<table>
<thead>
<tr>
<th>Title</th>
<th>Dispersal mode and assessments of recovery on the shores of Gruinard, the 'anthrax island'.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author(s)</td>
<td>Johnson, Mark P.</td>
</tr>
<tr>
<td>Publication Date</td>
<td>2008</td>
</tr>
<tr>
<td>Publisher</td>
<td>Springer Verlag</td>
</tr>
<tr>
<td>Link to publisher's version</td>
<td><a href="http://dx.doi.org/10.1007/s10531-007-9307-y">http://dx.doi.org/10.1007/s10531-007-9307-y</a></td>
</tr>
<tr>
<td>Item record</td>
<td><a href="http://hdl.handle.net/10379/310">http://hdl.handle.net/10379/310</a></td>
</tr>
<tr>
<td>DOI</td>
<td><a href="http://dx.doi.org/10.1007/s10531-007-9307-y">http://dx.doi.org/10.1007/s10531-007-9307-y</a></td>
</tr>
</tbody>
</table>
Dispersal mode and assessments of recovery on the shores of Gruinard, the ‘anthrax island’

Mark P. Johnson¹*, Sankurie Pye², and Louise Allcock¹,²

¹School of Biological Sciences, The Queen's University of Belfast, 97 Lisburn Road, Belfast, BT9 7BL, Northern Ireland

²Department of Natural Sciences, National Museums Scotland, Chambers Street, Edinburgh, EH1 1JF, UK.

*Author for correspondence m.johnson@qub.ac.uk
Abstract

Formaldehyde run-off was an unintended impact of the anthrax decontamination procedure on the island of Gruinard. The death of intertidal organisms was observed where formaldehyde reached the shore during 1986. The extent to which shores on Gruinard have recovered was assessed with survey work in 2000. Recovery estimates were based on the hypothesis that the process of recolonization is partly dependent on species’ dispersal capability.

Underdevelopment of the assemblage of species lacking planktonic dispersal stages (direct developers) is therefore evidence that the process of recolonization is ongoing, rather than complete. A novel multivariate test showed that, when comparing quadrats from Gruinard and nearby mainland shores, assemblages of direct developing molluscs were significantly more distinct than assemblages of molluscs with planktonic dispersal stages. The average densities of species with direct development were generally lower on Gruinard than on mainland shores. While some species with direct development have similar densities on Gruinard and on the surrounding shores, the recovery of the overall assemblage was still incomplete after 14 years. In contrast, the harvested species, Littorina littorea, appeared to benefit from the absence of humans visiting Gruinard’s shores. Populations of L. littorea on Gruinard contained significantly higher proportions of large individuals. Depending on the dispersal capabilities of different species, Gruinard is either still in recovery or acts as a reserve.

Key words: rafting, recolonization, spatial scale, structure index
Introduction

Patterns of species’ distribution and abundance are traditionally used in ecology to make inferences about the processes creating spatial variation in biodiversity. Such studies range from broad scale analysis of latitudinal gradients to studies of the intended or unintended impacts of habitat modification. As the large-scale destruction of biodiversity is generally unacceptable, many studies of the process of assemblage recovery and change are carried out in the context of ‘natural experiments’: volcanic eruptions, oil spills and other impacts. In theory, the dispersal capability of species is an important factor in the recolonization of disturbed sites. Evidence for dispersal-limited recolonization, however, is equivocal (Flinn and Velland 2005). If variation in dispersal does affect the recolonization process, this has implications for the design and effectiveness of protected area networks, particularly where there is an element of community reassembly (as is often the case in establishing marine reserves, Micheli et al. 2004). We were able to use an impact on the island of Gruinard to test whether dispersal mode has an influence on the recolonization process.

Gruinard (211 ha, 56° 56’ N, 5° 35’ W) is best known as a site of biological warfare trials during the Second World War. These trials contaminated the island with the causative agent of anthrax (Bacillus anthracis). The post war persistence of B. anthracis spores resulted in a ban on human occupation or livestock grazing (Miles et al. 1988). Continued monitoring of the island’s soils indicated that contamination was strongest around a site where bombs containing anthrax had been detonated (Manchee et al. 1994). As this site was relatively small, a biocide treatment was proposed to decontaminate the island. The biocide treatment, applied in 1986, used approximately 2200 m³ of 5% formaldehyde in seawater solution. Soils in a 4.1 ha area around the bombsite and at a coastal site where diseased animals were kept were irrigated with 50 l m⁻² of the formaldehyde solution (Manchee et al. 1994). Additional
treatments included injections down to the bedrock of 37% formaldehyde. These injections were targeted on sites where subsurface anthrax patches appeared to persist (Manchee et al. 1994). Unfortunately, the potential for formaldehyde run-off from the treatment area was underestimated. At least one section of shore was sterilized to the low water mark (Miles et al. 1988). Although some recolonization by common species with a plankonic dispersal stage (limpets, barnacles and green algae) was noted in Miles et al. (1988), there has been no comprehensive survey of Gruinard and adjacent shores since the decontamination was carried out.

Gruinard is in a bay that contains habitats found on the island, implying a potentially large supply of recruits to intertidal assemblages. Species recolonising following the formaldehyde treatment will arrive by rafting or by planktonic dispersal. Rafting is generally assumed to be a rare event (although see Colson and Hughes 2004), so species dependent on this mode of dispersal (direct developers that lack a free swimming larval stage) may be relatively rare on the island even some time after the disturbance from formaldehyde. In contrast, species with a planktonic dispersal scale of a few km are likely to reach Gruinard from an extensive area of source habitat. A relatively reduced contribution of direct developers to the existing island assemblages would therefore indicate that mode of dispersal affects the recolonization process. While the importance of life history characteristics on recovery processes is widely appreciated, explicit comparisons among species with different characteristics are generally rare (but see Reed et al. 2000). We propose and test the concept that multivariate comparisons between ‘direct developer’ and ‘planktonic disperser’ assemblages offer a route to identifying the extent of recovery in marine systems.
**Methods**

(a) **Survey work**

A survey of the intertidal diversity on Gruinard and in adjacent areas was carried out in September 2000 using a hierarchical design of two shores on Gruinard and two shores in Gruinard bay (Fig. 1). Shores were chosen at random from the available rocky shores accessible by boat or on foot. Comparison of the shores on Gruinard with those nearby tests the potential impact of the formaldehyde treatment against an estimate of the background level of biodiversity in the region. Estimates of smaller scale heterogeneity were made in the hierarchical design by sampling two sites separated by approximately 100 m at each shore. There were six 0.25 m$^2$ quadrats thrown haphazardly at each site, both at the mid tide level (MTL) and just above the level of spring tide low water (LWS).

The influence of dispersal mode on assemblage composition was tested using molluscs, a phylum where dispersal mode has been previously shown to affect spatial and temporal patterns of abundance (Johnson et al. 2001, Eckert 2003). In addition, molluscs have been considered to represent a good surrogate for intertidal biodiversity (Smith 2005).

Molluscs were collected from quadrats by removing all visible individuals. Macroalgae and other loose material (barnacle tests and attached shells) were also scraped from quadrats where present. Molluscs associated with the scraped material were collected using a freshwater wash and 1 mm sieve. Collected molluscs were fixed in formalin (4% in seawater) and transferred into industrial methylated spirits (74%) after four days. Species were identified using Tebble (1966), Jones and Baxter (1987), Graham (1988), Thompson (1988) and Reid (1996). The full list of species with authorities and dispersal modes are given Table 1. Details of dispersal mode follow Johnson et al. 2001, with additional information from

*Littorina neglecta* has been considered as an ecotype of *L. saxatilis* (Reid 1996). Separating the taxa, as done here, has little effect on the analyses, as the presence of *L. neglecta* does not contribute much to the differences between mainland and island. Processed material was catalogued and deposited in the National Museums Scotland (NMSZ:2003113).

(b) Multivariate analyses

Multivariate comparisons of assemblage variation among quadrats were made using the Bray-Curtis coefficient, following $x^{0.25}$ transformations of count data (Johnson et al. 2001). A Bray-Curtis dissimilarity coefficient of zero indicates identical assemblages in a pair of quadrats, with a coefficient of 100 indicating no species in common. Calculating all possible pairwise dissimilarities among quadrats gives a matrix of coefficients. Each number in such a dissimilarity matrix results from a comparison between a pair of quadrats at a particular scale (within a site, between sites in a shore, between shores on the island or mainland and between the island and mainland). Means of quadrats at the four scales can therefore summarize the spatial pattern of biodiversity. The means can be compared in a hierarchical dissimilarity plot (Lavery and Vanderklift 2002, Johnson et al. 2005). If species are distributed at random, the means will not change with scale and the line in a hierarchical dissimilarity plot will be horizontal. If there is additional variation at the mainland/island scale beyond that which exists when comparing pairs of shores, the mean dissimilarity will increase between the shore and mainland/island scales.

Each quadrat supplies information about the distributions of direct developers and planktonic dispersers. While these patterns can be analysed separately and then compared, the data can also be combined to provide a test of the relative change in life history assemblage.
composition with scale. A measure of the relative structure associated with different dispersal
modes can be calculated by subtracting the dissimilarity between a pair of quadrats calculated
using planktonic dispersers from the dissimilarity for the same quadrat pair calculated using
direct developers. A null expectation for values of this relative assemblage structure index
(abbreviated hereafter as ‘structure index’) would be for random fluctuations in means
calculated at different spatial scales. If the formaldehyde treatment has caused distinct
differences between the mainland and Gruinard associated with dispersal mode, then the
means for the structure index at different scales will not fluctuate randomly around the overall
average index value. In particular, a relatively stronger treatment impact on direct developers
will cause the structure index to peak at the largest spatial scale in the hierarchical design.

Differences from the null expectation of no change in structure index with spatial scale were
assessed with a randomisation test. By randomly assigning structure index values from pairs
of quadrats to each of the four scales in the hierarchical design, a distribution of means can be
produced. The number of quadrat pairs involved in this is a function of spatial scale. At the
within site scale there are 120 pairs, with 144 pairs between sites in a shore, 288 pairs
between shores on the island or mainland and 576 pairs between the island and mainland. To
generate a test statistic in the randomisation test, quadrat pairs were shuffled and allocated to
one of the four means with numbers of measurements divided as appropriate. The differences
between each mean and the overall mean structure index (n = 1128) were squared and then
summed to produce a test value that should lie close to zero under the null hypothesis of no
structure associated with means at different scales. The distribution of this test value after
1000 randomisations provides the basis for a test of the significance of the observed pattern of
structure index means. If the sum of squared differences between the observed means and the
overall mean lies in the tails of the derived distribution (α 0.05), then the hypothesis of no
spatial structure can be rejected. Rejection of the null hypotheses implies that the multivariate
distance between quadrats varies with development mode and that the magnitude of this effect
is a function of spatial scale. The largest spatial scale tested was the comparison between
mainland and island, allowing a test of the differential recovery hypothesis. Randomisation
tests were carried out using the Monte Carlo algorithms in Poptools
(http://www.cse.csiro.au/poptools/index.htm). As the design in Johnson et al. (2001) was
similar to the Gruinard survey, with the exception of a mainland-island comparison, data from
this study were also analysed for spatial pattern in the relative structure of direct developer
and planktonic disperser assemblages. This comparison was only possible for LWS as no
quadrats were sampled from MTL in Johnson et al. (2001).

**Results**

A total of 17 species with direct development and 27 species with some form of planktonic
dispersal were recorded in the survey. As would be expected, the average dissimilarity
between pairs of quadrats generally increased with spatial scale (Fig. 2). At the largest scale
of comparison, between mainland and island, there was no additional dissimilarity in the
planktonic disperser assemblage. Mainland and island shores were no more dissimilar than
pairs of island shores or pairs of mainland shores. The drop in mean dissimilarity of
planktonic dispersers at LWS from the between shore to the between island/mainland scale
implies that, for this assemblage, differences between Gruinard and nearby coasts are actually
less than the average difference between shores on Gruinard (or between shores on the
mainland coast). In comparison to the pattern observed in the planktonic disperser
assemblage, there was additional dissimilarity for direct developers when moving from a
between shore comparison to a between mainland and island comparison.
There were relatively large changes in the mean structure index calculated at different scales (Fig. 3). All three patterns in Figure 3 differed significantly from the null hypothesis of no change in structure index with spatial scale (p < 0.05). In most comparisons using data from Gruinard and the adjacent shores, pairs of quadrats were relatively more dissimilar on the basis of the planktonic disperser assemblage than was the case when using a direct developer assemblage. The exception to this pattern was when comparing quadrats between the island and the mainland. At this scale the relative dissimilarities between quadrats based on a direct developer assemblage were greater than the dissimilarities based on planktonic dispersers.

Patterns in previous work from the Isle of Man are virtually opposite to those found around Gruinard. At small scales, assemblages of direct developers provided a relatively high level of discrimination between quadrats. At the largest scale, among shores, the level of differentiation between assemblages was higher when comparing planktonic dispersers.

The contrasting results across scales with planktonic dispersers compared to direct developers are mostly due to differences in relative abundances rather than differences in the presence or absence of species. When hierarchical dissimilarity plots are calculated on a presence/absence basis, there is little or no increase in average dissimilarity from the between shore to the between island/mainland scale. The role of relative abundances in generating differences between the mainland and the island can be demonstrated by comparing average abundances between the two areas. Direct developers tend to be less abundant on the island. At MTL 63% of species had higher abundances on the mainland shores. This pattern was stronger at LWS, where 85% of direct developers had higher abundances on the mainland. A binomial test suggests that the pattern of greater mainland abundances of direct developers at LWS is significant (p < 0.01, null hypothesis of mainland and island having an equal probability of
higher abundances occurring). In contrast to the pattern observed in direct developers at LWS, species with planktonic dispersal were not significantly more likely to have higher mean abundances on the mainland. The percentages of planktonic dispersers with higher mainland abundances were 46% at LWS and 64% at MTL.

Discussion

Direct developer assemblages were generally different between Gruinard and nearby mainland shores. This pattern was particularly emphasized when using the structure index to compare direct developers with planktonic dispersers. In the assemblage of planktonic dispersers the differences between mainland and island were not marked. Direct developers appear to be less well represented on the island compared to adjacent shores. The contrast between dispersal modes supports the hypothesis that planktonic dispersers have been able to recover population sizes on Gruinard, while species dependent on rafting (direct developers) were still impacted 14 years after the formaldehyde treatment. Dethier et al. (2003) found that some species with low dispersal ability had failed to colonize a remote jetty (built in 1917, modified 15 years before surveys were carried out). There were, however, no consistent differences between colonization of the jetty by planktonic dispersers and direct developers (Dethier et al. 2003). A stronger contrast between dispersal modes in Gruinard may reflect a large supply of planktonic larvae from the abundant rocky intertidal habitat at short distances from the island. In comparison, the Ocean Shores jetty is considered one of the few rocky habitat sites in along the southern coast of Washington State (Dethier et al. 2003). The differences between Gruinard Island and mainland direct developer assemblages were largest at LWS. This included a significant proportion of species where average abundances were higher on the mainland. This pattern may also reflect the importance of rafting to the recolonization process. Presumably the tide limits opportunities for rafts to land and for
species to colonize on the low shore. Unless species migrate down from colonization events
further up the shore, this will cause lower immigration rates at LWS.

Gruinard has a simple topography, which can be approximated as cone-shaped with a near-
central peak at a height of 345 m. The formaldehyde treatment site was south of the island’s
centre, so much of the run off is likely to have entered the sea on the southern shores of the
island. This is reflected in the observations by Miles at al. (1988). Although tidal advection
and diffusion may have carried formaldehyde to the north shore of the island (where one of
the survey sites was located), the biocide concentration is likely to have been lower away
from the south of the island. Despite the probable between-shore variation in formaldehyde
impact, the direct developer assemblage on the island was still distinct from the mainland. In
other words, the between-shore variation on the island was still less than the multivariate
differences between island and mainland. Closer examination of the variation between the
shores on Gruinard supports the hypothesis of a differential impact. Average abundances on
the northern shore were higher for all species (n =11) with direct development for samples
taken at LWS. The pattern at MTL was not quite as strong, 78% (n = 14) of species present on
the island had higher abundances on the north shore compared to the south. The proportions
of species with higher abundances on the north shore are unlikely to have occurred by chance
if there was an equal probability of the largest mean occurring on the north or south of the
island (binomial test, p < 0.001 for LWS). The patterns for species with planktonic dispersal
do not suggest a greater impact on the south of the island, in agreement with the idea that
these species are able to recover more rapidly from the biocide treatment. At LWS 47% (n =
17) of species had higher abundances on the north coast while the equivalent figure for MTL
was 73% (n = 15). Neither of these proportions differs significantly from the expectations of
an even distribution of abundances between shores.
Even if the immediate impact of formaldehyde run-off on the north shore of Gruinard was minor, direct developers may still have been affected by the decontamination treatment. Direct developers may be more affected by the availability of local habitat than species with planktonic dispersal. For species with an ecologically significant larval supply, the amount of local habitat is not likely to influence local population size unless space becomes limiting. In contrast, the local persistence of direct developers is dependent on reproduction by local individuals. The chance of successful local reproduction is likely to be larger when the local habitat encompasses enough environmental heterogeneity that an event such as a storm cannot remove the entire population. The extent of local habitats will also be important if as, as hypothesised in Johnson (2006), species with direct development exist in small-scale metapopulations. In this situation, a metapopulation of direct developers exists as a network of patches where each patch is founded by a small number of colonization events. A consequence of this spatial structure is that the metapopulation needs a threshold number of patches (dependent on habitat extent) to persist. As yet little is known about the dispersal kernel for rafting species. Long distance dispersal occurs, but fine scale genetic structure in species with direct development suggests a generally low level of dispersal (Colson and Hughes 2004). If most recolonization events from rafting are dependent on nearby shores, the loss of a potential local source will reduce the number of patches on a shore. Hence the loss of species from the south of Gruinard may have affected shores on the northern coast by removing an important source of colonists. Better information on colonization and extinction rates for direct developers is needed to evaluate this hypothesis and the importance of habitat extent to species’ persistence.
An alternative hypothesis to a dispersal-based differential recovery is that the shores of Gruinard would differ from the mainland with respect to direct developers regardless of the formaldehyde treatment. As in any retrospective impact study, it is not possible to discount this possibility. The assemblages of direct developers and planktonic dispersers, however, contain species with a variety of overlapping life spans, trophic levels and preferred habitats. There is no clear environmental reason why such diverse assemblages should have varied in the manner observed. Differential recovery based on dispersal is the most parsimonious explanation for the observed patterns.

With the exception of the formaldehyde treatment, Gruinard has acted as a nature reserve. The military use, quarantine and current private ownership have all restricted public access and use of the island. There is no permanent dwelling on the island. One species that may have benefited from the absence of visitors is the winkle, *Littorina littorea*. This species is widely harvested around the UK and Ireland, both for local consumption and for export (Cummins et al. 2002). Populations on the island had a higher proportion of large individuals than the mainland shores. Pooling all individuals per shore, the average proportion of *L. littorea* $> 2.5$ cm shell length was 0.18 (SE 0.030) compared to 0.03 (SE 0.016) on the mainland ($t = 4.53, p < 0.05$). This result reflects those found in many studies of reserves (e.g., Roy et al. 2003) and presumably occurs as the consequence of 14 years without harvesting.

There are large differences in the structure index variation patterns seen in the Gruinard and Isle of Man surveys. The shores in the Isle of Man are not thought to have been affected by any major disturbance. The scale related changes in structure index reflect the interpretation of Johnson et al. (2001): Small-scale colonization events by direct developers cause this assemblage to be spatially relatively more structured than planktonic dispersers within sites.
and within shores. Among shores, however, hydrographic processes cause relatively larger
differences in species with dispersing larvae than in rafting species. Variation in structure
index within the Gruinard survey demonstrates the overriding influence of a difference in
direct developer assemblages at the island-mainland scale.

In conclusion, a comparison based on the dispersal capabilities of groups of species identified
a long-term (14 year) impact of the formaldehyde treatment on Gruinard. Studies based purely
on biodiversity without information on dispersal capability would not have identified this
impact. For example, a dissimilarity plot made from a matrix containing both direct
developers and planktonic dispersers suggests no mainland-island differences. It would be
useful to put a timescale on the recovery of limited dispersal species. At this stage, however,
there are few studies for comparison and potential causes of variation in recovery rates are
confounded. Reed et al. (2000) suggest regional differences in the recovery of ‘limited
dispersal’ species that range from 2 years to over 10 years. The Gruinard survey differs from
Reed et al. (2000) in the conspicuousness of the species, distance between sites and likely
content of founder assemblages following disturbance. A wider use of comparative
multivariate analyses is likely to improve our understanding of both the timescales of
assemblage recovery and the factors that influence this process.
Acknowledgements

Lesley Florence, Susan Chambers and Fiona Ware assisted with fieldwork. We thank the owners of the island for permitting access.
References


Ockelmann, K. W. (1965) Development types in marine bivalves and their distribution along
the Atlantic Coast of Europe. Proceedings of the first European Malacological
Congress (1962) p. 25-35.

Reed, D. C., Raimondi, P. T., Carr, M. H. and Goldwasser, L. (2000) The role of dispersal
and disturbance in determining spatial heterogeneity in sedentary organisms. Ecology
81: 2011-2026.


impacts and historical decline in body size of rocky intertidal gastropods in southern

there's a whelk there's a way. Biodivers Conserv 14:3565-3576.


**FIGURE CAPTIONS**

Figure 1. Gruinard Island and bay. Sampling sites are indicated with star symbols.

Figure 2. Hierarchical dissimilarity plots showing the change in mean dissimilarity between quadrats at different spatial scales. Survey data are divided into (a) species with planktonic dispersal stages and (b) species with direct development. Dotted lines are data collected at low water springs (LWS) and solid lines are data from the mid tide level (MTL). Error bars are SE.

Figure 3. Relative structure index values comparing the mean dissimilarity between quadrat pairs based on direct developer assemblages to the dissimilarity between the same pairs based on planktonic dispersers. (a) mid tide level, (b) low water springs and (c) comparison with Johnson et al. (2001) data for the Isle of Man. No equivalent of the mainland-island comparison occurs in the Isle of Man data. Positive values imply that quadrat pairs have relatively more divergent direct developer assemblages than planktonic disperser assemblages. Dotted lines show estimated 95% confidence intervals around the mean structure index value. Plots are centred on zero by subtracting the overall (n = 1128) mean index value from the averages calculated at each separate spatial scale.
Table 1. Taxa identified in material from the Gruinard survey. Dispersal modes, where known, are indicated by Pl = planktonic dispersal stage, Dd = direct development. Average abundances at the different shore heights (per quadrat) are indicated as 0 absent, * 0-1, ** >1-10, *** >10-100, **** >100-1000, ***** >1000 individuals.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Dispersal mode</th>
<th>Mainland MTL</th>
<th>Gruinard MTL</th>
<th>Mainland LWS</th>
<th>Gruinard LWS</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acmaea virginea</em> (Müller O.F., 1776)</td>
<td>Pl</td>
<td>0</td>
<td>*</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td><em>Alvania beani</em> (Hanley in Thorpe, 1844)</td>
<td></td>
<td>0</td>
<td>0</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td><em>Alvania punctura</em> (Montagu, 1803)</td>
<td>Pl</td>
<td>0</td>
<td>0</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td><em>Anomiacea</em></td>
<td></td>
<td>0</td>
<td>0</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Bittium reticulatum</em> (da Costa, 1778)</td>
<td>Pl</td>
<td>0</td>
<td>*</td>
<td>**</td>
<td>0</td>
</tr>
<tr>
<td><em>Brachystomia albella</em> (Lovén, 1846)</td>
<td></td>
<td>**</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Brachystomia eulimoides</em> (Hanley, 1844)</td>
<td></td>
<td>**</td>
<td>0</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td><em>Brachystomia lukisi</em> (Jeffreys, 1858)</td>
<td></td>
<td>**</td>
<td>0</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Brachystomia rissoides</em> (Hanley, 1844)</td>
<td></td>
<td>*</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Calliostoma ziziphinum</em> (Linnaeus, 1758)</td>
<td>Dd</td>
<td>0</td>
<td>0</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td><em>Cardiacea sp juv</em></td>
<td></td>
<td>0</td>
<td>0</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td><em>Cerithiopsis barleei</em> Jeffreys, 1867</td>
<td>Pl</td>
<td>*</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Species</td>
<td>Author</td>
<td>Page</td>
<td>Plate</td>
<td>Dies</td>
<td>Dd</td>
</tr>
<tr>
<td>--------------------------------------</td>
<td>------------------</td>
<td>------</td>
<td>-------</td>
<td>------</td>
<td>------</td>
</tr>
<tr>
<td><em>Cingula trifasciata</em> (Adams J., 1800)</td>
<td></td>
<td>Dd</td>
<td>***</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Collisella tessulata</em> (Müller, 1776)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td><em>Doto sp.</em></td>
<td></td>
<td>Pl</td>
<td>0</td>
<td>0</td>
<td>**</td>
</tr>
<tr>
<td><em>Euspira catena</em> (da Costa, 1778)</td>
<td></td>
<td></td>
<td>0</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td><em>Gibbula cineraria</em> (Linnaeus, 1758)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Gibbula umbilicalis</em> (da Costa, 1778)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>***</td>
<td>*</td>
</tr>
<tr>
<td><em>Helcion pellucidum</em> (Linnaeus, 1758)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>**</td>
<td>***</td>
</tr>
<tr>
<td><em>Hiatella arctica</em> (Linnaeus, 1767)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>*</td>
<td>***</td>
</tr>
<tr>
<td><em>Lacuna parva</em> (da Costa, 1778)</td>
<td></td>
<td>Dd</td>
<td>***</td>
<td>****</td>
<td>****</td>
</tr>
<tr>
<td><em>Lacuna vincta</em> (Montagu, 1803)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>**</td>
<td>***</td>
</tr>
<tr>
<td><em>Lasaea rubra</em> (Montagu, 1803)</td>
<td></td>
<td>Dd</td>
<td>***</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Lepidochitona cinerea</em> (Linnaeus, 1767)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td><em>Limapontia capitata</em> (Müller O.F., 1774)</td>
<td></td>
<td>Pl</td>
<td>**</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Limapontia senestra</em> (Quatrefages, 1844)</td>
<td></td>
<td>Dd</td>
<td>**</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Limapontia sp.</em></td>
<td></td>
<td></td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><em>Littorina fabalis</em> (Turton, 1825)</td>
<td></td>
<td>Dd</td>
<td>****</td>
<td>****</td>
<td>****</td>
</tr>
<tr>
<td><em>Littorina littorea</em> (Linnaeus, 1758)</td>
<td></td>
<td>Pl</td>
<td>***</td>
<td>***</td>
<td>**</td>
</tr>
<tr>
<td><em>Littorina neglecta</em> Bean in Thorpe, 1844</td>
<td></td>
<td>Dd</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>
Littorina saxatilis (Olivi, 1792)  
Margarites helicus (Phipps, 1774)  
Melarhaphe neritoides (Linneaus, 1758)  
Musculus sp  
Mysella bidentata (Montagu, 1803)  
Mytilus edulis Linnaeus, 1758  
Nassarius (Hinia) incrassata (Ström)  
Nucella lapillus (Linnaeus, 1758)  
Ocenebra erinacea (Linnaeus, 1758)  
Odostomia unidentata (Montagu, 1803)  
Onchidoridea  
Onoba semicostata (Montagu, 1803)  
Partulida spiralis (Montagu, 1803)  
Patella aspera Gmelin, 1791  
Patella vulgata Linnaeus, 1758  
Pleurobranchidae  
Retusa truncatula (Bruguière, 1792)  
Rissoa lilacina Récluz, 1843  
Rissoa parva (da Costa, 1778)  
Rissoella diaphana (Alder, 1848)
<table>
<thead>
<tr>
<th>Species</th>
<th>Genus</th>
<th>Dd</th>
<th>Pl</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Skeneopsis planorbis</em> (Fabricius, 1780)</td>
<td></td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td><em>Thracia phaseolina</em> (Lamarck, 1818)</td>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Tricolia pullus</em> (Linnaeus, 1758)</td>
<td></td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td><em>Turtonia minuta</em> (Fabricius, 1780)</td>
<td></td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td><em>Venerupis senegalensis</em> (Gmelin, 1791)</td>
<td></td>
<td>**</td>
<td>*</td>
</tr>
</tbody>
</table>