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PRIMARY RESEARCH PAPER

The European oyster *(Ostrea edulis)* and its epibiotic succession

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Abstract This study aimed to investigate intra- and inter-site differences in the epibiota on the European oyster *Ostrea edulis* of different ages and on hard substrata to assess their contribution to biodiversity. This research has shown that shells of *O. edulis* do show higher species diversity than non-living hard substrata and as oysters grow larger epibiotic diversity will increase. This investigation has revealed that *O. edulis* possesses biogenic engineering qualities and the value of *O. edulis* as a vehicle for increasing biodiversity should not be underestimated. Relatively few studies have examined the shell surfaces of *Ostrea edulis*, which, together with their associated epifauna provide a large portion of the natural hard substrata for sessile filter-feeding organisms, including oysters, in coastal and estuarine ecosystems. It can be considered a keystone species which has an influence on intertidal and subtidal community structures.

Keywords *Ostrea edulis* · Biodiversity · Epibiota · Succession

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Introduction

Large densities of oysters, particularly when they form reefs, are 'ecosystem engineers that create biogenic habitat important to estuarine biodiversity, benthic-pelagic coupling, and fishery production' (Lenihan & Peterson, 1998). Consequently, the ecological advantages which oyster assemblages provide are generally ignored to the detriment of the local marine environment (Hargis & Haven, 1995). Most studies on oyster communities, such as those undertaken in oyster restoration projects, have focussed on the diversity of the oyster assemblages themselves. Relatively few studies have examined the shell surfaces, which, together with their associated epifauna, provide a large portion of the natural hard substrata for sessile filter-feeding organisms, including oysters, in coastal and estuarine ecosystems (Myatt & Myatt, 1990) and for the early settlement stages of larger organisms. In commercial fisheries, epibiota on oysters have generally been regarded as spoiling factors (Yonge, 1966; Walne, 1974; Breitburg et al., 1995; Lenihan & Micheli, 2000). Indeed, Korringa (1946) concluded that a well-kept oyster was poor in species of 'vermin' and the shells of the Dutch oysters were rich in fauna with 68 species of sedentary and free-living animals recorded on both valves after cleaning for sale.

Korringa (1946) and Mistakidis (1951) carried out the two definitive studies on the epibiotic organisms found on the shell of the European oyster *Ostrea* *edulis*. Many of the species occurring regularly on the oyster shell were identified as characteristic epifauna of the oyster shell and true members of the oyster biocoenosis (Korringa, 1946). Both Korringa (1946) and Mistakidis (1951) recognised that *O. edulis* is not only a species beneficial to commercial fisheries but is also an important habitat for other organisms. In relation to marine conservation one of the greatest challenges lies in determining which characteristic species contributes most to their ecosystem. In the case of the coastal zone, oysters have been recognised as keystone species which can influence community structure (Ragnarsson & Raffaelli, 1999). This study aimed to investigate intra- and inter-site differences in the epibiota on *O. edulis* shells of different ages and on hard substrata to assess their contribution to biodiversity where oyster populations were undergoing natural recovery. The working hypotheses were that oyster shells would show higher diversity than non-living hard substrata and that as oysters grew older (larger) epibiotic diversity would increase.

Study area

Strangford Lough is located on the north east coast of Ireland in County Down and lies between 54°35′N and 54°20′N and between 5°41′W and 5°34′W. The Lough ranges in depth from 14 to 60 m, is approximately 32 km long and has a maximum width of 8 km (Gault et al., 1983; Service, 1993). It encloses an area approximately 150 km^2, has a tidal range of 3.5 m, an approximate volume of 1,252 × 10^6 m^3 and a tidal exchange of 350 million m^3 (Service, 1993). Salinity ranges from 32 to 34. The southern waters mix quite freely with the Irish Sea whilst the water in the northern basin is retained within the Lough for longer periods (Boyd, 1973).

Materials and methods

During July 2006 live *O. edulis* were collected from the most abundant intertidal oyster sites in Strangford Lough (Fig. 1). The sites are located in the northern basin of the lough in close proximity to a governmental Department of Agriculture sub-surface coastal monitoring buoy. The monitoring buoy recorded comparable physical parameters which included: a temperature range of 2–17.6°C, a mean salinity of 33, mean nutrient concentrations (μmol l^{-1}) of 2.8 ammonium, nitrate 13.5, phosphorus 2, and silicate 4.3 and a mean nutrient load (ton year^{-1}) of 1,202 nitrogen and 126 phosphorus for both sites during 2006 (www.afbini.gov.uk/costal).

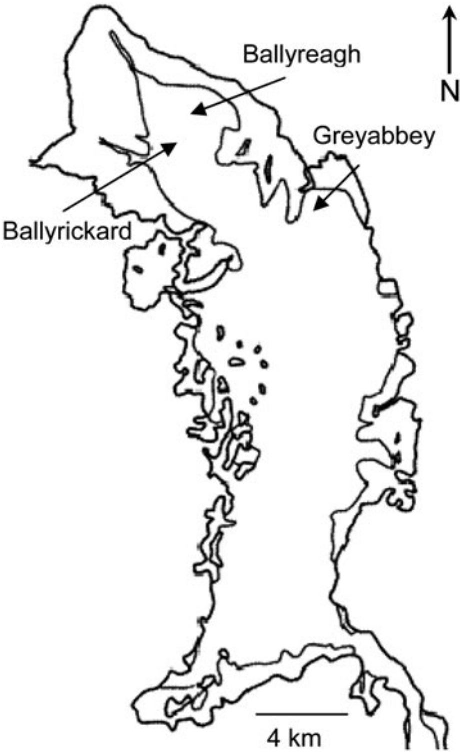

Fig. 1 Locations of survey sites in Strangford Lough, 2004

The first site Greyabbey is located at 54°31′6N, −5°33′6W near to a low water intertidal reef bordered by beds of *Mytilus edulis* and is regularly visited by shellfish gatherers (Smyth et al., 2009). The second site Ballyreagh is located at 54°34′3N, −5°40′7W, in a central channel which drains at low water and is bordered on each side by banks of *M. edulis*. Samples consisted of seventy-five oysters from each site. They were collected at each site at 0.3 m below admiralty chart datum from a 30 m × 10 m plot.

To investigate succession, oysters were separated into three size-classes based on shell lengths of <30 mm, <60 mm and >60 mm. Each size-cohort consisted of 25 oysters. On collection, each oyster was placed in a labelled zip-lock plastic sample bag taking great care not to disturb any of the epibiota of the shell. Oyster samples were immediately transferred to the laboratory and relaxed in 5% ethanol and then preserved in 70% ethanol (Mann et al., 1991). The area of coverage of the combined oyster sample was calculated, and the equivalent in loose hard substrata was collected and preserved accordingly. Each oyster was placed in a white photographic tray and examined using a dissecting microscope (×10 magnification). The procedure was repeated for the equivalent area coverage of hard substrata. Epibionts on the samples were identified to species, where possible and recorded.

In order to make an in situ comparison between the species abundance on the shell of *O. edulis* and on other hard substrata at Ballyreagh and Greyabbey, a quadrat survey was carried out within 30 × 10 m plots at each site. A 30-m transect was laid from corner to corner of the survey plot with 25 × 0.25 m^2 quadrats randomly sampled along the length of the transect line. The low shore location of the sample plots imposed time constraints due to the tidal cycle and restricted the recording of species to presence/absence. Digital images of each sample quadrat were taken for secondary analysis of species present. A species list of all epifauna recorded on hard substrata at each site was constructed from quadrat data and the corresponding digital imagery.

Data analysis

Since numbers of individuals were not recorded on hard substrata other than oyster shells, comparisons of communities on the respective substrata were based on numbers of species for univariate and presence/absence data for multivariate comparisons. Comparisons of communities on shells only were based on numbers of both species and individuals.

Diversity of the epibiota assemblages were compared using a variety of standard univariate indices and multivariate analysis. Univariate indices have limitations, and multidimensional analytical protocols are now considered to be the most appropriate tools for comparing biotic communities (Clarke & Warwick, 1994). PRIMER 5© was employed for multivariate analysis. Data were fourth root transformed, to achieve normality and to weight the relative contribution of abundant species by downgrading the skewing effect of dominant organisms. A Bray–Curtis similarity matrix was produced to determine the biological similarity of each pair of data sets, following the protocol outlined by Warwick & Clarke (1991).

The first stage of analysis involved clustering the data using a technique in which entities are sequentially linked together according to their similarity or dissimilarity producing a hierarchical dendrogram for site location and valve size and type. The Bray–Curtis similarity coefficient was applied to accurately reflect true similarity. The Multidimensional Dimensional Scaling (MDS) programme then subjected the data to ordination. In multidimensional scaling, the Bray–Curtis coefficients between each pair of sites are used to produce a map/plot which shows all relationships (Clarke & Green, 1988). A 'Stress' value of the plot is produced and is displayed in the top right-hand corner of the plot. This value measures how well the two-dimensional configuration represents the multidimensional set of relationships. When a stress value is <0.05 it can be considered an excellent expression, 0.1 is regarded as a good representation and values between 0.1 and 0.2 are still useful (Clarke & Warwick, 1994). The SIMPER programme on PRIMER 5© was used to create a similarity percentage breakdown and was employed to determine which species were responsible for the differences in the average Bray–Curtis similarity coefficients between the sites. Essentially this procedure computes the average dissimilarity between all pairs of the inter-group locations, and then breaks down the average into separate contributions from each species (Clarke & Warwick, 1994).

Results

Comparison of the diversity of epibiota on valves of *O. edulis* in different age categories

The three size-classes selected during the research provide a measure of successional change as on the oyster valve substratum. In the United Kingdom, *O. edulis* in the 30-mm size-class are considered to be 0–1 years of age (Walne, 1974) and, therefore, represent the first phase of epibiotic colonisation of the shell. A total count of 11 and 16 species were recorded on 0–1-year-old valves from Ballyreagh and Greyabbey, respectively. Shells in the 30–60-mm class are typical of 1–2-year-old oysters (Walne, 1974) representing the intermediate stages of community development. Oysters within this cohort had 28 species recorded at Ballyreagh and 39 species at Greyabbey. Oysters exceeding 60 mm in shell diameter are estimated to be 7–10 years old (Walne, 1974) and represent later stages in epifaunal community development with 38 and 78 species being recorded on shells >60 mm Ballyreagh and Greyabbey, respectively (Fig. 2a).

Species diversity and evenness measures for each replicate within size-class were calculated using the DIVERSE program on PRIMER 5©. The total number of species recorded showed a steady rise as valve size increased. At Ballyreagh numbers of epifaunal species ranged from a mean number ± 7 on the lower valves of 30-mm oysters to over 30 on oysters >60 mm in length. At Greyabbey, species numbers increased from 15, on 30-mm shells, to 78 on the upper valves of shells > 60 mm in length. Numbers of epibiotic species, numbers of individuals, Richness, Shannon-Wiener Diversity and Evenness for the size-cohorts 30 mm, <60 mm and >60 mm are displayed in Fig. 2a–c.

A one-way analysis of variance of the number of individual epibionts recorded on upper and lower oyster valves at each site in each size-class proved not to be significantly different (Table 1).

One-way ANOVA between the number of individual epibionts recorded in each size-class and site revealed significant differences (Table 2). The number of individuals and species on oyster shells was affected by size-class and site location. The most northerly of the two sites Ballyreagh produced a lower abundance of species richness and diversity throughout the three classes when compared with Greyabbey, which is situated on the northeastern shore of Strangford Lough.

Comparison of species composition on oyster shells and the neighbouring substratum

The presence/absence data for the survey plot and shell of *O. edulis* revealed the shell surface to have a greater abundance of species than the neighbouring substratum at both sites. The upper and lower valve

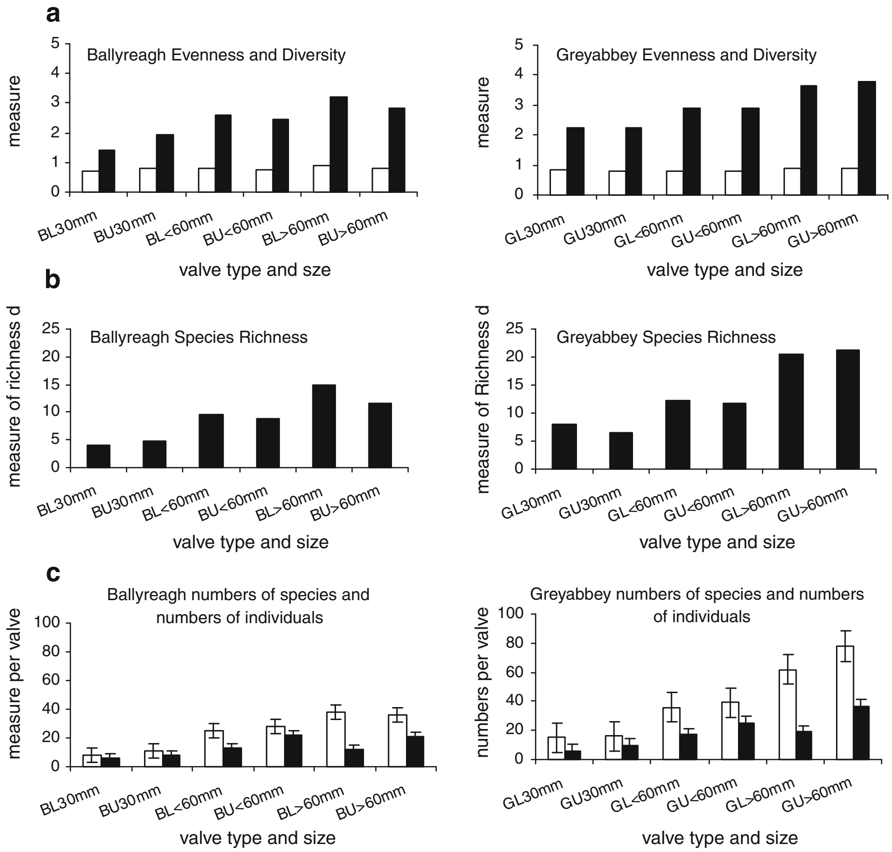

Fig. 2 **a** Number of species and number of individuals on upper and lower oyster valves in size classes 30, <60 and >60 mm (*solid*) total number of individuals, (*clear*) total number of species. **b** Species richness on upper and lower oyster valves in size classes 30, <60 and >60 mm. **c** Evenness of species distribution and species diversity on upper and lower oyster valves in size classes 30, <60 and >60 mm (*solid*) total number of individuals, (*clear*) Evenness J' (*solid*) Shannon H' (*loge*) diversity. *BL* Ballyreagh lower valve, *BU* Ballyreagh upper valve, *GL* Greyabbey lower valve, *GU* Greyabbey upper valve

Table 1 One-way ANOVA of the number of individual epibionts recorded on upper and lower oyster valves at each site in each size-class proved not to be significantly different

Variable	Source of variation	d.f.	*F*-stat	*P*-value
Valve	Species numbers (30 mm)	1	2.080	0.222
Valve	Species numbers (<60 mm)	1	0.844	0.410
Valve	Species numbers (>60 mm)	1	2.460	0.191

Table 2 One-way ANOVA between the number of individual epibionts recorded in each size-class and site revealed significant differences

Variable	Source of variation	d.f.	*F*-stat	*P*-value
Site	Species numbers (30 mm)	1	33.800	0.028
Site	Species numbers (<60 mm)	1	17.644	0.052
Site	Species numbers (>60 mm)	1	16.820	0.051

surfaces of *O. edulis* at Greyabbey produced a total of 78 species whereas random quadrat sampling on the substratum at the same site produced a total of 27 species. The differences at Ballyreagh were not so great, with 38 species recorded on the upper and lower valve surfaces of *O. edulis* and 21 species on the substratum (Fig. 3). One-way ANOVA revealed significant differences in the number of species colonising oyster valves and suitable hard substratum in the 30 mm ($F = 50.000$, d.f. 1, $P < 0.0021$) and >60 mm ($F = 20.000$, d.f. 1, $P < 0.011$) size categories. No significant differences existed in the <60 mm size-class.

When species composition data for both oyster valves and substrata were compared using MDS, two distinct groups are evident. The first group comprised oysters in the <60 and >60 mm size categories and substratum at Greyabbey. The second group consisted of all remaining samples. Within this group, oysters from Ballyreagh in the <60 and >60 mm size categories formed a clear sub-grouping (Fig. 3). Interestingly, oysters in the 30-mm size category from Greyabbey grouped more closely with this latter grouping and Ballyreagh substratum than it did with other Greyabbey samples. Upper and lower valves of oysters in each size category form high similarity pairs at each site. Differences within species numbers and diversity appear to be the influencing factors in similarity groupings in the two-dimensional multivariate plots (Fig. 3). The Greyabbey size-classes >60 mm and <60 mm and the Ballyreagh >60 mm all furnished high numbers of species and were grouped accordingly. The size-classes which recorded lower numbers of species, Ballyreagh 30 mm and <60 mm and Greyabbey 30 mm, were also grouped together (Fig. 3).

When the species composition data for the upper and lower valves of *O. edulis* were compared using Bray–Curtis Indices two distinct groups are evident. The first group comprised oysters in the 30- and-60 mm size categories at Ballyreagh and oysters from Greyabbey in the 30-mm category. The second group consisted of all the remaining samples and included oysters from Greyabbey in the <60 and >60 mm size categories and oysters >60 mm from Ballyreagh. The

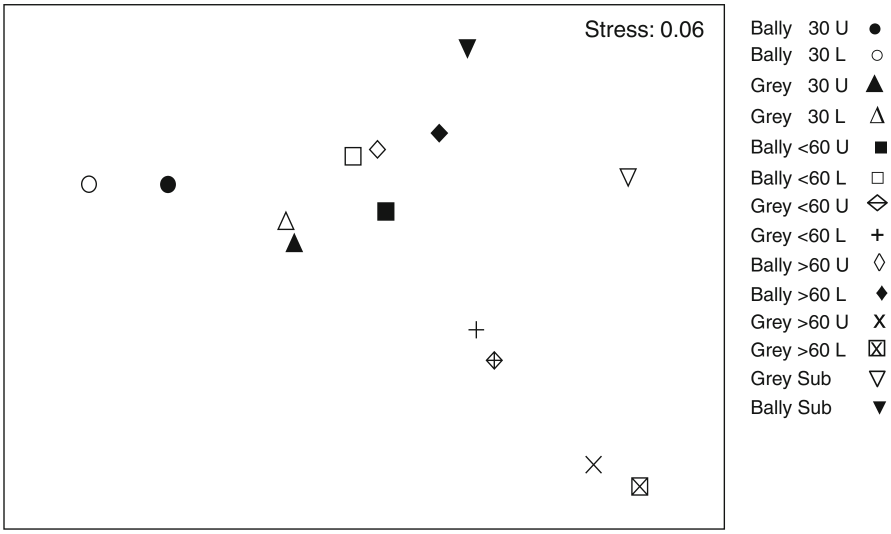

Fig. 3 MDS diagram based on Bray–Curtis similarity matrix based on the presence /absence for species and species diversity recorded on *O. edulis* valves in 30, <60 and >60 mm shell diameters and within $25 \times 0.25\ \text{m}^2$ quadrats at Ballyreagh and Greyabbey. Stress value of 0.06 indicates a good two-dimensional representation of the data

results indicate that site conditions and not the valve area are responsible for the differences in species diversity and numbers. However, more species were recorded on oyster valves than substratum at both Ballyreagh and Greyabbey (Fig. 2a).

SIMPER analysis, which determines the species that are mainly responsible for differences in Bray–Curtis similarities, was used to make inter- and intra-site comparisons of all three size-classes at the two sites. The six most abundant species which were recorded on the valves are generally considered to be 'fouling' species; *Elminius modestus,* nemertines, *Pomatoceros triqueter, Spirorbis spirorbis, Chondrus crispus* and *Mytilus edulis.* These were constantly recorded as the most common on all size-classes of oyster.

The SIMPER analysis revealed that site location influenced the epibiotic species composition and abundance of epibiota on oyster shells in all size-classes. The average dissimilarities between epibiotic communities on lower and upper valves of 30-mm oysters from Ballyreagh and Greyabbey was 36.472 and 30.370, respectively. *E. modestus, M. edulis* and *Gibbula cineraria* accounted for differences between the lower valves from the two sites whereas *Scytosiphon lomentaria, Enteromorpha intestinalis* and *C. crispus* accounted for differences between the upper valves.

The average dissimilarity between species data for the <60 mm lower valve cohorts was 45.633 and 42.034 for the upper valves. The species that differed most in frequency between sites were: *P. triqueter*, *S. spirorbis, Gammarella fucicola*, *Neoamphitrite figulus* and *Amphipholis squamata* on the surface of the lower valves and *Ralfsia verrucosa, Chaetogammarus marinus, Hymeniacidon perleve* and *G. cineraria* on the upper valves.

The average dissimilarity between species data for oysters >60 mm from Ballyreagh and Greyabbey were 44.64 for lower and 44.93 for upper valves. Species that differed most in frequency between sites were: Lithothamnia, *Lineus viridis, Modiolula phaseolina, Ralfsia verrucosa* and *Dumontia contorta* on the lower valves and *R. verrucosa, Liththothamnion glaciale,* Liththothamnia, and *Corallina officinalis* and *M. edulis* on the upper valve.

The average dissimilarity between species data for 30 and <60 mm oyster cohorts was 40.97. The species that differed most in frequency between the two size categories were *Anomia ephippium, Lineus viridis, Ectocarpus siliculosus* and *Leptochiton asellus* in the 60-mm and *Scytosiphon lomentaria* in the 30-mm category. The average dissimilarity between species data for 60 and >60 mm oysters from Ballyreagh was 38.87. Species that differed most in frequency between the two size categories were *E. modestus, S. spirorbis, Littorina littorea, Actinia equina,* and *Ciona intestinalis.*

The average dissimilarity between species for 30 and <60 mm oyster cohorts was 46.83. Species that differed most in frequency between the two size categories were *S. spirorbis* and *Tectura virginica* in the 30-mm and Liththothamnia*,* *R. verrucosa* and *Hymeniacidon perleve* in the 60-mm size category. The average dissimilarity between species data for <60 and >60 mm oysters from Greyabbey was 37.05. The species that differed most in frequency between the two size categories was *E. modestus* in the 60 mm and *Gammarella fucicola, Corallina officinalis, Hydroides norvegica* and *Tritaeta gibbosa* in the >60 mm size category.

Discussion

Temporal changes in epibiotic diversity on oyster shells

The current research into the epibiota on the shell of *O. edulis* is the first undertaken in Strangford Lough and no previous species lists are available for comparison. A number of factors may explain the differences in species diversity between the two survey sites. Ballyreagh is the most northerly *O. edulis* site surveyed in the present study and is situated in a channel between two extensive beds of *M. edulis*. The substrata of the upper northern regions of the Lough are dominated by fine muds and sands. Consequently the water column is generally turbid (Erwin, 1978; Brown et al., 1990; Kennedy & Roberts, 1999). Turbid conditions can be an influencing factor in species diversity. Moore (1977) described how suspended sediment and silted substrata restricted the settlement of planktonic larvae. The satisfactory settlement of many epifaunal organisms on hard substrata can be prevented by a layer of silt 1–2 mm in depth (Cole, 1949; Yonge, 1966; Hutchinson & Hawkins, 1992 Gosling, 2003). In a study of species abundance and diversity on intertidal oyster reefs in North Inlet, South Carolina, in waters considered to be turbid, Dame (1979) recorded a total of 37 species with a Shannon–Wiener diversity index of 2.2. Likewise in the state of Georgia at a similarly turbid site, Bahr & Lanier (1981) found a total of 42 epifaunal species on the shell of intertidal oysters with a Shannon–Wiener diversity index of 2.5. These results are comparable to those at Ballyreagh where a total of 38 species were recorded with a Shannon–Wiener index of 2.8 (Fig. 2b).

The turbidity of the water column in the northern basin of Strangford Lough is not the only limiting factor at Ballyreagh. The site is located 500 m from the Ballyrickard sewage outflow pipe. Ballyreagh would, therefore, be exposed to a potential high nutrient enrichment in the form of organic particulates and dissolved organic material which is also likely to increase suspended sediment and add to the level of turbidity at the site. The increased organic enrichment during periods of flood water run-off could result in eutrophication and increase the risk of de-oxygenation through microbial activity (Shumway, 1990; Dittman, 1997). Epibiota sensitive to these conditions will not colonise in this restrictive environment, and this was reflected in the species diversity index for Ballyreagh when compared with that of Greyabbey. A comparison of the total species list (Table 3) between the two sites shows the absence of species from Ballyreagh which are intolerant to long periods of siltation and de-oxygenation, e.g. *Halichondria panicea, Hymeniacidon perleve, Myxilla incrustans, Suberites* sp., Lithothamnia and *Corallina officinalis.* Porifera are unlikely to survive siltation for any significant length of time as the colonies rely on water movement for feeding and respiration. Sponges have a mechanism for shedding their complete outer tissue layer together with any debris (Bartol & Mann, 1997) but this probably incurs a high energetic cost. Mistakidis (1951) recorded a similar absence of sponges from turbid sites on the River Crouch in England. In the present study six species were consistently the most abundant in all three size-classes at both sites *E. modestus, M. edulis, P. triqueter, C. crispus,* Nemertea sp. and *L. cinerea.* These species were recorded in the first phase of colonisation of 0–1-year-old oysters and continued to dominate the epibiota on older oyster shells. These findings are comparable to those of Mistakidis (1951) and Waugh (1972) who also recorded the dominance of *E. modestus, M. edulis* and *P. triqueter* on all survey plots on the River Crouch in England.

Mytilus edulis was the most common species recorded on the Ballyreagh oysters and Hagmeier & Kändler (1927) reported large numbers of *M. edulis* on the oyster grounds of the North Friesian Shallows in Germany. This was due to the close proximity of large beds of adult mussels on the intertidal mud flats. Woodin (1976) suggested that large assemblages of suspension-feeding bivalves could have a negative effect on the recruitment of infaunal species due to increased consumption by filter feeders. Areas of low mussel coverage are capable of supporting greater numbers of species, as habitats suitable for both the mudflat fauna and mussel bed fauna are provided by the extra microhabitats provided within and between isolated clumps of mussels. The encroachment of *M. edulis* beds over the substratum can have negative impacts on the abundance and number of associated species. This suggests that high mussel coverage can have negative impacts such as a highly anoxic environment beneath mussel clumps, competition for food and space, and the filtration of pelagic larvae (Tsuchiya & Nishihira, 1985; Tsuchiya & Bellan-Santini, 1989; Lintas & Seed, 1994).

Chondrus crispus was the most abundant algal species recorded on the shell of *O. edulis* at both sites. The turbidity and nutrient levels at Ballyreagh are well within the tolerance range of *C. crispus*. Micheli & Peterson (1999) suggest that *C. crispus* is well adapted to living in lowlight conditions and is unlikely to be affected dramatically by any increases in turbidity. The sewage outflow may be an influencing factor in the abundance of *C. crispus* at Ballyreagh. Hydrographic conditions at both sites may account for the high abundance of species such as *C. crispus* and *M. edulis*. The spores of red algae are non-motile (Hatcher et al., 1989) and, therefore, entirely reliant on the hydrographic regime for dispersal.

The diversity of epibiota on oyster shells and the neighbouring substratum

The univariate and multivariate analysis techniques revealed no significant statistical differences between species numbers and diversity on upper and lower

Table 3 Total species list for substrata and oyster valve epibota

Total species list	*Ballyreagh substratum*	*Ballyreagh valve epibiota*	*Greyabbey substratum*	*Greyabbey valve epibiota*
Porifera				
Myxilla incrustans	0	0	0	1
Mycale macilenta	0	0	0	1
Halichondria panicea	0	0	0	1
Hymeniacidon perleve	0	0	0	1
Suberites sp.	0	0	0	1
Anthozoa				
Actinia equina	1	1	1	1
Nemertea				
Lineus longissimus	0	1	0	1
Lineus viridis	0	1	0	0
Annelida: Polychaeta				
Euphrosine foliosa	0	0	0	1
Hediste diversicolor	0	0	0	1
Pomatoceros triqueter	1	1	1	1
Spirorbis spirorbis	0	0	0	0
Lepidonatus squamatus	0	1	1	0
Lepidonotus clava	0	0	1	1
Serpula vermicularis	0	0	0	1
Neoamphitrite figulus	0	0	1	1
Sabellaria alveolata	0	0	1	1
Lanice conchilega	1	0	0	0
Hydroides norvegica	0	0	0	1
Eteone picta	0	1	0	0
Anaitides maculata	0	0	1	1
Oligochaeta				
Enchytraeus albidus	0	1	0	0
Crustacea: Cirripedia				
Eliminus modestus	1	1	0	1
Semibalanus balanoides	0	0	0	1
Copepoda				
Tisbe furcata	0	0	0	1
Isopoda				
Idotea neglecta	0	0	0	0
Idotea chelipes	0	0	0	1
Ischyroceridae				
Jassa falcata	1	0	0	1
Gammaridae				
Chaetogammarus marinus	1	0	0	1
Gammarella fucicola	0	1	0	0
Gammarus sp.	0	0	0	1
Hyalidae sp.	0	0	0	1
Caprellidea				
Caprella acanthifera	0	0	0	1

Table 3 continued

Total species list	*Ballyreagh substratum*	*Ballyreagh valve epibiota*	*Greyabbey substratum*	*Greyabbey valve epibiota*
Decapoda				
Porcellana platycheles	0	1	0	1
Carcinus maenas	1	1	1	1
Arthropod				
Tritraeta gibbosa	0	0	0	1
Mollusca: polyplacophora				
Leptochiton asellus	0	1	0	1
Leptochitona cinerea	1	1	1	1
Gastropoda				
Littorina littorea	1	1	1	1
Gibbula umbilicalis	0	0	0	1
Gibbula cineraria	1	1	1	1
Nucella lapillus	1	1	1	0
Tectura virginica	0	0	0	1
Tectura tessulata	1	1	1	0
Patella vulgata	1	1	0	1
Polinices catenus	0	0	0	1
Opisthiobranchia				
Facelina coronata	0	0	0	1
Archidoris pseudoargus	0	0	0	1
Pelecypoda				
Mytilus edulis	1	1	1	1
Ostrea edulis	1	1	1	1
Heteranomia squamula	0	1	1	1
Chlamys varia	0	0	1	1
Anomia ephippium	1	0	1	1
Modiolula phaseolina	0	0	0	1
Cerastoderma edule	1	0	0	0
Bryozoa				
Botrylloides leachi	0	0	0	1
Botryllus schlosseri	0	0	0	1
Electra pilosa	0	0	0	1
Tubulipora lilacea	0	0	1	1
Echinodermata				
Ophiura ophiura	0	0	0	1
Amphipholis squamata	0	0	0	1
Amphiura filiformis	0	0	1	1
Tunicata				
Ascidia conchilega	0	1	0	1
Ascidiella aspersa	0	1	0	1
Ciona intestinalis	0	0	0	1
Dendrodoa grossularia	0	0	0	1
Rhodophyta				
Mastocarpus stellatus	0	0	1	1
Gracilaria verrucosa	0	0	0	1

Table 3 continued

Total species list	*Ballyreagh substratum*	*Ballyreagh valve epibiota*	*Greyabbey substratum*	*Greyabbey valve epibiota*
Chondrus crispus	1	1	1	1
Ceramium rubrum	0	0	1	1
Nemalion helminthoides	0	1	0	0
Corallinales				
Corallina officinalis	0	0	1	1
Liththothamnia	0	0	0	1
Liththothamnion glaciale	0	0	1	1
Phaeophyta				
Fucus vesiculosus	1	1	1	0
Ectocarpus siliculosus	0	0	0	0
Fucus spiralis	1	1	1	0
Ralfsia verrucosa	0	0	0	1
Dumontia contorta	1	1	0	0
Scytosiphon lomentaria	0	0	0	0
Chlorophyta				
Ulva intestinalis	0	0	0	1
Ulva lactuca	0	1	0	1
Total	21	38	27	78

valves; however, multidimensional scaling revealed a clear grouping between the epibiotic species on upper and lower valves (Figs. 2a–c, 3). Cole (1949) described comparable results on *O. edulis* from beds at West Mersea, Essex, England, where both upper and lower surfaces of the shell showed equally high levels of biofouling. Cole (1949) and Yonge (1966) emphasised the fact that many *O. edulis* on soft ground lie with the hinge of the shell and part of both valves embedded in the substratum facing upwards at an angle of 45° to vertical. This positioning of settled oysters will facilitate an even colonisation of epibionts on both valves. Oysters found at Ballyreagh were on a soft mud substratum, and the majority of oysters settled in the 45° to vertical position.

Cole (1949) also suggested the evenness of epibiotic coverage on the shells was due to daily tidal disturbance when oysters were periodically turned on the ebbing and flooding tides. It is possible that tidal disturbance could explain the findings at Greyabbey as the survey plot is on a mixed shell gravel substratum located at a moderately exposed intertidal epifaunal reef. Oysters at the site could be subject to tidal tumbling as the valves are not fixed in soft substrata. Environmental factors between the two survey sites undoubtedly influenced species diversity because twice as many species were recorded on oyster valves at Greyabbey than at Ballyreagh. The findings at Greyabbey were similar to sites investigated by Korringa (1946) in the Oosterschelde in Holland, which displayed an equivalent substratum type, hydrographic conditions and a similar species count of 68 species on the oysters examined.

The significant differences in the number of species recorded on oyster valves and suitable hard substratum suggest that a pattern of succession exists during the species colonisation of oyster valves. Similar research has concurred with the current findings, Mobius (1893) listed 86 species on German oyster beds. Hagmeier & Kändler (1927) recorded 105 species on the same oyster grounds, and Mistakidis (1951) recorded 121 species at the Essex oyster grounds in England. The survey plots in comparable biodiversity studies were considerably larger than those in Strangford Lough, and it is quite possible that if a greater area had been examined at both sites the resulting species list might be considerably larger. The results suggest that the working hypotheses should be accepted and that oyster shells do show higher diversity than non-living hard substrata, and as oysters grow older (larger) epibiotic diversity will increase.

Conclusion

The loss of oysters and the habitat they create can have significant negative consequences for the sustainability economic value and biodiversity of ecosystems (Officer et al., 1982; Newell, 1988). The significance of species composition cannot be understated since organisms drive ecological processes and species differ in their traits. Species composition is likely to be one of the major determinants of stability, primary productivity, nutrient dynamics and invasibility. This research has shown that *O. edulis* possesses biogenic engineering qualities and the value of *O. edulis* as a vehicle for increasing biodiversity in Strangford Lough should not be underestimated in any future recovery programme.

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