Biofouling in suspended cultivation of the scallop *Pecten maximus* (L.)

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By

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Traditional scallop fisheries are under thereat from declining stocks and a growing desire to conserve seabed communities. Cultivation may supplement or replace declining fisheries, providing much needed employment in coastal areas. However, cultivation is labour intensive and thus farming must be efficient, particularly around the British Isles where scallops are slow growing and labour is expensive. Fouling of scallop shells and cultivation equipment by living organisms (biofouling) increases the weight and drag of cultivation equipment and is difficult and costly to remove. It may also decrease scallop growth. This thesis investigates fouling in suspended culture of juvenile *Pecten maximus* in a high current area off the Isle of Man. I aimed to describe net and scallop fouling communities and investigate how they influenced scallop growth. Biological control of fouling was also examined.

Fouling communities on cultivation nets were examined over 10 months for nets suspended at three depths (10, 14 and 18m), from two longlines. Communities on nets immersed at two different start dates were compared to differentiate the influence of seasonality and succession. A three-tiered community, including up to 72 species, was described. Sessile foulers provided a home for mobile scavengers and predators, which were prey for resident fish. The weight of fouling reached up to 60g per gram of netting. Multivariate analyses of percentage cover and weight data suggest that community composition was influenced more by seasonal recruitment, growth and senescence than duration of immersion. Winter nets were dominated by tube forming amphipods and small hydroids. Larger hydroids arrived in the spring and by summer they occluded all net surfaces. Hydroids seemed to facilitate the recruitment of other foulers, including solitary tunicates and mussels, which colonised during the summer and, with hydroids, dominated diverse autumn communities. Weight and cover of fouling generally declined with depth, particularly between 14 and 18m. Hydroids, saddle oysters, tunicates and mussels were important foulers of scallop shells.

An *in situ* study of the environment inside cultivation nets was intended to determine how net fouling and scallop growth might be coupled. To do this a range of factors important for scallop growth were measured in water samples collected from clean and fouled nets and open water sites. Water motion was also estimated from the dissolution of plaster spheres suspended inside nets. Net fouling reduced water movement and was often associated with high levels of plankton and organic particles. The precise effects of fouling varied with season and the age of the fouling community, but obvious negative effects on the environment (reduced oxygen levels, gross accumulation of nitrate, ammonia or inorganic matter) were absent.

The affect of net fouling on scallop growth and mortality was examined by comparing growth in clean and fouled nets, at three depths, on two longlines. On one occasion shell growth was highest in fouled nets, perhaps because of increased food levels. After a year scallop muscle and other soft tissue weights were least in fouled nets. This negative effect was tentatively attributed to direct interference from foulers (e.g. irritation or parasitism). Negative effects were, however, small and easily outweighed by reductions associated with the disturbance caused by frequent cleaning. There were no consistent interactions between the effects of fouling and depth but location was sometimes important.

In biological control trials a range of invertebrates was enclosed in pearl nets with scallops, for eight months. Urchins (*Psammechinus miliaris* (Gmelin) and *Echinus esculentus* L.) and hermit crabs (*Pagurus* sp.) reduced net fouling loads and cover by up to 50% without adversely affecting scallops. They also removed soft fouling organisms from scallop shells. Both types of organism reduced fouling by solitary and colonial tunicates but only urchins reduced hydroid cover. Top shells (*Calliostoma zizyphinum* (L.)), swimming crabs and starfish (*Henricia* sp.) did not consistently reduce fouling in the exposed study area.

This study challenges common assumptions about the effects of fouling on scallop growth and the environment inside cultivation nets. The results will help scallop farmers to tackle fouling problems. Although the study is specific to a Manx location, fouling is a ubiquitous problem and the results should be widely applicable.

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CHAPTER 1 - GENERAL INTRODUCTION

1.1 Overview

Traditional scallop fisheries are under threat from declining stocks and a growing desire to conserve seabed communities. Cultivation may supplement or replace declining fisheries, providing much needed employment in coastal communities all over the world. However, cultivation is labour intensive, which can be a problem where scallops are slow growing and labour is expensive. In these areas it is especially important that scallop farming is efficient. Fouling of scallop shells and cultivation equipment is a major problem because it is difficult to remove and can reduce scallop growth rates. This thesis examines the fouling problem in detail and investigates ways in which it may be ameliorated. Although the study is specific to a location off the Isle of Man, fouling presents a similar problem worldwide and it is thus hoped that the results will be widely applicable.

1.2 Problems with traditional scallop fisheries, why cultivate?

As a luxury food with high nutritional value (Hardy 1991, Edwards 1997) scallops are exploited worldwide. Large fisheries focus on roughly twenty (various authors in, Shumway 1991) of four hundred known scallop species (Brand 1991). These fisheries are important economically, socially and culturally as a traditional source of employment for coastal communities. Currently, however, fisheries are threatened by declining stocks and growing concern over gear damage to seabed communities.

Scallops are largely sessile, often slow-growing bivalves with relatively predictable distributions, making them easy to capture. They are also a lucrative crop making them worth pursuing even when fishing efforts are high and catches are low. Ease of capture and high fishing effort combine with variable recruitment patterns (see Orensanz *et al* 1991a), making scallops vulnerable to over-fishing. Worldwide over-fishing is thought to have caused the decline or collapse of important scallop fisheries (e.g. Young and Martin 1989, Ansell *et al.* 1991, Brand *et al.* 1991, Ito 1991, Orensanz *et al.* 1991b, Stotz 1997, Arnold *et al.* 1999). Management strategies including closed seasons, no-catch zones, minimum landing sizes, gear and effort restrictions and restocking have helped to conserve or restore stocks in some areas (e.g. Brand *et al.* 1991, Parsons 1991 *et al.*, Anon 1992, Holland and Jeffs 2000). However, these measures are often associated with reduced fishing effort and thus employment.

Scallops are generally caught using dredges (with metal bars, teeth or chains), trawls, and in some inshore areas, divers. Dredges are towed along or through the seabed, often altering

its character and influencing survival and recruitment of many non-target organisms (Kaiser and de Groot 2000). Organisms are disturbed or damaged by capture or contact with dredges (Hill *et al.* 1996, Jenkins *et al.* 2001). This can remove productive communities with a range of fragile, sensitive, and slow growing species; replacing them with sparse assemblages dominated by a few robust or fast-growing species such as crabs and starfish (Eleftheriou and Robertson 1992, Veale *et al.* 2000). Sensitive species include arborescent, sessile organisms such as eelgrass, bryozoans and hydroids (Orensanz *et al.* 1991a, and references therein, Collie *et al.* 1997). These are important settlement sites for the larvae of many organisms, including scallops (e.g. Schmidt 1983, Harvey *et al.* 1993), and hence their removal is likely to further reduce benthic diversity and productivity.

Substrate heterogeneity may also be reduced by dredging; fine sediment can be suspended and lost, leaving a flattened seabed with coarse or hard substrate (Caddy 1973, Currie and Parrie 1996). This reduces niche diversity and species that cannot survive siltation may also disappear (Hill *et al.* 1997). Benthic processes are closely coupled to the pelagic ones (e.g. Hilly 1991, Sullivan *et al.* 1991, Riisgård *et al.* 1995) and so dredging probably has repercussions throughout the water-column. Scallop dredging has thus been banned in some areas as a conservation measure (e.g. Bullimore 1985, Edwards 1993).

Two species of scallops are exploited around the British Isles, the great scallop (*Pecten maximus* (L.)) and the queen scallop (*Aequipecten opercularis* (L.)). Great scallops are most valuable and make up around half of all mollusc sales from the United Kingdom, with a first sale price of 30 million pounds in the year 2000 (Briggs 2000). Most are exported to France where they are regarded as a gastronomic delicacy (Edwards 1997).

The Isle of Man is surrounded by scallop beds that have been exploited since the 1930's (Ansell *et al.* 1991). Today, the Manx fishing industry is largely based on landings of great and queen scallops (Brand *et al.* 1991). Great scallops are worth roughly two thirds of all Manx fish and shellfish landings though by weight they represent less than half of the catch. In 2000, over one thousand tonnes of great scallops (live weight) were landed with a first sale value of £1.6 million (Brand and Beukers-Stewart 2001). However, around the Isle of Man, as elsewhere, great scallop stocks show signs of over-fishing (Brand *et al.* 1991). Most worryingly, the population is precariously dominated by young individuals, making it reliant on new recruits each year (Brand *et al.* 1991, Wilson 1994). Great scallops, which recess into the sediment are caught using spring-loaded, toothed dredges (see, e.g. Hardy, 1991). These dredges dig into the substratum and there are strong indications that regular dredging has altered the local seabed and its inhabitants (Hill *et al.* 1999, Veale *et al.* 2000).

Over-fishing and habitat alteration have occurred despite the establishment of conservation measures, including minimum landing sizes and a long closed season (June – October, inclusive), as early as 1943.

Locally and globally, there is therefore continued impetus to develop or expand scallop cultivation as a profitable industry to augment or replace traditional fisheries, providing jobs and relieving pressure on natural stocks and the seabed. In addition, cultivation of juvenile scallops for reseeding is an integral part of numerous stock enhancement schemes (e.g. Ventilla 1982, Tettelbach *et al.* 1997, Arnold *et al.* 1999, Wilson 2000).

1.3 Scallop cultivation

Declining fish stocks, increasing awareness of conservation issues and rising human populations mean that fish and shellfish aquaculture is set to increase globally (New 1999, Currie 2000, Naylor *et al.* 2000). However, concern over the use of chemicals, antibiotics, fish oil and fishmeal, and the increasing price of foodstuff might hamper the expansion of finfish and crustacean operations (Naylor *et al.* 2000, Berry and Davison 2001, Millar 2001). Bivalve cultivation does not rely on the addition of food (scallops are suspension-feeders) or chemicals to the sea, distancing it from these problems (Folke and Kantosky 1989, Sorgeloos 1999, Naylor *et al.* 2000). Scallops are in demand, and advances in hatchery technology coupled with exploitation of new species and new areas are increasing the production and efficiency of farming (Hardy 1991, Edwards 1997, Bourne 2000, Anon 2001). The future, therefore, seems promising for scallop cultivation.

Scallop farming began in Japan in 1930's and by 1998, 226 000mt of scallops were cultivated by the Japanese alone (FAO statistic, Anon 1998). This phenomenal success is based on research and technical advances, which now provide a foundation for scallop farming all over the world (Hardy 1991). A seven-fold rise in world production of cultivated scallops, coupled with declining fisheries captures meant that in 1996, more than 73% of scallops consumed were produced by aquaculture compared with 23% in 1987 (New 1999). China is the biggest producer, selling around a million metric tonnes in 1998 (FAO statistic, Anon 1998). With Japanese assistance, South America is also becoming an increasingly important producer. Chilean production, for example, rose from almost nothing (FAO statistic, Anon 1998) to over 20 000mt (SERNAPESCA, Sturla and Madrigal 2001) in the last decade. Current cultivation schemes have three main stages: spat production or collection, intermediate cultivation, and final on-growth to harvestable size. An overview of these stages is given below; more detailed descriptions are found in Ventilla

(1982), Hardy (1991) and numerous technical reports (e.g. Paul *et al.* 1981, Ventilla 1981, Millican 1997).

Scallop spat (newly settled shelled larvae) have been traditionally obtained from natural populations by suspending artificial collectors in the sea. Low or inconsistent spat-falls in some areas prompted research into hatchery production of larvae (e.g. Piquimil *et al.* 1991, Millican 1997) and many large operations, such as those in China now rely on spat from hatcheries (Chew 1990, Guo *et al.* 2000). However, scallop larvae are sensitive to rearing conditions making hatcheries costly, and sometimes unreliable (e.g. Leibovitz *et al.* 1984, Cropp and Frankish 1988, Piquimil *et al.* 1991, Millican 1997). Much cultivation thus continues to rely on spat from the sea and sometimes areas where scallop densities have been artificially enhanced (e.g. Ventilla 1982, Ito 1991). Once collected, spat are placed into Japanese style pearl nets, which are suspended in the water column from longlines or rafts. This intermediate cultivation stage lasts for up to six months and scallops grow to about 25mm.

Scallops can be grown through to marketable size by either suspended or bottom culture. Suspended culture methods include ear-hanging where scallops are attached directly to ropes with ties or cement; large horizontally divided "lantern nets", or smaller "pearl nets" which are often used for spat (see Hardy 1991). Many species grow fastest in suspended culture (e.g. Ventilla 1981, MacDonald and Thompson 1985, Wallace and Reinsnes 1985, Hardy 1991), probably because food is abundant in the water column compared with the seabed. However, elevated growth rates can be offset by the high cost of equipment and labour required for regular net cleaning and changing to remove fouling and reduce the density of scallops (Frishman *et al.* 1980, Wildish *et al.* 1988). On-growing on the seabed is often an economic alternative, particularly with slow growing species or in areas where labour is expensive. Using this method scallops can be sown onto the seabed where they grow to harvestable size without further attention (except perhaps removal of predators, Venitilla 1982, Ito 1991). This reduces both labour and capital costs, and produces an attractive, natural looking product (Hardy 1991). However, problems are associated with rights of ownership to the seabed and stock, and high losses of seeded scallops due to dispersal and predation (Volkov *et al.* 1982, Hardy 1991, Wilson 1994).

Around the British Isles, queen and great scallops are cultivated by a number of small producers on Irish and Scottish coasts. Most farms collect spat from the sea but recent advances in hatchery technology means that the industry may now become established where collection is impractical (Anon 1996). On-growing is carried out in both suspended

and bottom culture. Total production is low (< 200mt annually, FAO statistic, Anon, 1998), as farmers must overcome high labour costs and the slow growth of native species. Great scallops take roughly four years to reach marketable size whereas species produced in Japan and Chile can be sold after around one and a half years in cultivation (Hardy 1991, Piquimil *et al.* 1991, Guo *et al.* 2000). Queen scallops can be harvested after two years but they are small and have an average first sale price of 5 pence per shell compared with 50 - 65 pence for great scallops (Anon 2001). Recent biotoxin outbreaks, in both wild and cultivated scallops, have also created problems, causing shellfish farms to cease trading for several months (Anon 2001, Howard *et al.* 2001). These problems are, however, offset by high demand and stable markets which means that British scallop production is expected to increase substantially in the future (Edwards 1997). Scallop farms could become an important source of employment in isolated coastal areas, currently suffering from huge declines in traditional fishing industries.

Research into scallop cultivation around the Isle of Man began in 1975 when the feasibility of spat collection for cultivation of great and queen scallops was assessed (Brand 1976). Further work established methods of cultivating queen scallops in trays above the seabed (Brand *et al.* 1980, Paul *et al.* 1981). Wilson (1994) successfully grew both queen and great scallops using a variety of suspended and seabed techniques. Cultivation is now envisaged to supplement existing fisheries, providing scallops when prices are high and catches are low (e.g. Christmas time) and during the long fishery closed season. It could also provide young scallops for proposed stock enhancement schemes.

To enhance production and profitability scallop growers around the British Isles must maximise the efficiency of the long grow-out period for great scallops. Problems during this stage can be associated with predation, disease, toxic algae and parasites (Ventilla 1981, Hardy 1991). In suspended cultivation, increased labour and decreased growth rates associated with fouling may offset the benefits of increased growth (Barber and Davis 1997, Lu and Blake 1997, Lodeiros and Himmelman 2000). This thesis examines the problems of fouling with the aim of determining how they can be limited, and efficiency of suspended cultivation can be improved. This is more environmentally sound than introducing faster growing strains or exotic species which might degrade natural stocks and bring pests or disease (Minchin 1999, Beaumont 2000, Mortensen 2000, Berry and Davison 2001).

1.4 Fouling

Newly submerged surfaces are quickly colonised by aquatic flora and fauna (fouling or biofouling organisms). With a few exceptions, competition among these creatures is principally for space on substratum, rather than for food or other resources (see e.g. Connell 1961, Knight-Jones and Moyse 1961, Osman 1977). Thus, the build-up of fouling organisms generally proceeds until most bare substratum is covered (Richmond and Seed 1991). Colonisation begins with microscopic organisms such as bacteria and then diatoms (Wahl 1989); these are succeeded by macroscopic species and eventually a dynamic three-dimensional community organised by environmental factors and biological interactions (e.g. recruitment, competition and predation, Richmond and Seed 1991). Aspects of this fouling or colonisation sequence have been the subject of numerous studies (e.g. Osman 1977, Bingham 1993, Butler and Connolly 1999) as reviewed by Wahl (1989) and Richmond and Seed (1991). Physical and biological processes affecting mature fouling (or benthic) communities have also been studied repeatedly by ecologists examining rocky shores, seabeds and submerged panels (e.g. Connell and Slatyer 1977, Osman 1977, Green and Schoener 1982, Green *et al.* 1983, Hawkins and Hartnoll 1983, Breitburg 1985, Hartnoll and Hawkins 1985, Kullberg 1988, Farrell 1989, 1991).

Although fouling species vary geographically, similar surfaces are often fouled by comparable organisms. Ascidians, for example, are major foulers of oyster nets in Japan (Arakawa 1990), the USA (Dalby and Young 1993), Ireland (Skjaeggestad 1997), France (Mazouni *et al.* 2001), and Canada (Enright *et al.* 1993, MacNair and Smith 1999). However, as with pelagic systems, fouling communities in the tropics mature more quickly and show little seasonal change compared with their temperate counterparts (Richmond and Seed 1991). Within an area, substrate immersion history, water velocity, distance offshore, depth of water, surface orientation and seasonality cause roughly predictable changes in community composition (e.g. Pomerat and Reiner 1942, Page and Hubbard 1987, Taylor *et al.* 1997, Butler and Connolly 1999). Regular gradients are, however, blurred by irregular variation in response to random forces such as storms and larval supply (Paine 1966, Sutherland and Karlson 1977, Underwood and Fairweather 1989).

Fouling is a costly problem for major industries the world over. Ship owners are plagued by epiflora and fauna that hugely increase drag and thus fuel costs; wooden boats are also damaged by boring organisms (Wood 1986, Richmond and Seed 1991). Offshore oil and gas companies must similarly compensate for fouling-induced weight and drag on their

platforms (Edyvean 1987). Pipes transferring water from lakes or the sea are also blocked by a range of fouling creatures (Wood 1986, Richmond and Seed 1991). In aquaculture, fouling is not just a mechanical problem (it increases the need for equipment anchorage, strength and buoyancy), it can also interfere biologically with species under cultivation.

Mariculture is usually carried out inshore and often high in the water column for shelter and ease of access. Intensive cultivation also requires good water exchange. Fouling organisms thrive under these conditions (Richmond and Seed 1991) and so they rapidly accumulate on the nets and lines used for fish and shellfish cultivation. A build up of fouling organisms can reduce water exchange (Claereboudt *et al.* 1994b, Skjaeggestad 1997), possibly causing a build-up of waste products and reduced oxygen levels (Huguenin and Huguenin 1982, Enright 1993, Lu and Blake 1997). The fouling community itself can also consume oxygen further reducing levels (Cronin *et al.* 1999, Mazouni *et al.* 2001). Oxygen depletion can cause mortalities or reduced growth, particularly where cages are densely stocked (Boyd 1982, Laired and Needham 1988).

Most invertebrate foulers are suspension feeders and when the cultivated species also relies on this food source (e.g. species of carp or bivalves), food competition may occur, particularly because the flux of food particles is already impeded (Duggan 1973, Leighton 1979, Côté *et al.* 1993, Enright 1993, Wilson 1994, Lodeiros and Himmelman 1996, Lu and Blake 1997). The effects of food competition will vary between cultivated organisms; mussels for example are voracious and efficient feeders whose ration is unlikely to be affected by rope fouling unless food is already limited (Lesser *et al.* 1992).

Sessile or slow moving bivalves, such as scallops, with their hard shells are particularly vulnerable to fouling. Survival of scallops and oysters is reduced by entangling with foulers, which prevents individuals from opening their shells to feed and respire (e.g. Minchin and Duggan 1989, Roman 1991, Paul and Davies 1986, Lu and Blake 1997). Heavy fouling can also inhibit shell opening for vital processes (Cropp and Hortle 1992, Lodeiros and Himmelman 2000). Fouling is generally removed from nets by high pressure hosing, while scallops must be manually scraped (Hardy 1991). Both processes are labour intensive and stress scallops, which can reduce growth (Wildish and Kristmanson 1988, Parsons and Dadswell 1992, McDonough 1998, Laing *et al.* 2001). Fouling thus reduces the success of suspended scallop cultivation by increasing equipment and labour costs, while reducing scallop growth and survival (Minchin and Duggan 1989, Claereboudt *et al.* 1994a, Lodeiros and Himmelman 1996, Lodeiros and Himmelman 2000). Additionally, heavily

fouled shells are less attractive to consumers, reducing their value in live markets (Hardy 1991).

Despite its economic potential, no ubiquitous solution to the fouling problem has been discovered. Problems with tin and copper based antifoulants (e.g. Davies and Paul 1986, e.g. Minchin *et al.* 1995, Alzieu 1998) have focused attention on naturally derived chemicals, which deter larval settlement (e.g. Armstrong *et al.* 1999, Harder and Pei-Yuan 2000) or manipulating surface topography and energy to prevent larvae from attaching (e.g. Berntsson *et al.* 2000, Smith *et al.* 2000). Most research is, however, directed towards the lucrative shipping and engineering industries. Products are thus likely to be expensive and possibly useful only in high flow situations.

As bivalve cultivation proliferates, the need for an economic and environmentally sound solution to fouling problems intensifies (Claereboudt *et al.* 1994a, Lodeiros and Himmelman 1996, McDonough 1998). Molluscs are sensitive to copper, nickel and tin based formulas and also tend to accumulate these metals (e.g. Davies and Paul 1986, Minchin *et al.* 1995, Alzieu 1998). Natural antifouling techniques are therefore more attractive. Previous work has exploited epizooic sponges as a natural antifouling coating (Armstrong *et al.* 1999). Fish, crabs and gastropod molluscs have also been used successfully to reduce fouling on the nets in which fish and bivalves are grown (Hidu *et al.* 1981, Enright *et al.* 1983, Flimlin and Mathis 1993, Skjaeggestad 1997, Cigarria *et al.* 1998). Despite promising results, biological control is underdeveloped and there is a need for more research, particularly with respect to scallop cultivation (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, Minchin 1996).

1.5 Aims

This study had four chief aims; these are addressed in separate chapters. Together the chapters form a comprehensive analysis of fouling in suspended scallop cultivation in an exposed Irish Sea location.

Chapter 3: To provide a detailed description of pearl net fouling communities and their variation with depth, season and immersion history.
This information is used to formulate possible fouling control strategies. It also provides essential background descriptions for chapters 4, 5 and 6.

Chapter 4: To discover how fouling alters the environment inside pearl nets.

Factors important for scallop growth were measured to increase understanding of the mechanisms by which net fouling alters scallop growth.

Chapter 5: To establish if, and how, net fouling alters the growth of juvenile scallops around the Isle of Man for scallops at various depths, times and in two locations.
Scallop growth was monitored at the same time as fouling communities (chapter 3), helping to explain why the effects of fouling might vary with time and depth.

Chapter 6: To identify native invertebrates suitable for biological control of fouling and determine their optimal stocking densities for pearl nets.
It was hoped that developing an economic and environmentally sound method of fouling control might help to improve the efficiency of scallop cultivation.

CHAPTER 2 - GENERAL METHODS

2.1 Longlines

Longlines used in previous work around the Isle of Man were frequently damaged by bad weather and strong currents (Wilson 1994). The systems used in these experiments were therefore modified following extensive advice from the Marine Farming Unit at Ardtoe (Scotland) and FMP Henderson, Glasgow. The resulting design is described in detail (Figure 2.1) because it has weathered four rough winters without damage and may thus be useful for future research. Equipment suppliers are listed in Appendix 1.

Following diver surveys of the seabed, two longlines were deployed by the fishing boat, *Friendly Shore* (Castletown) according to instructions from the Seafish Industry Authority (Ardtoe). The two largest tyre weights (Figure 2.1) were positioned by the *R.V. Sula* working in conjunction with divers. Unfortunately the longlines were taught and could not be worked easily from the boat, subsurface buoys and nets were therefore attached by divers. When large numbers of pearl nets were deployed, a pulley system was set up between the boat and longline to provide nets as the divers worked. Small numbers of nets were brought to the longline by divers using air-filled lifting bags. Divers used wire brushes to remove fouling from the lines and re-secure (or mouse) the shackles at regular intervals. Cable ties (7mm) were used to mouse shackles because wire quickly rusted. Surface marker buoys were lost periodically as shackles or the bottoms of the buoys wore thin. This problem was minimised by attaching buoys with steel links that were welded through eyes in the bottom of the buoys and thimbles at the top of the ropes.

2.2 Scallops and pearl nets

Pecten maximus used in these studies were 2-3yrs old (65-100mm shell length) because they were easily obtained and previous studies onto the effect of fouling have used only spat or small juveniles (Côté *et al.* 1993, Claereboudt *et al.* 1994, Lodeiros and Himmelman 2000). A range of cages or nets are used for suspended cultivation (e.g. pocket nets, pearl nets, lantern nets, North West trays); of these, lantern nets are the most frequently used for intermediate culture or on-growing (Hardy 1991). However, because lantern nets are large and hold many scallops, their use would have limited replication in these experiments. Wide mesh pearl nets were therefore used for the experiments described in chapters 3, 4 and 5 because their small size facilitates replication, ease of handling and the creation of discrete experimental units for analyses. The pearl nets used had a plastic covered square wire frame base with sides of 34cm and black, monofilament mesh with 1.6cm^{-2} spacing. The mesh is

the same as that used for lantern nets and thus the results of these investigations are probably relevant for on-growth in both pearl and lantern nets. Fine mesh pearl nets ($0.6cm^{-2}$) were used for biological control trials (Chapter 6) because *Psammechinus miliaris*, *Calliostoma zizyphinum* and *Nucella lapillus* would not be retained by wide mesh nets and it was important to compare the different control organisms under similar conditions.

2.3 Study area

Two longlines (subsequently referred to as the north and south systems) were used to provide both spatial replication and insurance should one system be lost or damaged. The systems were positioned about 500m from the south west coast of the Isle of Man, in approximately 23m of water (Figure 2.2). This location was chosen because it is within a fisheries exclusion zone, where the use of mobile fishing gear is prohibited. Ideally, the longlines would have been positioned in areas with different current conditions but Manx inshore waters are heavily dredged for much of the year because they support both *Pecten maximus* and *Aequipecten opercularis*; there was therefore a high probability that equipment outside of the exclusion zone would be damaged. Additionally, this area was easily monitored from the coast and was readily accessible for sample collection and longline maintenance.

The tidal range in this area is 6m and peak flows are approximately $1 m s^{-1}$. Gross tidal flow runs parallel to the systems. However, rocky outcrops cause erratic local flow patterns that sometimes extended to the south system. Salinity is 34ppt and water temperatures reach a summer maximum of about 15°C and winter minimum of 6°C (T. Shammon, *pers. comm.* 2001. Port Erin Marine Laboratory, Isle of Man); the water column in this inshore area is not normally stratified (M. J. Bates, *pers. comm.* 2001. Port Erin Marine Laboratory, Isle of Man). In the north east of this area untreated sewage from Port Erin (population ca. 3000) is discharged in the lower intertidal (Figure 2.2). This probably increases concentrations of suspended solids locally. Plankton cycles in this area are characterised by a single peak in early summer (Graziano 1988, T. Shammon, pers. comm. 2001. Port Erin Marine Laboratory, Isle of Man).

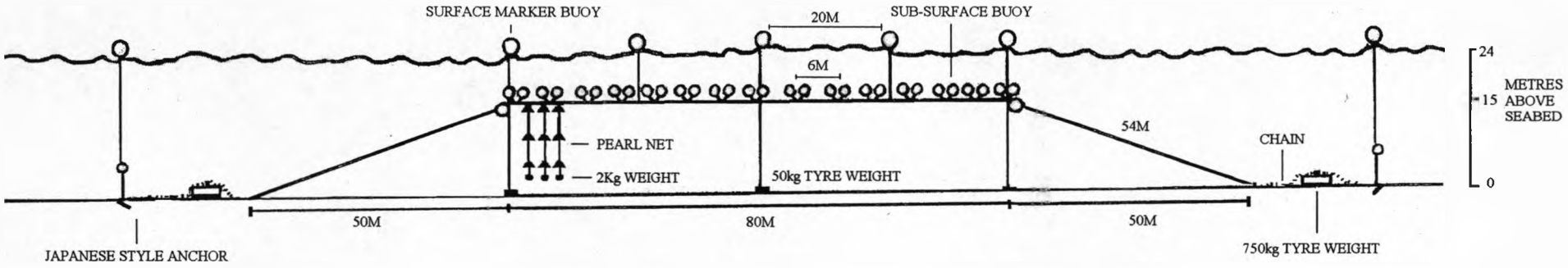


Figure 2.1. Longline system.

Ropes: 18mm "Seasteel" for all but attachment of subsurface buoys (8mm polypropylene). A double sheet bend joined the main headrope to a 2ft eye splice in the top of each warp. Warps were attached to chains with anchor bends. Down lines and surface marker buoys were spliced into the headrope. Subsurface buoys were threaded through eyes spliced into the headrope. Pearl nets were at 1.5m horizontal intervals. Load before fouling was a maximum of 390Kg.

Buoys: Surface markers were A3 (60") Polyform type; subsurface ones were 8" trawl floats along the headrope and a single 11" trawl float at the top of each warp.

Anchors: Steel Japanese anchors are described in Appendix 2. 750Kg tyre weights (angels) and 50Kg tyre weights were made from water-tight-concrete filled tractor and car tyres respectively. Steel loops were embedded in the concrete for attachment of shackles. 15m of long-link steel chain (22mm diameter), joined warps to anchors; angels were positioned in the centre of the chain. 7/8" x 1" D shackles joined ropes to tyre weights (via galvanised thimbles) and chains to anchors.

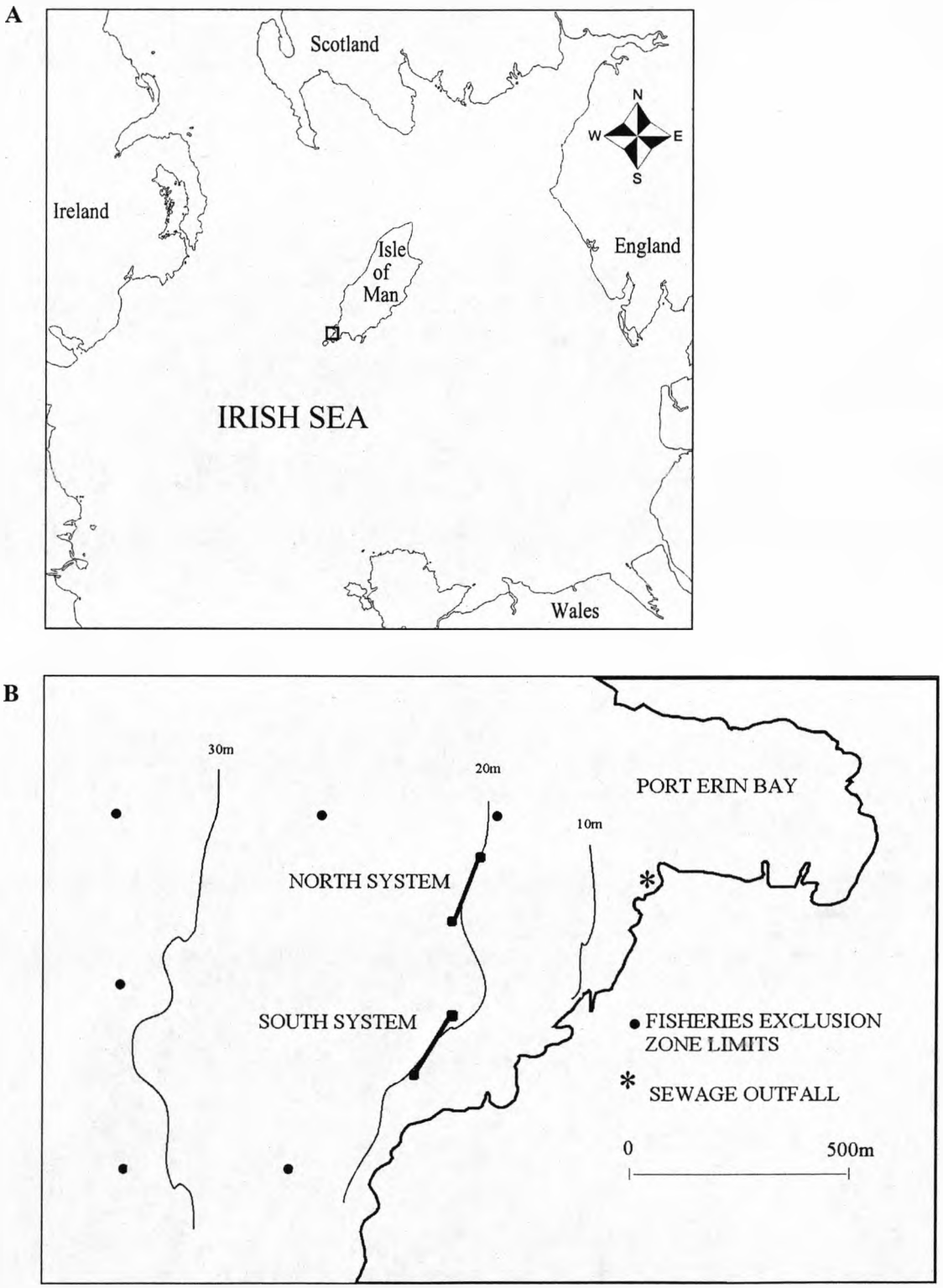


Figure 2.2. A, The Irish Sea; B, two longline systems off the South West coast of the Isle of Man.

2.4 Scallop tagging

Scallops were individually labelled so that their growth could be measured. A range of tagging methods have been used for molluscs. However, when this study began there was a dearth of literature on their application or success. Subsequently, Lemarié *et al.* (2000) reviewed a number of tags for freshwater mussels, though they stressed that for morphological and behavioural reasons tag retention is likely to vary between mollusc species. Previous experiments with great scallops (for example, Brand and Murphy 1992, Gruffydd 1992) have used button-tags where a hole is drilled through the anterior 'ear' of the shell and the tag is threaded onto a stainless steel wire. This method is not appropriate for use in suspended culture as the tags are likely to tangle with the netting. Prior to the current investigations a range of labelling techniques were tested, where shells were engraved or flexible tags were fixed to the shell using a range of chemical adhesives. The most successful tag-adhesive combination was then monitored in long-term field experiments (Chapters 1 and 3). Tagging results are described here along with recommendations for tagging strategies in future molluscan research.

Shell engraving, two types of flexible tag and six adhesives were tested in laboratory experiments. Five 2-3yr old scallops were used for each of 13 treatments with three types of tag or mark:

1) A binomial code of dots was marked on scallop shells by drilling to just below the periostracum with a small electric engraver and dental drill bit.

2) Micromarkers (labels for electric wiring, 2.5 x 4 x < 0.25mm, Brady Co Ltd., UK) or

3) Shellfish Tags (4 x 8 x 0.15mm, Hallprint Pty. Ltd., S.A. Australia) were attached to scallop shells.

Both Micromarkers and Shellfish Tags were attached with six different adhesives: standard epoxy resin, rapid epoxy resin, underwater epoxy resin, dental cement, cyanoacrylate gel, and cyanoacrylate fluid (super glue/crazy glue). When adhesives were used, scallops were roughly dried with a towel. Then both a small area near the umbo, and a shell groove, 10mm from the growing edge on the flat upper (left) shell valve, were thoroughly cleaned with a cotton bud. Adhesives were applied to the underside of the tag (tags were held with forceps), and/or the scallop shell, and pressed on with a cotton bud. When adhesives were touch dry (Table 2.1 gives adhesive drying times) the scallops were returned to sea-water tanks. Scallops were then held in tanks with running seawater and monitored for ill effects for one week. Tags, engraved marks and adhesives were assessed for ease of application,

legibility, visibility (the ease with which tagged scallops can be distinguished from non-tagged ones) and retention.

Following the investigation described above. Shellfish Tags and cyanoacrylate gel were used in long-term field experiments (Chapters 1 and 3). Five hundred and fifty 2-3 year old scallops were double tagged following the described method; the adhesive was left to cure for 2-4 minutes before immersion. The scallops were then kept in holding tanks for about 5 weeks, before being placed into pearl nets (10 scallops per net) and suspended, on the longlines described above, for 17 months. At 3-4 month intervals, scallops were retrieved and tag retention was recorded. When necessary, the tags were scraped to remove fouling organisms (algae, bryozoans and barnacles).

Of the six adhesives used in laboratory experiments, rapid epoxy resin, cyanoacrylate fluid and cyanoacrylate gel bonded strongly and quickly to tags and shells (Table 2.1). Standard epoxy resin took a long time to cure. Underwater epoxy resin and dental cement did not reliably bind to scallop shells. Two scallops tagged with standard epoxy resin died, probably due to being out of the water for 3 hours while the resin cured. No other scallops died or exhibited unusual behaviour. All tags were quick to apply and easy to clear of fouling, although the visibility of engraved dots declined quickly due to microfouling.

Shellfish Tags were selected for long-term experiments because of the ease with which they could be applied, their visibility, legibility and the quantity of data they carry (Table 2.2). Cyanoacrylate gel was used because it could be applied precisely and straight from the tube, whereas epoxy resins required mixing. Thus, the use of cyanoacrylate gel saved time and adhesive.

Long-term experiments using Shellfish Tags and cyanoacrylate gel lasted for 17 months. Of the 452 surviving scallops 74 (16%) lost tags from the umbo and only 2 (0.4%) lost tags from the grooves near the shell margin (Figure 2.3). Tag loss increased with time for scallops labelled on the umbo and in a groove (the probability that the slope of regression lines differed from zero was > 0.95 in both cases). However, the rate of tag loss remained stable over time (Figure 2.3). Fouling of tags was common, but generally easy to remove without damaging the tags.

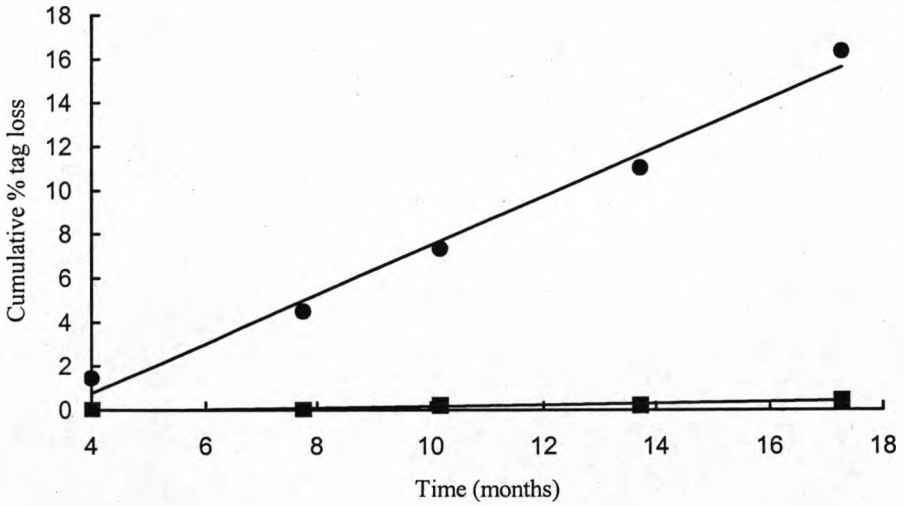


Figure 2.3. Tag loss in 452 scallops labelled on the umbo (circles, r = 0.99) and in a groove near to the shell margin (squares, r = 0.92).

Table 2.1. An assessment of adhesives used to bind labels to scallop shells.

Adhesive	Setting time	Strength of bond	Scallop Mortality (%)
Cyanoacrylate gel	1-2 minutes	Strong	0
Cyanoacrylate fluid	1-2 minutes	Strong	0
Standard epoxy resin	3 hours	Strong	40
Rapid epoxy resin	2-3 minutes	Strong	0
Underwater epoxy resin	10 minutes	Nil	0
Dental cement	6-8 minutes	Weak	0

Table 2.2. Evaluation of tags and marks. Visibility refers to the ease with which tagged scallops were distinguished from non-tagged scallops.

Tag	Ease of application	Information held	Legibility	Visibility
Micromarker	Awkward	Moderate (2 numbers)	Good	Moderate (small size)
Shellfish Tag	Simple	Good (1 letter, 2 numbers, various colours)	Good	Good (large + bright)
Engraved dots	Simple	Limited	Moderate	Moderate/poor (quickly fouled)

Engraving scallops was effective and economical; it could be a useful technique for small, short-term experiments where marked individuals are confined. However, rapid fouling and the small amount of information carried make engraving less suitable for long-term studies. If positioned in shell grooves, Shellfish Tags (Hallprint) are an effective way of labelling *P. maximus* for long-term studies. These results are consistent with the findings of Lemarié *et al.* (2000), who used Shellfish Tags and cyanoacrylate adhesive to mark freshwater mussels with a loss rate of 0.46% over two years. The results also compare favourably with other scallop tagging methods. For example, Brand and Murphy (1992) reported an initial ear-tag loss rate of 10% over 6 months.

Herald (1978) glued tags to saucer scallops (*Amusium balloti*) with adhesive and reported a higher tag loss on the lower (right) than the upper (left) shell valve. The present study also highlights the importance of tag position. The uneven surface within shell grooves probably provided the cyanoacrylate with more mechanical anchorage than the smooth surface of the umbo. Tagging within grooves also reduced the area of adhesive open to erosion/dissolution and provided a degree of protection from abrasion. This has implications for other species. For example, when tagging smooth and fast growing species such as *Mytilus edulis* (L.) labels may be best positioned near the growing edge of the shell where dense growth rings roughen the surface. During biological control studies (Chapter 6), tagged scallops were enclosed in pearl nets with seven species of gastropods, decapods or echinoids. Shellfish Tags were only removed by edible sea urchin (*Echinus esculentus*, L.) grazing. This should be considered if experiments are planned for sessile species where urchins are common.

Shellfish Tags were quicker, simpler and less damaging to apply than the ear-tags used in previous large-scale scallop mark-recapture experiments (Brand and Murphy 1992, Gruffydd 1992). Such experiments may benefit from using Shellfish Tags due to reduced labour and tag loss costs. However, tag retention should first be measured under seabed conditions, as these may differ from those in suspended culture. The success of tags in abrasive stream conditions (Lemarié *et al.*, 2000) and the fast water currents of suspended culture suggest strongly that these tags will prove suitable for seabed studies on *P. maximus*.

CHAPTER 3 – SHELL AND NET FOULING COMMUNITIES

3.1 Introduction

Encrusting sessile marine invertebrates often compete for space on substratum rather than for food or other resources (see e.g. Connell 1961, Knight-Jones and Moyse 1961, Osman 1977). Thus there is strong competition to occupy any available space, as summarised by Wahl (1989): "In the marine environment any solid, exposed, undefended surface will become fouled ... As substrate-bound nutrient uptake is of secondary importance to most sessile hard-bottomed organisms, all solid surfaces represent possible settlement sites for algae and sessile animals."

Fouling is therefore a ubiquitous problem in the marine environment (see Edyvean 1987, Richmond and Seed 1991), not least for scallop growers using suspended cultivation methods. Both scallops and nets become fouled which can cause decreased scallop growth (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, 2000) and increase the weight and drag of cultivation equipment (Hardy 1991, Aiken 1993). Predators including crabs and starfish may also recruit onto nets and reduce scallop growth and survival (Wilson 1994, O'Connor *et al.* 1998, Freites *et al.* 2000). The extended grow-out period for great scallops in British waters makes it imperative that farmers maximise scallop growth without greatly increasing the effort involved in husbandry.

Though there are few detailed investigations of fouling on aquaculture equipment, fouling communities on submerged panels, rocky shores and the seabed have been studied repeatedly by ecologists (e.g. Connell and Slatyer 1977, Osman 1977, Green and Schoener 1982, Green *et al.* 1983, Hawkins and Hartnoll 1983, Breitburg 1985, Hartnoll and Hawkins 1985, Kullberg 1988, Farrell 1989, 1991). Many of these studies describe processes that might shape and change net fouling communities. Species initially colonising new nets will be determined by the supply of invertebrate larvae and algal propagules, and their ability to settle and subsequently recruit on the net surface (e.g. Keough and Downes 1982, Bingham 1993). Later, changes in the fouling community may be driven by seasonal changes in the environment and, or, succession (e.g. Connell and Slatyer 1977, Jackson, 1977; Osman 1977, Dean and Hurd 1980, Farrell 1991, Hextall 1994). Further recruitment, competition, grazing, predation, and physical disturbance may be a part of these processes (e.g. Paine 1966, Lubchenko 1978, Buss 1979, Sousa 1979, Ayling 1981, Richmond and Seed 1991, Menge 2000) or impose separate temporal patterns (e.g. Hawkins and Hartnoll 1983, Hartnoll and Hawkins 1985, Tanner *et al.* 1994).

The most comprehensive studies of fouling in bivalve cultivation reveal two or three-tiered communities (Arakawa 1990, Lesser *et al.* 1992, Claereboudt *et al.* 1994, Mazouni *et al.* 2001). Sessile, suspension-feeders (bivalves, tunicates, barnacles, hydroids and fan worms) form the first tier and provide a habitat for motile species. This second tier includes scavengers, predators and sometimes deposit feeders (e.g. flatworms and amphipods). Finally, predatory fish may prey on both motile and sessile foulers.

Other records of net fouling come from research into fouling control, though they tend to consider a few principle foulers and not the whole community. These studies indicate that the same families or even species of organisms are important foulers across much of the world. Enright and her co-workers mention, mussels, ascidians, sponges, bryozoans and algae as important foulers on lantern nets and trays used for oyster cultivation in Canada (Enright *et al.* 1983, 1993, Enright 1993). Similar organisms combine with silt to foul cages off Maine, U.S.A. (Hindu *et al.* 1981), northwest Spain (Cigarria *et al.* 1998) and the Isle of Man (Wilson 1994). Minchin (1997), in Ireland, distinguishes hard fouling (barnacles, saddle oysters, bryozoans, mussels and spirobids) from soft fouling (ascidians), stating that hard fouling species often characterise more exposed conditions whereas soft fouling organisms favour deep, sheltered areas. Also in Ireland, Skjaeggestad (1997) identified feather stars and hydroids as key fouling species in addition to those detailed by Minchin (1997).

In nature scallop shells become fouled by a variety of organisms, and even support diverse communities (Wells *et al.* 1964, Bloom 1975, Hayward and Haynes 1976, Ward and Thorpe 1989, 1991, Berkman 1994). Fouling on scallops that naturally recess below the sediment, such as *Pecten maximus*, is often mainly limited to encrusting organisms (Ward and Thorpe 1989, K. Ross, unpublished data). However, in suspended culture shell fouling proliferates because conditions that favour scallop growth also benefit fouling organisms. Lodeiros and Himmelman (1996), for example, showed that fouling on the shells of cultivated *Euvola ziczac* can almost double upper valve weights. Such heavy fouling is associated with reduced growth and survival, probably because it inhibits shell opening for feeding and respiration (Cropp and Hortle 1992, Lodeiros and Himmelman 2000). In more robust species shell fouling may only be important at the spat stage, when it can bind shell valves together (e.g. Minchin and Duggan 1989, Roman 1991, Paul and Davies 1986, Lu and Blake 1997).

Community analysis is time-consuming and thus detailed studies of net or shell fouling have generally run only for short periods (Claereboudt *et al.* 1994, Taylor *et al.* 1997). Such

studies suggest that the abundance of fouling organisms varies in response to regular environmental cues, species succession and stochastic factors.

Predictable variation in the fouling community is caused by depth, surface orientation and season; this is generally attributed to light, temperature or food gradients and the availability and behaviour of larvae (e.g. Pomerat and Reiner 1942, Page and Hubbard 1987, Claereboudt *et al.* 1994, Taylor *et al.* 1997, Cronin *et al.* 1999). Predictably, algae dominate communities on nets close to the surface in spring and summer because of high light levels (Enright *et al.* 1983, Hextall 1994, Skjaeggestad 1997, Cigarria *et al.* 1998). Below the algal zone, and on downward facing surfaces, sessile animals are common although numbers of these may also decrease with depth in response to decreasing food, temperature and numbers of larvae (Brand *et al.* 1980, Heffernan *et al.* 1988, Arakawa 1990, Côté *et al.* 1993, Claereboudt *et al.* 1994, Hextall 1994). Seasonally, species tend to recruit and grow most in the summer, mortality or slow growth being associated with low water temperatures and light levels in the winter (e.g. Skjaeggestad 1997, Taylor *et al.* 1997, Cronin *et al.* 1999). Fouling communities can also vary predictably over short horizontal distances in response to differences in physiochemical conditions or the supply of larvae (Arakawa 1990, Cropp and Hortle 1992; Claereboudt *et al.* 1994, Butler and Connolly 1999). Arakawa (1990) also highlights the irregular occurrence of "blooms" of fouling organisms (fan worms, tunicates and mussels) in Hiroshima Bay.

This study aimed to describe the fouling of pearl nets used for scallop cultivation off the south west coast of the Isle of Man. Differences in the fouling community with depth, season and substrate immersion history were examined. Destructive sampling enabled macroscopic foulers in all layers of the three dimensional community and on all net surfaces to be identified. Major shell fouling organisms were also investigated. This provided essential background information for subsequent studies into the effects of fouling on the environment inside nets (Chapter 4) and scallop growth (Chapter 5). Thorough descriptions of the fouling communities on nets are rare and so information from this study might also be used to develop efficient fouling management strategies. Strategies could include biological control, where invertebrates are added to nets to remove foulers (e.g. Hidu *et al.* 1981, Enright *et al.* 1983, Minchin 1996, Cigarria *et al.* 1998).

3.2 Materials and methods

Several aspects of this study were costly and labour intensive; diving time and boat availability were also limited. The final design therefore represents a trade-off between collecting sufficient information to describe the dynamic fouling community and minimising sampling costs and effort. The experiment was conducted over a ten-month period because cultivation nets are not generally deployed for longer than this around the British Isles (as they are retrieved at regular intervals to reduce scallop densities and remove dead scallops, Hardy 1991, Wilson 1994).

3.2.1 Field work

Wide mesh pearl nets (1.6cm^2 spacing) were arranged vertically in strings of three and attached to two longlines (Figure 2.2) so that they were suspended at depths of approximately 10, 14 and 18m (Figure 2.1); each net contained 10 on-growing *Pecten maximus*. Temperatures at the three experimental depths were monitored continually using Stowaway Tidbit data loggers (Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532, USA) attached to the nets. Twenty strings of nets were deployed on each longline in November 1998; fourteen more strings were deployed on each longline in June 1999 (nets from the two deployment dates are referred to as series 1 and series 2 nets respectively). Initially, it was planned to sample two strings from each longline at monthly intervals for 10 months; unfortunately, sampling was often irregular (Table 3.1) because of bad weather, lack of boat crew and/or mechanical problems with the boat. Five sampling trips therefore followed each deployment, separated by between 30 and 76 days. Divers retrieved nets gently, sealing them in net bags (1mm mesh) before removing them from the longlines and bringing them to the surface with air-filled lifting bags. Mesh bags were preferable to plastic ones because they retained fouling organisms without collecting water. On arrival at the laboratory scallops were carefully removed from the nets. The nets were then transferred to plastic bags and kept in a freezer at approximately –20°C.

Table 3.1. Sampling dates and intervals for nets retrieved from north and south longline systems.

North	South	Series 1 Sample lable	Cumulative days north	south	Mean interval	Series 2 Sample lable	Cumulative days north	south	Mean interval
20.11.98	20.11.98	**0**	0	0					
11.2.99	8.2.99	**1**	83	80	82				
27.4.99	1.4.99	**2**	158	132	64				
11.6.99	2.6.99	**3**	221	220	76				
29.7.99	28.7.99	**4**	251	250	30				
30.7.99	31.7.99					**0**	0	0	0
14.9.99	14.9.99	**5**	298	298	48				
14.9.99	15.9.99					**1**	46	47	47
22.10.99	14.10.99					**2**	84	76	34
24.1.00	26.1.00					**3**	178	180	99
16.3.00	16.3.00					**4**	230	230	51
26.4.00	26.4.00					**5**	271	271	41

3.2.2 Laboratory analyses

Percentage cover

Percentage cover is a relevant measure of organism abundance because it influences the amount of water movement through nets and hence the environment for scallops inside. It is also relatively quick to measure. Percentage cover analyses were therefore carried out on all samples. Previous studies show that surface orientation can influence community composition; in this experiment differences between net surfaces (top inside, top outside, bottom inside, bottom outside) could have been increased by predator exclusion from inside surfaces and movement of scallops on net bottoms. The different surfaces were therefore recorded separately to make an accurate description of the entire net community. Approximate numbers of mobile species were also recorded.

Nets were defrosted at room temperature before analysis. They were then stretched flat over a board with nails around the edge. A quadrat strung with twine that marked 100 evenly spaced points was fitted on top of the net to measure the percentage cover of organisms on each surface (top inside, top outside, bottom inside, bottom outside). All species encountered below each point were recorded, as were uncolonised points. Species often grew over each other forming a multi-layered community so that total percentage cover could exceed 100%. Organisms were identified using Hayward and Ryland (1990). Nomenclature is from Howson and Picton (1997) and authorities are given therein. To find out whether freezing altered the size of "soft" fouling organisms (those without calcified shells or support), a preliminary study measured the percentage cover of ascidians and hydroids, before and after freezing. Results were compared using a *T*-test for dependent samples in the STATISTICA software package (v.5.5, StatSoft Inc.). Numbers of mobile species were recorded semi-quantitatively as rare (1-3 individuals per net), common (4-20 individuals) or abundant (>20 individuals). The size class of crabs (< 40mm, > 40mm) was also recorded because they are important scallop predators and their size influences prey capture (Hindu et al. 1981, Enright et al. 1993). Although mobile, brittle stars and feather stars were firmly attached to nets; they were therefore treated as sessile organisms and their abundance was assessed by percentage cover. The amphipod *Jassa falcata* frequently created mucus bound silt tubes; these were also measured as sessile fouling.

Species pooling

Where possible, organisms were identified to species level. However, the species below were pooled because: (1) specimens were small and could not be positively identified; (2) freezing removed species specific characters; (3) species from the same genus occurred concurrently and identification required that every individual be examined microscopically, or, (4) I lacked the taxonomic skill to distinguish species.

Table 3.2. Species pooling, reasons for pooling codes are given in text.

Pooled group	Species	Reason for pooling
Small hydroid	*Clytia hemispherica* and immature specimens including *Bougainvillia* spp. *Tubularia* spp. and *Eudendrium* spp.	1 & 3
Bougainvillia spp.	*B.ramosa, B.mucoides*	3
Tubularia spp.	*T.larynx, T.indivisa*	3
Halecium spp.	*H.Halecinum, H.beanii*	3
Eudendrium spp.	Undetermined	4
Echinoida	*Psammechinus miliaris, Echinus esculentus*	1
Liocarcinus spp.	*L.depurator, L.puber, L.corrugatus*	1 & 3
Hyas spp.	*H.araneus, H.coarctatus*	3
Inachus spp.	*I.phalangium, I.dorsettensis*	3
Macropodia spp.	*M.rostrata, M.deflexa*	3
Nereis spp.	*N.pelagica, N.zonata*	3
Galathea spp.	*Galathea strigosa* and *Galathea* indet.	3
Caprellidae	*Pseudoprotella phasma, Phtisica marina Caprella periantis, C.frentensis*	3
Anomia sp.	Undetermined	3
Aeolidae	*Facelina bostoniensis, Choryphella lineata*	2
Harmothöe spp.	*H.impar, H.fragilis, H.extenuata.*	3
Endeis spp.	*E.laevis, E.spinosa*	3

Wet and dry weights

The weight of different fouling organisms was measured for nets from a single depth and start date. This was time consuming because the intertwined and attached organisms were difficult to separate, but it illustrated patterns that were not apparent from spatial analysis. It

also identified small and rare species that could be recruitment stages of dominant foulers or favoured substrates for such species; they could also be important grazers or parasites.

The weight of different species groups per gram of netting was calculated for the top half of pearl nets suspended at 14m. Net tops were analysed in detail because variable fouling of the bottom surface due to scallop abrasion might have obscured treatment effects. Both wet and dry weights were measured. Though wet weights are quick to collect and most biologically relevant, it was thought that they might be inaccurate because similar organisms seemed to trap variable amounts of seawater and were inevitably allowed to desiccate for different times during sorting. Four sub-samples of equal area (totalling 25% of the net top) were removed systematically. The samples were then gently washed in a sieve with 1mm mesh spacing, until the water ran clear. The water was filtered to determine the mass of trapped silt. Mobile species were collected from the whole net because it was impossible to distinguish those from the top and bottom of the net; the mass of mobile species per net top was then estimated by halving these total weights. Fouling organisms were sorted into preweighed tin foil containers and weighed (giving the wet weight) before drying at 40°C to a constant dry weight. Rare species, weighing less than 0.2g per gram of netting, were recorded and given an arbitrary wet weight of 0.1g and a dry weight of 0.05g per gram of netting for statistical analyses. The total wet and dry weight of fouling organisms was measured for nets used in both weight and percentage cover analyses.

Fouling of scallop shells

Qualitative descriptions were made of common shell fouling organisms during series 1. Saddle oysters, mussels and solitary tunicates were identified as key shell-foulers and numbers per individual scallop shell were recorded.

3.2.3 Statistical analyses

Nets from series 1 (immersion date 20.11.98) and 2 (immersion date 30.7.99) were analysed separately, comparisons between them being qualitative. The experimental design was balanced and identical for both series. Both time (five treatments) and depth (three treatments) were fixed factors, replicated four times by sampling four nets (as discussed later replication was sometimes reduced). Multivariate techniques were used to assess changes in community composition with time and depth, and possible interactions between these factors. Univariate analyses were used to investigate changes in the amount of empty space, silt, and total wet and dry weights of fouling. Multivariate techniques also enabled qualitative comparisons of communities fouling different net surfaces to be made, but

quantitative comparisons were prohibited by the non-independence of surfaces belonging to the same net.

The proximity (ca. 250m, Figure 2.1B) of the longlines along the same depth contour meant that although conditions differ transiently (as discussed in Chapter 4) average conditions, and hence the fouling communities, would probably be similar. This assumption was supported by data from previous benthic studies in this area (Hextall 1994) and the consistency of water temperatures at all depths across the two systems. The four nets are therefore considered to be replicates and the results provide a specific description of succession in the study area only.

Multivariate analyses

To assess the effects of depth and time on community composition, the percentage cover of sessile species on all surfaces was combined for each net. Wet and dry weight data, for sessile and mobile species, were converted to values per gram of net so that the effects of time on this aspect of the community could also be assessed. Data sets including all species groups present in more than one sample were then analysed using non-parametric, multivariate techniques included in the PRIMER (Plymouth Routines in Multivariate Research) software package (Clarke and Warwick 1994). Bray-Curtis similarity indices (Bray and Curtis 1957) were calculated between all pairs of samples to produce a similarity matrix, after a square-root transformation was used to slightly down-weight the contributions to total similarity of the most abundant species. The similarity matrices were ordinated and clustered using non-metric MDS (multi-dimensional scaling) and hierarchical agglomerative clustering (on group-average linkage) respectively.

A priori tests for time effects were performed using one-way ANOSIM (analysis of similarity); when data were for more than one depth, separate tests were carried out for samples at each depth and for all depths pooled. When results showed a significant time effect, multiple comparison tests were used to identify which pairs of samples differed significantly and the magnitude of these differences. When interpreting the results of pairwise comparisons it should be borne in mind that with only four replicates in each group, the maximum significance level that can be achieved is $P = 0.03$. Adjustments for multiple comparisons were not therefore applied to P values because the tests had no power to detect the levels they deem significant (e.g. $P < 0.01$ under Bonferroni corrections). P values are presented for pairwise tests but should be interpreted with caution because they run an increased probability of type 1 errors. Instead, emphasis is put on global R values, which indicate the size of effect in each pairwise comparison (Clarke and Warwick 1994).

One-way ANOSIM were also used to test for depth effects with separate tests carried out for samples collected on different sampling dates and for all sampling dates pooled. Pairwise comparisons were then used to determine which depths differed; again the maximum significance level that could be detected was $P = 0.03$. The species contributing most to any differences found between treatments were determined using SIMPER (similarity percentages) analysis of square root transformed data. Shade diagrams were plotted using a Microsoft Excel macro written by L. Veale (Port Erin Marine Laboratory, Isle of Man, 2000), to identify patterns in species percentage cover and weight across treatments. The relative abundances of mobile species were included in the shade diagrams by scoring abundances, rare (1), common (4) and abundant (20) before calculating average values per treatment. MDS plots were used for qualitative comparisons of communities on different net surfaces and the two time series. When two-dimensional MDS plots had high stress values (>1.5) they were interpreted with reference to dendrograms from CLUSTER analysis (Clarke and Warwick 1994).

In two instances, replication was reduced to three nets. Unbalanced designs do not prohibit analyses using PRIMER (Clarke and Warwick 1994) but altered the design of some univariate analyses. The missing data were for a July weight sample, (percentage cover and total weight data was recorded for this net but it was omitted from other weight analyses), and a 10m October sample from series 2, lost from the freezer before any analysis had been made.

Univariate analyses

Within each month, average weekly temperatures provided four replicate measurements so that the influence of time of year, depth and longline system could be examined using a three-way analysis of variance (ANOVA). Time and depth were fixed factors and system was a random factor. One temperature logger was lost from 18m on the north system, and so only depths of 10 and 14m were included in this analysis. A second, two-way ANOVA (fixed factors time and depth) was then carried out to compare temperatures at all three depths on the south system only. Amounts of uncolonised space and total weights were examined using two-way ANOVA, where time and depth were fixed factors. The dry weight of silt was examined by one-way ANOVA with time as the only factor. When samples were missing (see above) only three replicates were used for ANOVA. Percentage cover data were arcsine transformed before analysis (Watt 1993). Heterogeneity of variance was tested for using Cochran's test (Winer 1971) and where necessary data were transformed. Some data were heterogeneous even after transformation, but ANOVA was still applied because the experimental design was balanced and fairly large (Underwood

1997). However, such analyses increase the probability of a type I error (Underwood 1997), and the results were interpreted with caution. When ANOVA indicated significant factors or interactions between factors, post-hoc Student-Newman-Keuls (SNK) tests were performed to determine which means differed. All analyses were carried out using GMAV5 (Underwood et al. 1998).

3.3 Results

3.3.1 Temperature

Water temperature followed a typical seasonal pattern ranging from 15°C in August and September to around 7°C degrees in February, March and April (Figure 3.1). Temperature loggers were deployed in February 1999, missing the first three months of the investigation, however measurements taken near to the study area suggest that the trend during this period was similar to 2000 (R. D. M. Nash, *pers. comm.*). ANOVA results (Table 3.3) showed that there were no significant differences between temperatures across the two longlines. May temperatures at 10m were significantly higher than at 14m, though the difference was less than 0.1°C; no other depth effects were revealed.

3.3.2 Community composition

Effects of freezing samples

Areas covered by fresh and frozen ascidians and hydroids did not differ significantly (Ascidians, $t = -.304$, df = 14, $P = 0.77$; Hydroids $t = -797$, df = 10, $P = 0.44$). It is therefore assumed that percentage cover results are representative of nets before freezing.

Percentage cover vs. wet weight as measures of community composition

Figure 3.2 highlights differences between weight and percentage cover results. Weight measures emphasise the importance of organisms such as sabellid worms, tunicates and bivalves that have a high mass per unit area. Less dense, but frequently occurring organisms such as hydroids are more prominent in percentage cover results. Additionally, separation of organisms for weight analyses revealed six small and cryptic species missed during percentage cover analysis (Figure 3.6). Despite their different emphasis, both types of data described similar changes in communities with time. Dry weight results have not been presented because they showed the same trends as wet weight data under both multi- and univariate analyses.

Surface effects

Inspection of MDS plots, CLUSTER diagrams and shade matrices revealed no consistent differences in the percentage cover of sessile species on the four net surfaces.

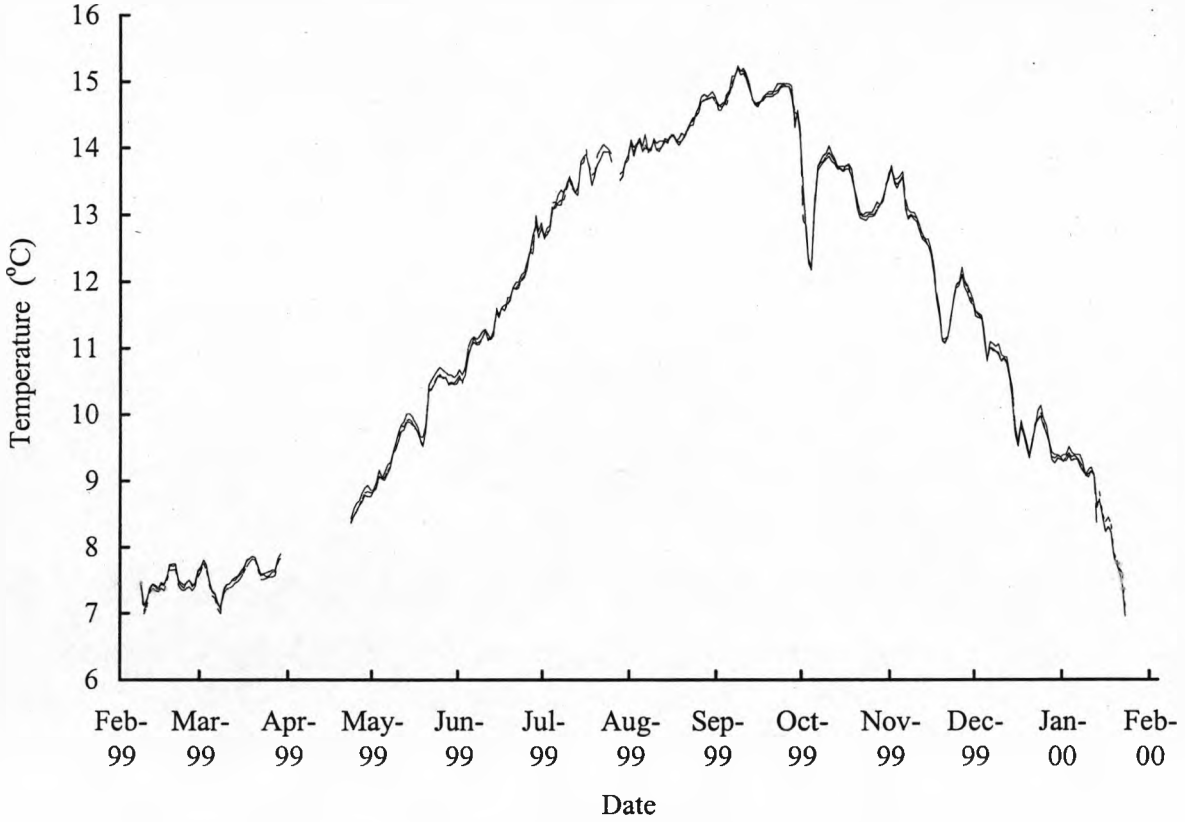


Figure 3.1. Water temperatures at 10m (solid line), 14m (short-dashed line) and 18m (long-dashed line). Data for 10 and 14m are average values for the two longline systems, data for 18m are for the south longline only. Data are missing when loggers were retrieved for downloading.

Table 3.3. Two and three way ANOVA and SNK multiple comparisons testing for the effect of longline system (A only), depth and time on water temperature (°C). A: Data for temperatures at 10m and 14m on both the north and south longline systems. B: Data for temperatures at depths of 10m, 14m and 18m on the south longline only. Results of Cochrans's tests are given and data are untransformed. Bold type indicates a significant results ($P < 0.05$).

Source	df	MS	*F*	*P*	*F* ratio versus
A.					
$C = 0.661, P > 0.05$					
System	1	0.018	0.07	0.80	Residual
Depth	1	0.004	0.02	0.90	System X Depth
Time	9	110.882	72038.15	**<0.01**	System X Time
System X Depth	1	0.144	0.54	0.46	Residual
System X Time	9	0.002	0.01	1.00	Residual
Depth X Time	9	0.008	3.37	**0.04**	System X Depth X Time
System X Depth X Time	9	0.002	0.01	1.00	Residual
Residual	120	0.267			
Total	159				
SNK Multiple comparison of depth, time interaction:					
Depths 1 and 2: **Feb. < March < May < Dec. < June < Nov. < July < Oct. < Aug. < Sept.**					
Depth had a significant effect in only in May, when the temperature was highest at 10m.					
B.					
$C = 0.106, P > 0.05$					
Depth	2	0.095	0.35	0.71	Residual
Time	8	87.526	321.27	**<0.01**	Residual
Depth X Time	16	0.003	0.01	1.00	Residual
Residual	81	0.272			
Total	107				
SNK Multiple comparison of time effects matched the pattern described above.					

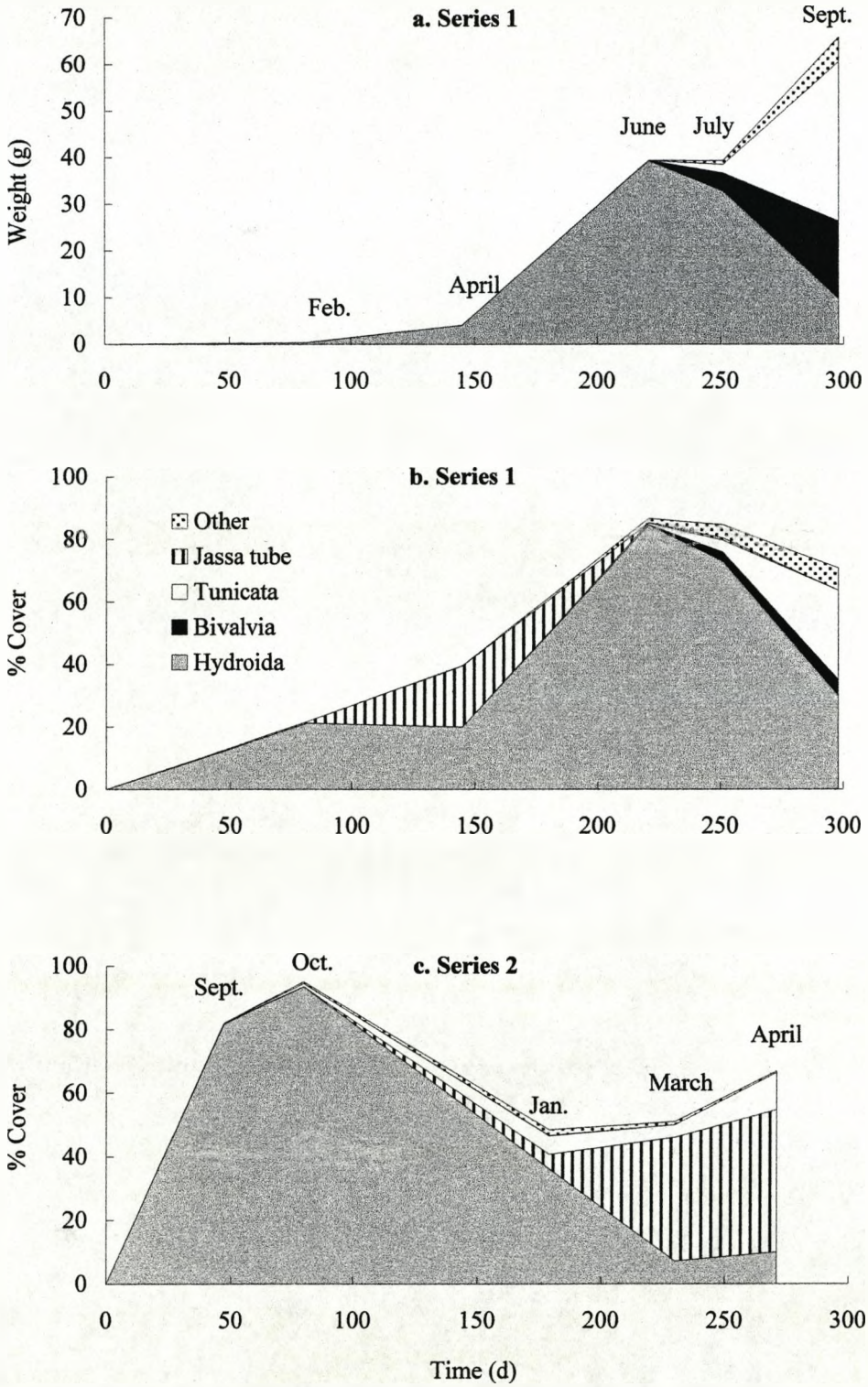


Figure 3.2. Changes in the wet weight (a, series 1 only) and percentage cover (b & c) of sessile fouling with time. Nets were suspended at 14m on the 20.11.98 (series 1) and 31.7.99 (series 2). Total percentage cover may exceed 100% as some species overlap spatially. Wet weight data are fouling loads per gram of netting. *Jassa* tubes were not included in weight analyses.

Changes with time

MDS ordinations of community data (Figures 3.3, 3.4 and 3.5) show progression over time (although samples from some periods overlap forming a gradient rather than discrete groups). This could be related to seasonal changes in the environment or increasing deployment times. All three MDS plots have the same arch shape: this type of plot often characterises communities responding to a strong environmental gradient (Clarke and Warwick 1994). It does not mean that the extreme samples are alike, instead those towards the ends of the arch are near to or more than 100% dissimilar (Clarke and Warwick 1994). The low stress values of these MDS plots means that they reflect differences between samples accurately (Clarke and Warwick 1994). Distances between the midpoints of samples from consecutive sampling dates on the MDS plot roughly reflect the time between sampling dates (this is most clear on the MDS of weight data). This suggests that rates of community change were similar throughout the investigation.

Series 1

Percentage cover and wet weight analysis identified 72 species on series 1 nets (Figure 3.6 with reference to Table 3.1). The percentage cover and weight of species included in PRIMER analyses are given in Appendices 3 and 4. Global ANOSIM results (all depths pooled) for series 1 percentage cover data found that samples from all five time-periods were significantly different (Table 3.4). When samples from different depths were analysed separately, however, communities from times one and two (February and April) did not differ greatly at any depth (R values are close to 0, Table 3.4). Differences between these times may have been blurred by slow winter fouling growth and scatter in April data due to the prolonged sampling period (26 days, Table 3.2). Samples from 18m were also indistinct at times three and four (June and July). Again, the time of sampling may have been important, as these sampling dates were separated by only 30 days (Table 3.2). Wet weight results group more discretely on the MDS than percentage cover data (Figure 3.5) and differences between samples on the five dates were all significant (ANOSIM results, Table 3.6). Interestingly, even April samples are strongly grouped though samples for this month were collected over an extended period.

The most striking feature of the shade matrix for series 1 (Figure 3.6) is the accumulation of species or, increase in species diversity, with time. Generally the low diversity, sparse, hydroid-amphipod dominated community of February and April shifted to a dense hydroid (*Tubularia*) turf in June and then developed into the more diverse and less dense *Mytilus-Ascidiella*-hydroid community of September samples. Descriptions of change in species

abundances with time (below) are based on shade matrices (Figure 3.6) and SIMPER results for both percentage cover and wet weight measures (Tables 3.7 and 3.8). SIMPER results and the shade matrix showed that patterns were generally conserved across all three depths and hence global results are described below; where different trends occurred they are highlighted.

Nets from the first two sampling dates of series 1 were colonised almost exclusively by hydroids and crustaceans. However, whilst February samples were characterised by high abundances of the hydroid *O. geniculata* and small hydroids (mainly *Clytia hemispherica*) April samples were dominated by amphipod (*Jassa falcata*) tubes and hydroids (*Tubularia* spp.). June samples were characterised by *Tubularia*, which often covered the nets completely; they lacked the small hydroids, *O. geniculata* and *J. falcata* tubes of earlier and later samples (though numbers of *J. falcata* were high). *Tubularia* was most prolific on top nets as *J. falcata* tubes had been previously. Kelps colonised nets at 10m in June samples and sessile species from other new taxa also begun to appear sporadically. Nudibranchs (aeolids and *Dendronotus frondosus*) were prolific in June with *Choryphella lineata* often numbering more than 15 individuals per net. Butterfish (*Pholis gunnelus*) and Lumpsuckers (*Cyclopterus lumpus*) were frequently observed around pearl nets from June onwards.

A large increase in diversity occurred during the short interval between June and July. This coincided with a decrease in dominance of *Tubularia*, which had lost many hydrothecae. *Bougainvillia* spp, tunicates (*Ascidiella scabra*), and mussels (*Mytilus edulis*) appeared in large quantities, and were particularly important in distinguishing June and July communities at 10 and 14m. Increased quantities of *Halecium* spp. and the first appearances of the solitary ascidian *Ciona intestinalis*, *Electra pilosa* (an encrusting bryozoan), and peacock worms (*Sabella pavonina*) in July were also important in discriminating the two communities. Mussels, tunicates, *E. pilosa*, *S. pavonina,* and *Bougainvillia* spp typically attached to the stems of *Tubularia.* Aeolid nudibranchs were rare in July samples, but their eggs were visible and numbers increased in September samples.

Tubularia abundance fell dramatically by September though it was still common to all samples. Abundances of *A. scabra, M. edulis,* and *S. pavonina* continued to increase whilst *Bougainvillia,* small hydroids, *E. pilosa* and *Diplosoma listerianum* (a colonial tunicate) overgrew increasingly large amounts of *Tubularia.* Hydroids also attached to the tests of *A. scabra*. Many of the organisms that appeared in July samples were also present in increased amounts in September, and, again additional species arrived.

Percentage cover and weight results described an increase in the amount of silt and algal debris trapped on nets from February until June. Quantities of both then dropped in July before rising again in September. ANOVA results (Table 3.9) showed that the weight of silt was significantly higher in June and September than all other months. The amount of uncolonised space varied significantly with both time and depth (Table 3.10). At depths of 10 and 14m uncolonised netting was highest in February, least in June and July and an intermediary amount in April and September (Figure 3.9). The pattern was similar at 18m except that April levels were not significantly different from high February values. The total weight of wet fouling increased significantly with time (Table 3.10), though February and April samples had similar weights, as did June and July samples (Figure 3.10); this pattern was conserved across all depth groups.

Series 2

Fifty-three species were identified from series 2 nets (Figure 3.7, Table 3.1), the percentage cover of species included in PRIMER analyses is given in Appendix 5. Global ANOSIM results for percentage cover data highlight significant differences between samples collected on all five dates (Table 3.4). Pairwise comparisons revealed, however, that within depth groups differences between consecutive sampling dates were often insignificant. Depth effects were only evident in January samples (Table 3.5).

The communities included an abundant and diverse array of mobile species (Figure 3.7). Like series 1, species tended to accumulate over time but the greatest increase in diversity occurred between the first and second sampling occasions. Nets were quickly covered in a thick *Tubularia* turf and a wide variety of mobile fauna, which dominated September and October communities, determining their proximity on the MDS plot (Figure 3.4). By January, *Tubularia* declined and new hydroid species (e.g. *Bougainvillia* spp.) and *J. falcata* tubes were an important feature of the community. This type of community persisted until April when prolific *J. falcata* tubes were colonised by a range of hydroids, tunicates and mobile organisms that had begun to arrive on earlier sampling dates (Figure 3.7). *Tubularia* cover began to increase again in April, drawing samples from the beginning and end of the time series together on the MDS plot (more than would be expected from the "arch effect", Figure 3.4). The following, detailed description of changes in fouling communities with time is based on percentage cover data described by the MDS plot (Figure 3.4), shade matrix (Figure 3.7) and SIMPER results (Table 3.7). Again, changes in organism cover with time were similar for all depths. Global trends (averaged over the three depths) are therefore discussed unless otherwise indicated.

Autumn communities were similarly characterised by high abundances of *Tubularia* and aeolid nudibranchs. Hydroid were, however, most abundant in October and it was this, along with the appearance of *D. listerianum* that principally differentiated sessile communities from the two sampling dates. One replicate from 18m is distinct from the other September samples on the MDS plot because it was very sparsely colonised, supporting only low abundances of both *Tubularia* and *Bougainvillia.* A large increase in diversity occurred between September and October. Mobile species included molluscs, crustaceans, polychaetes and bivalves. Some of these organisms occurred patchily across the sampling period (e.g. *D. frondosus* and *Cancer pagarus*) whilst others were sparse initially and increased later (e.g. *A. opercularis* and *S.marina*). The abundance of most mobile species plateaued in October. Maximum abundances of nereid worms, *Liocarcinus* spp., *S. marina* and *Endeis* spp. distinguished these communities from later ones.

The large distance between October and January communities on the MDS plot (Figure 3.4) mainly reflects changes in relative species abundance and not the appearance of new organisms (e.g. *Tubularia* cover fell from over 50% to less than 1%). The abundance of small hydroids was also reduced while *Bougainvillia*, *J. falcata* tubes and *A. scabra* became common. Abundances of mobile species were similar to January. March saw a decline in *Bougainvillia* and increasing cover by *J. falcata* tubes. The occurrence of other species was similar to January (explaining the intermingling of these samples on the MDS plot) though nudibranchs and their eggs had disappeared completely. April samples revealed a further increase in *J. falcata* tubes (Figure 3.2) with a slight increase in *Tubularia*, tunicates (*A.scabra* and *D.listerianum*) and nudibranchs. Low abundances of *J. falcata* tubes and *Tubularia* explain why one April replicate from 18m clusters atypically, near January samples on the MDS. As in series 1, the abundance of some species did not vary regularly with time or depth, instead they occurred sporadically, but often numerously, across times and depths (e.g. *Sertularia polyzonians* and *Inachus* spp.).

Amounts of uncolonised space changed significantly over time (Table 3.10). Levels were lowest on the first sampling date (September) rising through October to a peak in January and March before dropping slightly, but significantly, in April (Figure 3.9). The total wet weight of fouling also altered significantly with time though SNK tests failed to identify a trend (Table 3.11). Figure 3.10, however, suggests increased levels in April and, to a lesser extent, in October, following trends in total fouling abundance (measured by summing the percentage cover of all species, Figure 3.2) and not the area of net that was occluded (which does not take into account that the fouling community is multilayered).

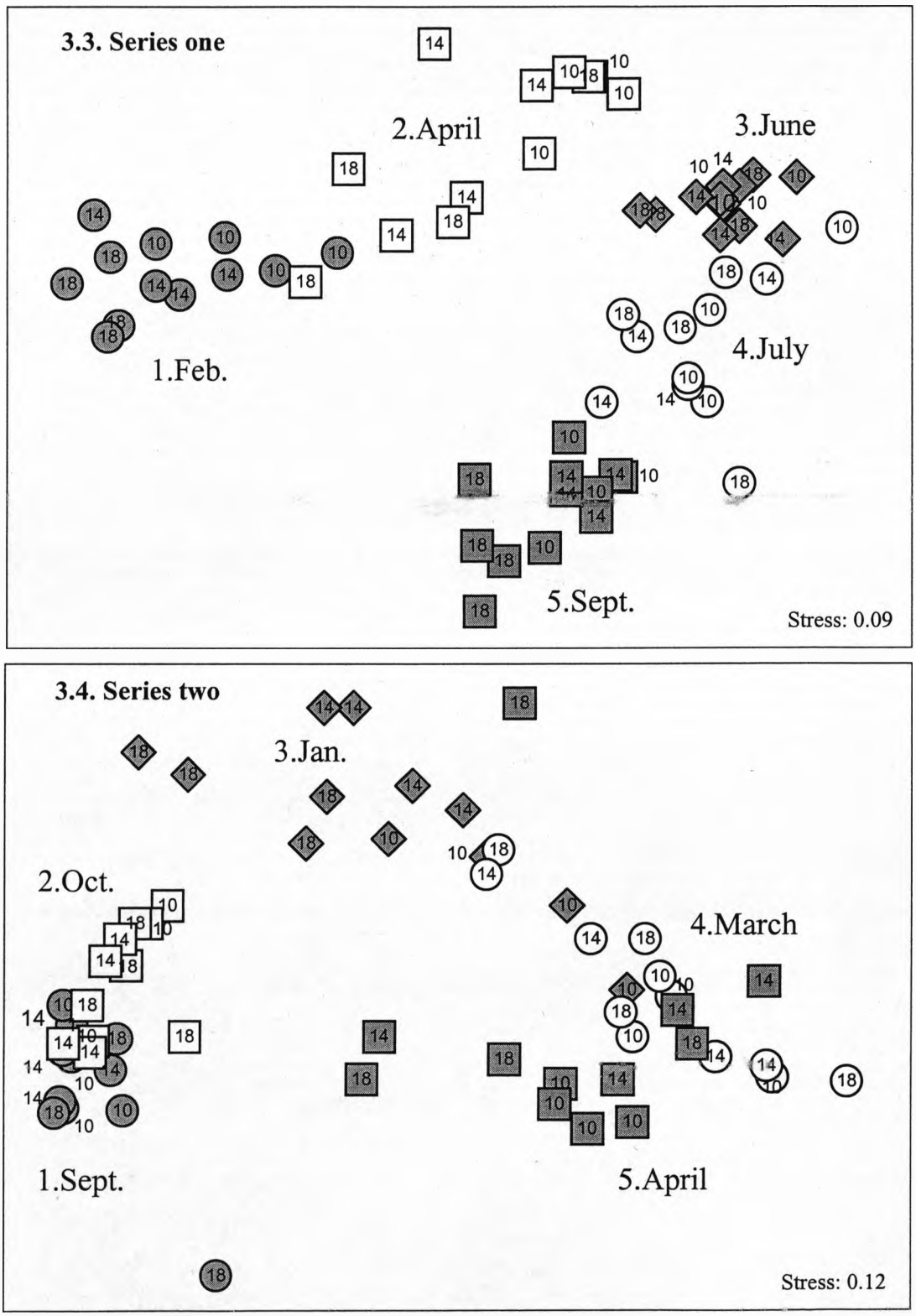
Changes with depth

Series 1

Univariate results showed that total wet weight decreased significantly with depth on every sampling date. The amount of uncolonised space was also highest on the deepest nets (at 18m), though this result was driven by a large difference between depths in April samples, when nets at 10 and 14m also differed significantly (Table 3.10). In contrast to the strong and relatively consistent depth effects identified in total fouling load and the amount of uncolonised space, ANOSIM results suggest that community composition (measured by percentage cover of sessile species) was generally unaffected by depth. SIMPER results show, however, that nets at 18m generally supported less *Tubularia* than shallower ones and that they were covered by relatively large areas of *Halecium* and *Bougainvillia.* There were no obvious trends in the abundance of mobile species with depth (Figure 3.3), though it should be borne in mind that numbers of these species were measured with little precision.

Series 2

Again, depth affected both the total wet weight of fouling and the amount of uncolonised space. Wet weight and the area of net covered by fouling were significantly reduced at 18m (Tables 3.10 and 3.11). Wet weights therefore reflect the area of net covered by fouling within sampling dates (when fouling organisms were similar), where they failed to across the sampling period (when fouling organisms differed, section 3.3.2). Multivariate analyses again suggest that the percentage cover of organisms was not affected by depth when time data were pooled. Global ANOSIM results within times identified a significant depth effect in January. Pairwise comparisons subsequently revealed that nets at 10 and 18m differed significantly although nets at 14m were similar to shallower and deeper ones (Table 3.5). Only small *Cancer pagarus* showed consistent variation between depths, being most common at 10m (Figure 3.4).



Figures 3.3 & 3.4. MDS ordinations of samples from 5 consecutive sampling dates (1, filled circles; 2, open squares; 3, filled diamonds; 4, open circles and 5, filled squares) for nets deployed on the 20.11.98 (series 1) and 31.7.99 (series 2). Numbers indicate the depth at which nets were suspended (10, 14 and 18m). Analysis was based on Bray Curtis similarity indices after square root transformation of percentage cover data.

Table 3.4. Results of ANOSIM analysis of fouling community structure measured by percentage cover data after square root transformation. Results from the two time series (deployed on 20.11.98, series 1 and 31.7.99, series 2) are presented seperately. Samples were compared between sampling dates at each depth and also within all depths pooled. Results of multiple comparisons between individual pairs of sampling dates are also presented. Bold type indicates a significant result ($P < 0.05$).

Time	Depth 10m		Depth 14m		Depth 18m		Global (all depths)	
	R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
Series 1								
Global (all times)	0.70	**<0.01**	0.79	**<0.01**	0.71	**<0.01**	0.90	**<0.01**
1 vs. 2	0.20	0.20	0.26	0.11	-0.09	0.71	0.87	**<0.01**
1 vs. 3	0.77	**0.03**	0.99	**0.03**	1.00	**0.03**	1.00	**<0.01**
1 vs. 4	0.81	**0.03**	1.00	**0.03**	0.99	**0.03**	1.00	**<0.01**
1 vs. 5	0.79	**0.03**	1.00	**0.03**	1.00	**0.03**	1.00	**<0.01**
2 vs. 3	0.65	**0.03**	0.70	**0.03**	0.56	**0.03**	0.86	**<0.01**
2 vs. 4	0.83	**0.03**	0.72	**0.03**	0.63	**0.03**	0.89	**<0.01**
2 vs. 5	0.98	**0.03**	0.83	**0.03**	0.66	**0.03**	0.98	**<0.01**
3 vs. 4	0.69	**0.03**	0.72	**0.03**	0.27	0.09	0.59	**<0.01**
3 vs. 5	1.00	**0.03**	1.00	**0.03**	1.00	**0.03**	1.00	**<0.01**
4 vs. 5	0.59	**0.03**	0.70	**0.03**	0.96	**0.03**	0.74	**<0.01**
Series 2								
Global (all times)	0.71	**<0.01**	0.73	**<0.01**	0.68	**<0.01**	0.74	**<0.01**
1 vs. 2	0.19	0.17	0.21	0.14	0.45	**0.03**	0.35	**<0.01**
1 vs. 3	0.98	**0.03**	0.92	**0.03**	0.88	**0.03**	0.91	**<0.01**
1 vs. 4	1.00	**0.03**	0.97	**0.03**	0.98	**0.03**	1.00	**<0.01**
1 vs. 5	0.99	**0.03**	0.97	**0.03**	0.66	**0.03**	0.89	**<0.01**
2 vs. 3	0.94	**0.03**	0.79	**0.03**	0.94	**0.03**	0.86	**<0.01**
2 vs. 4	1.00	**0.03**	0.97	**0.03**	0.95	**0.03**	0.98	**<0.01**
2 vs. 5	1.00	**0.03**	0.99	**0.03**	0.68	**0.03**	0.89	**<0.01**
3 vs. 4	0.32	0.11	0.47	0.06	0.89	**0.03**	0.51	**<0.01**
3 vs. 5	0.63	**0.03**	0.81	**0.03**	0.80	**0.03**	0.72	**<0.01**
4 vs. 5	0.06	0.34	0.12	0.23	0.10	0.17	0.35	**<0.01**

Table 3.5. Results of ANOSIM analysis of fouling community structure measured by percentage cover data after square root transformation. Results from the two time series (deployed on the 20.11.98 and the 31.7.99 respectively) are presented separately. Samples were grouped by depth and tested at each sampling occasion separately, and also within all sampling occasions pooled. Results of multiple comparisons between individual pairs of depths are also presented. Bold type indicates a significant result ($P < 0.05$).

Depth	**Time 1**		**Time 2**		**Time 3**		**Time 4**		**Time 5**		**Global**	
	R	***P***	***R***	***P***	***R***	***P***	***R***	***P***	***R***	***P***	***R***	***P***
Series 1												
Global (all depths)	-0.12	0.53	0.00	0.40	0.48	**<0.01**	-0.20	0.99	0.02	0.60	-0.03	0.85
10m vs. 14m	-0.13	0.86	-0.06	0.51	0.25	0.11	-0.18	0.91	0.05	0.34	-0.04	0.91
10m vs. 18m	0.09	0.26	0.15	0.26	0.65	**0.03**	-0.12	0.83	0.02	0.37	0.00	0.39
14m vs. 18m	-0.03	0.54	-0.06	0.49	0.54	**0.03**	-0.28	0.97	-0.12	0.91	-0.04	0.93
Series 2												
Global (all depths)	0.13	0.15	-0.01	0.41	0.44	**<0.01**	-0.13	0.83	0.05	0.26	-0.01	0.50
10m vs. 14m	-0.06	0.57	-0.03	0.43	0.18	0.17	-0.09	0.71	0.18	0.09	-0.01	0.50
10m vs. 18m	0.42	**0.03**	-0.07	0.51	0.62	**0.03**	-0.02	0.57	0.18	0.06	-0.02	0.24
14m vs. 18m	-0.02	0.57	0.11	0.34	0.45	0.09	-0.20	0.86	-0.12	0.91	-0.02	0.70

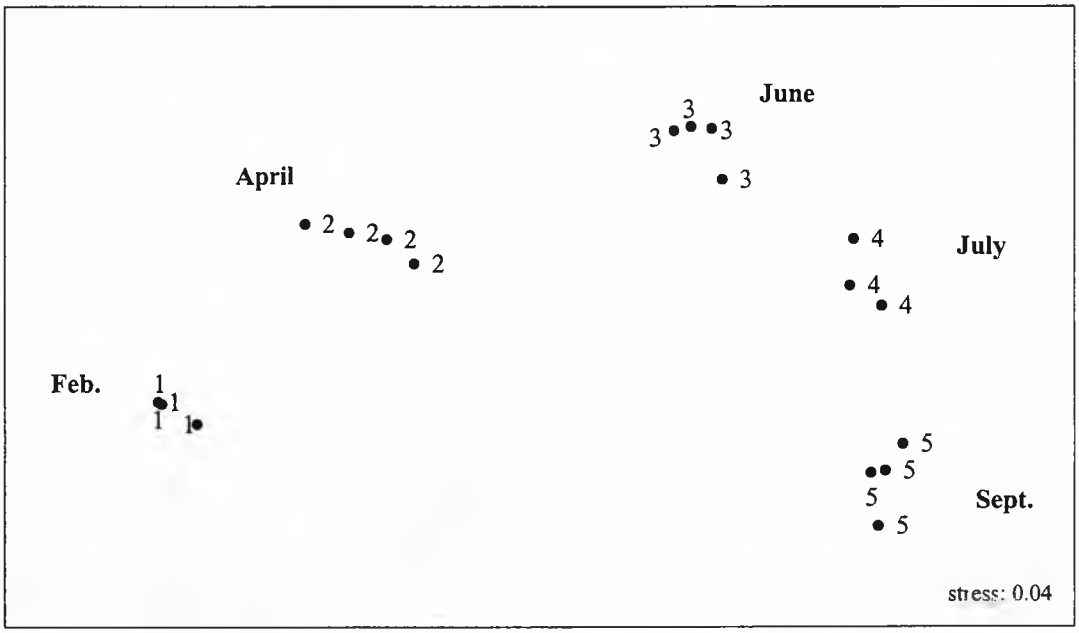


Figure 3.5. MDS ordination of samples from five consecutive sampling dates. Analysis was based on Bray Curtis similarity indices after square root transformation of wet weight data for nets suspended at 14m on 20.11.98 (series 1).

Table 3.6. Global and pairwise significances (P) and R values from 1-way ANOSIM of differences between the communities described above. Weight data were square root transformed and bold type indicates a significant result ($P < 0.05$).

Time	*R*	*P*
Global	1.0	**<0.01**
1 vs. 2	1.0	**0.03**
1 vs. 3	1.0	**0.03**
1 vs. 4	1.0	**0.03**
1 vs. 5	1.0	**0.03**
2 vs. 3	1.0	**0.03**
2 vs. 4	1.0	**0.03**
2 vs. 5	1.0	**0.03**
3 vs. 4	1.0	**0.03**
3 vs. 5	1.0	**0.03**
4 vs. 5	1.0	**0.03**

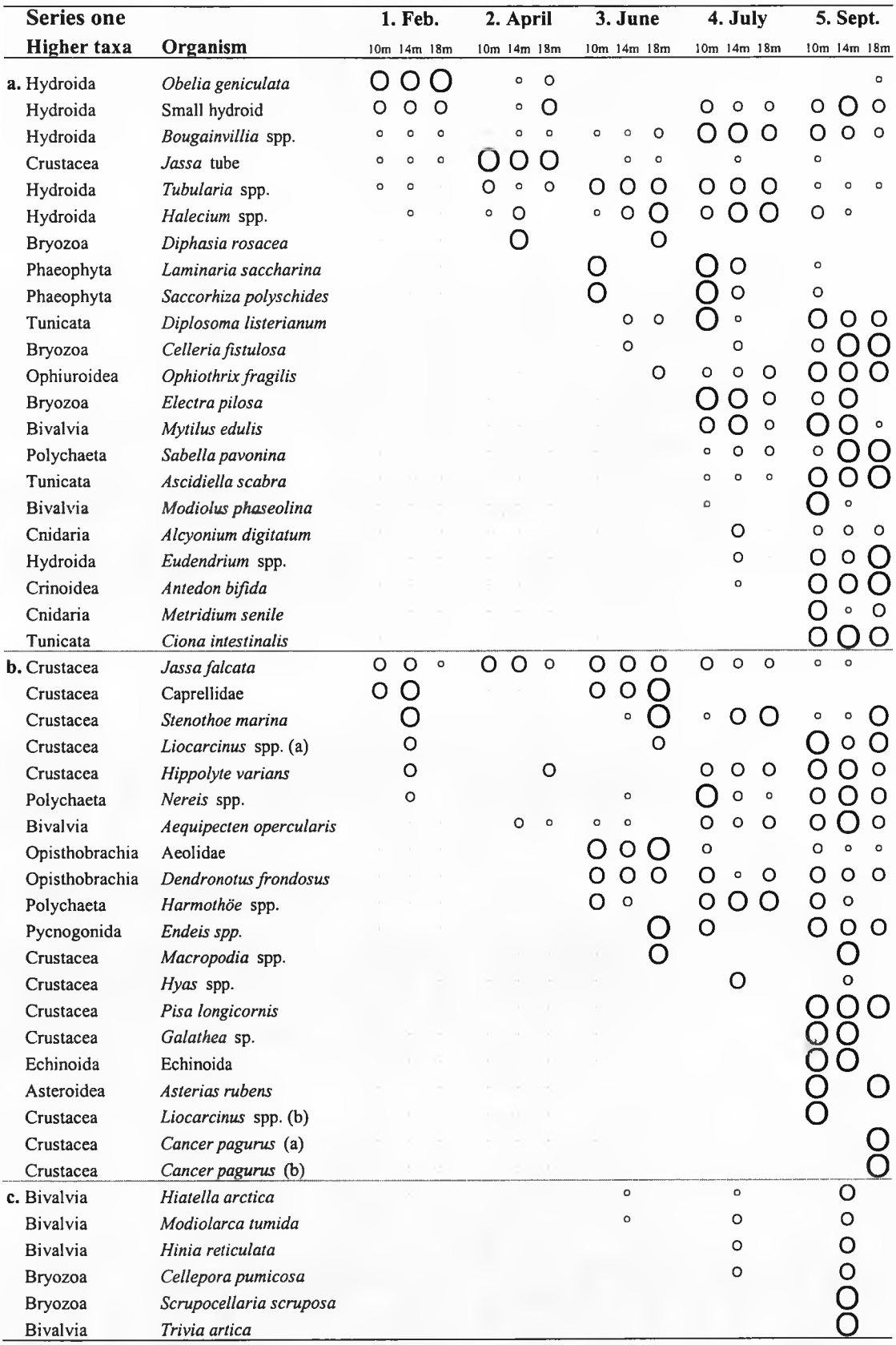


Figure 3.6. Relative abundance "within a sample" of each fouling organism present on more than one net, on five consecutive sampling dates and at three depths. Abundances of sessile (a), and mobile groups (b), were measured by percentage cover and inspection respectively, rare species (c), are those identified only by weight analyses. Circle size is proportional to relative abundance and organisms are sorted by differences between sampling dates. Crabs are labelled a (<4cm) and b (>4cm).

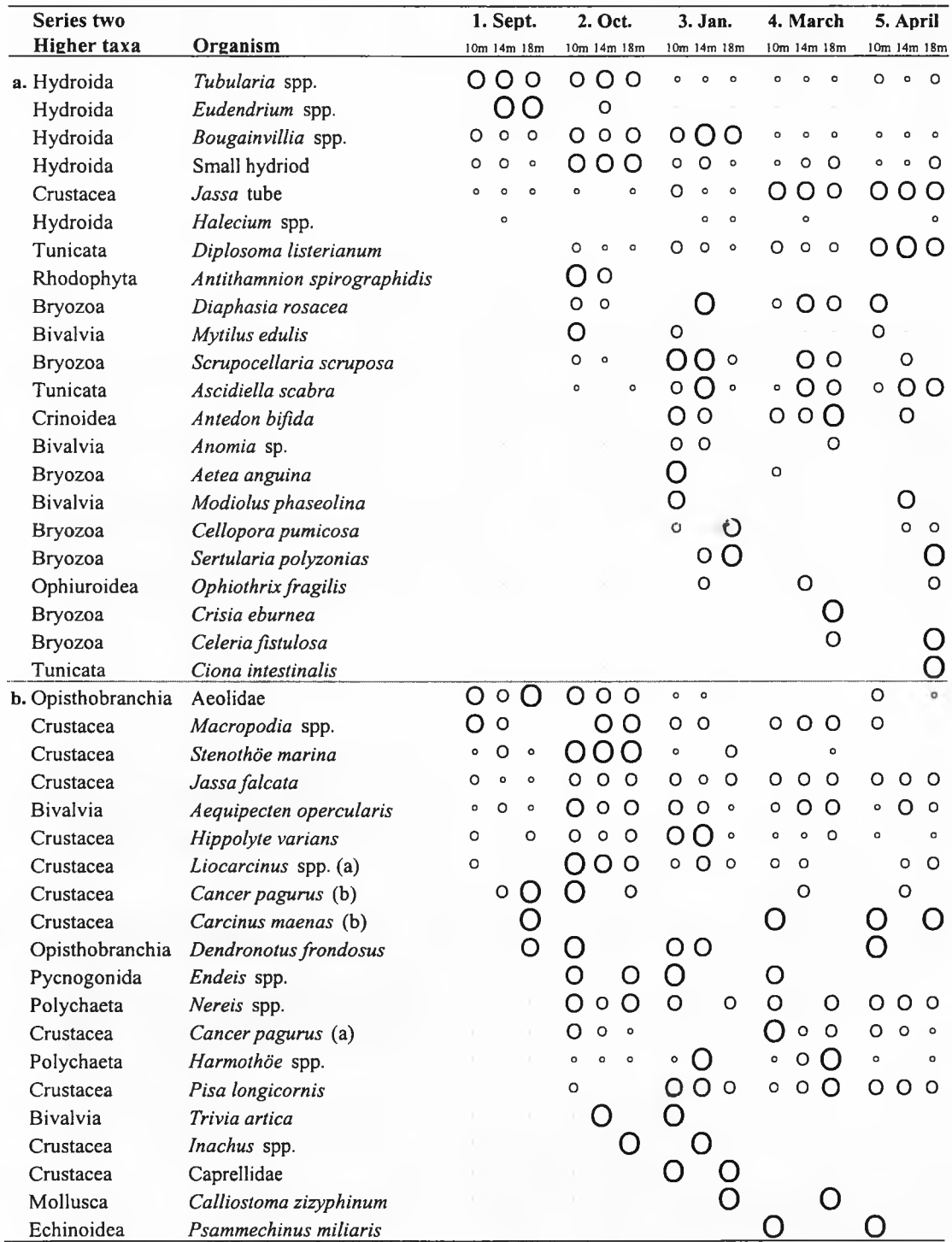


Figure 3.7. Relative abundance "within a sample" of each fouling organism present on more than one net, on five consecutive sampling dates and at three depths. Abundances of sessile (a) and mobile groups (b) were measured by percentage cover and inspection respectively. Circle size is proportional to relative abundance and organisms are roughly sorted by differences between sampling dates. Crabs are labelled a (<4cm) and b (>4cm).

Table 3.7. SIMPER results showing the sessile organisms mainly responsible for the Bray Curtis dissimilarity between consecutive sampling dates during series 1 and 2. Differences are based on square root transformed percentage cover data for all depths (global results, n = 12); a cut off point of 70% dissimilarity has been applied.

Organism	Average abundance (% cover)		Average dissimilarity/ SD	Contribution (%)	Cumulative contribution (%)
Series 1					
	1. Feb.	**2. April**			
Jassa tube	1	29	1.37	32	32
Tubularia spp.	2	23	1.56	27	59
O.geniculata	18	2	1.70	23	83
	2. April	**3. June**			
Jassa tube	29	0	1.75	35	35
Tubularia spp.	23	80	1.24	34	70
O.geniculata	2	0	0.97	8	77
	3. June	**4. July**			
Bougainvillia spp.	1	13	1.66	18	18
Tubularia spp.	80	59	1.10	14	31
A.scabra	0	3	2.15	10	42
E.pilosa	0	3	1.42	10	51
M.edulis	0	2	1.65	8	59
Small hydroid	0	2	1.16	7	66
Halecium spp.	1	1	1.03	5	72
	4. July	**5. Sept.**			
Tubularia spp.	59	11	2.04	19	19
A.scabra	3	34	2.42	19	38
Bougainvillia spp.	13	4	1.61	9	47
Small hydroid	2	5	1.42	6	53
M.edulis	2	4	1.56	6	59
E.pilosa	3	1	1.34	5	63
C.intestinalis	0	1	1.82	5	68
D.listerianum	1	1	1.51	4	72
Series 2					
	1. Sept.	**2. Oct.**			
Small hydroid	3	17	2.06	26	26
Tubularia spp.	67	53	0.95	25	51
Bougainvillia spp.	6	13	1.31	18	69
D.listerianum	0	1	1.49	9	78
	2. Oct.	**3. Jan.**			
Tubularia spp.	10	39	3.34	40	40
Small hydroid	21	3	1.82	13	53
Jassa tube	2	2	1.18	13	66
Bougainvillia spp.	4	3	1.41	10	76
	3. Jan.	**4. March**			
Jassa tube	0	39	1.50	31	31
Bougainvillia spp.	39	3	1.78	28	59
A.scabra	2	2	1.23	8	67
Small hydroid	4	3	1.28	7	74
	4. March	**5. April**			
Tubularia spp.	0	13	1.40	23	23
Jassa tube	39	48	1.02	21	44
D.listerianum	2	7	1.46	14	58
Small hydroid	3	2	1.46	10	69
A.scabra	2	2	1.36	10	78

Table 3.8. SIMPER results showing mobile and sessile organisms mainly responsible for the Bray Curtis dissimilarity between consecutive sampling dates during series 1. Differences are based on square root transformed wet weights per gram of netting, for nets at 14m (n = 4); a cut off point of 70% dissimilarity has been applied.

Organism	Average weight (g)		Average dissimilarity/SD	Contribution (%)	Cumulative contribution (%)
	1. Feb.	**2. April**			
Tubularia spp.	0.10	3.74	3.01	58	58
J. falcata	0.10	0.91	1.42	21	79
	2. April	**3. June**			
Tubularia spp.	3.74	38.89	4.61	65	65
J. falcata	0.91	0.94	1.25	6	71
	3. June	**4. July**			
M.edulis	0.03	3.27	5.85	16	16
A.scabra	0.00	1.84	4.83	13	29
Tubularia spp.	38.89	31.32	1.44	8	37
Bougainvillia spp.	0.40	1.01	1.59	8	45
J. falcata	0.94	0.07	1.56	7	52
E.pilosa	0.00	0.551	2.80	7	59
Halecium spp.	0.00	0.45	0.94	5	64
S.pavonina	0.00	0.15	5.20	4	68
M.phaseolina	0.00	0.10	12.55	3	71
	4. July	**5. Sept.**			
A.scabra	1.84	32.28	5.13	22	22
Tubularia spp.	31.35	7.47	2.51	16	38
M.edulis	3.27	15.05	6.08	11	47
S.pavonina	0.15	3.39	2.04	7	56
C.intestinalis	0.01	1.53	1.63	5	61
Bougainvillia spp.	1.01	2.03	1.14	3	64
A.opercularis	0.13	0.72	1.80	3	67
E.pilosa	0.51	1.02	1.39	2	69
D.listerianum	0.00	0.48	0.82	2	72

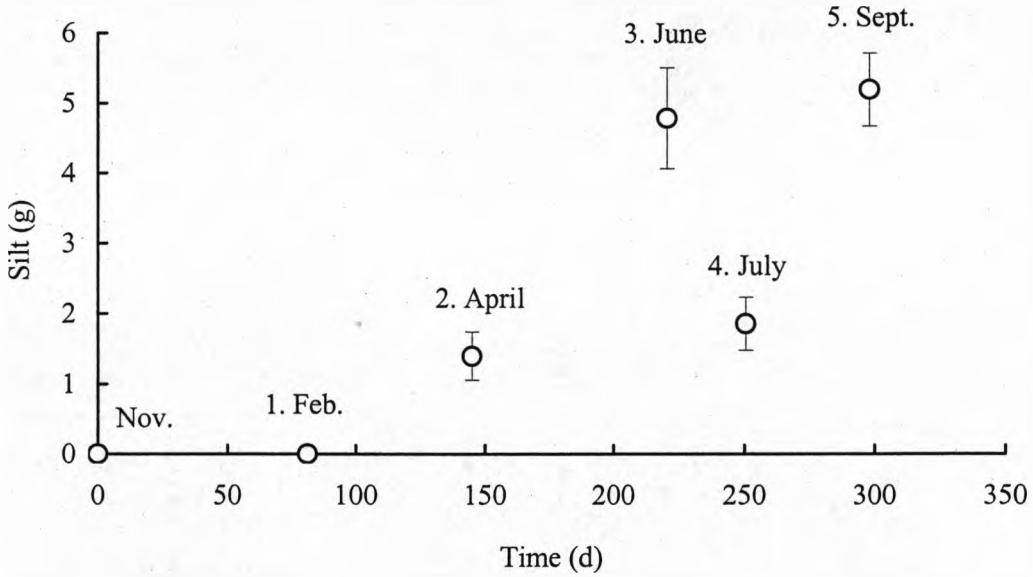


Figure 3.8. Changes in the mass of silt per gram of netting (mean +/- SE), with time. Nets were deployed on the 20.11.98 (series 1) and suspended at approximately 14m.

Table 3.9. One way ANOVA and SNK multiple comparison testing for the effect of deployment time on the mass of silt bound to pearl nets. Results of Cochran's test are given and data are untransformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	**df**	**MS**	***F***	***P***	***F* ratio versus**
$C = 0.6004, P > 0.05$					
Time	4	16	16	**<0.01**	Residual
Residual	10	1			
Total	14				

SNK multiple comparison of time groups:
1 = 2 = 4 < 3 = 5

Source of variation	df	MS	*F*	*P*	*F* ratio versus	
Series 1						
$C = 0.1724$, $P > 0.05$						
Time	4	3640	68	**<0.01**	Residual	
Depth	2	482	9	**<0.01**	Residual	
Time X Depth	8	137	2	**0.02**	Residual	
Residual	45	53				
Total	59					
SNK multiple comparisons:						
time groups	**1 > 2 > 5 > 3 = 4**				*depth groups*	**10m = 14m < 18m**
Interaction:	*Time 1:* 10m = 14m = 18m				*Time 4:* 10m = 14m = 18m	
	Time 2: **10m < 14m =18m**				*Time 5:* 10m = 14m = 18m	
	Time 3: 10m = 14m = 18m				*Depths 10m:* **1 > 2 = 5 > 4 = 3**	
					Depth 14 & 18m: **1 = 2 > 5 > 4 = 3**	
Series 2						
$C = 0.3743$, $P < 0.05$						
Time	4	1070	22	**<0.01**	Residual	
Depth	2	288	6	**0.01**	Residual	
Time X Depth	8	68	1	0.23	Residual	
Residual	30	48				
Total	44					
SNK multiple comparisons:						
time groups	**3 = 4 > 5 = 2 > 1**				*depth groups*	**10m = 14m < 18m**

Table 3.10. Two way ANOVA and SNK multiple comparisons testing for the effect of time (groups 1 - 5), and depth on the amount of uncolonised netting. Percentage cover data were arcsine transformed, results of Cochran's test are given and bold type indicates a significant result ($P < 0.05$).

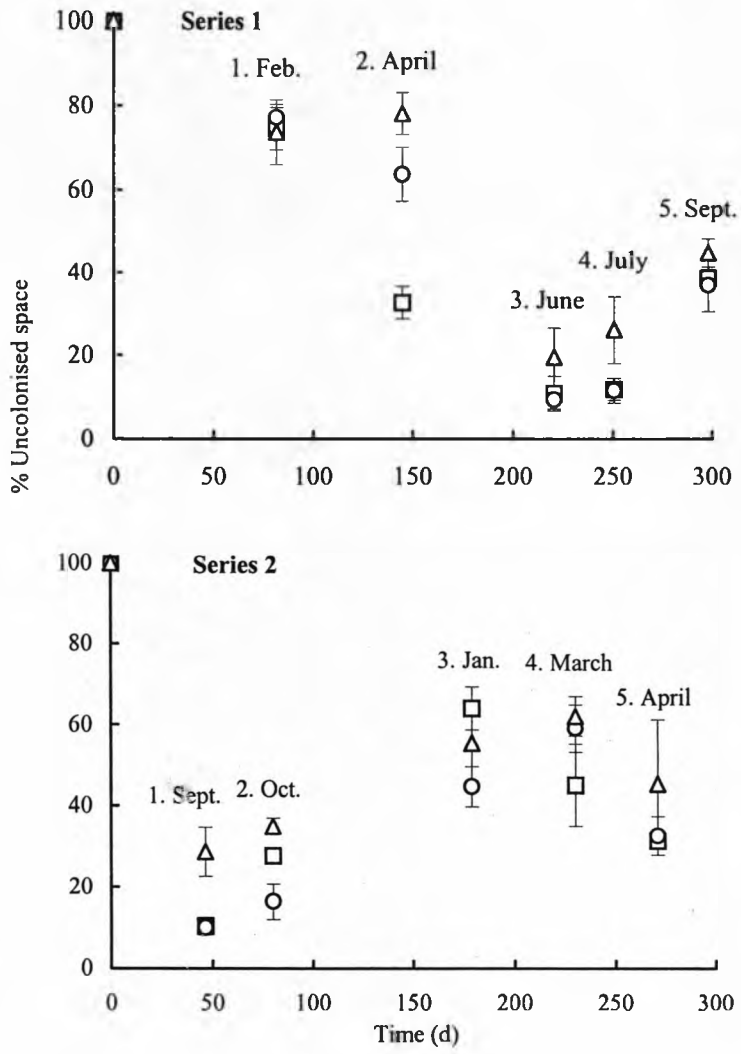


Figure 3.9. Changes in the amount of uncolonised netting (mean +/- SE) with average net deployment time, at depths of approx., 10m (squares), 14m (circles) and 18m (triangles). Initial deployments were made on the 20.11.98 (series 1) and 31.7.99 (series 2).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Series 1					
$C = 0.2133$, $P > 0.05$	4	12205	75	**<0.01**	Residual
Time	2	3571	22	**<0.01**	Residual
Depth	8	333	2	0.06	Residual
Time X Depth	45	162			
Residual	59				
Total					
SNK multiple comparisons:					
time groups: **1 = 2 < 3 = 4 < 5**			*depth groups*		**10m > 14m > 18m**
Series 2					
$C = 0.2856$, $P > 0.05$					
Time	4	852	14	**<0.01**	Residual
Depth	2	387	2	**0.03**	Residual
Time X Depth	8	53	1	0.82	Residual
Residual	30	97			
Total	44				
SNK multiple comparisons:					
no homogenous time groups			*depth groups*		**10m = 14m > 18m**

Table 3.11. Two way ANOVA and SNK multiple comparisons testing for the effect of time (groups 1-5), and depth on the total weight of fouling per gram of netting. Results of Cochran's test are given and data are untransformed. Bold type indicates a significant result ($P < 0.05$).

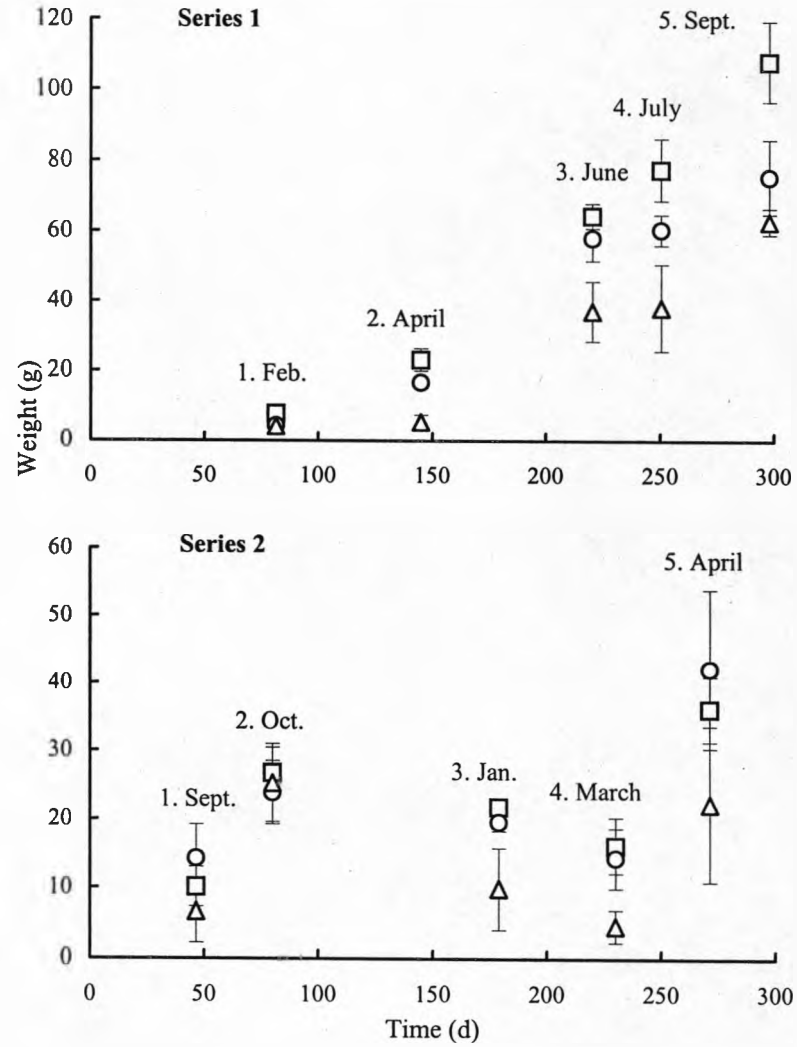


Figure 3.10. Changes in the wet weight of fouling per gram of netting (mean +/- SE) with average net deployment time, at depths of approx., 10m (squares), 14m (circles) and 18m (triangles). Initial deployments were on the 20.11.98 (series 1) and 31.7.99 (series 2). Note different scales on Y axes.

Effects of net deployment date (series 1 vs. series 2)

Nets collected at the same time of year were often characterised by similar foulers, even if they had been immersed at different times. Figure 3.2 highlights this strong seasonal variation in the fouling sequence. The most marked difference between series was the timing of peak hydroid (mainly *Tubularia*) abundance. During series 1, this occurred in June, 200 days after nets were deployed, and was preceded by a gradual rise in hydroid cover. By September (day 298), hydroid cover had dropped back to spring levels (<30%). In contrast, series 2 nets were rapidly colonised by hydroids so that average cover was around 80% in September and peaked in October, after only 80 days. Though *J. falcata* tubes proliferated early in both series, they were most abundant in April; after just 150 days of series 1 compared with 271 days of immersion for series 2. Bivalve fouling also differed between series: high abundances of *M. edulis* characterised late series 1 communities, whereas series 2 was sporadically colonised by low abundances of a range of bivalves. Tunicate proliferation was late and rapid during series 1 where a slight but perpetual cover occurred on series 2 nets.

MDS plots of series 1 and 2 (Figures 3.3 and 3.4) show that early communities were always distinguished from late ones. Later sampling occasions were less distinct during series 2 where samples tended to overlap across sampling dates. Final samples of series 2 were also similar to the first samples whereas these two sets of samples were completely dissimilar in series 1. Shade matrices (Figures 3.6 and 3.7) show that series 1 communities had a gradual increase in diversity with time with the final samples (day 298) being the most diverse. In contrast, the diversity of series 2 communities plateaued around 84 days. Although overall diversities were similar, series 1 supported more sessile species than series two (29 vs. 17 spp.); similar numbers of mobile species were identified from both series. Dominant organisms (hydroids, *J. falcata* and *A. scabra*) were similar in both series though species representing rare groups (bryozoans and algae) differed, and cnidarians and peacock worms appeared only during series 2 (Figures 3.6 and 3.7). Spring and summer/autumn samples generally cluster together on MDS results for both series combined (Figure 3.10); suggesting that samples group more strongly by season than immersion period. April and March samples had similarly high abundances of *J. falcata* tubes while summer and autumn samples shared high amounts of *Tubularia*. Seasonal similarities were, however, limited and samples from the two series were always separated at similarity level of 75% from CLUSTER analysis.

Univariate analyses of total weight and percentage cover data also exposed similar seasonal and depth effects across the two series, despite their different deployment dates. Wet

fouling load clearly increased with immersion period (from spring through to late summer) during series 1. Series 2 weights increased initially, dropping over winter and then increasing again the following spring (Figure 3.10). Wet weights from both series decrease at 18m while 10m and 14m samples were only distinct from each other during series 1 (Table 3.11). Trends in the amount of uncolonised space (Figure 3.9) roughly reflect hydroid abundance (Figure 3.2). The mesh of series 1 nets was up to 85% uncolonised between days 0 and 158 (November to April) but this dropped to around 20% for the next two, summer, sampling dates before increasing again in September (day 298). In contrast, series 2 nets were more thoroughly covered initially (ca. 20-60% empty space) but cover fell during the winter months (days 84-230) increasing again in the spring. Nets from both series were least covered at 18m (Table 3.11).

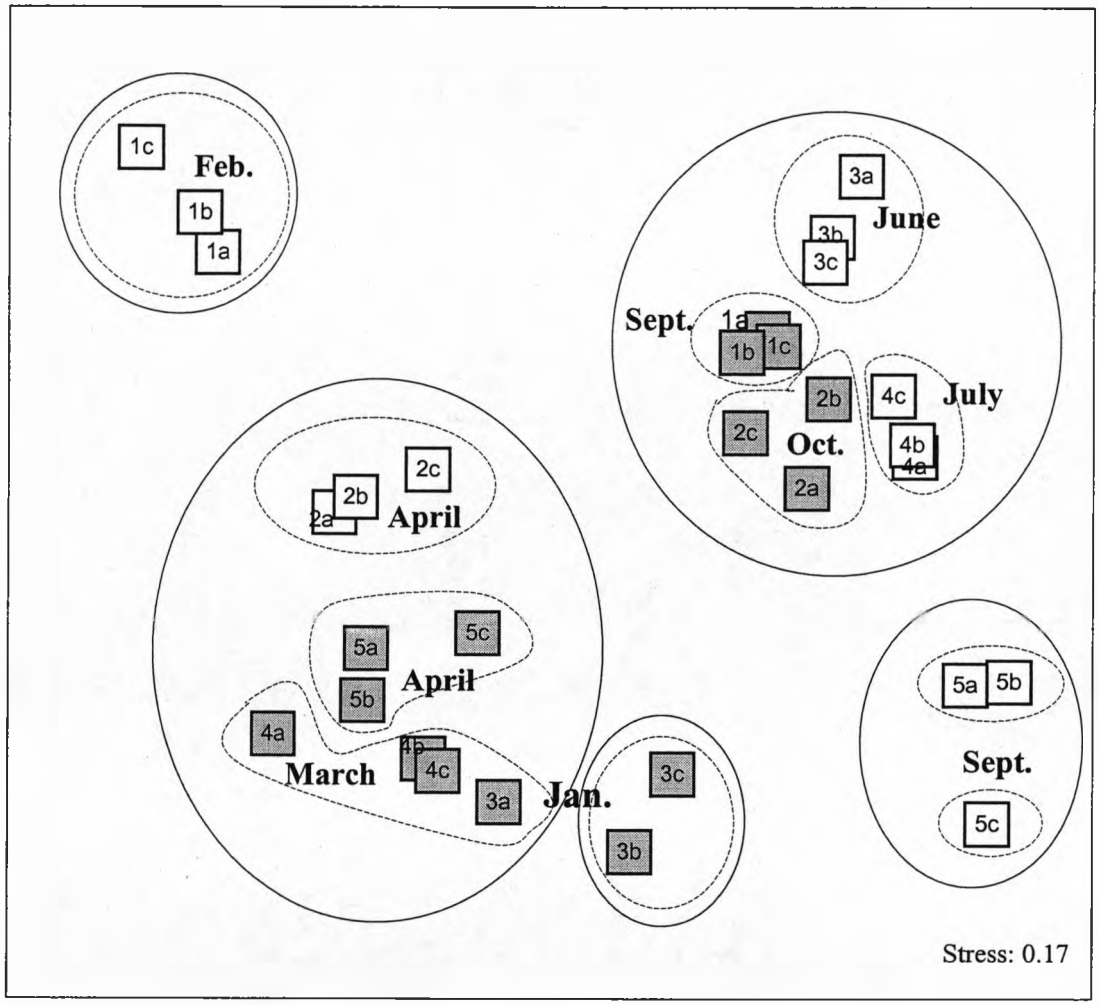


Figure 3.11. MDS ordination of Bray Curtis similarity matrix for square root transformed percentage cover data showing changes in sessile fouling communities with time for nets deployed on the 20.11.98 (series 1, open squares) and the 31.7.99 (series 2, filled squares). Data points are average results for all nets collected on each of five consecutive sampling dates (labled 1-5) from depths of 10m (a), 14m (b) and 18m (c). Samples are grouped at 50% (solid lines) and 75% (broken lines) levels of similarity from CLUSTER analysis.

3.3.3 Shell fouling

Scallop shells were fouled by the hydroids, bivalves, polychaetes and tunicates that colonised nets. The occurrence and abundance of shell foulers changed over time in the same way as net fouling organisms. *Tubularia*, *M. edulis* and ascidians sometimes bound scallops to the side of nets in July and September. In September *D. listerianum* also thickly covered the entire shell of many scallops. In addition to common net foulers, scallop shells were often fouled by the solitary tunicate *Dendrodoa grossularia*, spirobid worms and barnacles. *Dendrodoa grossularia* covered shells initially but was later replaced by *A. scabra* and an occasional *C. intestinalis*. Spirobid and barnacle fouling was sporadic but, where it did occur, abundances were high, reaching up to 100 individuals per scallop. Figure 3.12 shows gradual increases in the numbers and size of saddle oysters and solitary tunicates over time. In July and September, both saddle oysters and ascidians were most abundant at 18m. Mussels appeared in July and by September, they were often large (> 21mm) and concentrated on scallops in nets at 10 and 14m (Figure 3.12).

3.3.4 Scallop predators

Potential predators of scallops in series 1 included starfish (*Asterias rubens*) and crabs (*Liocarcinus* spp. and *C. pagarus*). All of these occurred patchily on the last sampling date. Small swimming crabs also appeared on other dates though they were most prolific on the final samples (Figure 3.6). A range of crabs also appeared on series 2 nets but they generally occurred sporadically across the whole sampling period (Figure 3.7).

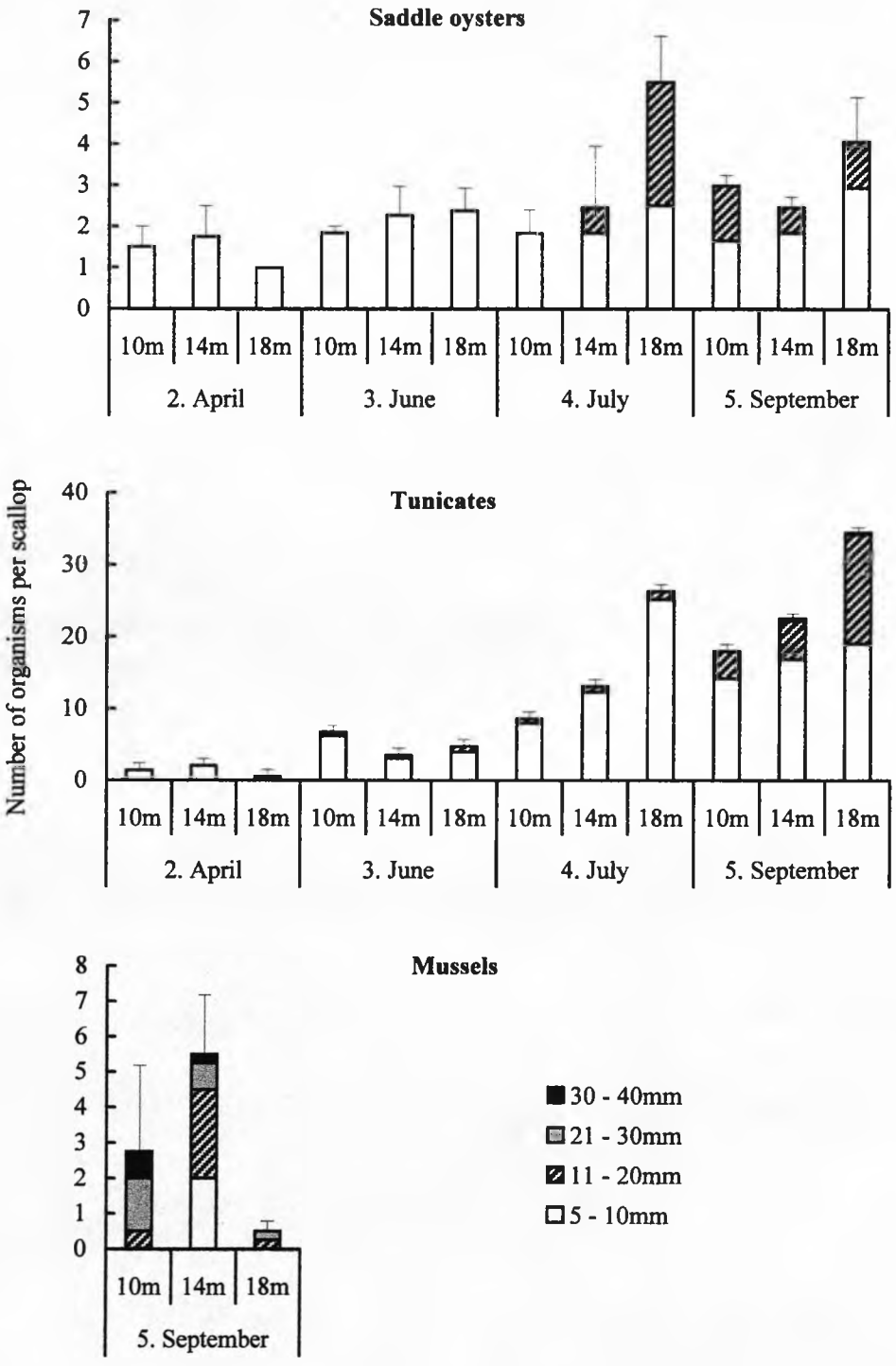


Figure 3.12. Numbers and sizes of common shell fouling organisms on individual scallops. Data are mean results (mean +/- SE) for five pearl nets suspended at 10, 14 and 18m, from 20.11.98 (Series 1). (Mussels were only counted in September.)

3.4 Discussion

The fouling community

The community studied here is similar to that described for nets and cages suspended at similar depths off other Irish Sea coasts (Minchin and Duggan 1989, Skjaeggestad 1997, McDonough 1998) and elsewhere around the world (e.g. Japan, Arakawa 1990; Canada, Claereboudt *et al.* 1994 and Enright *et al.* 1993; Venezuela, Lodeiros *et al.* 2000; USA, Hidu *et al.* 1981; Indonesia, Taylor *et al.* 1997; Spain, Cigarria *et al.* 1998, and Australia, Cronin *et al.* 1999). Off Port Erin, as in Hiroshima Bay (Arakawa 1990), the community can be split into three tiers whose composition changed over time. Sessile foulers often covered the entire net surface. The first species to arrive were hydroids (*Tubularia spp.*, *Bougainvillia* spp., *Obelia geniculata* and other small hydroids). Later, tunicates (*Ascidiella scabra*, *Diplosoma listerianum*, *Ciona intestinalis*), mussels (*Mytilus edulis*), and peacock worms (*Sabella pavonina*) became important. Scavenging and predatory, mobile foulers living amongst sessile species included amphipods, crabs, nudibranchs, and nereid worms. Finally, resident fish (*Pholius gunnellus* and *Cyclopterus lumpus*) probably preyed on sessile and mobile species. Major sessile foulers are discussed in most detail because they can affect scallop growth by entanglement or by changing the environment inside the nets (see Chapter 4). Mobile foulers and top predators are also considered because they could prey on or irritate scallops, or influence sessile foulers. They might also be usefully exploited for biological fouling control.

Net fouling communities were made up of species common in Manx waters (Bruce *et al.* 1963, Hextall and Mitchell 1994), but the dominant species differed from those on nearby hard substrata. Most noticeably the hard substrata lack heavy colonisation by tunicates, hydroids or mussels; instead, they are dominated by the plumose anemone, *Metridium senile,* the soft coral *Alcyonium digitatum* and *Echinus esculentus*, an urchin (*Pers. obs.* and M. J. Bates, *pers. comm.* 2001 Port Erin Marine Laboratory, Isle of Man). The absence of *Ascidiella* and mussels and dearth of hydroids on rock faces is probably explained by the removal of new recruits by urchin and mollusc grazing (Young and Chia 1984, Hextall 1994). *Alcyonium digitatum* and *M. senile* appeared on nets retrieved towards the end of series 1, though subsequently their spread may have been inhibited by competition for space with mussels and the instability of nets as a substrate.

Changes with time

Differences between time series highlight the importance of intra-annual, seasonal variation on the initial colonisation and subsequent dynamics of net-fouling communities. This was further illustrated by MDS plots for both series combined, which showed that samples collected in the same season (but with different immersion histories) were more similar than those that had been immersed for similar amounts of time but were collected in different seasons. As in other fouling studies (Svane 1988, Arakawa 1990, Hextall 1994) seasonal recruitment and senescence seems to have been the major cause of community change within each time series. Winter deployed nets (series 2) supported a gradual increase in species abundance and diversity culminating in a summer peak; samples from consecutive dates were generally differentiated by the appearance of new species. In contrast nets deployed at the end of July (series 2) were quickly and heavily colonised by a diverse array of species, the abundance of which declined through the winter months. Samples from different dates were characterised by changes in the abundance of a few dominant species. Colonisation patterns during this study are similar to those reported previously for this area (Brand *et al.* 1980, Hextall 1994, Wilson 1994) suggesting that the results provide an accurate example of regular seasonal variability. However, care should be taken in generalising from these results for a single year because the dynamics of benthic communities, particularly larval supply, can show huge inter-annual variation (Underwood and Fairweather 1989, Arakawa 1990, Richmond and Seed 1991)

Tubularia fouling was one of the most striking features of both time series; it often completely covered nets and weighed around 39g per gram of netting. The timing of maximum *Tubularia* fouling (in summer and autumn) seemed roughly independent of the immersion date. The timing of proliferation was probably determined by seasonal larval supply (Hextall, 1994) and high water temperatures promoting growth (Hughes 1983, Arakawa 1990). Positive intraspecific feedback may also have been important because chemicals from adult *Tubularia* can stimulate further larval settlement (Nellis and Bourget 1996). *Tubularia larynx* and *T. indivisa* have slightly different life cycles and growth strategies (Hughes 1983) though they occurred sympatricly during this study. Treating the two species as a single group may therefore have overlooked interactions between them and their possibly different relationships with other foulers.

Interestingly, the weight and cover of *Tubularia* on series 1 nets declined from June until September despite rising sea temperatures over this period. This seemingly premature decline was probably caused by the nudibranchs that proliferated in June. Many hydroid stalks lacked hydranths, which is a symptom of nudibranch predation (Hughes 1983,

Lambert 1991) and *Tubularia* is a preferred foods of all three nudibranchs identified in this study (Clark 1975, Hayward and Ryland 1990, Picton and Morrow 1994), though each may have exploited different areas of the hydroid colony (Lambert 1991).

Tubularia was an important structuring force in these fouling communities. As a "keystone species" (Tanner 1994) it probably facilitated the recruitment of many species and brought about the decline of others. Numerous *Tubularia* stalks provided a substrate for many sessile foulers, including bivalves, tunicates, small hydroids, bryozoans and tubeworms. Larvae of these species may have settled on *Tubularia* by chance, facilitated by its high surface area and reduced water-flow (Schmidt 1983). Many of the colonising species are, however, frequently associated with *Tubularia* (Hayward and Ryland 1990), suggesting more active processes were involved; perhaps larvae settled in response to physical or chemical cues (Harvey *et al.* 1993, 1997) or the availability of particular microhabitats (Schmidt 1983).

Like sessile species the abundance and diversity of amphipods, crabs, nudibranchs, pycnogonids and polychaetes also peaked when nets were heavily colonised by *Tubularia*. Many of these species probably benefited from the presence of *Tubularia* either directly (e.g. as a source of food or shelter from water movement) or indirectly through its interactions with other organisms (e.g. by encouraging amphipod settlement *Tubularia* provided food for nereid worms). Direct benefits have been recorded for amphipods that can prey on hydroids whilst gaining increased protection from their own predators and access to fast water currents for feeding (Gili and Hughes 1995, Cain 1998). *Tubularia* was also consumed by pycnogonids and nudibranchs. Mobile foulers that might prey on scallops included crabs (*Liocarcinus* spp. and *C. pagarus*) and starfish (*Asterias rubens*). They recruited most in summer months (Figures 3.6 and 3.7) and their small size means that they were unlikely to damage the intermediate sized scallops in nets. However, they could become a problem if scallop spat were suspended in nets or if nets were deployed for longer (Hidu *et al.* 1981, Minchin 1992, Freites *et al.* 2000).

Nudibranchs (*D. frondosus* and *Choryphella lineata* and *Facelina bostoniensis*) were important secondary foulers. Like *Tubularia,* they grow and reproduce most in the summer when water temperatures are high and food is abundant (Swennen 1961, Clark 1975). The decline of *Tubularia* coupled with stenotypic feeding habits and low water temperatures probably explain why nudibranch numbers generally declined through the winter.

Though hydroids frequently colonised *Tubularia* stalks (e.g. *Clytia hemispherica, Halecium* spp., *Filellum surpens*) the abundance of *Bougainvillia* spp. and *Obelia geniculata* tended to rise before or after peaks in *Tubularia* cover. Again, a causal relationship cannot be proved, and little information is available on the seasonal cycles and competitive abilities of these species. However, *O. geniculata* and *Bougainvillia ramosa* can recruit and grow year round (Jones 1993, Hextall 1994, Ballard and Myers 1996) but *O. geniculata* is readily overgrown by larger and more robust species (Hextall 1994). Reduced growth and recruitment of larger species in the winter probably enabled *O.geniculata* and *Bougainvillia* spp. to persist initially during series 1, whereas fast summer growth of *Tubularia* in series 2 may have pre-empted all of the available primary space, preventing other hydroids from settling, or overgrowing them before the nets were first sampled. Both species are also preyed on by nudibranchs (Lambert 1991, Cain 1998) and another possibility is that they were killed by nudibranchs that proliferated when *Tubularia* cover was high.

Jassa falcata tubes covered large areas of nets retrieved in winter and spring during both series. The amphipods were also prolific during summer and autumn months but dense hydroids might have obscured or disrupted their tubes at these times. High abundances of *J. falcata* were also found by McDonough (1998) on scallop nets in Strangford Lough, Northern Ireland and tube forming amphipods are important scallop shell foulers off Venezuela (Lodeiros and Himmelman 2000). *Jassa falcata* is a ubiquitous fouling species that proliferates in exposed conditions (Wakabara *et al.* 1983, Jacobi 1987), where detrital-food levels are high (Barnard 1958, Nair 1980, Dixon and Moore 1997) and abundant organic debris facilitate tube building (Ulrich *et al.* 1995). Female *J. falcata* breed inside their silty tubes, producing several broods throughout the year (Nair 1980, Borowsky 1983) though greatest growth and reproduction occurs during the summer when water temperatures are high (Nair 1980). Favourable conditions and high fecundity thus explain the rapid proliferation and subsequent persistence of *J. falcata.* A rough estimate suggests that, at their peak, over 200 adult *J. falcata* colonised one gram of netting, or that there were roughly 51 000 individuals m^2. Similarly, Nair and Anger (1980) found densities of 11 000-72 000 m^{-2} in the North Sea. Like *Tubularia*, small hydroids and *J. falcata* tubes formed a secure matrix that was inhabited by a diverse array of mobile species (Table 3.9).

Jassa falcata tubes often covered small hydroids, though it was impossible to tell whether the hydroids were killed or grew through the tubes so that they could feed. Many foulers do not settle or recruit onto silty substrates, or are quickly killed by smothering (e.g. Moore 1977, Devinny and Volse 1978, Minchin 1992, Sundberg and Kennedy 1993, Berkman 1994). Therefore, by covering large areas of netting in silty tubes, *J. falcata* might have

inhibited other species from colonising series two nets in the spring. During series 1, however, *Tubularia* was established before *Jassa* tubes providing an alternative, silt free, substrate for new species.

During series 1, the hydroid-amphipod dominated community was gradually succeeded by a more diverse one based principally on tunicates (mostly *Ascidiella scabra* but also *D. listerianum* and *Ciona intestinalis*), though *Mytilus edulis*, *Sabella pavonina, Electra pilosa* and a range of hydroids were also important (Figure 3.2, Tables 3.6 and 3.7). All of these late colonisers were frequently attached to *Tubularia* and, paradoxically, its presence may have stimulated or facilitated their settlement (Schmidt 1983, Harvey *et al.* 1993, 1997).

Gradual replacement of hydroids by ascidians and bivalves is a common fouling sequence (e.g. Clark 1975, Dean and Hurd 1980, Schmidt 1983, Claereboudt *et al.* 1994b, Hextall 1994). During series 1, this succession was probably initiated by the seasonal supply of larvae (Brand *et al.* 1980, Hextall 1994) and selectively grazing nudibranchs (Hughes 1983, Claereboudt *et al.* 1994a). Subsequently, a combination of factors may have enabled *A. scabra* and other late colonisers to replace *Tubularia*. Firstly, like *Tubularia,* larvae of *A. scabra* and *M. edulis* respond positively to the presence of conspecific adults (Svane *et al.* 1987, Richmond and Seed 1991, Seed and Suchanek 1992), encouraging their aggregation on nets. Secondly, once established, adult tunicates and mussels may have preyed on the larvae of other foulers before they could recruit (Dean and Hurd 1980, Osman *et al.* 1982, Breitburg 1985). Finally, late colonisers were active suspension feeders with robust supporting structures and predator defences, making them stronger competitors for food and space than hydroids (e.g. Dean and Hurd 1980, Russ 1982, Dalby and Young 1993, Hextall 1994).

The solitary tunicates found during series 1 are annual species whose dominance would have diminished with the onset of winter (Svane 1988, Hextall 1994, Skjaeggestad 1997). If nets are deployed early in the summer, they might therefore become dominated by long-lived *M. edulis* through the autumn and winter. Neither *M. edulis* nor *A. scabra* were abundant during series 2, probably because nets were deployed late in the year when larvae of both species have generally settled out of the water column (Mason and Drinkwater 1981, Hextall 1994). *Diplosoma listerianum*, however, persisted at low levels from July and eventually proliferated at the end of April (probably by asexual budding), when water temperatures began to rise.

Though cages and nets are unstable substrata, silt accumulation can be significant (Hidu *et al.* 1981, McDonough 1998), weighing up to 6g per gram of netting during this study. Silt was bound by amphipod tubes, between hydroids, and onto the cellulose tunics of *A. scabra*. The accumulation of silt was probably caused by a combination of biodeposition and the entrapment of dead foulers and organic debris from the water column. During series 1, the weight of silt generally increased with the total weight or percentage cover of the fouling community. However in July, weights of silt were atypically and consistently low (Figure 3.8). Wind and tide conditions were similar on June, July, and September sampling dates and the weeks leading up to them (wind data are from Ronaldsway meteorological office, Isle of Man) and so differences in water movement are unlikely to explain this result. Instead, *Tubularia* die-back may have released the silt. Later, the *A. scabra* community was established and, together with *M. edulis,* it seemed to form a solid, silt-binding matrix.

Changes with depth and the absence of surface effects

Previous studies, like this one, report that the weight and cover of fouling decreases with depth (Clareboudt *et al.* 1994, Lodeiros *et al.* 1998, Lodeiros and Himmelman 2000). Clareboudt *et al.* (1994) attribute such differences to decreases in water temperature, food, and larval settlement with depth. Other research suggests that low food concentrations, and not temperature, may explain why the growth of scallops and mussels in suspended culture decreases with depth (Page and Hubbard 1987, Lodeiros *et al.* 1998, and references therein). In this experiment, water temperatures were generally similar throughout the water column, the greatest difference (0.1°C) being unlikely to significantly affect the growth rate of poikilotherm fouling organisms (Lodeiros *et al.* 1998). Chlorophyll *a* measurements (Appendix 6) taken opportunistically twice during the experimental period, indicate that phytoplankton concentrations adjacent to the longlines decreased at 18m. Like scallops and mussels sessile foulers were suspension feeders, and this reduction in food is thus most likely to have limited their growth at depth. Larval supply and survival may also have been important. For example, Brand *et al.* (1980) showed that numbers of *Aequipecten opercularis* recruiting near to the study area decreased towards the seabed. Arakawa (1990) similarly reports that mussels and ascidians set most heavily in the top 10m of the water column.

Differences in the type of animal fouling on differently orientated surfaces are common and have been variously attributed to patterns of larval settlement, mortality or growth, in response to light intensity (Pomerat and Reiner 1942, Claereboudt *et al.* 1994a), silt accumulation (Lang *et al.* 1975, Harris *et al.* 1979) and predation (Harris and Irons 1982).

In this experiment, physical differences between surfaces (and hence differences in fouling organisms) may have been reduced by wide mesh spaces and the flexibility of the substrate.

Shell fouling

Pecten maximus usually recess under a thin layer of sediment, which protects their shells from heavy fouling. In suspended cultivation, however, this species readily accumulates shell-fouling organisms. In this experiment scallops were often bound to nets by hydroids, mussels and tunicates. This may have reduced scallop growth rates or increase mortality. Increased fouling of scallops in cages with wide mesh has been attributed to the ease with which fouling larvae can reach scallops (Manuel 2001). Similarly, in my study, increased shell fouling by ascidians and saddle oysters (*Anomia* sp.) at depth might be explained by reduced net fouling at 18m enabling larvae to enter nets unimpeded. In contrast, mussel fouling was least at 18m, probably reflecting the distribution of larvae in the water column.

Implications for fouling management

Tubularia, *O. geniculata*, *M. edulis* and *A. scabra* have been identified as the major sessile foulers in this study. *Obelia geniculata* is fragile and light, it thus seems unlikely to have affected scallop growth by altering the environment. However, it may harbour the polychaete *Polydora*, which is a scallop parasite (Mortensen *et al.* 2000). Here, as in other areas (Arakawa 1990, Claereboudt *et al.* 1994a) *Tubularia* often thickly covered entire nets, reducing the transfer of water to scallops (Chapter 4). *Tubularia* can also bind scallops (Claereboudt *et al.* 1994a, *pers. obs.*), and seems to encourage settlement of important sessile and mobile foulers. Cover of *M. edulis* and *A. scabra* was relatively patchy, but both species were observed to bind scallops, and as fast and efficient feeders (Barnes 1987, Lesser *et al.* 1992, Larsen and Riisgård 1997) they might also compete with scallops for suspended food particles. Finally, the high mass of tunicates and mussels (nets dominated by these organisms had a fouling load of around 3.75 kg whereas those covered in hydroids weighed just over 2 kg) increases the buoyancy requirement, and hence cost, of cultivation equipment (Hardy 1991). Strategies to control sessile fouling in this area might therefore concentrate on *Tubularia, M. edulis* and *A. scabra*.

Previous research suggests that fouling might be ameliorated by careful choice of cultivation site (Arakawa 1990, Claereboudt *et al.* 1994a). Unfortunately, the positioning of cultivation equipment generally represents a trade off between many factors (e.g. protection from weather, shipping and fishing, ease of access, water quality, and maximising scallop growth), and information about fouling may be absent or blurred by wide interannual variation. Within a particular location, fouling can be tackled by altering the vertical position of nets to avoid peak settlement depths (Arakawa 1990, Enright 1993), cleaning

nets soon after peak settlement (Enright 1993), chemical or physical deterrents on nets (Huguenin and Huguenin 1982, Paul and Davies 1986, Richmond and Seed 1991), luring fouling larvae to decoy lines (Arakawa 1990), or biological control (Hidu *et al.* 1981, Enright *et al.* 1983, Minchin and Duggan 1989, Cigarria *et al.* 1998). Results of this investigation suggest that mussel settlement could be reduced by setting nets low in the water column (ca. 18m) during June and July. However, low food at these depths might reduce scallop growth. Cleaning nets in September, after peak mussel and tunicate settlement, does not appear to facilitate significant proliferation of other fouling species, and therefore seems a sensible alternative. Periods of *Tubularia* recruitment are less well defined than those of mussels and tunicates. This hydroid might be best combated by altering the design of nets or using biological control.

Of the mobile foulers, *J. falcata* and nereid worms were often found inside scallops. Although this could be a sampling artefact it seems likely that these scavengers might enter scallops in search of food. Movement inside living scallops could both irritate and damage delicate ctenidia and mantle tissue, perhaps reducing scallop growth (Getchell 1991, Irlandi and Mehlich 1996). Crabs were also common and could be a problem if nets contained scallop spat (Hardy 1991, Freites *et al.* 2000). Controlling *Tubularia* might reduce the settlement and subsequent retention of crabs and worms but not *J. falcata,* which succeeded in the absence of sessile species. For this species then, as with *Tubularia*, biological control may be the best option.

Future work

Several studies have highlighted significant variations in fouling composition and intensity over short distances (e.g. Arakawa 1990, Claereboudt *et al.* 1994a, Butler and Connolly 1999). With a combination of literature research and field studies, it might be possible to roughly predict the intensity and type of fouling from various biological and physical parameters (e.g. distance off-shore, exposure, depth of water, substrate type, turbidity and current speed). Such information could help scallop growers to identify sites with potentially low fouling or the least harmful fouling species.

During this study, *Tubularia* colonies generally emanated from the knotted corners of the monofilament mesh; perhaps because knots sheltered newly settled larvae from strong water movement or offered a secure anchor for growing stolons. Other surface characteristics, such as colour and roughness can also affect the settlement of foulers (Norton and Fetter 1981, Arakawa 1990, Richmond and Seed 1991, Kerr *et al.* 1999). Work could therefore be

carried out to design nets and cages with physical surface characteristics that deter or inhibit the recruitment of foulers.

Finally, this work identified several scavenging or grazing crabs, urchins and molluscs that can succeed in the pearl net environment. These types of organisms have been successfully used to tackle fouling elsewhere (Hidu *et al.* 1981, Enright *et al.* 1983, Minchin and Duggan 1989, Cigarria *et al.* 1998) and will be considered as possible control organisms later in Chapter 6.

CHAPTER 4 – FOULING AND THE PEARL NET ENVIRONMENT

4.1. Introduction

The effects of fouling on the growth of scallops in suspended culture can be direct or indirect. Direct effects include mechanical interference with shell opening (Minchin and Duggan 1989, Roman 1991, Claereboudt *et al.* 1994a, Paul and Davies 1986, Lu and Blake 1997, Lodeiros and Himmelman 2000), irritation of the mantle (Getchell 1991), predation (Wilson 1994, O'Connor *et al.* 1998, Freites *et al.* 2000), parasitism (Leibovitz *et al.* 1984, Mortensen *et al.* 2000), and competition for space (Leighton 1979, Enright 1993). Indirect effects are caused by changes in the physio-chemical or food environment. Although they have not been investigated they are often invoked to explain how net-fouling reduces scallop growth (e.g. Duggan 1973, Leighton 1979, Huguenin & Huguenin 1982, Burnell & Slater 1989, Cropp & Hortle 1992, Enright 1993, Côté *et al.* 1993, Claereboudt *et al.* 1994a, Lodeiros & Himmelman 1996, Lu & Blake 1997, O'Connor *et al.* 1999). The aim of these experiments was thus to find out how a range of environmental factors that can affect scallop growth were influenced by net fouling. To do this physio-chemical conditions (water-movement, oxygen levels, concentrations of chemicals associated with anaerobic respiration and excretion) and food quantity and quality were measured *in situ*. It was hoped that information from this study might help scallop growers and researchers to tackle the problems of fouling.

Low water movement in fouled nets (Claereboudt *et al.* 1994b, Skjaeggestad 1997), probably alters both chemical and food conditions. Firstly, low flushing rates might combine with increased respiration and decay to reduce oxygen concentrations (Huguenin and Huguenin 1982, Enright 1993, Lu and Blake 1997) and encourage a build up of bacterial and invertebrate excretory products (e.g. ammonia) that can inhibit invertebrate growth (Hynes 1960). In finfish cages, fouling can reduce water exchange leading to oxygen depletion, and reduced growth or mortality of the culture organism (see, Cronin *et al.* 1999). Similarly, reduced water flow could prevent food from reaching scallops inside fouled nets (Duggan 1973, Huguenin and Huguenin 1982, Côté *et al.* 1993, Enright 1993, Claereboudt *et al.* 1994b, Lodeiros and Himmelman 1996, Lu and Blake 1997).

Shortage of food can limit the growth of scallops in suspended cultivation (Parsons and Dadswell 1992, Côté *et al.* 1994, Thorarinsdóttir 1994, Lodeiros *et al.* 1998) and hence fluctuations in food abundance are important. Suspension-feeding communities can deplete local food concentrations (e.g. Buss & Jackson 1981, Wildish & Kristmanson 1984, Fréchette *et al.* 1989, Asmus & Asmus 1991, Wildish & Saulnier 1993) and competition for

food between scallops and foulers, exacerbated by low water-flow, is often claimed to reduce the growth of scallops in fouled nets (Duggan 1973, Leighton 1979, Côté *et al.* 1993, Enright 1993, Wilson 1994, Lodeiros and Himmelman 1996, Lu and Blake 1997). Potential food particles are also trapped by non-feeding parts of fouling organisms and their nests or tubes (pers. obs.). Contrarily, fouling might increase food concentrations because suspension-feeding communities can release nutrients (Asmus and Asmus 1991, Arzul *et al.* 2001, Mazouni *et al.* 2001), large faeces (Mook 1981), larvae, and organic detritus. Fouling may also provide a substrate for benthic organisms. Scallops feed opportunistically, utilizing local food types, and so all of these particles might be exploited (Mikulich and Tsikhon-Lukaina 1981, Shumway *et al.* 1987, Cranford and Grant 1990, Alber and Valiela 1996).

Food quality, variously assessed by the size and organic and chemical composition of particles, can influence scallop growth more than food availability (Vahl 1980, Wallace and Reinsnes 1985, Wilson 1987, Lodeiros and Himmelman 2000). Suspension-feeding foulers could thus affect scallop growth rates by altering the type of seston inside nets. The relative abundance of organic and inorganic matter in the seston is important (Vahl 1980, Wallace and Reinsnes 1985). Fouling may enhance scallop growth if it produces mainly organic particles (e.g. larvae, pseudofaeces and debris), or depress growth by releasing more inorganic particles (e.g. silt and faeces). Suspension-feeders consume food selectively according to its size (e.g. Lesser *et al.* 1992, MacDonald and Ward 1994, Shumway *et al.* 1997, Brilliant and MacDonald 2000), density (Brilliant and MacDonald 2000), shape (Leighton 1979) and food value (e.g. Bayne *et al.* 1993, MacDonald & Ward 1994, Hawkins *et al.* 1996, Shumway *et al.* 1997, Brilliant & MacDonald 2000), although the last suggestion is disputed by Jørgensen (1996). The quality of food inside fouled nets could therefore be influenced by the selective feeding of foulers and scallops, and the presence of benthic organisms.

To determine how fouling changes the net environment, comparisons were made of conditions inside clean (recently submerged) and fouled pearl nets, containing intermediate sized *P. maximus*. Sites under the headrope of the longline with no nets were also included so that the effects of clean nets with scallops on the water-column could be separated from the effects of net fouling. The pearl net strings and two longlines used in these experiments were the same as those used in Chapters 3 and 5 to examine the process of net fouling and its effects on scallop growth. To investigate qualitatively whether the effects of fouling varied seasonally, experiments were carried out in June and November. In November, nets

with fouling communities at different stages of development were examined to see whether the composition of the fouling community influenced the net environment.

4.2. Materials and Methods

4.2.1. Field conditions and work

The longlines used in this experiment and the water surrounding them are described in Chapter 2. Longline head-ropes were approximately 10m below the surface (C.D.) on both sampling dates. June and November experiments were carried out in the year 2000, during early-spring and late-spring tides respectively; at these times the tidal range was 4-5m. Water temperatures and salinities were 12.4-12.3 °C and 34.1-34.2 p.p.t. during June sampling and 10.7-10.8 °C, 34.3 p.p.t., when sampling was carried out in November.

Weather conditions were not exceptional in either sampling period (Appendix 7). In June, mean rainfall and sunshine hours were slightly lower than average and strong breezes (force 6-7) also occurred a week before sampling. High rainfall (16 mm·day^{-1}) occurred one week before November sampling and mean rainfall for the month was higher than normal. Sunshine levels were lower than average during the November sampling period (ca. 0.2 h·day^{-1}).

Pearl nets were hung in strings of three, at 4 m vertical intervals, with a 2 kg weight attached below the lowest net. For logistical reasons only the top nets, hung about 0.15 m below the head-rope, were sampled. The nets used for nutrient samples contained ten 2-3 yr old *P.maximus* with a shell length of 6.5-8.5 cm. For water flow experiments nets contained 10 flat pebbles whose combined weight equalled that of 10 scallops. Pebbles were used instead of scallops because scallop movement may have abraded the plaster balls. Scallop sized pebbles were chosen so that water-flow and net movements matched those of nets containing scallops. Nets for flow measurements had loops in the central, supporting rope and a door so that plaster balls could be inserted and centrally fixed (Figure 4.1). Door fastenings and support were on net seams so that they did not change water-flow patterns (Figure 4.1).

In June and November, oxygen, ammonia, nitrate, chlorophyll *a*, particulate matter, plankton and water motion were measured in clean nets, fouled nets and open water sites. Open water sites were positions under the head-rope of the longline, at the same depth as experimental nets. In November, nets that had been immersed for different periods and hence supported different fouling communities were sampled; these are called long- and short-fouled treatments. The immersion times for each treatment are given in Table 4.1.

Technical problems delayed the second sampling period after clean nets had been deployed. To counteract this, fouling was thoroughly scrubbed from "clean" nets by divers one week prior to the second sampling effort. Treatments were arranged randomly, at 1 m intervals, along the two longlines. To prevent bias between treatments samples were collected and analysed in the random order that they were positioned on the longline. On each longline, treatments were replicated five times for nutrient experiments and four times for water motion experiments. Nutrient and water motion experiments were carried out side by side on the longlines. In the June experiment water motion was measured for 48 hours, during which time water samples were collected. In November bad weather meant that water motion could only be measured for 24 hours, a day after water samples were collected.

Diving was carried out from the R.V. Sula. Sampling sites were numbered with fluorescent tape. Syringes with 120mm Teflon tubing tips (3mm diameter) were used to collect samples in preference to permanent sampling tubes that would have been fouled or electronic probes that are expensive and hard to use accurately *in situ*. Divers collected a complete set of 15 or 20 nutrient samples (for example, all of the ammonia samples from one longline) using labelled syringes. Nets were not touched or moved to prevent disturbance both before and during sampling. Five millilitres of water was taken up outside the nets and expelled once the tip was in position; this should have removed any trapped debris from the syringe tip. Water samples were then collected slowly to minimise disturbance and sample contamination with water from outside the net. Dives lasted up to 20 minutes after which samples were returned to the boat. Samples were collected from nets by two pairs of divers deployed at 10-minute intervals. Sampling was alternated between longlines so that no more than two samples, totalling 160ml of water (1% of the net volume), were taken from a net in 4 hours.

Sampling and analysis procedures are outlined in Table 4.2; Appendix 8 details the order in which samples were collected. Prior to sampling all bottles and syringes were acid washed and rinsed in distilled water. Syringes used to collect oxygen samples were split in two (plunger and body) before diving to ensure that they did not retain any air bubbles.

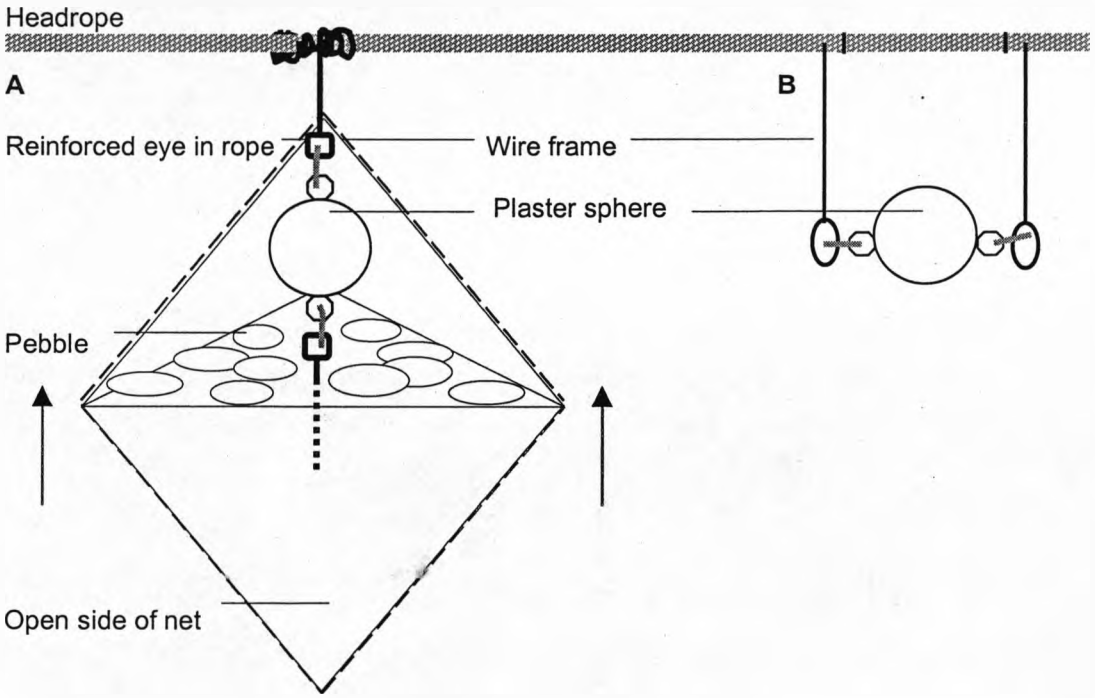


Figure 4.1. Pearl net (A), and wire frame (B, open water site) with plaster spheres to measure water motion. The open side of the pearl net was supported by a wire frame (dashed line) and was closed tightly with cable ties when the plaster spheres were in position. Grey bands are cable ties.

Table 4.1. Period for which nets were submerged before sampling, where two figures are given they are for the north and south system respectively. * Nets were cleaned seven days before sampling.

Sampling dates	Net type	Immersion date	Immersion time (weeks)
15-Jun. / 16-Jun.	Fouled	29-Feb., 22-Feb.	15, 16
	Clean	5-Jun	2
21-Nov. / 22-Nov.	Short-fouled	5-Jun	24
	Long-fouled	29-Feb., 22-Feb.	39, 40
	Clean*	25-Sept., 25-Sept.	8

Table 4.2. Treatment and analysis of dissolved and particulate matter in water samples collected by divers. *Filter papers were GF/F type and had a diameter of 25mm.

Sample	Volume	Action on Boat	Laboratory analysis	
			Immediately on return	**Later**
Ammonia and Nitrate	100ml	Syringes were capped and stored in the dark, on ice.	Samples were filtered* into bottles and frozen.	Ammonia and nitrate concentrations were determined using an Alpkem autoanalyser, (RFA 2).
Chlorophyll *a*	100ml	As above.	The filter paper* from ammonia samples was sealed in a bag and frozen.	Filter papers were soaked in 9ml of acetone for 24 hours. The concentration of chlorophyll *a* extracted was then measured with a Turner fluorometer.
Particulate matter	100ml	As above.	Samples were filtered* onto ashed papers and rinsed with 5ml of isotonic ammonium formate.	Filter papers were dried at 40°C to constant temperature, weighed, and then ashed overnight at 450°C and reweighed.
Oxygen	60ml	June samples were fixed by injecting Manganous sulphate and alkaline iodide into syringes. Fixed samples were stored in the dark, on ice. November samples were fixed and measured using a HANNA dissolved oxygen meter, (HI 93732).	Winkler titrations were carried out within 24 hours.	N.A.
Plankton	60ml	Samples were transferred to bottles with 1.2ml of neutral Lugol's iodine and a glass bead.	Samples were stored in the dark at a constant temperature.	Particles were counted, measured and categorised using inverted microscopy and SCION image analysis for widows.

4.2.2. Physiochemical conditions

Plaster of Paris spheres can be used to accurately measure time integrated water motion (Thompson *et al.* 1994); in these experiments they were a reliable alternative to expensive micro-flow meters. The spheres were made by combining 100g of Plaster of Paris ($CaSO_4$) for art with 90ml of distilled water. The plaster was mixed to a smooth paste, tapped to remove air bubbles and then poured into moulds. Moulds were plastic play-balls (70mm diameter) with a central wire; these were better than the epoxy resin, silicone rubber and plasticine moulds, used in preliminary trials, none of which sealed effectively. Filled moulds were then vibrated for 10 minutes to remove trapped air. Plaster spheres were removed from their moulds after approximately 12 hours and placed in a well-ventilated area to dry. After at least four weeks, spheres were dried at 30°C to a constant mass (accelerated drying at high temperatures can affect plaster's crystalline structure, Muus, 1968). After drying, spheres were weighed and their volume was measured by fluid displacement.

Before immersion, plaster spheres were wrapped in soft cloths to prevent chipping and minimises dissolution. Divers opened nets and used cable ties to fix spheres centrally (Figure 4.1) so that they were not abraded by contact with fouling organisms or nets. At open water sites wire was used to suspend spheres below the head-rope, level with the spheres inside nets (Figure 4.1). Once in position, the cloths were removed and the nets were resealed. To retrieve spheres divers snipped cable ties and wrapped spheres in soft cloths before bringing them to the surface. In the laboratory, spheres were dried to a constant mass.

Plaster dissolution rates (V_d) provide an indication of relative water motion and were used to describe treatment effects for analysis.

$$V_d = \frac{(W_1 - W_2)}{A\ T}$$

Where W_1 and W_2 are the weight of the sphere at the beginning and end of the experiment respectively, A is the mean surface areas of the sphere, calculated from start and end values, and T is the time over which spheres were immersed.

Velocity ratios were calculated as they provided an estimate of the magnitude of treatment effects on absolute water velocity. Velocity ratio equations were derived as follows:

$\frac{dW}{dt} = -k A \Delta C$ Thompson *et al.* (1994)

Where W is the weight of the sphere, t is time, k is the mass transfer coefficient, A is the exposed area of the sphere and ΔC is the concentration difference between dissolved plaster in the seawater at the plaster-seawater interface and in the bulk seawater.

Duration, temperature and salinity (and therefore ΔC) were identical for treatments on the same sampling dates, so:

$WL \propto A\ k$ where WL is weight loss and

$k \propto (V/D)^{0.5}$ where V is water velocity and D is the diameter of the sphere, (this relationship was derived from mass transfer equations in Skelland (1974) by L.Thompson, 2000, pers. comm., Appendix 9) so

$WL \propto A\ (V/D)^{0.5}$ which can be rearranged to give:

$V \propto D\ (WL/A)^2$

Therefore $V_f : V_c : V_o : V_l = [D_f (WL_f A_f)^2] : [D_c (WL_c A_c)^2] : [D_o (WL_o A_o)^2] : [D_l (WL_l A_l)^2]$

Where V_f, Vc, Vo and V_l are water velocities through fouled nets, clean nets, open water sites and long-fouled nets respectively.

June oxygen measurements were affected by a constant error, the cause of which could not be identified. To overcome this an oxygen meter was used in November, however this was only used successfully on the north system.

4.2.3. Food conditions

Particulate matter

The GF/F filter paper used to collect particulate matter had a pore size of 0.7µm. Particulate organic matter (PIM), particulate inorganic matter (PIM) and total particulate matter (TPM) were calculated as follows:

TPM = dry weight of filter paper and sample – filter paper ashed weight

PIM = ashed weight of filter paper and sample – filter paper ashed weight

POM = dry weight of filter paper and sample – ashed weight of filter paper and sample.

Plankton

It was hoped that plankton data would make it possible to identify any differences in the abundance and quality of food particles available to scallops. Samples were settled in a counting chamber following the methods of Utermöhl (Hasle, 1978). Dense samples were diluted with filtered seawater and completely enumerated to avoid the inaccuracy associated with counting plankton in random fields of view. To ensure that the precision of plankton counts was greater than 20% of the total count the volume of sample enumerated always contained more than 150 individuals of the most abundant organisms (Postel *et al.*, 2000). The density of detritus in samples was crudely assessed by counting detrital particles larger than 5μm along a vertical and horizontal transect of the counting chamber. Seston was recorded according to its type (small plankton, centric diatoms, pennate diatoms, diatom chains, solitary chain-forming diatoms, pelagic ciliates, benthic ciliates, dinoflagellates, flagellates, crustaceans, nematodes, invertebrate larvae, eggs and spores, and faeces) and maximum length (5-10, 11-20, 21-50, 50-100 and > 100μm). Small plankton was all organisms of 5-10μm; generally these were flagellates and diatoms.

4.2.4. Statistical analyses

Univariate analyses

June and November results were analysed separately. The experimental design was balanced with one random and one fixed factor (location and treatment respectively). There were three treatments in June (open-water sites, clean nets and fouled nets) and four in November (open-water sites, clean nets, short-fouled nets and long-fouled nets). Concentrations of plankton, faeces, detritus and nutrients and rates of plaster erosion for each treatment were examined using two-way analysis of variance (ANOVA). Oxygen measurements were only available for the north system and were analysed by one-way ANOVA, with treatment as a fixed factor. Heterogeneity of variance was tested for using Cochran's test (Winer 1971) and where necessary data were transformed. Some data were heterogeneous even after transformation but ANOVA was still applied because the experimental design was balanced and fairly large (Underwood 1997). However, such analyses increase the probability of a type I error (Underwood 1997), and the results were interpreted with caution. When ANOVA showed that the probability of a treatment effect was more than 0.05 and there was no interaction between location and treatment ($P > 0.25$), data for the two systems were pooled, this increased the power of ANOVA to detect treatment effects (Underwood 1997). When ANOVA indicate significant factors or interactions between factors, post-hoc Student-Newman-Keuls (SNK) tests were performed to determine which means differed. All analyses were carried out using GMAV5

(Underwood *et al.* 1998). Ammonia measurements were analysed by ANOVA and concentrations below the limit of detection were included as $5\mu g l^{-1}$, the highest undetectable value. This is a conservative approach which increased the probability of a type I error.

Multivariate analysis

June and November results were analysed independently. Plankton were put into 45 groups according to their size and type as described above. The data set was then analysed using non-parametric, multivariate techniques included in the PRIMER (Plymouth Routines in Multivariate Research) software package (Clarke and Warwick 1994). Bray-Curtis similarity indices (Bray and Curtis 1957) were calculated between all pairs of samples to produce a data matrix after a square-root transformation was used to slightly reduce the contributions to similarity of the most abundant species. The similarity matrices were ordinated and clustered using MDS (non-metric multi-dimensional scaling) and hierarchical agglomerative clustering (on group-average linkage) respectively. Two-dimensional MDS plots had low stress values (</= 0.1) and hence the dendrograms from CLUSTER analysis are not presented here. Instead, levels of similarity from cluster analysis are indicated on the MDS plots. *A priori* tests of the differences between locations and treatments were performed using a two-way, crossed ANOSIM (analysis of similarity), and the plankton groups contributing most to any differences found between the groups were determined using SIMPER (similarity percentages analysis). A shade diagram was plotted using a Microsoft Excel macro written by L. Veale (Port Erin Marine Laboratory, Isle of Man, 2000), to show how plankton group abundances varied between samples.

4.3. Results

4.3.1. Macrofouling communities

In June, "fouled" nets were almost entirely covered (> 90%) in the hydroids *Tubularia indivisa* and *T. larynx*; the amphipod *Jassa falcata* and its silt tubes were common as were the nudibranchs *Dendronotus frondosus, Coryphella lineata* and *Facelina bostoniensis.* Small hydroids (e.g. *Obelia* sp. and *Clytia hemispherica*) were present but occupied little space compared with the large *Tubularia* spp. "Clean" nets were sparsely colonised (< 5%) by small hydroids. The study was designed to qualitatively compare the effects of similar fouling communities at different times of year, however technical problems prevented sampling when the second set of nets was *Tubularia* dominated. Thus, the effects of fouling on different sampling dates were probably influenced by differences in the fouling communities as well as changes in the prevailing environment.

November fouling communities were more diverse than June ones and covered roughly 60 % of the net surfaces. Both long- and short-fouled nets were dominated by the tunicate *Ascidiella scabra*; hydroid cover was sparse and dominated by *Bougainvillia* type species, nudibranchs were present, but not as prolific as in June. Filamentous red algae grew on some short-fouled nets. Long-fouled nets supported more species than short-fouled ones, including, feather stars (*Antedon bifida*), cnidarians (e.g. *Metridium senile*, *Alcyonium digitatum*) and bivalves (*Mytilus edulis* and *Aequipecten opercularis*). Again, "clean" nets were sparsely colonised by small hydroids.

4.3.2. Physiochemical conditions

The plaster spheres used to measure water motion remained spherical throughout their deployment. In June 2000 water motion was similar on both longline systems (Figure 4.2). The mean ratio of water velocities in fouled nets, clean nets and open-water sites was approximately 1.0 : 2.0 : 2.0, only fouled nets significantly reduced water movement (Table 4.3). In November 2000 the mean ratio of water velocities was approximately 1.0 : 1.6 : 1.6 : 1.7 on the north system and approximately 1.0 : 1.3 : 1.7 : 1.8, on the south system for short-fouled nets, long-fouled nets, open-water sites and clean nets respectively (Figure 4.3). Although the lowest rates of plaster dissolution were recorded for short-fouled nets on both systems, the trend was not significant (Table 4.4). On the south system, long-fouled treatments also reduced water motion (Figure 4.3) and consequently average water motion was lowest on this system (but the variance of the data was heterogeneous, Table 4.4).

Overall nitrate concentrations were approximately ten times higher in November than June; they were not affected by treatment during either sampling period (Figure 4.2 and 4.3). In November, concentrations on the south system were significantly higher than the north system. However, this result should be treated with caution as variability of the data was heterogeneous. In June, only four ammonia measurements exceeded the minimum detection level of the autoanalyser (5 $\mu g \cdot l^{-1}$); these were all on the north system, which therefore had significantly higher results than the south system. There were no significant differences between treatments (Table 4.3). In November, all ammonia concentrations were less than 5$\mu g \cdot l^{-1}$ and mean oxygen saturation was highest in long-fouled nets (Figure 4.3), but this trend was not significant (Table 4.2).

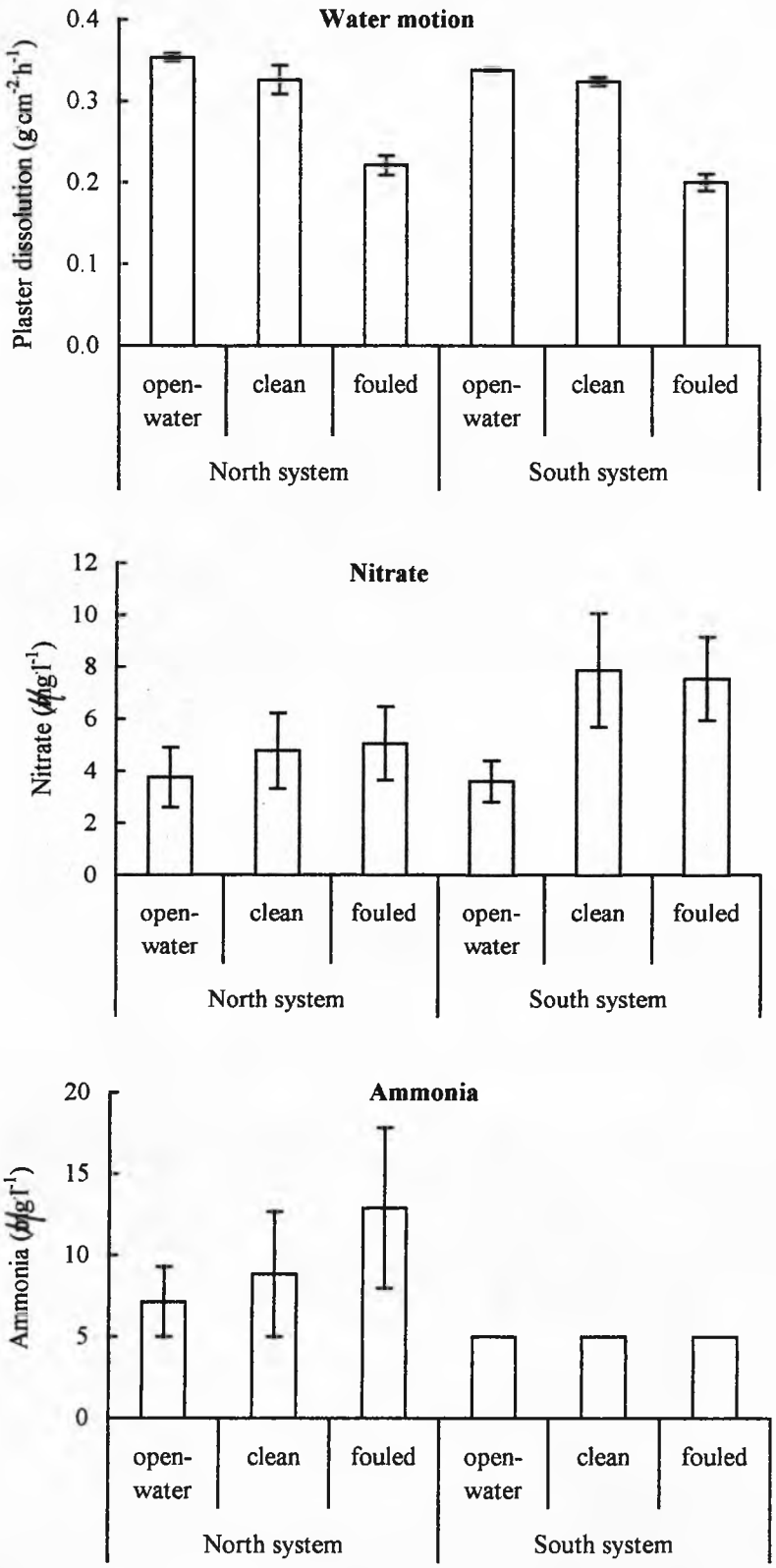


Figure 4.2. Physiochemical conditions (mean +/- SE) in clean and fouled pearl nets and open-water sites, in June 2000.

Table 4.3. Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on physiochemical conditions. Cochran's test results are given and data are not transformed unless indicated. (Bold type indicates a significant result, $P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Water motion					
$C = 0.4799, P > 0.05$					
Location	1	0.0012	3.18	0.091	Residual
Treatment	2	0.0425	196	**0.005**	Location X treatment
Location X treatment	2	0.0002	0.57	0.575	Residual
Residual	18	0.0004			
Total	23				
SNK multiple comparison of teatment results:					
North system: open-water = clean > fouled					
Nitrate					
$C = 0.3539, P > 0.05$					
Location	1	0.1242	2.22	0.149	Residual
Treatment	2	0.1141	2.91	0.256	Location X treatment
Location X treatment	2	0.0392	0.70	0.506	Residual
Residual	24	0.0558			
Total	29				
Ammonia					
$C = 5574, p < 0.05$					
Location	1	160.5453	4.41	**0.046**	Residual
Treatment	2	21.8963	1.00	0.500	Location X treatment
Location X treatment	2	21.8963	0.60	0.556	Residual
Residual	24	36.3827			
Total	29				

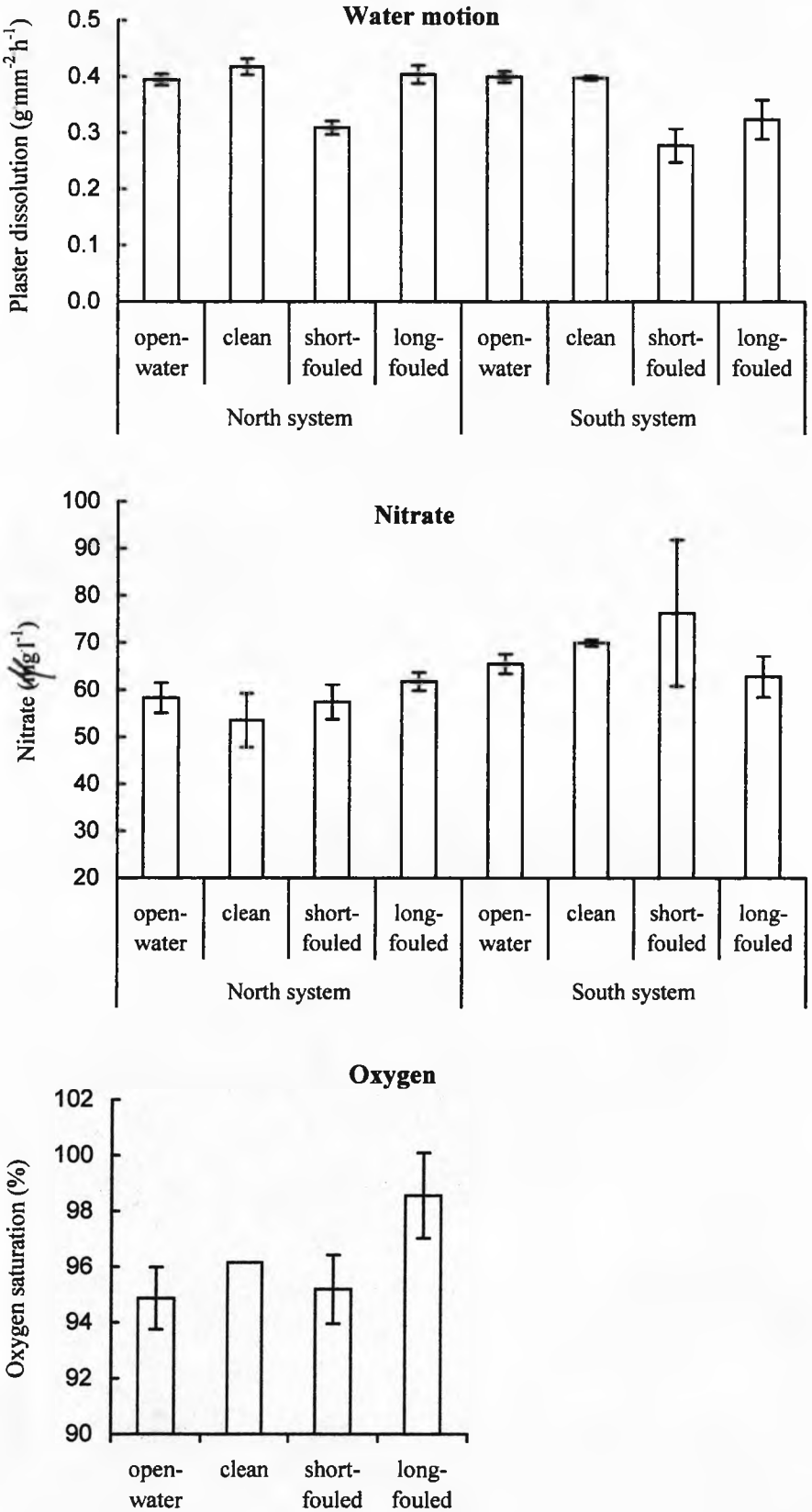


Figure 4.3. Physiochemical conditions (mean +/- SE) in clean and fouled pearl nets and open-water sites, in November 2000. Oxygen is shown for the north system only.

Table 4.4. Two way ANOVA of November data testing for the effect of location and treatment (clean nets, short-fouled nets, long-fouled nets and open-water sites) on physiochemical conditions. Cochran's test results are given and data are not transformed unless indicated. Oxygen data are for the South system and are analysed using a one-way ANOVA testing only for treatment effects. (Bold type indicates a significant result, $P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Water motion					
$C = 0.4719$, $P <$ **0.05**					
Location	1	0.0075	5.87	**0.023**	Residual
Treatment	3	0.0220	8.49	0.056	Location X treatment
Location X treatment	3	0.0026	2.02	0.137	Residual
Residual	24	0.0013			
Total	31				
Nitrate					
$C = 0.7594$, $P <$ **0.01**					
Location	1	6.0315	5.95	**0.021**	Residual
Treatment	3	0.3072	0.35	0.793	Location X treatment
Location X treatment	3	0.8730	0.86	0.471	Residual
Residual	32	1.0140			
Total	39				
Oxygen					
$C = 0.3771$, $P > 0.05$					
Treatment	3	0.0541	2.47	0.099	Residual
Residual	16	0.0219			
Total	19				

4.3.3. Food particles

Particulate matter

Particulate inorganic matter (PIM) concentrations were similar in June and November (Figures 4.4 and 4.5); November open-water replicates were lower and less variable than all other treatments (Figure 4.5), but not significantly so (Table 4.6). In June fouled nets on the south system supported exceptionally high PIM levels (Figure 4.4). No clear trends were obvious for the remaining treatments, which showed high variability between replicates and different trends on each system.

Particulate organic matter (POM) responded differently to treatment according to sampling date. In June, POM concentrations were 10-20 $mg\,l^{-1}$ higher in fouled nets than clean nets or open-water sites (Figure 4.4). However, the amount of POM in fouled nets was variable both within and between systems and so treatment effects were not significant. Differences between fouled nets on each system largely explain why POM concentrations were significantly higher on the south system (Table 4.6). POM concentrations for all treatments in November were similar to those for open-water and clean sites in June. Within and between treatment variability was lower than in June and there were no consistent treatment effects. Open-water values were significantly higher for the North than the South system (Table 4.6).

The ratio of PIM to POM in November was approximately double that in June (Figs. 4.4 and 4.5). In June fouled replicates had a significantly lower PIM to POM ratio than clean nets or open water sites (Table 4.5); all clean nets had lower PIM to POM ratios than open-water sites (Figure 4.6) but this trend was not significant. November results were highly variable and neither treatment nor location had a consistent effect (Figure 4.5). Total particulate matter (TPM) concentrations followed similar patterns to POM. In June, fouled nets on the south system supported significantly more TPM than clean or open-water sites (Figure 4.4). This trend was also apparent, but less pronounced and not significant, on the north system (Table 4.5). In November, TPM was significantly affected by treatment (Figure 4.5, Table 4.6) but differences were not consistent across systems and SNK tests failed to identify clear groups. Generally open-water sites and, on the south system, clean nets, contained the lowest and least variable TPM concentrations (Figure 4.5).

Detrital particles were more abundant in June than November. However, high variability within detritus measurements made treatment effects hard to distinguish (Figures 4.4 and 4.5). In June, open-water sites had consistently low detritus levels compared with all fouled

nets and clean nets on the north system, but this was not significant (Table 4.5). Result for clean nets on the south system were elevated by an outlying replicate. In November, detritus concentrations were similar in open-water sites and clean nets. Short-fouled nets supported significantly higher detritus concentrations than all other treatments and long-fouled nets supported significantly higher detritus concentrations than clean nets or open-water sites on the north, but not the south system (Table 4.6). The north system also had significantly higher levels of detritus.

Faeces (intact pellets) were more abundant in November than June (Figures 4.4 and 4.5); in both months faeces abundance showed the same trends for all size classes (Tables 4.4 and 4.5) and so only total abundances are presented graphically. In June, mean faeces concentrations were highest in fouled-nets on the south system (Table 4.5), but there was high variability between replicates. High faeces concentrations in fouled nets on the south system caused significant differences between locations in all but the 21-50 μm size category (Table 4.5). In the 21-50 μm size category fouled nets supported significantly more faeces on both systems (Table 4.5). In November faeces concentrations, for all size classes, were significantly greater in long-fouled nets than all other treatments (Table 4.6). Overall, concentrations in clean and short-fouled nets were also higher and more variable than those in open-water sites (Figure 4.5), but generally this trend was not significant (Table 4.6). Faeces concentrations at open-water sites were similar between replicates and across locations.

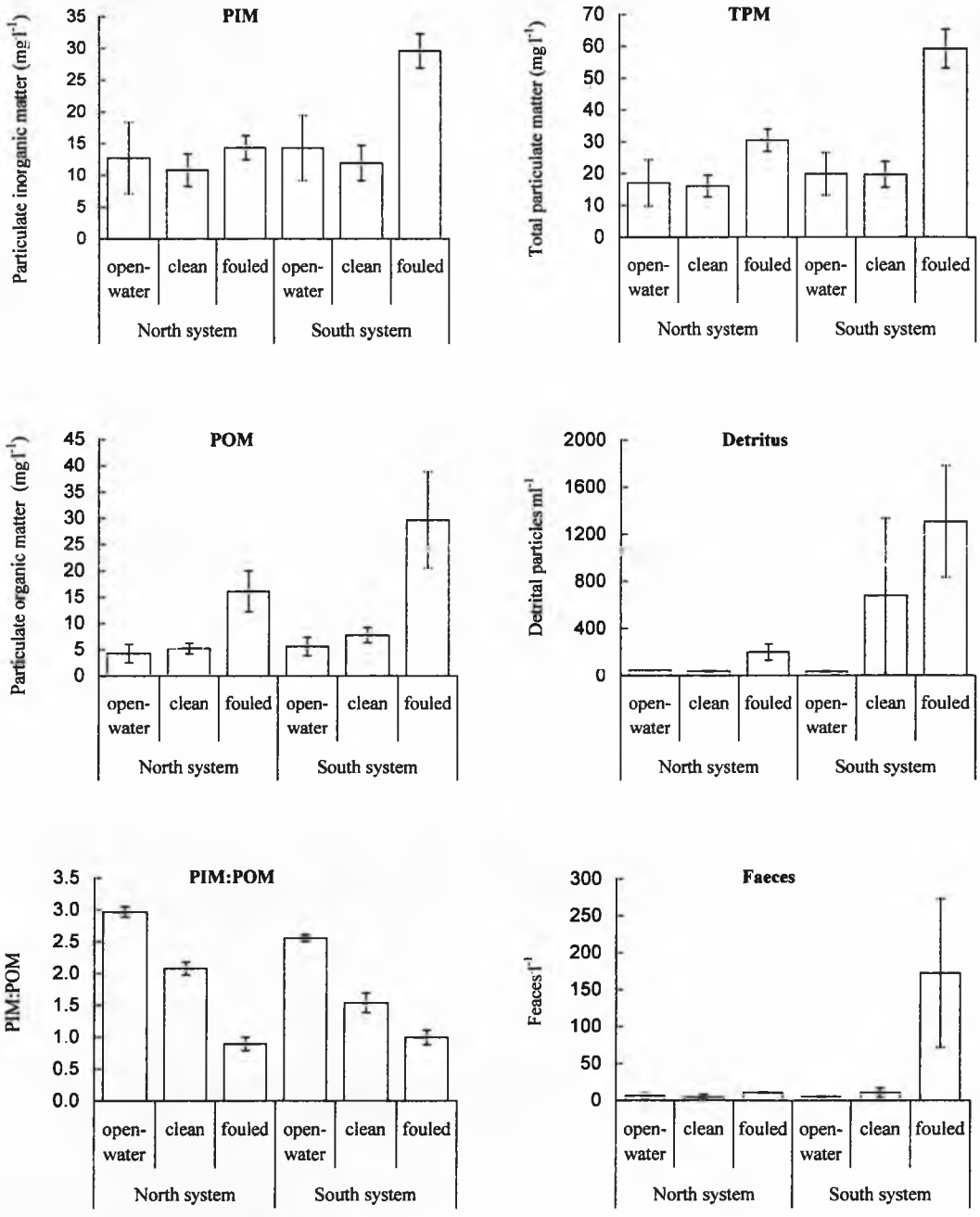


Figure 4.4. Concentrations and chemical properties of particulate matter (mean +/- SE) in clean and fouled pearl nets and open-water sites, in June 2000.

Table 4.5. Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on the abundance and chemical properties of the seston. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south sytems have been pooled. Cochran's test results are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
PIM					
$C = 0.3827$, $P > 0.05$					
Location	1	266.0162	3.83	0.062	Residual
Treatment	2	313.3311	1.94	0.340	Location X treatment
Location X treatment	2	161.2613	2.32	0.120	Residual
Residual	24	69.4180			
Total	29				
POM					
$C = 0.4098$, $P > 0.05$					
Location	1	253.9613	7.38	**0.012**	Residual
Treatment	2	991.0543	8.59	0.104	Location X treatment
Location X treatment	2	115.3071	3.35	0.052	Residual
Residual	24	34.4224			
Total	29				
PIM:POM					
Transformation = Ln (X+1), $C = 0.4331$, $P > 0.05$					
Location	1	0.0003	0.00	0.944	Pooled data
Treatment	2	0.3369	5.61	**0.001**	Pooled data
Location X treatment	2	0.0293	0.49	0.620	Pooled data
Residual	24	0.0627			
Total	29				
Pooled data	26	0.0601			
SNK multiple comparison of interaction:					
open-water = clean > fouled					
TPM					
$C = 0.3013$, $P > 0.05$					
Location	1	1039.8151	7.08	**0.014**	Residual
Treatment	2	2378.2781	4.35	0.187	Location X treatment
Location X treatment	2	547.3550	3.73	**0.039**	Residual
Residual	24	146.8783			
Total	29				
SNK multiple comparison of interaction:					
North system: open-water = clean = fouled					
South system: open-water = clean < fouled					
Open-water: North system = South system					
Clean: North system = South system					
Fouled: North system < South system					

Table 4.5 (cont.). Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on the abundance of all detrital particles and feaces in two size classes. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the north and south systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Detritus (>5 μm)					
Transformation = Ln (X+1), C = 0.5726, $P > 0.05$					
Location	1	1.31	2.37	0.150	Residual
Treatment	2	11.45	5.89	0.145	Location X Treatment
Location X Treatment	2	1.94	3.52	0.063	Residual
Residual	12	0.55			
Total	17				
Faeces (11-20 μm)					
Transformation = Ln (X), C = 0.3844, $P > 0.05$					
Location	1	4.89	11.16	**0.006**	Residual
Treatment	2	2.35	0.66	0.602	Location X Treatment
Location X Treatment	2	3.56	8.12	**0.006**	Residual
Residual	12	0.44			
Total	17				
SNK multiple comparison of interaction:					
North system: open-water = clean nets < fouled nets					
South system: open water = clean nets = fouled nets					
Open water: North system = South system					
Clean nets: North system = South system					
Fouled nets: North system < South system					
Faeces (21-50 μm)					
Transformation = Ln (X), C = 0.3083, $P > 0.05$					
Location	1	5.38	4.38	0.055	Pooled data
Treatment	2	12.22	9.95	**0.002**	Pooled data
Location X Treatment	2	1.48	1.21	0.328	Pooled data
Residual	12	1.19			
Total	17				
Pooled data	14	1.23			
SNK multiple comparison of treatment results:					
Open water = clean nets < fouled nets					

Table 4.5 (cont.). Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on the abundance of feaces in two size classes and the total abundace of faeces. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the north and south systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Faeces (51-100 μm)					
Transformation = Ln (X+1), C = 0.3680, $P > 0.05$					
Location	1	5.05	11.75	**0.005**	Residual
Treatment	2	3.89	1.77	0.362	Location X Treatment
Location X Treatment	2	2.20	5.13	**0.025**	Residual
Residual	12	0.43			
Total	17				
SNK multiple comparison of treatment results:					
North system: open-water = clean nets = fouled nets					
South sytem: open water = clean nets < fouled nets					
Open water: North system = South system					
Clean nets: North system = South system					
Fouled nets: North system < South system					
Faeces (>100 μm)					
Transformation = Sqrt (X+1), C = 0.5351, $P > 0.05$					
Location	1	3.63	9.96	**0.008**	Residual
Treatment	2	3.26	1.25	0.444	Location X Treatment
Location X Treatment	2	2.61	7.15	**0.009**	Residual
Residual	12	0.36			
Total	17				
SNK multiple comparison of interaction:					
North system: open-water = clean nets = fouled nets					
South sytem: open water = clean nets < fouled nets					
Open water: North system = South system					
Clean nets: North system = South system					
Fouled nets: North system < South system					
Total faeces (>5 μm)					
Transformation = Ln (X), C = 0.4550, $P > 0.05$					
Location	1	8.50	6.05	**0.028**	Pooled data
Treatment	2	10.62	7.56	**0.006**	Pooled data
Location X Treatment	2	2.03	1.44	0.269	Pooled data
Residual	12	1.30			
Total	17				
Pooled data	14	1.40			
SNK multiple comparison of treatment results:					
Open water = clean nets < fouled nets					

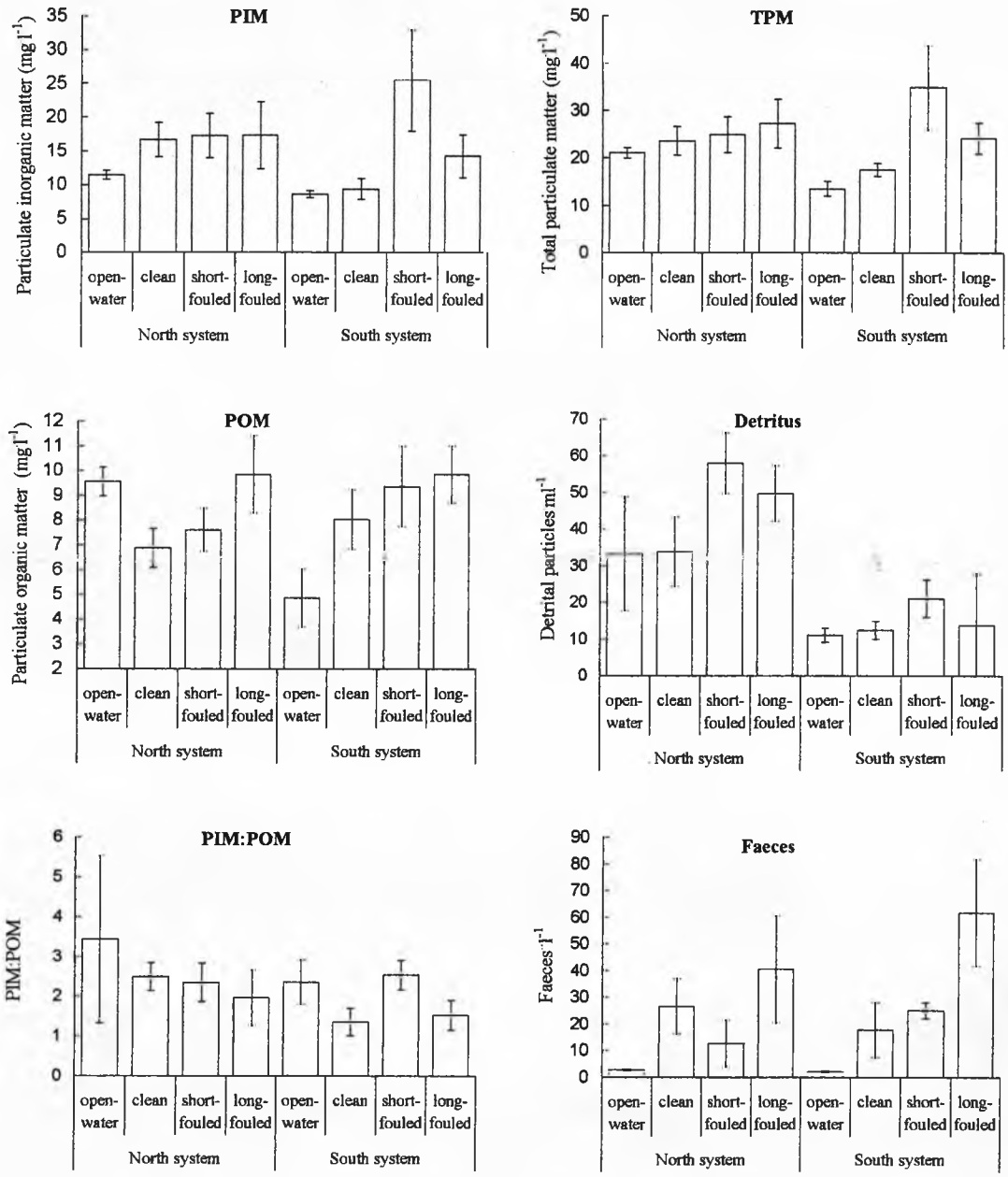


Figure 4.5. Concentrations and chemical properties of the seston (mean +/- SE) in clean and fouled pearl nets and open-water sites, in November 2000.

Table 4.6. Two way ANOVA and SNK multiple comparisons of November data testing for the effect of location and treatment (clean nets, short-fouled nets, long-fouled nets and open-water sites) on chemical properties of the seston. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south sytems have been pooled. Cochran's test results are given and data are not transformed unless otherwise indicated. (bold type indicates a significant result, $P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
PIM					
Transformation = Ln(X+1), C = 0.2924, *P* > 0.05					
Location	1	0.23	1.27	0.269	Residual
Treatment	3	0.60	2.16	0.272	Location X treatment
Location X treatment	3	0.28	1.50	0.232	Residual
Residual	32	0.19			
Total	39				
POM					
C = 0.2539, *P* > 0.05					
Location	1	2.45	0.34	0.565	Residual
Treatment	3	13.75	0.60	0.659	Location X treatment
Location X treatment	3	23.00	3.17	**0.038**	Residual
Residual	32	7.25			
Total	39				
SNK multiple comparison of interaction:					
Open-water: North system > South system					
Clean: North system = South system					
Short-fouled: North system = South system					
Long-fouled: North system = South system					
No homogeneous groups were identified within systems.					
PIM:POM					
C = 0.3345, *P* > 0.05					
Location	1	0.03	0.03	0.865	Residual
Treatment	3	1.06	0.44	0.742	Location X treatment
Location X treatment	3	2.41	2.31	0.095	Residual
Residual	32	1.04			
Total	39				
TPM					
Transformation = Sqrt (X+1), *C* = 0.3356, *P* > 0.05					
Location	1	0.04	0.04	0.844	Pooled data
Treatment	3	4.51	4.11	**0.013**	Pooled data
Location X treatment	3	0.85	0.78	0.514	Pooled data
Residual	32	1.12			
Total	39				
Pooled data	35	1.10			
SNK multiple comparison of treatment results failed to identify homogenous groups.					

Table 4.6 (cont.). Two way ANOVA and SNK multiple comparisons of November data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on the abundance of all detrital particles and feaces in two size classes. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the north and south systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Detritus					
$C = 0.2500$, $P > 0.05$					
Location	1	7.04	14.08	**0.002**	Residual
Treatment	3	10.49	1.91	0.304	Location X Treatment
Location X Treatment	3	5.49	10.97	**<0.001**	Residual
Residual	16	0.50			
Total	23				
SNK multiple comparison of interaction:					
North system: open-water = clean nets < long-fouled nets < short-fouled nets					
South system: open-water = clean nets = long-fouled nets < short-fouled nets					
Open water: North system = South system					
Clean nets: North system > South system					
Short-fouled nets: North system > South system					
Long-fouled nets: North sytem = South system					
Faeces (11-20 μm)					
$C = 0.5087$, $P > 0.05$					
Location	1	32.67	0.54	0.475	Residual
Treatment	3	209.63	23.18	**0.014**	Location X Treatment
Location X Treatment	3	9.04	0.15	0.929	Residual
Residual	16	61.05			
Total	23				
SNK multiple comparison of treatment results:					
Open-water = clean nets = short-fouled nets < long-fouled nets					
Faeces (21-50 μm)					
$C = 0.2866$, $P > 0.05$					
Location	1	84.38	0.88	0.360	Pooled data
Treatment	3	525.49	5.47	**0.007**	Pooled data
Location X Treatment	3	117.38	1.22	0.329	Pooled data
Residual	16	92.04			
Total	23				
Pooled data	19	96.04			
SNK multiple comparison of treatment results failed to identify homogeneous groups.					

Table 4.6 (cont.). Two way ANOVA and SNK multiple comparisons of November data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on the abundance of feaces in two size classes and the total abundace of faeces. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the north and south systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Faeces (51-100 μm)					
Transformation = Ln (X+1), $C = 0.54084$, $P > 0.05$					
Location	1	0.02	0.08	0.781	Residual
Treatment	3	5.58	9.91	**0.046**	Location X Treatment
Location X Treatment	3	0.56	2.94	0.065	Residual
Residual	16	0.19			
Total	23				
SNK multiple comparison of treatment results:					
Open-water = clean nets = short-fouled nets < long-fouled nets					
Faeces >100 μm					
$C = 0.4405$, $P > 0.05$					
Location	1	0.11	0.29	0.594	Pooled data
Treatment	3	2.33	6.43	**0.004**	Pooled data
Location X Treatment	3	0.28	0.77	0.524	Pooled data
Residual	16	0.38			
Total	23				
Pooled data	19	0.36			
SNK multiple comparison of treatment results:					
Open-water = clean nets = short-fouled nets < long-fouled nets					
Total faeces (>5 μm)					
$C = 0.3652$, $P > 0.05$					
Location	1	212.42	0.54	0.470	Pooled data
Treatment	3	2459.66	6.31	**0.004**	Pooled data
Location X Treatment	3	269.32	0.69	0.569	Pooled data
Residual	16	412.61			
Total	23				
Pooled data	19	389.98			
SNK multiple comparison of treatment results:					
Open-water = clean nets = short-fouled nets < long-fouled nets					

Plankton

Univariate analyses (quantity of plankton).

June plankton results are displayed in Figure 4.6 and Table 4.7. Small plankton (5-10μm plankton) and 11-20μm plankton were around one order of magnitude more abundant than other groups. Total plankton concentrations were significantly higher in fouled nets than clean nets or open water sites. This pattern was evident throughout the plankton size categories but it was not always significant because concentrations of plankton in fouled nets varied highly both within and between locations. Variation between systems was driven by differences between fouled treatments and was not consistent across size classes. However, in both the 51-100 and 100μm+ classes the south system supported significantly more plankton than the north system. Concentrations of plankton in clean nets and open-water sites were similar throughout size classes and locations, they were also less variable than concentrations in fouled nets. Plankton concentrations were around one order of magnitude higher in June than November.

Figure 4.7 and Table 4.8 display November plankton concentrations; the results are less consistent than in June. Small plankton were more abundant than any other size class and hence drove trends in total plankton abundance. Long-fouled nets supported the highest numbers of small plankton on both north and south systems, however this trend (and hence that for total plankton abundance) was not significant because of the high variability between replicate samples. Open-water sites and clean and short-fouled nets supported similar numbers of small plankton and their levels were less variable than in long-fouled nets. Numbers of 11-20μm plankton did not vary consistently between locations or treatments. Long-fouled nets supported significantly more 50-100μm plankton than other treatments. Clean and long-fouled nets supported significantly more plankton in both the 21-50μm and >100μm size classes than short-fouled nets and open-water sites on the north system, but on the south system there were no significant differences between treatments. Plankton of both 21-50μm and >100μm were, however, rare and so the precision with which they were enumerated was less than for other size classes.

Fouled nets (June) and long-fouled nets (November) supported the highest levels of chlorophyll *a* (Figures 4.6 and 4.7). Results for fouled and long-fouled treatments were also highly variable hence, although trends were similar on both north and south systems, they

were not statistically significant (Tables 4.7 and 4.8). In June chlorophyll *a* levels were significantly lower on the north system compared with the south system (Table 4.7).

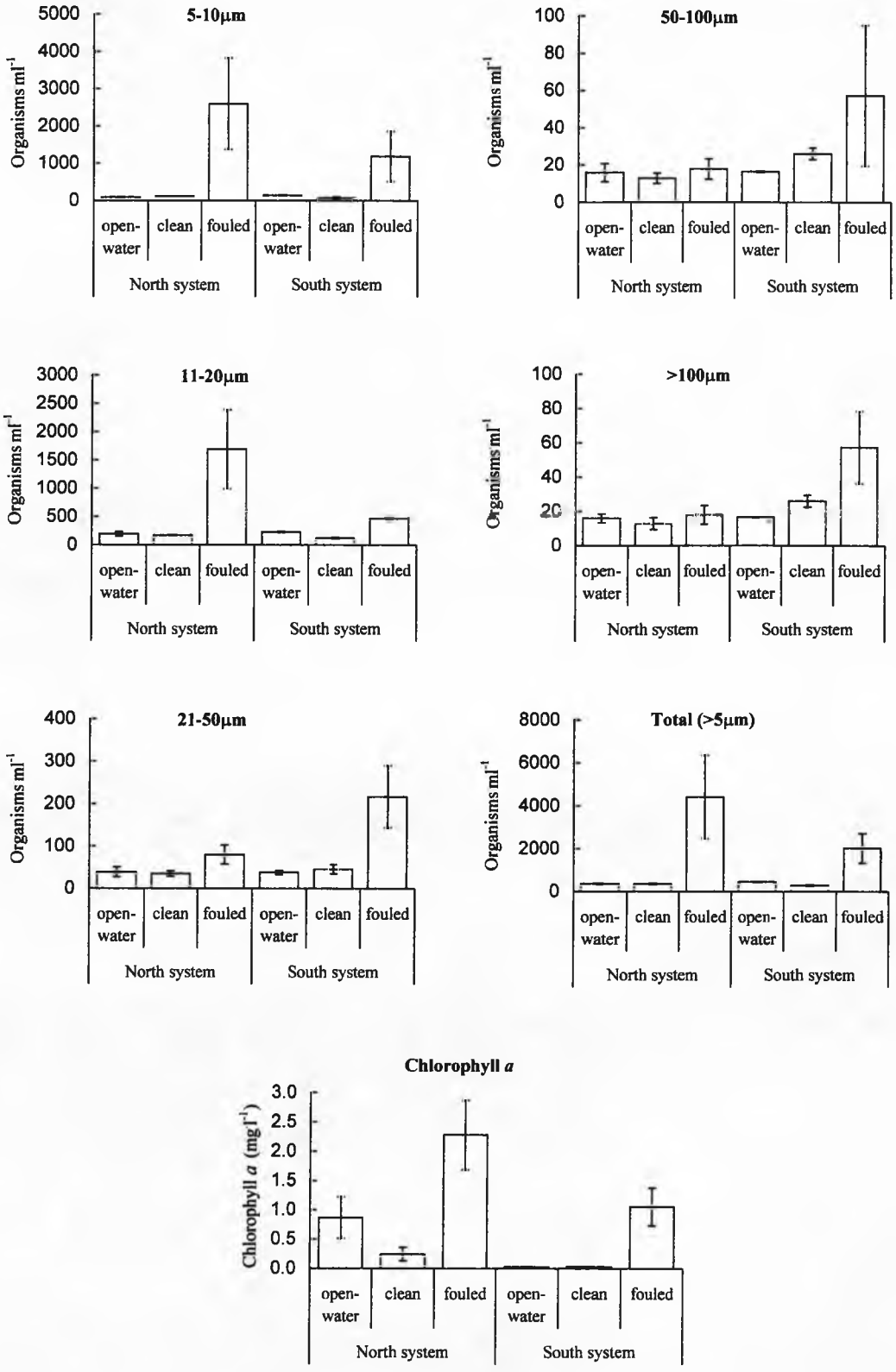


Figure 4.6. Concentrations of plankton in 5 size groups, total plankton and chlorophyll *a* (mean +/- SE), in clean and fouled pearl nets and open-water sites, in June 2000. Note different scales.

Table 4.7. Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on abundance of plankton in four size classes. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the North and South systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Plankton (5-10 μm)					
Transformation = Ln (X), $C = 0.7020$, $P <$ **0.05**					
Location	1	0.15	0.17	0.686	Residual
Treatment	2	11.44	22.56	**0.042**	Location X Treatment
Location X Treatment	2	0.51	0.58	0.576	Residual
Residual	12	0.88			
Total	17				
SNK multiple comparison of treatment results:					
open-water = clean < fouled					
Plankton (11-20 μm)					
Transformation = Ln (X+1), $C = 0.7042$, $P <$ **0.05**					
Location	1	0.15	0.18	0.678	Pooled data
Treatment	2	11.34	13.88	**0.001**	Pooled data
Location X Treatment	2	0.50	0.61	0.559	Pooled data
Residual	12	0.87			
Total	17				
Pooled data	14	0.82			
SNK multiple comparison of treatment results:					
open-water = clean < fouled					
Plankton (21-50 μm)					
Transformation = Ln (X+1), $C = 0.3366$, $P > 0.05$					
Location	1	0.75	4.04	0.068	Residual
Treatment	2	2.61	7.82	0.113	Location X Treatment
Location X Treatment	2	0.33	1.80	0.208	Residual
Residual	12	0.19			
Total	17				
Plankton (51-100 μm)					
Transformation = Ln (X+1), $C = 0.5262$, $P > 0.05$					
Location	1	1.15	8.01	**0.015**	Residual
Treatment	2	1.33	2.93	0.254	Location X Treatment
Location X Treatment	2	0.45	3.16	0.079	Residual
Residual	12	0.14			
Total	17				

Table 4.7 (cont.). Two way ANOVA and SNK multiple comparisons of June data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on abundance of plankton in two size classes, the total abundance over all size classes and chlorophyll *a* concentrations. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the North and South systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Plankton >100 μm					
Transformation = Ln (X+1), $C = 0.4092$, $P > 0.05$					
Location	1	1.68	7.92	**0.017**	Residual
Treatment	2	0.51	1.26	0.442	Location X Treatment
Location X Treatment	2	0.41	1.92	0.190	Residual
Residual	12	0.21			
Total	17				
Total plankton (>5 μm)					
Transformation = Ln (X+1), $C = 0.4092$, $P > 0.05$					
Location	1	279000	1.25	0.283	Pooled data
Treatment	2	16300000	7.29	**0.007**	Pooled data
Location X Treatment	2	2890000	1.29	0.305	Pooled data
Residual	12	2130000			
Total	17				
Pooled data	14	2240000			
SNK multiple comparison of treatment results:					
Open water = clean nets < fouled nets					
Chlorophyll a					
$C = 0.3252$, $P > 0.05$					
Location	1	39.2273	24.03	**<0.001**	Residual
Treatment	2	30.8130	7.02	0.125	Location X treatment
Location X treatment	2	4.3901	2.69	0.088	Residual
Residual	24	1.6327			
Total	29				

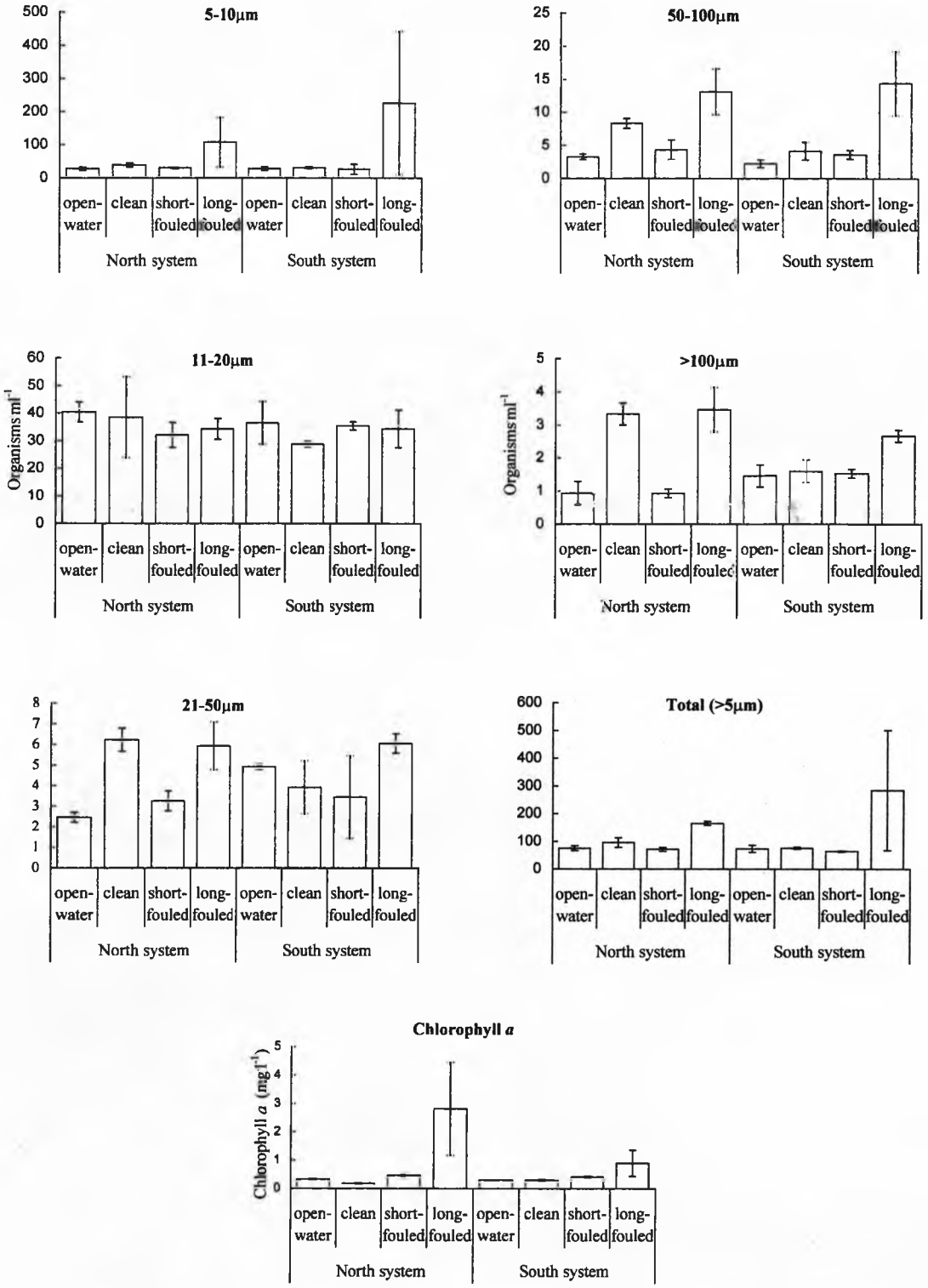


Figure 4.7. Concentrations of plankton in 5 size classes, total plankton and chlorophyll *a* (mean +/- SE) in clean and fouled pearl nets and open-water sites, in November 2000. Note different scales.

Table 4.8. Two way ANOVA and SNK multiple comparisons of November data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on abundance of plankton in four size classes. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the North and South systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (*Indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Plankton (5-10 μm)					
$C = 0.8896$, $P <$ **0.01**					
Location	1	4229	0.22	0.649	Residual
Treatment	3	28087	4.99	0.110	Location X Treatment
Location X Treatment	3	5624	0.29	0.835	Residual
Residual	16	19631			
Total	23				
Plankton (11-20 μm)					
$C = 0.5764$, $P > 0.05$					
Location	1	38.51	0.28	0.606	Residual
Treatment	3	74.15	14.99	0.026	Location X Treatment
Location X Treatment	3	4.95	0.04	0.991	Residual
Residual	16	139.37			
Total	23				
SNK multiple comparison of treatment results failed to identify homogenous groups.					
Plankton (21–50μm)					
$C = 0.3986$, $P > 0.05$					
Location	1	0.09	0.06	0.808	Residual
Treatment	3	9.02	1.59	0.357	Location X Treatment
Location X Treatment	3	5.68	3.70	**0.034**	Residual
Residual	16	1.53			
Total	23				
SNK multiple comparison of interaction:					
North system: open-water = short-fouled nets < clean nets = long-fouled nets					
South sytem: open water = clean nets = short-fouled nets = long-fouled nets					
Open water: North system < South system					
Clean nets: North system > South system					
Short-fouled nets: North system = South system					
Long-fouled nets: North sytem = South system					

Table 4.8 (cont.). Two way ANOVA and SNK multiple comparisons of November data testing for the effect of location and treatment (clean nets, fouled nets and open-water sites) on abundance of plankton in two size classes, the total abundance over all size classes and chlorophyll *a* concentrations. When there is no significant treatment effect or interaction between treatment and location ($P > 0.25$), data for the North and South systems are pooled. The results of Cochran's test are given and data are not transformed unless otherwise indicated. (Bold type indicates a significant result, $P < 0.05$.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Plankton (51-100 μm)					
Transformation = Sqrt (X+1), $C = 0.5045$, $P > 0.05$					
Location	1	0.47	1.37	0.259	Residual
Treatment	3	3.89	17.03	**0.022**	Location X Treatment
Location X Treatment	3	0.23	0.67	0.584	Residual
Residual	16	0.34			
Total	23				
SNK multiple comparison of treatment results:					
Open-water = clean nets = short-fouled nets < long-fouled nets					
Plankton >100 μm					
$C = 0.4619$, $P > 0.05$					
Location	1	0.74	1.98	0.179	Residual
Treatment	3	5.17	2.72	0.217	Location X Treatment
Location X Treatment	3	1.90	5.11	0.011	Residual
Residual	16	0.37			
Total	23				
SNK multiple comparison of interaction:					
North system: open-water = short-fouled nets < clean nets = long-fouled nets					
South sytem: no homeogeneous groups were identified					
Open water: North system = South system					
Clean nets: North system > South system					
Short-fouled nets: North system = **South system**					
Long-fouled nets: North sytem = South system					
Total plankton (>5 μm)					
$C = 0.9061$, $\boldsymbol{P < 0.01}$					
Location	1	3070	0.18	0.680	Pooled data
Treatment	2	42100	2.40	0.116	Pooled data
Location X Treatment	2	4990	0.29	0.755	Pooled data
Residual	18	18900			
Total	23				
Pooled data	20	17500			
Chlorophyll a					
$C = 0.9387$, $\boldsymbol{P < 0.01}$					
Location	1	2.69	1.50	0.230	Residual
Treatment	3	5.24	1.86	0.311	Location X treatment
Location X treatment	3	2.81	1.57	0.217	Residual
Residual	32	1.80			
Total	39				

Multivariate analyses (plankton type).

The MDS ordination of similarities between June samples (Figure 4.8) showed that in general fouled nets supported a different plankton community from clean nets and open-water sites. Fouled nets from different locations were also distinct. Differences between clean nets and open-water sites are blurred by differences between replicate samples, particularly those from open-water sites on the north system. ANOSIM revealed significant differences between both locations and treatments ($R = 0.42$, $P = 0.005$ and $R = 0.57$, $P = 0.001$ respectively). Pairwise comparisons found significant differences between fouled nets and both open-water sites ($R = 0.78$, $P = 0.01$), and clean nets ($R = 0.89$, $P = 0.01$), but, as indicated by the MDS plot, open-water sites and clean nets contained similar communities ($R = 0.278$, $P = 0.08$). SIMPER results (Table 4.9) show that differences in the abundance of small plankton, centric diatoms, flagellates, and pennate diatoms (11-20μm) were important in distinguishing locations and fouled nets from clean nets and open-water sites.

The shade matrix of June data (Figure 4.9) reveals that variability in abundances between replicates was high but fouled nets were characterised by high numbers of all plankton groups. Eggs and spores (21-50μm and >100μm), invertebrate larvae (>100μm), small plankton, centric diatoms (11-20μm), flagellates (11-50μm) and pennate diatoms (21-100+μm) were particularly common in fouled nets compared with clean and open-water sites. Nematodes and invertebrate larvae (51-100μm) were found only in fouled nets. Many plankton groups in clean and fouled nets were more abundant on the south system than the north one, explaining the separation of systems on the MDS plot. Consistently low abundances in the water sample 2NF explains its atypical position on the MDS plot: despite its low content this replicate still contained most of the plankton that characterised other samples from fouled nets. Pennate diatoms of all size classes were most abundant in fouled nets whereas large (>21μm) centric species had a more even distribution across treatments.

November samples contained fewer types of plankton than June samples (Figure 4.11). The MDS ordination of similarities also showed less distinct groups than in June (Figure 4.10). Two long-fouled samples clustered together at a 70% similarity level and two more were outliers from the main cluster with one clean sample. ANOSIM confirmed that there were no significant differences between locations ($R = 0.09$, $P = 0.26$). There was, however, a significant treatment effect ($R = 0.26$, $P < 0.01$), and pairwise comparisons showed that clean nets were different from both long- and short-fouled nets ($R = 0.24$, $P = 0.04$ and $R = 0.37$, $P = 0.01$); short- and long-fouled net also differed significantly ($R = 0.35$, $P = 0.01$).

Open-water sites had characteristics common to all other treatments (this is illustrated by Figure 4.11) and were not significantly different from long-fouled ($R = 0.28$, $P = 0.05$), clean ($R = 0.32$, $P = 0.06$) or short-fouled sites ($R = 0.06$, $P = 0.35$).

SIMPER results (Table 4.10) show that open-water sites, and clean and long-fouled nets, were primarily distinguished by the abundance of small plankton but that small flagellates and diatoms were also important. These plankton groups were also important in separating clean nets from short-fouled nets, but 11-20μm flagellates and not small plankton contributed most to treatment dissimilarity. Eggs and spores (11-20μm) were important in differentiating long-fouled treatments from open-water sites and short-fouled nets.

The November shade matrix (Figure 4.11) shows that both clean- and long-fouled nets were consistently characterised by high abundances of most plankton groups. High small plankton abundances characterised the two long-fouled nets that clustered together on the MDS plot. Centric diatoms, (11-20μm) and eggs and spores, (11-20μm) were also prevalent in these treatments. Dinoflagellates (11-20μm) and pennate diatoms (50-100μm) were common in both open-water and long-fouled sites. Pelagic ciliates (11-20μm), eggs and spores (11-20μm) and dinoflagellates (21-50μm) were less common in open-water sites than all other treatments. Short-fouled nets supported fewer diatoms than any other treatment. Variation among replicate samples was less than in June; generally differences were greatest among open-water sites.

November abundances of pennate and centric diatoms varied between size classes; in the 11-20μm range both groups were most abundant in clean- and long-fouled nets. In the 21-50μm size class centric diatoms were most common in open-water samples whereas pennate species were more abundant in nets, particularly fouled ones. Diatoms of 51-100μm were patchily distributed both within and between treatments; long-fouled nets had the highest abundance of pennate diatoms, whilst centric species were most common in both clean and long-fouled nets. Diatoms greater than 100μm followed similar trends to those of 51-100μm, except that pennate species were most common in both clean and long-fouled samples.

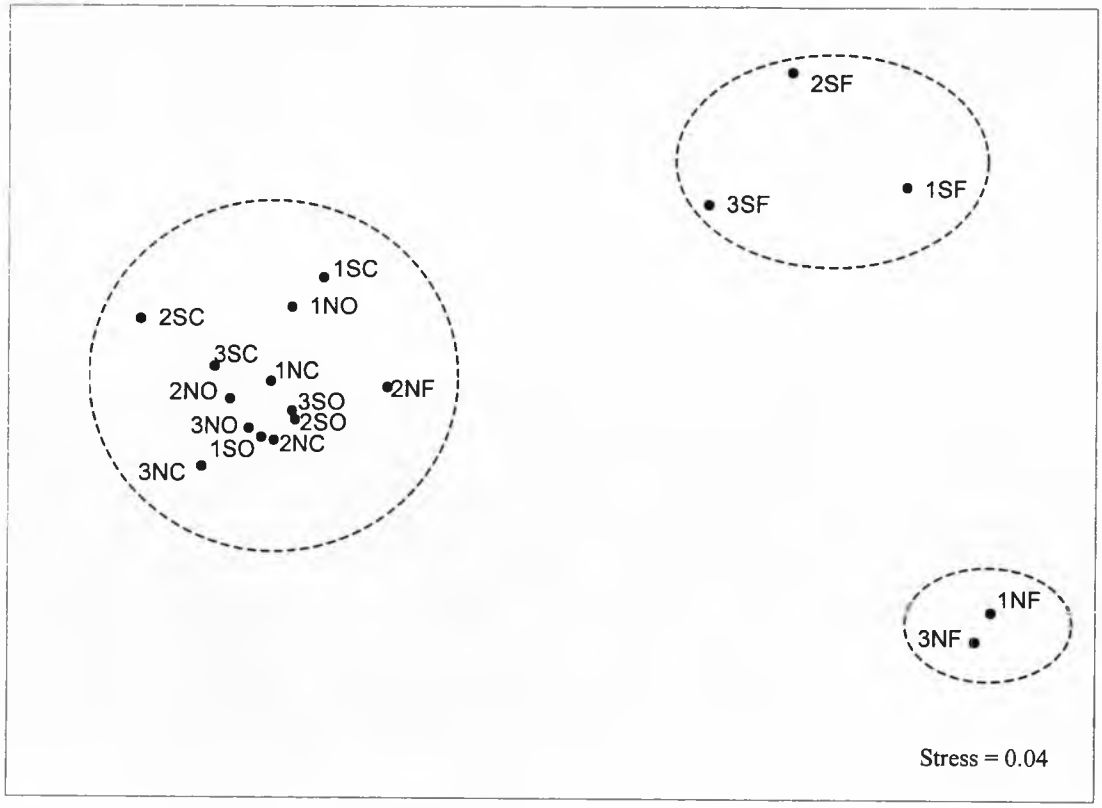


Figure 4.8. MDS ordination of Bray-Curtis similarity matrix for square-root transformed plankton-abundance-data (Appendix 7). Samples were collected in June 2000 and are labelled with their replicate number, location; north system (-N), south system (-S), and treatment; open-water sites (-O), clean nets (-C), and fouled nets (-F). Samples are grouped at a 70% level of similarity from CLUSTER analysis.

Table 4.9. SIMPER results showing the plankton groups principally contributing to differences between locations (A) and treatments (B - D), in June samples (when data were square root transformed). Abundances are per ml of sample. Numbers refer to plankton size classes: 1, 5-10μm; 2, 11-20μm; 3, 21-50μm; 4, 51-100μm; 5, >100μm.

A.

Plankton group	Average abundance		Contribution	Cumulative
	N system	S system	(%)	contribution (%)
Small plankton	935	469	20	20
Centric diatoms (1)	292	65	11	31
Flagellates (1)	184	30	8	39
Chain forming diatoms (1)	161	110	5	44
Pennate diatoms (1)	8	25	4	48
Pennate diatoms (2)	5	18	3	51

B.

Plankton group	Average abundance		Contribution	Cumulative
	Clean	Open-water	(%)	contribution (%)
Chain forming diatoms (1)	102	162	12	12
Small plakton	96	117	9	21
Pennate diatoms (1)	2	5	5	26
Chain forming diatoms (4)	3	0	4	30
Diatom chains (1)	2	6	4	34
Centric diatoms (1)	15	14	4	38
Flagellates (1)	10	13	4	42
Centric diatoms (2)	3	4	4	45
Diatom chains (2)	8	4	4	49
Chain forming diatoms (2)	12	16	3	52

C.

Plankton group	Average abundance		Contribution	Cumulative
	Clean	Fouled	(%)	contribution (%)
Small plankton	96	1893	25	25
Centric diatoms (1)	15	507	13	38
Flagellates (1)	10	298	9	48
Pennate diatoms (1)	2	42	4	52

D.

Plankton group	Average abundance		Contribution	Cumulative
	Fouled	Open-water	(%)	contribution (%)
Small plankton	1893	117	25	25
Centric diatoms (1)	507	14	14	39
Flagellates (1)	298	13	9	48
Pennate diatoms (1)	42	6	4	52

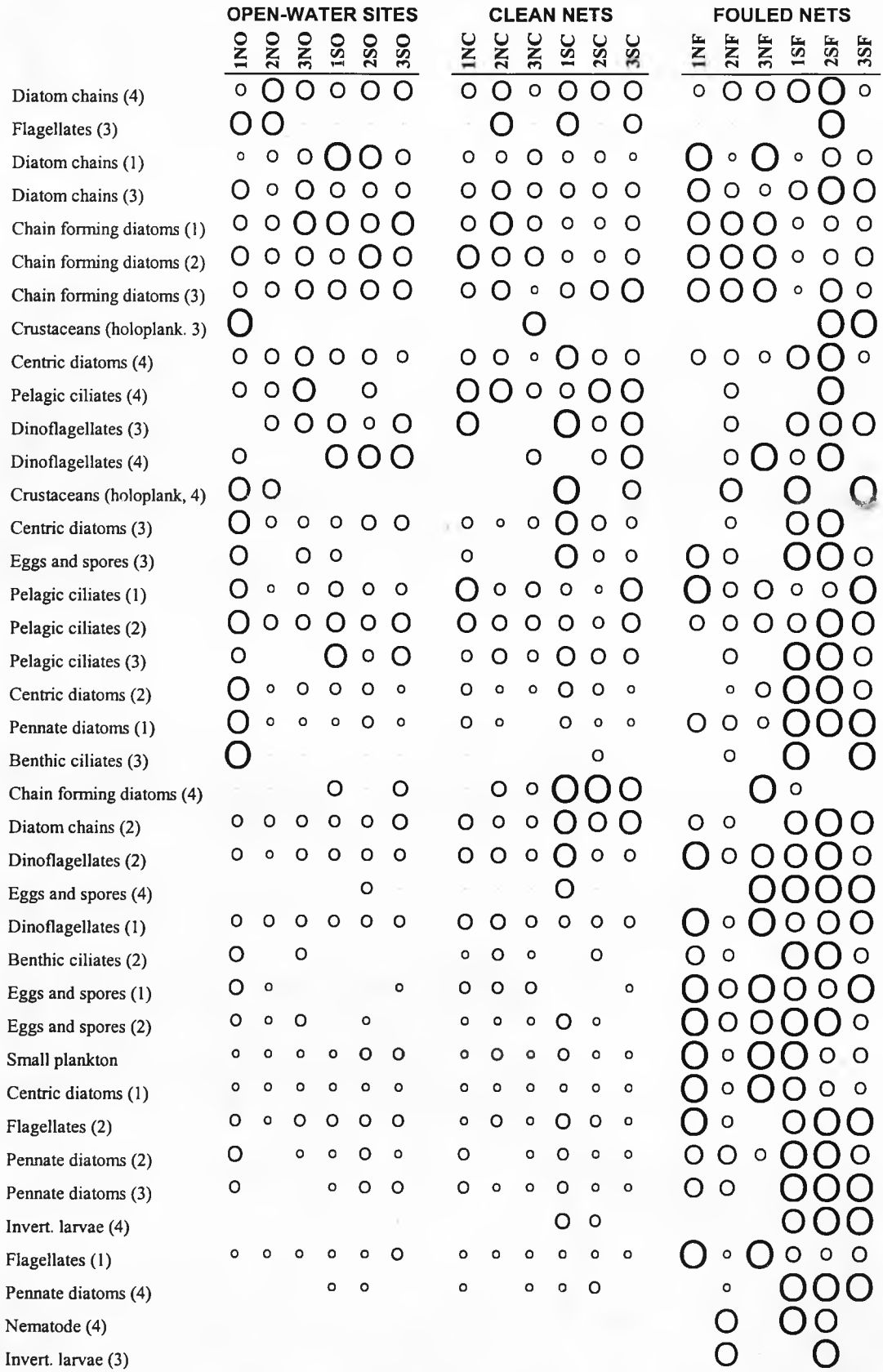


Figure 4.9. Relative abundance of each plankton category, present in more than one sample in June 2000. Numbers refer to plankton size classes: 1, 5-10μm; 2, 11-20μm; 3, 21-50μm; 4, 51-100μm; 5, >100μm. Samples are grouped by treatment; open-water sites (-o), clean nets (-c), and fouled nets (-f). Circle size is proportional to relative abundance. Categories are roughly sorted by abundance in the four treatments.

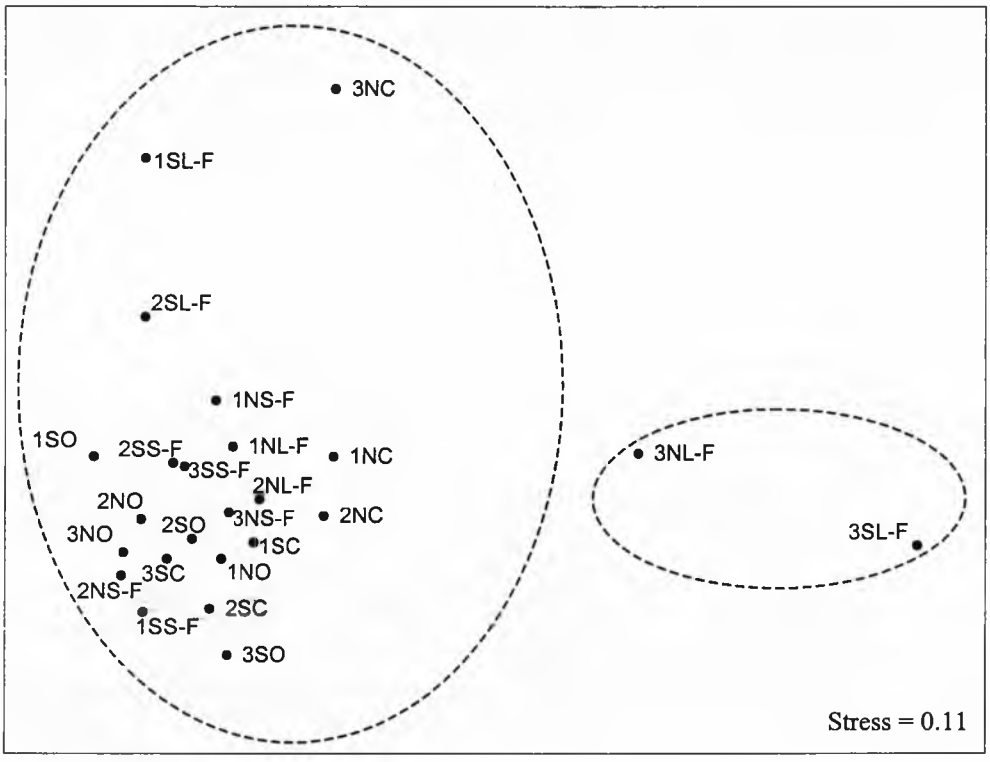


Figure 4.10. MDS ordination of Bray-Curtis similarity matrix for square-root transformed plankton-abundance-data (Appendix 8). Samples were collected in November 2000 and are labelled with their replicate number; location, north system (-N), south system (-S); and treatment, open-water sites (-O), clean nets (-C), short-fouled nets (-S-F), and long-fouled nets (-L-F). Samples are grouped at a 70% level of similarity from CLUSTER analysis.

Table 4.10. SIMPER results showing the plankton groups principally contributing to differences between Locations (A) and treatments (B - F), in November samples (when data were square root transformed). Numbers refer to plankton size classes: 1, 5-10μm; 2, 11-20μm; 3, 21-50μm; 4, 51-100μm; 5, >100μm.

A.

Plankton group	Average abundance		Contribution	Cumulative
	N system	S system	(%)	contribution (%)
Small plankton	51	78	23	23
Flagellates (1)	22	21	9	32
Centric diatoms (1)	4	3	7	39
Dinoflagellates (1)	7	7	5	43
Eggs and spores (2)	0	0	4	47
Pennate diatoms (1)	2	1	4	51

B.

Plankton group	Average abundance		Contribution	Cumulative
	Clean	Open-water	(%)	contribution (%)
Flagellates (1)	21	26	10	10
Dinoflagellates (1)	5	9	9	19
Small plankton	29	28	8	27
Centric diatoms (2)	2	2	5	32
Dinoflagellates (2)	1	0	5	37
Centric diatoms (3)	1	2	5	42
Diatom chains (3)	0	0	5	46
Eggs and spores (3)	0	0	4	51

C.

Plankton group	Average abundance		Contribution	Cumulative
	Short-fouled	Open-water	(%)	contribution (%)
Flagellates (1)	23	26	12	12
Small plankton	35	28	8	20
Centric diatoms (1)	4	2	7	27
Dinoflagellates (1)	5	9	7	34
Pennate diatoms (1)	3	1	6	41
Pennate diatoms (2)	1	0	5	45
Pelagic ciliates (1)	0	0	4	49
Eggs and spores (2)	0	0	4	53

D.

Plankton group	Average abundance		Contribution	Cumulative
	Long-fouled	Open-water	(%)	contribution (%)
Small plankton	167	28	36	36
Flagellates (1)	17	26	7	43
Diatoms (1)	7	2	7	50
Eggs and spores (2)	1	0	5	56

Table 4.10 (cont.). SIMPER results showing the plankton groups pricipally contributing to differences between Locations (A) and treatments (B - F), in November (when data were square root transformed). Numbers refer to plankton size classes: 1, 5-10μm; 2, 11-20μm; 3, 21-50μm; 4, 51-100μm; 5, >100μm.

E.

Plankton group	Average abundance		Contribution	Cumulative
	Clean	Short-fouled	(%)	contribution (%)
Flagellates (1)	21	23	13	13
Centric diatoms (1)	2	4	8	21
Monads	29	35	6	27
Pennate diatoms (1)	1	3	6	33
Eggs and spores (2)	0	0	5	38
Centric diatoms (3)	1	2	5	42
Pennate diatoms (2)	1	1	4	47
Chains (2)	0	0	4	51

F.

Plankton group	Average abundance		Contribution	Cumulative
	Clean	Long-fouled	(%)	contribution (%)
Monads	29	167	35	35
Centric diatoms (1)	2	7	7	42
Eggs and spores (2)	0	1	6	48
Dinoflagellates (1)	5	8	4	52

G.

Plankton group	Average abundance		Contribution	Cumulative
	Long-fouled	Short-fouled	(%)	contribution (%)
Monads	167	35	32	32
Flagellates (1)	17	23	10	42
Centric diatoms (1)	7	4	7	49
Pennate diatoms (3)	1	0	4	53

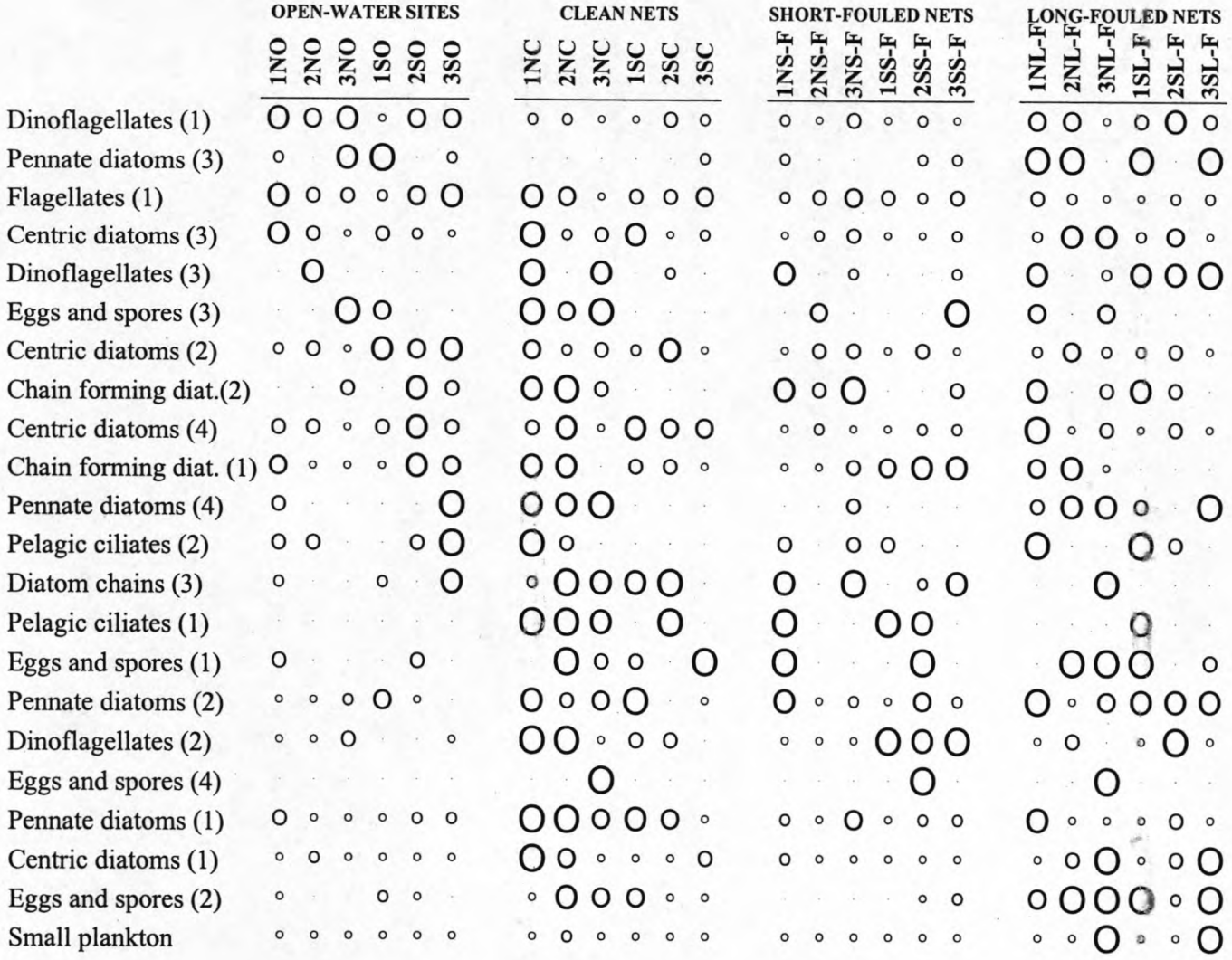


Figure 4.11. Relative abundance of each plankton category, present in more than one sample in November 2000. Numbers refer to plankton size classes: 1, 5-10μm; 2, 11-20μm; 3, 21-50μm; 4, 51-100μm; 5, >100μm. Samples are grouped by treatment; open-water sites (o), clean nets (c), short-fouled nets (s-f), and long-fouled nets (l-f). Circle size is proportional to relative abundance. Categories are sorted by abundance in the four treatments.

4.4 Discussion

The results of this study challenge common assumptions that fouling reduces food and oxygen levels. That conditions inside pearl nets differed from those outside is also an important discovery, which should be considered when researchers try to relate the growth of scallops in suspended culture to environmental parameters. The influence of fouling seems to vary seasonally. Although sampling was not repeated within seasons, experiments show that physio-chemical and biological conditions that influence the growth of suspension-feeders can vary over short-time periods (Fegley *et al.* 1992). Changes are caused by variations in the prevailing environment (random and regular) and biological cycles or rhythms (e.g. vertical zooplankton migration). June and November results are thus viewed as snapshot observations, providing an example of conditions at those times of year and not a precise description of, say, summer and winter environments.

Physiochemical conditions

Clean, wide-mesh nets, commonly used for on-growing intermediate sized scallops, had little effect on total water motion in this high current area. This was surprising because at water velocities similar to those in these experiments pearl nets with a mesh size of 12 mm^2 have been shown to reduce water movement by 6-7 % (Cole *et al.* 1996). Though low variability between open-water measurements in June (< 5 %, Figure 4.2) suggests that measurements of water motion were precise, Thompson and Glenn (1994) found that plaster clod cards (similar to plaster balls) had a precision of only 2.5-6.0 %, so measurements may not have been precise enough to detect small differences (< 5 %) in water velocities found by Cole *et al.* (1996). Alternatively, a small decrease in water-motion because of the net may have been negated by increased plaster dissolution if strings of nets acted like sails so that spheres in clean nets were moved through the water even when water currents were weak. Fouled nets approximately halved water-flow in June. Skjaeggestad (1997) similarly, reported that water-motion inside fouled cages, with 14 mm^2 spacing, was reduced by up to 68 % when fouling was at its peak.

Rates of plaster dissolution in November were more variable within treatments than in June probably because bad weather shortened the time for which the plaster spheres could be deployed (24 h cf. 48 h). This may have increased the influence of random events (e.g. abrasion or trapped debris) on measurements and may explain why no significant treatment effects were discovered. Chapter 3 describes how space opens up as the fouling community ages, and this explains the non-significant but consistent trend for short-fouled nets to

reduce water motion more than long-fouled nets (Figure 4.3). Skjaeggestad (1997) also proposed that effects of fouling on water motion are influenced by the composition of the community because both factors changed with depth and season. Off Port Erin November fouling communities were dominated by *Ascidiella scabra* whereas *Tubularia* spp. dominated in June. *Tubularia* spp. formed a dense turf with few gaps whereas the *A.scabra* community only covered about 65% of the net. Plaster spheres were an inexpensive and reliable way of measuring water-motion. Future experiments should, however, attempt to deploy them for longer (ca.72-96 h) as this would probably increase the precision of the measurements.

Laboratory experiments by Wildish and Saulnier (1993) show that some water-movement (>3 $cm \cdot s^{-1}$) is essential to prevent food depletion around *Placopecten magellanicus,* but velocities in excess of 6$cm \cdot s^{-1}$ inhibit feeding. Similar results were obtained by Cranford *et al.* (1994). Skjaeggestad (1997) also found that speeds of more than 6$cm \cdot s^{-1}$ inhibit feeding in *P.maximus.* As discussed by Bricelj and Shumway (1991), these flow rates seem very low as scallops regularly occur in areas where currents exceed 100 $cm \cdot s^{-1}$. Eckman *et al.* (1986) suggest that scallops may increase the free stream velocities at which they can feed by orientating with their anterior into the current; recessing into the boundary layer may also aid feeding in high currents. The laboratory findings are, however, reasonably consistent with the results of field experiments by Claereboudt *et al.* (1994b) and Cranford and Hargrave (1994). Claereboudt *et al.* (1994b) compared the growth of *P.magellanicus* inside and outside pearl nets. They found that scallops inside nets grew slower than those outside of nets in low current areas (<16 $cm \cdot s^{-1}$) and faster than those outside in high current areas (>90 $cm \cdot s^{-1}$). It was suggested that this was because, in high current areas, velocities that inhibited feeding were moderated by pearl nets, whereas in low current areas seston depletion inside nets limited scallop growth. Mean water velocity across the longlines in the current experiments was roughly 30 $cm \cdot s^{-1}$ and so scallop growth rates may have been improved by the reduction in water motion caused by fouling. Fouling may also have prevented local seston depletion by actively mixing the water and creating turbulent flow conditions (Fréchette *et al.* 1989, Larsen and Riisgård 1997).

On both sampling dates ammonia and nitrate levels were within the usual range for the area and time of year (T. Shammon, *pers. comm.* 2001. Port Erin Marine Laboratory, Isle of Man). They were also similar for all treatments indicating that neither clean nor fouled nets sustained a build up of decay or excretory products. Four high ammonia measurements in June may have been caused by the capture of detritus in water samples (kelp detritus was abundant and the northern longline is close to a sewage outfall pipe). Inorganic nitrogen is

absorbed by phytoplankton and it is possible that high numbers of phytoplankton reduced levels of nitrate and ammonia in fouled and long-fouled nets. Whilst replication of this experiment was sufficient to detect gross changes reflecting a build up of chemicals, further sampling would enable small changes in the abundance of inorganic nitrogen to be identified. Increased nitrogen could be important if it stimulates primary production within nets (see section 4.4.4).

Mean oxygen concentrations in November were above levels that stress scallops (Brand and Roberts 1973) and highest in long-fouled nets. This was unexpected because the nets were dominated by heterotrophs, and contradicts the suggestion by Huguenin and Huguenin (1982), Enright (1993) and Lu and Blake (1997) that low oxygen reduces the growth of scallops in fouled nets. Unfortunately, oxygen levels were not reliably measured in the summer when they were most likely to be depleted by high water temperatures, a dense, heterotrophic fouling community and anaerobic decay of abundant organic detritus. However, November oxygen concentrations followed the same trend as plankton numbers and chlorophyll *a*, which were both highest in fouled nets in June. Photosynthesis by benthic macroalgae in the fouling community may also have enhanced oxygen levels. In high current areas such as the study area, fouling might therefore enhance oxygen levels by supporting photoautotrophs. Interestingly, Mazouni *et al.* (2001) also reported a positive oxygen flux from oyster culture units in November, which contrasted with the negative flux at all other times of year. They attributed this to strong water movement and the presence of macroalgae.

Food conditions

Contrary to the assumption of Duggan (1973), Leighton (1979), Huguenin and Huguenin (1982), Côté *et al.* (1993), Enright (1993), Claereboudt *et al.* (1994b), Lodeiros *et al.* (1996), and Lu and Blake (1997) fouling did not reduce the quantity or quality of food particles available for scallops. Instead, net fouling was often associated with high numbers of phytoplankton and detritus, and a favourable PIM/POM ratio. Trends in plankton and detritus abundance discussed here were strong and consistent enough to be identified despite the low number of replicates (time constraints meant that only three water samples were analysed for each treatment), the notoriously patchy distribution of plankton (Hasle 1978) and variations in water velocity between sampling times. Analysing further samples would have increased the power of statistical tests to detect differences between treatments and provided a more precise description of food conditions.

Particulate matter

Proximity to the shore and the sewage outfall explains why this study area was characterised by high seston loadings (ca. 20mgl^{-1}) during both sampling periods; similar loadings were found by Cranford *et al.* (1994) and Lodeiros *et al.* (1998) in the water-column off Canada and Venezuela respectively. Both total particulate matter and POM concentrations were highest in fouled nets in June. This suggests that fouling traps, produces and perhaps supports the production of organic matter - a potential energy source for scallops. MacDonald *et al.* (1998) showed that even at high seston concentrations (15mgl^{-1}) scallop scope for growth may be reduced by the dilution of POM by PIM. Experiments suggest that when seston concentrations are not limiting a PIM/POM ratio of less than 3.5-4.0 is required by scallops to maintain a positive energy balance (Vahl 1980, Wallace and Reinsnes 1985), and maximum scope for growth (MacDonald *et al.* 1998). Cranford (1995) also predicted that scallops would not absorb any organic matter when POM levels are less than 14% (a PIM/POM ratio of >6). In this study, open-water sites in June had PIM/POM ratios of around 3, close to the critical value discussed above, and significantly higher than in fouled nets. In some instances, therefore, enhanced levels of POM in fouled nets could prevent high ambient PIM concentrations from depressing scallop growth rates. In November there were no consistent treatment effects in TPM, PIM or POM, the PIM/POM ratio was high (ca.1.5-3.5), even in fouled nets, and this might have affected scallop growth.

Rough enumeration of detrital particles indicated that they combine with phytoplankton to drive trends in TPM. Data were highly variable but suggest that detritus was produced and trapped in fouled nets in June and short- and long-fouled nets in November. Inclusion of a large detrital fragment or misplacement of the syringe tip, so that it scraped the surface of a scallop, could explain the outlying result for a clean net in June. Detritus included dead fouling organisms, faecal fragments and dying plankton (probably with associated bacteria). Such particles can be an important source of nutrition for scallops (Cranford and Grant 1990, Alber and Valiela 1995, 1996).

Mook (1981) found that some foulers package small food particles (<5μm) as large faeces or pseudo-faeces (>25μm) containing incompletely digested material. This conversion could make food particles more available for scallops because they retain large particles (>5μm) more efficiently than small ones (Bricelj and Shumway 1991). In June, faeces levels in all size classes were generally highest in fouled nets (Table 4.5). However, variability was high both within and between longline systems, suggesting that faeces were patchily distributed inside the nets. In November, faeces levels were consistently highest in long-fouled nets (Table 4.6) although water movement was least in short-fouled treatments.

Perhaps the tunicates dominating short-fouled treatments removed more faeces than the diverse community on long-fouled nets; alternatively, faeces may have been deposited in greatest numbers by organisms of the long-fouled community. On both sampling dates there were no significant differences between clean nets and open-water sites for any size of faeces so the influence of scallop faeces could not be determined. Only complete faecal pellets were counted and hence numbers are probably underestimated.

Plankton

Total plankton numbers at open-water sites were similar to those recorded by Graziano (1988) for the north-east Irish Sea. In both June and November 2000 plankton communities were dominated by plankton of 5-20μm reflecting Graziano's conclusion that 65% of primary production in this area was due to phytoplankton of 5-20μm. Chlorophyll *a* concentrations followed total plankton numbers reflecting the dominance of autotrophs in plankton samples.

Univariate analysis of plankton size classes and multivariate community analyses indicate that both actual and relative quantities of plankton types differed between treatments. There was no evidence that foulers depleted food resources and plankton numbers were often highest in fouled nets. Differences between treatments were thus probably driven by autochthonous production and this may have masked the removal of plankton by foulers. Net fouling may have encouraged primary production in June by releasing nutrients, retaining plankton in a favourable light environment or providing a substrate for benthic autotrophs. Increased primary production may in turn have supported heterotrophic and mixotrophic organisms such as dinoflagellates and ciliates.

Suspension-feeders have the potential to induce the growth of more phytoplankton than they consume (Asmus and Asmus 1991) because they can increase local inorganic and organic phosphate and nitrate concentrations, both directly through excretion and indirectly via bacterial decay of their faeces (e.g. Dame and Dankers 1988, Asmus and Asmus 1991 and references therein, Peterson and Heck 1999, Arzul *et al.* 2001, Mazouni *et al.* 2001). A possible mechanism by which suspension-feeding foulers and scallops could produce and retain nutrients is described in Figure 4.12. This might be important because in most marine systems, including the Irish Sea, phytoplankton are likely to be nitrate limited at certain times of year (Allen *et al.* 1998, Kennington *et al.* 1999). Similarly, Mazouni *et al* (2001) suggest that during summer months nutrient recycling by oyster culture units may drive primary production in the water column.

Proliferation of phytoplankton in fouled nets indicates that light levels were not reduced below their compensation point, even by thick *Tubularia* fouling. Perhaps strong sunlight in June penetrated the translucent stalks of this hydroid. Fouled nets may also have encouraged plankton growth and reproduction by preventing cells from sinking below the euphotic zone. The relationship between phytoplankton growth and net fouling may be better understood if future studies measured light attenuation by different fouling communities. Unfortunately, a photon meter was not available during this investigation.

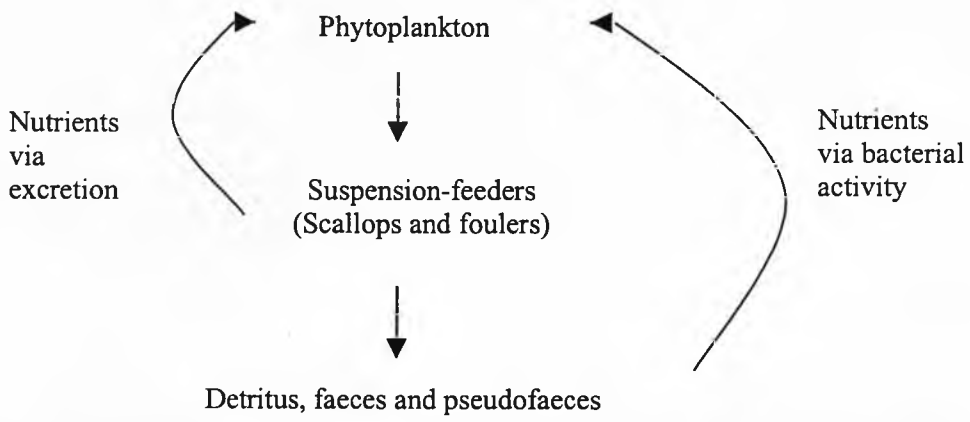


Figure 4.12. Mechanism by which nutrients might be retained and recycled in fouled pearl nets.

Benthic plankton are often suspended by turbulent coastal water and generally survive well in the water column (Newell and Newell 1979); this explains the prevalence of benthic ciliates and pennate diatoms in open-water samples (Figure 4.9). Many benthic species were, however, most common in fouled nets where they may have proliferated because of the conditions described above or the presence of a solid surface onto which they could attach or settle. Attached organisms may have been suspended by the passage of the sampling syringe, but movement of scallops and water currents are also likely to make them readily available as food for scallops.

There was some evidence that fouling enhanced plankton numbers in November, although low plankton abundances and patchy distributions made treatment effects hard to distinguish. Small plankton (<5μm) bloomed in some long-fouled nets; bloom-forming species are common in this area in the late spring (Kennington *et al.* 1999) and could

perhaps have been retained within fouled nets. Total plankton numbers were highest in long-fouled nets and although this result was only significant in the 50-100μm size range it was consistent across systems and matched (but masked by high variability) by the abundance of 5-10 μm plankton and chlorophyll *a* (obtained from water samples taken a day after plankton samples). Plankton of 21-50μm and >100μm were rare (1-6 plankton per ml) and hence enumerated with low precision: significant differences between numbers in clean and short-fouled nets on the north system may therefore be an artefact, particularly given the inconsistencies between systems when fouling communities were similar. Solitary tunicates are voracious and efficient feeders (Barnes 1987, Larsen and Riisgård 1997, and references therein) that can control plankton numbers in shallow or semi-enclosed areas (Riisgård *et al.* 1995). Tunicate dominance of fouled nets in November may thus have depressed plankton numbers (and possibly masked high production) more than the passive-feeding hydroid community that colonised nets in June. High nutrient concentrations and low plankton abundances make it unlikely that nutrients were limiting in November. Instead, retention in the euphotic zone, or provision of a hard substrate, might explain high plankton numbers in long-fouled nets.

It is interesting that long-fouled nets generally contained more plankton than short-fouled nets though fouling communities on both types of net were dominated by *A.scabra*. Short-fouling communities covered more of the net surface than long-fouling communities; hence, plankton removal by suspension-feeders (mainly *A.scabra*) was probably greatest in short-fouled nets. Numbers of pennate diatoms were lower in short-fouled nets than clean or long-fouled nets, perhaps because short-fouled nets were colonised by little other than *A.scabra* (compared to the more diverse long-fouling community). Ascidians have mechanical and chemical defences against predators (Vervoort *et al.* 1998) and fouling organisms (e.g. Stoecker 1978, Wahl and Banaigs 1991, Teo and Ryland 1995, Wahl *et al.* 1998). In short-fouled nets, benthic plankton may hence have lacked a substrate on which to attach and grow. The different immersion histories of short- and long-fouled nets could also explain their varied plankton abundances. Perhaps the plankton seeding high production in long-fouled nets arrived before short-fouled nets were deployed.

Changes in plankton abundance are only important if food limits scallop growth or if changes in food quality affect the rate at which scallops obtain energy. Scallop clearance or uptake rates increase with food levels up to a threshold level; uptake is then independent of food concentration (Palmer and Williams 1980, Skjaeggestad 1997) until, at very high food concentrations, uptake may again decrease (Cahalan *et al.* 1989, Lorrain *et al.* 2000). In

studies with juvenile *P.maximus* (6cm shell height) Skjaeggestad (1997) found a threshold concentration of between 9000-12000 *Tetraselmis suecica* cells ml^{-1}. Similarly, Cahalan *et al.* (1989) showed that the growth of juvenile *Agropecten irradians* increased with food up to concentrations of between 6000 and 15000 *Isochrysis galbana* cells ml^{-1}. In the current study total plankton cell densities in clean and open-water treatments were below 593 cells ml^{-1} in June and 105 cells ml^{-1} in November, far less than the threshold concentration discussed above. Increased cell numbers in fouled and long-fouled nets may well, therefore, have encouraged scallop growth.

Different types of plankton will vary in their food value to scallops depending on the ease with which they can be captured and digested, and their quality or biochemical composition. In this experiment, net fouling was often associated with a general increase in organism abundance rather than a new suite of plankton. There was, however, a notable increase in the relative abundance of small diatoms (5-20μm) and flagellates (10-20μm) in fouled nets in June and long-fouled nets in November. Pectinids retain particles smaller than 5-7μm less efficiently than larger particles (Bricelj and Shumway 1991, and references therein, Brilliant and MacDonald 2000). However, reduced retention efficiencies would probably have been out-weighed by the large increase in food availability. Invertebrate larvae (including decapods and echinoderms) and nematodes were only found in fouled nets in June: they were not numerically important as a food source but as potential predators and parasites they could have deleterious effects on scallop growth and survival. *Dinophysis* sp. appeared in water samples from two open-water sites in November and one fouled net in June (at concentrations of less than one per ml); these dinoflagellates can sometimes produce toxins known to cause diarrhoetic shellfish poisoning if they accumulate in scallops (Suzuki *et al.* 1996). Although concentrations were normal for this area (Shammon *et al.* 1997), problems could arise if, like other algal species, they were encouraged to bloom by conditions inside the fouled nets.

Implications

This is the first description of how fouling influences the environment inside nets used for shellfish cultivation. The results challenge the common assumption that fouling reduces food levels. Instead, in high current areas off the Isle of Man, fouling can be associated with increased food availability and does not necessarily encourage a build up of decay products, inorganic matter or an oxygen deficit, even when scallop densities are high. The results also show that the effects of fouling vary with composition or age of the fouling community and suggest that seasonal changes occur. These findings help to explain why scallops inside

pearl nets may grow faster than those outside pearl nets, in high current areas (Claereboudt *et al.* 1994b). It could also be inferred that negative effects of fouling on scallop growth are caused by fouling organisms mechanically interfering with scallops (e.g. binding them in unfavourable positions, inhibiting shell opening or disrupting feeding behaviour), or harbouring predators and parasites (Mortensen *et al.* 2000), rather than altering the net environment. Scallop growers in high current areas should perhaps strive to reduce the mechanical interference of foulers rather than trying to eliminate fouling altogether. Strategies might include biological control, which can keep bivalves clean and free to move, but does not completely remove biofouling (Hindu *et al.* 1981, Huguenin and Huguenin 1982, Enright *et al.* 1983, Minchin and Duggan 1989, Cigarria *et al.* 1998, Armstrong *et al.* 1999). This approach might benefit scallop growth by reducing mechanical interference whilst retaining the potential food enhancing properties of fouling.

This study shows that the net environment in which scallops grow can differ significantly from the water-column; this has important consequences for two areas of research. Firstly, studies often relate patterns of scallop growth in suspended culture to environmental conditions (e.g. Wallace and Reinsnes 1985, Côté *et al.* 1993, Claereboudt *et al.* 1994a, Emerson *et al.* 1994, Lodeiros and Himmelman 1994, Thorarinsdóttir 1994, Vélez *et al.* 1995, Kleinman *et al.* 1996, Lodeiros *et al.* 1998, Lodeiros and Himmelman 2000). This relationship may be described more accurately if future studies consider the influence of net fouling, or measure conditions inside the nets. On a wider scale, water-column-data have recently been used by researchers attempting to assess the affects of bivalve cultivation on nutrient and seston dynamics of bays, or predict the capacities of areas for shellfish cultivation (Pilditch *et al.* 2001 and references therein, Penney *et al.* 2001). Because of its potential to uncouple scallop processes from water-column seston conditions, the influence of net fouling should also be included in such models.

Further work

Fouling cover and scallop growth was not assessed quantitatively during this experiment because all available diver and boat time was exhausted. Instead, the relationship between fouling cover and scallop growth was determined over a different period (other conditions being constant) and assessed with reference to these results (Chapter 5). Simultaneous assessment of these factors in future studies would enable the interactions between fouling cover, the net environment and scallop growth to be described more accurately. This study used wide-mesh pearl nets containing intermediate sized scallops in a fast current area. Future work might examine the effects of fouling in low current areas or with the fine mesh nets used for growing spat. Studies to find out how common fouling assemblages (e.g.

hydroid, tunicate and mussel dominated communities) affect the net environment could help growers to choose cultivation sites, depths or methods of fouling control.

CHAPTER 5 – FOULING AND SCALLOP GROWTH

5.1 Introduction

Immersion in plankton rich water enables scallops in suspended cultivation to grow faster than on the seabed, under natural conditions (MacDonald and Thompson 1985, Wallace and Reinsnes 1985, Hardy 1991). Unfortunately, however, the conditions that promote scallop growth also encourage fouling on cultivation nets and scallop shells (e.g. Arakawa 1990, and references therein, Enright *et al.* 1993, Cigarria *et al.* 1998). This is costly because it increases the weight and drag of cultivation equipment and is difficult to remove (Hardy 1991, Aiken 1993). Fouling can also affect the growth and appearance of scallops.

Fouling of scallop shells and cultivation nets has been shown to reduce the growth of immature scallops (Claereboudt *et al.* 1994a, Lodeiros and Himmelman 1996, Lodeiros and Himmelman 2000). It has been suggested that net fouling organisms decrease scallop growth by competing for food and space, or reducing water flow through nets, and hence the transfer of food, oxygen and waste products (Duggan 1973, Leighton 1979, Huguenin and Huguenin 1982, Côté *et al.* 1993, Enright 1993, Claereboudt *et al.* 1994b, Lodeiros and Himmelman 1996, Lu and Blake 1997). Fouling of scallop shells increases the weight of upper valves and can bind upper and lower valves together. This increases mortality or reduces growth, probably because it inhibits scallop feeding and respiration (Minchin and Duggan 1989, Roman 1991, Paul and Davies 1986, Lu and Blake 1997, Lodeiros and Himmelman 2000). Other potentially negative effects of fouling include irritation of the mantle (Getchell 1991, Mortensen *et al* 2000), predation by foulers such as crabs and starfish (Wilson 1994, O'Connor *et al.* 1998, Freites *et al.* 2000) and parasitism by species including polychaete worms and amphipods (Leibovitz *et al.* 1984, Mortensen *et al.* 2000). However, the influence of fouling varies; some researchers have found or inferred that fouling does not affect bivalve growth (Wallace and Reinsnes 1985, Widman and Rhodes 1991, Lesser *et al.* 1992, Lodeiros *et al.* 1993, Lodeiros *et al.* 1999), while other experiments suggest that fouling might even have beneficial effects. Potentially beneficial effects of fouling include a positive influence on plankton abundance (Chapter 4) and moderation of fast water currents that might otherwise inhibit feeding (Côté *et al.* 1993, Devaraj and Parsons 1997).

The influence of fouling on bivalve growth may differ according to the type and intensity of fouling; this varies both geographically, and over small distances (e.g. Arakawa 1990, Cropp and Hortle 1992; Claereboudt *et al.* 1994, Butler and Connolly 1999). Within locations the intensity of fouling and hence its effect on scallop growth can change with

water depth and season (Leighton 1979, Arakawa 1990, Côté *et al.* 1993, Claereboudt *et al.* 1994a). The species and age of scallops being cultivated might also be important. Lodeiros *et al.* (2000) suggest that the susceptibility of cultivated species to fouling depends on their natural habitat. Species that naturally avoid fouling by recessing below a thin layer of sediment are more vulnerable when exposed than those that live above the sediment. Young scallops with small adductor muscles might also be more susceptible than adults if they lack the strength to break through entangling foulers. In addition, young scallops could struggle most to keep heavily fouled upper valves open for feeding and respiration. General predictions about the effects of fouling on scallop growth may therefore be inaccurate; instead, effects may be specific to cultivation areas and the age and species of scallop under cultivation.

This study aimed to determine how fouling influences the growth of intermediate sized *Pecten maximus* (60-90mm shell length) in wide mesh nets in an exposed area of the Irish Sea. Interactions between depth, season and fouling were also investigated. To do this scallop growth in clean, or minimally fouled nets, was compared with the growth of scallops in nets on which fouling was allowed to develop. The methods were similar to those of Clareboudt *et al.* (1994a), who investigated the effects of fouling on *P. maximus* spat over four months in Canada.

As in previous experiments, (Chapters 3 and 4) scallop nets were equally split between two longline systems (Section 2.1). Nets were also deployed at the same time as those used for fouling community analysis (Chapter 3). The results of this experiment could therefore be interpreted with reference to fouling community composition and the effects of fouling on the net environment (Chapter 4). Scallop growth rates can be depressed by frequent handling (Wildish and Kristmanson 1988, Parsons and Dadswell 1992, McDonough 1998, Laing *et al.* 2001). The influence of repeated handling on the results of this experiment was therefore assessed by comparing the growth of these scallops, which were frequently disturbed, with that of scallops deployed concurrently in undisturbed nets.

5.2 Materials and methods

5.2.1 Scallop collection and pearl net deployment

Juvenile scallops (*Pecten maximus*, shell length 60-90mm) were caught in dredges from two fishing grounds off the Isle of Man in July 1998. Scallops from the different grounds were then mixed and kept in a series of seawater tanks for two months. When natural food levels were low a mixture of fresh algae and algal paste was added to the tanks. Prior to their deployment, scallops were measured and double tagged with flexible plastic Hallprint tags, (described in Section 2.4) so that individual growth rates could be monitored. Ten scallops were then placed in each of 60 wide mesh pearl nets which were suspended in strings of three, approximately 10, 14 and 18m below the surface of the water (C.D), on two longline systems (Figures 2.1 and 2.2). Clean and fouled treatments were arranged randomly along each system.

5.2.2 Fieldwork

I intended to retrieved nets from the two longlines every six weeks, however this was prohibited by bad weather and technical problems, consequently sampling intervals were variable (Table 5.1) and collection from the different longlines was sometimes widely separated (Table 5.1). Nets were retrieved by divers who attached them to air filled lifting bags before slowly bringing them to the surface. Once on the surface, nets were transferred to fish boxes on the boat and kept damp on the short journey to shore. They were then hung in holding ponds or tanks. Scallop shell lengths were measured using a standard board with a sliding gauge and scallops were then replaced in their original fouled nets or new, clean ones. Care was taken to minimise scallop handling and emersion times. Dead scallops were recorded and replaced with healthy ones. Nets were then redeployed by divers, but unfortunately redeployment was often delayed (Table 5.1) and in July nets from the north line were boxed and taken to the boat on two occasions before they were finally redeployed. Fouling communities on nets were necessarily disturbed during collection and redeployment, to minimise impacts nets were treated gently and handled as little as possible. After 13 months all scallops were dissected, enabling the mass of muscle and other tissues to be measured before and after drying at 60°C, to a constant mass (giving wet and dry weights respectively).

Temperature was monitored continually at the three depths using *Stowaway Tidbit* data loggers (Onset computer corporation, 470 MacArthur Blvd., Bourne, MA 02532, USA) attached to nets.

Table 5.1. Sampling times and intervals for the two longline systems. Interval 1 is the time between consecutive retrieval dates and interval 2 is the time between net retrieval and redeployment (when nets were held in tanks).

Action	System	Nets		Interval (days)	
		Retrieved	Redeployed	1	2
0. Nov. '98	North	20.11.98	n.a.	n.a.	n.a.
Deploy nets	South	18.11.98	n.a.	n.a.	n.a.
1. Jan. '99	North	29.1.99	2.2.99	70	4
measure shells	South	29.1.99	1.2.99	72	3
2. March '99	North	31.3.99	19.4.99	61	19
measure shells	South	30.3.99	8.4.99	60	9
3. July '99	North	27.7.99	28.7.99	118	1
measure shells	South	12.7.99	26.7.99	104	14
4. Sept. '99	North	29.9.00	6.10.99	64	7
measure shells	South	29.9.00	6.10.99	79	7
5. Jan. '00	North	19.1.00	n.a.	112	n.a.
measure shells, wet & dry wt.	South	12.1.00	n.a.	105	n.a.

5.2.3 Experimental Design

The growth and mortality of scallops in clean and fouled nets was compared for scallops on two longlines and at three depths (approximately 10, 14 and 18m below the surface of the water, C.D). Five replicate nets represented each depth-longline-fouling combination (Table 5.2) so 60 nets were deployed in total. The growth of scallops in fouled nets was also compared with that in two strings of undisturbed fouled nets.

Table 5.2. Variables investigated during this experiment

Variable	Number of variables
Longline	2 (north and south)
Depth	3 (10, 14 and 18m)
Fouling	2 (clean and fouled)
Disturbance	2 (disturbed and undisturbed)

In addition to these variables, shell growth was compared over the five consecutive time periods (Table 5.1). However, measurements for different periods were treated separately

and qualitatively related to changes in fouling (Chapter 3) and environmental conditions measured here and in chapter 4.

Shell growth and scallop mortality

Shell growth and mortality were analysed separately for each time and for all times pooled. Throughout the experiment, scallops were of a size where shell-growth is independent of shell length or scallop age (Murphy 1986, Allison 1993). Mean rates of shell growth (G) were therefore calculated using the following equation.

$$G = \frac{L_2 - L_1}{t}$$

Where L_1 and L_2 are scallop shell lengths before and after time t respectively. To prevent pseudoreplication (Hurlbert 1984) mean shell-growth rates for each pearl net were calculated and used in subsequent analyses. Between the 20.7.99 and the 29.9.99, the initial, mean, growth rate of scallops added to nets on the north system, to replace dead scallops, differed from the mean growth of original scallops in the same net (paired t-test, df = 16, $t = 4.97$, $P < 0.01$). Initial growth rates of all replaced scallops were therefore excluded from analyses.

The main experiment was a balanced design involving two fixed factors (fouling and depth) and one random factor (location). Growth and mortality rates for each of the four time intervals and mean rates for the year were examined using three-way analysis of variance (ANOVA). Heterogeneity of variance was tested for using Cochran's test (Winer 1971) and data were transformed where appropriate. Shell growth data for the September 1999 – January 2000 period was heterogeneous even after transformation but ANOVA was still applied because with large and balanced designs this technique is robust to departure from homogenous variances (Underwood, 1997). However, such analyses increase the probability of a type I error (Underwood, 1997), and apparently significant results were interpreted with caution. When the ANOVA indicated significant factors or interactions between factors, post-hoc Student-Newman-Keuls (SNK) tests were performed to determine which means differed. All analyses were carried out using GMAV5 (Underwood *et al.*, 1998). Neither clean nor fouled nets were fouled when the nets were first submerged (November 1998 – January 1999). ANOVA were, however, carried out on data for this period to check for differences between the initial growth rates of scallops in clean and fouled nets as this could have influenced subsequent results.

Five nets at 18m were lost during the last sampling period. To maintain the balanced design of the experiment only three, randomly chosen, replicate nets per treatment were considered for this period and for analysis of growth and mortality rates for all times pooled. Hence, ANOVA for these periods had less power to detect treatment effects than analyses of all other time intervals.

Tissue weight

Soft tissue weights were approximately linearly related to shell length for the narrow size range of small scallops used in this experiment. Soft tissue weights were therefore standardised to give the weight per unit shell length. The relationship between tissue weight, location, depth and fouling was then examined using ANOVA and post-hoc SNK tests as described above. Data were average tissue weights (standardised to shell length) per net. For reasons given above, only three nets were considered per treatment and recently replaced scallops were excluded from the analysis.

Disturbance

When the nets analysed in Chapter 2 were collected for fouling community analysis the growth of scallops within was measured. These nets were not examined prior to sampling and therefore scallops inside were not experimentally disturbed. Nets and scallops were the same as those used in this experiment and the two sets of nets were deployed at the same time. The effect of frequent disturbance on scallop growth can therefore be gauged by comparing the growth of scallops in the undisturbed nets of Chapter 2 with those in the fouled nets in this chapter. Undisturbed nets were deployed on the two systems at three depths, in the same way as disturbed ones. However, only two sets of replicate nets were retrieved from each system at any given time. Undisturbed nets were also sampled at a different frequency to disturbed ones prohibiting qualitative comparisons between disturbed and undisturbed treatments.

5.3 Results

5.3.1 Temperature

Changes in water temperature are described in detail in section 3.3.; they followed a typical seasonal pattern ranging from 15°C in August and September to around 7°C degrees in February, March and April (Figure 3.1). Temperatures across the two systems and three depths were similar.

5.3.2 Shell growth

Initially, when clean and fouled nets were alike (because fouled nets had not yet accumulated fouling), growth rates of scallops in all nets were similar. The mean length of scallop shells decreased about 1$\mu m \cdot d^{-1}$ during this winter period (Figure 5.1). Subsequently fouling accumulated and fouled nets were easily distinguished from clean ones. However, pooled results for the year show that fouling did not affect mean scallop growth at any depth or location, and this was generally true for individual times (Table 5.3). Exceptionally, between January 1999 and March 1999 scallop growth tended to be highest in fouled nets for all system-depth combinations (Figure 5.1), though the difference was slight and not significant (Table 5.3). From July 1999 until September 1999 the growth of scallops on the north system was significantly higher in fouled nets than clean ones; on the south system growth was similar in both types of net (Table 5.3). Growth was greatest on the north system from March to July 1999. Differences between systems may have been related to sampling and redeployment dates (and hence holding times), which varied by up to two weeks between systems during both March and July (Table 5.1).

Shell growth from September 1999 to January 2000 was least at 18m (Table 5.3); this was also true for pooled growth results, but only for scallops in nets on the north system. Figure 5.1 indicates that, predictably, scallop shell growth varies over the year, being greatest in the summer months, when it reaches up to 14$\mu m \cdot d^{-1}$, whilst winter growth rates are low, or even negative.

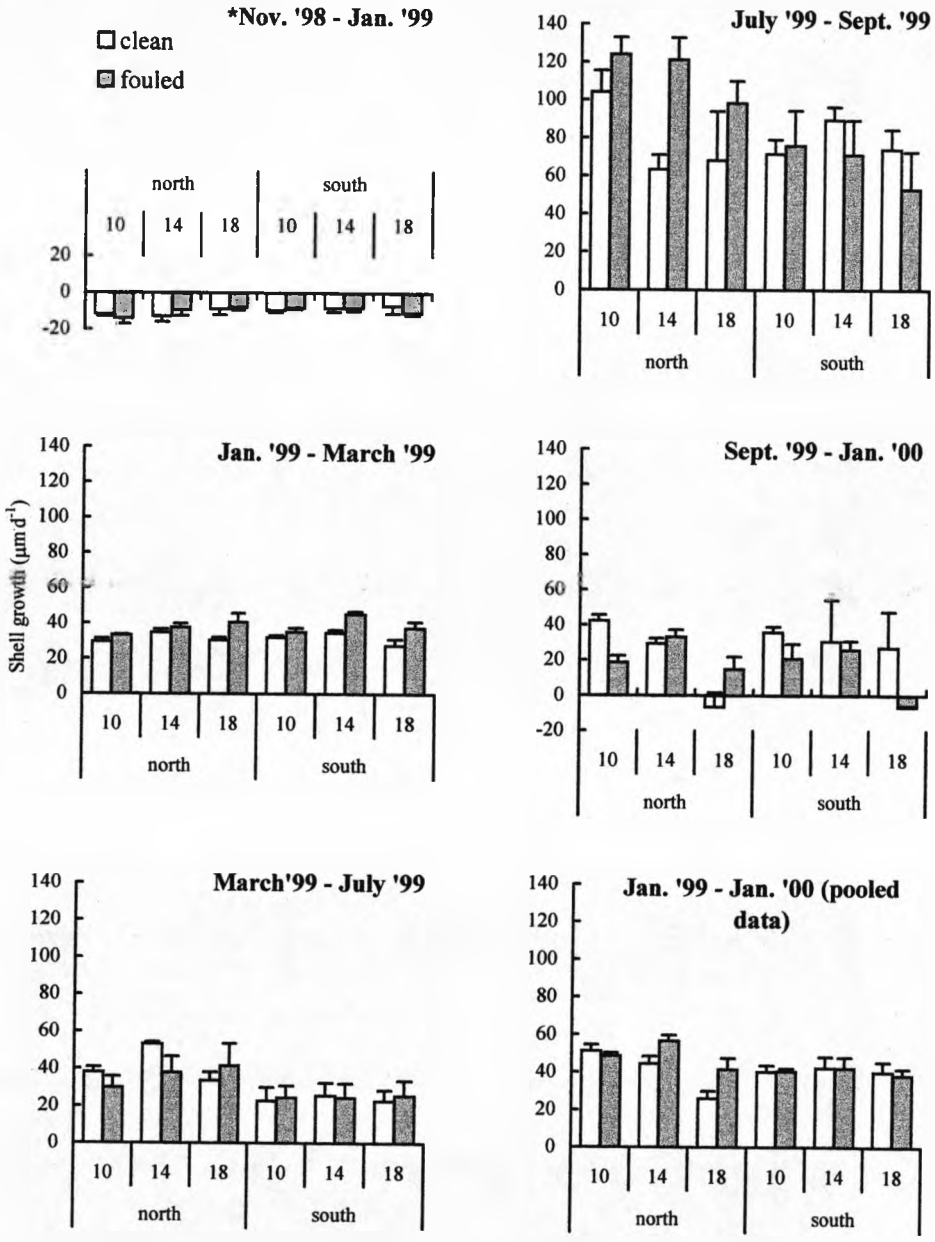


Figure 5.1. Daily growth rates of scallop shells (mean +/- SE) on north and south systems, in clean and fouled nets suspended at 10, 14 and 18m. Data are average results for 5 nets except September 1999 - January 2000, and pooled results, which are for 3 nets only. *Clean and fouled nets were the same during this period

Table 5.3. Three way ANOVA and SNK multiple comparisons of shell growth data testing for the effects of location, depth and fouling on shell growth over five consecutive periods and over the four final times pooled. Cochran's test results are given and data are not transformed unless otherwise indicated. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Nov. '98 - Jan. '99					
$C = 0.2195$, $P>0.05$					
System	1	0.6	2.3	0.14	Residual
Depth	2	0.2	0.8	0.55	System X Depth
Fouling	1	0.0	0.0	0.97	System X Fouling
System X Depth	2	0.3	1.0	0.38	Residual
System X Fouling	1	0.1	0.3	0.58	Residual
Depth X Fouling	2	0.1	0.6	0.63	System X Fouling X Depth
System X Fouling X Depth	2	0.2	0.8	0.44	Residual
Residual	48	0.3			
Total	59				
Jan. '99 - March '99					
$C = 0.2195$, $P>0.05$					
System	1	0.6	2.3	0.14	Residual
Depth	2	1.4	2.7	0.27	System X Depth
Fouling	1	4.9	6.8	0.23	System X Fouling
System X Depth	2	0.5	2.0	0.15	Residual
System X Fouling	1	0.7	2.8	0.10	Residual
Depth X Fouling	2	0.3	0.8	0.56	System X Fouling X Depth
System X Fouling X Depth	2	0.4	1.6	0.22	Residual
Residual	48				
Total	59				
March '99 - July '99					
$C = 0.2808$, $P>0.05$					
System	1	23.3	9.8	**< 0.01**	Residual
Depth	2	1.8	1.6	0.39	System X Depth
Fouling	1	2.9	0.6	0.57	System X Fouling
System X Depth	2	1.2	0.5	0.62	Residual
System X Fouling	1	4.5	1.9	0.18	Residual
Depth X Fouling	2	1.8	2.3	0.30	System X Fouling X Depth
System X Fouling X Depth	2	0.8	0.3	0.33	Residual
Residual	48	2.4			
Total	59				

Table 5.3 (cont.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
July '99 - Sept. '99					
$C = 0.2602$, $P > 0.05$					
System	1	64.7	6.1	**0.02**	Residual
Depth	2	21.8	1.4	0.41	System X Depth
Fouling	1	12.0	0.2	0.74	System X Fouling
System X Depth	2	15.4	1.5	0.24	Residual
System X Fouling	1	64.1	6.1	**0.02**	Residual
Depth X Fouling	2	1.3	0.2	0.86	System X Fouling X Depth
System X Fouling X Depth	2	7.6	0.7	0.49	Residual
Residual	48	10.6			
Total	59				
SNK multiple comparison of interaction:					
North: clean < fouled		Clean: north = south			
South: clean = fouled		**Fouled: north > south**			
Sept. '99 - Jan. '00					
$C = 0.4499$, $P < 0.05$					
System	1	0.0	0.0	0.95	Residual
Depth	2	20.2	27.2	**0.04**	System X Depth
Fouling	1	6.7	0.9	0.52	System X Fouling
System X Depth	2	0.7	0.2	0.79	Residual
System X Fouling	1	7.6	2.5	0.13	Residual
Depth X Fouling	2	2.8	0.3	0.75	System X Fouling X Depth
System X Fouling X Depth	2	8.2	8.2	0.09	Residual
Residual	24	2.1			
Total	35				
SNK multiple comparison of depths:					
10m = 14m > 18m					
Jan. '99 - Jan. '00 (pooled data)					
$C = 0.1724$, $P > 0.05$					
System	1	1.6	3.1	0.09	Residual
Depth	2	3.5	1.7	0.37	System X Depth
Fouling	1	1.4	0.8	0.54	System X Fouling
System X Depth	2	2.1	4.0	**0.03**	Residual
System X Fouling	1	1.8	3.5	0.07	Residual
Depth X Fouling	2	0.6	0.7	0.58	System X Fouling X Depth
System X Fouling X Depth	2	0.8	1.6	0.22	Residual
Residual	24	0.5			
Total	35				
SNK multiple comparison of interaction:					
10m: north > south		**North: 10m = 14m > 18m**			
14m: north = south		South: 10m = 14m = 18m			
18m: north = south					

5.3.3 Mortality

Mortality rates were generally low and not consistently affected by fouling. Exceptionally high mean mortalities at 18m on two sampling dates (Figure 5.2) reflected high mortalities in a single net, combined with above average mortalities in both clean and fouled nets at 18m on the north system (July - September 1999), and on both systems (September - January 2000). High mortalities were not specific to any fouling-system combination. High mortality rates on the south system between July and September 1999 coincide with low growth rates and a long period in holding tanks, as described above. Figure 5.3 also indicates that mortality rates varied over the year, being least from March until July 1999.

5.3.3 Soft tissue weights

Wet and dry weights showed slightly different trends. Dry weights are presented because they are probably most accurate. Wet weights can be roughly calculated according to the following equations:

Muscle wet wt. = 4.7 (+/-0.1) · muscle dry wt.

Other soft tissue wet wt. = 8.6 (+/-0.1) · other soft tissue dry wt.

Standardised muscle weights were significantly greater in clean nets than fouled nets (Table 5.5), although the difference between treatments was small. Other soft tissue was also negatively affected by fouling, but only on the south system. Like shell growth soft tissue weights were significantly greater on the north system (Table 5.5). Weights of soft tissue other than muscle and total soft tissue also decreased significantly at 18m (Figure 5.3, Table 5.5).

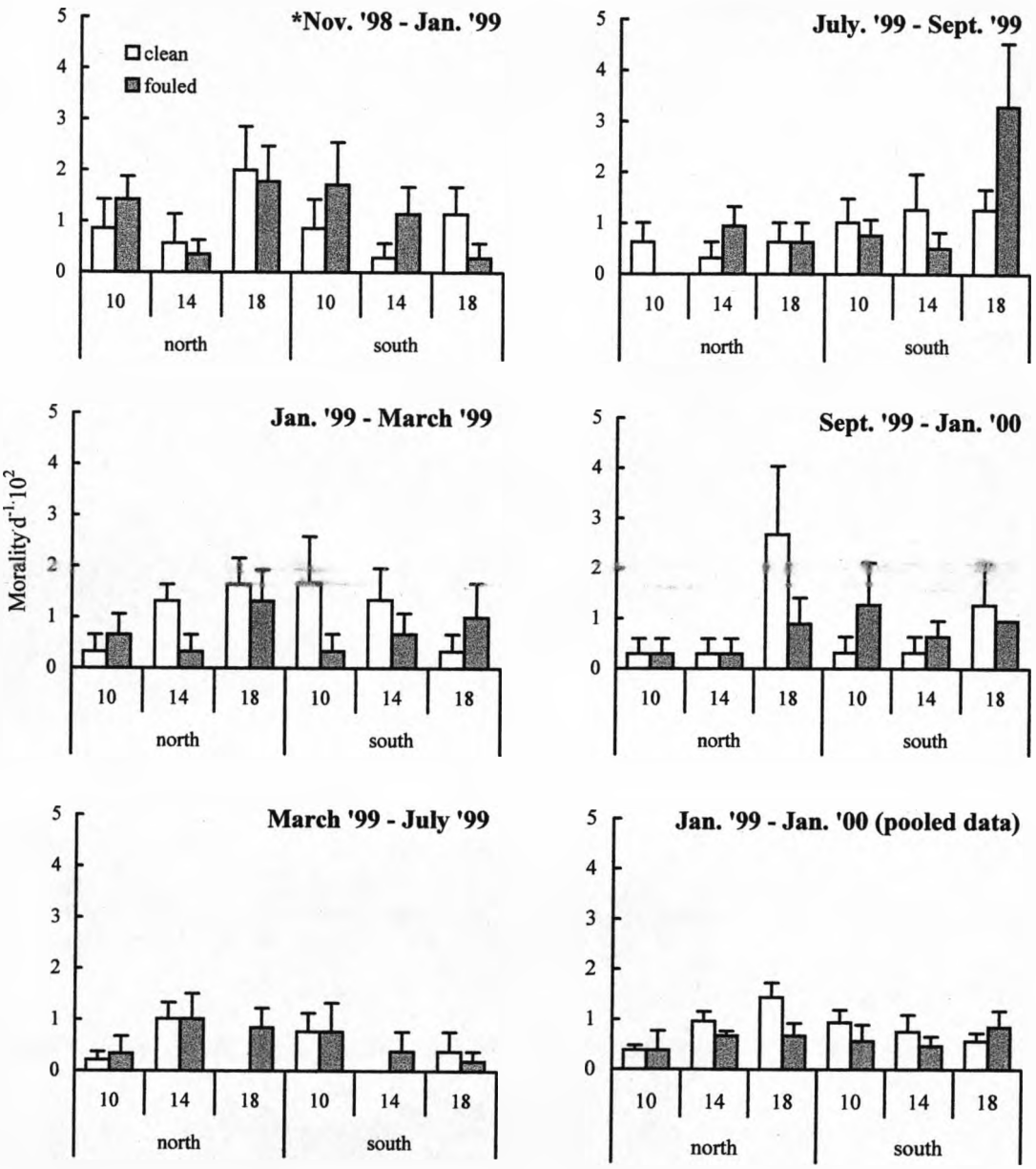


Figure 5.2. Daily mortality rates of scallops (mean +/- SE) on north and south systems, in clean and fouled nets suspended at 10, 14 and 18m. Data are average results for five nets except September 1999 - January 2000, and pooled results, which are for three nets only. *Clean and fouled nets were the same during this period.

Table 5.4. Three way ANOVA and SNK multiple comparisons of mortality data testing for the effect of location (system), depth and fouling on scallop mortality for five consecutive periods and for the four final times pooled. Cochran's test results are given and data are not transformed unless otherwise indicated. Bold type indicates a significant result, $P < 0.05$.

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Nov. '98 - Jan. '99					
$C = 0.2586$, $P > 0.05$					
System	1	0.0	0.0	0.85	Residual
Depth	2	0.4	0.3	0.74	System X Depth
Fouling	1	0.2	1.0	0.50	System X Fouling
System X Depth	2	1.0	2.1	0.13	Residual
System X Fouling	1	0.2	0.3	0.58	Residual
Depth X Fouling	2	0.7	1.0	0.50	System X Depth X Fouling
System X Depth X Fouling	2	0.7	1.3	0.27	Residual
Residual	48	0.5			
Total	59				
Jan. '99 - March '99					
$C = 0.1977$, $P > 0.05$					
System	1	0.8	1.1	0.29	Residual
Depth	2	0.5	0.3	0.80	System X Depth
Fouling	1	0.2	0.1	0.80	System X Fouling
System X Depth	2	1.8	2.5	0.09	Residual
System X Fouling	1	1.4	1.9	0.18	Residual
Depth X Fouling	2	0.5	0.3	0.75	System X Depth X Fouling
System X Depth X Fouling	2	1.4	1.9	0.16	Residual
Residual	48	0.7			
Total	59				
March '99 - July '99					
$C = 0.1977$, $P > 0.05$					
System	1	0.8	1.1	0.29	Residual
Depth	2	0.5	0.3	0.80	System X Depth
Fouling	1	0.2	0.1	0.80	System X Fouling
System X Depth	2	1.8	2.5	0.09	Residual
System X Fouling	1	1.4	1.9	0.18	Residual
Depth X Fouling	2	0.5	0.3	0.75	System X Depth X Fouling
System X Depth X Fouling	2	1.4	1.9	0.16	Residual
Residual	48	0.7			
Total	59				

Table 5.4. (cont.).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
July '99 - Sept. '99					
Transformation: Ln(X + 1) $C = 0.2292$, $P > 0.05$					
System	1	1.84	10.1	**<0.01**	Residual
Depth	2	0.20	32.4	**0.03**	System X Depth
Fouling	1	0.01	0.0	0.94	System X Fouling
System X Depth	2	0.01	0.0	0.97	Residual
System X Fouling	1	0.62	3.4	0.07	Residual
Depth X Fouling	2	0.45	1.5	0.40	System X Depth X Fouling
System X Depth X Fouling	2	0.30	1.7	0.20	Residual
Residual	48	0.18			
Total	59				
SNK multiple comparisons:					
System: north < south					
Depth: 10m = 14m < 18m					
Sept. '99 - Jan. '00					
$C = 0.3706$, $P > 0.05$					
System	1	0.00	0.0	0.92	Residual
Depth	2	0.38	29.0	**0.03**	System X Depth
Fouling	1	0.04	0.3	0.67	System X Fouling
System X Depth	2	0.01	0.1	0.91	Residual
System X Fouling	1	0.11	0.8	0.39	Residual
Depth X Fouling	2	0.25	1.5	0.40	System X Depth X Fouling
System X Depth X Fouling	2	0.17	1.2	0.32	Residual
Residual	24	0.14			
Total	35				
SNK multiple comparison failed to identify homogeneous groups					
Jan. '99 - Jan. '00 (Pooled data)					
$C = 0.1839$, $P > 0.05$					
System	1	0.00	0.2	0.68	Residual
Depth	2	0.00	0.7	0.60	System X Depth
Fouling	1	0.00	4.4	0.28	System X Fouling
System X Depth	2	0.00	2.2	0.14	Residual
System X Fouling	1	0.00	0.6	0.46	Residual
Depth X Fouling	2	0.00	0.0	0.98	System X Depth X Fouling
System X Depth X Fouling	2	0.00	2.0	0.15	Residual
Residual	24	0.00			
Total	35				

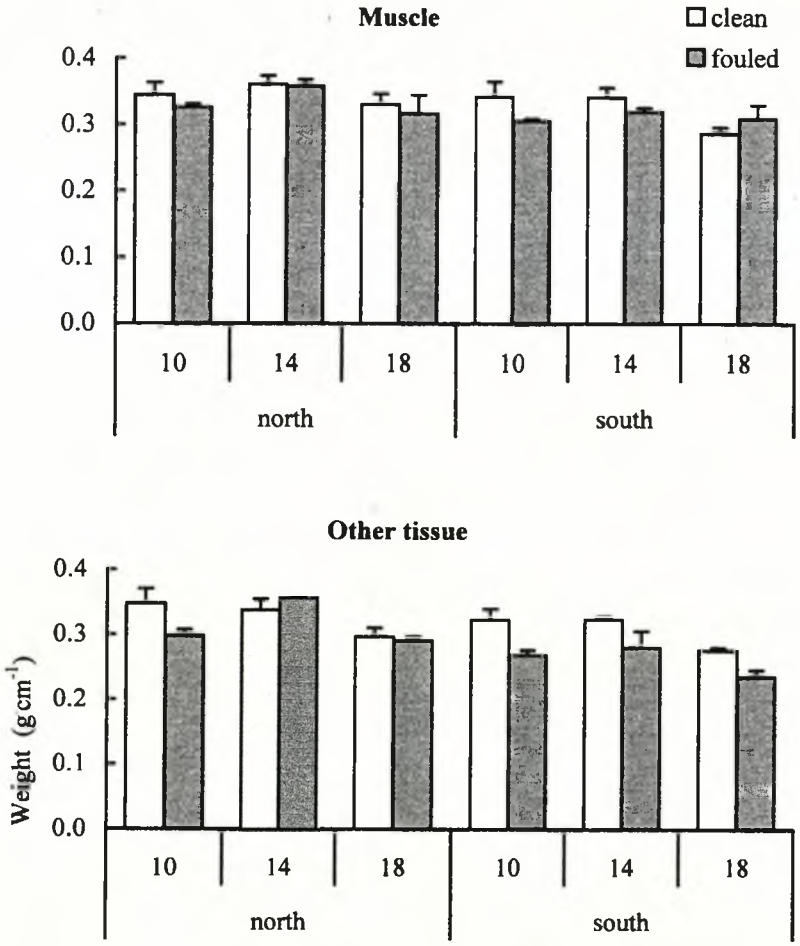


Figure 5.3. Dry weights of scallop tissue (mean +/- SE, standardised according to shell length) on north and south systems, in clean and fouled nets suspended at 10, 14 and 18m.

Table 5.5. Three way ANOVA and SNK multiple comparisons of dry weight data testing for the effects of location, depth and fouling on tissue dry weights. Cochran's test results are given and data are not transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Muscle					
$C = 0.2573$, $P>0.05$					
System	1	0.004	5.6	**0.03***	Residual
Depth	2	0.004	13.2	0.07	System X Depth
Fouling	1	0.001	76082.8	**<0.01****	System X Fouling
System X Depth	2	0.000	0.4	0.71	Residual
System X Fouling	1	0.000	0.0	1.00	Residual
Depth X Fouling	2	0.001	1.0	0.49	System X Depth X Fouling
System X Depth X Fouling	2	0.001	1.0	0.39	Residual
Residual	24	0.001			
Total	35				
*** north > south**		****clean > fouled**			
Other tissue					
$C = 0.2840$, $P>0.05$					
System	1	0.012	20.7	**<0.01**	Residual
Depth	2	0.008	37.0	**0.03**	System X Depth
Fouling	1	0.008	3.1	0.33	System X Fouling
System X Depth	2	0.000	0.4	0.70	Residual
System X Fouling	1	0.003	4.4	**0.05**	Residual
Depth X Fouling	2	0.001	2.1	0.33	System X Depth X Fouling
System X Depth X Fouling	2	0.001	1.1	0.36	Residual
Residual	24	0.001			
Total	35				
SNK multiple comparisons:					
Depth: 10m = 14m > 18m					
System X Fouling	North: clean = fouled				Clean: north = south
	South: clean > fouled				**Fouled: north > south**
Total dry weight					
$C = 0.1645$, $P>0.05$					
System	1	0.030	13.3	**<0.01***	Residual
Depth	2	0.022	19.9	**0.05**	System X Depth
Fouling	1	0.010	4.0	0.29	System X Fouling
System X Depth	2	0.001	0.5	0.62	Residual
System X Fouling	1	0.003	1.1	0.30	Residual
Depth X Fouling	2	0.004	1.6	0.39	System X Depth X Fouling
System X Depth X Fouling	2	0.003	1.2	0.31	Residual
Residual	24	0.002			
Total	35				
*** north > south**					
SNK multiple comparisons of depth effects failed to identify homogeneous groups.					

5.3.4 Disturbance

The mean growth of undisturbed scallops was at times almost three times that of frequently disturbed scallops (Figure 5.4). Differences between the two treatments were apparent between June and October and were reasonably consistent over the three depths. This needs careful interpretation, however, given differences in sampling dates. Total shell growth in undisturbed nets was generally greater on the north system, mirroring differences in the growth of disturbed scallops between the two systems. Mortality rates were similar in disturbed and undisturbed nets (Table 5.6).

Table 5.6. Mortality rates (mean +/- SE) for scallops in disturbed and undisturbed nets, on north and south systems. Data are average results for two nets between November 1998 and October 1999.

System	Depth	Mortality (numbers·d^{-1}·10^2)	
		Disturbed	Undisturbed
North	10m	1.1 (0.8)	1.6 (1.0)
	14m	0.9 (0.3)	1.0 (0.1)
	18m	1.4 (0.8)	1.6 (0.4)
South	10m	0.8 (0.8)	0.8 (0.5)
	14m	0.6 (0.0)	0.5 (0.5)
	18m	0.8 (0.5)	0.5 (0.2)

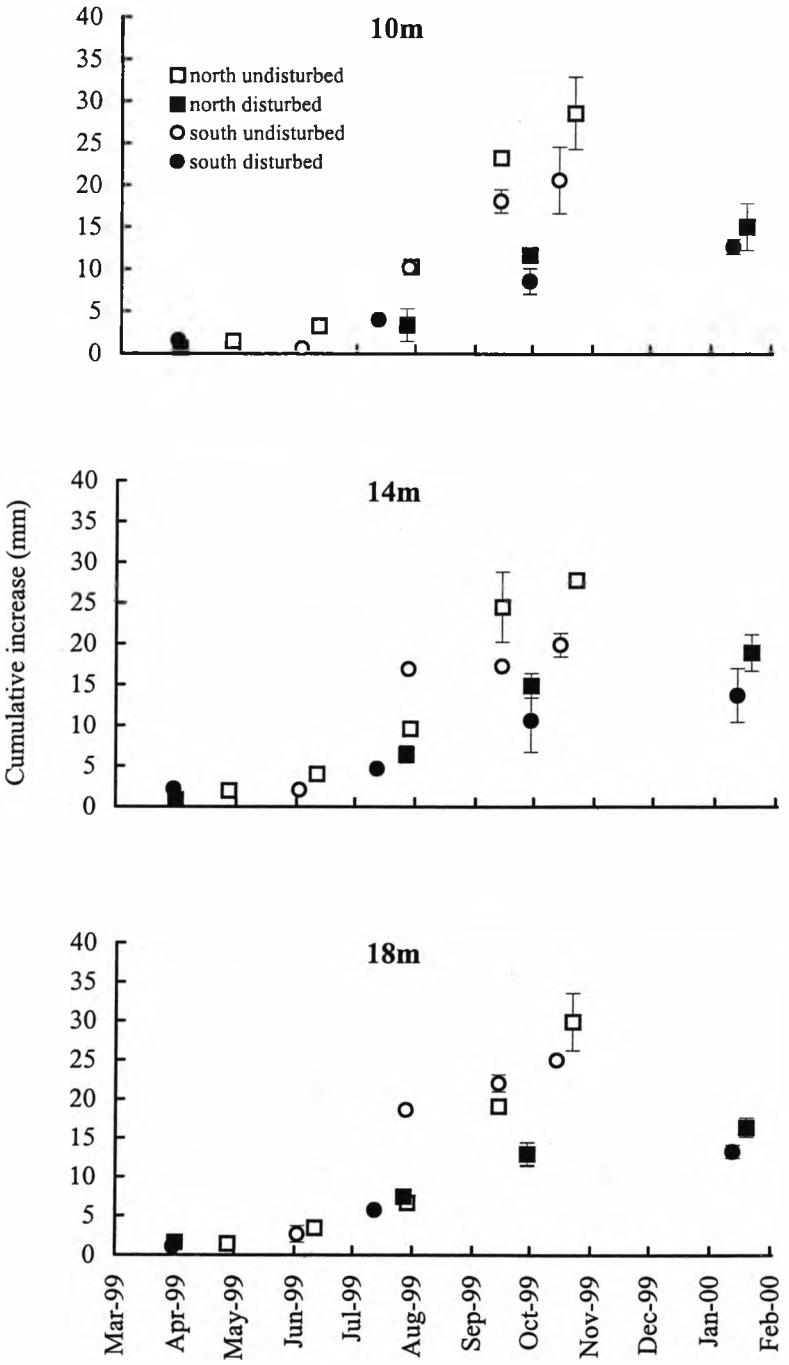


Figure 5.4. Cumulative increase in scallop shell length (+/- mean SE) for scallops in disturbed and undisturbed nets on north and south systems at 10, 14 and 18m. Data are average results for two nets except July data for undisturbed nets when only one net was sampled for all depths on the south system and 14m on the north system.

5.4. Discussion

The influence of fouling on scallop growth and mortality

Off Port Erin, the effects of fouling on scallop shell growth varied with time of year (or immersion period). Surprisingly, fouling enhanced shell growth rates, but only during summer months. Similarly, Lodeiros *et al.* (1996) and McDonough (1998) found differences in the effects of fouling over time. Negative effects seemed to diminish towards the end of both studies, though fouling had probably accumulated. In my experiment the effects of fouling could have been moderated by repeated handling and seasonal changes in the water column or fouling community. It should also be considered that sometimes "clean" nets bore a degree of fouling, particularly when measuring intervals were extended. This may have modified the apparent effects of fouling.

Geographical influences on the effects of fouling do not seem to have been investigated before, though the intensity of fouling is known to vary over small horizontal distances (e.g. Arakawa 1990, Cropp and Hortle 1992; Claereboudt *et al.* 1994, Butler and Connolly 1999). Off Port Erin, the effects of fouling on scallop shell growth varied between two nearby longline systems. In the summer, fouling enhanced shell growth on the north system but not the south one. Differences between systems were also reflected by the relatively high dry weight of soft tissue (other than muscle) in fouled nets on the north system. At this time, the nets were heavily colonised by hydroids, tunicates and bivalves. In June 2000, (a year after these experiments) physiochemical and food conditions inside fouled and clean pearl nets were compared (Chapter 4). Fouling reduced water flow and increased the abundance of plankton and detritus on both systems. However, plankton concentrations in fouled nets on the north system were more than twice those on the south system.

Ambient food levels probably limited scallop growth during this experiment (see Section 4.4). Thus, increased food coupled with high water temperatures appears to have promoted summer shell growth in fouled nets on the north system. This suggestion, however, hinges on a persistent, regular difference in summer plankton numbers between fouled nets on the two systems. Plankton levels were measured over 2 days and hence differences may have been transient. Long-lived, regular differences are hard to explain given the systems proximity and similar physiochemical conditions (temperature, depth of water, amount of water movement) and fouling communities. The direction of water movement was generally north to south across both systems, but east- west currents also crossed the south system as water swirled inside a headland (Figure 2.2). The north system was also exposed

to sunlight for slightly longer than the south system because it was further west of the steep coastline. Perhaps these differences in light and water currents affected plankton abundances and thus scallop growth in fouled nets. Net environments were also examined in November when space had opened up in the fouling community as annual species began to die back (Chapter 2). Again, plankton was most abundant in fouled nets. However, differences were an order of magnitude less than in June, and did not vary consistently between systems. This could explain why fouling only affected shell growth in the summer.

Previous work indicates that shell growth can be reduced by net fouling (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, McDonough 1998, Lodeiros and Himmelman 2000). It has also been inferred from other studies that in some areas fouling does not influence shell growth (Wallace and Reinsnes 1985, Widman and Rhodes 1991). Positive results have not previously been reported. When the environment inside nets was examined (Chapter 4), fouling did not seem to alter chemical, physical or food conditions in ways that could depress scallop growth. It is therefore suggested that when negative effects occur they are caused by direct interference between scallops and foulers. Disparities between the results of this study and those mentioned above may thus be related to the susceptibility of scallops to interference or variation in the intensity of direct interactions.

Previous studies used smaller scallops (< 70mm height, < 1.5yrs) than those used here (> 60mm, 2-3 yrs). Paul and Davies (1986) found that the shell growth of juvenile *Pecten maximus* (<60mm height) increased when pearl nets were treated with copper oxide based antifouling paint whereas larger scallops (> 70mm height) grew at the same rate in treated and untreated lantern nets. Differences are confounded by the different types of net used for large and small scallops and the possibility that the effects of copper (Davies and Paul 1986) differ with scallop size. However, they suggest that the effects of fouling may be greatest for small scallops. Perhaps the growth of small scallops was more sensitive to tissue cropping, interference by mobile foulers or binding by sessile species. For example, Kruczynsk (1972, cited in Getchell, 1991) showed that the growth of small scallops is reduced by pea crab infection (crabs live within the mantle cavity and are associated with soft tissue damage) whereas infection has no effect on the growth of adult scallops. Similarly, Wilson (1994) reports that around the Isle of Man the growth and survival of *P. maximus* spat is reduced by entangling foulers but that larger scallops (> 60mm height) were not affected by net fouling.

Alternatively, discrepancies between studies may be caused by differences in external conditions or equipment (earlier studies used pearl nets with 6-9mm mesh cf. 17mm in my

experiments). In previous studies (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, McDonough 1998, Lodeiros and Himmelman 2000), unlike this one, fouling might have created unfavourable physiochemical conditions. Experiments by Claereboudt *et al.* (1994b) indicate that the presence of pearl net mesh increases scallop growth in high current areas and reduces it in those with low flow. The effects of net fouling might be similarly influenced by water speed in different areas. Fine mesh reduces water flow more than wide mesh (Cole *et al.* 1996), which could encourage a build up of waste products, particularly if studies were carried out in low-current areas.

The mortality of intermediate sized scallops in this experiment was low and similar in clean and fouled nets. Occasional, high mortalities were probably caused by scallops falling together in unbalanced pearl nets. McDonough (1998), and Lodeiros and Himmelman (1996) also reported that net fouling did not influence scallop survival. Large scallops are probably less vulnerable to smothering than spat, and though scallops in this experiment sometimes became fixed to nets by hydroids, tunicates and the byssal threads of mussels, their valves were never bound together. Scallops had to be freed from entangling organisms for measuring and this may have moderated the effects of fouling over the year. However, scallops would naturally have been freed at intervals because the organisms that trapped them generally persisted for only limited periods (Chapter 3).

Tissue weights were reduced by net fouling. Unlike soft tissue growth shell deposition is largely irreversible (but see below) and growth of the two components is often weakly coupled (e.g. MacDonald and Thompson 1985, Côté *et al.* 1993). Low soft tissue weights may have been caused by negative effects of fouling in the winter when low food and water temperatures make scallops vulnerable to stress (McDonough 1998, Laing *et al.* 2001). Muscle tissue acts as an energy reserve, being utilised before other tissues when food is limited (Le Pennec *et al.* 1991, Thompson and MacDonald 1991). This could explain why the ratio of muscle tissue to shell length was reduced in fouled nets on the south system whilst other soft tissues were unaffected. Muscle weights are most important commercially. Although they were influenced by fouling, differences between fouled and clean nets were small. These differences could have been counteracted by allowing fouled scallops to grow for roughly one extra week in the spring or summer (giving them ca. 0.2mm extra shell length). Increased shell growth in the summer might also counteract this small reduction in the ratio of muscle to shell length. If scallop cultivation were to take place off Port Erin it seems unlikely that the costs of net cleaning would be outweighed by increased scallop growth.

Previous researchers have attributed the negative influence of net fouling to decreased food and oxygen, and the accumulation of waste products (e.g. Duggan 1973, Leighton 1979, Huguenin and Huguenin 1982, Burnell and Slater 1989, Cropp and Hortle 1992, Enright 1993, Côté *et al.* 1993, Claereboudt *et al.* 1994a, Lodeiros and Himmelman 1996, Lu and Blake 1997, O'Connor *et al.* 1999), although none of these factors were measured. Off Port Erin, fouling did not reduce food or oxygen, increase levels of waste products, or dilute organic food particles with inorganic matter (Chapter 4). Negative effects may thus be caused by net foulers interfering directly with scallops.

Dissection of scallops often revealed mobile foulers, especially amphipods (*Jassa falcata*) and nereid worms, inside the mantle cavity. This could have been a sampling artefact, but both species are omnivorous and may consequently have entered scallops in search of food. Irritation of the scallop mantle has been shown to reduce scallop growth rates, probably because it stimulates valve closure, inhibiting feeding (Irlandi and Mehlich 1996). Mobile foulers might also have attacked scallop tissue, reducing the energy available for new growth. In addition, the stinging nematocysts of the hydroid *Tubularia* could have irritated scallops if they made contact with delicate mantle tissue (Getchell 1991). Scallops sometimes had dark blisters on the inside of their shells and another possibility is that net fouling harboured scallop parasites such as the polychaete *Polydora* (Mortensen *et al.* 2000). Finally macroalgae, zoo- and phytoplankton and sessile invertebrates can produce allelopathic chemicals which inhibit the settlement and, or, growth of other invertebrates and algae (e.g. Davies *et al.* 1991, Friedlander *et al.* 1996, Arzul *et al.* 1999, Engel and Pawlik 2000). Scallop growth might therefore have been reduced by chemical interactions with foulers.

General patterns in scallop growth and mortality

Scallop tissue weights were highest on the north system and this difference was sometimes reflected in shell growth and mortality rates. It was also evident in shell growth rates for undisturbed scallops. Thus, the cause was probably variation in environmental conditions when scallops were deployed at sea and not differences between measuring intervals for the two systems. As discussed above, the direction of water movement, and perhaps sunshine hours, vary between the two systems and this might result in different food availability at the two sites. Scallops also orientate themselves and adjust their valve opening to maximise feeding efficiency (e.g. Hartnoll 1967, Eckman *et al.* 1989, Stokesbury and Himmelman 1995). Fluctuations in the direction of water movement on the south system might therefore have hindered feeding.

Scallop growth was often reduced at 18m, as was the abundance of fouling organisms (Chapter 3). Chlorophyll *a* measurements taken opportunistically, twice during the study, indicate that plankton abundance was less at 18m than at 10m and 14m (Appendix 6). Low food concentrations may therefore have limited scallop growth and survival at this depth. Similar reductions in scallop growth have also been attributed to food availability when, as shown for this area, vertical temperature gradients are negligible (Page and Hubbard 1987, Lodeiros *et al.* 1998).

Negative shell growth rates and the effect of handling

Seasonal shell growth patterns are consistent with other studies and probably reflect water temperatures, food availability, and the scallops reproductive cycle (Broom and Mason 1978, Wilson 1987, Allison 1994). However, consistently negative growth rates at the start of experiment were unexpected. Negative shell growth was also recorded for some treatments at 18m in January 2000. Scallop shell growth ceases in winter months due to low food ration and temperatures (Mason 1957, Broom and Mason 1978). In my experiment, scallops had been exposed to air and physical disturbance during collection, labelling and deployment, which can also interrupt shell growth (Parsons and Dadswell 1992, McDonough 1998, Laing *et al.* 2001). Examination of the aluminium plated measuring board used for these experiments confirmed that it was solid and had no surface imperfections. Trials also ruled out the possibility that shrinkage occurred due to the contraction of shell material in cold January water. Breakage during measurement was also eliminated after repeatedly measuring a number of scallops. Shrinkage was therefore a real phenomenon, perhaps caused by erosion or dissolution when shell growth had ceased (Day *et al.* 2000, Harper 2000).

Scallops in tanks and nets were maintained at high densities and their edges may have been scratched by frequent contact. There were, however, no signs of chipping which would likely have accompanied this type of abrasion. Measurement of labelled scallops retained in tanks over the winter period revealed similar reductions in shell length. This suggests that shrinkage was not related to abrasion caused by movement of pearl nets. Shell measurements were made between exhalant and inhalant areas where flow mediated processes of dissolution and erosion could be greatest. It has been shown that shell erosion occurs continually in limpets, probably because of sand scour, wave action, and grazing invertebrates (Day *et al.* 2000). Shell shrinkage, over a similar scale to that reported here, has also been reported for wild freshwater mussels (Downing and Downing 1993) and oysters cultivated subtidally in lantern nets (Wilson 1987), where dissolution might be more

important than erosion. In future studies, scallop biologists, ecologists and paleoecolgists should consider that the shells of living scallops can also shrink as well as grow.

Scallop handling is a necessary part of the net cleaning procedure, though in a commercial setting it would probably be carried out at sea. Whole nets can be retrieved and sprayed with high-pressure water hoses; alternatively, scallops may be transferred to new nets (J. Gallagher, *pers. comm.* 1998, Northwest Shellfish, Ltd., Northern Ireland, Lodeiros and Himmelman 1996). Previous research highlights negative effects of handling on scallop growth and mortality (Parsons and Dadswell 1992, and references therein, McDonough 1998, Laing *et al.* 2001). Off Port Erin, shell growth of scallops in undisturbed nets was in the upper range for wild growth in Manx waters (Mason 1957, Murphy 1986, Allison 1994) and was up to twice that of scallops in frequently disturbed nets. Measuring necessitated long handling times and aerial exposure, so the effects of disturbance may have been exaggerated in these experiments. In a commercial operation, nets left to accumulate fouling would not be handled. Hence, reductions in scallop growth due to fouling would probably be outweighed by the lack of disturbance associated with net cleaning. McDonough (1998) also suggests that the growth of juvenile *P. maximus* can be maximised by cleaning nets infrequently to reduce disturbance.

Future work and implications for fouling management

Net fouling had little effect on the growth or survival of intermediate sized *P. maximus* suspended in wide mesh nets in a high current area off the Isle of Man. In addition, disturbance during net cleaning seemed to reduce growth more than allowing fouling to accumulate. The costly process of net changing could therefore be minimised during the final stages of cultivation. However, other problems associated with fouling, such as the increased weight and drag of cultivation equipment should be considered.

Heavy fouling of scallop shells can reduce the growth and survival of *Pecten fumatus* and *Euvola ziczac* in suspended culture (Cropp and Hortle 1992, Lodeiros and Himmelman 2000). This is probably because the increased weight of the upper shell valve inhibits shell opening for feeding and respiration. Shell fouling was not manipulated during my experiments and might have affected growth in both clean and fouled nets. However, *P. maximus* is a larger, more robust species than either *P. fumatus* or *E. ziczac* and although it did accumulate fouling organisms, their mass was small relative to that of the shell valves (cf. 90% of the upper shell valve weight for *E. ziczac*, Lodeiros and Himmelman, 1996). Future studies might, however, examine the influence of shell fouling on the growth of *P. maximus*, particularly for small scallops and spat. Interestingly, anecdotal evidence suggests

that shell fouling is least when net fouling is greatest (Lodeiros and Himmelman 1996, Manuel 2001), presumably because the settling larvae of foulers do not reach scallops.

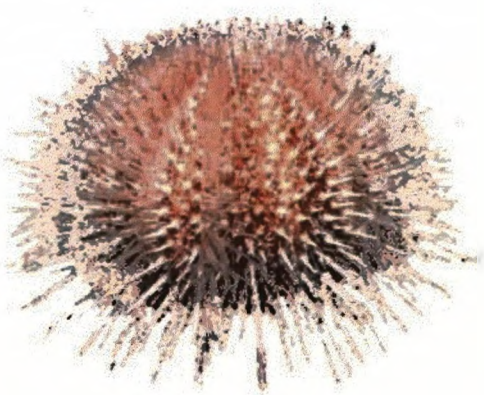
This study had several novel findings and implications that merit further study:
1. That negative fouling effects may be due to direct interactions between scallops and foulers. Studies might determine the affects of common mobile foulers (e.g. nereid worms and *Jassa falcata*) and *Tubularia* on the growth of scallops in tanks. Physical and chemical effects could be separated by enclosing scallops with free foulers or foulers enclosed in cages (i.e. Irlandi and Mehlich 1996).

2. That fouling can have a positive effect on scallop growth. Studies should try to establish which factors determine how fouling affects scallop growth. Factors to be considered include scallop size and species, season, type of fouling, type of net (particularly mesh size) and environmental conditions (e.g. water currents). Tissue weights should be measured where possible because they may differ from shell growth rates.

3. That shell loss can occur in living scallops. Shell loss, other than chipping has not been considered before. The possibility that shells might shrink is interesting for scallop biologists. It may also have important consequences for researchers using shell microchemistry to predict past environmental conditions in palaeoenvironmental studies (e.g. Kronick and Williams 1985, Zamarreno *et al.* 1996, Hickson *et al.* 1999). Studies could separate biological and physiochemical effects by examining shell loss from living and dead shells under a range of environmental conditions.

More generally, future studies should strive to minimise handling because it could mask treatment effects. Most studies have used small scallops, presumably because they are easy to acquire and handle. However, it should not be assumed that larger individuals will have the same response to fouling. Differences in fouling over short horizontal distances highlight the dangers of inadequate replication. Previous studies have examined growth in a single pearl net per treatment (e.g. Wallace and Reinsnes 1985, Claereboudt *et al.* 1994), which could give misleading results. Future studies should therefore try to maximise replication and avoid pseudoreplication.

CHAPTER 6 – BIOLOGICAL CONTROL OF FOULING



6.1 Introduction

Fouling is a ubiquitous problem for scallop growers using suspended cultivation methods (Duggan 1973, Leighton 1979, Heffernan *et al.* 1988, Aiken 1993, Barber and Davis 1997, Lu and Blake 1997). Costs are mainly associated with: increased weight and drag of cultivation equipment (Hardy 1991, Laing and Spencer 1997), reduced growth and survival of scallops (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, Lodeiros and Himmelman 2000) and removing fouling from cultivation nets and scallop shells (Heffernan *et al.* 1988, Aiken 1993, Enright 1993, Minchin 1996). Here, I investigate biological fouling control with the aim of providing an economic and environmentally sound way to reduce fouling.

Fouling is typically tackled by frequent net cleaning with high-pressure water hoses or regular net changes (e.g. Hardy 1991, Laing and Spencer 1997). This is labour intensive, increases equipment requirements, and stresses scallops, probably reducing their growth rates (Wildish and Kristmanson 1988, Parsons and Dadswell 1992, Enright 1993, McDonough 1998, Laing *et al.* 2001). Scallops are relatively stenotypic and cannot close their valves tightly to avoid unfavourable conditions. Control measures, such as saline dips and air-drying, used in oyster and mussel cultivation are therefore unsuitable. Other strategies include treating nets with antifouling chemicals (Huguenin and Huguenin 1982, Paul and Davies 1986, Yunbi *et al.* 1990, summary only), or careful equipment design (MacDonald, 1999). However, neither method is commonly used, presumably because of the potential for bivalves to accumulate or be detrimentally affected by toxic chemicals (e.g. Davies and Paul 1986, Alzieu 1998) and the high cost of new equipment. More recently, attempts have been made to exploit natural antifouling chemicals from marine plants and animals (e.g. Armstrong *et al.* 1999, Harder and Pei-Yuan 2000), or surfaces with low energy or micro-topographies that prevent larval attachment (e.g. Berntsson *et al.* 2000, Smith *et al.* 2000). The high costs of fouling and its removal provides impetus for the development of biological control methods.

Some fish and invertebrates feed on and remove sessile benthos from hard substrata under natural conditions (e.g. Jones and Kain 1967, Sutherland 1972, Hawkins and Hartnoll 1983, VanderVeer *et al* 1998). Biological control exploits these natural grazers or predators by adding them to cultivation nets. This can be a low cost, labour saving technique, which avoids the use of chemicals or new equipment. Ideally, the control organism is also

exploited, so that the method becomes a form of polyculture (e.g. Littlewood 1990, Ahlgren 1998).

Research suggests that biological control could improve the efficiency of bivalve cultivation. Survival of scallop and oyster spat can be increased by adding dog whelks (*Nucella lapillus*) or crabs to cultivation trays. The whelks and crabs prey on mussels that would otherwise smother and kill spat with their byssal threads (Hidu *et al.* 1981, Minchin 1996). Grazing gastropod molluscs target macroalgae, which proliferate on intertidal, or upper water oyster cages (Enright *et al.* 1983, Skjaeggestad 1997, Cigarria *et al.* 1998). Invertebrates, including hydroids and tunicates have also been removed by crabs, top shells (*Calliostoma zizyphinum*), sea urchins (*Psammechinus miliaris*) and fish (*Fundulus heteroclitus*) (Enright *et al.* 1993, Flimlin and Mathis 1993, Skjaeggestad 1997, L. Cook, *pers. comm.* 1999, Scottish Association of Marine Science, Argyll). Despite promising results, biological control is underdeveloped and there is a need for more research, particularly with respect to scallop cultivation (Claereboudt *et al.* 1994, Lodeiros and Himmelman 1996, Minchin 1996).

Previous studies have mainly considered plastic or metal cages, or algae dominated nets. The experiments described in this chapter involved pearl nets used for mid-water scallop cultivation where fouling is dominated by invertebrates. The aim was to identify a suite of possible control organisms and characteristics of their control (e.g. effectiveness with different fouling species). Growers might then choose organisms depending on the type of fouling and the availability of control organisms in their area. Only native organisms were considered because of the problems associated with introducing new species (e.g. Holmes and Minchin 1991, Lafferty and Kuris 1996). A range of control organisms was selected after consultation with researchers mentioned above, or because they might fulfil the following criteria (modified from Minchin, 1996):

1. They should reduce the amount of fouling on nets or scallops.
2. They should be readily available around the British Isles.
3. They should be omnivorous.
4. They should not prey on scallops (some species may not be suitable for use with very small scallops).
5. They should be tenacious enough to feed on moving vertical surfaces.
6. They should be large enough to be retained in cultivation nets.
7. They should survive well within cultivation nets.
8. They should not damage netting material.
9. They should not spread disease between scallops.

Four potential control organisms were identified after a preliminary experiment with seven species including crabs, urchins, gastropods and starfish. The four organisms were deployed in pearl nets for 8 months. Density is important because high densities of control organisms can lead to cannibalism (Flimlin and Mathis 1993) or scallop predation (Minchin and Duggan 1989), while low densities may provide insufficient fouling control. Organisms were thus tested at a range of densities where possible. The success of each organism was measured by its survival, effects on scallop growth, and ability to reduce common fouling species on different net surfaces and scallop shells.

6.2 Materials and methods

6.2.1 Preliminary investigations

Preliminary experiments examined the effects of various invertebrates on the growth of scallops and foulers in pearl nets. Starfish (*Henricia* spp., Gray 1814), sea urchins (*Psammechinus miliaris* Gmelin 1718, and *Echinus esculentus* L. 1785), hermit and swimming crabs (*Pagurus bernhardus* L. 1758, *Liocarcinus holsatus* Fabricius 1798 and *L. pusillus* Leach 1815), dog whelks (*Nucella lapillus* L. 1758) and top shells (*Calliostoma zizyphinum* L. 1758) were deployed in pearl nets with scallops for four months. When crabs were used small individuals were chosen to avoid scallop predation (Hindu *et al.* 1981, Enright *et al.* 1993). Percentage cover of fouling organisms on pearl nets and scallop growth was monitored for all treatments. Both types of urchins and hermit crabs yielded promising results and were therefore used in the more thorough investigations described below. Other organisms had no detectable effect on scallop growth or the amount of fouling on pearl nets or scallop shells. Swimming crabs also suffered heavy mortality. Though *C. zizyphinum* did not perform well in these trials, previous research indicates that it is effective elsewhere in the British Isles (Skjaeggestad 1997). It was therefore included in subsequent experiments.

6.2.2 Biological control organisms

Biological control organisms were collected by divers or obtained from fishermen who caught them unintentionally as by-catch when dredging for scallops (Table 6.1). *Psammechinus miliaris, E. esculentus* (< 5cm) and *Pagurus* sp. (in whelk shells, ca.3-8cm) were included at three densities so that optimal levels could be identified (Table 6.1). *Calliostoma zizyphinum* were difficult to find and were therefore included at a single density, close to the optimum level identified in previous experiments (Skjaeggestad 1997). An additional treatment including both a single *E. esculentus* and a single *Pagurus* sp. was also included in case they worked in synergy, removing different types of fouling or fouling from different surfaces (i.e. flat vs. overhanging). When hermit crabs were used, one or two spare shells were also added to each net (Enright *et al.* 1993). For each treatment, organisms were placed inside five replicate, scallop filled pearl nets on each of two longlines. At the end of the experiment, control organism survival was recorded (treatments were defined by initial densities of control organisms).

Table 6.1. Biological control organisms, source and density (number of individuals) in each treatment.

Organism	Number of treatments	Density	Source
Pagurus sp.	3	1, 2 & 3	By-catch
E. esculentus	3	1, 2 & 3	By-catch & diving
P. miliaris	3	3, 5 & 7	By-catch & diving
Pagurus sp. & *E. esculentus*	1	1 of each	By-catch & diving
C. zizyphinum	1	5	Diving

6.2.3 Scallops and cultivation nets

Juvenile scallops (*Pecten* maximus, shell length 70-95mm) were caught in dredges from fishing grounds off the Isle of Man, in June 2000. Scallops from different grounds were then mixed and kept in a series of seawater tanks. Scallops were tagged with flexible plastic Hallprint tags (section 2.3) so that individual growth rates could be monitored. Prior to deployment seven labelled scallops were measured and placed into each of 120 fine mesh (6mm) pearl nets with or without control organisms. Preliminary experiments showed that urchins could remove tags. Therefore, characteristic marks on scallop shells were recorded for additional identification when scallops were deployed with urchins.

Nets were suspended approximately 10m below the surface of the water (chart datum), on two longline systems (Figures 2.1 and 2.2). Nets were in strings of four, spanning a vertical depth of approximately 1.5m with a small concrete weight at the bottom. Previous work (Chapters 3 and 5) indicates that the growth of scallops and foulers does not vary over this depth range. However, potential bias was minimised by distributing treatments in a randomised block design where the four pearl net levels formed four blocks. A single empty net was also added to the top of each string, in case algae preferentially colonised these relatively well-lit nets.

Nets were suspended for 8 months, from 8/8/00 until 9/1/01 on the north longline system, and from 18/8/00 until 18/1/01 on the south system. Temperature was monitored continually on the two longlines using *Stowaway Tidbit* data loggers (Onset computer corporation, 470 MacArthur Blvd., Bourne, MA 02532, USA) attached to nets. On retrieval nets were maintained in seawater ponds, and within two days, the shell length of four

randomly selected scallops from each net was measured and dead scallops were counted. Dry weights of scallop adductor muscle and other soft tissues were also recorded after the tissues had been dried to a constant mass at 60°C. When control organisms were deployed at more than one density dry weight analysis was carried out on scallops in medium density treatments only.

6.2.4 Assessment of fouling on nets and scallops

Total amounts of fouling were assessed by weight and percentage cover. The weight of fouling is important because it affects equipment buoyancy; it is also an easy way to measure the precise abundance of fouling. Total wet weight of fouling per net was calculated by weighing empty nets before and after deployment (clean nets were immersed and both clean and fouled nets were placed on a rack to drain for 5 minutes before they were weighed).

The area of netting covered by fouling is also significant because it influences water flow through nets and hence the pelagic environment for scallops inside. This was measured by percentage cover. Nets were stretched flat over a board with nails around the edge. A quadrat strung with twine that marked 100 evenly spaced points was fitted on top of the net to measure the percentage cover of fouling. Species often grew over each other forming a multi-layered community so total percentage cover could exceed 100%. Thus, numbers of uncolonised points were also recorded. It was thought that control organisms might remove fouling preferentially from upper or lower net surfaces and hence the two were assessed separately. Organisms might also vary in their ability to inhibit different foulers and thus the percentage cover of common organisms (hydroids, colonial tunicates, solitary tunicates and amphipod tubes) was measured individually.

Control organisms were contained inside nets and were expected to clean inside surfaces better than outside ones. Fouling inside nets was therefore assessed using a semi-quantitative, ordinal scale based on the density of foulers per $100cm^2$.
Light fouling, < 1 organism.
Moderate fouling, 1-5 organisms
Heavy fouling, > 5 organisms
Again fouling was assessed separately for upper and lower surfaces, colonial tunicates were omitted from this analysis.

Shell fouling was measured using a similar scale, but four common groups of organisms were considered separately. Scoring was carried out for saddle oysters, hydroid colonies and solitary tunicates. Sabellid worms, anemones and colonial tunicates were measured together as "soft fouling". Four scallops were assessed from each net according to the following scale:

Rare, < 2 organisms per scallop

Frequent, 2 – 5 organisms per scallop

Abundant, 5+ organisms per scallop.

6.2.5 Experimental design and statistics

Experiments were designed to test whether scallop growth or the abundance of fouling varied between nets with no biological control organisms (control nets) and between treatment nets with one or three densities of biological control organisms (Table 6.1). Each type of biological control organism was assessed separately. Comparisons between biological control organisms were qualitative. Location (north or south system) was also included as a factor where possible, to determine whether treatment effects were consistent across the experimental area.

The experimental unit in these experiments was a pearl net. Hence, when assessing scallop growth and shell fouling mean results for all of the scallops in a net were used, rather than separate results for every scallop. This avoided pseudoreplication (Hurlbert 1984). Throughout the experiment, scallops were of a size where shell-growth is independent of shell length or scallop age (Murphy 1986, Allison 1993). Increases in shell lengths were therefore used in the analyses. Soft tissue weights were approximately linearly related to shell length, probably because the scallops were small and within a narrow size range. Tissue weights were therefore standardised to give the weight per unit shell length. Mean shell-growth rates, tissue ratios, and modal shell fouling abundances, were calculated for each pearl net and used in subsequent analyses.

Parametric analyses

Shell growth rates, tissue ratios, fouling weight and cover were examined by two-way analysis of variance (ANOVA). Location was included as a random factor with two levels and biological control was a fixed factor, with two or four levels (Table 6.1). Percentage cover data were arcsine transformed (Sokal and Rohlf 1995) and heterogeneity of variance was tested for using Cochran's test (Winer 1971). Hydroid percentage cover data for *E. esculentus* was heterogeneous, even after transformation. However, ANOVA was still

applied because with large and balanced designs this technique is robust to departure from homogenous variances (Underwood, 1997). This increases the probability of a type I error (Underwood, 1997), but treatment results were non-significant and thus the results are accurate. When there was no interaction between treatment and location ($P > 0.25$) data were pooled across locations, increasing power to detect treatment effects. Unpooled results are presented unless pooling revealed additional trends. When ANOVA indicated significant factors or interactions between factors, post-hoc Student-Newman-Keuls (SNK) tests were performed to determine which means differed. All analyses were carried out using GMAV5 (Underwood *et al.*, 1998).

Frequency analysis of categorical data

Fouling of scallop shells and inside net surfaces was analysed using Fisher's exact test (Sokal and Rohlf 1995). This type of analysis is sensitive to low frequencies and therefore results for north and south systems were pooled. The design was therefore a 2 x 3 or 4 x 3 Table depending on the number of treatments per control organism (Table 6.1). Analysis was carried out using SAS for Windows (version 8.2).

6.3 Results

6.3.1 Scallop growth

Shell growth was unaffected by biological control organisms except *Psammechinus miliaris* (Figure 6.1, Table 6.2). This urchin significantly increased shell growth rates, but only at a density of five urchins per net. Scallops with this treatment grew an average of 3mm more than those in control nets between September and January. Ratios of muscle and other soft tissue to shell length were not influenced by any control organisms. However, scallops from the north system had higher ratios than those from the south one (Figure 6.2, Tables 6.3 and 6.4). Scallop mortality was negligible (< 5%) for all treatments.

6.3.2 Control organism mortality

Mortalities were generally spread across treatments and not associated with a catastrophic event in any one net. *Calliostoma zizyphinum* suffered highest mortalities (38%). Urchin mortality was low and not influenced by density; *E. esculentus* mortality was slightly lower than *P. miliaris* (mean values were 4% and 13% respectively). Hermit crab survival was strongly influenced by density. All crabs deployed individually survived whereas a third in nets with two or three crabs died by the end of the experiment.

Scallop shell growth

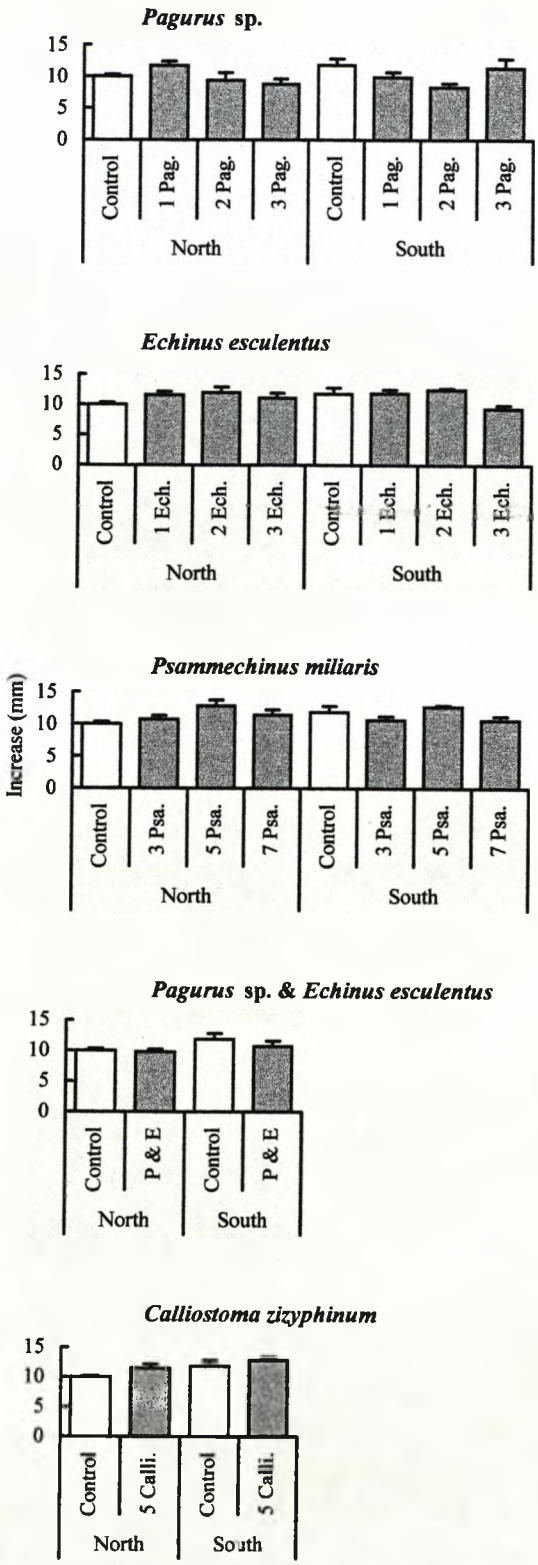


Figure 6.1. Increase in scallop shell lengths (mean +/- SE). Nets were suspended on north and south longline systems and contained scallops with various densities of control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.2. Two way ANOVA and SNK multiple comparisons of shell growth, testing for the effect of location and biological control. When no significant interaction between location and treatment occurred ($P > 0.25$) data for north and south systems have been pooled. Cochran's test results are given and bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3134, *P,* > 0.05					
Location	1	1.4	0.3	0.58	Residual
Treatment	3	9.0	0.8	0.58	Location x treatment
Location x treatment	3	11.6	2.6	0.07	Residual
Residual	32	4.4			
Total	39				
Echinus esculentus					
C = 0.2628, *P,* > 0.05					
Location	1	0.5	0.2	0.66	Residual
Treatment	3	7.9	1.5	0.38	Location x treatment
Location x treatment	3	5.4	2.3	0.09	Residual
Residual	32	2.3			
Total	39				
Psammechinus miliaris					
C = 0.2655, *P* > 0.05					
Location	1	0.3	0.2	0.71	Pooled data
Treatment	3	8.6	3.7	**0.02**	Pooled data
Location x treatment	3	3.2	1.3	0.28	Pooled data
Residual	32	2.3			
Total	39				
SNK multiple comparison of treatment effect:					
Control = 3 Psam. = 7 Psam. < 5 Psam.					
Pagurus sp. & Echinus esculentus					
C = 0.4695, *P* > 0.05					
Location	1	9.3	3.6	0.08	Residual
Treatment	1	2.3	2.3	0.37	Location x treatment
Location x treatment	1	1.0	0.4	0.54	Residual
Residual	16	2.6			
Total	19				
Calliostoma zizyphinum					
C = 0.5392, *P* > 0.05					
Location	1	11.3	4.4	0.05	Residual
Treatment	1	6.1	13.4	0.17	Location x treatment
Location x treatment	1	0.5	0.2	0.68	Residual
Residual	16	2.6			
Total	19				

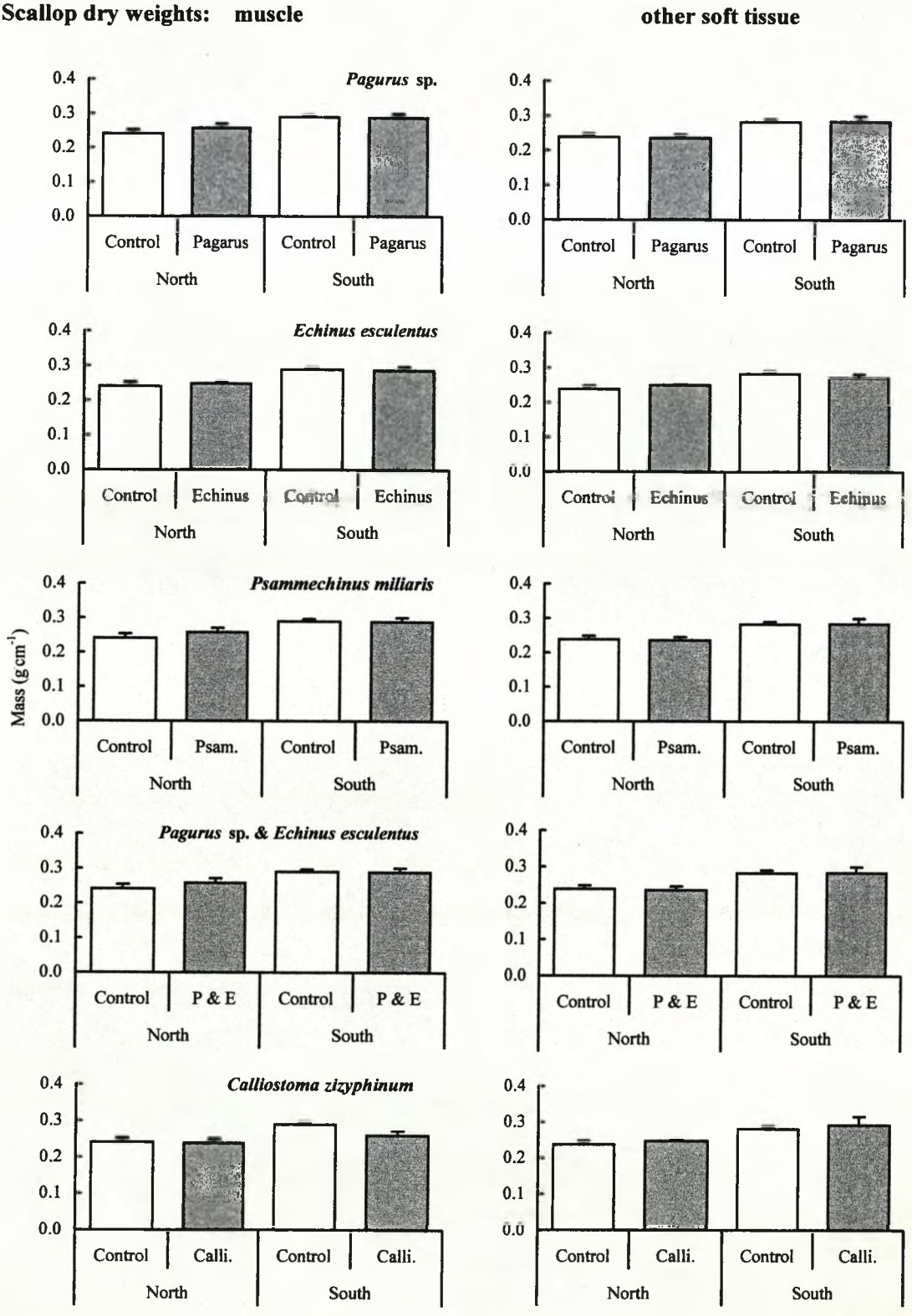


Figure 6.2. Dry weights of scallop muscle and other soft tissue (mean +/- SE, standardised to shell length). Nets were suspended on north and south longline systems and contained scallops with various densities of control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.3. Two way ANOVA and SNK multiple comparisons of muscle tissue dry weight data testing for the effect of location and biological control. Cochran's test results are given and bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Muscle					
Pagurus sp.					
C = 0.3206, *P*, > 0.05					
Location	1	0.0001	13.5	**<0.01**	Residual
Treatment	1	0.0000	1.0	0.50	Location x treatment
Location x treatment	1	0.0000	0.5	0.51	Residual
Residual	16	0.0000			
Total	19				
Echinus esculentus					
C = 0.3991, *P*, > 0.05					
Location	1	0.0001	19.4	**<0.01**	Residual
Treatment	1	0.0000	0.1	0.80	Location x treatment
Location x treatment	1	0.0000	0.3	0.57	Residual
Residual	16	0.0000			
Total	19				
Psammechinus miliaris					
C = 0.3249, *P* > 0.05					
Location	1	0.0001	11.1	**<0.01**	Residual
Treatment	1	0.0000	0.6	0.57	Location x treatment
Location x treatment	1	0.0000	0.6	0.44	Residual
Residual	16	0.0000			
Total	19				
Pagurus sp. & Echinus esculentus					
C = 0.5003, *P* > 0.05					
Location	1	0.0000	6.5	**0.02**	Residual
Treatment	1	0.0000	0.0	0.92	Location x treatment
Location x treatment	1	0.0000	2.1	0.17	Residual
Residual	16	0.0000			
Total	19				
Calliostoma zizyphinum					
C = 0.3117, *P* > 0.05					
Location	1	0.0001	8.9	**0.01**	Residual
Treatment	1	0.0000	0.7	0.55	Location x treatment
Location x treatment	1	0.0000	2.0	0.18	Residual
Residual	16	0.0000			
Total	19				

Table 6.4. Two way ANOVA and SNK multiple comparisons of dry weight data for soft tissue other than muscle, testing for the effect of location and biological control. Cochran's test results are given and bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Other soft tissue					
Pagurus sp.					
C = 0.4065, *P*, > 0.05					
Location	1	0.0001	23.4	**<0.01**	Residual
Treatment	1	0.0000	1.0	0.50	Location x treatment
Location x treatment	1	0.0000	0.3	0.57	Residual
Residual	16	0.0000			
Total	19				
Echinus esculentus					
C = 0.3767, *P*, > 0.05					
Location	1	0.0000	13.2	**<0.01**	Residual
Treatment	1	0.0000	0.0	0.95	Location x treatment
Location x treatment	1	0.0000	2.3	0.15	Residual
Residual	16	0.0000			
Total	19				
Psammechinus miliaris					
C = 0.4606, *P* > 0.05					
Location	1	0.0001	15.9	**<0.01**	Residual
Treatment	1	0.0000	1.0	0.50	Location x treatment
Location x treatment	1	0.0000	0.0	0.93	Residual
Residual	16	0.0000			
Total	19				
Pagurus sp. & Echinus esculentus					
C = 0.4925, *P* > 0.05					
Location	1	0.0001	8.8	**0.01**	Residual
Treatment	1	0.0000	0.1	0.84	Location x treatment
Location x treatment	1	0.0000	0.8	0.38	Residual
Residual	16	0.0000			
Total	19				
Calliostoma zizyphinum					
C = 0.3117, *P* > 0.05					
Location	1	0.0001	8.9	**0.01**	Residual
Treatment	1	0.0000	0.7	0.55	Location x treatment
Location x treatment	1	0.0000	2.0	0.18	Residual
Residual	16	0.0000			
Total	19				

6.3.3 Fouling on nets

General

Water temperatures were the same on both north and south longlines; they declined steadily from 15°C in September to 9°C in January, when the study finished. In nets with no biological control organisms (control nets) fouling organisms occluded around half of the net surface area. Hydroids (mainly *Tubularia* sp. and *Bougainvillia* sp.) were most abundant, with percentage covers of up to 40%. Other common organisms included the amphipod *Jassa falcata* and its silty tube, colonial and solitary tunicates (*Diplosoma listerianum* and *Ascidiella scabra* respectively). Queen scallops (*Aequipecten opercularis*) and erect bryozoans occurred frequently at low abundances. Most species were similarly abundant on both net surfaces, except hydroids, which proliferated on upper surfaces (Figures 6.4 - 6.7). Fouling varied between north and south systems, both total fouling mass and *A. scabra* cover was highest on the south system (Tables 6.5, 6.10 and 6.11). Generally, effects of biological control were independent of control organism density (Tables 6.5 - 6.15). Thus trends described below are for all densities unless otherwise stated.

Fouling mass

Mean fouling weights were least on nets with biological control for all of the organisms tested (Figure 6.3). Control nets had a mean fouling load of around 400g on the north system and 600g on the south system. In contrast nets with *P. miliaris, E. esculentus*, and *Pagurus* sp., supported around 300g of fouling on both systems. Mean weights of fouling on nets containing *C. zizyphinum* were only slightly less than control nets (Figure 6.3). Post hoc comparisons of ANOVA results show that the significant difference in fouling loads between systems was consistently driven by divergence of control nets, the south line supporting most fouling (Table 6.5).

Fouling loads were reduced significantly on the south line by control organisms other than *C. zizyphinum*, and *P. miliaris* (although nets with *P. miliaris* followed a similar trend to those with *E. esculentus* and *Pagurus* sp, Figure 6.3, Table 6.5). Variation between control nets on the north system was high making differences between control and treatment nets indistinct (Figure 6.3). Clearly significant differences were found only between control nets and those containing *Pagurus* sp. with *E. esculentus*. Control net weights were always significantly higher than nets with one or two densities of urchins and crabs but homogenous groups could not be identified (Table 6.5).

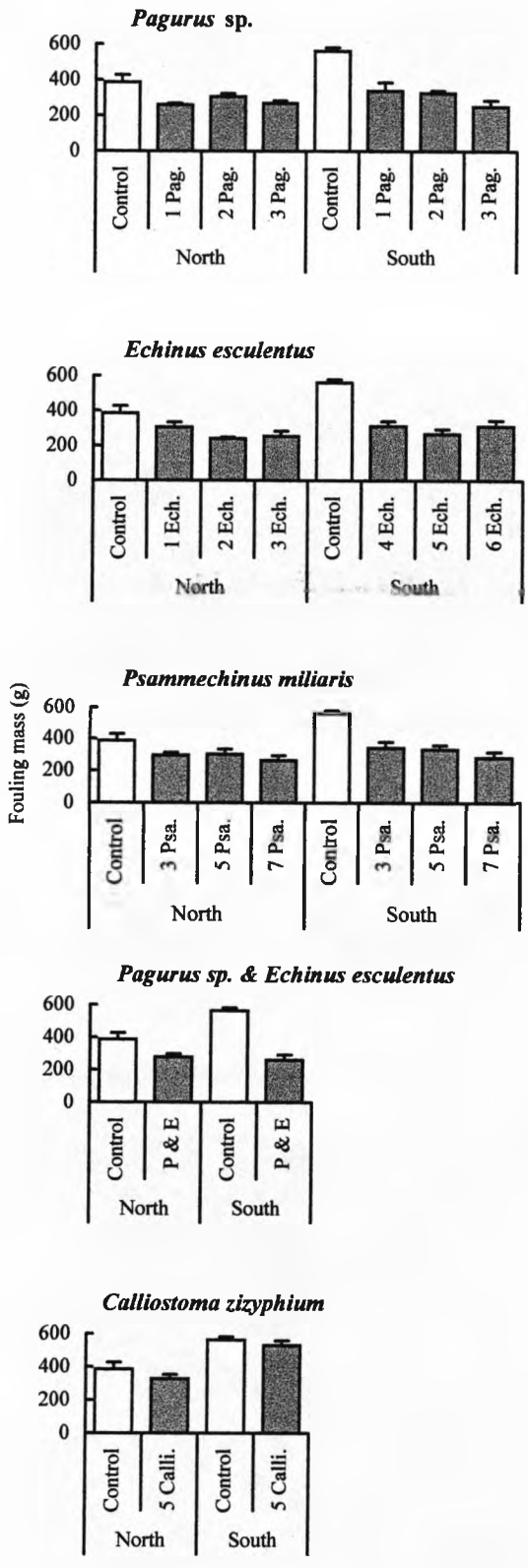


Figure 6.3. Weight of fouling (mean +/- SE) per net. Nets were suspended on north and south longline systems and contained scallops with various densities of control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.5. Two way ANOVA and SNK multiple comparisons of total fouling weights, testing for the effect of location and biological control. Cochran's test results are given and bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3526, *P*, > 0.05					
Location	1	41216	10.2	**<0.01**	Residual
Treatment	3	88632	4.9	0.11	Location x treatment
Location x treatment	3	17937	4.4	**0.01**	Residual
Residual	32	4037			
Total	39				
SNK multiple comparison of interaction:					
North: no homogeneous groups					
South: control > 1 Pag. = 2 Pag. = 3 Pag.					
Control: north < south					
1, 2 and 3 Pagurus: north = south					
Echinus esculentus					
C = 0.2683, *P*, > 0.05					
Location	1	45833	11.4	**<0.01**	Residual
Treatment	3	96813	6.8	0.07	Location x treatment
Location x treatment	3	14166	3.5	**0.03**	Residual
Residual	32	4019			
Total	39				
SNK multiple comparison of interaction:					
North: no homogenous groups					
South: control > 1 Ech. = 2 Ech. = 3 Ech.					
Control: north < south					
1, 2 and 3 Echinus: north = south					
Psammechinus miliaris					
C = 0.2368, *P* > 0.05					
Location	1	46649	10.3	**<0.01**	Residual
Treatment	3	77406	5.8	0.09	Location x treatment
Location x treatment	3	13277	2.9	0.05	Residual
Residual	32	4552			
Total	39				

Table 6.5. (Continued)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp. & Echinus esculentus					
C = 0.4824, *P* > 0.05					
Location	1	31284	7.0	**0.02**	Residual
Treatment	1	210330	4.5	0.28	Location x treatment
Location x treatment	1	47142	10.6	**0.01**	Residual
Residual	16	4470			
Total	19				
SNK multiple comparison of interaction:					
North & south: control > P & E					
Control: north < south					
P & E: north = south					
Calliostoma zizyphinum					
C = 0.4974, *P* > 0.05					
Location	1	178038	41.1	**<0.01**	Residual
Treatment	1	9901	12.7	0.17	Location x treatment
Location x treatment	1	781	0.2	0.68	Residual
Residual	16	4336			
Total	19				

Fouling area

Invertebrates varied in their ability to reduce different types of fouling, but generally trends were similar on both upper and lower outer net surfaces (Figures to 6.4 to 6.8). Again, variation between north and south systems was driven by differences in control nets. Hydroids were most abundant on the north system (Figure 6.4, Tables 6.6 and 6.7), while the tunicate *A. scabra* occurred most frequently on the south system (Figure 6.6, Tables 6.10 and 6.11). *Psammechinus miliaris* alone significantly reduced hydroid cover (Table 6.6 and 6.7). Although trends were similar on upper and lower surfaces, significant differences were only found for upper surfaces of nets on the north line (Table 6.6). Nets with *E. esculentus* and both *E. esculentus* and *Pagurus*, also showed this trend but differences were smaller and not significant. On the north line, nets containing *Pagurus* supported significantly higher hydroid cover than control nets (Figure 6.6, Tables 6.10 and 6.11).

Though tunicate cover was low it was often reduced by biological control (Figures 6.5 and 6.6). In each type of treatment *D. listerianum* cover was significantly reduced on at least one net surface (Tables 6.8 to 6.11). Differences were most distinct in nets with *C. zizyphinum* and *P. miliaris*, which were associated with significantly reduced cover on upper and lower surfaces (*post hoc* tests indicated that control nets were significantly higher than all *P. miliaris* densities but failed to distinguish between the densities). Nets containing *E. esculentus* had significantly less *Diplosoma* on upper but not lower surfaces. *Echinus esculentus* also tackled *A. scabra* efficiently, significantly reducing its cover on upper and lower surfaces (Tables 6.10 and 6.11). Similar trends occurred on nets containing *E. esculentus* with *Pagurus*, *P. miliaris* and *Pagurus*. However, these organisms only significantly reduced *A. scabra* cover on upper surfaces of nets on the north system (where levels were highest initially). No biological control organism reduced the cover of amphipod tubes (Tables 6.12 and 6.13). Instead, high and variable results for treatment nets indicate that occasionally biological control was associated with high tube densities (Figure 6.7).

Echinus esculentus was the only organisms to increase empty space on upper and lower net surfaces (post hoc tests failed to distinguish between treatments on upper surfaces but all were significantly higher than control nets, Tables 6.13 and 6.14). Nets with *P. miliaris* also showed this trend but differences were smaller and not consistent. Similarly, nets with both *Pagurus* sp. and *E. esculentus* significantly reduced the cover of fouling only on lower surfaces. The fouling community was multilayered and therefore the sum of fouling cover for all species would not necessarily reflect the amount of empty space. However, the two

were closely linked, when empty space was increased by 10% total cover was reduced by around 15%.

Control organisms were enclosed by nets and generally influenced fouling of inside surfaces more than those outside (Figure 6.9). Urchins significantly reduced fouling on upper surfaces, generally reducing heavy fouling to moderate levels. Results for *E. esculentus* suggest a degree of density dependence with 3 urchins producing more lightly fouled nets than one or two urchins. Both crabs and urchins significantly reduced fouling of lower surfaces. Levels were regularly reduced from heavy and moderate to moderate and light. *Calliostoma zizyphinum* did not significantly influence degree of fouling inside nets on either upper or lower surfaces.

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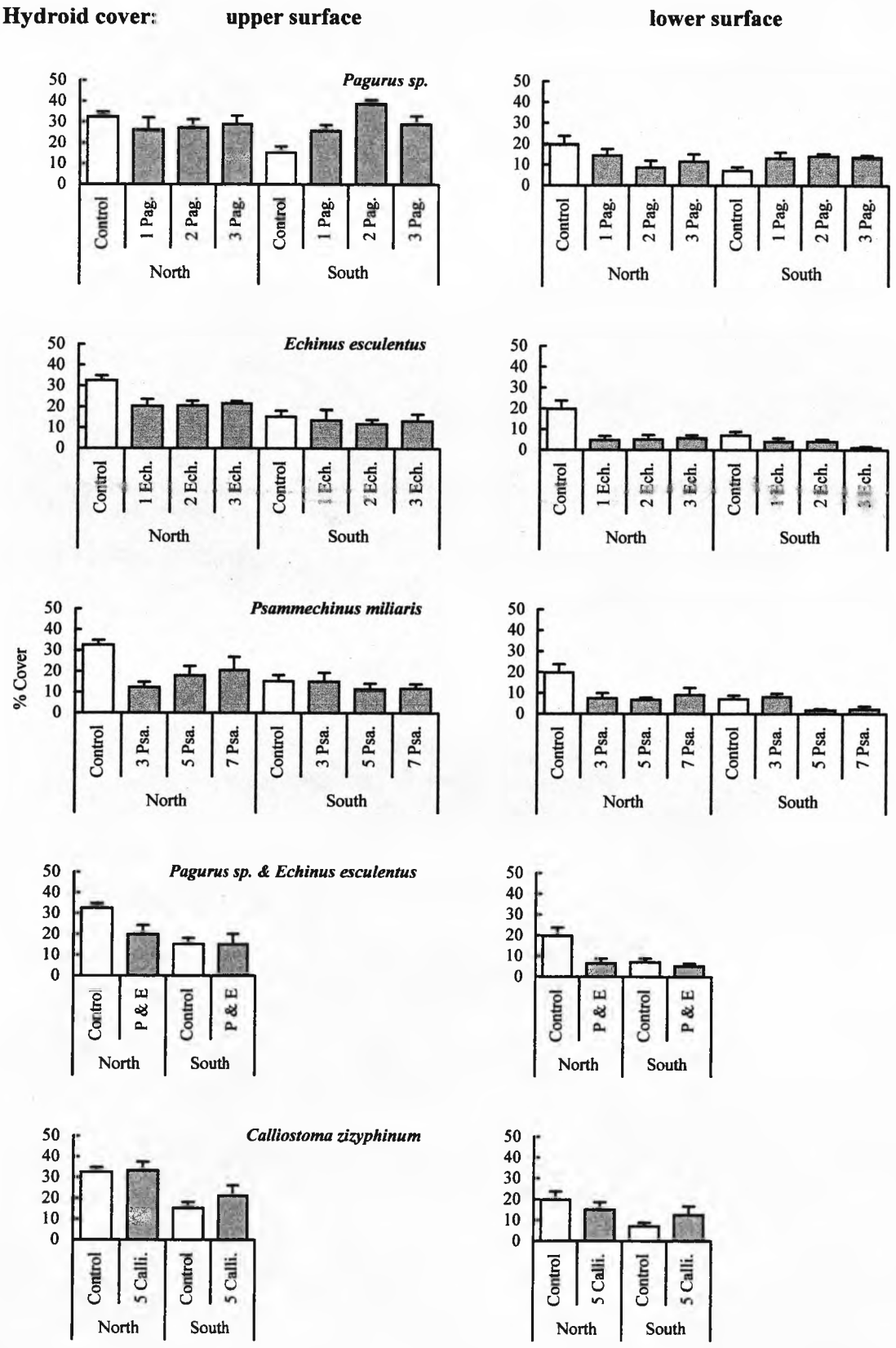

Figure 6.4. Percentage cover of hydroids (mean +/- SE), on outer net surfaces. Nets were suspended on north and south longline systems and contained scallops with various densities of biological control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.6. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of hydroids on upper net surfaces. Cochran's test results are given and data were arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3048, *P*, > 0.05					
Location	1	14	0.47	0.50	Residual
Treatment	3	71	0.44	0.74	Location x treatment
Location x treatment	3	163	5.2	**<0.01**	Residual
Residual	32	31			
Total	39				
SNK multiple comparison of interaction:					
North: Control = 1 Pagurus = 2 Pagurus = 3 Pagurus					
South: Control < 1 Pagurus = 2 Pagurus = 3 Pagurus					
Contol: North > South					
1 Pagurus: North = South					
2 Pagurus: North < South					
3 Pagurus: North = South					
Echinus esculentus					
C = 0.5221, P < 0.01					
Location	1	719	19	**<0.01**	Residual
Treatment	3	75	4.8	0.12	Location x treatment
Location x treatment	3	16	0.40	0.75	Residual
Residual	32	39			
Total	39				
Psammechinus miliaris					
C = 0.2248, *P* > 0.05					
Location	1	234	13	**<0.01**	Residual
Treatment	3	321	4.7	0.12	Location x treatment
Location x treatment	3	69	3.9	**0.02**	Residual
Residual	32	17			
Total	39				
SNK multiple comparison of interaction:					
North: SNK comparisons failed to identify homogeneous groups					
South: Control > 1 Psam. = 2 Psam. = 3 Psam.					
Contol: North > South					
1, 2 & 3 Psammechinus: North = South					

Table 6.6. (cont.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp. & Echinus esculentus					
C = 0.4563, $P > 0.05$					
Location	1	319	6.7	**0.02**	Residual
Treatment	1	129	1.5	0.44	Location x treatment
Location x treatment	1	88	1.8	0.19	Residual
Residual	16	48			
Total	19				
Calliostoma zizyphinum					
C = 0.3441, $P > 0.05$					
Location	1	43	1.0	0.33	Residual
Treatment	1	1575	12	0.18	Location x treatment
Location x treatment	1	135	3.2	0.09	Residual
Residual	16	42			
Total	19				

Table 6.7. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of hydroids on lower net surfaces. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3391, $P > 0.05$					
Location	1	4	0.11	0.74	Residual
Treatment	3	16	0.10	0.96	Location x treatment
Location x treatment	3	165	4.0	**0.02**	Residual
Residual	32	41			
Total	39				
SNK multiple comparison of interaction:					
North: SNK comparisons failed to identify homogeneous groups					
South: Control = 1 Pagurus = 2 Pagurus = 3 Pagurus					
Contol: North > South					
1, 2 & 3 Pagurus: North = South					
Echinus esculentus					
C = 0.2348 $P > 0.05$					
Location	1	351	10.0	**<0.01**	Residual
Treatment	3	269	3.1	0.19	Location x treatment
Location x treatment	3	88	2.5	0.08	Residual
Residual	32	35			
Total	39				
Psammechinus miliaris					
C = 0.2902, $P > 0.05$					
Location	1	442	10	**<0.01**	Residual
Treatment	3	206	2.2	0.26	Location x treatment
Location x treatment	3	92	2.2	0.11	Residual
Residual	32	42			
Total	39				
Pagurus sp. & Echinus esculentus					
C = 0.3373, $P > 0.05$					
Location	1	197	6.0	**0.03**	Residual
Treatment	1	244	1.8	0.41	Location x treatment
Location x treatment	1	139	4.3	0.06	Residual
Residual	16	33			
Total	19				
Calliostoma zizyphinum					
C = 0.5144, $P > 0.05$					
Location	1	76	1.2	0.29	Residual
Treatment	1	0	0.0	1.00	Location x treatment
Location x treatment	1	292	4.7	0.05	Residual
Residual	16	63			
Total	19				

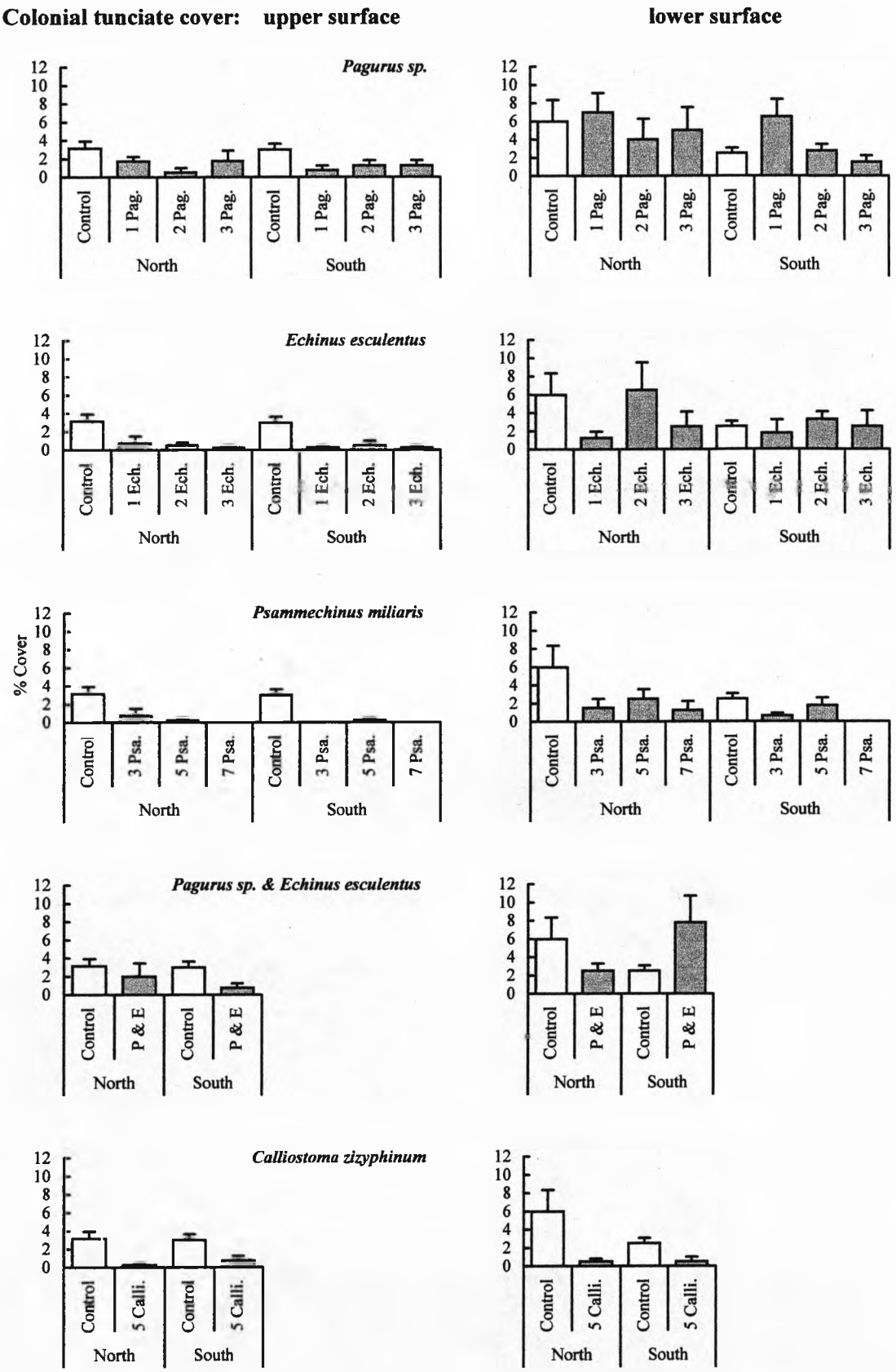

Figure 6.5. Percentage cover of *Diplosoma listeranium* (mean +/- SE), on outer net surfaces. Nets were suspended on north and south longline systems and contained scallops with various densities of biological control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.8. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of *Diplosoma listeranium* on upper net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.2266, $P > 0.05$					
Location	1	0.1	0.00	0.95	Pooled data
Treatment	3	69	3.7	**0.02**	Pooled data
Location x treatment	3	20	1.1	0.38	Pooled data
Residual	32	19			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogenous groups					
Echinus esculentus					
C = 0.2826, P > 0.05					
Location	1	0.8	0.070	0.80	Residual
Treatment	3	158	183	**<0.01**	Location x treatment
Location x treatment	3	0.9	0.070	0.97	Residual
Residual	32	12			
Total	39				
SNK multiple comparison of treatment effects:					
Control > 1 Echinus = 2 Echinus = 3 Echinus					
Psammechinus miliaris					
C = 0.4191, $P < 0.05$					
Location	1	2.5	0.33	0.57	Residual
Treatment	3	198	58	**<0.01**	Location x treatment
Location x treatment	3	3.4	0.45	0.72	Residual
Residual	32	7.4			
Total	39				
SNK multiple comparison of treatment effects:					
Control > 1 Psam. > 2 Psam. > 3 Psam.					
Pagurus sp. & Echinus esculentus					
C = 0.5969, $P > 0.05$					
Location	1	4.48	0.19	0.67	Pooled data
Treatment	1	146.11	6.33	**0.02**	Pooled data
Location x treatment	1	7.10	0.31	0.59	Pooled data
Residual	16	24.08			
Total	19				
Calliostoma zizyphinum					
C = 0.7532, $P < 0.01$					
Location	1	16.69	0.36	0.56	Residual
Treatment	1	397.26	1503204	**<0.01**	Location x treatment
Location x treatment	1	0.00	0.00	1.00	Residual
Residual	16	46.20			
Total	19				

Table 6.9. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of *Diplosoma listeranium* on lower net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagarus sp.					
C = 0.2306, $P > 0.05$					
Location	1	42	0.97	0.33	Residual
Treatment	3	72	4.3	0.13	Location x treatment
Location x treatment	3	17	0.38	0.76	Residual
Residual	32	44			
Total	39				
Echinus esculentus					
C = 0.2231, $P > 0.05$					
Location	1	30	0.64	0.43	Residual
Treatment	3	106	20	**0.02**	Location x treatment
Location x treatment	3	5.3	0.11	0.95	Residual
Residual	32	47			
Total	39				
SNK multiple comparison of treatment effects:					
Control = 2 Echinus > 1 Echinus = 3 Echinus					
Psammechinus miliaris					
C = 0.3108, $P > 0.05$					
Location	1	50	1.7	0.21	Residual
Treatment	3	130	28	**0.01**	Location x treatment
Location x treatment	3	4.7	0.16	0.92	Residual
Residual	32	30			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogenous groups					
Pagarus sp. & Echinus esculentus					
C = 0.4405, $P > 0.05$					
Location	1	13	0.26	0.62	Residual
Treatment	1	2.8	0.03	0.89	Location x treatment
Location x treatment	1	98	2.0	0.18	Residual
Residual	16	49			
Total	19				
Calliostoma zizyphinum					
C = 0.6577, $P > 0.05$					
Location	1	8.0	0.29	0.60	Pooled data
Treatment	1	334	12	**<0.01**	Pooled data
Location x treatment	1	12	0.45	0.51	Pooled data
Residual	16	28			
Total	19				

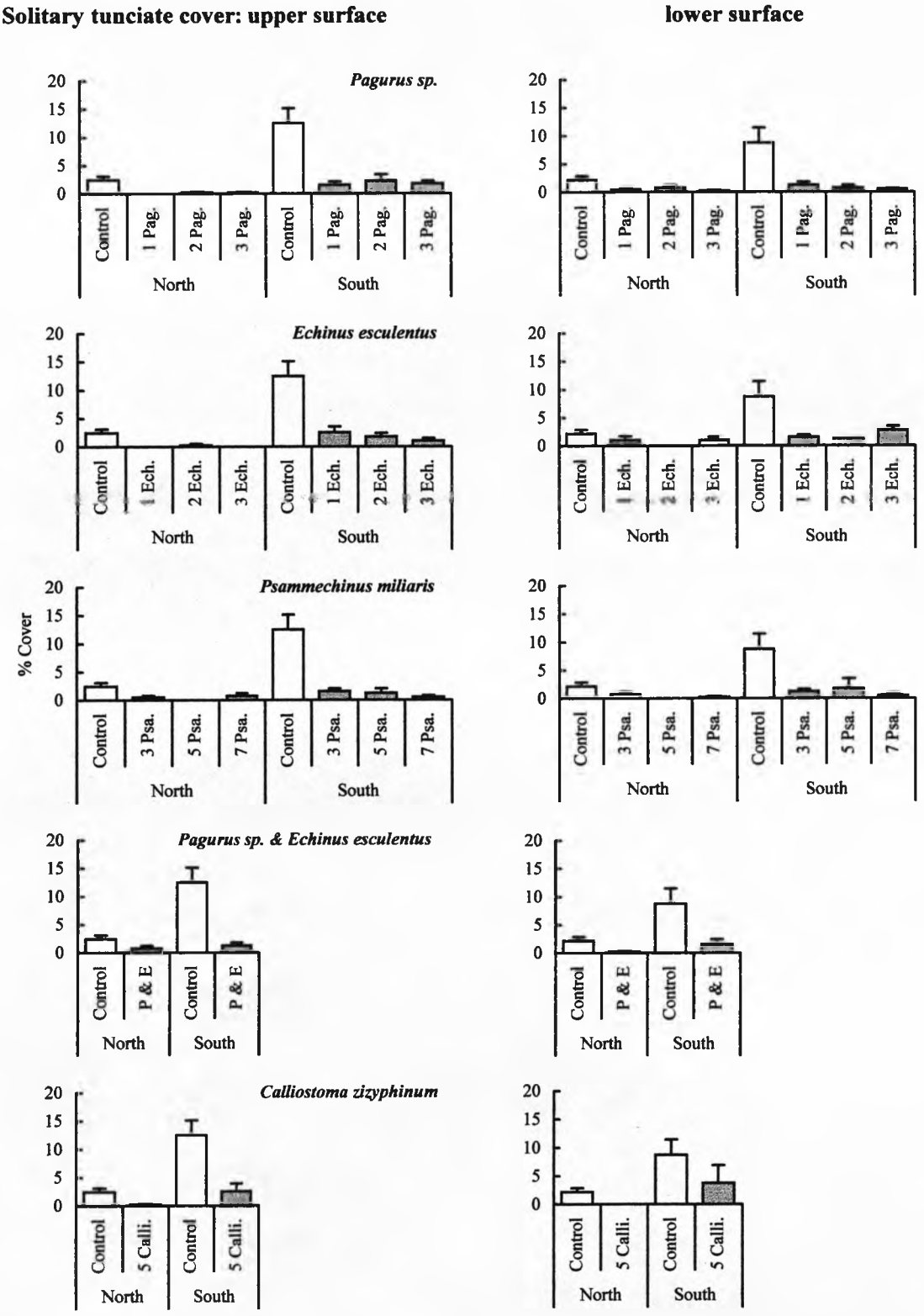

Figure 6.6. Percentage cover of *Ascidiella scabra* (mean +/- SE), on outer net surfaces. Nets were suspended on north and south longline systems and contained scallops with various densities of biological control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.10. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of *Ascidiella scabra* on upper net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.2958, $P > 0.05$					
Location	1	542	31	**<0.01**	Residual
Treatment	3	283	12	**0.04**	Location x treatment
Location x treatment	3	24	1.4	0.27	Residual
Residual	32	18			
Total	39				
SNK multiple comparison of treatment effects:					
Control > 1 Pagurus = 2 Pagurus = 3 Pagurus					
Echinus esculentus					
C = 0.2231, $P > 0.05$					
Location	1	549	36	**<0.01**	Residual
Treatment	3	305	11	**0.04**	Location x treatment
Location x treatment	3	29	1.9	0.15	Residual
Residual	32	15			
Total	39				
SNK multiple comparison of treatment effects:					
Control > 1 Echinus = 2 Echinus = 3 Echinus					
Psammechinus miliaris					
C = 0.3151, $P > 0.05$					
Location	1	538	16.99	**<0.01**	Residual
Treatment	3	554	5.0	0.11	Location x treatment
Location x treatment	3	111	3.5	**0.03**	Residual
Residual	32	32			
Total	39				
SNK multiple comparison of interaction:					
North: SNK comparisons failed to identify homogeneous groups					
South: Control > 1 Psam. = 2 Psam. = 3 Psam.					
Contol: North < South					
1, 2 & 3 Psam.: North = South					

Table 6.10. (cont.)

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp. & Echinus esculentus					
C = 0.2828, *P* > 0.05					
Location	1	246	10	**0.01**	Residual
Treatment	1	511	4.1	0.29	Location x treatment
Location x treatment	1	126	5.2	**0.04**	Residual
Residual	16	24			
Total	19				
SNK multiple comparison of interaction:					
North: Contol = P & E					
South: Contol > P & E					
Contol: North < South					
P & E: North = South					
Calliostoma zizyphinum					
C = 0.3846, *P* > 0.05					
Location	1	577	18	**<0.01**	Pooled data
Treatment	1	1143	8.1	0.22	Pooled data
Location x treatment	1	142	4.5	0.05	Pooled data
Residual	16	32			
Total	19				

Table 6.11. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of *Ascidiella scabra* on lower net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.2373, $P > 0.05$					
Location	1	121	6.3	**<0.01**	Residual
Treatment	3	223	5.3	0.10	Location x treatment
Location x treatment	3	42	2.2	0.11	Residual
Residual	32	19			
Total	39				
Echinus esculentus					
C = 0.2417, $P > 0.05$					
Location	1	549	36	**<0.01**	Residual
Treatment	3	305	11	**0.04**	Location x treatment
Location x treatment	3	29	1.9	0.15	Residual
Residual	32	15			
Total	39				
SNK multiple comparison of treatment effects:					
Control > 1 Echinus = 2 Echinus = 3 Echinus					
Psammechinus miliaris					
C = 0.3421, $P > 0.05$					
Location	1	156	7.2	**0.01**	Residual
Treatment	3	243	7.0	0.07	Location x treatment
Location x treatment	3	35	1.6	0.21	Residual
Residual	32	22			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogenous groups					
Pagarus sp. & Echinus esculentus					
C = 0.3492, $P > 0.05$					
Location	1	211	8.0	**0.01**	Residual
Treatment	1	337	5.2	0.26	Location x treatment
Location x treatment	1	65	2.5	0.14	Residual
Residual	16	26			
Total	19				
Calliostoma zizyphinum					
C = 0.6154, $P > 0.05$					
Location	1	331	9.1	**0.01**	Pooled data
Treatment	1	367	10	**0.01**	Pooled data
Location x treatment	1	6.3	0.2	0.68	Pooled data
Residual	16	38			
Total	19				

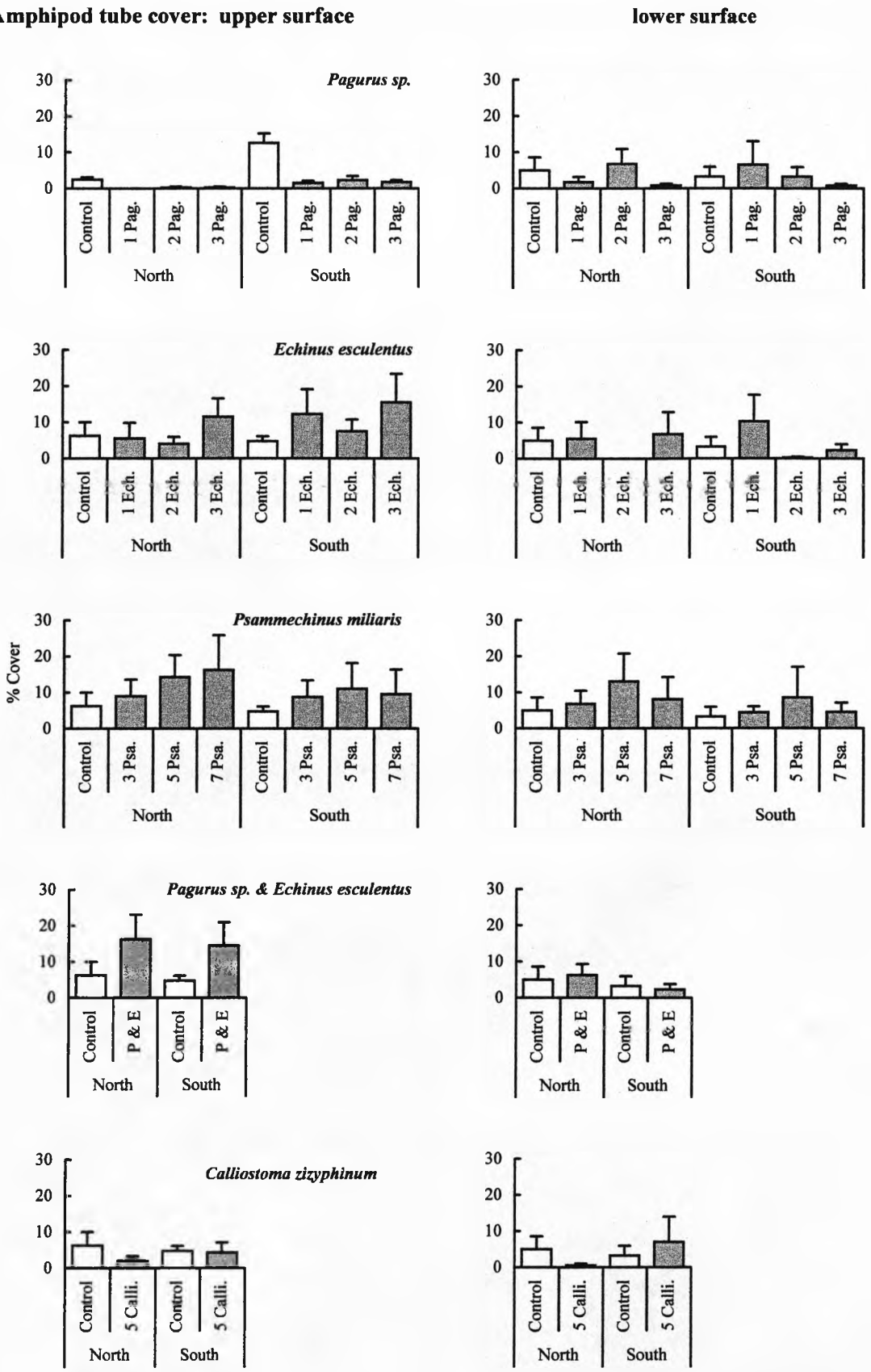

Figure 6.7. Percentage cover of amphipod tubes (mean +/- SE), on outer net surfaces. Nets were suspended on north and south longline systems and contained scallops with various densities of biological control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.12. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of amphipod tubes on upper net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.2218, $P > 0.05$					
Location	1	12	0.2	0.69	Pooled data
Treatment	3	294	3.7	**0.02**	Pooled data
Location x treatment	3	82	1.0	0.39	Pooled data
Residual	32	78			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogenous groups.					
Echinus esculentus					
C = 0.2493, $P > 0.05$					
Location	1	151	1.1	0.30	Residual
Treatment	3	96	6.8	0.07	Location x treatment
Location x treatment	3	14	0.1	0.96	Residual
Residual	32	135			
Total	39				
Psammechinus miliaris					
C = 0.2388, $P > 0.05$					
Location	1	45	0.2	0.63	Residual
Treatment	3	56	1.5	0.37	Location x treatment
Location x treatment	3	37	0.2	0.90	Residual
Residual	32	186			
Total	39				
Pagurus sp. & Echinus esculentus					
C = 0.4123, $P > 0.05$					
Location	1	2.6	0.02	0.89	Residual
Treatment	1	451	14	0.17	Location x treatment
Location x treatment	1	33	0.27	0.61	Residual
Residual	16	123			
Total	19				
Calliostoma zizyphinum					
C = 0.5506, $P > 0.05$					
Location	1	16	0.16	0.69	Residual
Treatment	1	393	34	0.11	Location x treatment
Location x treatment	1	12	0.12	0.73	Residual
Residual	16	96			
Total	19				

Table 6.13. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage cover of amphipod tubes on lower net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3160, $P > 0.05$					
Location	1	13	0.1	0.72	Residual
Treatment	3	65	2.7	0.22	Location x treatment
Location x treatment	3	24	0.3	0.86	Residual
Residual	32	97			
Total	39				
Echinus esculentus					
C = 0.2316, $P > 0.05$					
Location	1	13	0.2	0.64	Residual
Treatment	3	305	20	**0.02**	Location x treatment
Location x treatment	3	15	0.3	0.84	Residual
Residual	32	55			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogenous groups.					
Psammechinus miliaris					
C = 0.2525, $P > 0.05$					
Location	1	73	0.5	0.51	Residual
Treatment	3	32	1.1	0.48	Location x treatment
Location x treatment	3	30	0.2	0.91	Residual
Residual	32	164			
Total	39				
Pagurus sp. & Echinus esculentus					
C = 0.3041, $P > 0.05$					
Location	1	79	0.81	0.38	Residual
Treatment	1	2.2	0.21	0.73	Location x treatment
Location x treatment	1	11	0.11	0.75	Residual
Residual	16	97			
Total	19				
Calliostoma zizyphinum					
C = 0.5311, $P > 0.05$					
Location	1	9.4	0.080	0.79	Pooled data
Treatment	1	46	0.60	0.58	Pooled data
Location x treatment	1	75	0.61	0.45	Pooled data
Residual	16	124			
Total	19				

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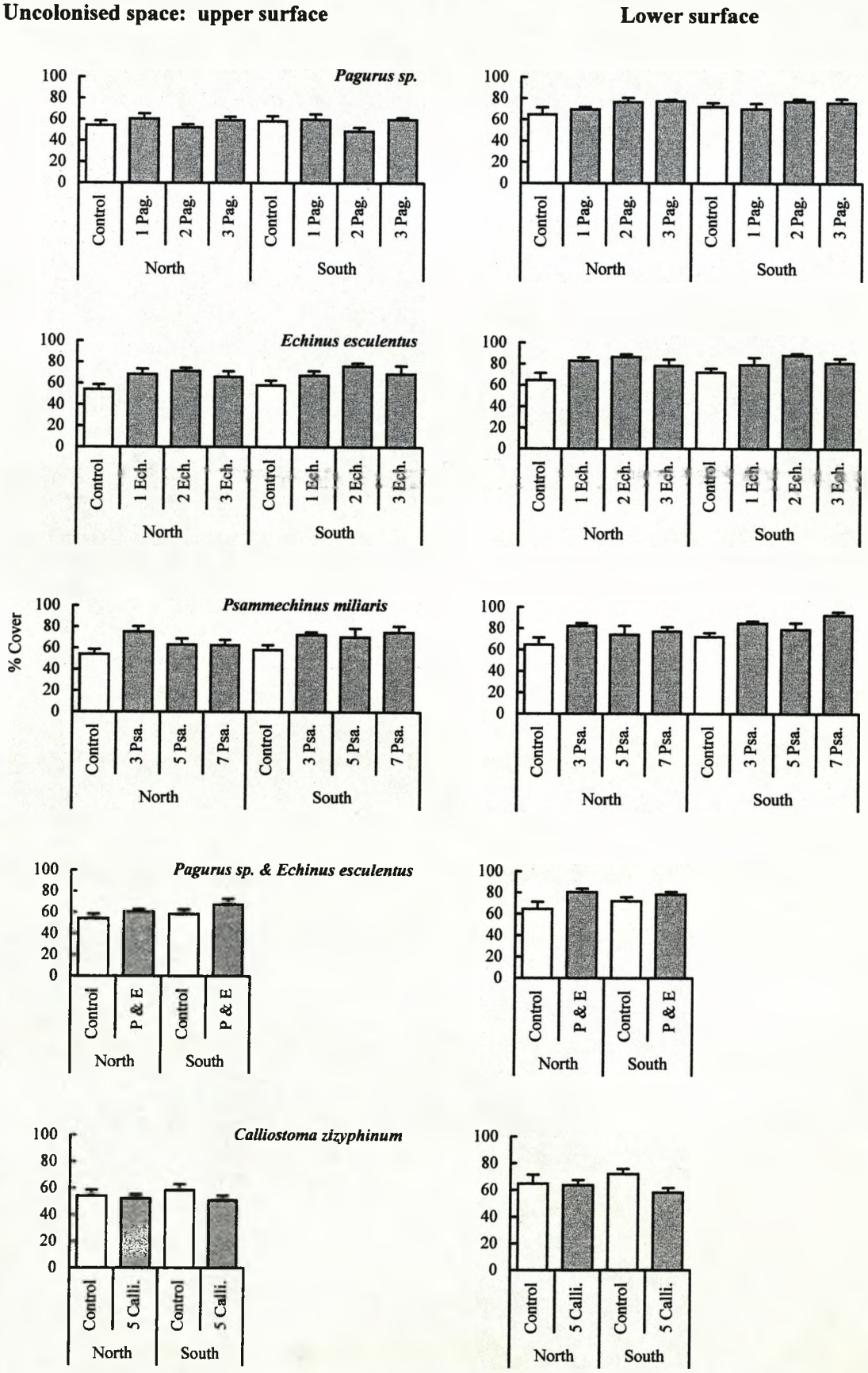

Figure 6.8. Percentage of unclonised mesh (mean +/- SE), on outer net surfaces. Nets were suspended on north and south longline systems and contained scallops with various densities of biological control organisms (grey bars), or just scallops (control nets, white bars).

Table 6.14. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage of uncolonised mesh on upper net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.2070, $P > 0.05$					
Location	1	0.4	0.020	0.90	Residual
Treatment	3	65	8.8	0.05	Location x treatment
Location x treatment	3	7.5	0.26	0.85	Residual
Residual	32	28			
Total	39				
Echinus esculentus					
C = 0.2306, $P > 0.05$					
Location	1	28	0.60	0.45	Residual
Treatment	3	203	27	**0.01**	Location x treatment
Location x treatment	3	7.5	0.16	0.92	Residual
Residual	32	47			
Total	39				
SNK multiple comparison of treatment effects:					
Control < 1 Echinus = 2 Echinus = 3 Echinus					
Psammechinus miliaris					
C = 0.2679, $P > 0.05$					
Location	1	72	1.2	0.29	Residual
Treatment	3	176	2.4	0.25	Location x treatment
Location x treatment	3	75	1.2	0.33	Residual
Residual	32	62			
Total	39				
Pagurus sp. & Echinus esculentus					
C = 0.3847, $P > 0.05$					
Location	1	59	1.6	0.22	Residual
Treatment	1	112	17	0.15	Location x treatment
Location x treatment	1	6.7	0.19	0.67	Residual
Residual	16	36			
Total	19				
Calliostoma zizyphinum					
C = 0.3356, $P > 0.05$					
Location	1	2.8	0.1	0.76	Pooled data
Treatment	1	40	3.5	0.31	Pooled data
Location x treatment	1	12	0.4	0.53	Pooled data
Residual	16	29			
Total	19				

Table 6.15. Two way ANOVA and SNK multiple comparisons of percentage cover data testing for the effect of location and biological control on the percentage of uncolonised mesh on lower net surfaces. Where no significant interaction between location and treatment occurred ($P > 0.25$) data for the north and south systems have been pooled. Cochran's test results are given and all data are arcsine transformed. Bold type indicates a significant result ($P < 0.05$).

Source of variation	df	MS	*F*	*P*	*F* ratio versus
Pagurus sp.					
C = 0.3415, $P > 0.05$					
Location	1	9.4	0.3	0.62	Residual
Treatment	3	79	7.6	0.07	Location x treatment
Location x treatment	3	10	0.3	0.84	Residual
Residual	32	37			
Total	39				
Echinus esculentus					
C = 0.2316, $P > 0.05$					
Location	1	13	0.23	0.64	Residual
Treatment	3	305	19.96	**0.02**	Location x treatment
Location x treatment	3	15	0.28	0.84	Residual
Residual	32	55			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogeneous groups.					
Psammechinus miliaris					
C = 0.3294, $P > 0.05$					
Location	1	318	4.7	**0.04**	Pooled data
Treatment	3	298	4.4	**0.01**	Pooled data
Location x treatment	3	78	1.1	0.35	Pooled data
Residual	32	67			
Total	39				
SNK multiple comparison of treatment effects failed to identify homogeneous groups.					
Pagurus sp. & Echinus esculentus					
C = 0.3041, $P > 0.05$					
Location	1	6.9	0.15	0.70	Pooled data
Treatment	1	263	5.8	**0.03**	Pooled data
Location x treatment	1	38	0.84	0.37	Pooled data
Residual	16	46			
Total	19				
Calliostoma zizyphinum					
C = 0.5654, $P > 0.05$					
Location	1	0.67	0.010	0.90	Residual
Treatment	1	115	1.8	0.41	Location x treatment
Location x treatment	1	64	1.42	0.25	Residual
Residual	16	45			
Total	19				

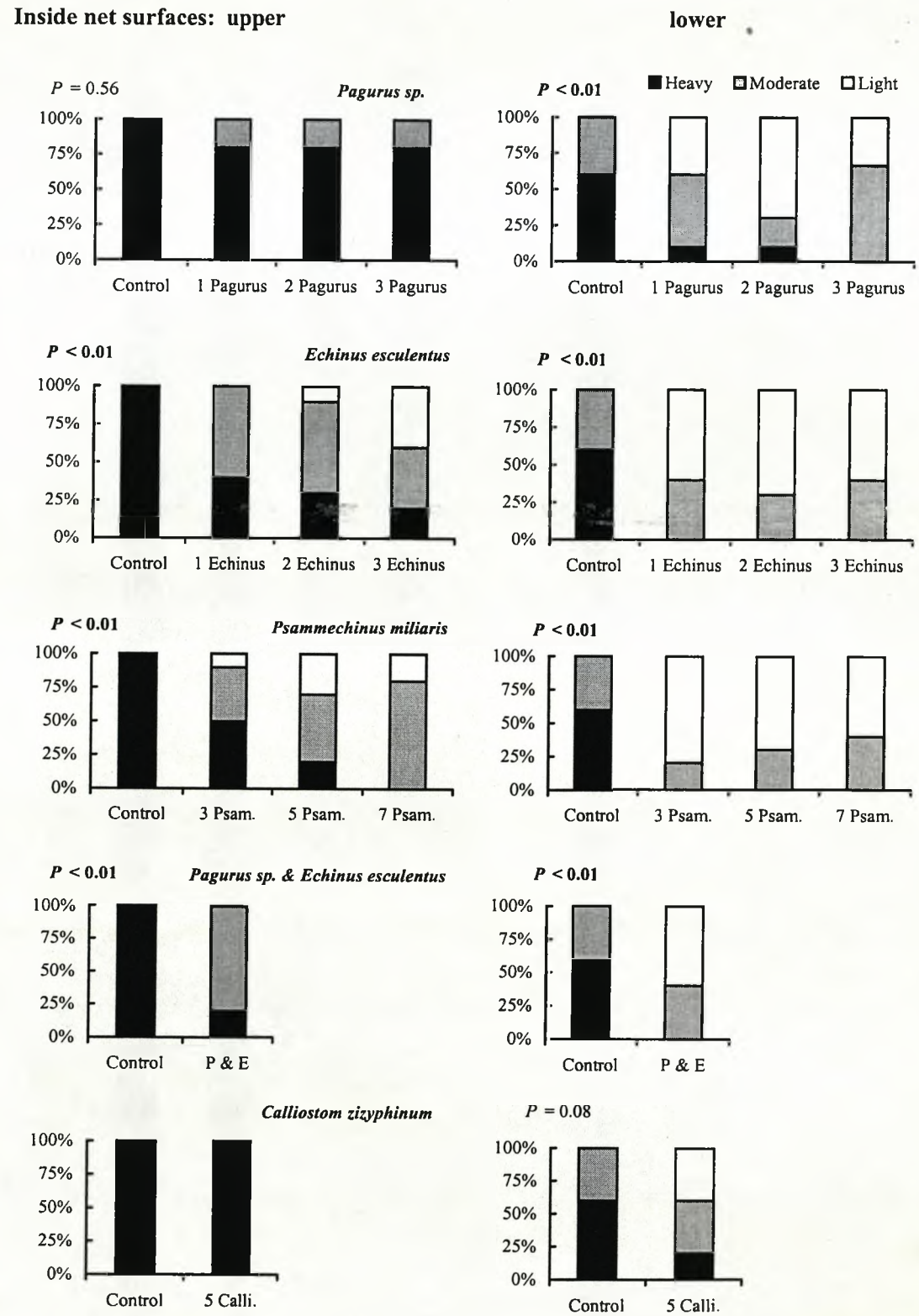

Figure 6.9. The degree of fouling on inside net surfaces with and without biological control organisms at various densities. The percentage of surfaces in each of three categories are shown. Data are for 10 nets and treatments are pooled across north and south longline systems. *P* values (from Fishers's exact tests) describe the probability that there is no significant difference between proportions in alternative treatments.

6.3.4 Scallop shell fouling

Scallop shells were frequently colonised by saddle oysters, tunicates and hydroids. A few barnacles or worms with calcareous tubes also sporadically fouled shells. Saddle oysters were the most prolific shell foulers, being abundant for most treatments and control nets. Occasionally, scallops in nets with urchins were free of saddle oysters. No biological control organism significantly influenced the abundance of organisms "soft-fouling" organisms (sabellid worms, anemones and colonial tunicates). However, there was a trend for reduced abundances in nets with high densities of urchins (Figure 6.10). Low sample sizes and tunicate abundance in control nets meant though shell fouling by solitary tunicates was rare in all nets with both *Pagurus* sp. and *E. esculentus*, treatment effects were not significant. The Significant treatment effect for tunicate fouling in nets with *Pagurus* sp. was driven by variation among crab densities (Figure 6.10). Hydroid cover was significantly reduced by both types of urchin and *Pagurus* (Figure 6.10).

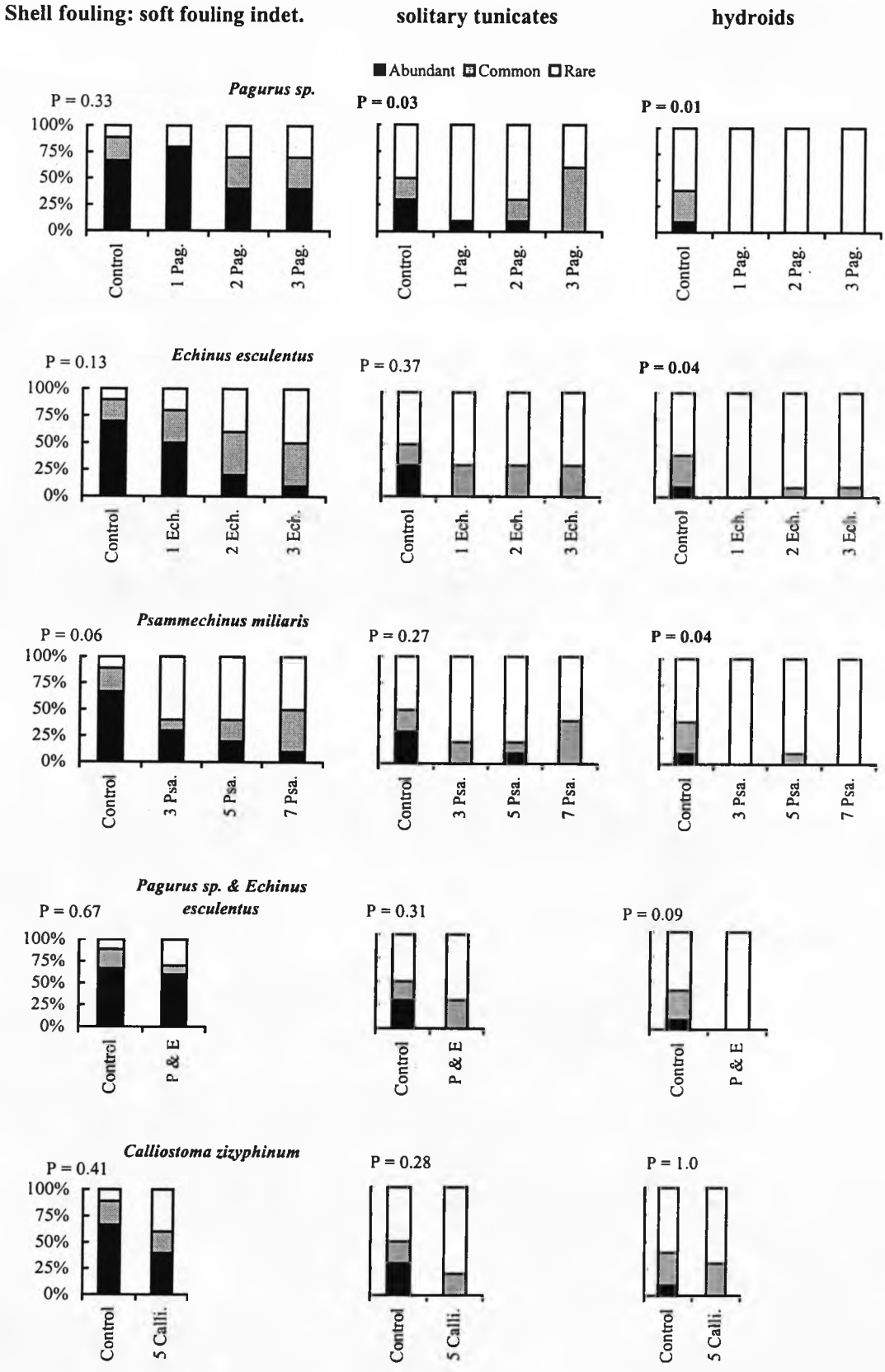

Figure 6.10. Amounts of fouling on scallop shells with and without biological control organisms at various densities. The percentage of shells in each of three categories are shown. Data are for 10 nets and treatments are pooled across north and south longline systems. *P* values (from Fisher's exact tests) describe the probability that there is no significant difference between proportions in alternative treatments.

Table 6.16. Main effects of biological control organisms on specific fouling organisms and total fouling cover and mass. Crosses indicate where control organism reduced fouling (for this overview cases where $P < 0.10$ have been included as a positive result because they represent strong trends that merit further study).

Treatment	Fouling organism				Total fouling			Shell fouling			
	Hydroids	Solitary tunicates	Colonial tunicates	*Jassa* tubes	Area inside	Area outside	Mass	Hard	Soft	Hydroids	Solitary tunicates
Pagurus sp.	-	X	X	-	X	X	X	-	-	X	-
Echinus esculentus	-	X	X	-	X	X	X	-	-	X	-
Psammechinus miliaris	X	X	X	-	X	X	X	-	X	X	-
Echinus esculentus & *Pagurus* sp.	-	X	X	-	X	X	X	-	-	X	-
Calliostoma zizyphinum	-	X	X	-	-	-	-	-	-	-	-

6.4 Discussion

Removal of fouling by control organisms

Urchins and hermit crabs have a strong potential for biological control of fouling in suspended scallop cultivation. Both are common and should be cheaply available around the British Isles. Once deployed they reduced fouling loads by up to 50%. This should lessen costs associated with buoyancy, anchorage, and cleaning of nets and scallops. Biological control is also expected to increase scallop marketability by removing shell fouling organisms, and enhance growth and survival by reducing disturbance. In addition, urchins might be profitably exploited as part of a polyculture system. Interestingly, swimming crabs and top shells were not efficient pearl net cleaners despite their ability to clean invertebrates from trays and cages in previous studies (Hidu *et al.* 1981, Minchin 1996, Skjaeggestad 1997).

Urchins were the most successful control organisms. This was perhaps unsurprising as where urchins proliferate naturally they often create large barren areas with little benthos (e.g. Forster 1959, Jones and Kain 1967, Lawrence 1975, Hagen 1983). Similarly, *Psammechinus miliaris* has been observed to reduce fouling on oyster trays (Maeaettae *et al.* 1989) and scallop nets (L. Cook, *pers. comm.* 1999, Scottish Association of Marine Science, Argyll). Both types of urchin (*P. miliaris* and *Echinus esculentus*) caused similar reductions in net and scallop shell fouling. They were the only control organisms to reduce hydroid cover, as well as colonial and solitary tunicate levels. Urchins also tolerated capture, handling and emersion well. *Echinus esculentus* survival in pearl nets was almost 100% over the 8-month experiment, slightly higher than *P. miliaris*. Both species are fragile, however, and care must therefore be taken not to crush them when deploying nets.

The cleaning ability of urchins was generally independent of their density (for the range of densities investigated here). Optimum densities are probably around five *P. miliaris* and two small *E. esculentus* per pearl net. However, this might vary seasonally, perhaps rising in the spring and summer when fouling proliferates (but see below). Choice of urchin could be based on species availability; although *E. esculentus* can grow up to approximately 15cm in diameter (cf. 5cm for *P. miliaris*) and so where space is limited only young specimens should be used.

Interestingly, urchins reduced total fouling loads and cover of hydroids and solitary tunicates to similar levels on both longline systems. This was despite significant differences in levels on control nets between the two systems. Lower inside net surfaces were almost

completely free of fouling in the presence of urchins, but fouling remained on the outside of nets, and, to a lesser extent, upper inside surfaces. It seems likely, therefore, that urchins had difficulty cleaning these surfaces, probably because they were hard to reach or cling to. Their ability to reach and remove fouling from outer surfaces might be improved with wider mesh nets, where the material is monofilament, rather than the split twine used here. Fouling can be associated with high concentrations of plankton and organic detritus (Chapter 4). In such instances, biological control could encourage scallop growth by retaining some of the food enhancing properties of net fouling while preventing it from binding or smothering scallops.

Urchins have several advantages over the other control organisms tested. Firstly, they are generalist grazers rather than predators (Barnes, 1987) and should probably be suitable for use with scallop spat. They are also large enough to be retained in wide mesh lantern nets. Importantly, urchins can also be produced in hatcheries (e.g. Hagen 1996, Grosjean *et al.* 1998, Kelly 2001), their roes might be lucratively exploited for human consumption (Keesing and Hall 1998, Kelly *et al.* 1999), and they may grow fastest and hence most profitably in suspended cultivation with other aquaculture species (Nuttall 1997, Kelly *et al.* 1998). Urchins thus seem to fulfil most of Minchin's criteria for biological control organisms (Minchin 1996). Further monitoring is, however, required to ensure that they do not become infected with, or spread, scallop diseases or parasites.

In preliminary trials hermit crabs were more effective at controlling fouling than swimming crabs, which suffered heavy mortality. Similarly, Enright *et al* (1993) found hermit crabs more efficient than walking crabs for removing fouling from lantern nets used in oyster cultivation. Presumably, shells offer protection from physical disturbance in suspended cultivation. Crabs reduced tunicate net fouling and soft fouling on scallop shells. However, they tended to concentrate on lower net surfaces, and have two inherent disadvantages. Firstly, the need to provide extra shells (to accommodate crabs as they grow) increases labour. Secondly, crabs are scallop predators and could kill bivalve spat unless their chelae were neutralized (Hardy 1991, Enright *et al.* 1993, Freites *et al* 2000). None-the-less, hermit crabs are readily available as by-catch from scallop dredging and might successfully tackle robust fouling organisms such as mussels (Hidu *et al.* 1981, Enright *et al*, 1993). They could be used where urchins are scarce. One crab should be added to each net for optimal cleaning and crab survival. Crabs and urchins together were less successful in removing fouling than urchins alone. However, the two species survived well together and could be used in conjunction if hermit crabs proved successful at removing fouling organisms other than those found here.

As in previous studies, the top shell *Calliostoma zizyphinum* reduced tunicate fouling on nets (Skjaeggestad 1997). This control organism was, however, less successful than the others tested, failing to reduce total fouling weights or cover. This may be in part due to its low survival in pearl nets, which reduced densities to an average of three snails per net. *Calliostoma zizyphinum* normally feeds on rocky surfaces (Campbell and Nicholls 1994). Its feeding and survival may thus have been limited by the constant flexing and motion of pearl nets in the relatively exposed conditions of this experiment.

Cover and weight of net fouling was rarely influenced by the density of crabs or urchins. Food may thus have been limiting for these omnivores. Despite this, urchin survival was high, possibly because they can exploit dissolved and suspended matter in addition to benthos (Pequgnat 1972, Kelly *et al.* 1998). The ability to survive winter months when food is limiting is advantageous because it means that urchins could probably be deployed year round at densities capable of removing prolific fouling in spring and summer months. Hermit crabs survived less well at high densities, their stocking densities might thus have to be adjusted seasonally according to food availability (although competition for space might also be important as crabs fight for territory, Barnes 1987).

Monitoring of biological control results is essential to ensure that removing one fouling organism does not encourage the growth of another. This is common in nature where predation or grazing removes dominant species facilitating recruitment of inferior competitors (Richmond and Seed 1991). In this study, proliferation of silty amphipod tubes was occasionally associated with urchin grazing (although tubes may just have been easier to identify in the absence of other fouling). This should be investigated if it is thought that amphipods adversely affect scallops. In one instance, hermit crabs were also associated with increased hydroid fouling (Figure 6.4). Off Port Erin, hydroids tended to be replaced by ascidians in the late summer (Chapter 3). Increased hydroid fouling might therefore have been aided by selective predation of hermit crabs on solitary tunicates.

Scallop growth

Reduced fouling in nets with biological control may not have consistently increased scallop growth for two reasons. Firstly, in the study area, even prolific fouling does not consistently reduce the growth of intermediate sized scallops (Chapter 5). Secondly, the experiment was carried out during autumn and winter when scallop growth is minimal (Broom and Mason 1978, Wilson 1987, Allison 1994) making treatment effects hard to distinguish. Interestingly, *P. miliaris* significantly increased scallop growth, but only at intermediate

densities (Table 6.2). Possibly, when urchins are present at high densities they reduce the time scallops spend feeding by frequently disturbing them (Irlandi and Mehlich 1996). Crucially, none of the biological control organisms tested adversely affected scallop growth rates. This has been a problem elsewhere when control organisms are deployed at high densities (Flimlin and Mathis 1993, Minchin 1996).

A major advantage of using biological control is that nets and scallops need not be manually cleaned. Cleaning is carried out frequently, particularly in the summer, when heavy fouling loads can make longlines vulnerable to damage and sinking. It is also important to prevent scallops from becoming trapped or smothered and to promote water flow through cages. However, cleaning necessarily disturbs scallops. Aerial exposure and handling reduces scallop growth and survival (Parsons and Dadswell 1992, and references therein, McDonough 1998, Laing *et al.* 2001). In this area, for example, frequent, prolonged, disturbance reduced scallop shell growth by up to 50% (Chapter 5). By preventing the build up of fouling on scallop shells and nets, biological control could thus increase cleaning intervals, reducing labour costs and raising production.

Shell fouling

Shell fouling is important for a number of reasons. Small scallops can be tightly bound by the byssal threads of mussels (Minchin and Duggan 1989), ascidian tunics (Wilson 1994, Lu and Blake 1997), tube forming polychaetes (Leibovitz, 1984) and hydroid stalks (Claereboudt *et al.* 1994). This inhibits shell opening, reducing growth and causing mortality. Similarly, heavy fouling of upper shell valves can hinder shell opening and thus reduce growth in both large and small scallops, particularly when the cultivated species has a relatively light shell (Cropp and Hortle 1992, Lodeiros and Himmelman 2000). Fouling might also harbour scallop parasites, for example, shell fouling by the hydroid *Obelia geniculata* has been associated with spat mortality because it encourages settlement of the shell boring polychaete *Polydora* (Mortensen *et al.* 2000). Both urchins and hermit crabs reduced hydroid and tunicate shell fouling and might thus be used to increase scallop survival in intermediate culture, or during the on-growth of species vulnerable to shell fouling. *Psammechinus miliaris* was the most successful shell cleaner, uniquely reducing levels of "other soft fouling" (mainly anemones and sabellid worms). Urchins also give shells a clean, "scrubbed" look (even removing labels attached with super-glue), which should improve marketability where scallops are sold in their shells.

None of the organisms tested was able to reduce saddle oyster fouling despite indications that *C. zizyphinum* can prevent recruitment of this bivalve (Minchin 1996). However,

saddle oysters were small and light, making them unlikely to influence scallop growth. They also fell from shells rapidly after emersion when scallops were still alive, and thus seem unlikely to be a problem fouler. In other areas oysters, barnacles and calcareous worms can be troublesome shell foulers, and are sometimes removed by adding dog whelks to enclosures (Minchin and Duggan 1989). Dog whelks might be used in conjunction with urchins where both hard and soft fouling species are a problem.

Further work

It is hoped that this study provides scallop growers with information on which to base their own biological control strategies. Obviously, methods will vary between locations. Reporting the success of new and current techniques along with details such as equipment specifications, main types of fouling and scallop size should facilitate further progress.

Crucially, experiments should be carried out over a whole intermediate-culture or on-growing cycle. The ability of organisms to tackle annual changes in fouling organisms (Chapter 3) and survive shifting environmental conditions could then be assessed. Optimum control organism densities might be adjusted accordingly.

This study points to several potential advantages of using urchins to control fouling of enclosures containing small scallops in intermediate culture. Trials are required to test these suggestions. If urchins prove successful elsewhere attempts should be made to develop polyculture and low-tech hatchery techniques (so that farmers can produce urchins on-site for fouling control) or economic means of distribution from purpose-built urchin hatcheries.

I have sometimes tentatively attributed differences between my results and those of previous researchers to equipment variation (for example trays versus nets). Urchins should therefore be tried in a range of enclosures such as lantern nets, Northwest plastic trays and pearl nets with different mesh sizes. It might also be possible to develop equipment that facilitates biological control. Attempts could also be made to retain control organisms on the outside of nets or on ear hung scallops. Suitable techniques might include tethering control organisms (various methods are available, e.g. Heck and Valentine 1995, Moksnes *et al.* 1998, Ryer *et al.* 1997), seeding equipment with juveniles, or encouraging juveniles to settle on cultivation equipment.

In some areas mussels cause heavy spat mortality. They had not set during this experiment and therefore it is not known whether they are efficiently tackled by urchins. Dog whelks can, however, reduce mussel damage (Minchin and Duggan 1989). Trials in areas where

mussels and hydroids or tunicates are a problem could therefore assess the effectiveness of urchins alone, and in combination with dog whelks.

CHAPTER 7 – GENERAL DISCUSSION

7.1 Introduction

Scallop cultivation is set to increase around the world (Bourne 2000), including the British Isles (Anon 2001a). Information from this thesis increases understanding of how fouling affects the growth of scallops in suspended cultivation. Better understanding and biological control should help to improve the efficiency and hence viability of cultivation. Biological control is promoted with sustainability in mind and the wish that scallop cultivation might develop to be a flagship for environmentally and socially responsible aquaculture. This thesis highlights spatial and temporal variation in the effects of fouling on scallop growth. Detrimental effects on spat mortality, marketability and equipment buoyancy are, however, ubiquitous. Principle net fouling genera are also similar the world over (e.g. Hidu *et al.* 1981, Enright *et al.* 1983, Arakawa 1990, Enright 1993, Minchin 1997, Cigarria *et al.* 1998), and thus the descriptions and techniques developed for Manx waters may be more widely applicable.

7.2 Ideas for scallop cultivation around the British Isles

High labour costs and the slow growth of native scallops mean that European scallop cultivation is unlikely to achieve the massive production levels of Japan, China or Chile. Instead increasing numbers of small, independent producers should appear, providing valuable employment and local revenue for coastal communities where traditional fishing industries continue to dwindle. Scallop farming is a much-cited means of diversification for inshore fishermen because it exploits their existing knowledge and is cheaper to set up and run than finfish production (Hardy 1991). Additionally, scallops are relatively easy to handle and process (Edwards, 1997). High demand from the continent (mostly France) and stable markets already make farming around the British Isles an attractive proposition (Edwards 1997, Anon 2001a). This could be further enhanced by the development of a significant domestic market. Recent concerns over red meat, increased awareness of health issues and interest in cooking could be exploited to increase demand in the U.K. Scallops might be marketed as a nutritious and glamorous treat, which can be attractively prepared in minutes.

Previous studies of fouling in bivalve cultivation have run for short time periods or provided qualitative descriptions of major foulers (e.g. Claereboudt et al. 1994a, Lodeiros and Himmelman 1996, 2000). The detailed and long-term investigation undertaken here gives a better understanding of fouling organisms and the processes governing their distribution in space and time. This should enable growers to target cleaning regimes or alter the position

of equipment to avoid problem species and take advantages of high growth rates in suspended culture (Ventilla 1981, MacDonald and Thompson 1985, Wallace and Reinsnes 1985, Hardy 1991). Using urchins to control fouling is another way in which fouling problems could be reduced. This method should have several economic and environmental benefits. Economic benefits include: increased scallop growth in the absence of cleaning disturbance, reduced cleaning costs and a potentially lucrative urchin harvest. Environmental benefits include: reduced fuel consumption for net cleaning (nets are usually cleaned at sea with high pressure water hoses), reduced waste (dead foulers and scallop faeces) to the marine environment and the redundancy of chemical antifoulants.

Restocking efforts have been proposed for planned new closed areas around the Isle of Man. Juvenile scallops were successfully reared in suspended culture (despite the apparent lack of suitable sheltered sites, Wilson 1994) using the equipment described in Chapter 2. It would therefore be feasible to grow juveniles for reseeding, though low and irregular spat falls (Brand et al. 1991) might necessitate setting up a hatchery. Elsewhere competition for sheltered sites with salmon farms and recreational facilities could force bivalve farmers to consider relatively exposed or even offshore locations (Sorgeloos 1999, Currie 2000, Berry and Davison 2001). These areas may not be suitable for traditional cultivation, because poor weather could prevent regular harvesting. Instead, such sites might support small-scale or opportunistic operations, perhaps run by fishermen to augment catches when fishing grounds are closed or scallop prices are high. Biological control could be especially appropriate in such situations, where regular cleaning is difficult. It may also be advantageous because it keeps scallops clean and untangled but leaves some fouling on the outside of cultivation nets. This should reduce high water currents that might otherwise inhibit feeding (Claereboudt *et al.* 1994b, Skjaeggestad 1997) and residual fouling might promote plankton growth, enhancing food levels.

7.3 Environmental considerations – a holistic approach

Powerful environmental groups are wary of fish and crustacean farming and have used their influence to block its expansion (Boyd 1999). Bivalve farming is generally considered an environmentally sound alternative because it does not require inputs of food, antibiotics or other chemicals (Folke and Kantosky 1989, Sorgeloos 1999, Naylor *et al.* 2000, Berry and Davison 2001). In current jargon, bivalve farmers have a small ecological footprint. However, we cannot afford to be complacent. In Chapter 4, it was demonstrated that fouled nets can encourage the growth of plankton but what if toxin producers proliferate along with other species? Accumulation of inorganic matter under farms can also alter benthic

communities (Skjaeggestad 1997, Berry and Davison 2001). Additionally, there are concerns that transfer of live bivalve seed could introduce diseases and pests, and alter the genetics of local shellfish stocks (Mackie and Ansell 1993, Heipel *et al.* 1999, Minchin 1999, Beaumont 2000, Mortensen 2000). Monocultures are also vulnerable to disease and parasites and may harbour them, threatening natural stocks (e.g. Pearson and Black 2001 in Berry and Davidson, 2001). Finally, waste shell and mantle material can also be difficult to dispose of. Care must be taken to investigate these potential problems so that they can be avoided or ameliorated. This should reduce both real environmental impacts and perceived ones; an astute move because, once lost, pubic opinion is notoriously hard to restore.

Emphasis on sustainable farming practices (as defined in Bruges 2001) should stimulate support for UK bivalve farmers. There is international pressure for aquaculture to adopt a holistic approach, considering socio-economic and environmental factors as part of the cultivation industry (Sorgeloos 1999, Naylor *et al.* 2000). There are difficulties with this approach, particularly where carnivorous species are intensively cultivated (see Boyd 1999). However, the principle can be successfully addressed bringing economic benefits (e.g. Jones and Iwama 1991, Kelly *et al.* 1998, Lombardi *et al.* 2001, Millar 2001) and deserves serious consideration (Bruges 2001). This is especially true when high value foods, such as scallops, are cultivated in wealthy countries. One way of reducing negative environmental effects is to cultivate different species together (e.g. Naylor *et al.* 2000, Neori *et al.* 2000). This means that waste matter or nutrients are retained within culture organisms instead of being lost to the wider environment.

Polyculture or integrated aquaculture is common in Asia where traditionally fish with different trophic or habitat requirements are grown together in ponds, efficiently sustaining and exploiting all available food sources (e.g. higher aquatic plants, zooplankton, phytoplankton and detritus) and zones of habitation (e.g. bottom dwellers, vertical surface cleaners, upper water species, Bardach *et al.* 1972). More recently, nutrient rich water from fish or shrimp farms has been used to promote the growth of algae, which are harvested or used as food for molluscs (e.g. Negroni 2000, Neori *et al.* 2000, Nelson et *al.* 2001). Bivalves and urchins have also been cultivated in salmon and shrimp enclosures, where they benefit from a rich diet including faeces and uneaten food pellets (e.g. Jones and Iwama 1991, Cook *et al.* 1998, Kelly *et al.* 1998, Soto and Mena 1999). Finally, fouling of salmon nets can be reduced by polyculture with sea cucumbers, themselves a lucrative crop (Ahlgren 1998). Cultivating urchins with scallops could become another example of successful polyculture. However, further work is required to determine how urchin growth and condition responds to the environment inside pearl or lantern nets.

With care, British scallop cultivation might continue to develop as an environmentally and economically sustainable industry, deserving support from the public and government organisations. Economically and socially, farming could provide employment in isolated coastal areas where traditional fishing and fish processing skills may otherwise be lost. Because scallop farms are generally owned by locally based individuals (Anon 2001a) some profit should remain in the locality rather than being exported to multinational corporations (Berry and Davison 2001). Communities may also enjoy and benefit from scallops as a nutritious and tasty fast-food (Hardy 1991).

Environmental benefits might first come from reduced fishing effort on traditional grounds conserving both scallops and non-target species. Frequent dredging can reduce the biodiversity and productivity of benthic habitats, which probably has knock-on effects for pelagic ecology in the waters above (Eleftheriou and Robertson 1992, Hill *et al.* 1996, Kaiser and de Groot 2000, Veale *et al.* 2000, Jenkins *et al.* 2001). Scallop larvae from scallops spawning on longlines may also gradually enhance natural stocks or cultivated juveniles might be used to reseed the seabed in stock enhancement programmes (e.g. Venitilla 1982, Tettelbach *et al.* 1997, Arnold *et al.* 1999, Wilson 2000). As discussed above, detrimental environmental effects are low. However, this study has highlighted some unexpected effects of cultivation on the environment and it is important to have a thorough understanding of all these processes so that a precautionary approach to potential problems can be adopted. Such an approach might include: using sites with high water-flow to inhibit the build up of waste and plankton (Skjaeggestad 1997, Millar 2001), using natural spat or those produced from local broodstock, stocking more than one species, exploiting shells to make medical products (Anon 2001b) and polyculture to reduce fouling without the need for chemicals. Bivalves are sensitive to pollution (e.g. Davies and Paul 1986, Minchin *et al.* 1995) and thus farmers have an interest in guarding a healthy marine environment from which we can all benefit.

7.4 Summary – findings of this thesis

This project had several novel findings that should help cultivators. Firstly, it provides the most detailed description to date of temporal patterns of fouling on cultivation nets. This should aid the development of fouling control strategies. The thesis also shows that contrary to popular belief fouling sometimes enhances scallop growth, most likely because it increases food availability inside nets. This has important consequences for scallop growers, particularly in oligotrophic sea areas such as offshore Islands. The possibility of

enhanced planktonic production within nets should also be considered by those modelling cultivation in an ecosystem context and researchers investigating relationships between the growth of cultivated scallops and environmental conditions. Finally, biological control studies yielded exciting results; epifaunal urchins were particularly successful, keeping both nets and scallop shells clean.

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Appendix 1 - Suppliers of material for longlines.

1. Japanese style anchors and metal loops: Metalco Engineering Ltd., Metals House, Athol Street, Port St. Mary, Isle of Man, IM9 5DS.

2. Chain, shackles and thimbles: F.P.M. Henderson Ltd., 27 Jordan Street, Glasgow, Scotland, G14 ORJ.

3. Trawl floats: Osprey Ltd., 6 Mynd Industrial Estate, Church Stretton, Shropshire, England, SY6 6EA.

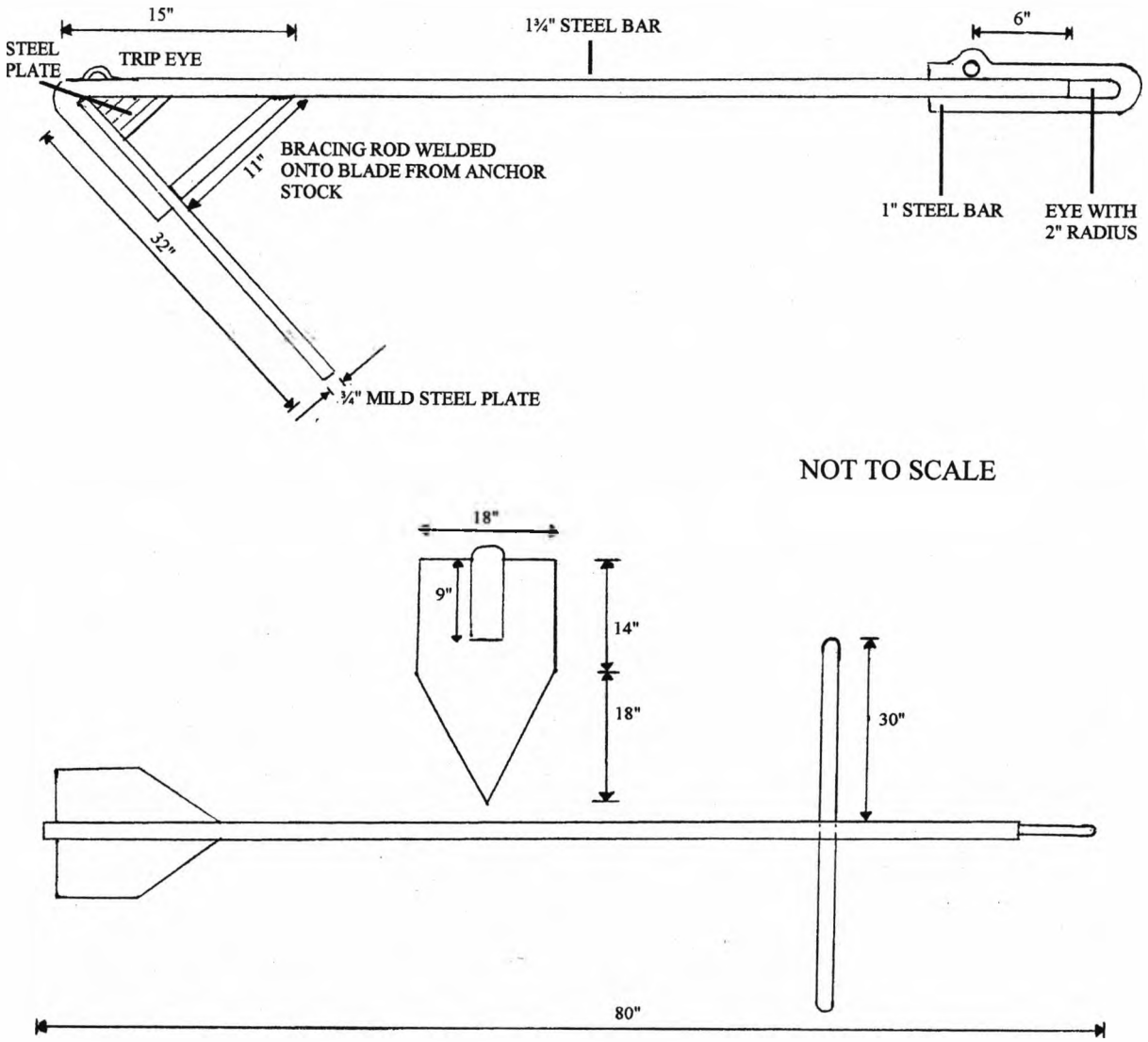
4. Polyform Buoys: Fishing Co-operatives (U.K.) Ltd., 20 Elgin Street Industrial Estate, Dunfermline, Fife, Scotland. KY12 7SN.

5. Seasteel rope: Gael Force, 12 Walker place, Inverness, Scotland, IVI 1TY.

6. Polypropylene rope: W & R Lewis, 286 Broomloan rd., Glasgow, Scotland G51 2DP.

7. Pearl nets: Zhanghiagang Haitain Netting Industrial Co. Ltd., No. 17, Renmid Rd. (M), Zhangjiagang City, Jiangsu, China. 215600.

Appendix 2 - Japanese style longline anchor.



After J. MacMillan, *Pers. comm.* 1998. Seafish Aquaculture, Marine Farming Unit, Ardtoe, Scotland.

Appendix 3 - Percentage cover of species groups during series 1.

(Data are average results for all net sufaces of four nets).

Time	1. February			2. April			3. June			4. July			5. August		
Depth (m)	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**
small hydriod	2.5	2.5	4.1	0.0	0.6	5.7	0.0	0.0	0.0	3.0	1.7	2.0	3.5	11.0	2.9
Tubularia spp.	1.8	0.6	0.0	34.8	11.8	19.1	91.7	78.9	76.0	70.7	68.9	68.5	11.8	16.4	4.7
Bougainvillia spp.	0.4	0.2	0.1	0.0	0.6	0.9	0.5	0.9	1.6	12.0	10.9	6.3	6.6	4.6	1.9
Eudendrium spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.3	2.3
Obelia geniculata	14.8	14.6	17.5	0.0	1.3	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Halecium spp.	0.0	0.1	0.0	0.1	0.5	0.0	0.2	0.5	1.3	0.6	1.4	1.3	0.6	0.1	0.0
Hiatella arctica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Modiolus phaseolina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	2.8	0.1	0.0
Mytilus edulis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	3.2	0.5	4.9	3.7	0.1
Ophiothrix fragilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1	0.2	0.5	0.6	0.6
Ophiocomina nigra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Ophiura albida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Antedon bifida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	1.1	0.9	1.9
Ciona intestinalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.6	0.9
Ascidiella scabra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	2.8	2.3	28.8	28.8	47.9
Diplosoma listerianum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	2.3	0.1	0.0	1.0	0.7	0.6
Celeria fistulosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.2	1.0	1.3
Scrupocellaria scruposa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Diphasia rosacea	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Jassa tube	1.3	0.6	0.2	52.3	21.9	21.0	0.0	0.1	0.3	0.0	0.4	0.0	0.2	0.0	0.0
Electra pilosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	2.4	1.5	1.3	2.4	0.0
Laminaria saccharina	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	2.2	0.6	0.0	0.1	0.0	0.0
Saccorhiza polyschides	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	2.0	0.3	0.0	0.2	0.0	0.0
Sabella pavonina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.4	0.4	3.1	2.2
Metridium senile	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.3
Alcyonium digitatum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.1	0.1

Appendix 4 - Wet weight of of species groups.

(Data are average weights per gram of netting for 4 nets suspended at 14m.)

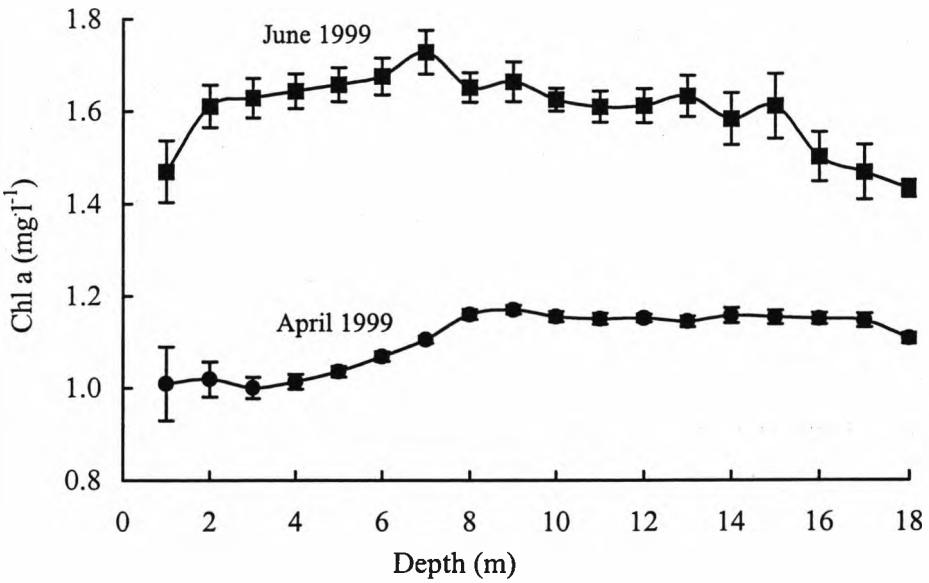
Time	1. Feb.	2. April	3. June	4. July	5. Aug.
Small hydroid	0.10	0.13	0.00	0.00	0.16
Tubularia spp.	0.10	3.74	38.89	31.32	7.47
Bougainvillia spp.	0.03	0.00	0.40	1.01	2.03
Obelia geniculata	0.16	0.14	0.00	0.00	0.00
Halecium spp.	0.00	0.08	0.00	0.45	0.18
Sabella pavonina	0.00	0.00	0.00	0.15	3.39
Nereis spp.	0.00	0.03	0.00	0.07	0.23
Harmothöe spp.	0.00	0.00	0.00	0.07	0.00
Trivia artica	0.00	0.00	0.00	0.00	0.07
Hiatella arctica	0.00	0.00	0.01	0.10	0.36
Modiolarca tumida	0.00	0.00	0.01	0.10	0.10
Mytilus edulis	0.00	0.00	0.03	3.27	15.05
Anomia ephippium	0.00	0.00	0.00	0.07	0.05
Hinia reticulata	0.00	0.00	0.00	0.07	0.10
Modiolus phaseolina	0.00	0.00	0.00	0.10	0.00
Ophiothrix fragilis	0.00	0.00	0.01	0.07	0.35
Antedon bifida	0.00	0.00	0.00	0.03	0.04
Echinoida	0.00	0.00	0.00	0.00	0.08
Ciona intestinalis	0.00	0.00	0.00	0.01	1.53
Ascidiella scabra	0.00	0.00	0.00	1.84	32.28
Diplosoma listerianum	0.00	0.00	0.00	0.00	0.48
Jassa falcata	0.10	0.91	0.94	0.07	0.00
Stenothöe marina	0.00	0.00	0.00	0.03	0.03
Endeis spp.	0.00	0.00	0.00	0.03	0.03
Hippolyte varians	0.00	0.00	0.00	0.00	0.03
Cellaria fistulosa	0.00	0.00	0.00	0.00	0.09
Electra pilosa	0.00	0.00	0.00	0.51	1.02
Cellepora pumicosa	0.00	0.00	0.00	0.03	0.08
Scrupocellaria scruposa	0.00	0.00	0.00	0.00	0.09
Diaphasia rosacea	0.00	0.00	0.00	0.03	0.03
Metridium senile	0.00	0.00	0.00	0.01	0.05
Alcyonium digitatum	0.00	0.00	0.00	0.00	0.05
Aequipecten opercularis	0.00	0.00	0.00	0.13	0.72
Dendronotus frondosus	0.00	0.00	0.07	0.16	0.06
Aeolidae	0.00	0.00	0.00	0.01	0.12
Liocarcinus puber	0.01	0.00	0.00	0.00	0.00
Inachus dorsettensis	0.00	0.00	0.00	0.00	0.01
Hyas spp.	0.00	0.00	0.00	0.07	0.02

Appendix 5 - Percentage cover of species groups during series 2.

(Data are average results for all net sufaces of three or four nets).

Time	1. February			2. April			3. June			4. July			5. August		
Depth (m)	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**	**10**	**14**	**18**
Tubularia spp.	328.6	288.3	181.4	196.2	251.8	184.2	0.8	0.6	4.9	2.5	1.4	1.7	52.8	34.7	73.9
Bougainvillia spp.	29.2	21.7	20.0	66.8	42.5	53.0	59.2	123.2	74.1	0.8	15.6	15.5	2.8	1.4	4.3
Eudendrium spp.	0.0	2.5	6.7	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halecium spp.	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.3	0.0	0.0	0.0	0.3
Aetea anguina	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Sertularia polyzonias	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	1.6	0.0	0.0	0.0	0.0	0.0	1.2
Modiolus phaseolina	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Mytilus edulis	0.0	0.0	0.0	0.4	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Anomia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Ophiothrix fragilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.3
Antedon bifida	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.3	0.0	0.3	0.3	1.1	0.0	0.3	0.0
Ciona intestinalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Ascidiella scabra	0.0	0.0	0.0	2.0	0.0	0.3	6.2	17.4	0.5	1.7	9.7	8.9	2.2	12.4	12.7
Diplosoma listerianum	0.0	0.0	0.0	6.8	4.0	1.6	11.4	5.7	2.0	9.0	6.1	5.3	20.6	34.1	30.5
Celleria fistulosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.5
Scrupocellaria scruposa	0.0	0.0	0.0	0.7	0.3	0.0	3.5	4.2	0.5	0.0	2.5	1.7	0.0	1.1	0.0
Diaphasia rosacea	0.0	0.0	0.0	0.4	0.3	0.0	0.0	2.5	0.0	0.3	0.8	0.6	0.8	0.0	0.0
Cellopora pumicosa	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.5	0.0	0.0	0.0	0.0	0.3	0.3
Crisia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Jassa tube	1.4	0.8	0.8	0.3	0.0	3.4	91.8	18.4	6.5	180.5	155.9	130.4	244.4	179.3	161.1
Antithamnion spirographidis	0.0	0.0	0.0	14.3	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 6 - The vertical distribution of chlorophyll *a*.



Changes in chlorophyll a (mean +/- SE) with depth from the surface, results are averages for replicates taken in the same area (n = 6 in June and n = 12 in April). Measurements were made between the north and south longline systems using a SeaTech fluorometer attached to a Seacat depth meter (SBE 19).

Appendix 7 - Weather conditions during net-environment studies.

Sampling dates are in bold, data are for Ronaldsway meteorological office, Isle of Man (ca. 6 miles from the sample site).

Date	Rain total (mm)	Sunshine Total (hrs)	Wind Direction (deg true)	Average Wind Speed (kt)
7 June	2.1	0.0	190	21
8 June	2.7	0.0	240	10
9 June	1.0	8.1	190	28
10 June	0.0	4.3	230	19
11 June	0.0	0.0	20	25
12 June	0.6	11.6	240	22
13 June	1.8	4.8	220	11
14 June	**0.0**	**7.7**	**150**	**9**
15 June	**0.0**	**10.0**	**80**	**11**
16 June	**0.0**	**7.9**	**240**	**11**
June average, 2000	1.2	6.4	186	15
June average, 1995-2000	2.0	7.3	217	10
14 November	15.6	0.2	210	13
15 November	0.0	6.5	280	14
16 November	0.0	2.7	290	16
17 November	4.5	0.0	255	15
18 November	1.0	3.7	290	17
19 November	0.1	3.9	300	9
20 November	4.3	0.8	120	12
21 November	**1.8**	**0.3**	**250**	**13**
22 November	**0.0**	**0.0**	**300**	**5**
Nov. average, 2000	5.5	1.8	228	16
Nov. average, 1995-2000	4.1	2.2	201	14

Appendix 8 - Order of sampling during net-environment studies.

Date	System	Sample
14-Jun	South	plaster spheres deployed
	North	plaster spheres deployed
15-Jun	South	Plankton
	South	Oxygen
	North	Plankton
	North	Ammonia / Particulate matter
	North	Oxygen
	South	Ammonia
16-Jun	North	Chlorophyll *a*
	South	Chlorophyll *a*
	South	plaster spheres retrieved
	North	plaster spheres retrieved
21-Nov	South	Chlorophyll *a*
	South	Oxygen
	North	Ammonia / Particulate matter
	North	Plankton
	South	Ammonia / Particulate matter
	South	Plankton
	North	Chlorophyll *a*
	North	Oxygen
22-Nov	South	plaster spheres deployed
	North	plaster spheres deployed
	South	plaster spheres retrieved
	North	plaster spheres retrieved

Appendix 9 - The mass transfer coefficient (*k*).

To show that $k \propto \sqrt{\frac{V}{D}}$ (where V is water velocity and D is the diameter of the plaster ball):

$N_{Sh} = 0.582\ N_{Re}^{1/2} N_{Sc}^{1/3}$ (1) (Skelland 1985)

Where N_{Sh} is the Sherwood number $\left(\frac{k\,D}{D_v}\right)$, (2)

N_{Re} is the Reynold number $\left(\frac{D\,V\rho}{\mu}\right)$ (3)

and N_{Sc} is the Schmidt number $\left(\frac{\mu}{\rho\,D_v}\right)$ (4)

In these dimensionless groups, D_v is the volumetric molecular diffusion coefficient, μ is the viscosity of the seawater and ρ is the seawater density.

Substituting equations 2, 3, and 4 into equation 1 gives:

$$\left(\frac{k\,D}{D_v}\right) = 0.582 \left(\frac{D\,V\rho}{\mu}\right)^{1/2} \left(\frac{\mu}{\rho\,D_v}\right)^{1/3} \quad (5)$$

Finally k is made the subject of equation 5:

$$k = \left[0.582\ D_v^{2/3} \left(\frac{\rho}{\mu}\right)^{1/6}\right] \sqrt{\frac{V}{D}} \quad \text{or} \quad k \propto \sqrt{\frac{V}{D}}$$

From L.Thompson, 2000 (pers. comm.).

Appendix 10 - Plankton numbers in June.

Plankton per ml of sample and the proportion of benthic organism (penante diatoms and cilitates). Numbers refer to plankton size classes: 1, 5-10µm; 2, 11-20µm; 3, 21-50µm; 4, 51-100µm; 5, >100µm. Lables identify the location; north line (n), south line (s) and treatment; open-water sites (-o), clean nets (-c), and fouled nets (-f) from where samples were taken.

	1NO	2NO	3NO	1SO	2SO	3SO	1NC	2NC	3NC	1SC	2SC	3SC	1NF	2NF	3NF	1SF	2SF	3SF
Small plankton	74	121	77	116	132	183	117	129	108	140	31	53	3931	137	3719	2536	501	531
Centric diatoms (1)	13	16	24	7	11	11	12	9	7	22	10	32	1004	69	1475	288	138	67
Centric diatoms (2)	15	1	3	2	4	1	5	0	1	8	3	1	0	1	5	26	73	9
Centric diatoms (3)	9	1	2	2	4	4	1	1	1	8	4	1	0	1	0	11	49	0
Centric diatoms (4)	7	5	8	7	6	4	7	7	1	12	6	7	5	5	3	17	37	4
Pennate diatoms (1)	22	1	2	2	4	2	5	1	0	6	1	1	19	14	8	49	104	55
Pennate diatoms (2)	6	0	1	1	3	2	3	0	1	4	1	1	11	14	5	58	82	11
Pennate diatoms (3)	1	0	0	0	1	1	1	1	0	2	1	1	5	3	0	21	34	11
Pennate diatoms (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	16	7
Diatom chains (1)	1	2	5	14	9	5	2	1	5	3	2	1	27	1	19	1	5	4
Diatom chains (2)	4	2	3	4	3	7	6	4	4	16	9	11	5	3	0	11	42	15
Diatom chains (3)	9	5	11	8	6	7	8	9	7	7	6	7	16	8	5	12	37	15
Diatom chains (4)	2	13	9	8	8	10	7	9	3	11	9	8	3	11	11	11	24	4
Chain forming diat. (1)	97	110	230	193	157	183	88	186	108	49	60	117	188	183	261	49	85	100
Chain forming diat. (2)	18	11	18	13	23	14	20	14	16	6	8	10	22	20	19	6	11	18
Chain forming diat. (3)	5	6	8	7	6	7	5	7	0	5	6	8	11	8	11	1	10	4
Chain forming diat. (4)	0	0	0	1	0	1	0	1	0	4	9	2	0	0	3	0	0	0
Pelagic ciliates (1)	2	0	1	2	1	1	4	1	2	1	0	3	5	1	3	1	2	11
Pelagic ciliates (2)	6	3	3	4	3	4	4	3	3	4	2	5	3	3	5	4	9	9
Pelagic ciliates (3)	1	0	0	3	0	2	0	1	1	2	1	1	0	1	0	4	9	2
Pelagic ciliates (4)	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	2	0
Benthic ciliates (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Benthic ciliates (2)	2	0	1	0	0	0	0	1	0	0	1	0	3	1	0	13	18	2
Benthic ciliates (3)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	2
Benthic ciliates (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dinoflagellates (1)	10	9	6	12	9	9	14	17	6	8	5	11	102	10	62	25	46	35
Dinoflagellates (2)	3	1	2	2	3	4	7	5	2	14	3	3	30	5	13	12	40	11
Dinoflagellates (3)	0	1	1	1	0	1	1	0	0	3	1	2	0	1	0	2	2	2
Dinoflagellates (4)	0	0	0	1	1	1	0	0	0	0	0	1	0	0	3	0	1	0
Flagellates (1)	11	9	6	9	19	21	12	18	7	12	3	6	977	14	597	63	52	83
Flagellates (2)	2	0	1	1	2	2	0	1	0	2	2	0	8	1	0	7	20	15
Flagellates (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Crust. holoplankton (3)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Crust. holoplankton (4)	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	2
Nematode (2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Nematode (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	1	0
Eggs and spores (1)	2	0	0	0	0	0	1	1	1	0	0	0	13	2	8	3	3	6
Eggs and spores (2)	2	1	1	0	0	0	0	1	0	3	0	0	27	5	8	16	12	4
Eggs and spores (3)	2	0	1	0	0	0	0	0	0	3	1	1	3	1	0	7	10	2
Eggs and spores (4)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	5	5	4
Meroplankton (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	7	0
Meroplankton (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	2
Phytoplankton indet. (1)	3	0	0	2	1	3	1	1	0	5	1	1	0	1	8	36	54	22
Phytoplankton indet. (2)	1	0	0	0	1	1	1	0	0	6	1	2	6	26	30	5	0	16
Phytoplankton indet. (3)	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
Zooplankton indet. (1)	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6
Zooplankton indet. (2)	1	0	2	0	0	1	0	0	0	1	0	0	0	0	0	2	2	2
Zooplankton indet. (3)	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	2	1	2
Zooplankton indet. (4)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Live indet. (1)	1	0	0	0	0	0	0	0	0	1	0	0	5	0	0	1	4	0
Live indet. (2)	1	0	0	0	2	0	0	0	0	1	0	0	3	0	0	1	12	0
Live indet. (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2
Live indet. (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Total	340	317	430	421	420	493	335	429	287	374	189	298	6435	555	6292	3339	1577	1101
% Benthic organisms	10	0	1	1	2	1	3	0	1	3	2	1	1	6	0	5	16	8

Appendix 11 - Plankton numbers in November

Plankton per ml of sample and the proportion of benthic organisms (pennate diaoms and cilitates). Numbers refer to plankton size classes: 1, 5-10µm; 2, 11-20µm; 3, 21-50µm; 4, 51-100µm; 5, >100µm. Lables identify the location; north line (n), south line (s) and treatment; open-water sites (o), clean nets (c), short-fouled nets (s-f), and long-fouled nets (l-f) from where saples were taken.

	1NO	2NO	3NO	1SO	2SO	3SO	1NC	2NC	3NC	1SC	2SC	3SC	1NS-F	2NS-F	3NS-F	1SS-F	2SS-F	3SS-F	1NL-F	2NL-F	3NL-F	1SL-F	2SL-F	3SL-F
Small plankton	37	21	26	20	26	39	30	51	35	34	32	26	31	27	33	29	26	24	33	33	259	10	12	658
Centric diatoms (1)	1	3	1	1	2	1	10	5	2	2	0	4	3	1	2	1	1	2	1	4	9	1	4	21
Centric diatoms (2)	2	2	1	3	3	4	3	2	2	2	3	1	1	2	2	1	2	1	2	3	2	2	2	1
Centric diatoms (3)	3	2	1	2	1	1	4	2	2	3	1	2	0	2	2	1	1	1	2	3	3	2	2	1
Centric diatoms (4)	1	1	0	1	1	1	1	1	0	1	1	1	0	1	0	0	1	1	2	0	1	0	1	0
Pennate diatoms (1)	2	1	1	0	1	1	5	5	2	2	2	1	1	0	2	1	1	1	2	1	1	1	2	1
Pennate diatoms (2)	0	0	1	1	0	0	1	1	1	2	0	0	1	0	1	0	1	1	2	0	1	2	1	1
Pennate diatoms (3)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	1
Pennate diatoms (4)	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diatom chain (3)	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Chain forming diat. (1)	1	0	0	0	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0
Chain forming diat. (2)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pelagic ciliates (1)	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelagic ciliates (2)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Dinoflagellates (1)	11	9	10	4	9	9	6	5	4	3	8	6	6	4	7	5	6	4	9	9	5	8	11	7
Dinoflagellates (2)	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0
Dinoflagellates (3)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Flagellates (1)	32	24	25	16	26	35	37	27	1	23	24	26	17	21	28	21	16	21	22	20	11	13	17	17
Eggs and spores (1)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eggs and spores (2)	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2
Eggs and spores (3)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Live indet. (1)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	4	0	0	0	0	0
Live indet. (2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Live indet. (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Total	91	63	68	51	72	94	103	105	54	77	74	68	66	58	83	62	59	62	86	79	296	41	55	713
% Benthic orgaisms	2	2	2	4	2	2	6	6	8	6	3	2	4	1	4	2	4	4	7	4	1	8	5	1