Temporal and spatial variability of zoobenthos recruitment in a north-east Atlantic marine reserve

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Submerged artificial surface imitates newly available habitat for settlement of marine fauna. It also enables study of the timing of benthic larval settlement. Such knowledge is important if the model of possible recovery after disturbance in protected areas is to be assessed. During this study recruitment of sessile benthic invertebrate fauna at spatial and temporal scales was investigated using artificial panels submerged in the Skomer Marine Nature Reserve (Wales, UK). Panels were exchanged monthly between May 2009 and September 2011 (with the exclusion of winter time). Recruitment was highly variable with regard to time and distribution; abundance and number of recruiting species varied significantly between sites (about 2 km apart from each other), depths (6 and 12 m), position on panels (top or underside) and years without any obvious trends. The highest number of individuals and highest values of species richness were at Bernies Rocks, at the greater depth and on the underside surface of panels. Bryozoans were the dominant taxa on panels in each studied year and month. Most macrofaunal species noted on panels exhibit a colonial life strategy with short-lived, non-feeding larval stage. Although many species settle all year round, levels of settlement usually peak in summer months, showing a seasonal recruitment pattern (Bugula fulva, Spirobranchus triquetus, Chorizopora brongniarti and Escharoides coccinea). Some species had a pronounced settlement peak in spring (e.g. Electra pilosa and Balanus crenatus).

Keywords: settlement, epifauna, colonization, seasonality, fouling community, hard substrate fauna, marine reserve, Skomer

INTRODUCTION

Most sessile marine benthic invertebrates possess complex life cycles with at least two contrasting stages: an adult sessile stage alternating with a mobile and dispersive larval phase. The larval stage duration has a direct effect on the adult distribution (Thorson, 1950). The longer the larvae persist at the planktonic stage, the further they can be distributed (Todd, 1998). Therefore colonization is not necessarily dependent on local reproductive success, but is influenced more by an external and unpredictable supply of new recruits (so-called ‘supply-side ecology’ theory formulated by Roughgarden (Levin, 1986)).

It is often difficult or impossible to observe marine invertebrate settlement in situ. One of the most practical ways used to infer settlement is to study their recruitment (Zea, 1993; Mariani, 2003). Settlement and recruitment are initial steps determining the structure of population of many species (Rodriguez et al., 1993). Settlement refers to a process of transformation from a pelagic to a benthic stage of life ending with metamorphosis, while recruitment is a process of establishing a population incorporating settlement and all early post-settlement events (Olafsson et al., 1994). Understanding the processes of recruitment is important as it is the first step of community development and has significant consequences for population dynamics and structure (Young, 1990). Knowledge about recruitment processes has broad practical application, especially in marine conservation. In particular, it can be used in developing models of community succession and community recovery after severe disturbance events, when freshly cleared substrate is available for recolonization. In many habitats, patterns of recruitment may determine the direction of subsequent colonization (Gaines & Roughgarden, 1985; Mullineaux & Butman, 1990), thus predictions of local recruitment could have implications for spatial management tools in marine protected areas (MPAs) (Santangelo et al., 2012).

This study is focused on the benthic, hard substrate assemblage of Skomer Island in Wales. Biological surveys in the investigation area date back to the 1980s and were mostly based on non-destructive stereophotographic sampling techniques (Bullimore, 1986). Surveys undertaken revealed the diverse and special nature of the area and helped lead to the designation of the Skomer Marine Nature Reserve in 1990. Since then, long-term monitoring programmes have been developed and conducted on intertidal and subtidal habitats, including sponge assemblages, algal communities, sediment...
Materials and methods

Study area

The study area, Skomer Marine Nature Reserve (Wales, UK), is located in St George’s Channel between the Celtic and Irish Seas (51°43′N 5°17′E) (Figure 1). The reserve covers about 1500 ha of seabed off the coast of Pembrokeshire. The area has a wide range of habitats, including algal communities on bedrock, boulders and cobbles. The shallow rocky subtidal has a wide range of habitats, including algal communities on bedrock, boulders and cobbles. The shallow site (6 m) is in kelp located on the north side of the island, 30 m from the cliff, on bedrock, boulders and cobbles. The shallow rocky subtidal of Skomer Island supports locally rich epifaunal assemblages (Lock et al., 2003).

The two sites selected were on different sides of Skomer Island about 2 km apart (Figure 1). Thorn Rock (T) is located on the south side with moderate currents (up to 1 m s⁻¹). It is wave exposed flat bedrock with occasional cobbles and boulders. The shallow site (6 m) is in kelp forest on bedrock, while the deeper site (12 m) is a reef dominated by massive sponges (Polymastia spp., Axinella spp. and Cliona celata) and bryozoan turf. The Bernies Rock (B) site is located on the north side of the island, 30 m from the cliff, on a boulder slope swept by strong currents (up to 1.5–2.5 m s⁻¹) but sheltered from wave action. A boulder and cobbles seabed dominated by kelp and red algae is characteristic of the shallow site (6 m). The deep site (12 m) is a boulder and cobbles seabed covered with bryozoan and hydroid turf and red algae.

Results

Epibenthic assemblage on panels

Number of taxa per panel over the total time period varied between 0 and 22, with an average of five taxa. In total 55 encrusting macrobenthic taxa belonging to eight phyla were recorded on panels between June 2009 and September 2011. Twenty-two taxa were identified to species level. The number of recruits per 30 d ranged between 0 and 197 per panel. Of the total of 8864 recruits, 71% were of colonial growth forms (such as bryozoans, hydrozoans, sponges) and 29% were unitary forms (polychaetes, bivalves, cirripedes). The majority of recruiting individuals possessed a short-lived, non-feeding larval phase (65%), while planktotrophic larvae were characteristic for 31% of individuals settled on panels. The remaining 4% of individuals had unknown reproductive strategies (mainly juvenile polychaetes).

Mean number of individuals that possess short-lived non-feeding larvae was higher in comparison to recruits with long-lived, planktotrophic larvae regardless of the position on infauna and several selected epifaunal species (e.g. Alcyonium glomeratum (Hassall, 1843), Euniceella verrucosa (Pallas, 1766), Pentapora fascialis (Pallas, 1766) (Lock et al., 2003; Bell et al., 2006; Burton et al., 2008)). This is the first experimental study undertaken in this area to gain an understanding of the spatio-temporal patterns of benthic assemblages at their early stage of development during a three-year long period. Owing to the special importance of this habitat it is crucial to further investigate inter- and intra-specific interactions of recruits and their role in early community development.

Here, we aim to investigate recruitment patterns of benthic larvae in relation to the position of the substrate (top vs underside surface of panels), depth and site, and to compare recruitment of species with two different life history strategies (colonial forms with short-lived larval phase and unitary forms with long-lived larval phase). The study also reveals information on monthly (seasonal) changes in the abundance and diversity of recruits over a three year period.

Sample and statistical analysis

Only the 10 × 10 cm² central squares of each panel were inspected in order to minimize the ‘edge effect’. Panels were examined under a binocular microscope to identify colonizing organisms to the lowest taxonomical level possible.

The number of colonial organisms was calculated as number of colonies. Since the panels’ immersion period varied over the study, results were standardized to a 30 d period. The obtained abundance data were transformed by log(x + 1) in order to meet assumptions about homogeneity of variance. The differences in abundance and species richness of recruits between the two sites (Bernies Rock and Thorn Rock), two depths (6 and 12 m), two positions on panels (underside and top) and three years (2009, 2010 and 2011) for an overall number of 420 replicates, were tested using multifactorial ANOVA (STATISTICA v.6, Statsoft). One-way ANOSIM pair-wise tests were used to check dissimilarities of species composition between the two sites, positions on panels, depths and years (PRIMER package v.6, Clarke & Warwick, 2001).

Sampling protocol

In order to minimize the influence of substrate heterogeneity and for ease of replication, three black, flat Perspex panels of similar size and shape (15 × 15 cm) were submerged in water at 6 and 12 m depths at each site in May 2009 (Figure 1). The panels were attached to a horizontal metal frame which was secured on the sea floor by metal bolts screwed into the seabed. Each set consisted of three panels and each panel was treated as a subsample. The panels were removed from each frame and replaced with a new set on a monthly basis from spring to autumn until the end of the study period in September 2011. The panels were not changed between October and April due to weather conditions.

The sea temperature at the time of deployment was 12.8°C at both sites and varied between 7.8°C in April 2010 and 16.7°C in August 2009.

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panel, site and depth (Figure 2). A very similar pattern was observed when comparing the two growth forms of settling epifauna. Colonial forms dominated the recruiting fauna on both surfaces of panels, at both sites and depths (Figure 2). Moreover, the patterns in number of recruits were consistent for species with short and long-lived larvae as well as for colonial and unitary forms. In each case, there were always higher numbers of recruits on the bottom surface of the panel, at Bernies Rock and at the deeper station (Figure 2).

Bryozoans were the most abundant group (6977 individuals) followed by bivalves (1191), polychaetes (1168), cirripedes (409), sponges (342) and hydrozoans (290). Eight taxa, namely the bryozoans Chorizopora brongniartii (Audouin, 1826), Electra pilosa (Linnaeus, 1767), Escharoides coccinea (Abildgaard, 1806), Haplopora impressum (Audouin, 1826), Microporella ciliata (Pallas, 1766), Tubuliporidae indet., Crisiidae indet., the bivalve Anomia ephippium Linnaeus, 1758, and the polychaete Spirobranchus triqueter (Linnaeus, 1758), dominated in terms of population abundance and were the most frequently recorded (occurring in over 20% of samples) settling on the panels. These species represented 63% of the total abundance.

Spatial and temporal recruitment fluctuation
Site, position on panels, depth and year were significant variables influencing both the number of taxa and abundance of recruits on experimental panels (see the results of ANOVA in Table 1). There were a number of significant interactions between variables showed by multifactorial ANOVA indicating that differences in abundance varied interactively across sites with time, depth and position on panels, while differences in recruit species richness varied across sites with time and position on panels (Table 1).

A higher number of both taxa and individuals settled on the underside of the panels, with the monthly mean of about 6.5 taxa and 32 individuals per panel. On the top surface of the panels the mean number of taxa and individuals were, respectively, three and nine per panel. There was a higher monthly mean number of taxa and number of recruits at 12 m depth.

Fig. 2. Mean (± standard error) number of recruits with different larval phase and different growth forms/30 d at Thorn Rock (site T) and Bernies Rock (site B), in shallow and deep stations and on the top and underside surface of panels.
respectively 6.1 taxa and 27 individuals) compared to 6 m depth (3.3 taxa and 14 individuals). Mean assemblage abundance and number of species were significantly higher at Bernies Rock, reaching on average 5.5 taxa and 26 individuals per panel compared to 3.9 taxa and 14 individuals in Thorn Rock. The assemblage significantly changed from year to year in terms of species richness and abundance. Post hoc comparison showed significant difference between 2010 and 2011 (Kruskal–Wallis test on species richness: $z = 3.17$, $P = 0.005$, on number of individuals: $z = 3.70$, $P = 0.001$) with the highest species richness and abundance in 2011 (Figures 3 & 4).

There was significant but low dissimilarity in species composition between the two sites (ANOSIM: global $R = 0.079$, $P = 0.001$), position on panels (ANOSIM: global $R = 0.287$, $P = 0.001$), two depths (ANOSIM: global $R = 0.071$, $P = 0.001$) and among three years (ANOSIM: global $R = 0.061$, $P = 0.001$).

There were large differences in average monthly species richness and abundance between top and underside surfaces of panels. On the top surface, the average abundance was patchy and varied temporally between sites and depths (Figure 3A, C). There was an opposite trend in abundance at 6 and 12 m depth at Bernies Rock in 2009 (Figure 3C). In the deeper sites the peaks were in July and August, while in shallow sites the number of individuals reached maximum abundance in June and then decreased. At both depths at Thorn Rock the maximum abundance was in September 2009 (Figure 3A). In 2010, clear peaks were observed in September at 12 m depth at Bernies Rock and Thorn Rock. Maximum abundance in 2011 was noted in May at 6 m depth at Bernies Rock due to the occurrence of Electra pilosa (Figure 3C). At Thorn Rock the peaks in abundance were in May and September at 12 m depth (Figure 3A).

### Table 1. ANOVA on number of taxa and number of individuals.

Significant values are in bold.

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![Fig. 3](https://example.com/figure3.png)

**Fig. 3.** Mean ($±$ standard error) abundance of fauna/30 days on the top and underside surfaces of panels at Thorn Rock (T) and Bernies Rock (B), and both depths 6 and 12 m.
On the underside of panels, the faunal distribution showed a similar temporal trend at the different sites and depths (Figure 3B, D). In 2009, peaks were observed in July at Thorn Rock at 12 m depth (Figure 3B) and at Bernies Rock at 12 m depth (Figure 3D). Density of recruits rose from low values in Spring 2010 to a maximum in September at both depths at Thorn Rock (34 individuals at 12 m depth and 29 at 6 m depth) and 12 m depth at Bernies Rock (125 individuals), while at 6 m depth at Bernies Rock the peak was in August (132 individuals) (Figure 3B, D). In 2011 at Thorn Rock the average monthly abundance of recruits reached high values from June to August at 12 m depth and in July, August at 6 m depth. At Bernies Rock the highest number of recruits was noted in August at 12 m depth (158 individuals) and a much smaller peak was in July at 6 m depth (28 individuals).

Large month-to-month fluctuations were noted in species richness (Figure 4). The differences between the top and underside surfaces of the panels were particularly evident at 6 m depth. At 12 m depth if we compare both sites separately there were some common patterns on both surfaces of the panels. At Thorn Rock peaks in species richness were observed in August 2009 (six taxa on the top surface and seven taxa on the underside surface), in July 2010 (six taxa on the top and underside surface) and in July 2011 (seven taxa on the top surface and 12 taxa on the underside surface) (Figure 4A, B).

At Bernies Rock, the maximum numbers of taxa were noted in July 2009 (five taxa on the top and nine taxa on the underside surface), in July and September 2010 (four taxa and six taxa on the top surface) and in August (14 taxa on the underside surface), in 2011 in August on both surfaces (seven and 13 taxa, respectively) (Figure 4C, D). The variability between depths and sites was great. Only on the underside of panels in 2010, there was a pattern of increasing number of species at both depths and both sites until the summer months and a sudden drop in October (Figure 4B, D).

Spatial and temporal fluctuation of epifaunal groups

There were clear differences in abundance of particular faunal groups in each month. Bryozoa dominated in all studied years and months reaching the highest mean value on the underside surface of panels in August 2010 (83 individuals) (Figure 5). The only exceptions were noted in July 2009 on both surfaces of panels in favour of bivalve *Anomia ephippium* (Figure 5) and in August on the top side of panels in favour of polychaetes. The dominance of Bryozoa on panels was less pronounced in 2009 compared to 2010 and 2011. The recruitment of bryozoans reached peaks in August 2010 (82 individuals) and August 2011 (60 individuals) on the underside of panels and in September 2010 (12 individuals) and May 2011 (25 individuals) on the top surface of panels. Bivalves showed large fluctuations across years with peaks in July and October 2009 (five individuals on the top surface and six taxa on the underside surface).
in July and 32 and 13 individuals on the underside surface in July and October respectively) and very low abundance (about 0) in 2011. The hydrozoan abundance was low throughout the study period, however they were absent from panels only in October 2010. Cirripedes occurred in low numbers on panels deployed in April, May, June (with maximum mean number of individuals of 4.5 in May 2011) and then they disappeared in September and October. Settlement of polychaetes reached peaks in August or September with the highest mean value in August 2010 (22 individuals). Poriferans were most abundant in April 2011 (1.3 individuals) and in September 2011 (5.3 individuals) on the top side of panels. The top surface of panels was colonized in the majority by hydroids and sponges (Figure 6), while bryozoans, Anomia ephippium, Balanus sp. and polychaetes dominated the under surface of panels in terms of number of individuals.

Species showed diverse temporal patterns of settlement (Figure 7). There were species that settled on panels in each studied month. These were E. pilosa, C. brongniarti and E. coccinea. Although they were present from April to October, some seasonal peaks were observed, for example in May for E. pilosa and in summer months for E. coccinea and C. brongniarti. The recruitment of Bugula fulva and S. triqueter was only in summer months (June, July, August). Few species colonized panels in spring (B. crenatus) and autumn (Haplopa impressum—not shown) or both (e.g. C. dumerilii and Escharella variolosa).

DISCUSSION

The process of larval recruitment is highly unpredictable and variable (Sutherland & Karlson, 1977; Keough, 1983; Hutchinson & Williams, 2001). In the present experiment we have observed significant differences at initial stage of assemblage development in epifaunal species richness and abundance at spatial and temporal scale.

Various factors are known to influence the epifaunal recruitment success, including light availability and sedimentation rate (Maughan, 2001), water currents (Hoffmann et al., 2012), type and characteristic of substratum (Anderson & Underwood, 1994), temperature (Privitera et al., 2011), presence of a microbial film (Keough & Raimondi, 1996) and presence of resident adults (Dean & Hurd, 1980). It is worth noting, however, that the response of individual species to different factors and their intensity is highly specific thus a combination of the above factors might drive a large fluctuation in the overall pattern of recruitment. Sessile marine invertebrates may be subject to heavy post-settlement mortality (Keough & Downes, 1982; Hunt & Scheibling, 1998). Our experimental design provided favourable conditions for recruits. The colonization of panels during any one month was not intense; less than 3% of space on the panels was colonized (personal observation). We also did not trace any grazing activities on panels’ assemblages. The inhibition of subsequent larval recruitment by resident adults, as described by Boyd (1972), is also unlikely to have occurred due to the short time of assemblage development and the large areas that remained available for settlement on the panels.

Recruitment density at the studied sites in the Skomer Marine Nature Reserve was low in terms of the number of recruiting individuals and species compared to other studies of temperate marine fouling invertebrates. Over a period of 5 yr at the sea lake Lough Hyne (south-west Ireland), Watson & Barnes (2004) noted a monthly mean number of recruits of up to 4000 per panel per 30 d. In the present study the maximum mean number of recruits reached 160 recruits. Such dissimilarity may be explained by...
Different characteristics of the coastline and hydrography at these two study areas. A semi-enclosed water body such as Lough Hyne ensures greater retention and accumulation of larvae at a given site. In contrast, sampling sites at Skomer Island are exposed to constant exchange of water masses, thus continuous inflow and outflow of larvae.

Most sessile species generally display one of two different life strategies (Jackson, 1986). In the present study, species

Fig. 7. Seasonal recruitment of selected species (mean ± standard error); for bryozoans (B) the number of colonies (equivalent to settlement events) is displayed rather than number of individual zooids.
with short-lived larvae are primarily also colonial while those with extremely long-lived larvae are mainly unitary forms. The panel assemblages in the two study sites, depths and on both upper and lower surfaces were dominated by colonial recruits with short-lived larvae. At open coast sites, like our study site, the most likely explanation for this is that the local larval pool of the surrounding habitat is more important in shaping encrusting assemblage than inflow of planktonic larvae with currents. Many bryozoan species exhibit an aggregation type of settlement (Ryland, 1976), while barnacles and spirobid tubeworms larvae display even stronger attraction to resident adults of the same species during settlement event, a phenomenon called ‘gregariousness’ (Crisp, 1974).

The patterns in number of recruits were consistent when comparing the two sites, two surfaces and two depths for both species with short and long-lived larvae as well as for colonial and unitary forms. In each case, there were always higher numbers of recruits on the bottom surfaces of panels, at Bernies Rock and at deeper stations. Environmental requirements are likely to be similar irrespective of the type of larva and growth form of recruits.

### Site and depth

The large variability in species richness and abundance of epifauna between sites only 2000 m apart is noteworthy. Numbers of individuals and numbers of species were markedly higher at Bernies Rock. The reason for this variation can be attributed to the differences in water dynamics between the sites, with Bernies Rock being more exposed to water currents but sheltered from wave action.

Many sessile benthic species have pelagic larva that are dispersed with ocean currents (Todd, 1998). However, the majority of recruiting species on our experimental panels produce short-lived lecithotrophic larvae which often occur only in near sea bottom habitat and have limited dispersal capabilities (e.g. Bryozoa (Mariani, 2003), Porifera (Maldonado & Bergquist, 2002)). Their recruitment will depend mainly on reproduction success of neighbouring parental colonies and physical factors at the site of attachment. Some of the recruits on the panels in the present study produce planktotrophic larvae (e.g. S. triqueter—Polychaeta: Serpulidae (Rouse & Pleijel, 2001), nauplii of cirripedes and veligers of the bivalve A. cuneatum (Bramanti et al., 2003), or cyphonautes of the bryozone E. pilosa (Ryland, 1970)) which may have travelled long distances with the water masses. In this case, current is a very important force which brings larvae from distant places (Scheltema, 1971). Water turbulence may influence the larval ability to encounter suitable substrate and to adhere to it (Pawlik et al., 1991; Todd, 1998). Turbulent flows may stimulate active selection of suitable habitat for settlement (Pawlik & Butman, 1993) and provide better conditions for filter-feeding animals (Todd, 1998), but if flow velocity exceeds a critical value, active selection for some larvae may be impossible (Maldonado & Young, 1996). The lower number of recruits at Thorn Rock may be a result of heavy wave action at the site. Possibly such conditions prevent larvae from settling in unfavourable sites and/or cause larval resuspension and bed-load transportation (Jonsson et al., 1991).

Higher abundance and species number were observed at the greater depth. Variation in number of settling larvae, even at smaller depth intervals of 0.5 m, has been described by Osman (1977) for many common species in Woods Hole. Lower wave and tidal forces at 12 m in comparison to the shallower location may provide an explanation. A higher energy environment might lead to increased mortality and overall prevent recruitment.

### Substrate position

Overall, a higher number of species and individuals attached to the underside surface of panels. Similar settlement preference for the under surface has been noted by many authors (e.g. Shin, 1981; Glasby, 1999; Maughan, 2001). The two sides of the panels vary in light intensity, with the underside being the shaded side. Explanation for selecting the underside surfaces of panels may as well be avoidance of competition for space with algae, which generally colonize the top surface of the panels (Breitburg, 1984). In addition, a deterrent effect of accumulated silt on the top of panels has been noted for Bryozoa (Maturo, 1959). However, in our study sites exposed to strong hydrodynamic conditions, we did not observe any effect of small silt cover on the recruitment process.

Differences in epifaunal abundance linked to the position on panels may be explained by the photonegative behaviour of larvae of many species. Such larval behaviour may have developed as a response to a risk of being smothered by silt (Maldonado & Young, 1996). By choosing sheltered areas of crevices juveniles are hidden from predators. Bryozoans and serpulid larvae tend to be more successful settlers on shaded, cryptic rather than exposed surfaces (Ward & Thorpe, 1989; Cotter et al., 2003) but a range of responses to light are possible for different species (Knight-Jones, 1951; Ryland, 1977). In the present study, the upper (unshaded) surface was preferred by hydroids and sponges. The results of an experiment conducted by Glasby (1999) did not show differences in sponge cover between shaded and unshaded treatments, while in contrast to our results, Bergquist & Sinclair (1968) and Sutherland & Karlson (1977) observed photonegative behaviour during the larval stage of shallow-water sponges. The planulae of hydrozoan species may be positively or negatively phototactic before settlement (Boero, 1984).

### Between-year variation and seasonality

The experimental results provide evidence of both seasonal and year to year variations in recruitment patterns of epifauna, both in terms of species richness and abundance of recruits. The peaks in abundance occur in the summer months (July—September). Phytoplankton peaks earlier in the season (Hickman et al., 2012), therefore reproduction of organisms is likely timed to maximize food availability for the adult organisms before larval release or for some of the larvae which can feed while in the water column, rather than for settling juveniles. However, even in summer, there was considerable variation in recruitment intensity. For instance the monthly mean at Bernies Rock at 6 m depth in August varied from 10 (in 2011) up to 135 (in 2010) individuals per underside surface of panel. The duration of peaks varied between years and the peak timing differed between depths and position on panels.

Recruits of some species are present on the panels throughout the whole study period from April to October. *Electra pilosa, C. bronquintari* and *E. coccinea* can colonize panels in
each month (with no data on winter months), however some seasonal peaks are observed. *Electra pilosa* reaches the highest abundance in May, while the top abundance of *C. brongniarti* and *E. coccinea* falls in summer. Examples of strong seasonal pattern in occurrence are *S. triqueter*, *Bugula cf. fulva* and *Haplopoma impressum* which appear on panels only in summer months or *B. crenatus* occurring in May. Only a few species (e.g. *C. dumerilii* and *Escharella variolosa*) peak in both spring and autumn. Any generalization is difficult, as reproductive activity of Bryozoa varies a lot from species to species and may be correlated with day-length, with cycle of planktonic production, and with temperature and other environmental factors (Ryland, 1976). Season and associated changes in physical environment have a marked effect on reproduction and larval availability of recruits and their abundance for many marine invertebrates (Sutherland & Karlson, 1977; Keough, 1983; Turner & Todd, 1993; Underwood & Anderson, 1994; Watson & Barnes, 2004). Most species reproduce during a limited time period (as in the present study) and early composition of the assemblage is mostly a function of larval abundance during the time of exposure (Osman, 1977).

**CONCLUSIONS**

Bryozoa was the dominant taxon during one month panel exposure in each month and year both in terms of species richness and abundance. The panel assemblages in the two studied sites, at both depths and on both upper and lower surfaces were dominated by colonial recruits with short-lived larvae.

Significant variability in the recruitment of fouling communities on experimental panels between top and underside surfaces were dominated by colonial recruits with short-lived larvae.

Insignificant variability in the recruitment of fouling communities on experimental panels between top and underside surfaces was dominated by colonial recruits with short-lived larvae. Significant patchiness in the present study is the primary determinant of structure in an ecological community of the marine epifauna in Bantry Bay, Ireland. *Journal of the Marine Biological Association of the United Kingdom* 83, 41–48.

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