Neopentadactyla mixta in circalittoral shell gravel or coarse sand

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

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2016-05-29

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/389]. All terms and the MarESA methodology are outlined on the website (https://www.marlin.ac.uk)

This review can be cited as:
Tyler-Walters, H. & Durkin, O.C., 2016. [Neopentadactyla mixta] in circalittoral shell gravel or coarse sand. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom.

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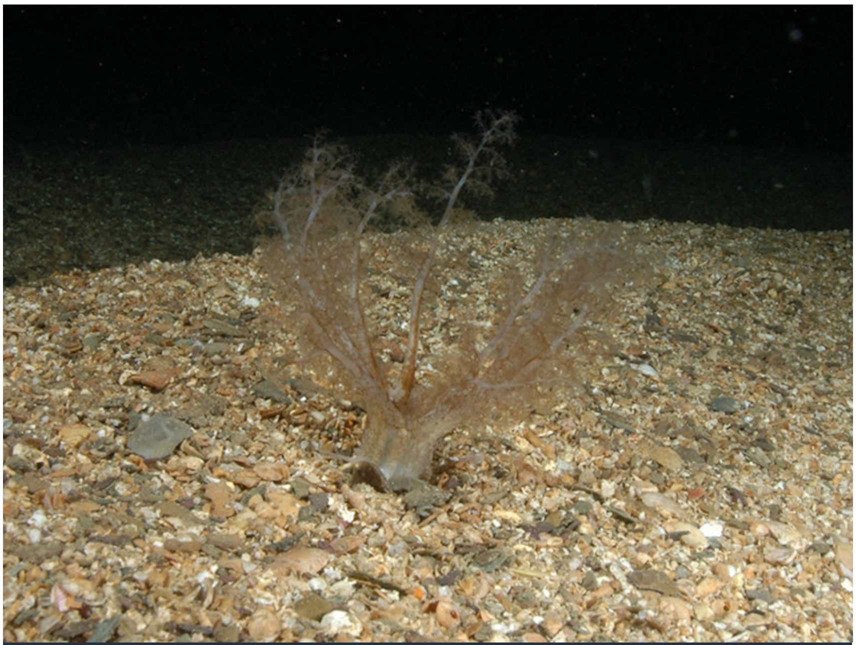

Neopentadactyla mixta **in circalittoral shell gravel or coarse sand**
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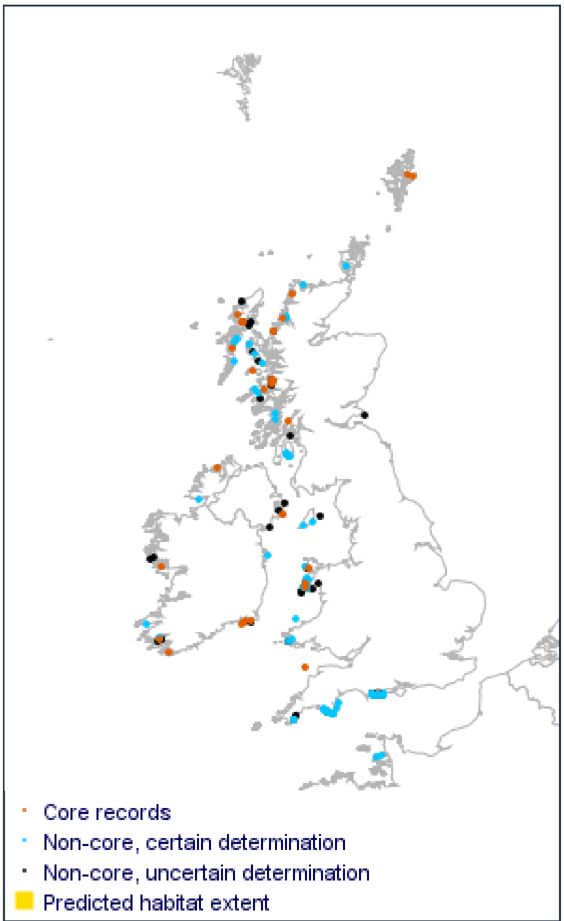

17-09-2018
Biotope distribution data provided by EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu)

Researched by Dr Harvey Tyler-Walters & Olivia Durkin **Refereed by** Admin

Summary

UK and Ireland classification

EUNIS 2008	A5.144	*Neopentadactyla mixta* in circalittoral shell gravel or coarse sand
JNCC 2015	SS.SCS.CCS.Nmix	*Neopentadactyla mixta* in circalittoral shell gravel or coarse sand
JNCC 2004	SS.SCS.CCS.Nmix	*Neopentadactyla mixta* in circalittoral shell gravel or coarse sand
1997 Biotope	SS.CGS._.Ven.Neo	*Neopentadactyla mixta* and venerid bivalves in circalittoral shell gravel or coarse sand

Description

Sublittoral plains of clean, shell, maerl, stone gravels or sometimes coarse sands, with frequent *Neopentadactyla mixta*. *Pecten maximus* may occur occasionally along with *Lanice conchilega*. Other epifaunal species may include *Ophiura albida*, *Pagurus* spp. and *Callionymus* spp. These sediments may be thrown into dunes by wave action or tidal streams. Widespread species such as *Cerianthus lloydii* and *Chaetopterus variopedatus* are present in many examples of this biotope. Scarcely recorded species such as *Molgula oculata*, *Ophiopsila annulosa* and *Amphiura securigera* may also be found. *Ophiopsila annulosa* only occurs in records from the south-west of the British Isles. It should be noted that *Neopentadactyla* may exhibit periodicity in its projection out of, and retraction into, the sediment (Picton 1993). (Information taken from the Marine Biotope Classification for Britain and Ireland, Version 04.05: Connor *et al.*, 2004).

Depth range

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

Additional information

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Listed By

- none -

Further information sources

Search on:

G G G JNCC

Habitat review

Ecology

Ecological and functional relationships

- The gravel sea cucumber, *Neopentadactyla mixta*, burrows in coarse, typically mobile shell sand, gravel or maerl where water flow is quite strong. The gravel sea cucumber is an infaunal burrower and is only visible when the tentacles are projected above the surface. When extended, the tentacular crown can be up to a quarter of the body length and have a spread of 140 square cm. The body is generally held in a u-shape within the sediment with the tentacles held in the water column and the terminal anus just at the surface. Food particles are trapped using special adhesive areas at the tips of the tentacles. To ingest food, a tentacle is inserted into the mouth, the buccal membrane constricts and the tentacle withdrawn, scraping off any adherent food particles.
- *Neopentadactyla mixta* lives gregariously and can reach densities of up to 400 per square metre in loose gravels such as maerl (Smith & Keegan, 1985). Such an abundance of burrowing sea cucumbers may prevent the colonization of other macrofauna and therefore excluding them from this biotope.
- Other echinoderms are also present and often abundant in this biotope. Brittle stars, *Ophiura albida*, *Ophiospila* sp., *Amphiura* sp., typically inhabit the top layer of sediment. The sea urchin *Echinus esculentus* is an important grazer.
- The dominant trophic group is suspension feeders. *Neopentadactyla mixta* is a passive suspension feeder and requires a reasonable flow of water to provide sufficient food particles. The tentacular crown is held up in the water column in order to feed. Predation is predominantly by fish, *Callionymus* sp., crabs, *Pagarus* sp., and starfish, *Asterias rubens*. If present in high abundance, the arms of *Amphiura* sp. can be an important food source for demersal fish (*Callionymus* sp.) providing significant energy transfer to higher trophic levels.
- *Melanella alba*, an eulimid gastropod is a temporary ectoparasite on *Neopentadactyla mixta*, piercing the skin and feeding on the internal organs.
- Cloak anemones, *Adamsia carcinopados*, occur attached to the gastropod shells of hermit crabs, *Pagurus prideaux*. The association appears to be obligatory between the two species and they are not generally found apart in normal circumstances and both degenerate quickly if separated. The base of the sea anemone secretes a chitinous membrane which effectively increases the size of the gastropod shell so as the crab grows it does not need to change shells.

Seasonal and longer term change

Neopentadactyla mixta spend much of the winter buried deep in aerobic mixed sediment. During this winter period, a torpid stage is entered with respiration and activity greatly reduced. Torpor exhibited by this species is marked by a considerable deterioration in body condition, a decline in tissue lipid content, and reduced metabolism. Given sufficient aeration, this species can tolerate long periods (up to 8 months) without feeding due to the use of long-term nutrient reserves stored as lipids and some proteins. The period of feeding cessation and torpor is backed up by previous workers unable to find populations of feeding *Neopentadactyla mixta* during winter months (Smith & Keegan, 1985). Smith (1981) reported a reduction of tissues in the gonad and substantial loss in gonad weight over the winter period with a concomitant loss of lipid.*Neopentadactyla mixta* also exhibit daily feeding activity rhythms. Although not necessarily representative of all populations, *Neopentadactyla mixta* exhibits regular daily and seasonal movements within the substratum. In the Kilkieran Bay population, individuals withdraw further into the sediment between 1-4 hours after sunrise and remain in the substratum for 1-2 hours, re-emerging over a period of up to four hours. The stimuli for the initiation of feeding activity remains unclear but it seems that light and temperature change are major cues affecting daily and seasonal feeding activity rhythms, respectively.

Habitat structure and complexity

The habitat of this biotope is complex. Maerl (dead and live) and gravel are often loose and mobile preventing colonization by many species. However, the majority of species within this biotope live below the gravel surface, notably deep burrowing fauna (Hall-Spencer & Atkinson, 1999). Burrowing fauna and tube building polychaetes (e.g. *Lanice conchilega*) are important for sediment stabilizing. The tubes modify benthic boundary layer hydrodynamics (Eckman *et al*., 1981), can provide an attachment surface for filamentous algae (Schories & Reise, 1993) and serve as a refuge from predation (Woodin, 1978; Zühlke *et al*., 1998). Tubes of *Lanice conchilega* can penetrate several tens of centimetres into the sediment. Such burrows and tubes allow oxygenated water to penetrate into the sediment indicated by 'halos' of oxidized sediment along burrow and tube walls. Other fauna probably help in stabilizing the substratum. The tube anemone *Cerianthus lloydii* extends above the sediment surface.

Productivity

Production in the biotope is mostly secondary, dependent upon detritus and organic material. Some primary production comes from benthic macroalgae and water column phytoplankton. The dominant trophic group therefore is suspension feeders. In the relatively shallow waters around the British Isles secondary production in the benthos is generally high, but shows seasonal variation (Wood, 1987). Generally, secondary production is highest during summer months, when temperatures rise and primary productivity is at its peak. Spring phytoplankton blooms are known to trigger, after a short delay, a corresponding increase in productivity in benthic communities (Faubel *et al*., 1983).

Recruitment processes

The majority of benthic marine invertebrates, particularly echinoderms, suffer high juvenile/post-settlement mortality (Gosselin & Qian, 1997), various environmental factors play an important role in the recruitment processes of echinoderms, such as, predation, disease and migration. Very little is known about settlement in holothuroids and no information has been found in relation to the life history strategies of *Neopentadactyla mixta*. Breeding is presumed to occur between April and September when the population is at the substratum surface. Holothuroids are predominantly gonochoristic and broadcast spawners, some are brooders or hermaphrodites. The larvae of some species show planktotrophy, others lecithotrophy, some direct development, others indirect. The scallop *Pecten maximus* appears to have a long breeding period with peaks in spring and autumn (Fish & Fish, 1996). The veliger larvae are planktonic for about three to four weeks and settle on a wide range of substrate including algae, bryozoans and hydroids. *Lanice conchilega* is a polychaete species with separate sexes. The species has two larval stages, the last stage; an aulophora larva lives for about 4-6 weeks in the plankton (Kessler, 1963). This species has a reported lifespan of 1-2 years (Beukema *et al*., 1978). Kuhl (1972) reported that the larvae of *Lanice conchilega* are released between April and October. Experimental data and field studies from the Wadden Sea revealed that the existence of 'hard substrate', preferentially tubes of conspecific adults, was a requirement for initial settlement of *Lanice conchilega* larvae, although single juveniles were also observed to settle on eroded shells of cockles and soft-shelled clams (Heuers, 1998; Heuers *et al.*, 1998). Tyler (1977) found that populations of *Ophiura albida* in the Bristol Channel had a well-marked annual reproductive cycle, with spawning taking place in May and early June. Spent adults and planktonic larvae were observed up to early October. In contrast the larger *Ophiura ophiura* had a more protracted breeding season.

Time for community to reach maturity

No information was found on the life history strategy of *Neopentadactyla mixta*. *Amphiura* sp. and *Pecten maximus* are long lived and take a relatively long time to reach reproductive maturity. It takes approximately 5-6 years for *Amphiura* sp. to reach maturity. Mortality of settling *Amphiura* sp. is reported to be extremely high, with less than 5% contributing to the adult population in any given year (Muus, 1981). *Pecten maximus* reaches sexual maturity within the first 2-3 years and has a lifespan of 10-20 years. The suggested lifespan for *Ophiura ophiura* in the west of Scotland is 5-6 years (Gage, 1990).

Additional information

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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
Salinity preferences	Full (30-40 psu)
Physiographic preferences	Enclosed coast / Embayment, Open coast
Biological zone preferences	Circalittoral, Lower infralittoral
Substratum/habitat preferences	Coarse clean sand, Gravel / shingle
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Exposed, Moderately exposed
Other preferences	

Additional Information

Species composition

Species found especially in this biotope

Rare or scarce species associated with this biotope

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Additional information

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The coarse sediment and the abundance of *Neopentadactyla mixta* define this biotope (SS.SCS.CCS.Nmix). *Neopentadactyla mixta* is recorded as frequent (ca 1-9 /100m^2) in coarse gravel (biotope SS.SCS.CCS.Nmix) and maerl (biotope SS.SMp.Mrl.Pcal.Nmix) and can reach high densities, for example, >400/m^2 on the west coast of Ireland (Könnecker & Keegan, 1973; Keegan *et al.*, 1985). It is the dominant and only important characterizing species within the CCS.Nmix biotope. The other characteristic species are found in a range of coarse sediment biotopes or are otherwise widespread. A significant reduction in the abundance of, or loss of, *Neopentadactyla mixta* would result in loss of the biotope as described in the habitat classification. Therefore, the sensitivity of the biotope is dependent on the sensitivity of *Neopentadactyla mixta*. The sensitivity of other characteristic species is mentioned where relevant.

Resilience and recovery rates of habitat

Little is known about the population dynamics of *Neopentadactyla mixta*, or their life history. Their abundance in coarse sediments might suggest either good local recruitment and or sporadic but high-level recruitment. For example, Keeghan *et al.* (1985) recorded adult densities of ca 420/m^2 together with juvenile densities of ca 15,000/m^2 (at different locations) on the west coast of Ireland. Breeding is presumed to occur between April and September when the population is at the substratum surface. *Neopentadactyla mixta* is dioecious, with large eggs (ca 300 µm in size) (Smith & Keegan, 1985). As a result, Southward & Campbell (2006) been suggested that larval development is lecithotrophic.

As a group, echinoderms are highly fecund; producing long-lived planktonic larvae with high dispersal potential. However, recruitment in echinoderms is poorly understood, often sporadic and variable between locations and dependent on environmental conditions such as temperature, water quality, and food availability. For example, in the heart urchin *Echinocardium cordatum* recruitment was recorded as sporadic, only occurring in 3 years out of a 10 year period (Buchanan, 1967). Millport populations of *Echinus esculentus* showed annual recruitment, whereas few recruits were found in Plymouth populations during Nichols studies between 1980 and 1981 (Nichols, 1984). Similarly, Bishop & Earll (1984) suggested that the population of *Echinus esculentus* at St Abbs had a high density and recruited regularly whereas the Skomer population was sparse, ageing and had probably not successfully recruited larvae in the previous 6 years.

Overall, there is no direct evidence of larval development, recruitment and/or population dynamics in *Neopentadactyla mixta*. As many echinoderms show sporadic and variable recruitment, any population could take anywhere from one year to perhaps ten years to recruit and recolonize a habitat from which they were reduced in abundance and or removed. Therefore, resilience is given a precautionary rank of **Medium** (2-10 years). However, the assessment of resilience is made by inference from the life history of members of the same phylum, so confidence is Low based on expert judgement.

Hydrological Pressures

	Resistance	Resilience	Sensitivity

Temperature increase (local)	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

Little information on temperature tolerances was found. The assessment is based on reported global distribution. The majority of records of *Neopentadactyla mixta* occur in the British Isles although its range extends from the Faeroe Islands, the west coast of Norway (Molde),the Barents Sea to the Bay of Biscay (Southward & Campbell, 2006; OBIS, 2016). Based on this evidence, it is likely to tolerate a chronic change in temperature.

Neopentadactyla mixta is not reported from shallow water, and it is only likely to be exposed to acute temperature changes due to thermal effluents. It is likely to withdraw into the sediment, away from the thermal plume, and be protected by the temperature of the interstitial waters. Only long-term acute change (greater than the benchmark) is likely to adversely affect the population. In winter months, it is probably too deep to be affected by significant decreases in temperature as it burrows to a depth of 30-60 cm into the substratum (Smith & Keegan, 1985). Smith & Keegan (1985) suggested that light or winter temperature might be one cue for seasonal torpor but noted that winter turbulence and increased turbidity, due to water movement, may also induce *Neopentadactyla mixta* to overwinter at depth.

Sensitivity assessment. Therefore, if exposed to a short-term acute change i.e. 5°C for a month, it will probably withdraw into the sediment and be unable to feed, resulting in a temporary loss of condition. Overall, a resistance of **High** is suggested, with a resilience of **High** so that the biotope is assessed as **Not sensitive** at the benchmark level.

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

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Sensitivity assessment. Therefore, if exposed to a short-term acute change i.e. 5°C for a month, it will probably withdraw into the sediment and be unable to feed, resulting in a temporary loss of condition. Overall, a resistance of **High** is suggested, with a resilience of **High** so that the biotope is assessed as **Not sensitive** at the benchmark level.

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

Echinoderms are restricted to the marine environment and one of the only stenohaline phyla in the animal kingdom (Russell, 2013). Although some species can acclimatise to hypo/hypersaline conditions, Russell (2013) did not mention *Neopentadactyla mixta* amongst them. Smith (1983) noted that hypo or hypersaline water caused the animal to withdraw its tentacles.

Neopentadactyla mixta is not reported from shallow water, and it is only likely to be exposed due to hypo/hypersaline effluents. Roberts *et al.* (2010b) reported that hypersaline effluents from desalination plants disperse with tens of metres of the discharge point but reported widespread alteration in seagrass and soft sediment communities in poorly flushed environment. Echinoderms and ascidians were amongst the most sensitive to hypersaline brine in the studies examined (Roberts *et al.*, 2010b). While hypersaline effluents are likely to sink to the seabed, and potentially penetrate into the sediment, the water movement characteristic of this biotope is likely to disperse the effluent and limit the effect to the immediate vicinity of any discharge point.

Sensitivity assessment. An increase in salinity above 40 psu is likely to be detrimental to *Neopentadactyla mixta* and interrupt feeding but if prolonged for a year (see benchmark) may result in the death of individuals in the vicinity of the discharge. Therefore, a precautionary resistance assessment of Medium is suggested but with Low confidence. Resilience is probably **Medium** so that sensitivity is assessed as **Medium**.

Salinity decrease (local)	None Q: Low A: NR C: NR	Medium Q: Low A: NR C: NR	Medium Q: Low A: Low C: Low

Echinoderms are restricted to the marine environment and one of the only stenohaline phyla in the animal kingdom (Russell, 2013). Although some species can acclimatise to hypo/hypersaline conditions, Russell (2013) did not mention *Neopentadactyla mixta* amongst them. Smith (1983) noted that hypo or hypersaline water caused the animal to withdraw its tentacles.

Sensitivity assessment. The biotope and *Neopentadactyla mixta* are only recorded from 'full' marine conditions. A reduction is salinity to reduced (18- <30 psu) for a year is likely to reduce feeding or drive *Neopentadactyla mixta* into the sediment where it cannot feed. Its seasonal torpor lasts from September to March each year, during which it loses condition significantly, it is unlikely to survive for a year without feeding. Therefore, a resistance of **None** is suggested but with Low confidence. Resilience is probably **Medium** so that sensitivity is assessed as **Medium**.

Water flow (tidal current) changes (local)	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

Neopentadactyla mixta occurs in maerl beds and coarse gravel sediments, both of which are associated with water flow either due to tidal streams (moderately strong to weak, Connor *et al.* 2004) or wave mediated water movement (exposed to moderately wave exposed). For example, the beds of *Neopentadactyla mixta* in coarse sediments examined by Konnecker & Keegan (1973) were found in tidal currents of up to 2.5 knots (ca 1.28m/s). Nevertheless, artificially increased current beyond the calm weather, spring tide, maximum of ca 1.5 m/s caused *Neopentadactyla mixta* to stop feeding a withdraw into its burrow, as did bombardment with dislodged sediment (Smith & Keegan 1985). Similarly, a heavy gale in August caused *Neopentadactyla mixta* to withdraw deep into the sediment for six to ten days (Smith & Keegan, 1985). The species regularly undertakes a ca six month long torpor period, during which it loses condition and lipid energy stores. Smith & Keegan (1985) suggested that the overwinter torpor may be a response to poor food availability coupled with increased turbulence experienced in winter at their study site. An increase in water flow may also modify the sediment, causing a loss of the sediment from the surface and mobilisation of the bed, although these sediments routinely bear mega-ripples caused by current flow and storms. However, a decrease in flow will probably result in deposition of fine sediments and detritus, resulting in a change in sediment type, and a complete change in the biological community,

Sensitivity assessment. Water flow (due to tidal flow or wave action) is an important structuring factor in habitats dominated by *Neopentadactyla mixta* (e.g. SS.SCS.CCS.Nmix and SS.SMp.Mrl.Pcal.Nmix), maintaining an open matrix of maerl or coarse sediment, removing fine sediments, allowing oxygenation deep within the sediment and providing adequate food supply to suspension feeders such as *Neopentadactyla mixta*. In areas of weak flow the biotope probably experience higher wave action, while in areas of moderate wave exposure, tidal flow is probably more important. However, a change in water flow of 0.1-0.2 m/s is probably of limited effect in the biotopes normal range of <0.5 to 1.5 m/s, especially if low flow occurs in wave exposed areas. Therefore, a resistance of **High** is suggested, with a **r**esilience of **High** so that the biotope is probably **Not sensitive** at the benchmark level.

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

The pressure benchmark is relevant only to littoral and shallow sublittoral fringe biotopes.

Wave exposure changes (local)	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

Neopentadactyla mixta occurs in maerl beds and coarse gravel sediments, both of which are associated with water flow either due to tidal streams (moderately strong to weak, Connor *et al.* 2004) or wave mediated water movement (Exposed to Moderately exposed). Smith & Keegan (1985) noted that a heavy gale at their study site in August caused *Neopentadactyla mixta* to withdraw deep into the sediment for six to ten days. The species regularly undertakes a ca six month long torpor period, during which it loses condition and lipid energy stores. Smith & Keegan (1985) suggested that the overwinter torpor may be a response to poor food availability coupled with increased turbulence experienced in winter at their study site.

Sensitivity assessment. Water flow (due to tidal flow or wave action) is an important structuring factor in habitats dominated by *Neopentadactyla mixta* (e.g. SS.SCS.CCS.Nmix and SS.SMp.Mrl.Pcal.Nmix), maintaining an open matrix of maerl or coarse sediment, removing fine sediments, allowing oxygenation deep within the sediment and providing adequate food supply to suspension feeders such as *Neopentadactyla mixta*. An increase in wave action may also modify the sediment, causing a loss of the sediment from the surface and mobilisation of the bed, although these sediments routinely bear mega-ripples caused by current flow and storms. However, a decrease in wave action (in areas of low water flow) will probably result in deposition of fine sediments and detritus, resulting in a change in sediment type, and a complete change in the biological community. However, a change in nearshore wave height of >3% but <5%) is unlikely to be significant. Therefore, a resistance of **High** is suggested, with a **r**esilience of **High** so that the biotope is probably **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.

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

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

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

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

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

No evidence was found

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	Low Q: Low A: NR C: NR	Medium Q: Low A: NR C: NR	Medium Q: Low A: Low C: Low

Neopentadactyla mixta probably needs coarse sediments to survive, as the open matrix provided by coarse sediments or maerls at depth, together with water flow, ensures that the water is oxygenated at depth in the sediment. *Neopentadactyla mixta* reduces its metabolism and oxygen consumption from 0.11 ml O_2/ gm dry wt. to 0.03 ml O_2/ gm dry wt. during its overwinter torpor (Smith & Keegan, 1985). Therefore, it might be able to survive lower oxygen levels overwinter than in spring, summer and autumn.

Lawrence (1996) reported mass mortality of echinoderms in the Gulf of Trieste due to hypoxia caused by a strong thermocline combined with high pelagic productivity and eutrophication. The brittlestar *Ophiura quinquemaculata* was killed with a few days, holothurians including *Ocnus planci* (as *Cucumaria planci*), starfish *Asteropecten* sp. and the remaining brittlestars were killed within a week. Echinoderms were shown to be intolerant of the effects of algal blooms, resulting in mortalities of the sea urchins *Echinus esculentus* and *Paracentrotus lividus*, and the holothurian *Labidoplax digitata* amongst other echinoderms, probably due to hypoxia caused by death of the algal bloom algae (Boalch, 1979; Forster, 1979; Griffiths *et al*., 1979; Lawrence, 1996). Diaz & Rosenberg (1995, Figure 5) suggested that shrimp and crustaceans were lost as oxygen levels dropped below ca 0.75 ml/l and that the macroinfauna was reduced below ca 0.4ml/l.

Vaquer-Sunyer & Duarte (2008) suggested a median sublethal oxygen concentration of 1.22 mg O_2/l (± 0.25) for a number of echinoderms reviewed in their study. Echinoderms were neither the most or the least sensitive of the taxonomic groups examined.

Sensitivity assessment. *Neopentadactyla mixta* may be more resistant of decrease oxygen levels while in it winter torpor. No information on juveniles was found. However, the species has a preference of coarse, mobile, deposits in areas of moderate to strong water flow (Konnecker & Keegan, 1973; Keegan et al., 1985). This suggests that it prefers well oxygenated habitats. The evidence from the Gulf of Trieste also suggests that echinoderms are sensitive to hypoxia. Therefore, a resistance of **Low** is suggested based on expert judgement. Resilience is probably **Medium** so that the biotope is assessed as **Medium** sensitivity at the benchmark level.

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

Nutrient enrichment can lead to increase in algal growth and algal blooms, whose subsequent death results in hypoxia or even anoxia. Nutrient enrichment can also result in increased bacterial growth in sediments, that also result in hypoxia. However, this biotope occurs in well flushed habitats so that only continuous of extreme enrichment is likely to be detrimental. But no direct evidence was found. However, the biotope is assessed as **Not sensitive** at the pressure benchmark of compliance with good status as defined by the WFD.

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

Organic enrichment due to sewage and other effluents has been implicated in the loss of maerl beds and a complete shift in their resident communities. For example in Brittany, numerous maerl beds were affected by sewage outfalls and urban effluents, resulting in increases in contaminants, suspended solids, microbes and organic matter with resultant deoxygenation (Grall & Hall-Spencer, 2003). This resulted in increased siltation, higher abundance, and biomass of opportunistic species, loss of sensitive species and reduction in biodiversity. Grall & Hall-Spencer (2003) note that two maerl beds directly under sewage outfalls were converted from dense deposits of live maerl in 1959 to heterogeneous mud with maerl fragments buried, under several centimetres of fine sediment, with communities dominated by only a few species by 1997. Similarly, changes in sediment community structure from diverse communities to communities dominated by opportunistic deposit feeders is well documented (Pearson & Rosenberg 1978; Diaz & Rosenberg 1995).

Sensitivity assessment. Although the evidence available could not be compared directly with the benchmark, the evidence suggests that organic enrichment could lead to a complete change in the community and loss of *Neopentadactyla mixta* populations. In addition, while this biotope is not characterized by maerl, the coarse sediment provides a similar open matrix, and would probably respond to organic enrichment in a similar manner. However, it is not possible to compare the reported evidence to the benchmark level of impact. Therefore, a resistance of **Low** is suggested. A resilience of **Low** is suggested as the habitat would need to recover before the species could return. Sensitivity is, therefore, assessed as **High.**

Physical Pressures

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

All marine habitats and benthic species are considered to have a resistance of '**None**' to this pressure and to be unable to recover from a permanent loss of habitat (resilience 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 not longer be a sedimentary habitat and would no longer support *Neopentadactyla mixta* or other infauna or epifauna.

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: High C: Medium	Very Low Q: High A: High C: High	High Q: High A: High C: Medium

Neopentadactyla mixta is recorded from coarse sand and gravel sediments. Könnecker & Keegan (1973) reported that it had a preference for gravel type substrata on the west coast of Ireland and that the highest densities of individuals occurred in loose, mobile deposits. Keegan *et al.* (1985) reported that it occurred in coarse sediments in moderate to strong tidal stream but that it was less common in other deposits. Connor *et al.* (1997a) reported that *Neopentadactyla mixta* occurred in biotopes from gravel, algal gravel (maerl) and coarse clean sand, while this biotope (CCS.Nmix is only recorded from sandy gravel habitats (Connor *et al.*, 2004). Therefore, a change in sediment type to fine sediments e.g. to fine sands, sands with gravel or muddy sands would result in a loss of the biotope as described by the habitat classification. *Neopentadactyla mixta* probably needs coarse sediments to survive, as the open matrix provided by coarse sediments or maerls at depth, together with water flow, ensures that the water is oxygenated at depth in the sediment. This is probably especially important as *Neopentadactyla mixta* overwinters for ca six months at depth (30-60 cm). A change is sediment type to 100% gravel wouls also result in loss of the biotope as described by the classification. *Neopentadactyla mixta* may also be lost, presumably, because the higher water flow associated with gravel habitats would preclude feeding.

Sensitivity assessment. Therefore, a resistance of **None** is recorded. As the change is permanent, resilience is **Very low** and sensitivity is assessed as **High**.

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

Neopentadactyla mixta lives in the sediment is a 'U-shaped' posture with its oral tentacles raised above the surface and its anus just below the surface of the sediment (Smith & Keegan, 1985). It is usually found in this position in its burrow 15-25 cm deep in the sediment (Könnecker & Keegan, 1973). However, in the winter months (ca September to March) its burrows into the sediment to a depth of 30-60 cm. It maintains this depth, even if the surface of the sediment is eroded or accreted (Smith & Keegan, 1985).

Sensitivity assessment. In spring to autumn, extraction of the sediment to 30 cm is likely to remove the majority of the resident population but in winter, the majority of the population would survive as long as suitable substratum remained after extraction. Therefore, a resistance of **None** is recorded to represent to worst case scenario. Resilience is probably **Medium** so that sensitivity is assessed as **Medium**.

Abrasion/disturbance of the surface of the substratum or seabed	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

The burrow of *Neopentadactyla mixta* in spring/autumn is 15-25 cm deep, and 30-60 cm deep during its winter torpor (Smith & Keegan, 1985). Therefore, it is unlikely to be directly impacted by surface abrasion. For example, in long-term studies of scallop dredging and subsequent recovery (Hall-Spencer & Moore 2000a, 2000b) deep burrowing species including *Neopentadactyla mixta* were not impacted and their abundance changed little over the four year period. It should be noted however that no information on juveniles was available. Therefore, a resistance of **High** is suggested. Resilience is probably also **High** (as there is no impact to recover from) so that biotope is assessed as **Not Sensitive**.

Penetration or disturbance of the substratum subsurface	Medium Q: Medium A: Medium C: Medium	Medium Q: Low A: NR C: NR	Medium Q: Low A: Low C: Low

In long-term studies of scallop dredging and subsequent recovery (Hall-Spencer & Moore 2000a, 2000b) deep burrowing species including *Neopentadactyla mixta* were not impacted and their abundance changed little over the four year period. However, experimental hydraulic blade dredging removed and damaged deep-burrowing species, including small numbers of *Neopentadactyla mixta* (Hauton *et al.* 2003), and affected the maerl bed to a depth of 9 cm. Hydraulic dredging in coarse sand and gravel may have similar effects.

Overall, penetrative gear may adversely affect *Neopentadactyla mixta* populations and a resistance of **Medium** is suggested. Resilience is likely to be **Medium** so that sensitivity is assessed as **Medium.**

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

This biotope occurs in well flushed areas subject to moderately strong to weak flow and/or wave exposed or moderately wave exposed conditions. *Neopentadactyla mixta* is a passive suspension feeder. It holds its tentacles into the water column and particles of food and detritus stick to the sticky mucus on the tentacles while filamentous algae lodge amongst the tentacles. The tentacles are them placed into the mouth and the food consumed (Smith, 1983). It feeds on unicellular and filamentous algae, diatoms, dinoflagellates, the exoskeletons of planktonic crustaceans and other organic material (Smith, 1983). Therefore, an increase in suspended sediment may increase food availability while an increase in turbidity may reduce phytoplankton abundance.

Smith & Keegan (1985) noted that a heavy gale at their study site in August caused *Neopentadactyla mixta* to withdraw deep into the sediment for six to ten days (Smith & Keegan, 1985). Smith & Keegan (1985) suggested that the overwinter torpor may be a response to poor food quality of the seston in winter months coupled with increased turbulence experienced in winter at their study site. Perhaps poor food quality was due to lack of phytoplankton in the winter months. Smith & Keegan (1983) also noted that in strong flow the tentacles became heavily turbated but were still held into the water column.

Sensitivity assessment. No direct measure of turbidity normally experienced by this biotope was found. Suspension feeders require good or constant water flow and a supply of seston. So an increase in suspended sediment could provide extra food. However, in turbid conditions, the suspension feeding apparatus may become clogged or overwhelmed by particulates and the animal stop feeding. The evidence of winter torpor in *Neopentadactyla mixta* may suggest that it avoids a natural increase in turbidity in the more stormy winter months, and/or avoids organic particulates in winter in preference for more energy rich phytoplankton in spring to autumn. Therefore, a resistance of **Medium** is suggested to represent the potential loss of feeding and food quality if the turbidity was to increase (e.g. from clear to intermediate; see benchmark) but with Low confidence. Resilience is probably **Medium** so that sensitivity is assessed as **Medium**.

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

Neopentadactyla mixta lives in the sediment is a ‘U-shaped’ posture with its oral tentacles raised above the surface and its anus just below the surface of the sediment (Smith & Keegan, 1985). It is usually found in this position in its burrow 15-25 cm deep in the sediment (Könnecker & Keegan, 1973). However, in the winter months (ca September to March) its burrows into the sediment to a depth of 30-60 cm. It maintains this depth, even if the surface of the sediment is eroded or accreted (Smith & Keegan, 1985).

Sensitivity assessment. The tentacular crown can expand to 140 cm^2 (Smith & Keegan, 1985) and probably extends to ca 4-5 cm above the substratum (expert opinion). However, the deposit of 5 cm of fine sediment would probably discourage *Neopentadactyla mixta* from feeding and it would probably withdraw into its burrow. Fine sediment will also penetrate the surface of the sediment in the affected area, significantly reducing water flow, and increasing the possibility of anoxia within the sediment. If the smothering sediment remained, it would result in a complete shift of the community and loss of the *Neopentadactyla mixta* population. However, in the areas of water movement in which these habitats occur it is unlikely that the smothering sediment would persist, depending on the local hydrography. As *Neopentadactyla mixta* can survive ca 6 months without feeding (Konnecker & Keegan, 1973; Smith & Keegan, 1985) it is likely that resistance is **High** and resilience is also **High.** Therefore, the biotope is assessed as **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

Neopentadactyla mixta lives in the sediment is a 'U-shaped' posture with its oral tentacles raised above the surface and its anus just below the surface of the sediment (Smith & Keegan, 1985). It is usually found in this position in its burrow 15-25 cm deep in the sediment (Könnecker & Keegan, 1973). However, in the winter months (ca September to March) its burrows into the sediment to a depth of 30-60 cm. It maintains this depth, even if the surface of the sediment is eroded or accreted (Smith & Keegan, 1985).

Sensitivity assessment. The tentacular crown can expand to 140 cm^2 (Smith & Keegan, 1985) and probably extends to ca 4-5 cm above the substratum (expert opinion). However, the deposit of 30 cm of fine sediment would probably discourage *Neopentadactyla mixta* from feeding and it would probably withdraw into its burrow. Fine sediment will also penetrate the surface of the sediment in the affected area, significantly reducing water flow, and increasing the possibility of anoxia within the sediment. If the smothering sediment remained, it would result in a complete shift of the community and loss of the *Neopentadactyla mixta* population. Smith & Keegan (1985) noted that a heavy gale at their study site in August caused *Neopentadactyla mixta* to withdraw deep into the sediment for six to ten days. However, in the areas of water movement in which these habitats occur it is unlikely that the smothering sediment would persist, depending on the local hydrography. As *Neopentadactyla mixta* can survive ca 6 months without feeding (Konnecker & Keegan, 1973; Smith & Keegan, 1985) it is likely that resistance is **High** and resilience is also **High.** Therefore, the biotope is assessed as **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. *Neopentadactyla mixta* is a passive suspension feeder in which small particulates stick to its mucus-covered tentacles. It seems logical that microplastics could also stick to its tentacles and be ingested, where they occur in these habitats. However, no evidence was found.

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

No evidence 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

Neopentadactyla mixta 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 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

Neopentadactyla mixta exhibits a diurnal feeding pattern. On the west coast of Ireland, individuals began to withdraw into the sediment about an hour after sunrise, and had all withdrawn within 2-3 hours and remained in the sediment for 1-2 hours before emerging again over a 4 hour period (Könnecker & Keegan, 1973). Yet Könnecker & Keegan (1973) also reported that they did not show an immediate response to strong white light. Smith & Keegan (1985) suggested that light may not be the cause of the diurnal behaviour.

Therefore, a change in incident light or shading from artificial structures may not affect feeding behaviour in *Neopentadactyla mixta*. Therefore, resistance is assessed as **High** so that resilience is also **High** and the biotope is assessed as **Not sensitive** to this pressure.

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 or propagules. But seed or propagule 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.

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 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

No evidence of the effects of non-native species in the UK was found. Grall & Hall-Spencer (2003) note that beds of invasive slipper limpet *Crepidula fornicata* grew across maerl beds in Brittany. As a result, the maerl thalli were killed, and the bed clogged with silt and pseudo-faeces, so that the associated community was drastically changed. Bivalve fishing was also rendered impossible. If overgrown by a *Crepidula* bed, the coarse sediment typical of this biotope would also suffer modification of the bed by silt and pseudo-faeces, with resultant changes in the resident community, including loss of *Neopentadactyla mixta*.

Crepidula is a potential threat to this biotope and, as recovery would require the removal of the *Crepidula* bed, is likely to result in permanent loss of the biotope. However, in the absence of any direct evidence, no assessment is made.

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

No evidence was available on the effect of microbial pathogens.

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

Scallops may be targeted in coarse sand and gravel habitats. Their removal may result in the physical effects discussed under 'abrasion' and 'penetration' pressures above. However, there are no clear relationships between the dominant important characterizing species *Neopentadactyla mixta* and other characterizing species. Therefore, a resistance of **High** is suggested so that resilience is also **High** and the biotope is assessed as **Not sensitive**.

Removal of non-target species	Medium Q: Medium A: Medium C: Medium	Medium Q: Low A: NR C: NR	Medium Q: Low A: Low C: Low

Scallops may be targeted in coarse sand and gravel habitats. Their removal may result in the physical effects discussed under 'abrasion' and 'penetration' pressures above. If the dominant important characterizing species *Neopentadactyla mixta* was removed as bycatch and its abundance reduced significantly, then the biotope would be lost. However, experimental hydraulic blade dredging removed and damaged deep-burrowing species, including small numbers of *Neopentadactyla mixta* (Hauton *et al.* 2003b), and affected a maerl bed to a depth of 9 cm. Hydraulic dredging in coarse sand and gravel may have similar effects. Due to the depth of it burrow, if only a few individual or juvenile *Neopentadactyla mixta* are vulnerable as bycatch, then a resistance of **Medium** is suggested. Resilience is likely to be **Medium** so that sensitivity is assessed as **Medium**.

Bibliography

Beukema, J.J., De Bruin, W. & Jansen, J.J.M., 1978. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea: Long-term changes during a period of mild winters. *Netherlands Journal of Sea Research*, **12**, 58-77.

Bishop, G.M. & Earll, R., 1984. Studies on the populations of *Echinus esculentus* at the St Abbs and Skomer voluntary Marine Nature Reserves. *Progress in Underwater Science*, **9**, 53-66.

Boalch, G.T., 1979. The dinoflagellate bloom on the coast of south-west England, August to September 1978. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 515-517.

Buchanan, J.B., 1967. Dispersion and demography of some infaunal echinoderm populations. *Symposia of the Zoological Society of London*, **20**, 1-11.

Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B., 2004. The Marine Habitat Classification for Britain and Ireland. Version 04.05. Joint Nature Conservation Committee, Peterborough. www.jncc.gov.uk/MarineHabitatClassification.

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.

Diaz, R.J. & Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.

Eckman, J.E., Nowell, A.R.M. & Jumars, P.A., 1981. Sediment destabilization of animal tubes. *Journal of Marine Research*, **39**, 361-374.

Faubel, A., Hartig, E. & Thiel, H., 1983. On the ecology of the benthos of sublittoral sediments, Fladen Ground, North Sea. 1. Meiofauna standing stock and estimation of production. *Meteor Forschungsergebnisse*, **36**, 35-48.

Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore.* Cambridge: Cambridge University Press.

Forster, G.R., 1979. Mortality of the bottom fauna and fish in St Austell Bay and neighbouring areas. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 517-520.

Gage, J.D., 1990. Skeletal growth bands in brittle stars: Microstructure and significance as age markers. *Journal of the Marine Biological Association of the United Kingdom*, **70**, 209-224.

Gosselin, L.A. & Qian, P., 1997. Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series*, **146**, 265-282.

Grall J. & Hall-Spencer J.M. 2003. Problems facing maerl conservation in Brittany. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, S55-S64.

Griffiths, A.B., Dennis, R. & Potts, G.W., 1979. Mortality associated with a phytoplankton bloom off Penzance in Mount's Bay. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 515-528.

Hall-Spencer, J.M. & Atkinson, R.J.A., 1999. *Upogebia deltaura* (Crustacea: Thalassinidea) in Clyde Sea maerl beds, Scotland. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 871-880.

Hall-Spencer, J.M. & Moore, P.G., 2000a. Impact of scallop dredging on maerl grounds. In *Effects of fishing on non-target species and habitats.* (ed. M.J. Kaiser & S.J., de Groot) 105-117. Oxford: Blackwell Science.

Hall-Spencer, J.M. & Moore, P.G., 2000b. *Limaria hians* (Mollusca: Limacea): A neglected reef-forming keystone species. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **10**, 267-278.

Hauton, C., Hall-Spencer, J.M. & Moore, P.G., 2003. An experimental study of the ecological impacts of hydraulic bivalve dredging on maerl. *ICES Journal of Marine Science*, **60**, 381-392.

Heuers, J., 1998. Ansiedlung, Dispersion, Rekrutierung und Störungen als strukturierende Faktoren benthischer Gemeinschaften im Eulitoral. Dissertation, Universität Bonn.

Heuers, J., Jaklin, S., Zülkhe, R., Dittmann, S., Günther, C-P., Hildenbrandt, H. & Grimm, V., 1998. A model on the distribution and abundance of the tube-building polychaete *Lanice conchilega* (Pallas, 1766) in the intertidal of the Wadden Sea. *Verhandlungen Ges Ökologie*, **28**, 207-215.

Keegan, B.F., O'Connor, B.D.S. & Könnecker, G.F., 1985. Littoral and benthic investigations on the west coast of Ireland - XX. Echinoderm aggregations. *Proceedings of the Royal Irish Academy. Section B- Biological, Geological and Chemical Science*, **85B**(7), 91-99.

Kessler, M., 1963. Die Entwicklung von *Lanice conchilega* (Pallas) mit besonderer Berücksichtigung der Lebensweise. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **8**, 425-476.

Konnecker, G. & Keegan, B.F., 1973. In situ behavioural studies on echinoderm aggregations. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **24**, 157-162.

Kuhl, H., 1972. Hydrography and biology of the Elbe Estuary. *Oceanography and Marine Biology: an Annual Review*, **10**, 225-309.

Lawrence, J.M., 1996. Mass mortality of echinoderms from abiotic factors. In *Echinoderm Studies Vol. 5* (ed. M. Jangoux & J.M. Lawrence), pp. 103-137. Rotterdam: A.A. Balkema.

Nichols, D., 1984. An investigation of the population dynamics of the common edible sea urchin (*Echinus esculentus* L.) in relation to species conservation management. *Report to Department of the Environment and Nature Conservancy Council from the Department of Biological Sciences, University of Exeter*.

OBIS, 2016. Ocean Biogeographic Information System (OBIS). http://www.iobis.org, 2016-03-15

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.

Roberts, D.A., Johnston, E.L. & Knott, N.A., 2010b. Impacts of desalination plant discharges on the marine environment: A critical review of published studies. *Water Research*, **44** (18), 5117-5128.

Russell, M., 2013. Echinoderm Responses to Variation in Salinity. *Advances in Marine Biology*, **66**, 171-212.

Schories, D. & Reise, K., 1993. Germination and anchorage of *Enteromorpha* spp. In sediments of the Wadden Sea. *Helgolander Meeresuntersuchungen*, **47**, 275-285.

Smith T.B. & Keegan, B.F., 1985. Seasonal torpor in *Neopentadactyla mixta* (Ostergren) (Holothuroidea: Dendrochirotida). In *Echinodermata. Proceedings of the Fifth International Echinoderm Conference. Galway, 24-29 September 1984.* (B.F. Keegan & B.D.S O'Connor, pp. 459-464. Rotterdam: A.A. Balkema.

Smith, T.B., 1981. Feeding and aspects of the nutritional biology of the dendrochirote holothurian *Neopentadactyla mixta* (Ostergren, 1898) and the ectoparasitic gastropod *Melanella alba* Bowdich (1822). Ph.D. Thesis, National University of Ireland, Ireland.

Smith, T.B., 1983. Tentacular ultrastructure and feeding behaviour of *Neopentadactyla mixta* (Holothuroidea: Dendrochirota). *Journal of the Marine Biological Association of the United Kingdom*, **63**, 301-311.

Southward, E.C. & Campbell, A.C., 2006. *Echinoderms.* The Linnean Society of London. Avon: The Bath Press. [Synopses of the British Fauna No. 56.]

Tyler, P.A., 1977a. Seasonal variation and ecology of gametogenesis in the genus *Ophiura* (Ophiuroidea: Echinodermata) from the Bristol Channel. *Journal of Experimental Marine Biology and Ecology*, **30**, 185-197.

Wood, E.M., 1987. *Subtidal Ecology*. London: Edward Arnold.

Woodin, S.A., 1978. Refuges, disturbance and community structure: a marine soft bottom example. *Ecology*, **59**, 274-284.

Zühlke, R., Blome, D., van Bernem, K.H. & Dittmann, S., 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. *Senckenbergiana Maritima*, **29**, 131-138.