



MarLIN

Marine Information Network

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

Ragworm (*Hediste diversicolor*)

MarLIN – Marine Life Information Network
Biology and Sensitivity Key Information Review

Georgina Budd

2008-05-08

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/species/detail/1426>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Budd, G.C. 2008. *Hediste diversicolor* Ragworm. 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/marlin.sp.1426.1>



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

(page left blank)



Hediste diversicolor at Wembury Point, Devon.
 Photographer: Fiona Crouch
 Copyright: Fiona Crouch

See online review for
 distribution map

Distribution data supplied by the Ocean
 Biogeographic Information System (OBIS). To
 interrogate UK data visit the NBN Atlas.

Researched by Georgina Budd

Refereed by Mike Kendall

Authority (O.F. Müller, 1776)

**Other common
 names** -

Synonyms *Nereis diversicolor* (O.F.
 Müller, 1776), *Nereis*
(Hediste) diversicolor (O.F.
 Müller, 1776)

Summary

🔍 Description

Hediste diversicolor is one of the commonest intertidal polychaetes in estuaries. Its body appears flattened with a prominent dorsal blood vessel. Adults may reach 6-12 cm in length and consist of between 90-120 chaetae bearing segments (chaetigers). Appendages on the head are conspicuous consisting of two antennae, and two palps, and four pairs of tentacles. The paired parapodia have dorsal and ventral chaetae and are used for crawling and swimming. The colour of *Hediste diversicolor* varies. Mature worms become a brighter green approaching and during spawning, otherwise specimens appear to be a reddish orange or brown. There has been considerable controversy over the name to be applied to this species and *Nereis diversicolor* is used by many authors.

📍 Recorded distribution in Britain and Ireland

Widespread along all British coasts where suitable habitat and substratum exist.

📍 Global distribution

Hediste diversicolor is widely distributed throughout north-west Europe on the Baltic Sea, North

Sea and along Atlantic coasts to the Mediterranean.

Habitat

Inhabits muddy substrata in a more-or-less permanent U or J-shaped burrow that may be up to 20 cm in depth. Also occurs under stones on mud where the burrow is adjacent to the stone. *Hediste diversicolor* is widespread in brackish water environments throughout north-west Europe.

↓ Depth range

Intertidal

🔍 Identifying features

- Head (prostonium) has four small eyes, two short antennae and two large biarticulate palps.
- Eversible pharynx with small conical chitinous teeth (paragnaths) on the proboscis.
- Four pairs of tentacular cirri, the dorsal cirri being longer than the ventral cirri.
- The neuropodial acicular ligules on the first two chaetigers have a finger-like post chaetal lobe.
- Cirri are much shorter than ligules on biramous parapodia.
- Notochaetae are long and taper to a fine point (homogomph spinigers) on biramous parapodia whilst neurochaetae may be long and tapering (homogomph and heterogomph spinigers) or have short blades with a hooked tip (heterogomph falcigers).
- In posterior chaetigers (about 40 in large animals), single stout falcigers replace heterogomph falcigers above the aciculum in neuropodia.
- Colour varies (see general biology) but mainly green or reddish.
- Prominent dorsal blood vessel.
- Inhabits mucous burrow.

Additional information

The form and distribution of paragnaths on the pharynx can be very useful in identification and Kinberg (1866, cited in Chambers & Garwood, 1992) assigned roman numerals to eight different areas of the pharynx that bear paragnaths. However, the number of paragnaths can vary considerably both within and between populations and this variation is thought to be a result of habitat and feeding preferences (Barnes & Head, 1977).

See Chambers & Garwood (1992) for further description and detail on identification.

✓ Listed by

Further information sources

Search on:

  

Biology review

☰ Taxonomy

Phylum	Annelida	Segmented worms e.g. ragworms, tubeworms, fanworms and spoon worms
Class	Polychaeta	Bristleworms, e.g. ragworms, scaleworms, paddleworms, fanworms, tubeworms and spoon worms
Order	Phyllodocida	
Family	Nereididae	
Genus	Hediste	
Authority	(O.F. Müller, 1776)	
Recent Synonyms	Nereis diversicolor (O.F. Müller, 1776) Nereis (Hediste) diversicolor (O.F. Müller, 1776)	

🌿 Biology

Typical abundance	High density
Male size range	60-120mm
Male size at maturity	60-70mm
Female size range	60-70mm
Female size at maturity	
Growth form	Vermiform segmented
Growth rate	
Body flexibility	High (greater than 45 degrees)
Mobility	
Characteristic feeding method	Non-feeding, Passive suspension feeder, Scavenger, Sub-surface deposit feeder, Surface deposit feeder
Diet/food source	
Typically feeds on	Mud, sand & detritus. Phytoplankton & plankton. Other macrofauna.
Sociability	
Environmental position	Infaunal
Dependency	Independent.
Supports	None
Is the species harmful?	No

🏛️ Biology information

Feeding

Hediste diversicolor is omnivorous and exhibits a diversity of feeding modes; carnivory, scavenging, filter feeding on suspended particles and deposit-feeding on materials in and on the surface layers of the sediment (Barnes, 1994). *Hediste diversicolor* feeds using an eversible pharynx and the sensory appendages on the head, namely palps and tentacles (M. Kendall, pers. comm.). < A conspicuous difference between *Hediste diversicolor* and the closely related polychaete *Nereis virens* is the unique ability of *Hediste diversicolor* to satisfy its metabolic requirements from a diet of

phytoplankton, like a typical obligate filter-feeder (Nielsen *et al.*, 1995).

The filter feeding mechanism was described by Harley (1950). A funnel-shaped net consisting of fine mucous threads is drawn across the burrow and a water current is driven through the net by undulating body movements (Fauchald & Jumars, 1979). This is best observed in a tank (M. Kendall, pers. comm.). When sufficient particles have accumulated on the net, they are consumed along with the entire net (Fauchald & Jumars, 1979). After an interval, the net is replaced (M. Kendall, pers. comm.). Riisgård (1991) suspected that *Hediste diversicolor* is a hitherto undervalued key organism in the control of phytoplankton in shallow brackish waters. It is unknown to what extent *Hediste diversicolor* utilizes its potential to subsist on suspended food particles in nature but can be considered a suspension feeder when a sufficient number of algal cells are present in the water (Riisgård, 1991).

When deposit feeding, Esnault *et al.* (1990) recognized two main types of searching behaviour exhibited by *Hediste diversicolor*. The first involved the worm crawling on the surface of the substratum prospecting for food, catching it with its jaws and ingesting it immediately. The second type saw the worm depositing a string of mucous on either side of its body on the substrate surface. When the worm retreated back into its burrow the mucous was brought back and built it into a pellet which can be consumed there and then or stored for consumption later on (Esnault *et al.*, 1990).

Olivier *et al.* (1995) found that juvenile *Hediste diversicolor* can select detritus on the sediment surface and accumulate it in their burrow. The juveniles irrigate the burrows thereby maintaining an aerobic condition that favours the decaying process of the plant debris by stimulating bacterial growth ('gardening').

Lucas & Bertru (1997) found bacteriolytic activity in the digestive system of *Hediste diversicolor* thus highlighting the ability of this species to feed on bacteria.

Colour

The variable colours of *Hediste diversicolor* approaching maturity and during spawning (see reproduction) are due to varying proportions of green (biliverdin), orange and brown (carotenoids) pigments. The green colour of mature males and females is caused by biliverdin present in the gut wall, the epidermis and coelomic cells and is formed by the breakdown of haemoglobin in the blood. In males, the white mass of sperm in the coelom gives it a lighter green colour (Dales, 1950). In mature specimens during and after spawning, the green appearance is also enhanced by a complete extraction of carotenoids from the body wall (Dales & Kennedy, 1954).



Habitat preferences

Physiographic preferences	Ria / Voe, Estuary, Enclosed coast / Embayment
Biological zone preferences	Lower eulittoral, Lower littoral fringe, Mid eulittoral, Upper eulittoral, Upper littoral fringe
Substratum / habitat preferences	Mud, Muddy sand, Sandy mud
Tidal strength preferences	Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Extremely sheltered, Sheltered, Very sheltered
Salinity preferences	Low (<18 psu), Reduced (18-30 psu), Variable (18-40 psu)
Depth range	Intertidal

Other preferences	No text entered
Migration Pattern	Non-migratory / resident

Habitat Information

Distribution & density

Hediste diversicolor is an euryhaline species and can withstand great variances in salinity. Smith (1956) reported that, in the Tamar estuary, England, individuals of this species living at the upstream limit regularly experience salinities less than 0.5 ppt. In marine dominated habitats, *Hediste diversicolor* behaves as a brackish water animal and is found in the least saline portion of the available ground (Smith, 1956). The distribution of *Hediste diversicolor* in high salinity areas is likely to be reduced as result of competition in the form of interspecific aggressions (Kristensen, 1988). In a study focussing on the distribution of nereid polychaetes in Danish coastal waters, Kristensen (1988) found that *Hediste diversicolor* could only maintain high population densities in marginal environments when the fitness of stronger competitors such as *Nereis virens* was reduced.

In estuaries the maximum density of the *Hediste diversicolor* population normally occurs in the middle regions, with density decreasing both towards the head and mouth of the estuary. Smith (1956), found that the maximum population density of *Hediste diversicolor* in the Tamar estuary corresponded to that portion of the estuary with the greatest salinity variation. The density of worms varies between locations and throughout the reproductive cycle. Numbers of juveniles may be over 100 000 per m² (Clay, 1967(c)). In the Ythan Estuary, Scotland, the density of adult *Hediste diversicolor* was reported to be 961 per m² (Chambers & Milne, 1975).

Burrows

The entrance to the burrows of *Hediste diversicolor* are 1-2 mm wide in soft mud and are best seen when a fork is inserted into the sediment and the handle pulled towards the user (M. Kendall, pers. comm.). Short shallow depressions radiate from the opening: these are made by the anterior part of the worm's body as it searches for food around it's hole, with the tail firmly anchored within the burrow. Burrow depth increases with body size (Esselink & Zwarts, 1989).

Whilst feeding at the mud surface the worm is particularly prone to predation by wading birds and fish. The burrow is thus an important refuge in which to retreat. Esselink & Zwarts (1989) found a seasonal variation in the depth of burrows of *Hediste diversicolor*. The deepest burrows were seen in winter and it is likely that this deeper burrowing is an adaptation to escape low temperatures. Burrow depth was seen to level off at 15 cm because at this depth the worm can retreat from the reach of most deep-probing predators including curlews and oyster catchers.

The individual burrow is a well-delimited territory but this territoriality is not extended outside the burrow (Scaps, 2002).

Life history

Adult characteristics

Reproductive type	Gonochoristic (dioecious)
Reproductive frequency	Semelparous / monotelously
Fecundity (number of eggs)	1,000-10,000
Generation time	1-2 years
Age at maturity	See additional text

Season	Spring - See additional text
Life span	See additional information

Larval characteristics

Larval/propagule type	-
Larval/juvenile development	Oviparous
Duration of larval stage	Not relevant
Larval dispersal potential	0 - 10 km
Larval settlement period	Not relevant

Life history information

Nereidae are monotelic, that is, they reproduce only once in their lifetime and then die (Olive & Garwood, 1981). *Hediste diversicolor* is gonochoristic (dioecious) and remains atokous throughout its life (Scaps, 2002).

In summer and autumn the sexes are externally indistinguishable being both reddish brown in colour. In any one population females are predominant, although to varying extent between localities (Dales, 1950; Clay, 1967 (c) and references therein). This observation led early workers to suggest parthenogenetic reproduction and hermaphroditism within *Hediste diversicolor* (Dales, 1950) but it is now acknowledged that these reproductive mechanisms are not found in *Hediste diversicolor*. *Hediste diversicolor* does not display epitoky or swarming behaviour associated with sexual reproduction like other nereid polychaetes, such as *Nereis succinea* and *Nereis virens*. The sex ratio in populations of *Hediste diversicolor* is heavily biased towards females. Olive & Garwood (1981) reported a ratio of females to males of approximately 4.6 : 1 in northeastern England.

Maturation & spawning

Colour differences between the sexes become more apparent upon maturation. Maturation and spawning are induced by a temperature rise in early spring to between 6°C and 11°C following a period of low winter temperatures. The male becomes bright green in colour. In contrast, the female appears darker green in colour which may be lacking on the ventral side. Reddish brown pigments may also still be visible in the female.

- Coelomic germ cells may be first recognizable in females that are at least 6 months old or about 7 cm in length. Eggs mature within the coelom surrounded by a loose mass of heterogenous corpuscles which the eggs gradually displace.
- Histolysis of the muscle layers and ingestion by phagocytes renders the female worm very brittle and enables the eggs to be released following rupture of the body wall, which is achieved by writhing within the burrow. In addition to a rise in temperature, the lunar cycle imposes a further synchrony on *Hediste diversicolor* so that spawning normally coincides with periods of new or full moon.
- Mature males crawl around outside in search of a mature female and discharge sperm through the nephridia, directly outside her burrow. Direct contact between the sexes is not a necessity. Pheromones are of particular use in the final stages of reproduction for co-ordinating processes such as mate location and the synchronization of gamete release and spawning at the population level. The existence of pheromones has been demonstrated in a number of polychaete species (Bentley & Pacey, 1992). Dales (1950) supposed that owing to the low numbers of males in populations of *Hediste diversicolor* there may be some chemical signal detectable to the opposite sex. The observations of

Bartels-Hardege & Zeeck (1990) support this supposition for the presence of chemical signals or sex pheromones, as males only released sperm outside burrows occupied by mature females.

- A period of increased activity follows the release of sperm, as the female and others in surrounding burrows, perform intense ventilation movements to draw sperm into their burrow. They may also carry sperm into the burrow using the proboscis in a feeding like manner. Fertilized eggs remain inside the burrow protected by the female. Both sexes die shortly after spawning.

Environmental factors

Bartels-Hardege & Zeeck (1990) induced spawning in the laboratory, in specimens of *Hediste diversicolor* from tidal flats of the Jadebusen (North Sea), outside the normal spawning period of early spring. Temperatures were not lowered to simulate winter conditions but maintained at 16°C. Mature specimens appeared after four weeks and released gametes after a further four weeks according to a semilunar cycle. Reproduction was sustained for a period of four months. Such an extended spawning was witnessed on the Jadebusen following an unusually warm winter. Spawning occurred from February until May and was less synchronized. In contrast, the same population spawned within two months (February - March) following lower winter temperatures in another year. They concluded that not only a threshold temperature was important for synchronized spawning but the timing of the rise in temperature following winter was also a significant factor (Bartels-Hardege & Zeeck, 1990).

Age at maturity

Generally *Hediste diversicolor* is reported to reach maturity between one and three years of age. Populations appear to show local characteristics in terms of spawning periods. Spawning may be limited to a short period in spring or extend over the summer. In the Thames Estuary, Dales (1950) reported specimens growing to maturity within one year, spawning in February, with some individuals surviving up to 18 months. Mettam *et al.* (1982), reported that *Hediste diversicolor* from the Severn Estuary matured rapidly in the spring and spawned at two years old. Olive & Garwood (1981), found that females in the Blyth Estuary, Northumberland, were in their second year before eggs began to appear, so most probably spawned in their third year. However, these authors also reported that spermatogenesis was only found to take about six months in the Blyth. They therefore suggested that there is a variable age at maturity and that this could have arisen either because the population were polymorphic in terms of their genetically determined age at maturity or if the age at maturity was variable and influenced by the environmental conditions (Olive & Garwood, 1981). Golding & Yuwono (1994) showed that, although full maturation of the gametes occurred, spawning was blocked by implanting cerebral ganglia from immature donors into the body cavity of adult hosts.

In the Ythan Estuary, Scotland, Chambers & Milne (1975) witnessed two spawning peaks in the population of *Hediste diversicolor*, the first occurring between January and March, and another between June and August.

Sensitivity review

This MarLIN sensitivity assessment has been superseded by the MarESA approach to sensitivity assessment. MarLIN assessments used an approach that has now been modified to reflect the most recent conservation imperatives and terminology and are due to be updated by 2016/17.

A Physical Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
Substratum Loss	High	High	Moderate	Low
<p><i>Hediste diversicolor</i> is infaunal and is reliant upon a muddy / sandy sediment in which to burrow. Physical removal of the substratum e.g. as a result of channel dredging activities would remove with it the entire associated population of <i>Hediste diversicolor</i>. The ability of postlarvae and larger juveniles and adults of <i>Hediste diversicolor</i> to swim, burrow and be carried by bedload transport can aid the rapid recolonization of disturbed sediments (Shull, 1997). Davey & George (1986), found evidence that larvae of <i>Hediste diversicolor</i> were tidally dispersed within the Tamar Estuary over a distance of 3 km and well away from areas of dense adult populations. However, this dispersal may not always lead the larvae to a favourable area and it is likely that there will be some loss.</p>				
Smothering	Low	Immediate	Not sensitive	Moderate
<p><i>Hediste diversicolor</i> inhabits depositional environments. It is capable of burrowing to depths of up to 0.3 m and reworking sub-surface modifications of its burrow through fine clays and sand. Smith (1955) found no appreciable difference in the population of a <i>Hediste diversicolor</i> colony which had been covered by several inches of sand through which the worms tunneled. It would not be adversely affected by smothering with additional sediments. However, smothering with impermeable materials would prevent <i>Hediste diversicolor</i> clearing the burrow to the sediment surface and prevent feeding. Larvae are more intolerant than adults as they are still acquiring the physical ability to burrow (see larval sensitivity).</p>				
Increase in suspended sediment	Tolerant*	Not relevant	Not sensitive*	Low
<p>Increased siltation maybe beneficial to feeding. As a surface-deposit feeder and suspension feeder <i>Hediste diversicolor</i> will be able to utilize suspended matter as a food resource. Increased deposition of silt onto the mudflats can raise the height of the mudflats and therefore increasing the exposure time of infaunal communities at low tide (Jones <i>et al.</i>, 2000). At the benchmark level however, this is unlikely to have an adverse effect on <i>Hediste diversicolor</i>.</p>				
Decrease in suspended sediment				
Desiccation	Low	High	Low	Low
<p><i>Hediste diversicolor</i> inhabits a burrow within the sediment which may be up to 0.3m deep. The species retreats within the burrow during periods of exposure and thus away from the desiccating factors of sunlight and wind. Residual surface and interstitial water prevent the burrow and thus <i>Hediste diversicolor</i> from drying. Therefore <i>Hediste diversicolor</i> is largely able to avoid desiccation. Specimens found at the upper limits in the intertidal zone may become stressed by desiccation if the substratum begins to dry, but <i>Hediste diversicolor</i> is sufficiently mobile to retreat back to damper substrata . Consequently this species is considered to have a low intolerance to the benchmark change in desiccating factors.</p>				

Increase in emergence regime

Low

High

Low

Low

Hediste diversicolor inhabits a burrow within the sediment which may be up to 0.3m deep. The species retreats within the burrow during periods of exposure and thus away from desiccating factors of sunlight and wind. Thus *Hediste diversicolor* can avoid some detrimental aspects of emergence (see desiccation). However, whilst in retreat within the burrow during extended periods of emergence, the ragworm is prevented from actively feeding at the surface and is likely to be prone to more intense predation pressure from wading birds as they have longer to search the mudflats. An increased emergence regime is also likely to cause a decline in the abundance of ragworms at the upper limits of the intertidal zone, as they may become stressed by desiccation if the substrata begin to dry and are prone to more extremes of temperature, but *Hediste diversicolor* is sufficiently mobile to gradually retreat back to damper substrata. Consequently, this species is considered to have a low intolerance to the benchmark change in emergence.

Decrease in emergence regime**Increase in water flow rate**

Intermediate

High

Low

Low

Hediste diversicolor characteristically inhabits littoral mudflats predominantly of clay (particles < 4 µm), silt (4-63 µm) and to a lesser extent very fine sand (63-125 µm) (Jones *et al.*, 2000). The type direction and speed of the currents control sediment deposition within an area. A change in two categories in water flow rate from weak and negligible to moderately strong and strong would entrain and maintain particles in suspension and erode the mud. As a result the scouring and consequent redistribution of components of the substratum would alter the extent of suitable habitat available to populations of *Hediste diversicolor*. Recovery of this species would be influenced by the length of time it would take for the potential habitat to return to a suitable state for recolonization by adult and juvenile specimens from adjacent habitats, and the establishment of a breeding population. This may take between one and three years, as populations differ in reaching maturity (Dales, 1950; Mettam *et al.*, 1982; Olive & Garwood, 1981), from the time that the habitat again becomes suited to the species.

Decrease in water flow rate**Increase in temperature**

Intermediate

High

Low

Moderate

The geographic range of *Hediste diversicolor* (see adult distribution) suggests that it is tolerant of a range of temperatures and a long term chronic temperature increase or decrease is unlikely to have an adverse effect on UK populations. *Hediste diversicolor* can tolerate temperatures from below zero under Baltic ice to high summer temperatures in Black Sea lagoons (Smith, 1977).

A decrease in temperature has been shown to be beneficial to *Hediste diversicolor* through reduction in numbers of their predators. A severe winter in the Wadden Sea in 1995/1996 saw an increased abundance of this species coinciding with a reduction in the numbers of *Carcinus maenus* and *Crangon crangon* (Armonies *et al.*, 2001). A similar increase in abundance was noted in the same area between 1978 and 1987 after a series of cold winters: mean density increased from 24 / m² to 151 / m² respectively (Beukema, 1990).

Species dwelling in the sediments are likely to be protected from direct effects of temperature change at the surface, for instance *Hediste diversicolor* burrows deeper in very cold and frosty weather (Linke, 1939). In addition, insensitivity to temperature change is limited by the insulating properties of the mud in which it lives (M. Kendall, pers. comm.).

Temperature change may adversely affect reproduction. Bartels-Hardege & Zeeck (1990) demonstrated that an increase from 12°C and maintenance of water temperature at 16°C

induced reproduction in specimens outside the normal period of spawning (see reproduction), and without a drop in temperature to simulate winter conditions the spawning period was prolonged and release of gametes was not synchronized. Poor synchronization of spawning could result in reduced recruitment, as gametes are wasted and mature specimens die shortly after gamete release. Therefore, an intolerance of intermediate has been recorded.

Decrease in temperature

Increase in turbidity Tolerant Immediate Not sensitive Low

Hediste diversicolor characteristically inhabits estuaries where turbidity is typically higher than other coastal waters. Changes in the turbidity may influence the abundance of phytoplankton available as a food source that may be attained through filter feeding. However, *Hediste diversicolor* utilizes various other feeding mechanisms and, at the benchmark level, the likely effects of a change in turbidity are limited.

Decrease in turbidity

Increase in wave exposure Intermediate High Low Low

Hediste diversicolor is infaunal, inhabiting a burrow in which it seeks refuge from predators and may partially emerge to seek and capture food. In addition, it inhabits low energy depositional environments. An alteration of factors within the environment that increases wave exposure is likely to cause erosion of the substrata and consequently, loss of habitat.

Recovery would be influenced by the length of time it would take for the habitat to return to a suitable state for recolonization by adult and juvenile specimens from adjacent habitats, and the establishment of a breeding population. This may take between one and three years, as populations differ in reaching maturity (Dales, 1950; Mettam *et al.*, 1982; Olive & Garwood, 1981), from the time that the habitat again becomes suited to the species.

Decrease in wave exposure

Noise Tolerant* Not relevant Not sensitive* Low

Hediste diversicolor may be able to detect some noise vibration but is not known to exhibit a significant response at the benchmark levels. However, wildfowl which prey upon estuarine infauna such as *Hediste diversicolor* are known to be disturbed by noise, consequently predation pressure upon *Hediste diversicolor* may be reduced for the length of time that the disturbance continues.

Visual Presence Tolerant Not relevant Not sensitive High

Hediste diversicolor demonstrates a distinct movement towards darkness (skototaxis) and it has been shown that feeding sensitizes the worm to light and influences their response to a sudden increase in illumination (Herter, 1926; Evans, 1966, in Clay 1967(c)). Otherwise, *Hediste diversicolor* lacks the visual ability to be affected by the visual presence of moving objects not normally found in the marine environment.

Abrasion & physical disturbance Intermediate High Low Low

The body of *Hediste diversicolor* may be physically damaged by mechanical interference as it has a fragile hydrostatic skeleton. Mechanical interference within the substratum, such as that caused by the dropping and dragging of an anchor or fishing gear, could physically damage ragworms within the path of the anchor and cause their displacement. Physical injury and displacement would hinder the ability of a ragworm to burrow rapidly back into the sediment to seek refuge from predation.

Regeneration of the lost body is often observed (M. Kendall, pers. comm.) however it is likely that some individuals may die and an intolerance of intermediate has been recorded.

Displacement Intermediate Immediate Very Low Low

Displacement from within the sediment to be left upon the sediment surface would increase the risk of *Hediste diversicolor* to predation but as a mobile burrowing species it is able to burrow rapidly back into the sediment and seek refuge. However, this is only possible if the animal is near its own burrow on a suitable substratum (M. Kendall, pers. comm.). The burrows of other worms are well defended through territorial behaviour.

Chemical Pressures

Synthetic compound contamination Intolerance High Recoverability Moderate Sensitivity Moderate Confidence High

Reports of the effects of synthetic chemicals on *Hediste diversicolor* illustrate that the intolerance of the species is highly dependent upon the molecular structure of the chemical, which determines the chemicals properties and use. For example:

1. Collier & Pinn (1998) observed significant differences in both the abundance and biomass of a benthic community from the Ythan Estuary, Scotland, experiencing contamination by Ivermectin. Ivermectin is the 22,23-dihydro derivative of avermectin β which has been shown to be highly efficient in the treatment of sea lice. *Hediste diversicolor* was the most intolerant species to Ivermectin in the benthic community studied. A rapid decline in both abundance and total biomass of *Hediste diversicolor* occurred within 7 days and with increasing concentration. An Ivermectin concentration of 8.0 mg m⁻³ caused 100% mortality within 14 days. Davies *et al.*, (1998) modelled factors influencing the concentration of Ivermectin reaching the seabed which ranged from 2.2 to 6.6 mg m⁻³. The upper limit of this range was only slightly less than the concentrations found to be toxic by Collier & Pinn (1998) and Black *et al.* (1997). Davies *et al.* (1998) concluded that there was a significant risk to benthic organisms within a radius of 50 m of salmon farms utilizing Ivermectin and that Ivermectin could accumulate (half life of Ivermectin in marine sediments > 100 days) within the sediment beyond a single treatment and reach toxic levels.
2. In contrast, Craig & Caunter (1990) examined the effects of the organosilicon compound, Polydimethylsiloxane (PDMS) in sediment on *Hediste diversicolor*. PDMS fluids are less dense than water and insoluble and form a discrete layer on the surface of the water. In an intertidal environment PDMS fluids are deposited upon the sediment surface at low tide and into contact with *Hediste diversicolor*. In laboratory tests, exposure to 10,000 mg PDMS per kg of sediment caused no deaths over 96 hours, and exposure to 1,000 mg PDMS per kg of sediment caused no deaths of *Hediste diversicolor* after 28 days.

Recovery of this species would be influenced by the length of time it would take for the potential habitat to return to a suitable state (e.g. factors such as the rate of decay of the synthetic chemical within the marine environment), recolonization by adult and juvenile specimens from adjacent habitats, and the establishment of a breeding population. This may take between one and three years, as populations differ in reaching maturity (Dales, 1950; Mettam *et al.*, 1982; Olive & Garwood, 1981), from the time that the habitat again becomes suited to the species.

Heavy metal contamination Intermediate Moderate Moderate High

Bryan (1984) reviewed metals in the marine environment and from the evidence available suggested that polychaetes were fairly resistant to heavy metals.

In *Hediste diversicolor* the acute toxicity is dependent on the rate of uptake of the metal, since this determines the speed with which the lethal dose is built up. The rate of intake is important because this determines whether the organism's detoxification mechanisms can regulate internal concentrations. The resistance of *Hediste diversicolor* is thought to be dependent on a complexing system which detoxifies the metal and stores it in the epidermis and nephridia (Bryan & Hummerstone, 1971; McLusky *et al.* 1986).

Hediste diversicolor has been found successfully living in estuarine sediments contaminated with copper ranging from 20 $\mu\text{m Cu/g}$ in low copper areas to $>4000 \mu\text{m Cu/g}$ where mining pollution is encountered e.g. Restronguet Creek, Fal Estuary, Cornwall (Bryan & Hummerstone, 1971). Attempts to change the tolerance of different populations of *Hediste diversicolor* to different sediment concentrations of copper have shown that it is not readily achieved suggesting that increased tolerance to copper has a genetic basis (Bryan & Hummerstone, 1971; Bryan & Gibbs, 1983).

Crompton (1997) reviewed the toxic effect concentrations of metals to marine invertebrates (see Table 5.12, Crompton, 1997). Annelid species, such as *Hediste diversicolor* were found to be at risk if metals exceeded the following concentrations during 4-14 days of exposure: $>0.1 \text{ mg Hg l}^{-1}$, $> 0.01 \text{ mg Cu l}^{-1}$, $> 1 \text{ mg Cd l}^{-1}$, $>1 \text{ mg Zn l}^{-1}$, $>0.1 \text{ mg Pb l}^{-1}$, $>1 \text{ mg Cr l}^{-1}$, $>1 \text{ mg As l}^{-1}$ and $>10 \text{ mg Ni l}^{-1}$.

In general, for estuarine animals heavy metal toxicity increases as salinity decreases and temperature increases (McLusky *et al.*, 1986). For example, Fernandez & Jones (1990) calculated 96 hour LC_{50} Zinc values for *Hediste diversicolor* at four salinities 5, 10, 17.5 and 30 psu at 12°C. The 96 hour LC_{50} at 17.5 psu and 12°C was 38 mg Zn l^{-1} , while at 5 and 10 psu it was 7 and 19 mg Zn l^{-1} respectively. Toxicity decreased with increasing salinity. When salinity remained constant at 17.5 psu, but temperature varied, the following 96 hour LC_{50} values for Zinc were recorded: 40 mg Zn l^{-1} at 6°C, 32 mg Zn l^{-1} at 12°C and 9.1 mg Zn l^{-1} at 20°C. Toxicity increased with increasing temperature. Accumulation of zinc was also greater at the lowest salinities and when the temperature was highest at 20°C. In a parallel experiment, the presence of sediment was found to reduce toxicity and body accumulation of zinc in *Hediste diversicolor*.

Recovery of this species would be influenced by the length of time it would take for the potential habitat to return to a suitable state (e.g. factors such as the decline of bioavailable metals within the marine environment), recolonization by adult and juvenile specimens from adjacent habitats, and the establishment of a breeding population. Since juveniles remain in the infauna throughout their development selection for metal tolerance can be expected to be operative from an early stage (Bryan & Gibbs, 1983).

Hydrocarbon contamination

Intermediate

High

Low

Moderate

The 1969 West Falmouth (America) spill of Grade 2 diesel fuel documents the effects of hydrocarbons in a sheltered habitat (Suchanek, 1993). The entire benthic fauna including *Hediste diversicolor* was eradicated immediately following the spill and remobilization of oil that continued for a period > 1 year after the spill, contributed to much greater impact upon the habitat than that caused by the initial spill. Effects are likely to be prolonged as hydrocarbons incorporated within the sediment by bioturbation will remain for a long time owing to slow degradation under anoxic conditions. Oil covering the surface and within the sediment will prevent oxygen transport to the infauna and promote anoxia as the infauna utilize oxygen during respiration. Although *Hediste diversicolor* is tolerant of hypoxia and

periods of anoxia, a prolonged absence of oxygen will result in the death of it and other infauna. McLusky (1982) found that petrochemical effluents released from a point source to an estuarine intertidal mudflat, caused severe pollution in the immediate vicinity. Beyond 500 m distance the effluent contributed to an enrichment of the fauna in terms of abundance and biomass similar to that reported by Pearson & Rosenberg (1978) for organic pollution, and *Hediste diversicolor* was found amongst an impoverished fauna at 250 m from the discharge.

Radionuclide contamination

Not relevant

Beasley & Fowler (1976) and Germain *et al.*, (1984) examined the accumulation and transfers of radionuclides in *Hediste diversicolor* from sediments contaminated with americium and plutonium derived from nuclear weapons testing and the release of liquid effluent from a nuclear processing plant. Both concluded that the uptake of radionuclides by *Hediste diversicolor* was small. Beasley & Fowler (1976) found that *Hediste diversicolor* accumulated only 0.05% of the concentration of radionuclides found in the sediment. Both also considered that the predominant contamination pathway for *Hediste diversicolor* was from the interstitial water. However, there is insufficient information available on the biological effects of radionuclides to comment further upon the intolerance of this species to radionuclide contamination.

Changes in nutrient levels

Tolerant*

High

Not sensitive*

Moderate

Nutrient enrichment favours the growth of opportunistic green macro-algae blooms which can cause declines in some species and increases in others (Raffaelli, 2000). Evidence (Beukema, 1989; Reise *et al.*, 1989; Jensen, 1992) suggested a doubling in the abundance of *Hediste diversicolor* in the Dutch Wadden Sea, accompanied by a more frequent occurrence of algal blooms that were attributed to marine eutrophication. Algae may be utilized by *Hediste diversicolor* in its omnivorous diet, so some effects of nutrient enrichment may be beneficial to this species.

Increase in salinity

Low

High

Low

Low

Hediste diversicolor is an euryhaline species, able to tolerate a range of salinities from full sea water down to 5 psu or less (Barnes, 1994). Consequently a change of one category from the MNCR salinity scale (see benchmark) for a duration of one year would not be restrictive to adults of *Hediste diversicolor*. Specimens already at the extreme ends of their salinity tolerance would be more intolerant of a short term change of two categories on the MNCR salinity scale but are sufficiently mobile to retreat to more hospitable conditions. Low salinities (< 8 psu) can have an adverse effect on reproduction (Ozoh & Jones, 1990; Smith 1964) (see larval sensitivity).

Decrease in salinity

Changes in oxygenation

Intermediate

High

Low

High

The littoral muds and muddy sands which *Hediste diversicolor* inhabits tend to have lower oxygen levels than other sediments. *Hediste diversicolor* is resistant to moderate hypoxia (Diaz & Rosenberg, 1995). The successful survival of this species under prolonged hypoxia was confirmed by the resistance experiments of Vismann (1990), which resulted in a mortality of only 15% during a 22 day exposure of *Hediste diversicolor* at 10% oxygen (ca. 2.8 mg O₂ per litre). *Hediste diversicolor* is active at the sediment/water interface where hydrogen sulphide concentrations increase during periods of hypoxia. Vismann (1990), also demonstrated that the high tolerance of *Hediste diversicolor* to hypoxia in the presence of sulphide is enabled by elevated sulphide oxidation activity in the blood. *Hediste diversicolor* may also exhibit a behavioural response to hypoxia by leaving the sediment (Vismann, 1990) which is enhanced

in the presence of sulphide. After 10 days of hypoxia (10% oxygen saturation) with sulphide (172-187 μM) only 35% of *Hediste diversicolor* had left the sediment compared to 100% of *Nereis virens*. Laboratory experiments in the absence of sediments, found that *Hediste diversicolor* could survive hypoxia for more than 5 days and that it had a higher tolerance to hypoxia than *Nereis virens*, *Nereis succinea* and *Nereis pelagica* (Theede, 1973; Dries & Theede, 1974; Theede *et al.*, 1973).

Biological Pressures

Intolerance Recoverability Sensitivity Confidence

Introduction of microbial pathogens/parasites

Not relevant

Insufficient information.

Introduction of non-native species

Not relevant

Insufficient information.

Extraction of this species

Intermediate High Low Low

Populations of *Hediste diversicolor* are dominated by females, males may constitute up to 40% of the population but several reports suggest that the proportion of males is frequently lower (< 20%) (see Clay, 1967(c.)). The sexes are externally indistinguishable except when approaching maturation and during spawning (see reproduction and adult general biology). Consequently extraction e.g. by bait digging, of 50% of the specimens from within an area is likely to remove more females than males. A reduction in the female proportion of the population prior to spawning could reduce recruitment to the population. The mechanical action of the digging, even if the worms were not actually taken, may also cause some damage to the bodies. Recovery is dependent on the reproductive success and survival of the remaining population and colonization by adults from unaffected areas.

Extraction of other species

Intermediate High Low Moderate

Many species in addition to *Hediste diversicolor* are taken from the intertidal environment for personal or commercial use as fishing bait. Techniques for extraction include hand digging, bait pumping and worm dredging (Fowler, 1999). Heiligenberg (1987) reported upon the effects of both hand and mechanical digging in the Dutch Wadden Sea. Hand and mechanical digging operating at a level to achieve a 50% reduction in *Arenicola marina*, caused a significant reduction in many of the common species, including *Hediste diversicolor*. A total of 1.9 g of other benthic animals were removed for every 1 g of *Arenicola marina*.

Mechanical disturbance of the substrata will also displace *Hediste diversicolor* causing specimens to be susceptible to predation (see abrasion & displacement).

Recovery is dependent on the reproductive success and dispersion of the remaining population and colonization by adults from unaffected areas.

Additional information

Chemical factors

Determining the concentration of metals to which *Hediste diversicolor* is exposed is not easy. Differences in the substratum concentrations of metals indirectly reflect the differences in metal partitioning between different sediment constituents and interstitial water. In turn metal partitioning affects the bioavailability of metals to infaunal animals (Luoma & Bryan, 1982). Polychaetes such as *Hediste diversicolor* are able to absorb metals from ingested sediment as well as

from solution in the surrounding water. Often it is difficult to determine which concentration, that of the sediment or interstitial water, is more significant in terms of exposure. *Hediste diversicolor* has a diversity of feeding modes which may also influence its exposure to chemical contaminants. Its omnivorous feeding behaviour would suggest that it takes whatever food dominates in the habitat. If the dominant food source is contaminated it will be an important route of exposure (Collier & Pinn, 1998; Bryan & Hummerstone, 1971). Wang *et al.* (1999) studied the assimilation efficiencies of trace metals (Ag, Cd, Co, Se & Zn) in a marine deposit-feeding polychaete, % *Nereis succinea*%, from ingested sediments. Their bioenergetic-based kinetic model indicated that most (>98%) of the Cd, Co, Se & Zn in polychaetes arises from sediment ingestion owing to the high ingestion rates of sediment ingestion in these animals. Wang *et al.* (1999) stated that environmental quality criteria must consider sediment as a potentially important source for metal uptake in benthic invertebrates.

Importance review

🔗 Policy/legislation

- no data -

★ Status

National (GB)
importance -

Global red list
(IUCN) category -

🇳🇱 Non-native

Native -

Origin -

Date Arrived

Not relevant

🏛️ Importance information

Food source

Hediste diversicolor is an important prey item for wading birds because it is common, profitable and detectable as well as accessible (Zwarts & Esselink, 1989). Direct observation and analysis of the diet of wading birds indicates that *Hediste diversicolor* constitutes the main prey of about 15 waders and is the dominant prey for the avocet *Recurvirostra avosetta*, grey plover *Pluvialis squatarola*, curlew sandpiper *Calidris ferruginea*, bar-tailed godwit *Limosa lapponica* and curlew *Numenius arquata* (see Goss-Custard *et al.*, 1977 and other references given in Zwarts & Esselink, 1989). Several flatfish prey on the macrobenthos of intertidal mudflats. Sole, *Solea solea*; dab, *Limanda limanda*, flounder, *Platichthys flesus* and plaice, *Pleuronectes platessa*, all include *Hediste diversicolor* in their diet.

Harvesting

Hediste diversicolor may be used as bait by anglers and are often sold commercially. They are harvested using a fork to turn over the substrata and collected. *Hediste diversicolor* is also used as a food source in aquaculture (Scaps, 2002).

Community importance

Hediste diversicolor has been implicated as an infaunal species that plays a confounding role in the colonization and establishment of pioneering saltmarsh species. Hughes *et al.*, (2000) reported that *Hediste diversicolor* reduced the success of *Zostera noltei* transplantation trials in southeast England. Plants protected from *Hediste diversicolor* had a higher survival rate, lower index of root damage and greater biomass than plants unprotected from the ragworm. In the laboratory, *Hediste diversicolor* was observed to grasp the leaves of *Zostera noltei* and pull them into the burrow. Hughes *et al.*, (2000) considered that these results indicate that herbivory and disturbance by *Hediste diversicolor* was responsible, in part, for the restriction of the distribution of *Zostera noltei* and maybe an important factor in limiting the success of transplanting experiments. Similarly, Emmerson (2000) demonstrated significant negative effects of *Hediste diversicolor* abundance on the survival of *Spartina anglica* seeds transplanted to sediment cores. Emmerson (2000) stated that there is a growing body of evidence indicating the importance of bioturbating infaunal invertebrates in regulating mudflat community structure (see Nowell *et al.* 1981; Levinton, 1995) and that their influence must be considered if the coastal defence functions of replanted saltmarshes are to be realized.

Bibliography

- Armonies, W., Herre, E. & Sturm, M., 2001. Effects of the severe winter 1995 / 1996 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. *Helgoland Marine Research*, **55**, 170-175.
- Bachelet, G., 1987. *Processus de recrutement et rôle des stades juvé d'invertébrés dans le fonctionnement des systèmes benthiques de substrat meuble en milieu intertidal estuarien.*, Thèse d'état, Université Bordeaux, France.
- Barnes, R.S.K. & Head, S.M., 1977. Variation in paragnath number in some British populations of the estuarine polychaete *Nereis diversicolor*. *Estuarine and Coastal Marine Science*, **5**, 771-781.
- Barnes, R.S.K., 1994. *The brackish-water fauna of northwestern Europe*. Cambridge: Cambridge University Press.
- Bartels-Hardege, H.D. & Zeeck, E., 1990. Reproductive behaviour of *Nereis diversicolor* (Annelida: Polychaeta). *Marine Biology*, **106**, 409-412.
- Bat, L., Gündoğdu, A., Akbulut, M., Çulha, M. & Satılmış, H.H., 2001. Toxicity of zinc and lead to the polychaete *Hediste diversicolor* (Müller 1776). *Turkish Journal of Marine Science*, **7**, 71-84.
- Beasley, T.M. & Fowler, S.W., 1976. Plutonium and Americium: uptake from contaminated sediments by the polychaete *Nereis diversicolor*. *Marine Biology*, **38**, 95-100.
- Bentley, M.G. & Pacey, A.A., 1992. Physiological and environmental control of reproduction in polychaetes. *Oceanography and Marine Biology: an Annual Review*, **30**, 443-481.
- Beukema, J.J., 1990. Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In *Expected effects of climatic change on marine coastal ecosystems* (ed. J.J. Beukema, W.J. Wolff & J.J.W.M. Brouns), pp. 83-92. Dordrecht: Kluwer Academic Publ.
- Black, K.D., Fleming, S. Nickell, T.D. & Pereira, P.M.F. 1997. The effects of ivermectin, used to control sea lice on caged farmed salmonids, on infaunal polychaetes. *ICES Journal of Marine Science*, **54**, 276-279.
- Bryan, G.W. & Gibbs, P.E., 1983. *Heavy metals from the Fal estuary, Cornwall: a study of long-term contamination by mining waste and its effects on estuarine organisms*. Plymouth: Marine Biological Association of the United Kingdom. [Occasional Publication, no. 2.]
- Bryan, G.W. & Hummerstone, L.G., 1971. Adaptation of the polychaete *Nereis diversicolor* to estuarine sediments containing high concentrations of heavy metals. I. General observations and adaption to copper. *Journal of the Marine Biological Association of the United Kingdom*, **51**, 845-863.
- Bryan, G.W., 1984. Pollution due to heavy metals and their compounds. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in the Oceans and Coastal Waters*, vol. 5. *Ocean Management*, part 3, (ed. O. Kinne), pp.1289-1431. New York: John Wiley & Sons.
- Chambers, M.R. & Milne, H., 1975. Life cycle and production of *Nereis diversicolor* O.F. Müller in the Ythan estuary, Scotland. *Estuarine and Coastal Marine Science*, **3**, 133-144.
- Chambers, S.J. & Garwood, P.R., 1992. *Polychaetes from Scottish Waters. Part 3. Family Nereidae*. Edinburgh: National Museums of Scotland.
- Clay, E., 1967c. *Literature survey of the common fauna of estuaries, 1. Cirratulus cirratus* O.F. Müller. *Imperial Chemical Industries Limited, Brixham Laboratory, PVM45/A/374*.
- Collier, L.M. & Pinn, E.H., 1998. An assessment of the acute impact of the sea lice treatment Ivermectin on a benthic community. *Journal of Experimental Marine Biology and Ecology*, **230**, 131-147.
- Craig, N.C.D. & Caunter, J.E., 1990. The effects of polydimethylsiloxane (PDMS) in sediment on the polychaete worm *Nereis diversicolor*. *Chemosphere*, **21**, 751-759.
- Crompton, T.R., 1997. *Toxicants in the aqueous ecosystem*. New York: John Wiley & Sons.
- Daan, R. & Mulder, M., 1996. On the short-term and long-term impact of drilling activities in the Dutch sector of the North Sea. *ICES Journal of Marine Science*, **53**, 1036-1044.
- Dales, R. P. & Kennedy, G.Y., 1954. On the diverse colours of *Nereis diversicolor*. *Journal of the Marine Biological Association of the United Kingdom*, **33**, 699-708.
- Dales, R. P., 1950. The reproduction and larval development of *Nereis diversicolor* O. F. Müller. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 321-360.
- Dales, R.P., 1958. Survival of anaerobic periods by two intertidal polychaetes, *Arenicola marina* (L.) and *Owenia fusiformis* Delle Chiaje. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 521-529.
- Davey, J.T. & George, C.L., 1986. Specific interactions in soft sediments: factors in the distribution of *Nereis (Hediste) diversicolor* in the Tamar Estuary. *Ophelia*, **26**, 151-164.
- Davey, J.T., 1994. The architecture of the burrow of *Nereis diversicolor*. *Journal of Experimental Marine Biology and Ecology*, **179**, 155-129.
- Davies, I.M, Gillibrand, P.A., McHenry, J.G. & Rae, G.H., 1998. Environmental risk of Ivermectin to sediment dwelling organisms. *Aquaculture*, **163**, 29-46.
- 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.
- Dries, R.R. & Theede, H., 1974. Sauerstoffmangelresistenz mariner Bodenvertebraten aus der West-lichen Ostsee. *Marine Biology*, **25**, 327-233.
- Eagle, G.A., 1983. The chemistry of sandy beach ecosystems - a review. In *Sandy beaches as ecosystems* (ed. A. McLachlan & T. Erasmus), pp. 203-224. The Hague, Netherlands: Junk.
- Emmerson, M., 2000. Remedial habitat creation: does *Nereis diversicolor* play a confounding role in the colonisation and establishment of the pioneering saltmarsh plant, *Spartina anglica*? *Helgoland Marine Research*, **54**, 110-116.
- Esnault, G., Retière, C. & Lambert, R., 1990. Food resource partitioning in a population of *Nereis diversicolor* (Annelida, Polychaeta) under experimental conditions. In *Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium, Oban, United Kingdom* (ed. M. Barnes & R.N. Gibson), pp. 453-467. Aberdeen: Aberdeen University Press.
- Esselink, P. & Zwarts, L., 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Marine Ecology Progress Series*, **56**, 243-254.
- Esselink, P., Van Belkum, J. & Esselink, K., 1989. The effect of organic pollution on the local distribution of *Nereis diversicolor* and *Corophium volutator*. *Netherlands Journal of Sea Research*, **23**, 323-332.
- Everson, C., 2000. Two species of lugworm. [On-line]. <http://ourworld.compuserve.com/homepages/BMLss/lugs.htm>, 2000-10-02
- Fauchald, J. & Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: an Annual Review*, **17**, 193-284.
- Fauchald, K., 1977. *The polychaete worms. Definitions and keys to the orders, families and genera*. USA: Natural History Museum of Los Angeles County.
- Fernandez, T.V. & Jones, N.V., 1990. The influence of salinity and temperature on the toxicity of zinc to *Nereis diversicolor*. *Tropical Ecology*, **31**, 40-46.
- Fowler, S.L., 1999. Guidelines for managing the collection of bait and other shoreline animals within UK European marine sites. *Natura 2000 report prepared by the Nature Conservation Bureau Ltd. for the UK Marine SACs Project*, 132 pp., Peterborough: English Nature (UK Marine SACs Project), <http://www.english-nature.org.uk/uk-marine/reports/reports.htm>
- Germain, P., Miramand, P. & Masson, M., 1984. Experimental study of long-lived radionuclide transfers (americium, plutonium, technetium) between labelled sediments and annelidae (*Nereis diversicolor*, *Arenicola marina*). In *International symposium on the behaviour of long-lived radionuclides in the marine environment*, (ed. A.Cigna & C. Myttenaere), pp. 327-341. Luxembourg: Office for Official Publications of the European Communities.
- Golding, D.W. & Yuwono, E., 1994. Latent capacities for gametogenetic cycling in the semelparous invertebrate *Nereis*. *Proceedings of the National Academy of Sciences*, **91**, 11777-11781.
- Gomez, J.L.C. & Miguez-Rodriguez, L.J., 1999. Effects of oil pollution on skeleton and tissues of *Echinus esculentus* L. 1758 (Echinodermata, Echinoidea) in a population of A Coruna Bay, Galicia, Spain. In *Echinoderm Research 1998. Proceedings of the Fifth European Conference on Echinoderms, Milan, 7-12 September 1998*, (ed. M.D.C. Carnevali & F. Bonasoro) pp. 439-447. Rotterdam: A.A. Balkema.
- Goss-Custard, J.D., Jones, R.E. & Newberry, P.E., 1989. The ecology of the Wash. 1. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology*, **14**, 681-700.
- Hailey, N., 1995. Likely impacts of oil and gas activities on the marine environment and integration of environmental considerations in licensing policy. *English Nature Research Report*, no 145., Peterborough: English Nature.
- Harley, M. B., 1950. Occurrence of a filter-feeding mechanism in the polychaete *Nereis diversicolor*. *Nature*, **165**, 734-735.
- Hayward, P.J. & Ryland, J.S. (ed.) 1995b. *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.
- Heiligenberg, T. van den., 1987. Effects of mechanical and manual harvesting of lugworms *Arenicola marina* L. on the benthic fauna of tidal flats in the Dutch Wadden Sea. *Biological Conservation*, **39**, 165-177.
- Heip, C. & Herman, R., 1979. Production of *Nereis diversicolor* O.F. Müller (Polychaeta) in a shallow brackish water pond. *Estuarine and Coastal Marine Science*, **8**, 297-305.
- Hughes, R.G., Lloyd, D., Ball, L., Emson, D., 2000. The effects of the polychaete *Nereis diversicolor* on the distribution and transplantation success of *Zostera noltii*. *Helgoland Marine Research*, **54**, 129-136.
- 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>
- Kristensen, E., 1988. Factors influencing the distribution of nereid polychaetes in Danish coastal waters. *Ophelia*, **29**, 127-140.
- Levinton, J., 1995. Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions and material fluxes. In *Linking species and ecosystems*, (ed. J.G. Jones & J.H. Lawton) pp. 29-36.
- Lucas, F. & Bertru, G., 1997. Bacteriolysis in the gut of *Nereis diversicolor* (O.F. Müller) and effect of the diet. *Journal of Experimental Marine Biology and Ecology*, **215**, 235-245.
- Luoma, S.N. & Bryan, G.W., 1982. A statistical study of environmental factors controlling concentrations of heavy metals in the burrowing bivalve *Scrobicularia plana* and the polychaete *Nereis diversicolor*. *Estuarine, Coastal and Shelf Science*, **15**, 95-108.

- Marty, R. & Retière, C., 1999. Larval-to-juvenile mobility activities of a holobenthic species, *Nereis diversicolor* (O.F. Müller) (Polychaeta: Nereidae) - their involvement in recruitment. *Bulletin of Marine Science*, **65**, 761-773.
- Marty, R., 1997. *Biologie de la reproduction et du développement de deux espèces d'annélides polychètes Nereis diversicolor* (O.F. Müller) et *Perinereis cultrifera* Grube. , Thèse de 3ème cycle, Université Rennes, France.
- McLusky, D.S., Bryant, V. & Campbell, R., 1986. The effects of temperature and salinity on the toxicity of heavy metals to marine and estuarine invertebrates. *Oceanography and Marine Biology: an Annual Review*, **24**, 481-520.
- Meador, J.P., Varanasi, U. & Krone, C.A., 1993. Differential sensitivity of marine infaunal amphipods to tributyltin. *Marine Biology*, **116**, 231-239.
- Mettam, C., Santhanam, V. & Havard, M.C.S., 1982. The oogenic cycle of *Nereis diversicolor* under natural conditions. *Journal of the Marine Biological Association of the United Kingdom*, **62**, 637-645.
- Moore, P.G., 1977a. Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanography and Marine Biology: An Annual Review*, **15**, 225-363.
- Nielsen, A.M., Eriksen, N.T., Iversen, J.J.L. & Riisgård, H.U., 1995. Feeding, growth and respiration in the polychaetes *Nereis diversicolor* (facultative filter-feeder) and *Nereis virens* (omnivorous) - a comparative study. *Marine Ecology Progress Series*, **125**, 149-158.
- Nowell, A.R.M., Jomars, P.A. & Eckman, J.E., 1981. Effects of biological activity on the entrainment of marine sediments. *Marine Geology*, **43**, 133-153.
- Olafsson, E.B., Peterson, C.H. & Ambrose, W.G. Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: an Annual Review*, **32**, 65-109
- Olive, P.J.W. & Garwood, P.R., 1981. Gametogenic cycle and population structures of *Nereis (Hediste) diversicolor* and *Nereis (Nereis) pelagica* from North-East England. *Journal of the Marine Biological Association of the United Kingdom*, **61**, 193-213.
- Olivier, M., Desrosiers, G., Caron, A., Retière, C. & Caillou, A., 1995. Réponses comportementales des polychètes *Nereis diversicolor* (O.F. Müller) et *Nereis virens* (Sars) aux stimuli d'ordre alimentaire: utilisation de la matière organique particulaire (algues et halophytes). *Canadian Journal of Zoology*, **73**, 2307-2317.
- Ozoh, P.T.E. & Jones, N.N., 1990. Capacity adaptation of *Hediste (Nereis) diversicolor* embryogenesis to salinity, temperature and copper. *Marine Environmental Research*, **29**, 227-243.
- Pacey, A., 2000. Sperm motility in *Arenicola marina* (L.).[On-line] , 2000-10-02
- 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.
- Philippart, C.J.M., 1994a. Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Marine Ecology Progress Series*, **111**, 251-257.
- Reise, K., 1979. Spatial configurations generated by motile benthic polychaetes. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **32**, 55-72.
- Riisgård, H.U., 1991. Suspension feeding in the polychaete *Nereis diversicolor*. *Marine Ecology Progress Series*, **70**, 29-37.
- Riisgård, H.U., 1994. Filter-feeding in the polychaete *Nereis diversicolor*: a review. *Netherlands Journal of Aquatic Ecology*, **28**, 453-458.
- Scaps, P., 2002. A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia*, **470**, 203-218.
- Shull, D.H., 1997. Mechanisms of infaunal polychaete dispersal and colonisation in an intertidal sandflat. *Journal of Marine Research*, **55**, 153-179.
- Smith, J.E., 1955. Salinity variation in interstitial water of sand at Kames Bay, Millport, with reference to the distribution of *Nereis diversicolor*. *Journal of the Marine Biological Association of the United Kingdom*, **34**, 33-46.
- Smith, J.E., 1964. On the early development of *Nereis diversicolor* in different salinities. *Journal of Morphology*, **114**, 437-464.
- Smith, R.I., 1956. The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *Journal of the Marine Biological Association of the United Kingdom*, **35**, 81-104.
- Smith, R.I., 1977. Physiological and reproductive adaptations of *Nereis diversicolor* to life in the Baltic Sea and adjacent waters. In *Essays on polychaetous annelids* (ed. D.J. Reish & R. Fauchald), pp. 373-390. Los Angeles: University of Southern California.
- Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist*, **33**, 510-523.
- Theede, H., 1973. Comparative studies on the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates. *Netherlands Journal of Sea Research*, **7**, 244-252.
- Theede, H., Schaudinn, J. & Saffè, F., 1973. Ecophysiological studies on four *Nereis* species in the Kiel Bay. *Oikos Supplementum*, **15**, 246-252,
- Vismann, B., 1990. Sulphide detoxification and tolerance in *Nereis (Hediste) diversicolor* and *Nereis (Neanthes) virens* (Annelida: Polychaeta). *Marine Ecology Progress Series*, **59**, 229-238.
- Wang, Wen-Xiong, Stupakoff, I. & Fisher, N.S., 1999. Bioavailability of dissolved and sediment-bound metals to a deposit-feeding

polychaete. *Marine Ecology Progress Series*, **178**, 281-293.

Zwarts, L. & Esselink, P., 1989. Versatility of male curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability. *Marine Ecology Progress Series*, **56**, 255-269.

Datasets

Bristol Regional Environmental Records Centre, 2017. BRERC species records recorded over 15 years ago. Occurrence dataset: <https://doi.org/10.15468/h1ln5p> accessed via GBIF.org on 2018-09-25.

Centre for Environmental Data and Recording, 2018. IBIS Project Data. Occurrence dataset: <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAtlas.org on 2018-09-25.

Cofnod – North Wales Environmental Information Service, 2018. Miscellaneous records held on the Cofnod database. Occurrence dataset: <https://doi.org/10.15468/hcgqsi> accessed via GBIF.org on 2018-09-25.

Environmental Records Information Centre North East, 2018. ERIC NE Combined dataset to 2017. Occurrence dataset: <http://www.ericnortheast.org.uk/home.html> accessed via NBNAtlas.org on 2018-09-38

Fife Nature Records Centre, 2018. St Andrews BioBlitz 2014. Occurrence dataset: <https://doi.org/10.15468/erweal> accessed via GBIF.org on 2018-09-27.

Fife Nature Records Centre, 2018. St Andrews BioBlitz 2015. Occurrence dataset: <https://doi.org/10.15468/xtrbyv> accessed via GBIF.org on 2018-09-27.

Fife Nature Records Centre, 2018. St Andrews BioBlitz 2016. Occurrence dataset: <https://doi.org/10.15468/146yiz> accessed via GBIF.org on 2018-09-27.

Kent Wildlife Trust, 2018. Biological survey of the intertidal chalk reefs between Folkestone Warren and Kingsdown, Kent 2009-2011. Occurrence dataset: <https://www.kentwildlifetrust.org.uk/> accessed via NBNAtlas.org on 2018-10-01.

Kent Wildlife Trust, 2018. Kent Wildlife Trust Shoresearch Intertidal Survey 2004 onwards. Occurrence dataset: <https://www.kentwildlifetrust.org.uk/> accessed via NBNAtlas.org on 2018-10-01.

Lancashire Environment Record Network, 2018. LERN Records. Occurrence dataset: <https://doi.org/10.15468/esxc9a> accessed via GBIF.org on 2018-10-01.

Manx Biological Recording Partnership, 2017. Isle of Man wildlife records from 01/01/2000 to 13/02/2017. Occurrence dataset: <https://doi.org/10.15468/mopwow> accessed via GBIF.org on 2018-10-01.

Merseyside BioBank., 2018. Merseyside BioBank (unverified). Occurrence dataset: <https://doi.org/10.15468/iou2ld> accessed via GBIF.org on 2018-10-01.

National Trust, 2017. National Trust Species Records. Occurrence dataset: <https://doi.org/10.15468/opc6g1> accessed via GBIF.org on 2018-10-01.

NBN (National Biodiversity Network) Atlas. Available from: <https://www.nbnatlas.org>.

OBIS (Ocean Biogeographic Information System), 2019. Global map of species distribution using gridded data. Available from: Ocean Biogeographic Information System. www.iobis.org. Accessed: 2019-03-21

South East Wales Biodiversity Records Centre, 2018. SEWBReC Worms (South East Wales). Occurrence dataset: <https://doi.org/10.15468/5vh0w8> accessed via GBIF.org on 2018-10-02.

South East Wales Biodiversity Records Centre, 2018. Dr Mary Gillham Archive Project. Occurrence dataset: <http://www.sewbrec.org.uk/> accessed via NBNAtlas.org on 2018-10-02

Suffolk Biodiversity Information Service., 2017. Suffolk Biodiversity Information Service (SBIS) Dataset. Occurrence dataset: <https://doi.org/10.15468/ab4vwo> accessed via GBIF.org on 2018-10-02.