



MarLIN

Marine Information Network

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

Seapens and burrowing megafauna in circalittoral fine mud

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

Jacqueline Hill & Dr Harvey Tyler-Walters

2018-03-19

A report from:

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

Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/habitats/detail/131>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Hill, J.M. & Tyler-Walters, H. 2018. Seapens and burrowing megafauna in circalittoral fine mud. 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.131.1>



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

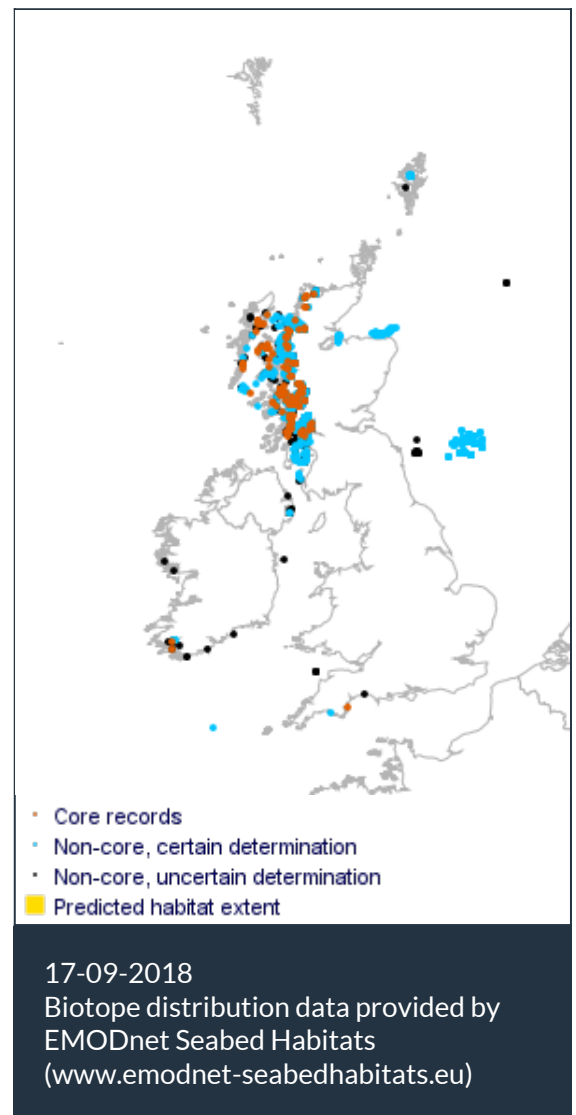
(page left blank)



Pennatula phosphorea and *Turritella communis* in muddy sediment.

Photographer: Mark Davies

Copyright: Joint Nature Conservation Committee (JNCC)



Researched by Jacqueline Hill & Dr Harvey Tyler-Walters

Refereed by Dr David Hughes and Dr Clare Greathead

Summary

☰ UK and Ireland classification

EUNIS 2008	A5.361	Seapens and burrowing megafauna in circalittoral fine mud
JNCC 2015	SS.SMu.CFiMu.SpMmeg	Seapens and burrowing megafauna in circalittoral fine mud
JNCC 2004	SS.SMu.CFiMu.SpMmeg	Seapens and burrowing megafauna in circalittoral fine mud
1997 Biotope	SS.CMU._SpMmeg	Seapens and burrowing megafauna in circalittoral soft mud

🔍 Description

Plains of fine mud at depths greater than about 15 m may be heavily bioturbated by burrowing

megafauna; burrows and mounds may form a prominent feature of the sediment surface with conspicuous populations of sea pens, typically *Virgularia mirabilis* and *Pennatula phosphorea*. These soft mud habitats occur extensively throughout the more sheltered basins of sea lochs and voes and are present in quite shallow depths (as little as 15 m) in these areas probably because they are very sheltered from wave action. The burrowing Crustacea present typically include *Nephrops norvegicus*, which is frequently recorded from surface observations although grab sampling may fail to sample this species. Indeed, some forms of sampling may also fail to indicate sea pens as characterizing species. This biotope also seems to occur in deep offshore waters in the North Sea, where densities of *Nephrops norvegicus* may reach 68 per 10 m² (see Dyer *et al.* 1982, 1983), Western Scotland in the Minches, and the Irish Sea. The burrowing anemone *Cerianthus lloydii* and the ubiquitous epibenthic scavengers *Asterias rubens*, *Pagurus bernhardus* and *Liocarcinus depurator* are present in low numbers in this biotope whilst the brittlestars *Ophiura albida* and *Ophiura ophiura* are sometimes present but are much more common in slightly coarser sediments. Low numbers of the anemone *Pachycerianthus multiplicatus* may also be found, and this species, which is scarce in the UK, appears to be restricted to this habitat (Plaza & Sanderson 1997). The infauna may contain significant populations of the polychaetes *Pholoe* spp., *Glycera* spp., *Nephtys* spp., spionids, *Pectinaria belgica* and *Terebellides stroemi*, the bivalves *Nucula sulcata*, *Corbula gibba* and *Thyasira flexuosa*, and the echinoderm *Brissopsis lyrifera*.

In northern deep fjordic sea lochs, CFiMu.SpMeg is represented by the sub-biotope CFiMu.SpMeg.Fun due to the presence of the tall sea pen *Funiculina quadrangularis*. IFiMu.PhiVir is similar to CFiMu.SpMeg but is found in shallower, less thermally stable waters and lacks the large burrowing species and the sea pen *Pennatula phosphorea*, and CFiMu.BlyrAchii shares a similar infauna but lacks *Pennatula phosphorea*. CFiMu.MegMax is similar in composition but dominated by burrowing macrofauna (i.e mud shrimps) and has a lower abundance of sea pens. (Information from the Connor *et al.*, 2004; JNCC, 2015).

↓ Depth range

10-20 m, 20-30 m, 30-50 m

🏛️ Additional information

The biotope does occur in shallower water, at 10-12 m in Loch Sween for example (D. Hughes pers. comm.). In some instances of this biotope *Asterias rubens*, *Pagurus bernhardus* and *Liocarcinus depurator* may be present in high numbers (D. Hughes pers. comm.). This biotope is also recorded in the Fladen Ground in the North Sea (Greathead *et al.*, 2011).

The following review of the ecology of the biotope examines both the sea pen epifauna and the burrowing megafauna. Therefore, the ecology review is applicable to both the CFiMU.SpMeg (inc. CFiMU.SpMeg.Fun) and CFiMu.MegMax biotopes, which are closely aligned (Connor *et al.*, 2004). Hughes (1998a) noted that the interaction between the sea pens and the bioturbation caused by burrowing megafauna was unknown. However, he also noted that sea pen and burrowing megafauna clearly co-exist and that the community of megafauna probably exhibits a 'mosaic' of communities depending on local disturbance (Hughes, 1998a).

✓ Listed By

- none -

Further information sources

Search on:



Habitat review

🔄 Ecology

Ecological and functional relationships

- The characterizing and other species in this biotope occupy space in the habitat but their presence is most likely primarily determined by the occurrence of a suitable substratum rather by interspecific interactions. Sea pens and burrowing megafauna are functionally and ecologically dissimilar and are not necessarily associated with each other but occur in the same muddy sediment habitats. For example, some sites with abundant burrowing megafauna have no sea pens (and vice versa). It is possible that sea pens might be adversely affected by high levels of megafaunal bioturbation, perhaps by preventing the survival of newly settled colonies. No single species can be considered a keystone species whose activity is essential to the structure of the community. In addition to sea pens and burrowing megafauna, the biotope often supports a rich fauna of smaller less conspicuous species, such as polychaetes, nematodes and bivalves, living within the sediment.
- There are however, some interspecific relationships within the biotope. For instance, the shrimp *Jaxea nocturna*, which often lives in association with the echiuran worm *Maxmuelleria lankesteri* (Nickell *et al.*, 1995), may benefit from the organic-rich mud pulled into its burrows by the worm. Nickell *et al.* (1995) found that numerous small bivalves and polychaete worms colonized the walls of *Maxmuelleria lankesteri* burrows. Mobile polychaetes such as *Ophiodromus flexuosus*, which normally live out on the sediment surface were also seen to enter burrows. The body of shrimps may offer a substratum for colonization. The ctenostome bryozoan *Triticella flava*, for example, grows a dense 'furry' covering on the antennae, mouthparts and legs of burrowing crustaceans. It is most commonly found on *Calocaris macandreae* but has also been found on several of the other crustacean burrowers present in the biotope (Hughes, 1998b). The mouthparts of *Nephrops norvegicus* harbour a small commensal sessile animal, the newly described *Symbion pandora* (Conway Morris, 1995). A few organisms have also been recorded in association with British sea pens. *Funiculina quadrangularis* is often host to the isopod *Astacilla longicornis*, which clings to the rachis, and the brittlestar *Asteronyx loveni*, which clings to the sea pen maintaining an elevated position above the seabed. However, *Asteronyx* is only found in deeper waters, usually below 100 m depth. There are also a few specialist predators of sea pens (see below). Although rare, the tube of the large sea anemone *Pachycerianthus multiplicatus*, which is only found in this biotope, creates a habitat for attached species (O'Connor *et al.*, 1977).
- The species living in deep mud biotopes are generally cryptic in nature. Predation is probably low because many species will be sheltered to some extent from visual surface predators such as fish. Evidence of predation on *Virgularia mirabilis* by fish seems limited to a report by Marshall & Marshall (1882 in Hoare & Wilson, 1977) where the species was found in the stomach of haddock. Observations by Hoare & Wilson (1977) suggest however, that predation pressure on this species is low. Many specimens of *Virgularia mirabilis* lack the uppermost part of the colony which has been attributed to nibbling by fish. The sea slug *Armina loveni* is a specialist predator of *Virgularia mirabilis*. *Nephrops norvegicus* is eaten by a variety of bottom-feeding fish, including cod, haddock, skate and dogfish. There are also numerous records of fish predation on thalassinidean mud shrimps such as *Calocaris macandreae* which has been found in the stomachs of cod and haddock. *Maxmuelleria lankesteri* has also been recorded in the stomachs of Irish sea cod (Hughes,

- 1998b). *Nephrops norvegicus* is carnivorous, feeding on brittle stars, polychaetes, bivalves and other crustaceans such as *Calocaris macandreae*.
- The bioturbatory activities of thalassinidean mud-shrimps such as *Callianassa subterranea* have important consequences for the structural characteristics of the sediment they inhabit. An important aspect of bioturbatory activity was emphasised by Johnston (1974) who showed that the activity of deposit-feeders results in the production of organic-mineral aggregates which may comprise as much as 70% of the sediment particle total. Such aggregation of particles must greatly increase the porosity of the sediments and so have a considerable influence on the transfer of chemicals by diffusion or other physical processes, as well as critically affecting environmental space for meio- and macrofauna and the bacterial flora. Such influences affect a variety of important ecosystem functions, including nutrient exchange (Nickell *et al.*, 1995), faunal community structure and biogeochemical cycling (e.g. Koike & Mukai, 1983; Waslenchuk *et al.*, 1983; Posey, 1986). Several studies have examined the effects of thalassinidean shrimp bioturbation on sedentary and mobile infaunal species. Tamaki (1988) found that *Callianassa japonica* had a positive effect on colonization by other mobile taxa, possibly by irrigating and fertilizing the sediment that stimulated the growth of microalgae and bacteria or by loosening up the sediment that eased burrowing and penetration. The abundance of sedentary species such as spionid polychaetes and some bivalves have been observed to be negatively correlated with abundance of Callianassid shrimps (e.g. Posey, 1986). The redistribution of organic matter within the sediment by effective bioturbating species, such as the deep burrowing mud shrimp *Callianassa subterranea* and the shallower burrowing *Nephrops norvegicus*, will influence depth distribution and community structure as well. However, the activities of the larger burrowers can either enhance or reduce the overall abundance of sediment macrofauna, depending on the species involved. Megafaunal activity creates a mosaic of disturbance patches which may be important to the maintenance of biodiversity in the sediment community (Hughes, 1998(b)). The presence and activity of *Callianassa* species has been shown to be linked to significant sediment and radioactive particulate resuspension (Roberts *et al.*, 1981; Colin *et al.*, 1986). Bioturbatory activities of deposit feeding genera such as *Nucula* and *Pectinaria* will also actively increase the rate of oxygen diffusion through finer sediments (Pearson & Rosenberg, 1978).
 - Where several species of burrowing megafauna occur together in the same biotope it is not unusual for burrows to interconnect. Tuck *et al.* (1994) found that 34% of *Nephrops* burrows at a site in Loch Sween showed evidence of interactions with other species, including *Maxmuelleria lankesteri*, *Jaxea nocturna* and *Leseurigobius friesii*. These interconnections are probably accidental and not indicative of any close symbiotic relationship between different burrowers. Such interconnections may improve ventilation and nutritional content of the burrows.
 - Mobile adults, such as *Nephrops norvegicus* and *Callianassa subterranea*, often show spacing out phenomena. Such behaviour is usually linked to territorial aggression (Gray, 1974).
 - The opening of the burrows of *Callianassa subterranea* provide temporary refuge for fish such as the black goby *Gobius niger* and *Pomatoschistus minutus*. Occasional errant polychaetes, particularly polynoid worms, inhabit the burrows (Nickell & Atkinson, 1995).
 - The burrowing and feeding activities of *Amphiura filiformis*, if present in high abundance, can modify the fabric and increase the mean particle size of the upper layers of the substrata by aggregation of fine particles into faecal pellets. Such actions create a more open fabric with a higher water content which affects the rigidity of the seabed (Rowden *et al.*, 1998). Such destabilisation of the seabed can affect rates of particle resuspension.
 - The arms of *Amphiura filiformis* are an important food source for demersal fish and *Nephrops norvegicus* providing significant energy transfer to higher trophic levels including

to humans. Increased nutrients and eutrophication processes may contribute to an increase in the accumulation of hydrophobic contaminants in *Amphiura filiformis* and their transfer to higher trophic levels (Gunnarsson & Skold, 1999).

- In their investigation of density dependent migration in *Amphiura filiformis* Rosenberg *et al.* (1997) calculated that in areas of high density of the species (3000 individuals per m²), the area of sediment at about 3 to 4cm depth covered by disks of *Amphiura filiformis* can be estimated as 22%. The capacity of such a density of brittle stars to displace sediment can be calculated at 0.18m² per hour. Thus, movement of *Amphiura filiformis* should generate a more or less continuous displacement of sediment and be of great significance to the biogeochemical processes in the sediment.
- The hydrodynamic regime determines whether a biotope, such as CMU.SpMeg, exists in a particular place by allowing deposition of fine sediment. The hydrography also affects the water characteristics in terms of salinity, temperature and dissolved oxygen. It is also widely accepted that food availability (see Rosenberg, 1995) and disturbance, such as that created by storms, (see Hall, 1994) are also important factors determining the distribution of species in benthic habitats.

Seasonal and longer term change

- Seapen and burrowing megafaunal communities appear to persist over long periods at the same location. Species such as the sea pen *Virgularia mirabilis*, the brittle star *Amphiura filiformis* and the mud shrimp *Calocaris macandreae* appear to be long-lived and are unlikely to show any significant seasonal changes in abundance or biomass. The numbers of some of the other species in the biotope may show peak abundances at certain times of the year due to the seasonality of breeding and larval recruitment. Immature individuals of *Liocarcinus depurator*, for example, are more frequent in the periods May - September.
- There are daily patterns of activity in some species. *Nephrops norvegicus*, for example, forages for food at night, returning to their burrows at sunrise. However, in deeper water (> 100m) this activity is reversed suggesting that activity is determined by light intensity. The echiuran *Maxmuelleria lankesteri* has been observed to feed only at night and so activity may also be related to light intensity. Movement of the sea pen *Virgularia mirabilis* in and out of the sediment may be influenced by tidal conditions (Hoare & Wilson, 1977).
- Burrowing activity of the mud shrimp *Callianassa subterranea* in the North Sea appears to be seasonal (Rowden & Jones, 1997). Relatively little activity was observed in the period January - April, before a steady increase through spring and early summer, reaching a maximum in at the end of the summer and a decline in autumn and winter. In January, when bioturbatory activity was low the seabed appeared essentially flat and smooth, whilst in September the bed was littered with numerous mounds and depressions. Tunberg (1986) found that *Upogebia deltaura* remained inactive in the deepest parts of its burrow during the winter. *Maxmuelleria lankesteri* is active all year round but seem to show peaks of activity in December and April when the proportion of easily-degradable organic matter at the sediment surface is at its highest (Hughes, 1998b).
- The behaviour of *Nephrops norvegicus* may be seasonal. In Loch Sween, *Nephrops* burrows were aggregated in groups during the late summer, which then broke up into a random distribution during the winter (Tuck *et al.*, 1994). Such aggregations may result when burrow complexes formed when juvenile animals settle in pre-existing adult systems, then break up as the juveniles gradually extend their own burrows and lose contact with those of the adults.

Habitat structure and complexity

- The biotope has little structural complexity above the sediment surface. Burrows and mounds of burrowing megafauna may form a prominent feature of the sediment surface with conspicuous populations of sea pens, typically *Virgularia mirabilis* and *Pennatula phosphorea*. However, apart from a couple of species of nudibranch the sea pens do not provide significant habitat for other fauna. Where present, the tube of the rare sea anemone *Pachycerianthus multiplicatus*, creates a habitat for attached species.
- However, dense populations of burrowers create considerable structural complexity, below the surface, relative to sediments lacking these animals. For example, *Callianassa subterranea* creates complex burrow systems in sandy mud sediments. The burrows consist of a multi-branched network of tunnels connected to several inhalent shafts, each terminating in a funnel shaped opening to the surface. These burrows allow a much larger surface area of sediment to become oxygenated, and thus enhance the survival of a considerable variety of small species (Pearson & Rosenberg, 1978). Burrows also create habitats for other animals such as clams and polychaetes. Burrows are also created by other crustacean species such as *Nephrops norvegicus* and *Calocaris macandreae* although these are not as complex as those of *Callianassa*. The echiuran worm *Maxmuelleria lankesteri* produces long-lasting burrows that provide a habitat for a variety of small polychaetes and bivalves but none of these appear to be obligate relationships (Jones *et al.*, 2000). In Scottish sea lochs the black goby *Gobius niger* will take up residence in burrows belonging to *Maxmuelleria lankesteri* and other species, frequently extending or changing the shape of the burrow opening. The squat lobster *Munida rugosa* is frequently found inhabiting burrows on the periphery of megafaunally-burrowed muds, close to coarser sediments. The sediment expelled by *Callianassa subterranea* forms unconsolidated volcano-like mounds, which significantly modify seabed surface topography (Rowden *et al.*, 1998).
- The bioturbatory activities of callianassids such as *Callianassa subterranea* have important consequences for the structural characteristics of the sediment. Many infauna are limited to the upper oxygenated layer, however, others penetrate deeper in irrigated burrows or possess long siphons capable of transporting oxygenated water into the sediment, which may result in an oxygenated layer around their burrows.

Productivity

Productivity in subtidal sediments is often quite low. Macroalgae are absent from CMU.SpMeg and so productivity is mostly secondary, derived from detritus and organic material. However, some shallower sites can have an extensive growth of benthic diatoms in the summer. Allochthonous organic material is derived from anthropogenic activity (e.g. sewerage) and natural sources (e.g. plankton, detritus). Autochthonous organic material is formed by benthic microalgae (microphytobenthos e.g. diatoms and euglenoids) and heterotrophic micro-organism production. Organic material is degraded by micro-organisms and the nutrients are recycled. The high surface area of fine particles provides surface for microflora.

Recruitment processes

The reproductive biology of British sea pens has not been studied, but in other species, for instance, *Ptilosarcus guernei* from Washington State in the USA, the eggs and sperm are released from the polyps and fertilization takes place externally. The free-swimming larvae do not feed and settle within seven days if a suitable substratum is available (Chia & Crawford, 1973). Thus, the

limited data available from these other species would suggest a similar pattern of patchy recruitment, slow growth, and long lifespan. As is typical of decapod crustaceans the female thalassinidean burrowers in the biotope carry fertilized eggs on the abdomen before hatching into planktonic larvae. The length of time the larvae spends in the plankton appears to vary between species. The larval stages of *Nephrops norvegicus* spend about 50 days in the plankton before settlement and it is thought to be about 28 days for *Callinassa subterranea*. In Northumberland, the life-history of *Calocaris macandreae* was found to be rather different. Animals produced eggs in January-February which hatched in September-October. Only about 100 eggs were produced in each batch and the large larvae had no free-swimming phase before settling. The larval stage of the echiuran *Maxmuelleria lankesteri* is completely unknown but the large, yolky eggs suggest that the planktonic stage is brief or absent. However, many of the species in the biotope appear to have planktonic larvae so recruitment to the biotope may often be from distant sources.

Time for community to reach maturity

There is very little known about community development for this biotope. Almost nothing is known about the life cycle and population dynamics of British sea pens, but data from other species suggest that they are likely to be long-lived and slow growing with patchy and intermittent recruitment. The burrowing decapods that characterise the biotope vary in their reproductive strategies and longevity. In the North Sea the lifespan of *Callinassa subterranea* appears to be 2-3 years (Rowden & Jones, 1994) and individuals become sexually mature in their first year. Time to sexual maturity is longer in *Nephrops norvegicus*, about 2.5 - 3 years, and for the very long-lived *Calocaris macandreae* individuals off the coast of Northumberland did not become sexually mature until five years of age, and produced only two or three batches of eggs in their lifetime. Although little is known of the life cycle of the echiuran worm *Maxmuelleria lankesteri* long-term observations of populations *in situ* have provided no evidence of any major fluctuations in population size, and it has been suggested that the species is long-lived with stable populations and low recruitment rates. Many of the other species in the biotope, such as polychaetes and bivalves, are likely to reproduce annually, be shorter lived and reach maturity much more rapidly. Since most key species reproduce regularly but take a while to grow, recruitment will be rapid but it will take several years to reach maturity and so it will probably take at least five years for the overall community to reach maturity.

Additional information

-

Preferences & Distribution

Habitat preferences

Depth Range	10-20 m, 20-30 m, 30-50 m
Water clarity preferences	No information found
Limiting Nutrients	No information found, Not relevant
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Physiographic preferences	Open coast, Sea loch / Sea lough
Biological zone preferences	Circalittoral
Substratum/habitat preferences	Mud

Tidal strength preferences	Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Extremely sheltered, Moderately exposed, Sheltered, Very sheltered
Other preferences	Muddy sediment

Additional Information

Species composition

Species found especially in this biotope

- [Pachycerianthus multiplicatus](#)

Rare or scarce species associated with this biotope

- [Pachycerianthus multiplicatus](#)

Additional information

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

CFiMu.Spnmeg and CFiMU.Spnmeg.Fun are similar to CFiMU.MegMax (Connor *et al.*, 2004) but differ in the relative abundance of sea pens (Spnmeg) and burrowing megafauna (MegMax). Connor *et al.* (2004) noted that MegMax often occurs in deeper water than Spnmeg but that the environmental factors that separate the biotopes are unclear. Hughes (1998a) suggested that the sea pen and burrowing megafauna communities exhibit a mosaic of patches of megafaunal communities depending on the level of disturbance. Hughes (1998a) also noted that the interaction between burrowing megafauna and sea pens was unknown, although they clearly co-exist.

Spnmeg and MegMax support a rich infauna of polychaetes, bivalves, burrowing sea urchins, brittlestars, and sea cucumbers, and a mobile epifauna of crabs and starfish. While the infaunal species composition varies between the biotopes, the infaunal and mobile epifaunal community is probably found across a range of circalittoral mud and deep mud habitats. Spnmeg.Fun is found in slightly deeper waters, typical of the fjordic sea lochs and the Minch, and is characterized by the presence of *Funiculina quadrangularis*. Spnmeg and Spnmeg.Fun may both support local populations of the rare burrowing anemone *Pachycerianthus multiplicatus* and occasional *Cerianthus lloydii*. Although *Pachycerianthus multiplicatus* is rare in the UK, loss of either burrowing anemone would not lead to a loss of the biotope.

Therefore, the sensitivity assessment of Spnmeg (and Spnmeg.Fun) concentrates on the epifaunal, suspension feeding, sea pens, because a significant reduction in their abundance would result in the loss of the Spnmeg biotope. The sensitivity of burrowing megafauna and other species is discussed where relevant.

Resilience and recovery rates of habitat

Studies of oogenesis in *Funiculina quadrangularis* and *Pennatula phosphorea* in Loch Linnhe, Scotland, demonstrated that they were dioecious, with 1:1 sex ratios, highly fecund, with continuous prolonged oocyte development and annual spawning (Edwards & Moore 2008; Edwards & Moore 2009). In *Pennatula phosphorea*, oogenesis exceeded 12 months in duration, with many small oocytes of typically 50 per polyp giving an overall fecundity of ca 40,000 in medium to large specimens, depending on size. However, <30% matured (synchronously) and were spawned in summer (July-August). Mature oocytes were large (>500 µm) which suggested a lecithotrophic larval development (Edwards & Moore, 2008). In *Funiculina quadrangularis* fecundity was again high, expressed as 500-2000 per 1 cm midsection, but not correlated with size, and again, only a small proportion of the oocytes (<10%) matured. Unlike *Pennatula phosphorea*, annual spawning occurred in autumn or winter (between October and January). Also, the mature oocytes were very large (>800µm), which suggested a lecithotrophic larval development (Edwards & Moore, 2009).

The lecithotrophic larval stage of *Funiculina quadrangularis* may result in a relatively long period of time in the water column and high potential dispersal ability and may explain the high gene flow observed between colonies of *Funiculina quadrangularis* in two Scottish sea lochs (Wright *et al.*, 2015). Wright *et al.* (2015) found limited genetic population subdivision within and between populations of *Funiculina quadrangularis* in Loch Linnhe and Loch Duich. However, the high genetic diversity and unique genotypes supported the absence of asexual reproduction in this species

(Wright *et al.*, 2015). No similar studies were available for *Virgularia mirabilis*, but Edwards & Moore (2009) noted that many sea pens exhibited similar characteristics. In a study of the intertidal *Virgularia juncea* fecundity varied with length (46,000 at 50 cm and 87,000 at 70 cm), eggs reached a maximum size of 200-300 µm in May and were presumed to be spawned between August and September (Soong, 2005).

Birkland (1974) found the lifespan of *Ptilosarcus gurneyi* to be 15 years, reaching sexual maturity between the ages of 5 and 6 years; while Wilson *et al.* (2002) noted that larger specimens of a tall sea pen (*Halipteris willemoesi*) in the Bering Sea were 44 years old, with a growth rate of 3.6 - 6.1cm/year.

Sea pens were shown to recover rapidly from displacement and removal from the seabed. *Funiculina quadrangularis* and *Pennatula phosphorea* were found to right themselves when dislodged, with all *Pennatula phosphorea* individuals re-established and 50% of *Funiculina quadrangularis* after 72 hours (Eno *et al.*, 2001). *Virgularia mirabilis* was found to withdraw into its burrow rapidly (ca 30 seconds) and could not be uprooted by dragged creels (Hoare & Wilson 1977; Eno *et al.*, 2001; Ambroso *et al.* 2013). *Pennatula phosphorea* and *Funiculina quadrangularis* recovered with 72-96 hours after experimental smothering for 24 hours by pot or creel and after 96-144 hours of smothering for 48 hours (Kinneer *et al.* 1996; Eno *et al.* 2001). In summary, all three sea pen species have been found to recover rapidly from the effects of dragging, uprooting and smothering (Eno *et al.*, 2001). However, a later study of the effects of experimental trawling damage in the sea whip *Halipteris willemoesi* suggests that recovery in *Funiculina quadrangularis* may have been over-estimated. *Halipteris willemoesi* is a functionally similar species to *Funiculina quadrangularis*, as it is tall, thin, and cannot withdraw into the sediment. Malecha & Stone (2009) simulated trawl damage in field populations in Alaskan waters, by abrading the sea whip with rubber disks (similar to rubber tire punch-outs used on the footrope of many trawls), dislodging them from the sediment and breaking the axial rod manually. All the specimens abraded repaired tissue damage and survived the experimental period. However, the authors noted that the experimental abrasion probably underestimated the effect of trawls as it did not include the mechanical force of the mobile gear and that even the smallest amount of tissue damage probably decreased the sea whip's ability to reproduce. Fifty percent of the dislodged sea whips were able to rebury and become erect within 18 days. Only 42% of the fractured sea whips were erect 18 days after treatment. However, only one specimen was erect after the 372 days of the experiment. There was no evidence to suggest that specimens could repair their damaged axial rods. After 372 days, 92% of the dislodged and 100% of the fractured specimens had substantial tissue loss and perished. Tissue loss was exaggerated by predation from nudibranchs, which appeared to be attracted to the experimental area, possibly due to the tissue damage suffered by the sea whips (Malecha & Stone, 2009).

Recovery from effects that remove a proportion of the sea pen population (e.g. bottom gears, hydrographic changes) will depend on recruitment processes and little is known about the life history and population dynamics of sea pens (Hughes, 1998a). Hughes (1998a) suggested that patchy recruitment, slow growth and long lifespan were typical of sea pens. Larval settlement is likely to be patchy in space and highly episodic in time with no recruitment to the population taking place for some years. Greathead *et al.* (2007) noted that patchy distribution is typical for sea pen populations. In Holyhead harbour, for example, animals show a patchy distribution, probably related to larval settlement (Hoare & Wilson, 1977). However, no information on larval development, settlement behaviour or dispersal was found.

Buchanan (1963) examined the population dynamics of *Calocaris macandreae* off the

Northumberland coast. The oldest individuals in that population appeared to be 9 years old and it was suggested that an age of almost ten years may be attained by a few (Buchanan, 1974). *Calocaris macandreae* are hermaphrodites and eggs are produced at five years old. Around 50 eggs are attached to the pleopods and are carried for nine months until September to October of the sixth year. Annual moults follow but the next batch of eggs takes two years to mature and the second laying is at the end of the seventh year with occasionally a third at the end of the ninth year. Mortality of a year group is almost wholly confined to the ninth and tenth years (Buchanan, 1974). Hughes (1998a) noted that age at maturity (5 years), low fecundity (producing only two to three batches of eggs in their lifetime) and long lifespan contributed to the stability of the population studied, which was very stable in numbers over a 10-year period. No evidence was found for recovery rates following disturbance.

Callianassa subterranea is sexually dimorphic in that the mature male bears an enlarged major chela. In the North Sea, females were found bearing eggs from April to September, and planktonic larvae were most abundant in August. Larvae spent about four weeks in the plankton before settlement. Large females may have a secondary breeding period in late winter. Their lifespan was 2-3 years (Rowden & Jones, 1994; Hughes, 1998a).

Nephrops norvegicus reach sexual maturity at 2.5-3 years of age in females and after three years in males (Hughes, 1998a). In the Irish Sea, *Nephrops norvegicus* individuals are not thought to live more than 8 or 9 years and sexually mature at about 2.5 - 3 years. However, in deeper waters such as the Porcupine Bank, they may survive over 15 years (Marine Institute, 2001). In Scottish waters, eggs are spawned and fertilized between August and November and carried by the females until the larvae hatch in April to August (Hughes, 1998a). Local populations of *Nephrops norvegicus* may vary considerably in density, size and growth rate (Tuck *et al.*, 1997) with fecundity also varying geographically (Eiriksson, 1970; Tuck *et al.*, 1997). The percentage of eggs lost during development can range from 32 - 51% with larval mortalities as high as 87% (Garrod & Harding, 1980) which could reduce recovery rates. As a result, *Nephrops norvegicus* do not produce large numbers of offspring. The pelagic larval stage lasting up to 50 days (Hughes, 1998a; Johnson *et al.*, 2013; Powell and Eriksson, 2013). This may support long-range dispersal and recolonization of depleted populations, but water currents may prevent larvae reaching locations away from source populations and may remove larvae from populations preventing self-recruitment in small stocks (Johnson *et al.*, 2013). Recolonization of depleted populations may also be limited by the requirement for existing burrows for successful recruitment (Tuck *et al.*, 1994, cited in Johnson *et al.*, 2013). Adults are essentially sedentary as tagging studies have revealed movements of no more than 100 m from their burrow in adult life (Chapman & Rice, 1971). Therefore, potential recruitment from other populations of *Nephrops norvegicus* is low as larvae do not have a high dispersal potential and adults show no evidence of migration (Marine Institute, 2001). The resilience of *Nephrops* populations is assessed as 'Medium' (2-10 years) although confidence in the quality of evidence for recovery is low as this assessment is based on expert judgement, taking into consideration the apparent long-term stability of *Nephrops* fishing grounds (Ungfors *et al.*, 2013).

Resilience assessment. In SpnMeg (and SpnMeg.Fun) the resilience assessment is based on the recovery rates of the sea pen epifauna as the important characterizing species within the biotope. The characteristic burrowing megafauna is likely to recover more quickly, with perhaps the exception of *Calocaris macandreae*.

Where the sea pens survive impact undamaged, that is resistance is 'High', recovery is rapid; a resilience of 'High' (<2 years). Where a proportion of the population is removed or killed, then the species has a high dispersal potential and long-lived benthic larvae, but larval recruitment is

probably sporadic and patchy and growth is slow, suggesting that recovery will take many years: a resilience of 'Low' (>10 years). The assessment is based on literature on the life history of the three sea pen species but not their population dynamics or information inferred from other species. Therefore, the quality, applicability and concordance of the evidence are 'Medium'.

The recovery rates for mud shrimp and *Nephrops* are likely to be dependent on the spatial scale of impact and the ability of adults to survive exposure and provide a potential supply of colonists. *Callinassa subterranea* is short lived but produces numerous offspring with a high potential dispersal range, which suggests that recolonization and recovery may be rapid, e.g. within a few years. The evidence from fishing grounds indicates that *Nephrops norvegicus* can persist in areas where they are subject to targeted removal, which suggests that the population can withstand and recover from repeated disturbances, but it is not clear what proportion of the population is removed and hence what the recovery rate to an undisturbed state would be. The evidence above suggests that the mud shrimp and *Nephrops* component of the biotope would probably recover within 2-10 years; a resilience of **Medium**, depending on the scale of removal. *Calocaris macandreae* may be an exception. *Calocaris macandreae* is long-lived, reaches sexual maturity only after five years, has a low fecundity and lacks a pelagic stage. Therefore, local recruitment may be good, where a population remains but recovery of the abundance and age structure of a significantly reduced population would probably be prolonged and where the population experienced a significant reduction in abundance (e.g. resistance is Low), then resilience is likely to be **Low** (10-25 years).

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Medium Q: Low A: NR C: NR	Low Q: Medium A: Medium C: Medium	Medium Q: Low A: Low C: Low

In shallow sea lochs, sedimentary biotopes typically experience seasonal changes in temperature between 5°C and 15°C (10°C) (Hughes, 1998a). Although unusually warm summers or cold winters may change the temperatures outside this range, benthic burrowing species will be buffered from extremes by their presence in the sediment. The sea pens typical of CFiMu.SpMeg (except *Funiculina quadrangularis*) can also withdraw into their burrows for protection. No information was found on the upper limit of sea pens tolerance to temperature. *Virgularia mirabilis* is recorded from western Europe, the Mediterranean, from Norway and Iceland to Africa in the North Atlantic, and to the Gulf of Mexico in North America (Hughes, 1998a; OBIS, 2016). *Pennatula phosphorea* is recorded in the North Sea and western British coasts but is absent from southern Britain (Hughes, 1998a). Hughes (1998a) suggested that records from the Mediterranean and North Atlantic are confused with other species. *Funiculina quadrangularis* is only recorded from north and west coasts of Scotland and Ireland in the British Isles (Hughes, 1998a), but is also recorded in the North Atlantic, the Mediterranean, North and South America, Japan and New Zealand (Manual 1981 cited in Hughes 1998a; OBIS, 2016).

The distribution of sea pens suggests that they are probably resistant to a 2°C change in temperature. However, sea pens are subtidal and occur at depth where wide and rapid variations in temperature are not common and so may be less resistant of a short-term increase of 5°C. Therefore, a resistance of **Medium** is suggested but with Low confidence. Resilience is probably **Low** so that sensitivity is assessed as **Medium**.

Temperature decrease (local)**Medium**Q: **Low** A: **NR** C: **NR****Low**Q: **Medium** A: **Medium** C: **Medium****Medium**Q: **Low** A: **Low** C: **Low**

In shallow sea lochs, sedimentary biotopes typically experience seasonal changes in temperature between 5°C and 15°C (10°C) (Hughes, 1998a). Although unusually warm summers or cold winters may change the temperatures outside this range, benthic burrowing species will be buffered from extremes by their presence in the sediment. The sea pens typical of CFiMu.SpMeg (except *Funiculina quadrangularis*) can also withdraw into their burrows for protection. No information was found on the upper limit of sea pens tolerance to temperature. *Virgularia mirabilis* is recorded from western Europe, the Mediterranean, from Norway and Iceland to Africa in the North Atlantic, and to the Gulf of Mexico in North America (Hughes, 1998a; OBIS, 2016). *Pennatula phosphorea* is recorded in the North Sea and western British coasts but is absent from southern Britain (Hughes, 1998a). Hughes (1998a) suggested that records from the Mediterranean and North Atlantic are confused with other species. *Funiculina quadrangularis* is only recorded from north and west coasts of Scotland and Ireland in the British Isles (Hughes, 1998a), but is also recorded in the North Atlantic, the Mediterranean, North and South America, Japan and New Zealand (Manual 1981 cited in Hughes 1998a; OBIS, 2016).

The distribution of sea pens suggests that they are probably resistant to a 2°C change in temperature. However, sea pens are subtidal and occur at a depth where wide and rapid variations in temperature are not common and so may be less resistant of a short-term increase of 5°C. Therefore, a resistance of **Medium** is suggested but with Low confidence. Resilience is probably **Low** so that sensitivity is assessed as **Medium**.

Salinity increase (local)**None**Q: **Low** A: **NR** C: **NR****Low**Q: **Medium** A: **Medium** C: **Medium****High**Q: **Low** A: **Low** C: **Low**

No information on the salinity tolerance of the three sea pens was found. Jones *et al.* (2000) suggested that *Virgularia mirabilis* was more tolerant of reduced salinity due to its distribution in shallower waters. MNCR data recorded *Virgularia mirabilis* and *Pennatula phosphorea* species from biotopes (SS.SMu.IFiMu.PhiVir; SS.SMu.CFiMu.SpMeg) that occur in full and variable salinity but *Funiculina quadrangularis* was only recorded in biotopes at full salinity. Recent analysis of survey data by Greathead *et al.* (2007), demonstrated that *Virgularia mirabilis* was the most ubiquitous of all three of the sea pens in Scotland, found in habitats nearer coastal areas and inner sea lochs. For example, *Virgularia mirabilis* is characteristic of the SS.SMu.IFiMu.PhiVir biotope, which can occur at depths of only 0-5 m. Greathead *et al.* (2007) suggested that *Pennatula phosphorea* was found in areas further from coastal areas and inner sea lochs, except in Loch Broom. *Funiculina quadrangularis* demonstrated a preference for deeper waters rather than any other physicochemical factor (Greathead *et al.*, 2007).

Pennatula phosphorea occurs in SS.SMu.CFiMu.SpMeg at depths of >10m, while *Funiculina quadrangularis* prefers deeper water (ca >20 m) where it is probably unexposed and hence intolerant to changes in salinity while *Virgularia mirabilis* is the most likely of the three sea pens to be exposed to variable salinity. Nevertheless, an increase in salinity to hypersaline conditions (>40 psu) for a year is probably detrimental to the sea pens and other epifauna, while deep burrowing species may be protected by their depth in the substratum. Therefore, *Funiculina quadrangularis* and *Pennatula phosphorea* probably have a resistance of **None** but the resistance of *Virgularia mirabilis* is probably **Low**. Resilience is likely to be at least **Low** and the resultant sensitivity is '**High**' for all three species. Due to the lack of direct evidence the assessment in resistance is made

with **Low** confidence.

Salinity decrease (local)

None

Q: Medium A: Low C: Medium

Low

Q: Medium A: Medium C: Medium

High

Q: Medium A: Low C: Medium

No information on the salinity tolerance of the three sea pens was found. Jones *et al.* (2000) suggested that *Virgularia mirabilis* was more tolerant of reduced salinity due to its distribution in shallower waters. MNCR data recorded *Virgularia mirabilis* and *Pennatula phosphorea* species from biotopes (SS.SMu.IFiMu.PhiVir; SS.SMu.CFiMu.SpnMeg) that occur in full and variable salinity but *Funiculina quadrangularis* was only recorded in biotopes at full salinity. Analysis of survey data by Greathead *et al.* (2007), demonstrated that *Virgularia mirabilis* was the most ubiquitous of all three of the sea pens in Scotland, found in habitats nearer coastal areas and inner sea lochs. For example, *Virgularia mirabilis* is characteristic of the SS.SMu.IFiMu.PhiVir biotope, which can occur at depths of only 0-5 m. Greathead *et al.* (2007) suggested that *Pennatula phosphorea* was found in areas further from coastal areas and inner sea lochs, except in Loch Broom. *Funiculina quadrangularis* demonstrated a preference for deeper waters rather than any other physicochemical factor (Greathead *et al.*, 2007).

Overall, the evidence suggests that *Virgularia mirabilis* is the most likely of the three sea pens to be exposed to variable salinity and its presence in shallow water biotopes suggests that it can tolerate occasionally reduced salinity while *Funiculina quadrangularis* is probably unexposed and hence intolerant to changes in salinity. *Pennatula phosphorea* occurs in SS.SMu.CFiMu.SpnMeg at depths of >10m where it is probably unexposed and hence intolerant to changes in salinity. Therefore, *Virgularia mirabilis* is probably resistant of variable salinity. But a decrease from full to reduced salinity for a year (the benchmark) e.g. from 32-35 units to 22-25 units for a year is probably more extreme. Therefore, *Funiculina quadrangularis* and *Pennatula phosphorea* probably have a resistance of **None** but the resistance of *Virgularia mirabilis* is probably **Low**. Resilience is likely to be at least **Low** and the resultant sensitivity is 'High' for all three species.

Water flow (tidal current) changes (local)

Low

Q: High A: High C: Medium

Low

Q: Medium A: Medium C: Medium

High

Q: Medium A: Low C: Medium

Sea pen biotopes (e.g. SS.SMu.CFiMu.SpnMeg) occur in low energy environments with weak (<0.5 m/sec) to very weak tidal streams (Connor *et al.*, 2004), which are a prerequisite for the fine mud sediments in which the sea pens occur (Hughes, 1998a). Of the three sea pens, *Virgularia mirabilis* occurs in coarser sandier muds with small stones and shell fragments e.g. SS.SMu.CSaMu.VirOphPmax (Hughes, 1998a; Greathead *et al.* 2007), and is probably more tolerant of current or wave induced flow than *Funiculina quadrangularis* and *Pennatula phosphorea* but the entire group is probably intolerant of increased flow. For example, Hiscock (1983) examined the effects of water flow on *Virgularia mirabilis*. As water flow rates increase, *Virgularia mirabilis* first responds by swinging polyps around the axial rod to face away from the current (at 0.12 m/s), then polyps face downstream. With further increase in flow, the stalk bends over and the pinnae are pushed together to an increasing amount with increasing velocity of flow (at 0.33 m/s). Finally, tentacles retract and at water speeds greater than 0.5 m/s (i.e. 1 knot) the stalk retracts into the mud (Hiscock, 1983). Best (1988) noted similar behaviour in the sea pen *Ptilosarcus gurneyi* and noted that filter efficiency, and hence feeding, increased with increased flow but then decreased once flow began to deform the shape of the sea pen. If water speeds remain at this level or above the sea-pen will be unable to extend above the sediment, unable to feed and could die. *Pennatula phosphorea* has a larger surface area due to its width, while *Funiculina*

quadrangularis is larger and less flexible, suggesting both species may be less tolerant of increased flow than *Virgularia mirabilis*. Greathead *et al.* (2015) suggested that the large surface area of *Funiculina quadrangularis* (compared to the other two sea pens) was a hindrance in strong currents but a potential competitive advantage in deeper quiescent waters as the amount of organic matter in the water column decreases with depth. In addition, long-term increases in water flow are likely to modify the sediment, removing the fine sediments the sea pens require in favour of sandier, coarser sediments. A change in sediment type could also affect the burrowing megafauna (see a change in sediment type below).

Sensitivity assessment. The biotope occurs in weak to negligible flow, so that a decrease in flow is not relevant. An increase in flow is probably directly detrimental to sea pens and may alter the sediment type in the long-term. An increase in water flow of 0.1-0.2 m/s for a year is may result in an increase in overall flow outside the preferred range for the sea pens, depending on location. Therefore, an increase in water flow may result in the removal or death of a proportion of the population of *Virgularia mirabilis*, and as the other sea pens are probably less tolerant of change, a resistance of **Low** is suggested, with a resilience of **Low**, resulting in a sensitivity of **High**.

Emergence regime 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

Changes in emergence are **Not relevant** to the biotope, which is restricted to circalittoral below 10 metres. The pressure benchmark is relevant only to littoral and shallow sublittoral fringe biotopes.

Wave exposure changes (local)

High

Q: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Sea pen biotopes (e.g. SS.SMu.CFiMu.SpMmeg) occur in low energy environments, extremely sheltered to sheltered from wave exposure (Connor *et al.*, 2004), a prerequisite for the fine mud sediments in which the sea pens occur (Hughes, 1998a). While *Virgularia mirabilis* occurs in coastal areas and inner sea lochs, these areas are still sheltered from wave action, and in sandier muds (e.g. the biotope SS.SMu.CSaMu.VirOphPmax) wave exposure was not recorded to be more than 'sheltered'. Therefore, it is likely that all of the sea pens, characteristic of this biotope, are intolerant of an increase in wave action. *Virgularia mirabilis* is probably the most tolerant of the three species while *Funiculina quadrangularis* is probably the most intolerant as wave exposure is attenuated by depth and *Funiculina quadrangularis* prefers deeper waters than the other sea pens.

A decrease in wave exposure is unlikely in the sheltered habitats they inhabit. However, a decrease in wave exposure elsewhere may be beneficial by providing additional habitat for colonization and hence an increase in their distribution.

Sensitivity assessment. An increase in wave exposure is likely to affect all three species adversely, limiting or removing the shallower proportion of the population, and potentially modifying sediment and therefore habitat preferences in the longer-term. In some cases, areas suitable for *Pennatula phosphorea* and *Funiculina quadrangularis* may become more suitable for *Virgularia mirabilis*. However, a 3-5% increase in significant wave height (the benchmark) is unlikely to be significant. The benchmark level of change may be no more than expected during winter storms even in the sheltered waters favoured by this biotope. Alternatively, such a small change in wave action may not penetrate to the depths at which this biotope occurs. Therefore, resistance is recorded as **High** at the benchmark level. Hence, resilience is **High** and the biotope is assessed as

Not sensitive at the benchmark level.

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.

In Norwegian fjords, Rygg (1985) found a relationship between species diversity in benthic fauna communities and sediment concentrations of the heavy metals Cu, Pb and Zn. Cu, in particular, showed a strong negative correlation and the author suggested a cause-effect relationship. Those species not present at sites where Cu concentrations were greater than ten times higher than the background level, such as *Calocaris macandreae*, *Amphiura filiformis* and several bivalves including *Nucula sulcata* and *Thyasira equalis*, were assessed as non-tolerant species. The tolerant species were all polychaete worms. Therefore, increased heavy metal contamination in sediments may change the faunal composition of the community and decrease overall species diversity. Some burrowing crustaceans, brittlestars and bivalves may disappear from the biotope and lead to an increasing dominance of polychaetes. But no information was found on the effect of heavy metals on sea pens.

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.

There was no information found on the effect of hydrocarbon pollution on the biotope. The best documented oil spill for protected habitats with soft mud/sand substrata is the West Falmouth, Florida spill of 1969. Immediately after the spill virtually the entire benthic fauna was eradicated following the incident and populations of the opportunistic polychaete *Capitella capitata* increased to abundances of over 200,000/m² (Sanders, 1978). Persistent toxicity of *Amoco Cadiz* oil in sediment prevented the start of the recovery period (Clark, 1997). *Callinanassa subterranea* appears to be highly intolerant of sediment contaminated by oil-based drilling muds (Daan *et al.*, 1992). Oil from spills would have to be dispersed deep into the water column to affect the biotope and since the biotope occurs in very sheltered conditions this is unlikely to occur. However, should the sediment become contaminated with oil there is likely to be the loss of many species.

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**. There was no information found on the effect of chemical pollutants on the biotope, probably because burrowing megafauna are generally too difficult to sample to be included in standard pollution monitoring studies. And there is no information available on the possible consequences of chemicals to British sea pens.

However, effects on some of the individual species in the biotope have been reported. Dahllöf *et al.*

(1999) studied the long-term effects of tri-n-butyl-tin (TBT) on the function of a marine sediment system. TBT spiked sediment was added to a sediment that already had a TBT background level of approximately 27 ng/g (83 pmol TBT/g) and contained the following fauna: *Amphiura* spp., *Brissopsis lyrifera*, the bivalve *Abra alba* and several species of polychaete. Within two days of treatment with a TBT concentration above 13.7 $\mu\text{mol}/\text{m}^3$ all species except the polychaetes had crept up to the surface and after six weeks these fauna had started to decay. Thus, increased contamination from TBT is likely to result in the death of some intolerant species such as brittlestars and heart urchins. Bryan & Gibbs (1991) report that crabs appear to be relatively resistant to TBT although some deformity of regenerated limbs has been observed. However, arthropods are very intolerant of the insecticide carbaryl (1-naphthol n-methyl carbamate; sold under the trade name Sevin®), which has been used to control burrowing shrimp in oyster farms (Feldman *et al.*, 2000). Ivermectin, an anti-louse treatment that was used in the salmon fish farming industry, has been shown to be highly toxic to sediment dwelling polychaetes (Hughes, 1998b). Different species will be affected by different chemicals but a general trend in areas of increasing pollution is a reduction in species diversity with habitats becoming dominated by pollution tolerant polychaete worms.

Nevertheless, this biotope is recorded as 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

In an investigation of bioturbation in the north-eastern Irish Sea, Hughes & Atkinson (1997) surveyed several sites close to the Sellafield (now Windscale) nuclear reprocessing plant. At a station immediately offshore from the Sellafield outfall pipeline a community similar to the CMU.SpMeg biotope was present. Burrow openings and shafts indicated the presence of the burrowing crustaceans *Callianassa subterranea*, *Goneplax rhomboides* and *Upogobia deltaura*. Epifauna were abundant, particularly *Ophiura ophiura* and *Asterias rubens*. The sea pen *Virgularia mirabilis* occurred at high density. Dragonets and small gobies were also common. Other species in the biotope such as *Nephrops norvegicus* and the echiuran worm *Maxmuelleria lankesteri* were also present at sites close to the outfall pipeline. Thus, the biotope occurs in bottom sediments that contain particles of long half-life radionuclides derived from the liquid effluent released from the reprocessing plant at Sellafield (now Windscale). 'No obvious effects' of the radionuclide effluent were observed (Hughes & Atkinson, 1997; Hughes, 1998a) but no information on the level of radiation was provided. Therefore, the biotope is may be resistant of such effluent but there is insufficient evidence to assess this pressure against the benchmark.

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

Medium

Q: Low A: NR C: NR

Low

Q: Medium A: Medium C: Medium

Medium

Q: Low A: Low C: Low

Virgularia mirabilis is often found in sea lochs so may be able to tolerate some reduction in oxygenation. However, Jones *et al.* (2000) reported that sea pen communities were absent from

areas which are deoxygenated and characterized by a distinctive bacterial community and Hoare & Wilson (1977) reported that *Virgularia mirabilis* was absent from sewage related anoxic areas of Holyhead harbour.

Large active animals with high respiratory demands will be most affected by oxygen depletion. In moderately hypoxic conditions (1 mg/l) *Nephrops norvegicus* compensates by increasing production of haemocyanin (Baden *et al.*, 1990). In the laboratory, this compensation lasted one week so at the level of the benchmark, the species will not be killed. However, at levels of about 0.6 mg/l the species died within 4 days. Catches of *Nephrops norvegicus* have been observed to be high when oxygenation in the water is low, probably because animals are forced out their burrows (Hughes, 1998a). Thalassinidean mud-shrimps are very resistant to oxygen depletion and enriched sulphide levels and many species can withstand total anoxia for several days (Hughes, 1998a).

Sensitivity assessment. The evidence suggests that severe hypoxic or anoxic conditions are likely to be detrimental to sea pen communities. However, sea pens may be resistant of short-term hypoxia due to their presence at depth in sheltered sea lochs. Nevertheless, Cole *et al.* (1999) suggested that most species would be affected at an oxygen concentration below 2 mg/l. Therefore, a precautionary resistance of **Medium** is suggested to represent to loss of a small proportion of the population but at **Low** confidence as the evidence is limited to a single observation, on only one of the British sea pen species. Resilience is probably **Low** so that sensitivity is assessed as **Medium** but also with **Low** confidence.

Nutrient enrichment

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not sensitive

Q: NR A: NR C: NR

Hoare & Wilson (1977) noted that *Virgularia mirabilis* was absent from part of the Holyhead Harbour heavily affected by sewage pollution. However, the species was abundant near the head of Loch Harport, Skye, close to a distillery outfall discharging water enriched in malt and yeast residues and other soluble organic compounds (Nickell & Anderson, 1977; cited in Hughes, 1998a), where the organic content of the sediment was up to 5%. *Virgularia mirabilis* was also present in Loch Sween in Scotland in sites where organic content was as high as 4.5% (Atkinson, 1989). Wilding (2011) noted that the abundance of *Pennatula phosphorea* was inversely correlated with predicted Infaunal Trophic Index (a predicted estimate of organic waste build-up) around salmon farms in Scotland, but that the effect only extended for 50 m from the cages.

Burrowing megafauna flourish in areas where the sediments are naturally high in organic matter, such as sheltered sea lochs (Hughes, 1998a). An increasing gradient of organic enrichment (e.g. in the vicinity of point sources of organic-rich effluent or sewage sludge dump sites) results in a decline in the suspension feeding fauna and an increase in the number of deposit feeders, in particular, polychaete worms (Pearson & Rosenberg, 1978). The effects of organic enrichment on burrowing megafauna and other infauna depended on the degree of enrichment and any resultant hypoxia, which depend on the sediment type and local hydrology.

Sensitivity assessment. Sublittoral muds may be expected to be high in organic matter and nutrients, and the presence of *Virgularia mirabilis* in areas of up to 4.5% organic carbon (Atkinson, 1989) and distillery effluent suggest a resistance to nutrient enrichment. Similarly, the characteristic burrowing megafauna are probably resistant of all but gross enrichment. Nevertheless, this biotope is recorded as **Not sensitive** at the pressure benchmark that assumes compliance with good status as defined by the WFD.

Organic enrichment**Medium**

Q: Medium A: Low C: Low

Low

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Low C: Low

Hoare & Wilson (1977) noted that *Virgularia mirabilis* was absent from part of the Holyhead Harbour heavily affected by sewage pollution. However, the species was abundant near the head of Loch Harport, Skye, close to a distillery outfall discharging water enriched in malt and yeast residues and other soluble organic compounds (Nickell & Anderson, 1977; cited in Hughes, 1998a), where the organic content of the sediment was up to 5%. *Virgularia mirabilis* was also present in Loch Sween in Scotland in sites where organic content was as high as 4.5% (Atkinson, 1989). Wilding (2011) noted that the abundance of *Pennatula phosphorea* was inversely correlated with predicted Infaunal Trophic Index (a predicted estimate of organic waste build-up) around salmon farms in Scotland, but that the effect only extended for 50 m from the cages.

Burrowing megafauna flourish in areas where the sediments are naturally high in organic matter, such as sheltered sea lochs (Hughes, 1998a). An increasing gradient of organic enrichment (e.g. in the vicinity of point sources of organic-rich effluent or sewage sludge dump sites) results in a decline in the suspension feeding fauna and an increase in the number of deposit feeders, in particular, polychaete worms (Pearson & Rosenberg, 1978). The effects of organic enrichment on burrowing megafauna and other infauna depended on the degree of enrichment and any resultant hypoxia, which depend on the sediment type and local hydrology.

For example, is a survey of Garoch Head sludge dumping grounds, Firth of Clyde, the burrowing megafauna (*Nephrops norvegicus*, *Callianassa subterranean*, *Calocaris macandreae*, *Lumpenus lampraetiformis* and *Cepola rubescens*) were abundant where organic content was <4% but absent where the organic content exceeded 6% (Smith, 1988, cited in Hughes, 1998a). *Calocaris macandreae* did not extend as far into the gradient as *Nephrops norvegicus* or *Lumpenus lampraetiformis* (Smith, 1988, cited in Hughes, 1998a). In Caol Scotnish, Loch Sween, bacterial mats of *Beggiatoa* were reported in the immediate vicinity of salmon cages in 1987. The burrowing megafauna (*Maxmuelleria lankesteri*, *Callianassa subterranea* and *Jaxea nocturna*) were abundant in unimpacted areas. But by 1988, the bacterial mats covered most of the seabed in the basin, the sediment was close to anoxic, and the burrows of megafauna were restricted to small areas free of *Beggiatoa*. After the removal of salmon cages in 1989, some recovery was apparent by 1990 with more burrows apparent, although the size of the individuals of *Maxmuelleria lankesteri*, *Callianassa subterranean* suggested that they had survived the loch basin during the peak of enrichment (Hughes, 1998a).

Sensitivity assessment. Sublittoral muds may be expected to be high in organic nutrients, and the presence of *Virgularia mirabilis* in areas of up to 4.5% organic carbon (Atkinson, 1989) suggest a resistance to organic enrichment at the benchmark level. Similarly, the characteristic burrowing megafauna are probably resistant of all but gross enrichment. Therefore, a precautionary resistance of **Medium** is suggested, and as resilience is probably **Low**, a sensitivity of **Medium** is recorded. However, *Pennatula phosphorea*, and by inference *Funiculina quadrangularis*, may be more sensitive.

A Physical Pressures**Resistance****None**

Q: High A: High C: High

Resilience**Very Low**

Q: High A: High C: High

Sensitivity**High**

Q: High A: High C: High

Physical loss (to land or freshwater habitat)

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 is '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.

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

If sedimentary substrata were replaced with rock substrata the biotope would be lost, as it would no longer be a sedimentary habitat and would no longer support sea pens and burrowing megafauna.

Sensitivity assessment. Resistance to the pressure is considered 'None', and resilience 'Very low' or 'None' (as the pressure represents a permanent change) and the sensitivity of this biotope is assessed as 'High'.

Physical change (to another sediment type)

None

Q: High A: Medium C: Medium

Very Low

Q: High A: High C: High

High

Q: Medium A: Low C: Medium

Virgularia mirabilis occurs in a number of biotopes, on substrata ranging from mud, sandy mud, and gravelly mud, with or with shell fragments or stones (Connor *et al.*, 2004). Greathead *et al.* (2007) suggested that the muscular peduncle of *Virgularia mirabilis* allowed it to occupy coarser muds than the other sea pens, and explained its presence in the Moray Firth and Firth of Forth, and its wider distribution in Scotland. Greathead *et al.* (2007) noted that *Pennatula phosphorea* was absent in the North Minch while *Funiculina quadrangularis* and *Virgularia mirabilis* were present, but that *Pennatula phosphorea* was abundant in soft, adhesive mud with high silt-clay content in Loch Broom. This may suggest a preference for fine muds. The MNCR only recorded *Pennatula phosphorea* from biotopes in 'mud'. Greathead *et al.* (2007) also noted that *Funiculina quadrangularis* had the most restricted distribution, probably due to a preference of depth and soft deep muds of sheltered loch basins, where it was abundant. Again, the MNCR only recorded *Funiculina quadrangularis* from biotopes in 'mud'. However, it was also recorded from areas of muddy sand in the South and North Minches and in the Fladen Grounds but in deep water. In addition, a 'mud' substratum was the most important factor in a habitat suitability index model for sea pens developed by Greathead *et al.* (2015). In their model, habitat suitability for *Funiculina quadrangularis* increased with mud content up to a maximum at 90-100% mud. *Pennatula phosphorea* and *Virgularia mirabilis* also had their maximum habitat suitability at 100% mud. All three species had zero habitat suitability at 0% mud. However, gravel content was also important. *Virgularia mirabilis* was the most tolerant of gravel content and was still recorded at 50% gravel while there were no records of *Pennatula phosphorea* and *Funiculina quadrangularis* above 40% and 30% gravel respectively (Greathead *et al.*, 2015).

Callianassa subterranea creates a complex lattice of galleries at 30-40 cm below the surface in the fine muds but burrows less deeply (9-23 cm) in coarse sediments (Rowden & Jones, 1995; Hughes, 1998a). *Calocaris macandreae* creates burrows with a total depth of 21 cm in muddy sediments with a high silt content but is not found in sandy sediments (Buchanan, 1963; Hughes, 1998a). *Nephrops norvegicus* burrows to 20-30 cm and is found in soft mud sediments. The large echiuran *Maxmuelleria lankesteri* burrows up to 80 cm into the sediment and is found in fine muds and muddy sands in deep water (10-80 m) (Nickell *et al.*, 1995; Hughes, 1998a).

A change in sediment type by one Folk class (see benchmark) is likely to adversely affect the sea pens. A change from 'mud and sandy mud' to 'sand and muddy sand' or 'mixed' would probably exclude *Pennatula phosphorea* and *Funiculina quadrangularis* (except where *Funiculina quadrangularis* occurs in deep basins) but not adversely affect *Virgularia mirabilis*, based on their reported distribution. It is also likely to result in a reduction in the abundance of most of the characteristic burrowing megafauna. Conversely, a change of sediment from coarse or sandy sediments to 'mud and sandy mud' will not affect *Virgularia mirabilis* but may allow the other sea pens to colonise. In all cases, a change in the sediment type is likely to change the associated community and result in loss of the sea pen population.

Sensitivity assessment. Sea pens have a narrow range of sediment type preferences, so their resistance to this pressure is **Low** for *Virgularia mirabilis* and **None** for the *Pennatula phosphorea* and *Funiculina quadrangularis*, and as resilience is **Very low** (the pressure is a permanent change), sensitivity is, therefore, **High**.

Habitat structure changes - removal of substratum (extraction)

None

Q: **Medium** A: **Low** C: **Medium**

Low

Q: **Medium** A: **Medium** C: **Medium**

High

Q: **Medium** A: **Low** C: **Medium**

Benthic trawls (e.g. rock hopper ground gear, otter trawls) will remove and capture sea pens (Tuck *et al.*, 1998; Kenchington *et al.*, 2011), albeit with limited efficiency. Nevertheless, dredging and suction dredging penetrates to greater depth and are likely to remove sea pens. Although *Virgularia mirabilis* and *Pennatula phosphorea* can withdraw into the sediment, they will not be able to avoid activities that penetrate into the sediment. Assuming their burrows are only deep enough to hold the entire animal (see Greathead *et al.*, 2007 for sizes), then *Virgularia mirabilis* burrows are up to 40 cm deep while *Pennatula phosphorea* burrows are only up to 25 cm. *Funiculina quadrangularis* can grow up to 150 cm in height above the sediment surface but cannot withdraw into a burrow.

Sensitivity assessment. Extraction of sediment to 30 cm (the benchmark) could remove most of the resident sea pens present. Hence, their resistance is probably **None**, and their resilience is at least **Low**, resulting in a sensitivity of **High**.

Abrasion/disturbance of the surface of the substratum or seabed

Medium

Q: **High** A: **High** C: **Low**

Low

Q: **Medium** A: **Medium** C: **Medium**

Medium

Q: **Medium** A: **Low** C: **Low**

In experimental studies (Kinnear *et al.*, 1996; Eno *et al.*, 2001), sea pens were found to be largely resilient to smothering, dragging or uprooting by creels or pots. In both *Pennatula phosphorea* and *Funiculina quadrangularis*, the pressure wave caused by approaching pots/creels bent the sea pen away, so that they were laid flat before contact. Kinnear *et al.* (1996) noted that *Pennatula phosphorea* and *Funiculina quadrangularis* were occasionally removed from the substratum by creels/pots. *Virgularia mirabilis* withdrew very quickly into the sediment when exposed to pots or creels, and so it was difficult to determine their response. However, all sea pens recovered from being dragged over by pots or creels within 24-72 h, with the exception of one individual *Funiculina quadrangularis*. Both *Pennatula phosphorea* and *Funiculina quadrangularis* were able to reinsert themselves into the sediment if removed as long as the peduncle remained in contact with the sediment surface, except in one specimen in which the peduncle was damaged. *Pennatula phosphorea* and *Funiculina quadrangularis* recovered with 72-96 hours after experimental

smothering for 24 hours by pot or creel and after 96-144 hours of smothering for 48 hours (Kinnear *et al.*, 1996; Eno *et al.*, 2001). However, a later study of the effects of experimental trawling damage in the sea whip *Halipteris willemoesi* suggests that recovery in *Funiculina quadrangularis* may have been over-estimated. *Halipteris willemoesi* is a functionally similar species to *Funiculina quadrangularis*, as it is tall, thin, and cannot withdraw into the sediment. Malecha & Stone (2009) simulated trawl damage in field populations in Alaskan waters, by abrading the sea whip with rubber disks (similar to rubber tire punch-outs used on the footrope of many trawls), dislodging them from the sediment and breaking the axial rod manually. All the specimens abraded repaired tissue damage and survived the experimental period. However, the authors noted that the experimental abrasion probably underestimated the effect of trawls as it did not include the mechanical force of the mobile gear and that even the smallest amount of tissue damage probably decreased the sea whip's ability to reproduce. Fifty percent of the dislodged sea whips were able to rebury and become erect within 18 days. Only 42% of the fractured sea whips were erect 18 days after treatment. However, only one specimen was erect after the 372 days of the experiment. There was no evidence to suggest that specimens could repair their damaged axial rods. After 372 days, 92% of the dislodged and 100% of the fractured specimens had substantial tissue loss and perished. Tissue loss was exaggerated by predation from nudibranchs, which appeared to be attracted to the experimental area, possibly due to the tissue damage suffered by the sea whips (Malecha & Stone, 2009).

Both *Virgularia mirabilis* and *Pennatula phosphorea* can withdraw into tubes in the sediment. In *Virgularia mirabilis* withdrawal from physical stimulus is rapid (ca 30 seconds) (Hoare & Wilson, 1977; Ambroso *et al.*, 2013). Birkland (1974) maintained that the only way to capture all of the sea pens in an area (quadrat) was to remove them slowly by hand until no more emerged. But several studies note that their ability to withdraw into the sediment in response to bottom towed or dropped gear (e.g. creels, pots, camera/video mounted towed sleds, experimental grab, trawl, or dredge) means that sea pen abundance can be difficult to estimate (Birkland, 1974; Eno *et al.*, 2001; Greathead *et al.*, 2007; Greathead *et al.*, 2011). The ability to withdraw also suggests that sea pens can avoid approaching demersal trawls and fishing gear. This was suggested as the explanation for the similarity in the densities of *Virgularia mirabilis* in trawled and untrawled sites in Loch Fyne, and the lack of change in sea pen density observed after experimental trawling (using modified rock hopper ground gear) over an 18 month period in Loch Gareloch (Howson & Davies, 1991; Hughes, 1998a; Tuck *et al.*, 1998). Kenchington *et al.* (2011) estimated the gear efficiency of otter trawls for sea pens (*Anthoptilum* and *Pennatula*) to be in the range of 3.7 – 8.2%, based on estimates of sea pen biomass from (non-destructive) towed camera surveys. However, species obtained by dredges were invariably damaged (Hoare & Wilson, 1977). It should be noted that *Funiculina quadrangularis* cannot withdraw into the sediment.

Hoare & Wilson (1977) noted that *Virgularia* was absent for areas of Holyhead Harbour disturbed by dragging or boat mooring, although no causal evidence was given (Hughes, 1998a). Sea pens are potentially vulnerable to long lining. Munoz *et al.* (2011) noted that small numbers of Pennatulids (inc. *Pennatula* sp.) were retrieved from experimental long-lining around the Hatton Bank in the North East Atlantic, presumably either attached to hooks or wrapped in line as it passed across the sediment. Hixon & Tissot (2007) noted that sea pens (*Stylatula* sp.) were four times more abundant in untrawled areas relative to trawled areas in the Coquille Bank, Oregon, although no causal relationship was shown. Greathead *et al.* (2011) noted that *Funiculina quadrangularis* was largely absent from Fladen fishing grounds in the northern North Sea, possibly due to its patchy distribution or fishing activities.

Trawl caught *Nephrops* females were reported to have fewer eggs on average than creel caught

females from the same area, during an experimental study, and that it was likely that the eggs may be lost due to physical abrasion (Chapman & Ballantyne, 1980). The proportion of eggs lost to abrasion ranged from 11-22 % in samples taken from the Clyde and West of Kintyre (Chapman & Ballantyne, 1980). *Nephrops* burrows are also likely to be damaged by abrasion. However, Marrs *et al.* (1998) reported that burrows were re-established within 2 days providing that the occupant had remained unharmed (Marrs *et al.*, 1998). The depth of the burrows constructed by characterizing megafauna (mud-shrimps and *Maxmuelleria lankesteri*) probably protects the species from surface abrasion and fishing activities. The burrow opening may be damaged (as above) but observations from Loch Sween suggest that they are re-established soon after experimental disturbance (Hughes, 1998a). Atkinson (1989) suggested that trawling was unlikely to affect burrowing megafauna (other than *Nephrops*) to 'any great extent'. Nevertheless, burrow density was lower in frequently trawled areas of Loch Fyne except in areas protected from trawling by submarine obstructions (Howson & Davies, 1991; Hughes, 1998a)

Sensitivity assessment. *Virgularia mirabilis* and *Pennatula phosphorea* can avoid abrasion by withdrawing into the sediment, but a frequent disturbance will probably reduce feeding time and hence viability. However, *Funiculina quadrangularis* cannot withdraw and is the tallest of all three of the sea pens (up to 2 m) and is the most likely to be displaced or removed by surface abrasion and towed gear. Surface abrasion by pots and creels is unlikely to affect the *Virgularia mirabilis* and *Pennatula phosphorea* adversely but may abrade or dislodge *Funiculina quadrangularis*. Towed gear is likely to remove a proportion of sea pens from the sediment, and if damaged they are likely to die, but if undamaged displaced and/or returned to suitable sediment *Virgularia mirabilis* and *Pennatula phosphorea* can probably recover relatively quickly. The evidence of the effect of abrasion on *Halipterus willemoesi* in Alaskan waters suggests that sea pens can recover from physical abrasion but that specimens that are dislodged or fractured are likely to die, especially in the presence of predators (Malecha & Stone, 2009). Therefore, as bottom gears (e.g. otter trawls) may remove a proportion of the population a resistance of '**Medium**' is suggested for *Pennatula phosphorea* and *Virgularia mirabilis* that can withdraw into the sediment and avoid direct impacts with bottom gears. However, as *Funiculina quadrangularis* cannot withdraw and is more likely to be removed by bottom gears, a resistance of '**Low**' is suggested where it is a dominant member of the community, as in CFiMu.SpNMeg.Fun. As the resilience is probably **Low**, the sensitivity of CFiMU.SpNMeg is assessed as **Medium** (for *Pennatula phosphorea* and *Virgularia mirabilis*) but the sensitivity of CFiMU.SpNMeg.Fun is probably **High**.

Penetration or disturbance of the substratum subsurface

Low

Q: High A: Medium C: Low

Low

Q: Medium A: Medium C: Medium

High

Q: Medium A: Low C: Low

The relevant evidence on the effects of fishing activities is present above under abrasion. Penetrative gear is likely to remove a greater proportion of the sea pen population, as it may remove them from their burrows, within the footprint of the activity. Therefore, resistance is assessed as **Low** for all three sea pen species. As resilience is probably **Low**, sensitivity is assessed as **High**.

Changes in suspended solids (water clarity)

High

Q: Medium A: Low C: Medium

High

Q: High A: High C: High

Not sensitive

Q: Medium A: Low C: Medium

The characteristic sea pen species live in sheltered areas, in fine sediments, subject to high suspended sediment loads. The effect of increased deposition of fine silt is uncertain but it is

possible that feeding structures may become clogged. When tested, *Virgularia mirabilis* quickly seized and rejected inert particles (Hoare & Wilson, 1977). Hiscock (1983) observed *Virgularia mirabilis* secretes copious amounts of mucus which could keep the polyps clear of silt. Kinnear *et al.* (1996) noted that *Funiculina quadrangularis* was quick to remove any adhering mud particles by the production of copious quantities of mucus. *Virgularia mirabilis* is also likely to be able to self-clean (Hiscock, 1983). No indication of the suspended sediment load was given in any evidence found.

If feeding is reduced by increases in suspended sediment the viability of the population will be reduced. Once siltation levels return to normal, feeding will be resumed therefore recovery will be immediate. Similarly, burrowing megafauna are unlikely to be affected adversely by changes in suspended sediment in the water column. Overall, resistance is probably **High**, hence, resilience is also **High**, and the sea pens are probably **Not sensitive** at the benchmark level.

Smothering and siltation rate changes (light)

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

Pennatula phosphorea and *Funiculina quadrangularis* were found to recover within 72-96 hours after experimental smothering by pots or creels for 24 hours and after 96-144 hours after 48 hours of smothering by pots or creels (Kinnear *et al.*, 1996; Eno *et al.*, 2001). However, smothering by a pot or creel differs significantly from 30 cm of fine sediment, which could clog feeding apparatus and exclude oxygen. Kinnear *et al.* (1996) noted that *Funiculina quadrangularis* was quick to remove any adhering mud particles by the production of copious quantities of mucus, once the source of smothering (in this case potting) was removed. Similarly, Hiscock (1983) observed *Virgularia mirabilis* secretes copious amounts of mucus, which could keep the polyps clear of silt and is also likely to be able to self-clean.

Where present, the characteristic burrowing megafauna (mud-shrimp and *Nephrops*) are unlikely to be affected adversely as they are active burrowers and *Nephrops norvegicus*, *Calocaris macandreae* and *Callianassa subterranea* were reported within the Garroch Head (Firth of Clyde) sludge dumping ground (Smith, 1988; cited in Hughes, 1998a). In addition, if the deposited sediment occludes burrow openings, then they would be reopened quickly. Observations from Loch Sween suggest that they are re-established soon after experimental disturbance (Hughes, 1998a).

All three species occur in deep, sheltered muddy habitats where the accretion rates are potentially high. Both *Pennatula phosphorea* and *Virgularia mirabilis* can burrow and move into and out of their own burrows. It is probable therefore that deposition of 5 cm of fine sediment will have little effect other than to temporarily suspend feeding and the energetic cost of burrowing. *Funiculina quadrangularis* cannot withdraw into a burrow but can stand up to two metres above the substratum, and so will probably not be affected adversely. However, no direct evidence was found. Therefore, a resistance of **'High'** is suggested, resulting in a resilience of **'High'** and sensitivity of **'Not sensitive'** at the benchmark level.

Smothering and siltation rate changes (heavy)

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

Pennatula phosphorea and *Funiculina quadrangularis* were found to recover within 72-96 hours after experimental smothering by pots or creels for 24 hours and after 96-144 hours after 48 hours of smothering by pots or creels (Kinnear *et al.*, 1996; Eno *et al.*, 2001). However, smothering by a pot

or creel differs significantly from 30 cm of fine sediment, which could clog feeding apparatus and exclude oxygen. Kinnear *et al.* (1996) noted that *Funiculina quadrangularis* was quick to remove any adhering mud particles by the production of copious quantities of mucus, once the source of smothering (in this case potting) was removed. Similarly, Hiscock (1983) observed *Virgularia mirabilis* secretes copious amounts of mucus, which could keep the polyps clear of silt and is also likely to be able to self-clean.

Where present, the characteristic burrowing megafauna (mud-shrimp and *Nephrops*) are unlikely to be affected adversely as they are active burrowers and *Nephrops norvegicus*, *Calocaris macandreae* and *Callianassa subterranea* were reported within the Garroch Head (Firth of Clyde) sludge dumping ground (Smith, 1988; cited in Hughes, 1998a). In addition, if the deposited sediment occludes burrow openings, then they would be reopened quickly. Observations from Loch Sween suggest that they are re-established soon after experimental disturbance (Hughes, 1998a).

All three species occur in deep, sheltered muddy habitats where the accretion rates are potentially high. Both *Pennatula phosphorea* and *Virgularia mirabilis* can burrow and move into and out of their own burrows. It is probable therefore that deposition of 30 cm of fine sediment will have little effect other than to temporarily suspend feeding and the energetic cost of burrowing. *Funiculina quadrangularis* cannot withdraw into a burrow but can stand up to two metres above the substratum, and so will probably not be affected adversely. However, no direct evidence was found. Therefore, a resistance of **High** is suggested, resulting in a resilience of **High** and sensitivity of **Not sensitive** at the benchmark level.

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	Not relevant (NR) 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 was found

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
---------------------------------	---	---	---

Some of the important characterizing species associated with this biotope, in particular, the sea pens, may respond to sound vibrations and can withdraw into the sediment. Feeding will resume once the disturbing factor has passed. However, most of the species are infaunal and unlikely respond to a noise disturbance at the benchmark level. Therefore, this pressure is probably **Not relevant** in this biotope.

Introduction of light or shading	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low
---	-----------------------------------	--	--

Hughes (1998a) suggested that sea pens were insensitive to light. In shallow water, *Nephrops* only forages outside their burrows at night, but in deeper waters (ca 100 m) *Nephrops* are active during

the day (Hughes, 1998a). while *Maxmuelleria lankesteri* is highly averse to light and its proboscis is only extended to the surface in the shallow waters of Loch Sween (Hughes, 1998a). Therefore, shading at the surface may alter the response of burrowing megafauna to daylight in the shaded area only but is otherwise unlikely to be detrimental. It is unlikely that artificial illumination would penetrate deep enough to affect the megafauna, except in the most shallow examples. However, the important characterizing sea pens are unlikely to be affected. Therefore, the biotope is probably **Not sensitive** to changes in light.

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

Most species within the biotope are burrowing and have no or poor visual perception and are unlikely to be affected by visual disturbance such as shading. Epifauna such as crabs have well developed visual acuity and are likely to respond to movement in order to avoid predators. However, it is unlikely that the species will be affected by visual disturbance at the benchmark level.

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

No evidence of genetic modification, breeding, or translocation in sea pens or burrowing megafauna was found.

Introduction or spread of invasive non-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

Sternopsis scutata is a non-native polychaete that has extended its range in inshore muddy sediments in the south west of the UK (Shelley *et al.*, 2008). However, in a mesocosm experiment, little effect on biological functioning was detected after the introduction of the polychaete and a

doubling of its biomass (Shelley *et al.*, 2008). The red king crab *Paralithodes camtschaticus* is a voracious, omnivorous benthic predator that has spread from the Barents Sea to the coast of Norway, where it is a threat to shell fisheries and demersal fisheries. It has not been recorded in UK waters to date (GBNNSIP, 2011).

No direct evidence on the effect of non-native species on sea pen and burrowing megafauna communities was found. However, this assessment should be revisited in the light of new evidence.

Introduction of microbial pathogens **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

The only major disease causing organism found in the biotope is the dinoflagellate parasite, *Hematodinium* sp. found in *Nephrops* populations from the west of Scotland, Irish Sea and North Sea (Hughes, 1998b). The parasite occurs in the blood and connective tissue spaces and appears to cause death by blocking the delivery of oxygen to the host's tissues (Taylor *et al.*, 1996). Infection is at its highest in the spring and early summer when a dense concentration of parasite cells in the blood give *Nephrops* an abnormal bright orange body and milky white ventral abdomen. Heavily infected animals become moribund, spend more time out of their burrows than healthy individuals making them more vulnerable to predation and fishing gear. Heavy infestation is fatal. The ecological consequences of *Hematodinium* infection and host mortality in *Nephrops* populations are unknown, but there are potential economic implications since the disease adversely affects meat quality. However, so far the *Nephrops* fishery has not suffered any serious decline. The infection appears to be cyclical. In the Clyde Sea, infection peaked in 1991-92 at 70% and had declined to 10 - 20% by 1996-7 (Hughes, 1998a).

However, no evidence was found on pathogen or parasite-mediated disease in sea pens.

Removal of target species **High**
Q: Low A: NR C: NR

High
Q: High A: High C: High

Not sensitive
Q: Low A: Low C: Low

Nephrops norvegicus is a characterizing species and *Nephrops* fisheries are of major economic importance. The species is fished throughout most of the geographic range of the biotopes in which it occurs including CMU.SpMeg. In trawled areas, it is likely that the density of *Nephrops norvegicus* has been reduced but Hughes (1998a) reports that most stocks have the potential to recover even after heavy fishing pressure. Atkinson (1989) concluded that trawling for *Nephrops* was unlikely to affect other megafaunal burrowers to any great extent. The upper section of burrows will be disrupted by trawling but observations in Loch Sween have shown that surface openings are soon re-established (Hughes, 1998a).

Sensitivity assessment. This pressure considers any biological effects resulting from the removal of target species. Sea pens are not targeted by commercial fisheries and hence are not directly affected by this pressure. Although *Nephrops* is targeted the ecological relationships between sea pens and burrowing megafauna are unclear (Hughes, 1998a). Direct effects of static or mobile gears that are targeting other species are assessed in under abrasion and penetration of the seabed pressures. Therefore, the biotope is considered to be **Not sensitive** (to the ecological effects only) of targeted removal of other species.

Removal of non-target species**Medium**

Q: High A: High C: Low

Low

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Low C: Low

Sea pens are not targeted by commercial or recreational fisheries but may be damaged or removed as by-catch and loss of the sea pens would change the biological character of the biotope. In observations of the impact of creeling activities, all three British species proved able to re-anchor themselves provided the basal peduncle remained in contact with the sediment surface (Kinnear et al., 1996; Eno et al., 2001) (see abrasion above). Sea pens were shown to recover rapidly from displacement and removal from the seabed. *Funiculina quadrangularis* and *Pennatula phosphorea* were found to right themselves when dislodged, with all *Pennatula phosphorea* individuals re-established and 50% of *Funiculina quadrangularis* after 72 hours (Eno et al., 2001). *Virgularia mirabilis* was found to withdraw into its burrow rapidly (ca 30 seconds) and could not be uprooted by dragged creels (Hoare & Wilson 1977; Eno et al., 2001; Ambroso et al. 2013). *Pennatula phosphorea* and *Funiculina quadrangularis* recovered with 72-96 hours after experimental smothering for 24 hours by pot or creel and after 96-144 hours of smothering for 48 hours (Kinnear et al. 1996; Eno et al. 2001). In summary, all three sea pen species have been found to recover rapidly from the effects of dragging, uprooting and smothering (Eno et al., 2001). However, a later study of the effects of experimental trawling damage in the sea whip *Halipteris willemoesi* suggests that recovery in *Funiculina quadrangularis* may have been over-estimated. *Halipteris willemoesi* is a functionally similar species to *Funiculina quadrangularis*, as it is tall, thin, and cannot withdraw into the sediment. Malecha & Stone (2009) simulated trawl damage in field populations in Alaskan waters, by abrading the sea whip with rubber disks (similar to rubber tire punch-outs used on the footrope of many trawls), dislodging them from the sediment and breaking the axial rod manually. All the specimens abraded repaired tissue damage and survived the experimental period. However, the authors noted that the experimental abrasion probably underestimated the effect of trawls as it did not include the mechanical force of the mobile gear and that even the smallest amount of tissue damage probably decreased the sea whip's ability to reproduce. Fifty percent of the dislodged sea whips were able to rebury and become erect within 18 days. Only 42% of the fractured sea whips were erect 18 days after treatment. However, only one specimen was erect after the 372 days of the experiment. There was no evidence to suggest that specimens could repair their damaged axial rods. After 372 days, 92% of the dislodged and 100% of the fractured specimens had substantial tissue loss and perished. Tissue loss was exaggerated by predation from nudibranchs, which appeared to be attracted to the experimental area, possibly due to the tissue damage suffered by the sea whips (Malecha & Stone, 2009).

The ability to withdraw also suggests that sea pens can avoid approaching demersal trawls and fishing gear. This was suggested as the explanation for the similarity in the densities of *Virgularia mirabilis* in trawled and untrawled sites in Loch Fyne, and the lack of change in sea pen density observed after experimental trawling (using modified rock hopper ground gear) over an 18 month period in Loch Gareloch (Howson & Davies, 1991; Hughes, 1998a; Tuck et al., 1998). Kenchington et al. (2011) estimated the gear efficiency of otter trawls for sea pens (*Anthoptilum* and *Pennatula*) to be in the range of 3.7 – 8.2%, based on estimates of sea pen biomass from (non-destructive) towed camera surveys. However, species obtained by dredges were invariably damaged (Hoare & Wilson, 1977). It should be noted that *Funiculina quadrangularis* cannot withdraw into the sediment.

Hoare & Wilson (1977) noted that *Virgularia* was absent for areas of Holyhead Harbour disturbed by dragging or boat mooring, although no causal evidence was given (Hughes, 1998a). Sea pens are potentially vulnerable to long lining. Munoz et al. (2011) noted that small numbers of Pennatulids (inc. *Pennatula* sp.) were retrieved from experimental long-lining around the Hatton

Bank in the north east Atlantic, presumably either attached to hooks or wrapped in line as it passed across the sediment. Hixon & Tissot (2007) noted that sea pens (*Stylatula* sp.) were four times more abundant in untrawled areas relative to trawled areas in the Coquille Bank, Oregon, although no causal relationship was shown. Greathead *et al.* (2011) noted that *Funiculina quadrangularis* was largely absent from Fladen fishing grounds in the northern North Sea, possibly due to its patchy distribution or fishing activities.

Sensitivity assessment. The removal of a proportion of the sea pen population as by-catch would change the character of the biotope. Therefore, a resistance of '**Medium**' is suggested for *Pennatula phosphorea* and *Virgularia mirabilis*. However, as *Funiculina quadrangularis* cannot withdraw and is more likely to be removed by bottom gears, a resistance of '**Low**' is suggested where it is a dominant member of the community, as in CFiMu.SpMg.Fun. As the resilience is probably **Low**, the sensitivity of CFiMU.SpMg is assessed as **Medium** (for *Pennatula phosphorea* and *Virgularia mirabilis*) but the sensitivity of CFiMU.SpMg.Fun is probably **High**.

Bibliography

- Ambroso, S., Dominguez-Carrió, C., Grinyó, J., López-González, P., Gili, J.-M., Purroy, A., Requena, S. & Madurell, T., 2013. *In situ* observations on withdrawal behaviour of the sea pen *Virgularia mirabilis*. *Marine Biodiversity*, **43** (4), 257-258.
- Aronson, R.B., 1990. Onshore-offshore patterns of human fishing activity. *Palaos*, **5**, 88-93.
- Atkinson, R.J.A., 1989. Baseline survey of the burrowing megafauna of Loch Sween, proposed Marine Nature Reserve, and an investigation of the effects of trawling on the benthic megafauna. *Report to the Nature Conservancy Council, Peterborough, from the University Marine Biological Station, Millport*, pp.1-59.
- Baden, S.P., Pihl, L. & Rosenberg, R., 1990. Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. *Marine Ecology Progress Series*, **67**, 141-155.
- Ball, B.J., Fox, G. & Munday, B.W., 2000a. Long- and short-term consequences of a *Nephrops* trawl fishery on the benthos and environment of the Irish Sea. *ICES Journal of Marine Science*, **57**, 1315-1320.
- Best, B.A., 1988. Passive Suspension Feeding in a Sea Pen: Effects of Ambient Flow on Volume Flow Rate and Filtering Efficiency. *The Biological Bulletin*, **175** (3), 332-342.
- Birkeland, C., 1974. Interactions between a seapen and seven of its predators. *Ecological Monographs*, **44**, 211-232.
- Bryan, G.W. & Gibbs, P.E., 1991. Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In: *Metal ecotoxicology: concepts and applications* (ed. M.C. Newman & A.W. McIntosh), pp. 323-361. Boston: Lewis Publishers Inc.
- Buchanan, J.B., 1963. The biology of *Calocaris macandreae* (Crustacea: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom*, **43**, 729-747.
- Chapman, C.J. & Ballantyne, K.A., 1980. Some observations on the fecundity of Norway lobsters in Scottish waters. *International Council for the Exploration of the Seas Council Meeting Papers*, C.M.1980/K:25.
- Chapman, C.J. & Rice, A.L., 1971. Some direct observations on the ecology and behaviour of the Norway lobster *Nephrops norvegicus* (L.). *Marine Biology*, **10**, 321-329.
- Chia, F.S. & Crawford, B.J., 1973. Some observations on gametogenesis, larval development and substratum selection of the sea pen *Ptilosarcus guernei*. *Marine Biology*, **23**, 73-82.
- Clark, R.B., 1997. *Marine Pollution*, 4th ed. Oxford: Carendon Press.
- Colin, P.L., Suchanek, T.H. & McMurtry, G., 1986. Water pumping and particulate resuspension by callianassids (Crustacea: Thalassinidea) at Enewetak and Bikini Atolls, Marshall Islands. *Bulletin of Marine Science*, **38**, 19-24.
- Connor, D.W., Dalkin, M.J., Hill, T.O., Holt, R.H.F. & Sanderson, W.G., 1997a. Marine biotope classification for Britain and Ireland. Vol. 2. Sublittoral biotopes. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06.*, *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06.*
- Conway Morris, S., 1995. A new phylum from the lobster's lips. *Nature*, **378**, 661-662.
- Crisp, D.J. (ed.), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-210.
- Daan, R., Groenewoud Van Het, H., Jong De, S.A. & Mulder, M., 1992. Physico-chemical and biological features of a drilling site in the North Sea, 1 year after discharges of oil-contaminated drill cuttings. *Marine Ecology Progress Series*, **91**, 37-45.
- Dahllöf, I., Blanck, H., Hall, P.O.J. & Molander, S., 1999. Long term effects of tri-n-butyl-tin on the function of a marine sediment system. *Marine Ecology Progress Series*, **188**, 1-11.
- Dauwe, B., Herman, P.M.J. & Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series*, **173**, 67-83.
- Davies, C.E. & Moss, D., 1998. European Union Nature Information System (EUNIS) Habitat Classification. *Report to European Topic Centre on Nature Conservation from the Institute of Terrestrial Ecology, Monks Wood, Cambridgeshire*. [Final draft with further revisions to marine habitats.], Brussels: European Environment Agency.
- Doherty, S.D., Brophy, D. & Gosling, E., 2009. Synchronous reproduction may facilitate introgression in a hybrid mussel (*Mytilus*) population. *Journal of Experimental Marine Biology and Ecology*, **378**, 1-7.
- Dyer, M.F., Fry, W.G., Fry, P.D. & Cranmer, G.J., 1982. A series of North Sea benthos surveys with trawl and headline camera. *Journal of the Marine Biological Association of the United Kingdom*, **62**, 297-313.
- Dyer, M.F., Fry, W.G., Fry, P.D. & Cranmer, G.J., 1983. Benthic regions within the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, **63**, 683-693.
- Edwards, C.B. & Moore, C.G., 2008. Reproduction in the sea pen *Pennatula phosphorea* (Anthozoa: Pennatulacea) from the west coast of Scotland *Marine Biology* **155**:303-314
- Edwards, D.C.B. & Moore, C.G., 2009. Reproduction in the sea pen *Funiculina quadrangularis* (Anthozoa: Pennatulacea) from the west coast of Scotland. *Estuarine, Coastal and Shelf Science*, **82**, 161-168.
- Eiriksson, H., 1970. On the breeding cycle and fecundity of the Norway lobster in south west Iceland. *International Council for the Exploration of the Seas Council Meeting Papers*, C.M.1970/K:6.
- Eno, N.C., MacDonald, D. & Amos, S.C., 1996. A study on the effects of fish (Crustacea/Molluscs) traps on benthic habitats and species. *Final report to the European Commission. Study Contract*, no. 94/076.

- Eno, N.C., MacDonald, D.S., Kinnear, J.A.M., Amos, C.S., Chapman, C.J., Clark, R.A., Bunker, F.S.P.D. & Munro, C., 2001. Effects of crustacean traps on benthic fauna *ICES Journal of Marine Science*, **58**, 11-20.
- Feldman, K.L., Armstrong, D.A., Dumbauld, B.R., DeWitt, T.H. & Doty, D.C., 2000. Oysters, crabs, and burrowing shrimp: review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. *Estuaries*, **23**, 141-176.
- Frid, C.L.J., Clark, R.A. & Hall, J.A., 1999. Long-term changes in the benthos on a heavily fished ground off the NE coast of England. *Marine Ecology Progress Series*, **188**, 13-20.
- Garrod, C. & Harding, D., 1980. Preliminary estimates of distribution, abundance and mortality of larvae and the size of the *Nephrops norvegicus* (L.) spring stock from larval surveys made off the north-east coast of England in 1976. *International Council for the Exploration of the Seas, Council Meeting Papers*, C.M.1980/K:18.
- GBNNSIP, 2011. Red King Crab, *Paralithodes camtschaticus*. Factsheet. [online]. York, GB Nonnative Species Secretariat. Available from: <http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=2533> [Accessed 05/05/2016]
- Gray, J.S., 1974. Animal-sediment relationships. *Oceanography and Marine Biology: an Annual Review*, **12**, 223-261.
- Greathead, C., Demain, D., Dobby, H., Allan, L. & Weetman, A., 2011. *Quantitative assessment of the distribution and abundance of the burrowing megafauna and large epifauna community in the Fladen fishing ground, northern North Sea*. Scottish Government: Edinburgh (UK).
- Greathead, C., González-Irusta, J.M., Clarke, J., Boulcott, P., Blackadder, L., Weetman, A. & Wright, P.J., 2015. Environmental requirements for three sea pen species: relevance to distribution and conservation. *ICES Journal of Marine Science: Journal du Conseil*, **72** (2), 576-586.
- Greathead, C.F., Donnan, D.W., Mair, J.M. & Saunders, G.R., 2007. The sea pens *Virgularia mirabilis*, *Pennatula phosphorea* and *Funiculina quadrangularis*: distribution and conservation issues in Scottish waters. *Journal of the Marine Biological Association*, **87**, 1095-1103.
- Gunnarsson, J.S. & Skold, M., 1999. Accumulation of polychlorinated biphenyls by the infaunal brittle stars *Amphiura filiformis* and *A. chiajei*: effects of eutrophication and selective feeding. *Marine Ecology Progress Series*, **186**, 173-185.
- Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: an Annual Review*, **32**, 179-239.
- Hiscock, K., 1983. Water movement. In *Sublittoral ecology. The ecology of shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.
- Hixon, M.A. & Tissot, B.N., 2007. Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon. *Journal of Experimental Marine Biology and Ecology*, **344** (1), 23-34.
- Hoare, R. & Wilson, E.H., 1977. Observations on the behaviour and distribution of *Virgularia mirabilis* O.F. Müller (Coelenterata: Pennatulacea) in Holyhead harbour. In *Proceedings of the Eleventh European Symposium on Marine Biology, University College, Galway, 5-11 October 1976. Biology of Benthic Organisms*, (ed. B.F. Keegan, P.O. Ceidigh & P.J.S. Boaden, pp. 329-337. Oxford: Pergamon Press. Oxford: Pergamon Press.
- Howson, C.M. & Davies, L.M., 1991. Marine Nature Conservation Review, Surveys of Scottish Sea Lochs. A towed video survey of Loch Fyne. Vol. 1 - Report. *Report to the Nature Conservancy Council from the University Marine Biological Station, Millport*.
- Howson, C.M., 1988. Marine Nature Conservation Review. Survey of Shetland, Foula and Fair Isle, 1987. Volume 1, Report. *Report to the Nature Conservancy Council from the Field Studies Council of Oil Pollution Research Unit, Orierton, Pembroke, Dyfed*.
- Howson, C.M., Connor, D.W. & Holt, R.H.F., 1994. The Scottish sealochs - an account of surveys undertaken for the Marine Nature Conservation Review. *Joint Nature Conservation Committee Report*, No. 164 (Marine Nature Conservation Review Report MNCR/SR/27)., *Joint Nature Conservation Committee Report*, No. 164 (Marine Nature Conservation Review Report MNCR/SR/27).
- Hughes, D.J. & Atkinson, R.J.A., 1997. A towed video survey of megafaunal bioturbation in the north-eastern Irish Sea. *Journal of the Marine Biological Association of the United Kingdom*, **77**, 635-653.
- Hughes, D.J., 1998a. Sea pens & burrowing megafauna (volume III). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. *Natura 2000 report prepared for Scottish Association of Marine Science (SAMS) for the UK Marine SACs Project.*, Scottish Association for Marine Science. (UK Marine SACs Project). Available from: <http://www.ukmarinesac.org.uk/publications.htm>
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC (Joint Nature Conservation Committee), 1999. *Marine Environment Resource Mapping And Information Database (MERMAID): Marine Nature Conservation Review Survey Database*. [on-line] <http://www.jncc.gov.uk/mermaid>
- Johnson, M.P., Lordan, C. & Power, A.M., 2013. Habitat and Ecology of *Nephrops norvegicus*. In Johnson, M.L. and Johnson, M.P. (eds.). *The Ecology and Biology of Nephrops norvegicus. Advances in Marine Biology*, vol. 64: Academic Press, pp. 27-63.
- Jones, L.A., Hiscock, K. & Connor, D.W., 2000. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. *Joint Nature Conservation Committee, Peterborough*. (UK

- Marine SACs Project report.). Available from: <http://www.ukmarinesac.org.uk/pdfs/marine-habitats-review.pdf>
- Kenchington, E., Murillo, F.J., Cogswell, A. & Lirette, C., 2011. Development of Encounter Protocols and Assessment of Significant Adverse Impact by Bottom Trawling for Sponge Grounds and Sea Pen Fields in the NAFO Regulatory Area. NAFO, Dartmouth, NS, Canada, 51 pp. <http://search.proquest.com/docview/1020851501?accountid=28412>
<http://archive.nafo.int/open/sc/2011/scr11-075.pdf>
- Kinnear, J.A.M., Barkel, P.J., Mojseiowicz, W.R., Chapman, C.J., Holbrow, A.J., Barnes, C. & Greathead, C.F.F., 1996. Effects of *Nephrops* creels on the environment. *Fisheries Research Services Report No. 2/96*.
- Koike, I. & Mukai, H., 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callinassa japonica* and *Upogebia major*. *Marine Ecology Progress Series*, **12**, 185-190.
- Lindley, J.A., Gamble, J.C. & Hunt, H.G., 1995. A change in the zooplankton of the central North Sea (55° to 58° N): a possible consequence of changes in the benthos. *Marine Ecology Progress Series*, **119**, 299-303.
- Loew, E.R., 1976. Light and photoreceptor degeneration in the Norway lobster *Nephrops norvegicus* (L.). *Proceedings of the Royal Society of London, Series B*, **193**, 31-44.
- Malecha, P.W. & Stone, R.P., 2009. Response of the sea whip *Halipteris willemoesi* to simulated trawl disturbance and its vulnerability to subsequent predation. *Marine Ecology Progress Series*, **388**, 197-206.
- Marine Institute, 2001. *Nephrops* biology [On-line]. Available from www.marine.ie/industry_services/fisheries/fisheries_biology, cited. 2002-01-24
- Marrs, S.J., Atkinson, R.J.A. & Smith, C.J., 1998. The towed underwater TV technique for use in stock assessment of *Nephrops norvegicus*. *International Council for the Exploration of the Sea Study Group on Life Histories of Nephrops La Coruña 4-8 May 1998*, CM 1998/G:9, pp. 88-98.
- Munoz, D.P., Murillo, F.J., Sayago-Gil, M., Serrano, A., Laporta, M., Otero, I. & Gomez, C., 2011. Effects of deep-sea bottom longlining on the Hatton Bank fish communities and benthic ecosystem, north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, **91** (4), 939-952.
- Nickell, L.A. & Atkinson, R.J.A., 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Marine Ecology Progress Series*, **128**, 181-197.
- Nickell, L.A., Atkinson, R.J.A., Hughes, D.J., Ansell, A.D. & Smith, C.J. 1995. Burrow morphology of the echiuran worm *Maxmuelleria lankesteri* (Echiura: Bonelliidae), and a brief review of the burrow structure and related ecology of the *Echiura*. *Journal of Natural History*, **29**, 871-885.
- O'Brien, P.J. & Dixon, P.S., 1976. Effects of oils and oil components on algae: a review. *British Phycological Journal*, **11**, 115-142.
- O'Connor, B., Bowmer, T., McGrath, D. & Raine, R., 1986. Energy flow through an *Amphiura filiformis* (Ophiuroidea: Echinodermata) in Galway Bay, west coast of Ireland: a preliminary investigation. *Ophelia*, **26**, 351-357.
- O'Connor, B., Keegan, G., McGrath, D. & Keegan, B.F., 1977. *Pachycerianthus multiplicatus* Carlgren, biotope or biocoenosis? In *Biology of Benthic Organisms*, (ed. B.F. Keegan et al.), pp. 173-183. Oxford: Pergamon Press.
- OBIS, 2016. Ocean Biogeographic Information System (OBIS). <http://www.iobis.org>, 2016-03-15
- OSPAR Commission, 2010. Background document for Seapen and Burrowing Megafauna communities. *OSPAR Commission Biodiversity Series*. OSPAR Commission: London. Available from: http://qsr2010.ospar.org/media/assessments/Species/P00481_Seapen_and_burrowing_megafauna.pdf
- Pearson, T.H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review*, **16**, 229-311.
- Plaza, J. & Sanderson, W.G., 1997. Rare sea bed species. In *Coasts and seas of the United Kingdom. Region 15 & 16: Northwest Scotland: the Western Isles and west Highland*, ed. J.H. Barne, C.F. Robson, S.S. Kasnowska, J.P. Doody, N.C. Davidson & A.L. Buck, pp. 116-121.
- Posey, M.H., 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callinassa californiensis*. *Marine Ecology Progress Series*, **31**, 15-22.
- Powell, A. & Eriksson, S.P., 2013. Reproduction: Life Cycle, Larvae and Larviculture. In Johnson, M.L. and Johnson, M.P. (eds.). *The Ecology and Biology of Nephrops norvegicus*. *Advances in Marine Biology*, vol. 64: Academic Press pp. 201-245.
- Roberts, H.H., Wiseman, W.J. & Suchanek, T.H. Jr., 1981. Lagoon sediment transport: The significant effect of *Callinassa* bioturbation. In *The Reef And Man. Proceedings Of The Fourth International Coral Reef Symposium. Manila (Philippines), 18-22 May 1981, Volume 1*. (ed. E.D. Gomez et al.), pp. 459-466.
- Rosenberg, R., Nilsson, H.C., Hollertz, K. & Hellman, B., 1997. Density-dependent migration in an *Amphiura filiformis* (Amphiuridae, Echinodermata) infaunal population. *Marine Ecology Progress Series*, **159**, 121-131.
- Rowden, A.A. & Jones, M.B., 1994. A contribution to the biology of the burrowing mud shrimp, *Callinassa subterranea* (Decapoda: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom*, **74**, 623-635.
- Rowden, A.A. & Jones, M.B., 1997. Recent mud shrimp burrows and bioturbation. *Porcupine Newsletter*, **6**, 153-158.
- Rowden, A.A., Jago, C.F. & Jones, S.E., 1998b. Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea. *Continental Shelf Research*, **18**, 1347-1363.
- Rowden, A.A., Jones, M.B. & Morris, A.W., 1998. The role of *Callinassa subterranea* (Montagu) (Thalassinidea) in sediment

- resuspension in the North Sea. *Continental Shelf Research*, **18**, 1365-1380.
- Rygg, B., 1985. Effect of sediment copper on benthic fauna. *Marine Ecology Progress Series*, **25**, 83-89.
- Sanders, H.L., 1978. Florida oil spill impact on the Buzzards Bay benthic fauna: West Falmouth. *Journal of the Fisheries Board of Canada*, **35**, 717-730.
- Shelley, R., Widdicombe, S., Woodward, M., Stevens, T., McNeill, C.L. & Kendall, M.A. 2008. An investigation of the impacts on biodiversity and ecosystem functioning of soft sediments by the non-native polychaete *Sternaspis scutata* (Polychaeta: Sternaspidae). *Journal of Experimental Marine Biology and Ecology*, **366**, 146-150.
- Soong, K., 2005. Reproduction and colony integration of the sea pen *Virgularia juncea*. *Marine Biology*, **146** (6), 1103-1109.
- Tamaki, A., 1988. Effects of the bioturbating activity of the ghost shrimp *Callianassa japonica* Ortmann on migration of a mobile polychaete. *Journal of Experimental Marine Biology and Ecology*, **120**, 81-95.
- Taylor, A.C., Field, R.H. & Parslow-Williams, P.J., 1996. The effects of *Hematodinium* sp. Infection on aspects of the respiratory physiology of the Norway lobster, *Nephrops norvegicus*. *Journal of Experimental Marine Biology and Ecology*, **207**, 217-228.
- Tuck, I.D., Atkinson, R.J.A. & Chapman, C.J., 1994. The structure and seasonal variability in the spatial distribution of *Nephrops norvegicus* burrows. *Ophelia*, **40**, 13-25.
- Tuck, I.D., Chapman, C.J. & Atkinson, R.J.A., 1997. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. I. Growth and density. *ICES Journal of Marine Science*, **54**, 125-135.
- Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E. & Basford, D.J., 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology Progress Series*, **162**, 227-242.
- Tunberg, B., 1986. Studies on the population ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassinidea). *Estuarine, Coastal and Shelf Science*, **22**, 753-765.
- Ungfors, A., Bell, E., Johnson, M.L., Cowing, D., Dobson, N.C., Bublit, R. & Sandell, J., 2013. Nephrops Fisheries in European Waters. In Johnson, M.L. and Johnson, M.P. (eds.). *The Ecology and Biology of Nephrops norvegicus*. *Advances in Marine Biology*, vol. 64, Academic Press, pp. 247-314.
- Waslenchuk, D.G., Matson, E.A., Zajac, R.N., Dobbs, F.C. & Tramontano, J.M., 1982. Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. *Marine Biology*, **72**, 219-225.
- Wilding, T. A., 2011. A characterization and sensitivity analysis of the benthic biotopes around Scottish salmon farms with a focus on the sea pen *Pennatulula phosphorea* L. *Aquaculture Research* 42: 35-40.
- Wilson, M.T., Andrews, A.H., Brown, A.L. & Cordes, E.E., 2002. Axial rod growth and age estimation of the sea pen, *Halipteris willemoesi* Kölliker *Hydrobiologia*, **471**, 133-142.
- Wright, E.P., Kemp, K., Rogers, A.D. & Yesson, C., 2015. Genetic structure of the tall sea pen *Funiculina quadrangularis* in NW Scottish sea lochs. *Marine Ecology*, **36** (3), 659-667.