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Soft sediment ecology of Lough Hyne Marine Reserve

-spatial and temporal patterns

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This thesis is presented to University College Cork, in candidature for the degree of

Doctor of Philosophy

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DECLARATION

I hereby declare that this thesis for the degree of Doctor of Philosophy submitted to the National University of Ireland, Cork is my own work and has not been previously submitted for another degree to this or any other university.

Signature

Date

ACKNOWLEDGEMENTS

‘Work with those that have both, knowledge and integrity’ reads a small fortune cookie slip that I got just before I came to Cork and for some reason it survived the journey across the Irish Sea and so I stuck it to my computer screen when I first got it (the PC screen). As it turned out I had the pleasure and good fortune to work with two people to whom this saying holds true: my very heartfelt thanks and best wishes for their respective futures go to my supervisors Dr Rob McAllen and Prof. John Davenport. Many thanks also to Dr Ruth Ramsay, my advisor.

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ABSTRACT

Distribution of soft sediment benthic fauna and the environmental factors affecting them were studied, to investigate changes across spatial and temporal scales. Investigations took place at Lough Hyne Marine Reserve using a range of methods. Data on the sedimentation rates of organic and inorganic matter were collected at monthly intervals for one year at a number of sites around the Lough, by use of vertical midwater-column sediment traps. Sedimentation of these two fractions were not coupled; inorganic matter sedimentation depended on hydrodynamic and weather factors, while the organic matter sedimentation was more complex, being dependent on biological and chemical processes in the water column. The effects of regular hypoxic episodes on benthic fauna due to a natural seasonal thermocline were studied in the deep Western Trough, using camera-equipped remotely-operated vehicle to follow transects, on a three-monthly basis over one year. In late summer, the area below the thermocline of the Western Trough was devoid of visible fauna. Decapod crustaceans were the first taxon to make use of ameliorating oxygen conditions in autumn, by darting below the thermocline depth, most likely to scavenge. This was indicated by tracks that they left on the surface of the Trough floor. Some species, most noticeably Fries' goby *Lesueurigobius friesii*, migrated below the thermocline depth when conditions were normoxic and established semi-permanent burrows. Their population encompassed all size classes, indicating that this habitat was not limited to juveniles of this territorial species. Recolonisation by macrofauna and burrowing megafauna was studied during normoxic conditions, from November 2009 to May 2010. Macrofauna displayed a typical post-disturbance pattern of recolonisation with one species, the polychaete *Scalibregma inflatum*, occurring at high abundance levels in March 2010. In May, this population had become significantly reduced and a more diverse community was established. The abundance of burrowing infauna comprising decapods crabs and Fries' gobies, was estimated by identifying and counting their distinctive burrow structures. While above the summer thermocline depth, burrow abundance increased in a linear fashion, below the thermocline depth a slight reduction of burrow abundance occurred in May, when oxygen conditions deteriorated again. The majority of the burrows occurring in May were made by Fries' gobies, which are thought to encounter low oxygen concentrations in their burrows. Reduction in burrow abundance of burrowing shrimps *Calocaris macandreae* and *Callianassa subterranea* (based on descriptions of burrow structures from the literature), from March to May, might be related to their reduced activity in hypoxia, leading to loss of structural burrow maintenance. Spatial and temporal changes to macrofaunal assemblage structures were studied seasonally for one year across 5 sites in the Lough and subject to multivariate statistical analysis. Assemblage structures were significantly correlated with organic matter levels in the sediment, the amounts of organic matter settling out of the water column one month before macrofaunal sampling took place as well as current speed and temperature. This study was the first to investigate patterns and processes in the Lough soft sediment ecology across all 3 basins on a temporal and spatial scale. An investigation into the oceanographic aspects of the development, behaviour and break-down of the summer thermocline of Lough Hyne was performed in collaboration with researchers from other Irish institutions.

Chapter 1

General introduction

Sublittoral soft sediment ecology

Seventy-one percent of the world is covered by sea-water, and most of the ocean floor is made up of soft sediments, so soft sediments are the second largest habitat on Earth after the water column (Snelgrove 1999). At the inner continental shelves, muds and sands are most common (37% and 47% of areas, respectively), while hard substrata (bedrock to cobble) are relatively rare (only 6%). The rest of the substratum is biotic in origin, being made up of maerl, living/dead shells and reefs (Kaiser et al. 2005). The size of the particles making up the substratum depends on hydrodynamic forces. Large particles such as cobble and sand settle out in high energy areas, while smaller and less dense particles such as silt and organic matter settle in areas of low current speeds, such as bays and inlets (Gray 1974, Gray & Elliott 2009). Hydrodynamic forces are also responsible for the sorting of particles, because soft sediments are rarely made up of one homogenous sediment type and grain size. The degree of mixing of grain sizes in a sample, also called sorting, can be represented by the sorting coefficient. A well-sorted substratum is found in high energy areas, while poorly sorted sediments occur in areas of low current flow. Large grains lead to large interstitial spaces, allowing water exchange and deep oxygen penetration into the sediment, while small grain sizes or poorly sorted sediments pack tightly together, and oxygen cannot penetrate as deeply. This sediment variability is correlated with the physicochemical properties of the substratum, making it either hospitable or non-hospitable to benthic marine fauna (Gray 1974, Thrush & Townsend 1986). Environmental gradients can be steep, especially in muddy sediments, where oxygen only penetrates a few millimetres into the sediments and therefore changes the redox potential from positive to negative (Snelgrove et al. 2000).

Invertebrates make up the majority of animals living in and on sediments. Animals living within the sediment are termed infauna, whilst animals living on the sediment surface, such as scallops, crabs and starfish are called epifauna (Snelgrove 1999). Infaunal animals are categorised by size, based mainly on the mesh size of sieves used to retain them. Microfauna are <63 µm, meiofauna 63-500 µm, and macrofauna 500 µm to approximately 5 cm. Invertebrates >5 cm in linear dimension are termed megafauna (Gray & Elliott 2009). These categories differ slightly in the literature; with some authors using sieves of 300 µm to collect macrofauna, while others use 1 mm sieves, depending on the research question and sampling location. Fauna retained in sieves with 300 µm aperture size and larger consist predominantly of species of the following phyla: Polychaeta, Mollusca, Crustacea and Echinodermata (Snelgrove 1999, Gray & Elliott 2009). Polychaete worms are most common, followed by bivalve molluscs, crustaceans and echinoderms (Snelgrove 1999). The mobility of infaunal animals as adults is often limited; many are sessile and depend on food from the water column (Snelgrove et al. 2000).

Most marine benthic invertebrates have a meroplanktonic larval stage which aids in the dispersal of populations (Thorson 1950). Larvae are capable of choosing suitable substrata aided by cues such as the presence of adult conspecifics, or appropriate organic matter contents and grain sizes, even though many of them are weak swimmers (Thorson 1950, Gray 1974). Large grain sizes in high current speeds can dislodge or kill soft shelled animals, while small particles such as silt can clog gills or feeding apparatus of some animals (Gray 1974).

Ocean currents, water depth and sediment type, combined with relatively long planktonic stages, lead to large-scale distribution patterns of benthic fauna, often spanning kilometres (Thorson 1950, Morrisey et al. 1992). The shape of coasts influences hydrodynamic forces and can lead to regional-scale distribution of environmental factors and benthic communities. Headlands and bays can change the current pattern, by reducing current speeds, leading to patchiness in meroplanktonic distribution and subsequent settlement to the benthos (Sponaugle et al. 2002, Rawlinson et al. 2005, Jessopp & McAllen 2008, von der Meden et al. 2012). Internal waves can also concentrate planktonic organisms, especially along coasts which can enhance patchy distribution of recruits (Lennert-Cody & Franks 1999). Small-scale heterogeneity of benthic communities is often maintained by biological processes such as predation and competition (Thrush 1986a, Morrisey et al. 1992). The size of small patches in soft sediments can vary from a few cm^2, caused by bioturbation of burrowing infauna, to several m^2 depending on local levels of disturbance, and the particular species affected by it. For example, Thrush (1986b) showed that accumulations of seaweed spreading approximately 1 m^2 over the seabed could affect benthic macrofaunal communities directly underneath and in close vicinity to the patch. This great variability of environmental factors leads to a mosaic of patches of faunal distribution (Morrisey et al. 1992).

Environmental conditions and communities also change over temporal scales. Changes over short time scales are often tide-driven, such as changes to salinity or temperature in estuaries, which occur over a matter of hours. Short-term periodic hypoxia can occur in some estuaries and last for several days (Pihl et al. 1991). Organic matter production in the water column is affected by seasonal fluctuations of sunlight and temperatures, especially in temperate and boreal seas (Smetacek et al. 1978, Riebesell 1989). The release of planktonic larvae of marine invertebrates is therefore often synchronised with phytoplanktonic blooms, so that planktotrophic larvae can make use of the abundant food source in the water column (Riebesell 1989).

Important environmental processes for benthic communities include the sedimentation of organic and inorganic matter and the ratios between them (Snelgrove 1999, Gray & Elliott 2009). Benthic organisms depend on organic matter settling out from the water column as a food source, especially in areas where sunlight cannot penetrate and therefore no primary production takes place (Quijón et al. 2008). Phytoplankton blooms occur in spring and autumn at temperate latitudes and provide fresh organic matter to the benthic communities once the bloom dies off (Smetacek 1980, Graf et al. 1982, Riebesell 1989). Surface productivity is enhanced in situations where eutrophication leads to excess nutrients in the water column. Enhanced surface water column productivity in turn leads to higher rates of deposition of organic matter onto the seafloor. This at first increases benthic productivity, with higher faunal biomasses and increased microbial activity. However, consequently the higher biological oxygen demand of the benthos can lead to local hypoxia and anoxia (Pearson & Rosenberg 1978, Heip 1995, Diaz & Rosenberg 2008). Diaz and Rosenberg (1995) defined hypoxia in the marine environment as corresponding to an oxygen content of 2.0 ml l^{-1} (2.8 mgl^{-1}) or less; a complete lack of oxygen is termed anoxia. However, Vaquer-

Sunyer and Duarte (2008) reviewed the literature on oxygen levels necessary for the survival for different taxa of animals and suggested that the value of 2.8 mg l^{-1} is set too low for many phyla and therefore that current management strategies to improve coastal oxygen conditions do not aim at high enough levels of oxygen in the water column.

Hypoxic conditions can occur anywhere in the marine environment, in the open sea they are mostly caused by strong upwelling, leading to oxygen minimum zones which can affect waters from 10 m to below shelf depths (Levin 2003). In coastal areas, four types of hypoxia have been recognised (Kemp et al. 2009). Permanent hypoxia is found in fjords and bays which are deeper than 100 m and are permanently stratified due to restricted circulation. Persistent seasonal hypoxia occurs in bays and estuaries up to a depth of 50 m, where seasonal water column stratification leads to reduced water exchange between bottom water and the surface. Episodic hypoxia occurs in productive microtidal bays with depths to 15 m, where wind is a main driver for water mixing, while diel hypoxia is typical in shallow bays where nocturnal biological oxygen consumption outstrips supply and is replenished during daytime due to photosynthesis in the water column (Kemp et al. 2009).

On an organism level, hypoxia at first leads to increased attempts by the animal to maintain oxygen delivery, for example by means of faster respiration rates or increase of oxygen carrying pigments but during periods of prolonged hypoxia animals reduce their activity and metabolic rate (Wu 2002). Mobile fauna, such as fish or non-burrowing crustaceans will move out of hypoxic areas, affecting faunal assemblages in nearby areas and causing changes to fisheries success (Wu 2002). Animals living in soft sediments are adapted to dealing with hypoxic conditions, and also with hydrogen sulphide. For example, thalassinidean shrimp build burrows in marine soft sediments and there, they are exposed to low oxygen and high hydrogen sulphide conditions, as well as hypercapnia (Atkinson & Taylor 2005). Adaptations to these conditions include lower oxygen consumption rates as compared to non-burrowing crustaceans, haemocyanins with high oxygen affinities and moderate Bohr values (which facilitate oxygen uptake during hypoxia) (Atkinson & Taylor 2005). Hypoxia can eliminate sensitive species, cause a reduction in growth rates and reproductive success leading to changes to the ecosystem (Wu 2002, Vaquer-Sunyer & Duarte 2008, Ekau et al. 2010).

Sheltered bays and estuaries with low water exchange rates can develop thermoclines which exacerbate hypoxic conditions because the water below the thermocline cannot be exchanged readily with oxygen-rich surface water. Geological evidence indicates that hypoxia in the marine environment has occurred naturally for millennia, but it is known to be spreading and intensifying due to anthropogenic eutrophication, particularly in coastal areas (Pearson & Rosenberg 1978, Diaz & Rosenberg 1995). The development of extensive anoxic conditions can lead to massive die-off events of benthic communities on a periodic or seasonal scale, which is followed by recolonisation in the winter (Rosenberg 1973, Kitching et al. 1976, Pearson & Rosenberg 1978, Tunnicliffe 1981). Opportunists often lead recolonisation and make use of plentiful organic matter that collected during the hypoxic event. Mobile fauna such as fish and epifaunal decapods move out of affected areas and return once conditions improve (Tunnicliffe 1981, Pihl et al. 1991, Breitburg 1992, Breitburg 2002, McAllen et al. 2009).

Marine hypoxic regions are predicted to spread even more in the future, due to further eutrophication driven by human population increases and agricultural intensification. This will be aggravated by increasing temperatures due to predicted climate change, that lead to greater stratification of the water column (Diaz & Rosenberg 2008, Vaquer-Sunyer & Duarte 2008). Additionally, increasing water temperatures cause higher metabolic rates in organisms and this can change life history traits, which may affect population size and biogeography (Pörtner & Farrell 2008, Hoegh-Guldberg & Bruno 2010).

The study site: Lough Hyne

Lough Hyne is situated on the southwest coast of Ireland (51°30” N, 9°18” W). It is a small marine lake (0.5 x 1 km), connected to the Atlantic via the Rapids, a narrow (<25 m) and shallow channel (a maximum of 4 m depth at high spring tide). The Rapids flow into the Lough at the Southeast Corner of the South Basin and are connected to Barloge Creek, a small natural harbour leading into the Atlantic. Barloge Creek (~2 m at low tide) also belongs to the marine reserve and the sandy sea floor is covered by seagrass and algae (Grave & Holmes 1998). A North and a South Basin, each 20-25 m deep, are separated by Castle Island. The Western Trough is much deeper with a maximum depth of 48 m (McAllen et al. 2009) and it connects the South and North Basin on the West. As opposed to many other coastal bays, freshwater influx is negligible at a volume of approximately 0.1 % of the Lough volume day^{-1} (Johnson & Costello 2002). Weather conditions are essentially constant across the entire study area due to its small size. In 1981, it became a marine reserve; since then it has been a no-take zone and anthropogenic disturbances such as dredging and trawling do not take place. However, an increase in nutrients from coastal waters has been measured in recent years (Jessopp et al. 2009). Even though the Lough is comparatively small, it features a wide variety of habitats ranging from rocky intertidal and subtidal cliffs to soft sediments which cover the South and North Basin as well as the Western Trough from a depth of approximately 12 m down (Bassindale et al. 1957, Kitching et al. 1976).

Due to the narrow inlet of the Rapids, the Lough also exhibits a wide range of current speeds from high at the Rapids (< 3 m s^{-1}) to virtually still water (< 0.001 m s^{-1}) in the North Basin (Bassindale et al. 1948). Water exchange is driven by tides and a shallow sill within the Rapids leads to a semi-diel, asymmetric tidal regime inside the Lough, with water flowing in over 4 hours and flowing out for 8.5 hours. Complete water exchange of the Lough has been calculated to take 80 days (Jessopp et al. 2009), effectively doubling a previously calculated estimation of 41 days (Johnson et al. 1995). The flora and fauna inhabiting Lough Hyne are marine (Bassindale et al. 1948) and biodiversity is high (Lilly et al. 1953, Costello & Myers 1991, Picton 1991, Bell & Barnes 2000).

Each summer, a thermocline forms at a depth of 25-26 m, affecting the Western Trough. Oxygen levels decline and H_2S forms below the thermocline during the course of the summer. In autumn, the thermocline breaks down once the top layers of water cool sufficiently, though autumn storms also have a role. In winter, the water column is normoxic. This thermocline and its effects on the fauna of Lough Hyne have been studied for decades, though it is likely to have occurred for millennia (Bassindale et al. 1957, Kitching et al. 1976, Rawlinson et al. 2004, McAllen et al. 2009). Kitching et al. (1976) investigated the changes in the soft sediment communities in the Western Trough over the course of three summers (1970-1972) using SCUBA surveys, crab potting and sediment sampling. They found that the abundance of animals was greatly reduced in the later months of summer each year (Kitching et al. 1976). They also noted that animals were most severely affected in the deeper parts of the Western Trough. They therefore suggested that anoxic and hydrogen sulphide rich water forms in the deeper parts at 48 m first, and subsequently spreads upwards to approximately 26 m. Rawlinson et al. (2004) studied vertical migration behaviour of zooplankton in the water column in the Western Trough and they discovered that the majority of zooplankton species avoided the water below the thermocline and adjusted their vertical migration patterns to stay above it. This was also confirmed by Hawkins et al. (2012), who demonstrated that water below the thermocline was clear of zooplankton in acoustic echograms at a depth of approximately 25 m. McAllen et al. (2009) utilised SCUBA surveys, crab potting and transect surveys using a camera attached to a remotely operated vehicle (ROV) to study changes in the benthic communities of the Western Trough. They compared communities present during hypoxic conditions with those occurring during winter, when conditions were normoxic. They observed that scavengers and predators used the improving oxygen conditions after break-down of the thermocline to dart below the thermocline depth, most likely to access food in the form of macrofauna that had died during anoxic conditions and moved up onto the top of the mud.

Study overview

Lough Hyne provides a unique set of features to facilitate the study of benthic fauna and the environmental factors affecting them. It is small, relatively shallow and sheltered, allowing for work to be carried out from small boats nearly 365 days per year. It is undisturbed by fisheries and the seasonal thermocline provides a model system for the global problem of hypoxia and its effects on marine communities. Due to the wide range of current speeds, it also provides an ideal study site for the investigation of coastal oceanographic processes such as sedimentation of organic and inorganic matter.

Using Lough Hyne Marine Reserve for the study of coastal subtidal benthic communities and habitats, this project aimed to address two major questions:

a) How do environmental conditions vary on spatial and temporal scales and how do they affect the benthic communities occurring in Lough Hyne?
b) How do benthic communities of the Western Trough cope with the seasonal presence of hypoxic conditions beneath a summer thermocline?

The two questions were addressed by studying benthic macrofauna at different sites within the Lough on a seasonal basis for one year. Physicochemical environmental conditions were investigated at the same intervals. Oxygen and temperature profiles were taken more frequently, usually monthly in the summer, as a water column profile at the deepest site of the Western Trough, in order to study the development of the thermocline and this data were taken for a period of 4 years. Sedimentation rates were measured on a monthly basis over 13 months.

Sedimentation rates of organic and inorganic matter are important environmental variables affecting benthic communities. They were measured monthly at six sites across the Lough over 13 months. The results of this study are presented in Chapter 2 and data on organic matter sedimentation rates were further used as environmental factors in the infaunal benthic community analyses presented in Chapter 5. The findings led to a publication in the *Journal of Marine Biology* which is attached to this thesis as Appendix 1. Additionally, sedimentation rates above and below the thermocline of the Western Trough were compared and these data were prepared for publication in a collaborative study on the thermocline behaviour in the Western Trough. For this publication, current speeds at 30 m depth when the thermocline was present and when it was absent in winter were also compared. Other aspects of the thermocline study were multisensory data (dissolved oxygen, temperature, pH and turbidity) of the breakdown of the thermocline. This study is under review in the journal *Estuarine, Coastal and Shelf Science* and is attached to this thesis as Appendix 2.

The effect of the seasonal thermocline on epifaunal communities was the focus of Chapter 3. Using a camera attached to a ROV, data on the abundance and the diversity of mobile benthic epifauna, such as fish, crabs and echinoderms were collected along transects above, within and below the summer thermocline depth. The ROV allowed non-destructive data collection and gave access to transects at depths below safe SCUBA limits.

For Chapter 4, two methods were used to study recolonisation of an area previously defaunated by the summer thermocline in the Western Trough of Lough Hyne. This study was repeated every 3 months from November 2009 to May 2010, when oxygen conditions deteriorated again. A camera attached to a ROV was used to identify and count burrows of decapods and fish above, within and below thermocline depth. Grab samples were used to collect macrofaunal samples above and below the thermocline and after taxonomic determinations were carried out and abundances estimated, statistical analyses were performed.

To learn about the diversity and abundance of soft sediment benthic fauna and to study spatial and temporal patterns of macrofaunal assemblages across the Lough, grab sampling was performed three-monthly at 5 sites around the Lough, and macrofauna identified, enumerated and then multivariate statistical analysis performed. In the course of this work, the holothuridean echinoderm *Rhabdomolgus ruber* was recorded for the first time and added to the list of species present at Lough Hyne. This finding extends the geographical range of this species, as previously it has only been found off Helgoland, Germany and near Cherbourg in France. It led to a publication in Marine Biological Records (Broszeit et al. 2010), which can be found in Appendix 3.

Finally, Chapter 6 considers the results presented in the earlier chapters in the light of previous research from the Lough and elsewhere; it also suggests areas of future research.

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Chapter 2

Comparison of inorganic and organic matter sedimentation in a natural laboratory – a one year study at Lough Hyne Marine Reserve, Ireland

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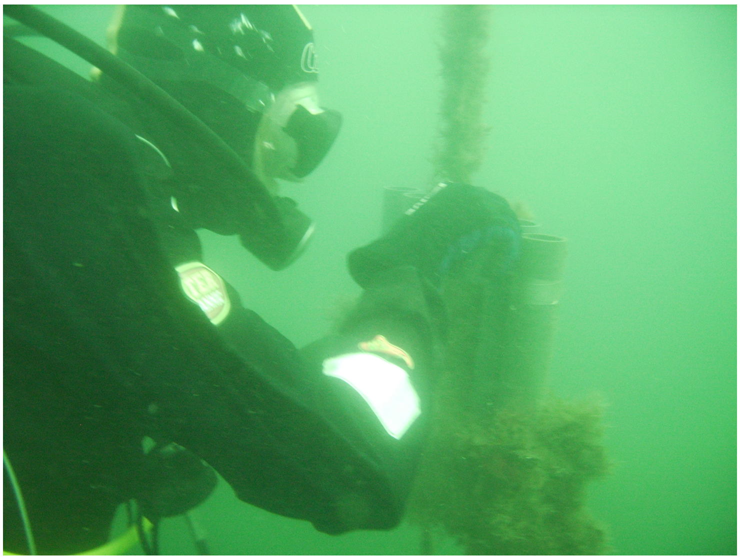
Material from this Chapter and additional data not presented here is submitted to *Estuarine, Coastal and Shelf Sciences*:

O'Sullivan, T., Broszeit, S., O'Sullivan, K., Davenport, J. and McAllen, R. High resolution monitoring of episodic stratification event in an enclosed marine system (Appendix 2)



ABSTRACT

Measuring sedimentation rates may provide useful information on the habitat preferences of marine organisms. To understand the effect of current speeds and meteorological conditions on sedimentation in the absence of other confounding factors (such as stirring up sediments by trawl fishing or anchoring), sedimentation of organic (OM) and inorganic (IOM) matter were measured at 6 sites in Lough Hyne Marine Reserve over the course of 13 months and expressed as sedimentation rate per day. During winter, both OM and IOM were imported to the Lough, peaking in December at Whirlpool, the site nearest to the Lough entrance, likely as a result of extreme weather conditions causing re-suspension of matter outside the Lough. Highest inorganic matter (IOM) sedimentation occurred in December at Whirlpool Cliff and was related to November wind speeds. Highest OM sedimentation also occurred in December at Whirlpool, but was not related to meteorological conditions. Decreasing current speed caused a decline in IOM sedimentation. However, no single environmental factor strongly influenced organic matter (OM) sedimentation. One-way ANOVAs on OM and log-transformed IOM data showed that sedimentation differed significantly amongst the six sites within the Lough. Increased plankton production in the Lough during summer led to increased OM sedimentation in areas of low current speed away from the entrance of the Lough.

1. INTRODUCTION

The settlement of matter out of the water column onto the seafloor is an important process for benthic fauna. Sinking organic matter provides a high-quality food source for marine benthic communities which, except where light can still penetrate and benthic photosynthesis occurs, are dependent on surface water production for energy input (Quijón et al. 2008). Sedimentation rates are largely influenced by the availability of nutrients in the surface water and by seasonality, which influences plankton growth. Dying phytoplankton blooms provide massive sedimentation events in short periods with a marked seasonality (Riebesell 1989), at least at medium and high latitudes. However, benthic communities can be adversely affected by high organic matter input as described by classic models (Pearson & Rosenberg 1978): an increase of organic materials at first causes an increase in benthic biomass and microbial metabolism, but eventually this leads to the complete depletion of oxygen. The consequences of anoxia in the benthic habitat and the overlying water column are massive die-off events in the benthic community (Heip 1995). This is studied in detail in Chapter 3 and 4 of this thesis. Additionally, areas of low water exchange, such as semi-enclosed bays and fjords, are known to develop temporal or permanent stratification of the water column. This is usually due to reduction of current speed by narrow and shallow inlets. The stratification worsens the hypoxic situation as it inhibits exchange of water across the thermocline. Seasonal or longer-term anoxia is a well-studied consequence of stratification and organic enrichment (Diaz & Rosenberg 1995).

Inorganic matter (IOM) such as gravel and sand will settle in areas exposed to strong hydrological forces such as subtidal currents and wind-driven waves (Gray & Elliott 2009). Finer particles remain in suspension longer and settle when the water velocity has fallen to a threshold value. Fine muds and silt settle in areas of low current velocity and here organic matter (OM) also settles out. Benthic animals choose their habitat according to factors such as current flow, grain size, stability and OM content. Because of negligible sedimentation of OM in high-energy areas, and the danger of being dislodged, few animals live in these sediments.

Lough Hyne is an ideal site to study coastal oceanographic processes as it is sheltered, comparatively shallow, and exhibits a wide range of flow rates within a relatively small area (Bassindale et al. 1957). A detailed site description has been given in Chapter 1. Within this body of water, the effects of current speed can be studied in the absence of (or much reduced) other confounding factors such as large distances between sampling sites or sampling across biologically and oceanographically different bodies of water. Weather conditions at any particular time are constant across the entire study area due to its small size, while previous studies have shown no significant spatial variation in either water chemistry (Total N, Total P, silicates) (Jessopp et al. 2009), or other factors likely to influence sedimentation in different areas of the Lough such as phytoplankton (Jessopp et al. 2009) and zooplankton abundance (Rawlinson et al. 2005). In addition, because it is a marine reserve, anthropogenic disturbances such as dredging and trawling do not take place, and therefore re-suspension of sediments, due to these processes, cannot influence the results.

Only limited work has been carried out previously on sedimentation within the Lough. Bell and Barnes (2002) focused on sedimentation onto rocky substrata to study environmental conditions for encrusting sponges. They found that for IOM, rates were higher in winter than in summer months, while sedimentation of OM was higher in summer than in winter. Interestingly, sedimentation was highest in areas of intermediate current speed such as Southwest, Goleen and cliff faces of the Western Trough.

The research reported here was designed to address the following questions:

a) How is sedimentation of organic and inorganic material distributed within the Lough and how does this change over time?
b) How do oceanographic and meteorological factors influence sedimentation rates?

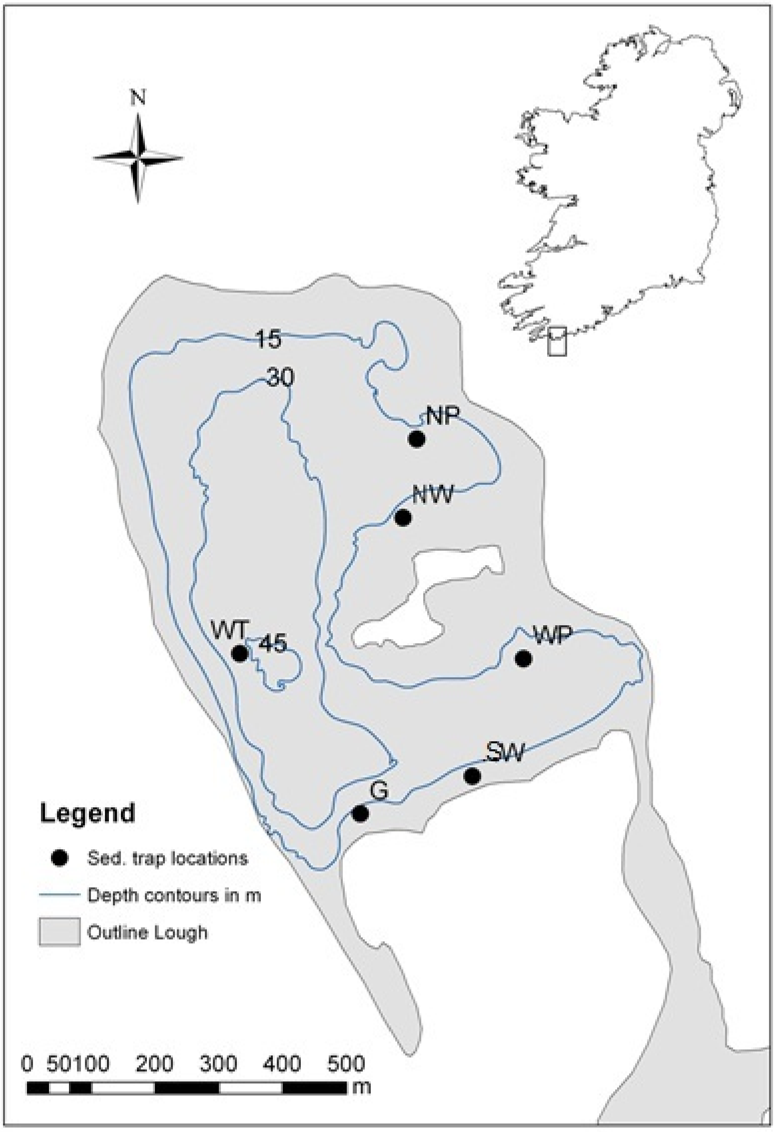


Figure 2.1: Sediment trap locations for the 13-month survey of Lough Hyne from June 2009 to July 2010. G = Goleen, NP = North Pier, NW = Northwest, SW = Southwest, WP = Whirlpool, WT = Western Trough. Depth contours of 15, 30 and 45 m are indicated in blue.

2. MATERIALS AND METHODS

2.1 Design and deployment of sediment traps

Sediment traps were deployed at six sites around Lough Hyne (Figure 2.1). Sites were chosen to reflect different localities and current speeds (based on previous studies) in the Lough ranging from fast (0.24 ms^{-1}) near Whirlpool Cliff to slow (0.02 ms^{-1}) in the northern part of the Lough. A 10 kg block of cement was used to anchor a rope in each location, and a surface buoy ensured that the rope was taut during the duration of the study. A sediment trap holder with six spaces for individual traps was suspended at a depth of 10 m from the surface buoy (Figure 2.2). A depth of 10 m was chosen to avoid measuring re-suspension from the sea floor. Due to the small tidal range of maximal 1 m, a surface buoy was chosen over a subsurface buoy and depth measured from the surface of the water.

Each trap was made of ABS (Acrylontrile Butadiene Styrene) drain pipe with an inner diameter of 45 mm and a length of 300 mm, sealed at the lower end with an ABS disc. The traps had an aspect ratio (width to height) of 1:6.67. This is above the recommended minimum of 1:3, while the diameter exceeded the recommended minimum of 40 mm (Håkanson et al. 1989). Four replicate traps in each carrier were filled to a depth of 70 mm with a 5% formalin/brine solution of 100 expressed in accordance to the practical salinity scale (psu) and measured with a WTW LF 330i conductivity meter (Wissenschaftlich-Technische Werkstaetten, Weilheim, Germany). Formalin preserved the organic material within the falling sediment, while the brine was necessary to achieve a dense layer in which the sediments would remain without re-suspension (Wakeham et al. 1993). Four tubes per site and month were chosen in case tubes were lost during the sampling interval and replication helped to confirm the representative nature of the collected data in relation to each site and month. A fifth trap was filled with seawater as a control. This control was only used to test the necessity of use of formalin for the monthly time span used, and data from the control tubes were omitted in the final analysis. A sixth trap in each holder was necessary for balance and was not removed during the course of the experiment. Traps were deployed and collected by SCUBA divers at intervals of approximately 4 weeks. Traps were sealed with drain pipe lids before removal from the trap holder and brought to the surface in a carrier in order to ensure the least possible disturbance to the trapped sediment. Each lid had a hole of 2 mm diameter drilled in the top to allow for pressure equalisation during the diving operations. After a pilot study to test functionality of the trap design, data collection was started in June 2009 and continued until July 2010.

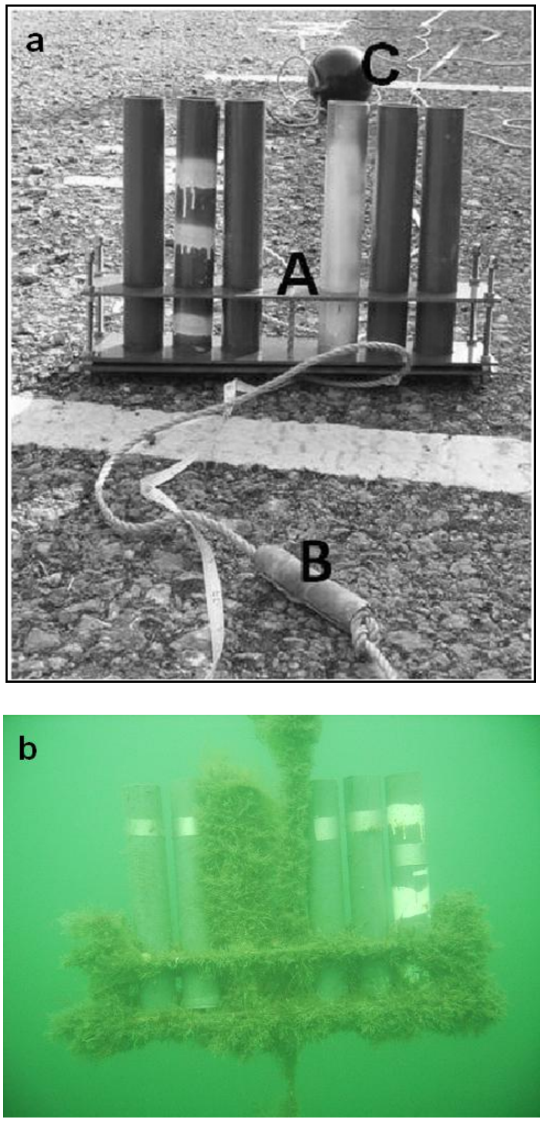


Figure 2.2: Six sediment traps in trap holder: a) before deployment, b) *in situ* at six sites spread across Lough Hyne, deployed from June 2009 to July 2010.. (A) A lead weight (B) rolled around the rope held the traps vertical in the water column. The surface buoy (C) ensured that the trap was suspended at the correct depth. Markings on the traps helped the divers to choose the correct trap on a given sampling occasion. The white trap remained in the holder throughout, purely for balance. The striped trap was the control.

2.2 Sediment analysis

In the laboratory, each trap was shaken vigorously to re-suspend the deposited material. A subsample of 55 ml was gently filtered through a pre-weighed 47 mm GF/C Whatman glass fibre filter using a KNF Neuberger Laboport vacuum pump. This was followed by a 50 ml wash with distilled water to remove salt (Håkanson et al. 1989). Filters were dried in an oven at 80 °C overnight, weighed, and ashed at 450°C for 6 h in a muffle furnace to remove organic matter before being reweighed. Sedimentation rates were calculated as g sediment m^{-2} d^{-1} for both organic and inorganic fractions.

2.3 Collection of factorial data for analysis

Current speed was measured using a Nortek Acoustic Doppler Velocimeter (Vector 3D current meter, Nortek AS, Norway) which was suspended vertically from a surface buoy anchored to the bottom by a 10 kg cement weight. Recording of current speed was conducted from January to March 2011 to ensure that re-suspension of sediment during equipment deployment and retrieval did not have any effect on sedimentation rates during the experiment. A change in current speeds at the sites was not expected between 2009 and 2011 as no changes to the water flow or the topography of the Lough were noted. To reduce interference due to the presence of the anchor rope, the velocimeter was placed in a steel frame that held it 50 cm away from the rope. A counterweight ensured upright position of the velocimeter during deployments. Using GPS, the velocimeter was placed at the same locations where the sediment trap holders had been previously held, and left to collect data for 2 weeks at each location to cover full spring and neap tidal cycles. Current speeds were measured at a depth of 5 m, halfway between the surface and the depth at which the sediment traps had been suspended, as this part of the water column is likely to carry the sediments that would be deposited in the sediment trap. Data were divided into current speeds at spring inflow, spring outflow, neap inflow and neap outflow, and mean maximum current speeds in each of these four categories subsequently used for analysis.

Weather data were obtained from MetÉireann, and consisted of mean hourly wind speeds (knots) for each month from the M3 weather buoy (51°13’0” N, 10°33’0” W), near Mizen Head, County Cork, and rainfall (mm) per month at

Valentia weather station, County Kerry. The distance from the M3 weather buoy to the Lough is approximately 90 km, while distance from the Valentia weather station to the Lough is approximately 85 km. Temperature was recorded at 30-min intervals in the South Basin. A Hobo Pro v.2 water temperature data logger (Onset Computer Corporation) was suspended from a mooring buoy at a depth of 5 m and logged temperature continuously throughout the study period. Distance to the Rapids was measured using the Path tool in Google Earth. For each site, a line was drawn from the inner mouth of the Rapids through the South Basin to the southern trap locations (marked using GPS data). For the two northern sites, two routes were measured: one moving east to west along the South Basin to the centre of the Western Trough, then northward and finally in an eastern direction north of Castle Island to the trap location. For a second set of measurements, a path was chosen that passed directly through the narrows between Castle Island and the East Shore to the trap location.

3. RESULTS

3.1. Data exploration

Data showed equal variances (Cochrane's test) for organic matter sedimentation (OM) while inorganic matter sedimentation (IOM) had equal variance only after $\log_{10}$ transformation. Current speed and distance from the Rapids were collinear, and rainfall and wind data were also collinear, so multiple regression analyses were not performed. Multiple linear regression was not performed on the data set as weather data were not collected at each individual sampling station and current speed was only measured once at each site, rather than continuously throughout the study period.

3.2 Environmental factors

Mean hourly wind speed (knots) and rainfall (mm) are graphically displayed in Figure 2.3. Lowest mean wind speed occurred in September 2009 (11.7 knots) and highest mean wind speed was recorded in November 2009 (19.8 knots). Highest rainfall was recorded in November 2009 with 362.8 mm, while lowest rainfall in the study period occurred in May 2010 (54.2 mm).

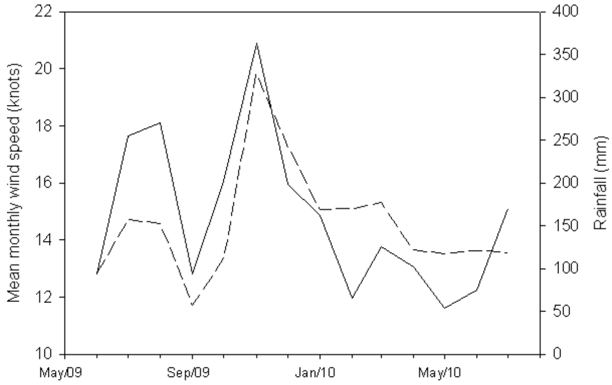


Figure 2.3: Mean hourly wind speed in knots recorded at the Irish M3 weather buoy (dashed line), and monthly rainfall at the Valentia recording station (solid line) during the study period. Data courtesy of MetÉireann.

Highest mean maximum current speed was recorded at Whirlpool during spring inflow (0.24 ms^{-1}) and lowest at Northwest during spring inflow (0.02 ms^{-1}) (Figure 2.4). Currents at North Pier were faster than at Northwest; indicating that there was tidal flow through the gap between the East shore and Castle Island.

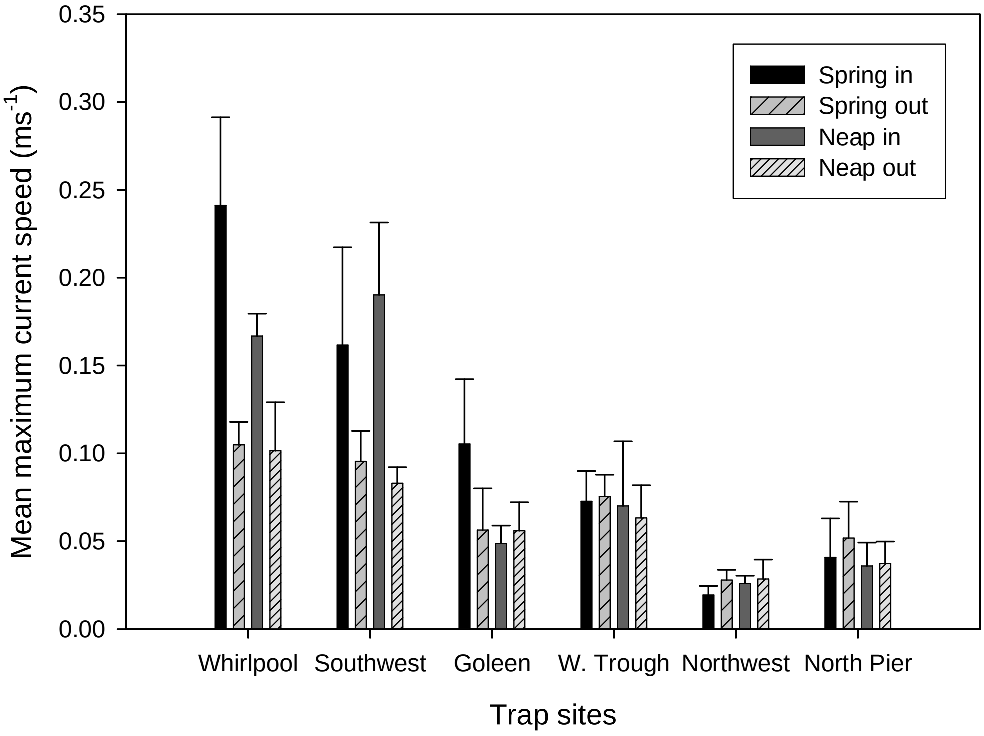


Figure 2.4: Mean maximum current speed of four tidal states (spring inflow, spring out flow, neap inflow, neap outflow) at each sediment trap site in Lough Hyne Marine Reserve. Error bars indicate standard deviation. Data were collected at each site over a spring and neap cycle in spring 2011.

3.3 Distribution of sedimentation in the Lough

IOM sedimentation rates ranged from 1.67 g m^{-2} d^{-1} at Northwest in September to 47.37 g m^{-2} d^{-1} at Whirlpool in December. OM ranged from 0.97 g m^{-2} d^{-1} at North Pier in January to 5.60 g m^{-2} d^{-1} at Whirlpool in December. Figure 2.5 shows IOM and OM sedimentation for each site over 13 months. Most noteworthy is a peak in IOM in December, particularly at the sites close to the entrance of the Lough, highest sedimentation being recorded at Whirlpool, followed by Southwest, then Goleen and Western Trough. Sedimentation rates at the two northern sites (Northwest and North Pier) showed an increase in IOM over the winter months (November to February), but not featuring such pronounced peaks as the southern sites in December. Similarly, a peak of OM occurred in December at Whirlpool Cliff and also to a lesser extent at Southwest and Goleen, but this pattern was not apparent in the data for the Western Trough, Northwest and North Pier.

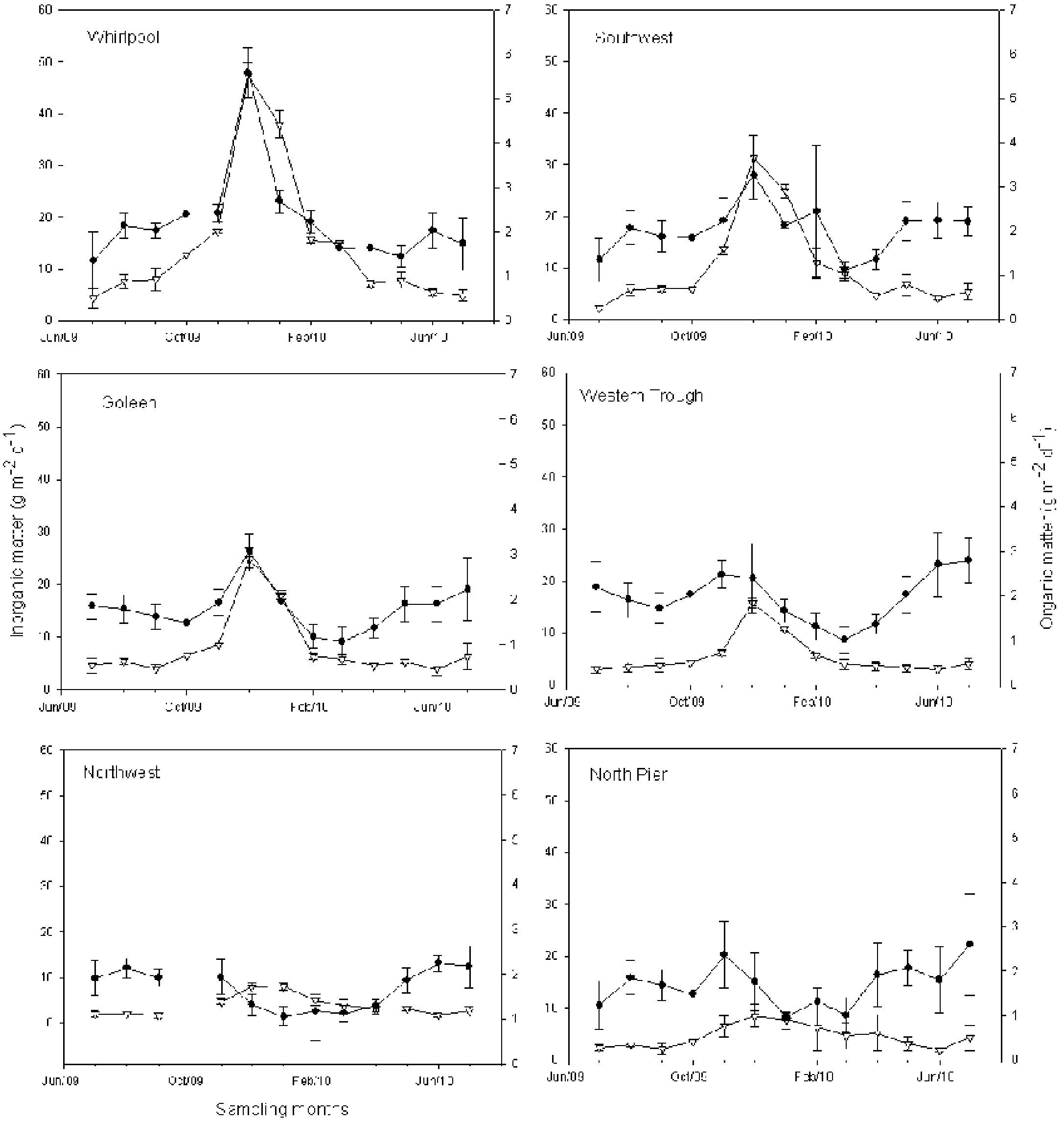


Figure 2.5: Sedimentation rates at six sites in Lough Hyne over the course of the study period (▿) inorganic matter sedimentation (●) organic matter sedimentation. Error bars indicate standard deviation. Most October samples were lost by accident. However, one sample from each site (except Northwest) remained for analysis.

A one-way ANOVA on log-transformed IOM data showed that IOM sedimentation rate was significantly different amongst sites (df = 5, F = 24.82, $P < 0.001$). Posthoc

Tukey pair-wise comparisons showed that most pairs exhibited statistically significant differences (Table 2.1a). Only four pairs did not; in each case they were sites adjacent to one another: Southwest-Goleen, Goleen-Western Trough, Western Trough-Northwest and Northwest-North Pier.

For OM data (untransformed), sites also differed significantly (one-way ANOVA, df = 5, F = 4.62, P < 0.001). Most pair-wise comparisons were non-significant (Table 2.1b); the only exceptions were between Whirlpool and other locations within the Lough (Whirlpool-Goleen, Whirlpool-Northwest and Whirlpool-North Pier).

Table 2.1: Post-hoc Tukey procedure to test at which sites sedimentation differed to a significant degree in Lough Hyne during the study period. a) IOM sedimentation, b) OM sedimentation. NS = not significant, * = significant: P < 0.05.

a)	Whirlpool	Southwest	Goleen	W. Trough	Northwest
Southwest	*				
Goleen	*	NS			
W. Trough	*	*	NS		
Northwest	*	*	*	NS	
North Pier	*	*	*	*	NS

b)	Whirlpool	Southwest	Goleen	W. Trough	Northwest
Southwest	NS				
Goleen	*	NS			
W. Trough	NS	NS	NS		
Northwest	*	NS	NS	NS	
North Pier	*	NS	NS	NS	NS

3.4 Effects of environmental conditions on sedimentation

Linear regression showed that, for IOM, wind speed during the previous month yielded the highest R^2 value ($R^2 = 0.39$, $P < 0.001$) of all environmental factors studied (Table 2.2). All other factors had lower R^2 values, though all relationships were statistically significant ($P < 0.05$). For OM, no single environmental factor had a particularly strong influence, and R^2 values were low ($R^2 < 0.1$) for all factors chosen, yet all had statistically significant effects ($P < 0.05$). Given the noticeable increase in OM from March 2010 onwards, additional regression analysis was carried out using mean and maximum monthly water temperatures (both for the same and previous month). Maximum temperature of the previous month showed a weak, yet statistically significant relationship ($R^2 = 0.1$, $P < 0.001$); other temperature relationships showed even lower R^2-values, though were statistically significant in all cases ($P < 0.05$).

Table 2.2: R^2-values and related p-values for linear regressions performed to explore which environmental conditions had an influence on inorganic and organic matter sedimentation rates in Lough Hyne during the study period.

		Inorganic		Organic	
	Factor	R^2	P	R^2	P
Weather	Wind speed previous month (knots)	0.39	<0.001	0.04	0.001
	Rainfall previous month (mm)	0.21	<0.001	0.09	<0.001
	Wind speed same month (knots)	0.15	<0.001	0.04	0.001
	Rainfall same month (mm)	0.02	0.023	0.04	0.001
Distance	Long route to North Basin (m)	0.17	<0.001	0.4	0.001
	Short route to North Basin (m)	0.17	<0.001	0.6	<0.001
Current speed	Spring inwards (ms^{-1})	0.22	<0.001	0.07	<0.001
	Spring outwards (ms^{-1})	0.16	<0.001	0.07	<0.001
	Neap inwards (ms^{-1})	0.15	<0.001	0.06	<0.001
	Neap outwards (ms^{-1})	0.19	<0.001	0.07	<0.001

4. DISCUSSION

This study of sedimentation over the course of one year clearly showed that IOM and OM sedimentation are governed by different environmental factors in this highly sheltered, semi-enclosed bay, and are therefore not tightly coupled. IOM sedimentation was influenced by weather and tidal factors and IOM was predominantly imported from outside the Lough. This was evidenced by IOM sedimentation rates being highest near to the Lough entrance and decreasing to lowest levels in the North Basin. Amongst the environmental factors considered, wind speed of the previous month had the strongest influence on IOM, probably because re-suspension of sediments in neighbouring coastal areas (caused by strong wind and wave action) takes some time to fully affect the sheltered Lough via Barloge Creek and the Rapids which connect the Lough to the Atlantic. Other potential sources of suspended particles such as dredging activity and river discharge can be excluded in this study as no dredging has taken place anywhere near the Lough entrance, and (rather unusual for temperate coastal bays) no rivers discharge into the Lough; the nearest river discharges into the Atlantic to the west of Baltimore, about 6 km west of Lough Hyne. Strong SW winds are a regular occurrence in SW Ireland and coastal areas are exposed to wave action and surge. However, the Lough itself is highly sheltered due to the semi-enclosed nature of the Lough and surrounding hills. Waves rarely exceed 1 m in amplitude even during strong storms (Bell & Barnes 2002). Of the 4 tidal regimes, spring inflow had the highest influence on IOM sedimentation, which supports the hypothesis that sediments were brought in from the outside and deposited near the entrance in the South Basin where flow is fastest (of all sites inside the Lough). Reduction in current speed leads to sedimentation of inorganic matter, heaviest sediments fall out first, while finer particles remain in the water column for longer (Gray & Elliott 2009). Additionally, if sediments are brought in at one point only, as appears to be the case with the Lough entrance, sedimentation will naturally decline with distance from point of entry as the water body loses suspended sediments with distance as velocity decreases.

In pairwise comparisons of sedimentation rates at each site it was shown that IOM sedimentation rate at Whirlpool was significantly different from IOM sedimentation at all other sites. These findings may be explained by the gradual reduction in flow rate with increasing distance from the Rapids causing progressive loss of sediments from the water column. Sites closest to each other showed IOM sedimentation rates that did not differ significantly, probably as a consequence of the sampling points being close together and the relationship between IOM sedimentation rate and distance from the Rapids already noted.

In contrast to IOM, none of the abiotic environmental factors tested had a strong influence on OM sedimentation individually. This suggests that variations in OM sedimentation rates are driven by biotic factors that were not measured in this study, or that a combination of abiotic factors influences settlement. OM is made up of several different components including: faecal material from nekton and zooplankton, dead and dying phytoplankton and zooplankton (made up of mero- and holoplankton), re-suspended organic material from sediments, plus debris derived from dislodged intertidal flora and fauna from the exposed shores of nearby coastal waters. For example, high winds can cause wind-driven turbulence, which promotes re-suspension of organic matter and dislodgement of intertidal flora and fauna (Gray & Elliott 2009, Davenport et al. 2011). This organic material, brought into the Lough during the winter months, may provide a valuable food subsidy for benthic animals that depend on productivity from elsewhere. Nutrient availability, plus rising light levels and temperatures influence phytoplankton growth in spring in temperate seas, causing spring blooms. Such blooms in turn lead to increased OM sedimentation (Smetacek et al. 1978, Smetacek 1980, Riebesell 1989). Zooplankton biomass increases with phytoplankton blooms and causes the production of further OM sedimentation either due to the animals’ faecal pellets, their moulted exoskeletons (in the case of crustaceans) or because of death. In addition, benthic marine animals release their meroplanktonic larvae in the summer and these also cause increases of OM sedimentation in the summer, due either to dead larvae or faecal pellets. A deferred high OM sedimentation may be caused by blooms of plankton at different time intervals. Sedimentation rates (IOM and OM together) were lower in Bell and Barnes’ study (2002) than the present study and OM peaked in April (data from all sites taken together), not during the winter months. As in this study they also found the lowest sedimentation (both OM and IOM) in the North Basin and a positive relationship between sedimentation and wind speed. By taking OM data from all sites together they were not able to see if OM was produced inside or brought in from the outside of the Lough. In the present study it was possible to hypothesise where OM was coming from at different stages of the study period. Previous studies on phyto- and zooplankton in Lough Hyne (Rawlinson et al. 2005, Jessopp & McAllen 2008) have shown that both components of the plankton community are produced inside Lough Hyne, but that some is also brought in from the outside. Nutrients have been shown to be brought in from the outside, causing increased occurrences of red tides even in the winter months, and year-round high levels of nutrients (Johnson & Costello 2002, Jessopp et al. 2009). In the present study it was shown that Lough Hyne may act as a sink for IOM from the outside and that nutrients may cause increased rates of phytoplankton blooms due to the semi-enclosed nature of the Lough.

The present study highlights the importance of understanding how coastal bays interact with their adjacent seas, particularly when such basins are considered for designation as marine reserves. Policies need to involve the clean-up of pollution, avoidance of eutrophication and limitations on permits for extractive activities in the areas neighbouring such enclosed bays. Further studies of the behaviour of separate components of the OM fraction are needed, as understanding what influences these components have will be valuable in understanding how these systems work internally and how they are connected to the wider ocean system.

Lough Hyne is a useful model area for future studies as it is a designated marine reserve, is easily accessible and allows observations on a confined body of water that shows marked variation in physical processes such as flow rates across a relatively short distance. Sedimentation data collected here can be used as baseline data for studies in systems where confounding factors such as differences in water chemistry or planktonic communities are encountered, or those experiencing anthropogenic disturbances. Data of organic matter sedimentation collected for this Chapter are further used in Chapter 5.

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Chapter 3

Seasonal oxygen-driven migration of mobile fauna

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Broszeit, S., Davenport, J., Bredendieck, K., Harman, L. and McAllen, R. Seasonal oxygen-driven migration of mobile fauna

ABSTRACT

Changes in mobile benthic fauna affected by anoxic conditions beneath a seasonal thermocline were studied at three-monthly intervals for one year at Lough Hyne. This marine lake features regular seasonal anoxia in the deepest part (the Western Trough). Building on previous studies of the effects of this anoxia on demersal fauna, a remotely-operated vehicle (ROV) was used to film the benthic assemblage. Transects above, within and below thermocline depth were filmed on each sampling occasion. Animals were identified and their sizes measured. Data on oxygen concentration of the water column were taken monthly during this period to correlate with the presence and absence of animals in the Trough. Most noteworthy was the establishment of a demersal fish assemblage during normoxic conditions in the deeper areas of the Trough. The Goby *Lesueurigobius friesii* was the most abundant species and its population contained all size classes. They are territorial and build burrows into which they retreated when the ROV approached. The main factor driving benthic faunal assemblages below thermocline depth was oxygen concentration, while the assemblage above the thermocline was never affected by hypoxia. Changes in transect animal abundance above the thermocline may have other controlling factors such as lack of food during winter or H_2S diffusing from the sediments below the thermocline. This study shows that mobile animals make use of areas affected by hypoxia as soon as conditions improve, and that some, such as *L. friesii* can establish resident communities.

1. INTRODUCTION

Hypoxia in the marine environment is a worldwide and spreading phenomenon. Coastal areas are particularly prone to hypoxic conditions, primarily due to stratification of the water column which is usually caused by the establishment of seasonal thermoclines. This reduces oxygen supply to lower layers and the decay of organic matter below the thermocline creates a biological oxygen demand that exceeds supply (Pearson & Rosenberg 1978, Heip 1995, Diaz & Rosenberg 2008). These factors occur naturally and geological evidence indicates that hypoxia has been a feature of marine habitats for millennia (Diaz & Rosenberg 1995). Hypoxia has been defined as corresponding to an oxygen content of 2.8 mg l^{-1} or less; a complete lack of oxygen is termed anoxia (Diaz & Rosenberg 1995). Ecologically, development of thermoclines can lead to massive die-off events of sessile/sedentary benthic assemblages during summer, followed by recolonisation in the winter (Kitching et al. 1976). Recolonisation is often led by opportunistic species (Heip 1995). High quantities of organic matter collected during the hypoxic event can support such opportunists, which in turn attract predators into the area (Pihl et al. 1991, Diaz & Rosenberg 1995, Nestlerode & Diaz 1998).

A thorough description of the study site Lough Hyne can be found in Chapter 1. A thermocline forms each year in early summer in the Lough, at a depth of 25-26 m, affecting the Western Trough, by reducing the supply of oxygen-rich water. Below the thermocline, oxygen levels decline and H_2S forms during the course of summer. In autumn, the top layers of water cool, causing the thermocline to break down, a process accelerated by autumn storms. During winter, the whole water column is normoxic. Kitching et al. (1976) studied the effect of the developing thermocline at different depths. They observed that the mud turned black and smelled of sulphide at 40 m and that animals died at that depth first. They suggested that anoxic conditions spread upwards and outwards from the deepest part of the trough. McAllen et al. (2009) compared benthic communities in winter (November, thermocline at 30-34 m; January, no thermocline present) and summer (August, thermocline at 26-28 m) using a remotely-operated vehicle (ROV), SCUBA and trapping experiments above and below the summer thermocline depth (August, November and January) to study benthic recovery processes. They found that mobile fauna (e.g. crustaceans) exploited improving oxygen conditions in autumn by darting below the thermocline depth into hypoxic waters to feed on organic matter. This was exemplified by *Palaemon serratus* being found in baited traps located below the breaking-down thermocline in November. Based on their findings the present study was designed to investigate the benthic faunal assemblage on a three-monthly basis over one year. The following questions were addressed:

a) How does the benthic assemblage of the Western Trough change in relation to seasonal oxygen conditions?
b) How do animals recolonise the hypoxic and anoxic areas of the Trough when these are re-oxygenated in winter?
c) Are there seasonal changes in the assemblage above the thermocline?

2. MATERIALS AND METHODS

2.1 Environmental monitoring

Monthly measurements of dissolved oxygen (mg l^{-1}) were taken in the Western Trough using a WTW OXI 197 Oxygen probe and meter attached to a 60 m cable. Readings were taken during each sampling month at the three study depths of 20, 30 and 40 m in the water column over the deepest part of the trough.

2.2 Remotely-operated vehicle survey

In August and November 2009, as well as in March and May 2010, a HYTEC H300 ROV system was deployed to follow three depth contours (each 40 m long) along the western slope of the Western Trough at 20, 30 and 40 m depths. Three up-slope transects were also taken, cutting across the middle and both ends of the transverse transects. A Sony FBC type analogue colour video camera was vertically-mounted on the ROV to film the sea bed, illuminated by four 75 watt halogen lights. The camera was equipped with two vertically-directed lasers installed 53 mm apart next to the lens. The lasers projected light spots onto the sea bed into the field of vision, thus permitting measurement of sizes of animals seen. Filming always took place between late morning and early afternoon to be able to compare data and for ROV scheduling constraints.

Images were recorded onto a Sony RDX-HX750 HDD/DVD 160 GB Recorder and burnt onto DVD. VideoLAN-VLC software (www.videolan.org/vlc/) was used for analysis. Snapshots were taken of all animals recorded; each was identified to species level where possible. Animals were counted and their size estimated using the calibrated laser scale in the image analysis software ImageJ (http://rsbweb.nih.gov/ij/). Statistical analysis was undertaken on univariate measurements of abundance, species richness and Shannon-Wiener diversity.

3. RESULTS

3.1 Environmental conditions

A thermocline began to form in June 2009, and declining hypoxic conditions were measurable from 25 m (O_2: 1.74 mg l^{-1}). The thermocline lasted until November. Subsequently, the water column returned to normoxic conditions until May 2010, when oxygen concentrations declined between 25 m (O_2 = 4.50 mg l^{-1}) and 30 m (O_2 = 1.29 mg l^{-1}).

Table 3.1: Oxygen concentrations (mg l^{-1}) in the Western Trough at 3 sampling depths in each sampling month over the deepest part of the Trough.

	August	November	March	May
20 m	8.02	9.21	9.83	7.13
30 m	0.00	6.80	9.93	1.29
40 m	0.00	2.27	9.70	1.18

3.2.1 Analysis of video footage

Uniform muds devoid of macrofauna and without burrows were encountered in August at and below 30 m when the thermocline had formed (Figure 3.1a: 40 m). Figure 3.1b shows unattached seaweeds that may have fallen or have been moved into the area by currents. The arrow indicates particle sedimentation that could be observed on all four sampling occasions. In Figure 3.1c the gastropod *Turritella communis* and the track it leaves on the seafloor is highlighted in the circle. Figure 3.1d shows crustacean tracks (probably left by portunid crabs) in November, while Figure 3.1e gives an example of tracks that could not be identified. Evidence of life below the thermocline depth in March can be seen in Figure 3.1f: a portunid crab (*Liocarcinus depurator*), and fresh burrows in the mud at 28 m depth. A fish (*Lesueurigobius friesii)* rests on the seafloor near a burrow in Figure 3.1g. In Figure 3.1h a live scallop *Pecten maximus* rests on the seafloor, with tentacles visible at the shell edge. The starfish *Marthasterias glacialis* was a regularly-observed species during this study (Figure 3.1i). In May 2010, the thermocline formed again, leaving the mud at 38 m devoid of macrofauna. The upper valve of a dead *P. maximus* sticks out of the mud in Figure 3.1j.

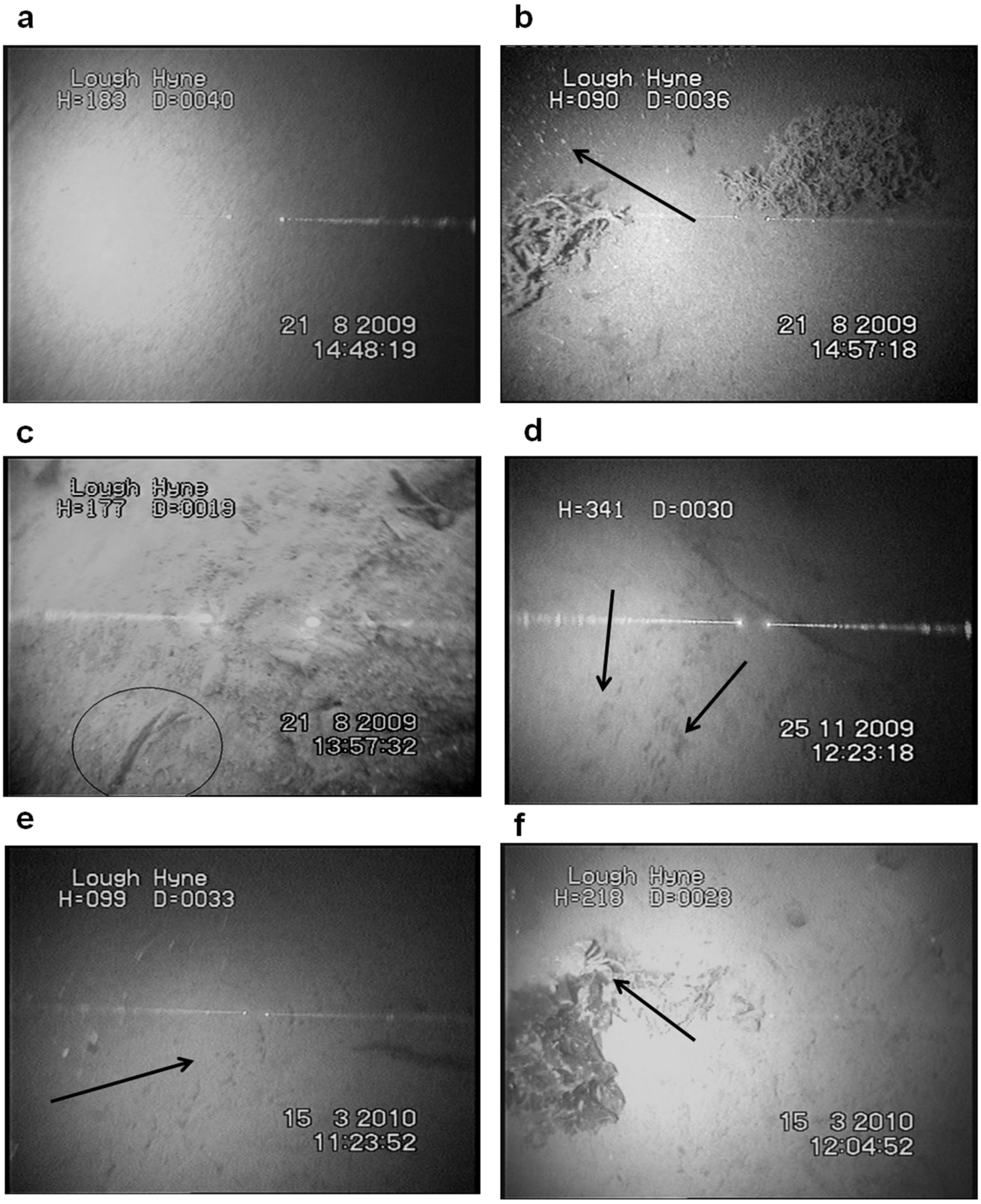

Figure 3.1: Snapshots taken from ROV videofootage taken in August, November 2009 and March, May 2010 at Western Trough of Lough Hyne at 20, 30 and 40 m depths. Transect length 40 m. See text for details. Note: In the top left hand corner of each image a heading (H) and a depth in metres (D) value are given. The two dots/lines are the laser pointers used for measuring animals and are 53 mm apart.

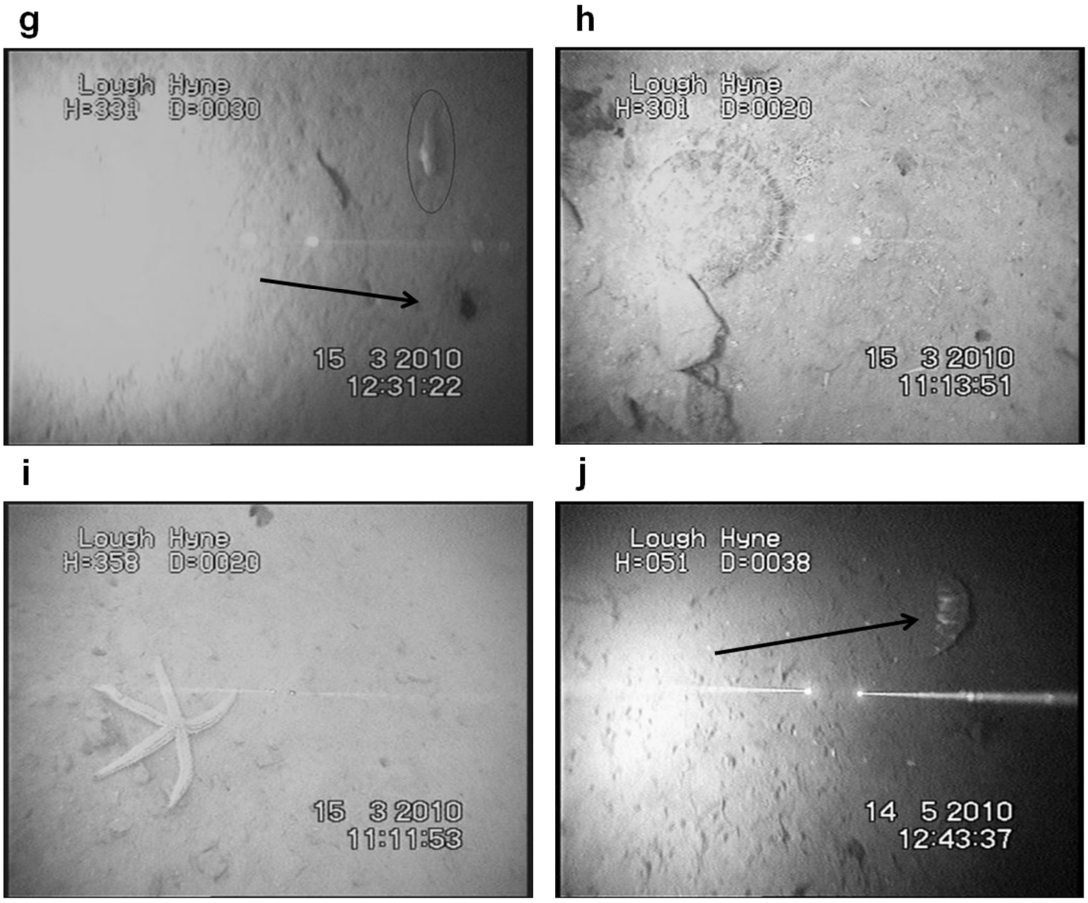

Figure 3.1 continued: Snapshots taken from ROV videofootage taken in August, November 2009 and March, May 2010 at Western Trough of Lough Hyne at 20, 30 and 40 m depths. Transect length 40 m. See text for details. Note: In the top left hand corner of each image a heading (H) and a depth in metres (D) value are given. The two dots/lines are the laser pointers used for measuring animals and are 53 mm apart.

During the study, 185 live, mobile animals (Crustacea, Echinodermata, Mollusca and Pisces) were recorded at all depths (Table 3.2). The largest number of sightings occurred in March (n = 122): 20 at 20 m depth, 74 at 30 m depth and 28 at 40 m depth. The lowest (n = 3) occurred in November 2009, two at 20 m and one at 30 m depth. In August, 14 animals were counted, all at a depth of 20 m and in May, 46 animals, 33 at 20 m and 13 at 30 m depth. With the exception of the scallop shell (Figure 3.1j), no dead or moribund animals were observed in the study.

Table 3.2: Abundances of a) Pisces b) Crustacea c) Mollusca and Echinodermata by species at each depth recorded at three-month intervals from August 2009 to May 2010 in the Western Trough of Lough Hyne using ROV equipment at 40 m long transects at 20 m, 30 m and 40 m depths.

a)	August 2009			November 2009			March 2010			May 2010			
	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	Total
PISCES													
Callionymus lyra	1	-	-	-	-	-	1	7	7	2	1	-	19
Ctenolabrus rupestris	6	-	-	-	-	-	-	-	-	2	-	-	8
Gobius niger	-	-	-	-	-	-	2	-	-	-	-	-	2
Gobiusculus flavescens	-	-	-	-	-	-	1	1	1	-	-	-	3
Lesueurigobius friesii	2	-	-	-	-	-	6	42	5	5	3	-	63
Platichtyhys flesus	-	-	-	-	-	-	-	-	-	-	1	-	1
Pomatoschistus minutus	1	-	-	-	-	-	3	17	6	4	3	-	34
Fish (unidentified)	-	-	-	-	1	-	-	1	3	7	1	-	13
Total	10	0	0	0	1	0	13	68	22	20	9	0	143

b)	August 2009			November 2009			March 2010			May 2010			
	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	Total
CRUSTACEA													
Carcinus maenas	-	-	-	-	-	-	-	-	1	2	-	-	3
Liocarcinus navigator	-	-	-	-	-	-	-	-	1	-	-	-	1
Liocarcinus depurator	2	-	-	-	-	-	-	4	-	4	-	-	10
Macropodia sp.	-	-	-	-	-	-	-	-	-	-	2	-	2
Maja brachydactyla	-	-	-	-	-	-	-	-	3	-	-	-	3
Portunid (unidentified)	-	-	-	2	-	-	1	1	-	-	-	-	4
Decapod (unidentified)	-	-	-	-	-	-	-	1	-	-	1	-	2
Total	2	0	0	2	0	0	1	6	5	6	3	0	25

	August 2009			November 2009			March 2010			May 2010			
c)	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	Total
MOLLUSCA													
Doris pseudoargus	-	-	-	-	-	-	-	-	-	-	1	-	1
Pecten maximus	-	-	-	-	-	-	1	-	-	-	-	-	1
Turritella communis	1	-	-	-	-	-	1	-	-	1	-	-	3
ECHINODERMATA													
Asterias rubens	-	-	-	-	-	-	1	-	-	1	-	-	2
Marthasterias glacialis	1	-	-	-	-	-	3	-	1	5	-	-	10

Fish (Table 3.2a) were the most abundant taxonomic group (143 sightings), and were the most species-rich (seven species). Except for the wrasse *Ctenolabrus rupestris*, which only occurred above the thermocline depth, they were all demersal fish. In August and November, only a few fish were recorded (10 in August at 20 m depth, one at 30 m depth in November), though conditions were normoxic (Table 3.1). In March, they were the most numerous group. In May, the water column was hypoxic from 28 m (2.03 mg l^{-1}) downwards and this was reflected in the number of animals found at depth: no fish occurred at 40 m and only nine at 30 m. Except for one fish that could not be identified, they were all demersal species.

Crustaceans (Table 3.2b) followed a similar pattern of occurrence as fish: in August and November they were only present twice, on each occasion above the thermocline, yet in March, five animals were visible at a depth of 40 m. Six animals were counted in March at 30 m. By May, the majority of crustaceans were at 20 m: two *Carcinus maenas* and four *Liocarcinus depurator*, while at 30 m two *Maja brachydactyla* and one unidentified decapod were seen.

Molluscs, sighted five times (Table 3.2c), occurred to a depth of 30 m, but left distinct tracks in March and May 2010 to a depth of 40 m on both occasions. These were probably left by *Turritella communis*, which was also the most common gastropod encountered. Echinoderms (12 sightings, Table 3.2c) occurred on every sampling occasion except November, but only one individual of *Marthasterias glacialis* at 40 m, all other echinoderms were encountered at 20 m. Ten echinoderm sightings were *M. glacialis,* while two individuals of *Asterias rubens* were encountered, one in March and one in May, both at 20 m depth.

Conditions remained normoxic at 20 m during the entire study period. Nonetheless, changes occurred in the number of animals and species on each study occasion. In August, 14 animals (seven species) were counted. In November, three animals were visible. Species richness and abundance of animals increased in March, with 20 animals of 10 species (five fish, one crustacean, two molluscan and two echinoderm species), and remained high in May, when 33 animals were identified from 10 species (five fish taxa, two crustacean, one molluscan and two echinoderm species).

A Friedman test comparing Shannon-Wiener diversity indexes (H') for each sampling depth and month showed that assemblages differed significantly amongst the three sampling depths (df = 2, P = 0.024), but not amongst months (df = 3, P = 0.086). This may be explained by the lack of animals at 40 m depth during three of four sampling occasions while fauna were always present at 20 m depth. Oxygen concentrations explained 26.6 % of the variation in animal abundances (P = 0.049).

3.2.2 Gobiid migration pattern

In March 2010, 53 Fries' gobies (*Lesueurigobius friesii)* were seen resting on the seafloor. Many were in close proximity to burrows (Figure 3.1g), into which they retreated when the ROV came close. The majority (42 animals) were recorded along the 30 m depth transect, and five along the 40 m depth transect. In May, eight Fries' gobies were seen at a maximum depth of 30 m. In August 2009, two Fries' gobies were both at a depth of 20 m, while none were visible in November 2009. Of the 53 gobies encountered in March 2010, total length could be measured for 47 individuals. The largest animal had a total length of 97 mm, and the smallest was 23 mm long. Figure 3.2 shows that a wide range of size classes was present in the Lough during March 2010 and that mature animals made up the bulk of the population.

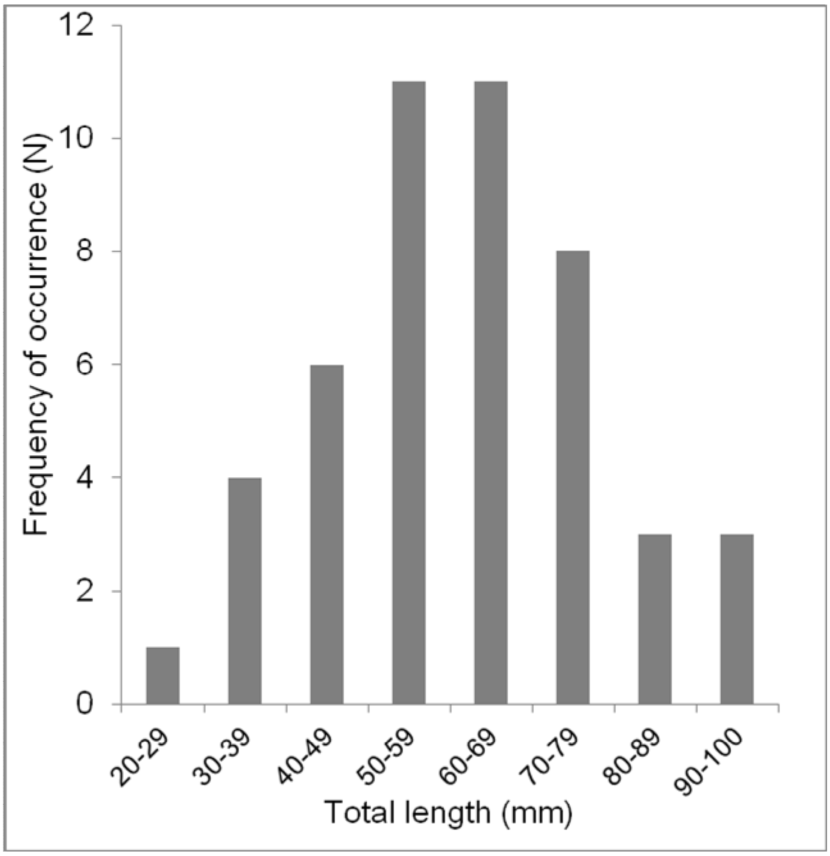

Figure 3.2: Size-frequency distribution of Fries' goby, *Lesueurigobius friesii* in the Western Trough at Lough Hyne in March 2010.

3.2.3 Animal tracks on sediment

In total, 119 animal tracks were recorded during the study period (Table 3.3). These were divided into three groups: gastropod, crustacean and of unidentifiable origin. Above the thermocline, tracks were visible on all four sampling occasions. In August, 19 tracks (11 crustacean, eight gastropod) were visible at 20 m. None were found below the thermocline depth in August. In November, 39 crustacean tracks were identified at 30 m depth and one at 20 m. This showed that crustaceans moved below the summer thermocline depth, possibly to feed. In November, 3 gastropod tracks were also found at 20 m. In March, tracks were evident to a depth of 40 m, while at 30 m, 20 of 27 tracks were crustacean, four gastropod and three unidentified. In May, two crustacean tracks occurred at 30 m and one molluscan track at 40 m, while the majority of tracks occurred at 20 m (n = 10 tracks).

Table 3.3: Animal tracks sighted during each sampling occasion in Lough Hyne Marine Reserve from August 2009 to May 2010 at three transect depths (40 m long each): 20m, 30m and 40 m.

	August 2009			November 2009			March 2010			May 2010			
	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	20 m	30 m	40 m	Total
CRUSTACEA	11	-	-	1	39	-	-	20	4	3	2	-	80
GASTROPODA	8	-	-	3	-	-	12	4	1	6	-	1	35
Unknown	-	-	-	-	-	-	-	3	-	1	-	-	4
Total	19	-	-	4	39	-	12	27	5	10	2	1	119

4. DISCUSSION

The present study has added to the growing body of information on the ecological effects of hypoxia on demersal fauna and their behavioural responses in both natural and anthropogenically induced hypoxia/anoxia. Fish were the most abundant group observed in the study. The total number of fish was highest in March when conditions were normoxic, indicating that they make use of the time that the Western Trough is habitable. Upon approach of the ROV, some of the Fries' gobies sought shelter in burrows, demonstrating that they continuously inhabited the area rather than just entering the Western Trough temporarily in a search for food as has been previously described for prawns, *Palaemon serratus* (McAllen et al. 2009) and in this study by observation of crustacean tracks. The populations of *Lesueurigobius friesii* consisted of fish of the entire size range for their species, which means that not only juveniles established themselves below summer thermocline depth. This species has previously been reported to occur in Lough Hyne at a depth of 15-30 m but else little was known about it at Lough Hyne (Wilkins & Myers 1991). When conditions became adverse through hypoxia, they apparently escaped into other (shallower and normoxic) areas of the Lough (involving lateral movements of 10s to 100s of metres), rather than remaining in the Trough. An alternative scenario that they might have died (as less mobile infauna do) is most unlikely as no dead or dying fish, behaving like zombies were encountered during the May sampling. Fish and some decapod crustaceans are the least tolerant taxa in terms of hypoxia and it has been hypothesised that this is due to their mobility which allows them to escape from hypoxic areas (Vaquer-Sunyer & Duarte 2008). Spreading into the Western Trough under normoxic conditions would help the fish to disperse, as they display territorial aggression (Gibson & Ezzi 1987). Adequate space may be an important factor, especially for the survival of juvenile fish (cf. Gibson & Ezzi 1978). In addition, Fries' gobies are known to feed mainly on polychaetes and small crustaceans (Gibson & Ezzi 1987) and previous studies spanning decades have shown that these groups are plentiful in the Western Trough under normoxic conditions (Kitching et al. 1976, McAllen et al. 2009). Wheeler (1969) recorded a maximum standard length of 130 mm for this species while they become mature at 40-50 mm standard length (50-60 mm total length)., which means that juveniles, as well as mature Fries' gobies made use of the Western Trough. Gobies tend to tolerate relatively low oxygen concentrations due to their benthic lifestyle (Breitburg 2002). Oxygen concentrations were 1.29 mg l^{-1} at 30 m in May in Lough Hyne and therefore *L. friesii* may move into more oxygenated waters. Kitching et al. (1976) suggested that, during formation of the thermocline, hypoxic conditions spread from the bottom upwards and outwards and this is confirmed by the oxygen profiles reported here. Such a pattern of hypoxia development would facilitate movement of fish towards normoxic conditions before their reproductive cycle commences. Results of this study suggest an up-slope migration as indicated by their change in maximum depth of occurrence between March and May and lack of dead or moribund animals below the forming thermocline in May. Studies on fish behaviour in relation to approaching ROVs have shown that some fish species react negatively to the associated light, sound and pressure changes (Stoner et al. 2008). *L. friesii* sought shelter upon approach of the ROV and this behaviour may have led to underestimation of fish abundances. Another source of underestimation may lie in diurnal changes in behaviour. Activity patterns of *P. minutus* have been studied in populations in the Baltic Sea and there it was found that they are more active at night when light levels are low to avoid visual predators (Ehrenberg & Ejdung 2008); the present study was performed in daytime for safety reasons, however changes in the faunal composition amongst seasons at mid-day sampling revealed the effect of the thermocline on populations.

Crabs also reacted to the changes in oxygen concentrations in relation to the thermocline. Most markedly, their tracks in November at 30 m showed that they can move into the hypoxic waters, probably to find food, as previously indicated for other decapods by McAllen et al. (2009). To learn more about the diversity of crustacean tracks, a tank experiment was set up, using five species of crustaceans: *Cancer pagurus, Carcinus maenas, Maja brachydactyla, Liocarcinus depurator* and *Pagurus prideauxi*. The experiment was unsuccessful due to the small size of the tank and the amount of stirred up sediment in the water column, due to which, no tracks could be assessed for several hours after letting animals enter the experimental tank. It was therefore not possible to identify the tracks further than to general crustacean level. In the present study only one unidentified fish was seen in November at 30 m, but numerous crab tracks at and below 30 m indicate that decapods were visiting the Western Trough while the thermocline was still breaking down. Scavenging crabs may benefit from organic matter brought in from the outside of the Lough during the winter months as demonstrated in Chapter 2, while the diet of fish such as Fries' gobies is more based on polychaetes and small crustaceans (Gibson & Ezzi 1987). They may therefore not risk entering the hypoxic area as their prey may not be abundant enough in November when recolonisation merely begins, as discussed in Chapter 4. By March, both decapods and their tracks were numerous below summer thermocline depth; as presumably they made use of enhanced abundances of prey such as polychaetes and small crustaceans that scavenge on decaying matter accumulated during the anoxic summer conditions. It should be noted that the portunid crabs observed in the Trough were predominantly swimming crabs; this means that they could potentially walk into the hypoxic areas to scavenge, and then readily swim upwards to reach normoxic water after feeding. Crustacean tracks were again encountered at 30 m in May, indicating that they migrated below thermocline depth to prey on dead and moribund infauna. This behaviour has been reported previously for fish and crustaceans in response to short-term hypoxic conditions for example Pihl et al. (1991) studied migration behaviour of three demersal fish species and two crustacean species in Chesapeake Bay and reported that most of them move out of hypoxic areas and move back in once conditions ameliorate. The only exception was the crustacean *Squilla empusa*, which moved out of hypoxic bottom waters but then remained where it had migrated to, rather than to return to deeper waters once oxygen conditions improved there.

Oxygen concentrations explained 26.6 % of the observed variation in animal abundances, implying that other factors play a role in faunal assemblage structure. These are likely to include seasonal variations in food availability, and H_2S concentrations. H_2S persistence in the sediments may also explain why few animals occurred in November at 30 m when normoxic water column conditions were recorded at that depth. Tunnicliffe (1981) studied the effects of anoxia on an epibenthic community in Saanich basin on Vancouver Island. That fjord-like system (maximum depth 220 m) developed anoxia in the summer months and anoxic water was flushed upward and out of the basin over the course of the winter months. During the rise of the anoxic layer to a depth of 100-130 m, crab numbers increased at 85 m indicating that they retreated there to avoid anoxic conditions at greater depth. Other authors also reported that fish may evade hypoxic conditions in fjordic systems exposed to seasonal hypoxic events. Jørgensen (1980) reports an increase in fish abundance close to shore in shallow waters of a Danish fjord (Limfjorden) during hypoxia in deeper waters, while crustaceans, *Carcinus maenas* and *Crangon crangon* were found moribund in the hypoxic zone and infauna moved onto the surface of the mud. Pihl et al. (1991) noted that fish catches were higher in oxic zones during hypoxia in the York River estuary (Chesapeake Bay, USA) and animals absent during hypoxic conditions returned to deeper waters when conditions improved. Our study has revealed that mobile animals not only used re-oxygenated areas as they became available for short-term activities such as scavenging, but that they also established a community and some built semi-permanent burrows. This was mainly exemplified by the Fries' goby that established a residential population encompassing all size classes in the Western Trough.

Using a three-monthly approach over one year in this study helped to elucidate how epifaunal assemblages change with the onset and break-down of the thermocline in the Western Trough of Lough Hyne. The experimental design allowed for a quantitative assessment of changes in the epifaunal assemblages which was not possible in the study of McAllen et al. (2009). Faunal assemblages differed between the studies. For example McAllen et al. (2009) recorded more scallops and *Palaemon serratus* than were encountered in the current study, but all observed species are regular inhabitants of Lough Hyne. Both studies, carried out in a tractable natural laboratory, revealed changes in faunal assemblages that can inform studies of fjords and loughs around the world that are affected by similar seasonal hypoxia.

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Chapter 4

Influence of natural hypoxic events on soft-sediment assemblages in a marine nature reserve

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ABSTRACT

Changes to benthic assemblages affected by a summer thermocline leading to first hypoxic and then anoxic conditions were studied during well-mixed water column conditions at Lough Hyne from November 2009 to May 2010. Sampling took place three-monthly, was backed with oxygen-temperature profiles, and was carried out in two ways. Video footage of the sediments was taken with a camera attached to a remotely operated vehicle and used to enumerate animal burrows above, at and below thermocline depth. For macrofaunal analysis, grab sampling above and below summer thermocline depth (STD) was employed. Hypoxic conditions below STD were still present in November and were forming again in May, normoxia being recorded in between. Faunal assemblages above STD changed slightly, possibly due to seasonal fluctuations. Below STD, anoxic summer conditions had left the sediments devoid of macrofauna and recolonisation took place from November to May, evident from both study approaches. Macrofauna showed classic post-disturbance recolonisation patterns below STD with a few species occurring in high numbers first before diversity increased and abundance decreased. Organic matter and oxygen are the main factors structuring the macrofauna, as established using multivariate analysis. Burrows occurred at 20 m throughout the study period, were absent at the deepest transect (40 m), but present just below summer thermocline depth during normoxia.

1. INTRODUCTION

In 2003, the OSPAR commission (Oslo-Paris Convention for the Protection of the Marine Environment of the North East Atlantic) added sea-pen and megafaunal burrowing communities to the list of communities and habitats to be protected (Diaz & Rosenberg 2008, Curd 2010). Trawling is one of the most direct threats to the benthic biodiversity of soft sediment marine communities, whilst other threats include eutrophication and increasing temperatures due to climate change. Chronic trawling disturbance can lead to dramatic reductions in the biomass of infauna and epifauna, of species diversity and to changes to trophic structures (Jennings et al. 2001, Curd 2010). Eutrophication leads to increased organic matter in the form of phytoplankton blooms. Their subsequent decay increases biological oxygen demand and – especially where stratification of the water column occurs – hypoxic/anoxic conditions, which have become a widespread and increasing problem around the world (Pihl et al. 1991, Diaz & Rosenberg 1995, Diaz 2001, Diaz & Rosenberg 2008, Rabalais et al. 2010). Increasing ocean temperatures lead to greater stratification and reduced mixing of water masses, while at an organism level they lead to higher metabolic rates which in turn can impact life-history traits and population size and dynamics (Pörtner & Farrell 2008, Hoegh-Guldberg & Bruno 2010). OSPAR stated that burrowing macrofaunal communities are not well understood in terms of how they function in the absence of such threats and how sensitive they are to naturally-occurring changes as these are likely to be masked by heavy trawling and other anthropogenic disturbances. For this reason, studying soft sediment communities of no-take zones such as marine protected areas (MPAs) and marine reserves is a valuable tool for understanding benthic ecological processes.

The study site Lough Hyne has been thoroughly described in Chapter 1. The water body of Lough Hyne and the benthic assemblages inhabiting it, are nearly cut off from the Atlantic, this is exemplified by an estimated flushing time of 80 days (Jessopp et al. 2009). This allowed studying the effects of a seasonal thermocline leading to a gradient from hypoxic to anoxic conditions on a soft sediment benthic community, that is most likely self-seeding, making it possible to compare directly the soft sediment assemblages above and below the summer thermocline depth (STD) and examine recolonisation processes.

The present study used sediment grab sampling and a camera-equipped remotely operated vehicle (ROV) to address the following research questions:

1. How do soft sediment assemblages re-establish themselves after temporary summer anoxic conditions have abated?
2. How do assemblages above and below the STD compare with each other?
3. Do infaunal macro- and megafauna recolonise in a comparable manner?

For the purpose of this study, animals collected by grab sampling were defined as macrofauna, while the term megafauna was used for those animals whose burrows were identified on the ROV video footage.

2. MATERIALS AND METHODS

2.1 Sampling schedule and site

Sampling was carried out in the Western Trough at intervals, from November 2009 (when the thermocline was breaking down) until May 2010, when the summer thermocline had begun to form again and oxygen levels below it were falling. The study period therefore encompassed the winter and early spring period when deep water was normoxic; summer sampling was unnecessary since sediments below the thermocline at that time are known to be devoid of fauna (Kitching et al. 1976, McAllen et al. 2009) as discussed in Chapter 3. Environmental monitoring and grab sampling were conducted every 3 months, but due to scheduling constraints, the remotely-operated vehicle (ROV) was unavailable in February 2010 and therefore this part of the survey was postponed to the beginning of March 2010.

The western part of the Western Trough was chosen for the ROV and grab sample studies. This area of the Trough is made up of uniform mud from about 12 m depth with occasional boulders occurring to a depth of 20 m, and was therefore ideally suited for this study.

2.2 Environmental conditions

Measurements of oxygen concentration (mg l^{-1}) and temperature (°C) were taken each sampling month (November 2009, February 2010, March 2010 and May 2010) from a boat moored to a permanent mooring buoy above the deepest point of the Western Trough (51° 30’ 144” N; 09° 18’ 139” W). A WTW OXI 197 oxygen-temperature probe and meter attached to a 60 m cable were deployed from the surface to 40 m depth and data were recorded at 1 m intervals. Due to a technical fault, temperature and oxygen readings were only available to 35 m in November.

2.3 Grab sampling

Preliminary grab samples at 48 m depth in the Western Trough collected in August 2009 confirmed the expected complete absence of live macrofaunal organisms during the summer. Sediment sampling for the infauna study reported here took place in November 2009, in February 2010 and in May 2010. At each study site, 4 samples were collected with a 0.05 m^2 van Veen grab. Two study depths were chosen to compare assemblages from above and below STD: the deepest part of the Western Trough (48 m) was used for assemblages below STD, while sampling at the 20 m depth contour along the western shore of the Western Trough was designated for assemblages from above the summer thermocline. At the 20 m depth contour, samples were not collected at the ROV transect site to avoid disturbing it. Depth was measured prior to each grab deployment ensuring that samples were taken from the correct depth (using a Speedtech SM-5 Depthmate portable sounder).

A subsample of 150 g wet weight from each grab sample was used for grain size analysis and organic matter content analysis. The sediment was dried in an oven for 48 hours at 80 °C. For grain size analysis, the method of Buchanan and Kain (1971) was followed. A sample of 25 g dry weight was mixed with 150 ml of 6 % hydrogen peroxide solution to remove organic matter. Sediment was stirred and left to soak overnight. Sediment was then washed with tap water in a sieve with 62 μm aperture size until the draining water remained clear. Distilled water was used for a final rinse to avoid fine particles from the tap water adding to the weight of the sample. The sample was again dried overnight at 80 °C. Each dry sample was passed through a series of Wentworth scale graded sieves (Wentworth 1922). Samples were driven through the sieves for 15 minutes by use of an Endecott Minor Sand Shaker, or, if particles had baked together, by gently brushing the sample through the grid with a soft brush. Median grain size and sorting coefficient were calculated using Gradistat v.6 (Blott & Pye 2001). Organic matter content (OM) was analysed by burning 1 g of dried sediment for 6 hours at 450 °C in a furnace. The sample was then reweighed and the difference calculated as percentage of overall weight.

For the macrofaunal assemblage analysis, the rest of each sample was sieved through a sieve with 500 μm aperture size, and the residue retained in the sieve stored in a 5 % formalin/seawater solution and stained with 0.1 g/100 ml Rose Bengal. Samples were then transferred into 70 % alcohol, sorted and identified to species level where possible. The reference collection made up of animals found in the present study was checked by staff of the environmental consultancy Marine Ecological Surveys, Limited, Bath, UK in June, 2011.

Two-way ANOVAs with Posthoc Tukey tests were carried out on abundance, species richness and Shannon-Wiener biodiversity indices of the biological data set. Multivariate analysis was only possible on data collected in February and May 2012 as samples collected in November at 48 m depth contained either no (three samples) or too few animals (one sample) to allow a multivariate analysis. Primer 6® (Plymouth Routines In Multivariate Ecological Research) was used to analyse species composition and relate it to the environmental conditions measured. For this, abundance data of all species were square-root transformed, then a Bray-Curtis similarity matrix was calculated. A non-metric multidimensional scaling plot (MDS) was used to visualise patterns of community structure. Next, the ANOSIM (Analysis of Similarities) routine was carried out on predefined groups (above and below STD, and February and May 2012). Finally, the BEST (environmental variables that ‘best’ explain the biological data) routine using the environmental variables: grain size, sorting, OM content, temperature and oxygen was carried out to relate environmental conditions with the biological data.

2.4 Remotely-operated vehicle survey

In November 2009, and in March and May 2010, a HYTEC H300 inspection class ROV system was deployed to follow three depth contours along the western slope of the Western Trough at depths of 20, 30 and 40 m for transect lengths of 40 m in each case. A Sony FBC type analogue colour video camera was vertically-mounted on the ROV to film the sea bed, which was illuminated by four 75 watt halogen lights. The camera was equipped with two vertically-directed lasers installed 53 mm apart on either side of the lens. The lasers projected light spots onto the sea bed into the field of vision, thus allowing size measurements. On all three occasions filming took place between late morning and early afternoon. Images were recorded onto a Sony RDX-HX750 HDD/DVD 160 GB Recorder. VideoLAN-VLC software (www.videolan.org.vlc) was used to analyse the footage as it allows manipulation of replay speed and the taking of snapshots.

For the video analysis, a series of screen shots were taken from each transect at each sampling date. The area filmed in each screen shot was measured by use of the laser pointers using ImageJ software (Rasband 1997-2012). The picture had to be a clear shot of the sea bottom with no obstructions such as sediment stirred up by the engine of the ROV. All visible burrows in each screen shot were assigned to a single burrow structure type and counted. Detailed descriptions of burrow structures of several species occurring in the Northwest Atlantic are available in the literature and were used in this study to help identification (Dworschak 1983, Nickell & Atkinson 1995, Astall et al. 1997, Atkinson & Froglia 2000, Atkinson & Taylor 2005, ICES 2011). Due to the variation in water clarity, it was not possible to evaluate equal sizes of sea floor on all occasions, but the mean transect size was 10.17 m^{-2} (SD = 4.78 m^{-2}) and data were expressed as burrow abundance m^{-2}.

3. RESULTS

3.1 Environmental conditions

Figure 4.1 displays temperature and oxygen readings for each sampling month. In November 2009, the summer thermocline at Lough Hyne substantially broke down, allowing oxygen levels to rise below thermocline depth. During breakdown, the thermocline moved downwards, improving oxygen conditions in deeper water. While oxygen concentrations were still low at 35 m depth in November, conditions were normoxic throughout the rest of the study period at all sampling depths until May 2010, when hypoxic conditions were measured again at 30 m and below. Temperatures were similar above and below STD in February and March 2010 (Figure 4.1). In November 2009 and in May 2010 temperatures differed strongly above and below the STD due to the thermocline with colder temperatures below the thermocline.

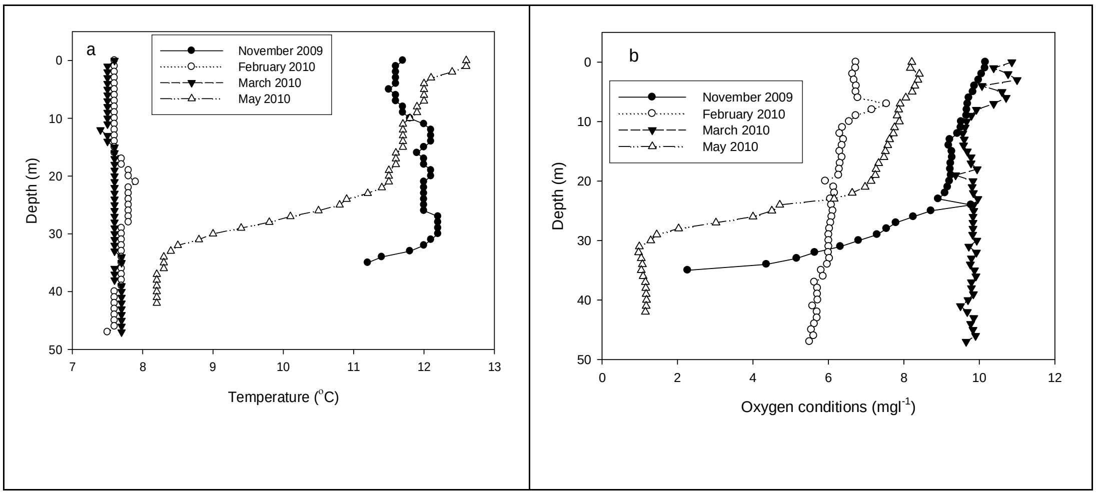

Figure 4.1: Vertical profiles of temperature in °C (a) and oxygen concentrations in mg l^{-1} (b) in the Western Trough, Lough Hyne during the study period.

3.2 Grab samples

The sediment at 48 m depth was made up of coarse to very coarse silt while at 20 m it consisted of very fine sand to very coarse silt (categorisation based on the Wentworth scale (Wentworth 1922)). Sediment was poorly sorted at both depths. OM content was significantly higher (2-way ANOVA, df = 1, F = 83.89, $P < 0.001$, performed on arcsin transformed data) at 48 m depth (mean = 10.21 %, SD = 0.27 %) than in samples at 20 m depth (mean = 6.52 %, SD = 1.53 %). The difference between months in terms of OM content were non-significant (2-way ANOVA, $df = 2$, $F = 3.61$, $P < 0.05$).

Table 4.1: Mean abundance m^{-2} of the 5 most dominant macrofaunal species identified from grab samples above and below STD in November 2009, February 2010 and May 2010 in the Western Trough of Lough Hyne. In November, only 2 species occurred at 48 m depth.

Sampling month	Below STD	Mean abundance	Above STD	Mean abundance
November 2009	*Chaetozone gibber*	5	*Kurtiella bidentata*	510
	Kurtiella bidentata	5	*Scalibregma inflatum*	310
			Nemertea	170
			Corbula gibba	85
			Amphiura chiajei	65
February 2010	*Scalibregma inflatum*	2980	*Scalibregma inflatum*	685
	Capitella capitata	620	Nemertea	160
	Capitella sp.	195	*Kurtiella bidentata*	105
	Malacoceros sp.	65	*Abra* sp.	90
	Kurtiella bidentata	15	*Glycera* sp.	80
May 2010	*Capitella capitata*	1015	*Scalibregma inflatum*	2432.5
	Scalibregma inflatum	210	*Lumbrineris* sp.	218.75
	Corbula gibba	135	Nemertea	137.5
	Malacoceros fuliginosus	125	*Lumbrineris tetraura*	25
	Abra alba	85	*Pseudopolydora* sp.	93.75

80 species in 32 families were identified in this study. These belonged to the following 8 phyla: Anthozoa, Mollusca, Polychaeta, Nemertea, Echinodermata, Sipuncula, Clitellata and Malacostraca. The most diverse group were the polychaetes with 42 species in ten families. The polychaete *Scalibregma inflatum* accounted for 52.5 % of all individuals counted (from all phyla). Table 4.1 lists

the mean abundance of the 5 most dominant species identified at each depth in November 2009, February 2010 and May 2010.

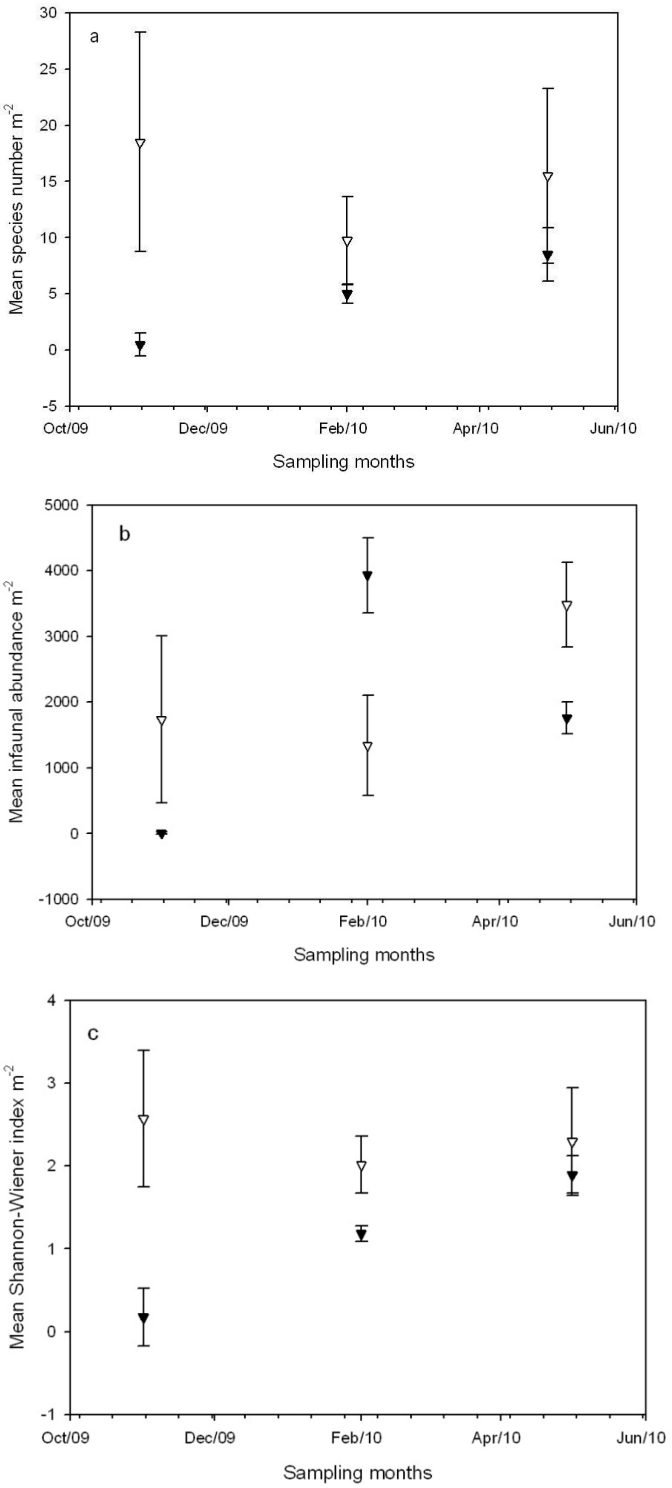

Figure 4.2: Univariate summaries of grab sample data at 20 m (open triangles) and 48 m (filled triangles) depth in November 2009, February 2010 and May 2010 in the Western Trough of Lough Hyne: mean species richness (a), mean abundance

m^{-2} (b) and mean Shannon-Wiener diversity indices (c). Error bars represent standard deviation. Note the different scales on the y-axes.

From Figure 4.2 it is evident that November samples below STD were characterised by virtual macrofaunal lifelessness, while above STD, species richness, abundance and biodiversity were high. By February, species richness and diversity index below STD had risen to values approaching those in sediments above STD, while abundances below STD were much higher than above STD. By May, species richness and biodiversity were similar at both depths, but abundances in deeper water had declined, while those in shallow water had risen.

Two-way ANOVAs with Posthoc Tukey tests on species richness, abundance and Shannon-Wiener diversity index revealed that species richness was significantly different between months (df = 2, F = 19.67, $P < 0.001$), being higher in November 2009 than in February 2010 ($P < 0.001$) and significantly higher in May 2010 than in February 2010 ($P < 0.001$), while depth was not a significant factor (df = 1, F = 0.15, $P > 0.5$). For abundance, the interactions between depths and amongst months were significant (df = 2, F = 24.83, $P < 0.001$) as might be expected from Figure 4.2b. For Shannon-Wiener diversity the interaction term between depth and month was also significant (df = 2, F = 9.83, $P < 0.001$).

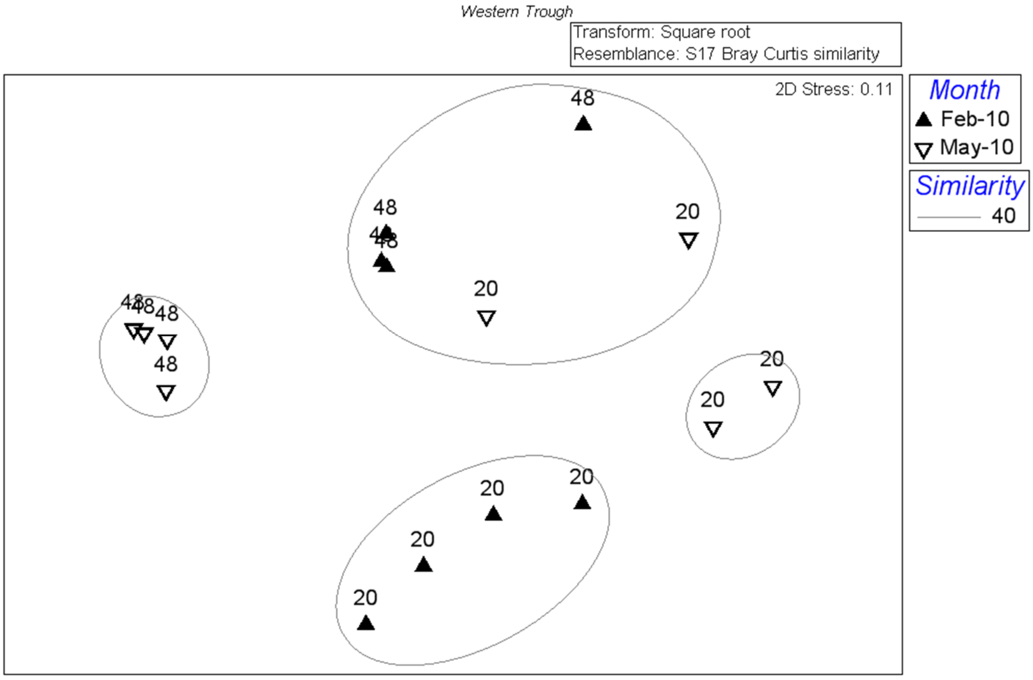

Figure 4.3: MDS plot of grab samples taken in February and May 2010 at Lough Hyne at 20 m and 48 m depth. Numbers above symbols indicate sampling depth. Four groups are indicated from the cluster analysis (40 % similarity).

The multidimensional scaling plot (Figure 4.3) shows 4 groups of samples based on 40 % similarity within these groups. Replicate samples from 20 m depth in February 2010 clustered into one group, and likewise replicate samples from 48 m depth in May 2010 clustered into a separate group. Similarity could also be found between samples from 48 m in February 2010 and 2 samples from 20 m in May 2010. To explore these clusters, a one-way ANOSIM was carried out on 4 sample groups: February 48 m, May 48 m, February 20 m and May 20 m. The global R calculated for assemblage composition differences between all 4 groups was significant: R = 0.814, P < 0.001. A posthoc Tukey test revealed that all pairwise comparisons between sample groups were significant except for two pairs: the between-group differences of samples collected in February at 48 m and May at 20 m samples and those collected at 20 m in February and at 20 m in May. This means that samples from February at 48 m were similar to samples collected in May at 20 m, as the MDS plot displays. It also means that samples collected at 20 m in February were similar to those collected in May at 20 m. Together these confirm winter recovery of the deep water assemblage.

The BEST routine was used to find the environmental factors which best explain the patterns observed in the biotic data. The best correlation was found for the combined effects of oxygen concentration and OM content ($\rho = 0.522$, $P < 0.001$).

3.3 Video analysis

Overall, five different megafaunal burrow structures were identified from the transect photos during the study. Figure 4.4 displays examples of the structures found. Burrows occurred to a sampling depth of 30 m on each sampling occasion, while none were found at 40 m depth on any sampling date. The greatest burrow diversity was found in March 2010, when all five structure types were visible. Figure 4.4a shows an individual Fries' goby resting on the bottom next to its burrow. Except for the burrows made by *Lesueurigobius friesii*, the inhabitants of the other burrow types were not visible in the video footage, therefore identification of burrows was based on burrow descriptions in the literature (as listed in section 2.4 of this chapter). In Figure 4.4b a burrow structure most likely made by the thalassinidean shrimp *Upogebia* sp. is encircled, the larger burrow opening visible is made by the goby *L. friesii*. The burrows of the thalassinidean crustacean *Calocaris macandreae* usually have 3 surface openings that produce a triangulate pattern as displayed in Figure 4.4c. A fresh burrow opening, conforming to descriptions of callianassid sp. is seen in Figure 4.4d. An example of an unidentified structure is depicted in Figure 4.4e. *Goneplax rhomboides* clear their burrow opening by sweeping sediment to the side with help of their claws, causing a typical pattern as displayed in Figure 4.4f.

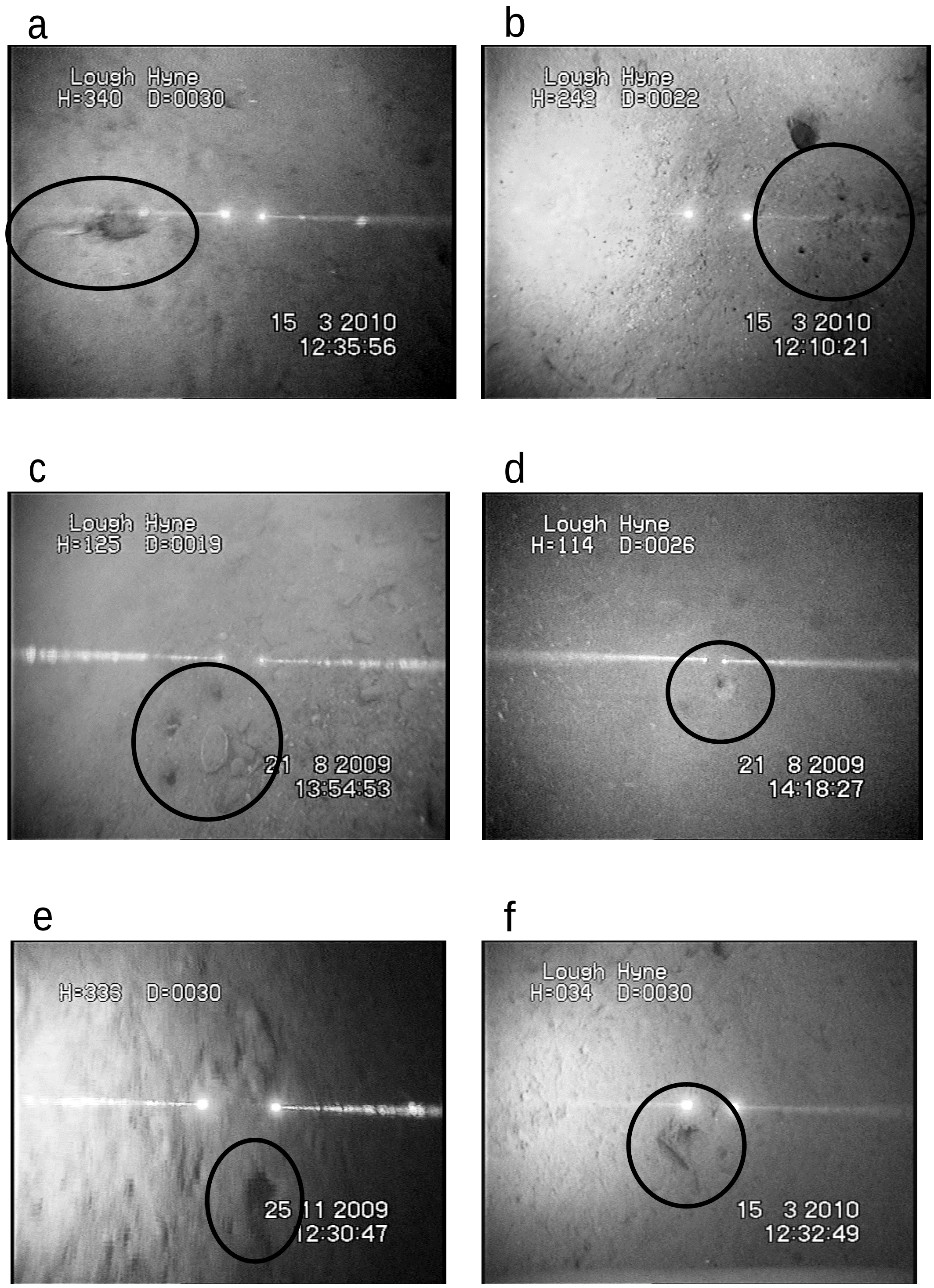

Figure 4.4: Burrow structures encountered during the study period in the Western Trough of Lough Hyne, conforming to structures described in the literature as belonging to: a) *Lesuerigobius friesii*, b) *Upogebia* sp. c) *Calocaris macandreae*, d) callianassid sp., e) an unidentified burrow, f) *Goneplax rhomboides.* In the top left corner a compass heading (H) and depth in m (D) is given, while the date and time of video capture is displayed in the lower right corner.

The most abundant burrow structure was made by *L. friesii*; the species occurred above and below STD during all sampling months (Figure 4.5). *Upogebia* sp. burrows were the second most abundant and occurred at a depth of 20 m on all three sampling occasions; while at 30 m it was encountered only in March and May 2010. The highest number of burrows was measured in May above the thermocline, which had begun to form by the time this sampling event took place, with the majority of these made by *Upogebia* sp. Burrows by *L. friesii* were still numerous in May at 30 m when the overall abundance of burrows was reduced and oxygen concentrations had fallen to 1.28 mg l^{-1} at 30 m.

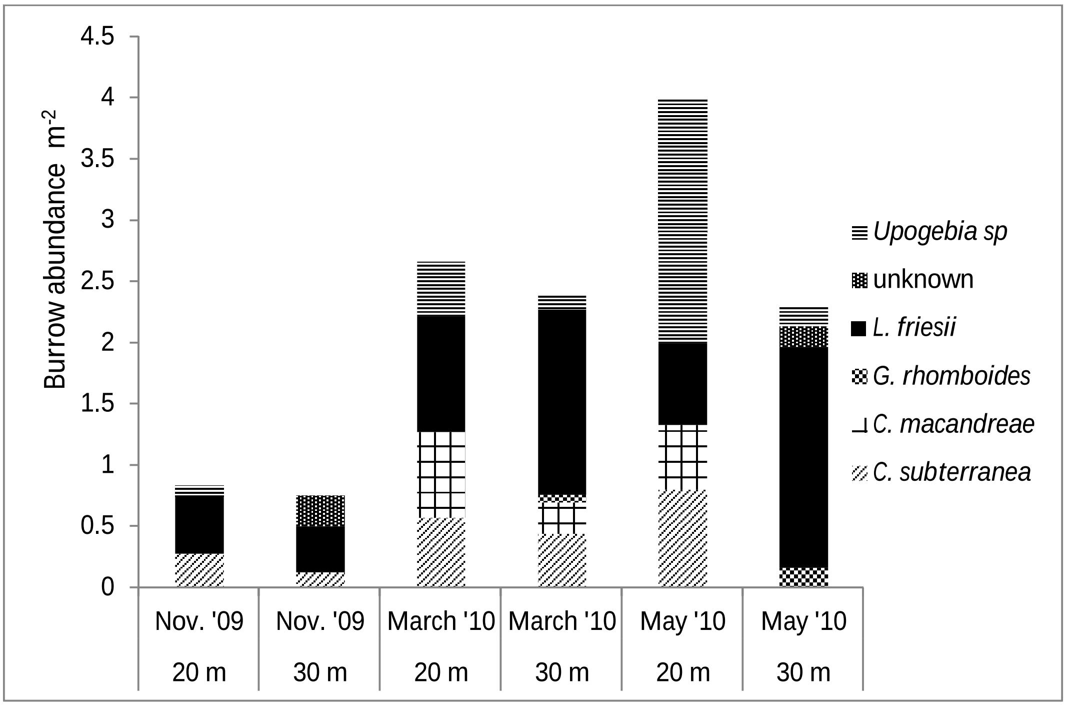

Figure 4.5: Changes in diversity and abundance of burrows at two depths in the Western Trough, Lough Hyne from November 2009 to May 2010.While conditions were normoxic at 20 m during the entire study period, oxygen conditions at 30 m depth were hypoxic in November 2009 and May 2010, but normoxic in February 2010. No burrows were found on the 40 m depth contour on any of the 3 sampling dates.

3.4 Comparing macrofauna and megafauna recolonisation below STD

Megafaunal burrow abundance above STD increased linearly from 0.83 m^{-2} burrows in November 2009 to 3.99 m^{-2} in May 2010 (2.66 m^{-2} in March 2010). Below STD, burrow abundance increased from November (0.75 m^{-2}) to March

2010 (2.39 m^{-2}), but then decreased slightly to May 2010 (2.29 m^{-2}). Recolonisation of macrofauna followed different patterns for both 20 m and 48 m samples. At 20 m depth, abundance reduced from November (1735 animals m^{-2}) to February (1340 animals m^{-2}) and then increased significantly in May (3470 animals m^{-2}). At 48 m depth, low abundance in November (10 animals) was followed by high abundance in February (3930 animals m^{-2}) and then fell to an abundance of 1650 animals m^{-2} in May 2010 (Figure 4.2b).

4. DISCUSSION

Conditions above the STD were normoxic throughout the study period and communities at this depth were therefore considered undisturbed in terms of adverse oxygen conditions; changes in assemblage composition above STD had to be due to other influences. Sediment grain size was similar throughout the study period and at both sampling depths, but OM was significantly higher below STD. The higher OM content may reflect the lack of macrofaunal bioturbation, feeding and remineralisation of sediment OM during the preceding anoxic summer conditions. It has been shown that bioturbation plays a major role in enhancing OM decomposition in marine sediments (Kristensen 2000).

A reduction in abundance, species richness and Shannon-Wiener diversity occurred at 20 m (permanently normoxic) in February 2010 (by comparison with November 2009) and then all three values increased in May 2010. Such seasonal changes are known to occur in shallow benthic communities of temperate oceans and are related to variations in temperature, primary production and light levels (Gray & Elliott 2009). Below STD, anoxic conditions had caused mass extinction of macrofauna before the study period commenced. Recolonisation by macrofauna at 48 m depth was shown by a linear increase in species number and Shannon-Wiener diversity index. Abundance peaked in February and then dropped in May. This is a classic post-disturbance profile, where at first a few species with high abundances make use of the available space and abundant OM before dying off and making space for a more diverse community (Odum 1969, Pearson & Rosenberg 1978). The polychaete *Capitella capitata,* for example, is an opportunistic species, colonising low oxygen - high OM sediments in high numbers before dying off and thereby making space for a more diverse community (Pearson & Rosenberg 1978 and references therein). Recolonisation revealed by the present study was dominated by the polychaete *Scalibregma inflatum*, which is surprising as they are not known to be a pioneer species and have not been found in such high numbers in Lough Hyne in previous studies (Kitching et al. 1976, Thrush & Townsend 1986) or in other soft sediment studies around the British Isles. However, they are believed to be detritus feeders and therefore would find plenty of food in the Western Trough (Fauchald & Jumars 1979). By May 2010, *S. inflatum* numbers had significantly reduced to less than

10 % of February densities, and *C. capitata* became dominant below STD. This may be related to a reduction in oxygen concentrations by May 2010; *C. capitata* is known to tolerate hypoxia (Pearson & Rosenberg 1978, Rosenberg 2001). Kitching et al. (1976) looked at seasonal variation of the community and recolonisation in the Western Trough, they found the polychaete *Pseudopolydora* sp. to dominate the habitat below STD with densities reaching several 1000s m^{-2} in early summer. Though the species did occur in our study at 48 m depth, it was only found in low numbers (20 m^{-2}) in May 2010. The reasons for such large difference in community composition (separated by five decades) are unknown.

Using multivariate analysis it was revealed that samples from 48 m depth in February were similar to those from May at 20 m depth. This is most likely due to the number of *Scalibregma inflatum* which dominated these two communities. Samples from 48 m depth were significantly different between February and May 2010 which also can be explained by the recolonisation and subsequent succession, for example the mass mortality of *S. inflatum* which is replaced by *C. capitata*. Changes to the communities above the STD are most likely due to seasonal cycles of population development, while changes below the STD can be explained by the availability of free space, high OM content and normoxic conditions during winter and subsequent deterioration of communities due to declining oxygen tensions.

Burrows made by megafauna were encountered at 20 m and 30 m depths, but not at 40 m depth. This is probably because summer hypoxia/anoxia develops earliest and is broken down last at this greatest depth, leaving too narrow a temporal window for colonisation by burrowing megafauna. However, McAllen et al. (2009), using ROV in the Western Trough of Lough Hyne, found evidence of burrowing megafauna at depth of 39-42 m in March 2005. This indicates that colonisation is possible and may vary from year to year. Rosenberg et al. (2002) studied the recovery of a Swedish fjord benthic (macrofaunal) community after anoxic conditions and there the recovery also took the longest in the deepest part of the fjord. These findings are also in agreement with those of Kitching et al. (1976), who found burrows in the Western Trough of Lough Hyne at 17-25 m depth during dive surveys during full water column normoxia but not at greater depths. They found burrows made by *Nephrops norvegicus, Calocaris macandraea* and gobies, while McAllen et al. (2009) found evidence of *Jaxea* sp. and *Calocaris* sp. in their ROV and SCUBA surveys. In our study, Fries' gobies (*L. friesii*) were responsible for the majority of burrows in all months at depth of 20 m and 30 m. Below the STD, their burrows were still numerous in May when oxygen conditions were already deteriorating. Fish are amongst the most sensitive of benthic megafauna to hypoxia and it has been suggested that this is counteracted because they are highly mobile, so can readily migrate away from adverse conditions. Hence they have limited physiological capacity to cope with hypoxia (Pihl et al. 1991, Breitburg 2002, Vaquer-Sunyer & Duarte 2008). Gobies are an exception to this rule due to their sedentary and burrowing life style, attachment to their burrows to avoid predators and egg-guarding behaviour when nesting. They are able to remain near their burrows until oxygen concentrations have reached nearly lethal concentrations (Breitburg 2002, Lissåker et al. 2003). This may explain why goby burrows were still found below STD in May 2010 when conditions were already hypoxic.

Like fish, most mobile crustaceans also readily migrate out of hypoxic areas (Tunnicliffe 1981, Pihl et al. 1991) and have low tolerances of hypoxic conditions (Vaquer-Sunyer & Duarte 2008). However, fossorial thalassinidean shrimps are an exception. They encounter severely hypoxic conditions in their burrows and can oxyregulate to near anoxic levels (Astall et al. 1997, Atkinson & Taylor 2005). Therefore, they remain in their burrows during hypoxic conditions and wait for oxygen levels to return to normal. They can maintain anaerobic respiration and survive anoxia for several days (Atkinson & Taylor 2005). A reduction of burrows of thalassinidean shrimps in May below STD in this study may be due to a reduced burrowing activity of thalassinideans rather than a sign of migration, as activities such as burrow maintenance are reduced in this group under hypoxic conditions (Atkinson & Taylor 2005). Given this behaviour and physiology, it is likely that they eventually die off in their burrows during summer anoxic periods at Lough Hyne, as this lasts for many weeks. Hence, the Western Trough may be a summer sink environmental patch for these crustaceans (as it probably is for most macrofauna), whereas it is likely that Fries' gobies migrate to and fro, avoiding significant mortality, as discussed in Chapter 3.

Even though the effect of coastal hypoxia on benthic communities has been the focus of much research for several decades (e. g. Kitching et al. 1976, Pearson & Rosenberg 1978, Tunnicliffe 1981, Diaz & Rosenberg 1995, Rosenberg et al. 2002, Pacheco et al. 2010), most study areas have also been disturbed by bottom trawling, confounding community analyses. OSPAR has consequently highlighted the need for research on soft sediment communities undisturbed by bottom trawling. Lough Hyne provides an ideal study area to address this issue. Separate communities within the same body of water affected by a seasonal thermocline, but undisturbed by bottom trawling for several decades were investigated in the present study. It was shown that even though the communities above and below the thermocline are in close proximity, they still differed significantly in their species' composition. This could only be explained by significant differences in OM and oxygen concentration at the two depths. Still, the communities must be interconnected in so far as that the permanently normoxic areas of the Lough can provide macrofaunal recruits (predominantly through planktonic larvae), or provide a summer refuge for such mobile species as the Fries' gobies.

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Chapter 5

Spatial and temporal changes in soft sediment communities at Lough Hyne in relation to current speed and other environmental factors

ABSTRACT

Temporal and spatial variation of benthic soft-sediment communities is influenced by small- and large-scale patterns of environmental factors. Current gradients influence communities on a large scale by shaping the habitat through sedimentation of organic and inorganic particles, as well as aiding the dispersal of larval stages of benthic marine fauna. Coastline configuration plays an important role in changing current speed, thereby changing larval dispersal and habitats. Temperature and organic matter settling onto the seafloor from the water column can vary on a spatial and temporal scale. Threats to coastal soft sediment communities include changes in seawater temperatures due to climate change, plus eutrophication which is known to increase organic matter in coastal marine systems. Lough Hyne, a small, semi-enclosed marine lake in the southwest of Ireland, offers an ideal site for basic ecological studies where anthropogenic influences are minimal, because it is a marine nature reserve. Lough Hyne features a current speed gradient that has already been shown to shape some hard substratum communities and taxa. Multivariate analysis was carried out on macrofaunal data collected seasonally for one year from grab samples, together with recordings of environmental variables along the current gradient. It was revealed that current speed, organic matter (settling out from the water column the previous month and organic matter in the sediment) and temperature acting together were important factors in shaping soft-sediment benthic communities. No single environmental factor had a strong influence on the benthic communities as revealed by first and second stage MDS.

1. INTRODUCTION

Marine benthic communities vary across spatial and temporal scales and can be patchily distributed (Gray 1974, Morrisey et al. 1992). Abiotic factors such as hydrodynamic forces play an important role in large-scale patterns of communities by shaping the physical habitat and aiding the dispersal of planktonic invertebrate larvae (Gray & Elliott 2009). Current speed also influences settlement of organic and inorganic matter to the seafloor with larger and denser particles settling out first, and lighter and organic particles settling in areas of low flow (Gray & Elliott 2009). Biotic factors such as predation and competition lead to small-scale changes in communities (Thrush 1986a, Thrush & Townsend 1986, Morrisey et al. 1992). Temperature and organic matter (OM) production in the water column also change seasonally; for example, phytoplankton blooms lead to peak inputs of fresh OM to the benthic communities in spring and autumn (Smetacek et al. 1978, Smetacek 1980, Riebesell 1989). The effect of each individual environmental factor on benthic habitats and communities usually cannot be studied separately as these factors usually work in union.

Coastline configuration influences water flow, by reducing current speed and water retention time in sheltered bays or by eddy formation around headlands (Archambault & Bourget 1999), all of which can lead to changes in recruitment of benthic communities from planktonic larval stages to the seafloor (Sponaugle et al. 2002, Rawlinson et al. 2005, Jessopp & McAllen 2008, von der Meden et al. 2012). Many coastal bays exhibit strong environmental gradients for example salinity gradients in estuaries (Ysebaert & Herman 2002), or an oxygen gradient where reduced current speeds are associated with high OM content and thermocline formation (Kitching et al. 1976). Similarly, pollution gradients have been identified from fjords and lagoons subject to eutrophication (Rosenberg 1973, Gamito 2008).

The study site at Lough Hyne has been described in detail in Chapter 1 and a map is displayed in Figure 5.1. Water exchange with the Atlantic is tidal-driven and, due to the narrow and shallow Rapids, water speed is high at the entrance of the Lough. It then slows down as it moves along the South Basin, while in the North Basin it is negligible (Bassindale et al. 1957, Broszeit et al. 2012). Thrush and Townsend (1986) studied spatial variation of macrofaunal soft-sediment communities along the current gradient in the South Basin of the Lough. They expected soft bottom benthic communities to change along the current gradient and related environmental variables. Instead, they found that distribution was more influenced by other abiotic and biotic factors such as anoxic bottom water seeping in from beneath the thermocline of the Western Trough, where the Western Trough and South Basin meet, local patches of increased organic matter input, or by the top-down influence of epibenthic predators. Current gradients played a more pronounced role in studies concerned with other taxa and communities. Watson and Barnes (2004) found differences in settlement patterns of hard-substratum communities between areas of high and low current speeds. Bell and Barnes (2000a, 2000b) found differences in sponge morphology and diversity that depended on current speed. The amphipod *Orchomene nana* had a significantly higher abundance in the South Basin than in the North Basin and it was suggested that this was due to lower current speed and longer water retention times in the North Basin which reduced the probability of these benthic scavengers detecting potential food sources by olfactory means (Morritt 2001).

Kitching et al. (1976) studied soft sediment benthic communities at Lough Hyne in the Western Trough only, comparing communities located above and below summer thermocline depths. Hence, there is a gap in knowledge of the macrobenthic community structures around the entire Lough and how they are influenced by environmental factors, especially if the current gradient has an effect on the Lough soft sediment communities as a whole.

The study reported here aimed to monitor environmental factors at different sites around the Lough, and assess how these influenced the soft sediment communities found at each site. It further aimed to understand how communities and environmental conditions changed on a seasonal scale.

2. MATERIALS AND METHODS

2.1 Sampling protocol

A three-monthly sampling regime commenced in May 2009 and continued until May 2010. Initially, 4 sites were chosen: Southeast, Goleen, Northwest and Northeast (Figure 5.1), their coordinates and depth are listed in Table 5.1. Sampling in the deeper parts of the Western Trough was omitted as this study is presented in Chapter 4. Data available from Chapter 4, collected in November 2009 and February and May 2010, above the thermocline were added to this chapter to increase areas covered.

Table 5.1: Depth, mean maximum current speed (spring inflow) and location of each sampling site, taken by a handheld depth meter, velocimeter and onboard GPS

	Southeast	Goleen	W.Trough	Northwest	Northeast
Depth (m)	21.2	5.9	21.7	18.7	17.4
Mean max. current speed (m^{-1})	0.2412	0.1054	0.0727	0.0194	0.0408
North	51°30.032'	51°29.855'	51°30.043'	51°30.269'	51°30.191'
West	9°17.898'	9°18.162'	9°18.333'	9°18.424'	9°18.050'

At each site, on each sampling occasion, 3 grab samples were taken using a 0.05 m^2 van Veen grab. Samples were placed in individual sample bags (450 x 600 mm, 120 g clear LDPE bags for food use). Samples were stored in a controlled temperature room at 4 °C overnight at the Environmental Research Institute, Cork and passed through a sieve with 500 μm aperture size within 24 hours of collection. A subsample of 150 g wet weight was taken from each sample for organic matter and grain size analysis before sieving commenced.

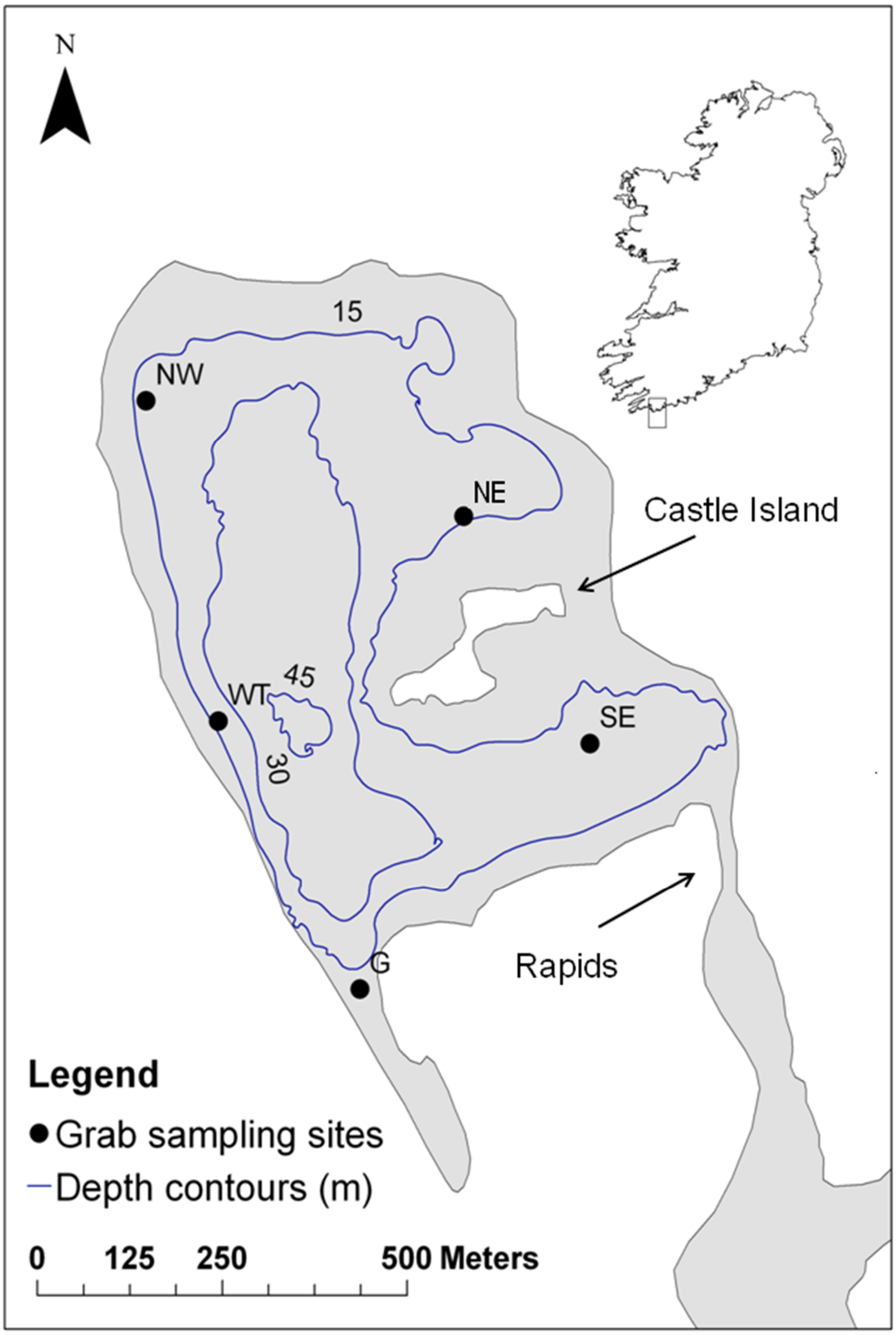

Figure 5.1: Depth contours of Lough Hyne and grab sampling sites used in this study. Numbers on contours are depth in m. SE = Southeast, G = Goleen, WT = Western Trough, NW = Northwest, NE = Northeast.

2.2 Environmental conditions

The subsample from each sediment sample was prepared for organic matter and grain size analysis following the protocol described in Chapter 4. Current speed measurements were taken in the water column near to the sampling sites at 5 m depth in 2010. Measurements had to be a few metres away from the sampling sites to avoid entangling of the rope that held the velocimeter with mooring buoys at the sampling locations. A Nortek Acoustic Doppler Velocimeter (Vector 3D current meter, Nortek AS, Norway) measured current velocity at sampling intervals of 10 min over a period of two weeks for one complete tidal cycle. The velocimeter was suspended vertically from a surface buoy anchored to the bottom by a 10 kg cement weight. To reduce flow interference due to the presence of the anchor rope, the velocimeter was placed in a steel frame that held it 50 cm away from the rope. A counterweight ensured that the velocimeter stayed upright during deployment. Data were divided into current speeds at spring inflow, spring outflow, neap inflow and neap outflow; and mean maximum current of spring inflow was subsequently used for analyses.

Measurements of temperature (°C) and oxygen concentration (mg l^{-1}) were taken just before sample collection at each site. A WTW OXI 197 oxygen-temperature probe attached to a 60 m cable was deployed to about 1 m above the sediment and oxygen and temperature readings were taken. Due to equipment failure, temperature and oxygen readings were not taken in May 2009 and February 2010. Depth was measured using a Speedtech SM-5 Depthmate portable sounder prior to the deployment of the probe, to ensure that oxygen and temperature readings were taken about 1 m above sediment. Sedimentation rate data collected for Chapter 2 (Broszeit et al. 2012) were used as an environmental factor in the analysis. Sedimentation rate of organic matter (OM) and inorganic matter (IOM) expressed as g m^{-2} day^{-1} during the month previous to the grab sample collection was chosen as a factor as this was hypothesised to influence communities at the collection date. For May 2009, no data were available because sedimentation rate data collection only commenced in June 2009.

To avoid collinearity amongst environmental variables, pairwise Pearson correlations were carried out on some variable groups after Kruskal-Wallis normality tests and if there was proof of a correlation, one factor was excluded.

2.3 Biological samples

For the community analysis, each grab sample was sieved through a 500 μm aperture size sieve, and the residue retained in the sieve stored in a 5% formalin/seawater solution and stained with 0.1 g/100 ml Rose Bengal. Samples were then transferred into 70 % alcohol, sorted and identified to species level where possible.

2.4 Data analysis

Primer 6® (Plymouth Routines in Multivariate Ecological Research) was used for analysis of environmental and biological data. For community analysis, the large dataset had to be reduced by removing all species that occurred less than 3 % of the time and in less than 3 % of the samples. Next, abundance data were $\log_{10}$ transformed and a Bray-Curtis similarity matrix calculated. Here, similarities are calculated between every pair of samples with similarity $S = 0$ if the two samples are totally dissimilar and $S = 1$ if the two samples are totally similar. $S = 0$ is satisfied if two samples have no species in common, while samples are said to be identical if the same species occur in the same proportion in both samples. In this way a triangular similarity matrix was prepared. The Bray-Curtis similarity is used in multivariate analysis as it is the only one that fulfils the requirement of not being influenced by joint absences. As Field et al. (1982) point out: “taking joint absences into account leads to the assumption that estuarine and abyssal samples are similar as they both lack outer-shelf species”. Based on this triangular matrix, multivariate analyses such as MDS and ANOSIM can be carried out. To visualise the patterns a non-metric multidimensional scaling plot (MDS) was prepared. A MDS places samples at a distance apart that reflects their dissimilarity to each other while reducing the dimensions to 2 and 3 dimensions. This reduction of dimensions can lead to distortion called stress and a high stress factor (> 0.2) indicates that the plot is inaccurate. In the next step, ANOSIM (Analysis of Similarities) was used to quantify the differences between samples, as with ANOVA in univariate analysis. Using the original data set, 2-way ANOSIM was carried out to test for significant seasonal and spatial differences. In order to elucidate which species were responsible for the patterns found in the ANOSIM analysis, the SIMPER analysis (similarity percentage) was performed. SIMPER calculates the contribution of each species to the overall Bray-Curtis similarity within groups and Bray-Curtis dissimilarity between each pair of groups (Clarke & Warwick 2001).

Finally the BEST (environmental variables that ‘best’ explain the biological data) routine was carried out: this routine finds the environmental conditions that best explain the biological patterns.

3. RESULTS

3.1 Environmental conditions

Mean maximum current speed at spring inflow tide at each site (Table 5.1) was chosen as the current speed factor since it was the highest current speed at each site and therefore most likely to influence sedimentation and biota. Current speed was highest at Southeast (0.2412 m s^{-1}) and lowest in Northwest (0.0194 m s^{-1}). Northeast had a higher current speed than Northwest (0.0408 ms^{-1}) due to the gap between Castle Island and the East Shore permitting ingress of fast-moving water from the South Basin.

All other environmental conditions used in the analysis are summarised in Table 5.2. OM content of the mud ranged from 7.70 % (mean of 3 replicate samples) in Northeast in August 2009 to a mean of 39.58 % in Goleen in November 2009. OM was always high at Goleen, and this was due to dense mats of a red filamentous alga *Rhodothamniella floridula*. Sediment OM content was also high at Northwest, but not at Northeast possibly due to the higher current speed at the Northeast site.

Sediments were mostly made up of clay and silt, mean median grain size being < 62 µm on most sampling occasions. However, in May 2009, a mean median grain size of 418.03 µm was measured at Southeast. The Western Trough had higher mean median grain size in November 2009 and May 2010 (90.05 and 107.81 µm, respectively). Sediments were poorly or very poorly sorted at all sampling occasions at all sites (sorting coefficient between 1.38 at Southeast in February and 2.72 at Western Trough in May 2010).

Temperatures were homogenous across the Lough in each sampling month, but differed clearly amongst months. The water was warmest in Goleen, in August 2009 (14.7 °C) and coldest in February 2010 in Goleen and Western Trough (7.5 °C at both locations). Conditions were normoxic on all sampling occasions. The lowest oxygen concentration was measured in February 2012 in the Western Trough (5.92 mg l^{-1}) and the highest at Goleen in August 2009 (9.82 mg l^{-1}).

Sedimentation rate data were collected monthly (Chapter 2), and therefore sedimentation data of the month prior to grab sampling were used for this analysis. This factor was considered to have the most influence on benthic communities while data of the same month may not fully influence processes in the sediment at the time of grab sampling. Organic matter (OM) sedimentation rates ranged from 0.93 g m^{-2} day^{-1} at Northwest in February to 2.78 g m^{-2} day^{-1} in the Southeast, also in February. OM in the trap in the previous month was tested for correlation with OM content in the sediment and the relationship was non-significant (R = 0.068, P = 0.628). Most sedimentation data from October 2009 were lost due to accidental spillage of the samples, therefore the ESTIMATE routine were used in PRIMER to calculate likely values.

Sedimentation rates of inorganic matter (IOM) were omitted from the data analysis as they were correlated to grain size collected with each grab sample (Pearson correlation on ranked IOM data, R = - 0.287, P = 0.031). Depth and OM content in the sediment were also negatively correlated (R = 0.354, P = 0.003), therefore OM was chosen for the analysis.

Table 5.2: Environmental conditions at the study sites during the study period. Values in brackets are SD. Oxygen and temperature were only measured once at each site on each sampling occasion and therefore no SD is given. NA = not available (due to equipment failure). Median grain size is a statistical parameter.

Month	Site	Temperature	Oxygen (mgl^{-1})	Mean median grain size (μm)	Sorting coefficient	Benthic OM (%)	Mean OM sedimentation (g m^{-2} day^{-1})
May-09	Southeast	NA	NA	418.03 (297.28)	2.18 (0.47)	10.15 (3.38)	NA
	Goleen	NA	NA	26.05 (3.04)	2.04 (0.24)	22.98 (7.66)	NA
	Northwest	NA	NA	32.38 (13.61)	1.86 (0.39)	33.32 (11.11)	NA
	Northeast	NA	NA	22.64 (1.33)	1.59 (0.04)	10.77 (3.59)	NA
Aug-09	Southeast	14.3	8.66	22.73 (1.72)	1.57 (0.04)	22.83 (7.61)	1.42 (0.47)
	Goleen	14.7	9.82	26.96 (9.69)	2.12 (0.57)	19.45 (6.48)	1.95 (0.26)
	Northwest	14.4	9.02	26.35 (2.19)	1.79 (0.04)	25.75 (8.58)	0.97 (0.13)
	Northeast	14.3	8.74	21.64 (2.34)	1.66 (0.04)	7.70 (2.57)	2.02 (0.39)
Nov-09	Southeast	12.5	8.9	19.76 (2.08)	1.49 (0.07)	25.59 (8.53)	2.40 (NA)
	Goleen	12.9	8.59	25.67 (1.53)	1.91 (0.31)	39.58 (13.2)	1.48 (NA)
	W. Trough	12.8	8.61	90.05 (50.93)	2.86 (0.13)	17.22 (5.74)	2.03 (NA)
	Northwest	12.9	8.08	37.49 (5.17)	2.35 (0.27)	24.87 (8.29)	1.48 (NA)
	Northeast	12.9	8.01	32.05 (2.21)	2.15 (0.07)	10.92 (3.64)	NA

Table 5.2 continued: Environmental conditions at the study sites during the study period. Values in brackets are SD. Oxygen and temperature were only measured once at each site on each sampling occasion and therefore no SD is given. NA = not available (due to equipment failure). Median grain size is a statistical parameter.

Month	Site	Temperature	Oxygen (mgl^{-1})	Mean median grain size (µm)	Sorting coefficient	Benthic OM (%)	Mean OM sedimentation (g m^{-2} day^{-1})
Feb-10	Southeast	7.5	NA	17.68 (0.38)	1.38 (0.03)	26.00 (8.67)	2.78 (0.21)
	Goleen	7.6	NA	23.91 (3.94)	1.74 (0.14)	37.16 (12.39)	2.02 (0.25)
	W. Trough	7.6	5.92	19.82 (2.04)	1.54 (0.11)	21.91 (7.30)	1.57 (0.24)
	Northwest	7.7	NA	26.89 (0.57)	2.11 (0.1)	28.94 (9.65)	0.93 (0.07)
	Northeast	7.8	NA	24.41 (1.54)	1.67 (0.05)	11.50 (3.83)	1.09 (0.24)
May-10	Southeast	10.9	8.1	19.10 (0.59)	1.45 (0.02)	23.49 (7.83)	1.64 (0)
	Goleen	11.1	8.81	26.14 (1.55)	1.78 (0.02)	33.71 (11.24)	1.28 (0.16)
	W. Trough	10.9	7.35	107.81 (70.9)	2.72 (0.43)	14.80 (4.93)	1.37 (0.27)
	Northwest	10.9	8.83	32.73 (6.02)	2.33 (0.18)	26.51 (8.84)	2.19 (0.55)
	Northeast	10.8	7.77	31.13 (2.33)	2.06 (0.10)	11.27 (3.76)	1.28 (0.16)

3.2 Biological analysis

180 animal species from 82 families were found during the study period. These belonged to the following phyla: Anthozoa, Crustacea, Echinodermata, Mollusca, Nemertea, Polychaeta and Sipuncula. Identification of Nemertea, Cumacea, Ostracoda and Tanaidacea requires expert taxonomic skills and so they were not identified further. The most diverse group was the Polychaeta with 76 species, followed by Mollusca and Crustacea with 37 taxa each. However, the recorded Crustacea diversity would have been higher if the Cumacea, Tanaidacea and Ostracoda could have been identified further. One echinoderm species, a small holothuridean *Rhabdomolgus ruber* has previously only been found in France and Helgoland. It was found for the first time in the grab samples of this study (Broszeit et al. 2010). For the multivariate analysis, the number of taxonomic entities was reduced to 54.

The stress value of the MDS plot was comparatively high (0.23) and due to the large number of samples, there was no pattern visible. Hence, the means of the 3 replicate samples at each site in each month were used in this step, which reduced stress to 0.17. The MDS ordination revealed community differences at a 48 % similarity (Figure 5.2). Goleen samples from November, February and May 2010 formed one group. This was most likely related to the high organic matter content (in the form of 3-dimensional algal mats) of the sediments at this particular site. Samples from May 2009 formed another group and included samples from the Western Trough in May 2009 which may be due to similarities in the communities in this particular season. The last group was made up of all of the other samples.

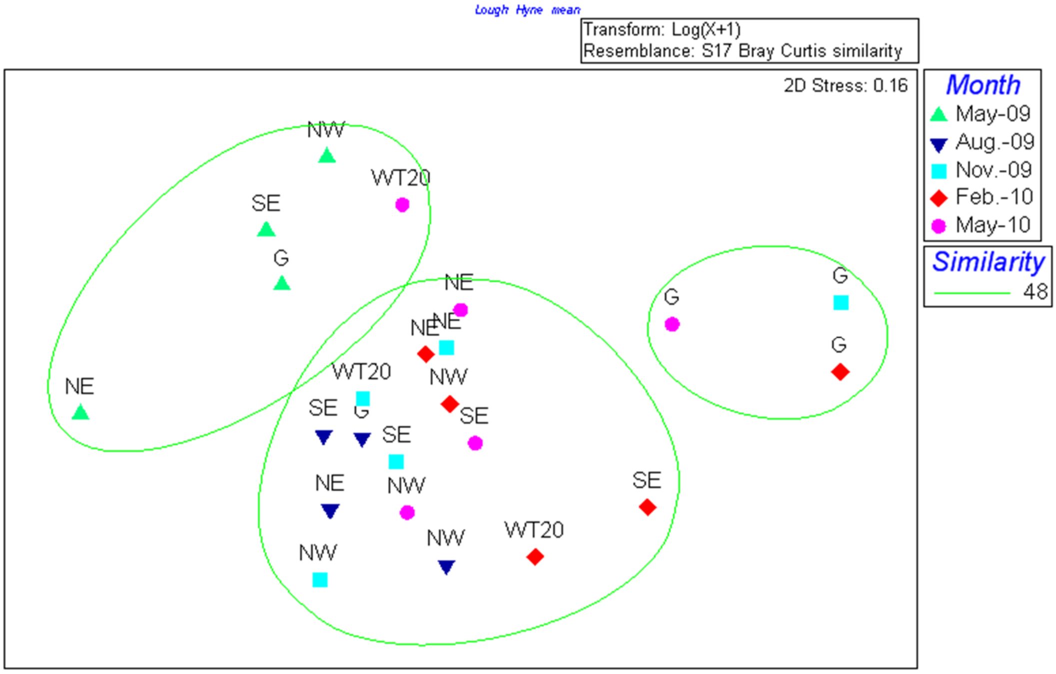

Figure 5.2: Non-metric multidimensional scaling plot of Lough Hyne soft sediment community data taken between May 2009 and May 2010 at 5 different sites. The green circles display 48% similarity between samples, forming 3 groups. Symbols represent different sampling dates and letters above the symbols represent sites (SE = Southeast, G = Goleen, WT20 = Western Trough, NW = Northwest, NE = Northeast).

The 2-way ANOSIM routine (factors: site and month) showed that there were significant differences amongst sites (R = 0.692, P = 0.001) and amongst months (R = 0.673, P = 0.001). All pairwise tests were significant (P < 0.005, for all pairwise tests).

The SIMPER routine revealed some slight patterns in the contributions of species to the similarity within groups (Table 5.3) and confirmed the results of the ANOSIM routine, that overall, there were only weak spatial or temporal patterns within the Lough. Goleen had more small-body-sized animals, particularly crustaceans, such as Tanaidacea and Cumacea than the other sites. Infaunal predators contributed to the average similarity amongst replicates in most of the samples that clustered together into the biggest group in the first stage MDS. The predatory taxa were: *Nephtys* sp., *Glycera* sp., *Lumbrineris* sp. and Aphroditidae. Predators occurred only once in May 2009 in sufficient abundance to contribute to average similarity, at Northwest. At Northeast, bivalves were contributing highly to the similarity within replicates, especially in May 2009, when four species contributed to similarity between replicates. However, in the other sampling months, they were less important, and no bivalves were sampled in May 2010.

Table 5.3: SIMPER (Similarity percentage) analysis results of $\log_{10}$ transformed abundance data, showing the species identified as contributing most to the community composition on each sampling occasion at a) Southeast and Goleen, b) Western Trough and c) Northwest and Northeast. Av.sim. = Average similarity, Av. Ab. = Average abundance (log transformed), Con. % = contribution to similarity.

a)	**Southeast**			**Goleen**		
May-09	Av. sim.: 51.84%			Av. sim.: 51.56%		
	Species	**Av.Ab**	**Con.%**	**Species**	**Av.Ab**	**Con.%**
	Tanaidacea	2.63	17.81	*Scalibregma inflatum*	3.16	17.84
	Cumacea	1.71	11.01	*Thracia* sp.	3.25	15.96
	Thracia sp.	1.76	9.13	*Corbula gibba*	3.26	14.77
	Amphiura chiajei	1.43	8.65	Nemertea	2.25	10.13
	Phascolion strombus	1.19	8.04	*Turritella communis*	1.52	5.75
Aug-09	Av. sim.: 57.48%			Av. sim.: 60.62%		
	Species	**Av.Ab**	**Con.%**	**Species**	**Av.Ab**	**Con.%**
	Nemertea	3.38	21.59	*Corbula gibba*	2.49	18.81
	Thyasira flexuosa	2.63	16.70	Nemertea	2.39	16.75
	Aphroditidae	2.22	13.30	*Thyasira flexuosa*	1.70	10.49
	Diplocirrus glaucus	1.71	10.04	*Abra prismatica*	1.43	9.53
	Scalibregma inflatum	1.76	8.71	Tanaidacea	1.19	8.86
Nov-09	Av. sim.: 67.15%			Av. sim.: 29.61%		
	Species	**Av.Ab**	**Con.%**	**Species**	**Av.Ab**	**Con.%**
	Capitella capitata	2.44	16.26	Tubificidae	1.85	52.83
	Nematoda	2.18	13.62	Ostracoda	1.29	11.47
	Aphroditidae	1.81	11.27	Nematoda	0.73	7.73
	Tubificidae	1.98	11.27	Cumacea	0.83	4.88
	Diplocirrus glaucus	1.44	8.92	*Lumbrineris* sp.	1.13	4.88
Feb-10	Av. sim.: 39.36%			Av. sim.: 58.09%		
	Species	**Av.Ab**	**Con.%**	**Species**	**Av.Ab**	**Con.%**
	Scalibregma inflatum	3.50	45.32	*Kurtiella bidentata*	1.89	25.08
	Capitella capitata	3.44	38.67	Tubificidae	1.75	23.66
	Glycera sp.	1.16	10.46	*Metaphoxus fultoni*	1.63	16.51
				Glycera sp.	0.69	10.83
				Tanaidacea	1.00	10.83
May-10	Av. sim.: 69.20%			Av. sim.: 77.54%		
	Species	**Av.Ab**	**Con.%**	**Species**	**Av.Ab**	**Con.%**
	Scalibregma inflatum	4.62	21.17	*Kurtiella bidentata*	4.97	15.47
	Nemertea	2.87	12.78	*Scalibregma inflatum*	4.36	14.83
	*Nephtys*sp. (juv.)	2.86	12.12	*Capitella capitata*	3.76	11.59
	Diplocirrus glaucus	2.44	9.90	*Metaphoxus fultoni*	2.70	9.10
	Kurtiella bidentata	2.51	9.68	*Nebalia* sp.	3.11	8.87

b)	**W. Trough**		
May-09	**NA**		
Aug-09	**NA**		
	Av. sim.: 59.80%		
Nov-09	**Species**	**Av.Ab.**	**Con.%**
	Kurtiella bidentata	3.28	16.95
	Nemertea	2.38	14.33
	Scalibregma inflatum	2.74	13.06
	Corbula gibba	1.71	9.81
	Aphroditidae	1.36	7.65
	Av. sim.: 57.01%		
Feb-10	**Species**	**Av.Ab.**	**Con.%**
	Scalibregma inflatum	3.72	42.07
	Abra sp.	1.83	18.34
	Glycera sp.	1.61	16.70
	Nemertea	1.84	9.28
	Corbula gibba	0.69	8.46
	Av. sim.: 45.15%		
May-10	**Species**	**Av.Ab.**	**Con.%**
	Scalibregma inflatum	4.52	39.66
	Nemertea	2.33	21.17
	Diplocirrus glaucus	1.29	7.62
	Cumacea	1.16	6.48
	Turritella communis	1.26	6.48

c)	**Northwest**			**Northeast**		
May-09	Av. sim.: 57.16%			Av. sim.: 17.67%		
	Species	**Av.Ab.**	**Con.%**	**Species**	**Av.Ab.**	**Con.%**
	Thracia sp.	3.43	25.65	*Corbula gibba*	1.49	26.43
	Scalibregma inflatum	2.5	19.00	*Angulus pygmaeus*	1.44	17.62
	Nemertea	2.34	17.03	*Melinna* sp.	0.46	11.92
	Corbula gibba	2.22	14.77	*Abra nitida*	1.03	8.81
	Glycera sp.	0.96	6.53	*Abra prismatica*	0.46	8.81
Aug-09	Av. sim.: 39.77%			Av. sim.: 47.88%		
	Species	**Av.Ab.**	**Con.%**	**Species**	**Av.Ab.**	**Con.%**
	Nemertea	2.44	34.44	Nemertea	2.39	33.00
	Scalibregma inflatum	2.08	24.53	*Abra prismatica*	2.2	28.46
	Thyasira flexuosa	0.96	13.35	*Turritella communis*	1.19	11.79
	Kurtiella bidentata	2.08	9.38	*Nephtys* sp.	0.83	9.93
	Nephtys sp. (juv.)	1.27	5.55	*Capitella capitata*	0.60	3.70
Nov-09	Av. sim.: 43.63%			Av. sim.: 64.86%		
	Species	**Av.Ab.**	**Con.%**	**Species**	**Av.Ab.**	**Con.%**
	Kurtiella bidentata	2.50	31.45	Nemertea	3.03	17.07
	Nemertea	1.62	18.4	*Exogene* sp.	2.82	14.73
	Corbula gibba	1.16	17.22	*Scalibregma inflatum*	2.51	14.16
	Nephtys sp.	0.69	13.54	*Lumbrineris* sp.	2.42	13.85
	Abra prismatica	1.06	7.86	*Kurtiella bidentata*	1.75	10.01
Feb-10	Av. sim.: 61.14%			Av. sim.: 63.26%		
	Species	**Av.Ab.**	**Con.%**	**Species**	**Av.Ab.**	**Con.%**
	Scalibregma inflatum	2.93	12.88	*Scalibregma inflatum*	3.62	27.71
	Corbula gibba	1.89	10.24	Nemertea	2.79	23.18
	Nemertea	2.47	9.34	*Corbula gibba*	1.44	10.66
	Tanaidacea	1.67	8.98	*Lumbrineris* sp.	1.06	7.00
	Turritella communis	1.63	6.71	Cumacea	1.19	6.98
May-10	Av. sim.: 59.60%			Av. sim.: 55.74%		
	Species	**Av.Ab.**	**Con.%**	**Species**	**Av.Ab.**	**Con.%**
	Scalibregma inflatum	2.85	21.16	*Scalibregma inflatum*	3.05	17.7
	Nemertea	2.46	19.65	Nemertea	2.52	14.32
	Nephtys sp. (juv.)	2.23	16.40	Tanaidacea	2.71	14.14
	Turritella communis	2.27	15.54	*Lumbrineris* sp.	2.27	11.00
	Amphiura chiajei	0.92	6.01	Cumacea	1.94	9.64

The best correlation between environmental and biological data using the BEST routine was found for the following combined factors: current speed, mean OM sedimentation rate, OM in the sediment and temperature ($\rho = 0.356$, $P = 0.001$).

3.3 Second stage analysis

To further investigate the patterns observed in the MDS plot (Figure 5.2) a second-stage MDS analysis was performed. In this analysis, the two crossed factors were analysed separately by producing similarity matrices for each factor level. In other words, since a series of data collection points are available for each site, it allows construction of a profile of community changes for each site, which can then be entered into a similarity matrix. These similarity matrices are summarised in Spearman rank correlations which are then entered into the two second-stage MDS (Figure 5.3), one for the factor ‘Month’ and one the factor ‘Site’. The analysis was carried out on the means of three replicate samples collected at each site and month due to statistical constraints.

In Figure 5.3a (factor month), November and February showed similar variation to each other, while the other three sampling occasions were more separated, indicating higher dissimilarity amongst them. In Figure 5.3b Northwest was separated from all sampling sites bar Northeast. This indicates that these two sites were more similar to each other than Northwest was to any other site. Figure 5.3b also indicates that there is no change of communities along the environmental gradient of current speed. If there had been, the sites would have been placed in order of reducing current speed along the Lough, with Southeast and Goleen close to each other, and Western Trough next to Goleen, then Northwest and Northeast.

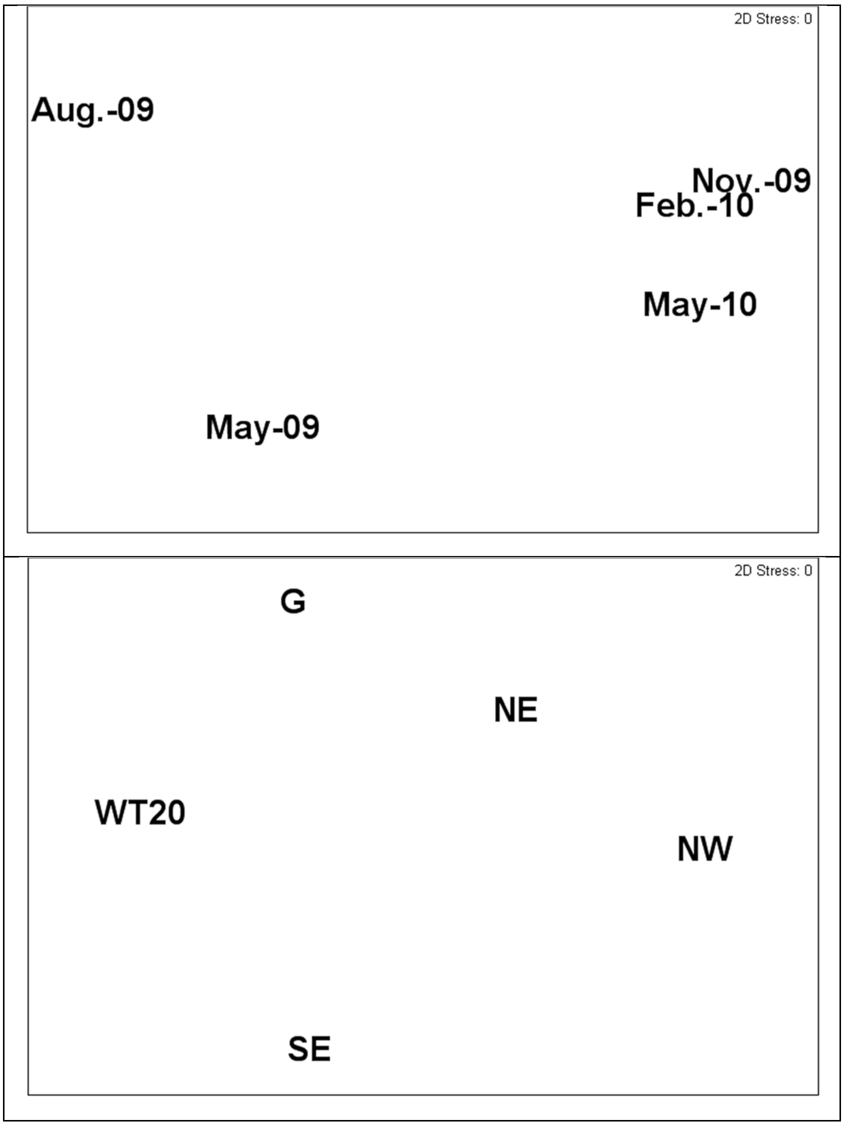

Figure 5.3: 2nd stage MDS (derived from Spearman correlations and converted to similarities) of soft sediment communities at Lough Hyne between May 2009 and May 2010 for both factors a) month and b) site. SE = Southeast, G = Goleen, WT20 = Western Trough, NW = Northwest, NE = Northeast.

4. DISCUSSION

The aims of this study were to look for patterns in the spatial and temporal dynamics of the soft sediment macrofaunal communities in Lough Hyne and to relate them to the measured environmental conditions. In general, such communities were fairly homogenous around the entire Lough during the study period. Current speed, amongst other environmental factors, played a significant role in shaping community structure around Lough Hyne. This is in accordance with studies conducted on hard-substratum communities (Watson & Barnes 2004) and sponge diversity (Bell & Barnes 2000b) and morphology (Bell & Barnes 2000a), yet in contradiction to Thrush and Townsend (1986), who found localised patterns were more important in shaping soft sediment benthic communities along a current gradient sampled at five sites in the South Basin of Lough Hyne.

Lough Hyne features a strong current gradient within a relatively small marine lake. As could be expected, low current speeds led to small grain sizes and poor sorting of sediments at most sites studied, except for the Southeast. OM content was higher in areas of low flow, such as Northwest and Goleen. Goleen was also shallower than the other sites, which allowed dense mats of *Rhodothamniella floridula* to grow, most likely because sunlight was able to penetrate to that depth. Temperatures were similar across the Lough on each sampling occasion, but varied strongly amongst seasons.

OM settling out from the water column is an important energy source for marine benthic communities, especially where sunlight cannot penetrate sufficiently to permit primary production to take place (Heip 1995). Lack of statistical evidence for a relationship between OM sedimentation and OM in the sediment can be explained by benthic processes such as microbial respiration and productivity removing OM from the sediment (Graf et al. 1982, Heip 1995). Highest sedimentation of OM occurred during the winter in Southeast and was most likely made up of sediments stirred up from the seafloor during storms outside the Lough and then transported inside (Chapter 2). Graf et al. (1982), studying OM sedimentation in the Kiel Bight, found that the quality of organic matter settling out in the winter is usually poor because it is stirred-up refractory material from the seafloor rather than fresh OM produced in the water column. In their study, OM sedimentation to the sediment was low in the summer, due to the pelagic food web using up the material in the water column. Therefore spring and autumn phytoplankton blooms were important food sources for benthic communities (Graf et al. 1982).

In the first stage MDS, most samples clustered together, indicating that communities were generally homogenous across the Lough and amongst the months. This means, that, even though there were spatial and temporal variations of environmental factors, as a whole, the communities across the Lough were to some extent similar to each other. Valderhaug and Gray (1984) studied a subtidal soft sediment community in Oslofjord over a period of 2 years and found that even though most environmental factors changed on a seasonal scale, most importantly the input of OM from the water column, the communities remained stable in terms of abundance and species richness over the sampling period. They argued that infaunal and epifaunal predators might be responsible for structuring the communities at their study sites. Infaunal predators may play a structuring role in the present study too; one predatory taxon distributed to average similarity (as measured in the SIMPER analysis) and was in nearly all of the samples that belong to the largest cluster of the 1st stage MDS, while the group consisting of May samples across different sites only had one predator at Northwest.

Two separate groups were formed by samples taken in Goleen and samples taken in May (2009 and 2010). The SIMPER routine revealed that small-bodied animals such as amphipods, ostracods were contributing most to the similarity amongst Goleen samples. They may have an advantage over larger bodied animals such as polychaetes in the dense mats of *R. floridula,* as they can move between the hair-like filaments of this alga and the dense mud it collects. The cluster of May samples (from 2009 and 2010) perhaps indicates that similar factors were acting on the communities in both years. The SIMPER routine did not reveal why May samples formed a separate group, but it may be due to the quality of organic matter sedimentation or temperatures. In addition, many planktonic larvae recruit to the benthic community in the spring. Their small body size and high abundance will change communities in the short-term, while only some will survive into autumn and winter.

The ANOSIM routine revealed that all samples were significantly dissimilar to each other indicating that, though they cluster together in the MDS, there are important differences that may have been due to small-scale and short-term changes to communities. Such changes could only be revealed by a higher sampling frequency spatially and temporally, beyond the scope and aims of the present study.

A combination of factors influenced the benthic communities such as current speed, OM content of the sediment and OM sedimentation, as well as temperature. Temperature may be the reason for the two winter sampling occasions (November and February) clustering close together in the second stage MDS. Nutritional value of OM sedimentation for benthic communities may be a second reason for this cluster and for the two May sampling occasions and August being separate from each other while OM content of the sediment and current speed could explain the second stage MDS of sites, particularly Northwest being closest to Northeast but separated from the other sites. Current speed is an important factor yet only in the context of its interplay with other environmental conditions. If it was the sole driver of the system, it could be expected that, in the second stage MDS, sites would form an array reflecting the water current measured at their site, so as that Southeast would be next to Goleen, then the Western Trough, then Northeast and finally Northwest, but this was not the case.

There was also evidence of patchiness occurring in the communities. Patchiness could be seen by the dominance of bivalves at Northeast in May 2009 and their subsequent reduction in importance as the study period progressed, even though the life span of all the bivalve species found exceeds the duration of the study period. Small-scale patchiness is an often-described feature of soft sediment benthic communities (Morrisey et al. 1992, Kendall & Widdicombe 1999). Several factors may cause patchiness such as epibenthic predators, bioturbation or competition (Thrush & Townsend 1986). Lough Hyne has an abundance of predators. For example, the swimming crab *Liocarcinus depurator* is caught regularly in large quantities in all areas of the Lough (McAllen, personal observation), while *Carcinus maenas* is another common predatory crab. Echinoderms, particularly the large starfish *Marthasterias glacialis* have been found in large numbers in some areas of the Lough, especially in the South Basin. Another starfish, *Luidia ciliaris*, is also a common predator of soft sediment communities and often found in Lough Hyne and all of these predators mentioned were also encountered on video footage of the Western Trough and these data are used in Chapter 3. Thrush (1986a) used these four species of predators in caging experiments in the South Basin of the Lough and found that *L. depurator* can significantly reduce the overall abundance of infauna, as well as the abundance of *Pseudopolydora pulchra*, a tube-building polychaete worm, while abundance of *Abra alba* and overall species richness were non-significantly, yet still negatively influenced. Another short-term cause of patchiness can be accumulations of large seaweeds (Thrush 1986b). Seaweeds, for example laminarians, dislodged from rocks and deposited on the sea floor can cause changes in the organic matter content, pH and oxygen content and cause localised shifts in macrofaunal community structures (Thrush 1986b). Patches of seaweed have been reported in the South Basin, and estimated at densities of 7 accumulations per 100 m^2 in the summer (Thrush 1986b). This number may be higher in autumn, when storms dislodge more seaweeds from the Atlantic coast and these are swept into the Lough. They were also encountered regularly in the Western Trough during ROV studies (Chapters 3 and 4).

Only a small number of macrofaunal studies in bays, estuaries or lagoons have looked at the effect of current speed, most being concerned with gradients of pollution (e. g. Rosenberg 1973), salinity (e. g. Ysebaert & Herman 2002) or hypoxia (Rosenberg et al. 2002, Veas et al. 2012). Also, second stage MDS is not often used in multivariate analysis but in this case it was useful to identify patterns that had been hidden in the two-way crossed set-up of samples.

This was the first study of soft sediment communities in all basins of Lough Hyne Marine Reserve. It showed that, though the communities are largely homogenous, there are important spatial and temporal differences and that these are caused by current speed, temperature and organic matter, the latter derived both from the sediment and the water column. The recently identified increase in nutrient input (Jessop et al. 2009) that is likely to increase OM availability to the Lough, may have important future impacts on the soft sediment communities of Lough Hyne. The present study should therefore serve as a baseline study for future community studies. Additionally, anticipated climate changes are likely to alter the annual temperatures of the Atlantic and the Lough - these may also impact Lough soft-bottom communities. Current regimes within the Lough are unlikely to change much over coming decades, particularly as the rebuilding of the western wall of the Rapids in 2006 has led to stable current speeds within the Rapids and Lough. Lough Hyne has been a marine reserve for over 30 years, and its soft-sediment communities have not been exposed to common anthropogenic threats occurring elsewhere, such as trawling and dredging. Ecological study is complicated by the number of environmental factors that influence benthic communities, all of which vary in intensity and act together (Bassindale et al. 1948). Lough Hyne therefore offers an ideal study site for disentangling the influences of non-anthropogenic environmental factors and providing a baseline for detecting the influence of large-scale environmental changes such as coastal eutrophication and climate change.

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Chapter 6

General discussion

GENERAL DISCUSSION

The present study used Lough Hyne to investigate temporal and spatial processes in the soft sediment benthos. Knowledge gained in this thesis is applicable to many temporal coastal systems worldwide due to common environmental conditions such as seasonal stratification leading to hypoxia and high variation in spatial patterns of environmental conditions. Also, the ecology of Lough Hyne soft sediment assemblages has not received much attention and therefore this study aimed to learn about the soft sediment assemblages and the environmental conditions affecting them. One major part of the project was concerned with the changes occurring to soft sediment assemblages in the Western Trough due to the stratification which leads to seasonal hypoxia.

The study of sedimentation rates showed that inorganic matter (IOM) and organic matter (OM) sedimentation are not closely linked and that they behave differently spatially and temporally (Chapter 2). IOM was brought into the Lough from the Atlantic outside, and input was enhanced during winter, due to strong wind speeds which stirred up sediments in coastal areas adjacent to the Lough. IOM sedimentation was also correlated with current speed on inflowing spring tides, providing yet further support for the inward transport of IOM from outside the Lough. This suggests that Lough Hyne is a sink for inorganic matter, particularly near the Rapids at the southeastern entrance to the Lough, where highest IOM sedimentation was measured. Further away from the entrance, in the North Basin, sedimentation of inorganic matter was significantly less than at the South Basin sites. This finding was reflected in the grain sizes measured for the study of infaunal communities around the Lough (Chapters 4 and 5). Grain sizes were generally small in Lough Hyne, mostly in the silt and clay fraction, as can be expected for an enclosed coastal bay (Gray & Elliott 2009). However, at the Southeast site, some grains were larger, and this was also true for grain sizes in the Western Trough at a depth of approximately 20 m. This is most likely due to the fact that the current loses speed and sediments rapidly along the South Basin, until it arrives at the western part of the Western Trough, which is where the samples mentioned were collected for grain size analysis.

OM sedimentation could not be solely correlated with the oceanographic processes measured in this study, as they would also depend on factors such as nutrients in the water column, for which no data were available. OM may either be produced *in situ* in the Lough as most likely happened in the summer periods of 2009 and 2010, or brought in from the Atlantic as occurred in the winter 2009/2010. Due to the small amount of direct freshwater influx of only 0.1 % of its volume day^{-1} (Johnson et al. 1995), OM coming from a freshwater source such as a river and its' catchment, as is common in coastal bays, is excluded at Lough Hyne. *In situ* production of OM may have important consequences for benthic fauna, as the nutritional value between freshly deposited pelagic OM, such as cells from phytoplankton or dead zooplankton has a higher nutritional value than OM resuspended during winter storms (Smetacek 1980). However, another source of winter OM (such as the material caught in the sediment traps used in this study) may come from intertidal flora and fauna that has been dislodged during winter storms (Davenport et al. 2011). Although there was no investigation of the type and source of the OM caught in the sediment traps, it was still demonstrable that OM quantities were correlated with benthic faunal processes (Chapter 5).

Organic matter settling out onto the seafloor can increase biological oxygen demand and thereby lead to hypoxic conditions, especially in coastal waters featuring reduced current flow and water column stratification. Hypoxic and anoxic events can lead to mass migration of mobile fauna and massive die-off events of sessile macrofauna. At Lough Hyne, a natural seasonal thermocline is believed to have occurred for millennia, and its effects on benthic and pelagic fauna has been studied for decades. Most recently, Rawlinson et al. (2004), using pumped water samples, discovered that zooplankton avoid the water column beneath the stratification and this was confirmed with echo sounding by Hawkins et al. (2012) in studies of sprat and zooplankton behaviour. In the present study, a visual quantitative approach was taken to study the effects of the thermocline on mobile fauna, and these data are discussed in Chapter 3. Mobile epifauna (mainly fish and crustaceans) were affected by the seasonal thermocline in that they probably migrated out of the Western Trough when the thermocline was present. This was particularly exemplified by the goby *Lesueurigobius friesii*, which migrated into the Western Trough to establish a resident population during periods of normoxic conditions. Portunid decapod crabs made use of ameliorating oxygen conditions by darting below the thermocline depth, possibly to scavenge food in November. This was shown by the abundance of tracks that they left on the sea floor. McAllen et al. (2009) caught prawns in pots in November 2006, indicating that not only portunid crabs behave in that manner. In the present study, only one unidentified fish was seen in the Western Trough in November 2009 as opposed to 39 crustacean tracks. This indicates that crustaceans make use of the Western Trough before fish move back in. This may have a physiological basis: decapods may be able to deal better with the hydrogen sulphide that is thought to be still present in November, than fish. Alternatively, the fish found in the Western Trough under normoxic conditions were mostly predators and therefore would not find food in the Western Trough, while scavenging decapods would find plenty of dead sessile macrofauna that did not survive the hypoxic summer conditions.

Burrowing crustaceans such as thalassinidean shrimps are known to tolerate low oxygen and high hydrogen sulphide conditions as a result of their fossorial life style, but only a few of their burrows were found in November below the summer thermocline depth. Unlike the goby *L. friesii*, thalassinideans do not readily migrate. Instead, after recruitment from the planktonic larval phase to the benthic adult stage, they build elaborate burrows which they rarely leave (Strasser & Felder 1998, Atkinson & Taylor 2005). The increase in abundance of thalassinidean burrows from November to March is therefore most likely due to new recruits.

Larger fauna such as gobies, burrowing crustaceans and echinoderms all help to oxygenate the sediment (which was high in organic matter content) by bioturbation. This in turn will help to move organic matter deeper into the sediment, encouraging deeper oxygen penetration and thereby make living conditions more favourable. It will also lead to a recycling of nutrients into the water (Snelgrove et al. 2000, Atkinson & Taylor 2005). Data collected for Chapter 4 indicate that macrofauna (collected by grab sampling) were sparse in the Western Trough below the summer thermocline depth in November. Most likely, this was due to the fact that their mode of recolonising previously uninhabitable areas is mainly accomplished by larval dispersal, which is why it would take a few months for benthic recovery to occur. By March 2010, macrofauna, epifauna and burrowing megafauna such as Fries' gobies and crustaceans such as *Upogebia* sp. were all plentiful in the Western Trough. This indicates that the habitat was favourable for macrofauna, which in turn attracted mobile predators into the area.

In the macrofaunal study presented in Chapter 4, a classical recolonisation pattern (Pearson & Rosenberg 1978) was observed: initial colonisation in March was performed chiefly by one opportunistic species, the polychaete *Scalibregma inflatum.* The following sample collection (in May) brought a greater benthic diversity and a significant reduction in *S. inflatum* abundance. The high abundance of predators encountered in the Western Trough during the March ROV sampling was likely in large measure responsible for the population crash of *S. inflatum*. This gave other species space to thrive. When comparing macrofaunal communities from above and below summer thermocline depth (STD), OM content of the sediment and oxygen concentration were the two environmental factors that best explained the spatial and temporal patterns of those communities. In the study presented in Chapter 5, comparing communities across the Lough (excluding communities below the STD in the Western Trough) and over an entire year, OM sedimentation also played a role, but other influential factors were temperature and current speed. As communities in the second study (Chapter 5) were not affected by hypoxia, it makes sense that oxygen did not play an important role and that temperature had a stronger temporal effect.

Sampling methodology

Sampling methods employed in marine ecology are by their nature selective and therefore, before an ecological study can be commenced, the appropriate approach has to be carefully considered. Also, the size and number of samples taken as well as the number of sampling sites, are a compromise between competing demands such as statistical precision, resources to sort and identify the samples (time and expertise), availability of sampling gear and ship capacity (Gray & Elliott 2009).

Study of sedimentation input to the soft sediment communities has not previously been done at Lough Hyne, but Bell and Barnes (2002) measured sedimentation above rocky cliffs in several places of Lough Hyne, which was useful data to compare with results of the current study. The traps and holders used in this study were designed by the author and supervisors and after a successful trial month, the study commenced. A monthly sampling interval was chosen as it was hypothesised that within a month enough sediment would accumulate to detect temporal changes. Also, environmental variables such as mean hourly wind speed and rainfall were data collected on a monthly basis by MetÉireann. Sedimentation data collected in this study are presented in Chapter 2. The method was successful and led to one publication in *Journal of Marine Biology* (Broszeit et al. 2012) presented in Appendix 1 and one collaborative publication, which is under review by *Estuarine, Coastal and Shelf Science* (Appendix 2).

All other sampling regimes followed in this study were on a three-monthly basis, in order to highlight seasonal changes and to reduce work load, both in the field and in the laboratory to a manageable level. A visual sampling approach was chosen to identify and enumerate the epifaunal communities of the Western Trough of the Lough. Using a camera attached to a ROV had several advantages over a SCUBA survey. Firstly, diving below 30 m depth is now considered hazardous, particularly in water rich in hydrogen sulphide as occurs during summer below the thermocline. Secondly, instead of divers recording what they encountered, video was collected that allowed repeated analysis of the transect, the taking of still images from the recordings and the exchange of information and stills with experts in the field to aid taxonomic identification. This was particularly important for the analysis of burrows discussed in Chapter 4. In many camera-aided benthic studies, the camera is mounted on a sledge. This has the advantage that the camera is always at the same height above the seabed, thus increasing size consistency of the video frame. In the present study this would have improved transect size consistency for the quantitative video analysis of burrow abundance. However, sledge sampling usually occurs along straight transect lines, over distances lasting several hundreds of metres. This is not possible at Lough Hyne due to its small size, also transects were lying parallel to each other so that direct comparisons could be made. Furthermore, the sledge runners would have stirred up the sediment leading to complete loss of visibility on consecutive transects and caused a large-scale disturbance to the benthos. Due to Lough Hyne's status as a marine reserve a permit for a sledge–operated sampling would therefore most likely not have been given. Data collected by ROV were presented in Chapters 3 and 4. Data from Chapter 3 have been accepted for publication in *Estuarine, Coastal and Shelf Science*, while data from Chapter 4 are under review by *Hydrobiologia*.

Due to its' status as a marine reserve, the use of other heavy sampling gear such as trawl nets is also not permitted at Lough Hyne and large research vessels cannot be used due to the shallow inlet. Therefore, a 0.05 m^2 van Veen grab used, which allowed a quantitative sampling approach and the destruction of sediments was localised to where the gear was dropped for sample collection. This could be deployed and retrieved by manual labour, because of the grab's small size and light weight, making a winch unnecessary. Samples were small enough to be sieved, sorted and analysed by one person. In the previous soft sediment studies carried out at Lough Hyne, sediment cores were collected by SCUBA divers (Kitching et al. 1976, Thrush & Townsend 1986). Using corers in the present study would have enabled comparing data with these former studies quantitatively. Likewise, other environmental variables such as redox potential of the sediment could have been measured. However, as mentioned above, SCUBA is no longer considered safe at the necessary sample depths and instruments to collect core samples remotely are too large and heavy for use in a small boat at Lough Hyne.

Summary and suggestions for future work

As described in Chapter 1, the unique features of Lough Hyne (it is small, sheltered, comparatively shallow, and features a wide range of habitats and environmental conditions) provide an ideal site to investigate general coastal soft sediment ecology. The research questions that were posed for this study were:

a) How do environmental conditions vary on spatial and temporal scales and how do they affect the subtidal benthic communities occurring in Lough Hyne?
b) How do benthic communities of the Western Trough cope with the seasonal presence of hypoxic conditions beneath a summer thermocline?

In Chapters 2, 4 and 5, environmental conditions and benthic communities and their variation on spatial and temporal scales are presented, fulfilling the first objective of this study. The effect of the thermocline on benthic macro - and epifauna has been studied for Chapters 3 and 4 and therefore, these chapters fulfil the second objective of the PhD programme.

This study helped to answer several questions about the Lough Hyne benthic ecosystem, yet it also opened new avenues of investigation which could not be addressed during the PhD programme because of limitations in time and funding. The following areas of research are suggested:-

Long-term changes to Lough Hyne soft sediment communities

Burrows of the crustacean *Nephrops norvegicus*, a commercially important inhabitant of soft sediments have been found in previous studies in Lough Hyne (Kitching et al. 1976, Thrush & Townsend 1986), yet in the course of the present study only a single burrow was found. Similarly, Kitching et al. (1976) and Thrush and Townsend (1986) both found the tube-building polychaete *Pseudopolydora pulchra* in high abundance, while in the present study they occurred in low numbers in the sediment grabs. In contrast, the polychaete *Scalibregma inflatum* was found to be highly dominant, particularly in the Western Trough, as demonstrated in Chapter 4. As many populations of marine organisms undergo cyclical abundance patterns (Barnes et al. 2002), this may also be true for these three species at Lough Hyne. However, the resident population of sea urchin *Paracentrotus lividus* has undergone dramatic abundance changes leading to a final collapse of the population (Barnes et al. 2002) with no signs of recovery (R. McAllen, personal communication) and detrimental effects for the shallow water ecology in the Lough. Further investigations into the ecological function of the three species (*N. norvegicus, P. pulchra* and *S. inflatum*) and how their change in abundance influences the ecology of Lough Hyne would be important. It would help to understand how the Lough ecology might change and how this could influence the biodiversity of the Lough, maintenance of which is a primary objective the designation of Lough Hyne as a marine reserve. In addition, Lough Hyne would be a suitable site for understanding ecosystem functioning due to its’ lack in fishing disturbance. The ecosystem functioning approach uses information on each macrofaunal species’ biology in terms of reproduction, movement and feeding (biological trait analysis) (Bremner et al. 2003). The aim of this approach is to understand, how these traits interact to lead to the distribution of species. It also helps to understand, which environmental conditions are necessary for each species to live in the sediment. With this approach, the health of the ecosystem can be assessed (Bremner et al. 2003).

Sources of organic matter

Knowing the origin, quality and composition of OM in the Lough would be useful in understanding benthic energy sources. Stable isotope analysis of sediment trap samples could give a clue to the origin of OM settling out of the water column at different times of the year. Stable isotope studies of organic matter in the topmost layers of the Lough sediments from various parts of the lough at different seasons (probably collected by SCUBA) would help to elucidate sources and composition of OM. The long-term aim would be to develop a trophic food web model.

Trends in thermocline development

One question that warrants further investigation concerns the annual development of the thermocline in Lough Hyne. Though its effects on benthic and pelagic communities have been studied for decades, there is an urgent need to understand which factors influence the development, longevity and break-down of the stratification. Information gathered in such a study will also help in making predictions of how it will be affected by local climate change and continuing eutrophication (Jessopp et al. 2009).

Meiofaunal and microfaunal processes and diversity in the Western Trough

In meiofaunal and microfaunal groups, some taxa are tolerant to or even prefer hypoxia to normoxic conditions and it would therefore be interesting to see how they affect/utilise OM in the sediment in the Western Trough, particularly how their assemblages change when macrofauna are absent during the anoxic summer conditions. A similar sampling regime to that employed in Chapter 4, and using cores from the grab samples would allow measurements of redox potential at different depths in the sediment. Additionally, the changes in abundance and diversity of microfauna and meiofauna at different depths in the sediment could be measured (for example comparing diversity and abundance in the top 0-1 cm with that in the 1-2 cm layer). Under anoxic summer conditions, macrofaunal bioturbation would not occur, leading to changes in the interstitial environment, affecting meio- and microfauna.

Lough Hyne has been used as a natural laboratory for marine research for nearly 100 years. The present study used methods not available to Kitching et al. (1976) or Thrush and Townsend (1986) such as a ROV or multivariate statistical analysis. Future advances in technology and increased statistical power will further improve our understanding of soft sediment processes, but it is hoped that the present study helped contribute to the advancement of our understanding of these processes.

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Appendix 1

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Research Article

Comparison of Inorganic and Organic Matter Sedimentation in a Natural Laboratory: A One-Year Study at Lough Hyne Marine Reserve, Ireland

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Measuring sedimentation rates may provide useful information on the habitat preferences of marine organisms. To understand the effect of flow rates and meteorological conditions on sedimentation in the absence of other confounding factors, sedimentation of organic (OM) and inorganic (IOM) matters was measured at 6 sites in Lough Hyne Marine Reserve (a semienclosed marine lake) over the course of 13 months. During winter, both OM and IOM were imported to the Lough, peaking in December at Whirlpool, the site nearest to the Lough entrance, likely as a result of extreme weather conditions causing resuspension of matter outside the Lough. Highest inorganic matter (IOM) sedimentation occurred in December ($47.36\,\mathrm{g\,m^{-2}d^{-1}}$ at Whirlpool Cliff) and was related to November wind speeds ($R^2 = 0.39$, $P < 0.001$). Decreasing current speed also caused a decline in IOM sedimentation. Highest OM sedimentation occurred in December at Whirlpool ($5.59\,\mathrm{g\,m^{-2}d^{-1}}$), but was not related to meteorological conditions. No single environmental factor strongly influenced organic matter (OM) sedimentation. One-way ANOVAs on OM and log-transformed IOM data showed that sedimentation differed significantly amongst the six sites within the Lough. Increased plankton production in the Lough during summer led to increased OM sedimentation in areas of low current speed away from the entrance of the Lough.

1. Introduction

The settlement of matter out of the water column onto the seafloor is an important process for benthic fauna. Sinking organic matter provides a high-quality food source for marine benthic communities which, except where light can still penetrate and benthic photosynthesis occur, are dependent on surface water production for energy input [1]. Sedimentation rates are largely influenced by the availability of nutrients in the surface water and by seasonality, which influences plankton growth. Dying phytoplankton blooms provide massive sedimentation events in short periods with a marked seasonality [2], at least at medium and high latitudes. However, benthic communities can be adversely affected by high organic matter input as described by classic models [3]: an increase of organic materials at first causes an increase in benthic biomass and microbial metabolism, but eventually this leads to the complete depletion of oxygen. The consequences of anoxia in the benthic habitat and the overlying water column are massive die-off events in the benthic community [4]. Additionally, areas of low water exchange, such as semi-enclosed bays and fjords, are known to develop temporal or permanent stratification of the water column. This is usually due to reduction of current speed by narrow and shallow inlets. The stratification worsens the hypoxic situation as it inhibits exchange of water across the thermocline. Seasonal or longer term anoxia is a well-studied consequence of stratification and organic enrichment [5].

Inorganic material such as gravel and sand will settle in areas exposed to strong hydrographic forces such as subtidal currents and wind-driven waves [6]. Finer particles remain in suspension longer and settle when the water velocity has fallen to a threshold value. Fine muds and silt settle in areas of low current velocity and here organic matter also settles out. Benthic animals choose their habitat according to factors such as current flow, grain size, stability, and organic matter content. Because of negligible sedimentation of organic matter in high-energy areas, and the danger of being dislodged, few animals live in these sediments, notable exceptions being venerid bivalve molluscs.

Lough Hyne (Lough Ine) on the SW coast of Ireland is a semi-enclosed fully marine lake that provides a natural laboratory for the study of the interactions of sedimentation and environmental factors. It is connected to the nearby Atlantic by a shallow, narrow channel (the “Rapids”) about 12 m wide (Figure 1) and between 1 m at ebb and at most 4 m deep at high tide. Due to this narrow inlet, the Lough exhibits a range of flow regimes from fast at the Rapids (up to $3\,\mathrm{m\,s^{-1}}$) to virtually still water ($<0.001\,\mathrm{m\,s^{-1}}$) in the North Basin. Freshwater influx is negligible [7] and salinity falls within the range of marine waters, resulting in the Lough’s flora and fauna being typically marine. Roughly speaking, the Lough can be divided into three parts: the South Basin and North Basin are approximately 20 m in depth and are divided from each other by Castle Island. The two basins are connected by the Western Trough, with a maximum depth of 48 m [8]. Lough Hyne is an ideal site to study coastal oceanographic processes as it is sheltered, comparatively shallow, and exhibits a wide range of flow rates within a relatively small area [9]. Within this body of water, the effects of current speed can be studied in the absence of (or much reduced) other confounding factors such as large distances between sampling sites or sampling across biologically and oceanographically different bodies of water. Weather conditions are constant across the entire study area due to their small size, while previous studies have shown no significant spatial variation in either water chemistry (Total N, Total P, silicates) [10], or other factors likely to influence sedimentation in different areas of the Lough such as phytoplankton [10], and zooplankton abundance [11]. In addition, because it is a marine reserve, anthropogenic disturbances such as dredging and trawling do not take place, and therefore resuspension of sediments due to these processes cannot impact the results.

Only limited work has been carried out previously on sedimentation within the Lough. Bell and Barnes [12] focused on sedimentation onto rocky substrates to study environmental conditions for encrusting sponges. They found that for IOM, rates were higher in winter than summer months, while sedimentation of OM was higher in the summer than winter. Interestingly, sedimentation was highest in areas of intermediate current speed such as Southwest, Goleen, and cliff faces of the Western Trough.

The research reported here was designed to address the following questions.

(a) How is sedimentation of organic and inorganic material distributed within the Lough and how does this change over time?

(b) How do oceanographic and meteorological factors influence sedimentation rates?

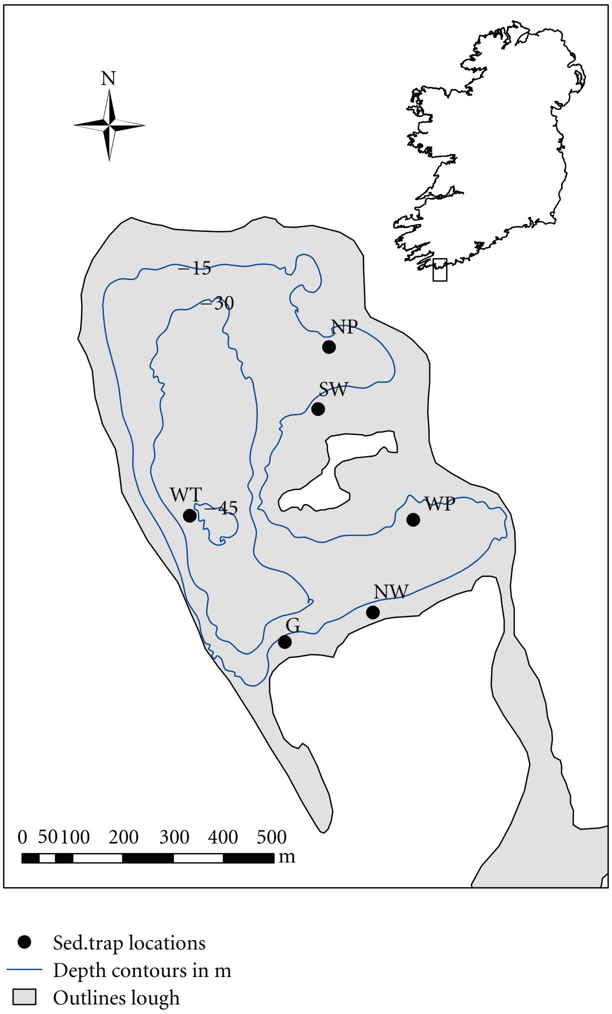


Figure 1: Sediment trap locations for the 13-month survey of Lough Hyne from June 2009 to July 2010. G: Goleen, NP: North Pier, NW: Northwest, SW: Southwest, WP: Whirlpool, WT: Western Trough.

2. Materials and Methods

2.1. Design and Deployment of Sediment Traps. Sediment traps were deployed at six sites around Lough Hyne (Figure 1). Sites were chosen to reflect different localities and current speeds (based on previous studies) in the Lough ranging from fast ($0.24\,\mathrm{m\,s^{-1}}$) near Whirlpool Cliff to slow ($0.02\,\mathrm{m\,s^{-1}}$) in the northern part of the Lough. A 10 kg block of cement was used to anchor a rope in each location, and a surface buoy ensured that the rope was taut during the duration of the study. A sediment trap holder with six spaces for individual traps was suspended at a depth of 10 m from the surface buoy (Figure 2). A depth of 10 m was chosen to avoid measuring resuspension from the sea floor.

Each trap was made of ABS drain pipe with an inner diameter of 45 mm and a length of 300 mm, sealed at the lower end with an ABS disc. The traps had an aspect ratio (width to height) of 1 : 6.67. This is above the recommended

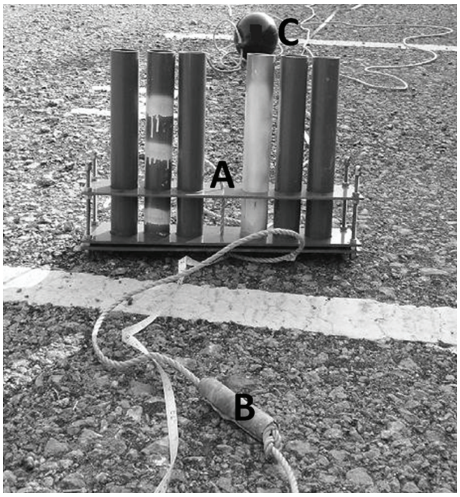


Figure 2: Six sediment traps in trap holder (A). A lead weight (B) rolled around the rope held the traps vertical in the water column. The surface buoy (C) ensured that the trap was suspended at the correct depth. Markings on the traps helped the divers to choose the correct trap on a given sampling occasion. The white trap remained in the holder throughout, purely for balance. The striped trap was the control.

minimum of 1 : 3, while the diameter exceeded the recommended minimum of 40 mm [13]. Four replicate traps in each carrier were filled to a depth of 70 mm with a 5% formalin/brine solution of 100 psu salinity. Formalin preserved the organic material within the falling sediment, while the brine was necessary to achieve a dense layer in which the sediments would remain without re-suspension [14]. Four tubes per site and month were chosen in case tubes were lost during the sampling interval and replication helped to confirm the representative nature of the collected data in relation to each site and month. A fifth trap was filled with seawater as a control. This control was only used to test the necessity of use of formalin for the monthly time span used, and data from the control tubes were omitted in the final analysis. A sixth trap in each holder was necessary for balance and was not removed during the course of the experiment. Traps were deployed and collected by SCUBA divers at intervals of approximately 4 weeks. Traps were sealed with drain pipe lids before removal from the trap holder and brought to the surface in a carrier in order to ensure the least possible disturbance to the trapped sediment. Each lid had a hole of 2 mm diameter drilled in the top to allow for pressure equalisation during the diving operations. After a pilot study to test functionality of the trap design, data collection was started in June 2009 and continued until July 2010.

2.2. Sediment Analysis. In the laboratory, each trap was shaken vigorously to resuspend the deposited material. A subsample of 55 mL was gently filtered through a preweighed 47 mm GF/C Whatman glass fibre filter using a KNF Neuberger Laboport vacuum pump. This was followed by a 50 mL wash of distilled water to remove salt [13]. Filters were dried in an oven at 80°C overnight, weighed, and ashed at 450°C for 6 h in a muffle furnace to remove organic matter before being reweighed. Sedimentation rates were calculated as g sediment $m^{-2}d^{-1}$ for both organic and inorganic fractions.

2.3. Collection of Factorial Data for Analysis. Current speed was measured using a Nortek Acoustic Doppler Velocimeter which was suspended vertically from a surface buoy anchored to the bottom by a 10 kg cement weight. Recording of current speed was conducted from January to March 2011 to ensure that resuspension of sediment during equipment deployment and retrieval did not have any effect on sedimentation rates during the experiment. The velocimeter was not available after completion of the sediment trap sampling and therefore current speed was measured in spring of 2011. To reduce interference due to the presence of the anchor rope, the velocimeter was placed in a steel frame that held it 50 cm away from the rope. A counterweight ensured upright position of the velocimeter during deployments. Using GPS, the velocimeter was placed at the same locations where the sediment trap holders had been previously held and left to collect data for two weeks at each location. Current speeds were measured at a depth of 5 m, halfway between the surface and the depth at which the sediment traps had been suspended. Data were divided into current speeds at spring inflow, spring outflow, neap inflow and neap outflow, and mean maximum current speeds in each of these four categories subsequently used for analysis. Weather data were obtained from Met Éireann and consisted of mean hourly wind speeds (knots) for each month from the M3 weather buoy (N51°13′0′′, W10°33′0′′), near Mizen Head, County Cork, and rainfall (mm) per month at Valentia weather station, County Kerry. The distance from the M3 weather buoy to the Lough is approximately 90 km, while distance from the Valentia weather station to the Lough is approximately 85 km. Temperature was recorded at 30 min intervals in the South Basin. A Hobo Pro v.2 water temperature data logger (Onset Computer Corporation) was suspended from a mooring buoy at a depth of 5 m and logged temperature continuously throughout the study period. Distance to the Rapids was measured using the Path tool in Google Earth. For each site, a line was drawn from the inner mouth of the Rapids through the South Basin to the southern trap locations (marked using GPS data). For the two northern sites, two routes were measured: one moving east to west along the South Basin to the centre of the Western Trough, then northward and finally in an eastern direction north of Castle Island to the trap location. For a second set of measurements, a path was chosen that passed directly through the narrows between Castle Island and the East Shore to the trap location.

3. Results

3.1. Data Exploration. Data showed equal variances (Cochrane's test) for organic matter sedimentation (OM) while inorganic matter sedimentation (IOM) had equal variance only after $\log_{10}$ transformation. Current speed and distance from Rapids were collinear, rainfall and wind data also, so

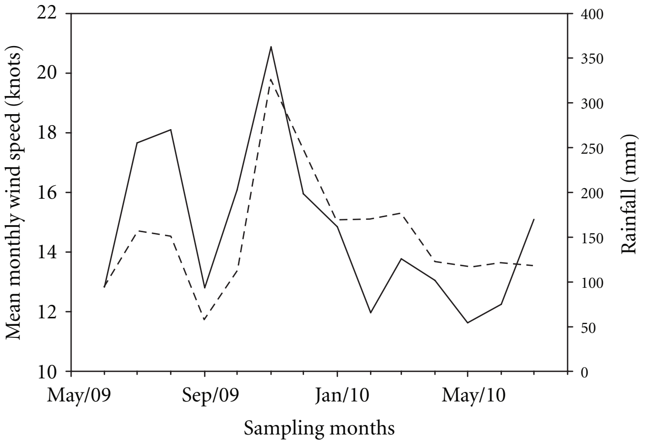


Figure 3: Mean hourly wind speed in knots recorded at the Irish M3 weather buoy (dashed line), and monthly rainfall at the Valentia recording station (solid line). Data courtesy of Met Éireann.

multiple regression analyses were not performed. Multiple linear regression was not performed on the data set as weather data were not collected at each individual sampling station and current speed was only measured once at each site, rather than continuously throughout the study period.

3.2. Environmental Factors. Mean hourly wind speed (knots) and rainfall (mm) are graphically displayed in Figure 3. Lowest mean wind speed occurred in September 2009 (11.7 knots) and highest mean wind speed was recorded in November 2009 (19.8 knots). Highest rainfall was recorded in November 2009 with 362.8 mm, while lowest rainfall in the study period occurred in May 2010 (54.2 mm).

Highest mean maximum current speed was recorded at Whirlpool during spring inflow (0.24 m s^{-1}) and lowest at Northwest during spring inflow (0.02 m s^{-1}) (Figure 4). Currents at North Pier were faster than at Northwest, indicating that there was tidal flow through the gap between the East shore and Castle Island.

3.3. Distribution of Sedimentation in the Lough. IOM sedimentation rates ranged from 1.67 g m^{-2} day^{-1} at Northwest in September to 47.37 g m^{-2} day^{-1} at Whirlpool in December. OM ranged from 0.97 g m^{-2} day^{-1} at North Pier in January to 5.60 g m^{-2} day^{-1} at Whirlpool in December. Figure 5 shows IOM and OM sedimentation for each site over 13 months. Most noteworthy is a peak in IOM in December, particularly at the sites close to the entrance of the Lough, highest sedimentation being recorded at Whirlpool, followed by Southwest, then Goleen and Western Trough. Sedimentation rates at the two northern sites (Northwest and North Pier) show an increase in IOM over the winter months (November to February), but not featuring such pronounced peaks as the southern sites in December. Similarly, a peak of OM occurred in December at Whirlpool Cliff and also to a lesser extent at Southwest and Goleen, but this pattern was not apparent in the data for the Western Trough, Northwest, and North Pier.

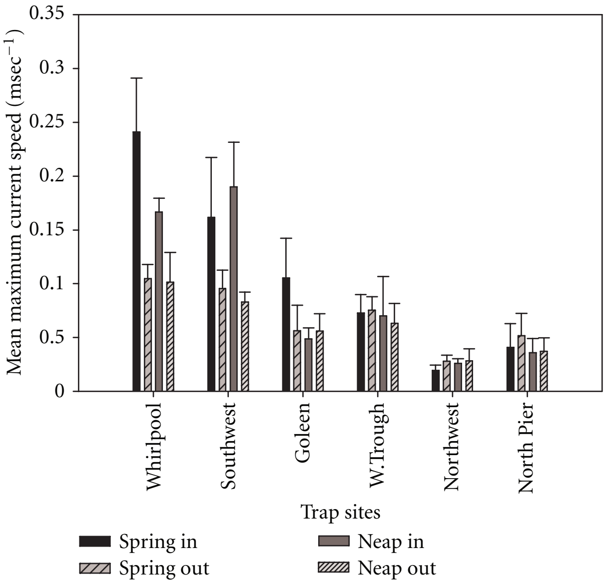


Figure 4: Mean maximum current speed of four tidal states (spring inflow, spring out flow, neap inflow, and neap outflow) at each sediment trap site in Lough Hyne Marine Reserve. Error bars indicate standard deviation. Data were collected at each site over a spring and neap cycle from January to March 2011.

Table 1: Post-hoc Tukey procedure to test at which sites sedimentation differed to a significant degree in Lough Hyne during the study period.

(a) IOM sedimentation

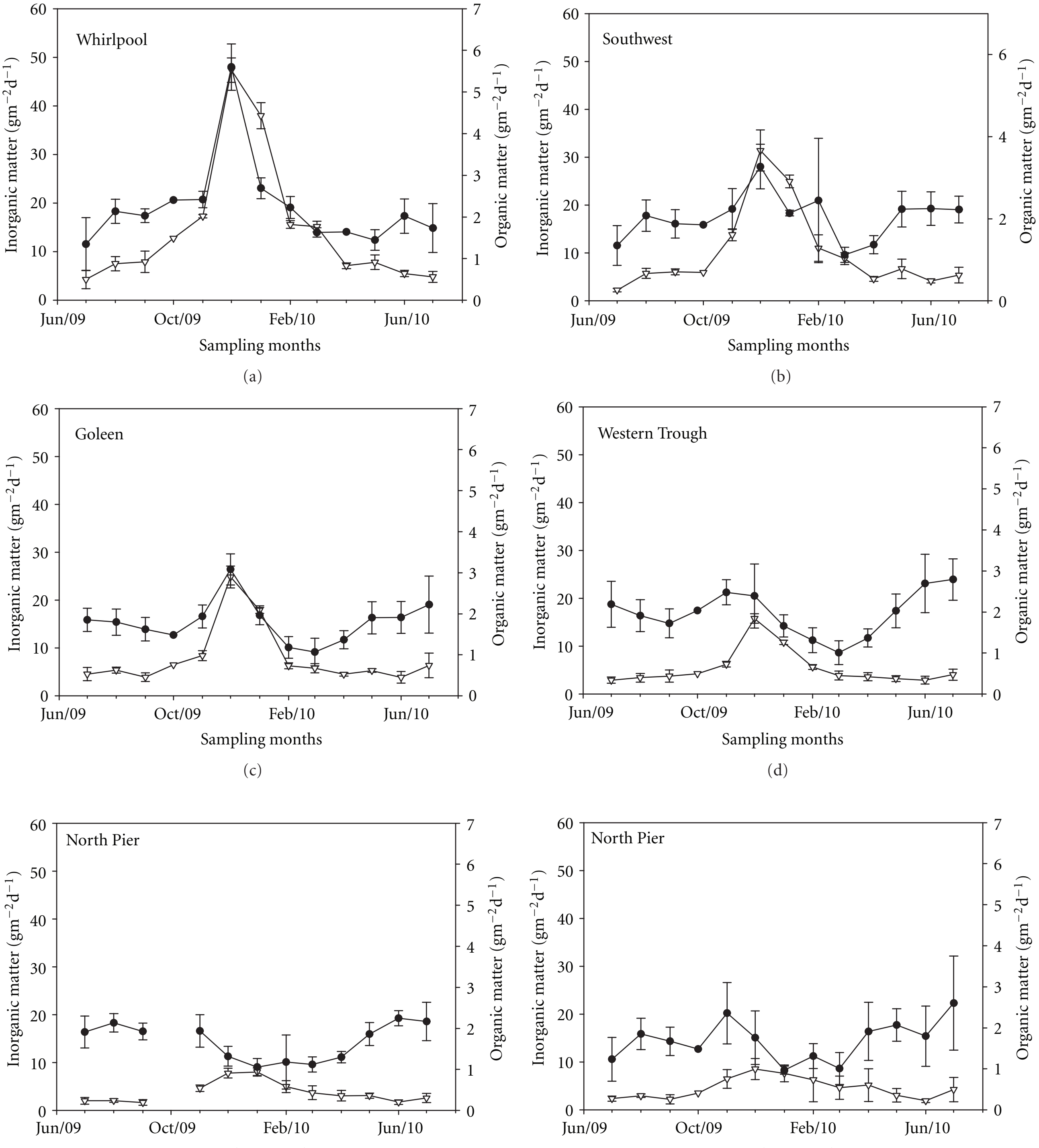
	Whirlpool	Southwest	Goleen	W. trough	Northwest
Southwest	*				
Goleen	*	NS			
W. trough	*	*	NS		
Northwest	*	*	*	NS	
North Pier	*	*	*	*	NS

(b) OM sedimentation

	Whirlpool	Southwest	Goleen	W. trough	Northwest
Southwest	NS				
Goleen	*	NS			
W. trough	NS	NS	NS		
Northwest	*	NS	NS	NS	
North Pier	*	NS	NS	NS	NS

NS: not significant, *: significant: $P < 0.05$.

A one-way ANOVA on log-transformed IOM data showed that IOM sedimentation rate was significantly different amongst sites ($F = 24.82$, $df = 5$, $P < 0.001$). Posthoc Tukeys pairwise comparisons showed that most pairs exhibited statistically significant differences (Table 1(a)). Only four pairs did not; in each case they were sites adjacent to one another: Southwest-Goleen, Goleen-Western Trough, Western Trough-Northwest and Northwest-North Pier.



(a) (b) (c) (d) (e) (f)

Figure 5: Sedimentation rates at six sites in Lough Hyne over the course of the study period; (▽): inorganic matter sedimentation, (•): organic matter sedimentation. Error bars indicate standard deviation. Most October samples were lost by accident. However, one sample from each site (except Northwest) remained for analysis.

Table 2: R^2-values and related P-values for linear regressions performed to explore which 370 environmental conditions had an influence on inorganic and organic matter sedimentation 371 rates in Lough Hyne during the study period.

Factor	Inorganic		Organic	
	R^2	P	R^2	P
Weather				
Wind speed previous month (knots)	0.39	<0.001	0.04	0.001
Rainfall previous month (mm)	0.21	<0.001	0.09	<0.001
Wind speed same month (knots)	0.15	<0.001	0.04	0.001
Rainfall same month (mm)	0.02	0.023	0.04	0.001
Distance				
Long route to North Basin (m)	0.17	<0.001	0.4	0.001
Short route to North Basin (m)	0.17	<0.001	0.6	<0.001
Current speed				
Spring inwards (ms^{-1})	0.22	<0.001	0.07	<0.001
Spring outwards (ms^{-1})	0.16	<0.001	0.07	<0.001
Neap inwards (ms^{-1})	0.15	<0.001	0.06	<0.001
Neap outwards (ms^{-1})	0.19	<0.001	0.07	<0.001

For OM data (untransformed), sites also differed significantly (one-way ANOVA, $F = 4.62$, $df = 5$, $P < 0.001$). Most pairwise comparisons were nonsignificant (Table 1(b)); the only exceptions were between Whirlpool and other locations within the Lough (Whirlpool-Goleen, Whirlpool-Northwest, and Whirlpool-North Pier).

3.4. Effects of Environmental Conditions on Sedimentation. Linear regression showed that, for IOM, wind speed during the previous month yielded the highest R^2 value ($R^2 = 0.39$, $P < 0.001$) of all environmental factors studied (Table 2). All other factors had lower R^2 values, though all relationships were statistically significant ($P < 0.05$). For OM, no single environmental factor had a particularly strong influence, and R^2 values were low (<0.1) for all factors chosen, yet all had statistically significant effects ($P < 0.05$). Given the noticeable increase in OM from March 2010 onwards, additional regression analysis was carried out using mean and maximum monthly water temperatures (both for the same and previous month). Maximum temperature of the previous month showed a weak, yet statistically significant relationship ($R^2 = 0.1$, $P < 0.001$); other temperature relationships showed even lower R^2 values, though were statistically significant in all cases ($P < 0.05$).

4. Discussion

This study of sedimentation over the course of one year clearly showed that IOM and OM sedimentation are governed by different environmental factors in this highly sheltered, semi-enclosed bay and are therefore not tightly coupled. IOM sedimentation was influenced by weather and tidal factors and IOM was predominantly imported from outside the Lough. This was evidenced by IOM sedimentation rates being highest near to the Lough entrance and decreasing to lowest levels in the North Basin. Amongst the environmental factors considered, wind speed of the previous month had the strongest influence on IOM, probably because resuspension of sediments in neighbouring coastal areas (caused by strong wind and wave action) takes some time to fully affect the sheltered Lough via Barloge Creek and the Rapids. Other potential sources of suspended particles such as dredging activity and river discharge can be excluded in this study as no dredging has taken place anywhere near the Lough entrance, and no rivers discharge into the Lough; the nearest river discharges into the Atlantic to the west of Baltimore, about 6 km west of Lough Hyne. Strong SW winds are regular occurrence in SW Ireland and coastal areas are exposed to wave action and surge. However, the Lough itself is highly sheltered due to the semi-enclosed nature of the Lough and surrounding hills. Waves rarely exceed 1 m in amplitude even during strong storms [12]. Of the four tidal regimes, spring inflow had the highest influence on IOM sedimentation, which supports the hypothesis that sediments were brought in from the outside and deposited near the entrance in the South Basin where flow is fastest (of all sites inside the Lough). Reduction in current speed leads to sedimentation of inorganic matter, heaviest sediments fall out first, while finer particles remain in the water column for longer [6]. Additionally, if sediments are brought in at one point only, as appears to be the case with the Lough entrance, sedimentation will naturally decline with distance from point of entry as the water body loses sediments along the way.

In pairwise comparisons of sedimentation rates at each site it was shown that IOM sedimentation rate at Whirlpool was significantly different from that at all other sites. These findings may be explained by the gradual reduction in flow rate with increasing distance from the Rapids causing progressive loss of sediments from the water column. Sites closest to each other showed IOM sedimentation rates that did not differ significantly, probably as a consequence of the sampling points being close together and the relationship between IOM sedimentation rate and distance from the Rapids already noted.

In contrast to IOM, none of the abiotic environmental factors tested had a strong influence on OM sedimentation individually. This suggests that variations in OM sedimentation rates are driven by biotic factors that were not measured in this study, or that a combination of abiotic factors influences settlement. OM is made up of several different components including: faecal material from nekton and zooplankton, dead and dying phytoplankton and zooplankton (made up of mero- and holoplankton), resuspended organic material from sediments, plus debris derived from dislodged intertidal flora, and fauna from the exposed shores of nearby coastal waters. For example, high winds can cause wind-driven turbulence, which promotes re-suspension of organic matter [6, 15] and dislodgement of intertidal flora and fauna. This organic material, brought into the Lough during the winter months, may provide a valuable food subsidy for benthic animals that therefore depend on productivity from elsewhere. Nutrient availability, plus rising light levels and temperatures influence phytoplankton growth in spring in temperate seas, causing spring blooms. Such blooms in turn lead to increased OM sedimentation [16, 17]. Zooplankton biomass increases with phytoplankton blooms and causes the production of further OM sedimentation either due to the animals' faecal pellets, their moulted exoskeletons (in the case of crustaceans), or because of death. In addition, benthic marine animals release their meroplanktonic larvae in the summer and these also cause increases of OM sedimentation in the summer, due either to dead larvae or faecal pellets. A deferred high OM sedimentation may be caused by blooms of plankton at different time intervals. Sedimentation rates (IOM and OM together) were lower in Bell and Barnes' study [12] than the present study and OM peaked in April (data from all sites taken together), not during the winter months. As in this study they also found the lowest sedimentation (both OM and IOM) in the North Basin and a positive relationship between sedimentation and wind speed. By taking OM data from all sites together they were not able to see if OM was produced inside or brought in from the outside of the Lough. In the present study it was possible to hypothesise where OM was coming from at different stages of the study period. Previous studies on both, phyto- and zooplankton in Lough Hyne [18, 19], have shown that both components of the plankton community are produced inside Lough Hyne but that some are also brought in from the outside. Nutrients have been shown to be brought in from the outside, causing increased occurrences of red tides even in the winter months, and year-round high levels of nutrients [10, 20]. In the present study it was shown that Lough Hyne may act as a sink for IOM from the outside and that nutrients may cause increased rates of phytoplankton blooms due to the semi-enclosed nature of the Lough.

Our study highlights the importance of understanding how coastal bays interact with their adjacent seas, particularly when such basins are considered for designation as marine reserves. Policies need to involve the cleanup of pollution, avoidance of eutrophication, and limitations on permits for extractive activities in the areas neighbouring such enclosed bays. Further studies of the behaviour of separate components of the organic matter fraction are needed, as understanding what influences these components have will be valuable in understanding how these systems work internally and how they are connected to the wider ocean system. Lough Hyne is a useful model area for future studies as it is a designated marine reserve, is easily accessible, and allows observations on a confined body of water that shows marked variation in physical processes such as flow rates across a relatively short distance. Sedimentation data collected here can be used as baseline data for studies in systems where confounding factors such as differences in water chemistry or planktonic communities are encountered, or those experiencing anthropogenic disturbances.

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Appendix 2

O’Sullivan, T., Broszeit, S., O’Sullivan, K., Davenport, J. and McAllen, R. High resolution monitoring of episodic stratification event in an enclosed marine system (submitted to *Estuarine Coastal and Shelf Science*)

High resolution monitoring of episodic stratification events in an enclosed marine system as a model for studying conditions in global oxygen minimum zones.

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Abstract

While hypoxic and anoxic environments have existed throughout geological time, their frequency of occurrence in shallow coastal and estuarine areas appears to be increasing. However, few data are available on the physicochemical conditions at the boundary between anoxic and normoxic layers, including the conditions required for both formation and dissipation of stratification. Advances in autonomous environmental sensing technology have produced robust sensors capable of detailed measurements in the inhospitable conditions created in such environments. In this paper, we present the first results acquired using autonomous high-frequency environmental sensors to record the physicochemical conditions at the interface within a stratified marine water column. We present the results of monitoring a seasonal stratification and deep-water renewal cycle at Lough Hyne Marine Reserve, Ireland, a seasonally anoxic semi-enclosed marine lake with uniquely favourable conditions for monitoring such phenomena. We present results of the effects of this thermocline on sedimentation rates and current speeds, indicating that current speeds below the thermocline were reduced when compared with current speeds measured at the same depth once the thermocline dissipated. We also present evidence that water column stratification formed a barrier to organic matter sedimentation into deeper waters.

Introduction

Marine water column stratification and the conditions involved in the formation and dissipation of hypoxic zones in the coastal oceans have been of increasing research effort in recent decades (Diaz 2001, Neretin et al. 2001, Rabalais, Turner & Wiseman Jr 2002, Canfield et al. 2010). This is driven by interest in the effects of coastal eutrophication and climate change on productivity, greenhouse gas cycling and evidence that the occurrence of hypoxic/anoxic zones has increased globally since the 1960s (Diaz, Rosenberg 2008). The formation of such zones is often related to high surface primary productivity combined with increased oxygen demand in poorly ventilated subsurface waters (Zaikova et al. 2010). A steep gradient of physicochemical conditions occurs between hypoxic and normoxic waters, profoundly affecting biological and physical processes within the water column. According to Diaz, hypoxia occurs when dissolved oxygen (DO) concentrations decrease below 2.8 mg L^{-1} (Diaz, Rosenberg 2008). Such DO concentrations affect the behaviour of benthic fauna, culminating in mass mortality for species unable to avoid locations and times when DO levels are reduced below 0.5 mg L^{-1}. Therefore, the study and understanding of these zones is important from a biological perspective and is of increasing importance in ecosystem management in coastal waters.

Although marine coastal hypoxic zones or oxygen minimum zones (OMZs) are now relatively common globally, few are readily accessible to detailed analysis using autonomous sensors. Lough Hyne Marine Reserve (LHMR), Ireland’s only statutory marine reserve, is one such accessible site and represents an important site in terms of biodiversity and conservation. LHMR covers an area of approximately 0.5 km^2 and encompasses a broad range of habitats and species within the boundaries of the reserve (Kitching 1987). Annual episodes of hypoxia/anoxia are known to occur in LHMR during summer months in an area of deep water (maximum depth 48 m) known as the Western Trough (McAllen et al. 2009). Records of anoxic conditions in the deeper water layers (> 25 m depth) of the Western Trough have been published sporadically for six decades, with the first detailed measurements taken in 1952 (Bassindale et al. 1957). Infrequent profiles of the water column since this early study have established that the water column in the Western Trough becomes highly stratified in the summer months and the presence of an oxy-thermocline is well established (McAllen et al. 2009, Kitching et al. 1976). However, the influence of this stratification on organic sedimentation has received little attention to date, and the conditions at the transition between the hypoxic and normoxic water parcels are poorly studied. This trend is common globally, due to the fact that many marine hypoxic zones are difficult to study due to limitations imposed by depth and necessity for expensive dedicated expeditions.

Experimental conditions for detailed examination of the processes involved in coastal hypoxia are ideal at LHMR, given the highly sheltered nature of the water body that minimizes wave action and wind-driven vertical mixing, plus the availability of detailed hydrographical models. These optimum conditions provide an unprecedented opportunity for study of the physicochemical conditions that result in marine water column stratification and the localised conditions created at the interface between layers. Thus, the aim of this study was to examine conditions resulting in formation and dissipation of water column stratification at LHMR, including both physicochemical conditions at the interface between water bodies, current speeds and sedimentation rates in the presence and absence of water column stratification.

Methods

Site Description

Lough Hyne is located on the south-western coast of County Cork (Grid reference N: 51.30.023 W: 9.18.218), Ireland. It is connected to the nearby Atlantic Ocean by a narrow width (~12 m) and shallow (3-4 m at high tide) channel called the Rapids located as illustrated in Figure 1-1.

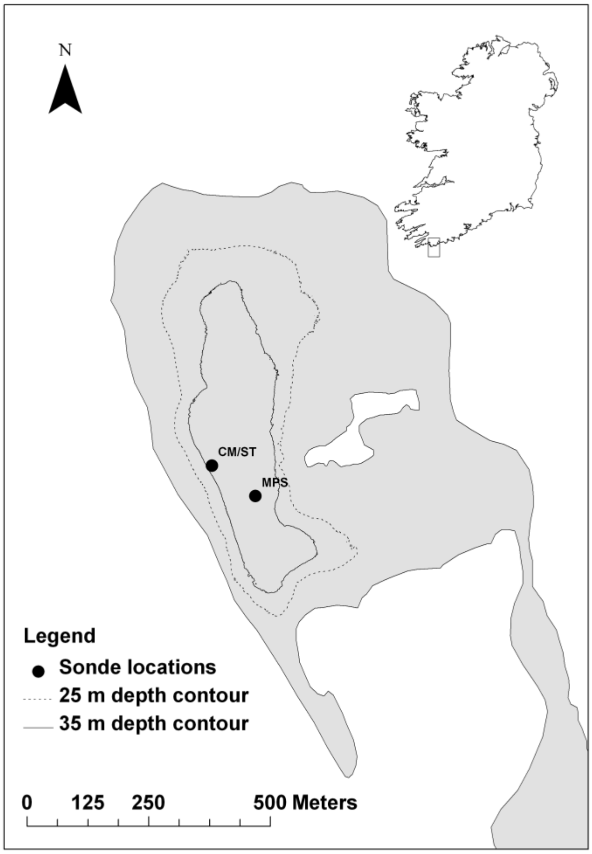

Figure 1-1: A map of Lough Hyne Marine Reserve, illustrating the outline shape of the Lough and the 25 and 35 m bathymetric contours of interest in this study. The area of greatest depth is known as the Western Trough and has a maximum depth of circa 50 m. Locations where sediment traps and environmental sensors were deployed during 2010/11 are indicated (CM/ST = Sediment Trap, MPS = Multiparameter Sonde)

Environmental data acquisition

Environmental conditions at LHMR during seasonal stratification were measured in 2011 using a multiparameter environmental sonde (YSI 6600 V2-2, YSI Hydrodata, Letchworth UK). Two sondes were equipped with a suite of sensors capable of measuring the parameters listed in Table 1-1.

Table 1-1: Environmental variables measured by each of the two deployed multiparameter sondes over the study period. Sondes collected data simultaneously using identical sensors, with the exception of the sonde deployed at the South Basin of Lough Hyne Marine reserve, which was fitted with additional sensors in the form of depth and pH meters.

Measured environmental variables	Western Trough 15 m	Western Trough 35 m
Temperature (ºC)	✓	✓
Conductivity (mS cm^{-1})	✓	✓
Optical Dissolved Oxygen (reported as both % saturation and mg L-1)	✓	✓
Turbidity (NTU)	✓	✓
Depth (m)	—	✓
pH	—	✓

The two sondes were deployed in the Western Trough of Lough Hyne at depths of 15 m and 35 m at the location shown in Figure 1-1. The depths chosen were based on historical measurements indicating that seasonal anoxia occurred below 25 m water depth during the summer season (Bassindale et al. 1957, Kitching et al. 1976, Thain, Jones & Kitching 1981), thus 15 m and 35 m depths were expected to correspond to conditions above and below the depth of the seasonal stratified boundary respectively. Sondes were anchored in place on a rope with a 25 kg weight at the point of greatest water depth in the Western Trough (Grid Reference N: 51.30.023 W: 9.18.218) and kept taut using a surface buoy.

Prior to deployment, each sonde was calibrated according to manufacturer's instructions and each sonde set to collect data synchronously before deployment. A sampling interval of 15 min was set for both instruments and data were periodically downloaded onsite. Collected data were analysed using the EcoWatch software for Windows (YSI Hydrodata, UK, version 3.18.00) and AQUARIUS 360° software (Aquatics Informatics Inc, BC Canada, version 3.0 R2), and statistically analysed with Origin (OriginLab, Northampton, MA).

Sedimentation rate measurements

Monthly sedimentation rate data were collected for one year from July 2009 to July 2010 above and below thermocline depth in the deepest part of the Western Trough of Lough Hyne as shown in Figure 1-1. A 10 kg weight was used to anchor a rope with the trap holders and a surface buoy ensured that the rope remained taut for the duration of the study. A sediment trap holder with spaces for 4 individual traps was suspended at a depth of 10 m from the surface buoy. Four traps were used at each depth in order to reduce loss of data due to breakage or loss of individual traps. A similar trap holder was suspended at 30 m depth.

Each trap consisted of a 300 mm length of Acrylonitrile butadiene styrene (ABS) drain pipe (internal diameter = 45 mm), sealed at the lower end with an ABS disc. The traps had an aspect ratio (width to height) of 1:6.67. This is above the recommended minimum of 1:3, while the diameter exceeded the recommended minimum of 40 mm (Håkanson, Floderus & Wallin 1989). The traps in each carrier were filled to a depth of 70 mm with a 5% formalin/brine solution of 100 ppt salinity. Formalin preserved the organic material within the falling sediment, while the brine was necessary to achieve a dense layer in which the sediments would remain without re-suspension (Wakeham et al. 1993). Traps were deployed and collected by SCUBA divers at intervals of about 4 weeks. Traps were sealed with drain pipe lids before removal from the trap holder and brought to the surface in a carrier to ensure the least possible disturbance to the trapped sediment. Each lid had a hole of 2 mm diameter drilled in the top to allow for pressure equalisation during the diving operations.

Sediment trap analysis

Each trap was shaken vigorously to re-suspend the deposited material. A subsample of 55 mL was gently filtered through a pre-weighed 47 mm diameter GF/C Whatman glass fibre filter using a KNF Neuberger Laboport vacuum pump. This was followed by a 50 mL wash of distilled water to remove salt deposits (Håkanson, Floderus & Wallin 1989). Filters were dried in an oven at 80 °C overnight, weighed, and ashed at 450 °C for 6 h in a muffle furnace to remove organic matter (OM) before being reweighed. Inorganic matter (IOM) was calculated by subtracting the weight of OM from the weight measured after first drying. Sedimentation rates were calculated as g sediment $m^{-2}day^{-1}$ for both organic and inorganic fractions and statistically analysed using Minitab V. 12.

Water movement in the Western Trough

Current speed measurements were taken twice in the Western Trough at 30 m depth in 2010. The first sampling took place in February and the second in August. The thermocline was confirmed as being absent in February and present in August, having formed in June 2010 at a depth of 25-26 m (S. Broszeit, unpublished data). A Nortek acoustic doppler velocimeter measured current velocity at sampling intervals of 10 min over a period of two weeks for one complete tidal cycle. The velocimeter was suspended vertically from a surface buoy anchored to the bottom by a 10 kg cement weight. In order to reduce flow interference due to the presence of the anchor rope, the velocimeter was placed in a steel frame that held it 50 cm away from the rope. Using GPS, the velocimeter was placed in the same locationon both occasions. Data were visualised using Excel from the Microsoft Office package and a smoother was added to visualise the trends. For this a moving average over 4 h was calculated.

Hydrographical and water volume calculations

To understand how much water is affected by the seasonal thermocline, water volume calculations for 25 m – 48 m depth were performed. During formation of the thermocline, anoxic conditions develop upwards from the deepest part of the Western Trough and conditions remain unfavourable there the longest after breakdown of the thermocline. Therefore, water masses were also calculated for below 35 m depth, at the depth of the lower multiparameter sonde and about halfway between the thermocline depth and the deepest part of the Lough. Calculation of the volume of water below the 25 and 35 m bathymetric contours was performed by importing the bathymetric data file into terrain modelling software, 12d (12d Solutions Pty Ltd, London, United Kingdom,). The bathymetric data was transformed into a triangulated irregular network (TIN), forming a 3-D surface mesh. To calculate the volume below 25 and 35 m depths, an artificial 2-D TIN with the same horizontal co-ordinate extents was created and positioned at each depth. The volume enclosed by the two TINs was then calculated and represents the volume below each of these depths.

Results

High-frequency environmental monitoring

Deployment of the two sondes at two depths within the water column allowed measurement of the precise conditions in the water column at LHMR as the seasonal stratification began to dissipate in September 2011. Measurement of dissolved oxygen values at a depth of 35 m in the Western Trough before September 13th 2011 confirmed anoxic conditions (DO levels approaching 0 mg L^{-1}) at this depth. In contrast, the water column at 15 m depth was well oxygenated (Mean value = 7.2 mg L^{-1}, SD = 0.34 mg L^{-1}, from measurements September 5th - 26th 2011). As the pronounced water column stratification became unstable in the second week of September 2011, DO concentrations at a depth of 35 m were found to increase rapidly until values comparable to those recorded at a depth of 15 m were reached. This transition from anoxia to normoxic conditions at a depth of 35 m occurred over a period of 4 days from the 13th - 17th September (Figure 1-2).

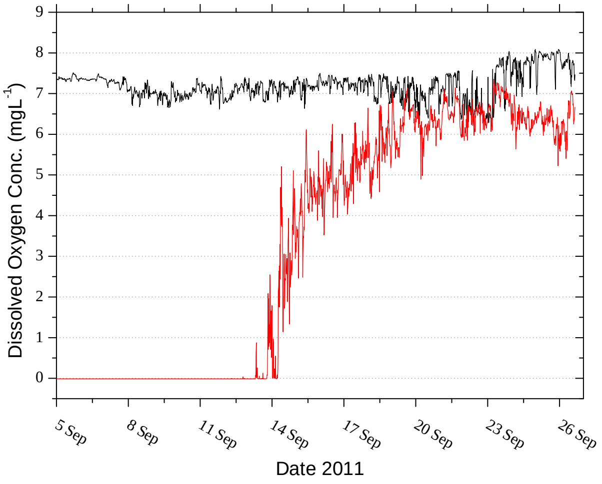

Figure 1-2: Dissolved oxygen concentrations at depths of 15 m (upper line) and 35 m (lower line) in the Western Trough of LHMR during August/September 2011. Dissipation of the stratified layer at a depth of 35 m is evident from the 13th of September as oxygen concentrations move from anoxia to DO concentrations similar to those measured at 15 m.

In contrast to the change in dissolved oxygen, change in the thermal stratification began to occur from the 5th September 2011. The sensors at 15 m recorded a continuously decreasing temperature at a rate of approximately 0.164 °C day^{-1}. This temperature decrease in the surface waters began from the 5th of September and continued until almost converging with the values obtained at 35 m, indicating complete mixing of the water column above a depth of 35 m. The mean temperature difference across the stratification boundary was 3.56 °C for the month prior to the beginning of the temperature decrease that resulted in dissipation of the thermocline (calculated from the 2nd August 2011 - 5th September 2011). In contrast to the cooling recorded by the sensor at 15 m, the temperature sensor at 35 m depth recorded a rapid 1.5 °C rise in temperature that largely occurred over a 3 day interval (12th - 15th September 2011) (Figure 1-3).

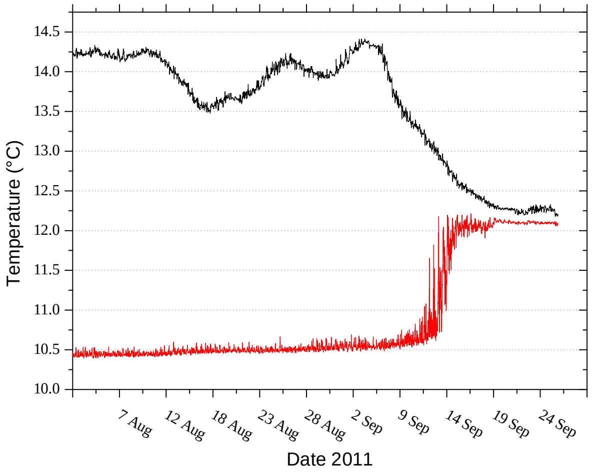

Figure 1-3: Temperatures at 15 m (upper) and 35 depths (lower) in the Western Trough of LHMR in August/September 2011. Breakdown of thermal stratification is illustrated by convergence of both the upper and lower water column temperatures.

The pH sensor at 35 m recorded changes in pH as the described changes in temperature and oxygen associated with dissipation of the stratified layer occurred. Although the occurrence of a seasonal thermocline and regular hypoxic events at Lough Hyne are documented since the 1950s (Bassindale et al. 1957), it was unclear how the presence of suspected high sulphide levels and hypoxic conditions affected pH at the interface between layers. High frequency measurement during this study illustrated the change in pH associated with the anoxic zone with a mean difference of almost 0.57 pH units between the upper and lower water volumes. During dissipation of stratification, pH values rapidly returned to a mean value of ≈ 8.1, consistent with the normal pH value expected in seawater. This confirms that the thermocline at Lough Hyne is coupled with a defined chemical gradient within the water column and the presence of a chemocline. However, fitting sigmoid curves (Boltzmann model, where A_1 is the low Y limit, A_2 is the high Y limit, x_0 is the inflexion (half amplitude) point and dx is the width) to both temperature and pH gradients through the stratified boundary, indicated that these two gradients are not coexistent. The temperature gradient through the stratified layer is steeper than that of pH (Temperature dx = 0.682, pH dx = 1.553, where dx is the width), indicating that the chemocline is distributed over a wider depth range than the thermocline and occurs over a larger water volume (Figure 1-4).

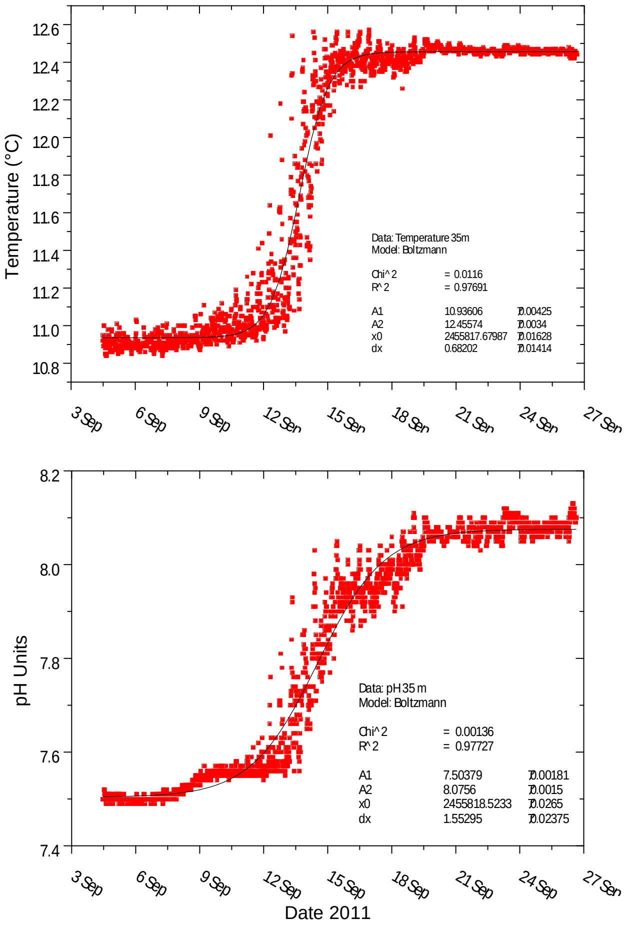

Figure 1-4: Graphs illustrating change in temperature (top) and pH (bottom) associated with the change from the normoxic water body and the anoxic waters at 35 m depth in the Western Trough of LHMR during September 2011. The sigmoid fit of the Botzmann model is shown for both parameters, where x0 = centre, dx = width, A1= initial Y value and A2 = final Y value. The values of both x0 and dx for pH are greater than those for temperature, indicating that pH change

occurs over a wider range of dates than temperature. This implies that the chemocline is of wider depth range than the thermocline.

Turbidity and water column stratification at LHMR

SCUBA divers transiting between the surface waters and the anoxic zone at LHMR have often reported a pronounced reduction in visibility at the interface between the upper mixed layer and the clear subsurface waters. Turbidity measurements in the water bodies above and below the stratification boundary were conducted at 15 min intervals during this study both before and during water column mixing. Measurements highlighted the low turbidity of the anoxic waters below the boundary layer, contrasting with the productive surface waters during stratification. However, as water column mixing occurred at 35 m in September 2011, a rapid increase in turbidity associated with the interface between the two layers was measured; this is consistent with the earlier reports of SCUBA divers (Figure 1-5). However, the cause of this turbidity signal at the transition between anoxic/normoxic conditions is not yet clear, although it may be speculated that it is a result of increased microbial activity, organic matter trapped at this boundary or suspended material resulting from the precipitation of sparing soluble metal sulphide particulates (Li et al. 2011).

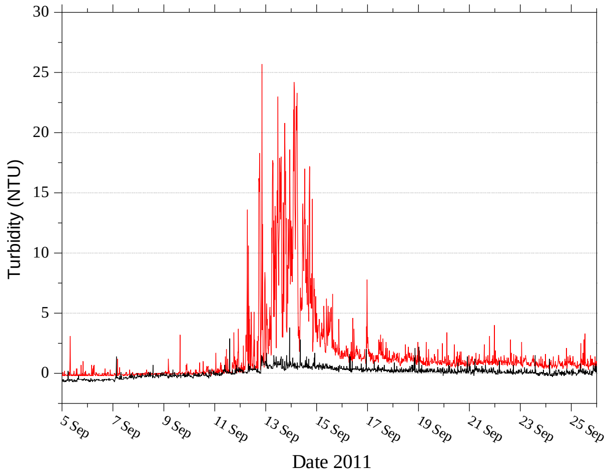

Figure 1-5: Turbidity measurements at a depth of 35 m (red) and 15 m (black) during September 2011 in the Western Trough of LHMR. The turbidity maximum associated with the boundary between the upper and lower (anoxic) water bodies is visible at 35 m, transitioning from very clear waters in the anoxic zone prior to the 12th September through to marginally increased turbidity associated with the normoxic waters of the upper layer.

Sedimentation of organic and inorganic matter

Sedimentation rates measured monthly from July 2009 to July 2010 indicated that highest sedimentation of OM occurred at 30 m in December of 2009 (4.65 $gm^{-2}day^{-1}$). In 2009, the thermocline dissipated in November and was absent until May 2010 (S. Broszeit, unpublished data), when pronounced temperature changes were measured at a depth between 26 and 30 m. OM sedimentation was higher at 30 m than at 10 m in months when no thermocline was present. When a thermocline was present, OM sedimentation was found to be higher at 10 m than at 30 m (Figure 1-6a). A two-way ANOVA of the OM data set was significant in the interaction term between depth and presence/absence of thermocline ($P = 0.005$). This result, together with real-time turbidity data from September 2011 (see above) and diver observations on reduced visibility within the thermocline compared to above or below the thermocline may be explained by the trapping of

OM at the thermocline. If the density of OM is lower than that of the water in the thermocline, it would slow down the sedimentation. Once the thermocline begins to dissipate and density changes due to an increase in temperature in the bottom water as demonstrated in Figure 1-3 this is likely to allow OM to sink to the sea floor.

Sedimentation of inorganic matter was higher in the 30 m traps than in the 10 m traps in all months studied (Figure 1-6b). Highest sedimentation occurred in December at 30 m (48.55 $gm^{-2}day^{-1}$). In January 2010 all traps were lost at 30 m and therefore no data is available for that month at this depth.

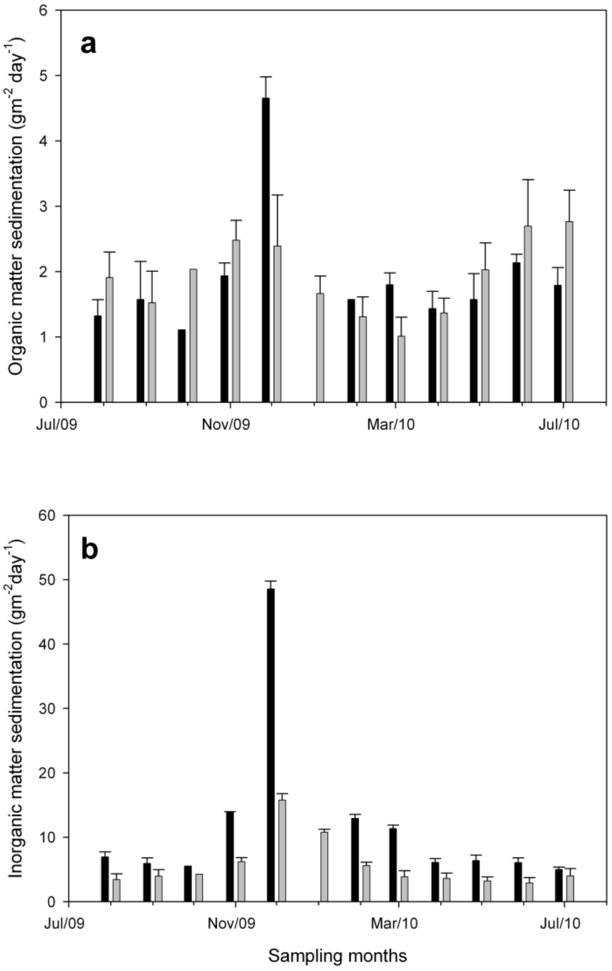

Figure 1-6: Sedimentation rates at 10 m (grey) and 30 m (black) depths at the Western Trough from July 2009 to July 2010, (a) organic matter sedimentation,

(b) inorganic matter sedimentation. Error bars indicate standard deviation. For clarity, scales on the y-axis axes of the two parts of the figure differ.

Current velocity in the Western Trough

There was a marked difference between measured current speeds in February and August 2010 in the Western Trough at Lough Hyne. While current speeds showed a greater maximum current speed (0.178 ms^{-1}) and greater variety (SD = 0.019 ms^{-1}) in February, current speeds were less varied (SD = 0.009 ms^{-1}) after thermocline formation and maximum current speed lower (0.063 ms^{-1}). The thermocline in 2010 had formed by June of that year and was at a depth of 25-26 m.

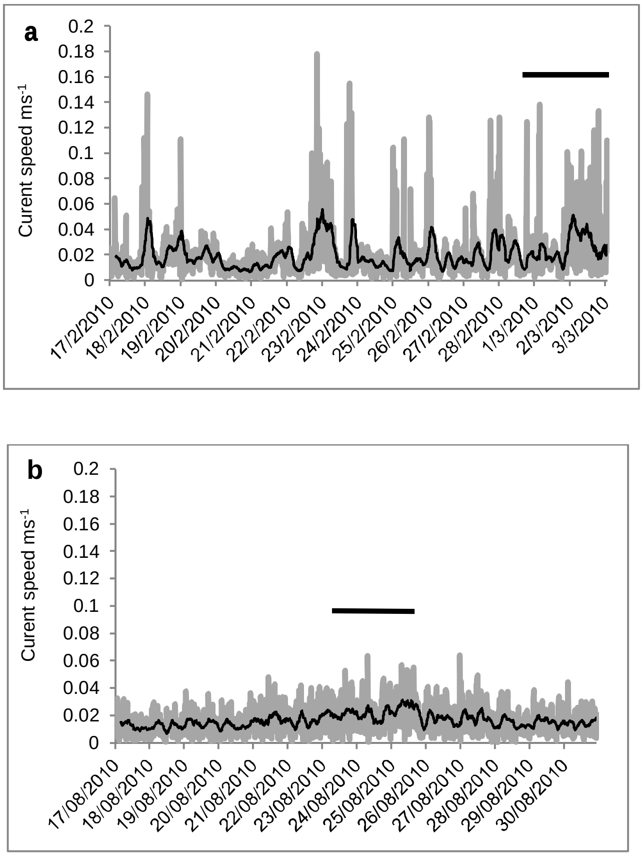

Figure 1-7: Current speed at 30 m depth in the Western Trough during February 2010 with well-mixed water column: (a) and August 2010 below thermocline: (b).

The grey line indicates actual readings while the black line is a smoother to visualise the trends (moving average over 4 hours). The black horizontal bar depicts spring tides.

This difference between current speeds at the same depth in LHMR can convincingly be explained by the presence of the thermocline which prevents disturbance of the underlying water body. This then prevents vertical and horizontal mixing at that depth and leads to a reduced current speed profile as seen in Figure 1-7.

Water volume calculations

The volume of anoxic water at LHMR represents 15% (1,514,017 m^3) of the total water volume present in the Lough when the thermocline is at 25 m depth. The volume of water below 35 m depth was calculated as 391,348 m^3. Therefore, during the breakdown of the thermocline approximately 1,122,669 m^3 of anoxic, low pH and hydrogen sulphide-rich (not measured in this study) water was mixed into the upper layers of the Lough water by the time the thermocline had moved down to 35 m depth. This may explain oxygen concentration reaching a low of approximately 6.5 mg L^{-1} measured at 15 m from approximately the 20th -23rd September 2011, after the breakdown of the thermocline.

Discussion

The aim of this research was to investigate the effects of the seasonally stratified water column at LHMR on conditions across the stratification boundary and organic matter sedimentation. Detailed investigation of the occurrence of hypoxia and seasonal anoxia at LHMR was first reported from 1952 (Bassindale et al. 1957). At present there is widespread interest in such conditions globally as it is reported that DO concentrations between 4.5 and 6.0 mg L^{-1} affect the growth of some marine organisms, while other aspects of metabolism are affected at between 2.0 and 4.0 mg L^{-1} and mortality can occur where concentrations are below 2.0 mg L^{-1} (Gray, Wu & Or 2002). DO concentrations in water below 25 m at LHMR during seasonal stratification events are not measurable with the current widely available DO sensor technology and approach 0 mg L^{-1}, indicating that most, if not all organisms in this layer would be affected. Dissipation of these anoxic waters into the overall water mass at LHMR during seasonal disruption of the stratified layer must result in a reduction in the overall DO concentration levels through LHMR as a whole. This is evident in the results from the present study, where concentrations approach 6.5 mg O_2 L^{-1} at a depth of 15 m in the water column, in comparison to normoxic concentrations.

Hydrodynamic conditions, rates of vertical mixing and exchange rates are important factors in the development of hypoxia/anoxia. This is certainly a factor at LHMR where seawater temperature flux and water column mixing are controlled by tidal cycles and input of fresh seawater through a narrow channel to the sea. This narrow channel known as the Rapids, controls tidal flow in and out of LHMR and results in a unique tidal regime (8.5 h ebb and 4 h flood), and rapid flow rates within the Lough (Bassindale et al. 1957, Lilly et al. 1953, Ebling et al. 1948). This unique bathymetry results in complete flushing times at Lough Hyne of approximately 80 days (Jessopp et al. 2011). These conditions together with increased nutrient input from the surrounding coastal waters (Jessopp et al. 2011) and bathymetry profile result in increased primary productivity in the surface waters of LHMR. The resulting high primary productivity ultimately contributes to high sedimentation rates that combined with the hydrographical conditions at LHMR produce the water column stratification as measured in this study. We have shown using real-time monitoring, that the characteristic temperature fluctuations present in the upper portion (10 m +) of the water column resulting from tidal influx from the Rapids are absent below the thermocline. Eventually, as seasonal cooling occurs (in September, 2011), this stratification becomes unstable resulting in a rapid mixing of the water column or suppression of the boundary between layers deeper into the water column (Figure 1-3).

In addition to experiencing profound anoxia, it has been demonstrated in this study that the lower water volume (25 – 50 m depth) is also reduced in pH and that a layer of suspended matter exists at the interface. It of interest to consider the consequences of releasing this toxic, colder seawater into the upper water column when mixing of the column occurs during dissipation of stratification. It is highly likely that seawater existing below the oxy-thermo-chemocline contains high levels of H_2S as evidenced by black anoxic sediments retrieved from the Western Trough and the odour of these sediments. To date no continuous measurements of dissolved H_2S have been attempted at LHMR, although high levels would undoubtedly have important biological impacts as has been shown in other locations (Lavik et al. 2008, Vaquer-Sunyer, Duarte 2010).

This study demonstrates the effect of the thermocline on several chemical and physical parameters of the Western Trough water column. The stratification of the water column leads to a reduced flow rate at a depth of 30 m compared with the period when the water column is mixed during the winter. The colder, higher salinity water volume below the summer thermocline leads to a densitydiscontinuity at the thermocline that acts as a barrier to exchange of water and OM. The reduction in sedimentation of particulate organic carbon has previously been shown in the Black Sea where a permanent thermocline exists (Wakeham et al. 2007). In the Gulf of Trieste a disruption of the stratification led to a sudden increase in total organic matter sedimentation below thermocline depth until the thermocline formed again (Posedel, Faganeli 1991). In the present study, the significantly reduced sedimentation below the thermocline could be explained by the short-term increase in turbidity when the stratification dissipated at the end of summer. Muddy substrates predominate in LHMR and the sediments in the Western Trough are particularly fine, being composed of silt (median grain size < 62 µm, and poorly sorted) with a high organic matter content (mean = 9.85 %, SD = 0.6 %) (S. Broszeit, unpublished data). Although this sediment may indeed result in increased turbidity at the interface, another possibility may involve microbial activity at this location.

In recent decades, Lough Hyne and its integrity as a reserve have suffered from anthropogenic influences due to increased recreational activity and development of the adjacent coastline (Johnson, Costello & O'Donnell 1995, Johnson, Costello 2002). Increased nutrient input into LHMR is thought to come from major estuaries along the coast, and nutrient rich waters are injected into LHMR during tidal water exchange rather than originating from direct agricultural runoff or freshwater input into LHMR. This has altered the water quality within LHMR which in turn may affect microbial/algal community composition and abundance (Jessopp et al. 2011). Year to year differences between the onset and the longevity of the thermocline are currently under investigation and although individual measurements of environmental parameters such as temperature and dissolved oxygen have been recorded intermittently over the period of scientific research within the Lough, no autonomous systematic monitoring programme is yet in place. The need for such a programme at Lough Hyne and the advantages to both reserve management and ecological studies in comparable locations have been pointed out by other researchers (McAllen et al. 2009, Jessopp et al. 2011).

Conclusions

This paper has presented the results of the first autonomous continuous sensing of the dissipation of the boundary between the upper well-mixed water column and the deeper anoxic waters at Lough Hyne Marine Reserve. This has resulted in a detailed examination of the biogeochemical conditions within the boundary layer of a stratified marine water body. Additional detailed measurements of the pH changes associated with the chemocline have also been presented for the first time for LHMR during the transition between normoxic and anoxic water bodies. Measurement of current velocity and sedimentation rates have demonstrated that water column stratification results in a reduction of organic matter sedimentation. These results, combined with the turbidity maximum measured at the boundary between the two layers as measured by continuous monitoring indicate that water column stratification in hypoxic zones may result in trapping of suspended material at the interface between hypoxic and normoxic waters.

From the historical studies and current real-time studies, Lough Hyne marine reserve presents an ideal location at which to study hypoxia/anoxia against a global backdrop of general increasing concern regarding coastal oxygen minimum zones. We propose this site as an ideal candidate for long-term environmental monitoring of such conditions, and that further detailed analysis of the relevance of this site as a model for the formation of oxygen minimum zones in general should be conducted as a matter of urgency.

Acknowledgments

We wish to thank Patrick Graham and Declan O' Donnell from the National Parks and Wildlife Service of Ireland for permission to conduct this work in Lough Hyne Marine Reserve. Luke Harman assisted with fieldwork. T. S. acknowledges the support of the Beaufort Marine Research Awards, carried out under the Sea Change Strategy and the Strategy for Science Technology and Innovation (2006-2013), with the support of the Marine Institute, funded under the Marine Research Sub-Programme of the National Development Plan 2007–2013. One of us (S. B.) acknowledges the support of the Crawford Hayes PhD studentship of University College Cork. No financial relations exist between the authors and the commercial identities mentioned in this study.

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Appendix 3

Broszeit S, Davenport J, McAllen R (2010) First documented record of *Rhabdomolgus ruber* (Echinodermata: Holothuridea) in Irish waters. Marine Biodiversity Records 3:1-3

Marine Biodiversity Records, page 1 of 3. © Marine Biological Association of the United Kingdom, 2010
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First documented record of *Rhabdomolgus ruber* (Echinodermata: Holothuridea) in Irish waters

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A small holothurian, Rhabdomolgus ruber*, was found in a number of grab samples from subtidal sedimentary sites within the Lough Hyne Marine Nature Reserve, West Cork, Republic of Ireland. Previously this species has only been recorded in waters off Helgoland, Germany and in the plankton near Cherbourg, France. This result significantly extends the known geographical range of this species to Irish waters.*

Keywords: *Rhabdomolgus ruber*, Holothurian, Lough Hyne, south-west Ireland, distribution, Synaptidae

Submitted 10 November 2009; accepted 7 April 2010

INTRODUCTION

Lough Hyne Marine Nature Reserve in West Cork, south-west Ireland is a highly sheltered inland marine lough, connected to the Atlantic Ocean by a narrow shallow channel, known as the 'Rapids'. Lough Hyne has been described as a biodiversity hotspot as it supports a high faunal diversity within a small geographical area (0.5 km^2) (Bell, 2007). This high biodiversity was the principal factor in its designation as Europe's first marine nature reserve in 1981 and it remains the Republic of Ireland's only marine nature reserve. A broad range of biodiversity studies has taken place in the variety of subtidal habitats within the Lough for over 100 years. However, the last study of the soft sediment fauna was performed by Thrush & Townsend (1986). Prior to that, Kitching *et al.* (1976) studied the soft sediment benthos of the Western Trough, the deepest part of the Lough. The present study commenced in May 2009 to reassess the soft sediment ecology and biodiversity within the Lough.

MATERIALS AND METHODS

Sediment samples were taken on 12 May 2009 by van Veen grab (0.05 m^2) inside Lough Hyne (see Figure 1). Sample depth except in the Western Trough was between 15 and 23 m. Four samples were taken at six sites (see Figure 1). Samples were fixed in 5% formalin for two days before being transferred to 70% ethanol for storage and later identification. Grain size was analysed following chiefly Buchanan & Kain (Buchanan & Kain, 1971). Organic matter was analysed by taking one gram of oven dried sediment sample (dried at 80°C for 48 hours) and burning it for six hours at 450°C before reweighing. This was repeated for a subsample of each sediment sample.

RESULTS

Ten of the 24 samples at five out of six locations contained 14 specimens of *Rhabdomolgus ruber* Keferstein. The species was absent from the Western Trough (sample depth 45 m). Table 1 lists locations, number of individuals found, median grain size and organic matter content. The specimens were between 4 and 18 mm long.

DIAGNOSIS

The collected specimens were identified using the echinoderm key of Southward & Campbell (2006). *Rhabdomolgus ruber* (Figure 2) is a cylindrical animal without tube feet or spicules. Ten finger-like tentacles were withdrawn into the body or partly protruded in the dead specimens (Figure 3). The alimentary canal is straight.

SYSTEMATICS

Class HOLOTHURIOIDEA Von Siebold, 1848
Order APODIDA Brandt, 1835
Family SYNAPTIDAE Verrill, 1867
Genus *Rhabdomolgus* Keferstein, 1863
Rhabdomolgus ruber Keferstein, 1863

DISCUSSION

The specimens collected in Lough Hyne are morphologically consistent with the existing descriptions of Keferstein (1863)

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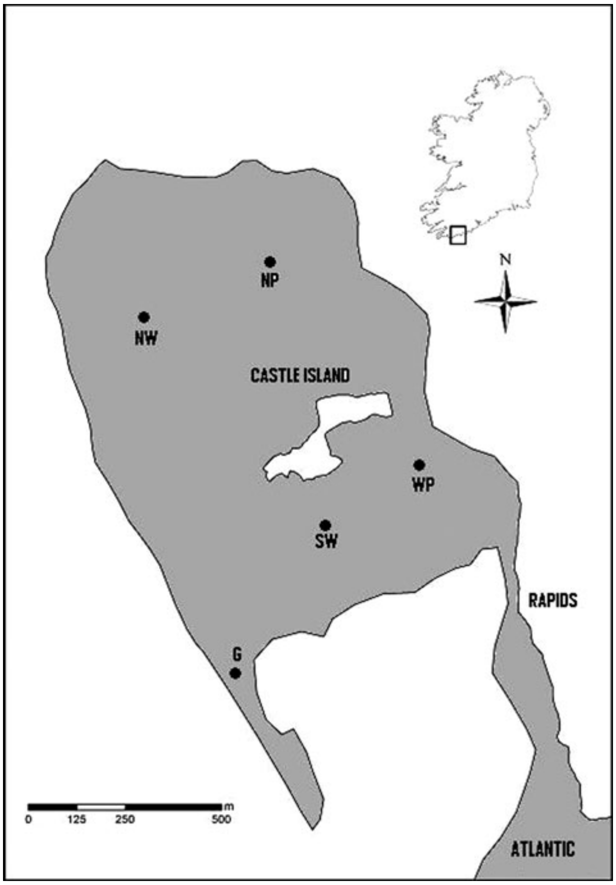

Fig. 1. Map of Lough Hyne. Five sampling stations where *Rhabdomolgus ruber* has been found in Lough Hyne. G, Goleen; NW, North-west; NP, North Pier; SW, South-west; WP, Whirlpool Cliff.

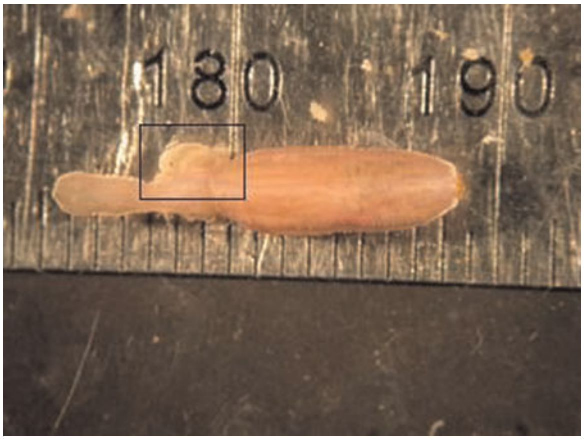

Fig. 2. *Rhabdomolgus ruber*. Sample specimen where some tentacles can be seen (box).

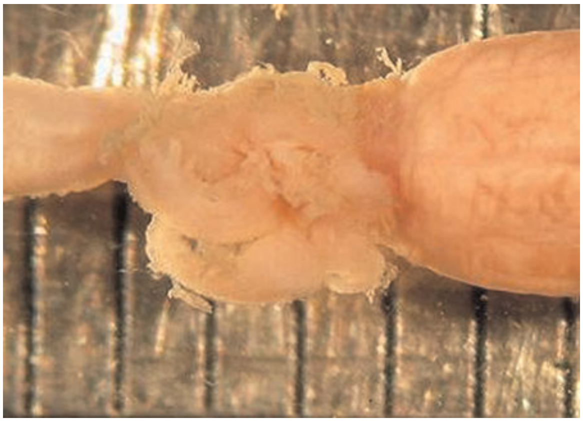

Fig. 3. Close-up of protruded tentacles of *Rhabdomolgus ruber*.

and Southward & Campbell (2006). The specimens found in Lough Hyne are bigger than described by those sources (up to 18 mm, rather than 10 mm maximum length as described by Keferstein). However, Keferstein (1863) based his description on a single specimen found near Cherbourg, France. Numerous specimens found at Helgoland (Menker, 1970) were much smaller (4–5 mm long), but at that site sediment grain size was larger, and the amount of organic matter lesser than at Lough Hyne (Table 1). These differences may help to explain the larger body size of the specimens found in our study.

Rhabdomolgus ruber was found at a depth of 19 – 21 m around Helgoland (Menker, 1970), while in Lough Hyne it presented itself at similar depths from 15 to 23 m. There are two reasons why it may not have been found in the Western Trough where samples were taken at a depth of 45 m. Firstly it may simply be restricted to the shallow subtidal. Secondly the Western Trough of Lough Hyne is known to develop a strong thermocline during the summer months, beneath which the water becomes anoxic and essentially lifeless (McAllen *et al.*, 2009). The grab samples taken in May 2009 were black and smelt of hydrogen sulphide. This indicates hypoxic/anoxic conditions on the sampling day, which are probably incompatible with survival in *R. ruber*.

The lack of previous records of this species may have two reasons: either it is slow at spreading its geographical distribution, or (more probably), it may have been previously overlooked (Southward, personal communication). Greenwood *et al.* (2000) found synaptid larvae in vertical plankton tows at the entrance to Lough Hyne and in the water column

Table 1. Sampling sites, frequencies of occurrence of *Rhabdomolgus ruber* and corresponding environmental conditions at six sampling locations.

Site	Number of grabs containing *R. ruber*	Number of individuals found (per site)	Median grain size (μm)	Organic matter content (%)
Whirlpool Cliff	1	2	1500	2.28
South-west	3	4	1520	3.29
Goleen	3	5	<40	7.93
Western Trough	0	0	<40	9.13
North Pier	2	2	<40	10.67
North-west	1	1	<40	3.63

over the Western Trough. Their samples were taken from a depth of 20 m. These may well have been larvae of *Rhabdomolgus ruber*, but further plankton sampling would be needed to confirm this.

ACKNOWLEDGEMENTS

Many thanks to E. Southward for help with identification of *Rhabdomolgus ruber*. Luke Harman and Catherine Russell helped with the collection of sediment samples. The Aquatic Services Unit, Environmental Research Institute Cork lent sampling equipment and gave advice. One of us (S.B.) acknowledges the support of the Crawford Hayes PhD studentship of University College Cork. We thank two anonymous referees for their valuable comments.

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Appendix 4

Grab sample species list

Appendix 4: Grab samples species list

May 2009 collection

27/05/2009	**South-east**	**Goleen**	**W. Trough 48m**	**North-east**	**North-west**
Abludomelita obtusata		1			
Abra alba		13	12	2	1
Abra nitida	2	22	5	13	
Abra prismatica	1	12	2	3	
Abra sp.	3	66		3	1
Abra tenuis		18			2
Actinothoe sphyrodeta	1				
Ampelisca gibba					1
Amphipholis squamata					2
Amphipoda	3				2
Amphiura chiajei	15	8	4	3	1
Amphiura filiformis			2		
Amphiura sp.		8			
Angulus pygmaeus				21	
Aphoelochaeta A		2			
Aphroditidae	7	4			4
Bivalve spat	5	14	5		4
Buccinum undatum					2
Calliopiidae	2				
Capitella capitata		10	30	2	
Capitella sp.			133		2
Chaetozone gibber	1				
Cheirocratus intermedius	1				
Cheirocratus sp.	2				1
Cheirocratus sundevalli					1
Corbula gibba	15	165	12	23	29
Monocorophium sextonae					1
Corophium volutator	1				
Cumacea	15	16		6	11
Diplocirrus glaucus	18	16		4	2
Galathea intermedia	1				
Gari tellinella		5			
Glycera sp. (juv.)			1		
Glycera sp.			7		8
Golfingia elongata		4			1
Golfingia margaritacea	1				

27/05/2009	**South-east**	**Goleen**	**W. Trough 48m**	**North-east**	**North-west**
Golfingia sp.		1			
Hesionidae	2			1	
Heteromastus sp.					3
Hippomedon denticulatus		6			
Hyalidae	1				
Kurtiella bidentata			2		
Leptochiton cancellatus	4				
Leucothoe incisa				1	
Leucothoidae		1			
Liocarcinus depurator		1			
Lumbrineris sp.	5			2	
Lumbrineris tetraura	20	5		17	16
Lunatia catena					1
Lysianassidae	7	7			6
Magelona alleni		1			2
Magelona minuta	3	1			1
Maldanidae					4
Mediomastus fragilis	1	4		1	15
Melinna cristata	1				
Melinna palmata		3		3	2
Metaphoxus fultoni	1				
Modiolarca tumida	1				
Mysia undata		2			
Mysta picta	1				3
Mytilidae		1			
Nebalia bipes	1				
Nemertea	11	45		18	34
Nephtys cirrosa				3	1
Nephtys hombergi				4	
Nephtys incisa	2			3	
Nephtys longosetosa	1				
Nephtys sp.	18	3		2	1
Nereididae		2			
Notomastus latericeus					1
Ophelina sp. (juv.)	4				
Ophiocten affinis		1			
Ophiura albida	1				
Ophiura ophiura		6			
Ostracoda	12	1		1	14

27/05/2009	**South-east**	**Goleen**	**W. Trough 48m**	**North-east**	**North-west**
Parvicardium ovale	1				1
Pecten maximus	1				
Pectinaria auricoma	2				
Pectinaria sp.		2		1	
Phascolion strombus	7	8			
Philine aperta	2	1			
Pholoe sp.	13				
Phoronida		1			
Phoxocephalidae		2			1
Platynereis dumerilii					3
Polyophthalmus picta	2				
Processa canaliculata					1
Pseudopolydora pulchra			1		
Pycnogonida	1				
Rhabdomolgus ruber	3	6		1	1
Scalibregma inflatum	7	84	265	3	72
Schistomeringos rudolphi	1				
Scolelepis foliosa	1				
Scolelepis squamata			81		
Semelidae		50			
Serpulidae	2				
Sipuncula	1	2			2
Spionidae		1	74		
Tanaidacea	40	24			10
Terebellidae					3
Terebellides stroemii		1		1	
Thracia sp.	18	118	2	17	120
Thyasira flexuosa	5	2		1	1
Thysanocardia procera	1	5			
Tonicella rubra	1				
Trachythyone elongata		2		1	1
Tubificidae	3				1
Turritella communis	4	18		2	

August 2009 collection

11/08/2009	**Southeast**	**Goleen**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abra alba				5	3
Abra nitida	11				4
Abra prismatica	13	10		25	
Abra sp.		1			2
Abra tenuis				2	
Amphipholis squamata	1				
Amphiura chiajei	9	14		1	1
Amphiura filiformis		3			
Aonides paucibranchiata					2
Aphroditidae	26	1			1
Buccinum undatum	1				
Capitella capitata		1		3	1
Chaetozone gibber	1				3
Chaetozone setosa					1
Chamelea gallina				1	
Cirratulid sp. (juv.)				1	1
Corbula gibba	4	34		7	1
Cossura longocirrata					1
Cumacea				4	
Diplocirrus glaucus	14	2		4	
Exogene sp.					6
Glycera sp. (juv.)					1
Hesionidae				1	
Kurtiella bidentata	34	22		5	70
Leucothoe incisa	2	1			
Leucothoe liljeborgi		2			
Leucothoe sp.				1	
Lumbrineris sp.	3			1	
Magelona minuta	1				
Magelona sp.				1	2
Malacoceros sp.					9
Maldanidae	1	1			
Marthasterias glacialis	1				
Mediomastus sp.					2
Melinna sp.	2	3		1	
Mysta picta		2			
Nassarius pygmaeus	1				

11/08/2009	**Southeast**	**Goleen**	**W. Trough 48 m**	**Northeast**	**Northwest**
Nematoda	4				2
Nemertea	86	32		30	35
Nephtys sp. (juv.)	1	5		2	16
Nephtys sp.	3	1		4	2
Ophelia sp.	8				
Ophiuridae (juv.)	1	1			
Ophiuridae	1				
Pariambus typicus	1				
Phascolion strombus	3	5			
Phoronida	1				
Processa canaliculata		1			1
Rhabdomolgus ruber	1	1			
Scalibregma inflatum	17	51		5	26
Sipuncula	2			1	
Sipuncula (juv.)		1			
Tanaidacea	9	7			
Tellimya ferruginosa	38	21		1	3
Terebellides stroemii	4	5		1	
Tharyx sp.	2				
Thyasira flexuosa	39	15		7	5
Thysanocardia procera		3			
Trachythyone elongata				1	
Tubificidae	15	2		3	
Turritella communis	1	11		8	6
Venus casina	1				

November 2009 collection

10/11/2009	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abra alba	5					
Abra nitida			8			
Abra prismatica	9				6	8
Abra sp.			4		1	4
Abra tenuis			9		4	
Akera bullata	2					
Ampharetidae (juv.)			1			
Amphipoda	1					
Amphiura chiajei			13		1	3

10/11/2009	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abra alba	5					
Amphiura filiformis			2			
Aonides paucibranchiata	1	5				
Aphoelochaeta A			2			
Aphroditidae	16		9			5
Capitella capitata	32	148	3		4	1
Caprellidae	1					
Chaetozone gibber				1		1
Chamelea gallina						1
Cirratulidae	2					
Cirratulus cirratus						1
Corbula gibba	4		17		19	7
Monocorophium sextonae		3				
Cossura longocirrata	1					
Cumacea		6	1		16	
Diplocirrus glaucus	10		6		14	1
Exogene sp.			4		59	
Glycera sp.		1				
Golfingia margaritacea			1			
Golfingia sp.			2			
Hediste diversicolor			1			
Hesionidae	3		1		1	2
Kurtiella bidentata	32	11	102	1	15	80
Leucothoe incisa			1		1	
Leucothoe sp.					1	
Loripes lucinalis			1			
Lumbrineris latreilli			1			
Lumbrineris sp.	2	15	8		34	2
Lumbrineris tetraura			7			
Magelona alleni			4			
Magelona sp. juv.)			1			
Magelona minuta			6			
Magelona sp.			2		1	
Maldanidae		1			1	
Mediomastus fragilis			1			
Melinna cristata			2			
Melinna elisabethae			1			
Melinna maculata			1			

10/11/2009	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abra alba	5					
Melinna palmata			1			
Metaphoxus fultoni		15			1	
Metaphoxus pectinatus			1			
Modiolula phaseolina	1					
Mysta picta					1	
Nassarius pygmaeus					1	1
Nematoda	25	4			1	
Nemertea	19	1	34		67	17
Nephtys sp. (juv.)	6		3			7
Nephtys sp.	3		1			3
Nereididae		3				
Nucula nitidosa			1			
Ophiura albida	1				1	
Ophiuridae			1			
Ostracoda		12				
Parvicardium minimum	1	1				
Pectinaria auricoma					1	
Pectinaria sp. (juv.)					1	
Pectinaria sp.			1			
Polyophthalmus picta		1				
Processa canaliculata					2	1
Protodorvillea kefersteini	1	2				
Retusa truncatula			1		1	
Rhabdomolgus ruber			1			1
Scalibregma inflatum	1		62		40	
Stenothoidae		3				
Tanaidacea		5	1		20	
Tellimya ferruginosa	17	11				
Thracia sp.		1				
Thyasira flexuosa	12		9		2	2
Thysanocardia procera			4			1
Tubificidae	22	17				
Turridae						1
Turritella communis			4		2	4

February 2010 collection

12/02/2010	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abra alba					2	7
Abra nitida	5				3	
Abra prismatica	1					8
Abra sp.			18			4
Abra tenuis					2	1
Aglaophamus pulchra			3			
Amphipoda						1
Amphiura chiajei						1
Aonides paucibranchiata	1				1	
Aonides sp.		9				
Aphoelochaeta A						1
Aphroditidae	4				1	7
Capitella capitata	142	1	11	124	3	4
Capitella sp.				39		
Chaetozone setosa						1
Corbula gibba	2		5	1	10	17
Corophiidae		3				
Crangonidae						1
Cumacea	3	4	1		8	17
Diplocirrus glaucus			1		4	5
Exogene sp.			2		11	1
Glycera sp. (juv.)	8					
Glycera sp.	1	3	16	1		
Hesionidae	4	1			1	3
Jassa sp.	6					
Kurtiella bidentata	13	18	21	3		65
Leucothoe sp.	1					1
Lumbrineris sp.	1				6	
Magelona sp.					3	
Malacoceros fuliginosus	17			1		
Malacoceros sp.	4			13		
Marthasterias glacialis	1					
Mediomastus sp.					1	1
Melinna sp.					1	

12/02/2010	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Metaphoxus fultoni		16				6
Modiolarca tumida			1			2
Modiolus barbatus	1					
Mysta picta	1				1	
Mytilus sp.			2			
Nassarius pygmaeus						5
Nebalia sp.		1				
Nematoda	39	4			2	12
Nemertea	17	1	32		46	47
Nephtys sp. (juv.)					1	10
Nephtys sp.			1			6
Nereididae (juv.)						9
Nereididae						1
Nucula sulcata				1		
Ophiothrix fragilis				2	1	
Ophiura albida						3
Ostracoda	1	2				13
Parvicardium minimum		1				
Phyllodocidae	1					
Pilumnus hirtellus	1					
Platynereis dumerilii	1					
Processa canaliculata					1	
Retusa truncatula					1	
Rhabdomolgus ruber					1	
Scalibregma inflatum	120	5	137	596	119	68
Spionidae	1	1	1	2		
Stenothoidae		1	1			
Tanaidacea		6			6	13
Tellimya ferruginosa	14					
Terebellida			9			
Terebellides stroemii	1				1	
Thyasira flexuosa	1		3		2	3
Tubificidae	1	15		1		2
Turridae						2
Turritella communis			1		5	15

May 2010 collection

07/05/2010	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Abludomelita obtusata			2			
Abra alba	6			17		4
Abra nitida	1	5		16		10
Abra prismatica	3			1	2	1
Abra sp.	2		1	1		
Abra tenuis		1	13	1	1	
Aglaophamus pulchra			4			
Amphiura chiajei		1	9		9	5
Amphiura sp.			1			
Aonides oxycephala		1				
Aonides paucibranchiata	8	31				
Aphroditidae	11		6		1	2
Bela brachystoma			1			
Capitella capitata	2	146		203	3	
Capitella sp.			1			
Chaetozone gibber	3					
Cirratulidae				2		1
Corbula gibba	18	1	1	27	2	1
Corophiidae		1				
Cumacea	6		9		22	1
Diplocirrus glaucus	35		10		12	4
Exogene sp.	2	2			6	1
Glycera alba			1			
Glycera sp. (juv.)	1					
Glycera sp.		17	4			1
Glycera tridactyla				3		
Hesionidae	2		1	1	6	4
Heteroclymene robusta		2				
Isaeidea		1				
Kurtiella bidentata	40	537	8	4	3	8
Leptrostraca					28	
Leucothoe liljeborgi			2			
Leucothoe sp.					1	
Lumbrineris sp.	3	17	35		35	
Lumbrineris tetraura			20			
Lunatia catena	1					

07/05/2010	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Magelona minuta			1			
Magelona sp.			3	1	4	
Malacoceros fuliginosus				25		
Maldane sarsi		3				
Maldanidae	1	3	1			
Mangelia sp.			1			
Mediomastus fragilis			15			
Melinna palmata			1			
Melinna sp.	1		2		2	
Metaphoxus fultoni	1	42				
Modiolarca tumida	1					
Modiolula phaseolina	2			2		
Modiolus barbatus		1				
Nassarius incrassata	1		1			
Nassarius pygmaeus						1
Nebalia sp.		78				2
Nematoda	16				24	
Nemertea	51	25	30	1	39	33
Nephtys incisa						3
Nephtys sp. (juv.)	53	1	1		20	28
Nephtys pulchra			14			
Nephtys sp.	5		1			4
Nereididae (juv.)			3	2	10	
Ophelia sp.	1					
Ophiothrix fragilis	2					
Ophiura albida	1	2			3	
Ostracoda		10				
P122	42					
Parvicardium minimum	2					
Parvicardium ovale					1	
Pectinaria sp.		1				
Phascolion strombus			4			
Phoxocephalidae		1				
Pilumnus hirtellus		1				
Polycirrus medusa	1					
Processa modica	1					
Protodorvillea kefersteini		4				
Pseudopolydora sp.			15	2		

07/05/2010	**Southeast**	**Goleen**	**W. Trough 20 m**	**W. Trough 48 m**	**Northeast**	**Northwest**
Pycnogodidae					1	
Retusa sp.					1	
Retusa truncatula			2			
Rhabdomolgus ruber		1	1			
Scalibregma inflatum	308	233	450	42	69	55
Sipuncula	1					
Sphaerodoridae		1				
Spionidae		18		1		1
Stegocephalidae		2				
Stenothoidae		2				
Tanaidacea	2	14	6		54	2
Tellimya ferruginosa	1					
Terebellidae (juv.)		2				
Terebellides stroemii			2			
Tharyx A						1
Thracia sp.		5				
Thyasira flexuosa	9	2	1			3
Trachythyone elongata						1
Tubificidae	7	9				
Turridae					3	
Turritella communis			12		14	31