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Marine Information Network

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

Dog whelk (*Nucella lapillus*)

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

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Group of *Nucella lapillus* and eggs on an overhang (the photograph is upside-down to aid identification).
 Photographer: Judith Oakley
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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	Dr Harvey Tyler-Walters	Refereed by	Dr John Crothers
Authority	(Linnaeus, 1758)		
Other common names	-	Synonyms	<i>Thais lapillus</i> (Linnaeus, 1758)

Summary

🔍 Description

The shell is broadly conical, bearing spiral ridges and consisting of a short pointed spire, dominated by the last whorl. The shell is usually up to 3 cm in height by 2 cm broad but may reach up to 6 cm in height (Crothers, 1985). The shell colour is variable, usually white, but may be grey, brown, or yellow, occasionally with contrasting (usually brown) spiral banding. A short, open siphonal canal leads from base of the aperture. The outer lip of the aperture is thin in young specimens, becoming thickened and toothed internally with age. The shell shape, shell thickness and relative size of the aperture vary with wave exposure. In some populations, mainly sublittoral or from the intertidal in North Kent, the growth lines extend outwards to form flounces or ruffles, and this variety of dog whelk is called *Nucella lapillus* var. *imbricata*. The animal itself is white or cream coloured with white speckles, and a flattened head. The head bears two tentacles, each bearing a eye about one third of the length of the tentacle from its base. The egg capsules of *Nucella lapillus* are vase shaped, about 8mm high, usually yellow, and found attached to hard substrata in crevices and under overhangs.

📍 Recorded distribution in Britain and Ireland

Common on all rocky coasts of Britain and Ireland.

📍 Global distribution

Found throughout the littoral zone of the North Atlantic from the Arctic to the Algarve in the east, Iceland and the Faroes, and from Long Island north to south west Greenland in the west.

🖼️ Habitat

Found on wave exposed to sheltered rocky shores from the mid shore downwards. Rarely present in the sublittoral but may be abundant in areas exposed to extremely strong tidal stress. They are gregarious and common amongst barnacles and mussels on which they feed.

↓ Depth range

Intertidal

🔍 Identifying features

- Shell solid with about 6 swollen whorls.
- Shell forms a short pointed spire, dominated by a large last whorl.
- Last whorl bears 11-14 spiral ridges.
- Siphonal canal open and short.
- Shell with low, strap-shaped spiral ridges, separated by narrow grooves and crossed by growth lines.
- Outer lip of aperture thin and smooth in young specimens but thick and toothed internally in shells that have ceased growth.
- Hypobranchial gland produces a purple secretion.

🏛️ Additional information

The taxonomy of *Nucella lapillus* was reviewed by Crothers (1985) and Kool (1993)

✓ Listed by



🔗 Further information sources

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Biology review

☰ Taxonomy

Phylum	Mollusca	Snails, slugs, mussels, cockles, clams & squid
Class	Gastropoda	Snails, slugs & sea butterflies
Order	Neogastropoda	Whelks, drills & cone snails
Family	Muricidae	
Genus	Nucella	
Authority	(Linnaeus, 1758)	
Recent Synonyms	Thais lapillus (Linnaeus, 1758)	

🌿 Biology

Typical abundance	Moderate density
Male size range	17 - 50+mm
Male size at maturity	
Female size range	Small-medium(3-10cm)
Female size at maturity	
Growth form	Turbinate
Growth rate	See additional information
Body flexibility	None (less than 10 degrees)
Mobility	
Characteristic feeding method	Predator
Diet/food source	
Typically feeds on	Barnacles and mussels (see Crothers, 1985).
Sociability	
Environmental position	Epifaunal
Dependency	Independent.
Supports	Host trematode parasites of sea birds, <i>Parorchis acanthus</i> and <i>Lepocreadium</i> sp.
Is the species harmful?	No But not edible, being distasteful (Crothers, 1985).

🏛️ Biology information

The ecology, physiology and genetics of *Nucella lapillus* has been extensively studied. Therefore, the following review is based on more detailed reviews by Fretter & Graham (1994) and Crothers (1985), to which the user should refer for further detail. The original references are given where appropriate.

Growth rate

Growth rates vary depending on wave exposure, prey type and starvation. Sheltered shore populations grow faster than wave exposed shore populations, resulting in larger more elongate shells (Osborne, 1977; Crothers, 1985; Etter, 1989). Feare (1970b) reported that juveniles

reached 10mm with a year, ca 15 mm at 2 years old and entered maturity at ca 20 mm at Robins Hood Bay in Yorkshire. Moore (1938a) reported that dog whelks reach 10-15 mm at 1 year, 21-26 at 2 years and 29.5 mm at maturity. Maturity was calculated to be reached at 2.5 years at which point shell growth stops (Fretter & Graham, 1994). However, Etter (1996) suggested that adults continued to grow but extremely slowly. Osborne (1977) noted that juveniles <12 mm grew at the same speed above which sheltered individuals grew faster than wave exposed individuals. Etter (1996) reported that juveniles grew 6 mm/150 days on wave exposed shores but 9 mm/150 days in sheltered conditions. Mussels supported the highest growth rates (Hughes & Drewett, 1985). Etter (1996) transplanted juveniles between shores of different wave exposure, and concluded that growth was determined by environmental factors and depressed by wave exposure since it reducing foraging or feeding time.

Crothers (1985) suggested that, although crabs select the largest first year class dog whelks, rapid growth may allow dog whelks to grow beyond the predators preferred size range and decrease their susceptibility to predation.

Feeding

Nucella lapillus is an important intertidal predator and preys mainly on barnacles and mussels but may also prey on cockles, other bivalves and gastropods.

- As in many neogastropods, the mouth and radula are born on an extensible proboscis, which in *Nucella lapillus* is approximately the same length as the shell in each individual (Barnes, 1980; Crothers, 1985).
- *Nucella lapillus* feeds by either
 1. pressing the proboscis between the valves of bivalves or plates of barnacles and removing flesh by the rasping radula, or
 2. by boring a hole in the shell of its prey and inserting the proboscis through the hole.
- The victims shell is bored by a combination of mechanical rasping by the radula in the proboscis and chemical attack by secretions of the accessory boring organ (ABO) situated in the sole of the foot.
- Once penetrated, the prey is narcotized by secretions of the accessory salivary glands, which also secrete a cement like substance that may help keep the proboscis attached to the prey (Andrews, 1991; Fretter & Graham, 1994). The hypobranchial gland also secretes a pharmacologically active choline ester that may be involved in narcotization (Carriker, 1981; Crothers, 1985), however its function is disputed by Fretter & Graham (1994).
- The dog whelk secretes digestive enzymes into the body of the prey and then ingests the resultant tissue 'soup' (Crothers, 1985).
- The 'gape' attack method is energetically more effective (Fretter & Graham, 1994) and is more likely to be used by dog whelks with experience of handling the prey than inexperienced dog whelks and results in a lower prey handling time than boring (Rovero *et al.*, 1999). Large dog whelks can also force the proboscis between the opercular plates of barnacles to apply the narcotic (Carriker, 1981; Fretter & Graham, 1994). The 'gape' attack is presumed to rely on successful application of the narcotic (Rovero *et al.*, 1999).
- Rovero *et al.* (1999) reported that the 'gape' attack method resulted in prey handling time (including inspection, narcotization and ingestion) of 49-51 hrs depending on experience, compared with a handling time of ca 100 hrs by boring. Morgan (1972) reported that boring could take 3 days to complete. Therefore, handling time can span several tidal cycles during which the dog whelk is vulnerable to desiccation, wave exposure and predation (Hughes & Drewett, 1985; Rovero *et al.*, 1999).
- It has been shown that experience of a particular food type reduces handling time (Dunkin

& Hughes, 1984; Hughes & Dunkin, 1984), which may partly explain dog whelks preference for a particular type of prey even in the presence of others.

- Once fed the dog whelk rests in a crevice or other shelter, up to 2-4 tides after feeding on barnacles and 7-9 tides after mussels (Hughes & Drewett, 1985). However, larger dog whelks have higher energy demands and rest for shorter periods (Bayne & Scullard, 1978).

Factors affecting feeding

- Crothers, (1985; Table 1) lists 24 potential recorded food species. *Nucella lapillus* usually favours *Semibalanus balanoides* > *Balanus* spp. > *Mytilus edulis* > *Elminius modestus* > (Crothers, 1985).
- Larger dog whelks tend to handle larger prey than small dog whelks. Hughes & Burrows (1993) found that dog whelks avoided mussels <5 mm and preferred 10-20 mm mussels (Hunt & Scheibling, 1998). Hunt & Scheibling (1998) noted that although juveniles (<3 mm) rarely fed on mussels <2 mm and post recruits (<5 mm) only rarely consumed mussels <5 mm both were capable of feeding on the full size range of mussels presented. Mussels > 40 mm seem to be safe from dog whelk attack, and Crothers (1985) suggested that 20 mm long mussels were optimum for a 30 mm long dog whelk (Bayne & Scullard, 1978; Crothers, 1985).
- Feeding rates vary, depending on size (hence shell thickness) of prey, temperature and season.
- Crothers (1985) suggested a mean annual consumption of 15-40 mussels per dog whelk (Largen, 1967a; Bayne & Scullard, 1978) and reported rates of 0.5 or 0.59 mussels/day or 1.1 *Semibalanus balanoides* /day in summer (Connell, 1961; Fretter & Graham, 1962; Anala, 1974).
- Largen (1967b) noted that feeding rates decreased with temperature, from an average of 16 barnacles or 0.7 mussels per week at 20 C to 10.2 barnacles and 0.4 mussels per week at 15 C.
- Connell (1961) noted that the time spent feeding on open rock surfaces decreased from about 60% in July to September to only 13% in January to March.
- Although foraging patterns on a given shore are similar, they vary between locations depending on the type of shore, its wave exposure, and local weather. Dog whelks from sheltered shores forage less in sunny, warm weather, whereas animals from wave exposed shores favoured calm periods even when sunny (Burrows & Hughes, 1989; Fretter & Graham, 1994).
- Stickle *et al.* (1985) demonstrated that starvation could overcome the dog whelks tendency to avoid stressful conditions e.g. low salinity. Feeding rates were reduced at low salinity and temperature, e.g. only 25% of dog whelks examined fed at 25 psu and 5C or 15 psu and 8.5C. When exposed to air (emersion) ingestion rates were affected by the air and water temperatures, the difference between these temperatures, salinity, humidity, weather conditions and appetite (Stickle *et al.*, 1985) (see sensitivity).
- Dog whelks avoid dense mussel beds, preferring the diffuse margins between the mussel bed and the surrounding barnacle dominated substratum, or solitary mussels (Petraitis, 1987; Fretter & Graham, 1994; Davenport *et al.*, 1996). This was partly because mussels can immobilise gastropods (*Nucella lapillus* and *Littorina littorea*) crossing the mussel bed with their byssus threads. Davenport *et al.*, (1996) found that although *Littorina littorea* broke free of at least 14 byssus threads within 45 mins, *Nucella lapillus* attached by 1-18 byssus threads took 4-12 hrs to escape. Some specimens, however, were found immobilised by at least 30 byssus threads. Dog whelks take a long time to feed, hence, increasing the chance of them being immobilised. Petraitis (1987) suggested that mussels

co-operated to flip over predatory dog whelks. However, Davenport *et al.*, (1996) found that byssus attachments occurred to areas of the shell closest to the substratum, there was no evidence of selective attachment to flip the shell over. Petraitis (1987) calculated that nearly 30% of dog whelks in a mussel bed perished due to being immobilised.

Shell shape, colour and sculpture variation

Nucella lapillus is highly variable in the appearance of its shell, depending on wave exposure and location (see Crothers, 1983; 1985 for review).

- Shell colour may be white, brown shading to black, mauve grading to pink, yellow shading to orange and rarely true orange, pink or black (Moore, 1936; Berry & Crothers, 1974; and Crothers, 1985, Plate 2). The white form predominates in the UK, but coloured shells predominate in the southern limits of its range (Portugal and Northern Spain) and in northern populations in Iceland (Crothers, 1985).
- *Nucella lapillus* also exhibits a variety of banded forms, with a mixture of un-banded, thin or thick banded (see Crothers, 1985 for discussion).
- Palmer (1984) demonstrated the inheritance of colour, banding and spiral shell sculpture using breeding experiments in *Nucella emarginata*. Similar breeding experiments have not been carried out in *Nucella lapillus* (Crothers, 1985), however it seems likely that colour and banding are under genetic control.
- In some populations, mainly sublittoral or from the intertidal in North Kent, the growth lines extend outwards to form flounces or ruffles, and this variety of dog whelk is called *Nucella lapillus* var. *imbricata*. The imbrication is genetically determined but may appear less marked due to abrasion (Largen, 1971; Crothers, 1985).
- The shell may also bear white dentiform tubercles on the inside edge of the shell lip, which develop once the shell has stopped growing (ca 2 years). However, interruption of growth earlier in life, possibly due to starvation or parasitism may result in additional rows of teeth (Crothers, 1985).

Shell shape variation

Variation in shell shape and length has been extensively studied (see Crothers, 1985 for a review). Key points follow.

- Sheltered shore animals grow faster than wave exposed individuals (Osborne, 1977) and sheltered shore populations have longer shells than wave exposed populations. Populations of exceptional length (up to 60 mm) occur subtidally or at extreme low water at Porlock Weir in the Severn Estuary, between Swanage and Kimmeridge, Dorset and at some sites in western Scotland (Crothers, 1985).
- *Nucella lapillus* from wave exposed shores tend to have shorter, squatter shells than those from sheltered shores, which are more elongate. A progression from squat to elongate form is seen with decreasing wave exposure (Cooke, 1895; Kitching & Ebling, 1967; Crothers, 1985). The shape of the shell can be expressed in terms of the shell length relative to the aperture length (see Crothers, 1985 for review). The possible reasons for the relationship between wave exposure and shell shape are noted below.
 - Short squat shells offer less resistance to water flow and wave action and exhibit a larger aperture and larger foot and hence increased pedal surface area, which increases their adhesion to the substratum (Cooke, 1895; Kitching & Ebling, 1967; Crothers, 1985; Etter, 1988).
 - Etter (1988) noted that the foot grows faster in wave exposed conditions rather

than in sheltered conditions and that foot size increased in dog whelks transplanted to more wave exposed shores but change little in the reciprocal transplant (Etter, 1988; Fretter & Graham, 1994).

- Longer, elongated shells have a relatively smaller foot but can hold a significantly greater volume of water within its mantle cavity when emmersed and are more tolerant of desiccation (see sensitivity) (Osborne, 1977, Kirby, 1994a).
- Short squat shells are more prone to predation, their rounded shape makes them easier to swallow for birds such as gulls and eider duck. In addition, the animal is not able to withdraw completely into the shell making them susceptible to crabs and oystercatchers whereas the elongate shell form can withdrawn completely and the narrow aperture does not allow crabs to gain adequate purchase on the shell. (Osborne, 1977) (see sensitivity to wave exposure).
- Crothers (1985) reported that the squat shell shape was absent from wave exposed sites in south-east England, the north coast of Wales, the Solway Firth and the Severn Estuary. Crothers (1985, Figure 33) suggested that the UK population of *Nucella lapillus* was divided into two groups, a south western group bearing the genes for the squat shell shape and another north-eastern form, which lacks the genes for the squat form and can only develop as the elongate form.

Genetic variation

In addition to the colour variation mentioned above, *Nucella lapillus* has been shown to demonstrate clines in allozyme (Day & Bayne, 1988; Day, 1990; Kirby, 1994a, b) and mitochondrial DNA polymorphisms (Kirby *et al.*, 1997), Robertsonian translocation (Staiger, 1957; Bantock & Cockayne, 1975; Page 1988; Pascoe & Dixon, 1994; Pascoe *et al.*, 1996), peri- and para-centric chromosomal inversions (Page 1988; Pascoe & Dixon, 1994; Pascoe *et al.*, 1996; Pascoe, 2002). Variation in chromosome number was found to vary greatly between different populations, within some populations and even within some individuals (Pascoe, 2002).

Habitat preferences

Physiographic preferences	Open coast, Strait / sound, Sea loch / Sea lough, Ria / Voe, Estuary, Enclosed coast / Embayment
Biological zone preferences	Lower eulittoral, Mid eulittoral, Sublittoral fringe
Substratum / habitat preferences	Artificial (man-made), Bedrock, Caves, Crevices / fissures, Large to very large boulders, Overhangs, Rockpools, Small boulders, Under boulders
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.), Very Strong > 6 knots (>3 m/sec.), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Exposed, Extremely exposed, Extremely sheltered, Moderately exposed, Sheltered, Very exposed, Very sheltered
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Depth range	Intertidal
Other preferences	No text entered
Migration Pattern	Non-migratory / resident

Habitat Information

- *Nucella lapillus* is widely distributed approximately between the 19 °C summer isotherm in the south and the -1 °C winter isotherm in the north (Moore, 1936), except in areas of reduced salinity such as the Baltic Sea (Crothers, 1985).
- Dog whelks occur below of mid tidal level, approximating to 10-75% emersion (Fretter & Graham, 1994).
- *Nucella lapillus* may form aggregations on the shore. In summer (May - October) aggregations of 20-500 individuals of mixed ages may form on the open rock surface of extensive shores (e.g. at Robins Hoods Bay) giving the appearance of a hunting pack (Feare, 1971; Lewis, 1964; Crothers, 1985). In winter individuals aggregate in crevices and pools, presumably to avoid dislodgement, since they have difficulty re-attaching in cold weather. Winter aggregations may form into pre-breeding and breeding aggregations in which the juveniles leave to feed but the adults remain (Feare, 1971; Crothers, 1985).

Life history

Adult characteristics

Reproductive type	Gonochoristic (dioecious)
Reproductive frequency	Annual protracted
Fecundity (number of eggs)	100-1,000
Generation time	2-5 years
Age at maturity	2.5 years
Season	Spring - Autumn
Life span	5-10 years

Larval characteristics

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

Life history information

Breeding occurs throughout the year but is maximal in spring and autumn.

Spawning

Adult *Nucella lapillus* may be seen spawning or copulating in spawning aggregations. Pre-spawning and spawning aggregations develop in early spring, sometimes summer, and may comprise 30 or (many) more individuals, dominated by adults. Pre-spawning aggregations may be difficult to distinguish from winter aggregations, except that the winter aggregations consist of all age classes. Winter and spawning aggregations occur in sheltered areas of the shore (e.g. crevices or under hangs and leeward faces), which are also perfect sites for spawning. Adults do not feed during mating and

spawning, and may remain in their winter aggregation sites for 4-5 months without feeding or moving significantly (Crothers, 1985).

Nucella lapillus lays its eggs in protective egg capsules on hard substrata in damp crevices and under stones. Copulation is repeated at intervals, between which a few egg capsules are laid, one at a time (Fretter & Graham, 1994). Larger females lay larger capsules, however most capsules are vase shaped, 9 -10 mm high, 3 -4 mm across and yellow to brown in colour. Capsules are cemented to the substratum by the ventral pedal gland and foot and is sealed with a 'plug' at the opposite end. (Crothers, 1985; Graham, 1988; Fretter & Graham, 1994). The gametogenesis, ovoposition and structure of egg capsules is discussed in detail by Ankel (1937), Fretter (1941), Feare (1970a), and Fretter & Graham, (1985, 1994).

Fecundity

The number of capsules laid depends on the female's food reserves, age and temperature, e.g. populations in the White Sea lay ca 20-30 capsules per season, while temperate Atlantic populations may lay 5 times this number. Although each capsule may contain ca 600 eggs, 94% of the eggs are unfertilized and function as 'nurse eggs' and are fed upon by the developing embryos (Fretter & Graham, 1994; Crothers, 1985). Capsules have been reported to release 12 -15 'crawl-away' hatchlings per capsule (Crothers, 1977), 13-36 hatchlings per capsule (Feare, 1970b) or 25-30 hatchlings per capsule (Graham, 1988). Fretter & Graham (1994) estimated that each female could produce 1030 hatchling per year. Etter (1989) noted that, in Massachusetts, adults from wave exposed shore laid about twice as many egg capsules and released about twice as many hatchlings per capsule (albeit ca 20% smaller) as adults from sheltered shores. The number and size of offspring produced was dependant on wave exposure, and formed a cline across the wave exposure gradient (Etter, 1989).

Impact of TBT on reproduction

The effects of tributyl tin (TBT), used in anti-fouling paints, on *Nucella lapillus* have been extensively documented and represent one of the best known examples of the effects of chemical pollution (see sensitivity). The following is based upon reviews by Hawkins *et al.* (1994) and Bryan & Gibbs (1991) to which the reader should refer for further detail.

- TBT is thought to increase the levels of testosterone in the female causing the development of male sexual characteristics, termed 'imposex' (Smith, 1980).
- With increasing TBT concentration a penis and vas deferens develop in the female, until the vas deferens occludes the genital papillae of the female, preventing release of egg capsules and effectively rendering the female sterile. The aborted capsules eventually build up until they rupture the capsule gland of the female, and kill the individual. The different stages of development are described by the vas deferens sequence (VDS) (Gibbs & Bryan, 1983). The degree of imposex may also be measured by the relative size of the female and male penises and termed the relative penis size (RPS).
- Both RPS and VDS have been used to estimate the degree of TBT contamination to which a population has been exposed and environmental monitoring of TBT (Bryan & Gibbs, 1991; Evans *et al.*, 1991; Moore *et al.*, 2000)

Larval development

The equivalent of the veliger stage occurs within the capsule. *Nucella lapillus* larvae feed on the nurse cells in the late veliger stage, during which development is halted for about 1 week. Development is slow and temperature dependant, taking ca 4 months in temperate areas but up to seven months in the White Sea, where the eggs overwinter (Fretter & Graham, 1994). Once larvae have become miniature adults they leave the capsule via the terminal plug, although if this exit is blocked by other hatchlings they may bore through the capsule wall. Hatchlings may be termed crawl-aways (Crothers, 1985; Fretter & Graham, 1994).

Longevity and mortality

Feare (1967) suggested that a large proportion of the 69% mortality of *Nucella lapillus* observed on the Yorkshire coast in the winter of 1965 -66 was due to predation by oystercatchers (*Haematopus ostralegus*). Adults are also preyed on by gulls and eiders, which swallow the dog whelk whole. Adults dog whelks of 40mm or more long are probably safe from birds (Crothers, 1985). Juveniles are eaten by rock pipits, turnstones, and purple sand-pipers. Feare (1970b) estimated juvenile mortality to be 90% within the first year, ca. 50% in the second year and 27% in the third. Feare (1967; 1970b) reported that the purple sand-piper favoured 2-5 mm long dog whelks (occasionally 8 mm) and accounted for most of the 90% mortality in juvenile dog whelks in the winter of 1965-66 in Robin Hood's Bay. Juveniles are also susceptible to crab predation. Feare (1967) reported that most of the juvenile mortality between summer and autumn 1966-67 (Robin Hood's Bay) was due to crabs. *Carcinus maenas* can handle dog whelks up to 15 mm in length whereas *Necora puber* can handle up to 25 mm (Crothers, 1985). Crothers (1985) suggested that lobsters, which can crush any size adult, may be a significant predator below low water. Feare (1970b) estimated a life expectancy of at least 6 years, although Crothers (1985) suggested that this may be an under-estimate.

Dispersal

Nucella lapillus lacks a dispersive pelagic larval phase. They are relatively inactive as adults, moving mostly at night (males more than females) but rarely far. Several movement estimates have been reported, for example, an average of 100 mm /tidal cycle (Connell, 1961), or 123 mm/day over barnacles and 329 mm/day over a cockle bed (Morgan, 1972; Fretter & Graham, 1994). Crothers (1985) reported that marked specimens were recovered within 30 cm of their release site after one year, and suggested that with an abundant food supply there was little stimulus to move far from their site of birth. Castel & Emery (1981) reported that adults do not move more than 30 m in their life-time. *Nucella lapillus* recolonizing Watermouth Cove in north Devon, following the effects of TBT pollution (Crothers, 1998), have advanced at least 30 m in a minimum of 13 years (Crothers, in prep). Palmer (1984) also noted that few *Nucella emarginata* moved more than 10 m in a year in the USA. Similarly, Gosselin & Fu-Shiang Chia (1995) reported that dispersal was limited to a few meters from the egg capsules in *Nucella emarginata* (in the USA). Poor dispersal as adult and hatchling results in low rates of recruitment from or migration between adjacent populations, and may lead to relatively high levels of genetic isolation and variation within the population (population sub-division).

However, Martel & Fu-Shiang Chia (1991) collected two hatchling *Nucella emarginata* drifting in the intertidal, suggesting that dispersal by passive transport by currents

can occur occasionally. Gosselin & Fu-Shiang Chia (1995) point out that occasional drifting by small numbers of hatchling, while rare, may still result in significant gene flow, and that since dislodgement increases with wave exposure, more gene flow (hence less population subdivision) may occur in wave exposed rather than sheltered shores.

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	Low	High	Moderate
Removal of the substratum would cause removal of adult and juvenile dog whelks together with their egg capsules. Therefore, an intolerance of high has been recorded. Given their poor dispersal ability, recruitment from other populations is likely to be slow, therefore a recoverability of low has been recorded.				
Smothering	Low	Immediate	Not sensitive	Moderate
Little information on the effect of smothering was found. However, dog whelks are found at the mouths of highly turbid estuaries, such as the Severn Estuary where rock pools are often filled with silt. Dog whelks are therefore probably not adversely affected by temporary smothering. If smothering occurs, there will be an energetic expenditure involved in freeing itself from the smothering material. Hence, an intolerance of low has been recorded.				
Increase in suspended sediment	Low	Immediate	Not sensitive	Low
<i>Nucella lapillus</i> is found in turbid estuaries such as the Severn estuary, and is, therefore, unlikely to be adversely affected by an increase in suspended sediment concentration. However, the accumulation of silt or mud may restrict their distribution in silty estuaries such as the Severn. In addition, the abundance of their prey (barnacles and mussels) may be restricted by increased suspended sediment, reducing their food supply. Therefore, an intolerance of low has been recorded.				
Decrease in suspended sediment	Tolerant	Not relevant	Not sensitive	High
<i>Nucella lapillus</i> is found on a variety of shores from wave exposed to sheltered and is, therefore, unlikely to be affected by a decrease in suspended sediment concentration. Hence, <i>Nucella lapillus</i> has been recorded as 'tolerant' to a decrease in suspended sediment.				
Dessication	Intermediate	High	Low	Moderate
Desiccation tolerance is dependant on the volume of water held inside the mantle cavity of the shell and hence the shell shape. Squat shells characteristic of some wave exposed shores have wider apertures and shorter spires which results in less water being retained within the shell when emersed and a greater rate of evaporation through the larger aperture. <ul style="list-style-type: none"> Boyle <i>et al.</i> (1979) demonstrated that the amount of water in the mantle cavity fell on drying at 20 °C for 6 hrs from 39% to 33% of the total water content of the animal, due to drainage and evaporation, with a resultant increase in ionic concentration. As expected higher shore animals, emersed for longer, showed a greater reduction in water 				

- volume on the shore. Etter (1988b) suggested that the evaporation of the mantle water resulted in cooling (see temperature below).
- Coombs (1973b) noted that desiccation was dependant on age and size. Small individuals (<16 mm, ca 1 year old) lost water more rapidly but survived a greater percentage water loss, and became comatose at a water loss of 50-55%; whereas large dog whelks (15-25 mm, ca 1-2 years old) became comatose after 35-40% water loss. Small and large individuals reach critical water loss after 6hr at 25 °C, however.
 - During emersion dog whelks were able to maintain normal aerobic respiration. Individuals that retained the most water during emersion also exhibited a higher oxygen consumption than those that retained less (Sandison, 1968; Houlihan *et al.*, 1981; Innes & Houlihan, 1985).
 - Sandison (cited in Lewis, 1964) reported 100% mortality in dog whelks exposed to drying for 7 days at 18 °C.
 - On sheltered shores, with relatively high temperatures the dog whelks are predominately white (Berry, 1983; Etter, 1988). Etter (1988b) reported that white shells reflected more light, and hence absorbed less heat, perhaps a mechanism for avoiding desiccation.

The effect of a change in desiccation will be dependent on the level of wave exposure. Increased desiccation on sheltered shores is likely to reduce the upper limit on dog whelks on the shore. Wave exposed shores are less susceptible to desiccation due to increase humidity due to wave action, however, the wave exposed shell form (squat shell shape) of *Nucella lapillus* is more intolerant of desiccation than the sheltered, elongate form. It should be remembered that on most shores of intermediate wave exposure, intermediate shell shapes will occur. Similarly, on shores with a large tidal range, the upper shores may experience a high level of desiccation since at low tide the sea is so far away that no spray reaches the upper shore (Crothers, pers comm.). Putting aside any migration downshore, desiccation at the level of the benchmark (see benchmark) is likely to result in high mortality.

An increase in desiccation is likely to reduce the upper limit of adult dog whelks on the shore and an intolerance of intermediate has been recorded. Gibbs *et al.* (1999) reported that dog whelks surviving a mass-kill were able to re-establish the population within 2 years but where there were few survivors, many years may be required. Therefore, a recoverability of high, to previous population levels, has been recorded (see additional information). Dog whelks displaced to the top of the shore (e.g. by wave action) will probably succumb to desiccation unless they are able to migrate to the lower shore before emersion.

Increase in emergence regime

Intermediate

High

Low

Moderate

The distribution of dog whelks on the shore is centred around the mid-tidal level and between 10-75% emersion (Fretter & Graham, 1994). Dog whelks extend higher upshore in Scotland or Norway than in south Britain (Dr John Crothers pers comm.), presumably because of the lower average air temperatures in more northern latitudes. In Norway, they can reach the uppermost *Semibalanus* and can eat-out their food supply.

Increased emersion would expose the population to increased risk of desiccation and a wider range of temperatures. Coombs (1973b) reported that dog whelks were unlikely to experience more than 3-4 hours of emersion at their preferred shore height, but also reported that dog whelks became comatose and reached

critical water loss after 6 hours at 25 °C, a temperature that may be experienced during a hot summer. Comatose animals are likely to be dislodged to lower on the shore, where they would escape the effects of increased emersion best, since they become relaxed, become more prone to desiccation. Therefore, some mortality of individuals at the upper limits of their range may occur as a result of an increase in emersion regime, and therefore an intolerance of intermediate has been recorded.

Decrease in emersion regime **Tolerant** Not relevant **Not sensitive** **Moderate**

The distribution of dog whelks on the shore is centred around the mid-tidal level between 10-75% emersion (Fretter & Graham, 1994). Decreased emersion would allow the population to follow their prey as they colonized further up the shore. However, it may also expose the individuals at the bottom of the shore to increased predation from crabs and starfish. It is likely that dogwhelks would migrate up the shore and the benefits of increased access to prey would balance out the possibility of increased predation, therefore an intolerance of tolerant has been recorded.

Increase in water flow rate **Low** **Very high** **Very Low** **Moderate**

Change to water flow rate mostly relevant to subtidal area. Etter (1988a) demonstrated that the tenacity of dog whelks to resist water flow was proportional to the pedal surface area. Tenacity of dog whelks from sheltered shores was lower than dog whelks from wave exposed shores. He also demonstrated that dog whelks from sheltered shores would develop a larger foot when transplanted to wave exposed shores. Therefore, *Nucella lapillus* exhibits considerable phenotypic plasticity in response to wave exposure and most likely current flow. Although, the most elongate specimens are probably highly intolerant of increases in water flow rates, hatchlings and juveniles, which are still growing, will probably adapt to the increase water flow regime. Therefore, an overall intolerance of low has been recorded. A recoverability of very high has been recorded to represent the time taken for juveniles to recolonize and adapt (see additional information below).

Decrease in water flow rate **Tolerant** Not relevant **Not sensitive** **Low**

It is unlikely that a decrease in water flow rate will directly affect dog whelks even though the longer foot associated with strong flows becomes superfluous. However, the biotope may change and prey species, predominantly barnacles, become less abundant. Etter (1988a) demonstrated that the tenacity of dog whelks to resist water flow was proportional to the pedal surface area. A decrease in water flow may result in an increase in the mean shell length of the population (depending on wave exposure) but *Nucella lapillus* is otherwise probably tolerant of a decrease in water flow.

Increase in temperature **Intermediate** **High** **Low** **Moderate**

Largen (1967) reported that feeding rate was maximal between 20 -22 °C and fell steeply to zero at 25 °C whilst crawling reached zero at 27 °C. Sandison (1968); (reported unpublished in Lewis, 1964) noted that heat coma occurred in *Nucella lapillus* at 27 -28 °C, and death at 32 -33 °C. Largen (1967) noted that feeding rates were temperature dependant, dog whelks averaged consumption of 16 barnacles or 0.7 mussels per week at 20 °C but only 10.2 barnacles and 0.4 mussels per week at 15 °C. Newell (1979) noted that oxygen consumption (hence

metabolic rate) fell with decreased temperature and starvation, being low in winter but high in summer. This resulted in a high scope for activity, and dog whelks responded rapidly to increases in temperature in the spring. Newell (1979) pointed out that dog whelks could adjust their metabolic rate with temperature and season. Stickle *et al.* (1985) also noted that feeding and ingestion rates decreased with decreasing temperature and salinity. Etter (1988b) noted that white shells reflected more light (reducing the rate of heating and the temperature reached within unit time) and that dog whelks were cooled by evaporation of the water retained within the shell during emersion. Increased temperatures also increase the risk of desiccation (see above), especially on sheltered shores. However, dog whelks demonstrate behavioural adaptations depending on the type of shore they inhabit, e.g. dog whelks from sheltered shores forage less in sunny, warm weather, whereas animals from wave exposed shores (higher humidity) favoured calm periods even when sunny (Burrows & Hughes, 1989; Fretter & Graham, 1994). In southern Britain mortality from high temperatures is probably more likely than from low temperatures (Dr John Crothers, pers comm.). Crothers (1985) suggested that the southern limit of dog whelk distribution was temperature dependant and noted that in Portugal dog whelks live inside mussels clumps and in Massachusetts, where water temperature may reach 25 °C, dog whelks may spend summer below the tide mark. Therefore, *Nucella lapillus* is probably relatively tolerant of temperature change within the normal range for the UK, and is probably tolerant to a change of 2 °C over a year. However, an acute temperature change (e.g. 5 °C) will probably interfere with feeding activity and in summer may result in direct mortality or indirect mortality due to heat coma and desiccation. Therefore an intolerance of intermediate has been recorded.

Decrease in temperature **Low** **Very high** **Very Low** **Moderate**

The northern geographical limit of *Nucella lapillus* is close to the 0 °C winter isotherm. Therefore, Crothers (1985) suggested that they were limited by ice, and that although dog whelks themselves could avoid ice in cracks and crevices, their prey (barnacles and mussels) could not avoid ice-scour. Cold torpor was apparent in dog whelks acclimated to 5 °C (Stickle *et al.*, 1985). Speed of movement increases rapidly above 5 °C (Largen, 1967), and activity begins at 3 °C, however, *Nucella lapillus* is totally inactive at 0 °C and will fall off steep substrata (Largen, 1967; Crothers, 1985). Dog whelks crept into sheltered crevices in winter and probably effectively hibernate over winter (Moore, 1936; Largen, 1967). Cold torpor is likely, therefore, to increase this species risk of being washed offshore or of predation. Low temperatures make dog whelks less tolerant of low salinity (Dr John Crothers, pers comm.). Feeding and ingestion rates also decrease with temperature. Largen (1967) noted that spawning began once temperatures increased to 9-10 °C, and was interrupted by a fall in temperature. Largen (1967) reported that dog whelks averaged consumption of 16 barnacles or 0.7 mussels per week at 20 °C but only 10.2 barnacles and 0.4 mussels per week at 15 °C. Newell (1979) noted that oxygen consumption (hence metabolic rate) fell with temperature and starvation, being low in winter but high in summer. This resulted in a high scope for activity, and dog whelks responded rapidly to increases in temperature in the spring. Newell (1979) pointed out that dog whelks could adjust their metabolic rate with temperature and season. Stickle *et al.* (1985) also noted that feeding and ingestion rates decreased with

decreasing temperature and salinity. During the severe winter of 1962/63, *Nucella lapillus* were reportedly unaffected in Anglesey, north Wales and the South Wales coast although many were reported killed in the Beaulieu River, Hampshire (Crisp ed., 1964). Overall, it appears that *Nucella lapillus* can survive temperatures as low as 3 °C and possibly 0 °C, although evidence for duration is lacking, the effects of low temperatures are sub-vital and an intolerance of low, at the level of the benchmark, has been recorded.

Increase in turbidity Tolerant Not relevant Not sensitive High

Nucella lapillus is an active carnivore and is unlikely to be adversely affected by increases or decreases in light attenuation due to turbidity and has been recorded as 'tolerant' to this factor.

Decrease in turbidity Tolerant Not relevant Not sensitive High

Nucella lapillus is an active carnivore and is unlikely to be adversely affected by increases or decreases in light attenuation due to turbidity and has been recorded as 'tolerant' to this factor.

Increase in wave exposure Intermediate High Low High

Dog whelks adapt to wave action through their shell shape and size of foot (Crothers, 1985). Etter (1988a) demonstrated that the tenacity of dog whelks to resist wave action was proportional to the pedal surface area. Tenacity of dog whelks from sheltered shores was lower than dog whelks from wave exposed shores. He also demonstrated that dog whelks from sheltered shores would develop a larger foot when transplanted to wave exposed shores. Therefore, *Nucella lapillus* exhibits considerable phenotypic plasticity in response to wave exposure and current flow. It is also found from very wave exposed to very sheltered shores. An increase in wave action, for example from sheltered to exposed (see benchmark) is likely to increase mortality due to dislodgement and result in loss of a proportion of the population. Very sheltered and sheltered shores are likely to be more intolerant of such an increase. Therefore, an intolerance of intermediate has been recorded. Recent juveniles colonizing the shore in autumn and winter in the UK, are likely to adapt their phenotype to the prevalent conditions. Therefore a recoverability of high (see additional information below) has been recorded.

Decrease in wave exposure Intermediate High Low High

Growth adaptations of the dog whelk to strong wave action result in a thinner shell and longer pedal opening. Therefore, although adhesion to the substrate will be more than adequate with an increase in shelter. However, wave exposed forms may be more liable to predation from crabs and to desiccation (see above). Therefore, an intolerance of intermediate has been recorded. Recent juveniles colonizing the shore in autumn and winter in the UK, are likely to adapt their phenotype to the prevalent conditions. Therefore a recoverability of high (see additional information below) has been recorded.

Noise Tolerant Not relevant Not sensitive High

While *Nucella lapillus* is probably sensitive to local vibration within its vicinity, possibly similar to that caused by a predator, it is unlikely to be adversely affected by noise of the type or levels addressed in the benchmark.

Visual Presence Tolerant Not relevant Not sensitive High

Nucella lapillus bears light sensitive eyes on its tentacles. However, its visual acuity is probably low and it is unlikely to be adversely affected by movement or shading due to anthropogenic activities.

Abrasion & physical disturbance **Low** Immediate **Not sensitive** **Moderate**

Shells of *Nucella lapillus* are likely to show signs of abrasion due to wave action or sediment scour. The flounces of *Nucella lapillus* var. *imbricata* may also be reduced due to abrasion. However, no information concerning the effect of abrasion such as trampling on dog whelks was found. It is likely that some individuals may be dislodged and some washed to deep water and lost as a result. The most adverse affect is likely to be indirect due to a loss of prey such as mussels or barnacles due to trampling or removal by an abrasive force. However, dog whelks are capable to switching to another prey source in the absence of their preferred prey, so an intolerance of low has been recorded.

Displacement **Intermediate** **High** **Low** **Moderate**

Displaced and dislodged individuals may become subject to increased desiccation if up turned, or washed to deep water and lost. However, Bryan (1968) reported that adults, presumably narcotized by oil and dispersants and washed below low water recolonized the shore within about 6 months, suggesting that displaced individuals could return to the intertidal. However, *Nucella lapillus* does not readily crawl across sediment, therefore individuals displaced to unsuitable substrata may not be able to return. Therefore, a precautionary intolerance of intermediate has been recorded. Recruitment from surviving adults and recolonization by juveniles from below water may result in recovery within about two years and a recoverability of high has been recorded (see additional information below).

Chemical Pressures

Synthetic compound contamination **Intolerance** **Recoverability** **Sensitivity** **Confidence**
High **Low** **High** **High**

The effects of tributyl tin (TBT), used in anti-fouling paints, on *Nucella lapillus* have been extensively documented and represent one of the best known examples of the effects of chemical pollution. The following is based upon reviews by Hawkins *et al.* (1994) and Bryan & Gibbs (1991) to which the reader should refer for further detail.

- *Nucella lapillus* (and other stenoglossan gastropods) are particularly intolerant of TBT contamination. Imposition is initiated at TBT concentrations low as <0.5 ng Sn/l. A proportion of females are sterilised at 1-2 ng Sn/l, and virtually all females are sterile at 3-5 ng Sn/l. Oogenesis was suppressed at >10 ng Sn/l, testis development may occur at 20 ng Sn/l and the sperm ingesting gland in some females remains undeveloped at 100 ng Sn/l (Gibbs *et al.*, 1988; Hawkins *et al.*, 1994). These values can be compared with concentrations of 430 ng Sn/l in the Crouch estuary and >2 µg Sn/l in some marine sites (Waldock & Miller, 1983).
- *Nucella lapillus* has been effectively exterminated from many areas in its European range (Gibbs *et al.*, 1991), especially in area of pleasure boating or shipping. In the south coast of England virtually all populations had been affected to some extent, and some were extinct

(Bryan & Gibbs, 1991; Hawkins *et al.*, 1994).

- Imposex is irreversible and recovery is dependant on recruitment of juveniles into the population.
- TBT has been banned from use of boats <20 m since 1987 since which time populations have begun to recover.
- Evans *et al.* (1996b) reported marked recovery of many populations from the North Sea and Clyde Sea and that although ports were 'hot spots' of TBT contamination the populations of *Nucella lapillus* were not sterile and produced enough offspring to survive. However, several populations in semi-enclosed areas with high boating activity in south west England had become extinct. Evans *et al.*, (1996b) also suggested that extinction of populations in Tarbert Harbour, western Scotland, the Clyde Sea, Lerwick in Shetland, the Solent, Channel Islands, Isle of Wight and east coast of the North Sea were probably due to TBT contamination.
- Moore *et al.* (2000) reported recovery of *Nucella lapillus* from the effects of TBT contamination in Yell Sound, adjacent to the Sullom Voe oil terminal in Shetland, with only 28% of females showing signs of imposex in their 1999 survey. The population in Sullom Voe itself, especially close to the terminal, had improved since 1991 but still had a low reproductive capacity.

Overall, *Nucella lapillus* is highly sensitive of TBT contamination, while females may be killed at concentrations above 5 ng Sn/l, imposex and hence reduced reproductive capacity can occur at lower concentration (above) and the population will decline due to natural mortality and poor recruitment. Where populations have become extinct, recovery is dependant on recolonization, and may take many years due to their poor dispersal capability (see additional information below). However, recoverability (*sensu MarLIN*) assumes that the impact has stopped or is removed. Bryan & Gibbs, (1991) and Hawkins *et al.* (1994), note that TBT is persistent in sediments and little recovery is likely until the ambient concentration of TBT falls below 4 ng/l.

Heavy metal contamination Low Very high Very Low Moderate

Bryan (1984) suggested that adult gastropod molluscs were relatively tolerant of heavy metal pollution. Bryan & Gibbs (1983) noted that *Nucella lapillus* accumulated Cu and Zn in the Fal estuary, but was excluded from the highly heavy metal contaminated Restronguet Creek. Food is the main route of uptake of iron (Fe) and zinc (Zn) in *Nucella lapillus* (Young, 1977). *Nucella lapillus* exhibits detoxification systems e.g. granules containing phosphate, calcium, zinc, magnesium (Mg) and copper occur in the digestive gland, which may explain their tolerance of high levels of Zn and copper (Cu), (Ireland, 1979; Bryan, 1984), Cadmium (Cd) is detoxified by storage as a metallothionien (Bryan, 1984). Therefore, an intolerance of low has been recorded.

Hydrocarbon contamination Intermediate High Low High

- The combination of oiling and subsequent treatment with dispersants after the *Torrey Canyon* oil spill (in March 1967) resulted in loss of *Nucella lapillus* from affected shores, however, Smith (1968) noted that where less dispersants

were used *Nucella lapillus* was amongst one of the most tenacious gastropods. Smith (1968) noted that the most resistant gastropods (such as *Osilinus lineatus* and to a lesser extent *Nucella lapillus*) were able to tightly close their shells with their operculum.

- The toxicity of the emulsifiers BP1002 (a non-ionic surfactant in an aromatic hydrocarbon solvent) has been examined by several workers. Smith (1968) reported that 10 ppm was adequate to inhibit crawling in gastropods and that *Nucella lapillus* was detached at this concentration. A concentration of >100 ppm was required to kill the majority of the dog whelk (after 24hr exposure at 12°C). Bryan (1968) noted that none died when exposed to 1ppm BP1002 and some survived longer than 2 hrs in neat BP1002. BP1002 was most toxic between 2.5-1000 ppm but less so above 1000ppm since the dog whelk was able to detect the emulsifier and close its shell. Surviving individuals recovered within 8 days. Crapp (1970a) reported that *Nucella lapillus* was severely affected by direct treatment with BP1002 in the field (exposed for ca. 6hrs at low tide). However, Crapp (1970b) reported that *Nucella lapillus* was relatively resistant, exhibiting a 1 hr LC₅₀ of between 10,000 -500,000 ppm, depending on season, being very resistant in winter. Crapp (1970b) also noted that individuals took longer to recover from exposure in winter.
- Exposure to petrol/water emulsions in Milford Haven as a result of the *Dona Marika* incident, caused gastropods to retract into their shells and resulted in a marked reduction in *Nucella lapillus* abundance, from Common to Rare. However, numbers increased within 9-11 months, mainly due to recolonization by adults that had presumably been narcotized or retracted, washed below low water and had taken some time to recover before returning to the shore (Blackman *et al.*, 1973; Baker, 1976).
- Smith (1968) and Bryan (1968) report similar rapid re-colonization from low water. Bryan (1968) noted that the majority of the recruitment was by juveniles that had presumably been living below low water during the spill and that the population had recovered within 2 years. However, both Smith (1968) and Bryan (1968) suggested that in areas of heavy treatment by dispersants, recovery may take much longer.
- Gelder-Ottaway (1976a) noted that *Nucella lapillus* and *Littorina littorea* were un-able to crawl through crude oil films. Gelder-Ottaway (1976b) exposed several species of gastropod to various oil/ water emulsions. After 6hrs exposure at 17-20 °C the toxicities of different oil emulsions to *Nucella lapillus* was as follows (percentage mortalities in brackets) leaded gasoline (54) > Kuwait crude

oil (18) > Kerosene (10) > diesel and No. 2 fuel oil (2-4).

However, no indication of concentrations used was given.

- Stickle *et al.* (1984) reported that *Nucella lima* (as *Thais lima*) was very tolerant of short term exposure to oil, but that tolerance declined with duration of exposure, e.g. the LC₅₀ to Cook Inlet crude oil after 7 days was >3000 ppm, but between 961 ppm after 21 days and 818 ppm after 28 days exposure.
- Ebert & Lees (1996) noted that growth of *Nucella lamellosa* was depressed on sites oiled by the Exxon Valdez spill in comparison to un-oiled sites.
- Nelson-Smith (1968) reported the *Nucella lapillus* was significantly affected at the upper end of its range on one shore, and markedly reduced in abundance on another after oiling and subsequent emulsifier treatment after the Chrissi P. Goulandris crude oil spill in Milford Haven. After the spill most gastropods were absent with *Steromphala umbilicalis*, *Steromphala cineraria*, and *Nucella lapillus* only represented by a few dead animals lodged in crevices. In areas that received less of this oil, such as Porthcolhen (near Padstow) and Marazion, *Nucella lapillus*, top-shells and winkles (except *Littorina littorea*) were numerous and unaffected.

Overall, while *Nucella lapillus* is probably more resistant to oiling and emulsifiers than most gastropods (except *Osilinus lineatus*), the above evidence indicates that population are severely affected by oil but especially emulsifiers depending on concentration.

Therefore, an intolerance of intermediate has been recorded.

Where, adults survive or juveniles are represent below low water, recolonization may take up to 2 years (see additional information below).

Radionuclide contamination

Not relevant

Insufficient information.

Changes in nutrient levels

High

Low

High

Moderate

Gibbs *et al.* (1999) reported a massive kill of *Nucella lapillus* in Bude Bay, north Cornwall. Gibbs *et al.* (1999) suggested that the mass mortalities may have been caused by eutrophication and summer algal blooms due to a new sewage outfall in the area that received only primary treated sewage. *Nucella lapillus* has been shown to be severely affected by toxic algal blooms. For example, Robertson (1991) reported up to 98-99% mortality of dog whelks exposed to a toxic bloom of *Chrysochromulina polylepis* in Gullmar Fjord, west Sweden in June 1988. As a result, the distribution and abundance were reduced, 1-2 yr. olds (three years recruitment) suffered heavy mortality and subsequent reproductive capacity was reduced (Robertson, 1991). Similarly, *Nucella lapillus* was shown to be severely affected by a bloom of *Gyrodinium aureolum* in south west Ireland in 1979 (Cross & Southgate, 1980) and strongly affected by a bloom of *Chrysochromulina polylepis* in the Kattegat, Skagerrak and

Norwegian coast of the North Sea, May -June, 1988 (Underdal *et al.*, 1989). Therefore, an intolerance of high has been recorded. Given their poor dispersal and recruitment from other populations, recovery may take many years (see additional information below).

Increase in salinity Low Very high Very Low Moderate

Kirby *et al.* (1994b) simulated the effects of hyper-osmotic shock due to evaporation of mantle cavity retained seawater in *Nucella lapillus*. Exposure to 35, 45, 55, 65 and 75 psu over periods of 6, 12 and 24 hrs at 15 °C resulted in an increase in alanine production, with concomitant decrease in aerobic respiration and, on return to 35 psu, an increase in nitrogen excretion due to increased protein metabolism. However, no mortalities were observed during the experiment, although the dog whelks remained in their shells for the duration of the experiment (Kirby pers. comm.). Kirby *et al.* (1994b) noted that the wave exposed (short spired shell) form of *Nucella lapillus* suffered a greater decrease in aerobic respiration and increase in protein metabolism and hence greater stress than the sheltered site forms. Kirby *et al.* (1994b) also noted a correlation between the physiological effects of hyperosmotic shock and different alleles at the leucyl-amino peptidase (*Lap*) locus suggesting a genetic component to hyper-osmotic shock tolerance. Overall, it appears that *Nucella lapillus* would tolerate an acute, short term increase in salinity, albeit at metabolic cost, suggesting an intolerance of 'low'.

Decrease in salinity Intermediate High Low Moderate

Nucella lapillus is unable to feed under brackish conditions and are likely to be absent from areas of fresh water influence on the shore (Crothers, 1985). Feare (1970b) noted that in rock pools at full salinity 100% of egg capsules hatched, whereas only 27% hatched in areas subject to fresh water runoff at low tide. Stickle & Bayne (1985) reported that, at between 5 -20 °C, dog whelks over 20 mm in length tolerated between 14.2 and 16.2 psu, whether exposed abruptly or after acclimation. In their experiments smaller dog whelks were able to tolerate salinities as low as 12.7 psu. Stickle *et al.*, 1985 noted that reduced salinity and temperature reduced feeding rates in *Nucella lapillus*, e.g. only 10% fed at 25 psu and 5 °C or 15 psu and 8.5 °C. They reported that *Nucella lapillus* was a poor volume regulator and did not quantitatively regulate their free amino acid pool. Crothers (1985) noted that *Nucella lapillus* is usually absent from estuaries and although found in the Severn Estuary it is restricted to the lower shore up-channel from Minehead where they presumably avoid reduced salinities. Therefore, a reduction in salinity below 18 psu is likely to adversely affect reproduction and feeding. Hence, a reduction in salinity at the benchmark level is likely to reduce the extent or abundance of *Nucella lapillus* and an intolerance of intermediate has been recorded. Gibbs *et al.* (1999) reported that dog whelks surviving a mass kill were able to re-establish the population within 2 years, except where mortalities were extensive, and a recoverability of high has been recorded (see

additional information below).

Changes in oxygenation

Intermediate

High

Low

Low

No information regarding tolerance to anoxic conditions was found. *Nucella lapillus* is able to maintain aerobic respiration when emmersed (Sandison, 1968; Houlihan *et al.*, 1981; Innes & Houlihan, 1985) and unlikely to suffer anoxia at low tide. *Nucella lapillus* is reported to be capable of anaerobic respiration (Sandison, 1966 cited in Gibbs *et al.*, 1999). Gibbs *et al.* (1999) suggested that its ability to respire aerobically at low tide would compensate for any anoxia experienced when immersed and that it is probably relatively tolerant of low oxygen conditions. Gelder-Ottaway (1976a) demonstrated mortalities (8-40%) in dog whelks held for 5 days in seawater under films of oil. Although the experiment was intended to demonstrate mortalities due to oil film, the death observed probably owed more to oxygen deficiency than the oil itself. Therefore, exposure to 2 mg/l O₂ for one week is likely to result in some mortality in dog whelk populations, and an intolerance of intermediate is recorded, although the ability to respire during emersion will probably keep mortalities to a minimum. Gibbs *et al.* (1999) reported that dog whelks surviving a mass kill were able to re-establish the population within 2 years, except where mortalities were extensive, and a recoverability of high has been recorded (see additional information below).



Biological Pressures

Intolerance

Recoverability

Sensitivity

Confidence

Introduction of microbial pathogens/parasites

Intermediate

High

Low

High

Intertidal gastropods often act a secondary hosts for trematode parasites of sea birds. *Nucella lapillus* may be infected by cercaria larvae of the trematode *Parorchis acanthus*. Infestation causes castration and continued growth (Feare, 1970b; Kinne, 1980; Crothers, 1985). Infected individuals may exhibit a deformed and enlarged shell, additional rows of teeth in the aperture, and an additional seventh whorl (Feare, 1970b). Feare (1970b) reported 15% infestation in one sample, in which the shells showed 3-4 rows of teeth. In one population, however, Feare (1970b) reported an infestation rate of 69%. Kinne (1980) notes that *Nucella lapillus* may also be infested with larvae of *Lepocreadium* sp., which cause reduced or non-functional gonads and a reduction in penis size in males. Castration of a proportion of the population may result in a reduction in recruitment and a reduced decline in population size eventually. Therefore an intolerance of intermediate has been recorded. Recoverability is dependant on recruitment from within the population. Gibbs *et al.* (1995) noted that a small number of individuals surviving the effects of an algal bloom (see nutrients) in north Cornwall, were able to re-establish the population within two years but noted that it

would probably take many years for the population to regain its former abundance. Therefore, a recoverability of high is reported.

Introduction of non-native species

Not relevant

Not relevant

The introduced American oyster drill *Urosalpinx cinerea* may feed on barnacles when not feeding on oyster spat and hence may compete with *Nucella lapillus* for either food or space. However, no further information was found.

Extraction of this species

Not relevant

Not relevant

Not relevant

Not relevant

Nucella lapillus is not subject to targeted extraction in the UK. However, whelks (including the dog whelk) were once collected for the production of Tyrian purple (see Baker, 1974 for review; Crothers, 1985).

Extraction of other species

Low

Very high

Very Low

High

Mussels are subject to extraction (see *Mytilus edulis*) and are a major food species for dog whelks where they occur. However, dog whelks are able to switch to a more abundant prey, such as barnacles (albeit slowly) if necessary and are therefore, likely to suffer a brief interruption in feeding and possibly temporary reduction in reproductive capacity. Therefore, an intolerance of low has been recorded.

Additional information

Recoverability

Nucella lapillus demonstrates low dispersal ability as adults and as juveniles (low vagility) (see reproduction and longevity). If a local population became extinct recovery would be dependant on recruitment from surrounding populations. Although passive dispersal by drifting has been observed in juveniles (Martel & Fu-Shiang Chia, 1995) it is probably an occasional event and would not contribute greatly to recruitment. On continuous stretches of coast recruitment could occur, albeit slowly, by crawling. However, in isolated bays recovery would take much longer. Gibbs *et al.* (1999) reported that the small numbers of dog whelks surviving a mass-kill in July -October 1995 were able to re-establish the population within two years. They also pointed out that in the worst affected parts of the area, the individuals were widely distributed so that breeding aggregations were not possible and suggested that it would take many years for dog whelks to regain their former abundance. However, on re-inspection six years after pre mass-kill in May 2001, the Bude population had recovered to its former abundance and areas of much higher mortality were well on their way to a full recovery (P. Gibbs pers. comm.).

In Watermouth Cove, north Devon, TBT pollution rendered *Nucella lapillus* extinct with the cove, whilst it remained common at the entrance (Crothers, 1998). Recolonization occurred after a maximum of 13 years (Crothers, in prep.).

Bryan (1968) examined the recolonization of Porthleven, south Cornwall after oiling and subsequent treatment with dispersants (BP1002) after the *Torrey Canyon* oil spill in March 1967. Although the population of *Nucella lapillus* was decimated in areas subject to dispersant treatment, the population recovered from 1-5 /m² in June 1967 to 100 /m² by November 1968 (ca 2 years). The majority of the initial recolonization was due to juveniles that had been feeding below low water at the time of the spill and suffered low levels of predation, since their predators were either killed or driven off by dispersant treatment. Fortunately the barnacle *Chthamalus stellatus* was particularly resistant to oil and dispersant so that recolonizing dog whelks had an adequate food source. However, Bryan (1968) noted that dog whelks were very slow to reappear in areas that received heavy dispersant treatment. Therefore it appears that populations of *Nucella lapillus* are capable of recovering with about 2-5 years if survivors are present either intertidally on below low water. However, should a population need to recruit from surrounding area recovery may take significantly longer.

Importance review

Policy/legislation

- OSPAR Annex V
- Features of Conservation Importance (England & Wales)

Status

National (GB) importance	Not rare/scarce	Global red list (IUCN) category	-
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Non-native

Native	-	Date Arrived	Not relevant
Origin	-		

Importance information

- *Nucella lapillus* is an important predator of mussels and barnacles on the rocky shore. The presence of dog whelks on the shore also mediates the effect of limpet grazing on fucoids and contributes to the cycle of barnacle - fucoid dominance. *Nucella lapillus* often shelters under fucoids, where their feeding on barnacles may undermine clumps of fucoids by killing the barnacles to which the holdfasts are attached. Similarly, reduced dog whelk abundance may result in increased barnacle density and hence reduced limpet grazing and allow fucoids to become established. No clear community effects resulting from the decline in dog whelks numbers due to TBT have been demonstrated (see Hartnoll & Hawkins, 1985 and Hawkins *et al.*, 1994 for reviews).
- However, in southwest Britain, where *Semibalanus balanoides* is less common, *Nucella lapillus* has a noted effect on mussel abundance (Dr John Crothers, pers comm.). At Porlock Weir, Somerset, mussels only thrive where a fresh water stream runs across the beach (Wilson *et al.*, 1985); elsewhere newly-settled mussel spat are targeted by dog whelks. There has been a noticeable increase in the abundance of mussels in Watermouth Cove, Devon following the demise of *Nucella lapillus* (Dr John Crothers, pers comm.).
- *Nucella lapillus* is preyed on by numerous sea birds and wildfowl, however, the dog whelk is not considered to be an important food source, except where alternative food sources are absent (Crothers, 1985).
- Whelks, including the dog whelk were once collected in Ireland for the production of the dye Tyrian purple (see Baker, 1974 for review).

- *Nucella lapillus* is listed in the UK Biodiversity Action Plan long list of species of conservation concern (Biodiversity Steering Group, 1995)

Bibliography

- Anala, J., 1974. *Foraging strategies of two marine invertebrates*. Ph.D. thesis, University of New Hampshire, Durham, USA.
- Ankel, W.E., 1937. Die feinere Bau des Kokons der Purpurschnecke *Nucella lapillus* (L.) und seine Bedeutung für der Laichleben. *Verhandlungen Deutschen Zoologischen Gesellschaft*, **39**, 77-86.
- Baker, J.M., 1976. Investigation of refinery effluent effects through field surveys. In *Marine Ecology and Oil Pollution* (ed. J.M. Baker), pp. 201-225. Barking: Applied Science Publishers Ltd.
- Baker, J.T., 1974. Tyrian purple: an ancient dye, a modern problem. *Endeavour*, **XXXIII**, 11-17.
- Bantock, C.R. & Cockayne, W.L., 1975. Chromosomal polymorphism in *Nucella lapillus*. *Heredity*, **34**, 231-245.
- Barnes, R.D., 1980. *Invertebrate Zoology*, 4th ed. Philadelphia: Holt-Saunders International Editions.
- Bayne, B.L. & Scullard, C., 1978. Rates of feeding by *Thais* (*Nucella*) *lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, **32**, 75-94.
- Berry, R.J. & Crothers, J.H., 1968. Stabilizing selection in the dog-whelk (*Nucella lapillus*). *Journal of Zoology*, **155**, 5-17.
- Berry, R.J., 1983. Polymorphic shell banding in the dog whelk *Nucella lapillus*. *Journal of Zoology (London)*, **200**, 455-470.
- Biodiversity Steering Group, 1995. *Biodiversity: the UK Steering Group report*, vol. 1 & 2. London: HMSO.
- Blackman, R.A.A., Baker, J.M., Jelly, J. & Reynard, S., 1973. The *Dona Marika* oil spill. *Marine Pollution Bulletin*, **4**, 181-182.
- Boyle, P.R., Sillar, M.Y. & Bryceson, K., 1979. Water balance and mantle cavity fluid of *Nucella lapillus* (L.) (Mollusca: Prosobranchia). *Journal of Experimental Marine Biology and Ecology*, **40**, 41-51.
- 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. & Gibbs, P.E., 1991. Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In: *Metal ecotoxicology: concepts and applications* (ed. M.C. Newman & A.W. McIntosh), pp. 323-361. Boston: Lewis Publishers Inc.
- Bryan, G.W., 1968. The effect of oil-spill removers ('detergents') on the gastropod *Nucella lapillus* on a rocky shore and in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **49**, 1067-1092.
- 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.
- Castle, S.L. & Emery, A.E.H., 1981. *Nucella lapillus*: a possible model for the study of genetic variation in natural populations. *Genetica*, **56**, 11-15.
- Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the

- barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61-104.
- Cooke, A.H., 1895. Molluscs. In *Cambridge Natural History*, vol. III, *Molluscs and Brachiopods*. London: Macmillan.
- Coombs, V.A., 1973. A quantitative system for age analysis for the dog-whelk *Nucella lapillus*. *Journal of Zoology*, **171**, 437-448.
- Coombs, V.A., 1973. Desiccation and age as factors in the vertical distribution of the dog-whelk *Nucella lapillus*. *Journal of Zoology (London)*, **171**, 57-66.
- Crapp, G.B., 1970a. Laboratory experiments with emulsifiers. In *Proceedings of a symposium organised by the Institute of Petroleum, at the Zoological Society of London, 30 November - 1 December, 1970. The ecological effects of oil pollution on littoral communities* (ed. E.B. Cowell), pp. 129-149. London: Elsevier Publishing Co. Ltd.
- Crapp, G.B., 1970b. Field experiments with oil and emulsifiers. In *Proceedings of a symposium organised by the Institute of Petroleum, at the Zoological Society of London, 30 November - 1 December, 1970. The ecological effects of oil pollution on littoral communities* (ed. E.B. Cowell), pp. 114-128. London: Elsevier Publishing Co. Ltd.
- Crisp, D.J. (ed.), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-210.
- Cross, T.F. & Southgate, T., 1980. Mortalities of fauna of rocky substrates in south-west Ireland associated with the occurrence of *Gyrodinium aureolum* blooms during autumn 1979. *Journal of the Marine Biological Association of the United Kingdom*, **60**, 1071-1073.
- Crothers, J.H., 1983. Variation in dog-whelk shells in relation to wave action and crab predation. *Biological Journal of the Linnean Society*, **21**, 259-281.
- Crothers, J.H., 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.) *Field Studies*, **6**, 291-360.
- Crothers, J.H., 1998. The size and shape of dog-whelks, *Nucella lapillus* (L.) recolonizing a site formerly polluted by tributyltin (TBT) in anti-fouling paint. *Journal of Molluscan Studies*, **64**, 127-129.
- Davenport, J., Moore, P.G. & LeCompte, E., 1996. Observations on defensive interactions between predatory dogwhelks, *Nucella lapillus* (L.) and mussels, *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, **206**, 133-147.
- Day, A.J. & Bayne, B.L., 1988. Allozyme variation in populations of the dog-whelk, *Nucella lapillus* (Prosobranchia: Muricacea) from the South West peninsula of England. *Marine Biology*, **99**, 93-100.
- Day, A.J., 1990. Microgeographic variation in allozyme frequencies in relation to the degree of exposure to wave action in the dogwhelk *Nucella lapillus* (L.) (Prosobranchia: Muricacea). *Biological Journal of the Linnean Society*, **40**, 245-261.
- Ebert, T.A. & Lees, D.C., 1996. Growth and loss of tagged individuals of the predatory snail *Nucella lamellosa* in areas within the influence of the Exxon Valdez oil spill in Prince William Sound. In *Proceedings of the Exxon Valdez Oil Spill Symposium, Anchorage, Alaska, 2-5 February 1993*, (ed. S.D. Rice, R.B. Spies, D.A. Wolfe & B.A. Wright), pp 349-361. Bethesda, Maryland: American Fisheries Society [American Fisheries Society Symposium no. 18]

- Etter, R.J., 1988. Asymmetrical developmental plasticity in an intertidal snail. *Evolution*, **42**, 322-334.
- Etter, R.J., 1988. Physiological stress and color polymorphism in the intertidal snail *Nucella lapillus*. *Evolution*, **42**, 660-680.
- Etter, R.J., 1989. Life history variation in the intertidal snail *Nucella lapillus* across a wave-exposure gradient. *Ecology*, **70**, 1857-1876.
- Etter, R.J., 1996. The effects of wave action, prey type and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, **196**, 341-356.
- Evans, S.M., Evans, P.M. & Leksono, T., 1996b. Widespread recovery of dogwhelks, *Nucella lapillus* (L.), from tributyltin contamination in the North Sea and Clyde Sea *Marine Pollution Bulletin*, **32**, 263-369.
- Evans, S.M., Hutton, A., Kendall, M.A. & Samosir, A.M., 1991. Recovery in populations of dogwhelks *Nucella lapillus* (L.) suffering from imposex. *Marine Pollution Bulletin*, **22**, 331-333.
- Feare, C.J., 1967. The effect of predation by shore-birds on a population of dogwhelks *Thais lapillus*. *Ibis*, **109**, 474.
- Feare, C.J., 1970a. The reproductive cycle of the dog whelk (*Nucella lapillus*). *Proceedings of the Malacological Society of London*, **39**, 125-137.
- Feare, C.J., 1970b. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus*. *Oecologia*, **5**, 1-18.
- Feare, C.J., 1971. The adaptive significance of aggregation behaviour in dogwhelks *Nucella lapillus* (L.). *Oecologia*, **7**, 117-126.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Fretter, V. & Graham, A., 1962. *British Prosobranch Molluscs*. London: Ray Society.
- Fretter, V. & Graham, A., 1985. The Prosobranch Molluscs of Britain and Denmark. Part 8. Neogastropods. *Journal of Molluscan Studies*. Supplement 15.
- Fretter, V. & Graham, A., 1994. *British prosobranch molluscs: their functional anatomy and ecology*, revised and updated edition. London: The Ray Society.
- Fretter, V., 1941. The genital ducts of some British stenoglossan prosobranchs. *Journal of the Marine Biological Association of the United Kingdom*, **25**, 173-211.
- Gelder-Ottaway, S., 1976. Some physical and biological effects of oil films floating on water. In *Proceedings of an Institute of Petroleum / Field Studies Council meeting, Aviemore, Scotland, 21-23 April 1975. Marine Ecology and Oil Pollution*, (ed. J.A. Baker), pp. 255-277. Barking: Applied Science Publishers Ltd.
- Gelder-Ottaway, S., 1976. The comparative toxicities of crude oils, refined oil products and oil emulsions. In *Proceedings of an Institute of Petroleum / Field Studies Council meeting, Aviemore, Scotland, 21-23 April 1975. Marine Ecology and Oil Pollution*, (ed. J.A. Baker), pp. 287-302. Barking: Applied Science Publishers Ltd.
- Gibbs, P.E. & Bryan, G.W., 1987. TBT paints and the demise of the dogwhelk, *Nucella lapillus* (Gastropoda). In *Oceans' 87 Proceedings, Volume 4: International Organotin Symposium*, pp. 1482-1487.

- Gibbs, P.E., Bryan, G.W. & Pascoe, P.L., 1991. TBT-induced imposex in the dogwhelk, *Nucella lapillus*: geographical uniformity of the response and effects. *Marine Environmental Research*, **32**, 79-87.
- Gibbs, P.E., Green, J.C. & Pascoe, P.C., 1999. A massive summer kill of the dog-whelk, *Nucella lapillus*, on the north Cornwall coast in 1995: freak or forerunner? *Journal of the Marine Biological Association of the United Kingdom*, **79**, 103-109.
- Gibbs, P.E., Langston, W.J., Burt, G.R. & Pascoe, P.L., 1983. *Tharyx marioni* (Polychaeta) : a remarkable accumulator of arsenic. *Journal of the Marine Biological Association of the United Kingdom*, **63**, 313-325.
- Gibbs, P.E., Pascoe, P.L. & Burt, G.R., 1988. Sex change in the female dogwhelk *Nucella lapillus*, induced by TBT from anti-fouling paints. *Journal of the Marine Biological Association of the United Kingdom*, **68**, 715-732.
- Gosselin, L.A. & Fu-Chiang Chia, 1995. Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. *Marine Ecology Progress Series*, **128**, 213-223.
- Graham, A., 1988. *Molluscs: prosobranchs and pyramellid gastropods (2nd ed.)*. Leiden: E.J. Brill/Dr W. Backhuys. [Synopses of the British Fauna No. 2]
- Hawkins, S.J., Proud, S.V., Spence, S.K. & Southward, A.J., 1994. From the individual to the community and beyond: water quality, stress indicators and key species in coastal systems. In *Water quality and stress indicators in marine and freshwater ecosystems: linking levels of organisation (individuals, populations, communities)* (ed. D.W. Sutcliffe), 35-62. Ambleside, UK: Freshwater Biological Association.
- Hayward, P.J. & Ryland, J.S. (ed.) 1995b. *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.
- Hayward, P.J. & Ryland, J.S. 1990. *The marine fauna of the British Isles and north-west Europe*. Oxford: Oxford University Press.
- Houlihan, D.F., Innes, A.J. & Dey, D.G., 1981. The influence of mantle cavity fluid on the aerial oxygen consumption of some intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **49**, 57-68.
- Howson, C.M. & Picton, B.E., 1997. *The species directory of the marine fauna and flora of the British Isles and surrounding seas*. Belfast: Ulster Museum. [Ulster Museum publication, no. 276.]
- Hughes, R.N. & Burrows, M.T., 1993. Predatory behaviour of the intertidal snail, *Nucella lapillus*, and its effect on community structure. In *Mutualism and community organization: behavioural, theoretical and food-Web approaches*, (ed. H. Kawanabe, J.E. Cohen, K. Iwasaki), pp. 63-83. Oxford: Oxford University Press.
- Hughes, R.N. & Drewett, D., 1985. A comparison of foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. *Journal of Molluscan Studies*, **51**, 73-77.
- Hunt, H.L. & Scheibling, R.E., 1998. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould)), *M. edulis* (L.) assemblages in tidepools and on emergent rock on a wave exposed rocky shore in Nova Scotia, Canada. *Journal of Experimental Marine Biology and Ecology*, **226**, 87-113.
- Innes, A.J. & Houlihan, D.F., 1985. Aquatic and aerial oxygen

consumption of cool temperate gastropods: a comparison with some Mediterranean species. *Comparative Biochemistry and Physiology*, **82A**, 105-109.

Ireland, M.P., 1979. Distribution of metals in the digestive gland-gonad complex of the marine gastropod *Nucella lapillus*. *Journal of Molluscan Studies*, **45**, 322-327.

Kinne, O. (ed.), 1980. *Diseases of marine animals*. vol. 1. *General aspects. Protozoa to Gastropoda*. Chichester: John Wiley & Sons.

Kirby, R.R., Bayne, B.L. & Berry, R.J., 1994a. Phenotypic variation along a cline in allozyme and karyotype frequencies, and its relationship with habitat, in the dog-whelk *Nucella lapillus*, L. *Biological Journal of the Linnean Society*, **53**, 255-275.

Kirby, R.R., Bayne, B.L. & Berry, R.J., 1994b. Physiological variation in the dog-whelk *Nucella lapillus* L., either side of a cline in allozyme and karyotype frequencies. *Biological Journal of the Linnean Society*, **53**, 277-290.

Kirby, R.R., Berry, R.J. & Powers, D.A., 1997. Variation in mitochondrial DNA in a cline of allele frequencies and shell phenotype in the dog-whelk *Nucella lapillus*. *Biological Journal of the Linnean Society*, **62**, 299-312.

Kitching, J.A. & Ebling, F.J., 1967. Ecological studies at Lough Ine. *Advances in Ecological Research*, **4**, 198-291.

Kitching, J.A., 1986. The ecological significance and control of shell variability in dogwhelks from temperate rocky shores. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed), 234-248.

Kool, S.P., 1993. The systematic position of the genus *Nucella* (Prosobranchia: Muricidae: Ocinebrinae). *Nautilus*, **107**, 43-57.

Largen, M.J., 1967. The influence of water temperature upon the life of the dog whelk *Thais lapillus* (Gastropoda: Prosobranchia). *Journal of Animal Ecology*, **36**, 207-214.

Largen, M.J., 1971. Genetic and environmental influences upon the expression of shell sculpturing in the dog-whelk (*Nucella lapillus*). *Proceedings of the Malacological Society*, **39**, 383-388.

Lewis, J.R., 1964. *The Ecology of Rocky Shores*. London: English Universities Press.

Martel, A. & Chia, F.S., 1991b. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*, **150**, 131-147.

Moore, H.B., 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to the environment. *Journal of the Marine Biological Association of the United Kingdom*, **21**, 61-89.

Moore, H.B., 1938a. The biology of *Purpura lapillus*. Part II. Growth. *Journal of the Marine Biological Association of the United Kingdom*, **23**, 57-66.

Moore, H.B., 1938b. The biology of *Purpura lapillus*. Part III. Life history in relation to environmental factors. *Journal of the Marine Biological Association of the United Kingdom*, **23**, 67-74.

Moore, J.J., James, B., Minchin, A. & Davies, I.M., 2000. Surveys of dog whelks *Nucella lapillus* in the vicinity of Sullom Voe, Shetland, August 1999. *Report to the Shetland Oil Terminal Environmental Advisory Group (SOTEAG)*, prepared by CORDAH Ltd and the Fisheries Research Services.

Morgan, P.R., 1972. *Nucella lapillus* (L.) as a predator of edible cockles. *Journal of Experimental Marine Biology and*

Ecology, **8**, 45-52.

Nelson-Smith, A., 1968. The effects of oil pollution and emulsifier cleansing on shore life in south-west Britain. *Journal of Animal Ecology*, **5**, 97-107.

Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Surveys Ltd.

Osborne, C.M., 1977. *Ecology of shell color polyphenism in the marine gastropod Thais lapillus in New England*. , Ph.D. thesis, University of Yale, Connecticut, USA.

Page, C., 1988. The chromosome complement of *Nucella lapillus* (L.), Mollusca: Gastropoda: Prosobranchia. *Caryologia*, **41**, 79-91.

Palmer, A.R., 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology*, **71**, 759-775.

Palmer, R.A., 1984. Species cohesiveness and genetic control of shell color and form in *Thais emarginata* (Prosobranchia, Muricacea): Preliminary results. *Malacologia*, **25**, 477-491.

Pascoe, P.L. & Dixon, D.R., 1994. Structural chromosomal polymorphism in the dog-whelk *Nucella lapillus* (Mollusca: Neogastropoda). *Marine Biology*, **118**, 247-253.

Pascoe, P.L., 2002. *Chromosomal variation in Nucella lapillus (L.) and other muricid gastropods*. , PhD thesis, University of Plymouth.

Pascoe, P.L., Patton, S.J., Critcher, R. & Dixon, D.R. 1996. Robertsonian polymorphism in the marine gastropod, *Nucella lapillus*: advances in karyology using rDNA loci and NORs. *Chromosoma*, **104**, 455-460.

Petraitis, P.S., 1987. Immobilization of the predatory gastropod, *Nucella lapillus*, by its prey *Mytilus edulis*. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, **172**, 307-314.

Robertson, A., 1991. Effects of a toxic bloom of *Chrysochromulina polylepis*, on the Swedish west coast. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 569-578.

Sandison, E.E., 1968. Respiratory response to temperature and temperature tolerance of some intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **1**, 271-281.

Smith, B.S., 1980. The estuarine mud snail, *Nassarius obsoletus*: abnormalities in the reproductive system. *Journal of Molluscan Studies*, **46**, 247-256.

Smith, J.E. (ed.), 1968. 'Torrey Canyon'. *Pollution and marine life*. Cambridge: Cambridge University Press.

Staiger, H., 1957. Genetic and morphological variation in *Purpura lapillus* with respect to local and regional differentiation of population groups. *Année Biologique*, **33**, 251-258.

Stickle, W.B., Moore, M.N. & Bayne, B.L., 1985. Effects of temperature, salinity and aerial exposure on predation and lysosomal stability in the dog whelk *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, **93**, 235-258.

Stickle, W.B., Rice, S.D. & Moles, A., 1989. Bioenergetics and survival of the marine snail *Thais lima* during long term oil exposure. *Marine Biology*, **80**, 281-289.

Underdal, B., Skulberg, O.M., Dahl, E. & Aune, T., 1989. Disastrous bloom of *Chrysochromulina polylepis*

(Pymnesiophyceae) in Norwegian Coastal Waters 1988 - mortality in marine biota. *Ambio*, **18**, 265-270.

Waldock, M.J. & Miller, D., 1983. The determination of total and tributyl tin in seawater and oysters in areas of high pleasure craft activity. *International Council for the Exploration of the Sea, CM Papers and Reports*, CM 1983/E:12, 16pp.

Wilson, C.M., Crothers, J.H. & Oldham, J.H., 1983. Realized niche: the effects of a small stream on sea-shore distribution patterns. *Journal of Biological Education*, **17**, 51-58.

Young, M.L., 1977. The roles of food and direct uptake from water in the accumulation of zinc and iron in the tissues of the dogwhelk, *Nucella lapillus* (L.) *Journal of Experimental Marine Biology and Ecology*, **30**, 315-325.

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.

Bristol Regional Environmental Records Centre, 2017. BRERC species records within last 15 years. Occurrence dataset: <https://doi.org/10.15468/vntgox> 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 NBNAAtlas.org on 2018-09-25.

Centre for Environmental Data and Recording, 2018. Ulster Museum Marine Surveys of Northern Ireland Coastal Waters. Occurrence dataset <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAAtlas.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.

Conchological Society of Great Britain & Ireland, 2018. Mollusc (marine) data for Great Britain and Ireland - restricted access. Occurrence dataset: <https://doi.org/10.15468/4bsawx> accessed via GBIF.org on 2018-09-25.

Conchological Society of Great Britain & Ireland, 2018. Mollusc (marine) data for Great Britain and Ireland. Occurrence dataset: <https://doi.org/10.15468/aurwcz> 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 NBNAAtlas.org on 2018-09-38

Fenwick, 2018. Aphotomarine. Occurrence dataset <http://www.aphotomarine.com/index.html> Accessed via NBNAAtlas.org on 2018-10-01

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/xtrbvj>

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.

Manx Biological Recording Partnership, 2018. Isle of Man historical wildlife records 1995 to 1999. Occurrence dataset: <https://doi.org/10.15468/lo2tge> 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.

Merseyside BioBank., 2018. Merseyside BioBank Active Naturalists (unverified). Occurrence dataset: <https://doi.org/10.15468/smzyqf> 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>.

Norfolk Biodiversity Information Service, 2017. NBIS Records to December 2016. Occurrence dataset: <https://doi.org/10.15468/jca5lo> accessed via GBIF.org on 2018-10-01.

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

Outer Hebrides Biological Recording, 2018. Invertebrates (except insects), Outer Hebrides. Occurrence dataset: <https://doi.org/10.15468/hpavud> accessed via GBIF.org on 2018-10-01.

South East Wales Biodiversity Records Centre, 2018. SEWBReC Molluscs (South East Wales). Occurrence dataset: <https://doi.org/10.15468/jos5ga> 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

The Wildlife Information Centre, 2018. TWIC Biodiversity Field Trip Data (1995-present). Occurrence dataset: <https://doi.org/10.15468/ljc0ke> accessed via GBIF.org on

2018-10-02.

Yorkshire Wildlife Trust, 2018. Yorkshire Wildlife Trust
Shoresearch. Occurrence dataset:

<https://doi.org/10.15468/1nw3ch> accessed via GBIF.org on
2018-10-02.