



# MarLIN

## Marine Information Network

Information on the species and habitats around the coasts and sea of the British Isles

### *Stuckenia pectinata* community

MarLIN – Marine Life Information Network  
Marine Evidence-based Sensitivity Assessment (MarESA) Review

Dr Harvey Tyler-Walters

2002-11-18

A report from:

The Marine Life Information Network, Marine Biological Association of the United Kingdom.

**Please note.** This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/habitats/detail/320>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Tyler-Walters, H., 2002. [*Stuckenia pectinata*] community. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom.  
DOI <https://dx.doi.org/10.17031/marlinhab.320.1>



The information (TEXT ONLY) provided by the Marine Life Information Network (MarLIN) is licensed under a Creative Commons Attribution-Non-Commercial-Share Alike 2.0 UK: England & Wales License. Note that images and other media featured on this page are each governed by their own terms and conditions and they may or may not be available for reuse. Permissions beyond the scope of this license are available [here](#). Based on a work at [www.marlin.ac.uk](http://www.marlin.ac.uk)

(page left blank)



A bed of fennel pondweed *Potamogeton pectinatus*.  
 Photographer: Martin Isaeus  
 Copyright: Martin Isaeus



Researched by Dr Harvey Tyler-Walters

Refereed by This information is not refereed.

## Summary

### ☰ UK and Ireland classification

EUNIS 2008 A5.542 Association with *Potamogeton pectinatus*

JNCC 2015 SS.SMp.Ang.A12 *Stuckenia pectinata* community

JNCC 2004 SS.SMp.Ang.A12 *Potamogeton pectinatus* community

1997 Biotope SS.IMU.Ang.A12 *Potamogeton pectinatus* community

### 🔍 Description

Consistently low salinity infralittoral mud with beds of *Potamogeton pectinatus*. *Potamogeton pectinatus* appears to replace *Ruppia* beds where the salinity is consistently low as opposed to variable. Other associated species are broadly similar to those characteristic of IMS.Rup, with blankets of filamentous green algae such as *Ulva intestinalis*, *Cladophora liniformis* and *Rhizoclonium tortuosum*. The grazing gastropods *Hydrobia ulvae* and *Potamopyrgus jenkinsi* are found in this biotope and juvenile *Mytilus edulis* have been observed settled on *Potamogeton* leaves and

amongst the algae. The nationally scarce charophyte *Lamprothamnium papulosum* may be found to some extent in this biotope but more often in neighbouring habitats. Mysids and sticklebacks *Gasterosteus aculeatus* can be found swimming amongst the vegetation. *Mya arenaria* may be found in some examples of this biotope but the infaunal component of this biotope requires further investigation. This biotope is further described as NVC type A12 (Rodwell 1995). (Information taken from the Marine Biotope Classification for Britain and Ireland, Version 97.06: Connor et al., 1997a, b).

### ↓ Depth range

-

### Additional information

This following review is based on more detailed reviews of *Potamogeton pectinatus* and its communities by Kantrud (1990), Verhoeven & van Vierssen (1978), Verhoeven (1980a) and van Vierssen & Verhoeven (1983), to which the reader should refer for further detail, together with reviews of general submergent macrophyte ecology by Haslam (1978) and Preston (1995).

### ✓ Listed By

- none -

### Further information sources

Search on:



## Habitat review

### 🔄 Ecology

#### Ecological and functional relationships

The rhizomes and roots of submerged macrophytes such as *Potamogeton pectinatus* help to stabilize and oxygenate the sediment surface, while the stems and leaves provide food and additional substratum for a variety of algae and invertebrates. Although the functional groups within the ecosystem probably remain fairly constant the abundance and diversity of species within each group varies with the habitat, especially the salinity regime (e.g. Verhoeven & van Vierssen, 1978; Verhoeven, 1980a; van Vierssen & Verhoeven, 1983).

- *Potamogeton pectinatus* provides primary production and substratum within the biotope. Few organisms, except waterfowl, feed on *Potamogeton pectinatus* spp. directly, however, decomposition of leaves and stems, especially in autumn and winter, support a detrital food chain within the biotope and probably also provide primary productivity to deeper water and the strandline (Verhoeven & van Vierssen, 1978; Verhoeven, 1980a; Byren & Davies, 1986; Kantrud, 1990).
- Additional, primary productivity is provided by microbial (e.g. diatoms) and macroalgal epiphytes growing on the leaves of *Potamogeton pectinatus*, and a floating mat of filamentous algae (e.g. *Ulva prolifera* and *Cladophora* spp.) in more saline situations, and, when present, stoneworts (e.g. *Chara aspera* and *Lamprothamnium papulosum*).
- *Potamogeton pectinatus* competes for light and space with other submerged macrophytes e.g. the stoneworts *Chara aspera* and *Lamprothamnium papulosum*, epiphytic microalgae and macroalgae (as above) or phytoplankton. With increasing or variable salinity *Potamogeton pectinatus* forms mixed stands with *Ruppia* species and may be replaced in the biotope IMS.Rup. In decreased salinity waters it competes with *Myriophyllum spicatum*, *Ranunculus baudotii* or *Zannichellia pedunculata* (van Vierssen & Verhoeven, 1983; Kantrud, 1990) forming mixed stands (NVC community A11; see Rodwell, 1995).
- *Potamogeton pectinatus* leaves may be used as substratum by algal epiphytes as above and faunal epiphytes such as bryozoans and hydroids (e.g. *Einhornia crustulenta*, *Conopeum seurati*, and *Cordylophora caspia*).
- The leaves of *Potamogeton pectinatus* and the algal mats may provide temporary substratum for juvenile anemones and bivalves (e.g. *Anemonia sulcata*, *Mytilus edulis*, *Cerastoderma glaucum*) and the larvae and pupae of aquatic insects (e.g. the shore fly, *Ephydra riparia*) (Verhoeven & van Vierssen, 1978; Verhoeven 1980a). Aquatic insects probably utilize any available aquatic macrophytes as substratum.
- The epiphytes and algal mats may be grazed by gastropods (e.g. *Hydrobia* spp. or *Potamopyrgus* spp.), amphipods (e.g. *Gammarus salinus* and other *Gammarus* species) and isopods (e.g. *Jaera* spp. and *Idotea* spp.) and probably mysids (Mauchline, 1980)
- Verhoeven & van Vierssen (1978) and Verhoeven (1980b) suggested that isopods and amphipods may feed directly on *Potamogeton pectinatus*. However, their most important role in the food chain was the breaking down of decomposing leaves into fine particles of detritus suitable for suspension and deposit feeders and microbes in the detrital food chain (Byren & Davies, 1986).
- The young leaves of *Potamogeton perfoliatus* were show to be the preferred food of freshwater caddis-fly larvae (Trichoptera) (Jacobsen & Sand-Jensen, 1994). Littoral Trichoptera species such as *Limnephilus lunatus* probably feed on *Potamogeton pectinatus* directly (Chen, 1976; van Vierssen & Verhoeven, 1983). Larvae of the beetle *Haemonia*

*appendiculata* were reported to feed on *Potamogeton pectinatus* (Kantrud, 1990).

- Suspension feeders filter both phytoplankton and detritus (organic particulates), for example amphipods e.g. *Corophium volutator*, the mysid e.g. *Neomysis integer*, bivalves e.g. *Cerastoderma glaucum* and *Mytilus* spat, hydroids, bryozoans, and polychaetes (*Hediste diversicolor*).
- Surface and infaunal deposit feeders include polychaetes (e.g. *Manayunkia aestuarina* and *Pygospio elegans*), oligochaetes (e.g. *Limnodrilus hoffmeisteri* and *Tubifex costatus*), amphipods (e.g. *Corophium volutator*), and chironomid larvae.
- Small invertebrates are preyed on by small mobile predators that use the *Potamogeton pectinatus* beds for shelter. For example, insect larvae (especially dragonfly larvae e.g. *Ischnura elegans*), water boatmen (e.g. species of *Sigara*), mysids, shrimp and sticklebacks (e.g. *Gasterosteus aculeatus* and *Spinachia spinachia*) (Verhoeven, 1980a; van Vierssen & Verhoeven, 1983).
- Generalist predators use, but are not closely associated with, the *Potamogeton pectinatus* beds, e.g. the eel *Anguilla anguilla*, and the goby *Pomatoschistus microps*.
- Several species of wildfowl feed directly on *Potamogeton pectinatus*, although the exact species will vary with location, season and salinity, e.g. the coot *Fulica atra*, the wigeon *Anas penelope*, the mute swan *Cygnus olor*, whooper swan and gadwall. Other species are omnivorous feeding on the vegetation and invertebrates, e.g. garganey, mallard, pintail, pochard, scaup, shoveler, teal, and tufted duck (Jupp & Spence, 1977; Kantrud, 1990; Preston, 1995).
- Mysids, shrimp and crabs probably act as scavengers within this biotope.

Detailed lists of species and their position within the habitat for several locations in Scandinavia and western Europe (Finland, the Netherlands, France and Portugal) are given by Verhoeven and his co-author (Verhoeven & van Vierssen, 1978; Verhoeven, 1980a; van Vierssen & Verhoeven, 1983), Jacobsen & Sand-Jensen (1994) and Cunha & Moreira (1995).

### Seasonal and longer term change

Most *Potamogeton* species, including *Potamogeton pectinatus*, are rhizomatous perennials, the majority of the plant dying back to tubers and either rhizomes with short leafy shoots or just rhizomes (Preston, 1995). *Potamogeton pectinatus* populations may act as perennials in some environments or annuals in others. For example, in a sheltered brackish pool in Yerseke, the Netherlands, *Potamogeton pectinatus* was perennial, dying back to rhizomes with leafy shoots and tubers, as well as producing a persistent seed bank. But, in a wave exposed lake, the population was annual, dying back to tubers only in winter (van Wijk, 1988, 1989a, Preston, 1995). Other populations may fall between the above two extremes (Preston, 1995).

In temperate areas, *Potamogeton pectinatus* is one of the first species to grow in spring. overwintering propagules begin to shoot in late March to June when water temperatures reach about 10 °C (Kantrud, 1990). Healthy stands can cover the water surface two weeks later. The plant dies back in late August to October, and most decomposes or is washed ashore before the winter freeze in north temperate zones (Kantrud, 1990). In meso-haline lagoons in the Netherlands, *Potamogeton pectinatus* flowers in mid May to mid July (Kantrud, 1990).

Growth of filamentous algae and algal mats is greatest in the summer months, potentially smothering and shading *Potamogeton pectinatus* (Kantrud, 1990). Van Vierssen & Verhoeven (1983) noted that the abundance and diversity of the coleopteran (beetle) and heteropteran (truebugs) fauna was positively correlated with the available pondweed cover. Cunha & Moreira (1995) reported seasonal changes in the macrofauna of *Potamogeton* and *Myriophyllum* beds in Portugal.

They reported that polychaetes showed little seasonal changes in abundance while molluscs and leeches showed high densities in spring to summer but low numbers or even absence in autumn to winter. Crustaceans (e.g. gammarids) were most abundant in autumn, while insects were rare but abundant in winter and summer. Oligochaetes were most abundant in winter, although some species of oligochaete were also abundant in spring. Seasonal changes in the macrofauna was related to seasonal changes in temperature, dissolved oxygen, tidal regime and low or high rainfall and hence freshwater runoff and salinity (Cunha & Moreira, 1995). Grazing bird species probably vary seasonally, with resident species feeding all year round and migrant birds grazing on rhizomes and tubers in the winter months.

### Habitat structure and complexity

The leaves and stems of *Potamogeton pectinatus* provide substratum and refuge for several species, while the rhizome and root system stabilize the sediment, and the transport of oxygen from the leaves to the roots oxygenates the sediment in the vicinity of the roots (the rhizosphere) changing the local redox potential, sediment chemistry and oxygen levels. Verhoeven and his co-author recognized the following elements of the submerged macrophyte *Ruppia* spp. communities, which are probably equally representative of *Potamogeton pectinatus* communities:

- the *Potamogeton pectinatus* and other associated aquatic macrophytes or macroalgae;
- mats of filamentous algae, e.g. *Cladophora* spp., and *Ulva* spp., that harbour high densities of invertebrates e.g. aquatic insects, chironomid larvae, amphipods, copepods and juvenile bivalves (Verhoeven & van Vierssen, 1978; Verhoeven 1980a; van Vierssen & Verhoeven, 1983);
- epiphytic species attached to the plants e.g. diatoms, filamentous diatoms, blue green algae, bacteria, fungi, hydroids, and bryozoans;
- temporary epiphytic species, e.g. larval or juvenile anemone, bivalves, and aquatic insects;
- species depositing eggs on *Potamogeton pectinatus* and other macrophytes, e.g. insects, hydrobids, and some fish;
- species living in tubes attached to plants, e.g. the amphipod *Corophium volutator*;
- species creeping over plants and other hard substrata but not the sediment, e.g. amphipods, isopods, gastropods, and insect larvae;
- species creeping over plants and the sediment bottom, e.g. *Hydrobia* spp. and *Potamopyrgus* spp.;
- benthic infauna, e.g. the oligochaete *Tubifex* spp., polychaetes *Hediste diversicolor*, *Arenicola marina* and *Manayunkia aestuarina*, the amphipod *Corophium volutator*, bivalves *Cerastoderma glaucum*, *Macoma baltica* and *Mya arenaria* and chironomids;
- mobile species in the vegetation canopy, e.g. sticklebacks, and
- mobile species occurring within the vegetation and the surrounding area, e.g. shrimps, crabs, mysids, gobies, and eels (Verhoeven & van Vierssen, 1978; Verhoeven 1980a; Howard-Williams & Liptrot, 1980; van Vierssen & Verhoeven, 1983).

Where the *Potamogeton pectinatus* beds accumulate sediment and/or lie adjacent to areas that dry out, the beds may be associated with a succession of terrestrial saltmarsh or marsh plants, e.g. reeds and sedges, forming a hydrosere. The reader is directed to Rodwell (2000) for further information on saltmarsh communities and Rodwell (1995) for further information on aquatic plant communities.

### Productivity

#### Primary productivity

*Potamogeton pectinatus*, other aquatic macrophytes, macroalgae and microalgae provide primary productivity in the community. *Potamogeton pectinatus* alone may be extremely productive, depending on location and conditions. For example, 840 individual plants/m<sup>2</sup> or shoot densities of 1000 shoots per m<sup>2</sup> were reported by Howard-Williams (1978; cited in Howard-Williams & Liptrot, 1980 and Kantrud, 1990). Growth rates and hence productivity is greatest early in the growth season. Values of 668 mg C/m<sup>2</sup>/day were reported in Loch Leven (Jupp & Spence, 1977), and may range between 548 -1400 C/m<sup>2</sup>/day depending on location (Kantrud, 1990). *Potamogeton pectinatus* biomass can be high, e.g. 72 g organic dry weight/m<sup>2</sup> in Loch Leven (Jupp & Spence, 1977), and 60 -210 g/m<sup>2</sup> in Canal de Mira, Portugal (Cunha & Moreira, 1995), while Kantrud (1990) suggested that a maximum standing crop of <200 g/m<sup>2</sup> might indicate limited growth. The below ground biomass varies between 4-78% of the total depending on grazing, substratum type (fine sediment or gravels and sand) and the allocation to vegetative production. The production of vegetative tubers and turions or seed can also be high, e.g. Kantrud (1990) reported that in culture 36,000 tubers, 800 turions, 6,000 seeds were produced from a single plant in single growing season, while over 4000 seeds /m<sup>2</sup> were observed deposited on substrata in the vicinity of *Potamogeton pectinatus* beds.

### Secondary productivity

The macrophyte primary productivity is only directly available to grazing water fowl and a few grazing invertebrates (e.g. trichopterans) (Jacobsen & Sand-Jensen, 1986; Kantrud, 1990). Microalgal and macroalgal primary productivity probably support a large number of grazing species such as molluscs and isopods. Fennel pondweed dies back rapidly shortly after flowering, with stems becoming washed ashore or decomposing on the bottom (Kantrud, 1990). Decomposition is accelerated by shredding and grazing invertebrates (e.g. amphipods) that increase the surface area for microbial decomposition, while other species feed on the microbes (Byren & Davies, 1986; Kantrud, 1990). Decomposed pondweed provides a food source for benthic filter-feeding and deposit feeding organisms (Kantrud, 1990). For example, Bryen & Davies (1986) reported 9 invertebrate taxa in bags of decomposing *Potamogeton pectinatus* in South Africa, with a maximum biomass of 64 mg of invertebrates per g dry weight of the pondweed, dominated by grazing amphipods and predatory dragonfly larvae.

The *Potamogeton pectinatus* beds themselves also support a high biomass of invertebrates, providing secondary production further up the food chain. For example Howard-Williams & Liptrot (1980) reported that the submerged macrophyte beds in the Swartvlei region of South Africa supported 410g/m<sup>2</sup> of the bivalve *Musculus* spp., 4000 individuals/m<sup>2</sup> of an amphipod (ca 0.27 g/m<sup>2</sup>), large numbers of juvenile marine fish, and a resident population of 2000 -3000 coot. Cunha & Moreira (1995) reported average annual invertebrate densities of 40,318 - 225,806 individuals/m<sup>2</sup> (of all species) in Canal de Mira, Portugal.

### Recruitment processes

#### *Potamogeton pectinatus*

*Potamogeton pectinatus* is a rhizomatous perennial, dying back in winter to leafy shoot bearing rhizomes and/or tubers in the winter months but may behave as an annual in some environments (see seasonal change). Fennel pondweed flowers in mid May to mid July, shortly after peak biomass of shoots is reached. Flowers are borne on long stalks (peduncles) to the water surface, where pollination by buoyant pollen occurs. But the peduncle is often not rigid enough to hold flowers at the surface and pollination can occur underwater between adjacent flowers by bubble pollination, although submerged pollination is not as efficient as at the water surface (Preston, 1995). Fruit (drupelets or achenes) begin to form about 3 weeks after flowering (Kantrud, 1990).



Mature fruit sink to the bottom or temporarily float and are deposited on shore and germinate from late March to early summer. Most fruit are recovered close to shore (Kantrud, 1990). Seedling mortality is high in shallow waters (<2m) due to physical damage and smothering by litter and stranded vegetation and in deeper water due to lack of light (Kantrud, 1990).

There is little evidence of the importance of reproduction by seed in *Potamogeton* species, seedlings are rarely observed in nature, and van Wijk (1988, 1989a) concluded that seed was probably only important for dispersal and survival to exposure to long-term desiccation or drastic variations in salinity (in effectively annual populations), and that the maintenance of populations was due to vegetative persistence or reproduction (Kantrud, 1990; Preston, 1995).

*Potamogeton pectinatus* may overwinter as rhizomes and/or tubers in the sediment. For example, in Swedish brackish waters, 100% of the biomass in wave exposed sands was reported to be tubers while in sheltered muds 75% of the biomass was overwintering shoots (Kautsky, 1987 cited in Kantrud, 1990). Tubers are produced by all populations of *Potamogeton pectinatus* and begin to develop as early as May. Germination of tubers begins in March and is stimulated by a cold snap or prior low temperatures (Kantrud, 1990; Preston, 1995).

*Potamogeton* species have considerable powers of dispersal (Preston, 1995). Pondweeds can disperse via specialized asexual propagules such as turions (see glossary of scientific terms), fragments of stems or rhizome or fruits that float (aided by their buoyancy) and can be carried long distances by currents or flood waters. For example, the fruit of *Potamogeton pectinatus* was reported to be able to float for 48-60 hours (Preston, 1995). Plant fragments may be transported on the bodies (e.g. feet) of water fowl, while fruits may be transported in their digestive tracts. A proportion of ingested fruit survive in the gut of birds. Viable fennel pondweed fruit were reported to take an average of 44 hours to pass through mallard ducks, potentially providing long-range dispersal. The abrasion received on passing through the gut may enhance germination (see Kantrud, 1990; Preston, 1995). The potential fecundity can be extremely high. For example, Yeo (1965 cited in Kantrud, 1990) grew 36,000 tubers, 800 turions, and 6,000 fruit from a single tuber and 63,300 fruit and 15,000 tubers from a single seed. Overall, *Potamogeton pectinatus* is considered to be a pioneering species, able to quickly colonize newly flooded areas or areas reclaimed from the sea, and often becomes dominant in areas that become temporarily unsuitable for other species, e.g. due to pollution (Kantrud, 1990).

### Other species

The microalgae and filamentous macroalgae found within the biotope are widespread and ubiquitous, producing numerous spores, and can colonize rapidly. Similarly, bryozoans and hydroids probably produce numerous but short lived pelagic larvae, so that local recruitment from adjacent populations is probably rapid. For example, *Einhornia crustulenta* is probably adapted to rapid growth and reproduction (*r*-selected), capable of colonizing ephemeral habitats, but may also be long lived in ideal conditions (Hayward & Ryland, 1998). In settlement studies, *Einhornia crustulenta* (as *Electra crustulenta*) recruited to plates within 5 -6 months of deployment (Sandrock *et al.*, 1991). Hydroids are often initial colonizing organisms in settlement experiments and fouling communities (Jensen *et al.*, 1994; Gili & Hughes, 1995; Hatcher, 1998). In settlement experiments in the Warnow estuary, *Cordylophora caspia* was found to colonize artificial substrata within ca one month of deployment, its abundance increasing from June to the end of September with a peak in July (Sandrock *et al.*, 1991). Similarly, Roos (1979) reported that *Cordylophora caspia* recruited to and grew luxuriantly on water lily stalks in summer after early reproduction of nearby colonies in early spring. *Cordylophora caspia* releases a planula larva, although planula may occasionally develop in the parent gonophores being released as juvenile polyps. Planula larvae swim or crawl

for short periods (e.g. <24hrs) so that while local recruitment may be good, dispersal away from the parent colony is probably very limited (Gili & Hughes, 1995). Fragmentation and rafting on floating debris may also provide other routes for short distance dispersal.

Boström & Bonsdorff (2000) examined the colonization of artificial seagrass beds by invertebrates. They reported colonization by abundant nematodes, oligochaetes, chironomids, copepods, juvenile *Macoma baltica* and the polychaete *Pygospio elegans* within 33-43 days. Disturbance by strong winds after 43 days resulted in a marked increase in the abundance of species by day 57, except for *Pygospio elegans*. They noted that settlement of pelagic larvae was less important than bedload transport, resuspension and passive rafting of juveniles from the surrounding area in colonization of their artificial habitats. The above observation suggests that most macrobenthic species in macrophyte beds may recruit rapidly.

Mobile species, such as the gammarids, small gastropods and mysids are probably able to recruit and colonize available habitats from the surrounding area. Hydrobid molluscs produce pelagic larvae capable of considerable dispersal and may also colonize new habitats by rafting. Coleoptera (beetles), Odonata (dragonflies) and Heteroptera (true-bugs), with adults capable of flight, will probably be able to colonize available habitats relatively quickly once established, although the ability to fly varies between species (van Vierssen & Verhoeven, 1983).

The sticklebacks *Gasterosteus aculeatus* and *Spinachia spinachia* may be associated with *Potamogeton pectinatus* beds. The males set up a territory and build nests, in which the female lays eggs that are subsequently fertilized and guarded by the males (Fishbase, 2000). The abundance of vegetation provided by the pondweed bed and its associated algal mats probably provides nesting material for the males and a refuge for developing juveniles. While associated with this biotope, sticklebacks are mobile species capable of colonizing the habitat from adjacent areas or the open sea.

### Time for community to reach maturity

*Potamogeton pectinatus* vegetation dies back in autumn and winter, and overwinters either as seed or rhizome, only to germinate or bud in early spring. Therefore, the *Potamogeton pectinatus* bed and its associated community (except the infauna) develops annually. Growth rates are high in spring and *Potamogeton pectinatus* can colonize space rapidly. Colonization by mobile species is probably rapid. Cunha & Moreira (1995, Figure 9) noted that peak abundance of molluscs, leeches and insects occurred in spring and summer, probably coincident with the peak of macrophyte biomass, while oligochaete and crustacean abundance peaked during late autumn and winter probably coincident with decomposition of senescent macrophytes. Therefore, the species richness and density of invertebrates fluctuates seasonally with macrophyte abundance or decomposition, suggesting that different invertebrate groups can colonize the pondweed beds readily, depending on season.

### Additional information

None entered

## Preferences & Distribution

### Habitat preferences

### Depth Range

## Water clarity preferences

**Limiting Nutrients** Nitrogen (nitrates), Phosphorus (phosphates), Calcium, Magnesium

**Salinity preferences**

**Physiographic preferences**

**Biological zone preferences**

**Substratum/habitat preferences**

**Tidal strength preferences**

**Wave exposure preferences**

**Other preferences** None known.

## Additional Information

Marine records of this biotope are restricted to Scottish saline lagoons (JNCC, 1999) but the equivalent NVC A12 community is characteristic of still to quite fast moving and often enriched, polluted and turbid eutrophic waters. NVC A12 is widely distributed in the warmer lowland waters of southern Britain with sporadic records in west and north Britain. NVC A12 has become increasingly common in pools, canals, ditches and streams contaminated by agricultural and industrial effluents (Rodwell, 1995).

## Habitat preferences

- *Potamogeton pectinatus* is restricted to habitats either permanently submerged or emersed for only 1-3 months.
- *Potamogeton pectinatus* grows down to 10m but optimal growth was reported at 7cm to 6m in depth, although the depth at which *Potamogeton pectinatus* survives is dependant on wave action, turbulence, turbidity and hence the substrata type.

*Potamogeton pectinatus* grows on a variety of substrata depending on wave action, e.g. clays, muds, sands, gravels, peats, rubble or bedrock.

- *Potamogeton pectinatus* is characteristic of persistently alkaline waters of pH 7-9 but absent from water below pH 6.3 or above pH 10.7 (Kantrud, 1990).
- *Potamogeton pectinatus* and *Potamogeton filiformis* are the only *Potamogeton* species to penetrate brackish water. *Potamogeton pectinatus* grows optimally between 5-14g/l in brackish waters with a maximum salinity tolerance of 8ppt Cl<sup>-</sup> (ca 15psu). It grows well below 4 ppt Cl<sup>-</sup> (ca 7.25psu) but is replaced by *Ruppia* dominated communities above 9 ppt Cl<sup>-</sup> (ca 16.25 psu), forming mixed stands at intermediate salinities (see IMS.Rup).
- *Potamogeton pectinatus* is characteristic of polluted, oxygen poor waters with high N or P levels but becomes less competitive at low P levels and probably requires Ca and Mg.
- Fennel pondweed is tolerant of moderate to fast current flows but this biotope occurs in very weak tidal streams in extremely to ultra wave sheltered lagoons.

Details from Verhoeven & van Vierssen (1978), Verhoeven (1980a), Kantrud (1990) Preston (1995) and JNCC (1999). Detailed accounts of the physical and chemical tolerance of *Potamogeton pectinatus* in fresh and saline waters and sediments are given by Haslam (1978), Kantrud (1990) and Preston (1995).

## Species composition

### Species found especially in this biotope

- *Cladophora flexuosa*
- *Cladophora liniformis*
- *Gasterosteus aculeatus*
- [Lamprothamnium papulosum](#)
- *Potamogeton pectinatus*
- *Potamopyrgus jenkinsi*

### Rare or scarce species associated with this biotope

- [Lamprothamnium papulosum](#)

### Additional information

A large number of species have been identified within *Potamogeton pectinatus* dominated communities. The *Potamogeton pectinatus* community NVC A12 included 14 other species of macrophyte (Rodwell, 1995). Verhoeven & van Vierssen (1978) reported 23 invertebrate species within mixed *Potamogeton pectinatus* and *Ruppia* spp. communities, while van Vierssen & Verhoeven (1983) reported 24 species of Coleoptera, and 12 species of Heteroptera in *Potamogeton pectinatus* dominated communities in the Netherlands. In addition, Cunha & Moreira (1995) identified 76 taxa in the *Potamogeton* and *Myriophyllum* beds in Canal de Mira, Portugal.

## Sensitivity review

### Explanation

*Potamogeton pectinatus* provides primary productivity, cover and substratum, and is the defining characteristic species within this biotope (Connor *et al.* 1997a; Rodwell, 1995). *Potamogeton pectinatus* is therefore considered to be key structural species. Grazers are probably important species in the food chain converting *Potamogeton pectinatus* and algal primary production to secondary production, directly available to their predators and to the wider community via the detrital food chain. In addition, their grazing activities probably control the growth of epiphytes that would otherwise shade or compete with the macrophytes. *Hydrobia ulvae* is included to represent gastropod grazers, while reference was made to *Gammarus salinus* and *Gammarus insensibilis* (the lagoon sand shrimp) to represent gammarid amphipod grazers. The hydroid *Cordylophora caspia* and bryozoan *Conopeum reticulum* have been used to represent brackish water epifauna. The mysid *Neomysis integer* has been used to represent the sensitivity of mysid species. Similarly, *Pomatoschistus minutus* has been used to represent the sensitivities gobies and other small fish.

### Species indicative of sensitivity

Community Importance	Species name	Common Name
Important other	<i>Conopeum reticulum</i>	A bryozoan
Important other	<i>Cordylophora caspia</i>	A hydroid
Important functional	<i>Gammarus insensibilis</i>	Lagoon sand shrimp
Important functional	<i>Gammarus salinus</i>	A gammarid shrimp
Important functional	<i>Hydrobia ulvae</i>	Laver spire shell
Important other	<i>Neomysis integer</i>	Opossum shrimp
Important other	<i>Pomatoschistus minutus</i>	Sand goby
Key structural	<i>Potamogeton pectinatus</i>	Fennel pondweed

### Physical Pressures

	Intolerance	Recoverability	Sensitivity	Richness	Confidence
Substratum Loss	High	High	Moderate	Major decline	High

Removal of the substratum, e.g. due to dredging, would remove the *Potamogeton pectinatus* beds, its rhizomes and tubes, associated species and infauna. Therefore an intolerance of high has been recorded. Recoverability is probably high (see additional information below).

	Intolerance	Recoverability	Sensitivity	Richness	Confidence
Smothering	Low	Very high	Very Low	Minor decline	Low

Haslam (1978) suggested that *Potamogeton pectinatus* was the most tolerant species of conditions in rivers affected by turbidity or sediment deposition due to coal mining effluent. *Potamogeton pectinatus* grows through additional layers of deposited sediment (Haslam, 1978). Rhizomes can be buried up to 15cm in the substratum while tubers can be found at 47cm below the surface of the substratum. Tubers planted at 20cm produced plants with reduced growth rates, so that growth is probably dependant on depth (Kantrud, 1990). Smothering during winter may result in reduced growth the following spring, although winter months are generally associated with increased scour due to high water flow rates and turbulence.

Smothering by flora and fauna may be of greater importance. Smothering and hence shading

by epiphytes and filamentous algae reduces growth rates in fennel pondweed in eutrophic conditions (Kantrud, 1990). The hydroid *Cordylophora* spp. was reported to grow on *Potamogeton pectinatus*, forming a gelatinous coating inhabited by harmful organisms, which suffocated and injured the pondweed (Kantrud, 1990). The accumulation of fine silt on the leaves was reported to harbour epiphytic diatoms and shade the plant, resulting in reduced growth (Kantrud, 1990). Smothering of the sediment surface by deposition of sediment is unlikely to adversely affect burrowing infauna such as polychaetes, oligochaetes and deposit feeding amphipods e.g. *Corophium* spp. But suspension feeders such as *Mya arenaria* or *Cerastoderma edule*, if present, are probably intolerant of smothering, especially as juveniles (see MarLIN reviews). Although the biotope would probably not be adversely affected, loss of intolerant suspension feeders will result in a loss of species richness.

Therefore, smothering by 5cm of substratum is unlikely to significantly harm the plants, although the build up of sediment may reduce growth rates in the following growth season, if it remains over winter. Smothering by algal mats and epiphytes and fauna may be more harmful but the pondweed beds will probably survive. Therefore, an intolerance of low has been recorded.

#### Increase in suspended sediment

Low

Very high

Very Low

No change

Low

*Potamogeton pectinatus* is considered to be tolerant of turbid waters (see below) (Haslam, 1978). The physical effects of suspended sediment (scour, clogging) are unlikely to adversely affect the pondweed. Many of the associated organisms, such as gastropods (e.g. *Hydrobia* spp.), hydroids (e.g. *Cordylophora caspia*), bryozoans (e.g. *Electra crustulenta* or *Conopeum seurati*), and crustaceans (e.g. *Gammarus salinus*) are typical of estuaries, salt marshes and lagoons that are characterized by high suspended sediment levels, and therefore likely to tolerate increased suspended sediment levels. The pondweed is likely to reduce water flow and increase siltation, so that increased suspended sediment is likely to increase the overall rate of accretion and raise the level of the substratum, potentially allowing emergent species to colonize in time. But increased accretion is likely to be minimal in a month (see benchmark). Therefore, an intolerance of low has been recorded. The major effect of increased suspended sediment levels is the change in turbidity (see below).

#### Decrease in suspended sediment

Low

High

Moderate

Rise

Low

A decrease in suspended sediment levels, and the resultant decrease in turbidity may allow other species to compete with *Potamogeton pectinatus*, e.g. *Myriophyllum alterniflorum*. But *Potamogeton pectinatus* is the dominating pondweed in brackish water conditions exemplified by this biotope, so that competition is likely to be minimal. A decrease in suspended sediment levels may reduce the food availability for suspension feeding invertebrates such as hydroids, bryozoans and mysids. Therefore, a biotope intolerance of low has been recorded.

#### Desiccation

Intermediate

High

Low

Minor decline

Low

*Potamogeton pectinatus* survives in submergent and emergent communities, tolerates fluctuating water levels and can survive aerial exposure, although it forms short plants in emergent communities (Kantrud, 1990). Kantrud (1990) reported that tubers were not dependant of surface water cover to germinate but were intolerant of desiccation as 60% failed to germinate in exposed to sediment moisture less than 23% for two weeks, while Preston (1995) reported that most *Potamogeton pectinatus* tubers were killed by 2 months desiccation. Fruit can survive emersion for over year, and will germinate in a few days once

wetted (Kantrud, 1990). Fruit production was only important for the long term population survival in areas subject to desiccation and/or drastic changes in salinity (van Wijk, 1988; 1989a). However, van Vierssen & Verhoeven (1983) reported that in pools in which the outer edges dry out in summer, *Potamogeton pectinatus* was restricted to deeper parts of the pools by competition from *Zannichellia pedunculata* and *Ranunculus baudotii*. *Zannichellia pedunculata* was able to reproduce and fruit quickly before the pools dried and *Ranunculus baudoti* survived as a land-form, while *Potamogeton pectinatus* did not form tubers until late summer and autumn, and was therefore excluded from areas of pools that dried in summer. Van Vierssen & Verhoeven (1983) therefore suggested that *Potamogeton pectinatus* was not tolerant of desiccation.

Mobile species such as gammarids, mysids and fish will probably avoid drying conditions and move to deeper water, while hydrobids are probably tolerant of desiccation, e.g. *Hydrobia ulvae* can survive emersed in sediment at the high strandline for over a week. But, bryozoans and hydroids are restricted to damp habitats on the shore, so that colonies on emergent plants are likely to be adversely affected.

Overall, an increase in desiccation at the benchmark level is likely to increase competition from desiccation tolerant emergent macrophytes, and decrease the upper extent of the fennel pondweed bed, especially where desiccation occurred early in the season, before reproductive propagules are formed. Therefore, an intolerance of intermediate has been recorded. Recovery is likely to be rapid, aided by remaining vegetative propagules and the surviving plants (see additional information below).

#### Increase in emergence regime

Intermediate High Low Minor decline Low

*Potamogeton pectinatus* is tolerant of water fluctuation (at least 0.5 -1.75m in brackish waters) and can survive periodic exposure in tidal conditions (Kantrud, 1990). A decrease in water level in turbid conditions may increase growth of the fennel pondweed by increasing light penetration. But an increase in emergence will expose the beds to increased risk of desiccation (see above) and competition from emergent macrophytes.

Mobile species (e.g. fish, gammarids and mysids) will probably avoid the factor and filamentous green algae (e.g. *Ulva* spp.) are probably tolerant of emersion, while emersed bryozoans and hydroids may be adversely affected due to the increased desiccation risk, potentially reducing species richness.

Therefore, an intolerance of intermediate has been recorded to represent the potential loss of the upper extent of the population. Recovery is likely to be rapid (see additional information below).

#### Decrease in emergence regime

Intermediate High Low Decline Low

*Potamogeton pectinatus* is tolerant of water fluctuation (at least 0.5 -1.75m in brackish waters) and can survive periodic exposure in tidal conditions (Kantrud, 1990). The effects of a decrease in emergence and hence increased immersion time and depth will depend on turbidity. In highly turbid waters, the resultant reduction in light levels is likely to reduce growth and biomass of shoots, rhizomes and reproductive propagules. For example, in clear brackish waters fennel pondweed survives changes of 2m in water level while a 10cm increase in highly turbid waters greatly reduced production (Kantrud, 1990). Van Vierssen & Verhoeven (1983) demonstrated a positive correlation between macrophytes cover and

insect species diversity, so that a decrease in pondweed biomass is likely to reduce the species richness. Alternatively, an increase in immersion may allow the pondweed to out-compete emergent macrophytes at lower turbidities and colonize a larger area.

Overall, a decrease in emergence may allow *Potamogeton pectinatus* and its associated community to increase in extent. Alternatively, increased average depth may result in a decrease in biomass and the species richness of the associated community, where additional habitat is not available for colonization. Therefore, an intolerance of intermediate has been recorded. Recoverability is likely to be rapid (see additional information below).

**Increase in water flow rate** Low Very high Very Low Minor decline Low

Although a deep rooted species, *Potamogeton pectinatus* was considered to have a low anchoring strength when compared to other macrophytes, depending on substratum, anchoring more firmly in coarse sediments than fine (Haslam, 1978; Kantrud, 1990). In summer, its rhizome system is difficult to erode (see wave action) but is easily damaged. The pondweed produces small plants in fast flow but large plants in slow flow (Haslam, 1978). Kantrud (1990) reported that currents >1m/s limited growth in the pondweed and one study, while the pondweed grew in currents up to 2m/s in another and concluded that *Potamogeton pectinatus* was tolerant of currents. However, Haslam (1978) suggested that the pondweed was intolerant of fast flow or storm flow.

This biotope has only been recorded from saline lagoonal habitats with very weak tidal streams on muddy substrata. An increase in water flow from very weak to moderately strong may reduce growth but would probably not damage the pondweed bed in most circumstances. The intolerant of the bed to damage is partly dependant on the substratum, with soft fine muds substrata being more susceptible to increased water flow. Strong to very strong currents, however would probably remove vegetation and some rhizome material, although a proportion of the plant will probably remain. Strong to very strong water flow may remove more plant material than can be compensated for by growth resulting in loss of the pondweed beds in the long term. In addition, increased water flow will favour coarser substrata although the pondweed can colonize a variety of substrata. The hydroid *Cordylophora caspia* and bryozoan *Conopeum reticulum* occur in a wide range of water flow regimes and are unlikely to be affected directly but a proportion may be lost if vegetation was removed. The crustacean fauna is found in strong water flow and will be probably unaffected by the increased water directly. Any loss of vegetation, and loosely attached filamentous algal mats will reduce their food supply.

However, at the benchmark level, although growth may be impaired the pondweed bed will probably survive. Therefore, an intolerance of low has been recorded. Recovery will probably be rapid (see additional information below). Communities in fine sediments may be more intolerant, and exposure to greater increases in water flow are likely to damage the bed resulting in lower biomass, cover and probably shorter plants, and probably reduced species richness.

**Decrease in water flow rate**

Not sensitive\*

Not relevant

*Potamogeton pectinatus* may dominate on soft sediments and slow water flow (Haslam, 1978) and its luxuriant growth may clog canals and streams, significantly reducing flow. It requires a modicum of water flow as an increase in water flow from 0.2 to equal to or >0.4mm/s increased its photosynthetic rate 1.5 fold (Kantrud, 1991). However, the above flow rate is



negligible compared to coastal waters. This biotope was recorded from very weak tidal streams or negligible water flow so that a further decrease in water flow is unlikely and not relevant has been recorded.

Increase in temperature    Tolerant\*    Not relevant    **Not sensitive\***    Rise    **Moderate**

Kantrud (1990) concluded that *Potamogeton pectinatus* had a wide temperature tolerance, commensurate with its cosmopolitan distribution, and was adapted to temperature fluctuation. However, temperature affects growth and reproduction. For example:

- van Wijk (1983) reported that tubers sprouted when water temperatures reached 5.5 °C in the field but that 25 °C was optimum for tuber germination in culture (Kantrud, 1990);
- fruit were reported to germinate at 8 °C and flowering began at 15 °C in Canadian lakes (Kantrud, 1990);
- optimum growth was observed at 23-30 °C, while little growth occurred at 37 °C and growth was slow at 10 °C;
- in experimental ponds fennel pondweed and other pondweeds died at 38 °C;
- in brackish waters growth was suppressed at 25 °C and the plants were covered in epiphytes, and
- maximum net photosynthesis occurred at 25-28 °C (Kantrud, 1990).

Thermal effluent from a Canadian power station, averaging 7 °C above ambient, resulted in earlier and heavier flowering, a higher standing crop and increased vegetative growth of *Potamogeton pectinatus*, replacing *Myriophyllum spicatum* (Haag & Gorhan, 1977). Similarly, fennel pondweed, increased in areas affected by thermal effluent on the Finnish coast, although it was replaced by *Myriophyllum spicatum* and *Cladophora glomerata* in area subject to the highest temperature increases and highest water flow (Kantrud, 1990).

The majority of the characterizing species have broad temperatures tolerances or are widely distributed to the north or south of Britain and Ireland, and unlikely to be affected by changes in temperature at the benchmark level. But an acute increase in temperature may adversely affect spring populations of *Neomysis integer* (see species review).

Overall, an increase in temperature may result in increased growth of *Potamogeton pectinatus* and ephemeral green algae, providing additional food and cover for the invertebrate fauna. However, excessive growth of ephemeral algae may smother the pondweed in brackish water conditions. Otherwise the pondweed and its associated community may benefit.

Decrease in temperature    **Tolerant**    **Not sensitive\***    **No change**    **Low**

Kantrud (1990) reported that *Potamogeton pectinatus* was distributed circumboreally, north to about 70° N and concluded that *Potamogeton pectinatus* had a wide temperature tolerance, commensurate with its cosmopolitan distribution. Kantrud (1990) reported that 5 °C was the lower limit of fennel pondweed growth, although tubers began to sprout at 5.5 °C. A cold snap was also reported to enhance tuber germination. In shallow water, fennel pondweed is likely to be damaged by frost if exposed but shoots may be found under ice in deeper waters (Kantrud, 1990).

The majority of the characterizing species have broad temperatures tolerances or are widely distributed to the north or south of Britain and Ireland, and unlikely to be affected by changes in temperature at the benchmark level.

Overall, the pondweed bed and its associated community is unlikely to be affected by long term decreases in temperature and will probably survive acute temperature decreases at the benchmark level.

**Increase in turbidity**      **Intermediate** **High**      **Low**      **Decline**      **Moderate**

*Potamogeton pectinatus* was considered to be of intermediate tolerance to turbid waters, compared with other macrophytes (Haslam, 1978) but tends to dominate highly turbid waters, e.g. due to suspended sediments, sewage or coal mining effluents, that are unsuitable for other macrophytes and was considered to have a high tolerance to turbid conditions by authors cited by Kantrud (1990). *Potamogeton pectinatus* exhibits local adaptations to turbid conditions in eutrophic (see nutrients) or brackish waters (van Wijk *et al.*, 1988; Kantrud, 1990) including increased tuber formation and increased shoot length allowing the plants to rapidly reach the water surface and develop a canopy. *Potamogeton pectinatus* is also shade tolerant, growing under overhanging trees and under emergent macrophytes (Kantrud, 1990). However, increased turbidity reduces growth, biomass and production in the pondweed. For example, 100ppm of suspended sediment reduced fennel pondweed production by 50% in culture and production was low in silted, carp infested waters with Secchi disks depths of <30cm. Increased water depth reduces the amount of light available to submergent plants and algae, so that increased water depth may be detrimental while a reduction in water depth may offset the effects of increased turbidity (see emergence) (Kantrud, 1990). Very high turbidity will exclude most pondweeds including *Potamogeton pectinatus*. For example, fennel pondweed was reported to be absent from a New Zealand lake in areas of 100-300ppm suspended sediment, and from lakes with Secchi depths of <20cm. Kantrud (1990) concluded that Secchi depths of <20cm usually indicated waters that would not support fennel pondweed growth. Kantrud (1990) also noted that growth of fennel pondweed improved water transparency by anchoring the substratum, reducing water turbulence, oxygenating the water column, and sequestering nutrients.

Increased turbidity will also probably reduce the growth of epiphytic or filamentous green algae and charophytes (e.g. *Lamprothamnium papulosum*) but most invertebrates are unlikely to be affected directly, although loss of macrophyte or algal productivity will reduce the food supply for grazers and ultimately decomposers and deposit feeders.

Overall, *Potamogeton pectinatus* is probably relatively tolerant of turbidity at the benchmark level, and is only likely to be excluded under extremely turbid conditions (see benchmark). However, high turbidity will probably reduce the productivity of community, in terms of both macrophyte and macroalgal primary productivity and hence secondary production. Therefore, the biotope would probably survive long term change to high turbidity and even to extreme turbidity in the short term (one month, see benchmark), depending on depth, although a proportion of the biomass will be lost and an intolerance of intermediate has been recorded. Nevertheless, while *Potamogeton pectinatus* is tolerant of high turbidity levels, increased turbidity has been implicated in its loss from some wetlands (Kantrud, 1990) and in moderate to highly turbid waters the pondweed is probably highly intolerant of any further increase in turbidity.

**Decrease in turbidity**      Tolerant\*      **Not sensitive** Rise      **Moderate**

In freshwater systems, a decrease in turbidity will probably allow other submergent macrophytes to invade the habitat, forming mixed stands and increasing competition with *Potamogeton pectinatus*. However, in brackish water exemplified by this biotope, few species other than *Myriophyllum spicatum*, *Potamogeton filiformis*, *Ranunculus baudoti*, charophytes are

likely to compete with the pondweed (see NVC A6 and A11, Rodwell, 1995). Therefore, the increased light is likely to increase the biomass and cover of the pondweed, and hence potential species richness and 'not sensitive\*' has been recorded.

**Increase in wave exposure** Intermediate High Low Decline Low

Haslam (1978) suggested that *Potamogeton pectinatus* was of intermediate tolerance to turbulence caused by wind generated wave action or boat wash in lakes. Submerged macrophytes are usually restricted to wave sheltered areas of lakes such as river inlets and protected bays (Kantrud, 1990; Preston, 1995), and *Potamogeton pectinatus* may be restricted to deeper waters in less sheltered sites. Fennel pondweed is likely to be torn or broken during storms but recover from underground rhizomes and tubers (Haslam, 1978). Haslam (1978) reported that in one example, rapid growth in early summer negated the effects of storm damage, while in autumn storm damage removed 80% of vegetation. Haslam (1978) suggested the recurrent storm damage may result in loss of a population. Increased wave action is likely to increase the turbidity due to resuspension of the sediments, or remove of suitable substrata. For example, Kantrud (1990) reported that fennel pondweed was still recovering 22 years after a storm, probably due to removal of substrata and increased turbidity due to plankton blooms.

Where present, *Potamogeton pectinatus* beds stabilize the sediment, and buffer wave action for other plants, e.g. Verhoeven (1980a) suggested that the upper zone of charophytes (*Lamprothamnium papulosum* and *Chara* spp.) in the brackish lake Swartvlei, the Netherlands, was dependant on the protection from wave action afforded by the deeper stands of *Potamogeton pectinatus*.

The majority of the associated invertebrate species are probably adapted to wave sheltered conditions, or fine sediments associated with wave sheltered conditions. Mobile species such as mysids, gobies and sticklebacks will probably move to deeper water to avoid wave turbulence. More sedentary gammarids or hydroids may be washed away, while the benthic infauna may be changed due to changes in the substrata from fine to coarser sediment, and a proportion of the epifauna and epiflora will be lost on removed vegetation.

Overall, this biotope is characteristic of extremely wave sheltered conditions, so that an increase in wave exposure from e.g. extremely sheltered to sheltered is likely to result in loss of a proportion of the biotope and an intolerance of intermediate has been recorded. The biotope is likely to be highly intolerant of a further increase, e.g. to moderate exposure, resulting in prolonged and low recoverability, as cited by Kantrud (1990).

**Decrease in wave exposure**

Not sensitive\*

Not relevant

This biotope is characteristic of extremely to ultra wave sheltered conditions, so that any further decrease in wave exposure is unlikely.

**Noise**

Tolerant

Not relevant

Not relevant

Not relevant

Not relevant

The majority of species in *Potamogeton pectinatus* dominated communities are unlikely to react to noise at the benchmark level. Wildfowl, however, are intolerant of disturbance from noise from e.g. shooting (Madsen, 1988) and from coastal recreation, industry and engineering works. For example, Percival & Evans (1997) reported that wigeon were very intolerant of human disturbance and, where wildfowling was popular, wigeon avoided *Zostera noltii* beds at the top of the shore.

**Visual Presence** Tolerant Not relevant Not relevant Not relevant Not relevant

The majority of species in *Potamogeton pectinatus* dominated communities have poor, if any, visual acuity, and are unlikely to react to visual disturbance. However, mobile fish may be disturbed by passing boats but probably with minimal effect. Wildfowl, however, are intolerant of disturbance from noise from e.g. shooting (Madsen, 1988) and from coastal recreation, industry and engineering works. For example, Percival & Evans (1997) reported that wigeon were very intolerant of human disturbance and, where wildfowling was popular, wigeon avoided *Zostera noltii* beds at the top of the shore.

**Abrasion & physical disturbance** Intermediate High Low Minor decline Low

The rhizome system of *Potamogeton pectinatus* is deep and extensive in summer and therefore difficult to erode, although easily damaged (Haslam, 1978). The pondweed bed will probably be damaged and torn by a passing anchor or mobile fishing gear (see benchmark) and a proportion of attached epifauna and epiphytes and filamentous algae will be lost. Recovery from remaining rhizomes and tubers will probably be rapid. Therefore an intolerance of intermediate has been recorded with a recoverability of high.

**Displacement** High High Moderate Major decline Low

*Potamogeton pectinatus* would probably be severely damaged and fragmented by displacement, resulting in loss of filamentous algae, epiphytes and epifauna, and the associated fauna. The mobile invertebrates and fish, e.g. gammarids, mysids and fish will probably be unharmed and migrate to adjacent areas. However, the community would probably be lost and an intolerance of high has been recorded. *Potamogeton pectinatus* is able to root from fragments of rhizome and stem, so that recovery will probably be rapid (see additional information below).

## Chemical Pressures

**Synthetic compound contamination** Intolerance Recoverability Sensitivity Richness Confidence

High High Moderate Major decline Moderate

Haslam (1978) suggested that *Potamogeton pectinatus* was very tolerant of sewage and industrial effluent pollution, often dominating affected waters where other plants can not survive. But herbicides and agricultural chemicals caused major damage, especially in still waters (Haslam, 1978). For example, Coyner *et al.* (2001) reported that the herbicide chlorsulfuron reduced growth rates, and vegetative production at 0.25 and 0.5ppb, while significant decrease in biomass and increased mortality occurred at greater than or equal to 1ppb chlorsulfuron. Several herbicides, including Atrazine and Diquat, have been used to control growth in *Potamogeton pectinatus* in irrigation ditches in North America (for details see Kantrud, 1990).

Similarly, most pesticides and herbicides were suggested to be very toxic for invertebrates, especially crustaceans (amphipods isopods, mysids, shrimp and crabs) and fish (Cole *et al.*, 1999). For example, Lindane was shown to be very toxic to gobies (*Gobius* spp.: see [Pomatoschistus minutus](#)) (Ebere & Akintonwa, 1992). The pesticide Ivermectin is very toxic to crustaceans, and has been found to be toxic towards some benthic infauna such as [Arenicola marina](#) (Cole *et al.*, 1999).

Therefore, synthetic chemicals found in agricultural, urban and industrial discharges are likely

to adversely affect the biotope. Herbicides in particular are likely to reduce growth and productivity of the pondweed beds, and may result in its loss. In addition, loss of particularly intolerant crustaceans may result in unchecked growth of epiphytes, which would again reduce photosynthesis and productivity of the pondweed beds. Overall, synthetic chemical contamination will at least result in a reduction in productivity, seed set and ultimately the extent of the *Potamogeton pectinatus* bed. Therefore, fennel pondweed is probably highly intolerant of herbicide contamination. Recovery is probably dependant on recolonization of the habitat (once the contaminants have dispersed or depurated) but will probably take less than 5 years.

### Heavy metal contamination

Intermediate High Low Decline Low

Haslam (1978) suggested that macrophytes were little affected by heavy metals, since a countrywide survey had not been able to detect any correlation between plant distributions and heavy metal concentrations of Cr, Co, Cu, Fe, Pb, Mn, Ni, Sn and Zn. The chemical constitution of waters and sediments inhabited by *Potamogeton pectinatus* (including heavy metals concentrations) was given by Kantrud, 1990). But Greger & Kautsky (1991) reported that sediment concentrations of 4µg Pb, 13 µg Cu and 38µg Zn /g dry weight of sediment reduced the biomass of the pondweed.

Cole *et al.* (1999) suggested that Pb, Zn, Ni and As were very toxic to algae, while Cd was very toxic to Crustacea (amphipods, isopods, shrimp, mysids and crabs), and Hg, Cd, Pb, Cr, Zn, Cu, Ni, and As were very toxic to fish. Gobies were reported to be particularly intolerant of Hg (see [Pomatoschistus minutus](#)). Bryan (1984) reported sublethal effects of heavy metals in crustaceans at low (ppb) levels.

Bryan (1984) suggested that polychaetes are fairly resistant to heavy metals, based on the species studied. Short term toxicity in polychaetes was highest to Hg, Cu and Ag, declined with Al, Cr, Zn and Pb whereas Cd, Ni, Co and Se were the least toxic. He also suggested that gastropods were relatively tolerant of heavy metal pollution.

The intolerance of crustaceans to heavy metal contaminants suggests that amphipod and isopod grazers would be lost, allowing rapid growth of epiphytes, and reduced turnover of the detrital food chain. Additional growth by the epiphytes and algal mats, unless they are adversely affected themselves, could potentially compete with pondweed stands for light and nutrients reducing productivity. Overall, in the absence of other evidence, the *Potamogeton pectinatus* beds would probably survive, with reduced productivity, but several members of the community may be lost (e.g. fish and crustaceans) resulting in a reduced species richness. Therefore, an intolerance of intermediate has been recorded. Recoverability would probably be high (see additional information below).

### Hydrocarbon contamination

High High Moderate Decline Moderate

Little information on the effects of hydrocarbon contamination from, for example oil spills, on *Potamogeton pectinatus* beds was found. Where they occur, oil spills are likely to persist for some time in sheltered, soft sediment habitats.

Suchanek (1993) noted that gastropods, amphipods, infaunal polychaetes and bivalves were particularly sensitive to oil spills. For example substantial kills of *Nereis*, *Cerastoderma*, *Macoma*, *Arenicola* and *Hydrobia* were reported after the *Sivand* oil spill in the Humber (Hailey, 1995). Single oil spills were reported to cause a 25-50% reduction in abundance of [Arenicola marina](#) (Levell, 1976). The toxicity of oil and petrochemicals to fish ranges from moderate to

high (Cole *et al.*, 1999). The water soluble fraction of oils was shown to cause mortality in sand gobies and fish, especially their larvae, are thought to be intolerance of polyaromatic hydrocarbons (PAHs) (see *Pomatoschistus minutus*). PAHs are significantly more toxic when exposed to sunlight (Ankley *et al.*, 1997), and may have a greater effect in clear shallow waters inhabited by pondweed communities.

Therefore, while there no evidence was found to suggest that *Potamogeton pectinatus* spp. would be directly affected by hydrocarbon contamination, its associated community may be lost. Loss of grazers may increase epiphytic fouling resulting in lower growth and productivity. However, given the likely persistence of oils in sheltered, sedimentary habitats, an overall intolerance of high has been recorded.

Recovery will depend on recolonization by the associated invertebrate community, which is likely to be rapid (see additional information below).

#### Radionuclide contamination

No information found

Not relevant

Insufficient information

Not relevant

#### Changes in nutrient levels

Tolerant\*

Not relevant

Not sensitive\*

Minor decline

Moderate

*Potamogeton pectinatus* is able to withstand a wide range of nutrient concentrations. It is capable of absorbing nutrients through its leaves and stems as well as its roots and influences nutrient cycling in natural waters (Kantrud, 1990). It requires Mg, Ca and P for active growth (Kantrud, 1990) but Ca is unlikely to be limiting in brackish water conditions. Kantrud (1990) suggested that *Potamogeton pectinatus* was seldom limited by nutrients.

*Potamogeton pectinatus* is characteristic of and often dominant in naturally eutrophic waters and polluted, oxygen-poor, waters high in nutrients due to agricultural runoff, sewage or municipal wastes (Haslam, 1978; Kantrud, 1990; Preston, 1995). However, hyper-eutrophicated conditions the biomass of the pondweed may decrease. Kantrud (1990) reported that extremely high nutrient concentrations injure or destroy the plant resulting in its replacement by algae, probably partly due to increased turbidity caused by increased phytoplankton blooms. Kantrud (1990) suggested that submerged macrophytes out-compete and hence inhibit the growth of algal epiphytes and phytoplankton in nutrient limited waters. However, phytoplankton blooms in eutrophic waters, either due to natural fluctuations in macrophyte abundance, phytoplankton predators, or eutrophic conditions, increases the turbidity by removing photosynthetically active light wavelengths, and hence, greatly reduce the biomass of the pondweed, often restricting it to shallow waters.

*Gammarus salinus* and *Cordylophora caspia* have been associated with polluted waters (see reviews), while most epiphytic and epistatic grazers would probably benefit from the increased algal growth stimulated by eutrophic conditions. But it was suggested that the nationally rare foxtail stonewort *Lamprothamnium papulosum* was intolerant of nutrient enrichment being absent from water with >20 µg/l, and preferring nutrient poor sites (Bamber *et al.*, 2001). Therefore, if present the foxtail stonewort will probably be lost due to nutrient enrichment.

Overall, *Potamogeton pectinatus* beds are probably tolerant of increase in nutrients at the benchmark level, and would possibly even benefit from enrichment, detrimental effects only manifesting at extreme high nutrient levels. Loss of a few intolerant species, e.g. some macrophytes and the foxtail stonewort will probably reduce species richness. Nevertheless, a

not sensitive\* has been recorded.

**Increase in salinity**      **High**      **High**      **Moderate**      **Minor decline** **Moderate**

*Potamogeton pectinatus* and *Potamogeton filiformis* are the only *Potamogeton* species to penetrate brackish water. *Potamogeton pectinatus* grows optimally between 5-14g/l in brackish waters with a maximum salinity tolerance of 8ppt Cl<sup>-</sup> (ca 15psu). It grows well below 4 ppt Cl<sup>-</sup> (ca 7.25psu) but is replaced by *Ruppia* dominated communities above 9 ppt Cl<sup>-</sup> (ca 16.25 psu), forming mixed stands at intermediate salinities (see [A5.5343](#)).

The nationally rare foxtail stonewort *Lamprothamnium papulosum* was reported to prefer 8-28psu but tolerate up to 32psu. Most brackish water species are adapted to a wide range or variable salinities, e.g. *Hydrobia ulvae*, *Gammarus salinus* and *Gammarus insensibilis*, however the mysid *Neomysis integer* is predominantly brackish water and has an upper tolerance limit of 20 - 25psu (see review).

Overall, a short term increase in salinity e.g. from low to variable for a week would probably stress the pondweeds and a few members of the invertebrate community but otherwise have limited effects. However, a long term change from e.g. reduced to variable salinity would probably result in loss of the *Potamogeton pectinatus* bed, and a change in the invertebrate community to more marine species, probably resulting in its replacement by *Ruppia* dominated communities in the long term (see [A5.5343](#)). Although the invertebrate fauna of brackish water *Potamogeton pectinatus* dominated communities and *Ruppia* dominated communities are similar, the biotope would effectively be lost and an intolerance of high has been recorded.

**Decrease in salinity**      **High**      **High**      Rise      **Low**

A further decrease in salinity e.g. from reduced to low or to freshwater, will probably exclude the marine or estuarine components of the invertebrate fauna, e.g. *Gammarus salinus* and bryozoans, while allowing more freshwater species to colonize, e.g. insects. *Potamogeton pectinatus* would probably experience greater competition from other submerged macrophytes, such as *Myriophyllum spicatum*, forming mixed stands similar to the more species rich NVC A11. Therefore, although many members of the faunal community will probably remain, and *Potamogeton pectinatus* would probably still be a dominant macrophyte, NVC A12 (the biotope) would probably become NVC A11 and be lost, therefore an intolerance of high has been recorded.

**Changes in oxygenation**      **Low**      **Very high**      **Very Low**      **No change**      **Low**

*Potamogeton pectinatus*, like many submergent macrophytes, is adapted to grow in hypoxic sediments. Air channels within the leaves and stem supply the roots with oxygen. Fennel pondweed is characteristic of polluted and oxygen-poor waters. In some cases its night-time respiration was reported to reduce dissolved oxygen to unacceptable levels in wetlands. Spencer & Ksander, (1997) reported that anoxic conditions caused propagules to sprout earlier than in aerobic conditions and noted no difference in the proportion of propagules that sprouted under either oxygen regime.

Most of the species identified as characterizing can probably tolerate low oxygen concentrations (e.g. *Cordylophora caspia*, benthic infauna, the mud snails *Hydrobia* spp. and the bryozoan *Conopeum* spp.) as they are characteristic of wave sheltered and low water flow environments subject to low oxygen conditions. Mobile gammarids and fish are probably able to avoid low oxygen conditions.

Overall, an intolerance of low has been recorded at the benchmark level. Recovery will

probably be rapid.

## Biological Pressures

	Intolerance	Recoverability	Sensitivity	Richness	Confidence
<b>Introduction of microbial pathogens/parasites</b>	Low	Very high	Very Low	Minor decline	Low

The loss of large areas of fennel pondweed and other macrophytes occurred in North American wetlands between 1918 and 1926. The decline was thought to be caused by fungal infection by *Rhizoctonia solani* and possibly other fungi. Fennel pondweed was particularly susceptible at 3-7psu. But Kantrud (1990) suggested that the evidence for direct role of pathogens in the decline was inconclusive. The aphid *Rhopalsiphum nymphaeae* uses several *Potamogeton* species as a secondary host, causing in-rolling of the leaf margin (Preston, 1995). The smut fungus *Doassansia martianoffiana* forms pustules of the underside of leaves of several *Potamogeton* species (Preston, 1995). Many species of invertebrates, including crustaceans and gastropods are secondary hosts for fish or bird parasites (see individual species reviews for examples).

Any form of infestation or disease is likely to reduce the viability of the infected population. Gastropod molluscs may also be castrated by heavy trematode infestation. Therefore, in the absence of other evidence an intolerance of low has been recorded.

<b>Introduction of non-native species</b>	Not relevant	Insufficient information	Not relevant
---	--------------	--------------------------	--------------

No information found.

<b>Extraction of this species</b>	Intermediate	High	Low	Minor decline	Moderate
-----------------------------------	--------------	------	-----	---------------	----------

*Potamogeton pectinatus* beds are a significant food plant for water birds. Water birds were reported to excavate holes in the bed 10 cm wide by 0.3 m deep in search of tubers. Water birds were estimated to remove 21% of the biomass, or 40% of the standing crop and 43% of tubers in separate studies (Jupp & Spence, 1977; Kantrud, 1990). For example, in Loch Leven losses from grazing were less than those caused by wave action, and tuber density was not affected by grazing (Jupp & Spence, 1977; Preston, 1995). Van Wijk (1988) reported that above and below ground biomass were reduced by grazing by coot, mallard and mute swan (Preston, 1995). But beds of fennel pondweed were reported to have remained for 20 years under heavy water bird grazing (Kantrud, 1990). Overall, a proportion of the standing crop and biomass would be removed by water bird predation and an intolerance of intermediate has been recorded by definition. But the bed would probably recover rapidly, possibly within the growing season depending on the time of year, and hence community will probably survive.

<b>Extraction of other species</b>	Not relevant	Not relevant	Not relevant	Not relevant	Not relevant
------------------------------------	--------------	--------------	--------------	--------------	--------------

## Additional information

### Recoverability

Zieman *et al.* (1984) noted that the recovery of seagrass ecosystems depended primarily of the extent or magnitude of damage to the sediments, i.e. the rhizome and root system. This is probably also true of aquatic macrophyte dominated communities.



*Potamogeton pectinatus* dies back in winter and grows back from over-wintering tubers and/or rhizomes, or from seed in annual populations. A single tuber or seed may be highly productive (see recruitment) and growth rates are high, especially in early spring (see productivity). Control of *Potamogeton pectinatus* may involve cutting back of the leaves and shoots (Rodwell, 1995). Fennel pondweed will not grow back immediately if cut late in the growing season, but in summer two or even three cuts may be required (Rodwell, 1995). Therefore, where tubers and/or rhizomes remain or a seed bank is present a well developed fennel pondweed bed is likely to develop within one growing season. Haslam (1978) reported that aquatic macrophytes could recover within a single growing season after shallow dredging, where a proportion of plant propagules remained. For example, after shallow dredging in the Great Ouse, *Potamogeton pectinatus* developed stable populations with 2-3 growing seasons (Haslam, 1978). But Haslam (1978) suggested that if plants are completely removed, recovery would probably take several years.

*Potamogeton* species have considerable powers of dispersal via specialized asexual propagules such as turions, fragments of stems or rhizome or fruits that float (aided by their buoyancy) and can be carried long distances by currents, flood waters, or by birds (Kantrud, 1990; Preston, 1995). *Potamogeton pectinatus* is considered to be a pioneering species, able to quickly colonize newly flooded areas or areas reclaimed from the sea, and often becomes dominant in areas that become temporarily unsuitable for other species, e.g. due to pollution (Kantrud, 1990).

The epiphytic and epifaunal species will probably recruit to the available habitats quickly, as will mobile species such as crustaceans, insects and fish (see recruitment).

Overall, recovery is likely to be rapid, probably within 1 year or at most 2-3 years where vegetative or sexual propagules remain in the sediment, or where neighbouring or upstream population exist. Where, the plants and propagules are completely removed or destroyed, recovery will take longer, but due to its potentially high dispersal potential, probably no longer than 5 years. Isolated habitats, e.g. lagoons, will depend on dispersal by water birds or flood waters from upstream populations, which could occur within a year or be protracted, although a stable population will probably establish quickly after recruitment.

## Bibliography

- Ankley, G.T., Erickson, R.J., Sheedy, B.R., Kosian, P.A., Mattson, V.R. & Cox, J.S., 1997. Evaluation of models for predicting the phototoxic potency of polycyclic aromatic hydrocarbons. *Aquatic Toxicology*, **37**, 37-50.
- Bamber, R.N., Gilliland, P.M. & Shardlow, M.E.A., 2001. *Saline lagoons: a guide to their management and creation* (interim version). Peterborough: English Nature.
- Boström, C. & Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series*, **205**, 123-138.
- Bryan, G.W., 1984. Pollution due to heavy metals and their compounds. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in the Oceans and Coastal Waters*, vol. 5. *Ocean Management*, part 3, (ed. O. Kinne), pp.1289-1431. New York: John Wiley & Sons.
- Byren, B.A. & Davies, B.R., 1986. The influence of invertebrates on the breakdown of *Potamogeton pectinatus* L. in a coastal marina (Zandvlei, South Africa). *Hydrobiologia*, **137**, 141-151.
- Cole, S., Codling, I.D., Parr, W. & Zabel, T., 1999. Guidelines for managing water quality impacts within UK European Marine sites. *Natura 2000 report prepared for the UK Marine SACs Project*. 441 pp., Swindon: Water Research Council on behalf of EN, SNH, CCW, JNCC, SAMS and EHS. [UK Marine SACs Project.], <http://www.ukmarinesac.org.uk/>
- Connor, D.W., Dalkin, M.J., Hill, T.O., Holt, R.H.F. & Sanderson, W.G., 1997a. Marine biotope classification for Britain and Ireland. Vol. 2. Sublittoral biotopes. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06., Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06.*
- Coyner, A., Gupta, G. & Jones, T., 2001. Effects of chlorsulfuron on growth of submerged aquatic macrophyte *Potamogeton pectinatus* (sage pondweed). *Environmental Pollution*, **111**, 453-455.
- Cunha, M.R. & Moreira, M.H., 1995. Macrobenthos of *Potamogeton* and *Myriophyllum* beds in the upper reaches of Canal de Mira (Ria de Aveiro, NW Portugal): community structure and environmental factors. *Netherlands Journal of Aquatic Ecology*, **29**, 377-390.
- Davies, C.E. & Moss, D., 1998. European Union Nature Information System (EUNIS) Habitat Classification. *Report to European Topic Centre on Nature Conservation from the Institute of Terrestrial Ecology, Monks Wood, Cambridgeshire*. [Final draft with further revisions to marine habitats.], Brussels: European Environment Agency.
- Ebere, A.G. & Akintonwa, A., 1992. Acute toxicity of pesticides to *Gobius* sp., *Palaemonetes africanus*, and *Desmocariss trispinosa*. *Bulletin of Environmental Contamination and Toxicology*, **49**, 588-592.
- FishBase, 2000. *FishBase. A global information system on fishes*. [On-line] <http://www.fishbase.org>, 2001-05-03
- Geger, M. & Kautsky, L., 1991. Effects of Cu, Pb and Zn on two *Potamogeton* species grown under field conditions. *Vegetatio*, **97**, 173-184.
- Gili, J-M. & Hughes, R.G., 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology: an Annual Review*, **33**, 351-426.
- Haag, R.W. & Gorham, P.R., 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submerged macrophytes in Lake Wabaman, Alberta. *Journal of Applied Ecology*, **14**, 835-851.
- Hailey, N., 1995. Likely impacts of oil and gas activities on the marine environment and integration of environmental considerations in licensing policy. *English Nature Research Report*, no 145., Peterborough: English Nature.
- Haslam, S.M., 1978. *River plants: the macrophytic vegetation of watercourses*. Cambridge: Cambridge University Press.
- Hatcher, A.M., 1998. Epibenthic colonization patterns on slabs of stabilised coal-waste in Poole Bay, UK. *Hydrobiologia*, **367**, 153-162.
- Hayward, P.J. & Ryland, J.S. 1998. *Cheilostomatous Bryozoa. Part 1. Aeteoidea - Cribrillinoidea*. Shrewsbury: Field Studies Council. [Synopsis of the British Fauna, no. 10. (2nd edition)]
- Howard-Williams, C. & Liptrot, M.R.K., 1980. Submerged macrophyte communities in a brackish South African estuarine-lake system. *Aquatic Botany*, **9**, 101-116.
- Jacobsen, D. & Sand-Jensen, K., 1994. Invertebrate herbivory on the submerged macrophyte *Potamogeton perfoliatus* in a Danish stream. *Freshwater Biology*, **31**, 43-52.
- Jensen, A.C., Collins, K.J., Lockwood, A.P.M., Mallinson, J.J. & Turnpenny, W.H., 1994. Colonization and fishery potential of a coal-ash artificial reef, Poole Bay, United Kingdom. *Bulletin of Marine Science*, **55**, 1263-1276.
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- Jupp, B.P. & Spence, D.H.N., 1977. Limitations of macrophytes in a eutrophic lake, Loch Leven. *Journal of Ecology*, **65**, 431-446.
- Kantrud, H.A., 1990. *Sago pondweed* (*Potamogeton pectinatus* L.): a literature review. U.S. Fish & Wildlife Service, Fish & Wildlife Resource Publication no. 176, version 16 July 1997. [On-line] <http://www.npwrc.usgs.gov/resource/literatr/pondweed/pondweed.htm>, 2002-07-03
- Levell, D., 1976. The effect of Kuwait Crude Oil and the Dispersant BP 1100X on the lugworm, *Arenicola marina* L. In *Proceedings of an Institute of Petroleum / Field Studies Council meeting, Aviemore, Scotland, 21-23 April 1975. Marine Ecology and Oil Pollution* (ed.

- J.M. Baker), pp. 131-185. Barking, England: Applied Science Publishers Ltd.
- Mauchline, J., 1980. The biology of Mysids. *Advances in Marine Biology*, **18**, 1-369.
- Preston, C.D., 1995. *Pondweeds of Great Britain and Ireland*. London: Botanical Society of the British Isles. [B.S.B.I. Handbook no. 8.]
- Rodwell, J.S. (ed.), 1995. *British plant communities, vol. 4. Aquatic communities, swamps and tall-herb fens*. Cambridge: Cambridge University Press.
- Roos, P.J., 1979. Two-stage life cycle of a *Cordylophora* population in the Netherlands. *Hydrobiologia*, **62**, 231-239.
- Sandrock, S., Scharf, E-M., von Oertzen, J.A., 1991. Short-term changes in settlement of micro- and macro-fouling organisms in brackish waters. *Acta Ichthyologica et Piscatoria*, **21**(Suppl.), 221-235.
- Spencer, D.F. & Ksander, G.G., 1997. Influence of anoxia on sprouting of vegetative propagules of three species of aquatic plant propagules. *Wetlands*, **17**, 55-64.
- Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist*, **33**, 510-523.
- Thorp, K., Dalkin, M., Fortune, F. & Nichols, D., 1998. *Marine Nature Conservation Review, Sector 14. Lagoons in the Outer Hebrides: area summaries*. Peterborough: Joint Nature Conservation Committee. [Coasts and seas of the United Kingdom. MNCR Series.]
- Thorp, K., 1998. *Marine Nature Conservation Review, Sectors 1 and 2. Lagoons in Shetland and Orkney*. Peterborough: Joint Nature Conservation Committee. [Coasts and seas of the United Kingdom. MNCR Series.]
- van Vierssen, W. & Verhoeven, J.T.A., 1983. Plant and animal communities in brackish supra-littoral pools ('dobben') in the northern part of the Netherlands. *Hydrobiologia*, **98**, 203-221.
- van Wijk, R.J., 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life-cycle under field conditions. *Aquatic Botany*, **31**, 211-258.
- van Wijk, R.J., 1989a. Ecological studies on *Potamogeton pectinatus* L. III. Reproductive strategies and germination ecology. *Aquatic Botany*, **33**, 271-299.
- van Wijk, R.J., 1989b. Ecological studies on *Potamogeton pectinatus* L. IV. Nutritional ecology, field observations. *Aquatic Botany*, **35**, 301-318.
- Verhoeven, J.T.A. & van Vierssen, W., 1978b. Distribution and structure of communities dominated by *Ruppia*, *Zostera* and *Potamogeton* species in the inland waters of 'De Bol', Texel, The Netherlands. *Estuarine and Coastal Marine Science*, **6**, 417-428.
- Verhoeven, J.T.A., 1980a. The ecology of *Ruppia*-dominated communities in western Europe. II. Synecological classification. Structure and dynamics of the macroflora and macrofaunal communities. *Aquatic Botany*, **8**, 1-85.
- Verhoeven, J.T.A., 1980b. The ecology of *Ruppia*-dominated communities in western Europe. III. Aspects of production, consumption and decomposition. *Aquatic Botany*, **8**, 209-253.