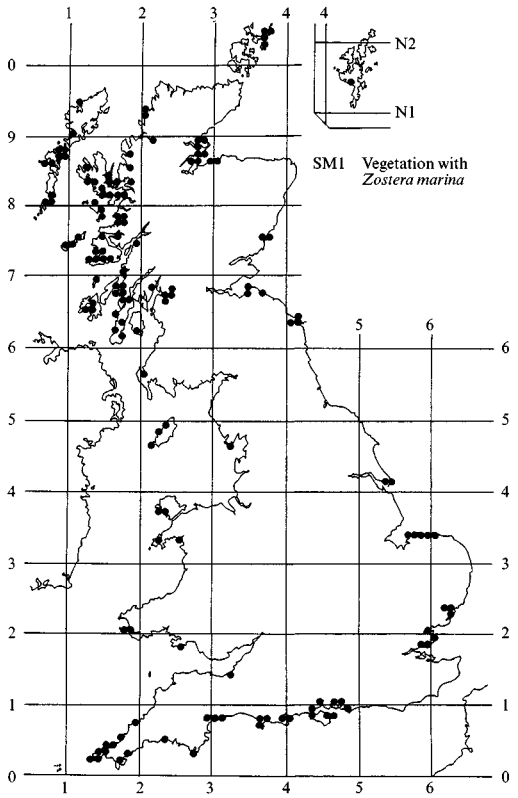

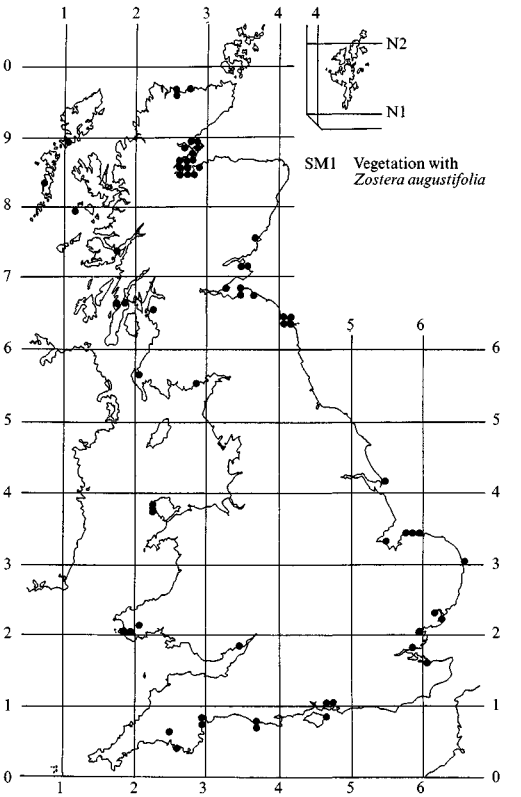

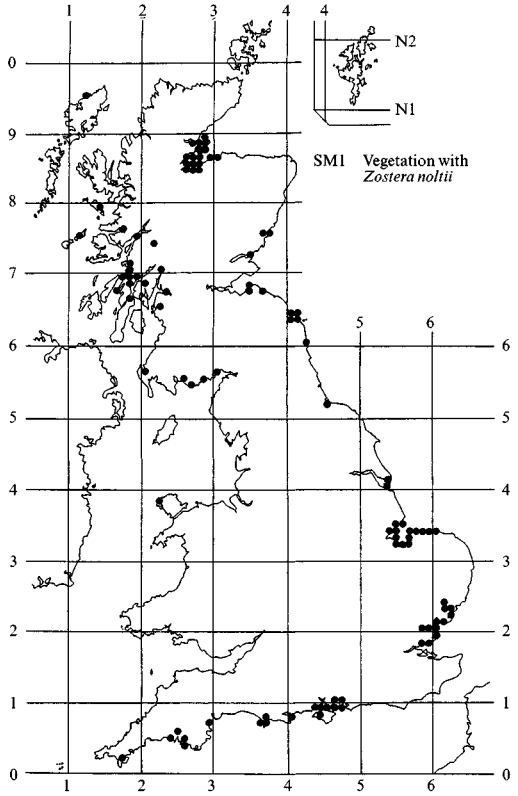

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