# Epibiont species richness varies between holdfasts of a northern and a southerly distributed kelp species

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All habitats are modified to some extent by the species that live within them. Kelp is known to have a very strong influence on the surrounding environment providing a habitat for a wide range of organisms including marine mammals, fish and invertebrates. Here we examine the consequences of a subtle shift in the relative abundance of two species of kelp, Laminaria digitata and Laminaria ochroleuca, and compare the holdfast epibiont assemblages on both. These species are morphologically very similar and both provide important biologically generated habitats. The distribution of these kelp species is predicted to alter as a consequence of climate change with L. ochroleuca extending its range northward and potentially outcompeting L. digitata in the north-eastern Atlantic. The epibiont flora we found on the holdfasts was from the class Rhodophyceae. Multivariate analysis showed that the richness of epibiont species associated with L. ochroleuca was significantly lower, a mean of 0.62 species per cm<sup>3</sup>, when compared to the northern species, L. digitata which had a mean of 1.13 species per cm<sup>3</sup>. Laminaria digitata also had more unique epibiont species indicating that species richness of holdfast assemblages is likely to decline if L. digitata is replaced by L. ochroleuca. These data illustrate the importance of studying biologically generated habitats when considering the potential consequences of climate change on marine assemblages.

Keywords: kelp, epibiont diversity, holdfasts, Laminaria, climate change

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## INTRODUCTION

All organisms have an influence on their surrounding habitat and modify the environment to some degree. For example, some organisms modify physical conditions or alter the flow of resources and therefore influence the composition of surrounding assemblages (e.g. Jones *et al.*, 1997). Through the provision of a modified habitat these organisms can increase habitat complexity and, depending on environmental conditions, ameliorate stress and provide refuges (Crain & Bertness, 2006). Other organisms may modify the environment and effectively reduce the diversity of species associated with it (Hall *et al.*, 1991).

Space is a limiting resource in many shallow water habitats (e.g. Seed & O'Connor, 1981) and the presence of large macrophytes such as kelp considerably increases the heterogeneity, often transforming relatively two-dimensional habitats into complex three-dimensional environments (Bruno & Bertness, 2001). The surface of kelp and the spaces between the haptera of their holdfasts provide a substantial amount of space for colonization (Seed & O'Connor, 1981). Biologically generated habitats such as this can substantially increase diversity since they create a patchwork of environmentally variable conditions (e.g. Thompson *et al.*, 1996). The holdfast is of interest in this

**Corresponding author:** A.J. Blight Email: ablighto1@qub.ac.uk study because it exhibits the highest diversity of all the kelp structures (Thiel & Vasquez, 2000; Norderhaug *et al.*, 2002; Christie *et al.*, 2003; Arroyo *et al.*, 2004). Moore (1973a), for example, lists 389 species found on holdfasts collected from the north-east coast of Britain. Hence, kelp holdfasts are an important biologically generated habitat and have a significant modifying influence on the environment (Christie *et al.*, 2003).

To date most studies of kelp forests as a habitat have focused on the abiotic factors that affect the flora and fauna associated with them, such as geography (Sheppard *et al.*, 1977), depth (Arroyo *et al.*, 2004), seasonality (Christie *et al.*, 2003), wave exposure (Lippert *et al.*, 2001; Arroyo *et al.*, 2004), water flow (Duggins *et al.*, 1990) and pollution (Jones, 1971). Most studies have examined a single kelp species and its associated fauna and flora (Jones, 1971; Moore, 1973b; Christie *et al.*, 2003; Arroyo *et al.*, 2004), and comparisons of the flora and fauna associated with the holdfasts of two or more species of kelp are rare (however, see Berdar *et al.*, 1978; Schultze *et al.*, 1990; Thiel & Vasquez, 2000; Lippert *et al.*, 2001). The consequences of subtle shifts in kelp distribution for epibiont species richness have not previously been described.

The current study set out to examine the consequences of subtle shifts in the relative abundance of biologically generated habitats provided by different kelp species. This was achieved by comparing the holdfast assemblages of two *Laminaria* species: *Laminaria digitata* (Hudson) Lamouroux and *Laminaria ochroleuca* De La Pylaie. These species have different geographical distributions but are very similar in their

morphology. Laminaria digitata is known to have diverse holdfast fauna and flora, and there is anecdotal evidence that L. ochroleuca also supports a diverse holdfast species assemblage but there are no quantitative data. Both species are found in low intertidal and shallow subtidal rocky habitats (Gibson et al., 2001; Smirthwaite, 2006). Laminaria digitata is a cold water species distributed from Norway to the Atlantic coast of Portugal where its southern limit is set by high summer temperatures (Hoek, 1982; Figure 1). In contrast, Laminaria ochroleuca has a more southerly distribution and ranges from Morocco to north-west Europe, reaching its northern limit around the south-west coast of England (Norton, 1985; Figure 1). Laminaria ochroleuca is of interest in the context of range shifts because it is progressively extending its range northward. From its recorded appearance in the far south-west of England (John, 1969), it has progressed along the south-west coast (Norton, 1985) to its current recorded distribution as far east as the Isle of Wight and northwards on the north Devon coast (Smirthwaite, 2006). These two species of kelp therefore provide an ideal model system to examine the effects of relatively subtle species replacements on the species richness of associated organisms living within such biologically generated habitats.

## MATERIALS AND METHODS

The survey site (Figure 1), Tinside on the south-west coast of England  $(50^{\circ}21.75'N, 4^{\circ}08.60'W)$ , situated in Plymouth Sound behind a breakwater, is moderately exposed to wave action and consists of a bedrock substrate. Sampling was undertaken using SCUBA between September and November 2004. Fifteen specimens of *Laminaria ochroleuca* and fifteen *Laminaria digitata* were collected during this period. All specimens were sampled from an area parallel to the shore, below mean low water spring (MLWS) at a depth



Fig. 1. Position of the survey site and the north-east Atlantic distribution (bold line) of (A) *Laminaria digitata* and (B) *Laminaria ochroleuca*.

of 1-3 m, where stands of the two *Laminaria* species overlapped in their distribution, in order to minimize any potentially confounding effects associated with the depth/ immersion gradient. The stipe and fronds were cut from each specimen about 5 cm above the holdfast which was then immediately covered in a fine muslin bag. The holdfast was very carefully dislodged from the substrate with a lever and immediately secured in the muslin bag to prevent the loss of mobile fauna.

The age of each holdfast was determined using a method set out by Kain (1963). A thin cross-section of the stipe was taken just above the holdfast. This was examined under a stereo dissection microscope to count the appropriate growth rings and the age of all the kelp specimens used for analysis was standardized to two years. Holdfast volume was determined by wrapping each holdfast in plastic food wrapping film and dipping it into a bucket of water, to mould the film to the outer shape of the holdfast. The total volume of the holdfast was then determined by displacement. The tissue volume was calculated by multiplying the wet weight of the cleaned holdfast tissue after epibiont collection by 1.3 (specific gravity of the tissue; after Jones, 1971). Tissue volume was then subtracted from the total volume of the holdfast to give the volume of potentially habitable space amongst the haptera of the holdfast. Haptera were removed to expose the inner structure and any associated flora and fauna. Identification was to species level wherever possible using Hiscock (1986) and Hayward & Ryland (2002).

## Data analysis

For each species of kelp linear regression was used to establish relationships between holdfast volume and the number of associated epibiont species. To determine if the number of epibiont species differed significantly between the two species of Laminaria, analysis of covariance (ANCOVA) was used to compare the relationship between kelp species and number of epibiont of species, with habitat volume as the covariate. All data were tested for normality using a Kolmogorov-Smirnov test and for homogeneity of variances using Levene's test. For all epibionts, particularly colonial organisms, data were reduced to presence/absence of species on each holdfast (N = 15). A Bray-Curtis similarity matrix was generated from the presence/absence data using PRIMER (Version 5.2.0) to give the similarity in assemblage composition between kelp species. To visualize the similarity of each holdfast a multidimensional scaling (MDS) ordination was plotted giving the position of each holdfast in two-dimensional space based on its epibiont composition. Analysis of similarity (ANOSIM) was then carried out to test for differences between the epibiont assemblages of the two kelp species. Similarity percentages (SIMPER) analysis was also used to identify characteristic epibiont species for L. digitata and L. ochroleuca and indicate their contribution to the level of similarity (within a species of kelp) and dissimilarity (between the two species of kelp).

## RESULTS

A total of 130 species of epibionts were found on the *Laminaria* holdfasts, of these 57 were associated solely with *Laminaria digitata* and 19 were solely with *Laminaria* 

ochroleuca. The most commonly occurring groups unique to L. digitata were the family Tubificidae and the anemone Urticina felina (Linnaeus). The most common species unique to L. ochroleuca were the ascidians Molgula spp, the entoproct Pedicellina nutans Dalyell and the molluscs Heteranomia squamula (Linnaeus) and Modiolarca tumida (Hanley). Appendix 1 gives a complete list of the epibiont species found on both kelps. The fauna common to both species were predominantly annelids, molluscs and bryozoans. The annelids were in turn dominated by polychaetes; 27 out of the 28 species found, and the molluscs by bivalves. The most common epibiont on L. digitata was the bryozoan, Callopora lineata (Linnaeus), which was present on 14 out the 15 holdfasts and the mollusc, Modiolus barbatus (Linnaeus), which was present on 13 holdfasts. For L. ochroleuca, the most common species was the ascidian, Dendrodoa grossularia (Van Beneden), which was present on 14 holdfasts. The majority of epifauna found on both species of Laminaria were filter feeding sessile species.

The number of epibiont species increased with holdfast habitat volume in both species of *Laminaria* (Figure 2). Linear regression found the slopes to be significantly different from zero, indicating a positive relationship between habitat volume and number of epibiont species for both *L. ochroleuca* ( $R^2 = 0.3855$ ,  $F_{1,13} = 8.16$ , P < 0.05) and *L. digitata* ( $R^2 = 0.4815$ ,  $F_{1,13} = 12.07$ , P < 0.05). Regression slopes were homogeneous ( $F_{1,26} = 2.92$ , P = 0.099) allowing an ANCOVA (Table 1) to be carried out which showed the effect of habitat volume as a covariate was highly significant for both species ( $F_{1,27} = 16.13$ , P < 0.001). The difference in epibiont species number was highly significant ( $F_{1,27} = 33.41$ , P < 0.001) with *L. ochroleuca* having far fewer epibiont species, a mean of 0.62 species per cm<sup>3</sup>, when compared to *L. digitata* which had a mean of 1.13 species per cm<sup>3</sup>.

An MDS plot of the holdfast assemblages for the two *Laminaria* species (Figure 3) had a stress value of 0.22 indicating the data are only partially represented by a two-dimensional plot (Clarke & Warwick, 1994) but were better represented by a three-dimensional plot (stress = 0.16). Hence although Figure 3 helps illustrate the separation in assemblage composition between holdfasts of *L. ochroleuca* and *L. digitata* it does not fully encapsulate the data therein. Subsequent ANOSIM indicated a significant difference in assemblage composition (R = 0.336, P = 0.001). SIMPER analysis showed that the *L. digitata* holdfast assemblage had an average similarity of 38.96%. The epibiont species

digitata

0.1998x + 9.5375 $R^2 = 0.3855$ 

Fig. 2. The relationship between holdfast habitat volume and number of epibiont species per holdfast for *Laminaria digitata* and *Laminaria ochroleuca* (N = 15). Regression lines found to be homogeneous.

Habitat Volume (ml)

 Table 1. Analysis of covariance data for number of epibiont species vs

 kelp species with habitat volume as the covariate.

df	Adj MS	F	Р
1	358.98	16.13	< 0.001
1	743.47	33.41	< 0.001
27	22.26		
29			
	df 1 27 29	df         Adj MS           1         358.98           1         743.47           27         22.26           29         2	df         Adj MS         F           1         358.98         16.13           1         743.47         33.41           27         22.26           29

df, degrees of freedom; Adj MS, adjusted mean square.

Celleporella hyalina (Linnaeus), Callopora lineata, Modiolus barbatus, Fabricia stellaris (Blainville), Anomia ephippium Linnaeus, Palmaria palmata (Linnaeus) Kuntze and Nematodes contributed 50.08% of this similarity. Laminaria ochroleuca holdfast assemblages had an average similarity of 36.41%. The epibiont species Dendrodoa grossularia, Celleporella hyalina and Celleporina hassallii (Johnston) contributed 46.37% of this. These three species had the highest individual contributions towards similarity for any of the species found inhabiting the holdfasts. Celleporella hyalina contributed towards the similarity of both species of Laminaria, which is indicated by its presence on 29 out the 30 holdfasts sampled. The average dissimilarity between the two Laminaria species was 68.71%. A wide variety of fauna and flora contributed towards this dissimilarity with no individual species contributing more than 2.42%. So while assemblages differed between L. digitata and L. ochroleuca this effect was not generated by marked differences in the occurrence of one or two particular epibiont species but rather the occurrence of numerous different epibionts on each species of kelp.

#### DISCUSSION

At broad spatial scales environmental factors, including depth, wave action and tidal elevation influence holdfast morphology and epibiont species richness, therefore affecting assemblage composition (Christie *et al.*, 2003). In addition, Arroyo *et al.* (2004) suggest that factors operating at a much smaller scale of resolution may have an even stronger influence on the distribution of meiofauna within a particular *Laminaria* bed. The epibionts found in this study were both macrofauna and



Fig. 3. Two-dimensional multidimensional scaling plot of the 30 holdfasts; 15 *Laminaria digitata* (filled squares) and 15 *Laminaria ochroleuca* (open circles), based on a presence/absence Bray–Curtis similarity matrix of epibiont species collected from each holdfast (stress = 0.22).

= 0.4535x + 13.172

= 0.4815

40

35

30 25

20 15

> 10 5 0

> > 0 5 10 15 20 25 30 35 40 45 50 55 60 65 70

Number of Epibiont Specie:

meiofauna, therefore, as well as broad scale factors, subtle and small scale effects may have been important in generating the differences between *Laminaria digitata* and *Laminaria ochroleuca* observed here.

The holdfast habitat volumes of both species of Laminaria examined had a positive relationship with epibiont species richness which was in agreement with previous studies (Jones, 1971; Sheppard et al., 1977; Thiel & Vasquez, 2000). Most of the epiflora found on the holdfasts were from the class Rhodophyceae, which accounted for 12 out of the 14 species of algae found, together with Himanthalia elongata (Linnaeus) Gray (Phaeophyceae) and *Ulva lactuca* (Linnaeus) (Chlorophyceae), however, these species only occurred on one L. digitata sample. Nine of the species of algae were unique to L. digitata and the most abundant of these were Ptilota gunneri Silva, Maggs & Irvine (four of the holdfasts) and Delesseria sanguinea (Hudson) Lamouroux (three of the holdfasts). Palmaria palmata was the single most abundant species and was common to both species of holdfast. Hill (2006) made the same observation in her description of L. digitata and other studies have also found a diverse flora associated with Laminaria hyperborea (Gunnerus) Foslie in Scotland (Whittick, 1983) and Helgoland (Schultze et al., 1990) which tend to be dominated by Rhodophyceae.

In a study of marine algal epifaunas, Seed & O'Connor (1981) reported that the majority of kelp epifauna consist of filter feeding, sessile species with bryozoans, hydroids, sponges and ascidians well represented and this was very much in agreement with the results of the present work. Filter feeding molluscs were well represented on both species of Laminaria in this study. Grazing molluscs were rare on L. digitata and completely absent on L. ochroleuca. Herbivores are generally rare amongst kelp epibionts and only a few species are known to directly graze on kelp (Nybakken, 2001). Three species of bryozoan were present on nearly all of the holdfasts sampled. One of which, Celleporella hyalina, was the most common species in this study and contributed the greatest towards any similarity of these two kelp species. A similar pattern of bryozoan abundance was obtained by Lippert et al. (2001) who examined the macroalgal epibionts in Kongsford (Spitsbergen). Polychaetes dominated the annelid epibiont species found in the present study and were also amongst the most abundant species present in the holdfast communities from Norway (Christie et al., 1998) and the Cantabrian Sea (Arroyo et al., 2004).

Laminaria ochroleuca had significantly lower epibiont species richness than L. digitata. Shepperd et al. (1977) and Arroyo et al. (2004) also found faunal richness to be lower on L. ochroleuca compared to other species of macroalgae but did not examine L. digitata. ANOSIM showed epibiont community composition to be significantly different between the two species of Laminaria. However, SIMPER analysis suggested a wide variety of fauna and flora contributed towards this dissimilarity explaining some of the variance within the kelp holdfast assemblages. This pattern may in part be a consequence of reducing the data to presence/absence scores. Analysis of abundance and biomass data places more emphasis on both rare and abundant species. However, it is not appropriate to use untransformed data in this manner when they consist of both counts and percentage cover information, as was the case in the present study. The outcomes may also be modified by low taxonomic resolution in some of the groups such as 'nematodes' and 'red encrusting algae'. None the less our data provide a robust indication of the patterns of the assemblages on these two species of kelp and indicate biologically, as well as statistically, important differences and are indicative of small scale differences between biological habitats as described by Arroyo *et al.* (2004).

A possible explanation for the difference in the epibiont species richness between these two Laminaria species is the increased production of antifouling chemicals by L. ochroleuca compared to L. digitata. Many large brown algae, including kelps, produce antifoulants and these exudates are known to hinder growth and settlement (Al-Ogily & Knight-Jones, 1977) and may be significant in determining epibiont abundance and species richness. Both L. digitata (Al-Ogily & Knight-Jones, 1977) and L. ochroleuca (Sheppard, 1976) are known to exude such antifoulants. Hellio et al. (2000) extracted the exudates of a variety of marine algae and examined their effects on the development of microorganisms. They found that the extracts from L. ochroleuca had high levels of antimicrobial activity, particularly against marine fungi (Hellio et al., 2000) and exudates were also found to inhibit microalgal growth and the attachment and germination of a variety of macroalgal spores (Hellio et al., 2002). In contrast, exudates of L. digitata only had slight antimicroalgal activity and were inactive against macroalgal spores (Hellio et al., 2002). Marine fungi and bacteria are significant contributors to biofilm formation which provides a substrate for the subsequent attachment of other epibiont organisms (Hellio et al., 2000). Therefore, the inhibition of this process by antifouling chemicals could potentially limit settlement of larger organisms and result in an impoverished epibiont assemblage on L. ochroleuca.

One of the primary factors that regulate the physiology and biogeography of marine algae is temperature (Adey & Steneck, 2001). The 'climate envelope' approach, which forecasts the response of a species' geographical distribution to a single climatic variable, e.g. temperature, has been the focus of many studies (Berry et al., 2002; Pearson & Dawson, 2003; Huntley et al., 2004). Organisms at the limit of their geographical ranges are likely to be some of the first to respond to temperature changes (Lewis, 1996; Herbert et al., 2003) and a general poleward movement of species ranges is predicted in response to warming (Parmesan, 1996; Sagarin et al., 1999). For example, warm water species have been seen to extend their northern range and abundance in the English Channel in response to climate changes (Herbert et al., 2003) and any future temperature rises in this location will favour warm water species such as L. ochroleuca over the cold water Laminaria species. Hence, the northward extension of L. ochroleuca's range and the consequences in terms of reduced epibiont species richness could influence an important biologically generated habitat and potentially have consequences at a broad scale of resolution. However, species will not necessarily react as predicted by climate envelope based on their current range alone (Simkanin et al., 2005). While species distributions are anticipated to change, a variety of factors including biological interactions, which are considered here, are likely to modify the outcomes that would be predicted using climate envelope in isolation. For instance, in the present data local populations of epibiont species are likely to be strongly influenced by shifts in the relative abundance of major habitat modifying species such as kelp. Depending on the extent of alternative habitat that is available, changes in distribution of these two

habitat-forming species of kelp will likely influence the abundance and possibly the presence or absence of epibiont species. Therefore, while climate envelope predictions are invaluable for initial assessments at a broad scale of resolution, in order to provide information at a scale relevant to management of habitats, predictions of species level responses to climate change should also take a more extensive account of biological interactions (Moore *et al.*, 2007).

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	L.d	L.o		L.d	L.o		L.d	L.o		L.d	L.o
Algae			Sphaerosyllis bulbosa	1	0	Halacaridae	6	2	Cerithiopsis tubercularis	1	0
Callophyllis laciniata	1	0	Spirorbis inornatus	9	4	Chironomidae			Heteranomia squamula	0	2
Ceramium sp.	1	0	Spirorbis tridentatus	2	0	Clunio marinus	3	0	Hiatella arctica	7	5
Chondrus crispus	1	0	Tharyx marioni	1	0	Cnidarians			Hydrobia ulvae	1	0
Corallina officinalis	2	1	Trypanosyllis coeliaca	3	1	Calycella syringa	2	0	Kellia suborbicularis	1	0
Delesseria sanguinea	3	0	Trypanosyllis zebra	7	2	Clytia hemisphaerica	5	4	Lasaea rubra	1	0
Himanthalia elongata	1	0	Typosyllis armillaris	1	0	Dynamena pumila	8	1	Modiolarca tumida	0	2
Lithophyllum incrustans	1	0	Tubificidae	7	0	Gonothyraea loveni	2	1	Modiolus barbatus	13	5
Lomentaria articulata	1	1	Ascidians			Grammaria abietina	0	1	Musculus marmoratus	0	1
Palmaria palmata	10	5	Ascidiella aspera	1	1	Laomedea flexuosa	1	1	Omalogyra atomus	1	0
Phytomatolithon purpureum	6	2	Ascidiella scabra	0	1	Obelia bidentata	1	0	Onoba semicostata	1	1
Polysiphonia sp.	1	0	Botryllus schlosseri	5	6	Orthopyxis integra	2	1	Patina pellucida	1	0
Ptilota gunneri	4	0	Ciona intestinalis	1	0	Sagartia elegans	3	0	Polyplacophora	1	0
Red encrusting algae	8	2	Dendrodoa grossularia	6	14	Sarsia eximia	1	0	Rissoa parva	4	0
Ulva lactuca	1	0	Didemnidae sp.	2	2	Urticina felina	6	0	Skeneopsis planorbis	1	1
Annelids			Molgula manhattensis	0	2	Crustaceans			Tectura virginea	1	0
Branchiomma bombyx	2	0	Phallusia mammillata	1	0	Chaetogammarus marinus	0	1	Tricolia pullus	0	1
Circeis armoricana	7	3	Bryozoans			Copepod	3	1	Turtonia minuta	1	0
Cirratulus cirratus	1	0	Aetea anguina	1	0	Corophium sextonae	8	4	Nematodes	12	7
Cirratulus filiformis	1	1	Bowerbankia gracilis	1	0	Elminius modestus	3	1	Nemerteans		
Exogone naidina	1	0	Bugula stolonifera	1	0	Gammaropsis maculata	0	1	Lineus ruber	1	0
Exogone verugera	0	1	Callopora lineata	14	7	Harpacticus uniremis	1	0	Nemertopsis flavida	0	2
Fabricia stellaris	12	4	Celleporella hyalina	15	14	Laophonte similis	4	0	Prosorhochnius claparedii	1	0
Grubea sp.	1	0	Celleporina hassallii	10	13	Mesochra lilljeborgi	1	0	Platyhelminthes		
Hydroides norvegica	1	1	Cryptosula pallasiana	1	0	Microdeutopus gryllotalpa	1	0	Plagiostomum vittatum	1	1
Janua pagenstecheri	4	6	Disporella hispida	1	0	Tigriopus fulvus	0	1	Pseudostomum quadrioculatum	3	0
Megalomma vesiculosum	1	1	Electra pilosa	7	4	Tisbe furcata	3	1	Porifera		
Neanthes irrorata	5	4	Membranipora membranacea	1	0	Echinoderms			Halichondria panicea	6	3
Neoamphitrite figulus	1	1	Phaeostachys spinifera	1	9	Amphipholis squamata	2	2	Hemimycale columella	0	1
Neodexiospira pseudocorrugata	3	5	Plagioecia patina	2	3	Ophiothrix fragilis	0	1	Hymeniacidon perleve	6	3
Nereis zonata	0	0	Scruparia ambigua	0	1	Entoprocts			Mycale macilenta	2	4
Nicolea venustula	0	1	Scruparia chelata	3	1	Pedicellina cernua	4	0	Scypha compressa	0	1
Platynereis dumerilii	8	4	Tubulipora plumosa	5	10	Pedicellina hispida	1	0	Sycon ciliatum	2	1
Polydora caeca	5	6	Umbonula littoralis	1	0	Pedicellina nutans	0	2	Pycnogonids		
Polydora ciliata	1	0	Walkeria uva	1	0	Molluscs			Anoplodactylus petiolatus	1	0
Polydora giardi	1	0	Chelicerata			Alvania punctura	1	0			
Pomatoceros triqueter	4	8	Erythraeidae	0	1	Anomia ephippium	10	9			