Zostera (Zosterella) noltei beds in littoral muddy sand

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

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2019-06-25

A report from:
The Marine Life Information Network, Marine Biological Association of the United Kingdom.

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This review can be cited as:
D'Avack, E.A.S., Tyler-Walters, H. & Wilding, C., 2019. [Zostera (Zosterella) noltei] beds in littoral muddy sand. 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.318.1

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A bed of ***Zostera noltei*** with ***Hydrobia ulvae*** visible on the mud surface.
Photographer: Mark Davies
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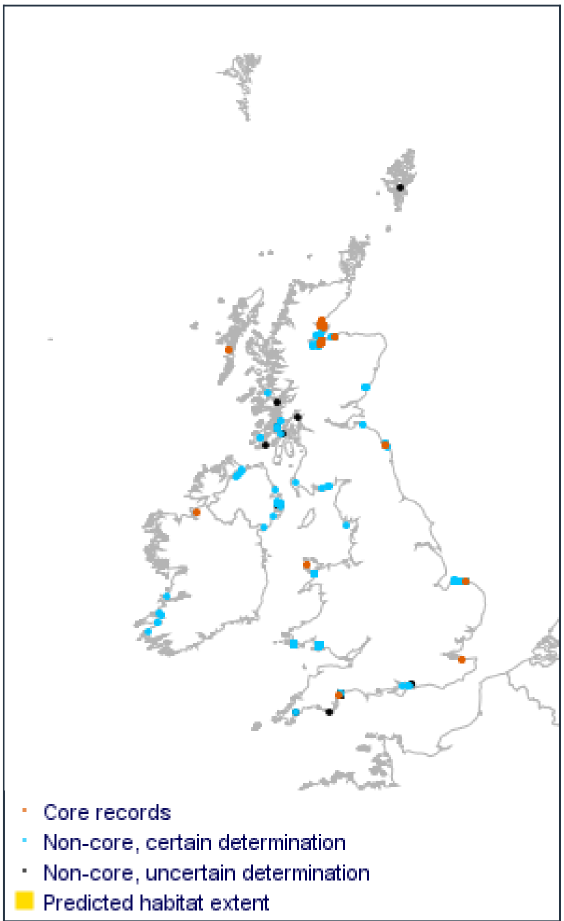

17-09-2018
Biotope distribution data provided by EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu)

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Summary

UK and Ireland classification

EUNIS 2008	A2.6111	*Zostera noltii* beds in littoral muddy sand
JNCC 2015	LS.LMp.LSgr.Znol	*Zostera (Zosterella) noltei* beds in littoral muddy sand
JNCC 2004	LS.LMp.LSgr.Znol	*Zostera noltii* beds in littoral muddy sand
1997 Biotope	LS.LMS.ZOS.Znol	*Zostera noltii* beds in upper to mid shore muddy sand

Description

Mid and upper shore wave-sheltered muddy fine sand or sandy mud with narrow-leafed eel grass *Zostera noltei* at an abundance of frequent or above. It should be noted that the presence of *Zostera noltei* as scattered fronds does not change what is otherwise a muddy sand biotope. Exactly what determines the distribution of *Zostera noltei* is not entirely clear. It is often found in small lagoons and pools, remaining permanently submerged, and on sediment shores where the muddiness of the sediment retains water and stops the roots from drying out. An anoxic layer is usually present below 5 cm sediment depth. The infaunal community is characterized by the polychaetes *Scoloplos armiger*, *Pygospio elegans* and *Arenicola marina*, oligochaetes, the spire shell *Peringia ulvae*, and the bivalves *Cerastoderma edule* and *Limecola balthica*. The green algae *Ulva* spp. may be present on the sediment surface. The characterizing species lists below give an indication both of the epibiota and of the sediment infauna that may be present in intertidal seagrass beds. The biotope is described in more detail in the National Vegetation Classification (Rodwell, 2000). This biotope should not be confused with Zmar which is a *Zostera marina* bed on the lower shore or shallow sublittoral clean or muddy sand. (Information taken from the Marine Biotope Classification for Britain and Ireland, Version 15.03, JNCC, 2015).

Depth range

Upper shore, Mid shore

Additional information

Please note, *Zostera noltei* (Hornemann) is the the accepted spelling of '*noltei*' but both '*Z. noltei*' and '*Z. noltii*' are found in the literature.

Listed By

- none -

Further information sources

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Habitat review

Ecology

Ecological and functional relationships

- The nature of intertidal ecosystems (immersion and emersion) means that seagrass beds are exposed to a range of varying environmental factors, such as temperature, desiccation and solar radiation (Massa *et al*., 2009).
- The transport of oxygen to the roots and rhizomes produces an oxygenated microzone around them, which increases the penetration of oxygen into the sediment.
- *Zostera* sp. support numerous epiphytes and periphyton, e.g. leaves may be colonized by microphytobenthos such as diatoms and blue green algae. The brown algae *Halothrix lumbricalis* and *Leblondiella densa* are only found on *Zostera* leaves and *Cladosiphon contortus* occurs primarily on the rhizomes of *Zostera* sp.
- Algal epiphytes, such as the diatoms *Cocconeis scutellum* and *Cocconeis placentula*, on the leaves of *Zostera noltei* are grazed by small prosobranch molluscs, for example, *Rissoa* spp., *Hydrobia* spp. and *Littorina littorea*.
- The sediment supports a diverse infauna, including deposit feeders such as, *Arenicola marina*, *Pygospio elegans*, *Scrobicularia plana*, *Limecola balthica*, and *Corophium volutator*; as well as suspension feeders such as *Cerastoderma edule* (Connor *et al*., 1997b; Davison & Hughes, 1998).
- *Zostera noltei* density and biomass can be influenced by the presence of high densities of lugworms (*Arenicola marina*), due to the sediment bioturbation (Philippart, 1994a).
- Lugworms (*Arenicola marina*) are also known to affect the densities of other species associated with *Zostera notii* beds, for example, *Pygospio elegans* (Reise 1985), *Corophium volutator* and juveniles of various worm and bivalve species (Flach 1992a & b)
- *Hediste diversicolor* are reported to eat the leaves and seeds of *Zostera noltei* plants (Hughes *et al*., 2000).
- The epifauna and infauna are vulnerable to predation by intertidal fish, and shore crabs (*Carcinus maenas*) at high tide.
- Since the decline of *Zostera marina* beds *Zostera noltei* has become the preferred food for dark-bellied Brent geese (*Branta bernicla*).
- Intertidal *Zostera noltei* beds are heavily grazed by overwintering wildfowl and are an important food source for Brent geese (*Branta bernicla*), wigeon (*Anas penelope*), mute and whooper swans (*Cygnus olor* and *Cygnus cygnus*).
- Intertidal seagrass beds are improtant spawning areas for transient fishes, with the tidal migration of garfish *Belone belone* being specifically directed at *Zostera noltei* beds for spawning. The eggs of the herring *Clupea harengus* were found at densities twenty times higher in seagrass beds than adjacent intertidal brown algal patches (Polte & Asmus, 2006).

Seasonal and longer term change

Zostera beds are naturally dynamic and may show marked seasonal changes. Leaves are shed in winter, although *Zostera noltei* retains its leaves longer than *Zostera marina*. Leaf growth stops in September/October (Brown, 1990). Leaves are lost, or removed by grazing or wave action over winter. For example, in the Wadden Sea, Nacken & Reise (2000) noted that 50% of leaves fell off, while Brent geese removed 63% of the plant biomass.
Zostera noltei overwinters as rhizome and shoot fragments, resulting in 'recruitment' of several

cohorts in the following spring (Marta *et al.*, 1996). However, Nacken & Reise (2000) noted that the *Zostera noltei* beds recovered normal shoot density and that grazing wildfowl helped to maintain a balance between accretion and erosion within the bed, without which recovery was inhibited. The rhizome of *Zostera noltei* has limited carbohydrate storage capability, Marta *et al.* (1996) and Dawes & Guiry (1992) regarded this species as ephemeral, taking advantage of seasonal increases in nutrients and light especially to grow rapidly in spring and early summer.

Where present, *Arenicola marina* spawns synchronously either once or twice a year; the precise timing depending on location (Howie, 1959; Clay, 1967; Bentley & Pacey, 1992). *Cerastoderma edule* spawns between March - August with a peak in summer, *Limecola balthica* spawns in February - March with another peak in autumn, whilst *Scrobicularia plana* spawns in summer (Fish & Fish, 1996).
Settlement of spat in intertidal bivalves is generally sporadic (see *Cerastoderma edule* for review). While *Limecola balthica* may be protected from low winter temperatures by its depth in the sediment, *Cerastoderma edule* is vulnerable to low temperatures in winter, especially in severe winters. Therefore, cockle mortality is likely over winter due to low temperatures, lack of food and predation, especially from wildfowl such as the oystercatcher (*Haematopus ostralegus*). Further mortality is likely in year one cockles due to exhausted energy reserves and predation by the shore crab *Carcinus maenas*. Epifaunal species, such as *Littorina littorea* and *Hydrobia ulvae* may suffer additional wildfowl predation over winter without the refuge provided by *Zostera noltei* leaves, however, being mobile they are able to seek alternative food sources.

Habitat structure and complexity

Leaves slow current and water flow rates under the canopy, which encourages settlement of fine sediments, detritus and larvae (Orth, 1992). Seagrass rhizomes stabilize sediment and protect against wave disturbance. Presence of seagrass increases species diversity by favouring sedentary species that require stable substrata (Orth, 1992; Davison & Hughes, 1998).

Zostera noltei provides shelter or substratum for a wide range of species, especially epiphytes and periphyton. Epiphytic species may be grazed by other species (Davison & Hughes, 1998) such as the mobile epifauna, *Hydrobia ulvae* and *Littorina littorea*present in seagrass beds. The sediment supports a rich infauna of polychaetes, bivalve molluscs and the mud amphipod *Corophium volutator*. Cockle beds (*Cerastoderma edule*) are often associated with intertidal seagrass beds. The sediment also includes a diverse meiofauna, for example many species of free-living turbellarians, ostracods and copepods (Asmus & Asmus, 2000b). In addition, intertidal seagrass beds are visited by several fish species when immersed.

Productivity

Seagrass beds are characterized by high productivity and biodiversity and are considered to be of great ecological and economic importance (Davison & Hughes, 1998; Asmus & Asmus, 2000b). Primary production is derived from phytoplankton, microphytobenthos and *Zostera* sp. In addition, organic carbon is derived from the input of detritus into the system (for estimates of g C/m▯2;/year see Asmus & Asmus, 2000b). Asmus & Asmus (2000b) reported that seagrass beds are sediment traps and nutrient sinks, which under storm conditions may become nutrient sources for the surrounding ecosystems, and are, therefore, important for the material flux in the ecosystem. For example, in the Sylt-Rømø Bight, Asmus & Asmus (2000b) estimated that the seagrass beds contributed significantly to material flux within the total intertidal system even though the seagrass beds only covered 12% of the intertidal area.

In periods when *Zostera noltei* dies off (winter), epiphytic algae and periphyton contribute significantly to the overall community productivity and above ground biomass (Welsh *et al.*, 2000; Philippart, 1995b). Philippart (1995b) estimated that by May on an intertidal mudflat off Terschelling, the Netherlands, periphyton biomass equalled *Zostera noltei* biomass, declining to 20% of the total above ground biomass by the end of September. Detritus food chains within the seagrass beds are driven by bacterial decomposition of dead seagrass tissue and other detritus. Dissolved organic matter (DOM) leaching from seagrass and bacterial decomposition supports high numbers of heterotrophic protists. Seagrass detritus is rich in micro-organisms, e.g. 1 g (dry weight) may support on average 9 mg of bacteria and protists, including heterotrophic flagellates and ciliates (Davison & Hughes, 1998). Dead seagrass leaves can be transported by currents to great depths or washed up on the shore; hence supporting detritus based food chains and communities in distant areas of the coast (Davison & Hughes, 1998). Although primary production is high, secondary production is similar in un-vegetated areas and seagrass beds (Asmus & Asmus, 2000b). Asmus & Asmus (2000b) presented a general food web for intertidal *Zostera* spp. beds, noting that loss of intertidal seagrass beds resulted in profound changes in the food web of the total ecosystem.

Recruitment processes

Zostera sp. are monoecious perennials (Phillips & Menez, 1988; Kendrick *et al.*, 2012; 2017) but may be annuals under stressful conditions (Phillips & Menez, 1988). *Zostera* sp. and seagrasses are flowering plants adapted to an aquatic environment. They reproduce sexually via pollination of flowers and resultant sexual seed but can also reproduce and colonize sediment asexually via rhizomes. Seagrass species disperse and recruit to existing and new areas via pollen, seed, floating fragments or reproductive structures, vegetative growth (via rhizomes), and via biotic vectors such as wildfowl (e.g. geese).

Genetic analysis of populations has revealed that sexual reproduction and seed are more important for recruitment and the persistence of seagrass beds than previously thought (Phillips & Menez, 1988; Kendrick *et al.*, 2012; 2017). Kendrick *et al.* (2012; 2017) concluded that seagrass species are capable to extensive long distance dispersal based on the high level of genetic diversity and connectivity observed in natural populations.

Zostera sp. flowers release pollen in long strands, dense enough to remain at the depth they were released for several days, therefore, increasing their chance of pollinating receptive stigmas. Pollen are long-lived (ca 8 hours) but not ideally for long-distance dispersal so that the pollen of *Zostera noltei* is estimated to travel up to 10 m, while that of *Zostera marina* travels up to 15 m, although most is intercepted by the canopy within 0.5 m (Zipperle *et al.*, 2011; McMahon *et al.*, 2014; Kendrick *et al.*, 2012; 2017). Pollination occurs mostly within the seagrass meadow or adjacent meadows, and outcrossing is high in Zostera sp. (Zipperle *et al.*, 2011). Zipperle *et al.* (2011) that the low level of inbreeding observed was due to self-incompatibility resulting in seed abortion or seedling mortality.

Seeds develop within a membranous wall that photosynthesises, developing an oxygen bubble within the capsule, eventually rupturing the capsule to release the seed. *Zostera* sp. seeds are negatively buoyant, and generally sink.

Hootsmans et al. (1987) reported that each flowering shoot of Zostera noltei produces 3-4 flowers containing 2-3 seed each. They estimated a potential seed production of 9000/m^2; based on the maximum density of flowering shoots in their quadrats in the Zandkreek, Netherlands. Most seeds were released in August in the Zandkreek but the actual seed densities were much lower than predicted (Hootsmans et al., 1987). However, the density of flowering shoots is highly variable. Phillips & Menez (1988) state that seedling mortality is extremely high. Fishman & Orth (1996) report that 96% of *Zostera marina* seeds were lost from uncaged test areas due to transport (dispersal) or predation. Phillips & Menez (1988) note that seedlings rarely occur within the eelgrass beds except in areas cleared by storms, blow-out or excessive herbivory. Den Hartog (1970) noted that although the seed set was high, *Zostera noltei* seedlings were rarely seen in the wild, suggesting that vegetative reproduction may be more important than sexual reproduction (Davison & Hughes, 1998). Experimental germination was increased by low salinity (1-10 psu) in *Zostera noltei* and no germination occurred at salinities above 20 psu, however germination was independent of temperature (Hughes et al., 2000). Hootsmans et al. (1987) noted that potential recruitment was maximal (32% of seeds) at 30°C and 10 psu, and no recruitment occurred at 30 psu and they estimated that, in 1983 <5>Zostera noltei plants in the Zandkreek originated from seed.

Conversely, Zipperle *et al.* (2009b) reported that the annual seed density was high and aggregated, in ranging from 367.5 to 487.5 per square metre in *Zostera noltei* meadows in the German Wadden Sea. Furthermore, 16-25% of seed germinated in the laboratory, and 12% in the field, and 205 of shoots observed in one year (2004) were seedlings, and that 7-33% of seedlings were from the local adult population, of which 30% were from seeds set 3 years earlier. They concluded that seeds were viable for at least 3 years, and formed a persistent seed bank within the sediment. They also noted that the remaining 70% of seedling recruitment was from either outside the meadow or from seeds older than 3 years. In addition, Manley *et al.* (2015) reported that seed density in *Zostera marina* meadows in Hog Island bay, Virginia, USA, decreased with increasing distance from the parent, that seed predation was low regardless of the distance from the edge of the bed, and that the seed density was strongly correlated with seed density from the previous year. They concluded that *Zostera* could quickly rebound from disturbances as long as a seed source remained.

Seeds have a limited dispersal range of a few metres although they may be dispersed by storms that disturb the sediment (Zipperle et al., 2009b; McMahon et al., 2014; Kendrick *et al.*, 2012; 2017). However, in New York, USA, Churchill et al .(1985) recorded 5-13% of *Zostera marina* seeds with attached gas bubbles and achieved an average dispersal distance of 21 m and up to 200 m in a few cases.

Seeds can also be dispersed within positively buoyant flowering branches (rhipidia) for weeks or months, and up to 100s of kilometres i.e. 20-300 km (McMahon et al., 2014; Kendrick *et al.*, 2012; 2017). Kendrick *et al.* (2012) noted that genetic differences between seagrass populations (inc. *Zostera marina* and *Zoster noltei*) showed limited differences regionally, i.e. <100>Zostera marina rhipidia fragments could be transported over 150 km (Kendrick *et al.*, 2012; 2017).

Seagrass seeds may also be transported in the gut of fish, turtles, dugong, manatees, and in the gut or on the feet of waterfowl (McMahon et al., 2014; Kendrick *et al.*, 2012; 2017). For example, 30% of freshwater eelgrass (*Naja marina*) seeds fed to ducks in Japan survived and successfully germinated after passage through their alimentary canals and potentially transported 100-200 km (Fishman & Orth, 1996). McMahon *et al.* (2014) noted that *Zostera* seeds are dormant and viable for 12 months or more. However, the extent of their biotic dispersal is unclear.

Seagrass reproduces vegetatively, i.e. by growth of rhizome. Vegetative reproduction was thought to exceed seedling recruitment except in areas of sediment disturbance (Reusch et al. 1998; Phillips & Menez 1988), although genetic analysis suggests a more complex process (Kendrick *et al.*, 2012; 2017). New leaves appear in spring and seedling appear in spring, and eelgrass meadows develop over intertidal flats in summer, due to vegetative growth. For example, a shoot density of 1000-23000 /m was reported in the Zandkreek estuary, Netherlands (Vermaat & Verhagen, 1996). Leaf growth stops in September/October and leaves are shed although *Zostera noltei* keeps its leaves longer than *Zostera marina* in winter. In the intertidal the combined action of grazing and wave action causes leaves to be lost over winter, and the plant reduced to its rhizomes within the sediment. For example, Nacken & Reise (2000) reported that 50% of leaves fell off while the rest were taken by birds in the Wadden Sea.

The rhizome of *Zostera noltei* is thinner than that of the longer lived *Zostera marina* and its growth is rapid and ephemeral in nature, taking advantage of seasonal increases in light and nutrients rather than metabolites stored in the rhizome (Marta *et al.*, 1996; Dawes & Guiry, 1992). Marta *et al.* (1996) reported shoot growth rates of ca 0.2 cm/day (winter minimum) to ca 0.8-0.9 cm/day (summer maximum) in the Mediterranean (with winter temperature of 12°C and summer maximum temperature of 23.2°C). Manley et al. (2014) reported a rhizome growth rate of 26 cm/yr in *Zostera marina*.

They also stated that the rhizomes were short lived, <1>et al. (2009a, 2011) reported that intertidal *Zostera noltei* probably persist for 4-5 years, although large clones in the Mediterranean were reported to be up to 14.7 years old. They also noted that although individual 'genets' may not be long-lived the *Zostera noltei* meadow in the German Wadden Sea had persisted since 1936. Similarly, examination of the population structure of a *Zostera marina* bed in the Baltic Sea suggested that individual genotypes (vegetatively produced clones) may be up to 50 years old and further suggested that the eelgrass bed at that site had been present for at least 67 years (Reusch *et al.*, 1998).

Recruitment and recovery of seagrass meadows depend on numerous factors, and is an interplay between seed recruitment to open or disturbed areas, the seed bank, and expansion by vegetative growth. Zipperle *et al.*, (2009a, b; 2010, 2011) suggested that intermediate levels of disturbance, typical of the Wadden Sea, enhanced recruitment. They suggested that disturbance may enhance dispersal of seed, enhance sexual reproduction via gap formation and increase outcrossing by reducing the size of vegetative clones. *Zostera noltei* seed and seedling density was higher in experimental pits dug to emulate greese feeding pits than controls, which concurred with observations by prior authors (Nacken, 1998; Zipperle *et al.*, 2010). For example, Tubbs &Tubbs (1983) reported that wildfowl were responsible for a reduction of 60 to 100% in *Zostera noltei* biomass from mid-October to mid-January. The removal of plants by wildfowl is part of the natural seasonal fluctuation in seagrass cover. Similarly, Nacken & Reise (2000) found that in intertidal *Zostera noltei*beds biomass was reduced by 63% due to wildfowl feeding. The beds, however, recovered by the following year and the authors suggested that this disturbance was necessary for the persistence of intertidal populations.

Similarly, Han *et al.* (2012) examined burial (up to 6 cm) and erosion (down to 6 cm) of *Zostera noltei* rhizomes in the Scheldt estuary, Netherlands. Survival of rhizomes was to all treatments was high (81-100%), and buried rhizomes extended and grew to their preferred depth quickly, i.e. within 21 days under 4 cm of burial. Han *et al.* (2012) noted that rhizomes were less likely to extend into experimental hollows than hills at the edge of the meadow but that *Zostera notlei* could fill gaps of 0.13 m^2 with 1 month. However, Zipperle et al., 2009a, 2011) reported that *Zostrea notlei* bed in the Königshafen, Wadden Sea, recovered up to 20% cover within four years after a 99% loss of cover due to a heat stress event, probably combined with increased sediment mobility, in 2003/04. Zipperel *et al.*, 2009a suggested that recover from severe events was possible as long as seedling recruitment and subsequent vegetative growth reached a density sufficient to survive winter mortality.

Recruitment is also affected by local environmental conditions, and isolation due to coastal geomorphology such as islands and inlets, hydrography and even biological structures. For example, a rare genetic selection was observed between subtidal and intertidal meadows of *Zostera marina* and genetic differentiation between *Zostera marina* populations was six times higher between Norwegian fjords than within fjords (Kendrick *et al.*, 2017). Reynolds *et al.* (2013) estimated that natural recovery of *Zostera marina* seagrass beds in the isolated coastal bays of the Virginian coast, USA would have taken between 125 and 185 years to recover from the substantial decline due to wasting disease in the 1930s. Although small patches were observed in the 1990s seagrass was locally extinct for 60 years. Seed transplantation in the late 1990s resulted in the restoration of ca 1600 ha of seagrass within 10 years Reynolds *et al.* (2013).

Potential recruitment may be hampered by competition with infauna such as the ragworm *Hediste diversicolor* or blow lug *Arenicola marina* (Philippart, 1994a; Hughes *et al.*, 2000). Hughes *et al.* (2000) noted that *Hediste diversicolor* consumed leaves and seeds of *Zostera noltei* by pulling them into their burrow, therefore reducing the survival of seedlings. The distribution of *Zostera noltei* can be restricted by burrowing and bioturbation of infauna such as *Hediste diversicolor* and *Arenicola marina*. Philippart (1994a) concluded that the blow lug populations in the Wadden Sea may have contributed to the decline in the *Zostera noltei* beds over the previous 25 years. The rhizome mat of the seagrass can inhibit burrowing and colonization of the seagrass bed by burrowing infauna (Hughes et al., 2000; Philippart, 1994a). At low densities, blow lug may be beneficial as they increase nutrient flux and oxygenation in the sediment. *Corophium volutator* has been reported to inhibit colonization of mud by *Salicornia* sp. (Hughes *et al.*, 2000) and where present may also inhibit *Zostera noltei* recruitment.

Epifaunal species such as *Hydrobia ulvae* are widely distributed, mobile, occur at high densities, and have a planktonic life cycle suggesting that they would recruit rapidly. Similarly *Littorina littorea* is likely to recruit rapidly.
Development of both *Arenicola marina* and *Pygospio elegans* starts in the female's tube. Larvae of *Pygospio elegans* are pelagic, while *Arenicola marina* larvae migrate up the shore. Recruitment in *Arenicola marina* is rapid, especially where there are adjacent populations present.
Recruitment in infaunal bivalve populations is sporadic due to variation in larval supply and post-settlement mortality. For instance, although recruitment in *Cerastoderma edule* is likely to occur annually, significant recruitment to the population may take up to five years.

Time for community to reach maturity

Zostera noltei is able to recover relatively quickly compared to other seagrass species (Marbà *et al.*, 2004). Nacken & Reise (2000) noted that *Zostera noltei* beds had returned to the previous abundance within a year following leaf loss and grazing by wildfowl. The majority of species associated with intertidal seagrass beds are not restricted to the biotope (Asmus & Asmus, 2000b), with the exception of *Zostera* sp. Specific epiphytes, and are likely to be present in the sediment or migrate into the developing bed. *Zostera noltei* is regarded as a relatively ephemeral species (Dawes & Guiry, 1992).

Additional information

No text entered.

Preferences & Distribution

Habitat preferences

Depth Range	Upper shore, Mid shore
Water clarity preferences	
Limiting Nutrients	Nitrogen (nitrates), Phosphorus (phosphates)
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Physiographic preferences	Enclosed coast / Embayment
Biological zone preferences	Eulittoral
Substratum/habitat preferences	Muddy sand, Sandy mud
Tidal strength preferences	
Wave exposure preferences	Extremely sheltered, Sheltered, Very sheltered
Other preferences	No text entered

Additional Information

Populations of *Zostera noltii* occur from the Mediterranean to southern Norway, the Black Sea, the Canary Islands and are regarded to prefer sea temperatures between about 5 - 30 C. However, Massa *et al*. (2009) found *Zostera noltii* to be tolerant of temperatures up to 37°C for an exposure period of 21 days. Therefore, they may not be sensitive to the range of temperatures likely in the British Isles (Davison & Hughes, 1998). Intertidal populations may be damaged by frost (den Hartog, 1987) and Covey & Hocking (1987) reported defoliation of *Zostera noltii* in the upper reaches of mudflats in Helford River due to ice formation in the exceptionally cold winter of 1987. However, the rhizomes survived and leaves are lost at this time of year due to shedding, storms or grazing with little apparent effect (Nacken & Reise, 2000).

Seagrass requires a particular light regime to net photosynthesize and grow. The intertidal is likely to be more turbid than the shallow subtidal occupied by *Zostera marina* due to runoff and re-suspension of sediment by wave and tidal action. Turbidity decreases light penetration and reduces the time available for net photosynthesis. However, intertidal *Zostera noltii* 'escapes' this turbidity since it is able to take advantage of the high light intensities at low tide (Vermaat *et al*., 1996).

Seagrass beds act as sinks for nutrients (Asmus & Asmus, 2000b) and as such, nitrogen may not be limiting in sparse intertidal seagrass beds. In sandy sediments phosphate may be limiting where it is adsorbed onto particles (Short, 1987; Jones *et al*., 2000).

Species composition

Species found especially in this biotope

- *Cladosiphon zosterae*

- *Halothrix lumbricalis*
- *Leblondiella densa*
- *Myrionema magnusii*
- *Punctaria crispata*
- *Rhodophysema georgii*

Rare or scarce species associated with this biotope

- *Halothrix lumbricalis*
- *Leblondiella densa*

Additional information

The MNCR survey recorded 185 species from this biotope. Asmus & Asmus (2000b, Table 1 and Figure 8) review species diversity in intertidal seagrass beds in the Sylt-Rømø. Davison & Hughes (1998) list representative and characteristic species of *Zostera* sp. beds. Species lists for major eelgrass beds are available for the Helford Passage (Sutton & Tompsett, 2000). Species lists are likely to underestimate the total number of species present, especially with respect to microalgal epiphytes, bacteria and meiofauna. Asmus & Asmus (2000b) noted that ostracods and copepods and fish were under estimated. However, many of the species found in intertidal seagrass beds are not specific to the community (Asmus & Asmus, 2000b). Therefore, although intertidal seagrass beds make a major contribution to primary and secondary production within the intertidal sedimentary ecosystem, loss of the seagrass beds would have a minor effect on species richness, especially with respect to the infaunal community (Asmus & Asmus, 2000b).

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

Zostera noltei is the main species creating this habitat as removing *Zostera marina* plants would result in the disappearance of this biotope. Although a wide range of species are associated with seagrass beds which provide habitat and food resources, these species occur in a range of other biotopes and are, therefore, not considered to characterize the sensitivity of this biotope (d'Avack *et al*., 2014). However, seagrasses worldwide have been shown to exhibit a three-way symbiotic relationship with the small lucinid bivalves (hatchet-shells, e.g. *Loripea* and *Lucinoma*) and their endosymbiotic sulfide-oxidizing gill bacteria (Van der Heide *et al*., 2012). In experiments, the sulfide-oxidizing gill bacteria of *Loripes lacteus* were shown to reduce sulfide levels in the sediment and enhance the productivity of *Zostera noltei*, while the oxygen relased from the roots of *Zoster noltei* was of benefit to *Loripes* (Van der Heide *et al*., 2012). Therefore, the effects of pressures on other components of the community are reported where relevant. Epiphytic grazers, such as *Hydrobia ulvae*, *Rissoa* spp. and *Lacuna vincta* remove fouling epiphytic algae that would otherwise smother *Zostera* spp. *Hydrobia ulvae* and *Lacuna* spp. have been shown to reduce the density of epiphytes on *Zostera noltei* in the Dutch Wadden Sea (Philippart, 1995a) and *Zostera marina* in Puget Sound (Nelson, 1997) respectively with subsequent enhancement of the productivity of sea grass. Nevertheless, *Zostera marina* is the main species creating this habitat and the removal or loss of *Zostera marina* plants would result in the disappearance of this biotope. Therefore, *Zostera noltei* is considered to be the most important species for the development of and, hence, sensitivity of the biotope, although the effects of pressures on other components of the community are reported where relevant.

Zostera noltei is the smallest of British seagrasses. The species occurs on sedimentary substrata, in sheltered or extremely sheltered locations with low current velocity. It is predominantly found in the intertidal region but can also be found subtidally. However, where water cover is permanent, *Zostera noltei* is often out-competed by *Zostera marina* (Borum *et al*., 2004).

Resilience and recovery rates of habitat

Zostera spp. are monoecious perennials (Phillips & Menez, 1988; Kendrick *et al*., 2012; 2017) but may be annuals under stressful conditions (Phillips & Menez, 1988). *Zostera* sp. and seagrasses are flowering plants adapted to an aquatic environment. They reproduce sexually via pollination of flowers and resultant sexual seed but can also reproduce and colonize sediment asexually via rhizomes. Seagrass species disperse and recruit to existing and new areas via pollen, seed, floating fragments or reproductive structures, vegetative growth (via rhizomes), and via biotic vectors such as wildfowl (e.g. geese). Genetic analysis of populations has revealed that sexual reproduction and seed are more important for recruitment and the persistence of seagrass beds than previously thought (Phillips & Menez, 1988; Kendrick *et al*., 2012; 2017). Kendrick *et al*. (2012; 2017) concluded that seagrass species are capable of extensive long distance dispersal based on the high level of genetic diversity and connectivity observed in natural populations.

Zostera sp. flowers release pollen in long strands, dense enough to remain at the depth they were released for several days, therefore, increasing their chance of pollinating receptive stigmas. Pollen are long-lived (ca 8 hours) but not ideally for long-distance dispersal so that the pollen of *Zostera noltei* is estimated to travel up to 10 m, while that of *Zostera marina* travels up to 15 m, although most are intercepted by the canopy within 0.5 m (Zipperle *et al*., 2011; McMahon *et al*., 2014; Kendrick *et al*., 2012; 2017). Pollination occurs mostly within the seagrass meadow or adjacent meadows, and outcrossing is high in *Zostera* sp. (Zipperle *et al.*, 2011). Zipperle *et al.* (2011) that the low level of inbreeding observed was due to self-incompatibility resulting in seed abortion or seedling mortality.

Seeds develop within a membranous wall that photosynthesises, developing an oxygen bubble within the capsule, eventually rupturing the capsule to release the seed. *Zostera* sp. seeds are negatively buoyant and generally sink. Hootsmans *et al.* (1987) reported that each flowering shoot of Zostera noltei produces 3-4 flowers containing 2-3 seed each. They estimated a potential seed production of 9000/m^2 based on the maximum density of flowering shoots in their quadrats in the Zandkreek, Netherlands. Most seeds were released in August in the Zandkreek but the actual seed densities were much lower than predicted (Hootsmans *et al.*, 1987). However, the density of flowering shoots is highly variable. Phillips & Menez (1988) state that seedling mortality is extremely high. Fishman & Orth (1996) report that 96% of *Zostera marina* seeds were lost from uncaged test areas due to transport (dispersal) or predation. Phillips & Menez (1988) note that seedlings rarely occur within the eelgrass beds except in areas cleared by storms, blow-out or excessive herbivory. Den Hartog (1970) noted that although the seed set was high, *Zostera noltei* seedlings were rarely seen in the wild, suggesting that vegetative reproduction may be more important than sexual reproduction (Davison & Hughes, 1998). Experimental germination was increased by low salinity (1-10 psu) in *Zostera noltei* and no germination occurred at salinities above 20 psu, however, germination was independent of temperature (Hughes *et al.*, 2000). Hootsmans *et al.* (1987) noted that potential recruitment was maximal (32% of seeds) at 30°C and 10 psu, and no recruitment occurred at 30 psu and they estimated that, in 1983 <5% of *Zostera noltei* plants in the Zandkreek originated from seed.

Conversely, Zipperle *et al.* (2009b) reported that the annual seed density was high and aggregated, in ranging from 367.5 to 487.5 per square metre in *Zostera noltei* meadows in the German Wadden Sea. Furthermore, 16-25% of seed germinated in the laboratory, and 12% in the field, and 20% of shoots observed in one year (2004) were seedlings, and that 7-33% of seedlings were from the local adult population, of which 30% were from seeds set 3 years earlier. They concluded that seeds were viable for at least 3 years, and formed a persistent seed bank within the sediment. They also noted that the remaining 70% of seedling recruitment was from either outside the meadow or from seeds older than 3 years. In addition, Manley *et al.* (2015) reported that seed density in *Zostera marina* meadows in Hog Island Bay, Virginia, USA, decreased with increasing distance from the parent, that seed predation was low regardless of the distance from the edge of the bed, and that the seed density was strongly correlated with seed density from the previous year. They concluded that *Zostera* could quickly rebound from disturbances as long as a seed source remained.

Seeds have a limited dispersal range of a few metres although they may be dispersed by storms that disturb the sediment (Zipperle *et al.*, 2009b, 2011; McMahon *et al.*, 2014; Kendrick *et al.*, 2012; 2017). However, in New York, USA, Churchill *et al.* (1985) recorded 5-13% of *Zostera marina* seeds with attached gas bubbles and achieved an average dispersal distance of 21 m and up to 200 m in a few cases. Seeds can also be dispersed within positively buoyant flowering branches (rhipidia) for weeks or months, and up to 100s of kilometres i.e. 20-300 km (McMahon *et al.*, 2014; Kendrick *et al.*, 2012; 2017). Kendrick *et al.* (2012) noted that genetic differences between seagrass populations (inc. *Zostera marina* and *Zoster noltei*) showed limited differences regionally, i.e. <100 km but increased with long-distances of hundreds of kilometres. In Swedish waters, a model predicted that *Zostera marina* rhipidia fragments could be transported over 150 km (Kendrick *et al.*, 2012; 2017).

Seagrass seeds may also be transported in the gut of fish, turtles, dugong, manatees, and in the gut or on the feet of waterfowl (McMahon et al., 2014; Kendrick *et al.*, 2012; 2017). For example, 30% of freshwater eelgrass (*Naja marina*) seeds fed to ducks in Japan survived and successfully germinated after passage through their alimentary canals and potentially transported 100-200 km (Fishman & Orth, 1996). McMahon *et al.* (2014) noted that *Zostera* seeds are dormant and viable for 12 months or more. However, the extent of their biotic dispersal is unclear.

Seagrass reproduces vegetatively, i.e. by the growth of rhizome. Vegetative reproduction was thought to exceed seedling recruitment except in areas of sediment disturbance (Reusch *et al.* 1998; Phillips & Menez 1988), although genetic analysis suggests a more complex process (Kendrick *et al.*, 2012; 2017). New leaves appear in spring and seedling appear in spring, and eelgrass meadows develop over intertidal flats in summer, due to vegetative growth. For example, a shoot density of 1000-23000 /m was reported in the Zandkreek estuary, Netherlands (Vermaat & Verhagen, 1996). Leaf growth stops in September/October and leaves are shed although *Zostera noltei* keeps its leaves longer than *Zostera marina* in winter. In the intertidal the combined action of grazing and wave action causes leaves to be lost over winter, and the plant reduced to its rhizomes within the sediment. For example, Nacken & Reise (2000) reported that 50% of leaves fell off while the rest were taken by birds in the Wadden Sea.

The rhizome of *Zostera noltei* is thinner than that of the longer-lived *Zostera marina* and its growth is rapid and ephemeral in nature, taking advantage of seasonal increases in light and nutrients rather than metabolites stored in the rhizome (Marta *et al.*, 1996; Dawes & Guiry, 1992). Marta *et al.* (1996) reported shoot growth rates of ca 0.2 cm/day (winter minimum) to ca 0.8-0.9 cm/day (summer maximum) in the Mediterranean (with a winter temperature of 12°C and summer maximum temperature of 23.2°C). Manley *et al.* (2015) reported a rhizome growth rate of 26 cm/yr. in *Zostera marina*.

They also stated that the rhizomes were short-lived, <1 year, presumably from one growing season to the next. However, Zipperle *et al.* (2009a, 2011) reported that intertidal *Zostera noltei* probably persist for 4-5 years, although large clones in the Mediterranean were reported to be up to 14.7 years old. They also noted that although individual 'genets' may not be long-lived the *Zostera noltei* meadow in the German Wadden Sea had persisted since 1936. Similarly, an examination of the population structure of a *Zostera marina* bed in the Baltic Sea suggested that individual genotypes (vegetatively produced clones) may be up to 50 years old and further suggested that the eelgrass bed at that site had been present for at least 67 years (Reusch *et al.*, 1998).

Recruitment and recovery of seagrass meadows depend on numerous factors and is an interplay between seed recruitment to open or disturbed areas, the seed bank, and expansion by vegetative growth. Zipperle *et al.* (2009a,b; 2010, 2011) suggested that intermediate levels of disturbance, typical of the Wadden Sea, enhanced recruitment. They suggested that disturbance may enhance dispersal of seed, enhance sexual reproduction via gap formation and increase outcrossing by reducing the size of vegetative clones. *Zostera noltei* seed and seedling density were higher in experimental pits dug to emulate geese feeding pits than controls, which concurred with observations by prior authors (Nacken, 1998; Zipperle *et al.*, 2010). For example, Tubbs & Tubbs (1983) reported that wildfowl were responsible for a reduction of 60 to 100% in *Zostera noltei* biomass from mid-October to mid-January. The removal of plants by wildfowl is part of the natural seasonal fluctuation in seagrass cover. Similarly, Nacken & Reise (2000) found that in intertidal *Zostera noltei* beds biomass was reduced by 63% due to wildfowl feeding. The beds, however, recovered by the following year and the authors suggested that this disturbance was necessary for the persistence of intertidal populations.

Similarly, Han *et al.* (2012) examined burial (up to 6 cm) and erosion (down to 6 cm) of *Zostera noltei* rhizomes in the Scheldt estuary, Netherlands. Survival of rhizomes was to all treatments was high (81-100%), and buried rhizomes extended and grew to their preferred depth quickly, i.e. within 21 days under 4 cm of burial. Han *et al.* (2012) noted that rhizomes were less likely to extend into experimental hollows than hills at the edge of the meadow but that *Zostera noltei* could fill gaps of 0.13 m^2 with 1 month. However, Zipperle *et al.* (2009a, 2011) reported that *Zostera noltei* bed in the Königshafen, Wadden Sea, recovered up to 20% cover within four years after a 99% loss of cover due to a heat stress event, probably combined with increased sediment mobility, in 2003/04. Zipperle *et al.* (2009a) suggested that recover from severe events was possible as long as seedling recruitment and subsequent vegetative growth reached a density sufficient to survive winter mortality.

Recruitment is also affected by local environmental conditions, and isolation due to coastal geomorphology such as islands and inlets, hydrography and even biological structures. For example, a rare genetic selection was observed between subtidal and intertidal meadows of *Zostera marina* and genetic differentiation between *Zostera marina* populations was six times higher between Norwegian fjords than within fjords (Kendrick *et al.*, 2017). Reynolds *et al.* (2013) estimated that natural recovery of *Zostera marina* seagrass beds in the isolated coastal bays of the Virginian coast, USA would have taken between 125 and 185 years to recover from the substantial decline due to wasting disease in the 1930s. Although small patches were observed in the 1990s seagrass was locally extinct for 60 years. Seed transplantation in the late 1990s resulted in the restoration of ca 1600 ha of seagrass within 10 years (Reynolds *et al.*, 2013). In addition, examination of seagrass meadows in Ria Formosa, Portugal, suggested that large and non-fragmented seagrass meadows had higher persistence values than small, fragmented meadows and, hence, that smaller patches were more vulnerable to disturbance (Cunha & Santos, 2009). Fonseca & Bell (1998) also suggested that loss of cover (below ca 50%) led to fragmentation, and loss of habitat structural integrity.

Potential recruitment may be hampered by competition with infauna such as the ragworm *Hediste diversicolor* or blow lug *Arenicola marina* (Philippart, 1994a; Hughes *et al.*, 2000). Hughes et al. (2000) noted that *Hediste diversicolor* consumed leaves and seeds of *Zostera noltei* by pulling them into their burrow, therefore reducing the survival of seedlings. The distribution of *Zostera noltei* can be restricted by burrowing and bioturbation of infauna such as *Hediste diversicolor* and *Arenicola marina*. Philippart (1994a) concluded that the blow lug populations in the Wadden Sea may have contributed to the decline in the *Zostera noltei* beds over the previous 25 years. The rhizome mat of the seagrass can inhibit burrowing and colonization of the seagrass bed by burrowing infauna (Hughes *et al.*, 2000; Philippart, 1994a). At low densities, blow lug may be beneficial as they increase nutrient flux and oxygenation in the sediment. *Corophium volutator* has been reported to inhibit colonization of mud by *Salicornia* sp. (Hughes *et al.*, 2000) and where present may also inhibit *Zostera noltei* recruitment.

Resilience assessment. Recovery of seagrass beds is dependent on numerous factors, including the supply of seed or other propagules, the remaining seed bank and vegetative growth but also the hydrodynamics (i.e. local and regional currents or isolation within bays or inlets), and the scale of the disturbance. Seagrass, and especially *Zostera noltei*, may recover quickly from small scale 'intermediate' disturbance, which may also enhance recruitment and resilience. *Zostera noltei* can recover quickly from the loss of cover up to 60 or 100% due to natural grazing and resultant pits. However, recovery may be prolonged after larger-scale effects, e.g. *Zostera noltei* recovered 20% of its prior cover after a 99% loss due to heat stress and sediment load within four years (Zipperle *et al.*, 2009a, 2011). Fragmentation of existing meadows may also increase their vulnerability to further disturbance (Fonseca & Bell, 1998; Cunha & Santos, 2009). In addition, recovery from the substantial loss of seagrass beds in the North Atlantic due to wasting disease in the 1930s has been limited (Davidson & Hughes, 1998). Seagrass beds remain nationally scarce in the UK and may have declined 25-45% in the last 25 years (although detailed datasets are lacking) but many beds remain under threat (Jackson *et al.*, 2013; Jones & Unsworth, 2015). Therefore, recovery from long-term, large-scale impacts may take several decades, especially where the loss of the seagrass beds result in changes in the habitat, loss of the seed bank or isolation slows recruitment. Therefore, where resistance is assessed as 'Medium' or 'Low', resilience is probably **'Medium'** and where resistance is 'None', resilience is probably **'Low',** depending on the effects of the pressure on the habitat.

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

Temperature is considered the overall parameter controlling the geographical distribution of seagrasses. All enzymatic processes, related to plant metabolism are temperature dependent and specific life cycle events, such as flowering and germination, are also often related to temperature (Phillips *et al.*, 1983). For seagrasses, temperature affects biological processes by increasing reaction rates of biological pathways. Photosynthesis and respiration increase with higher temperature until a point where enzymes associated with these processes are inhibited. Beyond a certain threshold, high temperatures will result in respiration being greater than photosynthesis resulting in a negative energy balance. Increased temperatures do also encourage the growth of epiphytes increasing the burden upon seagrass beds and making them more susceptible to disease (Rasmussen, 1977). Massa *et al.* (2009) investigated the thermal tolerance limits of *Zostera noltei* in a coastal lagoon system in Portugal. The study recorded that plant survival at 35°C and 37°C was 95% and 90% respectively. However, at 39°C and above the rate of shoot mortality was close to 100% (Massa *et al.*, 2009). *Zostera noltei* bed in the Königshafen, Wadden Sea, recovered up to 20% cover within four years after a 99% loss of cover due to a heat stress event, probably combined with increased sediment mobility, in 2003/04 (Zipperle *et al.*, 2009a, 2011). Cardoso *et al.* (2008) reported that the heat waves in 2003 and 2005 in the Mondego estuary, Portugal cut short the managed recovery of *Zostera noltei* beds from prior drought. Cardoso *et al.* (2008) noted that normal mean summer temperature of 21°C in 1961-1990 in central Portugal, was punctuated by heat waves of 23.8°C (mean) in August 2003 and 23.4°C (mean) in August 2005. Zipperle *et al.* (2009a) suggested that recovery from severe events was possible as long as seedling recruitment and subsequent vegetative growth reached a density sufficient to survive winter mortality.

Other species associated with seagrass habitats are also affected by changes in temperature. For instance, the gastropod *Lacuna vincta*, an important grazer found in seagrass beds, is near its southern range limit in the British Isles. Long-term increases in temperature due to human activity may limit the survival of the snail and restrict subsequent distribution whilst a short-term acute temperature increase may cause death. The loss of grazers could have detrimental effects on seagrass beds as the leaves provide a substratum for the growth of many species of epiphytic algae. These epiphytes may smother the *Zostera* plants unless kept in check by the grazing activities of gastropods and other invertebrates. Healthy populations of epiphyte grazers are therefore essential to the maintenance of seagrass beds.

Sensitivity assessment. A 5°C change in temperature over one month or a 2°C change in temperature over the period of a year is unlikely to cause direct mortalities as *Zostera noltei* is well within its thermal tolerance limits in the British Isles. Resistance is, therefore, considered 'High'. Recovery will be rapid once conditions return to normal resulting in a 'High' resilience score. The biotope is, therefore, assessed as 'Not sensitive' to a change in temperature at the pressure benchmark. However, in areas where seagrasses are already exposed to high temperatures, a change at the level of the benchmark may result in considerable losses.

Temperature decrease (local)	High Q: High A: High C: Medium	High Q: High A: Low C: Medium	Not sensitive Q: High A: Low C: Medium

Populations of *Zostera noltei* occur from the Mediterranean to southern Norway and *Zostera* sp. are regarded as tolerant of temperatures between about 5 -30°C. Therefore, they may tolerate the range of temperatures likely in the British Isles (Davison & Hughes 1998). Intertidal populations may be damaged by frost (Den Hartog, 1987) and Covey & Hocking (1987) reported defoliation of *Zostera noltei* in the upper reaches of mudflats in Helford River due to ice formation in the exceptionally cold winter of 1987. However, the rhizomes survived and leaves are usually lost at this time of year due to shedding, storms or grazing with little apparent effect (Nacken & Reise, 2000). Populations at the edge of the range are likely to be more intolerant of temperature change. Therefore, the biotope probably has a 'High' resistance and 'High' resilience to this pressure and is 'Not sensitive' at the benchmark level.

Salinity increase (local)	Medium Q: High A: Medium C: Medium	Medium Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium

In general, seagrass species have a wide salinity tolerance. Nejrup & Pedersen (2008) reported optimum salinities between 10 and 25 ppt. *Zostera noltei* is a euryhaline species found in the intertidal and more tolerant to extreme salinities than *Zostera marina*. Hypersaline conditions can affect the performance of angiosperms as changes in salinity may increase the energy requirements due to demanding osmotic adjustments (Touchette, 2007). For instance, a study by Vermaat *et al.* (2000) observed considerable mortalities of *Zostera noltei* plants at 35 ppt (25% survival for one test population and 60% for a second test population). Similarly, Fernández-Torquemada *et al.* (2006) found that both the growth and survival of *Zostera noltei* were significantly affected by high levels of salinity (>41 psu). Cardoso *et al.* (2008) also noted that periods of intense drought, associated with high salinities (>30) in the Mondego estuary, Portugal resulted in a decline in *Zostera noltei* biomass. Salinity also influences seed germination (Jackson pers comm.) so that persistent raised salinity may reduce recruitment from seed, recovery of the beds and possibly lead to its eventual decline. Cardoso *et al.* (2008) noted that the Mondego estuary remained at a salinity of 30-35 during the recovery phase, which may have explained its week recovery after the introduction of management. These findings suggest that *Zostera noltei* is ill-equipped to withstand extreme saline conditions. d'Avack *et al.* (2014) reported that phenotypic plasticity can play an important role in the ability of seagrasses to withstand external pressures such as changes in salinity. Changes in physiological and morphological characteristics of seagrass plants will enable species to cope with varying degrees of stress for an extended period of time (Maxwell *et al.*, 2014).

Sensitivity assessment. Even though *Zostera noltei* displays a wide tolerance to a range of salinities, an increase from 35 to above 40 units for the period of one year will cause some mortality of plants. This suggests that *Zostera noltei* will be adversely affected by activities such as brine discharges from a seawater desalination plant. Hence, resistance is assessed as **'Medium'**. Recovery by recolonization from surrounding communities will be fairly rapid once conditions return to normal so that resilience is assessed as **'Medium'**. The biotope is therefore assessed to have a **'Medium'** sensitivity to an increase in salinity at the pressure benchmark.

Salinity decrease (local)	High Q: Medium A: Medium C: Medium	High Q: High A: High C: High	Not sensitive Q: Medium A: Medium C: Medium

In general, seagrass species have a wide salinity tolerance. Nejrup & Pedersen (2008) reported optimum salinities between 10 and 25 ppt, while Den Hartog (1970) reported tolerance to salinity as low as 5 ppt. *Zostera noltei* is a euryhaline species found in the intertidal and more tolerant to extremes salinities than *Zostera marina*. Hyposaline conditions can, however, affect the performance of angiosperms as changes in salinity may increase the energy requirements due to demanding osmotic adjustments (Touchette, 2007). A study by Charpentier *et al.* (2005) investigated the consequences of a sudden decrease (from 15 to < 5) in water salinity on *Zostera noltei* over an extended period. The study found that *Zostera noltei* plants remained dominant for a period of 3 years after the initial drop in water salinity. The subsequent decline of seagrass beds in the area was not directly associated with low salinity but may have been the result of synergetic effects of sediment trapping and suspended particles brought along with decreased saline conditions. Once salinity levels returned to normal, *Zostera noltei* was able to rapidly recolonize from the shallow borders. Full recovery of *Zostera noltei* occurred within 10 years of the initial drop in salinity. d'Avack *et al.* (2014) reported that phenotypic plasticity can play an important role in the ability of seagrasses to withstand external pressures such as changes in salinity. Changes in physiological and morphological characteristics of seagrass plants will enable species to cope with varying degrees of stress for an extended period of time (Maxwell *et al*., 2014).

Most of the other intertidal species (e.g. *Hydrobia ulvae* and *Littorina littorea*) present in this biotope can also tolerate a wide range of salinities. Cardoso *et al.* (2008) however found that *Hydrobia ulvae* populations can be negatively impacted by changes in salinity observed during severe flooding. Similarly, both *Cerastoderma edule* and *Arenicola marina* have also been reported to be susceptible to a drop in salinities after heavy rains, especially at low tide.

Sensitivity assessment. *Zostera noltei* is more tolerant to changes in salinity than *Zostera marina* and a drop in salinity at the level of the benchmark is unlikely to result in mortality. Resistance is thus assessed as **'High'**. Recovery will be fairly rapid once conditions return to normal resulting in a **'High'** resilience. The biotope is, therefore, assessed as **'Not sensitive'** to a decrease in salinity at the pressure benchmark.

Water flow (tidal current) changes (local)	Medium Q: Medium A: Medium C: Medium	Medium Q: High A: Low C: Medium	Medium Q: Medium A: Low C: Medium

Human activities in coastal waters which alter hydrology have been implicated in the disappearance of seagrass beds. For instance, Van der Heide *et al.* (2007) noted that the construction of a dam in the Wadden Sea influencing the hydrological regime inhibited the recovery of *Zostera* plants after their initial decline following the wasting disease in the 1930s. The complex interactions existing between seagrass beds and water flow have been reviewed by d'Avack *et al.* (2014). Water flow determines the upper distribution of plants on the shore whilst plants mitigate the velocity of the flow by extracting momentum from the moving water. Reducing the flow increases water transparency and causes the deposition and retention of fine sediments. Increased flow rate, on the other hand, is likely to erode sediments, expose rhizomes and lead to loss of plants.

The highest current velocity a seagrass can withstand is determined by a threshold beyond which sediment resuspension and erosion rates are greater than the seagrasses ability to bind sediment and attenuate currents. In very strong currents, leaves might lie flat on the seabed reducing erosion under the leaves but not on the unvegetated edges which begin to erode. High velocity currents can thus change the configuration of patches within a meadow, creating striations and mounding in the seagrass beds. Such turreted profiles destabilise the bed and increase the risk of 'blow outs' (Jackson *et al*., 2013). Populations found in stronger currents are usually smaller, patchy and more vulnerable to storm damage.

A review by Koch (2001) determined that the range of current velocities tolerated by seagrass lies approximately between a minimum of 5 cm/s and a maximum of 180 cm/s. No exact numerical estimates were found for *Zostera noltei*. Recovery will depend on the species capacities to adapt to changes in water flow regime. A laboratory study by Peralta *et al.* (2006) on *Zostera noltei* demonstrated that plants are able to acclimate to hydrodynamic stresses by changing their architecture. When exposed to a water flow of 35 cm/s for four weeks, *Zostera noltei* plants had an improved anchoring system and changed leave morphology. The above ground/below ground biomass ratio was thereby reduced and the cross sections of leaves and rhizomes increased leading to a reduced risk of shoot breakage.

Sensitivity assessment: Any changes in hydrology will have a considerable impact on the integrity of the seagrass habitat. A change in water flow at the level of the benchmark of 10 to 20 cm/s for more than 1 year would cause some mortality in seagrasses. Therefore, resistance is assessed as **'Medium'**. Recovery will depend on the species capacities to adapt to changes in water flow regime but is considered to be fairly rapid. Resilience is thus assessed as **'Medium'** and sensitivity as **'Medium'** to changes in water flow at the pressure benchmark.

Emergence regime changes	Medium Q: High A: High C: High	Medium Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium

Seagrasses are generally not tolerant of exposure to aerial conditions, suggesting that the shallowest distribution should be at a depth below mean low water (MLW) (Koch, 2001). *Zostera noltei* grows predominantly in the intertidal zone and demonstrates a higher resistance to desiccation than *Zostera marina* which occurs more frequently in the subtidal. To understand the differences in desiccation tolerance between *Zostera* species, Leuschner *et al.* (1998) investigated the photosynthetic activity of emerged plants. The study found that after 5 hours of exposure to air during low tide, leaves of *Zostera noltei* had lost up to 50% of their water content. Decreasing leaf water content resulted in a reversible reduction in light-saturated net photosynthesis rate of the plant. The experiment further showed that photosynthesis was more sensitive to desiccation in *Z. marina* plants than in *Zostera noltei* under a given leaf water content. The experiment confirmed that *Zostera marina* is most susceptible to local changes in emergence regimes by being less tolerant of desiccation pressure. A review by d'Avack *et al.* (2014) reported that the limited tolerance of seagrass species to aerial exposure means that a decrease in relative sea level could force seagrass to grow deeper to reduce exposure to air. As the depth limit of seagrasses is set by light penetration, this change is likely to reduce the extent of suitable habitat. However, Cabaco *et* *al*. (2009) found that *Zostera noltei* displayed considerable plasticity at a physiological-, plant- and population-level along the intertidal zone, indicating the ability of the species to acclimate to the steep environmental gradient of this particular ecosystem. This plasticity will allow plants to cope with changes in emergence regime.

A decrease in emergence, on the other hand, could enable the biotope to expand further up the shore. A potential expansion is, however, dependent on available habitat and will be impossible where barriers such as dams and seawalls are present resulting in the net loss of plants.

Sensitivity assessment. *Zostera noltei* has a limited tolerance towards aerial exposure; resistance is thus assessed as **'Medium'**. Recovery will be enabled by recolonization from surrounding communities located further down the shore and via the remaining seed bank. Recovery is, therefore, considered to be fairly rapid resulting in a **'Medium'** resilience. The biotope is considered to have a **'Medium'** sensitivity to changes in emergence regime at the pressure benchmark.

Wave exposure changes (local)	Medium Q: Medium A: Medium C: Medium	Medium Q: High A: Low C: Medium	Medium Q: Medium A: Low C: Medium

An absolute wave exposure limit and maximum wave height for *Zostera* has not been established (Short *et al*., 2002) but an increase in wave action can harm plants in several ways. Seagrasses are not robust. Strong waves can cause mechanical damage to leaves and to the rest of the plant. By losing above ground biomass due to increased wave action, the productivity of seagrass plants is limited. Small and patchy populations, as well as seedlings, will be particularly vulnerable to wave exposure as they lack extensive rhizome systems to effectively anchor the plant to the seabed. Wave action also continuously mobilises sediments in coastal areas causing sediment resuspension which in turn leads to a reduction in water transparency (Koch, 2001) (see 'changes in suspended sediments' pressure). Photosynthesis can be further limited by breaking waves inhibiting light penetration to the seafloor. Wave exposure can also influence the sediment grain size, with areas of high wave exposure having coarser sediments with lower nutrient concentrations. Coarser sediments reduce the vegetative spreading of seagrasses and inhibit seedling colonisation (Gray & Elliott, 2009). Changes in sediment type can, therefore, have wider implications on the sensitivity of seagrasses on a long-term scale.

Sensitivity assessment. No evidence was available to determine the impact of this pressure at the benchmark level. However, exposure models from Studland Bay and Salcombe, where seagrass beds are limited to low wave exposure, show that even a change of 3% is likely to influence the upper shore limits as well as beds living at the limits of their wave exposure tolerance (Rhodes *et al*., 2006; Jackson *et al*., 2013). Change in wave exposure will impact the upper limit of seagrass and thus influence its wider distribution. At the benchmark level, an increase in wave exposure is likely to remove surface vegetation and the majority of the root system causing some mortality. Resistance is thus assessed as **'Medium'**. Recovery will depend on the presence of adjacent seagrass beds but is considered to be fairly rapid scoring a **'Medium'** resilience. The biotope, therefore, scores a **'Medium'** sensitivity changes in wave exposure at the pressure benchmark.

Chemical Pressures

	Resistance	Resilience	Sensitivity

Transition elements & organo-metal contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Hydrocarbon & PAH contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Synthetic compound contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence

Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

The effects of oxygen concentration on the growth and survivability of *Zostera noltei* are not reported in the literature. *Zostera* sp. leaves contain air spaces (lacunae) and oxygen is transported to the roots where it permeates into the sediment, resulting in an oxygenated microzone. This enhances the uptake of nitrogen. The presence of air spaces suggests that seagrass may be tolerant of low oxygen levels in the short-term, however, prolonged de-oxygenation, especially if combined with low light penetration and hence reduced photosynthesis may have a negative effect. Epifaunal gastropods may be tolerant of hypoxic conditions, especially *Littorina littorea* and *Hydrobia ulvae*. Infaunal species are likely to be exposed to hypoxic conditions, especially at low tide when they can no longer irrigate their burrows e.g. *Arenicola marina* can survive for 9 days without oxygen (Hayward, 1994). Conversely, possibly since it occupies the top few centimetres of sediment, *Cerastoderma edule* may be adversely affected by anoxia and would probably be killed by exposure to 2 mg/l oxygen for a week.

Sensitivity assessment. Overall de-oxygenation is not likely to adversely affect seagrass beds, especially in the lower intertidal where the biotope would experience periodic exposure to the air. Therefore, resilience is probably **High**, albeit with Low confidence, so that resistance is also **High** and the biotope is assessed as **Not sensitive** at the benchmark level.

Nutrient enrichment	Medium	Medium	Medium
	Q: Medium A: Medium C: Medium	Q: High A: Low C: Medium	Q: Medium A: Low C: Medium

During the past several decades, important losses in seagrass meadows have been documented worldwide related to an increase in nutrient load. Seagrasses are typically found in low energy habitats such as estuaries, coastal embayments and lagoons with reduced tidal flushing where nutrient loads are both concentrated and frequent. A typical response to nutrient enrichment is a decline in seagrass populations in favour of macroalgae or phytoplankton (Baden *et al*., 2003). Nutrient enrichment, especially of nitrogen and phosphorus, can lead to eutrophication. The mechanisms responsible for seagrass decline under eutrophication are complex and involve direct and indirect effects relating to changes in water quality, smothering by macroalgal blooms (Den Hartog & Phillips, 2000), and competition for light and nutrients with epiphytic microalgae and with phytoplankton (Nienhuis, 1996). In the Mondego estuary (Portugal), eutrophication triggered serious biological changes, which led to an overall increase in primary production and to a progressive replacement of seagrass *Zostera noltei* beds by coarser sediments and opportunistic macroalgae (Cardoso *et al*., 2004). Nutrients stimulate phytoplankton blooms that compete for nutrients but more importantly increase the turbidity and absorb light, reducing seagrass productivity (discussed in 'changes in suspended solids'). In general terms, algae are able to out-compete seagrasses for water column nutrients since they have a higher affinity for nitrogen (Touchette & Burkholder, 2000). Short and Burdick (1996) found that excessive nitrogen loading stimulated the proliferation of algal competitors that caused shading and thereby stressing *Zostera* plants. Many seagrasses have a positive response to nitrogen and/or phosphorous enrichment (Peralta *et al*., 2003), but excessive loads can inhibit seagrass growth and survival, not only indirectly through light reduction resulting from increased algal growth but also directly in terms of the physiology of the seagrass. Direct physiological responses include ammonium toxicity and water column nitrate inhibition through internal carbon limitation (Touchette & Burkholder, 2000). Indirect effects of nutrient enrichment can accelerate decreases in seagrass beds such as sediment re-suspension from seagrass loss (see 'changes in suspended solids' pressure). Jones & Unsworth (2015) concluded that seagrass habitats in the British Isles were nutrient enriched, with nitrogen levels 75% higher than the global average for *Zostera marina*, yet phosphate limited, and concluded that many beds in the vicinity of human populations were in a poor state.

Sensitivity assessment. The loss of seagrass beds worldwide has been attributed to nutrient enrichment, due in part to the likeliness of smothering by epiphytes, and the effects of reduced light penetration caused by eutrophication. For instance, a study by Greening & Janicki (2006) found that in Florida, the USA, recovery of seagrass beds was incomplete 20 years after nutrient enrichment causing an eutrophication event. Seagrass beds are regarded as highly intolerant (or of low resistance) to this pressure. However, the benchmark of this pressure (compliance with WFD 'good' status) allows for a 30% loss of intertidal seagrass beds under the WFD criteria for good status. Therefore, at the level of the benchmark resistance of seagrass beds to this pressure is assessed **'Medium'**. The resilience of seagrass beds this degree of impact is assessed as **'Medium'**. The sensitivity score is therefore assessed as **'Medium'**.

Organic enrichment	Medium	Medium	Medium
	Q: Medium A: Medium C: Medium	Q: High A: Low C: Medium	Q: Medium A: Low C: Medium

Organic enrichment may lead to eutrophication with adverse environmental effects including deoxygenation, algal blooms and changes in community structure (see 'nutrient enrichment' pressure). Evidence on the effects of organic enrichment on *Zostera* species is limited but abundant for other seagrass species. Neverauskas (1987) investigated the effects of discharged digested sludge from a sewage treatment on *Posidonia* spp. and *Amphibolis* spp. in South Australia. Within 5 years the outfall had affected an area of approximately 1900 ha, 365 ha of which were completely denuded of seagrasses. The author suggests that the excessive growth of epiphytes on the leaves of seagrasses was a likely cause for reduced abundance. A subsequent study by Bryars & Neverauskas (2004) determined that eight years after the cessation of sewage output, total seagrass cover was approximately 28% of its former extent. While these results suggest that seagrasses can return to a severely polluted site if the pollution source is removed, they also suggest that it will take many decades for the seagrass community to recover to its former state. The effects of organic enrichment from fish farms were investigated on *Posidonia oceanica* seagrass beds in the Balearic Islands (Delgado *et al*., 1999). The fish culture had ceased in 1991; however, seagrass populations were still in decline at the time of sampling. The site closest to the former fish cages showed a marked reduction in shoot density, shoot size, underground biomass, sucrose concentration and photosynthetic capacities. The shoot also had high P-concentration in tissues and higher epiphyte biomass compared to the other sites. Since water conditions had recovered completely by the time of sampling, the authors suggest that the continuous seagrass decline was due to the excess organic matter remaining in the sediment (Delgado *et al*., 1999).

It should be noted that coastal marine sediments where seagrasses grow are often anoxic and highly reduced due to the high levels of organic matter and slow diffusion of oxygen from the water column to the sediment. Seagrasses worldwide have been shown to exhibit a three-way symbiotic relationship with the small lucinid bivalves (hatchet-shells, e.g. *Loripes* and *Lucinoma*) and their endosymbiotic sulfide-oxidizing gill bacteria (Van der Heide *et al*., 2012). In experiments, the sulfide-oxidizing gill bacteria of *Loripes lacteus* were shown to reduce sulfide levels in the sediment and enhance the productivity of *Zostera noltei*, while the oxygen released from the roots of *Zoster noltei* was of benefit to *Loripes*. Nevertheless, the negative effects of the experimental addition of sulphide were not fully prevented by the presence of *Loripes* (Van der Heide *et al*., 2012). Therefore, while seagrasses or the *Zostera*-lucinid symbiosis are adapted to these anoxic sediment conditions if the water column is organically enriched, plants are unable to maintain oxygen supply to the meristem and die fairly quickly. The enrichment of the water column could, therefore, significantly increase the sensitivity of seagrasses to this pressure. Worldwide evidence suggests that nutrient enrichment is one of the biggest threats to seagrass populations (Jones & Unsworth, 2015).

Sensitivity assessment. The organic enrichment of the marine environment increases turbidity and causes the enrichment of the sediment in organic matter and nutrients (Pergent *et al*., 1999). Evidence shows that seagrass beds found in proximity to a source of organic discharge were severely impacted with important losses of biomass. Although no study was found on the British species, the evidence suggests that *Zostera noltei* will be negatively affected by organic enrichment. No evidence was found addressing the benchmark of this study. A deposition of 100 gC/m2/year is considerably lower than the amount of organic matter discharged by sewage outlets and fish farms. Resistance to this pressure is thus assessed as **'Medium'**. Therefore, resilience is assessed as '**Medium'** and sensitivity as **'Medium'.**

Physical Pressures

	Resistance	Resilience	Sensitivity

Physical loss (to land or freshwater habitat)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

All marine habitats and benthic species are considered to have a resistance of '**None'** to this pressure and to be unable to recover from a permanent loss of habitat (resilience of '**Very Low'**). Sensitivity within the direct spatial footprint of this pressure is, therefore **'High'**. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure. Adjacent habitats and species populations may be indirectly affected where meta-population dynamics and trophic networks are disrupted and where the flow of resources e.g. sediments, prey items, loss of nursery habitat etc. is altered.

Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

A change to another seabed type (from sediment to hard rock) will result in a permanent loss of suitable habitat for seagrass species. Resistance is thus assessed as **'None'.** As this pressure represents a permanent change, recovery is impossible as a suitable substratum for seagrasses is lacking. Consequently, resilience is assessed as **'Very low'**. The habitat, therefore, scores a **'High'** sensitivity. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

Physical change (to another sediment type)	Low Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

Seagrass beds occur almost exclusively in shallow and sheltered coastal waters anchored in sandy and muddy bottoms. A physical change to another seabed type such as a change in Folk class at the benchmark level will, therefore, have a detrimental effect on seagrass beds as they will be excluded from the newly created habitat. A change towards a coarser sediment type (e.g. gravelly sediments; see benchmark) would inhibit seagrasses from becoming established due to a lack of adequate anchoring substratum. A more mud dominated habitat, on the other hand, could increase sediment re-suspension and exclude seagrasses due to unfavourable light conditions. In an unpublished experiment, little difference in seagrass growth rates was seen between mud and sand substrata but significantly lower growth rates were observed when mud was changed to sandy gravel (Jackson, pers comm., 2019). In addition, this biotope (Znol) is only recorded from muddy sand in the UK (JNCC, 2015) and presumably reflects the interplay of sediment type, wave energy and currents. Therefore, resistance was assessed as **'Low'**. As this pressure represents a permanent change, recovery is impossible without intervention as a suitable substratum for seagrasses is lacking. Consequently, resilience is assessed as **'Very low'.** The habitat, therefore, scores a **'High'** sensitivity. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

Habitat structure changes - removal of substratum (extraction)	None Q: High A: High C: High	Very Low Q: High A: Low C: Medium	High Q: High A: Low C: Medium

The extraction of sediments to 30 cm (the benchmark) will result in the removal of every component of seagrass beds. Roots and rhizomes are buried no deeper than 20 cm below the surface (see ' 'penetration and/or disturbance of the substratum below the surface of the seabed').

Resistance is, therefore, assessed as **'None'** for and resilience is considered **'Very low'** resulting in a **'High'** sensitivity score.

Abrasion/disturbance of the surface of the substratum or seabed	Low Q: High A: High C: High	Medium Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium

Seagrasses are not physically robust. The leaves and stems of seagrass plants rise above the surface and the roots are shallowly buried so that they are vulnerable to surface abrasion. Activities such as trampling, anchoring, power boating and potting are likely to remove leaves and damage rhizomes. The removal of above-ground biomass would result in a loss of productivity whilst the removal of roots would cause the death of plants. Seagrasses are limited to shallow, protected waters and soft sediments. These areas are often open to public access and are widely used in commercial and recreational activities.

Trampling and vehicles: human wading in shallow coastal waters is a common activity that inherently involves trampling of the substratum. Trampling may be caused by recreational activities such as walking, horse-riding and off-road driving. These activities are likely to damage rhizomes and cause seeds to be buried too deeply to germinate (Fonseca, 1992). Negative effects of human trampling on seagrass cover, shoot density, and rhizome biomass, have been reported by Eckrich & Holmquist (2000) for the seagrass *Thalassia testudinum*. The study found that recovery occurred within a period of seven months after trampling ceased but the reduced cover was still visually distinguishable 14 months after the experiment. A study by Major *et al.* (2004) found that trampling impact varied depending on substratum type. A significant decrease in shoot density as a result from trampling was only observed at a site with soft muddy substratum with no impact detected on hard packed sand substratum. Damage from trampling is thus dependent on the substratum type with seagrass beds growing on soft substrata being most vulnerable to this pressure.

Hodges and Howe (1997) documented the impact of vehicular access on *Zostera angustifolia* beds in Angle Bay, Wales after the Sea Empress oil spill. Vehicle use, required for the initial clean up, resulted in patchy beds, criss-crossed with wheel ruts up to 1 m deep. Unauthorized activities before the spill, including vehicles associated with bait digging and the use of motorbikes, created ruts that were still visible over a year later.

Boating activities: boats passing in close proximity to seagrass beds can create waves. Turbulences from propeller wash and boat wakes can resuspend sediments, break off leaves, dislodge sediments and uproot plants. The re-suspension of sediments is further assessed in 'changes in suspended sediment' pressure. Koch (2002) established that physical damage from boat wakes was greatest at low tide but concluded that negative impacts of boat-generated waves were marginal on seagrass habitats. The physical impact of the engine's propellers, shearing of leaves and cutting into the bottom, can also have damaging effects on seagrass communities. In severe cases, propellers cutting into the bottom may completely denude an area resulting in narrow dredged channels through the vegetation called propeller scars. Scars might expand and merge to form larger denuded areas. A study in Florida looking at the seagrasses *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightei* determined that recovery of seagrass to propeller impact depend on species (Kenworthy *et al.*, 2002). For *Syringodium filiforme* recovery was estimated at 1.4 years and for *Halodule wrightei* at 1.7 years, whilst recovery for *Thalassia testudinum* was estimated to require 9.5 years. Variations in recovery time were explained by different growth rates. However, it is not appropriate to assume that recovery rates are similar from one geographical or climatic region to another and more in-depth research is needed for *Zostera* species around the British Isles.

Potting: static gear is commonly deployed in areas where seagrass beds are found, either in the form of pots or as bottom set gill or trammel nets. Damage could be caused during the setting of pots or nets and their associated ground lines and anchors, by their movement over the bottom during rough weather and during recovery. Whilst the potential for damage is lower per unit deployment compared to towed gear (see 'penetration and/or disturbance of the substratum below the surface of the seabed' pressure), there is a risk of cumulative damage if use is intensive. Wall *et al*. (2008) categorized seagrass beds as being highly sensitive to high intensities of potting (pots lifted daily, with a density of over 5 pots per ha) and medium sensitive to lower levels (pots lifted daily, less than 4 pots per ha). However, no direct evidence was found to confirm these estimates.

Grazing: Nacken & Reise (2000) investigated physical disturbance caused by Brent geese (*Branta b. bernicla*) and wigeon (*Anas penelope*) feeding on *Zostera noltei* in the northern Wadden Sea. To graze on leaves and shoots above the sediment and on rhizomes and roots below, birds reworked the entire upper 1cm layer of sediment and excavated pits by trampling. As a result, birds pitted 12% of the seagrass bed and removed 63% of plant biomass. Plants recovered by the following year with the authors suggesting that seasonal erosion caused by herbivorous wildfowl was necessary for the persistence of *Zostera noltei* beds (Nacken & Reise, 2000). Similarly, Davison & Hughes (1998) suggested that *Zostera* sp. can rapidly recover from 'normal' levels of wildfowl grazing. Physical disturbance may, however, be detrimental to seagrass beds as soon as the ‘normal’ level caused by grazing birds is exceeded by human activities.

Experimental: Zipperle *et al.* (2009a,b; 2010, 2011) suggested that intermediate levels of disturbance, typical of the Wadden Sea, enhanced recruitment. They suggested that disturbance may enhance dispersal of seed, enhance sexual reproduction via gap formation and increase outcrossing by reducing the size of vegetative clones. *Zostera noltei* seed and seedling density were higher in experimental pits dug to emulate geese feeding pits than controls, which concurred with observations by prior authors (Nacken, 1998; Zipperle *et al*., 2010). Boese *et al.* (2009) examined the recolonization of experimentally created gaps within intertidal perennial and annual *Zostera marina* beds in the Yaquina River Estuary, USA. The experiment looked at two zones, the lower intertidal almost continuous seagrass and an upper intertidal transition zone where there were patches of perennial and annual *Zostera marina*. The study found that recovery began within a month after disturbance in the lower intertidal continuous perennial beds and was complete after two years, whereas, plots in the transition zone took almost twice as long to recover.

Sensitivity assessment. In summary, a wide range of activities gives rise to this pressure with intertidal habitat being more exposed as they are more readily accessible than subtidal beds. Seagrass plants are not physically robust and their root system is located in the upper layer of the sediment making them prone to damage by abrasion. The resilience and recovery of seagrass beds to abrasion of the seabed surface depends on the frequency, persistence and extent of the disturbance. Factors such as the size and shape of the impact will also influence the sensitivity of seagrass to this pressure. There is also considerable evidence that the type of substratum plays a role in determining the magnitude of impact. Soft and muddy substratum is thought to be more easily damaged than harder more compact ground. Finally, temporal effects should also be taken into account. The state of the tide will influence the magnitude of damage as will seasonal effects with damage induced in winter being more likely to have a lesser impact than damage occurring during the growing season. Overall, studies suggest little resistance to abrasion resulting in **'Low'** resistance. Physical disturbance and removal of plants can lead to increased patchiness and destabilisation of the seagrass bed, which in turn can lead to reduced sedimentation within the seagrass bed, increased erosion, and loss of larger areas of plants (Davison & Hughes, 1998). Recovery will, however, be fairly rapid resulting in **'Medium'** resilience. Overall this biotope, therefore, has a **'Medium'** sensitivity to this pressure.

Penetration or disturbance of the substratum subsurface	None	Low	High
	Q: High A: Medium C: Medium	Q: High A: Low C: Medium	Q: High A: Low C: Medium

Seagrass species are vulnerable to physical damage. Activities such as digging and raking for clams, anchoring and mooring will penetrate the substratum to an average depth of 5 cm removing plant biomass above and below ground. Penetration to the substratum to a depth greater than 5 cm will directly impact seagrass habitats as the plant is confined to the upper layer of the sediment. All biomass (leaves, rhizomes) will be completely removed leading to the death of the plant. Seagrass beds are often associated with commercially important bivalves. Fisheries targeting these species are therefore likely to impact seagrass habitats and are the most widespread (and best studied) activities giving rise to this pressure on this habitat.

Clam digging and clam raking: Racking and digging for shellfish is a common practice in the intertidal zone. In southern Portugal clam harvesters dig up intertidal sediments dominated by the seagrass *Zostera noltei*, using a hand-blade, which breaks and removes the shoots and rhizomes of plants. Cabaço & Santos (2007) found that clam harvesting activities change the species population structure by significantly reducing shoot density and total biomass, particularly during August, when the harvest effort is highest. Experimental harvest revealed a short-term impact on shoot density, which rapidly recovered to control levels during the following month. By experimentally manipulating rhizome fragmentation, the authors determined that plant survival was only reduced when fragmented rhizomes were left with less than two intact internodes; fragmented rhizomes having 2 to 5 internodes were not significantly affected, even though growth and production were lower with fewer internodes. The results of this study suggest that *Zostera noltei* is adversely affected by clam harvesting, however, the species is able to rapidly recover from this physical disturbance. Similary, Branco *et al.* (2018) observed no significant difference in the photosynthetic efficiency *Zostera noltei i*n areas subject to a single incidence of experimental hand raking for clams in the first few centimetres of sediment, using traditional techniques, in the Mira estuary, Portugal, although it was unclear if the seagrass itself was damaged in the process. In the same study area, Alexandre *et al.* (2005) looked into the effects of clam harvesting on sexual reproduction. Disturbed meadows showed significantly lower vegetative shoot density but significantly higher reproductive effort. These results were confirmed by manipulative experiments and suggest that *Zostera noltei* responded to clam harvesting disturbance by both increasing its reproductive effort and extending its fertile season. Boese (2002) investigated the effects of manual clam harvesting on *Zostera marina* by raking and digging for clams in experimental plots in Yaquina Bay, USA. After three monthly treatments, measures of biomass, primary production (leaf elongation), and percent cover were compared between disturbed and undisturbed plots. The study found that clam raking treatments visibly removed large numbers of seagrass leaves and some below-ground rhizomes. However, two weeks after the end of the experiment, no statistical difference in percentage cover was observed between disturbed and control plots indicating a fast recovery rate.

Clam digging, on the other hand, caused visual differences in percentage cover for 10 months after the end of the experiment, although differences were not statistically significant. Boese (2002) concluded that recreational clamming is unlikely to have a major impact on seagrass beds in the Yaquina estuary. The author calls, however, to view the results with caution as multi-year disturbances were not investigated and differences in sediment characteristics are likely to influence the resistance and resilience of seagrasses to this pressure. Similarly, Peterson *et al.* (1987) found that hand raking and moderate clam-kicking (a commercial harvesting method in which propeller wash is used to dislodge hard clams) resulted in a reduction in *Zostera marina* biomass by approximately 25%. No differences between control and experimental areas were apparent one year after the experiment. However, at a higher intensity, clam-kicking reduced seagrass biomass to about half of control levels and recovery remained incomplete four years after the end of the experiment (Peterson *et al.*, 1987).

Anchoring and mooring: an anchor landing on a patch of seagrass can bend, damage and break seagrass shoots (Montefalcone *et al.*, 2006) and an anchor being dragged as the boat moves driven by wind or tide causes abrasion of the seabed. Milazzo *et al.* (2004) found that the extent of damage depended on the type of anchor with the folding grapnel having the greatest impact. The study further determined that heavier anchors (often associated with larger boats) will sink deeper into the substratum and thereby cause greater damage. A technical paper by Collins *et al.* (2010) using SCUBA divers found bare patches (typically 1–4 m^2) were caused by anchoring by leisure boats in Studland Bay, UK. The study further determined that average shear vane stress was significantly higher in intact seagrass beds compared to scars indicating a less cohesive and more mobile substratum caused by anchors. Axelsson *et al.* (2012) also investigated anchor damage in Studland Bay. The study did not provide consistent evidence of boat anchoring impacting the seagrass habitat in this location. The study did, however, observe higher shoot density and percentage cover of seagrass in a voluntary anchor zone compared to a control area where anchoring occurred. The authors recommended longer monitoring in order to determine whether the trend was caused by natural variations or the effects of anchor exclusion. Traditional mooring further contributes to the degradation of seagrass habitats. A traditional swing mooring is a buoy on a chain attached to a static anchoring block fixed on the seabed, to buffer any direct force on the permanent block, the chain lies on the seabed where it moves around with wind and tides, as the chain pivots on the block it scours the seabed. In proximity to seagrass beds, the chain usually removes not only the seagrass above ground parts such as leaves and shoots but also the roots anchored in the sediment. Further sediment abrasion may occur in the vicinity to the anchoring blocks due to eddying of currents. The blocks themselves may increase the competition of seagrass with other algae as they provide ideal settlement surfaces. Boats might also moor on intertidal sediments. When the tide goes out, the boat sits directly on top of the soft sediment. Walker *et al.* (1989) found that boat moorings caused circular or semi-circular depressions of bare sand within seagrass beds between 3 to 300 m^2 causing important habitat fragmentation. The scours created by moorings in the seagrass canopy interfere with the physical integrity of the meadow. Though relatively small areas of seagrass are damaged by moorings, the effect is much greater than if an equivalent area was lost from the edge of a meadow. Such mooring scars have been observed for Zostera marina around the UK such as in Porth Dinllaen in the Pen Llyna'r Sarnau Special Area of Conservation, Wales (Egerton, 2011) and at Studland Bay (Jackson *et al.*, 2013).

Trawling: Neckles *et al.* (2005) investigated the effects of trawling for the blue mussels *Mytilus edulis* on *Zostera marina* beds in Maquoit Bay, USA. Impacted sites ranged from 3.4 to 31.8 ha in size and were characterized by the removal of above- and belowground plant material from the majority of the bottom. The study found that one year after the last trawl, *Zostera marina* shoot density, shoot height and total biomass averaged respectively to 2-3%, 46-61% and <1% that of the reference sites. Substantial differences in *Zostera marina* biomass persisted between disturbed and reference sites up to seven years after trawling. Rates of recovery depended on initial fishing intensity but the authors estimated that an average of 10.6 years was required for *Zostera* shoot density to match pre-trawling standards.

Dredging and suction dredging: the effects of dredging for scallops on *Zostera marina* beds were investigated by Fonseca *et al.* (1984) in Nova Scotia, USA. Dredging was carried out when plants were in the vegetative stage on hard sand and on soft mud substrata. The damage was assessed by analysing the effects of scallop harvesting on seagrass foliar dry weight and on the number of shoots. Lower levels of dredging (15 dredges) had a different impact depending on substrata, with the hard bottom retaining a significantly greater overall biomass than a soft bottom. However, an increase in dredging effort (30 dredges) led to a significant reduction in seagrass biomass and shoot number on both hard and soft bottoms. Solway Firth is a British example of the detrimental effects of dredging on seagrass habitats. In the area, where harvesting for cockles by hand is a traditional practice, suction dredging was introduced in the 1980s to increase the yield. A study by Perkins (1988) found that where suction dredging occurred, the sediment was smoothened and characterized by a total absence of *Zostera* plants. The study concluded that the fishery was causing widespread damage and could even completely eradicate *Zostera* from affected areas. Due to concerns over the sustainability of this fishing activity, the impacts on cockle and *Zostera* stocks, and the effects on overwintering wildfowl, the fishery was closed to all forms of mechanical harvesting in 1994.

Sensitivity assessment. The deployment of fishing gears on seagrass beds results in physical damage to the above surface part of the plants as well as to the root systems. Seagrasses do not have an avoidance mechanism; resistance to this pressure is therefore assessed as **'None'.** The recovery of seagrass beds after disturbance to the sub-surface of the sediment will be slow with the speed depending on the extent of removal. Rates may be accelerated where adjacent seed sources and viable seagrass beds are present but can be considerably longer where rhizomes and seed banks were removed. Using a model simulation, it has been suggested that with favourable environmental conditions, seagrass beds might recover from dragging disturbance in six years; conversely, recovery under conditions less favourable to seagrass growth could require 20 years or longer (Neckles *et al.*, 2005). Resilience is thus assessed as **'Low'**. The mechanical harvest of shellfish damaging the sub-surface of the sediments poses a very severe threat to seagrass habitats, yielding a **'High'** sensitivity score.

Changes in suspended solids (water clarity)	Low Q: High A: High C: High	Low Q: High A: Low C: Medium	High Q: High A: Low C: Medium

Irradiance decreases exponentially with increasing depth, and the suspended sediment concentration has a direct linear effect on light attenuation (Van Duin *et al.*, 2001). Changes in suspended solids will thus reduce the light available for seagrass plants necessary for photosynthesis. Impaired productivity due to a decrease in photosynthesis will affect the growth and reproductive abilities of plants. Turbidity also results in a reduction of the amount of oxygen available for respiration by the roots and rhizomes thus lowering nutrient uptake. The resulting hypoxic conditions will lead to a build-up of sulphides and ammonium, which can be toxic to seagrass at high concentrations (Mateo *et al.*, 2006). Davison & Hughes (1998) reported considerable declines in seagrass populations related to increases in turbidity from dredging in the Wadden Sea.

Water clarity is a vital component for seagrass beds as it determines the depth-penetration of photosynthetically active radiation of sunlight. Seagrasses have light requirements an order of magnitude higher than other marine macrophytes making water clarity a primary factor in determining the maximum depth at which seagrasses can occur. The critical threshold of light requirements varies among species ranging from 2% in-water irradiance for *Z. noltei*, to 11 to 37% for *Z. marina* (Erftemeijer & Robin, 2006). These differences in the light requirement for *Zostera* are reflected by the position of species along a depth gradient with *Zostera noltei* occurring predominantly in the intertidal and *Zostera marina* found at greater depth in the subtidal. However, differences in light requirements also vary within species. For example, the minimum light requirement for *Zostera marina* in a Danish embayment was 11% in-water irradiance, whereas the estimated light requirement for the same species in the Netherlands was 29.4% in-water irradiance (Olesen, 1993). This variability within species is likely attributed to photo-acclimation to local light regimes. A study by Peralta *et al.* (2002) investigated the effects of reduced light availability on *Zostera noltei* in Spain. The authors determined that plants were able to tolerate acute light reductions for a short period of time (below 2% of surface irradiance for two weeks) by storing and mobilizing carbohydrates at a low level of irradiance. However, *Zostera noltei* are likely to be less tolerant of chronic, long-term reductions in light availability. In a six month long experiment in the Dutch Wadden Sea, Philippart (1995) found that shading induced a 30% decrease in the leaf growth rate, a 3-fold increase in the leaf loss rate, and an 80% reduction in the total biomass of *Zostera noltei*. The decreasing growth rate is most probably the result of a reduction of photosynthesis due to shading. The increased leaf loss may have been the result of enhanced deterioration of leaf material under low light conditions. The study also established that during the summer period, the maximum biomass of *Zostera noltei* under the control light conditions was almost 10 times higher than those under the low light conditions (incident light reduced to 45% of natural light conditions). The summer is a critical period for maintenance and growth of vegetative shoots. The effects of shading may, therefore, be most severe during the summer months.

Changes in suspended solids leading to turbid conditions over a prolonged period of time are, therefore, likely to adversely impact seagrass species. The extent of damage will depend on individual seagrass beds. Older, more established perennial meadows have greater carbohydrate reserves and are thus more able to resist changes in light penetration than annual plants (Alcoverro *et al.*, 2001). Seagrass plants found in clear waters may be able to tolerate sporadic high turbidity (Newell & Koch, 2004). However, where seagrass beds are already exposed to low light conditions, then losses may result from even short-term events (Williams, 1988).

Sensitivity assessment. Turbidity is an important factor controlling production and ultimately survival and recruitment of seagrasses. Seagrass populations are likely to survive short-term increases in turbidity, however, a prolonged increase in light attenuation, especially at the lower depths of its distribution, will probably result in loss or damage of the population. A score of **'Low'** was therefore recorded for resistance. A loss of seagrass beds will promote the re-suspension of sediments, making recovery unlikely as seagrass beds are required to initially stabilise the sediment and reduce turbidity levels (Van der Heide *et al.*, 2007). A high turbidity state appears to be a highly resilient alternative stable state; hence return to the seagrass biotope is unlikely resulting in **'Low'** resilience. *Zostera noltei* should be considered intolerant of any activity that changes the sediment regime where the change is greater than expected due to natural events, yielding a **'High'** sensitivity score.

Smothering and siltation rate changes (light)	Medium	Medium	Medium
	Q: Medium A: Medium C: Medium	Q: High A: Medium C: Medium	Q: Medium A: Medium C: Medium

Several studies have documented the deterioration of seagrass meadows by smothering due to excessive sedimentation. Consequences of enhanced sedimentation for seagrass beds depend on several factors such as the life history stage as well as the depth and timing of burial. Early life stages of seagrass, smaller in size than adult plants, are most vulnerable to this pressure as even a small load of added sediment will lead to the complete burial. Cabaço & Santos (2007) determined that *Zostera noltei* is highly sensitive to burial and erosion disturbances due to the small size of this species and the lack of vertical rhizomes. Buried plants, however, produced longer rhizome internodes as a response to burial, suggesting an attempt to relocate the leaf-producing meristems closer to the sediment surface. The carbon content of leaves and rhizomes, as well as the non-structural carbohydrates (mainly the starch in the rhizomes), dropped significantly during the experimental period, indicating an internal mobilisation of carbon to meet the plant demands as a consequence of light deprivation. However, shoots did not survive more than 2 weeks under complete burial. Cabaço & Santos (2007) concluded that *Zostera noltei* was highly sensitive to burial disturbance and determined that the threshold for total shoot loss was between 4 cm and 8 cm of burial. The study did not observe any recovery within 2 months of the experiment. Han *et al.* (2012) found that mortality of *Zostera noltei* plants was related to sediment depth with survival rapidly decreasing when rhizomes were buried deeper than 1 cm. Similar to Cabaço & Santos (2007), Han *et al.* (2012) observed that *Zostera noltei* was able to relocate rhizomes to the depth at which the rhizomes of undisturbed plants were most frequently found. However, contrary to the previous study Han *et al.* (2012) concluded that *Z. noltei* is well adapted to cope with sediment disturbances of limited amplitude (i.e. ± 6 cm) by rapidly relocating their rhizomes to the preferential depth. Tu Do *et al.* (2012) investigated the recovery of *Zostera noltei* beds in Arcachon Bay in France after burial resulting from dredging activities (10 cm, mainly discharged in a main single event). The study found that seagrass beds had completely disappeared within 6 months with plants only partly recovering 5 years after the initial disturbance.

Other factors influencing the sensitivity of *Zostera noltei* to smothering is the frequency and the timing of deposition of material. The timing of the siltation event plays a particularly important role for intertidal beds. At low tide, for instance, the seagrass bed is exposed with plants lying flat on the substratum. The addition of material would immediately smother the entire plant and have a greater impact on leaves and stem than if added on plants standing upright. The resistance of intertidal beds to this pressure may thus vary with time of day. In addition, sudden burial has a more pronounced negative effect on the survival response of *Zostera noltei* than continuous burial (Han *et al*., 2012).

Sensitivity assessment. The above studies suggest that *Zostera noltei* is intolerant of smothering with some discrepancy between the critical threshold depths of burial. All studies, however, indicate that at the level of the benchmark (5 cm of fine material added to the seabed) some mortalities will occur resulting in a **'Medium'** resistance score. Some plants will survive by successfully relocating rhizomes closer to the sediment surface. With the benchmark set at 'material added to the seabed in a single event', the sensitivity will be greater than if burial occurred in a continuous way. In addition, seagrass beds are restricted to low energy environments, suggesting that once the silt is deposited, it will remain in place for a long period of time so habitat conditions will not reduce exposure. Resilience is therefore assessed as **'Medium'**. The biotope is assessed as **'Medium'** sensitivity to siltation at the pressure benchmark.

Smothering and siltation rate changes (heavy)	None Q: High A: High C: High	Very Low Q: High A: Low C: Medium	High Q: High A: Low C: Medium

Zostera noltei is sensitive to smothering by excessive siltation (see light smothering above). Studies have found that the seagrass is capable of producing longer rhizome internodes as a response to burial in an attempt to relocate leaf-producing meristems closer to the sediment surface (Cabaço & Santos, 2007; Hall *et al*., 2012; Tu Do *et al*., 2012). All studies indicate that seagrass species are sensitive to an increase in sedimentation rates at the benchmark level of 30 cm. In addition, seagrass beds are restricted to low energy environments, suggesting that once the silt is deposited, it will remain in place for a long period of time so habitat conditions will not reduce exposure. Resistance is assessed as **'None'** as all individuals exposed to siltation at the benchmark level are predicted to die and consequent resilience as **'Low'**. Sensitivity based on combined resistance and resilience is therefore assessed as **'High'.**

Litter	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

Not assessed.

Electromagnetic changes	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence

Underwater noise changes	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Species characterizing this habitat do not have hearing perception but vibrations may cause an impact. However, no studies exist to support an assessment.

Introduction of light or shading	Low Q: High A: High C: Medium	Medium Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium

Seagrasses have light requirements an order of magnitude higher than other marine macrophytes making water clarity a primary factor in determining the maximum depth at which seagrasses can occur. The critical threshold of light requirements varies among species ranging from 2% in-water irradiance for *Zostera noltei*, to 11 to 37% for *Zostera marina* (Erftemeijer & Robin, 2006). These differences in the light requirement for *Zostera* are reflected by the position of species along a depth gradient with *Zostera noltei* occurring predominantly in the intertidal and *Zostera marina* found at greater depth in the subtidal. However, differences in light requirements also vary within species. For example, the minimum light requirement for *Zostera marina* in a Danish embayment was 11% in-water irradiance, whereas the estimated light requirement for the same species in the Netherlands was 29.4% in-water irradiance (Olesen, 1993). This variability within species is likely attributed to photo-acclimation to local light regimes. A study by Peralta *et al.* (2002) investigated the effects of reduced light availability on *Zostera noltei* in Spain. The authors determined that plants were able to tolerate acute light reductions for a short period of time (below 2% of surface irradiance for two weeks) by storing and mobilizing carbohydrates at a low level of irradiance. However, *Zostera noltei* are likely to be less tolerant of chronic, long-term reductions in light availability. In a six month long experiment in the Dutch Wadden Sea, Philippart (1995) found that shading induced a 30% decrease in the leaf growth rate, a 3-fold increase in the leaf loss rate, and an 80% reduction in the total biomass of *Zostera noltei.* The decreasing growth rate is most probably the result of the reduction of photosynthesis due to shading. The increased leaf loss may have been the result of enhanced deterioration of leaf material under low light conditions. The study also established that during the summer period, the maximum biomass of *Zostera noltei* under the control light conditions was almost 10 times higher than those under the low light conditions (incident light reduced to 45% of natural light conditions). The summer is a critical period for maintenance and growth of vegetative shoots. The effects of shading may, therefore, be most severe during the summer months.

Sensitivity assessment. Overall, the effects of shading could mirror those of reduced water clarity (increased turbidity) depending on the scale of the artificial structure. Therefore, a resistance of **'Low',** with a resilience of **'Medium'** and sensitivity of **'Medium'** is suggested, albeit with low confidence.

Barrier to species movement	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant – this pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Physical and hydrographic barriers may limit the dispersal of seed. But seed dispersal is not considered under the pressure definition and benchmark.

Death or injury by collision	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant to seabed habitats. NB. Collision by grounding vessels is addressed under 'surface abrasion'.

Visual disturbance	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Translocation of seagrass seeds, rhizomes and seedlings is a common practice globally to counter the trend of decline of seagrass beds. *Zostera marina* is the seagrass species most commonly translocated. Williams & Davis (1996) found that levels of genetic diversity of restored eelgrass *Zostera marina* beds in Baja California, USA, were significantly lower than in natural populations. The loss of genetic variation can lead to lower rates of seed germination and fewer reproductive shoots, suggesting that there might be long-term detrimental effects for population fitness. Williams (2001) affirmed that genetic variation was essential in determining the potential of seagrass to rapidly adapt to a changing environment. Transplanted populations are, therefore, more sensitive to external stressors such as eutrophication and habitat fragmentation, with reduced community resilience, compared to natural populations (Hughes & Stachowicz, 2004). Even though restoration efforts tend to focus on *Zostera marina*, transplantations of *Zostra noltei* (Martins *et al*., 2005) have also been undertaken. Similar reductions in genetic diversity are expected, making the transplanted populations particularly sensitive to external stressors.

Translocation also has the potential to transport pathogens to uninfected areas (see 'introduction of microbial pathogens' pressure). The sensitivity of the 'donor' population to harvesting to supply stock for translocation is assessed for the pressure 'removal of target species'. No evidence was found for the impacts of translocated beds on adjacent natural seagrass beds. However, it has been suggested that translocation of plants and propagules may lead to hybridization with local wild populations. If this leads to loss of genetic variation there may be long-term effects on the potential to adapt to changing environments and other stressors.

Sensitivity assessment: Presently, there is no evidence of loss of habitat due to genetic modification and translocation of seagrass species. However, if hybridization occurred and genetic diversity was reduced, then the affected populations may become more susceptible to change and, hence, more sensitive.

Introduction or spread of invasive non-indigenous species	Low Q: Medium A: Medium C: Medium	Low Q: High A: Low C: Medium	High Q: Medium A: Low C: Medium

The effect of non-native species on seagrass species was reviewed by d'Avack *et al.* (2014). The review reported several non-native invasive plants as well as invertebrate species negatively impacting British seagrass beds. These included *Sargassum muticum*, *Spartina anglica*, *Codium fragile* ssp. *tomentosoides*, *Didemnum vexillum*, *Urosalpinx cinerea* and *Magallana gigas.*

For example, the cord-grass *Spartina anglica* is non-native grass, which was recorded to have negative effects on seagrass beds. This hybrid species of native (*Spartina alterniflora*) and an introduced cord-grass species (*Spartina maritima*) colonizes the upper part of mud flats, where due to its extensive root system, it effectively traps and retains sediments. *Spartina anglica* has rapidly colonized mudflats in England and Wales due to its fast growth rate and high fecundity. Deliberate planting to stabilise sediments accelerated its spread throughout Britain (Hubbard & Stebbings 1967). By consolidating the sediments the plant is responsible for raising mudflats as well as reducing sediment availability elsewhere. Butcher (1934) raised concerns that its pioneering consolidation may result in the removal of sediments from *Zostera* beds. Declines in *Zostera noltei* due to the encroachment of *Spartina anglica* were observed in Lindisfarne National Reserve in north-east England (Percival *et al.* 1998). The reduction in *Zostera noltei* beds had a direct impact on wildfowl populations as the food availability for the wildfowl was reduced on the top of the shore. This pressure will affect the upper limits of the intertidal rather than subtidal biotopes.

Sensitivity assessment: d'Avack *et al.* (2014) found that invasive flora had the greatest impact on seagrass bed but pointed out extensive knowledge gaps on how invasive species influence the health of *Zostera* beds in UK waters More research is thus needed in order to fully comprehend this pressure. Resistance is assessed as **'Low'.** Return to 'normal' conditions is highly unlikely if an invasive species would come to dominate the biotope. Indeed recovery would only be possible if the majority of the NIS were removed (through either natural or unnatural process) to allow the re-establishment of other species. Therefore, actual resilience is assessed as **'Low'** resulting in an overall **'High'** sensitivity score.

Introduction of microbial pathogens	Medium Q: Medium A: Medium C: Medium	Medium Q: High A: Low C: Medium	Medium Q: Medium A: Low C: Medium

Historic records show that seagrass species, in particular, *Zostera marina*, are highly susceptible to microbial pathogens. During the 1930s, a so-called 'wasting disease' decimated *Zostera marina* populations in Europe and along the Atlantic Coast of North America with over 90% loss (Muehlstein, 1989). Wasting disease resulted in black lesions on the leaf blades which potentially lead to loss of productivity, degradation of shoots and roots, eventually leading to the loss of large areas of seagrass (Den Hartog, 1987). Wasting disease is caused by infection with a marine slime mould-like protist called *Labyrinthula zosterae* (Short *et al*., 1987; Muehlstein *et al*., 1991). Recovery of seagrass beds after the epidemic has been extremely slow or more or less absent in some areas such as the Wadden Sea (Van der Heide *et al*., 2007).

The disease is less likely at low salinities, however, and *Zostera noltei* was little affected (Rasmussen, 1977; Davison & Hughes, 1998). Hence, *Zostera noltei* populations did not suffer to the same extent even though the disease also occurs in this species (Vergeer & Den Hartog, 1991).

Sensitivity assessment. *Zostera noltei* is susceptible to microbial pathogens but unlikely to suffer the level of mortality experienced by *Zostera marina*. Therefore, a resistance of **'Medium'** is recorded, with a resilience of **'Medium,** resulting in a sensitivity of **'Medium'**.

Removal of target species	Low Q: Medium A: High C: High	High Q: High A: Medium C: Medium	Low Q: Medium A: Medium C: Medium

Seagrass is not targeted by a commercial fishery at present. However, seeds and shoots are harvested currently for extensive transplantation projects aimed at promoting seagrass populations in areas denuded by natural or anthropogenic causes. Divers are most commonly employed to remove material from the source population, an activity with a low overall impact on seagrass habitats. In the USA, however, a mechanical seed harvesting technique was invented and put into practice (Orth & Marion, 2007). The mechanised harvester was able to drastically increase the number of *Zostera* seed collected from a source population (1.68 million seeds in one day compared to 2.5 million seeds collected by divers in one year). However, the large-scale removal of seeds, the productive output of seagrasses, can affect the integrity of the natural seagrass beds. To date, no mechanical harvesting has been employed in the UK. The ecological impact of seed collection by divers is low; the harvesting of *Zostera* in British waters has, therefore, a minimal effect on natural seagrass habitats. The effect of the translocation of species is covered in the pressure 'genetic modification and translocation of indigenous species'. The direct physical effects on seabed habitats from activities are described below in 'abrasion/disturbance' of the substratum on the surface of the bed' and 'penetration and/or disturbance of the substratum below the surface'.

Harvesting of seagrasses as a craft material is a small but growing industry. However, the present legislation for the conservation of seagrasses will discourage the expansion of this industry (see Jackson *et al.* (2013) for a full list on the political framework for seagrass protection in the UK).

Seagrass beds are not considered dependent on any of the organisms that may be targeted for direct removal e.g. oysters, clams and mussels. However, an indirect effect of fisheries targeting bivalves is a change in the water clarity, crucial for the growth and development of *Zostera* species. Indeed bivalves have been shown to significantly contribute to the clearance of the water column which subsequently increases light penetration, facilitating the growth and reproduction of *Zostera* species (Wall *et al*., 2008). Newell & Koch (2004) using modelling, predicted that when sediments were resuspended, the presence of even low numbers of oysters (25 g dry tissue weight m^2) distributed uniformly throughout the domain, reduced suspended sediment concentrations by nearly an order of magnitude. A healthy population of suspension-feeding bivalves thus improves habitat quality and promotes seagrass productivity by mitigating the effects of increased water turbidity in degraded, light-limited habitats (see 'changes in suspended solids' pressure). Bivalves also contribute pseudofaeces to fertilise seagrass sediments (Bradley & Heck Jr, 1999).

Seagrass plants may be directly removed or damaged by static or mobile gears that are targeting other species. These direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of target species on this biotope.

Sensitivity assessment. Seagrass beds have no avoidance mechanisms to escape targeted harvesting of leaves, shoots and rhizomes. Resistance to this pressure is, therefore, assessed as **'Low'**. A study by Nacken & Reise (2000) investigated the removal of *Zostera noltei* plants caused by Brent geese (*Branta b. bernicla*) and widgeon (*Anas penelope*) in the northern Wadden Sea. Birds removed 63% of plant biomass. Plants recovered by the following year with the authors suggesting that seasonal erosion caused by herbivorous wildfowl may be necessary for the persistence of *Zostera noltei* beds (Nacken & Reise, 2000). The study suggests that recovery from the removal of target species will be rapid resulting in **'High'** resilience score. Added anthropogenic disturbance may, however, be detrimental to seagrass beds as soon as the 'normal' level caused by grazing birds is exceeded by human activities. Overall the sensitivity of this biotope is deemed **'Low'** to this pressure.

Removal of non-target species	None Q: Low A: Low C: NR	Low Q: Low A: Low C: NR	High Q: Low A: Low C: NR

Filter-feeders such as mussels, clams and scallops are often associated with seagrass beds. Fisheries targeting these bivalves employ methods such as trawling, dredging, digging and raking which all result in the non-targeted removal of seagrass species. The direct physical effects of such fishing methods on seagrass are described in detail for the pressures 'abrasion' and 'penetration and/or disturbance of the substratum'.

Seagrasses may be directly removed or damaged by static or mobile gears that are targeting other species. These direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of non-target species in this biotope.

Sensitivity assessment. Seagrass habitats are not dependent on any other organisms but the incidental removal of seagrass as by-catch could be detrimental and could remove the biotope (see the evidence presented under 'penetration and/or disturbance of the substratum' above). Therefore, resistance is considered to be **'None',** resilience **'Low**' and a sensitivity **'High'**.

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