COMMISSIONED REPORT

Commissioned Report No.251

Conservation of the Native Oyster Ostrea edulis in Scotland

(ROAME No. F02AA408)

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COMMISSIONED REPORT

Summary

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Background

Native oyster (*Ostrea edulis*) populations in Scotland have declined significantly in abundance and distribution since the 19th century, mainly as a result of over-exploitation. Most of the remaining populations are thought to exist in west coast sea lochs. The native oyster is the subject of a UK Species Biodiversity Action Plan, the Native Oyster Species Action Plan (NOSAP), so there is a requirement to consider what conservation measures are appropriate.

This project aimed to develop advice on the conservation management of the native oyster in Scotland, based on an assessment of the current status of extant populations, reviews of the history of oyster exploitation in Scotland, and conservation and fisheries management practices in the UK and elsewhere. Sites throughout the west and north coasts of Scotland were surveyed for oysters and detailed population studies were carried out at three of these sites.

Main findings

- Native oysters occur mainly in small, scattered populations fringing sea lochs around the west and north coasts of Scotland, usually at low population density. The only managed fishery is in Loch Ryan, which appears to have a large, self-sustaining population. There is evidence of unlawful gathering of oysters on a wide scale having a severe impact on small populations.

- Population density and abundance at the Argyll sites were within the range of estimates for other British and European populations, but were much lower than in Loch Ryan at present and in the Firth of Forth historically.

- Native oysters were attached to all hard materials surveyed, but with an apparent preference for oyster shell and other shell types (‘cultch’). However, shell material was sparse and patchy. There was no evidence of competition for space with other sessile species surveyed.

- Detailed analysis of the small-scale distribution of oysters indicated a potential for limited reproductive success, owing to the distances between adult oysters. Sparseness and patchiness of oysters is probably exacerbated by a lack of cultch and by unlawful gathering.

- Genetic analyses indicated that past translocations of oysters have probably masked any former local differences, but more-widely separated populations can still be differentiated. A Skye population appeared very distinctive, but was represented by only a small sample, so further studies are desirable to ascertain whether this population is deserving of special conservation status.

A range of management measures were reviewed in relation to their applicability to conserving native oysters in Scotland. Low population densities and unlawful gathering are the two key issues to be addressed. Effective control of unlawful gathering is essential if remaining populations are to persist. Measures to increase broodstock density or habitat availability may also be required to sustain some populations.

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CONSERVATION OF THE NATIVE OYSTER, *OSTREA EDULIS*, IN SCOTLAND

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1 INTRODUCTION

1.1 The Native Oyster Species Action Plan

At the Rio Earth Summit in 1992, the Convention on Biological Diversity was agreed and signed by 159 governments as part of a strategy to protect global biodiversity. The goals of the Convention were "…the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits from the use of genetic resources" (Anon., 2005). Article 6 of the Convention stated that countries were to develop national strategies for the conservation and sustainable use of biodiversity. In response, the U.K. government held a two-day seminar to discuss the key issues with respect to Britain and published "Biodiversity: the U.K. Action Plan" (1994), which outlined the strategy for the conservation of national biological diversity in the United Kingdom (U.K.). The "U.K. Biodiversity Steering Group" was also created in 1994, which published "Biodiversity: the U.K. Steering Group Report – meeting the Rio Challenge". This provided criteria for identifying threatened and declining key species and habitats throughout Britain and set targets for protecting national biodiversity. The U.K. Government endorsed the initiative in 1996 and six volumes of Action Plans were published, encompassing 391 species action plans (SAPs), 45 habitat action plans (HAPs) and 162 local biodiversity action plans (BAPs) (Anon., 2004a). Volume 5 of the Tranche 2 Action Plans, specific to British maritime species and habitats was published in 1999. The native European flat oyster (*Ostrea edulis* L.) was identified therein as a "priority species" and assigned a species action plan – the Native Oyster Species Action Plan.

O. edulis is a sessile bivalve mollusc of the family Ostreidae, class Pelecypoda. It is distributed throughout Europe from Norway to the Black Sea (Anon., 2003) and has been cultivated in Europe since Roman times (Plinius, 1st century; Günther, 1897; Yonge, 1960). However, several factors have contributed to a decrease in abundance and contraction in range of native oyster stocks throughout Europe, principally since the 19th century. In Britain, these factors have included high levels of commercial exploitation during the 19th and 20th centuries (Anon., 1885-1977; Orton, 1927), unlawful exploitation (Anon., 1885-1977; Guillotreau & Cunningham, 1994; Anon., 1997; Donnan, 2003), mass mortality caused by severe weather events (Anon., 1885-1977; Orton, 1940; Cole, 1956; Waugh, 1964), disease (Orton, 1923; Cole, 1951) and predation by and competition with indigenous and non-indigenous species (Cole, 1951; Utting & Spencer, 1992). Lowered reproductive output has also been linked with tri-butyl tin (TBT) pollution, which retards the alternation between sexes and inhibits larval production in *O. edulis* (Thain, 1986). Current estimates of the abundance of stocks around Britain are much lower than those made during the 1800s and many beds have been extirpated. As a result of the decline of the species around Britain, the stated objectives and targets of the Native Oyster Species Action Plan are to maintain and increase the abundance of the native oyster stocks, and expand the existing geographical distribution within U.K. inshore waters (Anon., 1999).

1.2 Current status of *Ostrea edulis* stocks in the United Kingdom

"The U.K. Biodiversity Action Plan – Native Oyster Species Information Review" was published in 2001, highlighting the current known distribution, abundance and fisheries exploitation of stocks around the United Kingdom (Gardner & Elliot, 2001). Complementary to this review, research initiatives are in progress to assess the main issues affecting the stocks and aid the development of practical measures to meet the aims and objectives of the Native Oyster Species Action Plan.

1.2.1 England and Wales

Scattered wild populations of *O. edulis* are found around the coastlines of England and Wales. Over the past two centuries, the majority of the populations have been commercially exploited at high levels and have been reduced to low levels of density and abundance (Gardner & Elliot, 2001). For example, current density estimates of *O. edulis* in Milford Haven, Wales, are less than 0.2 oysters per m^2 (Cooke, 2003). Although the current density and abundance of many of these natural populations are thought to be low, several are of sufficient abundance to sustain small-scale fisheries, managed under Several or Regulating Orders (Gardner & Elliot, 2001). Cultivation of native flat oysters is also practised in many areas. Typical management practices for both cultivated and fished stocks involve a combination of relaying of broodstock and juveniles, cultch (dead shell) supplementation and harrowing to decrease silt layers on settlement material and therefore increase spat settlement opportunities (Gardner & Elliot, 2001).

Since the 1980s, infection by the protistan disease-forming *Bonamia ostreae* has caused high levels of mortality in localised stocks of *O. edulis* in England. *B. ostreae* is a parasitic haplosporidian that infects the haemocytes of *O. edulis*, causing discoloration and ulcers on the gill and mantle tissues and adult mortality levels up to 60% in infected stocks (ICES, 2005). It was first discovered in Normandy (France) in 1979, with the translocation of infected oysters causing the spread of the disease elsewhere in Europe. There has been widespread mortality of cultivated and fished stocks since the introduction of the parasite to England in the 1980s. A significant body of research has now been published investigating the life cycle of *B. ostreae* and the development and selective breeding of *Bonamia*-resistant stocks (see www.bonamia.com for recent publications). Oyster stocks in England and Wales are also subject to competition from slipper limpets (*Crepidula fornicata*) and predation by the whelk tingle (*Urosalpinx cinerea*), both non-indigenous species introduced with consignments of oysters from America during the 19th century (Utting & Spencer, 1992).

There are several initiatives in England contributing to the goals of the Native Oyster Species Action Plan. Oyster beds at the Holy Isle (Northumberland) have been restocked, although the success of this action has not been published (C. Askew, pers. comm., 2005). There has been research into the effects of cultch type and stocking density on the survival and immunocompetence of *O. edulis* larvae and quantification of the competitive interactions with *C. fornicata* (Hawkins *et al*., 2005). Upcoming research will investigate the effects of harrowing and the development of pond-culture methods for spat production with the aim of restocking *O. edulis* populations in southern England (C. Askew, pers. comm., 2005).

1.2.2 Northern Ireland

Lough Foyle, Larne Lough, Strangford Lough, Inner Dundrum Bay and Carlingford Lough are the main sites in Northern Ireland commercially exploited for *O. edulis* (Gardner & Elliot, 2001). Lough Foyle is the only site with a natural bed that is still commercially exploited, although the site was restocked with spat in the 1970s (Gardner & Elliot, 2001). Although *B. ostreae* is known to infect natural populations in Eire, the parasite has not been discovered in Northern Ireland (Culloty & Mulcahy, 2001).

The Centre for Marine Resources and Mariculture (C-Mar), Queen's University, Belfast, has carried out research into *O. edulis* in Northern Ireland funded by the Department of Agriculture and Rural Development. This research has focussed on restoring the stocks and fishery of Strangford Lough. High levels of exploitation in the late 19th century led to the depletion of these stocks (Kennedy, 1999). Initial surveys of oyster population density, abundance and spatfall within the Lough were made in 1997. It was concluded that the density and abundance of the population was insufficient to allow natural regeneration of the stocks. Spatfall in the area was attributed to the cultivation of an imported *O. edulis* stock in Reagh Bay (Kennedy & Roberts, 1999). The availability of suitable settlement substrata was also found to be low. In 1996/97 there were importations of spat and adult broodstock and cultch material was supplemented to increase the habitat available for larval settlement.

The second phase of research in Northern Ireland has included further surveys of density, abundance and spatfall in 2003/04 to assess the impact of the restocking programme, and has furthered research into a supportive breeding programme. The findings of this research have yet to be published but the results are anticipated to form the basis of management for a long-term sustainable fishery programme (Anon., ca. 2003).

1.2.3 Scotland

Despite the compilation of the Native Oyster Information Review (Gardner & Elliot, 2001), there is a paucity of up-to-date information regarding the status and demography of wild *O. edulis* stocks in Scotland. Past efforts to conserve wild stocks or determine the suitability of stocks for commercial exploitation have provided an indication of where oyster beds have been present in the past, and provide some demographic history (Anon., 1885-1977; Millar, 1961; Bunker, 1999). After the collapse of the main flat-oyster fisheries in the early 20th century, two large-scale investigations were conducted into restoring the flat-oyster stocks of Scotland. During the early 1920s, the Fishery Board for Scotland attempted to restore beds along the west coast by relaying thousands of oysters originating from Skye and Holland. A lack of funding resulted in the termination of the project in 1923, two years after it was initiated. There are no records of the outcome of this project (Anon., 1885-1977).

During the 1950s, Dr Robin Millar, of the former Scottish Marine Biological Association conducted the second large-scale research project into the status and restoration of native oyster stocks in Scotland with the goal of developing commercial fisheries (Millar, 1961). This research involved documenting the presence or absence of oysters in locations around Scotland historically known for oyster production. In addition, the growth, "fattening" and reproductive potential of several stocks (wild and imported) were also investigated. During this research, thousands of *O. edulis* from Brittany (France) were imported and re-laid in Linne Mhuirich, West Loch Tarbert, Loch Ryan and a quarry on Easdale Island (Argyll). It was concluded that Loch Ryan was the most suitable area in Scotland for the breeding and growth of oyster populations. Linne Mhuirich was also satisfactory although the area available for the development of a fishery was small. Restocking using foreign broodstock and the establishment of hatcheries were suggested as methods of increasing stock abundance in areas considered for restoration and fishery exploitation. Millar also regarded Scottish sites suitable for oyster cultivation because non-indigenous pests and diseases were not present, and warned that stock should not be brought in from areas where such non-indigenous species were present. However, the main disadvantage to the development of oyster fisheries in Scotland was that commercial development of the beds would involve high transportation costs because the sites were remote. Other small-scale surveys of specific populations have been made for either conservation (Connor, 1990; Harding, 1996; Bunker, 1999) or commercial interests (Anon., 2004b), but these have not contributed directly to any national research or management plans for the species.

1.3 Conservation and restoration of *Ostrea edulis* stocks in Europe

Throughout the early history of the European fisheries for *O. edulis*, the re-laying of juveniles and broodstock was the principal method of preventing the depletion of commercially exploited stocks (Anon., 1885-1977; Korringa, 1946; Cole, 1951; Yonge, 1960). However, this practice contributed to the depletion of donor stocks, such as the Firth of Forth (Anon., 1885-1977; Yonge, 1960), and generally did not prevent the collapse of fisheries that were exploited at high levels (Key & Davidson, 1981).

The first large-scale collapse of fisheries and associated restoration of stocks occurred in France. Peak landings of 100 million oysters per year were recorded in the early 19th century but by the mid-19th century, local populations had become extirpated and exploitation of the remaining beds was no longer economically viable (Yonge, 1960). The restoration of the French *O. edulis* fisheries was attributed to the efforts of Monsieur Coste, a French embryologist, who introduced Italian methods of oyster cultivation based on the formation of stone reefs, to the French environment. Coste formed “oyster parcs” by laying tonnes of shell cultch and broodstock, and providing additional fascines (bundles of sticks) as spat collectors. Trials in the Bay of Brieuc were so successful that “parcs” were constructed throughout the depleted oyster-producing regions. Following initial success in restoring oyster beds, rapid progress was made in France in the development of oyster cultivation methods. Firstly, the French developed a method of collecting spat on stacks of semi-cylindrical roof tiles that were covered in a friable cement of sand and lime, allowing easy removal of the spat. Stacks of tiles provided a protected substratum for the larvae to settle and grow upon until they were collected. Secondly, the French developed “ambulances”, wire covered trays into which the spat were placed after removal from the tiles. These ambulances protected the spat from predators until they were large enough to be re-laid on the exposed “parcs” (Yonge, 1960). The French method of restoration, using a combination of cultch supplementation, spat collectors and the importation of broodstock, was also used to restore the stocks of *O. edulis* in the Oosterschelde, Netherlands, in the late 1930s (Korringa, 1946).

In the late 1800s, restoration of depleted stocks of *O. edulis* in Norway took a different approach. Although natural beds of *O. edulis* were found in sheltered areas around the coastline, natural inlets from the main fjords, called “polls”, provided the most sheltered environment with water temperatures suitable for larval development. However, the muddy substratum of the polls was unsuitable for laying oysters, so broodstock and cultch material for spat collection was suspended in the water column (Korringa, 1976). Hanging culture dates back to the 4th century, when the Romans used this method for oyster cultivation in what is now Italy (Yonge, 1960). This method has not often been recorded in recent literature as a technique with commercial applications, but is appropriate for cultivation in areas where the substratum is unsuitable for laying oysters directly on the ground. In conclusion, the combination of creating a suitable and protected environment for reproduction and growth of oysters has been key to the re-establishment of *O. edulis* stocks in other European countries.

Investigations into habitat suitability for *O. edulis* in Britain have mostly been limited to the settlement of larvae onto different cultch types (Knight-Jones, 1952; Millar, 1961; Kennedy &

Roberts, 1999; Palmer, 2002), although few studies have related this to the availability of cultch in the natural environment (Kennedy & Roberts, 1999). Throughout the history of *O. edulis* fisheries in Britain, there has been widespread use of cultch supplementation usually by adding dead, clean shell material to increase spat settlement (Gardner & Elliot, 2001).

Importations of broodstock have also been used extensively to restore degraded fisheries in Britain (Millar, 1961; Key & Davidson, 1981; Gardner & Elliot, 2001) and are still being recommended as a method for restoring depleted populations (Kennedy & Roberts, 1999; Laing *et al*., 2005). It has been suggested that millions of broodstock oysters are necessary to ensure the restoration of a population (Korringa, 1946; Laing *et al*., 2005). However, there is a lack of research on the number of individuals necessary for the long-term survival of unexploited populations of *O. edulis*. Furthermore, there are no recorded long-term population surveys of density or abundance available for the existing populations of *O. edulis* in Scotland, including those commercially exploited. In comparison, in England, the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) makes annual assessments of the *O. edulis* stocks in the Solent and the Fal estuary. Accurate monitoring of stocks is necessary to assess the success of any management measures aimed at restoring, maintaining or improving the growth of populations.

A comprehensive Cost-Benefit Analysis was prepared by CEFAS, comparing a range of strategies for restoring depleted and extirpated *O. edulis* populations in Britain (Laing *et al*., 2005). The main restoration strategy proposed consisted of enhancing the natural habitat by laying cultch and importing sufficient disease-free stock to establish a naturally-regenerating population. The factors identified as potentially limiting the success of restoration programmes included disease, pests, the availability of suitable substratum and current population density and abundance. Accordingly, it was suggested that initial restoration attempts be made in areas free from pests, disease and pollution. It was suggested that restoration programmes should be supported for at least 25 years to ensure success. Stakeholder participation in management plans was also identified as being fundamental to the success of any programme.

1.4 Research Aims and Objectives

The aims of the research were to assess the status of *O. edulis* in Scotland and to present suitable guidelines for the conservation of the native oyster in Scotland. Specifically, the objectives were:

- To conduct a review of existing data on oyster abundance and distribution in Scotland to give an historical perspective;
- To conduct a review of native oyster management practices within the U.K. and in comparable oyster fisheries overseas;
- To assess the current status of oyster stocks via a survey of representative sample locations in Scotland;
- To assess the demography of oyster populations at selected study sites;
- On the basis of the results, to prepare advice on the conservation management of the native oyster in Scotland.

1.5 Study Sites

Three study sites on the west coast of Scotland were selected for detailed investigations of oyster demography: West Loch Tarbert (Argyll), Linne Mhuirich, Loch Sween (Argyll) and Loch Ailort (Highlands) (Figure 1.1). These sites were chosen because they contained the greatest population densities within the water bodies visited, as indicated by past work, local knowledge and preliminary site surveys. Furthermore, most sites could be accessed even during stormy weather conditions. Additional sites on the west and north coasts and the islands of Scotland were also visited (Figures 1.1, 6.2a). Basic demographic data were obtained for these sites and oysters removed for genetic studies.

1.5.1 West Loch Tarbert

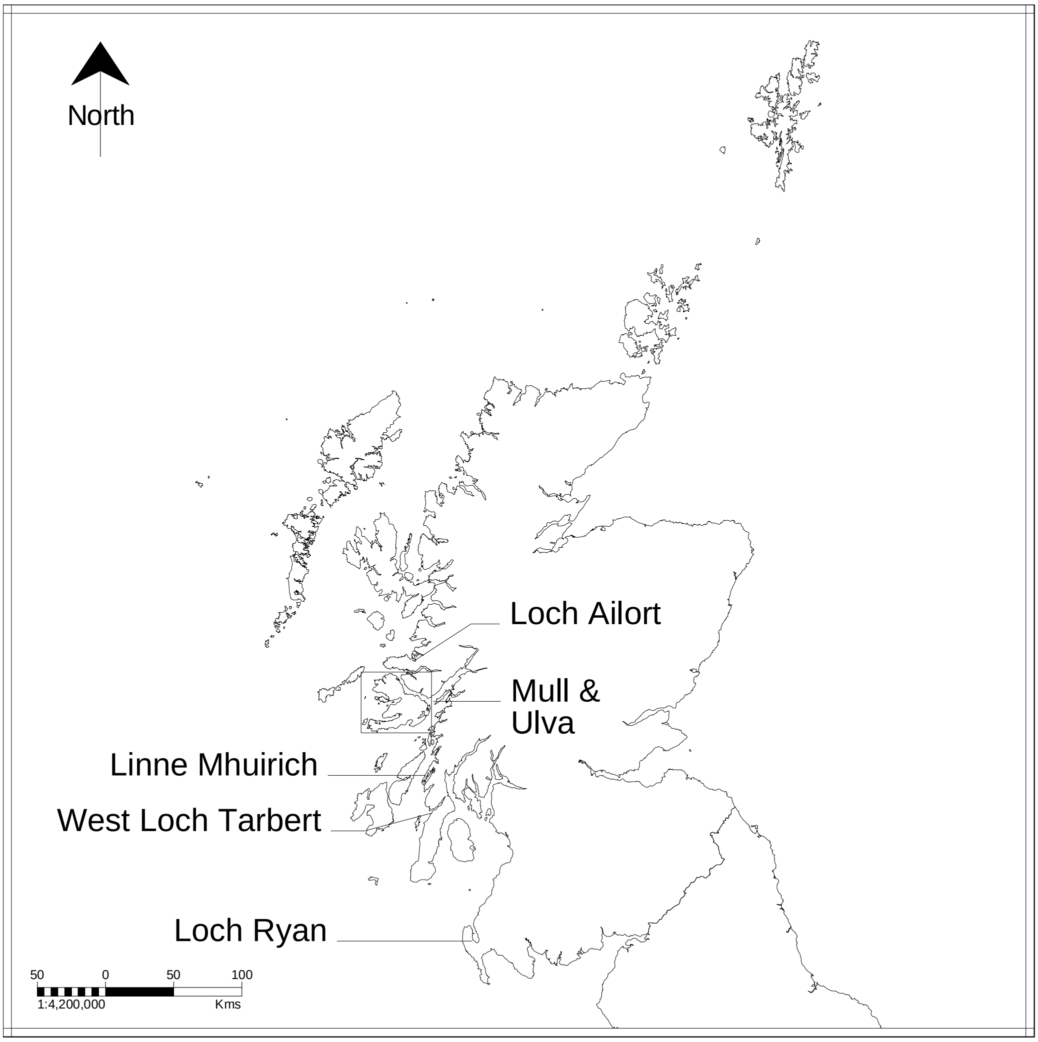
West Loch Tarbert (Argyll) is 16 km long with a shallow sill of 8 m depth at the mouth of the loch (Edwards & Sharples, 1986). The basin behind the sill reaches a depth of 32 m, although the majority of the loch has a maximum depth of approximately 10 m (Millar, 1961; Howson, 1990). There are large sediment banks at the head of the loch and at the sill, and 23% of the loch bed is intertidal (Howson, 1990). The tidal range (between mean high and low water springs) is 0.9 m (Edwards & Sharples, 1986) and the tidal pattern is irregular (Lewis & Powell, 1960). Two rivers discharge into West Loch Tarbert: the Abhainn na Cuile at the head of the loch on the north-west shore (NR830680) and the Bardaravine River next to Wood House (NR830650). Freshwater run-off was estimated at approximately 1.37×10^6 m^3 y^{-1} and the salinity reduction as 20 (Edwards & Sharples, 1986). Millar (1961) found that reduced salinity conditions were generally confined to the uppermost layers with minimal reduction in salinity near the sea bed.

The study sites in West Loch Tarbert (WLT1 and WLT2) were characterised by a gentle slope with mud or mixed sediment at WLT1 and a combination of coarse and mixed sediments at WLT2. Bedrock was present along the littoral fringe and was covered by biogenic reef (*Mytilus edulis*) in some places. The habitat in the lower infralittoral is mud (Millar, 1961). Underwater visibility was generally poor during site visits (<2 m) due to high turbidity. After storms, visibility dropped to less than 1 m.

Temperature was recorded every hour using a VEMCO© "Minilog" placed on the sea bed in subtidal waters alongside the slipway at Rhu. Data are available from 9 February 2004 to 12 December 2005. In 2004, the average monthly temperature ranged from 5.5°C in February to 19.4°C in May (Table 1.1, Figure 1.2a), with the daily average temperature ranging from 3.3°C in February to 21.9°C in May. In 2005, the monthly average temperature ranged from 6.8°C in January to 17.2°C in July (Table 1.1, Figure 1.2a), with the daily average temperature ranging from 5.4°C in January to 19.7°C in July.

Most of the lands adjacent to the sites are owned and managed by the Forestry Commission. There are a few scattered houses in the vicinity of the study sites. *Crassostrea gigas* are cultivated near the mouth of the loch by Seacroft Oysters (NR760590). There is also a pier at the head of the loch where a small number of fishing boats are moored.

Figure 1.1 Map of Scotland showing the location of main research sites



The oyster populations located at WLT1 and WLT2 have been unlawfully exploited in recent years. There were several reports of unlawful gathering of native oysters at WLT2 during the period of the present research. Oysters had been placed in cages in the subtidal waters around WLT2 for monitoring growth for the present study. It was discovered in March 2005 that the cages had been slit open and the oysters removed.

1.5.2 Linne Mhuirich (Loch Sween)

Linne Mhuirich is an arm of Loch Sween (Argyll) and is approximately 4 km in length, with a breadth of between 200 to 500 m (Millar, 1961). There is a maximum depth of 13 m in the lower reaches, although the majority of Linne Mhuirich is less than 3 m deep. Linne Mhuirich is separated from Loch Sween by a narrow channel with a maximum depth of 3 m, known as the “Linne Mhuirich Rapids” (Lumb, 1986). The tidal range is 0.67 to 0.85 m (Millar, 1961). The tidal pattern is irregular and is influenced by local weather regimes (Lewis & Powell, 1960). The catchment of Linne Mhuirich is considered to be small and it is thought that salinity is not reduced greatly by freshwater runoff and precipitation (Millar, 1961).

The chosen study sites (LM2 and LM1) were in the sublittoral fringe and upper infralittoral areas of Linne Mhuirich. The habitat has a very gentle slope with coarse sediment and rock. Underwater visibility was always good during site visits (>3 m). Temperature was recorded every hour using a VEMCO© “Minilog” placed in the subtidal waters near the centre of the LM1 oyster bed. Data are available from 26 January 2004 to 12 December 2005. In 2004, the average monthly temperature ranged from 5.3°C in January to 17.4°C in August (Table 1.1, Figure 1.2b), with the daily average temperature ranging from 4.0°C in February to 18.9°C in August. In 2005, the average monthly temperature ranged from 6.1°C in February to 17.1°C in June (Table, 1.1, Figure 1.2b), with the daily average temperatures ranging from 3.9°C in February to 21.4°C in May.

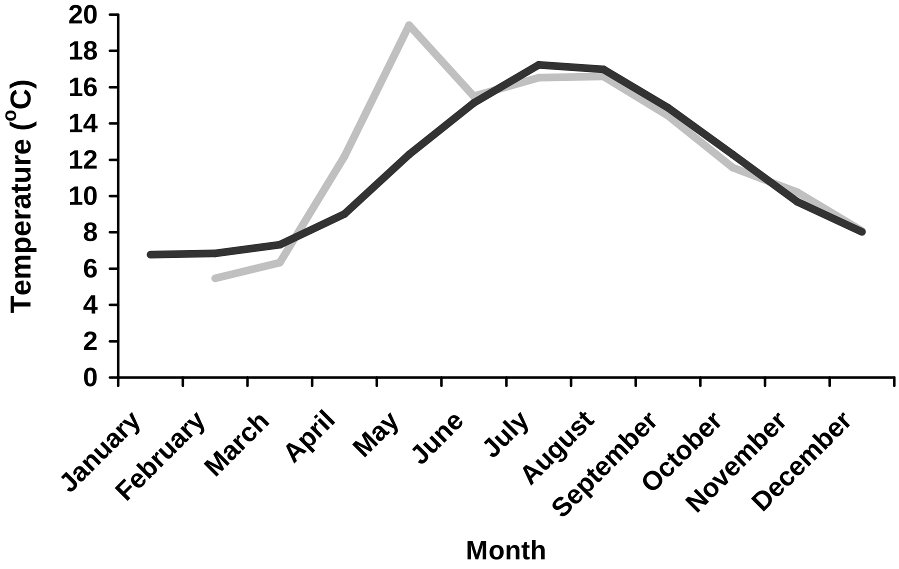
The oyster population at LM2 has been unlawfully exploited in recent years with numerous reports during the period of the present research.

Table 1.1 Mean monthly temperatures for Linne Mhuirich and West Loch Tarbert in 2004 and 2005.

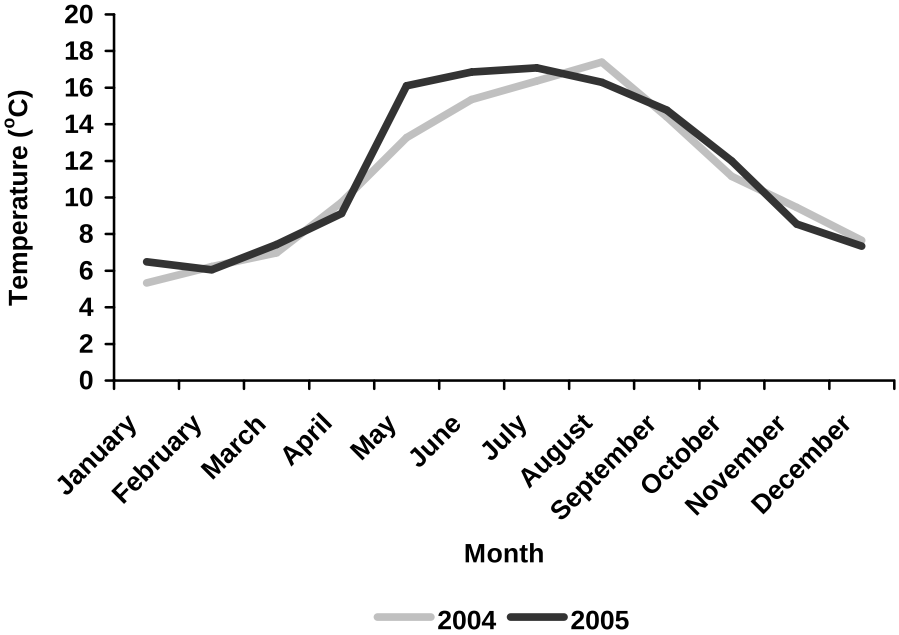
Month	**West Loch Tarbert**		**Linne Mhuirich**	
	2004	**2005**	**2004**	**2005**
January	---	6.8	5.3	6.5
February	5.5	6.8	6.2	6.1
March	6.3	7.3	7.0	7.4
April	12.2	9.0	9.7	9.1
May	19.4	12.3	13.3	16.1
June	15.5	15.1	15.4	16.9
July	16.5	17.2	16.4	17.1
August	16.6	17.0	17.4	16.3
September	14.4	14.9	14.4	14.8
October	11.6	12.3	11.2	12.0
November	10.2	9.7	9.5	8.5
December	8.1	8.0	7.7	7.3

Figure 1.2 Mean monthly temperatures in 2004 and 2005. (a) West Loch Tarbert. (b) Linne Mhuirich.

a.



b.



1.5.3 Loch Ailort

Loch Ailort (Highlands) is 8.1 km long and contains 3 sills. There is a maximum depth of 43 m in the upper reaches of the loch. The mean tidal range is 4.3 m. Several large burns discharge into Loch Ailort and runoff is estimated at 1.34×10^6 m^3 y^{-1} and the reduction in salinity is estimated at 8.8 (Edwards & Sharples, 1986).

The chosen study sites (LA1 and LA2) were in the sublittoral fringe and infralittoral area of Loch Ailort. The majority of this bay is intertidal. The bay is adjacent to a basin bounded by a 5 m deep sill to the east and 4 m deep sill to the west. The maximum depth of this basin is 14 m. The site has a very gentle slope and is dominated by coarse sediments and bedrock. A burn discharges into the loch at the north-west corner of the bay. Underwater visibility was generally good during site visits (>2 m) with low turbidity. Water temperature was not recorded at this site.

The shores to the north of this bay are part of the Ardnish Estate and are not cultivated or used for pasture. An oyster hatchery is being established to the east of Eilean na Gualainn (NM720790). The owners of this development have collected approximately 400 oysters from the southern shores of Loch Ailort. These oysters are kept in cages and used to monitor growth (M. Cooper, pers. comm., 2003). Marine Harvest operates salmon cages at the head of the loch with onshore facilities at Kinlochailort. *C. gigas* are cultivated on trestles by Mr H. MacLaren at the head of the loch on the shore adjacent to Kinlochailort. Abandoned mussel lines are situated to the east of Eilean nan Trom.

Unlawful gathering of oysters from Loch Ailort has been reported in recent years and from the bay to the east of Eilean nan Trom during the period of the present research.

2 THE SCOTTISH OYSTER FISHERIES: AN HISTORICAL REVIEW

2.1 Introduction

The importance of *O. edulis* as an exploited biological resource in Scotland has fluctuated throughout history. Oyster beds were once numerous throughout Scotland and were important to local people as a source of protein (Anon., 1885–1977; Young, 1886; Millar, 1961). As early as the 14th century, oyster beds were used for economic purposes, such as rent and tax payments (Young, 1886). By the 18th century, the fisheries were commercial and supplying a European market, with the abundance of high quality oysters supporting the success of the Scottish oyster fisheries (Anon., 1885–1977). However, economic success, in combination with inefficient management, resulted in the exhaustion of the oyster stocks and the decline of the fisheries. There were several unsuccessful attempts to revive the fisheries during the 20th century (Anon., 1885–1977), but by the 1950s, all the commercial native oyster fisheries had collapsed (Millar, 1961; Hugh-Jones, 2003). The stocks were left either totally exhausted or in a state of serious depletion. In order to protect the stocks that have survived to the present day and preserve this part of the biological heritage of Scotland, conservation and perhaps restoration efforts are necessary. Lessons from history allow us to understand the factors responsible for the original decline of the beds and prevent their recurrence. This review documents the history of the main oyster producing regions and the rise and fall of the Scottish oyster fisheries, based predominantly on the information from the Fishery Board for Scotland Annual Reports (1885–1977) and Millar (1961).

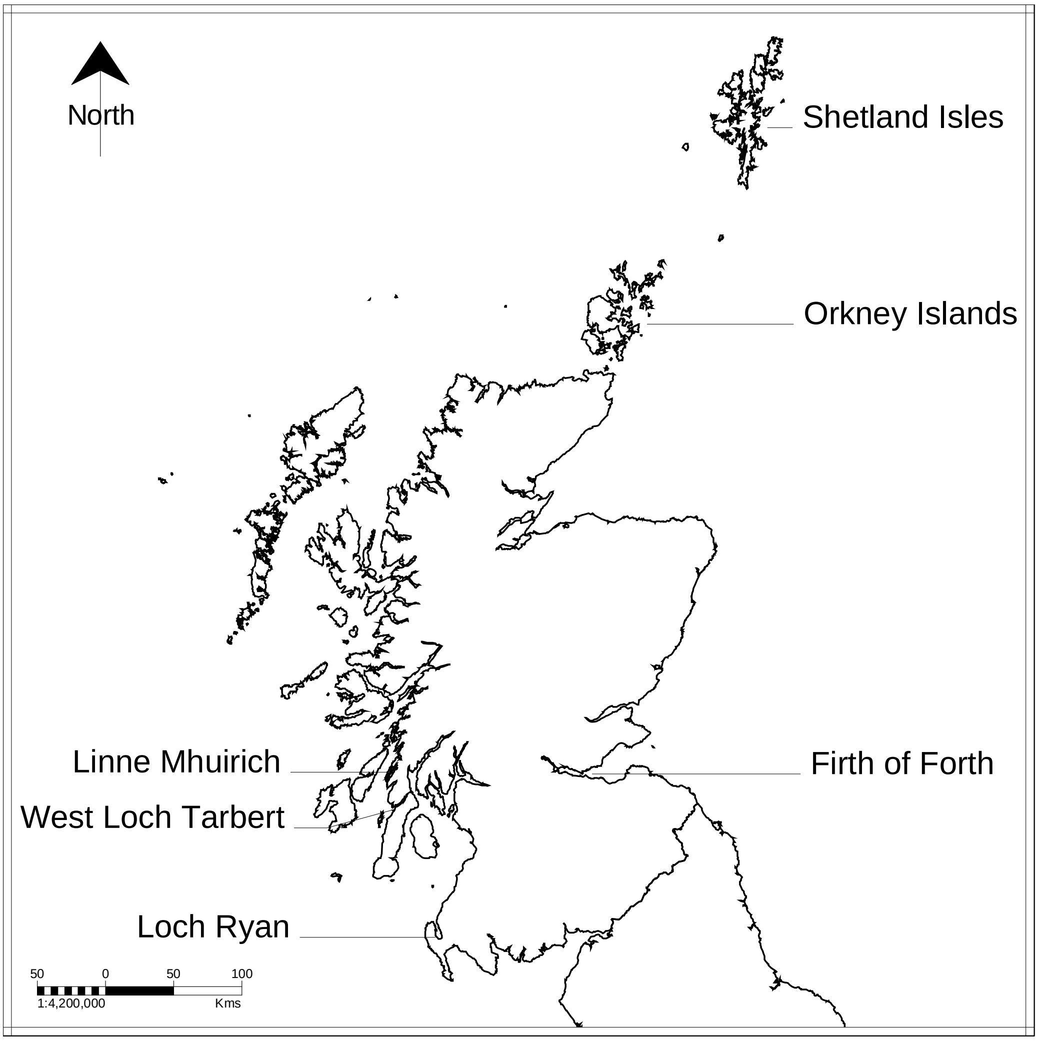
2.2 The west coast fisheries

Oyster beds along the west coast and around the islands of Scotland were once numerous, reflecting the availability of suitable habitat within the many sheltered bays formed by the rugged and indented coastline. Shell middens excavated around Scotland have indicated the pre-historic importance of oysters as a source of dietary protein since Mesolithic times (Anon., 1885–1977; Young, 1886; Mellars & Andrews, 1987; Coull, 1996). Prior to the development of commercial fisheries during the 17th century, many rural communities harvested local beds for subsistence use. Certainly, *O. edulis* continued to be a common dietary component for Scots until oysters started to become scarce during the late 1800s. From that time onwards, the main oyster beds contributing to commercial landings of *O. edulis* were in Loch Ryan, West Loch Tarbert, Orkney and Shetland (Figure 2.1). By the end of the 19th century, while other beds throughout Scotland were dwindling, production in Loch Ryan and West Loch Tarbert was sustained by cultivation. The oyster beds in Linne Mhuirich, Loch Sween (Figure 2.1) were also cultivated but did not contribute to commercial landings.

2.2.1 Loch Ryan, Ballantrae district

The Ballantrae district was historically the second most productive area for *O. edulis* in Scotland after the Leith fishery district on the east coast. Several natural oyster beds within Ballantrae allowed the formation of small fisheries such as Farlieston Bay, Luce Bay and Wigtown Bay, all of which were exploited to exhaustion and abandoned by the late 19th century. The productivity of the district though was largely due to the Loch Ryan fishery, which became the major producer in Scotland throughout the 20th century.

Figure 2.1 Map of Scotland showing the location of the principal oyster fisheries and cultivation sites in Scotland from the 18^{th} – 20^{th} century.



The right to gather oysters in Loch Ryan was originally granted to Captain Andrew Agnew and his wife Margaret in 1701 and subsequently passed to the Wallace family (Shaw & Dunlop, 1824; pers. comm., D. Hugh-Jones, 2005). Written records for the fishery exist only from 1884, although Lt Col. W.T.F.A. Wallace reported in 1876 that oysters had been gathered from Loch Ryan since the early 1800s and there were court cases concerning the Loch Ryan fishery in 1822 and 1866. In order to prevent the depletion of stock, the Wallace family regulated the oyster fishing in Loch Ryan. However, the right to gather oysters from the intertidal sand-bank known as the “Spit” was not included in the Loch Ryan charter. The Spit was reported to “abound with oysters” and local fishermen gathered from this area in an uncontrolled and unregulated manner until the population was exhausted. This gathering was unlawful, but the Crown, which owned the fishing rights, did not prevent this exploitation (Young, 1887). The fishery regulated by the Wallace family also suffered from unlawful exploitation, but a lack of evidence prevented many prosecutions at that time. Nevertheless, the Loch Ryan fishery established itself and became the principal contributor to Scottish oyster landings from the early 1900s.

Records show that the landings from the fishery fluctuated greatly with periods of intense exploitation and high landings followed by rapid declines in production (Hugh-Jones, 2003). Peak production was reached in 1913, when landings of over 1.3 million oysters were recorded. During this period, 30 boats were landing approximately 130 tonnes annually. Over the next few years, production declined rapidly as the effects of sustained high exploitation levels took their toll. Landings continued to fall until 1957, when the fishery was deemed uneconomic (Millar, 1968; Hugh-Jones, 2003). Millar (1961) concluded that the persistence of the Loch Ryan fishery until this time was a result of private ownership and the associated supervision, maintenance and control of the fishery by the proprietors.

Experimental cultivation aimed at restoring the fishery commenced in 1957, with the introduction of many thousands of Brittany oysters by the Scottish Marine Biological Association (Millar, 1963). Millar (1961) commented that there had been other importations from France, Holland and Essex throughout the history of the fishery, but these had gone unrecorded. The fishery was resumed in 1976 under the management of the Colchester Oyster Fishery Company, with four working boats landing 61 tonnes of oysters annually. Under the management of B & B Shellfish from 1987, oysters were re-laid and annual landings were restricted to 15 tonnes (Hugh-Jones, 2003). Since 1998, the Loch Ryan oyster fishery has been managed by Loch Ryan Shellfish Ltd. Landings continue to be restricted, ranging between 10 and 15 tonnes annually, under-sized oysters and shell material are re-laid (Hugh-Jones, 2003), and prospects for the future include developing the stock as a natural hatchery for supply to other areas (D. Hugh-Jones, pers. comm., 2004).

2.2.2 West Loch Tarbert, Inveraray District.

The natural beds of oysters in West Loch Tarbert were once prolific, although in the late 19th century, it was the use of cultivation techniques that allowed the fishery to be the primary producer within the Inverary district, and to contribute significantly to Scottish oyster landings.

Cultivation of the beds commenced in 1887 after a Several Order was granted to “Messrs. Hay & Co.” for the oyster fishing rights in West Loch Tarbert. A breeding pond stocking 4,000 oysters was constructed at Rhu to enhance spat collection. Some 700,000 oysters originating from Loch Sween, the Hebrides and France were brought in as fattening stock. Oysters were also transferred from the outer reaches of the loch, since the beds at the head of the loch were considered to be better for fattening. The fishery expanded quickly and the oysters were reported to be of good quality and were fetching high prices of 10 shillings per hundred on the Glasgow market in 1898. By 1890, the beds were estimated to hold approximately 1 million oysters and were being fished intensively. In 1897, when proprietorship of the beds changed to a Mr Rafferty, 110,000 oysters were being harvested per half a season, with only 43,000 oysters used to restock. Intense exploitation eventually led to the decline of the West Loch Tarbert fishery around 1912, and thereafter this fishery contributed only a small percentage to total Scottish landings.

During the 1940s and 1950s, Millar (1961) conducted cultivation experiments on the oyster beds in West Loch Tarbert. Over 200,000 oysters from Brittany were laid in the beds to investigate the growth and fattening potential of the loch. Millar concluded that a large stock of oysters would be necessary to maintain a regular fishery, and estimated that the beds could hold a stock of approximately 5 million oysters. Although there was a large population of the starfish, *Asterias rubens*, which preys upon *O. edulis*, Millar concluded that West Loch Tarbert was a suitable area for oyster cultivation. The current stock of *O. edulis* within the loch is not commercially exploited, although there have been incidents of unlawful gathering recently (N. Duncan, pers. comm., 2003) and applications have been made to develop the stock for commercial purposes (see section 3.6.2.3).

2.2.3 Linne Mhuirich (Loch Sween), Campbeltown District

There were no recorded commercial landings of *O. edulis* in the Campbeltown District from the 1880s onwards. However, the history of oyster farming in Loch Sween dates back to the mid 19th century (C. Pollock, pers. comm., 2003). Accounts of oyster cultivation are documented from 1891 after an Order was granted to Colonel Malcolm and Major Campbell of “Loch Sween Oysters and Mussels”. Cultivation was based in one of the natural oyster beds within Linne Mhuirich, an arm of Loch Sween. Smith (1894) reports that approximately 3 million oysters were obtained locally from Loch Sween and re-laid in a narrow strip along the south-east shore of Linne Mhuirich. As these were mostly attached to rocks, and therefore unsuitable for market, they were to form the breeding stock “to establish a permanent, natural, self-sustaining fishery” (Smith, 1894). A market stock of 10,000 oysters was obtained from Arcachon (France) via Whitstable (England) and laid for fattening. Breeding ponds were also constructed and spat collection tiles were hung to increase the recruitment of the natural stocks. All these efforts were frustrated by adverse weather conditions, including a severe frost in 1894–95 causing high mortality in the adult oysters and strong wave action washing the imported oysters ashore. The proprietors eventually ended their cultivation attempts in 1895.

As in Loch Ryan and West Loch Tarbert, Millar (1961) laid Brittany oysters in Linne Mhuirich to research the potential for growth and fattening. Millar concluded that this site was also suitable for the breeding and reproduction of oysters. Mr T. Stevenson obtained the fishing rights after this time and laid *O. edulis* obtained from mainland Europe, but severe weather conditions caused high mortality in the introduced stock (Alkins, 1977). There is currently no legitimate commercial exploitation of the populations in Linne Mhuirich, although there have been frequent instances of unlawful gathering of oysters from the north-west shore.

2.2.4 Orkney and Shetland

Dredging of oyster beds in Shetland waters, including the areas of Basta Voe and the Burra Isles, resulted in the exhaustion of the Shetland oyster populations by the late 19th century. After 1885, the official fishery records show that oyster landings were small and sporadic in Shetland. Wild oysters are still found around Shetland and there has been interest in using these oysters as broodstock in the development of a local hatchery (J. Irvine, pers. comm., 2004).

There were prolific oyster beds in Orkney that were frequently described in the literature. For example, in 1529 John Bellendenm wrote, "*Firth alia est parochial ubi Ostrea abunde capiuntur*" ("The [Bay of] Firth is another area where oysters are fished in abundance") (Young, 1886). The former abundance of native oyster beds around Orkney is also highlighted by the repeated documentation of the use of oysters for land rent payments during the 16th century, when for instance, between 40 and 500 oysters were gathered by hand for each payment. However, from as early as 1693, there are reports of decreasing stock abundance resulting from uncontrolled gathering by local people (Young, 1886).

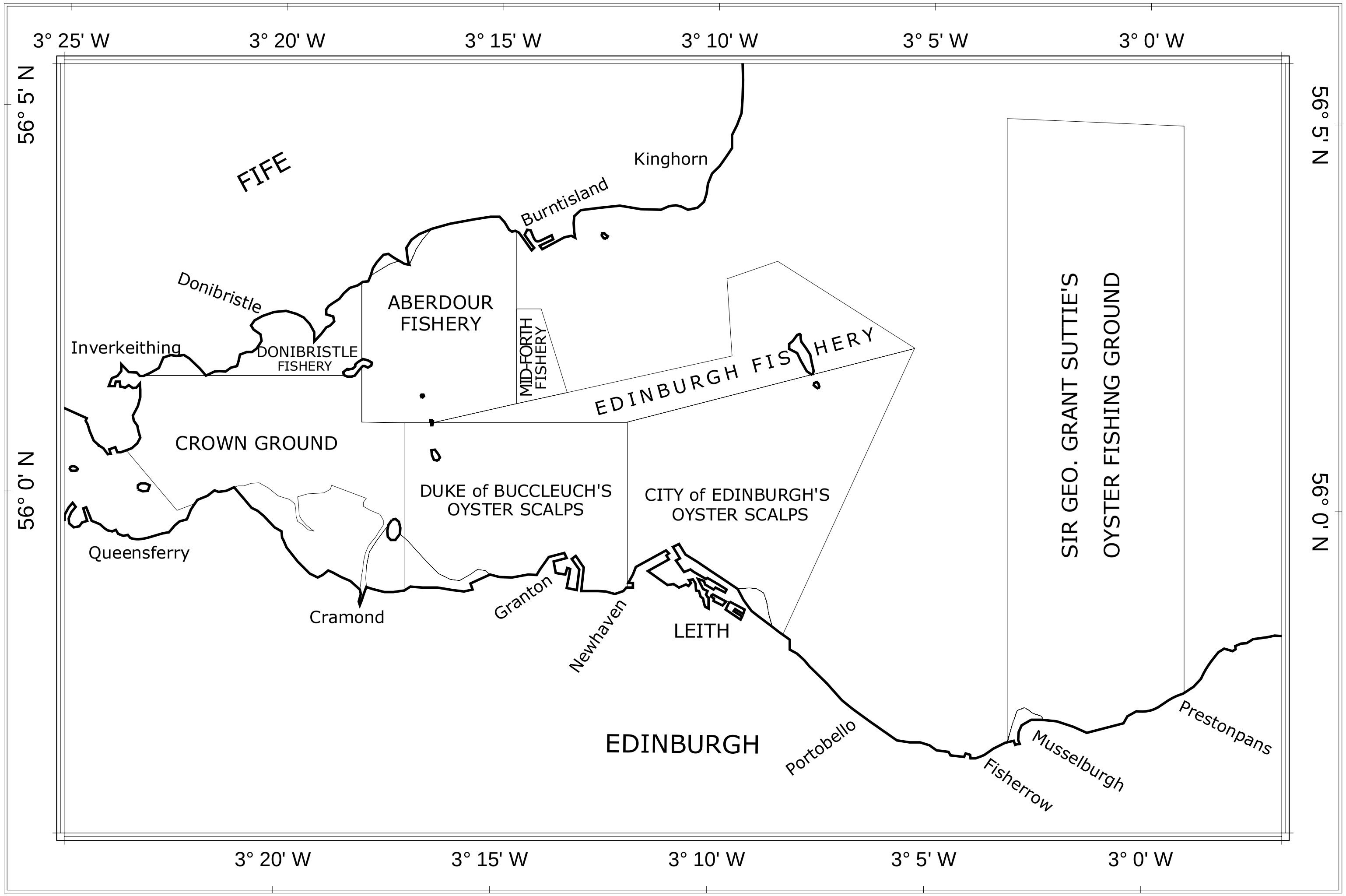
The main commercial fishing areas in Orkney were the beds in the Bay of Firth and Deerness. Smaller fisheries also operated in Long Hope Bay and Widewall where layings, presumably from the main beds, were used to supplement the natural stocks. Oysters from Orkney were considered plentiful, of high quality and were expensive. For instance, during the 19th century, the English market was reported to be paying up to 12 shillings per hundred. In addition, vessels from mainland Britain started fishing in the Bay of Firth after previously unexploited stocks were located. Reports state that these vessels, which started fishing in 1871, took far greater quantities than the locals and by 1880, the Bay of Firth beds had become exhausted. Such high levels of fishery exploitation, in addition to a lack of harvesting regulations or protection of the wild oyster stocks, contributed to the exhaustion of the natural beds.

Efforts to revive the beds and the fisheries began after a syndicate was formed in 1908. The Secretary of State granted protection of the stocks to the syndicate in 1910, and in 1912 the beds were cleaned, laid with cultch and 800,000 English oysters. A peak in production was seen a few years later and the greatest annual landings for Orkney were recorded in 1915 with 15,300 oysters. Landings rapidly declined thereafter and the beds were declared economically extinct by 1918. Further attempts at bed conservation were made, including restocking using Danish oysters, but all attempts failed as a result of the poor condition of consignments, laying on unsuitable substratum and unfavourable environmental conditions. The cultivation attempts of the syndicate finally ended in 1937. Wild oysters have not been found around Orkney for the past ten years (D. Gowland, pers. comm., 2004). *O. edulis* from the Seasalter hatchery, England, were introduced into eight sites in 1989–90. *O. edulis* is still cultivated at one of these sites for research and development purposes (D.Gowland, pers. comm., 2004).

2.3 The east coast fisheries

Of the 15 fishing districts on the east coast, the Leith district, encompassing the famous Firth of Forth oyster beds (Figure 2.2), was the only recorded contributor to Scottish oyster landings. The Moray Firth and the Firth of Tay also contained natural oyster beds but these did not contribute to the reported Scottish landings during the period over which official records were kept. Applications for a Regulating Order for the Firth of Tay oyster fishery were made twice in the late 1800s but in both cases were withdrawn. In the 1880s, English oystermen discovered dense beds in the Moray and Cromarty Firths. Exploitation using dredges was intensive, with peak landings of 25,000 oysters in 1884, after which the beds became exhausted. After this time the only notable east-coast oyster landings were from the Firth of Forth.

Figure 2.2 Map of the former Firth of Forth oyster beds, showing the boundaries of ownership (redrawn from Fulton, 1895).



2.3.1 The Firth of Forth, Leith district

Stretching over 25 km of the southern shoreline and covering over 166 km^2, the oyster beds in the Firth of Forth were the most prolific and, from the 13th century, the most commercially important in Scotland. Ownership of the rights to gather oysters in the Forth was divided among private individuals, corporate bodies, local government and the Crown (Figure 2.2). Forth oysters had a reputation of such good quality that they were in demand not only by local markets but also throughout Scotland, England and Europe. Fulton (1895) stated that at a very conservative estimate, at the turn of the 19th century the Forth fisheries were landing 30 million oysters annually. Nonetheless, the quantity and quality of oysters and high levels of fishing effort, plus the lack of enforced management policies were the principal factors leading to the decline of the Firth of Forth beds. This section summarises the detailed report made by Fulton (1895), which focused principally on the fate of the beds owned by the City of Edinburgh.

From the 13th century, oysters were very cheap and were widely consumed. In the 16th century, the price of oysters started rising, prompting the commercial exploitation of the stocks. Exports of oysters to "foreign" markets were common, and were blamed repeatedly for the depletion of the Forth beds. In the 1660s, the Town Council of Edinburgh was forced to prohibit fishing by, and sales to, other European countries, in particular the Netherlands, in attempts to protect the beds. Intense exploitation again became problematic in 1742, when it was noted that "…unless a stop be put to such spulzies, and the theftnous practices timeously, that the very breed of oysters may be quite extirpate and carried off, to the great and irreparable loss, both of this country and the community". The Council again issued regulations. These included restrictions on selling to other countries, including England, without official approval, fishing only by local boats (not including those from Fife), the introduction of a closed season (10 April – 4 September), a minimum size for exported oysters and the oyster fishermen were to aid in the enforcement of the restrictions. As occurred in 1660s, the regulations were complied with for a short time allowing the beds to flourish before the old practices were resumed.

The beds exploited by the "East Country" fishermen (Fisherrow, Cockenzie and Prestonpans) were the first of the Forth beds to become exhausted. These beds were public grounds or leased from proprietors. Landings by this group in the 1780s were estimated at around 18 million per season for 40 boats working a 4-day week. The majority of these were juvenile oysters, which were exported to the English and Dutch markets. In 1786, the East Country fishermen had exhausted the public and leased beds that they regularly fished and were reported to be exploiting oysters unlawfully from the City beds. Legal proceedings followed where the titles and rights were officially confirmed for the different sections of the oyster beds. The regulations of 1742 were reiterated in 1788 and, in addition, a minimum landing size of 1.5 inches diameter was imposed for market oysters in an attempt to regulate the exportation of juvenile oysters.

The City of Edinburgh owned one of the most valuable fisheries for which the Newhaven fishermen had leased the fishing rights since 1510. The Newhaven fishermen were responsible for exporting great quantities to "foreign" markets, in particular the Netherlands and England. When, in 1751 it became apparent that the regulations on exportation were ineffective, the Council revoked the fishing rights of the Newhaven fishermen and transferred them to a Leith merchant, on the condition that the oysters were sold only to the Edinburgh market. By 1786, the Newhaven fishermen had re-gained the fishing rights. Over the period 1773–1786, daily landings in the Forth had fallen from several thousand to 400–500 oysters per boat. Exports were blamed for this decrease in oyster productivity, but these had also declined on account of the scarcity and rising cost of oysters.

Landings from the Forth oyster beds showed an increase at the turn of the 19th century, followed by an all time low at the end of the 1820s, with a recorded daily catch of 150–200 oysters per boat. The Council again issued strict regulations banning the exportation of oysters and began leasing the City-owned beds, for which the Newhaven fishermen paid £50 rent per year. In addition, a fine of £100 was to be levied on any fisherman breaking the fishing regulations. As a result of these measures fishing was controlled and natural regeneration increased the productivity of the beds. However, this increase in productivity promoted a return to "reckless fishing". Between 1834 and 1836 nearly 60 million oysters were exported from Newhaven to stock the Essex and Kent beds. Attempts were again made by the Council in 1836 to curtail this exploitation and exportation by restricting daily harvests to 792 oysters per person, with catches to be sold only to the Edinburgh market and permission for exportation to be sought from the Council.

Eventually in 1839, the Town Council permitted exports to England through an English syndicate, which paid £600 annually to rent the City beds. As part of the contract the Council abolished their size restrictions but established landing quotas. Denied fishing rights again, unlawful harvesting by the Newhaven fishermen became frequent, causing large losses to the syndicate. Fishermen from up to 60 boats, which leased the beds on either side of the City of Edinburgh beds were involved in the unlawful activity. Unlawful exploitation was facilitated by the lack of adequate demarcation of the beds. In addition, the Newhaven fishermen would not work for the syndicate and 70 boats and crew had to be hired at expense from England. The perceived losses from unlawful exploitation and the extra expenses incurred caused the syndicate to increase their landings in order to achieve compensation and several actions were levied against the City for these losses. In 1841, the City allowed the lease to be broken and the rights were returned to the Newhaven fishermen.

Exports to the English markets, in particular of young brood oysters, continued throughout the 19th century. Similar regulations and restrictions, as detailed above, were periodically issued but were not adequately enforced or followed. Extra fees and rents were also repeatedly levied on the fishermen of the City beds. In 1865, a report to the Council by Dr James McBain, an Edinburgh naturalist, declared the beds would soon cease to be productive owing to the scale of exploitation. The only action to occur as a result was the appointment of an officer to enforce the regulations. The Duke of Buccleuch, who owned the fishing rights to the Buccleuch beds, eventually withdrew these rights from the Newhaven fishermen on account of their poor fisheries management. In 1867 he transferred the rights to an Edinburgh fish merchant, Mr J. Anderson, who also held rights to other privately-owned fishings and the Crown fishings. This restricted the fishermen to the public and City beds only, although the Duke of Buccleuch had leased the Buccleuch beds on the condition that Mr Anderson employed the Newhaven fishermen. In 1868, seeking to protect the beds further, the private owners applied for and were granted Mussel Fishery Orders for the area of the oyster beds in an attempt to prohibit fishermen gathering mussels (*Mytilus edulis*) and "inadvertently" landing oysters. At this time the Board of Trade declared the beds to be in a state of "semi-exhaustion" owing to their poor management. Remedial measures were attempted, including the re-laying of local oysters and cultch preservation, but unlawful exploitation hampered these efforts. By the 1870s, the fisheries were beginning to close owing to exhaustion of the different beds. The last of the Forth oyster fisheries eventually ceased in 1920. Surveys carried out in 1957 and 1996 found no living oysters, indicating that the Forth oyster population was extinct (Millar, 1961; Harding, 1996).

2.4 Exploitation of oyster populations

Details of the early oyster fisheries are scarce (Fulton, 1891; Coull, 1996), but records indicate that economic development of the commercial fisheries greatly expanded in the early 19th century driving exploitation to unsustainable levels. This expansion was partially driven by improving fisheries technology and the developing transport network. By the mid-17th century, the main method for gathering oysters was dredging using sail- or oar-powered boats, superseding the primitive harvesting methods of gathering oysters by hand or using glass-bottomed bucket and tongs (Yonge, 1960). Early oyster dredges were similar to their modern counterparts. Present-day oyster dredges are triangular with two metal arms attached to a flat bar that scrapes oysters and other seabed materials into an attached bag. Modern bags are approximately 1 m wide and formed of linked metal rings. Early dredges were of the same design except that they were only 0.5 m in width, with the lower half of the bag made from perforated hide and the upper from twine. The early dredges were manual, being manoeuvred by a “catch-stick” attached to the mouth of the bag or being dragged by a rope attached to the boat (Yonge, 1960). The introduction of steam-powered boats in the mid-1800s also increased the effective fishing effort by allowing larger dredges to be used over great distances (Anon., 1885–1977). Furthermore, in addition to the introduction of railways in 1840, steam-boats provided links to a wider geographical market than had previously been possible (Coull, 1996).

Initially, the improvements in harvesting methods accompanied by developments in transport increased the value and income from oysters, causing increased competition between fishermen and driving exploitation to unsustainable levels (Coull, 1996). As detailed in part 2.3.1, regulations were repeatedly laid down for the fisheries and although the lessees were required to enforce these regulations, there was no official enforcement or supervisory body. Large quantities of both broodstock and juvenile oysters and also the dead shells known as cultch, that are necessary for larval oyster settlement, were removed as a result of the lack of enforcement (Fulton, 1891). Ultimately, this contributed to depletion of the stocks, causing an imbalance between the levels of exploitation and the capacity for natural regeneration of the stocks necessary to sustain the fisheries. Reports from Shetland indicate a similar disregard for the sustainability of shellfish stocks: “…the Shetlanders are said to have nearly exhausted the large whelks known as buckies, and to be fast destroying the mussel scalps, as they have already done the oyster-beds…” (Tudor, 1883, cited in Young, 1886).

Although the rights to oyster fishing belong to the Crown or those subjects to whom the rights have been granted (see Appendix 1), unlawful gathering was common throughout the history of the oyster fisheries in Scotland (Anon., 1885–1977). Early indications of the exhaustion of oyster stocks throughout Scotland, related to the high levels of both commercial and unlawful exploitation, led to the passing of the Oyster Fisheries (Scotland) Act 1840. This created offences of theft and attempted theft for trespassing on other people’s right to gather oysters or oyster beds.

Although there were many reports of unlawful fishing of oysters in the Firth of Forth (see section 2.3.1), the first prosecution of unlawful gathering of oysters was made under this Act in 1842 against Prestonpans fishermen trespassing upon the Newhaven beds. It was hoped that this prosecution, which was accompanied by a nominal fine, would publicise the new legislation (Broun, 1844; Fullarton, 1889). Another example of a successful prosecution under the 1840 Act was in 1866, when two fishermen who had been licensed to dredge for oysters in Loch Ryan took a quantity of undersized oysters (as defined in their permit) and were successfully convicted of theft (Anon., 1866). Nevertheless, the legal right to gather oysters was not widely acknowledged in Scotland and this was made apparent in interviews conducted by Archibald Young, the Inspector for Salmon Fisheries, in 1886. Young (1888) concluded that, "… people all along the [west] coast look upon oyster scalps and mussel beds as their natural property, and have been accustomed, in ignorance or defiance of law, to help themselves for years to what does not belong to them…".

Although successful prosecutions against unlawful gathering had been made, there were numerous reports of failed prosecutions. Young (1888) documented Mr MacAndrew, the Provost of Inverness, describing the beds in the Moray Firth as containing oysters of high quality. These were discovered by English fishermen "…and for several years they fished persistently until the oysters were practically exhausted, and now they cannot be found in sufficient quantity to pay for dredging". Further on, MacAndrew stated, "efforts were made to stop the fishing, but it was found that no person had a legal right…". Even in areas where the ownership rights were clear, confusion arose about who should protect the beds. For instance, the English syndicate that held the lease for the fishing rights to the City of Edinburgh oyster beds had several arguments with the Town Council of Edinburgh about which party was responsible for protecting the stocks from unlawful exploitation.

The interviews documented by Young in both 1886 and 1888 state repeatedly that the perceived lack of legal protection for stocks dissuaded parties from investing in, and cultivating the wild oyster stocks. In 1877, Several and Regulating Orders were introduced by an amendment to the Sea Fisheries Act of 1868. Through these orders the Government aimed to encourage cultivation of shellfish stocks in an attempt to revive declining fisheries. The official power for regulation of these Orders was ascribed to the Board of Trade. Notable cultivation efforts of native oyster stocks in Scotland were those in West Loch Tarbert (see section 2.2.2) and Linne Mhuirich (see section 2.2.3), with the former contributing to commercial landings. However, in other areas where cultivation was attempted the techniques employed were often unsuitable, leading to increased mortality of the stocks. In addition, the level of unlawful exploitation of the cultivated stocks was rarely controlled effectively. For example, layings made by locals in the Moray Firth were dredged out without permission by Colchester boats (Young, 1888). Orders were expensive to apply for and this economic burden coupled with losses from unlawful exploitation undoubtedly discouraged many applications. Ultimately the oyster beds were *de facto* open-access and both cultivated and natural fisheries were poorly regulated or unregulated. The reports by Young (1886, 1888) indicate that Government support had been called upon for some time but the introduction of Several and Regulating Orders had come too late for the conservation of the oyster fisheries.

It was in 1904 that Parker, a mussel merchant from Greenock, challenged a decree that the Lord Advocate had obtained on the Crown's behalf, which declared that the Crown had exclusive rights to fish mussels in the Clyde estuary (see Appendix 1). The right to fish for mussels is of the same character as that for oysters, and offences of theft or attempted theft were also created by the Mussel Fisheries (Scotland) Act 1847. The House of Lords ruled that there was not a public right to fish for mussels. Thus, the public did not have a legal right to harvest oysters either. However, the long-standing ambiguity surrounding the right to gather oysters, protection for the stocks and a lack of sufficient prosecutions resulted in high levels of unlawful exploitation that continued unhindered.

2.5 The decline of the oyster fisheries

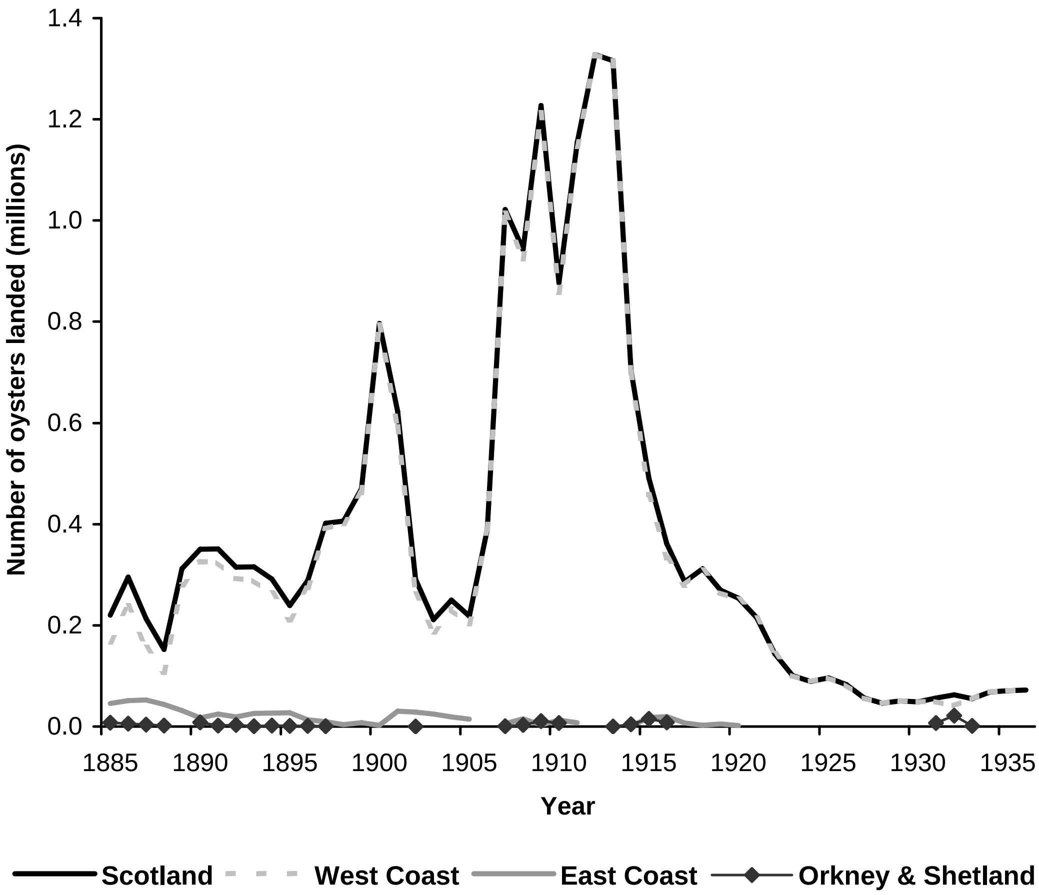
The rise and fall of the oyster fisheries in Scotland is described best using examples from the Firth of Forth, as this was the largest and most productive fishery in Scotland. Annual landings from the Newhaven fishery alone totalled 59.8 million oysters from 1834–1836, with a total value of £12,579 (Anon., 1885–1977). At this time, 50 to 60 boats each with a five-man crew were dredging for the whole season (Coull, 1996). These landings were far in excess of those documented by the Fishery Board for Scotland (1885–1977) (Figure 2.3), by which time landings from Newhaven had decreased greatly. For instance, recorded landings from dredging during the 1874–75 season in the Newhaven district were 815,850 oysters. This decreased to 55,140 oysters by 1882–1883 and no landings were recorded in the following season (Fulton, 1895). Similarly, annual landings from the Leith fishery also decreased from millions to thousands of oysters during the 19th century (Anon., 1885–1977).

Changes in the landing patterns of the principal oyster fisheries provide some indication of the scale of decline in oyster production throughout Scotland. For most of the history of Scottish oyster fisheries, the wild oyster beds of the Firth of Forth, which covered 166 km^2, were the most productive beds in Scotland. However, official fishery records indicate that by the end of the 19th century, the fisheries on the west coast were producing nearly 100% of landings of *O. edulis* (Figure 2.3). The Loch Ryan fishery (Ballantrae district), which covers an area equivalent to only 9% of the former Forth beds, contributed over 90% to these west coast landings from the early 1900s. Furthermore, at the height of the Firth of Forth fishery in 1836, landings were in excess of 59 million oysters for the Newhaven district alone, whereas at the height of the Loch Ryan fishery in 1913, total annual landings were only 1.3 million oysters.

After the decline of the Firth of Forth fishery, official records indicate that the level of exploitation in the remaining Scottish oyster fisheries remained high over the turn of the 20th century. Landings in the Ballantrae district increased from approximately 200,000 oysters in 1900 to over 700,000 oysters in 1902. Production from the Inverary district crashed from over 150,000 oysters in 1890 to 40,000 in 1894 but increased to 130,000 in 1897 after the discovery of un-exploited beds, which were rapidly dredged to exhaustion. From the late 19th century onwards, market demand for oysters was also increasing and as landings increased so did their value (Anon., 1885–1977). Market demand, in addition to the decline in landings of other oyster fisheries around Scotland, supported the high levels of fishing effort on the west coast. Landings of oysters from Loch Ryan increased until 1913 (Anon., 1885–1977; Hugh-Jones, 2003), after which, landings from this fishery also decreased until the fishery was deemed economically extinct in the 1950s.

In the early 1920s, the Fishery Board for Scotland commenced a large-scale cultivation programme to restore the native oyster beds along the west coast. Oysters were imported from Holland and used to supplement areas of natural stocks. The long-term aim was to establish a central breeding station that could be used to supply small cultivation areas. However, the project was short-lived and terminated in 1923 owing to a lack of financial resources and interest in an extinct fishery.

Figure 2.3 Annual landings of O. edulis *in Scotland from 1885–1936 (Anon., 1885–1977).*



2.6 Other potential factors

Although high levels of exploitation were the primary cause of the depletion of the oyster beds in Scotland, other factors such as extreme weather events, low levels of recruitment and pollution may also have contributed. Periods of extreme cold weather have caused high levels of mortality in stocks where *O. edulis* populations are found in very shallow water (Anon., 1885–1977). Although wild stocks are susceptible to mortality caused by low temperature (Orton, 1940), such mortality has only been recorded in Scotland in association with cultivation efforts where stocks have been re-laid in shallow waters, such as in Linne Mhuirich (Smith, 1894) and Orkney (Anon., 1885–1977). This suggests that a higher level of success may have been achieved had suitable habitat in deeper waters been used for the cultivation efforts. Although predation has rarely been suggested as a contributor to the decline of oyster fisheries, predation has been linked to high levels of mortality in cultivated stocks (Anon., 1885–1977; Young, 1888).

Low environmental temperatures were also suggested as a contributing factor to the decline of the Firth of Forth beds, although these claims were refuted since larval oyster settlement was observed during the periods when the fisheries were closed (Fulton, 1895). Fulton (1895) also rejected claims that industrial and sewage pollution contributed to the decline of the Firth of Forth beds because of a lack of evidence. Nevertheless, pollution was linked to the extinction of mussel beds in Argyll, which had previously been depleted as a result of high levels of exploitation (Young, 1888).

Low levels of recruitment to populations have often been suggested as a factor contributing to the decline of many exploited oyster stocks (Anon., 1885–1977). Fluctuations in recruitment to oyster populations are common as Fulton (1895) commented; had the oyster fisheries been properly regulated, poor recruitment would not have influenced the decline (as was proven by reports of successful fisheries based on shellfish with similar recruitment patterns). Overall, stocks that had been reduced to low levels by overexploitation would have been more susceptible to the effects of variable recruitment, adverse environmental conditions and predation.

2.7 The wider experience

Scotland was not the only country to experience declines in oyster stocks; parallel situations occurred throughout Europe (Fulton, 1895; Fullarton, 1889) (see section 1.3). Survival of the French oyster beds was due to the effective response of the French Government, which invested money into the development of cultivation techniques suitable for the populations in France. Ownership rights were simple as the Government owned the rights to the foreshore and leased them to *ostreiculturists*. Since both the Government and the lessee derived income from the beds, both provided protection. This simple, but effective, system supported by the French Government allowed France to restore the fisheries, providing landings greater than before (Fullarton, 1889). This comparison highlights the lack of support received by the Scottish oyster fishermen and how important Government support could have been to the survival of the fisheries.

Harvesting marine species until exhaustion has been documented throughout the fisheries literature and is usually driven by a lack of incentive to protect open-access resources (Jennings *et al*., 2001). Hardin (1968) called this the “tragedy of the commons”; each person exploiting an open-access resource aiming to maximise his gain by exploiting the resource without limits, until that resource collapses. Hardin suggested that the tragedy of the commons could be avoided through resource privatisation, with ownership providing the incentive to regulate exploitation on a sustainable basis. In order to prevent indiscriminate fishing, Several and Regulating Orders were established by the Sea Fisheries Act 1868 as a supportive measure for those that held the fishing rights to oyster stocks. However, as discussed, high levels of unlawful exploitation undermined this legislation and exploitation of *O. edulis* stocks continued as though it was a "common" resource. As a result, those that legally exploited the stocks did so without restraint in order to recoup their economic investment in the stocks.

"With regard to the oyster and mussel beds on the shores of [the Loch Carron] district, I have no doubt both could be cultivated and much improved. But the people are so numerous – so constantly collecting whelks along the shores, which now brings them considerable profit – that not an oyster is to be got. At one time we could get oysters in abundance. Now none are to be found. The cost of protecting such an extensive coast from the depredations of the people would be enormous. It would require an army of watchers. So that it appears to me useless and absurd for the proprietor to incur any expense. The oyster and mussel beds are limited to small portions of the coast, far separated from each other" (Mr McIver – Factor at Scourie, cited in Young, 1888). This quote adequately states the problems associated with the wild oyster beds, which are still faced in Scotland today. Unlawful exploitation remains a major concern for the survival of the Scottish wild oyster beds. This stems from the same reasons as detailed for unlawful exploitation over a century ago. Interviews conducted during the course of the present study, indicate that the ownership rights to the oyster stocks are still unclear and, in general, shellfish including oysters are still regarded as an open-access resource by many people. Wild oyster stocks are also found in many unconnected beds covering a vast geographical area along the west coast of Scotland. The coastline is highly indented and many beds are found in isolated areas, making the task of preventing unlawful exploitation difficult and potentially very expensive. However, there exists a range of fisheries and conservation measures that can be investigated for suitability to address the issues pertinent to the management of the present day oyster stocks in Scotland (see section 8).

2.8 Conclusion

Three main issues can be identified from the history above as contributing to the decline of the Scottish oyster fisheries: unsustainable levels of exploitation driven by technological improvements, market demand and a lack of effective management, unlawful exploitation and confusion over the legal issues pertaining to the rights to gather oysters. In the words of Fulton (1895) "…the temptation of great and immediate gain proved too strong for fishermen". Reports dating back to the 18th century warned of the exhaustion of the beds. However, a lack of effective support and adequate control of the fisheries meant that high levels of exploitation and reckless fishing techniques were allowed to persist. This led to the decline and "serial depletion" of local beds, eventually causing the collapse of the Scottish native oyster fisheries.

Historically, oyster fisheries were based upon exploiting wild beds, but today, the Loch Ryan oyster fishery is the only large-scale commercial fishery using wild stocks. Several other wild oyster populations have also survived and small-scale exploitation of these stocks and interest in developing them for commercial purposes is increasing. Interviews conducted during the course of this study indicate that small-scale native oyster cultivation is also being increasingly practised alongside the cultivation of non-native *Crassostrea gigas* and other shellfish stocks. The future of the remaining oyster beds is therefore dependent on the development and enforcement of an effective management system, which addresses the threats posed to the survival of the remaining wild beds. Suitable cultivation techniques and biological monitoring are needed to allow the oyster beds to be maintained and to flourish. Support from all levels of stakeholders involved with oyster stock management is necessary in order to achieve the goals of maintaining and expanding the current range and abundance of the oyster beds in Scotland. Finally, issues that pose a threat to the existence of current oyster stocks, such as unlawful exploitation, an issue that has persisted from the times of the historic fisheries, need to be addressed.

3 POPULATION ESTIMATES OF SELECTED WILD *OSTREA EDULIS* POPULATIONS IN SCOTLAND

3.1 Introduction

The objectives of the Native Oyster Species Action Plan are to expand the existing geographical distribution and abundance of the native oyster within UK inshore waters (Anon., 1999). This is to be achieved through management and protection targets that include maintaining the existing stock abundance, ensuring adequate recruitment and preventing the spread of disease through controlling stock density. Although these targets appear to be aimed at stocks that support commercial fisheries, the same targets should also be met for wild populations.

Loch Ryan contains the largest known wild population in Scotland and is exploited for commercial purposes. The main fishing areas are north of Lefnoll point, the Wig and the west side of the loch (Figure 3.1). Recent population estimates made by Royal Haskoning, using 0.1-m Van Veen grabs, indicate there are approximately 5.7 million adults (>70 g) and 52 million spat oysters in the Lefnoll area alone, which covers approximately 1.6 km^2 (T. Hugh-Jones, pers. comm., 2005). Commercial use of populations is not limited to Loch Ryan and a few small-scale enterprises also exploit wild populations of *Ostrea edulis* around Scotland. However, there is a paucity of information on the smaller populations of *O. edulis*, including those that are currently exploited. Detailed records of the historical local fisheries are also scarce and introductions of non-native broodstock are suspected to have been made in many areas, but have gone unrecorded (Millar, 1961). One-off studies have been made on a few extant populations (Paisley, 1994, cited in Bunker, 1999; Bunker, 1999; Anon., 2004b), but these have used differing methods and are therefore not directly comparable. Furthermore, the current distribution of extant populations is uncertain and knowledge about the existence of local beds is often not shared because of concern about unlawful exploitation (pers. obs.). It is believed that many small populations have become extinct since the turn of the 20th century (Millar, 1961).

Oysters are regarded as a luxury food item with a relatively high market value. In general, marketable oysters have a shell length of approximately 5 to 8 cm, which equates to an age of approximately 4 to 6 years. Unlawful exploitation, driven by the high value of oysters, is one of the greatest threats to remaining populations (Bunker, 1999; Donnan, 2003; pers. obs., 2004). The extent of unlawful exploitation throughout Scotland is unknown but it is thought that significant reductions in population size have occurred (Donnan, 2003).

The aim of the present study was to estimate the population density and abundance of native oysters at three sites on the west coast of Scotland and determine their size-frequency distribution. Since two different survey methods were used in two years, a limited comparison of the efficacy of the methods is possible.

Figure 3.1 The Loch Ryan basin. Low water spring line is indicated by the blue line.

3.2 Methods

3.2.1 Sites surveyed

In 2004, 15 sites within seven geographical locations were surveyed in Scotland using the multi-level transect survey method (Figure 1.1) (Krebs, 1999). Table 3.1 lists the locations, survey sites, dates and number of transects completed. Transects were located randomly throughout the oyster populations, except at sites where only one or two transects were completed, when transects were placed in areas of highest density.

In 2004 and 2005, population density, abundance and size-distributions were estimated for Linne Mhuirich (Loch Sween, Argyll), West Loch Tarbert (Argyll) and Loch Ailort (Highlands) (see sections 1.5.1 – 1.5.3). It should be noted that other, unsurveyed areas within these sites may also contain oysters. Population estimates were made using multi-level transect surveys in 2004 and belt-transect surveys in 2005. The belt transects were used in 2005 in order to obtain more precise estimates.The total area to be surveyed was determined as the extent of the firm substratum (usually sand with a mixture of shell and pebbles) in the area of the oyster populations. Data were collected for each site using SCUBA or snorkelling, in shallow (<5 m) subtidal and intertidal waters.

3.2.2 Population surveys

3.2.2.1 Multi-level transect surveys

Each survey area was divided into sections of 50 m length along the shore and each section sub-divided into a grid with rectangular cells of 50 x 5 m. In each section, one grid cell was randomly selected for surveying. The grid cells were surveyed in a random order and located using a GPS receiver. Within selected cells, a transect was marked using a 30-m tape measure placed parallel to the shoreline. Sampling was done by placing a 1 m^2 quadrat on both sides of the tape at three randomly chosen distances within each 10 m subsection, giving a total surveyed area of 18 m^2 per transect. Direct counts of the number of living oysters and potential predator (*Asterias rubens* and *Carcinus maenas*) and competitor species (*Anomia ephippium* and *Mytilus edulis*) were made. Dial callipers were used to measure the height and length of living oysters to the nearest 0.1 mm. Percentage cover by different substrata was determined, including sand, hard substrata (rocks, stones, pebble and gravel) and shell (cultch). Percentage cover of algae was also recorded. The negative binomial distribution was used to determine the number of transects necessary for a 25% level of precision of estimates. However, adverse weather conditions limited the number of transects that could be surveyed at the sites.

The mean density and abundance (with 95% confidence limits) of oysters were estimated using the formulae for two-level sampling (Cochran, 1977). Oyster counts were log(x+1)-transformed prior to analysis to normalize the data. The estimates have been back-transformed in order to present population densities (m^{-2}) and abundances.

The mean cover of the different substrata and mean density of *A. rubens, C. maenas, A. ephippium* and *M. edulis* were estimated for all sites, with 95% confidence limits estimated for sites with more than two transects. The percentage cover data were arcsine-transformed and the species counts were log(x+1)-transformed prior to analysis to normalize the data.

Table 3.1 Survey sites and details of transects completed. MLT = multi-level transects, BT = belt transects.

Location and Site	Dates of MLT surveys	Dates of BT surveys	Number of transects	
			MLT	BT
LOCH RYAN (STRANRAER)				
LR1	09/02/2004 to 13/02/2004		5	0
WEST LOCH TARBERT (ARGYLL)				
WLT1	13/04/2004 to 16/04/2004	04/04/2005 to 08/04/2005	8	8
WLT2	07/06/2004 to 11/06/2004	04/04/2005 to 08/04/2005	8	9
LINNE MHUIRICH (LOCH SWEEN, ARGYLL)				
LM2	29/03/2004 to 01/04/2004	02/05/2005 to 06/05/2005	12	12
LM1	01/06/2004 to 04/06/2004	02/05/2005 to 10/05/2005	9	12
LM3	30/03/2004		2	0
LOCH AILORT (HIGHLANDS)				
LA1	06/09/2004 to 10/09/2004	22/08/2005 to 25/08/2005	9	11
LA2	06/09/2004 to 10/09/2004		2	
LA3		23/08/2005	0	7
LOCH SCRIDAIN (MULL)				
M1	10/05/2004 to 14/05/2004		1	0
LOCH NA KEAL (MULL)				
M2	10/05/2004 to 14/05/2004		1	0
SOUND OF ULVA (ULVA/MULL)				
M3	10/05/2004 to 14/05/2004		1	0
U1	10/05/2004 to 14/05/2004		1	0
U2	10/05/2004 to 14/05/2004		1	0
U3	10/05/2004 to 14/05/2004		1	0
U4	10/05/2004 to 14/05/2004		1	0

3.2.2.2 Belt-transect surveys

Each survey area was divided into sections of 20 m length along the shore and each section sub-divided into a grid with rectangular cells of 20 x 2 m. Randomly selected cells were located by measuring alongshore and offshore coordinates with a tape measure. Within selected cells, transects were marked with a 20 m tape measure placed parallel to the shoreline. Sampling was done by placing 1 m^2 quadrats on both sides of the tape and surveying contiguously along transects to give a total surveyed area of 40 m^2. All live oysters within the quadrats were counted and the shell height and length of each individual was measured to the nearest 0.1 mm with dial callipers.

Oyster counts were log(x+1)-transformed prior to analysis to normalize the data, but the estimates have been back-transformed in order to present the mean density, abundance and 95% confidence limits.

3.2.3 Unlawfully gathered oysters

Unlawful gathering of native oysters in Linne Mhuirich, West Loch Tarbert and Loch Ailort was reported after the completion of the surveys in 2004. The effects of unlawful exploitation on population estimates cannot be quantified as the two survey methods differ. However, recovery of oysters unlawfully gathered from the Linne Mhuirich area in February 2005 provided some data on the size-range of oysters being taken. The contents of each bag were counted, measured with dial callipers to the nearest 0.1 mm and the oysters returned to known locations within Linne Mhuirich. The size-frequency distribution was compared with that of the surveyed population in Linne Mhuirich to determine whether unlawful gatherers were selecting a specific size range of oysters.

3.3 Results

3.3.1 Multi-level transect survey habitat and species data

The density of oysters recorded was generally low (<1 m^{-2}) for most sites (Table 3.2). The estimated density of *O. edulis* was greater at LM2 (Linne Mhuirich) and LR1 (Loch Ryan) (<2 m^{-2}) and at M1 (Loch Scridain, Mull), where the estimated mean density was 3.5 m^{-2} (Figure 3.2 a). The maximum number of oysters counted within quadrats generally ranged from 2 to 8 oysters, except for the three sites mentioned, which had maximum counts ranging from 20 to 28 oysters (Table 3.2).

Species that could be potential spatial competitors with *O. edulis*, such as *A. ephippium*, *M. edulis* and algal species were recorded at low densities at the majority of sites (Figures 3.2 b-d). However, *A. ephippium* was present at much higher densities (~4 m^{-2}) at WLT1 and WLT2 compared to *O. edulis* (~ 0.6 m^{-2}) (Figures 3.2 a-b). The densities of the predatory species *A. rubens* and *C. maenas* were generally low throughout all sites (Figure 3.2 e-f) and *A. rubens* was not recorded at 50% of the sites surveyed. The availability of hard substrata at the sites surveyed was generally high, with mean percentage cover often greater than 45% (Figure 3.3 a). The availability of settlement substrata for larval oysters in the form of dead shell (cultch) was generally low (Figure 3.3 b).

3.3.2 Population surveys

All density and abundance results for Linne Mhuirich, West Loch Tarbert and Loch Ailort refer to the total area of the grid used to locate transects. In places, the oyster bed may have extended beyond the grid but preliminary surveys indicated that the grid encompassed the majority of the population. The survey data from both methods were fitted to the negative binomial distribution. Table 3.3 lists the survey statistics and Table 3.4 lists the results of the density and abundance estimates for both survey methods. The estimates for the multi-level survey method had relatively low levels of precision, with percentage relative precision (PRP) of 25–65% of the mean depending on the location. With the exception of LA1, the belt-transect method showed an increase in the PRP of estimates by 25–48%, with PRPs ranging from 13–15%. The PRP of the multi-level transect estimates was more precise for LA1. Two additional transects were required in LA1 in order to attain a similar level of precision to that obtained using the multi-level survey method (Table 3.3).

The belt-transect method consistently provided narrower confidence limits around the mean (Figure 3.4). For all sites except for LM2 and LA1 the estimates of the belt-transect method fell within the confidence limits of the multi-level survey method. A comparison between the two survey methods showed that the difference between the density estimates was more than 60% for LM2 and LA1. This is substantially greater than the 11–18% difference between the estimates for the other sites (Table 3.4).

The *k*-value of the negative binomial distribution indicates the level of clumping of the sampled populations (Krebs, 1999). The *k*-values for the two survey methods were similar at each site with differences varying by approximately 5% (Table 3.3), suggesting that there was no major difference in the indicated degree of clumping. However, the *k*-value for the belt-transect survey at WLT2 was 50.7% lower than that of the multi-level survey (Table 3.3). This suggests that the spatial distribution surveyed using the belt-transect method was more clumped. This difference in the apparent spatial distribution was also recorded for the population at LA1, where the *k*-value was lower by 45.7% for the belt-transect estimates (Table 3.3).

For all sites, the major peaks in size-classes were the same for each method, except that the peaks in the belt-transect surveys were in marginally larger size-classes (Figure 3.5). For all sites except WLT2, the peaks in size-classes were more pronounced for the belt-transect surveys in which more oysters were sampled. LM2 is the only site at which fewer oysters were sampled in the belt-transect method compared to the multi-level survey method.

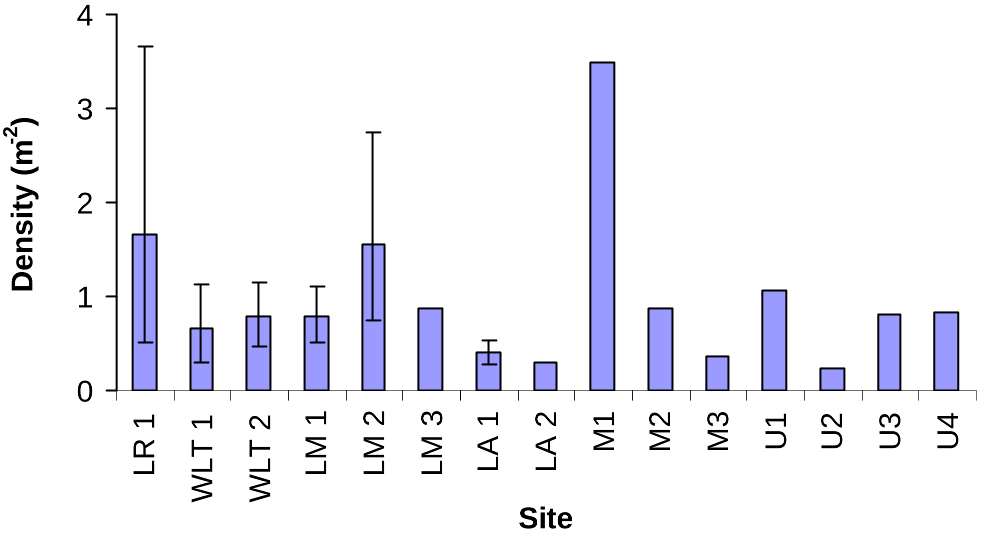
Table 3.2 Estimates of O. edulis *density per transect for the multi-level transect survey (2004).*

Location	Total number of oysters counted	Upper confidence limit	Mean oyster density (m^{-2})	Lower confidence limit	Range	Minimum height (cm)	Maximum height (cm)
Loch Ryan (Stranraer)							
LR1	251	2.006	1.650	1.142	0–20	0.90	9.74
West Loch Tarbert (Argyll)							
WLT1	139	1.110	0.658	0.303	0–5	1.84	8.80
WLT2	158	1.156	0.787	0.481	0–7	0.41	10.75
Linne Mhuirich (Loch Sween, Argyll)							
LM1	185	1.094	0.784	0.520	0–8	1.09	10.97
LM2	630	2.65	1.553	0.785	0–28	0.11	11.03
LM3	42	n/a	0.863	n/a	0–5	2.07	9.55
Loch Ailort (Highlands)							
LA1	102	0.129	0.402	0.119	0–6	1.07	10.49
LA2	17	n/a	0.307	n/a	0–4	0.09	9.82
Loch Scridain (Mull)							
M1	133	n/a	3.498	n/a	0–27	2.81	10.5
Loch na Keal (Mull)							
M2	23	n/a	0.880	n/a	0–4	3.50	8.90
M3	11	n/a	0.370	n/a	0–5	2.35	7.80

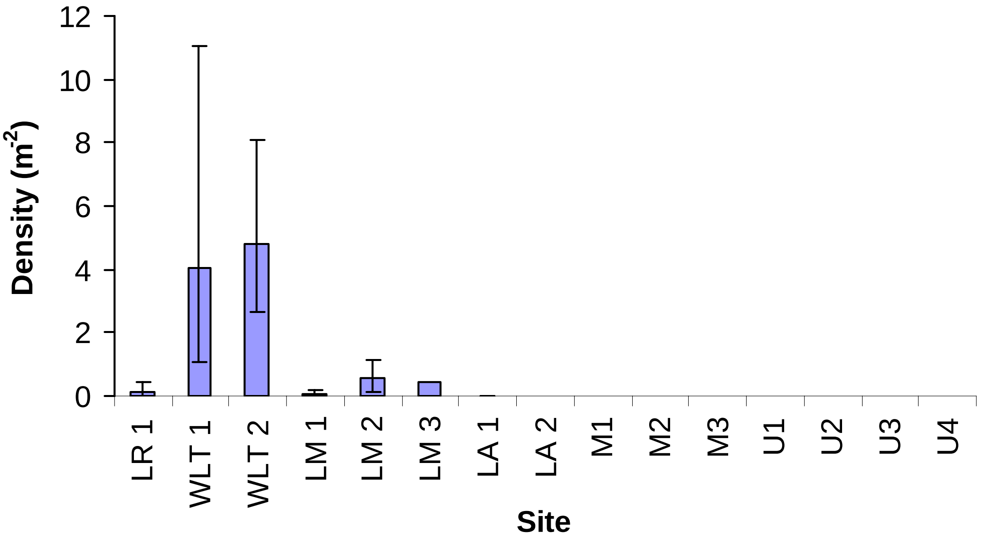
Location	Total number of oysters counted	Upper confidence limit	Mean oyster density (m^{-2})	Lower confidence limit	Range	Minimum height (cm)	Maximum height (cm)
Sound of Ulva							
U1	24	n/a	1.073	n/a	0–3	2.72	10.86
South Ulva							
U2	7	n/a	0.240	n/a	0–2	3.17	8.12
U3	26	n/a	0.799	n/a	0–8	2.98	9.82
Loch Tuath (Ulva)							
U4	29	n/a	0.828	n/a	0–8	3.14	10.68

Figure 3.2 Mean density of O. edulis *(a), mean density or cover of potential competitor species (b-d) and predator species (e-f) surveyed in the multi-level transect surveys (2004).*

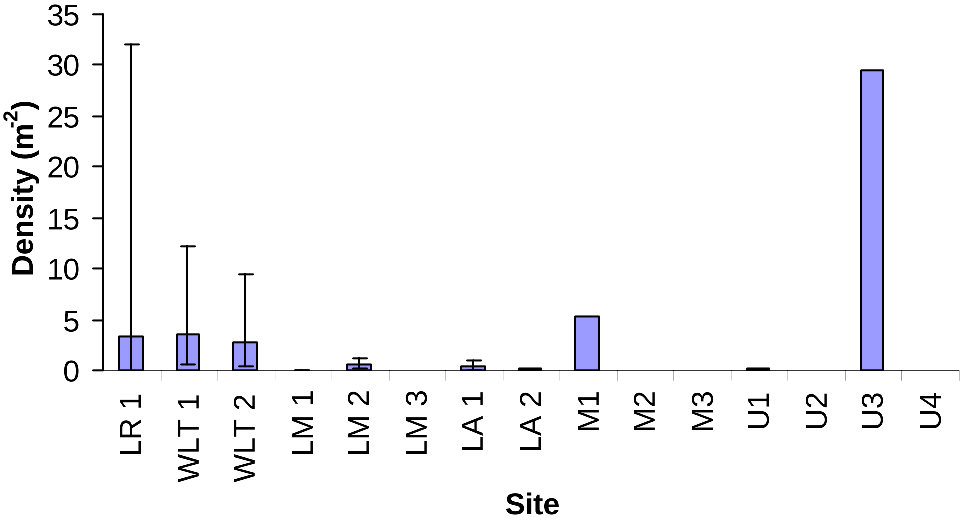
a. Ostrea edulis



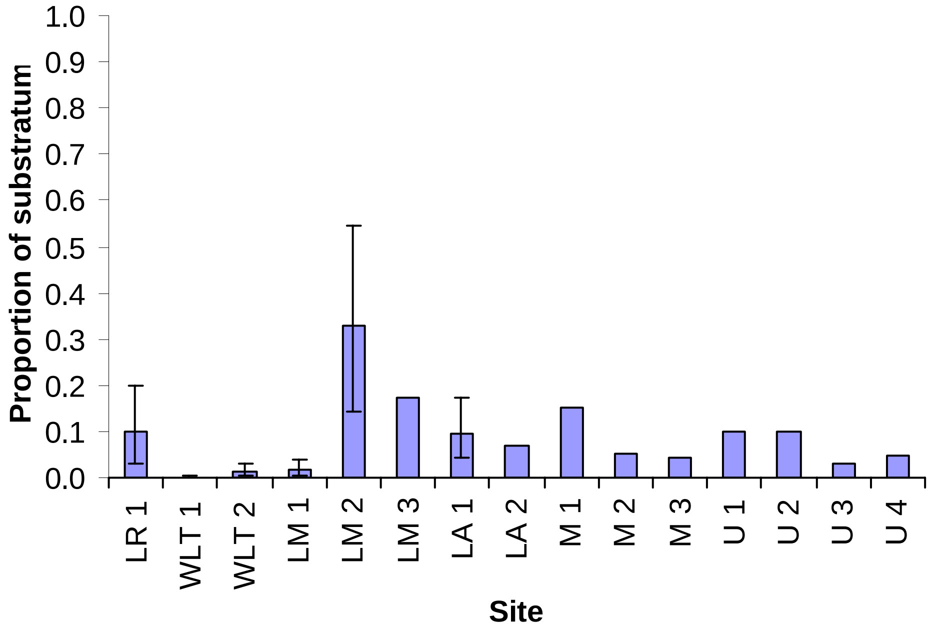
b. Anomia ephippium



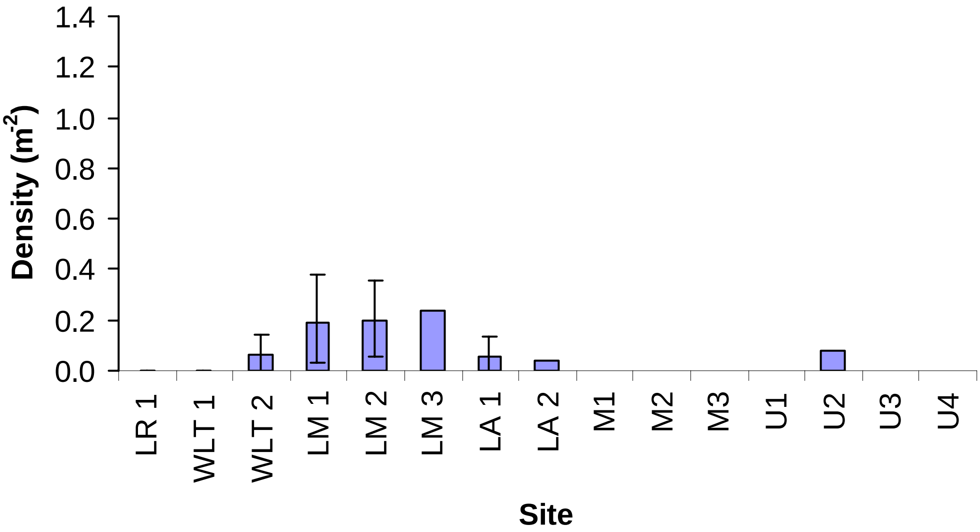
c. Mytilus edulis



d. Algae



e. Asterias rubens



f. Carcinus maenas

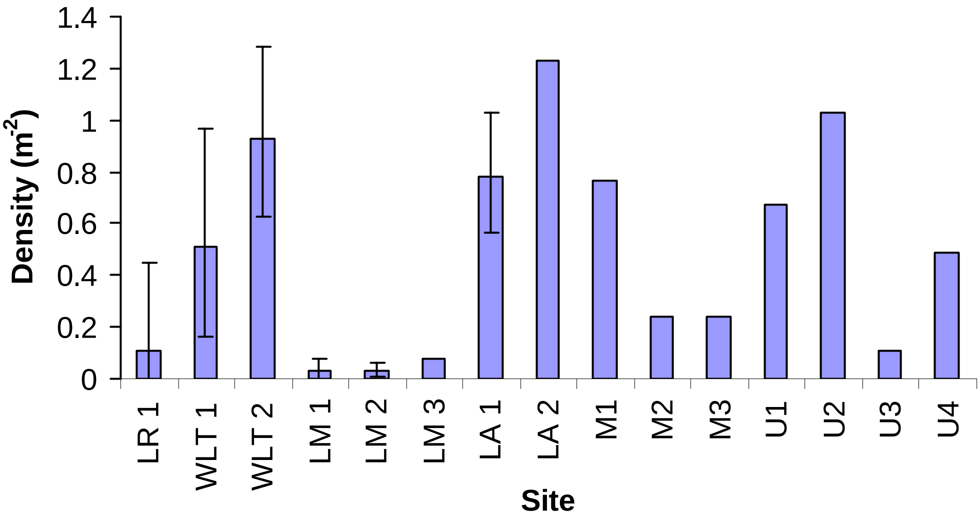
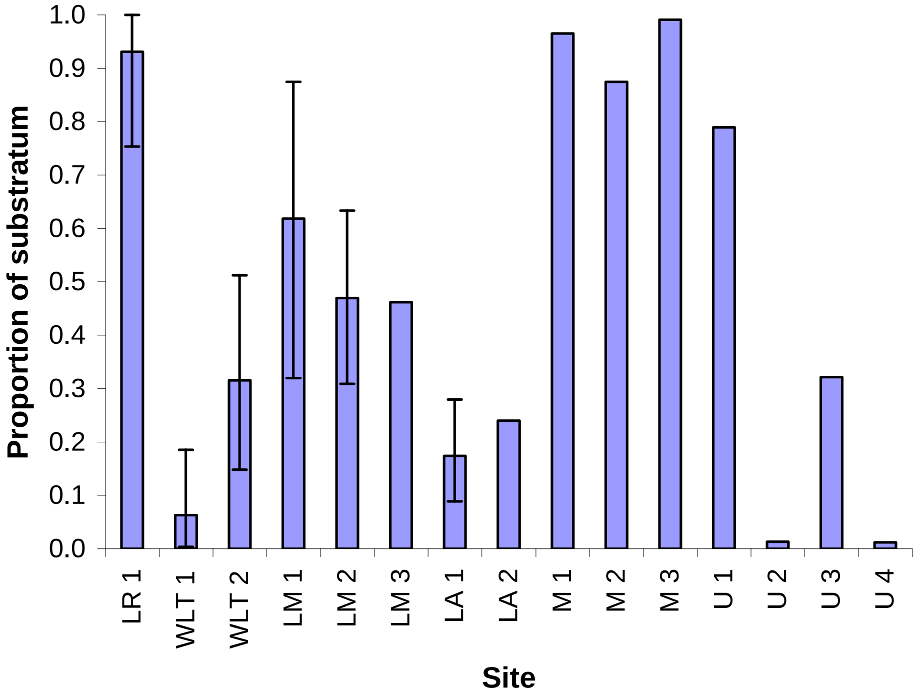


Figure 3.3 Mean proportional cover of substratum types per transect at surveyed sites.

a. Hard substratum



b. Shell

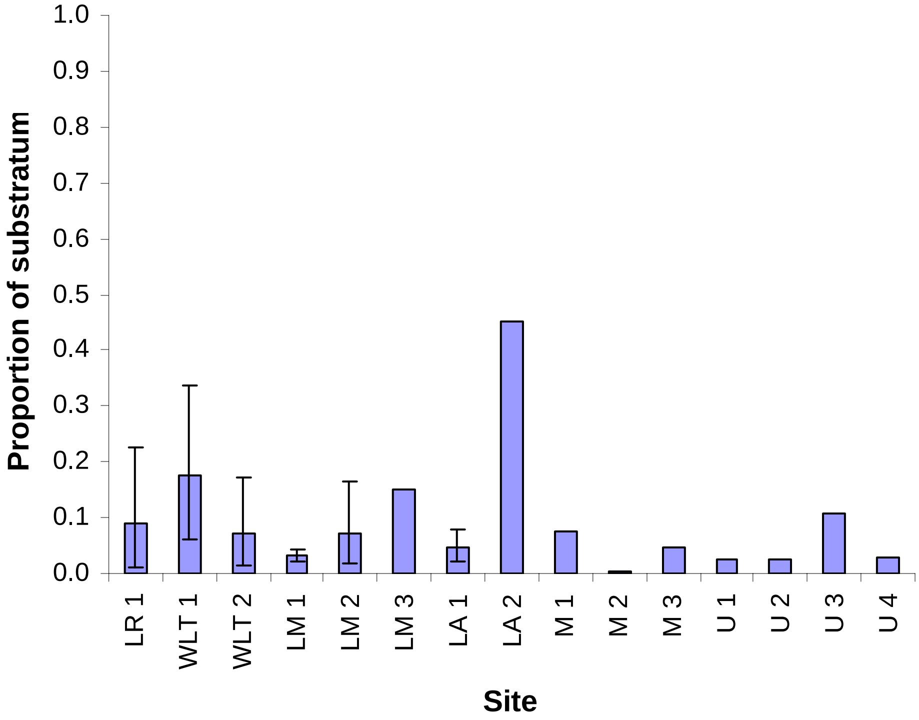


Table 3.3 Survey statistics. k = parameter of the negative binomial distribution. MLT = multi-level transect, BT = belt transect, BT: Estimates of belt-transect surveys using additional transects to increase the precision of estimates.*

Location	Method	Percentage Relative Precision (%)	*k*
WEST LOCH TARBERT			
WLT1	MLT	61.3	1.253
	BT	13.3	1.258
WLT2	MLT	42.8	2.136
	BT	13.3	1.052
LINNE MHUIRICH			
LM2	MLT	60.0	0.549
	BT	15.2	0.523
LM1	MLT	36.6	1.331
	BT	14.6	1.218
	BT*	11.0	1.194
LOCH AILORT			
LA1	MLT	26.5	0.635
	BT	32.6	0.262
	BT*	25.5	0.345
LA3	BT	44.0	0.394

Location	Method	Upper confidence limit (m^{-2})	Mean density (m^{-2})	Lower confidence limit (m^{-2})	Upper confidence limit	Mean abundance	Lower confidence limit	Area (m^2)	Maximum number of oysters
WEST LOCH TARBERT									
WLT1	MLT	1.110	0.658	0.303	22 193	13 160	6 601	20 000	5
	BT	0.852	0.750	0.653	17 049	15 002	13 068	20 000	6
WLT2	MLT	1.156	0.787	0.481	37 557	25 578	15 648	32 500	7
	BT	0.733	0.645	0.562	21997	19 360	16857	30 000	9
LINNE MHUIRICH									
LM2	MLT	2.650	1.553	0.785	66 250	38 818	19 632	25 000	8
	BT	0.607	0.525	0.448	15 174	13 132	11 193	25 000	10
LM1	MLT	1.094	0.784	0.520	16 415	11 762	7 799	15 000	28
	BT	0.796	0.689	0.591	11 890	10 332	8 865	15 000	12
	BT*	0.900	0.800	0.715	13 349	12 002	10 719	15 000	12
LOCH AILORT									
LA1	MLT	0.554	0.435	0.324	4 159	3 259	2 429	7 500	6
	BT	0.173	0.130	0.088	1 299	975	664	7 750	4
	BT*	0.193	0.153	0.115	1 448	1 150	862	7 500	4
LA3	BT	0.107	0.074	0.042					3

Table 3.4 Estimates of population density and abundance for Linne Mhuirich, West Loch Tarbert and Loch Ailort. Abbreviations as above

Figure 3.4 Mean population density (± 95% confidence limits) estimated from multi-level transect surveys and belt-transect surveys.

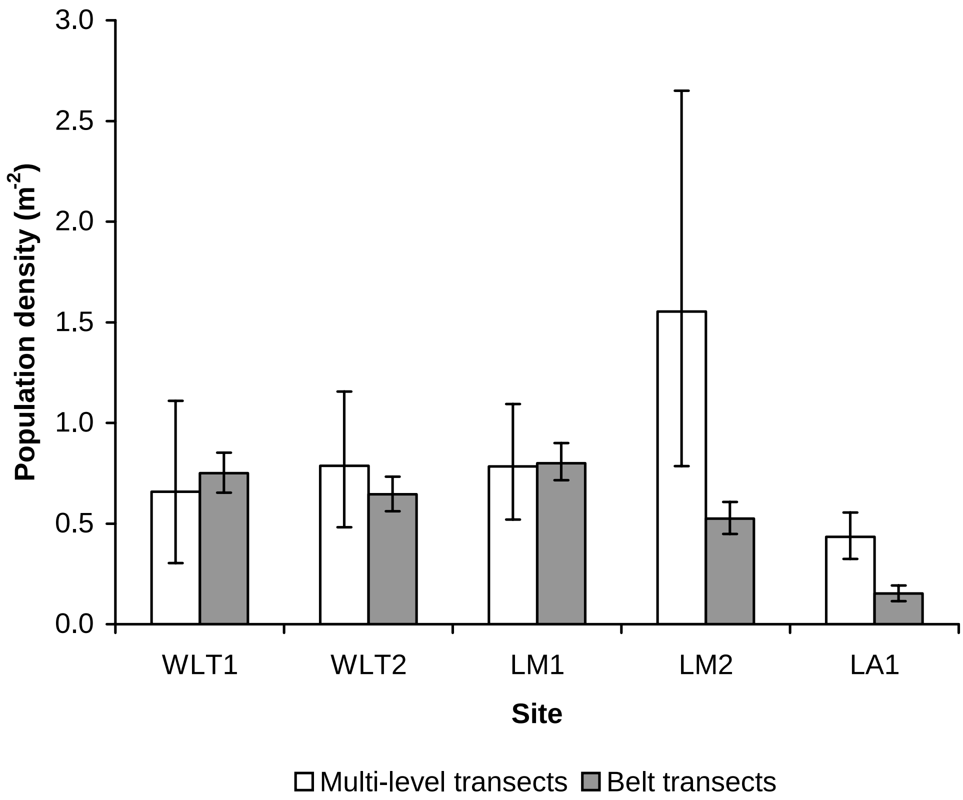
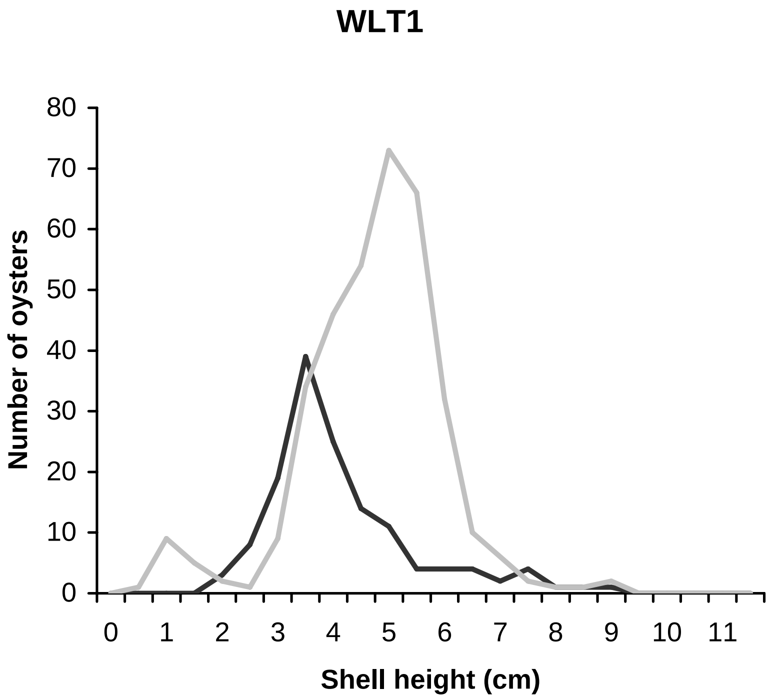
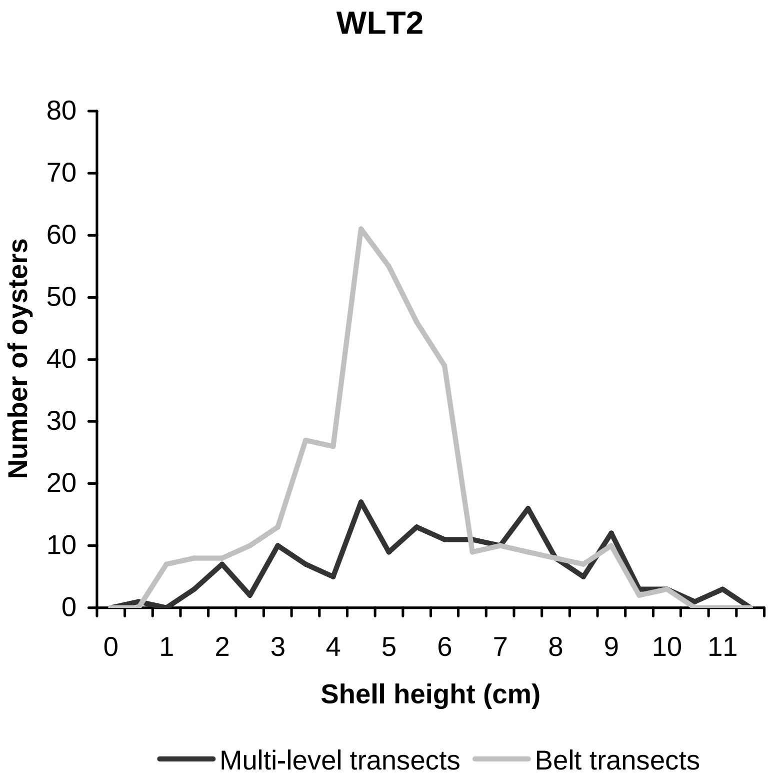


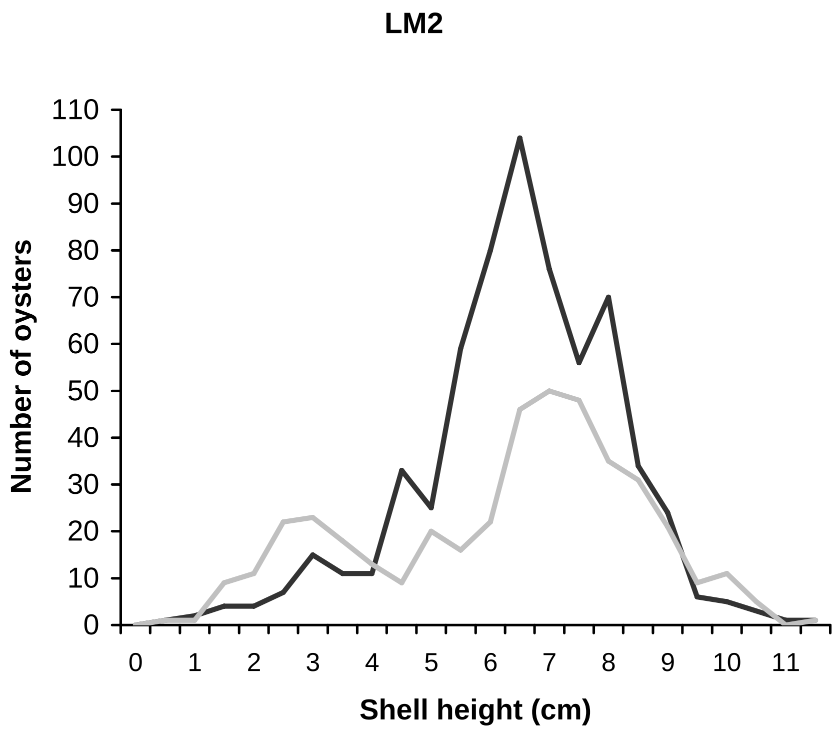
Figure 3.5 Size-frequency distributions of surveyed oysters at (a) West Loch Tarbert, (b) Linne Mhuirich and (c) Loch Ailort for multi-level transects (2004) and belt transects (2005). Only the most precise estimates are presented. Size-classes for shell height were based on 0.5 cm intervals and are represented by the first measurement of the category.

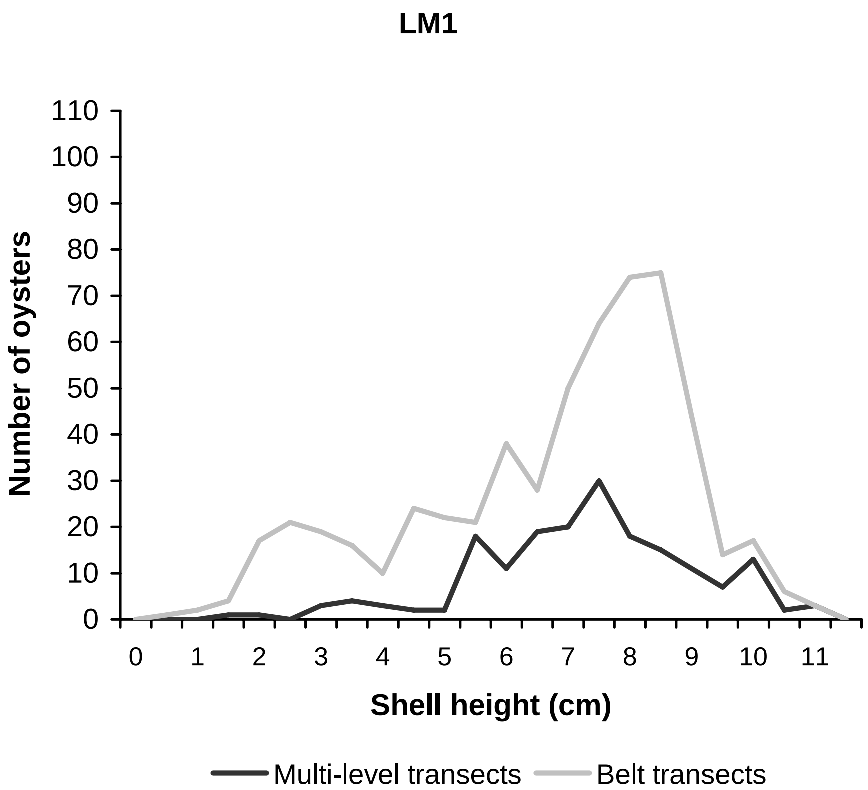
a West Loch Tarbert



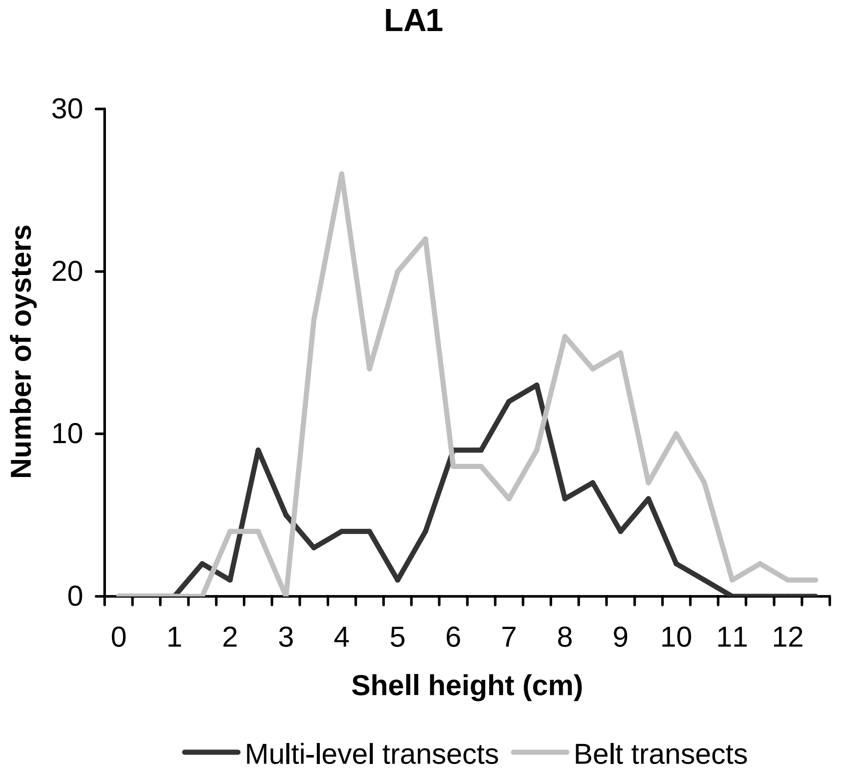


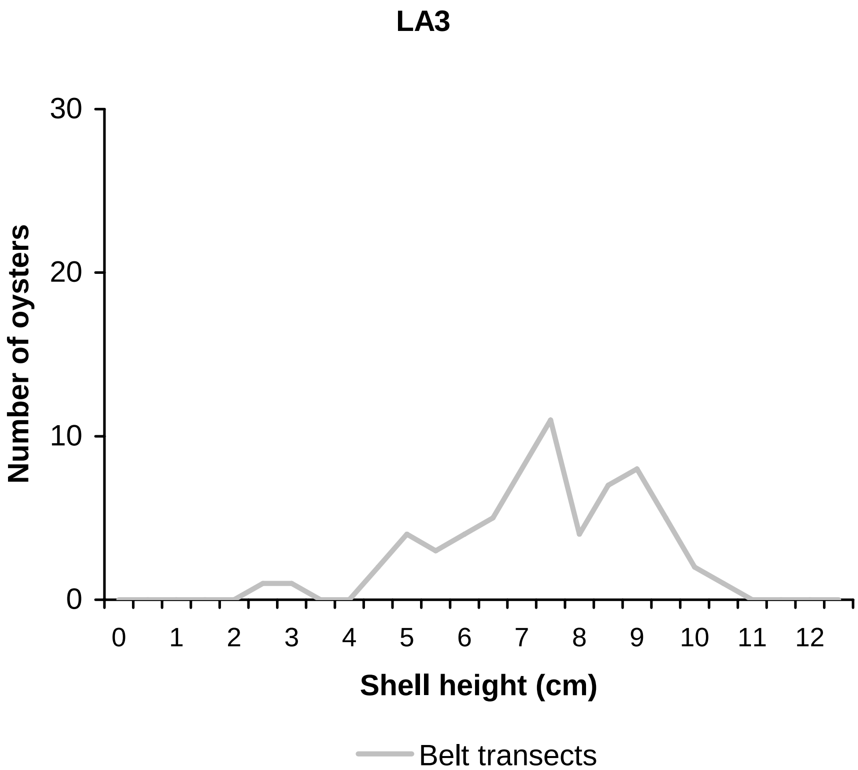
b. Linne Mhuirich





c. Loch Ailort





In West Loch Tarbert (Figure 3.5 a), the population at WLT1 was dominated by small to medium-sized (3–6 cm) oysters in 2004 and predominantly medium-sized (5–7 cm) oysters in 2005. In 2004, peaks were less obvious in the size-frequency for the WLT2 population with a higher proportion of oysters in the medium-size ranges (4–7 cm) and a few smaller and larger individuals. However, in 2005, there was a more pronounced peak in the size-range of 5–7 cm. At both sites in West Loch Tarbert, a small increase in the number of small-sized oysters (1–2 cm) was apparent. Overall, the oysters surveyed at both sites in Linne Mhuirich were generally from larger size-classes (6–9 cm) (Figure 3.5 b). However, the 2005 surveys show a small peak in the smaller size-classes (<4 cm). The LA1 population in Loch Ailort shows two peaks in the 2004 survey, one of smaller sizes (2–3 cm) and a second in the middle to large size range (5–8 cm) (Figure 3.5 c). Both of these peaks are small due to the low number of oysters surveyed. These peaks shifted to medium-sized oysters (4–6 cm) and larger oysters (8–11 cm) in the 2005 surveys. The oyster population at LA3 was also surveyed in 2005. The majority of these oysters were in the medium-large size range (5–10 cm) (Figure 3.5 c).

3.3.3 Unlawfully gathered oysters

The three bags of unlawfully gathered oysters contained 118, 250 and 364 oysters, respectively. Of the 732 oysters measured, only 18 oysters were less than 5 cm and in most cases these were attached to larger oysters. Comparison of the size-frequency distributions shows that a range of sizes of oysters are present in the Linne Mhuirich population but the oysters that were gathered were concentrated in the medium to large size range (Figure 3.6). Over 55% of the oysters were attached to a substratum or showed evidence of forceful removal from a substratum (Figure 3.7). Less than 20% of these oysters were attached to larger substrata, such as rock or stone.

Figure 3.6 Size-frequency distribution of oysters unlawfully gathered from Linne Mhuirich. Shell height is represented by the mid-point of the size-class interval.

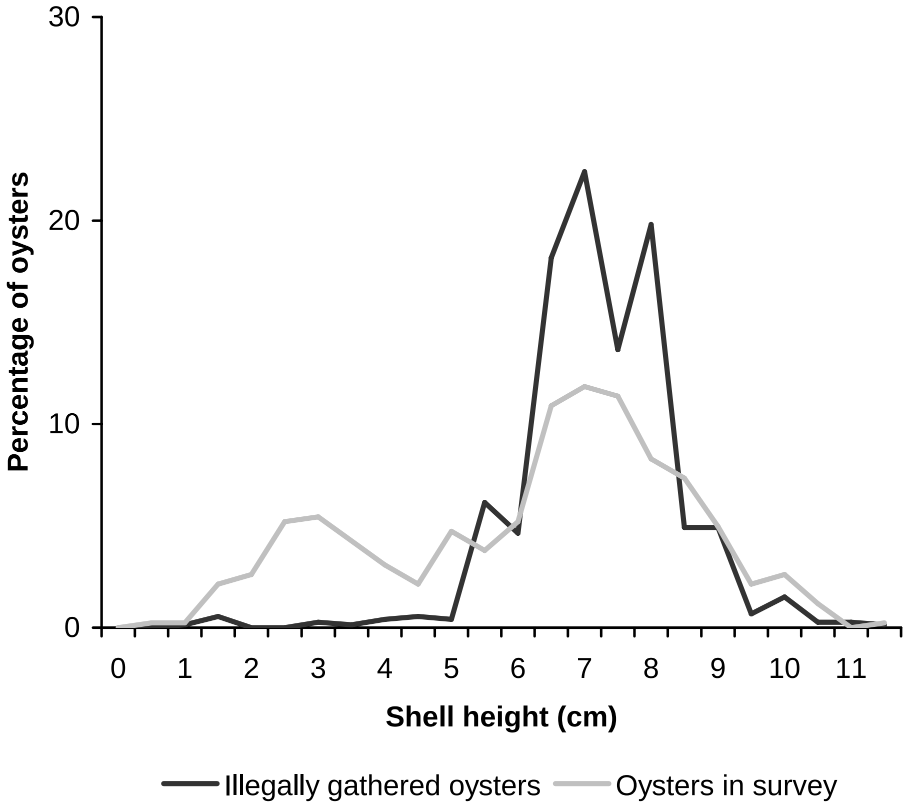
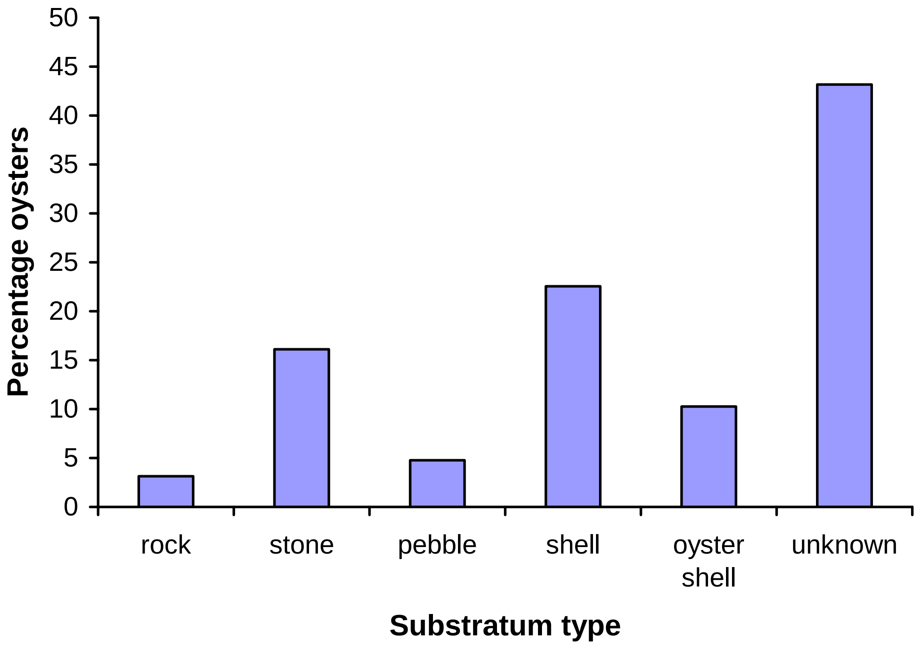


Figure 3.7 The percentage of unlawfully gathered oysters attached to different substratum types.



3.4 Discussion

3.4.1 General status of wild populations

Although full population surveys could not be completed at all the sites visited, surveys indicate that a range of high- and low-density populations exist throughout Scotland. Overall, the associated predator and potential competitor species of *O. edulis* were at low densities. However, *A. ephippium* occurs at relatively high densities in sites at West Loch Tarbert, indicating that it could be a potential competitor with *O. edulis*. Substrata suitable for larval settlement were also present at relatively high abundances at all the sites surveyed. Further research will be necessary to determine whether species interactions or the availability of habitat suitable for larval settlement could be limiting factors to the growth of populations of *O. edulis* (Section 4) and whether density and abundance are sufficient for populations to be self-sustaining (Section 5).

3.4.2 Sampling design

Increasing the number of replicates decreases the standard error and thereby increases the precision of marine benthic studies (Vézina, 1988). The use of SCUBA for underwater visual census creates logistical restrictions on the number and length of replicates that can be attained in a specific period of time. As conservation projects are often constrained by financial factors (Sutherland, 2000), the most efficient survey method should be used in order to maximise the resources available. Several census methods have been used for estimating marine benthic population characteristics throughout the literature, including belt-transects (Shepherd, 1986; Pascual *et al*., 2001; Trewfik & Guzman, 2003), multi-level transects (Richardson *et al*., 1993; Kennedy & Roberts, 1999; Wright-López *et al*., 2001) and adaptive cluster sampling (Woodby, 1998). In the current study, estimates using belt-transect data were found to have higher levels of precision and therefore produced more reliable results.

The precision of estimates varied greatly among sites for both methods owing to the sparse and patchy nature of the oysters within the habitat, with quadrat counts following a negative binomial distribution. More precise estimates and narrower confidence limits were obtained for all sites using the belt-transect method. However, when the same number of transects were compared, the precision of the estimates obtained from the belt-transect surveys at LA1 were slightly lower than that of the multi-level transects. This small difference can be attributed to the random selection of transects. For all sites, except WLT2 and LA1, comparison of the *k*-values showed a difference of approximately ±5%, whereas the *k*-value for the belt-transect surveys was 50.7% less at WLT2 and 45.7% less at LA1 than for the multi-level transects. This indicates greater patchiness of the individuals in the belt-transect surveys compared with the multi-level surveys at these two sites. Given the small difference in *k*-value at each of the other sites, it is unlikely that the change in sampling design was the main cause of this pronounced difference. All sampling grids included both sparse and dense areas and the transects surveyed were selected randomly. Since the surveys in 2004 and 2005 used differing methods, it is difficult to draw any firm conclusions. Nevertheless, belt-transect surveys are expected to be less affected by patchiness in a population (Krebs, 1999), so the spatial distribution of these populations is likely to have changed between the two years.

Reports of unlawful exploitation of the *O. edulis* populations at WLT2 and LA1 were made during the period between the two surveys (see sections 3.6.2.3 and 3.6.5.1). Although the numbers of oysters that were taken could not be quantified, unlawful exploitation could have increased the patchiness within the population causing the *k*-value and the precision of estimate to decrease. Unlawful harvesting was also reported for Linne Mhuirich, but the *k*-values for the two surveys only differed by approximately 4%. The spatial distribution of the population at LM2 is characterised by a small number of dense patches within a large area of sparsely distributed oysters. Oyster counts within individual quadrats in the LM2 multi-level surveys ranged principally between 0–4 m^{-2}, but the maximum number counted ranged up to 28 oysters. The range in oyster counts was narrower in the belt-transects, with the maximum count being 12 oysters (Table 3.4). Although unlawful exploitation of the Linne Mhuirich population occurred, this may not have affected the *k*-value of the surveys since relatively dense areas were still preserved. In contrast, there was no distinct difference in the range of oyster counts within quadrats at WLT2 and LA1 between the two survey methods. Therefore, the decrease in the *k*-value suggests that unlawful exploitation from the populations at WLT2 and LA1 may have increased the patchiness.

3.4.3 Population estimates and unlawful exploitation

Previous estimates of population density at Linne Mhuirich, as well as density and abundance estimates for populations elsewhere in Europe have been made in recent years (Table 3.5). Comparisons among these estimates should be made cautiously, owing to the use of different survey methods. The present estimates of *O. edulis* population densities in Linne Mhuirich, West Loch Tarbert and Loch Ailort (Table 3.4) lie within the range of the values reported for the other European populations (Table 3.5). However, the estimated density at LM1 in the current study was considerably lower than that found by Paisley (1994 cited in Bunker, 1999), which in turn was thought to be much lower than historical values. Bunker's (1999) estimate of population density in Linne Mhuirich was lower than Paisley's, but is nevertheless greater than the upper confidence limits of the present estimates at that site. Kennedy & Roberts (1999) used a multi-level survey method to estimate population density and abundance in the northern part of Strangford Lough, Northern Ireland. The 2004 estimates using the multi-level method indicate that the Scottish sites surveyed had higher densities than in Strangford Lough, where the density was 0.0018 m^{-2}, averaged over the two regions of the lough where oysters were found. However, since the total area of these regions of Strangford Lough (61.687 km^2) was much larger than the Scottish sites, the total estimated abundance there (109,975 oysters) was greater than at any one of the Scottish sites. With the exception of Strangford Lough, the surveyed populations of *O. edulis* in Scotland appear to be more abundant than other British populations.

Size-frequency distributions indicate that there have been recent recruitments in Linne Mhuirich and Loch Ailort, with peaks around the size-class of 3 cm (Figure 3.5 b). However, the small size peak suggests that these recruitment events may have been weak. Other sites also showed peaks in smaller oysters (<5 cm). The appearance of peaks in 2005 of small-sized oysters (<4 cm) at many of the sites could be attributed to the larger area surveyed in the belt-transects. In addition, the annual growth occurring between the survey dates could have increased the visibility of the smaller oysters to the survey divers, thus increasing their chance of being sampled. The Linne Mhuirich populations showed a wider size-range than the West Loch Tarbert populations (Figure 3.5 a). The lack of larger-sized oysters (>7 cm) in the West Loch Tarbert populations could be an artefact of past unlawful exploitation, when SCUBA divers were thought to have removed many thousands of oysters (N. Duncan, pers. comm., 2004). However, differences in the size-frequency distributions among sites and among years will also be influenced by differences in growth and survival

Table 3.5 Estimates of density and abundance of wild O. edulis *populations in Europe, from non-commercial data sources over the past 25 years.*

Location	Year	Survey method	Abundance	Density (m^{-2})	Reference
SCOTLAND					
Linne Mhuirich	1994	Dive survey: method unknown	Unknown	3 - 4	Paisley (1994), cited in Bunker (1999)
	1999	Dive survey: single belt transect (2 m x 100 m).	Unknown	1.3	Bunker (1999)
NORTHERN IRELAND					
Strangford Lough	1999	Dive survey: multi-level transect surveys	109 975	0.0018	Kennedy & Roberts (1999)
WALES					
	2003	Dive survey: unspecified transect method	Unknown	< 0.2	Cooke (2003)
SPAIN					
Galician Rias	1984	Unknown	300 000		Ruiz *et al*. (1992)
Ría de Ortigueira	1989	Unknown	10 000		Saavedra (1997)

rates, data for which are not currently available. Therefore it is difficult to interpret these differences in size-frequency distributions.

The size-frequency of the unlawfully gathered oysters in this study indicates that medium- to large-sized oysters (5–9 cm) (Figure 3.6) are selected, probably because the oysters were to have been sold for human consumption. Smaller oysters that were included in the unlawful catch could be considered inadvertent bycatch, since small oysters made up a small percentage of the catch and in most instances were attached to larger oysters. Although unlawful gathering has been frequently reported in Linne Mhuirich, large-sized oysters (>7cm) are still present at LM2. This is because dense patches of oysters at LM2 are often found attached to large rocks from which the oysters cannot easily be removed (see sections 4.3.2). Furthermore, the majority of oysters that were gathered were either attached to light-weight substrata or were unattached. This indicates that the substratum to which the oysters are attached influences their selection for gathering.

Although the effects of unlawful exploitation on population density cannot be quantified, the effects are perceptible in the populations at LM2 and LA1. The size-frequency distributions indicate that LM2 is the only site for which the belt-transect method, which covered a larger survey area, sampled fewer individuals than the multi-level survey design (Figure 3.5 b). Correspondingly, density estimated by the belt transect was less than 63% of the estimates by the multi-level transect. Furthermore, in both areas, the upper confidence limits of the density estimates for the belt-transect method fell below the lower confidence limits of the multi-level survey method. For all other sites, the confidence limits for the belt-transect survey estimates fell between the confidence limits of the multi-level survey estimates (Figure 3.4, Table 3.4). Since unlawful exploitation is known to have occurred several times between the surveys, it is plausible to attribute the change in density and abundance of the LM2 population primarily to the effects of unlawful exploitation. A similar conclusion can also be drawn for the change in density and abundance in the Loch Ailort population, since local reports suggest that approximately 2,000 oysters were unlawfully taken in December 2004.

3.5 Current Status of *Ostrea edulis* populations around Scotland

This section is a compilation of site information and local knowledge gathered during site visits and provides a summary of the status of the wild *O. edulis* populations (Table 3.6).

Table 3.6 Summary of the status of known wild O. edulis *populations based on recent (post 2003) information and records of live oysters.*

Location	Status	Brief summary
DUMFRIES & GALLOWAY		
Loch Ryan	Extant	*O. edulis* are found over the majority of the shallow (<5 m) inner basin. A commercial fishery operates within this area.
ARGYLL		
Loch Melfort	Unknown	Occasional live oysters have been found in recent years.
West Loch Tarbert	Extant	Beds found in shallow waters (<5 m) around margins of the upper loch. Some scattered oysters found on the northern bank also. Unlawful exploitation of the populations is a severe problem. A *C. gigas* farm is located in the outer reaches of the loch.
Loch Sween	Unknown	*O. edulis* have been reported in Loch Sween in the past. Around the Ulva Islands, exploratory dives did not find any live oysters. Oysters have been reported around the Castle Sween area but this sighting has not been confirmed.
Loch Sween (Linne Mhuirich)	Extant	Two main bed areas found in shallow (<3 m) waters. Unlawful exploitation of the population in the Tayvullin-Dun Mhuirich area is a severe problem. *O. edulis* are also present in low numbers in other areas around Linne Mhuirich.
MULL		
Broadford Bay	Unknown	Anecdotal reports suggest that oysters were present but dredging activities in this area may have smothered the remaining oysters.
Loch na Keal	Extant	*O. edulis* populations have been reported in several areas of this Loch. Unlawful exploitation has been reported in this area.
Loch Scridain	Extant	A large bed is present within the loch. Unlawful exploitation has been reported in this area.
Loch a' Chumhainn	Extant?	*C. gigas* and *O. edulis* are farmed in the subtidal areas on the southern banks. *O. edulis* have been reported living wild in the subtidal areas also.

Location	Status	Brief summary
North Mull	Extant?	*O. edulis* beds are reported to be present and provide the source of broodstock for a local hatchery (Tobermory Oysters). The hatchery owner would not disclose the whereabouts of the source bed.
HIGHLANDS & ISLANDS		
Loch Ailort	Extant	Oyster beds are located around the shallow (<5 m) waters in several areas of the loch. A commercial *O. edulis* hatchery is planned for this loch and wild oyster collection has occurred. Oysters have also been collected for breeding trials for a hatchery development in Drumnadrochit. Unlawful exploitation is also a potential problem.
Loch Eriboll	Extinct?	Oysters have been collected from this area for a variety of purposes, mainly from the head of the loch. Unlawful exploitation is also a major problem. Recent exploration of this area suggests that it has now become extinct. However, anecdotal reports suggests that there may be a deeper bed in the area.
Kyle of Tongue	Extinct?	No evidence of live oysters was found in this area. Commercial growing of hatchery *O. edulis* occurs in the intertidal area to the north of Tongue House.
Skye	Extant?	Anecdotal evidence suggests that there are several locations around Skye where oysters can be found. Unlawful exploitation is a severe problem in some of these areas.
Uist	Extant?	Possibility of live *O. edulis* reported by Dr Hall-Spencer in 2004.
Orkney	Extinct	Anecdotal reports suggests that all oyster beds around Orkney have become extinct.
Shetland	Extant?	Anecdotal reports suggests that there is one oyster bed that still contains oysters (see section 3.6.7.1).

3.6 Observations and local information from around Scotland

3.6.1 Dumfries and Galloway

3.6.1.1 Loch Ryan

Loch Ryan has a long history of harvesting, restocking and cultivation of wild *O. edulis* populations, which occur throughout the loch from Craignure to Stranraer (see section 2.2.1). Loch Ryan is currently operated as a commercial fishery, managed by Loch Ryan Shellfish Ltd.

3.6.2 Argyll and Bute

3.6.2.1 Loch Melfort

Two living oysters were found attached to moorings in Loch Melfort in 2004 by Peter Richardson, the Projects Manager of Kames Fish Farming Equipment Ltd. In the 1950s, Millar (1961) laid Brittany oysters in two bays at the head of the Loch. Oysters have been identified by SNH personnel at the head of Loch Melfort.

3.6.2.2 Loch Fyne

Loch Fyne Oysters have previously cultivated *O. edulis*, but cultivation efforts were terminated as they were deemed to be uneconomical. Currently Loch Fyne Oysters cultivate *C. gigas* and *M. edulis* at Ardkinglas, Cairndow. A salmon farm operated by Pan-Fish is also located nearby.

3.6.2.3 West Loch Tarbert

There are a several areas containing *O. edulis* around the infralittoral areas in West Loch Tarbert. The populations in West Loch Tarbert have suffered from frequent occurrences of unlawful exploitation over the past five years. Reports of unlawful exploitation from West Loch Tarbert were made in 2004 and 2005 by Mr Neil Duncan.

Mr & Mrs Stewart of Campbeltown have recently submitted proposals for the development of an *O. edulis* “ranching” operation in the subtidal area at Rhu. SeaCroft Oysters is a *C. gigas* farm in the lower reaches of the loch and is owned and managed by Neil Duncan. A more detailed history of West Loch Tarbert is provided in section 2.2.2.

3.6.2.4 Linne Mhuirich (Loch Sween)

There is a long history of harvesting, cultivation and restocking of the wild *O. edulis* populations in Linne Mhuirich (see section 2.2.3). There are two main populations in this area and unlawful exploitation is common. Isolated *O. edulis* are also found in the Linne Mhuirich tidal rapids and other bays.

A holiday couple camping at Castle Sween, who have their own boat, informed the project team that for several years they have taken oysters from the Castle Sween area and re-laid them in Linne Mhuirich. It is unknown what quantity have been re-laid or for how many years this has been happening.

Approximately 450 oysters were confiscated from a poacher in December 2003, originating from the Linne Mhuirich area, and these were re-laid by SNH personnel. Another 732 oysters unlawfully harvested from Linne Mhuirich were seized in February 2005. These have been re-laid by UMBSM personnel.

Mr Tom Stevenson, who used to manage the fishery in Linne Mhuirich in the 1960s, has recently started doing his own survey work (for non-commercial personal interest) in the intertidal and shallow subtidal areas of Linne Mhuirich. SNH have been in correspondence with him over this matter.

3.6.2.5 Loch Sween

Alan Berry used to cultivate *O. edulis* in Loch Sween, but this was terminated when the quality of the water deteriorated, making the stock unfit for market. There have been reports of *O. edulis* populations in several locations in Loch Sween. An exploratory survey of the Ulva Islands area found no living *O. edulis*. The status of the other areas is unknown. However, a survey of littoral molluscs conducted for the Natural Conservancy Council in 1982, did not record *O. edulis* at a site to the east of Castle Sween (Smith, 1982).

3.6.2.6 Bute

Isolated oysters have been found in the intertidal area of St. Ninian's Bay. This site was visited in May 2005. The *O. edulis* found were mostly larger individuals of 8–10 cm diameter with very occasional smaller individuals of around 4 cm diameter. The oysters were mostly isolated individuals with occasional patches of 3–5 individuals. There was a lack of dead oyster shell in the area. Winkle pickers frequently collect from this area, so it is possible that *O. edulis* have also been collected in the past.

3.6.2.7 Loch Ceann Traigh

Mr John Timothy MacMillan, of Rowanmere, Acharacle, Argyll, was granted a Several Order to fish for oysters and scallops. The Order came into force on 5 December 1997 and was granted for 15 years. It is unknown whether a natural population of *O. edulis* exists or if the species is being cultivated by Mr MacMillan.

3.6.3 Mull and Ulva

3.6.3.1 Loch Tuath

Mr Jamie Howard has cultivated *C. gigas* in this loch for over ten years. The area holds 80 trestles, with eight oyster bags per trestle. *C. gigas* have been imported from Herm, Channel Isles. There is a lack of water movement in this area and weed grows quickly on the bags. There has been a build up of Cyanobacteria since the trestles were introduced. Wild *O. edulis* are also found in this area.

A biodiversity survey conducted in 1983 recorded occasional *O. edulis* (Smith & Gault, 1983). It should be noted that "occasional" was used to refer to single individuals in the Smith & Gault (1983) study. The current status of any potential population in this area is unknown.

3.6.3.2 Sound of Ulva

There is some small-scale cultivation of *O. edulis* in this area. The native population has been supplemented with *O. edulis* re-laid from the south side of Ulva and *O. edulis* from the Isle of Colonsay were imported around 1997. The origin of the Colonsay stock is unknown. There have been losses of *O. edulis stock* to *A. rubens*, but oysters above 30–40 g are thought to have higher survival rates. Algal coverage has also increased in recent years.

3.6.3.3 Loch na Keal

O. edulis are found scattered subtidally in this region and it is suspected that unlawful exploitation takes place at a number of sites. A biodiversity survey conducted in 1983 recorded *O. edulis* as "common" or "occasional" in sites around Loch na Keal (Smith &

Gault, 1983). It was not possible to survey the same sites and the current status in these areas is unknown.

One site in Loch na Keal is used for farming *C. gigas* on trestles. *O. edulis* were originally found in the area and were cultivated in the past but this proved unprofitable. Free-living *O. edulis* have been collected from underneath the trestles and placed into two shallow brick-lined compartments (approximately 3 m^2). There are boat moorings in the outer reaches of this bay and a scallop fishing operation is based on the other side of the island.

Another part of this loch is known for Palourdes (*Tapes decussatus*) and there are no reports of unlawful exploitation of the oyster population in this area. It is inaccessible without a boat and there is a watchman in the employ of the Inch Kenneth Estate, which overlooks the bay.

Simon Howitt, a local fishmonger and shellfish picker, intends to apply for a lease to ranch *O. edulis* on an off-shore reef area within Loch na Keal.

3.6.3.4 Ulva (other areas)

A large population of *O. edulis* used to be present near Gometra. It is claimed that approximately eight years ago, a person could collect “a hundredweight” of *O. edulis*. Unlawful exploitation of the population is known to occur in this area by visitors to the island. An exploratory survey of the subtidal area found a few isolated oysters.

It is claimed that travelling people are responsible for most of the unlawful exploitation of oysters around Mull and Ulva. Many areas on Mull have been blocked off to prevent travellers setting up camps. Locals also claim that they suspect that some people with access to small boats are responsible for removing oysters from the more remote sites that cannot be reached from the road.

3.6.3.5 Loch Scridain

Local clam divers have found *O. edulis* down to depths of 10–15 m, where they occur as fully-grown specimens in clumps. The prevailing winds in that area are south-westerly and Mr Howitt speculated that the foreshore bed receives spat from these offshore beds. We were unable to survey these deeper areas for logistical reasons. In places, the intertidal and shallow subtidal areas have an abundant population of *O. edulis*.

A biodiversity survey conducted in 1983 recorded a natural population of abundant *O. edulis* in the central loch and occasional *O. edulis* in the inner loch (Smith & Gault, 1983). In addition, the report stated that a small oyster farm at Eilean an Fheòir cultivated *C. gigas* and *O. edulis*. The *O. edulis* were originally from the natural population found in the area.

3.6.4 Mull (other areas)

3.6.4.1 Loch a’ Chumhainn

Mr David Wathen has cultivated *O. edulis* in the shallow subtidal area of this loch since the late 1970s. He used to import 8–10,000 per year from the Orkney hatchery until it closed four years ago. He has now changed to a supplier from Morecombe, Lancashire. Mr Wathen operates under a Collection License from the Crown Estate and uses tray cultivation. Mr Wathen stated that a few years ago divers found oysters living on the sea-bed in the deeper reaches of the loch. The current status of any natural population is unknown.

3.6.4.2 Tobermory Bay

There is an *O. edulis* hatchery operating in the Port na Coite area of Tobermory Bay, owned and managed by Mr David Flockhart. Scallops and *C. gigas* are also cultivated. Mr Flockhart stated the hatchery was started using wild *O. edulis* broodstock collected from a local population. Mr Flockhart would not reveal the location of this population. Occasional *O. edulis* were recorded in 1983 to the west of Calve Island (Smith & Gault, 1983).

3.6.4.3 Broadford Bay

Anecdotal reports suggest that *O. edulis* were present in Broadford Bay. However, it is speculated that dredging activities causing high levels of sedimentation in this area may have exterminated the population.

3.6.5 The Highlands and Islands

3.6.5.1 Loch Ailort

This area contains wild populations of *O. edulis*. There are no recorded fishing, harvesting, restocking or re-laying activities in this area. The only possibility may have been in the early 20th century when the Government were trying to revive the west coast oyster beds (see section 2.5). The loch is difficult to navigate and there is very little boat traffic, except for that associated with the salmon farm at the head of the loch and pleasure craft. Millar did not mention this area in his 1961 report, suggesting that this was not a well-known bed. However, local knowledge suggests that this bed has been known since the time of Bonnie Prince Charlie. A road was only constructed along the southern shore in 1965; the only access before this point was via the postal track. This suggests that if any exploitation of the beds was occurring, it was from local gathering. Unlawful exploitation of the beds has been reported in recent years. In summer 2004, snorkellers and divers were suspected of removing oysters. An Aberdeen farmer who owns a holiday home in the area informed us that his relatives have re-laid at least 100 oysters from the southern shores.

Exploratory surveys have revealed beds at several sites within Loch Ailort. A mollusc survey conducted in 1978 recorded the presence of *O. edulis* but no comment was made on their abundance or density (Smith, 1978). The first visit by the project team in June 2004 revealed some abundant populations, although no detailed surveys were made at that time. On return in September 2004, few oysters were found in the same area.

O. edulis are also present in low numbers at the head of the loch, where *C. gigas* are cultivated on trestles. The foreshore in this area and the *C. gigas* cultivation belong to Mr Hugh McLaren of Inverailort Estate.

Graham and Marilyn Cooper have recently started the development of a hatchery for *O. edulis* based at Roshven farm. In June 2004, the Coopers stated that they have collected 400 oysters from the southern shores of Loch Ailort. They aggregated these oysters in trestles and have reported good growth and survival. Preparations for the development of the hatchery are in the early stages.

3.6.5.2 Loch Moidart

There are reports that *O. edulis* used to be farmed in Loch Moidart where there was also a hatchery. It is speculated that broodstock was taken from Loch Ailort, conditioned and spawned in the hatchery there and then re-laid in Loch Moidart.

Currently, *C. gigas* are cultivated in the south channel of Loch Moidart by Mr Bill McDermott. He is currently re-developing his business to include *O. edulis*, which are to be grown on the sea bed. Mr McDermott plans to build a hatchery at Drumnadrochit, where he will cultivate local (i.e. West Lochaber) spat for relaying on his farm. Mr McDermott is currently using broodstock from Kinloch Ailort for breeding trials.

3.6.5.3 Loch Kishorn

An *O. edulis* fishery used to be based at Loch Kishorn but it has now closed. The status of any natural wild or stock with other origins is unknown.

3.6.5.4 Skye

O. edulis is reported to occur at several locations in Southern Skye. Exploratory surveys were conducted at low spring tides in three areas, but live oysters in very small numbers were found only at two sites.

3.6.5.5 Uist

There have been unconfirmed sightings of live *O. edulis* in the waters around Uist during research diving work in Summer 2004. The abundance and status of any potential populations is unknown.

3.6.6 Sutherland

3.6.6.1 Loch Eriboll

The intertidal and shallow subtidal area at the head of Loch Eriboll and mouth of Lochan Havurn was formerly known as one of the most productive beds for *O. edulis* along the north coast of Scotland. It has been used numerous times as a source of broodstock for oyster farming, such as the hatchery in Orkney. This area has been subject to high levels of unlawful exploitation in recent years, allegedly by travelling people. Exploratory surveys of this area revealed approximately 25 oysters in the whole bay area. A local biology teacher believes that there may be a deeper subtidal bed area somewhere in the loch. However, exploratory dives of the deeper areas of the Lochan Havurn area found a shallow sloping expanse of sand with no dead or live oyster shell present. This lack of shell suggests that it is unlikely that oysters are washed up from deeper areas to the infralittoral area.

There was some cultivation of *O. edulis* in the mid-reaches of the loch, but this operation is believed to have closed.

3.6.6.2 Kyle of Tongue

Historically, there were *O. edulis* populations in the Kyle of Tongue and empty oyster valves still remain around the foreshore. There is no evidence that there are currently any wild *O. edulis* in the Kyle of Tongue. Tom and Angela McKay cultivate *O. edulis* and *C. gigas* in the infralittoral zone just north of Tongue House. *O. edulis* were originally bought from a hatchery in Orkney, which used broodstock derived from Loch Eriboll. The McKays prefer to lay the native oysters on the seabed, but will use bags if there is a threat of mortality from predation or some other cause. Prior to collection, the stock suffered high mortalities from unknown causes (the McKays contended that this was associated with high sedimentation caused by trawling at the mouth of the Kyle).

3.6.7 Shetland and Orkney

3.6.7.1 Shetlands

Anecdotal reports suggest that a small *O. edulis* population may be extant in the waters around Unst. There are plans to develop a hatchery based on this population by a small Shetland business in collaboration with Dr Joe Irvine, the UHI Research and Commercialisation Manager of the Shetland Business Innovation Centre. Shetland Shellfish

Management Organisation Ltd. hold a Regulating Order for shellfish fisheries around Shetland, which includes *O. edulis* as a named species.

3.6.7.2 Orkney

Local information has suggested that there are no surviving *O. edulis* populations around Orkney. There used to be a hatchery in Orkney that obtained broodstock from Loch Eriboll but this closed due to the difficulties of rearing *O. edulis* spat.

3.6.8 Other Areas

Other areas of Scotland that may have *O. edulis* populations are those in which Millar (1961) laid Brittany oysters during the 1940s and 1950s. These included:

- Loch Craignish;
- Loch Gair;
- Balvicar Bay;
- Clachan, Seil, Argyll;
- Loch Creran (Ardnaclach, South Shian Bay);
- Loch Feochan;
- Loch Don, Isle of Mull;
- Loch Striven;
- Isle of Lewis (Loch Leurbost, Loch Barraglom, Loch Erisort, Breasclete Bay, Little Loch Roag);
- Isle of Soay;
- Loch Torridon (Ob Mheallaidh, Dubh Airde Bay, Boathouse Bay);
- Loch Ewe;
- Loch Tournaig;
- Inverness Firth;
- Munlochy Bay (Inverness Firth).

These areas have not been surveyed and it has not been possible to obtain local information for these areas. Therefore, the status of any potential populations in these areas is unknown.

A preliminary shore survey of Loch Craignish was made; no evidence of live *O. edulis* was found and information from local boat owners suggests that there are no live oysters present in this loch. The construction of a small boat harbour is thought to have increased the level of sedimentation and restricted water flow around Eilean Mhic Chroin and potentially caused loss of local marine fauna. However, the existence or extinction of *O. edulis* in this area has not been confirmed and there is concern about the local marine area in relation to urban development proposals.

A survey of the molluscan fauna of the shores of Loch Carron in 1978 recorded the presence of *O. edulis* within a *Cerastoderma edule* bed at Bagh an t-Strathaidh (Smith, 1978). A follow-up survey in 1985 found only one live oyster present in the *C. edule* bed plus many dead oyster shells (Smith, 1985). *O. edulis* were also recorded at Sruth Mor, Loch Laxford in 1979 (Smith, 1981). Details of the abundance or density of the species were not given. The current status of this area is not known but it seems unlikely that there are any *O. edulis* left in this area.

O. edulis was also placed in Loch Aline by clam divers (D. Donnan, pers. comm., 2006). The origin of the oysters is unknown, as is the numbers introduced and the numbers currently remaining.

4 SETTLEMENT SUBSTRATUM AVAILABILITY AS A LIMITING FACTOR FOR THE ABUNDANCE OF *OSTREA EDULIS* POPULATIONS IN SCOTLAND

4.1 Introduction

Availability of habitat has been suggested as a principal factor in determining individual or population size in several marine species (Caddy, 1986; Steger, 1987; Caddy & Stamatopoulos, 1990; Beck, 1995; Holbrook *et al*., 2000; Halpern, 2004; Reed *et al*., 2004). Caddy (1986) and Caddy & Stamatopoulos (1990) have proposed the demographic "bottleneck" theory based upon this concept. For species in which the post-larval stage is dependent on physical habitat availability, limited habitat availability could restrict recruitment affecting specific cohorts or ontogenetic stages, thereby causing a demographic bottleneck (Caddy, 1986; Caddy & Stamatopoulos, 1990; Beck, 1995). This theory is of relevance to the conservation and fisheries management of the native flat oyster, *Ostrea edulis*, in Scotland where wild populations are small and potentially declining.

O. edulis larvae are pelagic for a period of 7 to 12 days, after which settlement occurs with larvae attaching to solid substratum and metamorphosing into spat (juvenile oysters) (Korringa, 1952; Yonge, 1960). Key factors determining recruitment success in oyster populations are the number of larvae retained within the area of the oyster bed that successfully settle and metamorphose, and the availability of suitable substratum for larval attachment (Korringa, 1946; Millar, 1963; MacKenzie, 1970; Abbe, 1988). The settlement preferences of oyster larvae have been researched extensively, with authors concluding that the larvae prefer the underside of dark coloured settlement surfaces (Cole, 1936; Cole & Knight-Jones, 1939; Walne, 1979). However, most of these studies have concentrated on settlement onto artificial surfaces and within laboratory situations. Those studies that have investigated spatfall in natural populations have surveyed the numbers of spat on dead-shell cultch material sampled *in situ* (Knight-Jones, 1952; Millar, 1961; Kennedy & Roberts, 1999; Palmer, 2002). On natural oyster beds, settlement surfaces include the shell of living and recently dead oysters (Cole & Knight-Jones, 1939; Korringa, 1946; MacKenzie, 1970), other shellfish (dead or alive) (Cole & Knight-Jones, 1939; MacKenzie, 1970; Korringa, 1976) and other hard substrata, such as stones, wood or concrete (Korringa, 1976; Abbe, 1988).

It is often perceived that settlement substrata are widely scattered and only available at low abundance in the natural environment (Cole & Knight-Jones, 1939; Millar, 1963; MacKenzie, 1970). In addition, exploitation removes oyster shell, so decreasing the overall availability of this particular settlement substratum (Korringa, 1946). Therefore, commercial oyster management practices have often provided supplemental cultch material (e.g. dead clean shell or limed tiles) to increase the surface area available for larval settlement (Yonge, 1960; Korringa, 1976; Abbe, 1988). This practice has also been recommended by several authors as a way to increase the production of populations (Korringa, 1946; MacKenzie, 1970; McKelvey *et al*., 1993). Cultch supplementation practices are suitable for commercial fisheries because:

1. The beds are regularly maintained by the fishery (Korringa, 1946);
2. If used in conjunction with broodstock supplementation, the level of larval production is high enough to ensure that the effects of cultch supplementation are maximised (Korringa, 1946; Abbe, 1988); and
3. The costs of the labour and financial investment are recovered from the economic gains of stock production.

Wild *O. edulis* beds that are not managed for commercial gain do not necessarily fulfil these criteria. In addition, conservation techniques are often limited by practical and financial restraints (Sutherland, 2000). It is therefore necessary to identify the factors that are potentially limiting the capacity of a population to be self-sustaining.

This study aims to investigate the settlement characteristics of *O. edulis* in wild populations and to determine whether the availability of settlement substratum could limit recruitment. This will also include a survey of the habitat preferences of other sessile species that compete for space. The presence of these species could render areas of otherwise suitable substratum unsuitable for the settlement of oyster larvae. Investigation of these characteristics will allow a resource assessment to determine whether suitable habitat is a limiting factor to population abundance in the natural environment.

4.2 Methods

The oyster habitat at LM1 (Linne Mhuirich), LM2 (Linne Mhuirich), WLT2 (West Loch Tarbert) and LA1 (Loch Ailort) was divided into alongshore sections of 25 m length. Eight sections were randomly chosen and surveyed. A 25-m tape measure was laid parallel to the shore along the mid-line of the bed section. Twenty 1-m^2 quadrats, divided into 5 cm squares, were placed at randomly-chosen alongshore and offshore co-ordinates on each side of the tape measure. The percentage cover of the following substrata was estimated: sand, gravel (<5 mm), pebbles (5–20 mm), stone (20–150 mm) and rock (>150 mm). The percentage cover of native flat oyster shell and other shell types lying on top of the other substrata were also recorded. The numbers of living *O. edulis* and *Anomia ephippium* were counted and the substratum to which they were attached was recorded. The percentage cover of the following sessile organisms and the substratum to which they were attached was also recorded: algal species, tubeworms (*Pomatoceros* spp.), barnacles (*Chthamalus montagui*, *Semibalanus balanoides*), mussels (*Mytilus edulis*), and tunicates (*Ciona intestinalis*, *Ascidiella aspersa*).

Red “Marley” ridge tiles, 45 cm x 30 cm x 8 cm, were used as spat collectors. Spat collectors were laid in two lines parallel to the shoreline, spaced 5 m apart, with the lower line approximately 1 m from the lower edge of the coarse-sediment substrata. Forty-six tiles were laid in total, with 23 on each line. The tiles were placed at intervals of 20 m. At each interval, the tiles were placed singly or in a pair as determined randomly. Tiles were laid in Linne Mhuirich in June 2004 and removed in February 2005, then re-laid in June 2005 and removed in December 2005.

4.2.1 Analysis

To increase the number of samples, observations of tunicate species were combined, as were observations of barnacle species. Manly’s α was calculated to determine whether the abundance of a species on a particular substratum was in proportion to the availability of that substratum. The α value is the measure of probability that an individual will settle upon a particular substratum when all substrata are of equal availability:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum_{j=1}^{m} \frac{r_j}{n_j}} \qquad 4.1$$

Where:
α_i = Manly's α (preference index) for substratum type i;
r_i , r_j = proportion of individuals attached to substratum type i or j;
n_i, n_j = proportion of substratum type i or j in the environment;
m = number of substratum types available.
i and j = 1, 2, 3,…, m.

The α values are normalised so that:

$$\sum_{i=1}^{m} \alpha_i = 1 \qquad 4.2$$

If $\alpha_i = 1/m$ attachment is in proportion to the availability of the substratum in the area. If $\alpha_i > 1/m$, then attachment on substratum i occurs at a greater frequency than would be expected on the basis of the areal extent of that substratum. Conversely, if $\alpha_i < 1/m$, settlement occurs at a lower frequency than would be expected (Krebs, 1999).

Anderson-Darling tests were used to test the assumption of normality of data sets. Oyster count data and the percentage cover of each substratum were compared with the negative binomial distribution. Species density was calculated by dividing the counts of *O. edulis* or *A. ephippium*, or the percentage cover of the species, by the proportion of substratum (within the quadrat) to which they were attached. Permuted multivariate analysis of variance was used to test for differences in substratum composition among sites and plots (PERMANOVA v1.6) (Anderson, 2005). Permuted analysis of variance (ANOVA) was used to test for differences in the percentage cover of individual substrata and substratum-specific densities of species among sites and plots. The availability of gravel and pebble were not used in permuted ANOVA involving species densities or abundance since the number of records of attachment to these substrata were very low. Relationships between the average substratum-specific species density and average availability of substratum within sites were tested using Spearman's rank correlation. Wilcoxon's signed ranks tests were used to determine whether the mean substratum-specific densities of *O. edulis* were different from those of *A. ephippium* within sites.

The average abundance of oysters was calculated for each plot and differences among sites were tested using ANOVA followed by Fisher's pairwise comparisons. The average percentage cover of substrata per plot was calculated. The average values of flat oyster shell and other shell types were used as covariables in analysis of co-variance (ANCOVA) to determine if the mean abundance of oysters varied with the availability of shell. The average values of gravel, pebble, stone and rock were used as covariables in a second ANCOVA test to determine if the mean abundance of oysters varied with the availability of hard substrata. The substrata groups were tested separately because of the differences in the recorded percentage covers. Forward stepwise fitting of the ANCOVA models was used to determine the models with best-fit. ANCOVA models were tested for all sites surveyed and for the Argyll sites only.

Chi-square tests of association were used to test for the association between small (≤5 cm) and large (>5 cm) *O. edulis* individuals and the substrata to which they were attached. Flat native oyster shell and other shell types were combined and gravel and pebble were excluded from the analysis.

Mann-Whitney U-tests were used to determine if the number of spat settled on tiles was related to the depth, configuration, or side of the tiles.

4.3 Results

4.3.1 Substrata

Within sites, all substrata recorded were fitted to the negative binomial distribution. The composition of substrata differed among sites and the effect of plot contributed to the variance in the composition within sites (Table 4.1, Figure 4.1). The composition of substrata was significantly different between WLT2, LM1 and LM2, and between LM1 and LA1. LM1 and WLT2 had significantly more oyster shell and other shell than LA1 (Table 4.2). WLT2 had a significantly greater percentage cover of other shell types than the other Argyll sites but also had more sand. The percentage cover of gravel was significantly different between sites although paired comparisons were not sufficiently powerful to determine where the differences lay. The percentage cover of pebble was not significantly different between sites. The percentage cover of stone was greater at LM1 compared to WLT2 and LA1 and the percentage cover of rock was greater at LM2 than WLT2.

4.3.2 Ostrea edulis

The level of precision of oyster estimates achieved for sites was greater than 25% for LM1 and WLT2, 32% for LM2 and 40% for LA1, as indicated by the negative binomial distribution. The mean abundance of oysters was significantly different among sites ($F_{3,28} = 9.27$, $P < 0.01$). Pairwise comparisons indicated that oyster abundance was lower at LA1 compared to all other sites and LM2 had a significantly greater abundance than WLT2 (Figure 4.2). Stepwise fitting of ANCOVA models, for all sites, using the different shell categories as covariables, indicated that the relationship between oyster abundance and other shell types depended on site and was positively related to the percentage cover of oyster shell regardless of site. In addition, the relationship between other shell and the number of oysters was not the same at all sites (Table 4.3). For all sites and using hard substrata as covariables, stepwise fitting of ANCOVA terms indicated that there were differences in the abundance of oysters between sites but did not show any clear relationship with the percentage cover of any hard substratum (Table 4.3). After LA1 was removed from the analysis, the mean abundance of oysters did not vary significantly among sites ($F_{3,28} = 1.81$, $P = 0.19$).

The substratum-specific densities of *O. edulis* differed significantly among sites for the substrata other shell, stone and rock. The effects of plot significantly contributed to the variance within sites (Figure 4.3, Table 4.4). The density of *O. edulis* on other shell was significantly greater at WLT2 compared to all other sites and densities differed significantly among plots at WLT2. The density of *O. edulis* on stone was significantly lower at LA1 than at LM1 or LM2. The density of *O. edulis* on rock was significantly greater at LM2 than at LM1 or WLT2. Differences in the densities on stone and rock among plots within sites were not significant within any site. There were no significant correlations between the average substratum-specific densities of *O. edulis* and the average percentage cover of substrata within sites (Table 4.5)

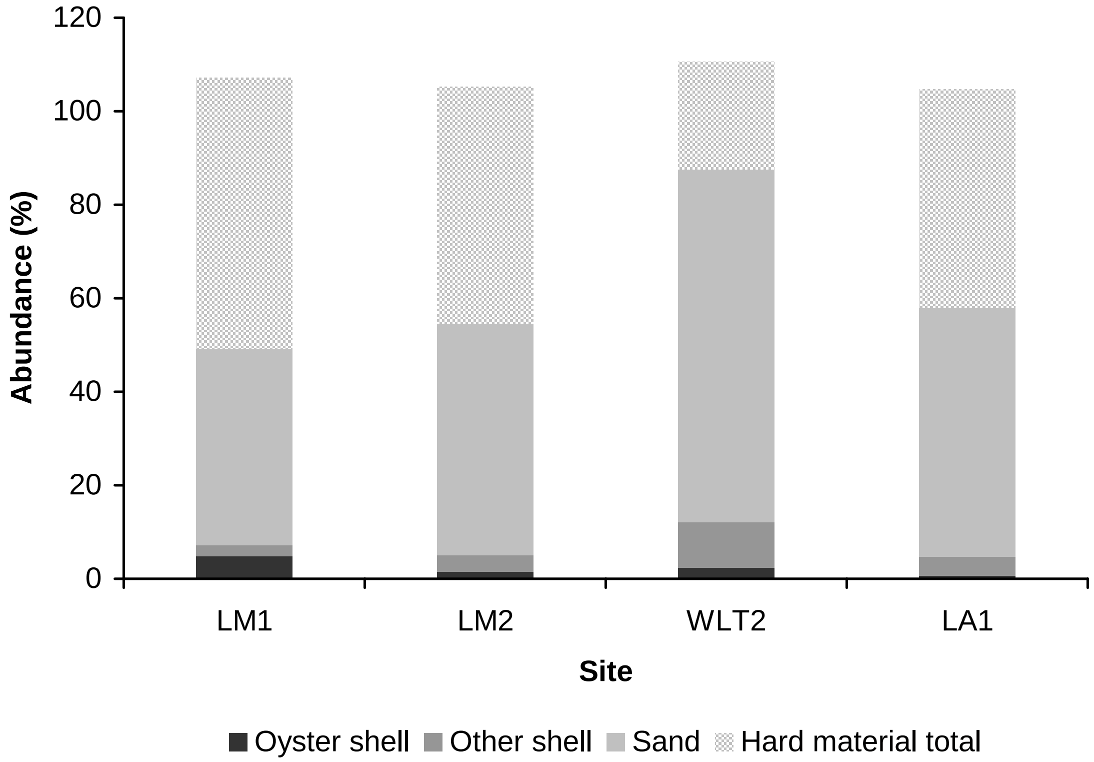
There was no association between the size of *O. edulis* and the substrata to which individuals were attached at any site. Tests of association could not be made at LA1 because there were too few data.

Table 4.1 Results of permuted ANOVA tests for the difference in the composition of substrata among sites and plots and paired comparisons between sites. F and P are the statistic and probability calculated by the permuted ANOVA test for n-1 degrees of freedom. t and P are the statistic and probability calculated for the paired comparison tests. Paired tests were only significant after correction for multiple comparisons, using the Bonferroni correction, when the P-value was <0.01. Significant values are in bold.

	F	**P**
Permuted ANOVA		
Site (d.f. 3, 28)	5.83	**<0.01**
Plot (d.f. 28, 608)	7.14	**<0.01**
Paired comparisons		
	t	**P**
LM1 v LM2	2.45	0.01
LM1 v WLT2	4.27	**<0.01**
LM1 v LA1	2.71	**<0.01**
LM2 v WLT2	2.66	**<0.01**
LM2 v LA1	0.81	1.00
WLT2 v LA1	2.35	0.10

Figure 4.1 Average percentage abundance of (a) shell groups, sand and hard substrata and (b) sand and hard substratum types at the surveyed sites.

a.



b.

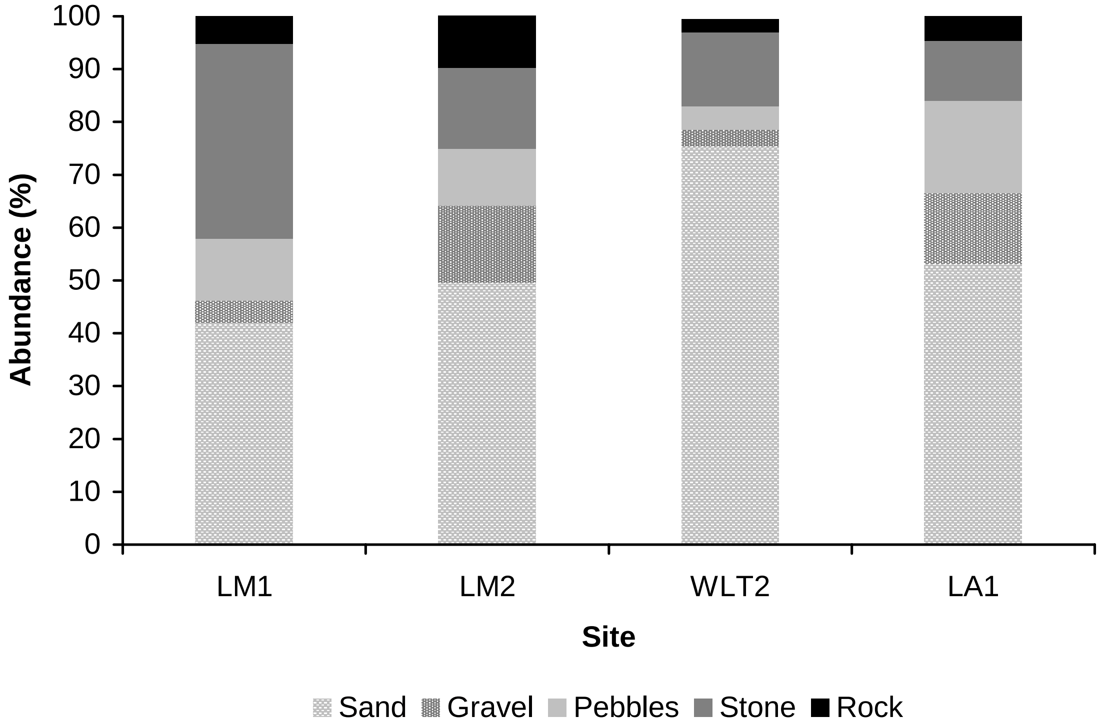


Table 4.2 Results of permuted ANOVA tests of the differences in substratum abundance among sites and plots and paired comparisons between sites. Significant values are in bold.

	Oyster shell		Other shell		Gravel		Pebble		Stone		Rock		Sand	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Permuted ANOVA														
Site (d.f. 3, 28)	8.49	**<0.01**	11.49	**<0.01**	4.65	**<0.01**	2.23	0.07	4.97	**<0.01**	2.98	0.01	5.62	**<0.01**
Plot (d.f. 28, 608)	2.23	**<0.01**	3.13	**<0.01**	5.34	**<0.01**	3.73	**<0.01**	7.29	**<0.01**	2.49	**<0.01**	6.82	**<0.01**
Paired comparisons														
	t	**P**	**t**	**P**	**t**	**P**			**t**	**P**	**t**	**P**	**t**	**P**
LM1 v LM2	1.97	0.04	2.08	0.02	1.76	0.06			3.00	0.01	1.78	0.05	0.97	0.35
LM1 v WLT2	0.62	0.70	3.61	**<0.01**	0.79	0.58			3.52	**<0.01**	1.70	0.05	4.39	**<0.01**
LM1 v LA1	4.33	**<0.01**	2.62	**<0.01**	2.00	0.05			3.69	**<0.01**	0.77	0.59	1.00	0.39
LM2 v WLT2	1.82	0.04	2.78	**<0.01**	1.91	0.05			0.51	0.86	2.52	**<0.01**	3.02	**<0.01**
LM2 v LA1	1.79	0.61	0.65	0.67	0.63	0.63			0.42	0.96	1.56	0.1	0.75	0.57
WLT2 v LA1	3.57	**<0.01**	2.53	**<0.01**	2.33	0.02			0.79	0.50	1.16	0.27	2.17	0.03

Figure 4.2 Average abundance of O. edulis *within surveyed plots within sites (±95% confidence limits).*

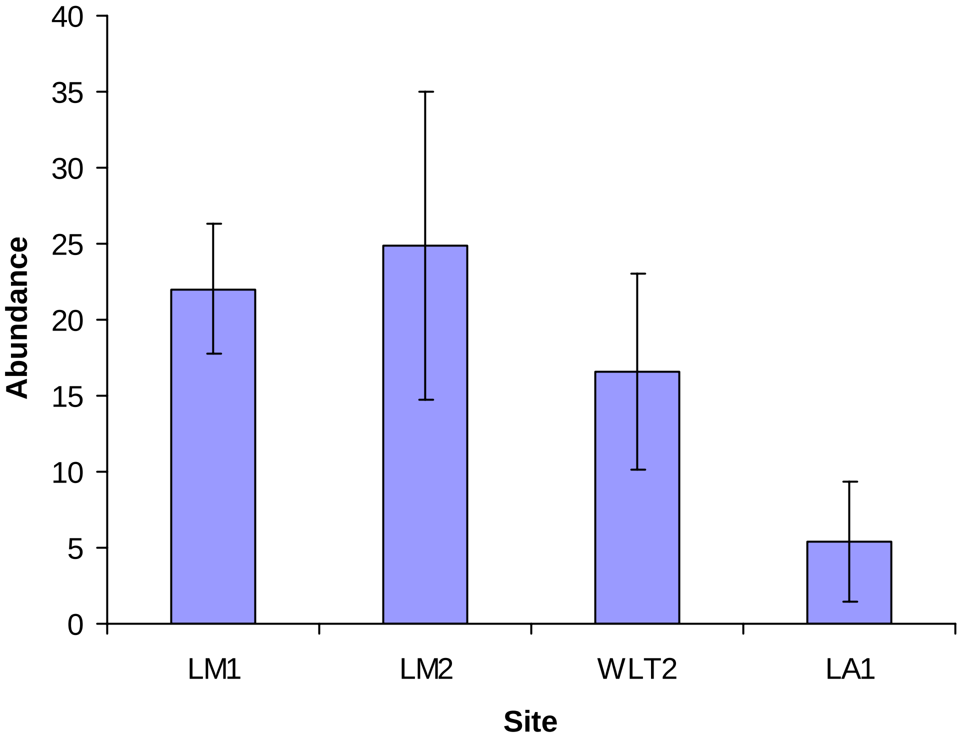
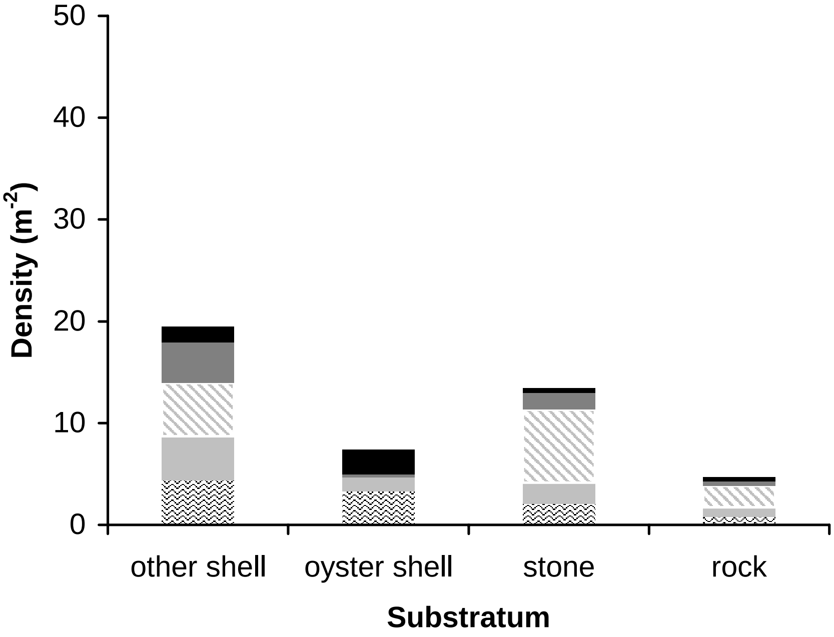


Table 4.3 Results of stepwise ANCOVA models testing the relationship between the abundance of oysters among sites with the mean abundance of substrata types. The results of two models are presented, the first using the mean abundance of shell groups as covariables and the second using the mean abundance of hard substrata as covariables. Significant values are in bold.

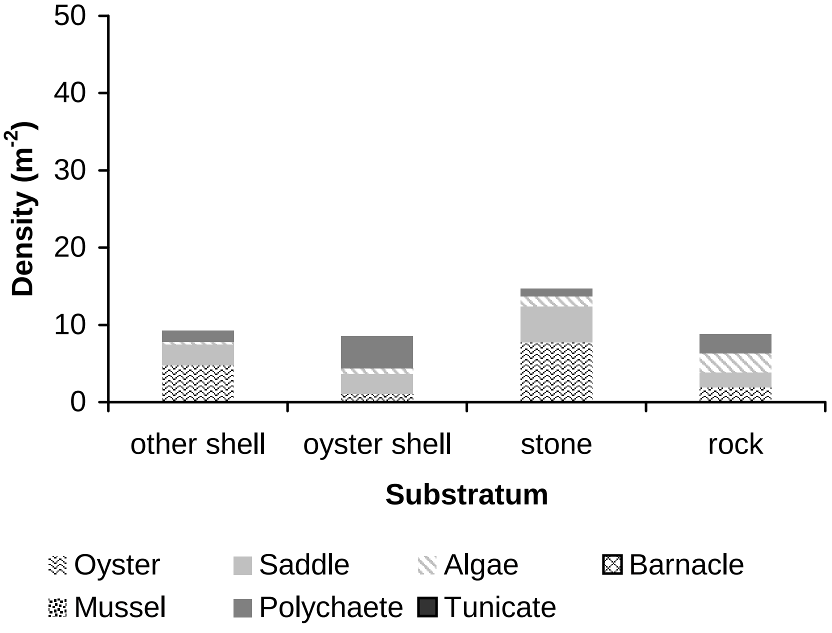
Model factors	**$F_{1,3}$**	**P**	**Model factors**	**$F_{1,3}$**	**P**
Site	8.75	**<0.01**	Site	4.79	**0.01**
Other shell	4.63	**0.04**	Gravel	0.42	0.52
Oyster shell	8.18	**0.01**	Pebble	0.05	0.89
Site x Other shell	5.06	**0.01**	Stone	4.05	0.06
			Rock	2.68	0.11

Figure 4.3 Comparison of the substratum-specific densities of species upon different substrata within (a) LM1, (b) LM2, (c) WLT2 and (d) LA1.

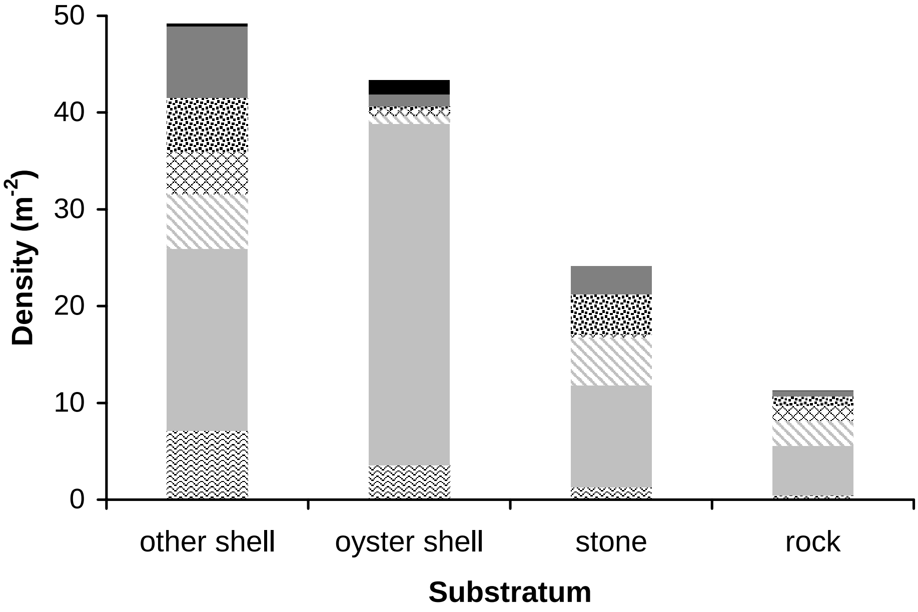
a.



b.

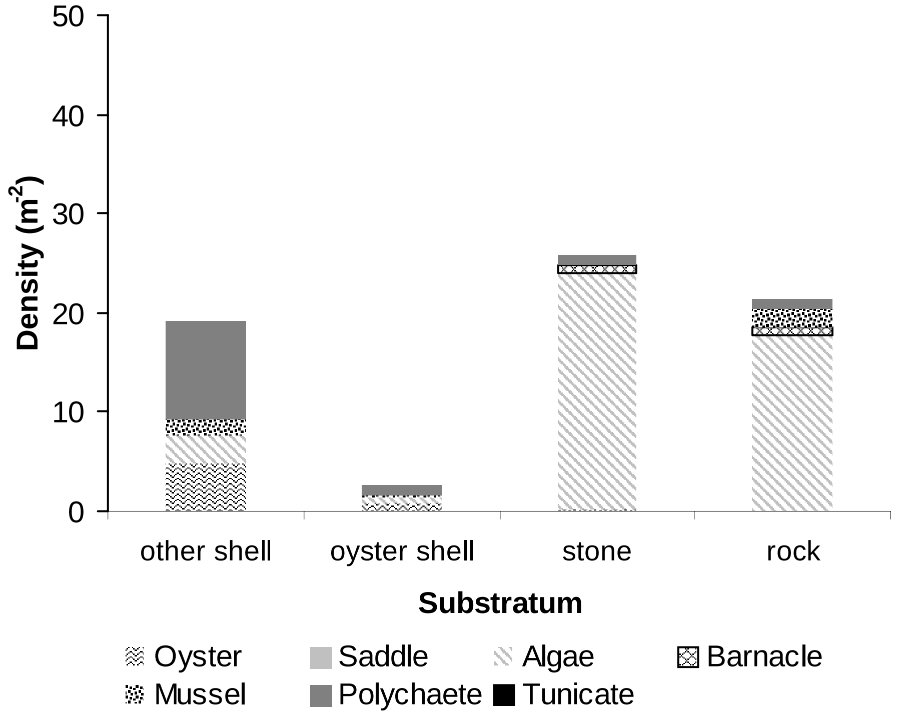


c.



50
40
30
20
10
0
Density (m-2)
other shell
oyster shell
stone
rock
Substratum

d.



50
40
30
20
10
0
Density (m-2)
other shell
oyster shell
stone
rock
Substratum
Oyster
Saddle
Algae
Barnacle
Mussel
Polychaete
Tunicate

*Table 4.4 Results of permuted ANOVA for differences in the density of species attached to substrata among sites and plots and paired comparisons between sites. Abbreviations as above. Blank cells indicate that too few data were available to calculate tests. **Also some problems with the programme crashing so full results cannot be given at the present time.** Significant values are in bold.*
(a) Flat oyster shell, (b) other shell types, (c) stone and (d) rock

a.

Flat oyster shell	***O. edulis***		***A. ephippium***		**Algal species**		**Barnacle species**		**Mussels**		**Tubeworm species**		**Tunicate species**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Site	1.45	0.06	3.88	**<0.01**							0.99	0.39		
Plot	1.05	0.15	1.70	**<0.01**							1.28	**<0.01**		
Paired comparisons														
	t	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
LM1 v LM2														
LM1 v WLT2				**<0.01**										
LM1 v LA1			n/a	n/a										
LM2 v WLT2				**<0.01**										
LM2 v LA1			n/a	n/a										
WLT2 v LA1			n/a	n/a										

b.

Other shell types	***O. edulis***		***A. ephippium***		**Algal species**		**Barnacle species**		**Mussels**		**Tubeworm species**		**Tunicate species**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Site	3.11	**<0.01**	15.23	**<0.01**	4.11	**0.01**			4.37	**0.01**	8.66	**<0.01**	0.59	0.79
Plot	1.30	**<0.01**	1.78	**<0.01**	1.45	**<0.01**			1.7	**<0.01**	3.01	**<0.01**	1.45	**<0.01**
Paired comparisons														
	t	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
LM1 v LM2				**<0.01**	1.64	0.05								
LM1 v WLT2		**<0.01**		**<0.01**	0.26	0.28								
LM1 v LA1			n/a	n/a	0.02	0.02								
LM2 v WLT2		**<0.01**		**<0.01**										
LM2 v LA1			n/a	n/a										
WLT2 v LA1		**<0.01**	n/a	n/a					1.75	0.06				

c.

Stone	***O. edulis***		***A. ephippium***		**Algal species**		**Barnacle species**		**Mussels**		**Tubeworm species**		**Tunicate species**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Site	5.36	**<0.01**	3.26	**0.01**	6.55	**<0.01**	0.88	0.47			**3.81**	**0.01**		
Plot	1.31	**<0.01**	2.360	**<0.01**	3.90	**<0.01**	1.33	**<0.01**			**3.08**	**<0.01**		
Paired comparisons														
	t	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
LM1 v LM2	1.47	0.09	1.13	0.27	2.02	0.01					1.01	0.33		
LM1 v WLT2	0.69	0.79	2.39	**<0.01**	0.70	0.72					1.37	0.18		
LM1 v LA1	2.49	**<0.01**	n/a	n/a	1.60	0.08					1.13	0.28		
LM2 v WLT2	1.93	0.02	1.34	0.17	1.85	0.04					1.96	0.03		
LM2 v LA1	2.57	**<0.01**	n/a	n/a	2.42	**<0.01**					-0.41	1.00		
WLT2 v LA1	2.04	0.03	n/a	n/a	1.85	0.01					2.09	0.03		

d.

Rock	***O. edulis***		***A. ephippium***		**Algal species**		**Barnacle species**		**Mussels**		**Tubeworm species**		**Tunicate species**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Site	2.34	**<0.01**	0.76	0.87	2.91	**<0.01**	0.78	0.76			1.13	0.32		
Plot	1.11	**0.01**	1.19	**<0.01**	2.11	**<0.01**	1.23	**<0.01**			2.01	**<0.01**		
Paired comparisons														
	t	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
LM1 v LM2		**<0.01**			0.54	0.91								
LM1 v WLT2					0.20	0.94								
LM1 v LA1					2.16	0.01								
LM2 v WLT2					0.84	0.57								
LM2 v LA1		**<0.01**			2.09	**<0.01**								
WLT2 v LA1					2.12	**<0.01**								

Table 4.5 Results of Spearman's rank correlation testing the association between substratum availability and species densities. Significant values are in bold.

LM1	Flat oyster shell		Other shell types		Stone		ROCK	
	r_s	P	r_s	P	r_s	P	r_s	P
Species								
O. edulis	-0.04	0.93	0.30	0.47	0.12	0.78	0.46	0.26
A. ephippium	-0.17	0.69	0.35	0.40	-0.02	0.96	-0.48	0.23
Algal species	n/a	n/a	0.66	0.08	0.52	0.18	0.49	0.22
Tubeworms	0.63	0.10	0.71	**0.05**	0.26	0.53	-0.44	0.27
Tunicates	0.19	0.65	-0.19	0.65	0.07	0.86	n/a	n/a

LM2	Flat oyster shell		Other shell types		Stone		ROCK	
	r_s	P	r_s	P	r_s	P	r_s	P
Species								
O. edulis	-0.22	0.60	-0.40	0.33	-0.32	0.44	0.24	0.57
A. ephippium	0.10	0.81	0.66	0.08	0.11	0.80	-0.32	0.44
Algal species	0.43	0.29	0.58	0.14	-0.17	0.69	0.11	0.80
Tubeworms	n/a	n/a	-0.92	**<0.01**	0.83	**0.01**	0.58	0.13

WLT2	Flat oyster shell		Other shell types		Stone		ROCK	
	r_s	P	r_s	P	r_s	P	r_s	P
Species								
O. edulis	0.51	0.20	-0.07	0.87	0.19	0.65	n/a	n/a
A. ephippium	0.52	0.18	0.36	0.39	0.41	0.32	0.60	0.12
Algal species	n/a	n/a	-0.31	0.46	-0.10	0.82	0.26	0.53
Barnacle species	0.61	0.11	0.29	0.48	0.30	0.46	0.12	0.77
Mussels	0.19	0.65	0.71	**0.05**	0.20	0.64	0.11	0.78
Tubeworms	-0.41	0.32	-0.31	0.46	-0.12	0.78	0.17	0.69
Tunicates	0.34	0.41	-0.07	0.86	n/a	n/a	n/a	n/a

LA1	Flat oyster shell		Other shell types		Stone		ROCK	
	r_s	P	r_s	P	r_s	P	r_s	P
Species								
O. edulis	n/a	n/a	0.05	0.91	n/a	n/a	n/a	n/a
Algal species	0.74	**0.04**	0.21	0.61	0.55	0.16	0.57	0.14
Barnacles	n/a	n/a	n/a	n/a	-0.60	0.12	0.27	0.53
Mussels	n/a	n/a	-0.48	0.23	n/a	n/a	0.05	0.91
Tubeworms	0.44	0.27	0.13	0.76	0.32	0.44	0.27	0.52

4.3.3 Potential competitor species

The abundance of the potential competitor species monitored in the surveys differed among sites and among substrata within sites. For all tests of differences among sites and plots, there was a significant difference in the substratum-specific densities of species between plots (Table 4.4). Differences between sites will be presented in the following sections. The mean substratum-specific densities of species were, in general, not significantly correlated with the mean availability of substrata within sites (Table 4.5). The percentage of quadrats with a species attached to a particular substratum followed the same trends as the differences in the substratum-specific densities of species among sites.

A. ephippium was attached to all substrata at all sites except LA1 (Figure 4.3, Table 4.4). The densities of *A. ephippium* were significantly different among sites for flat oyster shell, other shell types and stone. The effect of plot contributed significantly to the variation within sites. The densities of *A. ephippium* on flat oyster shell and other shell were significantly greater at WLT2 compared to LM1 and LM2. The density of *A. ephippium* on stone was significantly greater at WLT2 than at LM1. There were no significant differences among sites in the density on rock. The densities of *A. ephippium* were significantly greater than *O. edulis* at WLT2, on other shell ($P = 0.01$), oyster shell ($P = 0.02$) and stone ($P = 0.02$) (Figure 4.4). There were no significant differences in the densities of the two oyster species at LM1 or LM2.

Algal density on other shell types and stone was lower at LM2 than LM1 or WLT2 (Figure 4.3, Table 4.4). LA1 had the greatest density of algal species on stone and rock. Although the percentage of quadrats containing algal species on rock was greater at LA1 than the other sites, the percentage of quadrats containing algal species on stone was greater at LM1 compared to LA1. There were insufficient records of algal species density on oyster shell to make a comparison among sites.

Barnacles were only present in surveys at WLT2 and LA1. Sufficient records for site comparisons were only available for the density of barnacles on other shell, which was greater at WLT2 than LA1 (Figure 4.3, Table 4.4). Barnacles on oyster shell were not found in the survey at LA1. Tubeworms were recorded at all sites on all substrata. Tunicates were only recorded at LM1 and WLT2. Sufficient observations were only available for site comparisons of the density of tunicates on oyster shell, which was not significantly different among the sites. Mussels were recorded attached to all substrata but were only present in surveys at WLT2 and LA1 (Figure 4.3, Table 4.4). There were sufficient observations to make a comparison among sites for the density of mussels on other shell only, which was greater at WLT2 than LA1. The density of mussels was also significantly related to the availability of other shell at WLT2 (Table 4.5).

The density of tubeworms on other shell types was lowest at LM2 and greatest at WLT2 and LA1 (Figure 4.3, Table 4.4). However, there were significant correlations between tubeworm density and the availability of other shell at LM2 and LM1 (Table 4.5). The density on oyster shell was greatest at LM2 compared to the other sites. The density of tubeworms on stone was greater at WLT2 compared to LM2 and LA1. There was no significant difference between WLT2 and LM1, although the percentage of quadrats containing tubeworms on stone was greater at LM1 than WLT2. Furthermore, the density of tubeworms on stone was significantly correlated with the availability of stone at LM2 (Table 4.5). The density of tubeworms on rock was not significantly different among sites.

All species showed a preference for attachment to oyster shell at all sites except *O. edulis* at LM2, algal species at WLT2 and tubeworms at LM1 (Table 4.6). *O. edulis*, *A. ephippium*, mussels and tubeworms showed a preference for attachment to other shell types at all sites

Figure 4.4 Difference in the density of O. edulis *and* A. ephippium *on substrata at WLT2.*

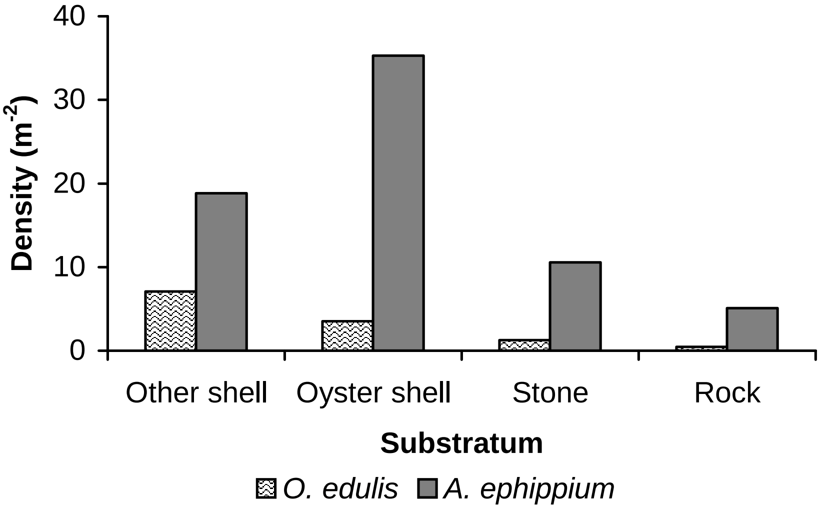


Table 4.6 Manly's α indices for species' preferences of attachment to substrata within sites. Values greater than α = 0.167 indicate a greater frequency of attachment upon a substratum given the availability of that substratum in the environment. Significant values are in bold.

O. edulis	**LM1**	**LM2**	**WLT2**	**LA1**
Oyster shell	**0.505**	0.156	**0.376**	**0.353**
Other shell	**0.251**	**0.336**	**0.483**	**0.599**
Gravel	0.012	0.030	n/a	n/a
Pebble	0.016	0.008	n/a	n/a
Stone	0.125	**0.277**	0.08	0.033
Rock	0.090	**0.219**	0.061	0.016

A. ephippium	**LM1**	**LM2**	**WLT2**	**LA1**
Oyster shell	**0.169**	**0.341**	**0.537**	n/a
Other shell	**0.558**	**0.361**	**0.225**	n/a
Gravel	n/a	n/a	n/a	n/a
Pebble	0.006	0.037	n/a	n/a
Stone	0.122	0.159	0.111	n/a
Rock	0.145	0.102	0.110	n/a

Algal species	**LM1**	**LM2**	**WLT2**	**LA1**
Oyster shell	n/a	**0.295**	0.051	**0.192**
Other shell	**0.382**	0.114	**0.351**	**0.185**
Gravel	n/a	n/a	n/a	0.010
Pebble	0.105	0.107	n/a	0.060
Stone	**0.190**	0.115	**0.265**	**0.210**
Rock	**0.323**	**0.370**	**0.333**	**0.344**

Barnacle species	**LM1**	**LM2**	**WLT2**	**LA1**
Oyster shell	n/a	n/a	**0.290**	n/a
Other shell	n/a	n/a	**0.288**	0.109
Gravel	n/a	n/a	n/a	n/a
Pebble	n/a	n/a	n/a	n/a
Stone	n/a	n/a	0.086	**0.235**
Rock	n/a	n/a	**0.336**	**0.656**

Mussel	LM1	LM2	WLT2	LA1
Oyster shell	n/a	n/a	**0.180**	**0.262**
Other shell	n/a	n/a	**0.392**	**0.324**
Gravel	n/a	n/a	n/a	n/a
Pebble	n/a	n/a	n/a	n/a
Stone	n/a	n/a	0.150	0.029
Rock	n/a	n/a	**0.255**	**0.384**

Tubeworm species	LM1	LM2	WLT2	LA1
Oyster shell	0.099	**0.357**	**0.246**	**0.300**
Other shell	**0.588**	**0.236**	**0.434**	**0.482**
Gravel	0.009	n/a	n/a	n/a
Pebble	0.069	n/a	n/a	0.002
Stone	0.108	**0.173**	**0.171**	0.080
Rock	0.061	n/a	0.062	n/a

Tunicate species	LM1	LM2	WLT2	LA1
Oyster shell	**0.663**	n/a	**0.840**	n/a
Other shell	**0.217**	n/a	0.086	n/a
Gravel	n/a	n/a	n/a	n/a
Pebble	n/a	n/a	n/a	n/a
Stone	0.058	n/a	0.012	n/a
Rock	0.061	n/a	0.062	n/a

at which they were recorded. Algal species also showed a preference for other shell except at LM2. Barnacles showed a preference for attachment to other shell at WLT2 as did tunicates at LM1. *O. edulis* also showed a preference for stone and rock at LM2. Tubeworms showed a preference for stone, and algal species showed a preference for rock at LM2. Although the preferences of *O. edulis* were shared with other species at the same sites, the only species density significantly correlated with the density of *O. edulis* was the density of algae on stone at LM2 (Table 4.7).

4.3.4 Settlement Tiles

There was no significant difference in the number of spat caught at each depth in either 2004 ($U = 1980.5$, $P > 0.05$) or 2005 ($U = 506.0$, $P > 0.05$). There was also no significant difference in the number of spat caught using the two configurations of tiles in 2004 ($U = 1554.4$, $P > 0.05$) or 2005 ($U = 329.0$, $P > 0.05$). In 2004, significantly more spat were caught on the concave underside (mean = 2.55) of the tiles compared to the convex top-side (mean = 0.23; $U = 1277.0$, $P < 0.01$). Spat were only caught on the concave underside of tiles in 2005 (mean = 0.24).

Table 4.7 Results of Spearman's Rank Correlation testing the association between the density of O. edulis *and the densities of the surveyed potential competitor species. Significant values are in bold.*

LM1	**Flat oyster shell**		**Other shell types**		**Stone**		*Rock*	
	r_s	P	r_s	P	r_s	P	r_s	P
A. ephippium	0.33	0.42	-0.39	0.37	0.29	0.49	-0.09	0.83
Algal species	n/a	n/a	0.12	0.77	0.10	0.82	-0.10	0.81
Tubeworms	0.58	0.14	0.68	0.06	0.24	0.57	-0.49	0.22
Tunicates	0.18	0.67	-0.71	0.05	-0.07	0.86	n/a	n/a

LM2	**Flat oyster shell**		**Other shell types**		**Stone**		*Rock*	
	r_s	P	r_s	P	r_s	P	r_s	P
A. ephippium	0.51	0.20	-0.06	0.89	0.46	0.26	0.42	0.30
Algal species	0.52	0.19	-0.22	0.60	**0.84**	**0.01**	0.22	0.61
Tubeworms	0.01	0.98	0.58	0.13	-0.33	0.42	0.26	0.54

WLT2	**Flat oyster shell**		**Other shell types**		**Stone**		*Rock*	
	r_s	P	r_s	P	r_s	P	r_s	P
A. ephippium	0.39	0.35	0.29	0.49	0.24	0.57	n/a	n/a
Algal species	0.01	0.99	0.19	0.65	0.10	0.82	n/a	n/a
Barnacle species			-0.32	0.44	-0.30	0.46	n/a	n/a
Mussels	0.28	0.51	0.10	0.82	0.12	0.77	n/a	n/a
Tubeworms	0.02	0.96	0.07	0.87	0.12	0.78	n/a	n/a
Tunicates	0.33	0.42	-0.34	0.41	n/a	n/a	n/a	n/a

LA1	**Flat oyster shell**		**Other shell types**		**Stone**		*Rock*	
	r_s	P	r_s	P	r_s	P	r_s	P
Algal species	n/a	n/a	0.61	0.11	n/a	n/a	n/a	n/a
Barnacles	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Mussels	n/a	n/a	0.60	0.12	n/a	n/a	n/a	n/a
Tubeworms	n/a	n/a	0.44	0.27	n/a	n/a	n/a	n/a

4.4 Discussion

4.4.1 Substrata availability and Ostrea edulis

The abundance of *O. edulis* populations depends on a variety of interacting factors. This study has focussed on the availability of substrata suitable for the settlement of larval oysters and the potential competitive interactions with other sessile species, which also settle upon the available substrata. All substrata were recorded at all sites but *O. edulis* were not attached to all substrata within all sites. Substrata were characterised by an aggregated distribution suggesting the availability of substrata was heterogeneous. The availability of gravel and pebble varied among sites but the maximum availability of gravel was over 69% and of pebble was 50% at all sites. However, *O. edulis* was only recorded attached to gravel once at both LM1 and LM2 and attachment to pebble was recorded four times at LM1 and twice at LM2. Manly's α index of preference also suggested that *O. edulis* showed a strong "avoidance" of attachment to either gravel or pebble. The low frequency of attachment to substrata that were characterised by high availability suggests that gravel and pebble either are not suitable for settlement by larvae, or the survival rate of *O. edulis* attached to these substrata is low.

Overall, Manly's α indicated that attachment of *O. edulis* was greater on flat oyster shell and other shell types than would be expected given the availability of these substrata. The percentage cover of these substrata was less than 5%, except at WLT2 where the mean percentage cover of other shell types was 12%. The presence of biotic reefs at WLT2, formed by *M. edulis*, account for this difference in the abundance of other shell among the sites. The density of *O. edulis* on other shell was also greater at WLT2 compared to the other sites surveyed, indicating that increased levels of shell could affect the abundance of oysters.

Stepwise ANCOVA models also indicated that the difference in the abundance of oysters between sites was related to the availability of shell. Shell abundance was, in general, significantly more abundant at the Argyll sites than at LA1. In accordance with population estimates (see section 3.3.2), the abundance of *O. edulis* was significantly lower at LA1 than the other sites, and after removal from the analysis, the abundance of oysters did not differ significantly among the Argyll sites. Stepwise fitting of models should be treated with caution because the final model can differ depending on the sequence of steps. However, tentative conclusions can be drawn and the model supports the conclusion that the availability of shell could have a significant influence on the abundance of populations of *O. edulis*.

Other investigations of spat settlement have also concluded that the spat of *O. edulis* show a preference for shell (Cole & Knight-Jones, 1939; Kennedy, 1999). Surveys of spat have shown that spat settle in greater numbers on the concave side of the shell (T. Hugh-Jones, pers. comm., 2005). Laboratory studies (Cole & Knight-Jones, 1939), field studies (Hopkins, 1937, cited in Cole & Knight-Jones, 1949; Knight-Jones, 1951) and the field-studies using ridge tiles in this research have also found that spat are found in greater numbers on the concave side of settlement materials. The accumulation of silt on the upper surfaces of settlement material prohibits the settlement of larval oysters (Knight-Jones, 1951) and may have influenced the settlement patterns of spat in the current study. Furthermore, the ciliary pumping activity of *O. edulis* is not suited to environments of high turbidity (Yonge, 1960) and it has been suggested that settlement on the underside of surfaces decreases the level of sedimentation to which the spat are exposed, thus increasing the chance of settlement and survival (Cole & Knight-Jones, 1949; Knight-Jones, 1951). Other substrata within the environment do not necessarily provide such protection and it is possible that spat survival is therefore higher when attached to shell compared to other settlement substrata.

The preference of attachment of *O. edulis* at LM2 did not include flat oyster shell, instead a preference for stone and rock was indicated. Furthermore, the frequency of large oysters attached to rock at LM2 and stone at WLT2 was greater than expected, whereas small oysters were attached to shell more frequently than expected at both sites. Although the populations at these sites have relatively high abundances within Scotland (see sections 3.3.2 & 3.4.3), there have been numerous reports of unlawful exploitation of these oyster populations in recent years. A study on unlawfully gathered oysters found that oysters were less likely to be collected if they were attached to large stones or rock (see section 3.4.3). However, there is no evidence in the current study to suggest that unlawful gathering has influenced the observed pattern of attachment of large and small oysters within these sites.

4.4.2 Competitive interactions

The present study does not provide evidence for competitive interactions between *O. edulis* and the other sessile species surveyed. Although the majority of species showed the same preferences of substratum attachment as *O. edulis*, overall, the densities of the other sessile species did not show any association with the density of *O. edulis* on the substrata surveyed. There was no consistent pattern in substratum-specific species densities among sites. Furthermore, differences in substratum-specific species densities were the same as those exhibited by the percentage of quadrats containing species attached to a substratum. This suggests that the differences in density were highly influenced by the presence of the species on a substratum as opposed to the relative amount of substrata occupied by the species. Nevertheless, the patterns of density and abundance of some of the surveyed species are of significance.

The patterns of density on different substrata among sites and the attachment preferences of *A. ephippium* showed a high level of similarity to those exhibited by *O. edulis*. The densities of *A. ephippium* were also greater at WLT2 than the densities of *O. edulis* on three of the four suitable substrata. The densities of tubeworms were significantly correlated with the availability of other shell types at LM1 and other shell types and stone at LM2. However, the densities of tubeworm species on other shell types were low and did not show significant associations with the densities of *O. edulis.*

The density of algal species was significantly correlated with the density of *O. edulis* on stone at LM2. The attachment preferences of algal species were also wide-ranging including the majority of the suitable substrata at all the sites surveyed. The algae species surveyed included fucoids. The percentage of substrata covered where these species attach is small. However, a large volume of water can be dominated by the thalli of these species and could have a potential influence on water movement and larval movement within the water column. It has been suggested that the increase in fucoid density in the Solent has contributed to the decline in population recruitment of oysters in recent years (G. Mills, pers. comm., 2005).

These patterns of settlement by *A. ephippium*, tubeworms and algal species indicate that changes in substrata could influence the competitive interactions of these species with *O. edulis*.

4.5 Conclusions

At the sites surveyed, substrata were patchy and sand was a dominant component of the seabed. There is no published information on the carrying capacity of substrata for *O. edulis*. However, although *O. edulis* were recorded attached to all the substrata in the surveys, the species did not show any evidence of a relationship with the availability of substrata to suggest that the total availability of substratum was a limiting factor to population growth. However, there was evidence that an increase in the availability of shell could increase larval settlement in these populations. The patchy nature of the substrata, the high percentage availability of sand and homogeneous settlement patterns suggest that if the availability of settlement substrata were increased, settlement by larval oysters may increase. This is supported by the increased frequency of attachment to shell at WLT2 compared to the other sites where the availability of shell is significantly lower. Shell was also the preferred substratum for attachment at all sites. Thus, it is possible that habitat enhancement using cultch supplementation techniques could increase the settlement of *O. edulis* larvae in wild populations around Scotland. Although the total availability of substrata suitable for settlement is quite high, the patchy nature of its spatial dispersion is potentially causing a demographic bottleneck within the surveyed populations.

Although there was no evidence of competitive interactions that could limit the population growth of *O. edulis*, there were indications that *O. edulis* had similar settlement patterns to other species. Increasing the availability of habitat could promote the growth of other species, thus increasing the likelihood that competitive interactions will develop.

5 DO ALLEE EFFECTS POTENTIALLY LIMIT THE RECRUITMENT SUCCESS OF *OSTREA EDULIS* IN SCOTLAND?

5.1 Introduction

Allee effects refer to the decrease in individual fitness resulting from reduced social interactions at low population density (Allee *et al*., 1949; Courchamp *et al*., 1999; Gyllenberg *et al*., 1999; Stephens & Sutherland, 1999; Chen *et al*., 2002). Several authors have proposed that recruitment limitation caused by Allee effects has contributed to the collapse of several exploited marine stocks (Quinn *et al*., 1993; Myers *et al*., 1995; Frank & Brickman, 2000; Stoner & Ray-Culp, 2000; Gascoigne & Lipcius, 2004). Therefore, the recognition of Allee effects in recruitment processes is important for conservation and fisheries management to ensure the maintenance of sustainable populations (Stoner & Ray-Culp, 2000).

Marine invertebrates exhibit several social behaviours that can facilitate successful fertilisation, including the formation of breeding aggregations and spawning synchrony (Yund, 2000). However, several commercially exploited marine invertebrates exhibit depensation, i.e. recruitment is disproportionately low at low population densities (Breen & Adkins, 1980; Peterson & Summerson, 1992; Quinn *et al*., 1993; Stoner & Ray-Culp, 2000; Gascoigne & Lipcius, 2004). Recruitment failures in populations of queen conch (*Strombus gigas*) (Stoner & Ray-Culp, 2000) and abalone (*Haliotis* spp.) (Shepherd & Brown, 1993; Babcock & Keesing, 1999) have been associated with high levels of exploitation decreasing the ability to form adequately-sized breeding aggregations. For free-spawning species such as abalone, the distance between members of the opposite sex, gamete longevity and dilution are important factors for fertilisation success (Breen & Adkins, 1980; Shepherd, 1986). Thus, population density is a critical factor for the efficacy of reproduction in many marine invertebrate species.

Ostrea edulis is a protoandrous, alternating hermaphrodite species that changes sex successively throughout its lifespan (Orton, 1922, 1927, 1933, 1937a). The breeding season in Scotland extends from May until August (Millar, 1961, 1964). Functional males are broadcast spawners, releasing sperm morulae (packets) that break apart on contact with sea water (Orton, 1927). Egg production in females is highly variable (Walne, 1964), but has been shown to increase linearly with shell length (Cole, 1941; Walne, 1964) and body weight (Utting *et al*., 1991). Functional females use their inhalent current to collect sperm within the mantle cavity where the eggs are accumulated prior to fertilisation (Orton, 1927). Embryos attach to the mantle and gills and are brooded for a period of between 6 and 15 days before they are released as larvae (Orton, 1927, 1933; Millar, 1964; Walne, 1964). Sexual maturity of *O. edulis* in Britain is thought to occur between 3 and 4 years-of-age (Spark, 1924, cited in Orton, 1927; Cole, 1941; McKelvey *et al*., 1993), although functional males have been recorded at 1 year of age after exceptionally warm years (Dantan, 1913, cited in Dodd *et al*., 1937; Orton, 1922, 1937a).

Spawning and larval production in *O. edulis* is temporally variable within and between populations. Gametogenesis, spawning and larval development are related to environmental and physiological factors. The threshold temperatures for these processes differ between geographic regions (Korringa, 1956; Loosanoff, 1962; Wilson & Simons, 1985). For instance, higher temperatures increase the rate of larval development and consequently reduce the duration of the planktonic phase (Korringa, 1956). Temperature variations that influence metabolic processes, combined with food availability, affect the levels of glycogen and lipids available for growth and reproduction (Orton, 1927; Walne & Mann, 1975; Mann, 1979).

These factors also influence the contribution of an individual during the breeding season. The time to change to a functional female state ranges from months to years in wild populations, whereas the change to a functional male starts while larvae are being brooded and can be completed within weeks (Orton, 1927, 1933). Functional females are more numerous earlier in the breeding season (Cole, 1941; Millar, 1964), although males have been found to outnumber females in wild populations throughout the breeding season (Orton, 1933; Cole, 1941; Millar, 1964).

Larvae are present in the water column throughout the breeding season but show production maxima (Orton, 1933; Millar, 1964; Korringa, 1957a, 1957b) that have been linked with the lunar cycle (Korringa, 1957a). Larval production is greatest in the first production maximum (Cole, 1941; Korringa, 1957a, 1957b; Millar, 1964), coinciding with the time of highest gamete production by both sexes (Orton, 1927; Cole, 1941). Depletion of reserves, resulting in lower egg production by individuals functioning as females during a second spawning, has been proposed as a factor contributing to lower production in subsequent maxima (Orton, 1927, 1933; Cole, 1941). During periods of less favourable environmental conditions, it has been hypothesised that gamete ripening is delayed so that individuals may only spawn as one sex during a season (Cole, 1941; Loosanoff, 1962). As a result of the energy requirements of alteration between functional sexes, only a proportion of a breeding population will contribute to each fertilisation event (Millar, 1964) and spawning season (Orton, 1933).

Variability in the timing of an individual spawning and the duration of change between functional sexes, can cause the sex ratio of a population to deviate from 1:1. Estimates of the proportion of sexes in wild populations range from a 1:1 sex ratio (Orton, 1933; Cole, 1939, cited in Cole, 1941) to a 3:1 male to female sex ratio (Millar, 1964). The consequences of a skewed sex ratio could include the decreased availability of one gamete type, acting as a limiting factor to recruitment success. Since population density can have a significant effect on the success of fertilisation in broadcast spawners, the effects of a skewed sex ratio in small populations could have a severely limiting effect on the levels of recruitment, and prevent a population from being self-sustaining. Overall, the variability in the reproductive physiology and behaviour of *O. edulis* cause larval production to be highly variable. Furthermore, the frequency of successful recruitment events has been estimated to range from every year in Loch Ryan (T. Hugh-Jones, pers. comm.) to periods of 2 to 3 years every 6 to 8 years in Lough Foyle (McKelvey *et al*., 1993).

Unlawful exploitation of *O. edulis* removes broodstock from wild populations (see section 3.4) and can act to reduce the density of conspecifics. Since Allee effects have been proposed as a factor increasing the probability of extinction in small populations (Courchamp *et al*., 1999; Stephens & Sutherland, 1999), determining whether *O. edulis* are susceptible to Allee effects is necessary for the effective conservation and fisheries management of this species. The aim of this study was to determine whether wild populations were susceptible to Allee effects by analysing the spatial dispersion of individuals at different geographical scales and examining the effects of spatial pattern and distance from conspecifics on fertilisation success. In addition, the study aimed to determine whether unlawful exploitation of populations could increase the potential of Allee effects by reducing population density.

5.2 Methods

Six spatial maps were made at both LM1 and LM2 to investigate whether the spatial distribution of oysters differed with distance from the centre of the bed towards the edge and between exploited and unexploited areas. The LM1 maps were made on 6–9 June 2005 and the LM2 maps between 26–30 September 2005. Individual *O. edulis* were mapped within 36-

m^2 plots, spaced 20 m apart, with the first plot located at the approximate alongshore centre of the bed area. A buffer zone of 1 m width around the boundary of the plot was also mapped. Sub-division of the plots into 1-m^2 quadrats, which were further subdivided into squares of 10 x 10 cm, was used to increase the accuracy of the maps. Each 10 x 10 cm square was mapped individually. Distances between the central points of oysters were measured using a tape measure to the nearest centimetre and the length and height of mapped oysters were measured with dial callipers to 0.1 mm.

Anderson-Darling tests were used to test the assumption of normality for the quadrat counts and inter-individual distances. Mann-Whitney U-tests were used to determine whether the counts of oysters within 1-m^2 subdivisions within the plots were different between the two sites. Kruskal-Wallis tests followed by Dunn's multiple comparison procedure (Orlich, 2000) were used to investigate the differences in the counts between plots within sites.

To investigate the spatial pattern of the mapped populations at the site level, Morisita's index of dispersion, I_d, and the standardised Morisita index of dispersion were calculated for each site (Krebs, 1999). Morisita's index of dispersion is calculated by:

$$I_d = n\left[\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}\right] \qquad 5.1$$

Where:
n = Sample size,
x = Quadrat counts

The standardised Morisita index, I_p, was derived by calculating critical values for Morisita's index of dispersion: the uniform index (M_u) (Equation 5.2) and the clumped index (M_c) (Equation 5.3).

$$M_u = \frac{\chi^2_{0.975} - n + \sum x_i}{\left(\sum x_i\right) - 1} \qquad 5.2$$

Where:
$\chi^2_{0.975}$ = The 97.5% critical value of χ^2 with *n*-1 degrees of freedom,
x_i = Number of organisms in quadrat *i* (*i* = 1,…*n*)
n = Number of quadrats.

$$M_c = \frac{\chi^2_{0.025} - n + \sum x_i}{\left(\sum x_i\right) - 1} \qquad 5.3$$

Where:
$\chi^2_{0.025}$ = The 2.5% critical value of χ^2 with *n*-1 degrees of freedom,

Morisita's standardised index of dispersion, I_p, was then calculated for $I_d \geq M_c \geq 1$:

$$I_p = 0.5 + 0.5\left(\frac{I_d - M_c}{n - M_c}\right) \qquad 5.4$$

The standardised form of the index varies from –1 to +1, with 95% confidence limits at –0.5 and +0.5 (Krebs, 1999). Values of I_p = 0, indicate a random dispersion. An aggregated dispersion is indicated by values greater than zero and a uniform pattern by values less than zero.

Two tests were used to analyse spatial pattern at the scale of the local neighbourhood. Firstly, the variance to mean (*I*) ratio was calculated on a 1-m^2 basis for each plot and the significance tested using the χ^2 goodness-of-fit test (Campbell & Clarke, 1971). Random dispersion is indicated by a value of 1 and aggregation by values greater than 1. Secondly, nearest-neighbour distances were analysed using Clark and Evans (1954) R-statistic:

$$R = \frac{\sum r_i}{n} 2\sqrt{\rho} \qquad 5.5$$

Where:
r_i = Distance to nearest-neighbour for individual *i*,
n = Number of individuals in the study area,
ρ = The density of oysters in the study area.

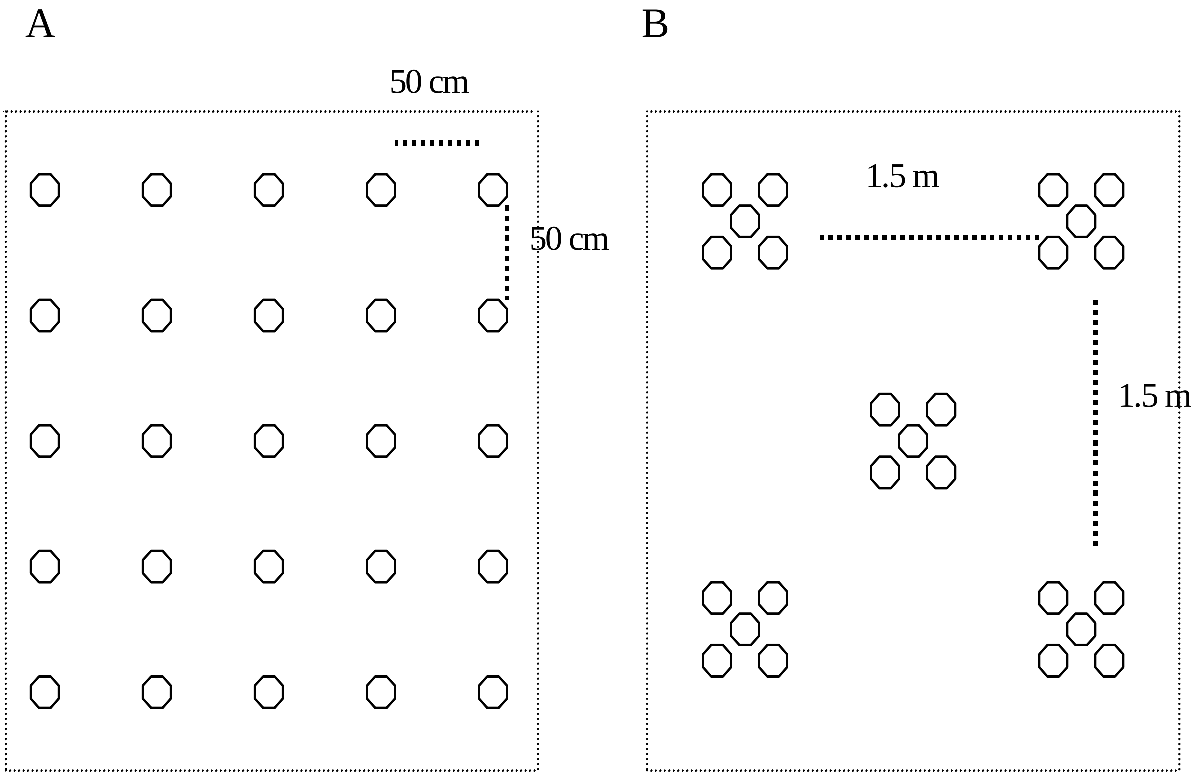
Values of R = 1 indicate a random spatial pattern. An aggregated spatial pattern is indicated by values of R approaching zero and a regular pattern by values approaching an upper limit of 2.15 (Krebs, 1999). Significance was tested using the χ^2 goodness-of-fit test to a negative exponential distribution (expected under random dispersion) (Campbell & Clarke, 1971). The R-statistic was calculated for distances between individual oysters and their first, second and third nearest-neighbours for the total mapped population and for distances between sexually mature oysters (> 40 mm shell length) and their first sexually mature nearest-neighbour. Pearson's product moment correlation was used to test the association between the density of oysters (m^{-2}) and the mean distance to the n^{th} nearest-neighbour. The Dunn-Šidák correction factor was used to correct the probability for multiple comparison correlations.

5.2.1 Experimental investigation of the factors influencing fertilisation

The six plots mapped at LM1 were cleared of all oysters and each oyster was labelled with a reference specific to its coordinates on the spatial map. Each plot was randomly assigned to an aggregated or non-aggregated spatial pattern, with three replicates of each treatment. Labelled oysters were then placed in the central 2 m^2 of the plots in the assigned pattern. The non-aggregated pattern was composed of oysters placed in a regular spatial pattern with neighbour distances of 50 cm. The aggregated pattern consisted of 5 groups of 5 juxtaposing oysters, with each group placed 1.5 m apart from the others (Figure 5.1). These distances were chosen in order to utilise the full central 2 m^2.

Anderson-Darling tests were used to test the assumption of normality for the distribution of the number of brooding oysters per plot. A two-sample t-test was used to determine whether the number of oysters brooding larvae differed between plots with an aggregated or random spatial pattern. One-way analysis of variance and Fisher's pairwise comparisons were used to determine if the number of brooding oysters differed with distance along the bed.

Figure 5.1 Experimental plot layout for a non-aggregated (A) and an aggregated (B) spatial pattern.



5.3 Results

There were significant differences in density among plots at LM1 ($H = 55.35$, d.f. = 5, $P < 0.01$) and LM2 ($H = 74.30$, d.f. = 5, $P < 0.01$). At LM1 the density was greatest in the central plots and lowest towards the edge of the bed. The pattern at LM2 was less clear, but plots nearer the centre of the bed were more dense than plots towards the edge (Figure 5.2, Table 5.1). The overall density at LM2 was significantly lower than at LM1 ($W = 50959.0$, $P < 0.01$).

At the site level, Morisita's and standardised Morisita indices indicated that, within plots, *O. edulis* had a pattern of dispersion significantly different from random, tending toward aggregation (Table 5.2). Variance to mean ratios indicated that the dispersion of oysters within plots at LM1 was characterised by a random spatial pattern, with the exception of the 40-m plot. The dispersion of oysters within the first two plots at LM2 were also characterised by a random spatial pattern, whereas the oysters within the 40-100-m plots were characterised by an aggregated spatial pattern (Table 5.3).

Distances between first nearest-neighbours in plots at LM1 suggested that oysters were characterised by a random spatial pattern except in the 20 and 40-m plots (Table 5.4). The R-statistic for the 40-m plot was 1.01 but was significantly different from a random spatial pattern. The actual and expected mean distances between neighbours were both 32 cm, but, 23% of the nearest-neighbour distances were greater than 50 cm. A comparison of the observed and expected distances according to a negative exponential distribution, indicated that the pattern of the 20-m plot tended towards a regular spatial pattern. The R-statistic for the 40-m plot was 0.81, suggesting an aggregated spatial pattern. Distances between first nearest-neighbours at LM2 were all significantly different from a random spatial pattern, with R-statistic values indicating aggregated spatial patterns. At LM1, nearest-neighbour distances between mature oysters indicated a random spatial pattern, except for the 40- and 80-m plots. R-statistic values were 0.81 in the 40-m plot and 0.85 in the 80-m plot, indicating that the mature oyster groups within these plots were aggregated. At LM2, distances between mature oysters were significantly different from a random spatial pattern in all plots, with R-statistic values indicating an aggregated pattern.

At LM1, there was a significant inverse correlation between plot density and the mean distance between nearest-neighbours for all the mapped oysters ($r = -0.935$, $P < 0.01$) and sexually mature oysters ($r = -0.936$, $P = 0.01$). At LM2, this association was significant for mature oysters ($r = -0.89$, $P = 0.02$), but not for all the mapped oysters ($r = -0.714$, $P = 0.11$) (Figure 5.3). The mean distance between all mapped individuals in plots and their first nearest-neighbours ranged from 21–60 cm at LM1 and 19–37 cm at LM2. Distances between sexually mature oysters and their first nearest sexually mature neighbour ranged between 21–58 cm at LM1 and 20–28 cm at LM2 (Figure 5.3). R-statistic values indicated that these distances were characterised by a random spatial pattern at LM1, whereas at LM2, the spatial pattern tended towards aggregation (Figure 5.4). However, there were no significant differences between sites in the mean distance to the nearest-neighbours for all oysters ($W = 49.0$, $P = 0.13$) or the mature populations ($W = 42.0$, $P = 0.69$).

Figure 5.2 Comparison of the mean density of oysters within plots at LM1 and LM2.

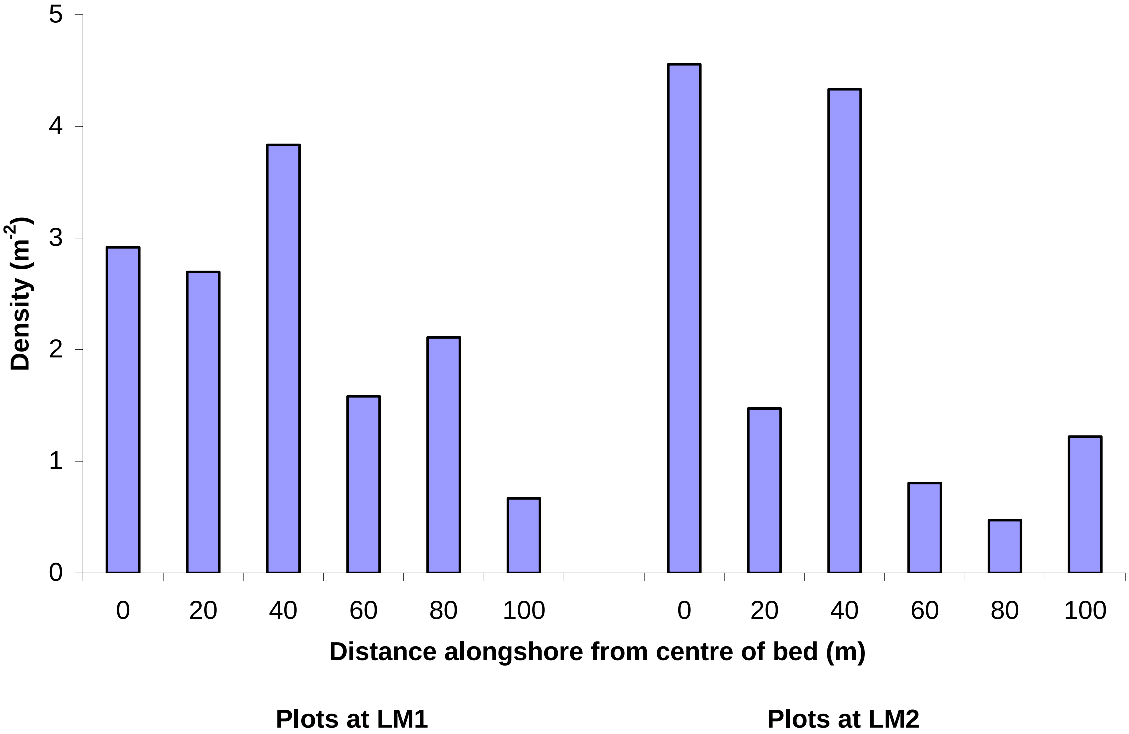


*Table 5.1 Differences in the abundance of mapped oysters among plots within sites. Z values are significant when they are greater than the critical value of 2.45, with a family error rate of 0.2 and a probability of **P = 0.05 and ***P <0.01.*

LM1			LM2		
Plots	**Z**		**Plots**	**Z**	
1 v 4	3.21	***	1 v 2	4.09	***
1 v 6	5.54	***	1 v 4	6.20	***
2 v 4	2.63	**	1 v 5	6.74	***
2 v 6	4.97	***	1 v 6	5.30	***
3 v 4	4.05	***	2 v 3	2.76	**
3 v 5	3.72	***	2 v 5	2.65	**
3 v 6	6.38	***	3 v 4	4.87	***
5 v 6	3.66	***	3 v 5	5.41	***
			3 v 6	3.97	***

Table 5.2 Spatial pattern of O. edulis *recorded in 6-m^2 plots at LM1 and LM2, determined by Morisita's index and the standardised Morisita index. Departures from a random spatial pattern are indicated by a significantly high χ^2 value and values of the standardised index >0.5.*

	LM1	**LM2**
Morisita's index	1.18	1.43
χ^2	95.50	177.64
Probability	<0.01	<0.01
Standardised Morisita index	0.52	0.54

*Table 5.3 Spatial dispersion of individuals within plots determined by the variance to mean (I) ratio. Plots are numbered using their distance alongshore from the centre of the bed (m). These departures from a random spatial pattern are significant at probabilities of *P < 0.05 and ***P <0.01.*

	LM1					**LM2**				
Plot	***I***	**d.f.**	**χ^2**		*Pattern*	**I**	**d.f.**	**χ^2**		**Pattern**
0	1.24	3	1.22		Random	2.01	7	7.89		Random
20	1.48	5	9.35		Random	2.08	3	4.60		Random
40	2.08	6	14.50	*	Aggregated	4.04	7	55.98	***	Aggregated
60	1.75	3	1.79		Random	4.31	2	119.47	***	Aggregated
80	1.51	4	4.61		Random	3.08	1	4.56	*	Aggregated
100	0.94	1	0.20		Random	4.21	2	17.51	***	Aggregated

*Table 5.4 R-statistics for neighbour distances between all mapped oysters and mature oysters only. Significant departures from a random spatial pattern are given at n – 1 degrees of freedom and probability of ***P < 0.01.*

a. LM1.

	PLOT											
	0 m		20 m		40 m		60 m		80 m		100 m	
TOTAL POPULATION												
R_1	0.98		1.01		0.81		0.95		0.96		1.00	
χ^2	8.41		17.56	***	37.50	***	9.65		6.64		6.19	
Pattern	random		regular		aggregated		random		random		random	
R_2	1.51		1.66		1.39		1.34		1.49		1.75	
χ^2	30.12	***	187.08	***	37.50	***	14.62		53.44	***	45.53	***
Pattern	regular		regular		regular		random		regular		regular	
R_3	1.83		1.95		1.82		1.74		2.11		2.22	
χ^2	47.65	***	358.46	***	446.45	***	70.17	***	270.89	***	72.56	***
Pattern	regular		regular		regular		regular		regular		regular	
MATURE POPULATION												
R_1	0.89		0.98		0.81		0.95		0.94		0.91	
χ^2	8.37		8.95		34.83	***	7.79		13.97		6.99	
Pattern	random		random		aggregated		random		random		random	

b. LM2

	PLOT											
	0 m		20 m		40 m		60 m		80 m		100 m	
TOTAL POPULATION												
R_1	0.82		0.72		0.65		0.43		0.48		0.58	
χ^2	42.73	***	42.35	***	171.58	***	56.02	***	20.10	***	113.59	***
Pattern	aggregated		aggregated		aggregated		aggregated		aggregated		aggregated	
R_2	1.32		1.13		1.11		0.84		0.60		0.82	
χ^2	104.63	***	27.53	***	4.01		29.95	***	17.33	***	84.64	***
Pattern	regular		regular		random		aggregated		aggregated		regular	
R_3	1.82		1.64		1.51		1.31		1.01		1.10	
χ^2	532.42	***	132.13	***	108.93	***	21.60	***	2.22		59.33	***
Pattern	regular		regular		regular		regular		random		regular	
MATURE POPULATION												
R1	0.79		0.83		0.68		0.49		0.58		0.63	
χ^2	41.35	***	0.90		121.42	***	57.25	***	11.55	***	106.91	***
Pattern	aggregated		random		aggregated		aggregated		aggregated		aggregated	

Figure 5.3 Relationship between the density of O. edulis *within plots and the distance to the first nearest neighbour.*

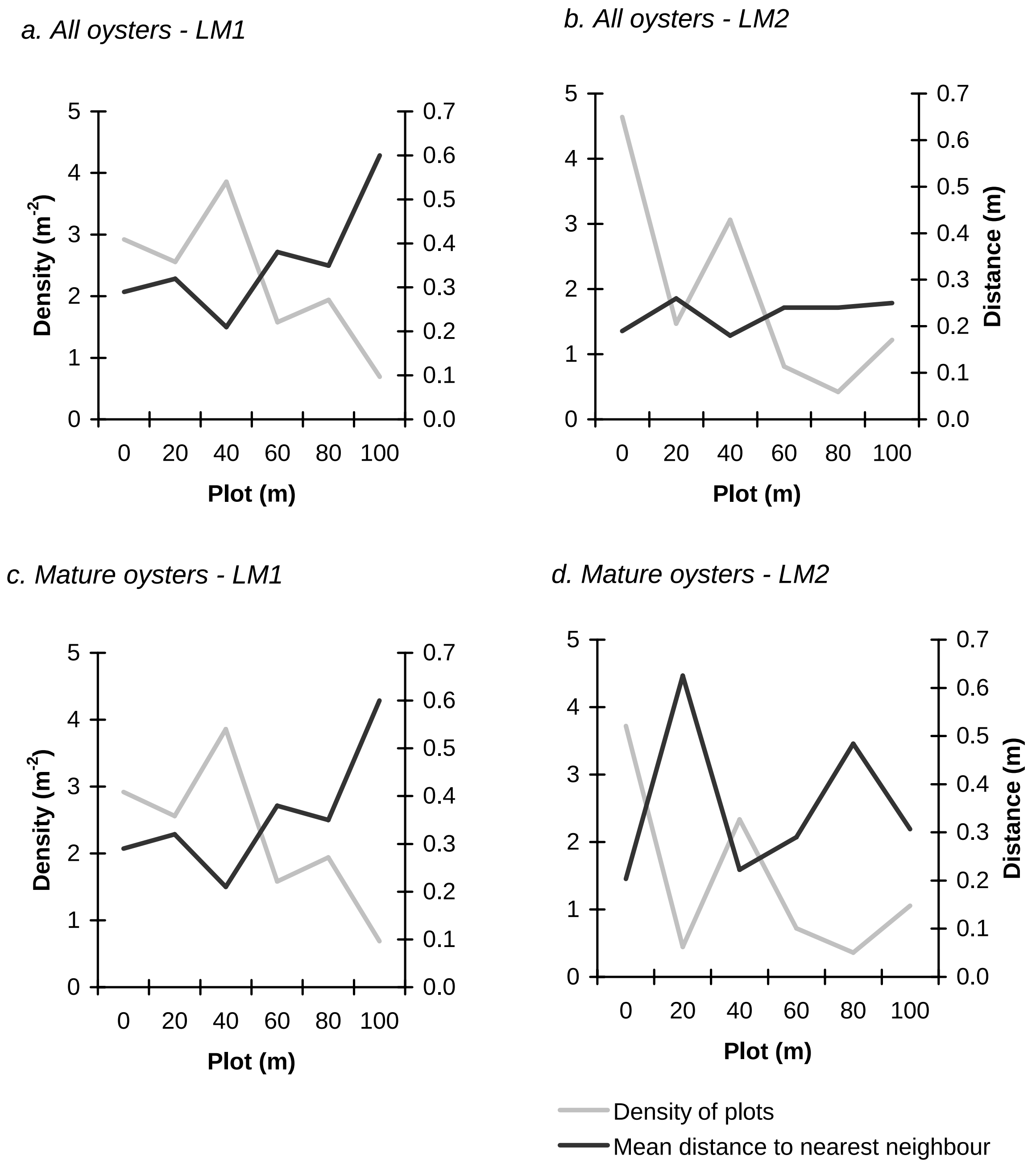
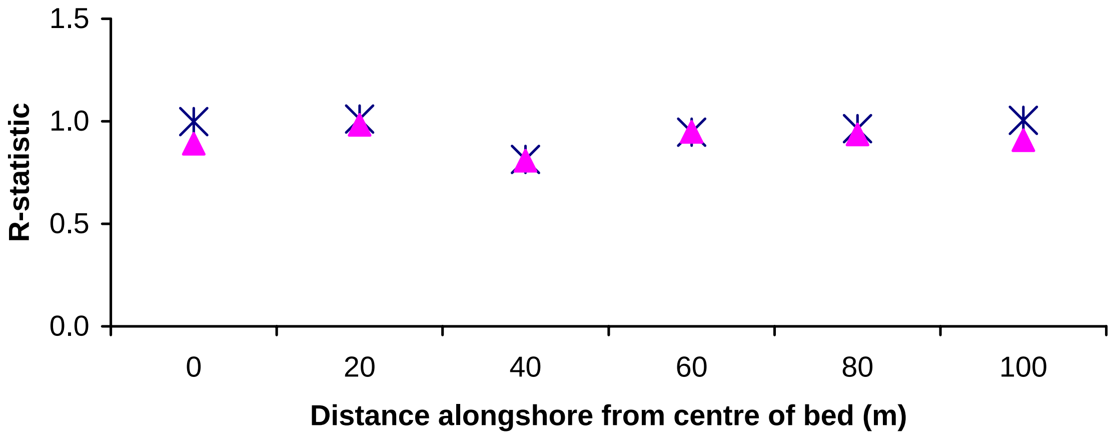


Figure 5.4 Changes in the R-statistic for distances between all mapped individuals and their first nearest neighbour and distances between first nearest neighbours of mature-mature individuals. R = 1 indicates a random spatial pattern, R < 1 indicates an aggregated spatial pattern and R > 1 indicates a regular spatial pattern.

a. LM1



b. LM2

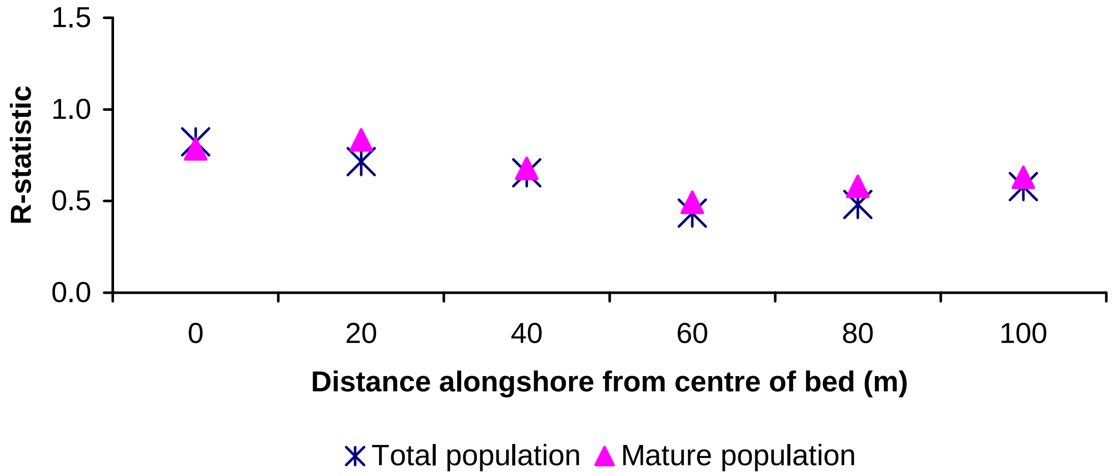
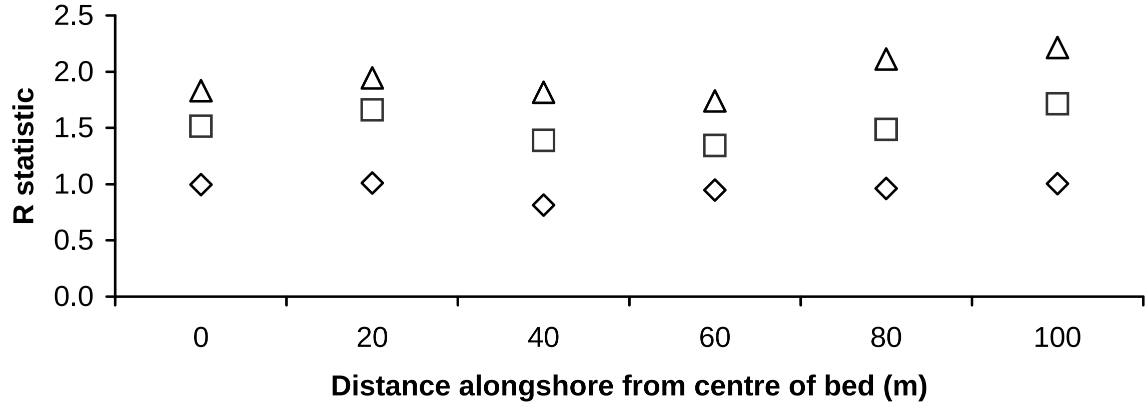
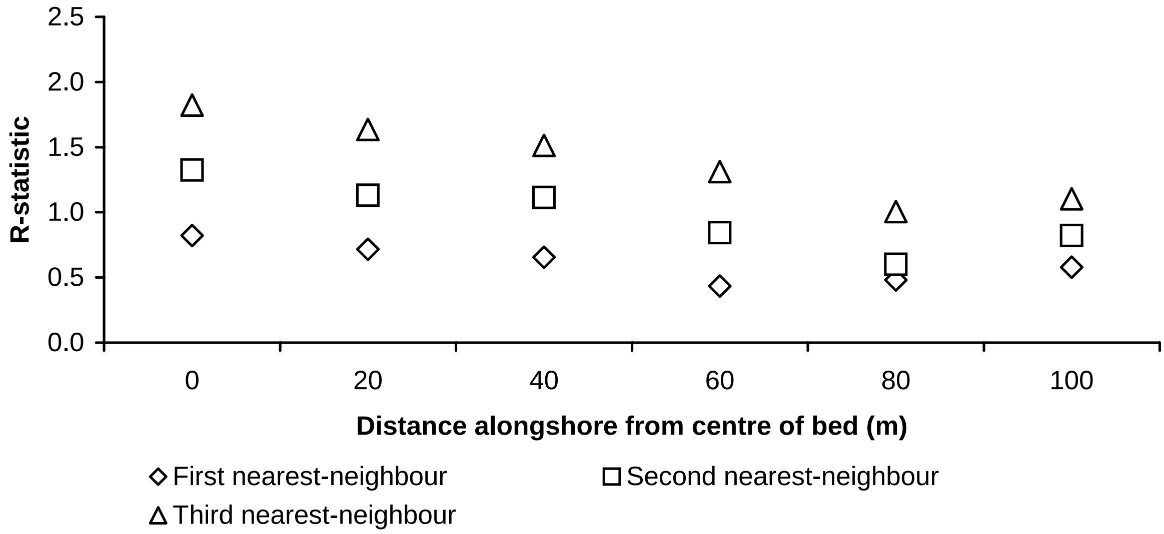


Figure 5.5 Changes in the R-statistic between individuals and the first, second and third nearest neighbour. R = 1 indicates a random spatial pattern, R < 1 indicates an aggregated spatial pattern and R > 1 indicates a regular spatial pattern.

a. LM1



b. LM2



At both sites, R-statistic values indicated that the spatial patterns of oysters tended towards a regular spatial pattern as the neighbourhood was increased from the first to the third nearest-neighbour (Figure 5.5). There was a significant inverse association between plot density and the distance to the third nearest-neighbours at LM1 (r_2 = -0.880, P = 0.02) but there was no significant relationship at LM2. Mean distances between the third nearest-neighbours ranged between 46–133 cm at LM1 and 42–78 cm at LM2.

5.3.1 Manipulated plots

The number of brooding oysters did not differ significantly with the spatial pattern of manipulated plots (t = -0.75, d.f. = 3, P = 0.51). There was a significant difference in the number of brooding oysters within plots ($F_{5,144}$ = 2.31, $P < 0.05$). Fisher's pairwise comparisons indicated that plot 2, containing eight brooding oysters, differed significantly from all other plots except for plot 3, which contained five brooding oysters. However, the number of brooding oysters in plot 3 was not significantly different from any of the other plots, which ranged from one to three brooding oysters. There was no correlation between the number of brooding oysters and the original density of the plots (r = 0.52, $P > 0.05$).

5.4 Discussion

The geographical scale of analysis influenced the apparent spatial pattern of oysters in Linne Mhuirich. At the site level on a scale of tens of metres, oysters at both LM1 and LM2 displayed an aggregated spatial pattern. This finding agrees with the estimates of population density and abundance in section 3.3.2, in which transect data for both sites fitted the negative binomial distribution. At the individual neighbourhood scale, variance to mean ratios based on 1-m^2 quadrats and distances between nearest-neighbours showed differences in spatial pattern between and within sites. Oysters within plots at LM1 were, on the whole, characterised by a random spatial pattern. There was a discrepancy between the results of the variance to mean ratio and the nearest-neighbour distance analysis for the 20-m plot, which was due to the large proportion of nearest-neighbour distances greater than the average. It would be expected that as density increases, the distance to the nearest-neighbour decreases. This is observed in the 40-m plot at LM1, which was the most dense of the LM1 plots (3.86 m^{-2}) and had the lowest average distance between nearest-neighbours (21 cm).

The dispersion of oysters within plots at LM2 did not follow the same trends as at LM1. With the exception of plots 1 and 3, oyster densities within plots were low at LM2 compared with LM1. Variance to mean ratios indicated that the spatial dispersion of the high-density plots at LM2 was random, whereas nearest-neighbour distance analysis indicated aggregated patterns. However, both variance to mean ratios and nearest-neighbour distances indicated aggregated spatial patterns for the low-density plots at LM2, whereas at LM1, both analyses indicated a random spatial pattern in low-density plots. The aggregated patterns indicated for oysters at low density at LM2 could be related to the spatial availability of habitat suitable for larval settlement within the plots. However, in a previous study, the suitable substrata surveyed were characterised by aggregated spatial patterns at the site level for both LM1 and LM2 (see section 4.3.1). Therefore, this characteristic alone is unlikely to have resulted in the different spatial patterns between the two sites.

Gathering of oysters is only known to occur at LM2 and is selective for oysters of a size consistent with sexual maturity (see sections 3.3.2 and 3.4.3). However, sexually mature oysters were present in all plots at LM2 and nearest-neighbour distances indicated that they were also characterised by aggregated spatial patterns. A comparison of the corresponding plots within the two sites highlighted the fact that natural variation exists within oyster beds, making it difficult to isolate the effects of unlawful exploitation on local density. However, the variations in density do not explain the differences in spatial pattern of the oysters between the two sites. In section 3.3.2, analysis of the substratum to which unlawfully gathered oysters were attached showed that over 80% were attached to shell, pebbles or were not attached and showed no signs of forced removal. Oysters that are attached to substrata that are cumbersome, such as large stone and rock, are less likely to be collected. Only 3% of the unlawfully gathered oysters surveyed had damage to the valve indicative of forced removal from substrata. It may be, therefore, that the aggregated spatial patterns of oysters at low densities at LM2 result from a combination of habitat availability and unlawful exploitation selecting oysters attached to lightweight substrata.

On the whole, the spatial pattern of oysters in plots was unaffected by the removal of sexually immature individuals from the analyses. However, as the neighbourhood of individuals within the surveyed plots was increased from the first to the third nearest-neighbour, changes in the R-statistic showed a tendency towards regular spatial patterns, because the distances between individuals increased significantly compared with those of first nearest-neighbours. Furthermore, the mature oysters at both sites showed an inverse relationship between density and the distances between first nearest-neighbours, as expected. The change in the R-statistic and relationship with density suggest that the size of the clumps at the neighbourhood scale was small at both sites for both the total populations and for mature oysters.

For marine species that expel gametes into the water column, simulation experiments have shown that fertilisation success of eggs decreases as distance increases from the source of sperm (Denny & Shibata, 1989; Levitan, 1991). This drop in fertilisation success is the result of dilution and diffusion of sperm in the external environment. Synchronised spawning events, the retention of eggs by females prior to fertilisation with sperm that has been collected from the external environment and the release of gametes as concentrated packets, have been suggested as adaptations that overcome the inefficiencies of external fertilisation in the marine environment (Denny & Shibata, 1989). These are all characteristics of the reproductive behaviour of *O. edulis* and may increase the effective distance over which sperm can fertilise eggs and provide an advantage when individuals exist at low population density. However, population density and abundance also have a significant influence on the fertilisation success of individuals (Levitan, 1991; Levitan & Young, 1995). Field experiments using the sea urchin *Diadema antillarum* have shown that although gamete production increases with body size, fertilisation success was lower when large-bodied individuals were at low density compared to higher densities of smaller bodied individuals (Levitan, 1991). Although clumping was observed in areas of low density, “clump” size appeared to be restricted to the first nearest-neighbour.

Experimental manipulation of oysters in this study did not reveal any relationship between the spatial pattern and the number of brooding individuals. Permission was granted to collect no more than 150 oysters for this research, so the experimental plots were based on only 25 individuals each. It is therefore possible that the plot size and distance between oysters within plots was not sufficient to reveal links between brooding and spatial pattern, if any relationship exists. Furthermore, the sex and stage of gonad development could not be determined prior to manipulation. Therefore, the sex ratio and number of oysters contributing to any fertilisation event during the experimental period would have differed between the experimental plots and would have greatly influenced the number of potential brooding oysters. It was also impossible to determine which oysters may have spawned in the male-phase during the experiment because of individual variation in the rate of sex-change in the gonad physiology. It is possible that the female oysters within the plots fertilised the eggs with sperm originating from outside the boundaries of the experimental plots. This would require the male gametes of *O. edulis* to be viable over distances of several metres and, if this were so, it would reduce the influence of density on Allee effects. However, current velocity, tides and turbulence are environmental factors that affect sperm concentrations by causing dilution, thus influencing fertilisation success with distance from the sperm source (Pennington, 1985; Denny & Shibata, 1989; Yund, 1990; Levitan, 1991; Levitan *et al*., 1992). The hydrodynamic factors and potential sperm concentrations were not considered in this study, but will have played an important role in determining the number of brooding individuals within the plots. This experiment should be repeated in a laboratory environment in order to ensure stringent controls on the starting and environmental conditions.

Fluctuations in the sex ratio of populations also act to decrease the likelihood that the nearest-neighbour of an individual is of the opposite sex. Current estimates of oyster population density are less than 1 m^{-2} for both sites (see section 3.3.2). In this study, the densities in plots at LM1 ranged from 0.69–3.86 m^{-2} and from 0.42–4.67 m^{-2} at LM2 attesting to the patchy nature. Low overall population densities, patchy local densities and clump-sizes of individuals being restricted to first nearest-neighbours suggest that fertilisation success among oysters in Linne Mhuirich oyster is potentially low.

Immature oysters were recorded within all plots at both sites, so it can be assumed that some spatfall has occurred in recent years and hydrodynamic factors have not limited larval transport to the areas surveyed. In a previous study, spat collection tiles located at the LM1 site also indicated that larval settlement occurred throughout the bed area (see section 4.3.4). Laboratory and field-based research has shown that when larval production is high, the abundance of spat settling upon collectors is high (Walne, 1964). Loch Ryan contains the largest known extant oyster population in Scotland and in a year with lower spatfall, a maximum of 100 spat were recorded on a collection tile with a total surface area of 0.045 m^2. The spat collectors laid at LM1 (see section 4.2) had a total surface area of approximately 0.27 m^2. In 2004, the maximum number of spat recorded on a single tile was ten, whereas in 2005, 11 spat were found settled on a total of 46 tiles, with three individuals the maximum number of spat recorded on a single tile. If we assume that the recruitment pulse in 2004 represents a low spatfall in Linne Mhuirich, the difference in the scale of the spatfall compared to Loch Ryan can be attributed to the difference in the scale of abundance between the two populations. Loch Ryan has a population abundance estimated in the millions (see section 3.1), whereas Linne Mhuirich has an estimated population abundance of approximately 50,000 oysters (see section 3.3.2).

Determining whether these spatfalls represent good or poor recruitment years in Linne Mhuirich is difficult. Recruitment in *O. edulis* populations is known to be highly variable, both temporally and spatially (Korringa, 1956; McKelvey *et al*., 1993). Several European scientists have suggested that 15˚C is the critical temperature necessary to trigger breeding in *O. edulis* (Orton, 1922; Korringa, 1956). In Scotland, the breeding season extends from May to August (Millar, 1963). The average monthly temperature in Linne Mhuirich was, on average, higher in 2005 compared to 2004, with the critical temperature for breeding attained a month earlier in 2005 (16.09˚C in May) compared to 2004 (15.36˚C in June) (see section 1.5.2). Thus, the lower spat recruitment in 2005 cannot be attributed to a potential delay in the onset of spawning caused by ambient temperatures. Korringa (1956) stated that the magnitude of larval production depended upon the number of female-phase oysters breeding in that year. As the sex ratio of the population for each year is unknown, it is possible that fewer individuals bred in the female-phase in 2005 compared to 2004. This would account for the differences in recruitment between the two years. However, the Linne Mhuirich population has been shown to have areas of low density and inter-individual distances that increase markedly as second and third nearest-neighbours were considered, suggesting that Allee effects could be influencing fertilisation success and therefore larval production.

As years with high spatfalls have been recorded up to eight years apart (McKelvey *et al*., 1993) and the recruitment data in this study only spans a 2-year period, it is impossible to determine what constitutes a high spatfall in Linne Mhuirich. The size range of the Linne Mhuirich population suggests that there have been low levels of recruitment in previous years (see sections 3.3.2 & 3.4.3). This suggests that the Linne Mhuirich population recruits hundreds of spat per year during periods of low recruitment, but can lose hundreds of adult oysters to unlawful exploitation in a day (see section 3.3.2) in addition to natural mortality. Therefore, there is potentially a deficit in the number of recruited individuals, thus preventing the population from being self-sustaining.

5.5 Conclusions

Characteristics of the *O. edulis* sub-populations in this survey, including the fluctuating sex ratio of the species, small local-neighbourhood clump sizes and areas of very low neighbourhood densities, suggest that Allee effects could be important in limiting recruitment success within the *O. edulis* population within Linne Mhuirich. Furthermore, selective removal of sexually mature oysters by unlawful gathering can increase the potential of Allee effects by decreasing the population density and abundance.

6 GENETICS OF SCOTTISH POPULATIONS OF THE NATIVE OYSTER, *OSTREA EDULIS*: GENE FLOW, HUMAN INTERVENTION AND CONSERVATION

The research in this section was conducted by A. R. Beaumont, University of Wales, Bangor, under a subcontract to UMBSM. The report by Beaumont has been edited to fit within the overall project report.

6.1 Introduction

Ostrea edulis is a bivalve mollusc that has supported important aquaculture and fisheries activities throughout Europe for hundreds of years. However, what was once a widely abundant species has now become relatively rare in nature, almost certainly due to human activities. Dramatic declines in population sizes were experienced across Europe towards the end of the 19th century and in the early part of the 20th century (see sections 1.3 and 2.7).

Like other sedentary marine bivalves, oysters have a life history that involves a planktonic larval dispersal phase. Depending on the length of larval life, the prevailing oceanographic conditions and the availability of suitable habitat, marine bivalve species are to a greater or lesser extent subdivided into populations that are relatively genetically distinct. When there is little gene flow (i.e. few larval exchanges) per generation between populations, forces such as random genetic drift (non-directional) and selection (directional) will change allele frequencies at gene loci leading to identifiable and quantifiable genetic differences between populations. Such population genetic differentiation is an important part of natural biodiversity below the level of species. Without doubt, within-species genetic diversity is of critical value both for recovery in the event of serious population decline and also as a repository of the future evolutionary potential of the species.

Because failing stocks of oysters in one region of Europe were often replenished with oysters from other regions (Millar, 1961; 1963; Magennis *et al*., 1983), the likely consequences will have been a homogenization of any naturally evolved underlying population genetic differentiation. In the particular case of Scotland, there have been recorded (and probably unrecorded) translocations of significant numbers of oysters into the region from Europe, and between sites within the region (Figure 6.1). As part of the Native Oyster Biodiversity Action Plan, and in relation to stock regeneration (Laing *et al*., 2005), it is important to establish whether translocations or other aquaculture activities have effectively homogenized any original population genetic differentiation, or whether there remain any sites where unique genetic populations can be identified.

Genetic differentiation of populations can be identified using a number of genetic markers (Carvalho & Hauser, 1998; Beaumont & Hoare, 2003). Until recently allozymes were the major markers used. Studies using allozymes (e.g. Johannesson *et al*., 1989; Saavedra *et al*., 1993; Saavedra *et al*., 1995) were not able to detect fine-scale genetic differentiation in European stocks of *O. edulis*. Johannesson *et al*. (1989) and Saavedra *et al*. (1993) identified a general low level of genetic variability of *O. edulis* relative to other bivalves and a low level of genetic differentiation in Atlantic stocks (Wright's (1965) F_{st}, a measure of genetic differentiation, was 0.062). Saavedra *et al*. (1995) reported evidence for two ancient Atlantic and Mediterranean stocks that have subsequently become merged. Mean G_{st} (equivalent to Wright's (1951) F_{st}) was 0.088 indicating little differentiation across an area from the eastern Mediterranean to Norway, almost the entire range of the species in Europe.

Figure 6.1 Recorded and anecdotal records of translocations of O. edulis *into and within Scotland. Code letters and numbers refer to Table 6.1.*

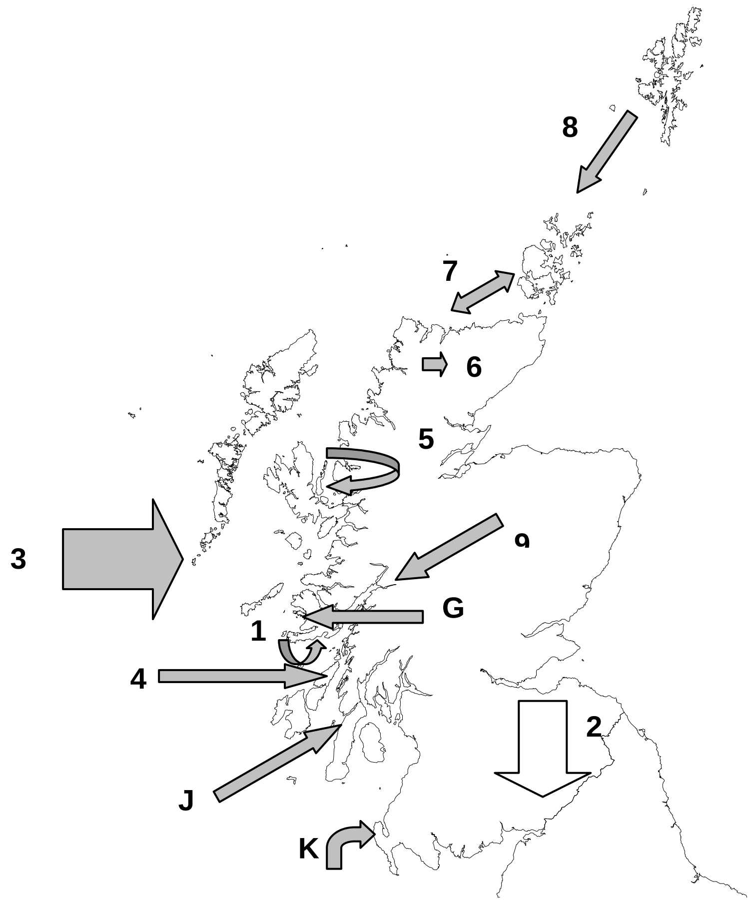


Table 6.1 Recorded and anecdotal records of translocations of O. edulis *into and within Scotland, as indicated in Figure 6.1.*

	Date	Details of translocation
A	1900s	Unknown quantities from Skye and Holland laid in unrecorded layings along west coast (Anon., 1885–1977).
	1950s	Thousands of oysters from Brittany (France) re-laid in 19 locations along west coast (Millar, 1961).
B	1990s	*O. edulis* from Loch Eriboll used to stock a hatchery in Orkney, which was used to stock a cultivation programme in the Kyle of Tongue (A. MacKay, pers. comm. 2003).
C	1800s	Unknown quantities from unknown locations re-laid in Long Hope Bay, St Margaret's Hope Bay and Widewall (Young, 1886).
	1912	800,000 oysters from an unknown location re-laid in Orkney (Millar, 1961).
	1920s	Oysters from Denmark re-laid in Orkney beds (Millar, 1961).
D	19th century & 1990s	Loch Eriboll stock re-laid in Kyle of Tongue (A. MacKay, pers. comm. 2003).
E	20th century?	Oysters from Loch Ainort removed to stock Broadford Bay (Millar, 1961).
F	1880s	Unknown quantities from Morbihan (France) re-laid in Loch Creran (Anon., 1885-1977).
	1894	Two consignments from Holland were re-laid in Loch Creran (Anon., 1885–1977).
G	From 1970s	Stock from Seasalter (England) layed in Mull (D. Wathen, pers. comm. 2003). Stock was also brought from the Orkney hatchery until early 2000.
H	1990s	Oysters moved from south Ulva to other locations around Ulva. *O. edulis* from the Isle of Colonsay also re-laid around Ulva (J. Howard, pers. comm. 2004).
I	1890s	40,000 oysters from Arcachon (France) *via* Whitstable (England) re-laid in Loch Sween (Smith, 1894; Millar, 1961).
	1947	Few thousand oysters from Brittany re-laid in Loch Sween (Millar, 1961).
J	1886	700,000 oysters from Loch Sween, the Hebrides and France re-laid in West Loch Tarbert (Anon., 1885–1977). Further restocking from unknown areas in the late 1800s (Millar, 1961).
	1950s	201,000 oysters translocated from Brittany to West Loch Tarbert (Millar, 1961).
K	1800s	Unknown quantities from France, Holland and Essex layed in Loch Ryan (Millar, 1961).
	1958–1960s	Thousands of oysters from Brittany re-laid in Loch Ryan (Millar, 1963).
L	18th & 19th centuries	Millions of oysters taken from the Firth of Forth and re-laid in England, France and Holland (Fulton, 1895; Millar, 1961; Anon., 1885-1977).
	1870s	30,000 oysters from an unknown source laid in unknown locations within the Firth of Forth (Fulton, 1895).

Allozyme markers are not ideal for identifying genetic differentiation because they are not very variable (usually from two to five alleles per polymorphic locus). Also this variability may often be determined and maintained by selection rather than random genetic drift (Karl & Avise, 1992) thus leading to false conclusions about true gene flow between populations.

Microsatellite DNA markers are highly polymorphic (usually from 5–30 alleles at a locus), and have a high mutation rate that makes them ideal for population genetic studies (Bruford & Wayne 1993; Zane *et al*., 2002). Several microsatellite loci have now been developed for *O. edulis* (Naciri *et al*., 1995; Morgan *et al*., 2000: Sobolewska *et al*., 2001; Launey *et al*., 2002) and there are now two reports of their use to investigate population genetic differentiation in *O. edulis* (Launey *et al*., 2002; Sobolewska & Beaumont, 2005).

Launey *et al*. (2002) demonstrated significant genetic variation based on 5 microsatellite loci between two major regions — the Atlantic-western Mediterranean region and the eastern Mediterranean region (Overall $F_{st} = 0.019$). Within each region there was much less variation and little to discriminate between Atlantic populations except at the northern limit of the species distribution (Norway). Using four different microsatellite loci to those used by Launey *et al*. (2002), Sobolewska & Beaumont (2005) focused more on North Atlantic (including Scottish) populations and took into account whether the populations sampled were derived from hatchery-produced seed or not. As expected, samples derived originally from hatchery seed showed significantly fewer alleles per locus and significantly reduced expected heterozygosity compared with wild populations. A sample of oysters from Norway was the most genetically distinct from all others and hatchery-sourced populations were also relatively distinct from other wild populations. However, overall genetic differentiation was not extensive (F_{st} excluding hatchery-derived populations = 0.02) suggesting relative genetic homogeneity between samples.

In the study reported here, we have focused on investigating the genetic variation at six microsatellite loci in a number of populations from around the Scottish coast. Samples from Brittany, the Netherlands and Norway are included as out-groups and also because several of the recorded importations of large numbers of oysters into Scotland have come from Brittany and the Netherlands.

6.2 Methods

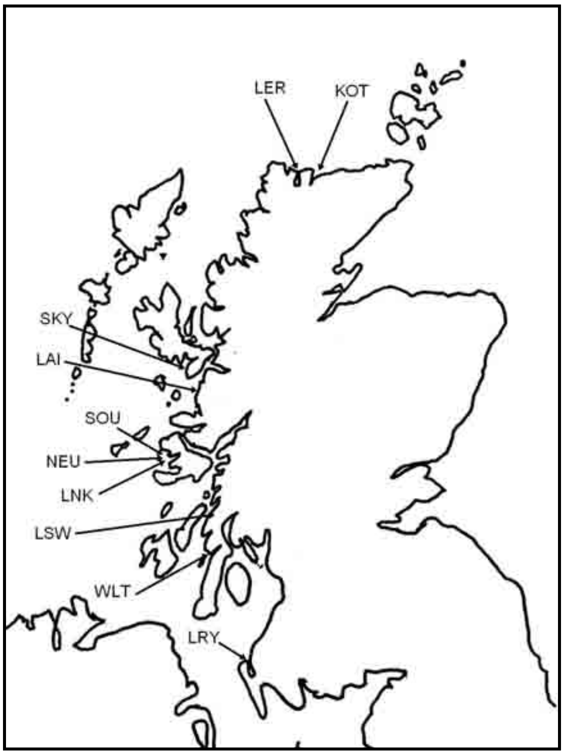
Oysters collected from sites in Scotland (Figure 6.2a) were dissected at the University Marine Biological Station, Millport (UMBSM) and samples of gill and adductor muscle tissue were placed in microtubes in 90% alcohol for transport to the School of Ocean Sciences (SOS), University of Wales, Bangor, during 2004. Norwegian oyster samples (Figure 6.2 b) were provided in a similar way, as tissue in 90% alcohol. Oysters from The Netherlands and Brittany (Figure 6.2b) were sent either fresh or frozen to SOS, dissected and preserved in 100% alcohol. All samples were held at 4-6^{o}C until use.

Oyster DNA was extracted using a standard phenol-chloroform method (Sambrook *et al*., 1989) following proteinase K and CTAB treatment (Wilding *et al*., 1997). Concentration and quality of the extracted DNA was measured using a Biophotometer that estimates the ratio between absorbance at 260 and 280 nm wavelengths. Initial trials indicated that slightly better quality DNA could be extracted from gill tissue compared with adductor muscle tissue so gill was used as the main source of oyster DNA.

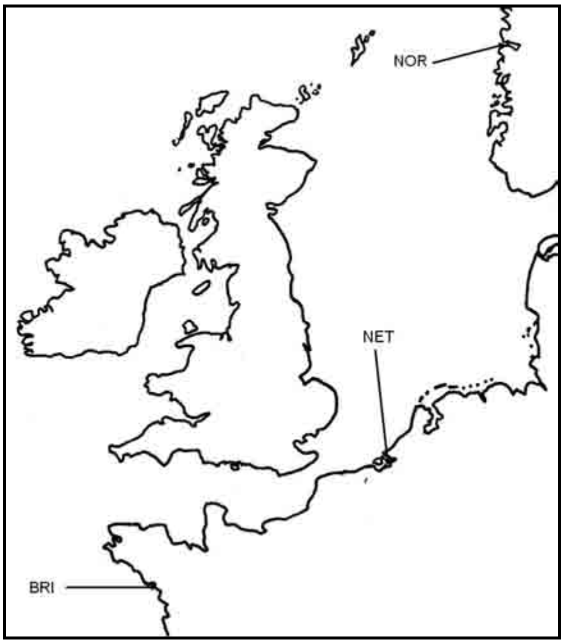
Initial trials were carried out to select suitable microsatellite loci from those published (Naciri *et al*., 1995; Morgan *et al*., 2000; Sobolewska *et al*., 2001; Launey *et al*. 2002). Suitable loci

Figure 6.2 Sample sites in Scotland and Europe of populations of O. edulis *for genetic analysis at six microsatellite loci. Population abbreviations (from north to south): Norway (**NOR**), Loch Eriboll (**LER**), Kyle of Tongue (**KOT**), Skye (**SKY**), Loch Ailort (**LAI**), Sound of Ulva (**SOU**), North East Ulva (**NEU**), Loch na Keal (**LNK**), Loch Sween (**LSW**), West Loch Tarbert (**WLT**), Loch Ryan (**LRY**), The Netherlands (**NET**) and Brittany (**BRI**).*

a. Sample sites around Scotland



b. Sample sites in northern Europe



were those that gave a range of variability (from 3 up to 30 alleles), exhibited different size ranges but had similar annealing temperatures (to allow multiplexing of pairs of loci), responded reliably during PCR and could be easily scored. Firstly, we used the authors' published methods and checked for PCR product on ethidium bromide-stained 0.8% agarose mini-gels. Loci that did not produce clear strong bands on mini-gels were not investigated.

Six microsatellite loci were selected for routine amplification of oyster samples, three from Launey *et al*. (2002) (*Oed.*J12, *Oed*.T5 and *Oed*.U2) and three from Morgan *et al*. (2000) (Oe1/63, Oe1/64 and Oe2/72) (Table 6.2). Minor modifications to the authors' published methods were required for most loci. In spite of considerable effort spent trying to optimise PCR by varying concentrations of template DNA, dNTPs and $MgCl_2$, and by adjusting the thermal cycling protocol, reliable scoring was not always possible for all individuals in all populations. Such problems are not uncommon when using PCR methods in a non-robotic DNA laboratory where occasional slight variations in the environment or in procedures are inevitable. Details of the process of optimisation of PCR for each locus and the final methods employed are described by Truébano García (2004) and Hönig (2005).

PCR products were separated on a 0.25 mm thick, 6.5% polyacrylamide slab gel in a LiCor DNA sequencer that uses a laser Infra Red detector to pick up a signal from one of the primers used in PCR amplification. Molecular weight standards were run alongside the samples and LiCor SAGA© software was used to provide pictures of the gels and to analyse them based on DNA fragment size. All gel images were carefully checked by eye to ensure that the automatic analysis was detecting and selecting fragment sizes correctly.

Microsatellite genotype data were analysed using a number of packages (TFPGA, (Miller, 1997); F-STAT (Goudet,1995) and BOTTLENECK (Cornuet & Luikart, 1996)). Numbers of alleles, allele frequencies and expected and observed heterozygosities were calculated. Agreement with the Hardy-Weinberg model was tested using exact tests and Wright's (1951) F-statistics were calculated according to Weir & Cockerham (1984). Nei's (1978) unbiased genetic distances were calculated for all pairwise comparisons between populations and used within a UPGMA routine to produce a dendrogram illustrating the genetic relatedness between oyster populations. A bootstrapping procedure is employed to calculate the proportion of permuted data sets (re-sampling with replacement over loci) that result in the formation of a node seen in the original data set and these proportions are indicated at each node in the dendrogram. For each population, Cornuet & Luikart's method (1996) was used to estimate the probability that a population has recently undergone a genetic bottleneck. Correlation between geographical distance and genetic distance was estimated by a Mantel test within TFPGA. Geographical distances between populations were simply measured as nearest coastline distances.

Table 6.2 Genetics of Scottish O. edulis *populations. Published source of microsatellite loci, locus names, types of repeat motif, size ranges of PCR product and numbers of alleles detected.*

Locus name	**Repeat motif**	**Size range**	**Number of alleles**	**Author**
Oedu.J12	$(GT)_{14}$	202-276	34	Launey *et al*. (2002)
Oedu.T5	$(CA)_{15}$	104-178	30	Launey *et al*. (2002)
Oedu.U2	$(AC)_{21}$ $(AG)_{7}$	146-226	30	Launey *et al*. (2002)
Oe1/63	$(GT)_{9}$	90-114	13	Morgan *et al*. (2000)
Oe1/64	$(GT)_{n}$ interrupted	130-174	19	Morgan *et al*. (2000)
Oe2/72	$(CA)_{n}$ $(TA)_{n}$ $(GT)_{n}$ interrupted	300-310	6	Morgan *et al*. (2000)

6.3 Results

This is the first study to use the following loci of Morgan *et al*. (2000): Oe1/63, Oe1/64 and Oe2/72 in a wider population analysis. Using just 20 oysters trawled from Southampton Water (UK), these authors recorded seven alleles at the Oe1/63 locus, four at the Oe1/64 locus and three at the Oe2/72 locus. In our wider survey we have detected a further six, fifteen and three alleles respectively for these loci. Launey *et al*. (2002) do not give total numbers of alleles detected at their three loci, *Oed*.J12, *Oed*.T5 and *Oed*.U2, that we have used in our study.

Table 6.3 shows allele frequencies at the six loci across 13 populations. Some samples failed to amplify at certain loci so there is essentially a complete data set for all six loci for eight populations (although five loci for Sound of Ulva) and a second data set including three loci for all 13 populations (but only two loci for Loch na Keal). Some analyses were carried out separately on the "six locus" data set and the "three locus" data set. The full data set is given in the format of an input file for the TFPGA analysis programme (Miller, 1997) in Appendix 2. Mean numbers of alleles across all populations range from 3.3 for locus Oe2/72 up to 18.8 for locus *Oed*.U2 and mean heterozygosity is highest at the *Oed*.J12 locus (0.919) and lowest at Oe2/72 (0.472) (Table 6.4).

In every case where there is a significant deviation from the Hardy-Weinberg model ($P<0.001$ following Bonferroni adjustment), the deviation is in the direction of deficiency of heterozygotes ($H_o<H_e$) (Table 6.4). Across all 61 tests, there are 51 instances of Ho< He (-ve) and only 10 instances of $H_o>H_e$ (+ve) and this is a significant ($P<0.05$) difference from an equal number of positives and negatives that would be expected if loci were generally in Hardy-Weinberg equilibrium in all populations. Overall values of mean F_{is} are strongly positive for both the three locus (F_{is} = 0.193) and the six-locus (F_{is} = 0.148) data set confirming an overall deficiency of heterozygotes relative to the expectations of the Hardy-Weinberg model.

Using all eight populations for which there are data at six loci, genetic differentiation according to Wright's F_{st} (1951) is 0.048. The three locus data set has a similar value (F_{st} = 0.051) indicating that the inclusion of a further four populations does not significantly alter the estimate of the level of genetic differentiation. Pairwise comparisons between all populations using Nei's (1978) unbiased genetic distance (*D*) based on all available data for all populations are given in Table 6.5. The highest values of *D* are found when comparing the Skye population with all others (mean *D* = 0.8107): this compares with the next highest mean *D* of 0.5877 for the Norway population. These high values of *D* indicate that these two populations are relatively distinct, genetically, from all others. Figure 6.3 shows a dendrogram of 12 populations based on data at three loci, which illustrates the genetically distinct nature of the Skye and Norway samples. The Netherlands and Brittany samples cluster together suggesting that they are quite similar to one another, but they differ from Scottish and Norwegian samples. There appear to be two main groupings among the Scotland sites (apart from Skye): Group A that includes Loch Ailort, Loch Ryan, Loch Sween and Loch Eriboll and Group B consisting of the Ulva region, West Loch Tarbert and the Kyle of Tongue. The Loch na Keal sample is excluded from Figure 6.3 because there are only data for two loci, but when included (dendrogram not shown) it clusters within the geographically proximate Ulva grouping.

Table 6.3 Allele frequencies for loci in 10 Scottish and three European populations of O. edulis*. Alleles are given as size in base pairs followed by notation (in brackets) for the TFPGA input file (Appendix 2). For population abbreviations see Figure 6.2.*

Population **Allele** ***Oed.* J12**	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
202 (1)							0.011						
204 (2)						0.025							
206 (3)					0.029				0.012				
208 (4)					0.014								
210 (5)										**0.141**			
212 (6)			0.019		0.014		0.011		0.036				
214 (7)							0.023		0.060		0.088		
216 (8)		**0.125**		0.056	0.043	**0.100**		0.021	0.024	0.031	**0.132**		**0.147**
218 (9)			0.039		0.071		0.023	0.063		**0.203**		**0.100**	
220 (10)			**0.115**		0.014		**0.148**	0.021	**0.202**	0.047		0.050	
222 (11)	**0.141**		0.019	**0.278**	**0.143**		0.057	0.063	**0.107**	0.094	0.044	0.050	**0.147**
224 (12)	0.016	0.063	**0.173**	**0.111**	0.014	**0.150**	0.068	**0.188**	0.036		**0.118**	**0.100**	**0.177**
226 (13)	0.016	**0.125**		0.056	0.043	**0.200**	0.011	0.063	0.036	0.063		0.050	0.059
228 (14)		**0.188**	0.019		0.057	**0.175**	0.046	0.063		0.016	0.088		
230 (15)	0.031	**0.250**	0.058		0.043			0.083	0.083	0.031	0.059		
232 (16)			0.039		**0.100**	0.025	0.057	0.042	0.095		0.029		0.029
234 (17)	0.094		0.077	0.056		0.050	0.034	0.021		**0.109**	0.059	**0.100**	0.059
236 (18)		0.063			0.057		0.034		0.012	0.016	0.044		0.029
238 (19)	0.203	0.063	0.039		0.029		0.034	0.042	0.060	0.063	0.059		**0.118**
240 (20)	0.047	0.063	**0.154**	0.056	0.014	0.050	0.057	0.021	0.024				
242 (21)			0.019		0.014		0.034	0.083	0.024	0.016	0.074	**0.150**	
244 (22)	0.016		0.019		0.086	**0.150**	0.091	0.063	0.083	0.016	0.059		0.059
248 (23)	**0.281**		0.077	**0.111**	0.057		0.057	0.021	0.012		0.015	0.050	0.059
250 (24)	0.063		0.039	**0.111**	0.014	0.025	0.011	0.042		0.031	0.044	0.050	0.059
252 (25)	0.016		0.039		0.043	0.025	0.034	0.083	0.036		0.044	**0.150**	0.029
254 (26)	0.047				0.043	0.025	0.011			0.031			
256 (27)	0.016	0.063	0.058		0.014		0.057		0.012		0.029		0.029
258 (28)	0.016			**0.111**			0.011		0.012			**0.150**	
260 (29)					0.014		0.023	0.021		0.031	0.015		

Population Allele *Oed.* J12	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
262 (30)					0.014		0.011		0.012	0.031			
264 (31)					0.014				0.024	0.016			
266 (32)										0.016			
268 (33)							0.046						
276 (34)				0.056									

Population Allele *Oed.* T5	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
104 (1)							0.022						
106 (2)	0.088	**0.206**	**0.107**	**0.181**	**0.368**	0.068	**0.111**	0.043	**0.318**	**0.119**	**0.293**	0.053	0.033
108 (3)												0.053	**0.100**
110 (4)			0.018				0.011	**0.114**		0.036			
112 (5)						0.011			0.080		0.012		
114 (6)							0.011	0.086				0.026	0.033
116 (7)					0.053			0.043					
118 (8)	0.029		**0.250**	**0.318**	**0.132**	**0.409**	**0.189**	**0.229**	**0.136**	**0.333**	0.098	0.053	
120 (9)		**0.118**			0.092	0.011	**0.111**	0.071	0.034	0.012	0.061	0.079	0.067
122 (10)		**0.177**					0.022	0.029	0.011				
124 (11)			**0.143**	0.091	**0.145**	**0.102**	**0.111**	0.014	0.046	0.060	0.073	0.026	0.033
126 (12)		**0.324**	0.018		0.013	0.023			**0.102**	0.036	0.061	0.053	0.067
128 (13)		0.029	0.018		0.040				0.046		0.037	0.053	
130 (14)		0.029	0.018			0.023	0.022	0.029	0.023		0.012	**0.132**	0.033
132 (15)	0.074	0.029	0.089	0.046		0.034	**0.156**	0.043	0.034	0.071	0.012	0.026	
134 (16)			**0.161**	**0.136**	0.026	0.046	0.011	0.014	0.011		0.061		
136 (17)					0.013	**0.102**	0.067		0.034	**0.107**	0.012	**0.132**	0.033
138 (18)	**0.250**		0.054		0.053	0.068	0.044	0.029	0.011	0.071	0.061	0.079	**0.233**
140 (19)	**0.132**				0.013	0.023	0.022	0.029	0.034	0.012		0.053	**0.133**
142 (20)	0.029			0.046		0.011	0.033	0.029	0.011	0.060			0.033
144 (21)	0.029			0.091	0.013	0.011	0.033	**0.100**	0.023	0.036	0.049		
146 (22)	**0.265**	0.088	0.036			0.011		0.029	0.011		0.024		

Population Allele *Oed.* **T5**	NOR	LER	KOT	SKY	LAI	SOU	NEU	LNK	LSW	WLT	LRY	NET	BRI
148 (23)			0.054	0.046				0.014	0.023	0.012	0.037	**0.105**	0.033
150 (24)	0.059		0.018	0.046	0.013	0.023	0.022			0.024	0.024		
152 (25)			0.018		0.013	0.011		0.029	0.011	0.012	0.024	0.026	0.067
154 (26)	0.015							0.014				0.053	0.033
156 (27)	0.029				0.013						0.012		0.033
158 (28)						0.011					0.024		
160 (29)													0.033
178 (30)								0.014			0.012		

Population Allele ***Oed. U2***	NOR	LER	KOT	SKY	LAI	SOU	NEU	LNK	LSW	WLT	LRY	NET	BRI
146 (1)			0.036			**0.229**							
148 (2)									0.019				
152 (3)	**0.103**						0.048		0.019		0.018		
154 (4)	0.059										0.036		
156 (5)	0.015		**0.179**		0.018	0.063			0.093	0.021	0.054		
158 (6)			0.036		0.054	0.021	0.032			0.042	0.071		
160 (7)	0.029		0.071		0.054	0.021	0.032		0.093	0.063	**0.143**		
162 (8)	**0.235**		0.071		0.036	0.021	0.048		0.093	**0.104**	0.018		
164 (9)	0.015		0.071		0.071	0.042	0.097				0.071		
166 (10)	0.015		0.089				0.032		0.019	0.042	0.071		
168 (11)	0.074		0.036			0.021	0.016			0.042	0.054		
170 (12)			0.089		0.071	**0.125**	0.065		**0.130**	**0.146**	0.071		
172 (13)			0.036		0.036	0.021	0.081		0.074	0.021	0.054		
174 (14)			0.018		0.018	0.042	0.032		0.074	0.063	0.036		
176 (15)	0.029				0.071	0.042	0.081		0.037	**0.104**	0.018		
178 (16)			0.036		**0.161**	0.083	0.065			0.021	0.089		
180 (17)			0.018		0.036				0.074	0.063			
182 (18)					0.071		0.048		0.056	0.063	0.036		
184 (19)	0.088		0.036		0.036		0.032		0.037	0.021			

Population **Allele** ***Oed. U2***	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
186 (20)	0.074		0.054		0.036	**0.146**	**0.113**		0.056	0.021	0.054		
188 (21)			0.054		0.054		0.016			0.042	0.036		
190 (22)	0.059		0.054		0.054		0.048		0.019	0.021			
192 (23)	**0.147**				0.054		0.032		0.074	0.083	0.018		
194 (24)	0.029				0.018	0.042	0.016						
196 (25)						0.021	0.016		0.019		0.036		
198 (26)	0.029				0.036	0.021	0.032						
200 (27)									0.019		0.018		
202 (28)			0.018		0.018	0.021	0.016						
208 (29)						0.021							
226 (30)										0.021			

Population **Allele** **Oe 1/63**	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
90 (1)						0.081							
92 (2)									0.011				
94 (3)						0.032	**0.141**		0.054		0.043		
96 (4)				**0.750**	0.052	0.032	0.094			0.013	0.043	**0.375**	**0.333**
98 (5)		0.063	**0.125**		**0.155**		**0.266**			0.040	0.029		
100 (6)	**0.265**	**0.125**	**0.146**	**0.125**	0.086	**0.129**	**0.109**		0.065	**0.145**	0.043	**0.188**	0.083
102 (7)	**0.235**	0.063	**0.125**	0.063	**0.121**	0.065	**0.188**		0.033	**0.250**	0.071		0.083
104 (8)	**0.162**	**0.219**	0.063		**0.172**	**0.242**	0.016		**0.359**	**0.184**	**0.100**	**0.250**	0.083
106 (9)	**0.132**	0.094	0.083	0.063	**0.172**	**0.145**			**0.109**	**0.184**	**0.300**	0.063	0.083
108 (10)	**0.147**	**0.219**	0.063		**0.172**	**0.210**	**0.125**		**0.217**	0.092	**0.229**		**0.333**
110 (11)	0.059	**0.219**	**0.375**		0.035	0.048	0.031		**0.120**	0.040	**0.129**	0.063	
112 (12)			0.021		0.035				0.022	0.053	0.014	0.063	
114 (13)						0.016	0.031		0.011				

Population Allele Oe 1/64	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
130 (1)											0.040		
132 (2)											0.020		
134 (3)											0.040		
136 (4)					0.042	0.022							
138 (5)											0.080		
140 (6)						0.022					0.080		
142 (7)											0.040		
144 (8)	0.059				0.021	0.022			0.036				
146 (9)	**0.221**		**0.136**		**0.125**	**0.130**	**0.107**		**0.196**		0.040		
148 (10)	**0.118**		**0.159**		**0.229**	**0.174**	**0.179**		**0.143**	**0.104**	0.060		
150 (11)	0.044					**0.109**				**0.271**	0.040		
152 (12)	0.088				**0.188**	0.022			0.071	0.021	0.020		
154 (13)	0.059				**0.375**	**0.326**	**0.393**		**0.554**		**0.220**		
156 (14)	**0.103**		**0.300**			**0.109**	**0.321**			**0.313**	**0.300**		
158 (15)	0.015		**0.364**		0.021	0.022				**0.104**	0.020		
160 (16)	**0.265**		0.023			0.022				**0.188**			
162 (17)	0.015					0.022							
164 (18)	0.015												
174 (19)			0.023										

Population Allele Oe 2/72	**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**
300 (1)							0.036			0.022	0.080		
302 (2)											0.020		
304 (3)					**0.105**		0.036		0.056		0.080		
306 (4)	**0.833**		**0.833**		**0.579**		**0.643**		**0.630**	**0.630**	**0.500**		
308 (5)	**0.152**		**0.167**		**0.316**		**0.286**		**0.315**	**0.348**	**0.320**		
310 (6)	0.015												

Table 6.4 Number of individuals scored (N), number of alleles (Na), heterozygosity expected (He), heterozygosity observed (Ho) and probability (P) of Hardy Weinberg Equilibrium at six microsatellite loci in 13 populations of O. edulis. *For population abbreviations see Figure 6.2.*

Population Locus		**NOR**	**LER**	**KOT**	**SKY**	**LAI**	**SOU**	**NEU**	**LNK**	**LSW**	**WLT**	**LRY**	**NET**	**BRI**	**Mean**
J12	N	32	8	26	9	35	20	44	24	42	32	34	10	17	25.6
Na		14	9	17	10	24	12	25	18	21	19	17	11	13	16.2
He		0.854	0.908	0.923	0.909	0.948	0.889	0.948	0.936	0.920	0.915	0.938	0.936	0.918	0.919
Ho		0.594	0.875	0.808	0.889	0.771	0.600	0.705	0.792	0.762	0.656	0.765	0.700	0.765	0.745
P		**<0.001**	0.768	0.035	0.805	**<0.001**	**<0.001**	**<0.001**	0.011	0.001	0.002	**<0.001**	0.006	0.618	
T5	N	34	17	28	11	38	44	45	35	44	42	41	19	15	31.8
Na		11	8	14	9	15	18	17	20	19	15	20	16	16	15.2
He		0.842	0.822	0.879	0.861	0.819	0.805	0.902	0.913	0.862	0.851	0.887	0.945	0.924	0.870
Ho		0.618	0.706	0.821	1.000	0.553	0.705	0.733	0.800	0.750	0.810	0.781	0.947	0.867	0.776
P		0.003	0.158	0.252	0.642	**<0.001**	0.055	**<0.001**	0.008	0.231	0.604	0.416	0.009	0.618	
U2	N	34	0	28	0	28	24	31	0	27	24	28	0	0	31.5
Na		15	-	18	-	20	18	22	-	18	19	20	-	-	18.8
He		0.896	-	0.936	-	0.947	0.908	0.954	-	0.942	0.944	0.949	-	-	0.935
Ho		0.912	-	0.750	-	0.893	0.958	0.871	-	0.889	0.875	0.786	-	-	0.867
P		0.438	-	0.001	-	0.082	0.020	0.349	-	0.133	0.111	0.005	-	-	
1/63	N	34	16	24	8	29	31	32	0	46	38	35	8	6	25.6
Na		6	7	8	4	9	10	9	-	10	9	10	6	6	7.8
He		0.818	0.851	0.809	0.442	0.875	0.858	0.849	-	0.798	0.845	0.832	0.800	0.818	0.806
Ho		0.706	0.750	0.250	0.250	0.655	0.613	0.625	-	0.783	0.711	0.571	0.750	0.833	0.625
P		0.116	0.151	**<0.001**	0.145	0.004	**<0.001**	**<0.001**	-	0.044	0.017	0.008	0.725	1.000	
1/64	N	34	0	22	0	24	23	14	0	28	24	25	0	0	24.3
Na		11	-	6	-	7	12	4	-	5	6	13	-	-	8.0
He		0.821	-	0.753	-	0.769	0.838	0.725	-	0.640	0.788	0.853	-	-	0.773
Ho		0.882	-	0.636	-	0.583	0.652	0.286	-	0.714	0.667	0.680	-	-	0.638
P		**<0.001**	-	0.194	-	0.097	0.015	**<0.001**	-	0.016	0.355	0.004	-	-	

Population Locus		NOR	LER	KOT	SKY	LAI	SOU	NEU	LNK	LSW	WLT	LRY	NET	BRI	Mean
2/72	N	33	0	24	0	19	0	14	0	27	23	25	0	0	23.6
Na		3	-	2	-	3	-	4	-	3	3	5	-	-	3.3
He		0.287	-	0.284	-	0.569	-	0.521	-	0.511	0.492	0.647	-	-	0.472
Ho		0.333	-	0.333	-	0.632	-	0.429	-	0.407	0.478	0.800	-	-	0.487
P		1.000	-	1.000	-	0.751	-	0.222	-	0.477	1.000	0.727	-	-	
Mean N		33.5	13.6	25.3	9.3	28.8	28.4	30	29.5	35.7	30.5	31.3	12.3	12.7	
Mean Na		10.0	8.0	10.8	7.7	13.0	14.0	13.5	19.0	12.7	11.8	14.2	11.0	11.7	
Mean He		0.758	0.860	0.764	0.737	0.821	0.860	0.816	0.925	0.779	0.806	0.851	0.894	0.887	
Mean Ho		0.674	0.777	0.600	0.713	0.681	0.706	0.608	0.796	0.718	0.699	0.730	0.799	0.822	

Table 6.5 Pairwise comparisons of genetic differences between populations of O. edulis *using Nei's (1978) unbiased genetic distance (D) based on up to six loci over 13 populations. For population abbreviations see Figure 6.2.*

Population	NOR	LER	KOT	SKY	LAI	SOU	NEU	LNK	LSW	WLT	LRY	NET
LER	0.7578											
KOT	0.2756	0.6153										
SKY	1.2307	1.8714	0.5857									
LAI	0.3391	0.4010	0.1998	0.7538								
SOU	0.8072	0.5445	0.2396	0.8371	0.3022							
NEU	0.3347	0.8614	0.0603	0.7169	0.1239	0.3295						
LNK	1.0688	0.8587	0.2259	0.2242	0.5730	0.2027	0.2495					
LSW	0.3880	0.2760	0.2103	1.2189	0.0627	0.3050	0.1874	0.5943				
WLT	0.2667	0.7561	0.2399	0.8361	0.2953	0.4057	0.2337	0.3291	0.3841			
LRY	0.3906	0.2546	0.1417	0.9070	0.1192	0.3297	0.1640	0.3949	0.1806	0.2162		
NET	0.7925	0.8674	0.6401	0.2146	0.6775	0.6460	0.7368	0.3242	0.6088	0.6019	0.7115	
BRI	0.4004	0.6366	0.2825	0.3323	0.4985	0.5331	0.6135	0.5286	0.6531	0.7483	0.3522	0.1992

A second pairwise comparison (Figure 6.4) was made between eight populations for which there are data at all six loci (or five loci — Sound of Ulva). As in Figure 6.2, the Norway sample is clearly different from all others. Of the Scottish samples, Loch Ryan, Loch Sween and Loch Ailort group together as they did in the three-locus analysis and Kyle of Tongue and North East Ulva oysters cluster together. West Loch Tarbert oysters appear relatively different from other Scottish populations.

No populations of oysters showed any evidence of a recent bottleneck based on Cornuet & Luikart's (1996) method. A Mantel test for correlation between Nei's (1978) unbiased genetic distance and geographic distance between populations was not significant ($r = 0.1579$, $P > 0.05$).

Figure 6.3 Dendrogram of genetic relatedness (Nei's (1978) Genetic Distance, D) between populations of O. edulis *based on data at three microsatellite loci. Numbers at nodes are proportions of permuted data sets that support the node.*

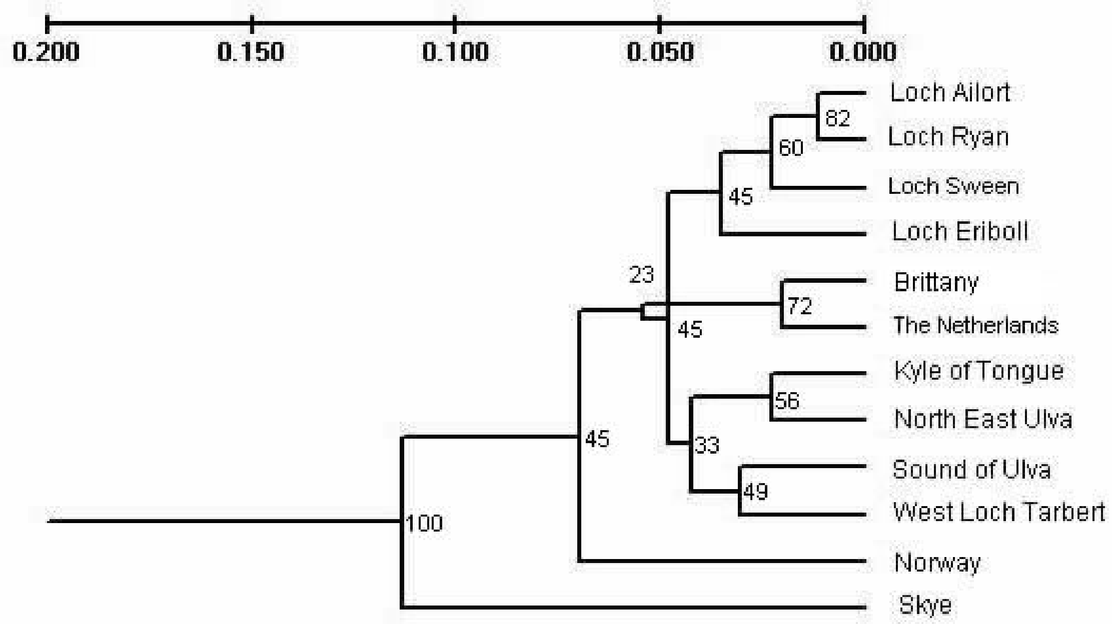
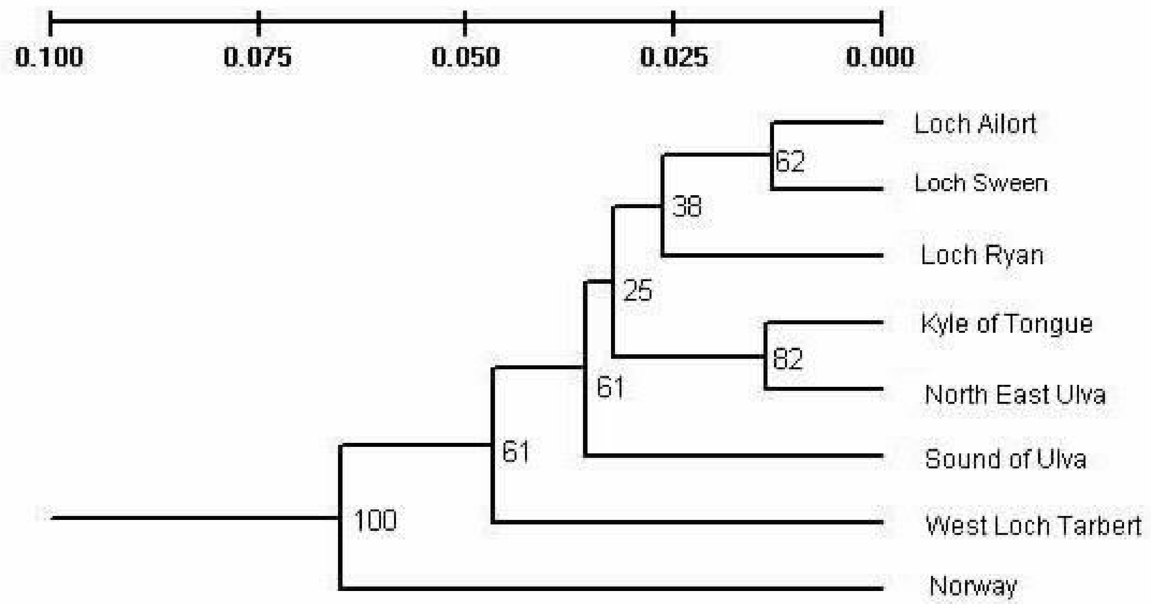


Figure 6.4 Dendrogram of genetic relatedness (Nei's (1978) Genetic Distance, D) between populations of O. edulis *based on data at six microsatellite loci (five for SOU). Numbers at nodes are proportions of permuted data sets that support the node.*



6.4 Discussion

The failure to achieve a full data set of genotypes at six loci for all the 13 populations sampled was disappointing. There can be several reasons for failure to score genotypes at microsatellite loci reliably and these include variable quality of extracted DNA, contaminant-inhibition of PCR, difficulty in identification of bands due to “stutter” and the existence of homozygotes for null alleles. It is probable that all four reasons have contributed to the reduced data set in this instance. In addition, for some populations only a few individuals were sampled.

For populations where all six loci were scored, mean numbers of alleles per locus ranged from 10.0 to 13.5, which is less than the mean value reported by Launey *et al*. (2002) but within the range previously reported by Sobolewska & Beaumont (2005) for four different microsatellite loci in northern European populations. At highly polymorphic loci, the number of alleles identified is very dependent upon the sample size and in some cases the sample sizes in this study are really quite small. Truébano García (2004) has demonstrated a strong correlation between the number of alleles detected and sample size in a portion of this data set ($r = 0.733$, $P<0.001$). As in other studies of highly polymorphic microsatellites, mean expected heterozygosity is high at most loci (ranging from 0.773 to 0.919). The exception is locus Oe2/72 where there are only three common alleles and mean expected heterozygosity is 0.472.

The general deficiency of heterozygotes relative to the Hardy-Weinberg model has been a very common finding in allozyme studies of marine bivalves (Zouros & Foltz, 1984; Gaffney, 1994). The same pattern seems to be emerging at microsatellite loci in oysters: Launey *et al*. (2002) and Sobolewska & Beaumont (2005) both report significant deficiencies of heterozygotes at microsatellite loci.

It is very unlikely that the significant heterozygote deficiencies in this data set are caused by some systematic factor such as inbreeding, because there is no consistent pattern at particular loci or in particular populations (Table 6.3). Significant deficiencies occur at all loci except Oe2/72, and are not restricted to particular populations. Also the Wahlund effect, the accidental sampling of cryptic population substructure within populations, is ruled out because of the general lack of allele frequency differences between populations.

Although microsatellite loci are generally expected to be neutral, some evidence that indirect selection, where the microsatellite locus is linked to a coding locus, has been detected in oysters by Boudry *et al*. (2002). This could be the cause of some of the heterozygote deficiencies, but by far the most likely cause is the presence of null alleles (alleles that fail to be visualised under the analytic conditions). Null homozygotes do not score on gels and null heterozygotes are scored incorrectly as homozygotes leading to a deficiency of heterozygotes. In hatchery crosses, null alleles have sometimes been detected at allozyme loci (Gaffney, 1994, Hoare & Beaumont, 1995) but null alleles are far more common at microsatellite loci (McGoldrick *et al*., 2000; Boudry *et al*. 2002).

The analysis of population genetic differentiation identifies the Skye sample as being rather different to all others and the Norway sample as being different to all except the Skye population. This result in relation to the Norway sample agrees with the findings of Launey *et al*. (2002) and Sobolewska & Beaumont (2005) who also found Norwegian populations of *O. edulis* to be distinct from other European populations. This current study used some of the loci of Launey *et al*. (2002), but none of those developed by Sobolewska *et al*. (2001) and used by Sobolewska & Beaumont (2005). Confirmation of a pattern identified by variation at a number of different microsatellite loci by different authors strengthens the conclusion that Norwegian *O. edulis* may represent a genetic resource that has not been significantly affected by human activity. Conservation of Norwegian oysters as a separate population is therefore of importance and importations of oysters from elsewhere should be strictly controlled.

The small sample size of the Skye population gives rise to concern over the significance of its genetic distinctiveness. Only 11 individuals were available for genotyping, and some of these failed to amplify at all loci. How important is the sample size? Of the three loci scored, only one (Oe1/63) shows a large difference in allele frequency from other samples. The Oe1/63 [96] allele is at high frequency (0.750) in Skye, but absent from, or rare in all other Scottish populations (highest frequency 0.094 in North East Ulva). In order for Skye to group among the other populations in its region, it should have a similar frequency of allele Oe1/63 [96]. If the *true* frequency of this allele in the Skye population is around 0.09 we can ask what is the probability, in a sample of eight oysters, of sampling by chance, individuals that give a frequency of 0.75 for this allele? Simple probability calculations provide a probability of much less than 0.001 for this event. Sample size needs to be down as low as 3–5 individuals before this becomes a likely event. It is therefore unlikely that the distinctness of Skye sample is simply a sampling effect.

Although the Oe1/63 [96] allele is rare or absent in Scottish populations (other than Skye) it is relatively common in the southern samples from the Netherlands (0.375) and Brittany (0.333). In the 1950s unknown quantities of 2–3 year old Brittany oysters were imported to various sites in Scotland including Skye (Millar, 1961). It is possible that the high frequency of the Oe1/63 [96] allele in the Skye population is the result of a founder effect from this stocking event. If this is a real founder effect, it is important to consider why we do not see evidence of founder effects at other Scottish sites that were stocked in similar way. This could indicate that gene flow between Skye and other Scottish populations is less frequent than gene flow within these other Scottish populations. Therefore, even though Skye may currently be different due to importation, it could have been different before importation due to relatively restricted gene flow.

Considering the Skye data at other loci, Norway has allele *Oed*.J12 [248] at high frequency (0.281) but this is rare (<0.08) or absent at all other sites except Skye where its frequency is 0.111. At the *Oed*.T5 locus, Skye shares its three most common alleles *Oed*.T5[106], *Oed*.T5[118] and *Oed*.T5[134] with many other Scottish populations, but these alleles are rare or absent in the Brittany sample. This is not what would be expected if there had been a founder effect. Because of the small sample size of the Skye population, it is not possible to decide with certainty what may have been the cause of the apparently distinct genetic nature of the sample analysed. However, there are some intriguing possibilities and further work is required to elucidate the true genetic relatedness of the Skye population to others in the region.

There is suggestion of a further subdivision of populations within the Scottish samples (excluding Skye), in which Loch Ryan, Loch Ailort, Loch Sween and Loch Eriboll cluster together distinct from the Ulva populations, Kyle of Tongue and West Loch Tarbert (Figure 6.3). This grouping is partially, but less clearly, supported by the six loci data set (Figure 6.4). Because of the relatively weak bootstrap support for this node in both dendrograms it is probably not safe to treat these as significant groupings. Nevertheless, it is important to note that these suggested groupings have no obvious link to their geographical position – Loch Eriboll (the most northerly Scottish population) groups with Loch Ryan (the most southerly one) and oysters from the Kyle of Tongue, close to Loch Eriboll and probably derived from Eriboll oysters via a hatchery in Orkney, cluster in the other group.

Cornuet & Luikart (1996) developed the idea that following a severe reduction in population size (a “bottleneck”) the equilibrium between the number of alleles and heterozygosity at a locus is disturbed. A slight excess of heterozygosity over that predicted by the Hardy-

Weinberg model is expected for several generations following a bottleneck. They developed a computer programme (BOTTLENECK) to test for this discrepancy and it has become a recognised test for genetic data. However, in the case of bivalves, where *deficiencies* of heterozygotes are a common feature of genetic data, the test is unable to identify *excess* heterozygosity effectively. Although significant bottlenecks were not detected in our data, it is possible that the populations could have suffered bottlenecks. Whether or not there have been significant bottlenecks at any time in the populations that were sampled in this study, it is instructive to note that the general level of genetic variation is high. As with microsatellite loci in other organisms (Sunnucks, 2000), many variant alleles are present and heterozygosity is high at the loci tested. This would not support the idea of significant population size reductions having taken place in the recent past.

If there has been little influence of human intervention on population structure in *O. edulis*, we would expect to find that pair-wise genetic distances correlate to some extent with geographic distances between pairs of populations. The result of a Mantel test of this correlation is not significant ($P>0.05$) and this supports the contention that human activities have been sufficiently strong over recent centuries to override any random genetic drift that could establish and maintain natural population differentiation. However, the simplistic measure of geographic distance used in the test does not take into account the potential oceanographic factors that could restrict or enhance larval travel between any two points or populations. Thus the Mantel test result should be taken with caution.

7 REVIEW OF FISHERIES AND CONSERVATION MANAGEMENT MEASURES

7.1 Introduction

7.1.1 Invertebrate fisheries

Coastal, shallow-water fisheries for marine invertebrates have been exploited worldwide to the extent that many wild stocks are now considered to be over-exploited (Thorpe *et al*., 2000) or endangered (Tegner, 1996; Hobday *et al*., 2001). Poor understanding of the biology of the exploited species (Ludwig *et al*., 1993; Castilla & Fernàndez, 1998; Hobday *et al*., 2001) and a reliance on management practices that do not incorporate important ecological factors (Castilla & Fernàndez, 1998) have been suggested as reasons for such over-exploitation. Other factors include unlimited exploitation driven by the prospect of wealth and the large variation in natural variability that masks the effects of overexploitation (Ludwig *et al*., 1993). Widely-used management measures (so-called “technical measures”) aimed at regulating stock exploitation, such as minimum landing sizes, gear restrictions and closed seasons, have not been effective in many fisheries (Harrison, 1986; Friere *et al*., 2002). With the emphasis of management on the conservation of stocks, protection of the environment and the development of sustainable fisheries, it is important to evaluate and identify effective management strategies for specific stocks. Management measures such as protected areas and stock enhancement, which have been used effectively in several coastal fisheries, are becoming more popular for invertebrate fisheries as “alternative” management measures. This review aims to analyse the range of management measures available for invertebrate fisheries and their use in conservation and fisheries management. Specifically, the use of the management measures for conserving and managing isolated wild stocks of the commercially valuable bivalve *Ostrea edulis* in Scotland will be discussed.

7.1.2 The conservation and fisheries importance of Ostrea edulis

Three factors work simultaneously to determine the abundance of natural populations: demographic variation, environmental variation and genetic factors (Primack, 1998). Natural levels of demographic variation can lead to population size becoming small, leaving the population vulnerable to further reduction through environmental variation and genetic factors, thus increasing the chance of extinction (Primack, 1998). Fishing increases mortality rates, decreasing stock density and abundance, potentially altering the sex ratio and changing the size of age at maturity (Botsford *et al*., 1997; Policansky & Magnuson, 1998; Nielson & Kenchington, 2001). Such impacts on the demography of populations play an important role in the sustainability of exploited stocks.

Historically, the high value of *O. edulis* has led to over-exploitation of wild stocks, causing the extirpation of many wild populations and the contraction of the geographical range (Korringa, 1946; Anon., 1999). Wild populations of *O. edulis* have also been subject to high levels of unlawful exploitation for decades (see sections 2.4 & 2.5). In Scotland, unlawful gathering of oysters is one of the most important current issues affecting the survival of the remaining populations. Fisheries-associated activity based on *O. edulis* is currently limited to the Loch Ryan population, which is exploited on a commercial scale, and populations in Argyll and the Highlands, which are exploited on a small-scale basis for hatchery-based supportive breeding programmes.

Proposals for the cultivation and exploitation of wild populations of *O. edulis* around Scotland are becoming more frequent (see section 3.6). Although fisheries management may have a variety of socio-economic objectives, it is necessary that exploitation is managed in such a way that stock security and future production are not jeopardised. UK policy drivers, such as the Sustainable Development Strategy (DEFRA, 2005) and the Marine Stewardship Report (DEFRA, 2002), advocate sustainable development and the regulation of exploited marine stocks and ecosystems. However, an alternative to the development of oyster stocks for fisheries purposes is the option of conservation management. The aims of conservation management are to determine the main threats to the species and associated ecosystem and develop practical approaches to prevent declines in populations and prevent degradation of habitat. Both of these approaches can be used to form a national plan for the management of *O. edulis* stocks around Scotland.

7.1.3 Current fisheries management measures

Many sea-fisheries are based on species that are highly fecund, have a larval dispersal phase and have stocks covering wide geographic ranges (Jamieson, 1993, cited in Peterson, 2002; Hobday *et al*., 2001; Nielsen & Kenchington, 2001). These factors have been mistaken as characteristics that ensure the persistence of a species even in the event of high exploitation pressure (Tegner, 1996). For instance, in the 19th century, the Sea Fisheries Committee, which was established to review the state of British marine fisheries, interpreted these biological characteristics as those of species that should be resilient to exploitation (Caird *et al*., 1891). The Committee recognised that *O. edulis* stocks in Britain, although characterised by these biological traits, had been declining for several years. However, they attributed stock declines to spat failures, variable recruitment and high mortality levels in early life-history stages (Anon., 1868; Caird *et al*., 1891). The Committee did not recognise that fishing could be compounding these biological issues, stating "that this decrease has not arisen from overfishing, nor from any causes over which man has direct control". The management measures in operation at the end of the 19th century included fishing rights, a minimum landing size and a closed season that covered the spawning period. These measures were not adequately enforced (see section 2.4) and high levels of exploitation resulted in the collapse of the commercially exploited *O. edulis* stocks throughout Scotland during the early 20th century. These management measures are still applicable to commercial *O. edulis* fisheries.

7.2 Management measures

7.2.1 Minimum landing sizes

A minimum landing size (MLS) is one of the most common technical measures in invertebrate fisheries (Jamieson, 1993, cited in Peterson, 2002), and is intended to allow a species to mature sexually and reproduce a number of times prior to being harvested (Tegner, 1989; Hobday *et al*., 2001). The efficacy of this control has come under scrutiny. For example, Berg & Olsen (1989) reviewed the *Strombus gigas* fishery in the Caribbean and estimated that up to 94% of the stock might be fished before reaching reproductive age. Furthermore, Hobday *et al*. (2001) suggested that for irregularly recruiting species, an individual may not successfully reproduce in the period between age at sexual maturity and age at harvest set by the MLS. This could occur because the MLS was less than the length at which the species became sexually mature. The minimum landing size for *O. edulis* in England and Wales is 63 mm (Anon., 1868; Caird *et al*., 1891; Bannister, 1986), which generally corresponds to an age of approximately five to six years in British waters

(Drinkwater & Howell, 1985). The size limit should therefore potentially allow individuals to reproduce for a period of two to three years. As the market preference is for oysters of the MLS, individuals from stocks exploited for commercial purposes will rarely reach the size at which they achieve maximum reproductive output (99 mm) (Bannister, 1986). This suggests that exploitation using the current MLS could result in depressed levels of recruitment for exploited stocks and could potentially lead to recruitment over-fishing. One technique for overcoming this would be to increase the size limit, although this could have an economic impact on the fishery at least in the short term (Rothschild *et al*., 1994).

7.2.2 Legal rights

Legal rights are a spatial management measure that should, theoretically, control levels of exploitation through the ownership of harvesting rights and therefore exclusive access to stocks (Galstoff *et al*., 1930; Kennedy, 1989; Castilla & Fernandez, 1998; Orensanz & Jamieson, 1998; Whitmarsh, 1998). There are various forms of legal rights influencing the exploitation of oyster stocks in Scotland. The common law right to gather wild *O. edulis* belongs to the Crown, except in places where the right has been granted to individuals or corporations (and possibly transferred subsequently), or acquired by prescriptive possession (Appendix 1). A right to fish for oysters may be acquired by permit or lease from the fishery owner. Several and Regulating Orders can also be granted under the Sea Fisheries (Shellfish) Act 1967 for specific periods to persons intending to develop a fishery or fisheries for certain named shellfish species. Several and Regulating Orders grant certain rights in relation to named shellfish species within a designated area for a period of up to 60 years, but usually for shorter periods. Several Orders grant the exclusive right of fishing, dredging, cultivating, depositing and taking the named shellfish species within a designated area, subject to any stipulated restrictions or exceptions, usually for a period of five to ten years. Several Orders also restrict all other fishing activities within the limits of the shellfish fishery, except for those using hook-and-line or pelagic nets. In 2000, the 1967 Act was amended to permit additional fishing implements within the designated area if they do not disturb or injure the shellfish and are specified in the Several Order (Sea Fisheries (Shellfish) Amendment (Scotland) Act 2000).

Regulating Orders confer powers to regulate a fishery, for example by imposing regulations or restrictions, levying tolls or issuing licences to fish for named species. A right to fish for oysters may therefore be acquired through a licence issued under an appropriate Regulating Order. Regulating Orders are generally granted for periods of 20–30 years. Although the grantee has powers to regulate fishing within the designated area, they do not hold the property rights to the named species and therefore lack the legal protection afforded by Several Orders. Furthermore, regulations and restrictions need ministerial approval, which, if granted, is normally given at the time of the Order.

Taking or dredging for oysters without permission from a private bed or a bed subject to an order is likely to constitute criminal offence under the Oyster Fisheries (Scotland) Act 1840 or the Sea Fisheries (Shellfish) Act 1967, or both. Any criminal damage or injury caused to the fishery may also be prosecuted under the Criminal Damage Act 1971 or the Theft Act 1968 (although in some circumstances there may be uncertainty in law about the ownership of wild oysters prior to them being gathered; see Appendix 1).

On the whole, oyster stocks in Scotland are small and often located in geographically separated loch systems (Millar, 1961). Cultivation and exploitation of wild stock is currently practised by individual private enterprises with Loch Ryan containing the largest exploited *O. edulis* stock, which covers an area of approximately 15 km^2. The legal right to fish *O. edulis* in England is more complex, partly owing to the different legal position (there is no patrimonial right to gather oysters belonging to the Crown), the geographical coverage of populations and the number of stakeholders involved with their exploitation within individual areas. For example, the Solent oyster fishery which covers 104 km^2 (Gardner & Elliot, 2001) is characterised by a patchwork of fishing rights including three Several Orders, a regulated fishery and areas of public fishery (Guillotreau & Cunningham, 1994). The Southern Sea Fisheries Committee is responsible for the overall management of the Solent fisheries, but separate management committees are responsible for fishery regulation measures under the different rights (Guillotreau & Cunningham, 1994; Gardner & Elliot, 2001). Guillotreau & Cunningham (1994) conducted a survey of the Solent oyster fishermen and found evidence that catch per unit effort (CPUE) was better in the Several Order fisheries, where access is most limited. However, confidentiality issues associated with the Several Order fisheries meant that CPUE and stock abundance data could not be evaluated, therefore, the conclusion of limited access resulting in increased catches was a tentative one. Since the survey, the spread of the parasite *Bonamia ostreae* has caused mass-mortality of the stocks throughout the Solent (Laing *et al*., 2005).

Although the Solent covers a large area within which separate committees regulate different areas, unlawful exploitation is still a serious problem affecting the stocks. Guillotreau & Cunningham (1994) reported the closure of two Several Order fisheries owing to high levels of unlawful exploitation. Furthermore, policing of the Calshot Oyster Fishery was discontinued because the costs of unlawful exploitation were greater than the benefits of employing a warden. Unlawful exploitation has been a major factor causing the depletion of stocks within privatised areas (Guillotreau & Cunningham, 1994; Anon., 1997).

Oyster stocks are also susceptible to over-exploitation through the use of unsuitable regulation measures. For example, historical evidence shows that the combination of high levels of exploitation combined with unlawful exploitation caused the collapse of oyster stocks in Scotland (see section 2.8). Oyster stocks in other countries, such as the American oyster (*Crassostrea virginica*) fishery of Chesapeake Bay, United States of America, have also reported fisheries collapse or depletion resulting from over-exploitation (Kennedy, 1989; Rothschild *et al*., 1994). Although similar technical measures have been used throughout invertebrate fisheries, the perspective of management needs to encompass the individual characteristics of exploited populations and the environment in which they are found. Population assessments are useful in determining these characteristics and the effects of management measures, and can be used to evaluate and adapt management strategies when necessary.

Bannister (1986) stated that population surveys were more useful for advising oyster fisheries for short-term management than fisheries models, because of the high natural mortality and irregular recruitment of populations. The use of population surveys however, is not widespread in Scotland. The application for Several and Regulating Orders requires a population survey of the stocks the applicant wishes to exploit, with applications considered on a site-by-site basis. However, legislation does not stipulate that further population surveys are required for ensuring the maintenance of stocks, although they could be made a condition of the Order. Without this information, it is impossible to determine the success of management measures with respect to the sustainability of stocks.

7.2.3 Temporal fisheries closures

Temporal fisheries closures can have various purposes. For example, closures of fisheries during specific times of the year are used to protect stocks during a critical period, such as the reproductive season. More frequent, e.g. weekly, closures can be used to restrict fishing effort. Total bans on fisheries exploitation can be applied for indefinite periods of time to allow for stock regeneration. These types of closure rely on natural productivity to increase stock abundance but their efficacy relies on making certain assumptions: there is sufficient broodstock, there is sufficient suitable habitat available for settlement and the population is not subject to unlawful exploitation, disease, adverse environmental affects or high levels of predation. Closure to fishing during the reproductive season is beneficial for marine invertebrates because the abundance and density of the breeding aggregation is maintained (Caddy, 1989; Aiken *et al*., 1999; Peterson, 2002). However, the use of seasonal closures makes further assumptions that are also applicable to long-term closures. Allee effects (see section 5.1) are only prevented if the size and density of the breeding aggregation is sufficient to sustain the population prior to closure (Peterson, 2002). Furthermore, stocks will only benefit if the populations under protection act as a source of larvae and favourable hydrodynamics ensure self-sustainability of populations through the retention of larvae (Jennings, 2001). For example, larvae of abalone species are thought to exhibit localised settlement, suggesting that migration of larvae to isolated populations is unlikely (Tegner, 1993). These factors will be discussed more fully in subsequent sections.

Both types of fisheries closure have been used in the management of *O. edulis* stocks in Scotland. Seasonal closures in marine invertebrate fisheries generally have been uncommon until recent decades, whereas wild *O. edulis* fisheries in the UK have been subject to a closed season to protect the spawning stock for over 100 years. The national closed season currently extends from 14 May until 4 August (Anon., 1999). However, as with other marine invertebrate fisheries, total bans on exploitation have been imposed after stocks have collapsed following unsustainable levels of exploitation. In 1954, the Loch Ryan oyster fishery was closed after it became economically unviable (Millar, 1961; Hugh-Jones, 2003). Millar (1968) surveyed Loch Ryan in 1957 and found that only 3% of the remaining stock was of large size, i.e. made up of individuals greater than 60 g. After 5 years without exploitation, this figure had increased to approximately 50%, with a further increase of 14% by 1967. Millar concluded that these changes resulted from a release from fishing pressure

Natural regeneration does not always follow a fishery closure. *O. edulis* stocks in the Firth of Forth on the east coast of Scotland continued to decline even after the fishery was closed in the early 1920s. Studies of recruitment to stocks of *O. edulis* in Denmark concluded that populations required many years of high recruitment for stock regeneration (Spärk, 1951). *Mercenaria mercenaria* (hard clam) stocks in North Carolina, which were considered severely depleted, showed no evidence for effective compensatory recruitment during a 20-year closure of the fishery (Peterson, 2002). The density of *Strombus gigas* populations in Florida remained below the critical densities required for mating after an 8-year fishery closure (Berg *et al*., 1992, cited in Stoner & Ray-Culp, 2000). Several authors have suggested that in most cases, shellfish stocks may need some form of stock enhancement in order to ensure successful recruitment, especially in the case of species with irregular recruitment (Goldberg *et al.,* 2000; Stoner & Ray-Culp, 2000; Beale & Gayle Kraus, 2002; Peterson, 2002). It should be noted that hydrodynamics also play an important role in the potential regeneration of stocks that have a larval dispersal stage. For instance, Loch Ryan is considered to be a self-contained population (Millar, 1968). Therefore, larval retention in this area could have played a key part in the success of the natural regeneration of these stocks.

7.2.4 Marine Protected Areas

Marine protected areas (MPAs) provide a spatial form of stock protection (Caddy, 1989; Botsford *et al.,* 1997; Done & Reichelt, 1998; Lauck *et al.,* 1998; Edgar & Barrett, 1999; Aiken *et al.,* 1999; Sumaila *et al*., 2000; Jennings, 2001; Manríquez & Castilla, 2001). MPAs were defined by the World Conservation Union as “any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (cited in Allison *et al.,* 1998). MPAs have become a popular management tool, since they are seen as a precautionary approach to marine management (Lauck *et al*., 1998). However, like temporal fisheries closures, MPAs are often established after the effects of fishing have been recognised (Wallace, 1999).

By controlling or prohibiting fishing effort, MPAs can fulfil a range of potential functions (Botsford *et al*., 1997; Stoner & Ray, 1996; Allison *et al.,* 1998; Lauck *et al.,* 1998; Sumaila *et al*., 2000), although few of the potential benefits have been supported by empirical evidence (Stoner & Ray, 1996; Edgar & Barrett, 1999). However, research has shown MPAs to be of value in protecting and conserving invertebrate stocks. For example, release from fishing pressure associated with MPA establishment was found to increase the abundance, biomass and density of spawning aggregations of the muricid gastropod *Concholepas concholepas* (Chilean loco) within MPAs (Manríquez & Castilla, 2001). The population size-structure of protected *Haliotis* spp. shifted towards larger individuals within a Tasmanian reserve (Edgar & Barrett, 1999). Although the benefits of MPAs have been shown for stocks within the protected areas, there is little evidence of beneficial effects on adjacent exploited populations (Manríquez & Castilla, 2001). Surveys of *S. gigas* in the Exuma Cays, Bahamas, compared larval transport to a population within a MPA with that in a fished area and showed that larval transport to the exploited population, which was located upstream of the MPA, was lower. In addition, juvenile abundance was greater in the MPA as a result of the location and protection offered (Stoner & Ray, 1996). The authors concluded that if reserves acted as sources of larvae with fished areas located in downstream "sink" areas, reserves could potentially enhance larval supply to fished areas. However, the survey also highlighted that exploitation of juveniles and young adults from fished areas before they had migrated to deep-water spawning sites was detrimental to the spawning stock of the area (Stoner & Ray, 1996). This suggests that the potential benefits of MPAs to fished areas may be limited without suitable effort controls.

For the protection of marine stocks, the design and implementation of MPAs should aim to encompass a sufficient proportion of the stocks and habitat required by these stocks, so that the MPA is self-replenishing (Stoner & Ray, 1996). MPAs can act as a source of recruits to other populations, providing protection from the effects of over-exploitation (Allison *et al*., 1998; Lauck *et al*., 1998). In order to determine if a protected stock is self-replenishing, the factors affecting successful recruitment such as Allee effects (see section 5.1), the effective population size, larval dynamics and the effects of density dependence on growth, survival and fecundity should be known (Jennings, 2001; Sale *et al*, 2005).

Genetic studies investigating the level of genetic differentiation between stocks are necessary, providing information for the decision of which stocks should be protected. Maintaining high levels of genetic variation within managed populations is important for their adaptive potential to respond to environmental changes (see section 6.1). High levels of genetic variation in donor stocks also increase the likelihood of success if stock enhancement is used as a management measure to restore degraded populations (Hindar *et al*., 1991; Ryman, 1991; Ryman & Laikre, 1991). Combined larval genetics and coastal oceanography research is also necessary to determine whether stocks are connected and which stocks act as sources or sinks (Tegner, 1993; Allison *et al.,* 1998; Jennings, 2001; Manríquez & Castilla, 2001). A network of MPAs could provide a countrywide strategy for the protection of stocks. However, to ensure the efficacy of reserves, their geographical size and number needs to be determined with relation to species movements (Allison *et al.,* 1998; Lauck *et al.,* 1998; Edgar & Barrett, 1999; Jennings, 2001). For instance, reserves of small size are thought to be sufficient for the protection of sessile or sedentary invertebrate species, but insufficient for species that can migrate outside the boundary of the MPA depending on the migration rate (Edgar & Barrett, 1999).

It is an offence to release organisms into and remove resident organisms from sites protected under U.K. legislation (Wildlife & Countryside Act 1981; Natural Heritage (Scotland) Act 1991). However, increasing abundance and biomass of protected populations increases the temptation for unlawful exploitation of stocks within marine reserves (Lauck *et al.,* 1998). Insufficient protection from unlawful exploitation led to the loss of transplanted green abalone (*Haliotis fulgens*), a species of high commercial value, from Californian MPAs (Tegner, 1993). Co-management and incentive regimes have been suggested as techniques for combating unlawful exploitation and ensuring high levels of public support (Allison *et al*., 1998; Sumaila *et al*., 2000).

Community and ecosystem benefits are also gained in addition to the protection of the stocks within MPAs. Recovery of stocks involves complex interactions between the target stock, the protected community and the environment. Restoration of *Crassostrea virginica* reefs in Chesapeake Bay led to ecosystem benefits directly resulting from the filtering activity of the oysters, leading to improved water quality (Cressman *et al*., 2003). Since exploitation of target stocks may alter community and habitat structure, in addition to the demographic effect on target populations, recovery of stocks and the goals of MPAs should therefore take these effects into account (Jennings, 2001). For instance, the designation of an MPA in Chile resulted in a community structure different to that considered "normal" by the investigators (Duran & Castilla, 1989, cited in Edgar & Barrett, 1999). MPAs should therefore be viewed as an ecosystem management tool and provide an opportunity for an holistic approach to management.

7.2.5 Stock enhancement

Variations in recruitment over time influence the capacity for regeneration in depleted populations (Tegner, 1989; Goldberg *et al*., 2000). Stock enhancement has been used to supplement depleted stocks for many species of marine invertebrates including *Argopecten irradians* (bay scallops) (Peterson & Summerson, 1992; Peterson *et al*., 1996; Goldberg *et al.,* 2000), *Mercenaria mercenaria* (Kassner & Malouf, 1982), *C. virginica* (Southworth & Mann, 1998) and *O. edulis* (Yonge, 1960; Millar, 1961; Key & Davidson, 1981; Spencer, 2002). Stock enhancement involves translocating wild broodstock or juveniles, or releasing hatchery-bred stock.

Translocations have been advocated as a beneficial way to restore degraded *O. edulis* stocks in the UK (Laing *et al*., 2005) and have had a high success rate in past restoration attempts (Millar, 1968; Key & Davidson, 1981). For instance, translocation of French stock to the Solent was credited with the establishment of new populations after heavy recruitment in both the host and adjacent areas (Key & Davidson, 1981). Temporary translocations, in the form of "spawner sanctuaries" have also been proposed as a method for increasing the recruitment of stocks and maximising the effective population size of small populations (Peterson & Summerson, 1992; Peterson *et al.,* 1996; Goldberg *et al.,* 2000). Spawner sanctuaries are protected areas such as cages, in which broodstock can be aggregated for the spawning season to increase the density of conspecifics and the likelihood of successful fertilisation. Peterson & Summerson (1992) and Goldberg *et al*. (2000) have demonstrated the success of spawner sanctuaries, using non-local broodstock, to increase the abundance of *A. irradians* after high levels of exploitation caused stocks to be depleted.

Translocations have, however, led to the introduction of non-indigenous pest and disease species. The protozoans *Bonamia ostreae* and *Marteliosis refringens* have caused mass mortality of oyster stocks in Europe and Southern England (Baud *et al*., 1997; Culloty & Mulcahy, 2001; Spencer, 2002). The gut parasite *Mytilicola intestinalis* has been recorded in oysters in Loch Ryan (Mason & Fraser, 1986). Although this parasite was not found in recent investigations of the stocks (Pendrey, 2004) and is not lethal to the oyster host, the effects of *M. intestinalis* could be detrimental to other shellfish species (Hepper, 1956; Theisen, 1987; Utting & Spencer, 1992). In order to prevent the spread of disease, movement of shellfish throughout Europe and non-European countries is controlled within approved disease-free zones. Movements need to be notified to the fisheries department 24 h in advance and movement documents from the official health protection service must accompany each consignment. Shellfish businesses in the UK must also be registered under the Fish Farming and Shellfish Farming Business Order 1985.

American whelk tingles (*Urosalpinx cinerea*) and slipper limpets (*Crepidula fornicata*) were introduced into England with consignments of *C. virginica* (Utting & Spencer, 1992). *U. cinerea* and European rough tingles (*Ocenebra erinacea*) are predators of young oysters and have caused high levels of mortality in spat and juvenile *O. edulis* in southern England (Cole, 1951; Utting & Spencer, 1992; Laing *et al*., 2005). *C. fornicata* competes with *O. edulis* for space and food and is a recognised pest species in both mainland Europe and England (Cole, 1951; Korringa, 1951b; Utting & Spencer, 1992). Another species that does not directly affect oysters is *Sargassum muticum* (a brown alga native to Japan), which was introduced into Europe through consignments of *O. edulis* and *Crassostrea gigas* (Critchley & Dijkema, 1984; Rueness, 1989). This non-native species has rapidly spread throughout England (Rueness, 1989) and has recently been found in Loch Ryan (D. Donnan, pers. comm., 2004; pers. obs.) and the Clyde Sea Area around Cumbrae. The unauthorised release of non-native species into the wild environment in Britain is an offence under the Wildlife and Countryside Act (1981) and licenses are required for any intentional releases.

7.2.5.1 Species biology and stock enhancement

Although translocation of broodstock for the restoration of oyster populations has produced immediate results in some fisheries (Millar, 1961; Southworth & Mann, 1998), broodstock is expensive (Tegner, 1989; Southworth & Mann, 1998) and of limited availability from hatcheries and non-local populations (Kassner & Malouf, 1982; Tegner, 1989; Goldberg *et al.,* 2000). Furthermore, removing broodstock for translocation could result in the overexploitation of the donor stock, as has occurred numerous times in the history of *O. edulis* cultivation (Fulton, 1895; Yonge, 1960). Spawner sanctuaries have the advantage of being temporary and can be returned to their native environment. However, for species with reproductive physiologies linked to seasonal factors, increased residence times in the host environment may be necessary to achieve reproductive synchrony (Millar, 1968; Kassner & Malouf, 1982; Tegner, 1993; Goldberg *et al.,* 2000). Gametogenesis, spawning and larval development occur at different temperatures in geographically separated stocks of *O. edulis* (Korringa, 1957b; Millar, 1968; Wilson & Simons, 1985). Millar (1968) investigated the differences in the gametogenic cycle between transplanted French stock and native Scottish stock in Loch Ryan. Millar found that the native stock spawned earlier than the introduced oysters in the first year but the French stock established synchrony with the native after several years. Other investigations have also revealed that the breeding cycle of *O. edulis* adapts within years to new environmental regimes (Shpigel, 1989).

Genetic studies are valuable for ensuring the success of stock enhancement. These include parentage studies of recruits (Chiu Liao, 1997; Goldberg *et al*., 2000; Peterson, 2002), evaluating the genetic contributions of different stocks to a population (Policansky & Magnuson, 1998) and determining the genetic effects at the individual and population level (Hindar *et al.,* 1991; Ryman, 1991). Introductions of non-local stock could alter the genetic structure of wild populations. Hindar *et al*. (1991) reported that the interbreeding of released cultured fish and wild populations could lead to the "breakdown of adapted gene complexes" and the "homogenisation of population structure through swamping a region with a common gene pool”. If a population is experiencing a “bottleneck”, then the introduction of stock could help increase genetic variation.

On the other hand, if the population is small, the introduction of non-local stock could cause further losses of genetic variation (Hindar *et al*., 1991; Ryman, 1991; Ryman & Laikre, 1991; Policansky & Magnuson, 1998) and loss of local adaptation. Genetic drift and migration both cause a loss in heterozygosity of the population and the effects of genetic drift are large in small populations. Therefore, if non-local stock is introduced to a small population and hybridisation occurs, there may be an overall loss of genetic variation (Ryman, 1991; Ryman & Laikre, 1991; Policansky & Magnuson, 1998). Past studies reveal that there are no predictable genetic effects related to the introduction of exogenous stock into wild populations (Hindar *et al*., 1991). Since genetic variation is a prerequisite for adaptation to changing environmental and biological conditions, any loss of heterozygosity would decrease the evolutionary potential of the population (Ryman, 1991).

Hatchery-produced seed or half-grown oysters raised in disease-free areas may provide a less expensive option than the translocation of broodstock depending on the intended time-scale of the programme (Laing *et al*., 2005). Growth of hatchery-produced *O. edulis* is the main method of production in Spain, which no longer has any commercially-viable natural populations (Laing *et al*., 2005). The benefits of reseeding using hatcheries are that they can provide a disease- and pest-free source of stock (Millar, 1961). Hatchery broodstock can be obtained from stocks cultivated over several generations, or from supportive breeding programmes that collect broodstock from wild populations, then harvest and rear the spat in hatcheries (Ryman, 1991; Ryman & Laikre, 1991).

Hatchery stocks are potentially susceptible to genetic problems, owing to the small number of broodstock used (Hedgecock *et al*., 1992; Ryman, 1991; Ryman & Laikre, 1991). Supportive breeding has been linked to increased levels of inbreeding as a result of decreased effective population sizes in both the donor and hatchery populations (Hedgecock *et al*., 1992; Hindar *et al*., 1991; Ryman, 1991; Ryman & Laikre, 1991). Furthermore, in other species, environmental differences between the hatchery and the natural habitat have caused lowered rates of growth and survival of introduced hatchery stock (Stoner, 1994; Lee Blankenship & Leber, 1995; Policansky & Magnuson, 1998). Therefore, re-seeding programmes require juveniles that have the vigour and adaptability for growth, survival and eventual reproduction in wild environments (Stoner, 1994).

7.2.5.2 Stock enhancement and national and international policy guidelines

The benefits of species translocations have often been outweighed by the biological costs. As a result, the use of translocations as a conservation measure has come under debate and other methods of *in situ* conservation are recommended (McLean, 2003). However, as part of the U.K. Biodiversity Action Plan, the Joint Nature Conservation Committee (JNCC) revised and updated policy guidelines for translocations. The JNCC policy covers i) species that have lived in the wild in the U.K. in historic times but are now extinct, ii) proposals to translocate individuals of native species within the current or recent historic range, and iii) proposals to translocate individuals of native species beyond the current or recent historic range (McLean, 2003). These policy guidelines provide an evaluation process for determining the necessity of translocations, which identifies the need for surveys to establish the current status of the species at the site of interest, the reasons for the decline of the species and the potential for the success of translocations. Post-translocation monitoring is also recommended to assess the outcome of the translocation. These policy guidelines are to be used in conjunction with the more detailed IUCN Guidelines for Reintroductions (1995). It should be noted that these guidelines were developed for conservation purposes and do not mention translocations for commercial venture (such as fisheries).

7.2.6 Habitat enhancement

Oyster larvae settle gregariously upon hard substrata, particularly shell (Cole & Knight-Jones, 1939; section 4.1). As a result, the availability of suitable substrata for settlement is considered as one of the most important factors for recruitment success to oyster populations (Korringa, 1946; Knight-Jones, 1951; Palmer, 2002). Commercial oyster fisheries frequently spread additional clean, unfouled cultch (empty shell) immediately before the spawning season to enhance spat settlement (Galstoff *et al*., 1930; Key & Davidson, 1981; Abbe, 1988; Kennedy, 1989; Rothschild *et al*., 1994; Southworth & Mann, 1998). The use of spat collectors is another technique that can enhance spat settlement (see section 4.1) and extensive use of spat collectors, in conjunction with stock enhancement have proved a valuable combination for restoring depleted oyster populations (see section 1.3).

A wide range of materials for spat collection have been investigated, including shell (Galstoff *et al.,* 1930; Cole & Knight-Jones, 1939; Abbe, 1988; Spencer, 2002), bundles of twigs (Galstoff *et al*., 1930; Spencer, 2002), roofing tiles (Yonge, 1960; Spencer, 2002) and other man-made materials, such as PVC pipe (Spencer, 2002) and cement boards (Butler, 1955). Dead shell has been widely used as a spat collector for several species of oyster in both scientific research and in fisheries. Dead shell can also be dredged from areas before relaying (Rothschild *et al*., 1994; Kennedy & Roberts, 1999). However, empty shell may harbour disease. For instance, deposition of empty cockleshell material in the Netherlands was linked to an outbreak of *Ostracoblabe implexa*, a fungus that infects flat oysters. As a result, cockleshell was replaced with mussel shell, which degrades more quickly, preventing the establishment of the fungus (Korringa, 1951a; Spencer, 2002). Furthermore, mussel and oyster shell are also considered to be more efficient spat collectors (Key & Davidson, 1981).

For any spat collector to be effective, the settlement material must be clean (although a degree of marine bacterial fouling is desired) and free from fouling by macro-organisms when it is laid (Cole & Knight-Jones, 1939). Collectors must be laid just before larval settlement commences, to minimise fouling and maximise the settlement of target species, thus decreasing the potential for interspecific competition (Galstoff *et al.,* 1930; Cole, 1951; Knight-Jones, 1951; Abbe, 1988). Use of collectors therefore requires knowledge of the environmental factors that influence spawning and the spawning periods of each stock (Galstoff *et al*., 1930). In addition, settlement studies in Chesapeake Bay found that the abundance of *C. virginica* spat was three times greater in areas characterised by gyres compared to other downstream areas (Southworth & Mann, 1998). Thus, knowledge of local hydrodynamics patterns is useful to maximise the success of collectors (Galstoff *et al*., 1930; Key & Davidson, 1981). Portable collectors can be used in areas where oyster settlement is low because the substratum is not considered suitable for larval settlement of population growth (Galstoff, *et al*., 1930). Artificial spat collectors also have a three-dimensional structure that provides a larger surface area for attachment. Studies have shown that spat attached to such artificial collectors can have higher growth rates than on effectively, two-dimensional carpets of cultch (Galstoff *et al*., 1930; Rothschild *et al.,* 1994; Southworth & Mann, 1998).

The success of habitat enhancement depends upon sufficient larval settling, growing and surviving upon the additional substrata (Galstoff *et al*., 1930; Korringa, 1946; Key & Davidson, 1981; Abbe, 1988; Dayton *et al*. 1989). The variable nature of the reproductive strategy of *O. edulis* makes it difficult to predict the level of larval production (Abbe, 1988; Hedgecock *et al*., 1992; section 5.1). Artificial reefs constructed in the Piankatank River region of Chesapeake Bay to restore the *C. virginica* population were deemed unsuccessful because of low levels of natural recruitment. For this reason, habitat enhancement is often used in conjunction with stock supplementation.

7.3 Additional legal aspects

Coastal activities and the proximity to waste discharge sites can affect the water quality of shellfish beds (Cole, 1951). Shellfish intended for market require to be purified of contaminants if the harvesting area falls below an "A" classification (Food Safety (Live Bivalve Molluscs and Other Shellfish) Regulations, 1992). This involves extra costs to fisheries, as depuration is needed to produce stock of market quality, and in extreme cases pollution has led to the closure of oyster fisheries (Cole, 1951; A. Berry, pers. comm., 2004). Shellfish poisoning caused by algal toxins can also have economic impacts on fisheries through harvest bans. Algal toxins are monitored under the Food Safety (Fishery Products and Live Shellfish) (Hygiene) Regulations 1998, by requirement of the Shellfish Hygiene Directive 91/492/EEC. Shellfish waters are also regulated for other microorganisms, heavy metals and organic contaminants under the EC Shellfish Waters Directive (79/923/EEC), which is to be superseded by the Water Framework Directive (2000/60/EC). Water quality in shellfish-producing areas is required to meet the standards set under The Surface Waters (Shellfish) (Classification) (Scotland) Regulations 1971 and The Surface Waters (Shellfish) (Scotland) Directions 1998 (as amended).

7.4 Financial considerations of potential management strategies

Laing *et al*. (2005) conducted a Cost Benefit Analysis (CBA) of the different options for *O. edulis* stock regeneration in the UK. Natural regeneration, cultivation in hatcheries, cultivation using ponds as hatcheries and the laying of half-grown imported oysters were compared using the preconstruction, construction and operational costs, including 24-h surveillance costs. The authors concluded that the operational costs of hatcheries excluded the use of hatchery stock for short-term (20 years) regeneration programmes. Importing half-grown oysters into a site or preparing a site to promote the natural regeneration of a depleted population were the most economically viable options for a regeneration programme over 20 years. However, the authors also highlighted the high risk factor associated with recruitment success under the natural regeneration option.

One feature of the CBA was the inclusion of substratum preparation for all regeneration options. Habitat enhancement is also a widespread feature in commercial oyster fisheries, as harvesting removes the shell that would otherwise act as a substratum for settlement. This suggests that any fisheries or conservation management strategy for *O. edulis* stocks should incorporate guidelines for habitat maintenance. Protection of the habitat and the species may be achieved through the implementation of fisheries closures and MPAs. Fisheries closures offer temporary relief from fishing activity compared to MPAs, which are devised as a permanent management measure for the protection of species and habitats. For many of these management measures, the hydrodynamics of the area need to be investigated to ensure that the goals of achieving a self-sustaining population and/or providing a source of recruits to other stocks are achieved. Further biological requirements that require adequate consideration are the potential for Allee effects and genetic considerations. The requirement for a sufficiently large population is highlighted by the results of genetic studies indicating that the effective population size of marine organisms is typically orders of magnitudes lower than the census population size (Hedgecock *et al*., 1992; Saavedra, 1997; Hauser *et al.,* 2002). Although native oyster populations in Scotland have been termed "genetically healthy" in terms of their level of genetic variation (Truébano-Garcia, 2004), studies of *O. edulis* indicate that the species can suffer from increased homozygosity and founder effects when bred from small populations (Saavedra & Guerra, 1996; Bierne *et al*., 1998; Naciri-Graven *et al*., 2000).

A second feature of the CBA was the recommendation that all stock regeneration options received 24-h surveillance (Laing *et al*., 2005). As already mentioned, unlawful exploitation is a major problem for the existence of *O. edulis* stocks in Scotland and has contributed significantly to the decline of many populations (see section 2.4). Surveillance measures are not always financially viable (Guillotreau & Cunningham, 1994; Anon., 1997). Unlawful exploitation is also a problem for other coastal shellfish stocks in other countries (Bourne, 1986; Tegner, 1993). Although the rights to gather *O. edulis* are restricted in Scotland, the species is often treated as an open-access resource and is usually found with other species of shellfish that are legitimately gathered, such as palourdes (*Venerupis decussata*). Without suitable public awareness about private harvesting rights, suitable controls on shellfish harvesting, or adequate surveillance of *O. edulis* populations, unlawful exploitation will continue to be a threat to the existence of the stocks in Scotland.

8 THE APPLICABILITY OF MANAGEMENT MEASURES FOR *OSTREA EDULIS* POPULATIONS IN SCOTLAND

8.1 Introduction

The management measures reviewed in section 7 have their origins in fisheries. However, this does not preclude the use of these measures for conservation objectives. Consideration of both fisheries and conservation-style management would be appropriate for developing an holistic management programme for the remaining wild stocks of *Ostrea edulis* around Scotland. Issues that need to be considered when evaluating management strategies include the biological characteristics of the species, such as demographic and genetic variation, ecosystem considerations, and the political, social and economic factors associated with the management measures. The static spatial structure of sedentary shellfish stocks (Orensanz & Jamieson, 1998) also makes them vulnerable to over-exploitation within the boundaries of many "traditional" management measures, such as gear restrictions, minimum landing sizes and closed seasons (Bourne, 1986). This spatial aspect needs to be given proper consideration too, in order to prevent the sequential depletion of exploited populations (Bourne, 1986).

8.1.1 Summary of findings

Current population estimates indicate that the densities of the surveyed wild populations of *O. edulis* around Scotland are generally greater than that of other British populations (see section 3.4). Although substrata suitable for larval settlement have high percentage covers within the surveyed environments, increasing the cover of shell could further increase larval settlement (see section 4.4.1). However, larval settlement is low in most years, potentially because of Allee effects in low-density populations (see section 5.4) and the variable nature of annual recruitment (McKelvey *et al*., 1993). However, levels of genetic variation in populations around Scotland are high and this suggests that the sampled populations have a reasonably effective population size (see section 6.4).

O. edulis populations around Scotland are often found in remote locations (Millar, 1961) where there is a lack of enforcement and wild stocks of shellfish, such as palourdes (*Venerupis decussata*), are often exploited legitimately under common law. Although *O. edulis* is not an open-access resource, arguably it has become subject to the "tragedy of the commons" (Hardin, 1968) as a result of unlawful exploitation and a lack of effective protection (see sections 2.4 & 2.7). Unlawful exploitation has become one of the main threats to the survival of stocks around Scotland (see section 3.4) and is therefore a primary issue that needs to be addressed in any management programme.

8.2 Population assessments

The lack of a long time-series of population estimates for the wild *O. edulis* populations in Scotland makes it difficult to draw conclusions about natural population dynamics and the effects of unlawful exploitation. Regular assessments of commercially exploited populations are also lacking, making it impossible to determine accurately the effects of current fisheries associated activities in Scotland. The aims of the Native Oyster Species Action Plan (1999) are to maintain and expand the current geographical range and abundance of *O. edulis*. Long-term population surveys are central to the attainment of these goals and for the efficacy of any conservation or fisheries management measures. It is therefore advised that regular population assessments become a mandatory feature of the future management of the wild populations of *O. edulis* around Scotland.

Population estimates should be based on methods that provide the highest level of precision possible with the available resources. The current research suggests that, at present densities, belt-transects provide greater levels of precision per unit effort than quadrat-based methods (see sections 3.3.2 & 3.4.2). Therefore, it is recommended that future surveys using underwater visual census be based on belt-transects or similar methods.

8.3 Enhancement techniques

8.3.1 Broodstock enhancement

The lack of population assessments also makes it difficult to determine whether the populations around Scotland are declining or expanding. However, unlawful gathering of oysters is known to be reducing the density and abundance of some populations (see section 3.4.3). The findings of section 5 suggest that Allee effects could be decreasing fertilisation success in populations of low density. Furthermore, studies investigating the natural regeneration of depleted populations have led to conflicting conclusions about the efficacy of this process (see section 7.2.5). However, a combination of stock and habitat enhancement has been used successfully to restore many depleted stocks of *O. edulis* throughout Europe (see section 1.3). Laing *et al*. (2005) have also suggested these measures form part of contemporary restoration programmes for *O. edulis* populations around Britain (see section 7.4).

Genetic evidence provides support for the proposal that millions of broodstock oysters would be required to restore a depleted population of *O. edulis* (Korringa, 1956; Laing *et al*. 2005). Using allozyme studies, Saavedra (1997) concluded that a wild population of *O. edulis* in Spain, with an estimated population census size of 10,000 individuals, had an effective population size of only 248 individuals. The 50/500 rule determines the number of individuals necessary to maintain the genetic characteristics over the short- and long-term (Franklin, 1980). Application of this rule to Saavedra's estimate suggests that approximately 50,000 individuals would be necessary to maintain the short-term genetic heterogeneity of a population and 5 million individuals would be necessary to maintain the long-term adaptive potential of the population. With the exception of Loch Ryan, these figures vastly exceed the current estimates of population abundance of *O. edulis* around Scotland. However, the level of genetic variation in populations around Scotland is high, indicating reasonably effective population sizes (see section 6.4). In order to determine whether stock enhancement is necessary, population census data are required to determine the dynamics of populations over several years.

Pilot studies investigating the growth, survival and reproductive traits of stock placed into a "foreign" environment are recommended before large-scale enhancement programmes are commenced (see section 7.2.5). Although much research has been done on the growth and survival of *O. edulis* under laboratory conditions, there are relatively few studies investigating these aspects within Scottish waters (Millar, 1961; Drinkwater & Howell, 1985; Beaumont & Gowland, 2002).

Survival and growth is influenced by environmental conditions, making some areas more suitable for oyster population development than others (Cole, 1951; Millar, 1961; Drinkwater & Howell, 1985; Beaumont & Gowland, 2002). In general, the findings of spat growth studies have found that mortality is greatest after the initial introduction and is affected by the size and batch of seed used (Drinkwater & Howell, 1985; Utting, 1988). Since spat are susceptible to predation by *Carcinus maenas* and *Asterias rubens* (Hancock, 1955), protective caging, using heavy plastic mesh bags, can be used to increase survival (Cole, 1951; Drinkwater & Howell, 1985). Older oysters show better growth when cages are not used (Hawkins *et al.*, 2000). Growth of oysters at all ages is affected by temperature and food availability (Galstoff *et al*., 1930; Walne & Mann, 1975; Drinkwater & Howell, 1985; Utting, 1988), and is inversely related to stocking density (Hawkins *et al*., 2000). Drinkwater & Howell (1985) found that for 10-mm spat, the maximum stocking density was 380 m^{-2}. Optimal stocking densities for older oysters have rarely been documented, although Knight-Jones (1951) recommended 3-year old oysters be stocked at densities of 50 m^{-2} and stated that increasing stocking density would result in greater spatfall. Caution should be taken with stocking at high densities, since this leads to stress in individuals making them more susceptible to disease (Hawkins *et al*., 2005). A further note of caution; translocation of brooding *O. edulis* should be avoided as disturbance can cause premature spawning of larvae (Orton, 1927, 1933; pers. ob.).

Translocations of stock between water bodies can enhance the movement and introduction of non-indigenous species (see section 7.3). Current legislation does exist to prevent movements and introductions of non-indigenous species, but caution is advised. It is recommended that stock derived from wild populations out with Scotland should not be used for stock enhancement programmes or for any other fisheries-associated activity. The reason is to prevent the introduction and spread of disease and competitor species, such as *Bonamia ostreae, Crepidula fornicata* and *Urosalpinx cinerea*, which are abundant in other parts of the United Kingdom and mainland Europe (see sections 1.2.1 & 7.2.5). This caution should also apply to other species that are cultivated within Scottish waters. Although there are no published reports of the existence of an established population, *C. fornicata* has been identified within the Clyde Sea Area (G. Moore, pers. obs.). Also, Scottish Natural Heritage (SNH) has recently identified the non-native algal species, *Sargassum muticum,* in sealochs in southern Scotland (see section 7.2.5). Species translocations within Scotland should, therefore, also be assessed for their potential impact on the host ecosystem.

An alternative strategy to stock enhancement, which has been used by “Loch Ryan Shellfish Ltd”, is to increase the density of the oyster population by concentrating the population in a smaller area. This could also be achieved by placing the oyster within enclosed cages such as spawner sanctuaries using local stock (see section 7.2.5). Increased broodstock density should lead to increased spawning success and larval recruitment (Peterson & Summerson, 1992; Peterson *et al.,* 1996; Goldberg *et al.,* 2000). However, the effects of concentrating oysters could increase the susceptibility of the stock to unlawful gathering and the spread of disease.

Changes in genetic variation caused by inter-breeding between stocks of different origins can affect the long-term sustainability of a species (see section 7.2.5.1). There are indications that populations of *O. edulis* around Skye could have unique genetic characteristics (see section 6.4). It is therefore recommended that the populations around Skye are considered as a separate resource from mainland Scotland populations, until further genetic work can establish the genetic status of the Skye populations. Translocations into or out of populations around Skye should be avoided and the Skye populations should potentially be considered of high conservation importance. Although it is suspected that there have been high levels of translocations among other populations in the past, current estimates indicate that genetic variation is high within certain Scottish populations (see section 6.4). This indicates that translocations between these Scottish stocks should not have any adverse genetic consequences. However, genetic variation should be assessed for any population that is to be potentially used in translocation or enhancement programmes, both prior to and following the commencement of any programme. It is possible that there are, as yet, undiscovered “original” native Scottish populations.

Introduction of juvenile oysters has been suggested as an alternative long-term option for restocking populations since they can be derived from disease and pest-free sources, such as pond-culture or hatcheries (Millar, 1961; Laing *et al*., 2005). Currently, Tobermory Oysters (Mull) owned by David Flockhart, is the only *O. edulis* hatchery in Scotland and culture methods are still being developed. Other hatcheries are also being developed. Graham and Marilyn Cooper are in the early developmental stages of establishing a hatchery at Loch Ailort and Bill McDermot is developing an inland hatchery (see sections 3.6.3.2 & 3.6.3.3). *O. edulis* from Loch Ailort is the intended broodstock for both of these hatcheries.

The genetic issues of hatchery-produced stock and supportive breeding are discussed in part 7.2.5.1. Population census surveys indicate that Loch Ailort has the lowest population density and abundance of the surveyed populations (see section 3.3.2). Although hatchery development is a potential method for producing stock for regeneration programmes and is extensively used in Spain (Laing *et al*., 2005), supportive breeding programmes carry a high risk of creating deleterious genetic effects within the donor and hatchery populations. Therefore, it is of concern that two hatchery enterprises exploit the stocks of Loch Ailort for hatchery purposes when the wild population abundance is already low. Hatchery-reared stock bred from wild populations around Scotland provides a viable method for restoring degraded *O. edulis* populations. Therefore, to maximise the success of the hatchery programmes and protect the small Loch Ailort population, the hatcheries should be encouraged to use parent stock from other genetically similar populations around Scotland (e.g. Loch Ryan, Loch Sween and Loch Eriboll, see parts 6.3 & 6.4). This method also raises important economic and social advantages, by providing support to small enterprises and is, therefore, to be encouraged as a potential management method for the restoration of stocks around Scotland.

8.3.2 Habitat enhancement

Stock enhancement is used in conjunction with habitat enhancement in order to maximise the benefits of increased larval production (see section 4.1). The availability of hard substrata in oyster producing areas is variable and the availability of cultch (dead shell) is generally low (see sections 3.3.1, 4.3.1 & 4.4.1). Although substrata suitable for larval settlement are present at all sites surveyed, low levels of larval production and the patchy nature of available substrata, may make habitat a limiting factor to population growth (see section 4.4.1). Further investigations of substrata availability would be required for each site for which stock enhancement was to be considered.

A potential source of cultch is the shellfish industry, which produces shell as a waste product. However, all “waste” products are subject to strict environmental legislation under U.K. law. The level of purification that would be required to transform “waste” shell into a product suitable for habitat enhancement could be prohibitive in terms of cost for cultch supplementation to be feasible. Cultch supplementation has also been linked with the spread of disease in *O. edulis* populations (see section 7.2.6). Empty flat oyster and other shell types are often present in the upper benthic layers where wild populations have existed. Exhuming this shell has been suggested as an alternative low-cost source of shell (Kennedy, 1999) and has been shown to be an effective spat collector (Cole & Knight-Jones, 1939). However, there are many practical difficulties associated with the suggestion. Disturbance of the habitat could have detrimental impacts on any extant population of *O. edulis* or other shellfish species in the vicinity through increased turbidity, burial or re-mobilisation of metals. The depth of water covering the areas of buried shell and the quantity of shell that would be required for cultch supplementation could make the recovery process logistically unfeasible. Furthermore, if shell is transferred between areas this could also facilitate the movement of non-indigenous species. Individuals of *O. edulis* attached to light-weight cultch, such as shell, are subject to higher levels of unlawful gathering than individuals attached to other, heavier substrata (see section 3.4.3). As with other management measures, the benefits need to be weighed against the potential impact of unlawful exploitation.

One major criticism of stock enhancement is that ecosystem degradation can result from exceeding the carrying capacity of the environment (Folke *et al*., 1998). Habitat enhancement could also have environmental impacts by changing hydrodynamic patterns. Although the survey results suggest that predator and competitor species of *O. edulis* are presently at low densities, enhancement measures could have a positive effect on the population growth of these species (see sections 4.4.1 & 7.2.6). Therefore an ecosystem perspective should be adopted when considering enhancement measures. Historically important areas should have the characteristics necessary for stock enhancement (Stoner, 1994), unless there has been some major environmental change since the depletion of the stock, such as the establishment of a new faunal community or pollution. Therefore, in addition to surveys of population abundance, community assessments should be carried out before and during stock enhancement programmes, in order to monitor the community response and ensure adequate environmental conditions.

8.4 Marine protected areas

Marine protected areas (MPAs) have primarily been used as a technique to conserve populations subject to high levels of exploitation or to protect species and habitats at risk from damaging fishing activities (see section 7.2.4). MPAs allow an ecosystem approach to management by providing protection for species, associated habitat and the ecosystem as a whole. MPAs can also have geographical benefits that range out with the site of a population considered for protection.

Genetic studies have suggested that oyster populations around Scotland could be linked by larval transport (Truébano-Garcia, 2004), although studies of this hypothesis are lacking. Anecdotal evidence indicates that larval transport can be important for the sustainability of populations. For instance, stocks of *O. edulis* were removed from the Beauly River after infection by *B. ostreae.* Recruitment levels in the Solent stocks were considered to be much lower after the removal of the Beauly stock (G. Mills, pers. comm., 2005). This suggests that the Beauly River acts as a source of recruits to the Solent population. Marine reserve networks could, in theory, protect larval source populations and maintain the supply of larvae to sink populations, ensuring the sustainability of stocks. However, larval transport studies among the populations around Scotland would be required to ensure the benefits of a MPA network.

The efficacy of MPAs for a single site would depend upon the natural dynamics of the population being protected, the interaction with the ecosystem and the potential links with other populations. Furthermore, reports of unlawful exploitation of commercially valuable invertebrate species from within MPAs (Tegner, 1993) imply that the efficacy of protection afforded to the species would greatly influence the success of the MPA.

8.5 Fisheries

The Loch Ryan *O. edulis* population is currently estimated to have a population abundance of tens of millions of oysters (T. Hugh-Jones, pers. comm., 2005). This is the only commercial oyster fishery within Scotland and must adhere to current British fisheries policy, including the minimum landing size, seasonal closure and ownership of fishing rights. Loch

Ryan Shellfish Ltd lease the rights to the oyster fishing from Ben Wallace, who is the proprietor of the right to fish oysters in Loch Ryan. Annual landings are restricted to between 10 and 15 tonnes, although there is scope for this to increase in the future. Landings are kept to a minimum as the managers have adopted a conservation approach, taking the view that living oysters within Loch Ryan are the only source of recruits to the population and provide the best settlement material for larval oysters. Management measures have included aggregating the oysters in several areas within Loch Ryan and experimenting with habitat enhancement (T. Hugh-Jones, pers. comm., 2004).

It is estimated that individuals in Loch Ryan reach a marketable size after an average period of 10 years (T. Hugh-Jones, pers. comm., 2004). Oysters in other populations around Britain normally reach maturity at about 3 to 4 years-of-age. If the market maturity time is longer in Loch Ryan, the contribution of an individual to population recruitment will be much greater compared with individuals of other populations. Loch Ryan is also unique because of the abundance of the oyster population, with an estimated population abundance of millions of individuals compared with estimates of tens of thousands in other Scottish stocks (see section 3.1, 3.3.2 & 3.4.3). As discussed in part 7.2.1, the current MLS is less than the estimated shell length for optimum contribution by an individual to population recruitment. For wild populations, where applications are made for commercial development, an introduction of regulation on the MLS could be imposed as a conservation strategy contributing to the long-term sustainability of stocks. Furthermore, if this management measure is stipulated during the developmental stages of any application, this should avoid any deleterious economic impact on the enterprise.

Management policy in Loch Ryan involves re-laying cultch. This is beneficial to the population and the fishery as it allows the levels of suitable substrata for larval settlement to be maintained. This management measure could also be introduced as a conservation strategy for potential oyster fisheries development.

The proprietors and associated management of the Loch Ryan oyster fishery have often been commended for the conservation approach to management taken (Anon., 1886–1977; Millar, 1961) and the current proprietors are no exception. There is no evidence to suggest that the current management measures could lead to exhaustion of the stocks in Loch Ryan. However, stock assessments of the Loch Ryan population are sporadic and not made in association with the management of the fishery, so it is difficult to assess the impacts of the current management measures accurately. Bannister (1986) suggested that regular monitoring of stocks provided a more accurate short-term approach to fisheries management. Regular monitoring of the Loch Ryan population should be encouraged in order to assess the efficacy of management, protect the stocks from failures in management and maximise economic gain. However, caution is advised with respect to this last point and the conservative approach to management already in operation at Loch Ryan should be maintained.

For any fisheries-associated exploitation of wild *O. edulis* stocks in Scotland, it is recommended that regular independent assessments should be made a mandatory condition of a Several or Regulating Order, to provide evidence of success in the management measures adopted.

As discussed earlier, larval transport can potentially link geographically separated populations, with management measures taken in one area affecting stocks in other areas (see section 8.4). The influence of hydrodynamic factors is not limited to larval transport and changes in coastal use could impact on the management of *O. edulis* populations around Scotland. Waste discharge and coastal development can have detrimental effects on the potential success of fisheries-associated activities. For example, dredging of 276,000 m^3 of sediment from the northern channel of Loch Ryan is planned for expansion of the existing ferry terminal at Cairnryan.

Environmental consultants Royal Haskoning carried out an Environmental Impact Assessment that determined, among other factors, the impact of the development on the hydrology and oyster population (Lindsey *et al*., 2005). Current tidal movement and sediment transport is predominantly from north to south. Oysters were recorded in surveys approximately 400 m to the south of the proposed development site but not within the site itself. Modelling studies illustrated that the 18-month dredging operations would not change the hydraulic patterns within the loch or alter sediment transport. During the operations there is likely to be an increase in suspended sediment within the bottom 0.5 m of Loch Ryan and an increase in sedimentation of up to 20 mm to the south of the development by the end of the dredging operations. This was predicted to be mostly deposited in the Cairnryan port development area, along the south-east shores of Loch Ryan and in the central part of the southern basin. After dredging operations are terminated, ferries will no longer use the southern basin and will only operate within the northern channel of the loch. The impacts to the oyster population and the associated fishery determined by the consultants are detailed in Table 8.1.

Table 8.1 Summary of impact assessment of port development in Loch Ryan (Lindsey et al.*, 2005).*

Impact	Assessment	Comment
CONSTRUCTION PERIOD		
Loss of substrata/habitat	Negligible, adverse significance	Oysters are not found within the reclamation area.
Sedimentation mobilisation, smothering and disturbance	Minor, reversible, adverse significance	Estimated maximum 12–16 mm sediment deposition to south of development, but will only extend 250 m from development.
OPERATIONAL PERIOD		
Loss of substrata	No Impact	No maintenance dredging
Change of habitat due to movement of ships and prop wash	Minor, long-term and adverse significance	Habitat directly south of the development will be subject to localised smothering rendering the habitat unsuitable for oysters.

The authors assessed the impacts to be negligible or minor to the oyster population of Loch Ryan because the main areas of habitat loss and increased sedimentation were identified as out-with the area in which oysters are found. In addition, the intended method of construction (backhoe dredging) was considered to cause less environmental disturbance than other methods of dredging. As regular dredging of the shipping channel, which extends throughout the southern basin, will no longer be required, it was postulated that sediment transport within the southern basin would return to a “more natural state”. The long-term effect of the cessation of maintenance dredging, which was not mentioned in the report, would possibly decrease the level of sedimentation that the Loch Ryan oyster population is exposed to.

The conclusions of the assessment are limited to the area surrounding Cairnryan. However, if the modelling studies are accurate and increased sedimentation is restricted to the suggested localised areas within Loch Ryan, there is no reason to suggest that the current oyster population and fishery (which is predominantly based south of Cairnryan, the Scar and the west side of the loch) will be at risk from the effects of smothering or reduced larval settlement resulting from habitat degradation (see section 4.4.1). However, oysters within the Cairnryan area are at the most risk from unseen adverse impacts. The assessment contained recommendations of post-construction monitoring of the benthic fauna adjacent to the site and cultch-laying as a mitigation measure to safeguard the oyster population in this area (Lindsey *et al*., 2005).

It is important that coastal development is suitably regulated to prevent any detrimental impacts to *O. edulis* stocks and the managers of stocks receive adequate support from authorities in such matters.

In several areas around Scotland, native oysters are cultivated alongside the introduced Pacific oyster (*Crassostrea gigas*). Although *C. gigas* can produce larvae that settle in British waters, environmental temperatures are too low in winter for the survival of *C. gigas* spat (Child & Laing, 1998). Increasing sea temperatures around Britain, associated with climate change, could allow *C. gigas* to recruit successfully and grow within areas where it is currently cultivated. *C. gigas* is a more efficient filter-feeder and has higher growth rates than *O. edulis* (Mann, 1979). This suggests that if *C. gigas* can recruit successfully and establish populations within Scottish waters in the future, there could be a serious risk of competition with *O. edulis*.

8.6 Unlawful gathering

Unlawful exploitation of populations of *O. edulis* in Scotland has been frequent in recent years and is likely to continue because the species has a high market value, populations are found in remote locations and, therefore, are easy to collect without detection. There has also been a lack of effective prosecution of those caught unlawfully removing *O. edulis*. Unlawful exploitation of populations of *O. edulis* is also a significant problem throughout Britain, causing the closure of privatised fisheries (Guillotreau & Cunningham, 1994) in addition to the depletion of wild stocks (see sections 2.4 & 3.4.3).

Recent efforts in Scotland have concentrated on coordinating the response of police with local reports of unlawful gathering in Argyll. Success of this network has so far been limited for a number of reasons. Firstly, the legal status of the right to fish for *O. edulis* in Scotland is not widely acknowledged (see section 2.4) and is often confused by the common access right to gather other shellfish species (with the exception of mussels). Viewpoints of official bodies have often been contradictory regarding the right to gather *O. edulis* and gathering has been allowed if it has been limited to small numbers “for the pot”. Secondly, the system is based upon reports made by local people about suspected unlawful gathering but these allegations have been difficult to prove. Furthermore, unlawful gathering can go unreported in some areas because of the fear of retribution (M. Cooper, pers. comm., 2005). Since this initiative is still in its infancy, the management of the system requires strict review and development in order to advance its potential. This development and the expansion of the system is critically required as there is currently no other formal system of pro-active protection for wild *O. edulis* stocks in Scotland.

An alternative approach was taken to combating unlawful gathering in Loch Ryan. In an attempt to prevent unlawful gathering of the oysters, Mr Wallace acquired the rights to the foreshore to remove any uncertainty regarding the rights to gathering of oysters in Loch Ryan. This approach to removing “grey areas” was also taken by proprietors of oyster fishing rights in the Firth of Forth, when they acquired the rights to mussel fishing for the oyster bed areas (see section 2.3.1). It was suggested at a recent meeting of the Technical Committee of the Shellfish Association of Great Britain that both of these approaches had potential for development using current legal tools. Another suggested approach was to investigate the use of Anti-Social Behaviour Orders as a method of excluding people, who were repeatedly accused of unlawful gathering, from water bodies containing *O. edulis* populations. Legal advice would be required on the application of this approach in Scotland.

The market forces driving unlawful exploitation are largely unknown but some details are available. The development of shellfish transport to continental Europe, has allowed unlawfully gathered oysters to be smuggled out of Britain rapidly, by hiding them under the legitimate stock within vivier-tanks (G. Mills, pers. comm., 2005). Marine stocks being transported out of Britain are subject to checks and registers, but after the first sale there is no right of inspection. This presents opportunities for unlawfully gathered oysters to be added to stocks being transported to continental Europe. Details of a British market are unknown. The issues surrounding unlawful gathering are complex and decades of attempts to stop this activity have not provided a solution to the problem. It is advised that communication among stakeholders in different parts of Britain is increased, with discussions focusing on the successes and failures of previous and current attempts to stop unlawful gathering.

8.7 Concluding remarks

The goals and objectives of the Native Oyster Species Action Plan are to maintain and expand the existing geographical distribution of oysters stocks in UK inshore waters, and to maintain and increase the existing abundance of these stocks. These are pertinent goals for Scotland where small population size and unlawful exploitation are the two key concerns for the persistence of stocks of *O. edulis*. Clearly, the highest priority is to prevent further decline in existing populations and to increase their abundance, if possible. If resources allow, consideration could be given to re-establishing oysters in former grounds.

In order to achieve these goals, two main issues urgently need to be addressed. The first is to improve the current system for combating unlawful exploitation, as if this practice is continued, the effects will undermine any management measures attempted. Furthermore, to maintain the existing geographical distribution of stocks, the current efforts to combat unlawful exploitation need to be extended throughout Scotland from the main current focus in Argyll. Secondly, a regular monitoring programme of the stocks throughout Scotland needs to be established so that populations most in need of intervention can be kept under review. If statutory bodies do not have the resources to commit their own staff to a national oyster monitoring programme, consideration should be given to how local conservation-minded people could be recruited, trained and coordinated to monitor oyster beds in their area in a standardised way.

Populations that are given priority status would be those showing continual decreases in density and abundance over several years. Once priority populations are identified, further studies to determine the cause of population decline should be undertaken. Past experiences (see section 1.3) have shown that programmes using a combination of stock and habitat enhancement have been successful in restoring declining populations. However, U.K. policy and IUCN guidelines encourage other methods of conservation to be used before considering stock enhancement (see section 8.3.1). For instance, spawner sanctuaries, using local stock, provide a possible alternative that should be considered prior to stock enhancement.

If stock enhancement is considered necessary, the IUCN guidelines should be used in the design of any translocation programme. If oysters are translocated into an existing population, the donor stock should be genetically similar. Oysters being translocated are subject to health checks under the Fish Health Regulations (1997). In addition, to decrease the chance of introducing non-native species, oysters should be taken from an area with a similar (or the same, where possible) species composition to that of the recipient stock. Native oyster populations in areas that contain stocks with a potentially unique or distinct genetic makeup, such as in Skye (see section 6.4), should be allowed to regenerate naturally, if possible. For such populations, habitat enhancement could be considered, if necessary, although extreme care must be exercised to ensure that alien species, pests or diseases are not introduced with any imported material, such as shells. Translocations of stock should only be considered as a last resort if a genetically-distinct population continues to decline in abundance. Any stock enhancement programme should ideally be complemented by studies of the genetic variation of both the donor and recipient populations, prior to and following translocations.

Marine Protected Area status for biotopes containing *O. edulis* will only be useful if they are adequately policed and protected. MPAs subject to a regular monitoring programme would aid in assessing the impacts of management measures on both the oyster population and its supporting biotope. However, owing to the paucity of research on *O. edulis* larval transport, there is inadequate information on which to base the design of an effective MPA for conserving native oyster populations (Sale *et al*., 2005).

As interest in cultivation of *O. edulis* is increasing within Scotland, measures to encourage a conservation-style approach to fisheries management should take high priority as a method of maintaining and protecting populations that are exploited (see section 8.5). This includes the need to make population assessments of exploited stocks a mandatory requirement for the granting of Several and Regulating Orders. It would also be useful to establish a Geographical Information System database that can incorporate information relating to the different oyster populations. For instance, information that could be included would be population assessment data, biotope features and details of the management of stocks in different areas, e.g. ownership of the right to oysters, whether the population is exploited for fisheries purposes, how many are gathered annually etc. This database would provide a powerful consultation tool for regulating the levels of exploitation under Several and Regulating Orders.

All management measures are susceptible to externalities such as climate change, pollution events and unlawful exploitation, and there is a level of uncertainty attached to all management strategies. National guidelines have failed to prevent stock collapses in the past. Therefore, each local bed should be considered separately and management strategies tailored to suit the requirements of each population. However, a precautionary approach to management is strongly recommended. This would involve developing a range of complementary management measures throughout Scotland that take account of the ecological differences between populations, the influence of hydrodynamic features, other coastal users and wider ecosystem factors. This approach should provide insurance against failures of particular management plans in localised areas. A principle of precautionary management should be to do no further harm, so any proposed measure should be considered against an option of “take no action”. For example, the risks of adverse effects from introducing cultch or translocating oysters should be assessed carefully in relation to the likelihood of benefits accruing in the long-term, and where the balance of probabilities is unfavourable or uncertain, the proposed measure should not be implemented.

Finally, the development of native oyster management programmes should consider the timescale and financial backing available to achieve the desired goals, such as stock regeneration and sustainability, which are long-term objectives. Most of the forms of management discussed above will take many years for benefits to accrue. However, the remote locations of *O. edulis* populations and the high level of unlawful exploitation suggests that unless an effective solution is found for the problem of unlawful gathering, other measures to conserve native oysters in Scotland could well prove to be futile.

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APPENDIX 1: RIGHT TO GATHER OYSTERS IN SCOTLAND

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A1.1 Background

The decline of native oyster (*Ostrea edulis*) populations around the British Isles has been attributed mainly to overexploitation from the middle of the nineteenth century, when the advent of steam technology and rail transport led to industrialisation of the fisheries. Other deleterious agents include the introduction of alien pathogens, predators and competitors, often as an inadvertent consequence of attempts to improve fisheries (Orton, 1937; Cole, 1951). Native oyster populations in the United Kingdom have declined to such an extent that the species is now the subject of a Biodiversity Action Plan under the International Convention on Biodiversity (Lockwood, 2001). In Scotland, oysters are absent from areas that formerly supported pre-eminent fisheries, such as in the Firth of Forth (Yonge, 1960). It seems that *O. edulis* is largely restricted to isolated populations in west coast sea lochs and these are currently threatened by unauthorized fishing (Donnan, 2003). There appears to be a lack of public awareness of the laws regarding oyster gathering, the law of the foreshore and seabed is under review (Mackay et al., 2003; Anon., 2005b) and management of inshore fisheries in Scotland is being reorganised (Anon., 2005a). It is therefore timely to review the legal status of oysters and oyster fishing in Scotland.

A1.2 Common law rights

In Scotland, the right to gather native oysters (*Ostrea edulis*) is a patrimonial property right of the Crown, unless the right in a particular place has been acquired by exclusive grant from the Crown or by "prescriptive possession" (Stewart, 1892; Reid, 1993). The common law public right to gather shellfish does not extend to oysters or mussels. A temporary right to gather oysters may be acquired by a lease or permission from the owner, by a Several Order made under the Sea Fisheries (Shellfish) Act 1967, or by a licence issued by the grantee of a Regulating Order made under that Act.

Over hundreds of years, the Crown has made grants of oyster fishings in Scotland to individual subjects and bodies corporate. For example, the Loch Ryan fishery was granted to an ancestor of the current proprietor in 1701 (Shaw & Dunlop, 1824; D. Hugh-Jones, pers. comm.) and Fulton (1896) lists several grants of oyster fishing rights in the Firth of Forth to the City of Edinburgh from the 14th to the 17th centuries. In Scotland, the right to gather oysters is separate from the ownership of the foreshore, seabed or the oysters themselves: in law, it is a "separate tenement", analogous to the right to fish for salmon (Stewart, 1892; Reid, 1993; Gill et al., 1998). It is therefore possible that the right of ownership in an area of foreshore or sea bed and the right to gather oysters there are held by different persons. A grant of the foreshore or sea bed from the Crown does not include the right to gather oysters, unless it is specifically included (Stewart, 1892; Reid, 1993). Where a more general right of "fishings" is included in the title, it is possible for the holder to acquire the right to gather oysters by exclusive possession for the "prescriptive period", which has previously been as long as 40 years, but is currently ten years, or twenty years in cases involving the Crown (Inglis, 1994).

It has in the past been argued that the Crown holds the right to gather oysters in trust for the public and that there is therefore a public right to gather oysters in a particular place until an exclusive grant, or other restriction, is made in respect of that place. However, the case of

Parker *versus* Lord Advocate, which was settled in the House of Lords in 1904, established that this is not so (Anon., 1902a,b, 1904). That case concerned mussels (*Mytilus edulis*), but the principle applies also to oysters. In 1896, the Board of Trade, on behalf of the Crown, leased the right to gather mussels from beds in the estuary of the River Clyde between Greenock and Port Glasgow to the Fishery Board for Scotland (Anon., 1898). The Fishery Board sub-let the right to Dr J.H. Fullarton, a former Fishery Board employee, who intended to conduct experiments in mussel cultivation. For many years, mussels had been gathered commercially from these beds to supply bait for long-line fishing. Fullarton's efforts were hampered by continued fishing by local mussel fishermen. Prosecution of a mussel merchant (Maurice Parker) and two mussel fishermen for theft under the Mussel Fisheries (Scotland) Act 1847 was unsuccessful until a decree was obtained declaring that the Crown had "sole and exclusive property in and right to the mussel beds". Parker contested the validity of this decree in the Court of Session (the supreme civil court in Scotland) and appealed to the House of Lords, arguing that mussel fishermen had exercised a public right of gathering mussels in the Clyde estuary since time immemorial and also that shellfish legislation giving statutory powers to ministers to grant several and regulating orders had removed the Crown's right to grant mussel fishings. Ultimately, these arguments were rejected by the Courts and the decree was upheld. The House of Lords affirmed the decision of the Court of Session that the right to gather mussels (and the separate right to gather oysters) is personal to the Crown, rather than being held in trust for the public (Anon., 1902a,b, 1904).

A1.3 Statutory protection of private rights

McKay & Fowler (1997) erroneously stated that oysters and mussels were "removed from the public fishery" by the Oyster Fisheries (Scotland) Act 1840 (hereafter the 1840 Act) and the Mussel Fisheries (Scotland) Act 1847 (the 1847 Act), respectively. On the contrary, as noted in the case of Parker *v*. Lord Advocate (Anon., 1902b), rather than altering the rights to those species, these Acts recognised antecedent ownership by the Crown, private individuals and institutions. The 1840 and 1847 Acts (which are still in force) made it an offence of theft, punishable by imprisonment for up to one year, to remove oysters or mussels without permission from the owner of the "oyster bed, laying or fishery", or "mussel bed, scalp laying [*sic*], or fishery", respectively, in which they were located. Attempting to gather mussels or oysters with bottom-towed gear, or any other implement, without permission was made an offence of attempted theft, punishable by a fine (now level 1 on the standard scale) or a shorter prison term. The first prosecution under the 1840 Act was in 1842 and resulted from a boundary dispute in the Firth of Forth between oyster fishermen from Prestonpans and from Newhaven (Broun, 1844).

A1.4 Ownership of oysters

There seems to be some uncertainty in common law about the ownership of oysters themselves (as distinct from the right to gather them), which turns on the degree to which they can be considered to have attached to the substratum and, in legal terms, therefore, have "acceded" to the *solum* (ground). If oysters are judged to be *partes soli* (part of the ground), they are "heritable property" and belong to the proprietor of the ground to which they are attached (even though that proprietor may not have the right to gather them). In relation to mussels, the decision in the case of Parker *v.* Lord Advocate concluded that scalps (the rocks or banks of sand or mud on which mussels occur) were indeed *partes soli*, but it was left undecided whether the living mussels were (Anon., 1902b). The alternative view is that, because oyster beds include loose material and unattached oysters, the degree of attachment is insufficient for the principle of accession to apply. In that case, oysters would be "moveable property", *res nullius* (ownerless things) and would become the property of the first person to appropriate them by collection or by marking out for cultivation (Reid, 1993). This is the legal status of wild salmon under common law in Scotland. A wild salmon is ownerless until caught, when it becomes the property of its captor. However, if the captor did not have the right of salmon fishing in that place, he has committed a criminal offence and the fish is forfeit (Reid, 1993).

Since 1867, and now under the Sea Fisheries (Shellfish) Act 1967, legislation has provided that oysters on or in a privately-owned oyster bed "sufficiently marked out or sufficiently known as such", or in a bed that is the subject of a Several Order and marked out as directed by the Order, are the absolute property of the owner of the bed, or the grantee, respectively. If an oyster bed is not sufficiently marked out or sufficiently known as being privately-owned, ownership of the oysters is not ascribed by the 1967 Act and a charge of theft could not be maintained under the 1840 Act (which uses similar wording about demarcation and knowledge of private ownership). This may be the case with some natural oyster beds, or beds that were formerly cultivated but have been left unattended for some time. It was presumably for this reason that in the case of Parker *v.* Lord Advocate, it was necessary for the Crown to obtain a decree declaring ownership of mussel beds in the Clyde estuary before a prosecution for theft was successful (even though notices intimating ownership of the mussel beds had been posted in Port Glasgow in 1897). The 1967 Act indicates that measures to make ownership known may include buoying or otherwise marking the limits of an oyster bed and publishing, posting or distributing notices of the limits. In cases where ownership of an oyster bed is not adequately made known, the only recourse against unauthorised exploitation would seem to be civil proceedings to uphold an exclusive right to gather oysters.

Where native oysters occur at low density and many of them are not attached to the substratum, the question may arise as to what constitutes an "oyster bed". The Sea Fisheries (Shellfish) Act 1967 defines a "shellfish bed" as "any bed or ground in which shellfish are usually found or which is used for the propagation or cultivation of shellfish". No definition was given specifically for "oyster bed", but if the general definition can be applied to oysters, the term "usually found" suggests that the ground on which scattered oysters may lie could be considered an "oyster bed" if there is evidence that oysters have normally been present over some period of time leading to the present or ending only recently (depending on interpretation of the word "usually"). The definition does not indicate a minimum density of shellfish required to form a bed; indeed the word "usually" implies that at some times there may be no shellfish "in" the ground at all. Scattered oysters *may* therefore be considered to be in a bed and therefore afforded statutory protection by the 1840 and 1967 Acts, but this interpretation has not been tested in the courts, as far as we are aware.

A1.5 Interaction between common law and statute law

The Sea Fisheries (Shellfish) Act 1967 seems to create the possibility of a conflict between a statutory right and a common law right, because it defines the owner of the oysters themselves as the owner of the bed, rather than as the holder of the incorporeal property right of gathering oysters in that place. In Scots law, these may not be the same person. This situation may arise most commonly where the Crown has granted the foreshore or sea bed to a subject proprietor but has retained the right to gather oysters, or *vice versa*. For example, the proprietor of the Loch Ryan oyster fishery does not own the sea bed (Anon., 1902c). There may therefore be some uncertainty about the protection afforded by the Sea Fisheries (Shellfish) Act 1967 to oyster beds or fishings in Scotland in some circumstances. It should be noted that the ambiguity can be resolved by the proprietor or his lessees obtaining a Several Order, as has been done in relation to Loch Ryan to eliminate uncertainty about the rights to oysters on the foreshore there (D. Hugh-Jones, pers. comm., 2005). It is interesting to note that the wording of the 1840 Act (with application in Scotland only) acknowledges the distinction between ownership of the ground and of the fishings, and therefore appears to be more compatible with Scots law than the 1967 Act (with application in Great Britain).

Notwithstanding this potential legal complication, in many parts of Scotland, both the right of ownership of the ground and the right to gather oysters are retained by the Crown, and in some places both have been acquired by a single subject proprietor. In these cases, the legal situation is clear: the Crown or proprietor, as appropriate, has exclusive ownership of and right to the oysters on the ground. Taking oysters without permission would be in breach of the common law, an offence under the 1967 Act and an offence of theft under the 1840 Act.

A1.6 Situation after abolition of the feudal system

The Crown's rights in mussels and oysters in Scotland are part of the *regalia minora*, or minor property rights of the Crown, established with the introduction of the feudal system in the 12th century (Stewart, 1892). Where these rights were not 'alienated' (granted by the Crown), they were unaffected by the abolition of the feudal system of land tenure in Scotland in 2004 (Gill et al., 1998). Where a right to gather oysters was alienated, the holder of the feudal *dominium utile* of the right became the outright owner with the abolition of the feudal system, as with other types of heritable property in feudal tenure (Abolition of Feudal Tenure etc. (Scotland) Act 2000). In Scots law, the incorporeal right of oyster fishing is considered a type of "land" (Anon., 1902c).

In March 2003, as part of the ongoing process of land reform, the Scottish Law Commission proposed that the common law right to gather shellfish from the foreshore and seabed should become a statutory public right, and that this should be extended to include gathering of mussels and oysters, except where there has been an exclusive grant of the right to gather these species (Mackay et al., 2003). The Scottish Law Commission proposed that "if native oysters or mussels are or become endangered species", they can be protected by conservation legislation. Mackay et al. (2003) cited a successful legal action by Fife Council in 2002 to prevent commercial cockle (*Cerastoderma edule*) collection in Pettycur Bay, Firth of Forth. Commercial cockle collection in the Firth of Forth has subsequently been prohibited by a Special Nature Conservation Order (Anon., 2004), although the aim of that order was to protect the food source of sea bird species of conservation significance (Anon., 2003). Measures aimed directly at safeguarding shellfish stocks have, however, been made under fisheries legislation. For example, cockle collection using vessels or vehicles is prohibited in the Solway Firth [Inshore Fishing (Prohibition of Fishing for Cockles) (Scotland) Order 1995, as amended].

At the time of writing (September 2005), the Scottish Executive is considering how to proceed with reform of the law of the foreshore and seabed (Anon., 2005b). If a statutory public right to gather oysters is to be created, it would be advisable at the same time to implement and publicize statutory measures to protect native oyster populations from eradication by uncontrolled gathering. Any such statutory measures would need to be accompanied by clarification of who is to be responsible for enforcing them and consideration would need to be given to the resource implications of this decision.

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APPENDIX 2: NATIVE FLAT OYSTER, *OSTREA EDULIS*: MICROSATELLITE DATA SET FOR TFPGA

No of loci = 6

J12(34 alleles) **T5**(30) **U2**(30) **1/63**(13) **1/64**(19) **2/71**(6)

Max no of alleles = 34

No of populations = 13

Pop 1 Norway
Pop 2 Loch Eriboll
Pop 3 Kyle of Tongue
Pop 4 Skye
Pop 5 Loch Ailort
Pop 6 Sound of Ulva
Pop 7 NE Ulva
Pop 8 Loch na Keal
Pop 9 Loch Sween
Pop 10 West Loch Tarbert
Pop 11 Loch Ryan
Pop 12 Netherlands
Pop 13 Brittany

The initial number on each line of the input file indicates the population number.
Data are provided as genotypes at each locus. Alleles are numbered from 01 through to the highest number for each locus. (To link these numbers to actual allele sizes at each locus, see Tables 6.2(a)-(f) in main body of the report).
The genotype for the first locus is given as four numbers (e.g. first individual for Norway = 2323 – a homozygote for allele 23) followed by a comma, then the genotype at the second locus (1919, homozygote for allele 19) followed by a comma, the genotype at the third locus (1923, a heterozygote for alleles 19 and 23) and so on.
Where a genotype could not be scored for an individual, “0000” is entered.

Pop No.	J12	T5	U2	1/63	1/64	2/71

1, 2323,1919,1923,0607,1316,0404 Pop 1 **Norway**
1, 1111,1818,2226,0610,0916,0404
1, 1723,1922,0715,0609,1214,0404
1, 1119,0815,2022,0810,0916,0404
1, 2323,1818,0308,0708,0912,0404
1, 1924,0822,0308,0606,1215,0404
1, 2323,1818,1122,0709,1116,0404
1, 1717,0222,0319,0607,1116,0405
1, 2323,2222,2326,0610,0916,0404
1, 1125,2424,0308,0707,1114,0405

1, 2428,1520,2323,0710,1016,0405
1, 1115,0219,0808,0609,0916,0405
1, 1923,2222,0811,0810,0809,0000
1, 1127,1922,0408,0808,0916,0405
1, 2026,1520,0324,0909,0912,0404
1, 1719,1818,0823,0606,0916,0405
1, 1919,2224,0823,0608,0916,0404
1, 1919,1919,1922,0711,0913,0404
1, 1319,1922,0408,0707,1414,0404
1, 0000,0202,0320,0808,0916,0404
1, 2323,1822,0411,1010,1313,0404
1, 1923,1522,1519,0711,0909,0404
1, 1117,1822,0511,0609,0912,0405
1, 1923,1821,0819,0607,1616,0406
1, 1222,2227,0408,1111,1214,0405
1, 2424,1924,0919,0710,0810,0404
1, 2323,1822,0720,0607,0810,0404
1, 0000,1818,1123,0608,1016,0404
1, 2020,1518,0820,0608,0810,0404
1, 1923,1826,1023,0909,1016,0405
1, 1723,0202,2323,0609,1016,0404
1, 1115,2222,0820,0810,1417,0404
1, 2626,1822,0824,0607,1418,0404
1, 1119,2127,0308,0710,1016,0405

2, 0000,1315,0000,0710,0000,0000 Pop 2 **Loch Eriboll**
2, 0000,1012,0000,0711,0000,0000
2, 0000,1212,0000,0000,0000,0000
2, 0000,1022,0000,0811,0000,0000
2, 1527,1012,0000,0505,0000,0000
2, 0000,0209,0000,0910,0000,0000
2, 1515,1014,0000,1111,0000,0000
2, 1419,0209,0000,0911,0000,0000
2, 0000,0202,0000,0000,0000,0000
2, 0814,0909,0000,0911,0000,0000
2, 1420,0000,0000,1011,0000,0000
2, 1315,1212,0000,0810,0000,0000
2, 0000,0212,0000,0610,0000,0000
2, 0000,0210,0000,0610,0000,0000
2, 0000,1222,0000,0608,0000,0000
2, 1218,1012,0000,0610,0000,0000
2, 0813,0222,0000,0808,0000,0000
2, 0000,1212,0000,0808,0000,0000

3, 1727,0815,1321,0810,1314,0404 Pop 3 **Kyle of Tongue**
3, 1225,0000,0000,0606,1013,0404
3, 1619,0818,0814,0811,1319,0405
3, 1223,0822,0000,0505,1414,0404
3, 0000,0808,1010,0000,0000,0000
3, 1223,1116,1016,0510,1014,0404
3, 1520,0216,1017,0808,0000,0404
3, 1720,1124,2028,1010,0913,0405
3, 0000,1516,0505,1010,1414,0404
3, 0000,0808,0707,1010,0000,0404
3, 2020,1111,1120,0505,1414,0404

3, 1227,1516,0722,1010,1313,0404
3, 0616,0000,0606,0910,1415,0405
3, 0000,0815,0709,0909,1013,0404
3, 1214,0223,0912,0606,0000,0405
3, 1021,1116,1619,0505,1014,0405
3, 2024,0416,0808,0410,1314,0405
3, 0000,1625,0505,1010,1014,0000
3, 1010,0814,0822,1010,1414,0404
3, 1525,0208,0510,1010,1013,0405
3, 1022,1123,0512,0000,0000,0000
3, 1720,0202,0522,0000,0000,0000
3, 1727,0815,1321,0000,0000,0000
3, 1115,0808,1221,0000,0000,0000
3, 0909,0000,0000,0000,0000,0000
3, 1220,0811,0112,0606,1313,0404
3, 2024,1623,0111,0707,0910,0404
3, 1019,0216,0919,0000,0909,0405
3, 2323,1218,0920,0404,0913,0404
3, 1212,1118,0505,0407,0913,0404
3, 1012,1322,0512,0404,1414,0404

Pop 4 **Skye**

4, 0000,0208,0000,0409,0000,0000
4, 1220,0208,0000,0404,0000,0000
4, 1117,0823,0000,0000,0000,0000
4, 1123,0815,0000,0407,0000,0000
4, 1124,0816,0000,0000,0000,0000
4, 1111,1120,0000,0404,0000,0000
4, 1324,0811,0000,0606,0000,0000
4, 0000,0216,0000,0000,0000,0000
4, 2834,0208,0000,0404,0000,0000
4, 0812,1621,0000,0404,0000,0000
4, 2328,2124,0000,0404,0000,0000

Pop 5 **Loch Ailort**

5, 0330,0808,0707,0811,1213,0000
5, 1323,0202,1219,0000,1313,0404
5, 1115,0202,0621,0608,0913,0405
5, 1420,0212,0616,0808,0913,0404
5, 1114,0000,1226,0000,0000,0000
5, 1113,0000,2328,1012,0000,0505
5, 1114,0213,1524,0708,0909,0405
5, 1518,0707,1820,1010,1315,0404
5, 1822,0000,0609,0810,1212,0404
5, 0000,0927,0926,0000,1012,0405
5, 0816,0707,1616,0609,0913,0405
5, 1113,0225,1820,1010,1313,0405
5, 1025,0817,1315,0810,1013,0405
5, 0415,0808,0716,0710,1212,0404
5, 0000,1118,1622,0000,0912,0305
5, 0808,0000,1723,0910,0000,0404
5, 2525,0816,1822,0000,1012,0405
5, 0331,0000,1921,0911,0404,0000
5, 1222,1111,0921,0000,1010,0304
5, 1818,0000,1216,0000,0000,0405
5, 0923,1111,0913,0810,1013,0305
5, 0921,1818,1723,0000,0813,0000

5, 0923,2124,1616,0000,1013,0000
5, 0000,0208,1214,0709,1012,0000
5, 0000,0000,1522,0809,1313,0000
5, 0000,0000,0508,0407,1313,0000
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5, 0609,0216,1618,0709,1010,0304
5, 0000,0000,0000,0505,0000,0000
5, 0000,0213,0000,0709,0000,0000
5, 0000,0211,0000,0505,0000,0000
5, 0922,0811,0000,0000,0000,0000
5, 0000,0811,0000,0505,0000,0000
5, 0000,0911,0000,0608,0000,0000
5, 0000,0809,0000,0505,0000,0000
5, 1922,0202,0000,0606,0000,0000
5, 1126,0202,0000,0507,0000,0000
5, 1629,0918,0000,0000,0000,0000
5, 0000,0202,0000,0000,0000,0000
5, 1124,0202,0000,0000,0000,0000
5, 0000,0202,0000,0000,0000,0000
5, 2222,0213,0000,0000,0000,0000
5, 1119,0909,0000,0000,0000,0000
5, 1623,0000,0000,0000,0000,0000
5, 1111,0202,0000,0000,0000,0000
5, 2626,0202,0000,0912,0000,0000
5, 1616,0911,0000,0404,0000,0000
5, 1616,0219,0000,0000,0000,0000

Pop 6 **Sound of Ulva**

6, 0719,0215,0812,0810,0913,0000
6, 0000,1116,0112,0609,1313,0000
6, 0820,0808,0112,0808,1113,0000
6, 0221,0808,0120,0106,0911,0000
6, 0215,0216,1125,0106,0415,0000
6, 0523,0814,1416,0607,0916,0000
6, 0824,1124,1316,0310,1013,0000
6, 0205,0509,0524,0708,1010,0000
6, 0808,0811,0115,0310,1313,0000
6, 0221,0811,0120,0106,1013,0000
6, 0220,0208,0126,0106,1313,0000
6, 0221,0818,0120,0410,0913,0000
6, 0707,0818,0512,0808,1013,0000
6, 0215,0824,2020,0106,1112,0000
6, 0720,1118,0112,0808,0000,0000
6, 0303,0815,1529,0808,1414,0000
6, 0222,0808,0112,0608,1014,0000
6, 0810,0811,1424,0707,1017,0000
6, 1018,1111,0616,0000,1113,0000
6, 0721,1828,0901,0000,0610,0000
6, 1024,0216,0716,0000,0811,0000
6, 1823,1521,0928,0000,1414,0000
6, 0223,0808,0120,0000,0909,0000
6, 0223,1118,0520,0000,1313,0000
6, 1313,0817,0000,1010,0000,0000
6, 0000,0808,0000,0000,0000,0000
6, 0813,0817,0000,0000,0000,0000
6, 1722,1425,0000,0000,0000,0000

6, 1625,0816,0000,0411,0000,0000
6, 1313,1717,0000,1011,0000,0000
6, 0822,0808,0000,0810,0000,0000
6, 1422,0817,0000,1010,0000,0000
6, 1212,0808,0000,0808,0000,0000
6, 1414,0808,0000,0810,0000,0000
6, 1313,1717,0000,0000,0000,0000
6, 0822,0812,0000,0000,0000,0000
6, 2020,1219,0000,0000,0000,0000
6, 1224,0819,0000,0909,0000,0000
6, 1212,0808,0000,1010,0000,0000
6, 1422,0817,0000,0911,0000,0000
6, 2226,1822,0000,0909,0000,0000
6, 1414,0817,0000,0913,0000,0000
6, 0814,0202,0000,0909,0000,0000
6, 1217,0820,0000,0000,0000,0000

Pop 7 **North East Ulva**

7, 1723,1515,0923,0305,1414,0404
7, 0000,0000,0909,0506,1010,0405
7, 1026,0815,1526,0608,0000,0000
7, 1723,0208,0000,0000,0000,0000
7, 0000,0216,1520,0407,1010,0404
7, 1921,0208,1012,0506,1414,0405
7, 0110,0209,1522,0000,0000,0000
7, 1224,0815,1219,0000,0000,0000
7, 0621,0919,1223,0507,1414,0404
7, 0912,0821,0307,0607,0000,0000
7, 1033,0811,1416,0404,1313,0305
7, 1020,0820,0916,0510,1313,0105
7, 0000,1115,1319,0506,0000,0505
7, 0000,0819,0808,0606,1313,0404
7, 1929,0000,2020,1010,0913,0000
7, 1920,0420,1018,0507,0913,0404
7, 0000,0815,1616,0303,1313,0404
7, 2727,0811,0306,0404,0913,0405
7, 3333,1114,1825,0305,1414,0405
7, 1214,0202,1822,0507,1014,0404
7, 2127,0811,1315,0710,0000,0000
7, 1212,1420,0613,0303,0000,0000
7, 0000,1515,1320,0303,0000,0000
7, 1433,0000,0915,0304,0000,0000
7, 1423,0815,0720,0000,0000,0000
7, 1014,0808,0813,0000,0000,0000
7, 1329,1518,0314,0000,0000,0000
7, 1722,0811,1226,0000,0000,0000
7, 1627,1818,0921,0000,0000,0000
7, 1025,1111,1120,0000,0000,0000
7, 1127,0101,2228,0000,0000,0000
7, 2525,0815,2024,0000,0000,0000
7, 0707,0210,0000,0507,0000,0000
7, 2323,0217,0000,0505,0000,0000
7, 1010,0000,0000,0000,0000,0000
7, 0000,0924,0000,0000,0000,0000
7, 1122,1717,0000,0711,0000,0000
7, 1630,0924,0000,0707,0000,0000

7, 2020,0000,0000,1010,0000,0000
7, 2028,0915,0000,0000,0000,0000
7, 1118,0817,0000,0000,0000,0000
7, 1118,0621,0000,1013,0000,0000
7, 1218,0918,0000,1013,0000,0000
7, 0911,0915,0000,0000,0000,0000
7, 1622,1717,0000,0507,0000,0000
7, 1010,0909,0000,0000,0000,0000
7, 1022,0202,0000,0000,0000,0000
7, 1010,1021,0000,0000,0000,0000
7, 0000,0000,0000,0505,0000,0000
7, 2222,0000,0000,0711,0000,0000
7, 1616,0915,0000,0000,0000,0000
7, 2222,1111,0000,0505,0000,0000

8, 1320,0811,0000,0000,0000,0000 Pop 8 **Loch na Keal**
8, 1322,0916,0000,0000,0000,0000
8, 0000,1930,0000,0000,0000,0000
8, 1021,1925,0000,0000,0000,0000
8, 0000,0814,0000,0000,0000,0000
8, 1225,0808,0000,0000,0000,0000
8, 0000,0208,0000,0000,0000,0000
8, 2121,0821,0000,0000,0000,0000
8, 1724,0208,0000,0000,0000,0000
8, 1625,0923,0000,0000,0000,0000
8, 1315,0215,0000,0000,0000,0000
8, 1215,0626,0000,0000,0000,0000
8, 0000,0722,0000,0000,0000,0000
8, 1124,0609,0000,0000,0000,0000
8, 1225,0609,0000,0000,0000,0000
8, 1522,1818,0000,0000,0000,0000
8, 1125,2020,0000,0000,0000,0000
8, 1522,0921,0000,0000,0000,0000
8, 0821,1425,0000,0000,0000,0000
8, 1129,0707,0000,0000,0000,0000
8, 0000,0608,0000,0000,0000,0000
8, 0000,0415,0000,0000,0000,0000
8, 0000,0622,0000,0000,0000,0000
8, 1923,0408,0000,0000,0000,0000
8, 1414,0421,0000,0000,0000,0000
8, 0000,0821,0000,0000,0000,0000
8, 0912,0608,0000,0000,0000,0000
8, 0000,1521,0000,0000,0000,0000
8, 1212,0810,0000,0000,0000,0000
8, 1419,0808,0000,0000,0000,0000
8, 1216,0404,0000,0000,0000,0000
8, 0909,0421,0000,0000,0000,0000
8, 1212,0810,0000,0000,0000,0000
8, 0000,0821,0000,0000,0000,0000
8, 0000,0404,0000,0000,0000,0000

9, 1120,0202,1219,0810,1013,0404 Pop 9 **Loch Sween**
9, 0000,0211,1314,1011,0913,0405
9, 0000,0814,0507,1011,1013,0405
9, 1015,0217,1725,0808,0913,0405

9, 0712,0213,1417,0810,1013,0404
9, 0000,0508,0822,0308,0913,0505
9, 0612,0922,0723,0809,1212,0505
9, 1518,1717,1215,0810,1013,0505
9, 0711,0219,0815,0609,1313,0305
9, 1122,0211,0307,0810,1013,0405
9, 0000,0515,1219,0609,1213,0404
9, 1125,0823,0712,0810,0913,0405
9, 1122,0209,0512,0312,1013,0404
9, 0831,0219,1717,0311,1313,0404
9, 0731,0521,1014,0910,1013,0405
9, 0716,1521,1423,0809,1313,0404
9, 1623,0508,2020,0709,0913,0505
9, 1628,0000,0508,0808,0910,0304
9, 0000,1519,0512,0709,1213,0404
9, 1925,0209,0507,0608,0913,0404
9, 1219,0205,0818,0811,0913,0000
9, 0000,0208,1223,0606,1313,0405
9, 1920,0811,1327,0310,0913,0304
9, 0716,0212,0820,0810,0913,0404
9, 1330,1123,1818,0310,1313,0405
9, 1111,0225,1323,0810,1313,0404
9, 1919,1313,0000,0810,0808,0404
9, 1111,0205,1302,0210,0913,0404
9, 1016,0208,0000,0611,0000,0000
9, 1027,0202,0000,0808,0000,0000
9, 1313,0208,0000,0810,0000,0000
9, 1010,0210,0000,0808,0000,0000
9, 1622,0212,0000,0000,0000,0000
9, 1021,0000,0000,1010,0000,0000
9, 1010,0202,0000,0808,0000,0000
9, 1522,1214,0000,0811,0000,0000
9, 1016,0220,0000,0813,0000,0000
9, 1022,0512,0000,0810,0000,0000
9, 1010,0808,0000,0808,0000,0000
9, 1622,1318,0000,0811,0000,0000
9, 1525,0808,0000,0912,0000,0000
9, 0622,0202,0000,1111,0000,0000
9, 1521,1216,0000,0810,0000,0000
9, 1010,0202,0000,0000,0000,0000
9, 1010,1212,0000,0808,0000,0000
9, 0810,0000,0000,1011,0000,0000
9, 1515,1212,0000,0709,0000,0000
9, 0306,0000,0000,0911,0000,0000

Pop 10 **West Loch Tarbert**

10, 0909,0825,0719,0809,1416,0405
10, 1126,0808,1521,0610,1016,0404
10, 1131,0218,0716,0809,1114,0404
10, 1524,0820,1115,0610,1114,0405
10, 0929,0215,0812,0709,1111,0000
10, 0508,0821,1017,0910,1111,0404
10, 0000,0000,0612,0607,1216,0404
10, 0000,0211,0623,0606,1416,0405
10, 1919,0208,1223,1212,1415,0404
10, 0930,1120,1222,0707,1016,0405

10, 1129,0000,1017,0507,1616,0404
10, 1718,0823,0815,0707,1016,0505
10, 0000,0220,0813,0707,1111,0404
10, 0924,0811,0508,0709,1414,0405
10, 1726,0808,1414,0610,1114,0404
10, 1313,0808,1818,0507,1014,0405
10, 1332,0811,0817,0507,1415,0405
10, 0509,0817,1220,0607,1011,0405
10, 0917,0815,1421,0707,1414,0505
10, 0519,0819,0723,0708,1414,0405
10, 0921,1518,1830,0808,1114,0404
10, 1930,0821,1523,0609,1515,0104
10, 0000,0211,1115,0912,1115,0505
10, 1314,0818,1212,0609,1116,0405
10, 0000,0817,0000,0000,0000,0000
10, 0909,0815,0000,0708,0000,0000
10, 0000,1217,0000,0709,0000,0000
10, 0000,1824,0000,0000,0000,0000
10, 0922,1824,0000,0000,0000,0000
10, 0909,0821,0000,1111,0000,0000
10, 0000,0209,0000,0410,0000,0000
10, 0000,0815,0000,0808,0000,0000
10, 1017,1717,0000,0610,0000,0000
10, 1010,0420,0000,0608,0000,0000
10, 1115,0817,0000,0000,0000,0000
10, 0505,1218,0000,0809,0000,0000
10, 0817,0208,0000,0710,0000,0000
10, 0505,1517,0000,0809,0000,0000
10, 0000,0820,0000,0000,0000,0000
10, 1111,1717,0000,0912,0000,0000
10, 0505,0812,0000,0811,0000,0000
10, 0000,0404,0000,0909,0000,0000
10, 1717,0808,0000,0000,0000,0000
10, 0000,0202,0000,0808,0000,0000

Pop 11 **Loch Ryan**

11, 0729,0225,1621,0910,1115,0405
11, 1122,0830,0314,0000,0000,0105
11, 0000,0202,2527,0306,0514,0405
11, 1927,0213,0923,0808,0613,0405
11, 0718,0000,0711,0707,1414,0405
11, 0718,1111,1212,1010,1014,0405
11, 0000,1523,0520,0809,0714,0204
11, 1221,0211,0812,0000,1414,0405
11, 0000,1623,0418,0810,0614,0105
11, 0812,0223,0509,0707,1414,0304
11, 0000,0222,0407,0410,0513,0405
11, 0000,0808,1218,0310,0513,0305
11, 1225,1221,0707,0310,0000,0000
11, 1212,0221,0606,0608,0111,0404
11, 0808,0202,1421,0000,1313,0000
11, 0000,0811,0507,1010,0614,0505
11, 1224,1116,0925,0911,0713,0405
11, 1414,0808,0707,0000,0512,0404
11, 1722,1321,0613,0909,1013,0405
11, 0000,0000,1116,1111,1414,0104

11, 1625,1722,1010,0709,0310,0304
11, 0707,0000,1620,0000,0106,0404
11, 0000,0000,0609,0000,0000,0304
11, 0711,0000,1520,1011,1414,0405
11, 1824,0208,1316,0404,1313,0104
11, 1116,0208,1113,0511,0209,0000
11, 0000,1121,1010,0811,0309,0404
11, 0000,1316,0716,0909,1313,0405
11, 1919,0224,0000,0909,0000,0000
11, 0821,0218,0000,1011,0000,0000
11, 1414,0209,0000,0909,0000,0000
11, 1521,0928,0000,0909,0000,0000
11, 1525,1418,0000,0909,0000,0000
11, 1419,0202,0000,0509,0000,0000
11, 1224,1827,0000,0609,0000,0000
11, 0827,1824,0000,1010,0000,0000
11, 0000,0909,0000,0811,0000,0000
11, 1517,0216,0000,0000,0000,0000
11, 1422,0216,0000,0912,0000,0000
11, 0000,0209,0000,0911,0000,0000
11, 2121,1212,0000,0910,0000,0000
11, 0000,0000,0000,1010,0000,0000
11, 1517,0212,0000,0000,0000,0000
11, 0812,0228,0000,0000,0000,0000
11, 0822,0512,0000,0000,0000,0000
11, 0000,0000,0000,0000,0000,0000
11, 1723,0202,0000,0000,0000,0000
11, 0808,1825,0000,0000,0000,0000

Pop 12 **The Netherlands**

12, 0000,1318,0000,0000,0000,0000
12, 0000,1217,0000,0000,0000,0000
12, 2121,1723,0000,0608,0000,0000
12, 1725,1426,0000,0000,0000,0000
12, 0000,0919,0000,0000,0000,0000
12, 0000,1426,0000,0606,0000,0000
12, 1021,0617,0000,0812,0000,0000
12, 0000,0914,0000,0408,0000,0000
12, 1325,0325,0000,0408,0000,0000
12, 1725,0309,0000,0000,0000,0000
12, 0000,1723,0000,0000,0000,0000
12, 1212,1723,0000,0000,0000,0000
12, 0000,0000,0000,0411,0000,0000
12, 0000,0811,0000,0000,0000,0000
12, 1123,1214,0000,0404,0000,0000
12, 2828,0815,0000,0000,0000,0000
12, 0924,1823,0000,0000,0000,0000
12, 0928,1318,0000,0409,0000,0000
12, 0000,1419,0000,0000,0000,0000
12, 0000,0202,0000,0000,0000,0000

Pop 13 **Brittany**

13, 0811,2529,0000,0000,0000,0000
13, 1111,0309,0000,0410,0000,0000
13, 1123,0000,0000,0409,0000,0000
13, 1322,0000,0000,0000,0000,0000
13, 0819,1219,0000,1010,0000,0000

13, 0823,0000,0000,0407,0000,0000
13, 1819,0219,0000,0810,0000,0000
13, 1317,1827,0000,0000,0000,0000
13, 0000,0000,0000,0000,0000,0000
13, 0000,1718,0000,0000,0000,0000
13, 0808,0918,0000,0000,0000,0000
13, 1724,0000,0000,0406,0000,0000
13, 1622,1925,0000,0000,0000,0000
13, 1212,1818,0000,0000,0000,0000
13, 1225,1114,0000,0000,0000,0000
13, 1219,1823,0000,0000,0000,0000
13, 1212,0618,0000,0000,0000,0000
13, 1924,1926,0000,0000,0000,0000
13, 1127,0303,0000,0000,0000,0000
13, 0000,1220,0000,0000,0000,0000
13, 0000,0000,0000,0000,0000,0000