

NOTES ON THE IDENTITY AND ECOLOGY OF *ROCELLARIA DUBIA* (BIVALVIA: GASTROCHAENIDAE)

NICK (NJW) OWEN

Ecologist, Wool, Dorset

Abstract *Rocellaria dubia* is under-recorded in the British Isles due to its habit of boring into hard substrata leaving only its siphons showing. The calcareous siphonal tubes which cover the siphons persist for a considerable time and can be used to identify *R. dubia* with a high degree of certainty. This paper provides descriptions and images of its siphonal tubes intended to assist with the correct identification of further records of this cryptic species. In the British Isles *R. dubia* siphonal tubes are colonised by a wide range of epibionts and the use of SACFOR abundance recording (for an animal of 1–3cm) based on the siphonal tubes is tenable.

In the British Isles *R. dubia* appears restricted to calcareous substrata including carbonate-cemented sand- and mud-stones and is an important eroder of these. It is highly tolerant of sediment veneers. Open bivalve bores under fine sediment veneers offer microhabitats to small sediment infauna by harbouring pockets of deeper sediment less subject to periodic 'clearance' than the surrounding sediment. The importance of biogenic erosion by *R. dubia* and other borers on subtidal rock exposures may be significantly under-estimated at the time of writing.

Key words *Gastrochaenidae*, *siphonal tube*, *substratum*, *crypt*, *biogenic erosion*.

INTRODUCTION

The flask shell, *Rocellaria dubia* (Pennant, 1777) formerly *Gastrochaena dubia*, is well known in the Mediterranean where it can cause serious damage to submerged antiquities (e.g. marble statuary) and to concretes used in civil engineering, especially where calcareous aggregates are used (Morton *et al.*, 2011). In the British Isles and adjacent waters, this bivalve is under recorded due to its cryptic lifestyle and the small size of its siphonal tubes, which are the main indicator of its presence. Given the 'right' substratum it can be 'Common', and it is capable of modifying communities. It is probably an important contributor to the biological erosion of sublittoral substrata. In order to increase the number of British Isles records the in-situ recognition features (the siphonal tubes and bores) are described here. The substrata on which the animal can be found, aspects of the ecology of the animal and its role as a habitat modifier are also discussed.

Species Description and Habitat

Fig. 1 is a photograph of one valve of an *R. dubia* shell, which can attain a length of 25mm (Tebble, 1976). The large anterior ventral gape is not visible but the pattern of growth ridges on this specimen would seem to indicate that it is in excess of ten years old. Like Tebble (1976) and other

publications, Hayward and Ryland (2005) give a full description of the shell of the species and state that it bores into "sandstone, limestone and organic carbonates, lower shore and shallow sublittoral". No mention is made of its appearance in situ or that *R. dubia* produces a calcareous lining to its bore. This lined bore is known as the crypt. Compared with true piddocks (Pholadidae) which bore into easily-eroded shales and clays as well as calcareous rocks, it is very difficult to find free *R. dubia* valves to identify. Full descriptions of the anatomy of the species (and of other related species) and the mechanism by which it bores fall outside the scope of this paper and have been summarised by Morton *et al.* (2011).

Mediterranean records exist of the species boring into coralline algal crusts (Fava *et al.*, 2016) and as a borer of live or dead bivalves such as oysters and venerids or living with its crypt free in sediments (Morton *et al.*, 2011). There are old British Isles records of this latter behaviour reported (Jeffreys, 1865 in Albano, 2003) and of *R. dubia* boring into mollusc shells (Tebble, 1976) including through oyster shells and on into sediment beneath (Woodward, 1880 reported by Albano, 2003). In British Isles waters, *R. dubia* primarily seems to inhabit solid rock substrata in the subtidal. Records exist from the intertidal but there are few in the NBN dataset (Fig. 2). From the NBN data, it seems that *R. dubia* is more likely to be recorded by divers



Figure 1 *Rocellaria dubia* NMW.1915.237; Tenby, Wales. IMG no: M010832.

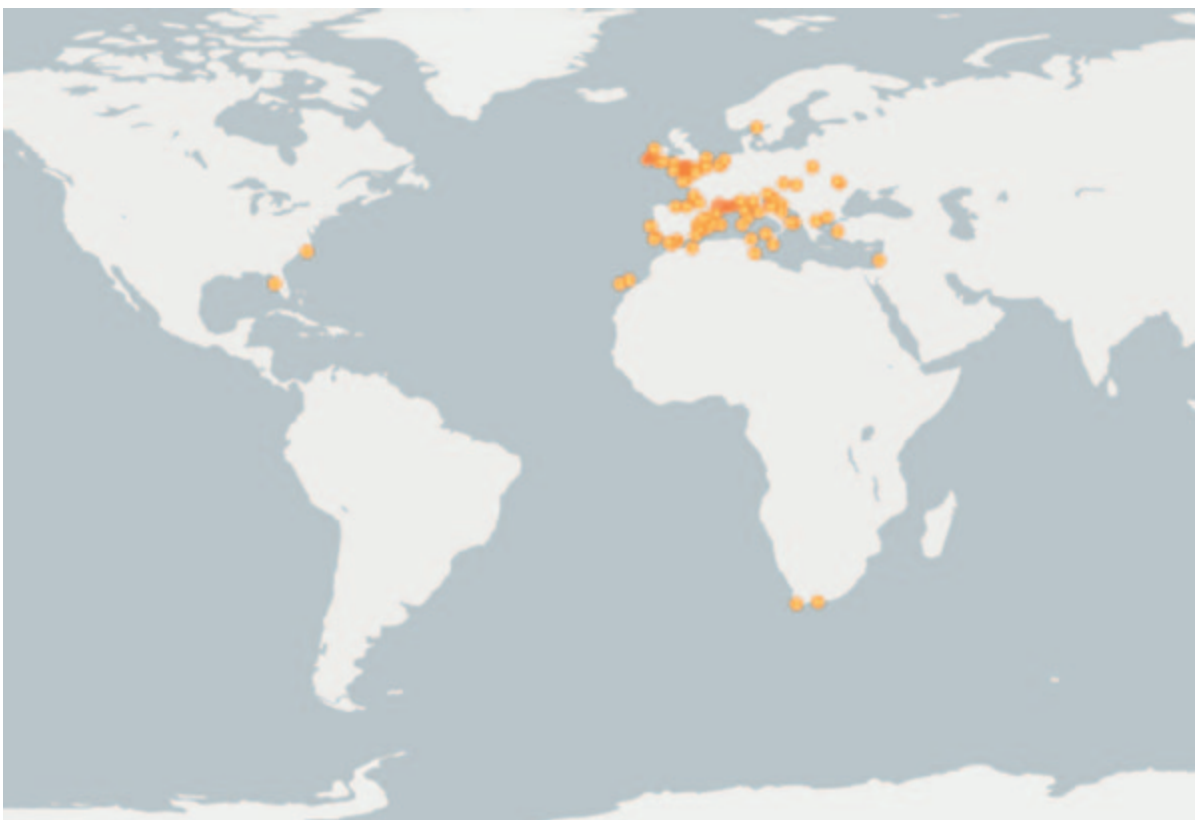


Figure 2 Worldwide distribution of *Rocellaria dubia*, screenshot from GBIF.org (09 January 2022).



Figure 3 British Isles distribution of *Rocellaria dubia* from the NBN Gateway, January 2022

rather than by shore workers or by those using benthic sampling equipment from vessels.

DISTRIBUTION

Rocellaria dubia has a widespread distribution, concentrated in the Mediterranean, the north-east Atlantic, and the southern North Sea. GBIF also has one record off west Florida and three off South Africa, plus several on dry land in Europe. The Florida record is a mis-identification and the South African records may be confusion with *Rocellaria cuneiformis*. The apparent gaps in the core distribution may be due to under-recording and an absence of exposures of substratum of suitable composition between currently-known parts of the range. There is also the possibility of confusion with closely related species, errors in data entry or the inadvertent inclusion of fossils, especially in 'range outliers'. Fig. 3 is a snapshot of the British Isles distribution from the NBN website. Note the cluster of records in Devon and Dorset where Seasearch divers are accustomed to recognising the species from its siphonal tubes. Anthropogenic disturbance of metastable sediments where *R. dubia* might otherwise exist 'free' in its crypt might explain an apparent lack of recent records of this type in British Isles waters.

IDENTITY: *ROCELLARIA DUBIA* SIPHONAL TUBES

In-situ recognition of *R. dubia* depends on spotting its siphonal tubes. *R. dubia* bores using a mixture of chemical solution of carbonates in the substratum and abrasion by the shell valves Morton *et al.* (2011). In British Isles waters, apart from some old records, *R. dubia* appears to be restricted to calcareous rock: limestones, chalk, carbonate-cemented sandstones and mudstones, and organic carbonates such as oyster and venerid shells as shown on the Aphoto marine website (Fenwick, 2012). The initial entry into the substratum is narrow and the bore then swells as the animal grows and burrows deeper to produce a flask-shape, hence the common name of the species. The tissues of the mantle and siphons produce a calcareous lining to the bore, the 'crypt' which extends upwards to cover the outside of the twinned siphons and this hard, calcareous 'siphonal tube' often projects beyond the surface of the substratum. If the bore breaks through into a void such as a pre-existing bore in rock or through the side of the shell of a living or dead bivalve, the crypt wall covers this hole. The 'neck' of the flask remains occupied by the siphonal tube and the shell remains out of sight below the substratum surface inside the crypt.

The siphonal tube is distinctive (Schiaparelli *et al.*, 2005) approximately 4×3mm and typically a few millimetres in height, although height is highly variable. They can be found on suitable bedrock as well as on suitably stable cobbles and pebbles. In recent years Seasearch divers in Dorset have occasionally referred to the species as ‘shotgun piddock’. Morton *et al.*, (2011) record that the animal’s siphons are linked by an inter-siphonal septum which is accommodated by the absence of a wall between the bores of the siphonal tube (Fig. 4). Morton *et al.*, (2011) also showed that *R. dubia* was able to secrete a new siphonal tube if the animal was removed from its crypt. The same workers reported Schiaparelli *et al.* (2005) as showing that the “size of the siphonal tube of *R. dubia* is strongly correlated with shell valve dimensions and the volume of the borehole made by its inhabitant”. Siphonal tubes often exhibit annulations marking stages in extension of the tube (‘growth striae’, Albano, 2003).

In poor visibility on silty sites, siphonal tubes may be felt before they are seen as the protruding siphons feel scratchy-sharp under the fingers. This sensation is similar to noticing the sand-grain tubes of the worm *Sabellaria spinulosa*, the bore of which is similar in size to *R. dubia* siphonal tube bores. Whilst *Sabellaria* tubes can form reefs, they can also be found scattered amongst turf and protruding from sediment veneers and can be found paired on occasion (Fig. 5).

R. dubia siphonal tubes are too small to show up in most drop-down video and are difficult to spot in diver-shot wide angle video. Being of calcareous material, the siphonal tubes are often of similar colouration to the surroundings

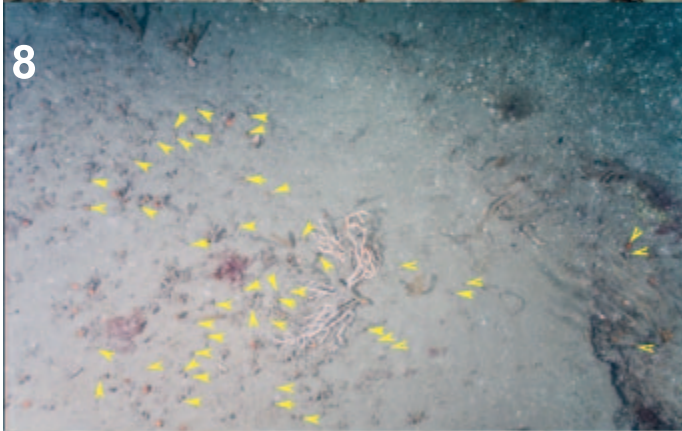
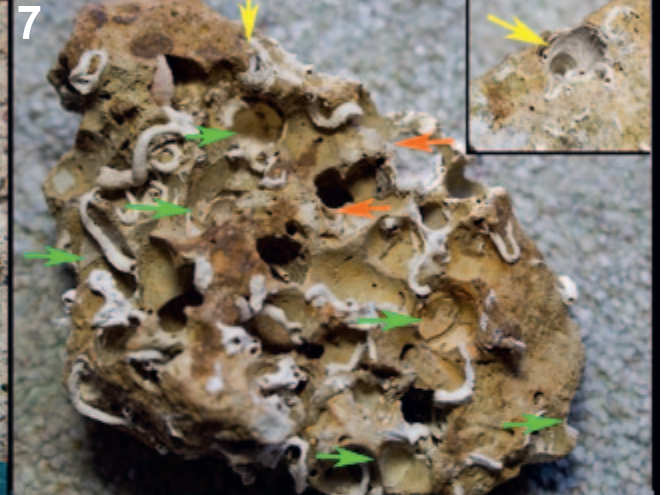
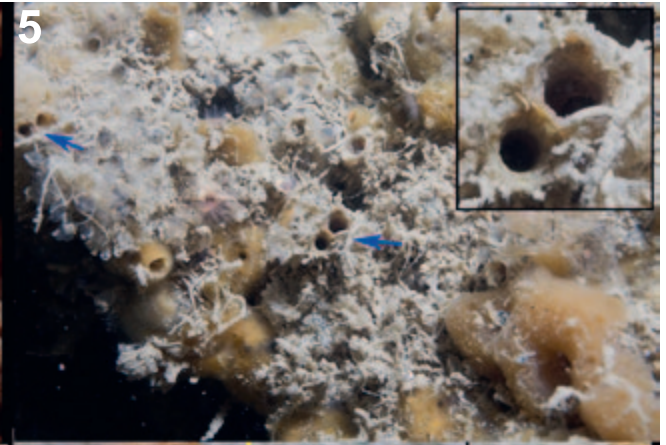
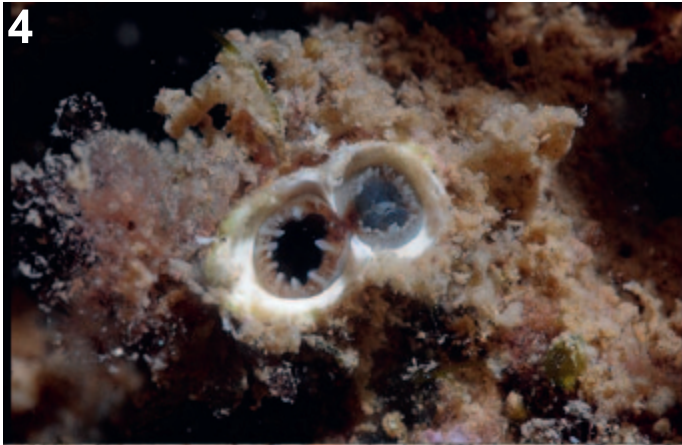
and are often partly hidden amongst animal turf or algae. Unlike some ‘piddocks’ and *Hiatella rugosa*, (Fig. 17) the actual siphons are not brightly coloured although brown pigment may be present (Fig. 4). The siphonal tubes do turn up as ‘by-catch’ in good quality macro photographs but if not recognised in a photograph as ‘belonging’ to *R. dubia*, identification is currently problematic as nothing like it is easily found in the current literature. If one searches on *R. dubia* by name there are many photographs of the siphonal tubes online. The ‘Habitats’ website (Picton *et al.*, 2020) shows *R. dubia* in situ, as well as giving details of the valves of the shell. Other website mentions exist e.g. DORIS (<https://doris.ffesm.fr/index.php/Especies/Rocellaria-dubia-Mye-perce-pierre-2774>).

IDENTITY: *ROCELLARIA DUBIA* BORES

Whilst other bivalve borers in British Isles waters may produce a calcareous lining to the bores (e.g. Teredinidae in wood, Hayward and Ryland, 2005), the robustness of *R. dubia*’s crypt seems distinctive. Donovan *et al.* (2007) excavated and examined bivalve bores in pebbles of carboniferous limestone from Marloes Bay, Pembrokeshire and linked the presence of a calcareous lining in a ‘clavate’ bore to *R. dubia* rather than to *Hiatella arctica* which was posited to have nestled in vacant *R. dubia* bores.

Due to factors such as overgrowth by biota and the presence of silt, the small size of the bores makes it difficult to use the crypt lining to identify *R. dubia* bores in situ in the subtidal. Fig. 7 shows a recovered rock sample from the circalittoral off Portland, Dorset with many lined

Figures 4–11 4 *R. dubia* (Babbacombe, Devon) pair of siphons slightly retracted within a siphonal tube densely colonised by epibiota. Note absence of any wall between the bores © Keith Hiscock. 5 Paired *Sabellaria spinulosa* tubes (blue arrows) (Samphire Ridges, Kent) inset of the central arrowed tubes showing sand-grain construction and a wall between the tubes. 6 Silty, diverse, short animal turf (Lyme Bay, Dorset) including *R. dubia* (yellow and black arrows), ‘piddock’ siphons (2 species, left pointing arrows) and solitary tunicates (3 species, paired arrows). 7 Rock sample (Portland, Dorset) with *R. dubia* lined bores indicated. Yellow (downward) arrow indicates the base of a broken siphonal tube. Inset shows the reverse of the same (opened) crypt. The orange (rightward) arrows indicate the ‘shoulders’ of two *R. dubia* crypts which appear to have been laid down following removal of a former surface of the clast – both these are missing their siphonal tubes. The green arrows indicate the bases of opened crypts with lining material visible. 8 *R. dubia* (Lyme Bay, Dorset). Yellow arrows mark siphonal tubes. 9 *R. dubia* siphonal tube to the left of a juvenile *Atrina fragilis* measuring 25mm along the gape (Beer Fans, Lyme Bay, Devon). Sediment/biogenic fragment veneer was approximately 50mm in depth when observed. 10 *R. dubia* siphonal tube on silt veneer, West Tennants, Lyme Bay, Devon sponge-encrusted. 11 *R. dubia* siphonal tubes colonised by a colonial tunicate (possibly *Didemnum coriaceum*) (West Tennants, Lyme Bay, Devon). Note extreme length of tubes – the animals appear to extend their tubes to keep the entrances clear of the overgrowing tunicate.



(*R. dubia*) and unlined (other) bivalve bores. A yellow arrow indicates a *R. dubia* siphonal tube broken off flush with the specimen surface and the 'figure-8' shape just discernible in the photograph. The inset shows the same crypt broken open with the lining a paler colour than the parent rock.

THE ABUNDANCE OF *ROCELLARIA DUBIA* IN BRITISH ISLES WATERS

Published material (e.g. Morton *et al.*, 2011) contains indications that in some parts of its range *R. dubia* can be very common. In the UK context, numerical assessments of frequency at a given location or of overall population size on a site or in a habitat are not available. A few numerical records exist in the NBN database but appear to refer to number in an individual sample and the numbers given are small. The bulk of the records are SACFOR abundances (Hiscock (ed.) 1996) and many of these are 'R' (<1/m²) or 'O' (1/m²). This is understandable as the siphonal tubes are the only sure sign of presence and they are often hidden amongst other species. However, an idea of population size and density can often be gained from dived data because divers will often take photographs which show habitat. If *R. dubia* siphonal tubes show up as 'by-catch' in many images from a dive, then it is reasonable to assert that there was a significant population of the species on that dive or even in a biotope recorded on that dive.

Fig. 8 is an image taken as a record of a broken-off *Eunicella verrucosa*. The resolution is high enough to zoom in and mark 42 *R. dubia* siphonal tubes around the *Eunicella* in an area of silt veneer over flat, apparently smooth, bedrock with various species growing through including *Epizoanthus couchii* and *Alcyonidium diaphanum*. The area shown is approximately 70cm×70cm. The density of 'definite' *R. dubia* siphonal tubes in this image multiplies up to 85 per square metre. Based on the size class into which the valves will fall (1–3cm), the *R. dubias* in the image are recorded as 'Common' on the MNCR SACFOR scale (10–99/m²) (Hiscock (ed.) 1996). Note that only 'definite' *R. dubias* have been marked and several other 'possibles' exist in this image. The three siphonal tubes on the right on a thin slab with a more-diverse turf, thinner silt layer and (recorded by probing) a pitted surface have not

been included in the numerical assessment. The area in the top right corner has a deeper silt/biogenic fragments layer and no *R. dubia* siphonal tubes visible.

R. dubia siphons react quickly to disturbance of the water column by retracting. This might seem to make estimates of numbers of living individuals hard to arrive at but it should be remembered that live tubes can be extended to keep the siphons clear of a sediment veneer surface or of overgrowing epibionts whereas dead tubes cannot. Live tubes will be repaired if damaged (Morton *et al.*, 2011) whereas dead tubes will not. It is therefore reasonable to assume that where *R. dubia* siphonal tubes are visible in a veneer community or amongst turf, most will be alive so SACFOR estimates of abundance of the species will be adequate but will require care to arrive at.

ROCELLARIA DUBIA AS A HABITAT MODIFIER

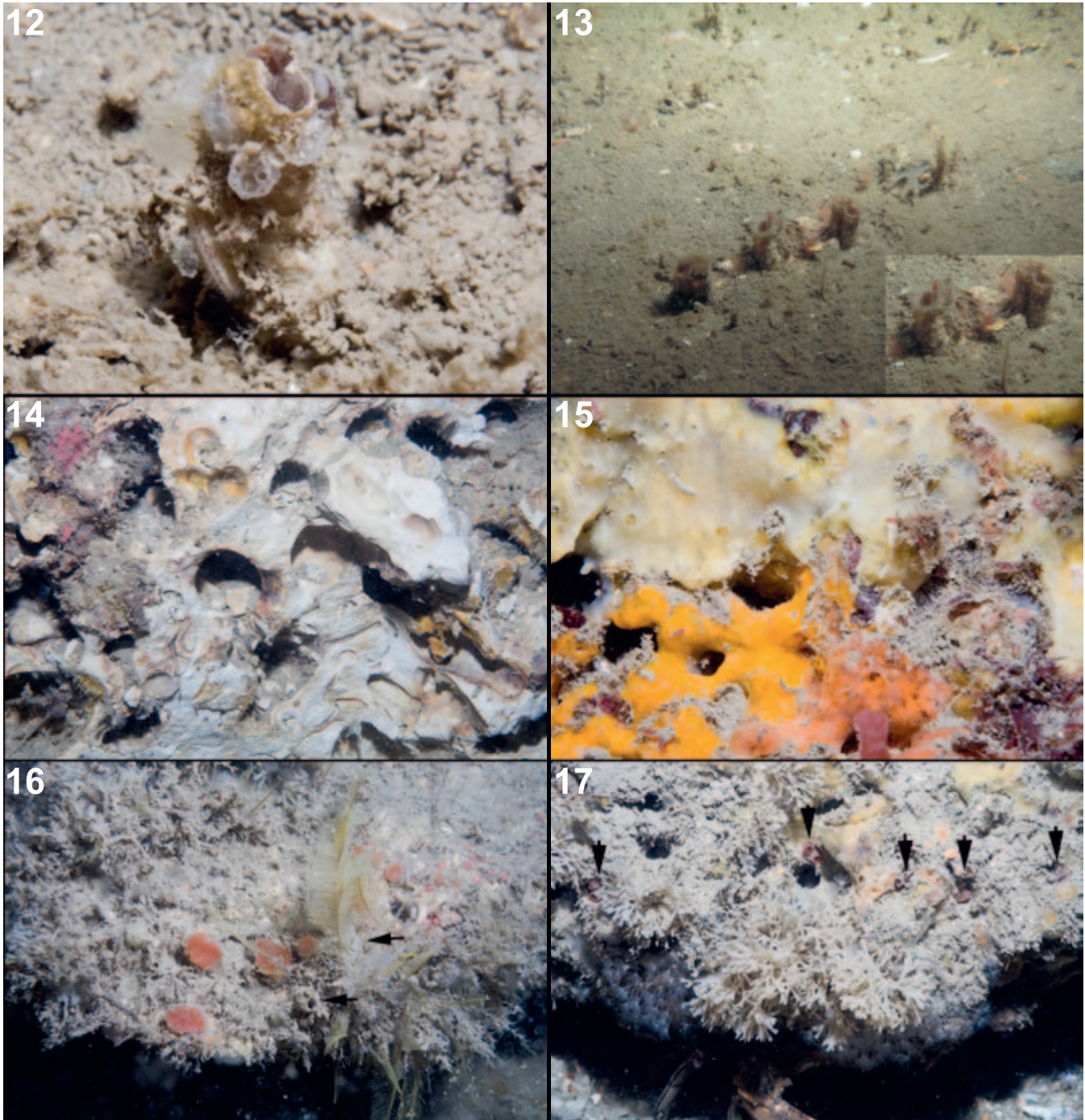
Siphonal Tubes as Substratum

Bare *R. dubia* siphonal tubes are often recorded, especially in sediment veneer biotopes where the sediment depth has recently decreased from a maximum, e.g. Fig. 9. In many instances siphonal tubes protruding above the surface of rock or sediment veneer are colonised as a substratum in their own right. Figs 9 to 12 show some of the wide range of species that have been recorded.

R. dubia siphonal tubes are maintained for the lifetime of the animal which is comparatively long-lived (Fig. 1). The siphonal tubes are thus persistent features of a habitat where they occur. The tubes are also fairly tough and are likely to last beyond the death of the animal unless removed through gross physical damage. They may survive (whether live or dead) a sediment veneer 'maximum' which kills/removes overgrowing epibionts, therefore offering vacant substratum for re-colonisation when veneer depth decreases. Where present, *R. dubia* siphonal tubes can act as a significant modifier of biotopes, increasing overall biodiversity.

Vacant R. Dubia Bores as Microhabitat

Fig. 7 indicates that *R. dubia* bores may make up a significant component of the bivalve bores present at a given point. Many of the bivalve bores in the figure contain the skeletal remains of species such as *Spirobranchus* sp. (tubes), bryozoan crusts and a juvenile pectinid bivalve. On



Figures 12–17 12 *R. dubia* siphonal tube colonised by tunicates, erect bryozoans, sponges and a juvenile pectinid bivalve. 13 Shotgun Reef, Lyme Bay © Nigel Topham. Inset shows one of two *Edwardsia* sp. 14 & 15 Portland stone bedrock, Portland, Dorset 14 Honeycombed by bivalve and worm bores. 15 Bored rock densely colonised by sponges and other biota. 16 *R. dubia* siphonal tubes on an overhanging bedrock edge amongst dense faunal turf (Beer Fans, Lyme Bay, Devon). 17 same site as 16 with siphons of *Hiatella rugosa* (the wrinkled rock borer or red nose), and obvious empty bivalve bores.

non-veneer sites, bivalve bores would offer some refuge from grazing by species such as *Echinus esculentus* (not present in Lyme Bay or points east) and the smooth surfaces of vacant bores could offer preferred lodgement for juveniles of

some sessile species. On veneer sites, especially where the sediment veneer is silt, vacant bores fill with sediment which is more stable than the bulk of the sediment component of the veneer and offers niches for small 'sediment' biota such

as *Edwardsia* sp. (Fig. 13) *Amphiura* spp. and juvenile *Cerianthus lloydii*. This could add significantly to the species list for a site whilst blurring the identification criteria for the site as a veneer.

ROCELLARIA DUBIA AND SEDIMENT VENEERS

Part of the 'Reefs' category of habitats, veneer biotopes are hard surfaces with an overlay of sediment. The biota attached to the hard surface often includes characteristic species including the sponges *Adreus fascicularis* and various *Polymastia* spp., plus the stoloniferous anthozoan *Isozoanthus sulcatus*. In the infralittoral, algae such as *Ahnfeltia plicata* and *Xiphisiphonia ardreana* may be present. To qualify as a sediment veneer, the layer of silt must be mobile (Owen, 2019 and Interpretation Manual of European Union Habitats, Eur28, 2013) and the depth and periodicity of such a layer will therefore vary. The hard substratum under a sediment veneer can be rocky reef, boulders, stony reef or biogenic reef. Evidence (such as many of the photographs in this paper and Schiaparelli *et al.*, 2005) is accumulating that *R. dubia* is highly tolerant of sediment veneers. The ability to quickly extend its siphonal tube (Morton *et al.*, 2011) allows *R. dubia* to cope with increases in depth of a mobile sediment layer. The presence of *R. dubia* shows up especially clearly on silt veneers due to its exposed siphonal tubes often supporting more-visible epibionts (Figs 9 to 12).

ROCELLARIA DUBIA BORES AND EROSION OF REEFS

R. dubia in the Mediterranean is considered to be an important eroder of calcareous substrata and it can be 'Common' in British Isles waters. As seen in Fig. 7 and Schiaparelli *et al.*, 2005, it can be an important contributor to biogenic erosion of hard substrata by boring bivalves. Other biota (worms, sponges) are also significant eroders of rock and although such erosion is difficult to show in photographs, Figs 14 to 17 combine to give an idea: Figs 14 and 15 illustrate the effects of boring species including bivalves on just one site in the upper circalittoral off Portland in Dorset, showing where the outer face of vertical bedrock has spalled away revealing a honeycomb of bores beneath and a short distance away, an intact surface supporting a dense animal turf.

Fig. 16 shows an undercut piece of circalittoral bedrock outcrop on Beer Fans in the middle of Lyme Bay with *R. dubia*. Elsewhere on the same site, Fig. 17 shows the red siphons of *Hiatella rugosa* (wrinkled rock borer, black arrows), plus numerous apparently empty mollusc bores. The substratum in both photographs is densely covered in animal turf and probing with the fingers showed that the rock was intricately pitted and eroded. On other sites with silt veneer biotopes including *R. dubia*, the silt layer often obscures horizontal rock surfaces, but finger-probing often reveals similar pitting which can also be seen on verticals and edges.

Along the Devon and Dorset coasts, there are many outcrops of horizontally-bedded or gently dipping beds of calcareous hard sedimentary rock (HSR) interspersed with beds of less-resistant clay or shale. In these locations the HSR can often be observed to form a 'roof' over considerable voids, the back wall of which can frequently be seen to be made of softer beds, pieces of which, full of mollusc and other bores, may be found on the floor of the overhang. In other places fractures in a horizontal surface of apparently solid HSR can be seen with crab- or lobster-dug 'tailings piles' containing holey pieces of softer rock. *Conger conger* can be seen inhabiting some of these fractures, indicating that the void behind a small hole may go back a considerable distance. Other sites show areas of HSR, which forms a 'crazy paving' of interlocking broken slabs or even several layers of HSR slabs.

These observations point to biogenic erosion being an under-appreciated force in non-igneous rock in the circalittoral and lower infralittoral in British Isles waters with effects of boring biota combing with tunnelling by crustaceans to 'convert' bedrock reef to boulder reef as the soft layers erode away and the unsupported harder layers collapse and fracture. During this process the exposed rock surfaces gradually fragment, reducing the sizes of rock pieces. Where the rock is calcareous, *R. dubia* is an important part of this process.

ACKNOWLEDGEMENTS

The observations contained in this paper were recorded over several years off the coasts of Dorset and Devon, primarily on dives organised by and reported through Seasearch.

All photographs are copyright of the author with the exception of those credited otherwise with thanks.

Thanks are due to any and all of the various Seasearch dive buddies who have had to put up with the author 'wafting' and to Lin Baldock for encouragement and comments on drafts.

REFERENCES

- ALBANO PG 2003 Mediterranean Gastrochaenidae (Mollusca: Bivalvia) *Bolletino Malacologico* **38** (9–12): 135–138. Societa Italiano di Malacologia.
- FENWICK D 2012 *Rocellaria dubia* on *Venus verrucosa* shell. Aphoto Marine Website (aphotomarine.com) http://www.aphotomarine.com/images/marine_bivalves/bivalve_rocellaria_dubia_flask_shell_19-05-12_2.jpg
- CONNOR DW, ALLEN JH, GOLDING N, HOWELL KL, LIEBERKNECHT LM, NORTEN KO & REKER JB 2004 *The Marine Habitat Classification for Britain and Ireland Version 04.05* JNCC, Peterborough ISBN 1 861 07561 8 (internet version): www.jncc.gov.uk/MarineHabitatClassification
- DORIS *Données d'Observations pour la Reconnaissance et l'Identification de la faune et la flore Subaquatiques*. The *R. dubia* page is at: <https://doris.ffesm.fr/index.php/Especes/Rocellaria-dubia-Mye-perce-pierre-2774>
- DONOVAN SK, FEARNHEAD FE & UNDERWOOD CJ 2007 Recent borings in limestone cobbles from Marloes Bay, southwest Wales. *Lethaia*, **40** 233–236.
- EUROPEAN COMMISSION DG ENVIRONMENT 2013 *Interpretation Manual of European Union Habitats*, Eur 28. April 2013. Page 13.
- FAVA F, PONTI M & ABBIATI M 2016 Role of Recruitment Processes in Structuring Coralligenous Benthic Assemblages in the Northern Adriatic Continental Shelf. *Plos One* **11** (10) <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0163494>
- GBIF 2021 (Global Biodiversity Information Facility) at: *Rocellaria dubia* (Pennant, 1777) in GBIF Secretariat. GBIF Backbone Taxonomy. Checklist dataset <https://doi.org/10.15468/39omei> accessed via GBIF.org in June 2021.
- HAYWARD PJ & RYLAND JS 2005 (Eds) Handbook of the marine fauna of North-West Europe. OUP.
- HISCOCK K 1996 (ed.) Marine Nature Conservation Review: Rationale and methods. Coasts and seas of the United Kingdom. MNCR series. Joint Nature Conservation Committee, Peterborough: SACFOR scale abundances <https://mhc.jncc.gov.uk/media/1009/sacfor.pdf>
- IRVING R 2009 The identification of the main characteristics of stony reef habitats under the Habitats Directive. Summary report of an inter-agency workshop 26–27 March 2008. *JNCC Report No.* 432.
- MORTON B, PEHARDA M, PETRIC M 2011 Functional morphology of *Rocellaria dubia* (Bivalvia: Gastrochaenidae) with new interpretations of crypt formation and adventitious tube construction and a discussion of evolution within the family. *Biological Journal of the Linnean Society* **104**: 786–804.
- OLIVER PG, HOLMES AM, KILLEEN IJ & TURNER JA 2016 *Marine Bivalve Shells of the British Isles*. Amgueddfa Cymru – National Museum Wales. Available from: <http://naturalhistory.museumwales.ac.uk/britishbivalves> [Accessed: 06 June 2021].
- NBN (National Biodiversity Network) Atlas at: https://records.nbnatlas.org/occurrences/search?taxa=&q=lsid%3ANHMSYS0021054513&fq=&wkt=&lat=&lon=&radius=&dir=&offset=240&max=20#tab_map Viewed June 2021.
- OWEN NJW 2019a *A Diver's Guide to Sediment Veneers* Dorset Seasearch, limited circulation.
- OWEN NJW 2019b Sediment Veneers *Bulletin of the Porcupine Marine Natural History Society* **11** 36–43.
- PICTON, BE MORROW, CE (eds.) Encyclopedia of Marine Life of Britain and Ireland <http://www.habitas.org.uk/marinelife/>
- SCHIAPARELLI S, FRANCI G, ALBERTELLI G & CATTANEO-VIETTI R 2005 A Nondestructive Method to Evaluate Population Structure and Bioerosion Activity of the Boring Bivalve *Gastrochaena dubia*. *Journal of Coastal Research* **21**(2) 383–386.
- TEBBLE N 1976 *British Bivalve Seashells, A Handbook for Identification*. Royal Scottish Museum/HMSO (Edinburgh) second edition.

