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The role of fronts, eddies and bubbles on the distribution, abundance and advection of gelatinous zooplankton: new insights for finfish aquaculture

Thesis presented by

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for the degree of

Doctor of Philosophy

University College Cork

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23rd March 2018

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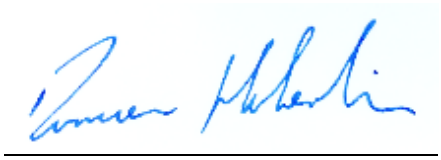
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Declaration

The thesis submitted here is my own work and has not been submitted for another degree, either at University College Cork or elsewhere.



Michael Damien Haberlin

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General Abstract

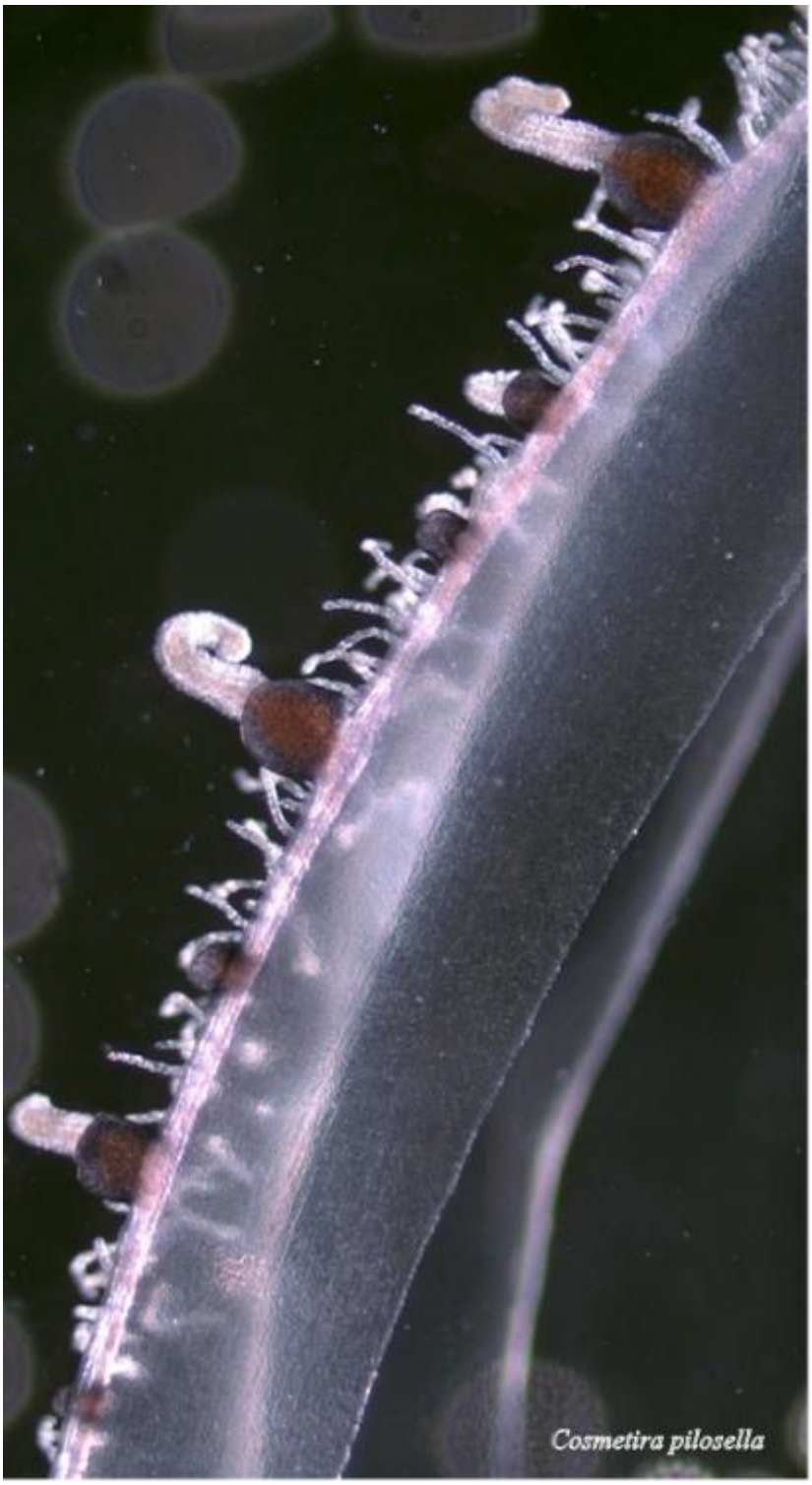
The past three decades, from 1990 to the present, have seen a considerable increase in the number of studies investigating the ecology of gelatinous zooplankton, driven in no small part by the negative socio-economic impacts of gelatinous zooplankton. Despites some exciting progress, some important gaps remain, particularly with regard to how physical and oceanographic processes influence the distribution and abundance of gelatinous zooplankton. It is well established that these are central processes in the formation of the patchy distribution of phytoplankton and large vertebrate pelagic predators, however, few studies have elucidated the role of such processes on gelatinous zooplankton. Therefore, the central theme of this thesis was to investigate the influence of mesoscale processes (fronts and eddies) on gelatinous zooplankton ecology. In addition, two strategies with the potential to reduce the impact of harmful jellyfish species at finfish farms were investigated: 1) the use of an artificial front as a barrier and; 2) the efficacy of a non-toxic antifouling coating to reduce hydroid biofouling.

Temporal sampling in southwest Ireland and a compilation of historic observations revealed a low siphonophore diversity in Irish waters, with *Muggiaea atlantica* being the most abundant species by an order of magnitude. The occurrence of siphonophores in the southwest of Ireland indicated the influence of physical drivers and shared trends with the Western English Channel suggested a physical link between both regions. The Celtic Sea Front was the most likely physical link between both regions and its annual formation had a profound impact on gelatinous zooplankton distribution in the region for a period each year.

Sampling carried out during July 2015 revealed two distinct gelatinous communities separated by the Celtic Sea Front; a cold mixed water community in the

Irish Sea and a warm water stratified community in the Celtic Sea. The gelatinous abundance (656 indiv. m^{-3}) and biomass (2085 mg C 1000 m^{-3}) was higher in the Celtic Sea. The mean gelatinous contribution to the total zooplankton biomass was 4 - 6%, reaching a maximum of 16% in the Celtic Sea. There was no evidence that the front enhanced the abundance of biomass of gelatinous taxa, however, it is likely that the front influenced the community and biomass through broader scale advective processes. A survey in the northwest Atlantic also showed that a mesoscale warm core eddy had a profound influence on the gelatinous zooplankton, with a 12-fold decline in gelatinous zooplankton inside the eddy. Some larger calycophoran genera were present in the eddy, along with several large crustacean genera, nonetheless, most zooplankton taxa were poorly represented, suggesting an oligotrophic eddy core.

An investigation of mitigation strategies for finfish aquaculture demonstrated that a bubble curtain may be of limited use due to the ability of small objects to pass through the bubble plume. Tests also showed, the potential rate of 'jellyfish' transmission through the bubble curtain is affected by wave height and frequency, meaning sites which experience high wave energy would negatively impact the bubble curtain. Experimental trials of a novel non-toxic coating applied to nylon netting typical to salmon farm cages showed no effect on the ubiquitous fouling hydroid *Ectopleura larynx*. Although the coating was effective at reducing microscopic fouling and enhanced clean-ability of nets, the stolon system of the macrofouling hydroids was extremely adaptable and the complex surface topography of the multi-stranded nylon provides a surface which is physically easy for the hydroids to anchor to.



Chapter 1

General Introduction

Gelatinous zooplankton

Gelatinous zooplankton is a broad term that refers to organisms with a body mass that is composed mostly of water, usually above 95% water (Larson, 1986; Arai, 1997; Anderson, 1998). This definition encompasses organisms from a range of taxonomic groups including Cnidaria, Ctenophora, pelagic Tunicata, Chaetognatha, Polychaetae, Mollusca and the larval stages of many non-crustacean zooplankton (Haddock, 2004). Terms like gelatinous zooplankton, gelata (Haddock, 2004) and jellyfish, while in some sense intuitive, do little to convey the diversity of form, function and life history traits they describe, and it is increasingly apparent that gelatinous zooplankton form an important component of pelagic ecosystems (Robison, 2004; Doyle et al., 2014; Lucas et al., 2014; Hamilton, 2016). In this study, the term gelatinous zooplankton is used in reference to Cnidaria, Ctenophora and pelagic tunicates only, and where other gelatinous or semi-gelatinous zooplankton are discussed the distinction is made clear in each instance.

The phylum Cnidaria is the most diverse group containing two monophyletic clades, the class Anthozoa (7500 spp.) and the Medusozoa (3786 spp.) (Daly et al., 2007; Mapstone, 2015). The medusozoa contains four Classes, the Hydrozoa (3500 spp.), Scyphozoa (200 spp.), Cubozoa (36 spp.) and Staurozoa (50 spp.) (Daly et al., 2007; Mapstone, 2015). Cnidarians derive their name from the possession of a specialised type of cell, called a cnidocyte, which is capable of producing organelles called cnidae. A type of cnidae called nematocysts are capable of piercing the skin of prey and injecting venom. Cnidarian tentacles are loaded with cnidocytes and are used to capture a wide variety of zooplankton prey including other cnidarians (Purcell,

1981; Purcell, 1991; Purcell, 1997; Sabatés et al., 2010). The phylum Ctenophora is less diverse, containing 150 - 250 described species, although more are known to exist (Dunn et al., 2015; Giribet, 2016; Jager and Manuel, 2016). Some ctenophores possess adhesive tentacles and use them for prey capture, however, other genera engulf or use lobed arms to manipulate prey (Harbison et al., 1978; Jager and Manuel, 2016). The majority swim via ciliary action, with some species able to use their body to 'paddle' through the water, and therefore they lack the agility of many cnidarians. The tunicates are a diverse group containing over 2000 species, with two relatively species poor pelagic groups, the class Thaliacea (72 spp.) and class Appendicularia (20 spp.) (Holland, 2016).

Both groups move by jet propulsion and unlike the cnidarians and ctenophores, they are omnivorous filter feeders that consume small particles (Holland, 2016). Although characterised by a similar gelatinous form, these groups contain animals that are vastly different from each other, however, a unifying characteristic is the ability to exploit often transient and patchy resources to reproduce rapidly (Graham et al., 2001; Dawson and Hamner, 2009; Holland, 2016). In the first instance, being composed largely of water allows these animals to grow faster than non-gelatinous species, giving them a competitive advantage (Pitt et al., 2013). The thaliaceans alternate between sexual and asexual generations, allowing them to respond rapidly when primary productivity increases (Holland, 2016). The appendicularians have a simpler life cycle, reproducing sexually, but can develop to adult size in 24 hours and have short life spans, e.g. 10 days for *Oikopleura diocia*, which means they are equally adept at utilising primary productivity (Holland, 2016). The Ctenophora are largely hermaphroditic and are capable of reproducing at an early developmental stage (paedogenesis) (Ruppert and Barnes, 1994). Furthermore, as adults, gametes are

released continuously while food is available, and these traits allow populations to develop rapidly (Ruppert and Barnes, 1994).

Medusozoa reproductive strategies are diverse and include broadcast spawning, direct development and an alteration between sexual and asexual reproduction and multiple generations per season (Russell, 1953; Russell, 1970; Lucas et al., 1995; Bouillon et al., 2006; Arai, 1997; Blackett et al., 2015). Coastal aggregations are predominately meroplanktonic species that utilise an asexual polyp stage, while the oceanic species are predominantly holoplanktonic species with direct development, although there are exceptions in both cases (Bouillon et al., 2006). Medusozoa are voracious insatiate predators and this combined with reproductive flexibility allows populations to increase rapidly when prey are available (Purcell, 1997; Graham et al., 2001; Dawson and Hamner, 2009; Lucas et al., 2014; Blackett et al., 2015). The availability of prey is a key concept in population dynamics and dependent on a range of factors, the swimming ability, physiology and behaviour of both predator and prey determine successful foraging (Folt and Burns, 1999; Arai, 1997; Benoit-Bird et al., 2013). Just as important is the physiological and behavioural responses of predator and prey to the physical environment, and processes that create intense physical gradients, discontinuities, horizontal or vertical flows, and zones of divergence or convergence can influence gelatinous zooplankton populations (Owen, 1981; Arai, 1992; Graham et al., 2001; Deibel and Paffenhofer, 2009).

Eddies & Fronts

Fronts and eddies are ubiquitous pelagic features that arise from several different physical processes and create zones of coherent horizontal and/or vertical flow which often separate different water masses (Owen, 1981; Belkin et al., 2009; Chelton et al., 2011). Frontal systems are generally linear and interact with

topography, tides and weather to produce upwelling and downwelling zones (Owen, 1981; Le Fèvre, 1987; Raine, 2014). An eddy can be thought of as a special type of front where the linear flow encloses a circular bowl shaped parcel of water, and can also induce vertical flows (Stommel, 1958; Owen, 1981; Dufois et al., 2016). Both features can result from interactions between topography and hydrography in shallow coastal waters, but can also be found in deep pelagic regions independent of topography (Stommel, 1958; Owen, 1981; Rossby, 1996; Shoosmith et al., 2005). The geographic range of both features is variable; the major ocean gyres form large scale (>250 km) quasi stationary eddies and contribute to the major oceanic frontal systems, whereas the meso-scale (100 – 250 km) features are generally transient, seasonal, or both (Graham et al., 2001; Kaiser, 2011). Both features have a profound influence on primary productivity, vertical mixing of nutrients and energy and lateral oceanic circulation (Tranter et al., 1980; Benitez-Nelson et al., 2007; McGillicuddy et al., 2007; Belkin et al., 2009; Chelton et al., 2011; Zhang et al., 2014; Faghmous et al., 2015; Dufois et al., 2016; McGillicuddy, 2016). A substantial body of literature shows spatial coherence between fronts and eddies and higher trophic levels such as birds, sharks, marine mammals, mesopelagic fish, and sea turtles (Brandt, 1981; Owen, 1981; Olson and Backus, 1985; Olson et al., 1994; Schick et al., 2004; Worm et al., 2005; Bakun, 2006; Doyle et al., 2008b; Belkin et al., 2009; Scales et al., 2014a). Likewise, the distribution of mesozooplankton (0.2–20 mm), macrozooplankton (2-20 cm) and nekton are influenced by fronts/eddies (Brandt, 1981; Davis and Wiebe, 1985; Olson and Backus, 1985; Wiebe et al., 1985; Boyd et al., 1986; Bakun, 2006; Lara-Lopez et al., 2012; Schultes et al., 2013; McGinty et al., 2014).

The available literature on gelatinous zooplankton with respect to frontal/eddy systems is relatively sparse, and biased towards scyphomedusae, nonetheless, it

indicates that frontal systems and eddies often partition distinct gelatinous communities (Davis and Wiebe, 1985; Wiebe et al., 1985; Pagès and Gili, 1992; Pages and Schnack-Schiel, 1996; Graham et al., 2001; Guerrero et al., 2016). Graham et al. (2001) summarised that small and mesoscale fronts are more likely to promote aggregation, whereas, the large-scale oceanic fronts serve to separate distinct water masses and their respective communities. The reasons for this appear two-fold: small and meso-scale features exhibit stronger flows, leading to the passive aggregations of weakly swimming gelatinous taxa via convergent currents. Secondly, many of the studies have focused on small and meso-scale features, mainly in the neritic domain, where higher productivity and thus prey availability potentially lead to active aggregations (Arai, 1992; Folt and Burns, 1999; Graham et al., 2001).

Much of the research which has focused on gelatinous zooplankton in the oceanic domain, was concerned with geographic and vertical distribution (Alvariño, 1971; Pugh, 1977; Pugh, 1984; Roe et al., 1984; Mackie et al., 1987; Angel and Pugh, 2000). Siphonophores have often been the dominant group (Pugh, 1977; Williams and Conway, 1981; Mackie et al., 1987) and their distribution is influenced by the major hydrographic currents (Pugh, 1977; Pugh, 1984; Mackie et al., 1987; Larson et al., 1991). Vertically, siphonophores are most abundant and diverse in the epipelagic zone (0 – 200 m depth) (Mackie et al., 1987; Mapstone, 2009) and therefore oceanic eddies are likely to play an important role in their ecology/distribution. The distribution of hydromedusae and scyphomedusae in the oceanic domain are poorly understood and while some studies suggest they are predominantly in the meso-pelagic zone (200 – 1000 m depth) (Larson et al., 1991), other studies combining methods indicate a wider vertical distribution (Hosia et al., 2008; Stemmann et al., 2008; Hosia et al., 2017). A broader vertical distribution would mean meso-scale eddies are potentially an

important influence over oceanic medusozoa. The Warm Core Rings project in the 1980s, showed that warm eddies contained distinct zooplankton communities, including gelatinous taxa, that could develop substantially in 2-3 months, shifting to a larger predatory community (Davis and Wiebe, 1985; Wiebe et al., 1985). Species level detail was lacking in the study, however, a shift to larger zooplankton would favour certain gelatinous taxa, most likely large siphonophores (Purcell, 1981; Mackie et al., 1987).

Frontal systems in the neritic domain are often characterised by very different gelatinous communities on either side, with coastal neritic species on the inshore side and oceanic species on the offshore side (Graham et al., 2001; Guerrero et al., 2016). However, this is not always the case and some studies reveal little influence of frontal systems on the gelatinous community (Schultes et al., 2013; Luo et al., 2014). Few studies support the idea that fronts directly support bottom up increases in the majority of gelatinous taxa, except perhaps for the pelagic thaliaceans - doliolids (Deibel, 1985; Luo et al., 2014). Nonetheless, observations of increases in small hydromedusae associated with upwelling suggest, that on occasion, aggregations are the result of both passive and behavioural factors (Arai, 1992). The peak abundance of hydromedusae has been recorded on the offshore side of frontal systems in several regions (Pagès and Gili, 1992; Mianzan and Guerrero, 2000; Schultes et al., 2013), however, no causal relationship between the front and the gelatinous predators was suggested.

The Celtic Sea Front and the Ushant Front in the Celtic Sea, in the north east Atlantic, are two relatively well studies features (Cooper, 1952; Cooper, 1960; Cooper, 1967; Pingree and Griffiths, 1978; Le Fèvre et al., 1983; Le Fèvre, 1987; Pingree and Le Cann, 1989; Horsburgh et al., 1998; Pingree et al., 1999; Beaugrand

et al., 2000; Brown et al., 2003; Fernand et al., 2006; O'Boyle and Raine, 2007; Hill et al., 2008; Raine et al., 2010; McGinty et al., 2014; Raine, 2014), and have a profound impact on primary productivity, and form part of a circulation that conveys plankton around the Celtic Sea (Hill et al., 2008). Interactions between weather and the frontal system is known to advect Harmful Algal Blooms (HABs) into sensitive habitats with intensive aquaculture operations (Raine et al., 2010). These interactions are effectively intrusions of oceanic shelf water into inshore areas and similar events are thought to have, on occasion, brought high densities of hydromedusae into inshore regions in Ireland, Norway, Scotland and Germany (Greve, 1994; Båmstedt et al., 1998; Cronin et al., 2004). The neritic siphonophore *Muggiaea atlantica* has become a serious problem species in Ireland for the salmon farming industry (Baxter et al., 2011a), and there is considerable circumstantial evidence that the Celtic Sea frontal systems may advect the now resident English Channel *M. atlantica* population (Blackett et al., 2015) into Irish coastal waters during the summer/autumn.

Interactions between jellyfish and finfish aquaculture

The presence of gelatinous zooplankton and particularly 'jellyfish' blooms in coastal regions has led to a range of negative interactions with human activities including tourism, fishing, power plants intakes, catastrophic trophic cascades, and finfish aquaculture (Purcell et al., 2007). In the case of finfish aquaculture, the problem species have predominantly been cnidarians, although occasionally ctenophores have also caused problems (Båmstedt et al., 1998), and documented events began in the 1950s (Purcell et al., 2013). Thus far the salmon aquaculture industry has suffered most, and the industry in northern Europe, e.g. Scotland, Norway, and Ireland, has been hardest hit (Doyle et al., 2008a; Baxter et al., 2011a; Rodger et al., 2011a). To a lesser extent, salmon operations in Chile, Australia, Asia, and North America have

also been affected (Adams et al., 2004; Palma et al., 2007; Rodger et al., 2011a). The issue can be divided into two categories; 1) high mortality events caused by extreme densities of usually, but not exclusively, scyphomedusae, i.e. *Pelagia noctiluca*, and 2) a chronic elevated background mortality caused by small inconspicuous hydromedusae, i.e. *Muggiaea atlantica* or *Phialella quadrata*. High mortality events can result in 100% mortalities, such as has occurred in Glenarm Bay, Northern Ireland, during 2007 (Doyle et al., 2008a) and estimates of background mortalities range from 12 – 80% over several years (Rodger, 2007). The second category of chronic impact also contains the hydroids, which while not strictly planktonic, does include the shedding of polyps and this process has injured caged fish in the Mediterranean (Bosch-Belmar et al., 2017). Baxter et al. (2012a) has also demonstrated that both attached colonies and colonies shed into the water cause gill damage (sloughing, necrosis & haemorrhage) and clouding of the cornea in young salmon during controlled tests.

It is increasingly difficult to assess the cause of gill damage and fish moralities at fish farms as other biological agents and pathogens often co-occur with jellyfish and disentangling the exact contribution of each agent is difficult (Rodger et al., 2011b). In addition, some jellyfish species may carry the bacteria, *Tenacibaculum maritimum*, thereby injuring and infecting fish at the same time (Ferguson et al., 2010; Delannoy et al., 2011), which further complicates post mortem analysis. Aquaculture food production is the fastest growing food production system globally, and currently finfish aquaculture output is estimated at over US $99 billion (FAO, 2016). The Food and Agricultural Organisation of the United Nations has projected substantial increases in finfish aquaculture output of over 40% in the coming years, which is likely to lead to an increase in interactions between fish farms and harmful jellyfish in some

regions (Boero et al., 2016). In Ireland, the salmon industry produces approximately €50 million worth of fish annually, with losses of approximately 50% during some recent years (Marine Harvest Ireland Ltd., pers. comm.). Furthermore, climatic changes and increasing sea temperatures are likely to have unpredictable effects, as gelatinous taxa may potentially increase or decrease in abundance, and other taxa may shift in latitude bringing 'new' harmful species into a region (Boero et al., 2016). A good example of this, is the now resident population of the siphonophore *Muggiaea atlantica* in the English Channel, where it was previously considered seasonal and transient (Blackett et al., 2014; Blackett et al., 2015). Despite this recent work, knowledge of these species remains poor and knowledge of other potentially harmful species is non-existent.

Mitigation against harmful jellyfish

Currently farmers have no early warning system and even if they did, the strategies for dealing with high densities of harmful jellyfish are limited. The least stressful strategy for the fish is to control their shoaling depth, to avoid the highest densities of jellyfish; this involves cessation of feeding which makes fish circulate deeper in the cage (Marine Harvest Ireland Ltd., pers. comm.). Newer cage designs also have moveable lids which can corral the fish at variable depths to achieve the same end. On occasion, fish will be harvested early to remove them from harm's way, however, this is not simple and specialised vessels take time to arrive on location, meaning fish may well be unmarketable by that time (Marine Harvest Ireland Ltd., pers. comm.). Where fish are known to be injured, antibiotics can be added to feed to offset secondary infections. All of these strategies add substantial economic cost to the industry and impact the welfare of the fish, and therefore other strategies are sought which might offer protection to farms.

A bubble curtain, or pneumatic barrier is one proposed method for protecting finfish aquaculture cages, and although the system is apparently in use at some power stations, as protection against jellies and at salmon farms as protection against harmful phytoplankton (Canadian Pond Ltd., pers. comm.), there are no published data on the efficacy of the system. In principle the system is simple; compressed air is delivered to a perforated hose lying across the seabed and the escaping air bubbles create a vertical current as they expand and rise to the surface (Lo, 1996). The vertical current in theory should entrain the harmful zooplankton and lift them to the surface to be removed or flow around the 'protected' area. The majority of research on this system has been carried out in the engineering field, as an oil spill retention strategy, and while effective for surface oil, the system was not 100% effective for sub-surface oil. Wind and current were evidently influential on the efficacy of the system as an oil barrier (Lo, 1996), however, whether these results are applicable to gelatinous animals which do not rest on the surface like oil is unknown. Many farms are off grid and rely on diesel power generation and the prospect of running powerful compressors continuously is economically unattractive, nonetheless, if such a system was combined with a greater understanding of the ecology of harmful species it could well become a viable mitigation strategy.

Biofouling is ubiquitous in marine ecosystems and the fouling of a surface begins immediately upon immersion in seawater (Whelan and Regan, 2006; Callow and Callow, 2011; Mieszkin et al., 2013). The process is initially a physical interaction between a surface and the ambient water, whereby organic molecules such as proteins, carbohydrates and polysaccharides settle on a surface, creating a 'slime' layer (Mieszkin et al., 2013). This stage is followed by the settling and binding of bacteria and other microbes to the surface, which is subsequently followed by larger macro-

fouling organisms such as mussels, barnacles and hydroids (Guenther et al., 2010; Callow and Callow, 2011; Fitridge et al., 2012). The macrofouling community that ultimately develops on a surface is influenced by species availability, geography, hydrography, season, temperature and the physical and chemical properties of a surface (Yebra et al., 2004; Chambers et al., 2006; Dobretsov et al., 2006; Scardino et al., 2009; Banerjee et al., 2011; Callow and Callow, 2011; Baxter et al., 2012a; Fitridge et al., 2012; Blöcher et al., 2013a; Buskens et al., 2013; Mieszkin et al., 2013).

Biofouling in the finfish aquaculture industry is deleterious for the structural integrity of cage arrays and fish health (Guenther et al., 2011; Baxter et al., 2012a; Fitridge et al., 2012; Floerl et al., 2016; Bosch-Belmar et al., 2017). Heavily fouled cages can increase the stress on anchoring systems, reduce the flow through of fresh oxygenated water, reduce the dispersal of fish excrement, increase pathogen presence and directly injure fish through hydroid stings (Braithwaite and McEvoy, 2004; De Nys and Guenther, 2009; Baxter et al., 2012a; Fitridge et al., 2012; Floerl et al., 2016). One hydroid species, *Ectopleura larynx*, is a dominant fouling organism on salmon cages (Braithwaite and McEvoy, 2004; Greene and Grizzle, 2007; Baxter et al., 2012a; Kassah, 2012; Blöcher et al., 2013a). Its presence on nets and in the water has been shown to injure fish (Baxter et al., 2012a), and the shedding of mature polyps has been correlated with increased injuries (Bosch-Belmar et al., 2017). The current mitigation strategy against biofouling includes the application of copper based biocidal coatings and subsequent *in situ* high pressure cleaning of cages. Neither method has proved to be effective against *E. larynx* in the long term; the biocidal coating loses effectiveness after *ca.* six months (Braithwaite et al., 2007), and the cleaning creates a plume of stinging debris that can spread active propagules to adjacent structures and cause gill damage (Floerl et al., 2016).

Scope of the thesis

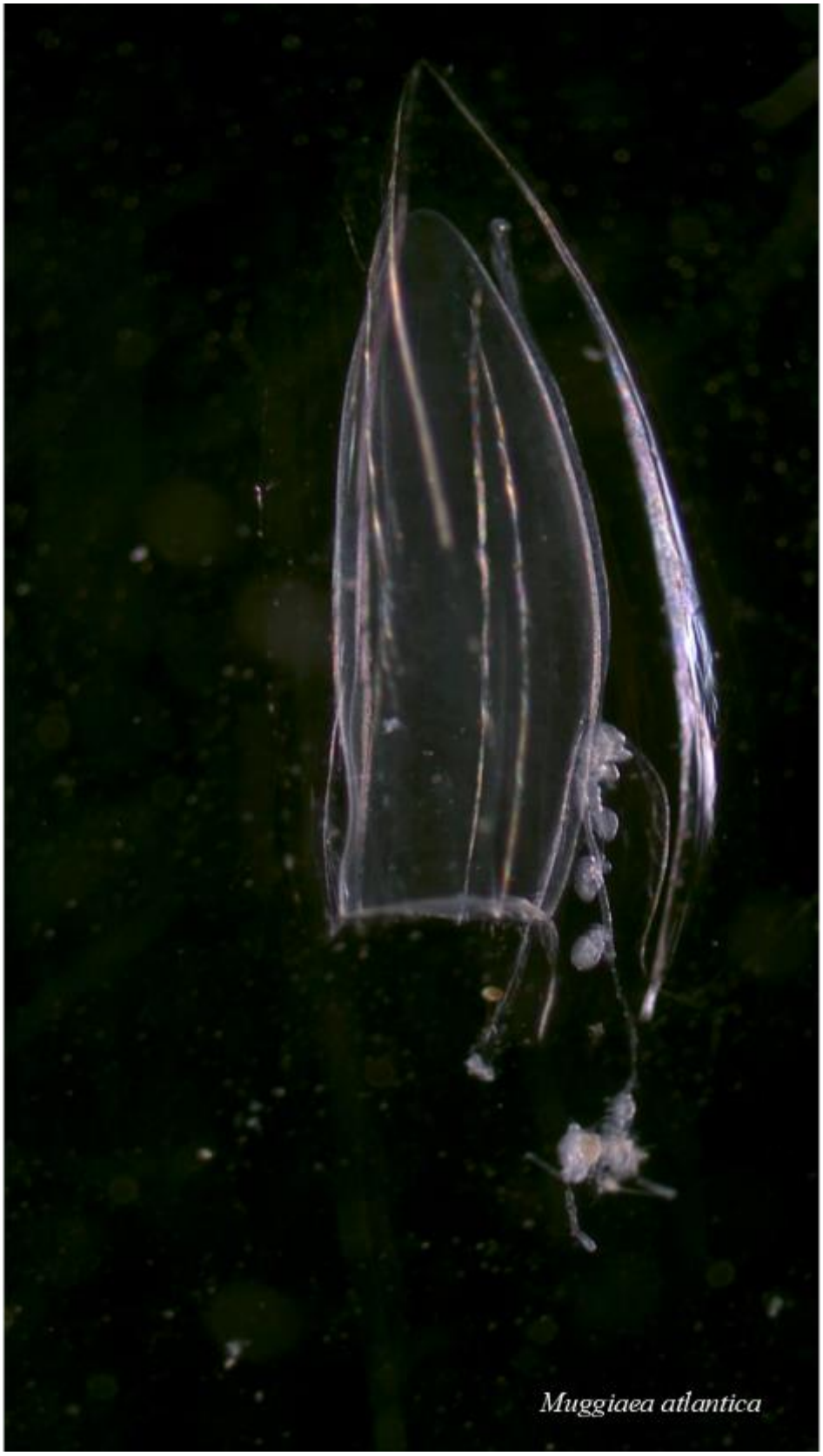
The current research was carried as part of a collaboration between University College Cork, including the Marine and Renewable Energy Centre (MaREI), the School of Biological, Earth and Environmental Sciences (BEES), and Marine Harvest Ireland Ltd., and referred to as Aqua-MaREI. Part of the research was also carried out in collaboration with Galway and Mayo Institute of Technology and the Environmental Protection Agency (EPA) funded 'Ecosystem Tipping Points Project'. The Aqua-MaREI project was set up to investigate the ecology of harmful gelatinous zooplankton and the key processes driving abundance and distribution. In addition, the project addressed potential mitigation strategies that might reduce the impact of harmful species on caged fish.

This thesis sought to enhance our understanding of gelatinous zooplankton by addressing key gaps in our understanding; including the relationship between spatial and temporal heterogeneity and physical processes, and the application of that knowledge to mitigation strategies. The mitigation strategies investigated included the use of a 'bubble curtain' or a pneumatic barrier as a protective screen against harmful species, and the application of a novel non-toxic antifouling coating as a deterrent to fouling hydroids.

Through the Aqua-MaREI project and in collaboration with Plymouth Marine Laboratories, the occurrence and distribution of siphonophores in the southwest of Ireland and the Western English Channel were investigated (Chapter 2). This research sought to examine current data with respect to historic observation, and with respect to data from the adjacent, potentially related, pelagic ecosystems. The Celtic Sea Front is a seasonal oceanographic feature between the Celtic Sea and the Irish Sea, and is also part of a larger circulation that physically connects otherwise disparate regions of

the Celtic Sea (Hill et al., 2008). A plankton survey during July 2015 sought to investigate the influence of the front over the Celtic Sea gelatinous zooplankton assemblage (Chapter 3). The contribution of gelatinous zooplankton to the total zooplankton assemblage was investigated, which has not been done before in Irish waters. Another survey in April 2015 crossed the north Atlantic form Ireland to Newfoundland, and offered a unique opportunity to investigate a meso-scale warm core eddy situated within the North Atlantic Current (Chapter 4). This oceanic feature is analogous to the Celtic Sea front and presented an opportunity to compare meso-scale processes in the oceanic and neritic domains and their respective influence over gelatinous zooplankton. To date, this is the first study, to the best of our knowledge, to describe the gelatinous taxonomic variation across a warm core eddy.

In collaboration with Marine Harvest Ireland Ltd., the Aqua-MaREI project carried out two specific projects on potential mitigation measures to protect finfish farms from harmful gelatinous species. The first experiment involved testing the efficacy of a bubble curtain system as a barrier to jellyfish; both field and laboratory experiments were carried out using real and model jellyfish (Chapter 5). The results are described within the context of substantial biological and physical data from two aquaculture sites in Ireland (relating to Chapter 2) in an effort to assess the practicality of the system. The second experiment was the investigation of a novel anti-fouling coating as a deterrent to the fouling hydroid *Ectopleura larynx*. The efficacy of the coating as a fouling-release agent was also examined in cleaning tests (Chapter 6).



Chapter 2

Diversity and occurrence of siphonophores in Irish coastal waters

This chapter has been published in a similar format as a peer-reviewed publication: Haberlin, D., Mapstone, G., McAllen, R., McEvoy, A.J. and Doyle, T.K., 2016, January. Diversity and occurrence of siphonophores in Irish coastal waters. In *Biology and Environment: Proceedings of the Royal Irish Academy* (Vol. 116, No. 2, pp. 119-129). Royal Irish Academy.

Abstract

Siphonophores are at times amongst the most abundant invertebrate zooplankton predators in the oceans. Historically, siphonophores have been under-sampled and of the studies conducted there has been a bias towards oceanic oligotrophic waters where they are considered to be more abundant and diverse. In temperate coastal regions, comparatively less is known about the diversity and abundance of siphonophores, where periodic blooms can restructure the plankton communities and have been correlated with high mortalities in the salmon aquaculture industry. To address this lack of knowledge, plankton samples were collected during two periods (March 2009-March 2011 and April 2014- November 2015) from a coastal embayment in the southwest of Ireland. In total, three siphonophore species were found, the calycophoran *Muggiaea atlantica*, and the physonects, *Nanomia bijuga* and *Agalma elegans*. *Muggiaea atlantica* was the most abundant species (250 colonies m^{-3}), with densities an order of magnitude higher than either physonect. *Muggiaea atlantica* displayed a distinct seasonality, whereas the physonect species were sporadic in occurrence. Comparing siphonophores in Bantry Bay, Ireland, and the Western English Channel (Plymouth Marine Laboratory's L4 station) indicates both regions share a similar pattern of inter-annual occurrence and provides novel information on the seasonality and occurrence of siphonophores in Irish coastal waters.

Introduction

Siphonophores are at times amongst the most abundant non-crustacean invertebrate predators in the oceans (Purcell, 1981; Williams and Conway, 1981; Pugh, 1984; Pugh et al., 1997). With 177 species (Mapstone, 2015), the majority are described as holoplanktonic, cosmopolitan in distribution and more frequently encountered in deep oceanic waters (Totton and Bargmann, 1965; Mackie et al., 1987; Mapstone, 2014). Historically, they have largely gone undetected, primarily as a result of the difficulty of sampling very delicate animals (Haddock, 2004). As such, compared to crustacean zooplankton, quantitative data on siphonophores are relatively scarce. Where good quantitative data have been gathered, particularly with the use of *in situ* techniques, there has been a bias towards warm oligotrophic waters where diversity was known to be high (Hamner, 1975; Mills, 1995). However, where submersible transects have been used in regions of low and high productivity, the same siphonophore diversity has been recorded (Mills, 1995) and long term sampling in the upwelling region west of Vancouver Island, Canada, (Denman et al., 1981) revealed a relatively high diversity (Mapstone 2009). Recently, the occurrence of siphonophores in coastal waters has received a lot of attention because of their negative impact on the salmon aquaculture industry. Abundance of the small calycophoran siphonophore, *Muggiaea atlantica* Cunningham, 1892, has been correlated with mass mortalities of farmed salmon in Ireland (Cronin et al., 2004; Baxter et al., 2011a), Scotland (Nickell et al., 2010) and Norway (Fosså et al. 2003). The abundance of the physonect *Apolemia uvaria* Lesueur, 1815 has also been correlated with fish mortalities in Norway (Båmstedt et al., 1998). Furthermore, there is growing evidence that unidentified small jellyfish contribute significantly to annual fish mortality rates in Ireland and Scotland, through injury to the fish and as a vector of secondary bacterial infection (Ferguson et

al., 2010; Rodger et al., 2011a; Rodger et al., 2011b). *M. atlantica* can have a dramatic impact on the plankton community through top-down predation on copepods, in Helgoland during 1989 unusually high *M. atlantica* densities reduced the copepod population to 10% of the long-term mean (Greve, 1994). The decline in copepods released phytoplankton from predation and contributed to changes in nutrient concentrations in the region, causing a late autumn phytoplankton bloom (Greve, 1994). While most siphonophores are considered oceanic, there is evidence that some species can reside in coastal waters for extended periods, i.e., 1-2 years. In Norway a year-long study found the physonect *Nanomia cara* Agassiz, 1865 to be semi-resident in deep Norwegian fjords (Hosia and Båmstedt, 2008). Observations in the Gulf of Maine showed a similar occurrence of *N. cara*, but recorded higher densities and in shallow areas above 30m depth (Rogers et al., 1978; Mills, 1995). Studies in Ireland (Baxter et al., 2011a), Portugal (Marques et al., 2006) and Chile (Palma et al., 2011), showed *M. atlantica* to be present for much of the year and occasionally a dominant member of the macrozooplankton community. By contrast, the current knowledge of siphonophores in Irish waters is largely based on qualitative observations from the early twentieth century, with only Ballard and Myers (2000) and Baxter et al. (2011a) generating quantitative data on small gelatinous zooplankton. Much of the literature referencing the impact on salmon aquaculture is based on post-mortality reports, with no data recorded prior to the events. Here, an additional two years of zooplankton samples from Bantry Bay was used to supplement the previous work carried out by Baxter et al. (2011a) and Baxter (2011). Historical occurrences of siphonophores in Irish waters were collated, and in combination with the recent quantitative data were used to comment on the occurrence and seasonality of siphonophores in temperate coastal waters.

Material and Methods

Seasonal abundance of siphonophores was studied over two periods; from March 2009 - March 2011 (Baxter, 2011a) and from April 2014 - November 2015. Approximately one year of data (April 2009 – March 2010) from the earlier work was published previously by Baxter et al. (2011a) and Baxter (2011). All samples were taken at the Roancarrig salmon farm (Marine Harvest Ireland Ltd.), situated in Bantry Bay, southwest Ireland (51.654° N, -9.774° W) (Fig. 2.1).

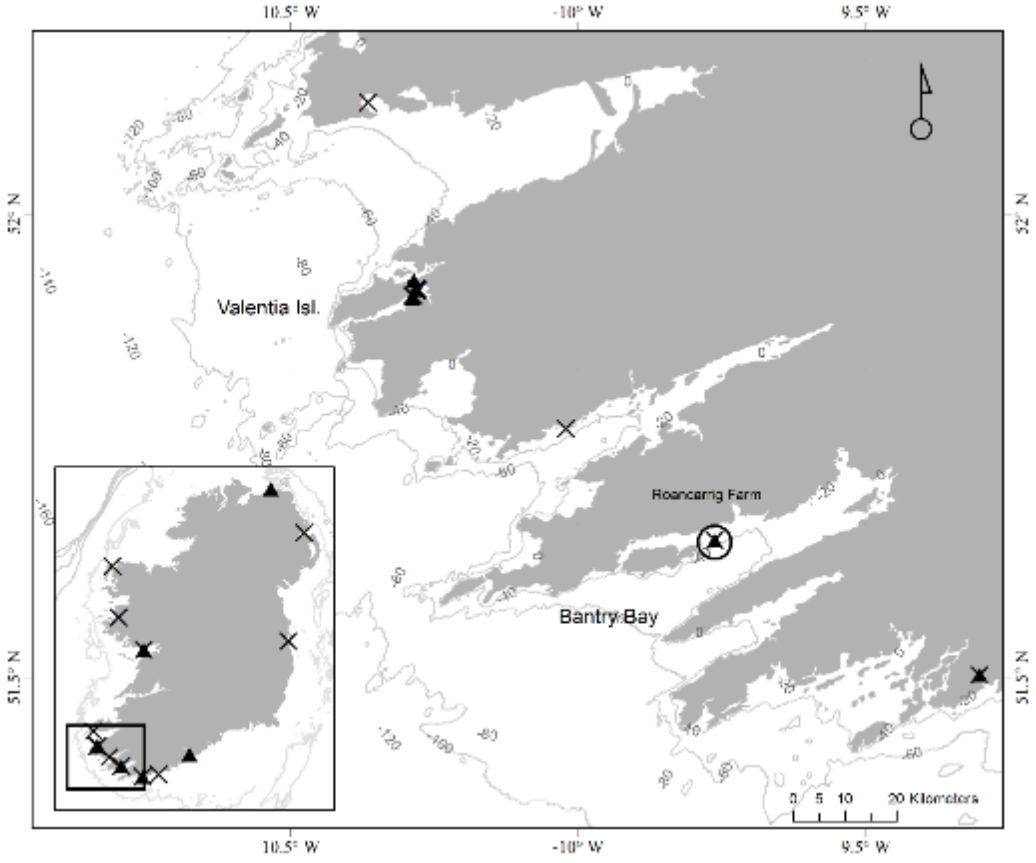


Figure 2.1: The southwest coast of Ireland, with the sample site in Bantry Bay and (inset) historic observations of siphonophores around the Irish coastline. Symbols on the map indicate calycophoran (▲) and physonect (x) sightings. The Roancarrig farm site is represented by the open circle.

Bantry Bay is a smoothly sloping bay with limited estuarine characteristics and is heavily influenced by wind and coastal currents (Raine et al., 2010; Raine, 2014). The bay is 35 km long, running in a south-west to north-east direction, experiences weak tidal circulation, and becomes thermally stratified in the summer (Raine, 2010). The intense stratification leads to a two layer, wind-driven oscillatory flow, exchanging water between the bay and adjacent shelf waters (Edwards et al., 1996). During the 2009-11 study, samples were collected using a 0.4 m ring net with 200 µm mesh (Baxter, 2011; Baxter et al., 2011a). Five vertical plankton tows were taken at five stations around the Roancarrig farm, fortnightly during April-October and monthly at all other times (Baxter, 2011; Baxter et al., 2011a). Assuming 100% filtering efficiency over a short vertical distance, volume was calculated from the depth of water sampled (Baxter, 2011; Baxter et al., 2011a). During the 2014-15 study, samples were collected using a 0.5 m ring net with 200 µm mesh with a high length to mouth diameter ratio, designed to minimise damage to gelatinous zooplankton. Triplicate samples were taken at a single station (~25m depth) by hauling vertically from ~4m above the sea bed to the surface and a non-reverse flowmeter was used to calculate the volume of water filtered. The mean volume filtered was 3.5 ± 0.06 m^{-3} (± SE). All samples were fixed immediately in a 4% formalin sea water solution. Although the ring nets used in each study differed in mouth diameter and length, both nets would be expected to have comparable efficiency (McGowan and Fraundorf, 1966).

Samples were analysed using a Zeiss dark-field stereomicroscope (Stemi 2000) and all gelatinous zooplankton were counted and identified to the lowest possible taxonomic level. Physonects consist of a single pneumatophore and multiple nectophores, the number of which depends on species and maturity (Totton and Bargmann, 1965). Pneumatophores and nectophores were counted and the presence of

other fragments noted, i.e. bracts, palpons and gastrozooids. Physonect abundance was based on pneumatophore counts, and due to their consistent presence there was no necessity to estimate abundance using nectophores counts. For *Muggiaea atlantica* abundance, all identifiable nectophores and bracts were counted. The number of anterior nectophores can be used to represent the total number of polygastric stages, since *Muggiaea* species do not develop a posterior nectophore (Totton and Bargmann, 1965). Eudoxid abundance was taken as the number of full intact eudoxids plus the number of eudoxid bracts. Polygastric and eudoxid counts were summed to give a figure for total abundance. Data were presented as the mean number of colonies ± 1SE m^{-3} for physonects, and mean number of polygastric or eudoxid stages ± 1SE m^{-3} for *Muggiaea atlantica*. To examine trends on a wider scale, results from this study were compared with data from a plankton monitoring station called L4 (50° 15.00' N, 4° 13.02' W) in the western English Channel. Plymouth Marine Laboratory (PML) collects and maintains the L4 dataset which is stored at the British Oceanographic Data Centre (BODC) (www.BODC.ac.uk). Since 1988 weekly duplicate plankton samples, collected with a WP2 200 µm mesh net, have been analysed and enumerated for zooplankton species. Siphonophore species have only been identified to species level at L4 since 2009. Data were presented as the mean number of colonies ± 1SE m^{-3} for physonects, and mean number of polygastric or eudoxid stages ± 1SE m^{-3} for *Muggiaea atlantica*. All data points were presented according to the date collected.

Investigation of physonect growth

To investigate possible growth in colony size through the summer, preserved nectophores collected from June to August 2014 were measured across their width. There were insufficient nectophores in other months or in other years to include in the analysis. In addition, the nectophores collected during 2009-11 had deteriorated and

were not suitable for measurement. Nectophores that were badly damaged or misshapen were also not used for measurements. All measurements were taken from calibrated images using a Micron Optical 5mp digital camera with the stereomicroscope. All analysis was carried out using R (R Core team, 2016)

Results

In total 260 samples were collected on 60 sampling days, from April 2009 to November 2014. Three siphonophore species were recorded in the samples: the calycophoran *Muggiaea atlantica* and two Agalmatidae physonects, *Nanomia bijuga* (Fig. 2.2) and *Agalma elegans* Sars, 1846. Athorybiid larvae of *A. elegans* (Fig. 2.3) were also recorded in several samples. *Muggiaea atlantica* and *N. bijuga* were present in all four years with *M. atlantica* the most abundant species, being an order of magnitude more abundant than the other species, 234 ± 14 (± SE) indiv. m^{-3} in 2009 (Fig. 2.4). *M. atlantica* was present on 33 days, with polygastric and eudoxid stages occurring on 28 days (Fig. 2.4). The mean percentage of eudoxids across those sample days was 64 ± 4% (± SE). *M. atlantica* was notably absent in 2014, except for a small number of individuals (< 1 indiv. m^{-3}) in November and December. *Nanomia bijuga* were present on 17 (28%) sampling days and the mean density was less than 1 colony m^{-3} on all sampling days except during June 2014 when the mean density reached 9.8 ± 2.3 (± SE) colonies m^{-3}. *Agalma elegans* polygastrics and athorybiid larvae were not present in all years. Athorybiid larvae were recorded on six days, three of which were consecutive monthly samples from October, November and December in 2014. Their mean density was less than 1 colony m^{-3} on all sample days, except in Nov 2014 when the mean density reached 11.5 ± 1.7 (± SE) colonies m^{-3}. *Agalma elegans* was present on 4 (7%) sampling days and never exceeded 1 colony m^{-3}. The presence of *M. atlantica* suggested a distinct seasonality, first appearing in June/July and with peak density in 2009, 2010 and 2013 occurring in October. The presence of *N. bijuga* would also appear to be seasonal, with fifteen of the seventeen positive sampling days between May and August. *Agalma elegans* colonies and athorybiid larvae appeared to be aseasonal.

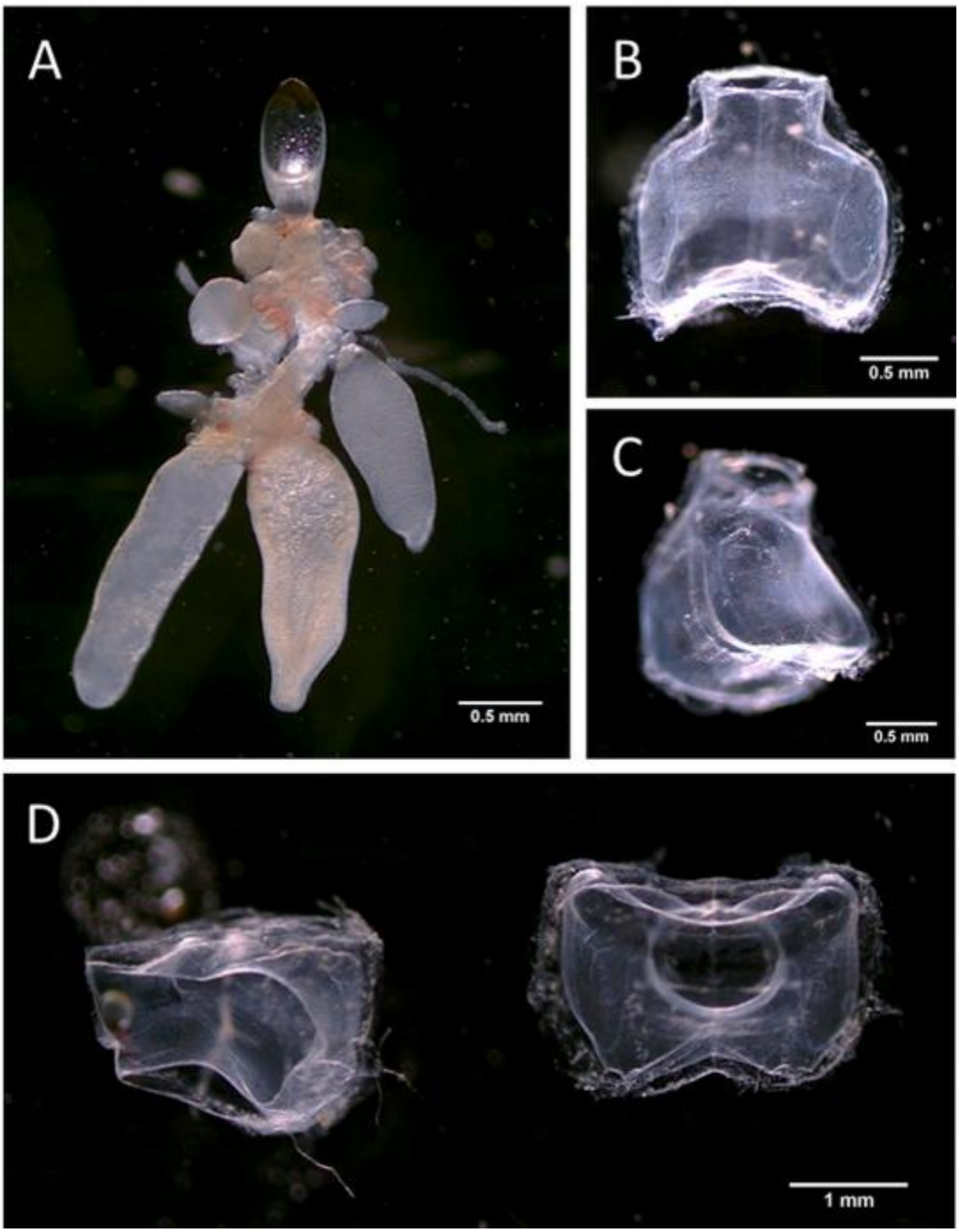


Figure 2.2: *Nanomia bijuga* colony from Bantry Bay, September 2015; A, Pneumatophore, nectosome and siphosome, with no nectophores attached; (B-D), *N. bijuga* nectophores from the same sample as colony in (A); (B) Upper view; (C) Lateral view; (D) Lateral view on the left and proximal view on the right.

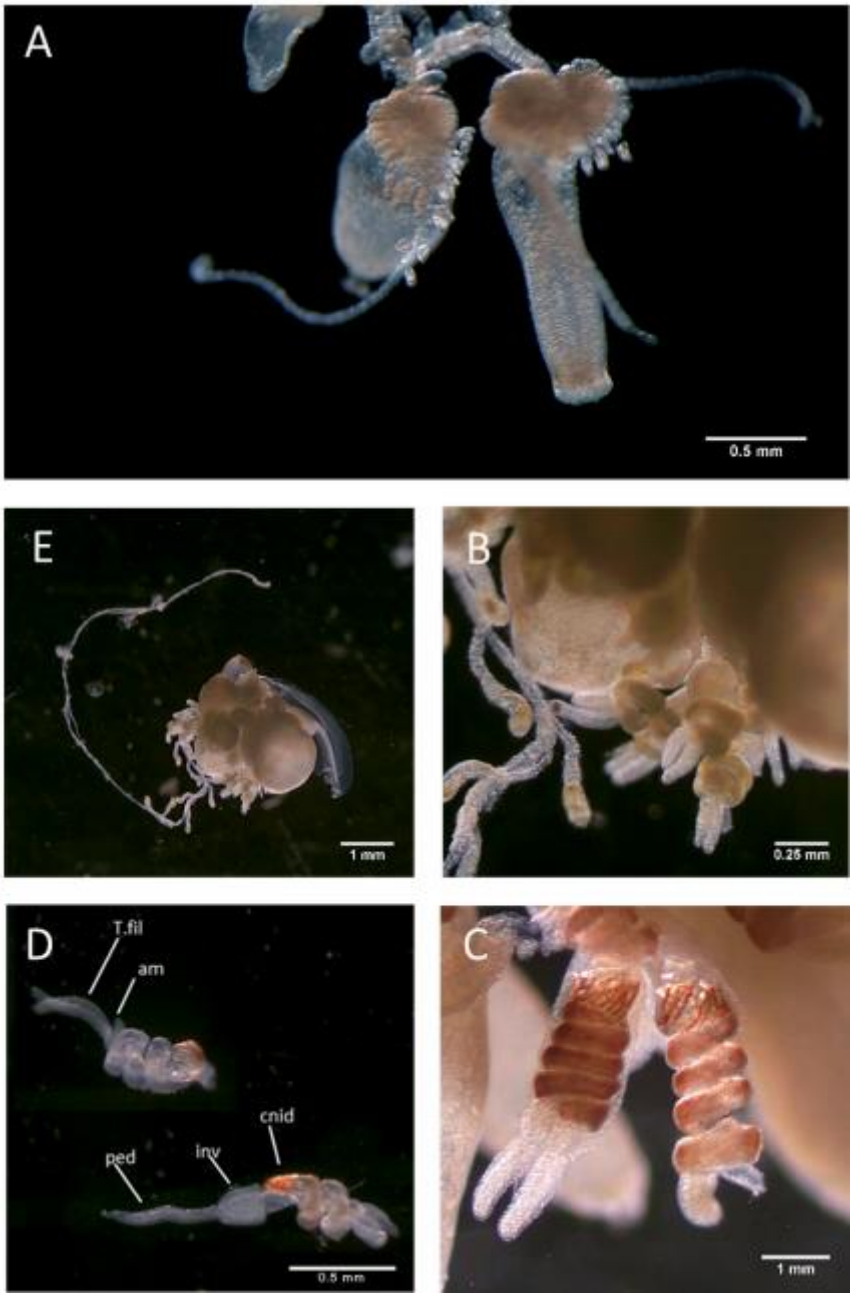


Figure 2.3: Physonect zooids: A, *Nanomia bijuga* colony, part of the stem bearing three young cormidia and their tentacles bearing larval tentilla; (B) small developing definitive tricornuate tentilla on an *Agalma elegans* larva; (C) large definitive tentilla of an adult *A. elegans*; (D) developing definitive tentilla of an adult *A. elegans*; (E) *A. elegans* larva with both larval tentilla and developing definitive tentilla; ped = pedicel, inv = involucrum, cnid = first coil of the cnidoband beginning to show red pigment, T.fil = 2 terminal filaments, am = ampulla.

The historical literature contained records for ten siphonophore species (Table 2.1): six physonects, four calycophorans and one cystonect. Many observations were recorded under older synonyms, which have been updated to the current accepted synonym using the world register of marine species (Schuchert 2016). The literature is biased towards south and west coasts, with the majority of observations coming from Valentia Island, S.W. Ireland (Fig. 2.1), and is dominated by physonects (Table 2.1). While all of the historic records of the genus *Nanomia* are recorded as the species *Nanomia cara*, molecular phylogenetic analysis provides strong evidence that this commonly encountered physonect is *Nanomia bijuga* (Baxter et al., 2012b).

Comparison with the L4 dataset

Samples taken on 319 days (2009-15) showed the occurrence of siphonophores at L4 displays a marked similarity to the data from Bantry Bay. *Muggiaea atlantica* was the most abundant species, two orders of magnitude higher than either physonect and, like Bantry, showed a distinct seasonality (Fig. 2.5). Peak abundance was earlier at L4, with highest densities recorded during July to September in 2009, 2010 and 2013 (Fig. 2.5). The peak abundance of *M. atlantica* at L4 reached more than 2000 indiv. m^{-3} on one occasion in July 2010. *M. atlantica* was present on 250 days, with polygastric and eudoxid stages occurring on 215 (67%) days. The mean percentage of eudoxids across those 215 days was 76 ± 2% (± SE). *M. atlantica* was almost completely absent during 2014, with densities of less than 1 indiv. m^{-3} during January, September, October and December only. *Nanomia bijuga* was present on 80 (25%) sample days, showing a distinct peak in abundance during June 2014 of 25 nectophores m^{-3}, with 35 of those days occurring in May and June. *A. elegans* at L4 was rare, occurring on 16 (5%) days with nectophore counts never exceeding 6 nectophores m^{-3}.

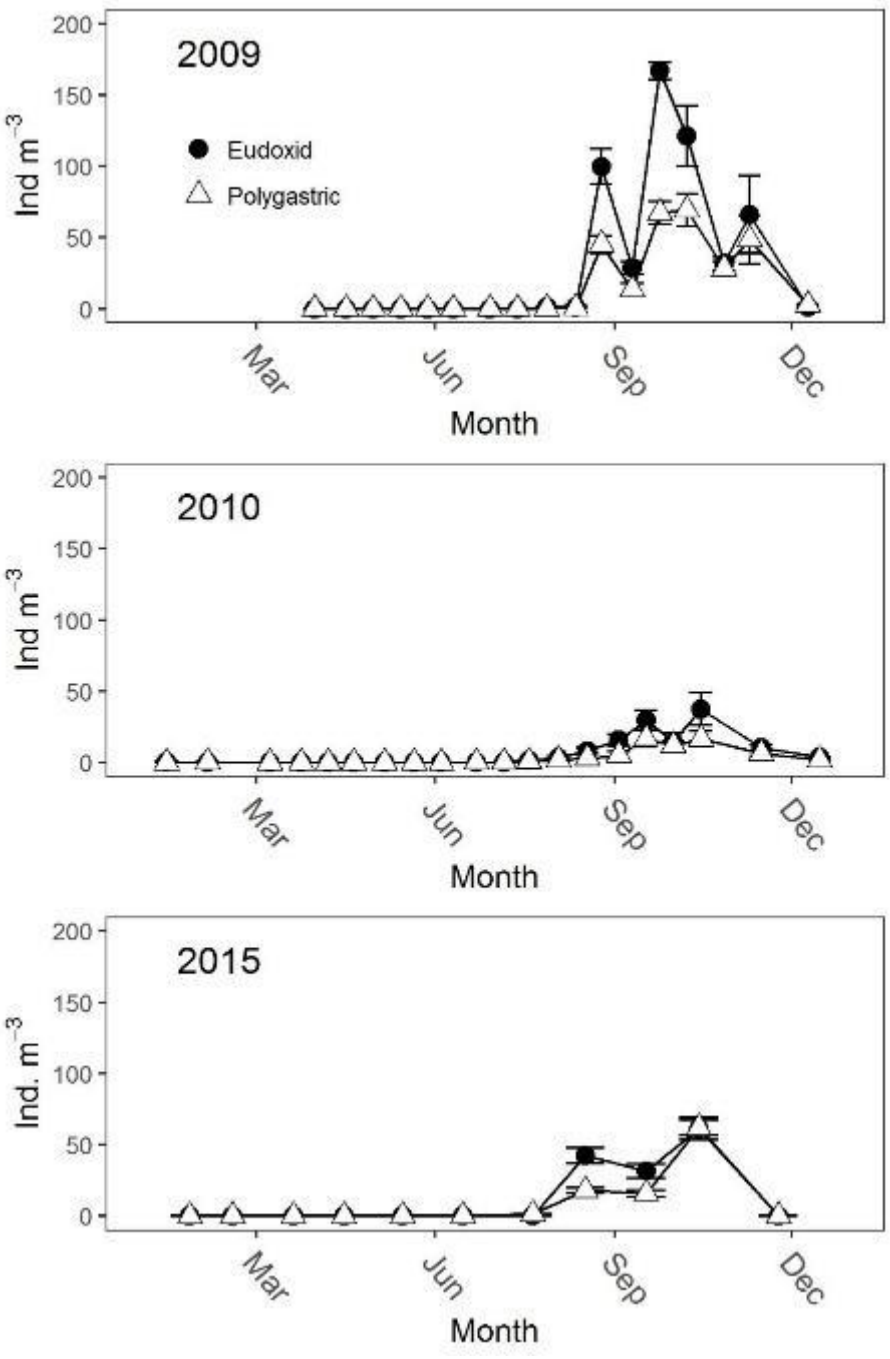


Figure 2.4: Mean seasonal abundance of *Muggiaea atlantica* polygastric and eudoxid colonies in Bantry Bay during the years 2009, 2010 and 2015. *Muggiaea atlantica* was almost entirely absent during 2014, therefore the data are not shown.

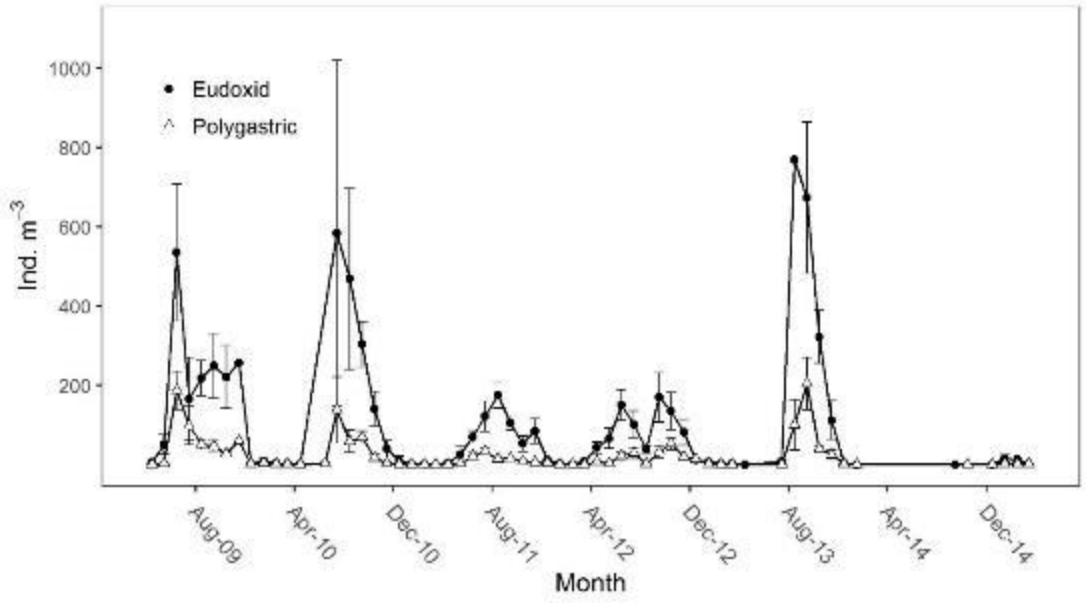


Figure 2.5: Mean monthly abundance of *Muggiaea atlantica* polygastric and eudoxid colonies at L4 station (Western English Channel) during the years 2009 to 2015.

Nanomia nectophore Growth

11 samples collected during 2014 and 2015 were used to analyse nectophore to pneumatophore ratio and nectophore size, with a total of 116 pneumatophores and 741 nectophores (ratio of 1 to 6.4). The maximum number of nectophores counted with one pneumatophore was 22. There was no apparent increase in nectophore numbers during the peak abundance in 2014, the ratio of nectophores to pneumatophores in June (91 to 550, ratio of 1 to 6) and July (14 to 81, ratio of 1 to 5.8) remained consistent. There was no apparent increase in nectophore size during June, July and August, 2014. Although a significant difference in width was found across the three months (Kruskal-Wallis, df =2, p = < 0.001), post hoc analysis showed no change between June (1.42 ± 0.005 mm, N=80) and July (1.38 ± 0.007mm, N=43) (Kruskal-Nemenyi, p = > 0.05), but a significant decrease between July and August (0.77 ± 0.009 mm, N=17) (Kruskal-Nemenyi, p = <0.01). Due to the smaller sample size in

August (N=17) and the possibility that all of the nectophores originate from a single colony, the decline in size may not be representative of the *Nanomia bijuga* population in general. No colonies were found with nectophores still attached, and loose gastrozooids and palpons were observed in many samples. All of the pneumatophores found were attached to a stem and the nectosome and siphosome were readily discernible, although usually tightly contracted (Fig. 2.2). Minute budding zooids were visible on many colonies below the pneumatophore, some of which were beginning to resemble nectophores.

Discussion

Abundance and seasonality

In this study, consistent quantitative sampling effort at a single site in Irish coastal waters revealed a low diversity of siphonophore species. *Muggiaea atlantica* was the most abundant species, consistently appearing in June/July and increasing in abundance before peaking in October/November (Figs. 2.4 & 2.5). The two physonect species did not have a readily observable pattern in either occurrence or abundance, appearing to be aseasonal, with *Nanomia bijuga* being more abundant and occurring more frequently than *Agalma elegans*. Despite the largely anecdotal nature of the historic literature, the pattern of temporal occurrence is broadly similar with the patterns found in this study. Historic observations around Ireland are dominated in early years (pre-1960) by physonects, whereas more quantitative methods in later years (post-1960), found *M. atlantica* to be the most abundant species (Table 2.1). The older literature is most likely biased towards reports of physonects due to their ability to float and their larger size, making them more easily detected by earlier observers.

There are few comparable studies of siphonophores in similar coastal environments; nonetheless, work in other locations provides interesting comparisons. *Nanomia cara* was the most common species in several Norwegian fjords (Hosia and Båmstedt, 2008), with peak abundance in May/June. Hosia and Båmstedt (2008) reported a maximum density of less than 1 colony m^{-3}, which is low compared to the 9.8 colonies m^{-3} in Bantry Bay. *Nanomia cara* was recorded throughout the year by Hosia and Båmstedt (2008), and the size and ratio of their nectophores to pneumatophores increased into the winter, indicating growth. Far higher densities of *N. cara* were documented in the Gulf of Maine, with densities reaching up to 7–8 colonies m^{-3} in 1975–6 (Rogers et al., 1978) and possibly 50–100 colonies m^{-3} in 1992–3 (Mills, 1995). Likewise, in the Gulf of Maine, *N. cara* colonies were found throughout the winter months, however, no seasonality was apparent (Rogers et al., 1978). Descriptions by Hosia and Båmstedt (2008) and Rogers et al. (1978) indicated that colonies can grow large, with nectophores in Norway reaching up to 8mm in width (Hosia and Båmstedt, 2008); compared with a maximum width of 2mm in Bantry. Rogers et al. (1978) described colonies of 0.2–3.5 m in length from a submersible, with 30–40 nectophores per colony in their larger individuals. In contrast, this study generally found smaller colonies, with a ratio of 6.4 nectophores per pneumatophore.

The diversity, abundance and seasonality of siphonophores appears to vary across different geographic regions, although *M. atlantica* has been consistently reported in many temperate coastal regions (Marques et al., 2006; Palma et al., 2007; Mapstone, 2009; Blackett et al., 2014). In Chilean coastal waters siphonophore diversity was higher, with 11 species recorded during a series of cruises in 2003 (Palma et al., 2007) and 2006 (Palma et al., 2011). During winter and spring *M. atlantica* was the dominant siphonophore with a peak abundance in spring (> 255

indiv. m^{-3}) and only one physonect species, *Pyrostephos vanhoeffeni*, (<1 indiv. 100 m^{-3}) was recorded. *Muggiaea atlantica* was the only siphonophore recorded in an estuarine environment in Portugal, peaking in May/June with densities reaching ~360 colonies m^{-3} (Marques et al., 2006). This density is comparable with those recorded in Ireland, whereas the peak density in May/June is much earlier and indicative of the earlier annual plankton blooms at these lower latitudes (Wroblewski 1989). In the main, siphonophore diversity appears to increase in deep water oceanic ecosystems (Mackie et al., 1987; Pages and Gili, 1992), although this would appear to not be the case in tropical coastal regions, where > 30 species have been recorded in shallow (*ca.* 20 m depth) lagoon habitats (Pages et al., 1989). Notably, *M. atlantica* is not well represented in tropical regions, and this well be due to a lack of suitable prey in oligotrophic water (Purcell, 1982). Both *A. elegans* and *Nanomia* spp. have a wide distribution and do not appear restricted to neritic waters like *M. atlantica* (Mapstone, 2009). This is possibly due to a preference for larger less common prey (Purcell, 1981) which allows them to inhabit oligotrophic waters. However, the identity of *Nanomia* spp. remains ambiguous and there may well be variants or sub-species with varying life histories, and varying geographic distributions (Mapstone G. M., pers. comm.).

Nanomia Identification

Nanomia bijuga was the most abundant physonect throughout the present study, yet it is absent from the historic Irish literature and only first identified from plankton samples in 2009 (Baxter et al., 2011a; Baxter et al., 2012b). Baxter et al. (2012b) found it to be widespread at numerous sites along the south and southwest coasts of Ireland, although the abundance was low by comparison with *M.* atlantica. Baxter et al. (2012b) confirmed the identification of *N. bijuga* by matching Irish and Pacific samples using phylogenetic analysis of the 18S rDNA sequence. The 18S sequence is

highly conserved within cnidarians and can be problematic for species level differentiation (Berntson et al., 1999; Cartwright et al., 2008). However, *N. bijuga* is the most intensely sequenced siphonophore (Dunn et al., 2005) and this match is the best available data to date.

The taxonomy and nomenclature of the genus *Nanomia* is confusing and identifying colonies unequivocally using existing descriptions (Agassiz, 1865; Bigelow, 1911; Totton and Bargmann, 1965; Kirkpatrick and Pugh, 1984; Bouillon and Mar, 2004) is difficult. The original descriptions of *N. cara* (Agassiz, 1865; Fewkes, 1888) show a marked similarity to both colonies from Bantry Bay, and the colonies described from Valentia Island during the 1880s (Browne et al., 1898). Certain features, including the small size of the colonies with generally less than 10 nectophores and the tiny larval tentilla (Fewkes, 1888) (Fig. 2.3) have likely led to the continued application of the name *Nanomia cara* when it was not appropriate. Likewise, the suggestion that *N. bijuga* was a warm water congener of *N. cara* (Bigelow, 1911; Kirkpatrick and Pugh, 1984; Mackie et al., 1987) and therefore less likely to occur in the north Atlantic may have biased identification. Identifying physonect siphonophores from net caught preserved samples is often difficult as the morphology of nectophores is altered by mechanical disturbance and the preserving agents used. *In situ* sampling and examination of narcotised intact specimens, and further phylogenetic analysis is needed to consolidate the *Nanomia* nomenclature.

Table 2.1: Historical observations of siphonophores from around the Irish coastline and adjacent seas.

Species	Year	Month	Location	Max No.	Paper
Agalma elegans	1857	Unknown	Dun Laoghaire	unknown	(Jeal and West, 1970)
	1894	Unknown	Isle of Man	'several'	(Browne et al., 1898)
	1905, 1906	June	Valentia Isl.	1	(Delap and Delap, 1905; Jeal and West, 1970)
	1908	June – Sept.	Valentia Isl.	'plentiful'	(Delap, 1924)
	1909	June – July	Valentia Isl.	' a number'	(Delap, 1924)
	1965	June	Galway Bay	Unknown	(Fives, 1971)
	1986	Nov	Killary Harbour	1	(Ryan et al., 1986)
	2009-2011		Bantry Bay, southwest coast	1	(Baxter et al., 2011a; Baxter et al., 2012b)
	2015	July-Sept	South & southwest coast	6	D. Haberlin Unpublished data
Nanomia cara	1895-1898	March-Dec	Valentia Isl.	very abundant	(Browne et al., 1898)
	1905	Unknown	Valentia Isl.	unknown	(Jeal and West, 1970)
	1906	Oct – Nov	Valentia Isl.	'A few'	(Jeal and West, 1970)
	1951	May	Valentia Isl.	'A specimen'	(Totton, 1954)
	1972	Unknown	Galway Bay	2	(Boyd et al., 1973)
	1986	May/June	Killary	1	(Ryan et al., 1986)
Nanomia bijuga	2009-2010	July-Sept	South & west coasts	$3m^{-3}$	(Baxter et al., 2011a; Baxter et al., 2012b)
Forskalia edwardsi†	1856	Unknown	Belfast Lough, Dun Laoghaire	Unknown	(Stephens, 1904; Jeal and West, 1970)
Physophora hydrostatica	1969	May	Blind Harbour, Mayo	1	(Jeal and West, 1970)
Apolemia uvaria	2011	July	Donegal	1	D. Haberlin, Unpublished data
	2012	Aug	Cork	1	D. Haberlin, Unpublished data
Muggiaea atlantica	1896-1898	July-Nov	Valentia Isl.	'abundant'	(Browne et al., 1898)
	1904	May-Nov	Valentia Isl.	Very abundant	(Delap and Delap, 1905)
	1967-1969	Jan-Dec	Galway Bay	2140	(Jeal and West, 1970; Boyd et al., 1973)
	1993-1994	Aug-Dec	Lough Hyne	$10\ m^{-3}$	(Ballard and Myers, 2000)
	2009-2010	June-Feb	Bantry Bay	$250\ m^{-3}$	(Baxter et al., 2011a)
Muggiaea kochii	1971	Sept, Nov	Cork Harbour	1	(Boyd et al., 1973)
*Chelophyes appendiculata**	1841,1844	unknown	Giants' Causeway, Bundoran	'several'	(Hyndman, 1841; Stephens, 1904)
*Sulculeolaria biloba**†	1899-1905	Apr-July	Valentia Isl.	'several'	(Delap and Delap, 1905; Jeal and West, 1970)
Physalia physalis	1835-1970	All seasons	All coasts	very abundant	(Stephens, 1904; Jeal and West, 1970)

†Recorded as *Forskalia contorta* : *Recorded as *Diphya elongata* (Hyndman 1841) and *Diphyes elongata* (Stephens 1904)
*†Recorded as *Galeolaria* sp. (Delap and Delap 1905), was subsequently identified as *S. biloba* (Jeal and West 1970).

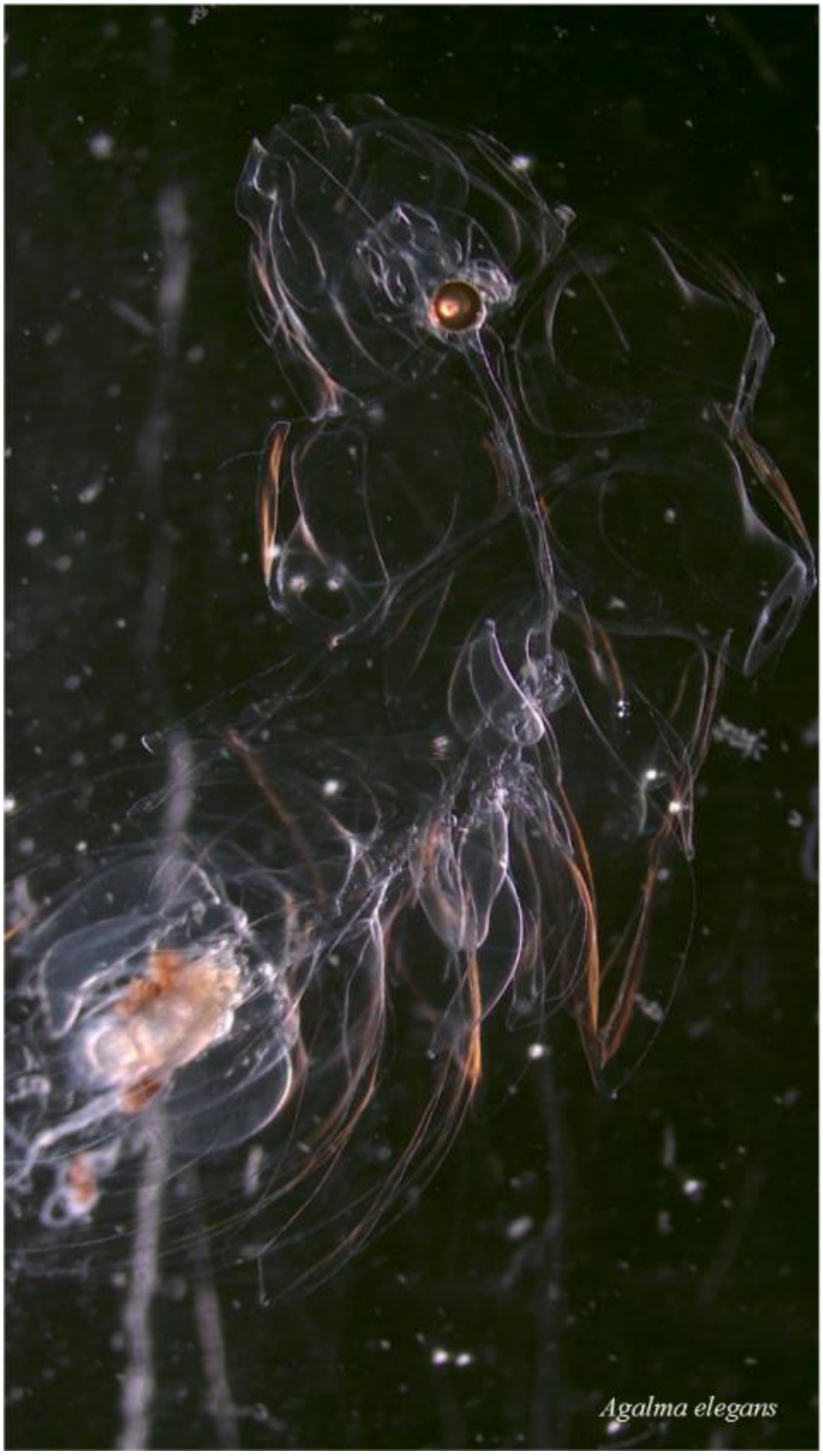
Oceanographic drivers

The presence of siphonophores in coastal waters has been correlated with intrusions of oceanic water in Norway (Båmstedt et al., 1998; Fosså et al., 2003; Hosia and Båmstedt, 2008) and Ireland (Cronin et al., 2004). Furthermore, in the southwest of Ireland and particularly in Bantry Bay, advective processes have been known to cause intrusion of harmful algae into the bay through wind driven exchange with shelf waters (Raine and McMahon, 1998; Raine et al., 2010). While species may be initially advected into a bay, subsequent stratification and front formation can lead to their retention (Graham et al., 2001) and the formation of a seasonally resident population. These intrusions may also be transient and brief, for example, in Bantry Bay in November 2014, athorybiid larvae of *A. elegans* appeared suddenly, reaching more than ten colonies m^{-3} but by the following month they had disappeared. The occurrence of *A. elegans* in Bantry Bay and L4 is consistent with previous studies, which consider the species to be uncommon, oceanic and epipelagic in distribution (Mapstone, 2009). The abundances at both locations are probably indicative of the abundance in oceanic waters lying to the south and southwest of Ireland and England. By inhabiting the epipelagic zone, *A. elegans* would be more likely to be advected into the southern coastlines of Ireland and England by the prevailing westerly and south-westerly winds.

In contrast, *M. atlantica* is a neritic species confined primarily to coastal regions (Mapstone, 2009) and displays a distinct seasonality in both Bantry Bay and the western English Channel. The presence of eudoxid stages demonstrates that it is reproducing in Bantry Bay. However, considering the far higher densities recorded at L4 (Figs. 2.4 & 2.5), this would suggest that the conditions in Bantry Bay are less favourable than those at L4. Nonetheless, in Bantry Bay in 2009 and 2015, *M. atlantica* reached densities (> 150 colonies m^{-3}) which are known to negatively impact on caged salmon (Cronin et al., 2004). The life cycle of *M. atlantica* including sexual and asexual reproduction, is a trait shared with many bloom-forming

scyphozoan jellies (Dawson and Hamner, 2009), and enables *M. atlantica* to reproduce rapidly, particularly when temperature and prey densities are elevated (Carré and Carré, 1991; Blackett et al., 2014). The negligible presence of *M. atlantica* at both Bantry and L4 in 2014 suggests that both areas are linked and that the population in Bantry may be seeded from surrounding neritic waters. Research into harmful algal blooms (HABs) has demonstrated that the Celtic Sea can be a source of HABs along the southwest coast of Ireland (Raine, 2014). A coastal current brings Celtic Sea HABs into the southwest region where local wind patterns can cause an exchange of bay and shelf water, thereby advecting HABs into the Bay (Raine et al., 2010). This would indicate that both the oceanography of the Celtic Sea and the southwest region, coupled with distinct changes in the wind patterns, could have a strong influence over the presence of *M. atlantica* in the southwest.

In summary, plankton samples in Bantry Bay demonstrate low siphonophore diversity, with *Muggiaea atlantica* being the most abundant species. *Muggiaea atlantica* displayed a marked seasonality while the physonect species occurred more sporadically. The occurrence of *M. atlantica* and *Nanomia bijuga* in the Irish southwest and the western English Channel appear broadly similar, and *Nanomia bijuga* is more common than previously thought in both regions. The patterns displayed here are likely driven by the interactions between coastal and oceanic waters which are highly variable from year to year. Under the current continuous increase in sea temperature, it is plausible that *M. atlantica* will eventually overwinter in Irish coastal waters, establishing a resident population, as has happened in the western English Channel (Blackett et al., 2014).



Chapter 3

The influence of a thermohaline front on the gelatinous zooplankton community of a shelf sea

This chapter has been submitted for peer-review publication: Haberlin, D., Raine, R., McAllen, R. and Doyle, T.K., 2018, The influence of a thermohaline front on the gelatinous zooplankton community of a shelf sea. Submitted to *Limnology and Oceanography*

Abstract

Thermohaline fronts are a ubiquitous phenomenon across continental shelf seas that are known to enhance primary productivity and aggregate biomass. The enhanced productivity at fronts provides favourable conditions for higher trophic levels, however, the influence on gelatinous zooplankton is poorly understood. Sampling carried out during July 2015 found two distinct gelatinous communities across the Celtic Sea Front; an Irish Sea community in the cooler mixed water which was largely composed of neritic taxa, and a Celtic Sea community in the warmer stratified water which contained a mixed neritic and oceanic community. The gelatinous abundance (656 indiv. m^{-3}) and biomass (2085 mg C 1000 m^{-3}) was higher in the Celtic Sea and was dominated by *Aglantha digitale*, *Lizzia blondina* and *Nanomia bijuga*. The mean gelatinous contribution to the total zooplankton biomass was 4 - 6%, reaching a maximum of 16% in the Celtic Sea. Physonect siphonophores were surprisingly widespread, contributing >25% of the gelatinous biomass, suggesting their ecological role is underestimated. Multivariate analysis of the zooplankton biomass indicated that water column structure, coupled to the underlying topography, was the key driver of variation in the zooplankton community. There was no evidence that the Celtic Sea front enhanced zooplankton biomass at the front, however, it is likely that the front influences the community and biomass through broader scale advective processes.

Introduction

A defining characteristic of virtually all planktonic taxa is their patchy temporal and spatial distribution in pelagic and neritic ecosystems. Spatial patchiness is influenced both by physical oceanographic processes and the inherent biological and behavioural adaptations specific to each species (Folt and Burns, 1999). Since the 1970s, frontal systems, which encompass a range of oceanographic processes, have been identified as regions of enhanced biological activity (Pingree et al., 1979; Owen, 1981; Le Fèvre, 1987; Olson et al., 1994). The advent of remote satellite sensing has revealed that frontal systems are ubiquitous across marine ecosystems, ranging in size from 10s to 100s of km (Belkin et al., 2009; McGillicuddy, 2016). Ocean colour sensing has explicitly linked frontal systems and primary productivity (McGillicuddy, 2016) and a growing body of literature records enhanced abundance of marine vertebrates at frontal systems (Owen, 1981; Bakun, 2006; Scales et al., 2014b; Sousa et al., 2016). However, how frontal systems influence the abundance, diversity and advection of zooplankton is less clear and this is particularly the case for gelatinous zooplankton (Purcell, 2009).

Gelatinous zooplankton are an important and at times dominant component of neritic ecosystems (Boero et al., 2008). The variability in reproductive strategies, including metagenic, hermaphroditic and multiple intra-annual generations allows many gelatinous taxa to reproduce rapidly or ‘bloom’ under favourable conditions (Purcell et al., 2007; Boero et al., 2008; Hamner and Dawson, 2009). The majority of gelatinous zooplankton are predators, consuming a wide variety of meso-zooplankton prey (Purcell et al., 2007), and therefore a frontal system which increases meso-zooplanktonic prey numbers provides a favourable environment for gelatinous

predators (Shiganova, 1998; Purcell, 2005; Blackett et al., 2015). The response of individual gelatinous species to this environment will be driven by inherent reproductive traits; some holoplanktonic species with short generation times and high fecundity are particularly pro-adapted to exploit stable frontal systems with sustained high prey concentrations, leading to a true bloom (Graham et al., 2001; Hamner and Dawson, 2009). Species with longer generation times and a polyp stage, i.e. large scyphomedusae, are more likely to be aggregated by advective processes (Graham et al., 2001).

Much of the literature on the distribution and abundance of gelatinous zooplankton along fronts pertains to large scyphozoan species (Graham et al., 2001; Brodeur et al., 2008; Sabates et al., 2010). In contrast, quantitative data on smaller gelatinous zooplankton are sparse. Across all taxa, available evidence indicates that along large scale oceanic fronts, the front often acts as a boundary between distinct communities (Russell, 1953; Pages and Schnack-Schiel, 1996; Pages et al., 1996; Graham et al., 2001; Hosia et al., 2008). Mesoscale seasonal fronts in coastal seas coincide with partitioning of large scyphomedusae in NW Europe (Doyle et al., 2007b; Bastian et al., 2011) and aggregations of scyphomedusae have been recorded along frontal systems associated with islands, river plumes and tidal forces (Graham et al., 2001; Colombo et al., 2003). Frontal systems in upwelling regions are also associated with high abundance of scyphomedusae (Sparks et al., 2001; Suchman and Brodeur, 2005) and hydromedusae, particularly siphonophores (Pagès and Gili, 1992; Pagès et al., 1992; Pages et al., 2001). Yet, other studies on shelf fronts have found no enhanced hydromedusae abundance along the frontal system (Guerrero et al., 2016).

The Celtic Sea, located to the south of Ireland on the broad northwest European continental shelf, has a strong oceanic influence and experiences profound seasonal

changes. Most of the Celtic Sea becomes thermally stratified in spring and summer (Cooper, 1967). Tidal influences produce a marked tidal front in summer along the boundary between stratified Celtic Sea water and the tidally mixed waters of the Irish Sea, a front referred to as the Celtic Sea Front (CSF) (Pingree and Griffiths, 1978; Le Fèvre, 1987). The increasing effect of the tide close to the coast around the Celtic Sea produces a bottom density front which drives a strong but narrow baroclinic anti-clockwise flow along the north coast of southwest England, continuing along the Celtic Sea Front and then westwards along the south coast of Ireland, where the flow continues up the west coast of Ireland (Brown et al., 2003; Fernand et al., 2006).

Tidal fronts, including the Celtic Sea Front, can be associated with elevated levels of phytoplankton (Holligan, 1981). In summer, this frontal system can promote Harmful Algal Blooms (HABs) (Raine, 2014) which are subsequently carried along the southern Irish coast towards the bays of southwest Ireland (Farrell et al., 2012) where they occasionally have a detrimental impact on the shellfish industry (Raine et al., 1990; Raine and McMahon, 1998; Raine, 2014). Bays along this coastline also hold important salmon aquaculture farms, which have also been negatively impacted by harmful jellyfish species, predominantly the scyphozoan *Pelagia noctiluca* and the siphonophore *Muggiaea atlantica* (Baxter et al., 2011a). The fact that there is evidence of a connection between *M. atlantica* populations found in the English Channel and the west coast of Ireland (Haberlin et al., 2016), it is possible that *M. atlantica* may be driven by the same process which advect HABs into the region. Studies in the region indicate the Celtic Sea Front separates distinct crustacean zooplankton communities (McGinty et al., 2014), however, no study to date has investigated the role of the Celtic Sea Front in relation to gelatinous zooplankton distribution. Therefore, the aim of this study was to investigate the distribution, abundance and biomass of gelatinous

zooplankton across the seasonal Celtic Sea Front, to determine if the front aggregated gelatinous zooplankton and to investigate if *Muggiaea atlantica* are advected along the front.

Material and Methods

Study site

The Celtic Sea Front (CSF) is located across St. George's Channel between the Welsh and Irish coasts (Fig. 3.1A). The front itself forms during April/May when solar radiation begins to heat the Celtic Sea and stratification occurs (Simpson, 1981). A characteristic of this front is a large meander which extends southward into the Celtic Sea and is readily apparent in satellite Sea Surface Temperature (SST) images (Fig. 3.1B). The bathymetry ranges from *ca.* 40 m to 110 m, the deepest region being in the centre of St. George's Channel, coincident with and driving the overlying meander (Brown et al., 2003).

Samples were collected between the 13th and 17th July 2015 from the *R.V. Prince Madog*, at which time the front had become well established (Fig. 3.1B). Five transects were carried out in the study area, with Transect 1 (T1) being predominantly coastal transect 50 km long, T2 being the longest transect running 150 km south east from Ireland. Transect 3 (T3) began at the Welsh coast moving directly east over the Celtic Deep stopping on the central axis of St. George's Channel. From this point, Transect 4 (T4) started and proceeded north into the Irish Sea, stopping approximately 6 km north of the CSF. From this point Transect 5 (T5) started, proceeding southwest through the Irish Sea and crossing back into the Celtic Sea. In total, 49 zooplankton samples were taken using a 1-metre diameter, 270 µm mesh plankton net with a flowmeter attached. The cod end was emptied into a small aquarium in order to count ctenophores, particularly *Bolinopsis infundibulum* O. F. Müller 1776, which does not preserve well. Upon completing the ctenophore count, the sample was immediately fixed in 4% buffered formalin and filtered (50 µm) sea water solution.

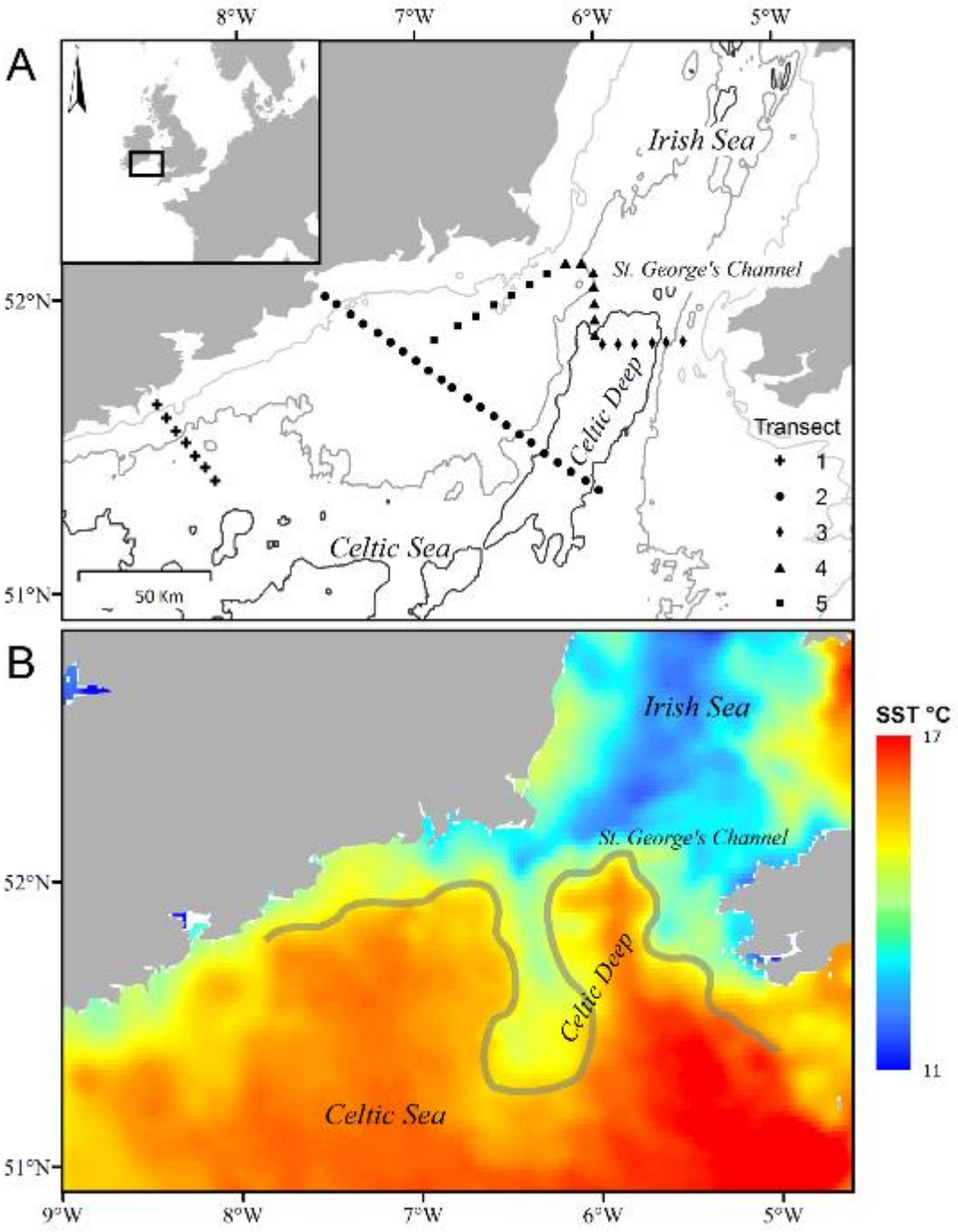


Figure 3.1: Study site in the north eastern Celtic Sea with A; major geographic features and contours (50 m, 80 m and 110 m) displayed and B; mean sea surface temperature for mid July 2015 and the SST front edge (thick grey line) which marks the Celtic Sea Front (CSF).

Zooplankton analysis

Samples were analysed under laboratory conditions using a Zeiss dark-field stereomicroscope (Stemi 2000), quantifying the dominant taxa and identifying all gelatinous zooplankton and fish to the lowest taxonomic level. All copepods were grouped as a single taxon, and rarer taxa such as phoronid larvae were noted as present or absent. Quantitative data were gathered from subsamples using a Folsom splitter and entire samples were analysed for larger taxa, for example the larger hydromedusae like *Leuckartiara octona* Fleming 1823. Biomass data and biometric conversions for dry mass (DM) and carbon content (C) were sourced from existing literature (Supporting Information Table. S3.2). Where possible biometric equations for the specific species were used and applied to the mean sizes found. Where this was not possible relationships for closely related or morphologically similar species were used: equations for *Clytia hemisphaerica*, Linnaeus 1767, were used to determine *Laodicea undulata*, Forbes & Goodsir 1853, biomass. For *Agalma elegans*, Sars 1846, (N = 11) and *Nanomia bijuga*, Delle Chiaje 1844, (N = 1), samples collected, opportunistically, by hand (snorkelling) along the southern Irish coastline during July and August 2015, were used to get the biovolume per colony and then converted in the same way as the above.

Temperature and salinity analysis

A conductivity, temperature & depth (CTD) (Seabird, SBE 911) profile was taken at each station (N = 98), profiling from the surface to approximately 10 m above the seabed. The parameters recorded were, density (kg m^{-3}), salinity (PSU), temperature (°C) and chlorophyll-*a* fluorescence (µgl $^{-1}$). Each profile was analysed using the

'Oce' package (Kelley and Richards, 2017) for oceanographic data analysis implemented in R (R Core Team, 2017). The surface readings (0-1 m) were removed from each profile, to exclude any diurnal heating effect. Each profile was then clipped, retaining only the downcast, and interpolated to 1 m intervals. The processed profiles were then analysed to extract the depth of maximum cline intensity according to the methods used by Reygondeau and Beaugrand (2010). This method defines the depth of the cline as the depth of the maximum gradient over 5 m rolling mean values. The calculated depths were checked against the raw CTD profiles and there was good agreement, with the top of the cline picked from profiles. Data for the top and bottom 5 m of each CTD cast were averaged and used as the top/bottom parameter for subsequent analysis. This had little impact on bottom values, but would smooth out any diel variation at the surface. In addition, the maximum fluorescence was extracted, as this was not always at the surface. Finally, a measure of water column stability, the Brunt–Väisälä frequency or buoyancy frequency was calculated for each cast.

Statistical analysis

The zooplankton abundance (individuals m^{-3}) and carbon content (mg C 1000 m^{-3}) were compiled into station by species matrix. The matrices were then square root transformed twice to down weight the dominant taxa and then transformed again into (non-parametric) Bray–Curtiss dissimilarity matrices. From these matrices, non-metric multidimensional scaled ordination (MDS) and cluster analysis were used to identify distinct communities (Clarke and Warwick, 2001). Some species were dropped due to rare occurrence, e.g. *Euphysa aurata,* Forbes 1848 was recorded once across the entire survey, however, many which contributed <1% across the dataset were retained, as dropping them would discard valuable information about changes in

the zooplankton community (Poos and Jackson, 2012). For example, using the 1% criteria of Clarke and Warwick (2001) would have excluded *Muggiaea atlantica* Cunnigham 1892, a species of interest in this study. The different MDS ordinations, based on abundance, dry mass, and carbon biomass, were compared using Procrustes analysis, which rotates one ordination to achieve maximum similarity with a second ordination, by minimizing the sum of squared differences. The ENVFIT and BIO-ENV functions were used to investigate which environmental parameters were most influential. ENVFIT fits environmental parameters onto a community ordination, and BIO-ENV finds the best subset of environmental parameters, so that the Euclidean distances of scaled environmental parameters have the maximum (rank) correlation with community dissimilarities. The ANOSIM (Clarke, 1993) test was used to determine whether the clusters were significant and ADONIS (Permutational Multivariate Analysis of Variance) (Anderson, 2001) was also used to determine which environmental variables were most significant in explaining the clusters. All community and multivariate analysis was carried out using the 'Vegan' package (Oksanen et al., 2017) in R. Differences between clusters for individual species were tested using single factor ANOVA, or a Kruskal Wallis test where the parametric model was a poor fit. Potential relationships between individual environmental variables and individual taxa were investigated using Pearson's correlation. All mean values are presented with standard deviation unless stated otherwise.

Front edge detection

Analysis was carried out using ArcGIS. The open source package, Marine Geospatial Ecology Tools (Roberts et al., 2010) was used to implement a single image edge detection algorithm (Cayula and Cornillon, 1992), which can detect the SST fronts in raster images. The raster image was created from ODYSSEA North West Shelf Sea

Surface Temperature data, downloaded from the Copernicus data portal. This is a processed gap free data-set on a 0.02° x 0.02° resolution grid, created by the Group for High Resolution Sea Surface Temperature (GHRSST) using combined satellite and *in situ* observations (www.copernicus.eu.org).

Results

Oceanographic data

The CTD profiles clearly indicated the changing vertical structure of the water column, particularly along T2, T3, T4 where parts of the Celtic Deep were sampled (Figs. 3.2 - 3.5). The water column over the Celtic Deep was intensely stratified with the strongest physical gradients recorded along T2 and T3. The shallow stations during T1 and T3, highlight the relatively narrow corridor (*ca.* 10 km) of tidally mixed water, characteristic of coastal water in the region (Brown et al. 2003). T1 and T2 both started within *ca.* 4 km of the coastline and T1 is mixed within 10-15 km of the coastline and weakly stratified thereafter. In contrast, T2 appeared to retain a pycnocline approaching the near coast stations. There was also evidence of some mixing between 90 to 110 km along T2 (at 80 m contour) and thereafter the water column stratified again over the Celtic Deep (Figs. 3.2 – 3.5). Plots of temperature, salinity and fluorescence conformed to the same general pattern (See supplementary material, Figs. S3.1 – S3.3). The highest fluorescence values were recorded along T1 and T2 (Celtic Sea) at *ca.* 30 m depth (Fig. 3.5) and the depth of the sub-surface chlorophyll maximum was positively correlated with the pycnocline ($r = 0.97$, $p < 0.001$). The highest surface fluorescence was recorded at stations in T1, T3, T4 and T5 (east of the SST front), the lowest values were all recorded during T2 and remained low within the mixed water evident between the 90 to 110 km mark (Fig. 3.5). Bottom density fronts were evident along transects T2 – T5, indicative of along front flows (Fig. 3.2).

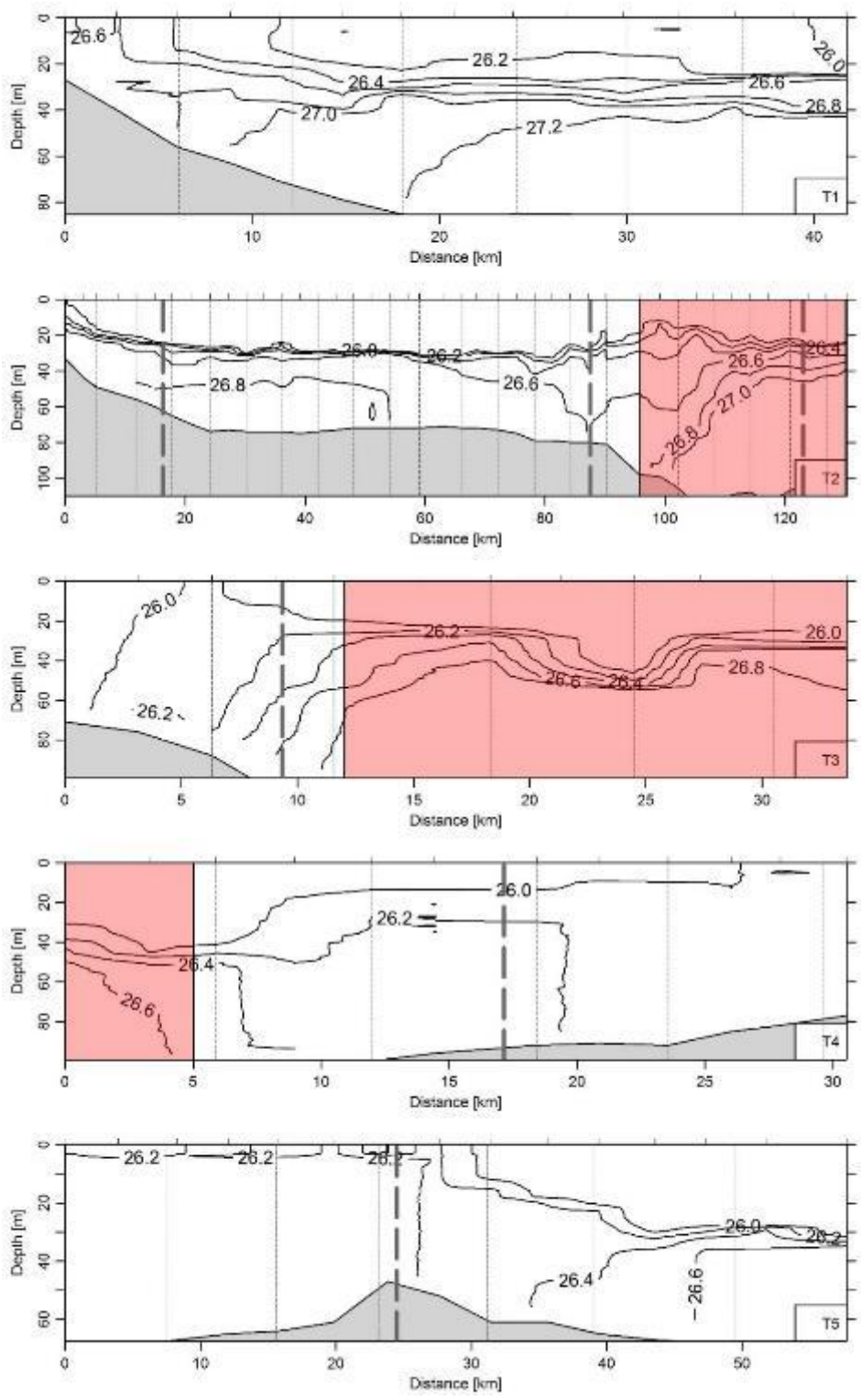


Figure 3.2: Density (kg m^{-3}) contours for the 5 transects, T1 – T5. CTD stations (*ca.* every 3 km) are marked along the top x axis. Zooplankton sample stations (*ca.* every 6 km) are indicated by vertical dotted lines. The heavy dashed line represents the position of the Celtic Sea Front (CSF). Note, plots are scaled differently on the x axis. The red shading marks the Celtic Deep boundary.

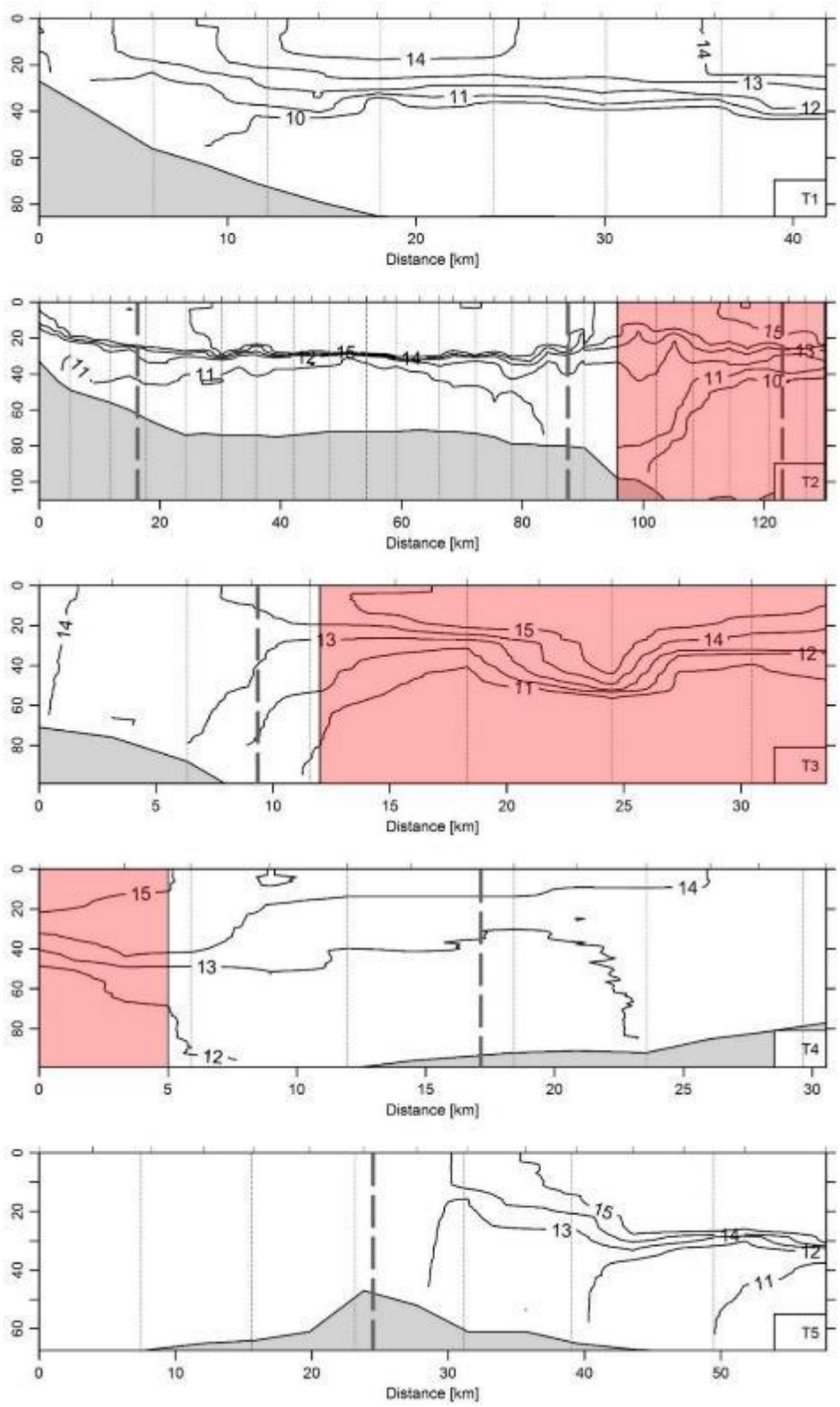


Figure 3.3. Temperature (°C) contours for the 5 transects, T1 – T5. CTD stations (*ca.* every 3 km) are marked along the top x axis. Zooplankton sample stations (*ca.* every 6 km) are indicated by vertical dotted lines. The heavy dashed line represents the position of the Celtic Sea Front (CSF). Note, plots are scaled differently on the x axis. The red shading marks the Celtic Deep boundary.

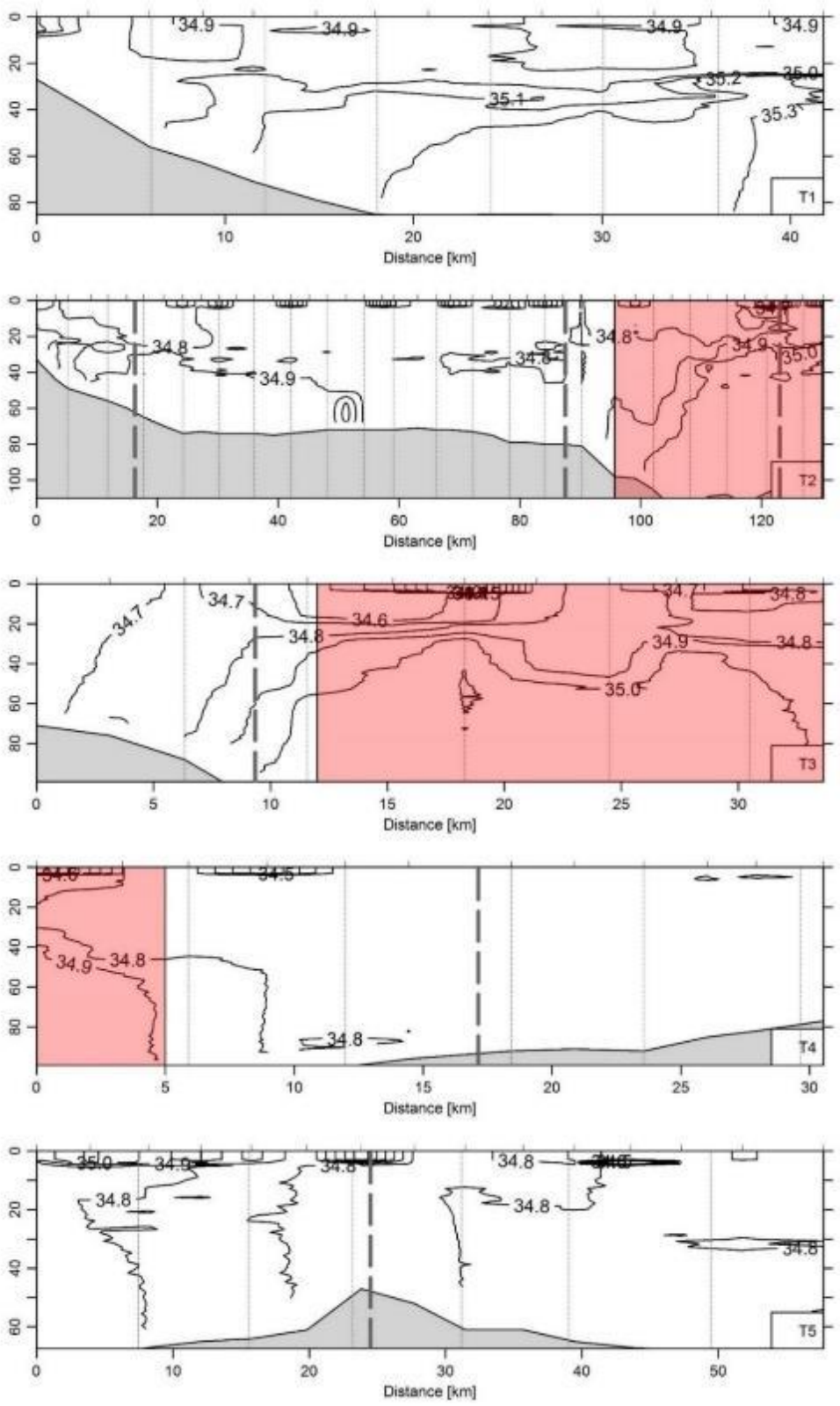


Figure 3.4. Salinity (PSU) contours for the 5 transects, T1 – T5. CTD stations (*ca.* every 3 km) are marked along the top x axis. Zooplankton sample stations (*ca.* every 6 km) are indicated by vertical dotted lines. The heavy dashed line represents the position of the Celtic Sea Front (CSF). Note, plots are scaled differently on the x axis. The red shading marks the Celtic Deep boundary.

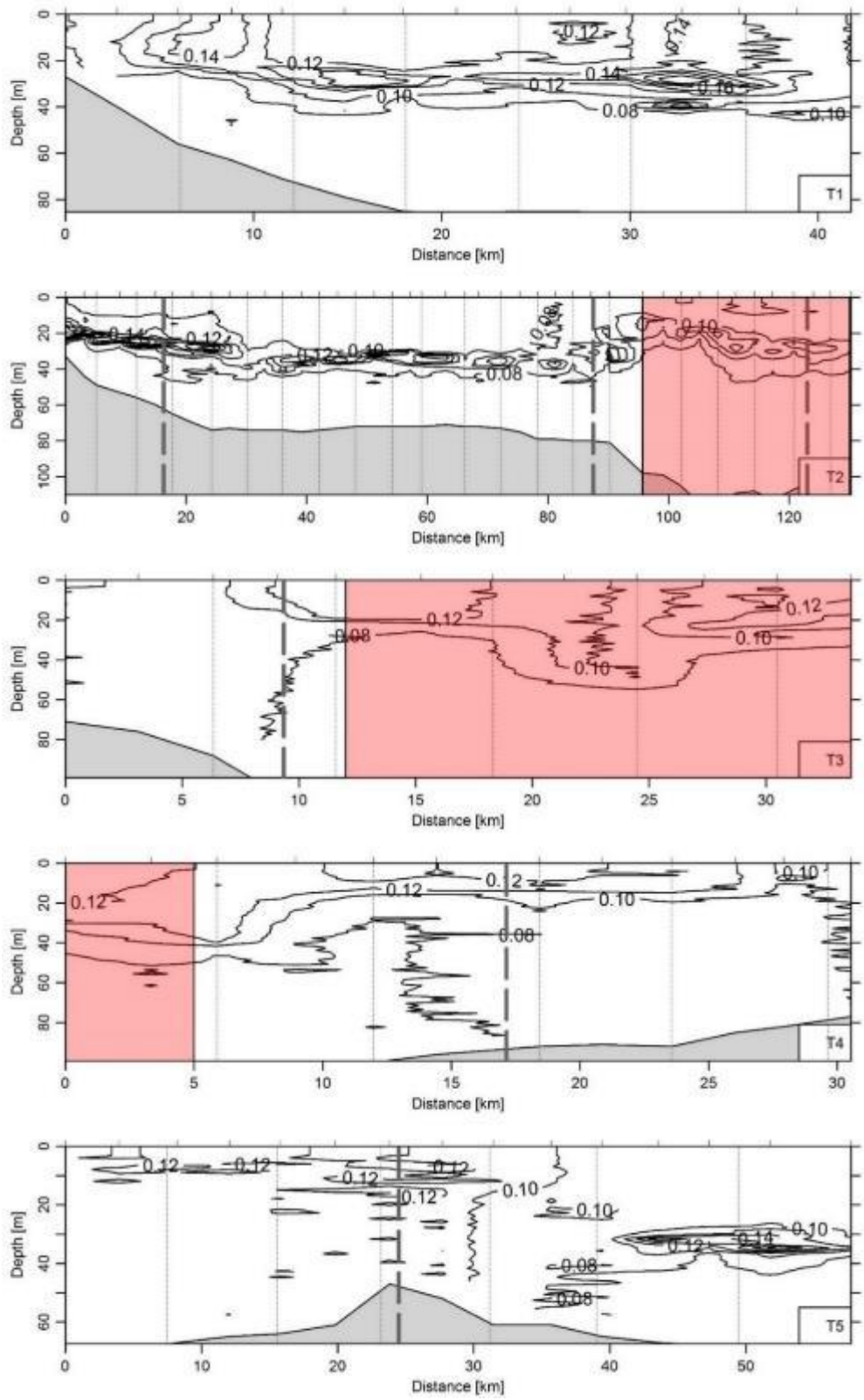


Figure 3.5. Chlorophyll a fluorescence (µgl $^{-1}$) contours for the 5 transects, T1 – T5. CTD stations (*ca.* every 3 km) are marked along the top x axis. Zooplankton sample stations (*ca.* every 6 km) are indicated by vertical dotted lines. The heavy dashed line represents the position of the Celtic Sea Front (CSF). Note, plots are scaled differently on the x axis. The red shading marks the Celtic Deep boundary.

Zooplankton data

In total 74 taxa were identified from the 49 samples collected (Appendix A, Table. S3.1). The mean number of taxa across all stations was 24 ± 5.4. Included were, 17 hydromedusa species, three ctenophore species and a single scyphozoan species. Cluster and MDS analysis of zooplankton abundance (indiv.m^{-3}) identified three distinct and significantly different communities (ANOSIM, $R = 0.88$, $p < 0.001$) (Fig. 3.6A): 1) a Celtic Sea community in stations to the west of the cooler mixed water that intrudes into the Celtic Sea, with one station lying east of the SST front; 2) a Celtic Deep community which included only stations beyond the 100 m contour, bar one, and 3) an Irish Sea community which included all the stations with intense vertical mixing and some stations within the Celtic Deep (Fig. 3.6B).

Several hydromedusae were widespread across the survey area, with *Aglantha digitale,* Müller 1776, *Clytia hemisphaerica, Agalma elegans*, *Nanomia bijuga, Lizzia blondina*, Forbes, 1848, and *Leuckartiara octona* all recorded at >60% of stations. *A. digitale* and *L. blondina* were by an order of magnitude, the dominant hydromedusae throughout the survey area reaching a mean of 200 ± 247 m^{-3} and 88 ± 159 m^{-3} respectively, and present at 80% and 75% of stations respectively. Of the ctenophores, *Pleurobrachia pileus*, Müller 1776, was the most widespread, present at 94% of stations, with a mean abundance of 0.25 ± 0.23 m^{-3}. Other gelatinous zooplankton common across the survey area were the pelagic polychaete *Tomopteris* sp. (present at 82% of stations), appendicularians (present at 98% of stations), *Clione* sp. molluscs (present at 53% of stations) and *Sagitta elegans,* Verrill, 1873, (present at 90% of stations). *Tomopteris* sp. was particularly abundant in Celtic Sea water reaching a maximum of 26.7 m^{-3} at station 16 (T2) with a mean abundance of 4.8 ± 6.20 m^{-3} across all stations.

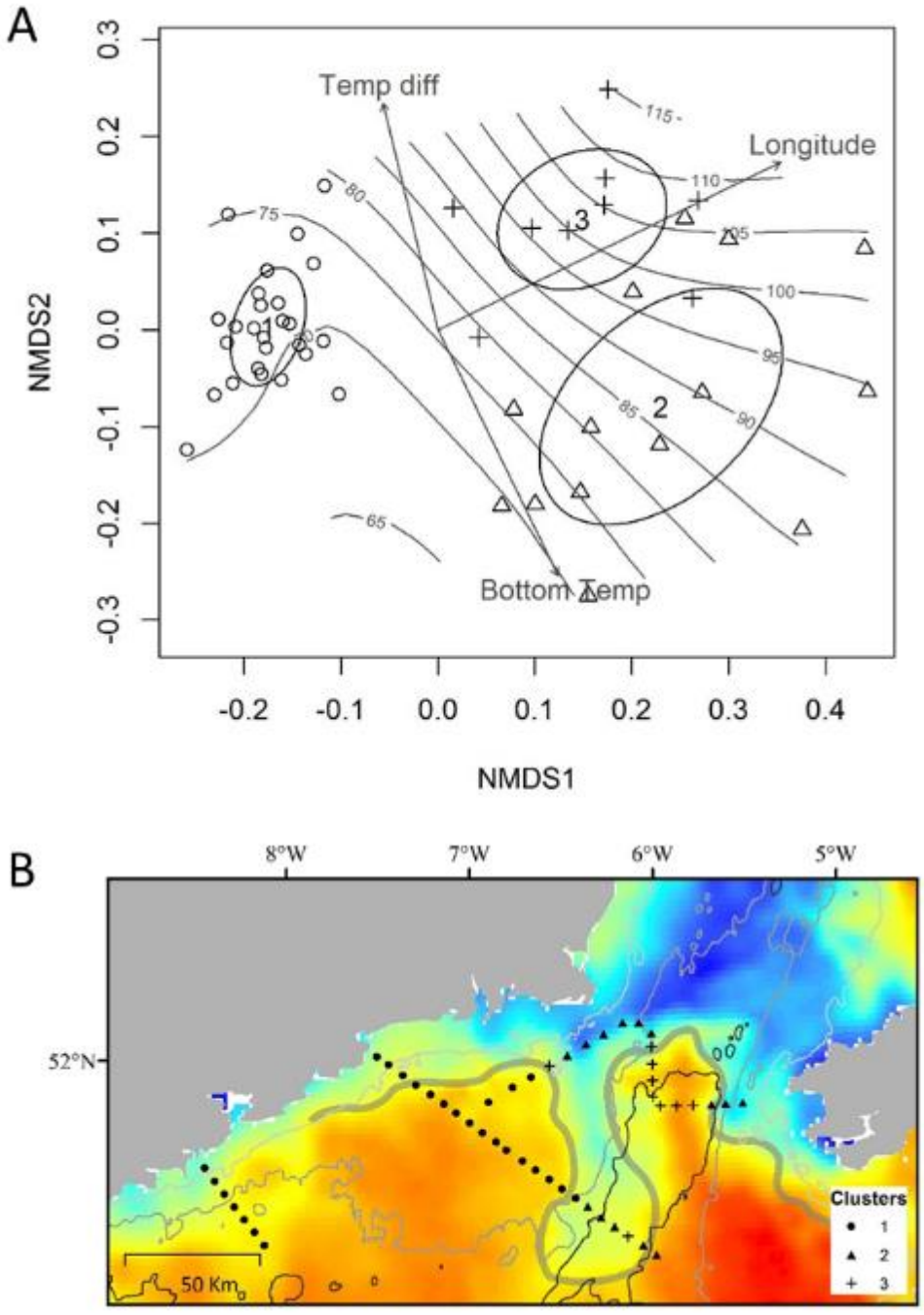


Figure 3.6: A; Non-metric multidimensional scaled ordination (Stress = 0.13) of zooplankton abundance, using Bray-Curtiss dissimilarity matrix (indiv. m^{-3}), with stations symbolised according to hierarchical clustering, identifying three communities. Influential environmental parameters are indicated by a fitted surface, for bathymetry, and vectors for temperature difference, bottom temperature and longitude. B; Map of survey stations coded by the hierarchical clustering, i.e. as in the NMDS plot.

Clione sp. was also abundant throughout Celtic Sea water reaching a maximum of 33.1 m^{-3} and a mean of 3.4 ± 7.0 m^{-3}. Non-gelatinous zooplankton were dominated by copepods, Limacinidae molluscs, decapod larvae and polychaete larvae from the families Poecilochaetidae, Magelonidae, polynoidae and Sabellariidae (Appendix A, Table. S3.1). The decapod larvae including both zoea and megalops stages, were most abundant in Celtic Deep and Irish Sea stations reaching mean abundances of 0.27 ± 1.03 and 12.3 ± 19.02 indiv. m^{-3} respectively. Twenty-five species of fish larvae were identified in total. *Arnoglossus laterna*, Walbaum, 1792, *Callionymus* spp., *Sardina pilchardus*, Walbaum, 1792, *Scomber scombrus* Linnaeus, 1758, and Gobidae were the most widespread, recorded at *ca.* 30% of stations. Gobidae larvae were the most widespread, recorded at 63% of stations (Table S3.1). The highest abundance of fish larvae was found within shallow (< 80 m) Celtic Sea region, and they were largely absent from the deeper stations. Phytoplankton from the *Ceratium* genus was abundant at stations near the southern coastline, reaching > 83,000 cells m^{-3} during T1. Its occurrence appeared to be largely restricted to shallower (< 80 m depth) mixed water and it was absent from deeper stratified water (> 80 m depth). The presence of *Ceratium* was considered noteworthy because of the high density, however, it was not included in any subsequent analysis.

Analysis of dissimilarities between the communities (SIMPER) showed that the shift in community structure was primarily driven by *Limacina* sp., *A. digitale, P. elegans,* Appendicularia and copepods (Table 3.1). The dissimilarity between the Celtic Sea and Irish Sea community was driven by *Limacina* sp. species (44%), copepods (25.5%) and *A. digitale* (15%). The dissimilarity between Celtic Sea and Celtic Deep was also driven by *Limacina sp.* species (42%) and copepods (30%) and

A. digitale (15%). The dissimilarity between the Celtic Deep and Irish Sea community was dominated by copepods (75%), Appendicularia (10%) and *L. blondina* (8%).

Table 3.1: Mean abundance ± SD (indiv. m^{-3}) of the zooplankton taxa which drove the dissimilarity between the three different communities according to the SIMPER analysis, and the results of ANOVA tests for individual taxa showing where between group differences in abundance were significant.

Taxa	Abundance (indiv. m^{-3})			ANOVA
	Celtic Sea	Celtic Deep	Irish Sea	
Copepoda	839 ± 885	820 ± 950	720 ± 400	$F_{2,46}$ = 0.106, p = >0.1
Decapoda	12.5 ± 9.7	0.5 ± 0.8	20.5 ± 33.2	$F_{2,46}$ = 2.995, p = >0.05
Limacina sp.	1258 ± 895	9.6 ± 21.7	4.13 ± 4.7	$F_{2,46}$ = 21.97, p = <0.005
Clione sp.	6.50 ± 8.59	0 ± 0	0.180 ± 0.063	$F_{2,46}$ = 6.327, p = <0.001
Tomopteris sp.	8.0 ± 6.9	1.7 ± 2.4	0.7 ± 1.2	$F_{2,46}$ = 10.6, p = <0.001
Polychaete larvae	19.40 ± 14.03	1.4 ± 2.2	7.9 ± 9.3	$F_{2,46}$ = 10, p = <0.001
Ichthyoplankton	1.3 ± 1.4	0.1 ± 0.2	0.44 ± 0.63	$F_{2,46}$ = 5.6, p = <0.005
Echinodermata	26.1 ± 30.7	26.80 ± 17.35	6.92 ± 14.20	$F_{2,46}$ = 2.94, p = >0.05
Appendicularia	104.6 ± 116.3	91.1 ± 93.1	24.5 ± 24.2	$F_{2,46}$ = 3.32, p = <0.05
Sagitta elegans	16.2 ± 12.6	2.8 ± 4.0	1.2 ± 1.9	$F_{2,46}$ = 14.02, p = <0.001
Ctenophora	0.22 ± 0.26	0.32 ± 0.18	0.34 ± 0.19	$F_{2,46}$ = 1.35, p = >0.1
Aglantha digitale	375 ± 221	1.95 ± 4.77	0.11 ± 0.22	$F_{2,46}$ = 32.1, p = <0.001
Lizzia blondina	155 ± 195	30 ± 37	0.2 ± 0.9	$F_{2,46}$ = 6.05, p = <0.005
Clytia hemisphaerica	0.04 ± 0.10	5.53 ± 3.84	7.06 ± 6.96	$F_{2,46}$ = 15.85, p = <0.001
Agalma elegans	0.2 ± 0.2	0.18 ± 0.10	0.03 ± 0.04	$F_{2,46}$ = 5.58, p = <0.01
Muggiaea atlantica	0.0015 ± 0.0080	2.27 ± 2.52	0.23 ± 0.57	$F_{2,46}$ = 41.95, p = <0.001
Mitrocomella polydiademata	0.0017 ± 0.0060	0.08 ± 0.17	0.010 ± 0.025	$F_{2,46}$ = 4.87, p = <0.05
Leuckartiara octona	0.08 ± 0.11	0.050 ± 0.013	0.008 ± 0.013	$F_{2,46}$ = 4.87, p = <0.05
Total Cnidaria	656 ± 368	134 ± 89	35 ± 25	$F_{2,46}$ = 27.86, p = <0.001
Total zooplankton abundance	2829 ± 1181	994 ± 1003	802 ± 445	$F_{2,46}$ = 23.6, p = <0.001
No. Taxa	27 ± 4	19 ± 3	21 ± 5	$F_{2,46}$ = 21.75, p < 0.001
Shannon index	1.30 ± 0.31	0.66 ± 0.40	0.5 ± 0.29	$F_{2,46}$ = >30, p < 0.001

Permutational analysis within the SIMPER routine indicated where a dissimilarity is significant and copepods were only significantly different between the Irish Sea and Celtic Deep (Table 3.1). Testing individual taxa for differences gave results which in the main agreed with the SIMPER analysis, however, some taxa e.g. copepods and ctenophores, were shown to not change significantly between the 3 communities (Table 3.1). The ENVFIT function indicated that numerous environmental parameters had a significant correlation with the zooplankton abundance NMDS ordination (p <0.05), except for halocline depth and intensity, surface fluorescence, max fluorescence, vertical change in fluorescence and bottom salinity. Many of these parameters were collinear and the majority were collinear with bathymetry. The subset of environmental parameters with the best correlation, with the zooplankton abundance NMDS ordination (using BIOENV), included only the bottom temperature and bathymetry (Mantel, $R = 0.52$, $p < 0.001$).

Zooplankton biomass

NMDS and cluster analysis of the zooplankton biomass (mg C 1000 m^{-3}) (Fig. 3.7) produced a slightly different clustering to that produced by the abundance analysis (Fig. 3.6A). The Celtic Sea community was retained as previously, six stations over the Celtic Deep, previously clustered within the Irish Sea community, shifted into the Celtic Deep community. It was evident that the Celtic Deep and Irish Sea stations rotated more when comparing both ordinations, however, a procrustes comparison of the zooplankton abundance and biomass NMDS ordinations demonstrated a positive and significant correlation ($r = 0.96$, $p = 0.001$), suggesting that minor rotation was enough for some stations to switch between communities. The changes between Celtic Sea water, Celtic Deep water and Irish Sea water communities were significant (ANOSIM, $r = 0.85$, $p < 0.001$) and driven primarily by copepods and *A. digitale*.

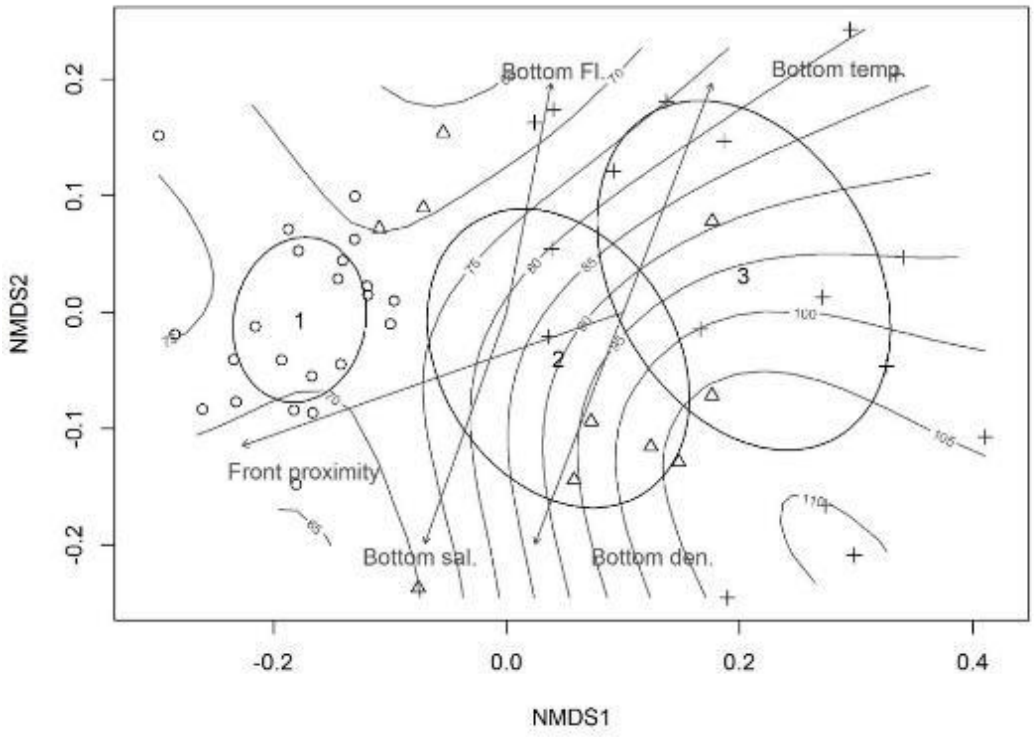


Figure 3.7: NMDS ordination (Stress = 0.16) of total zooplankton biomass (mg C 1000 m^{-3}) with the most significant variables displayed. Depth is displayed as a fitted surface and the remaining parameters are displayed as vectors with the direction and length indicating the direction and magnitude of influence. The stations are coded by symbols according to the cluster analysis, open circles are Celtic Sea community, open triangles are Irish Sea community and crosses are Celtic Deep community.

Analysis of dissimilarities between the communities (SIMPER) showed that the shift in community structure was driven by copepods, decapod larvae, *Clione* sp., *Tomopteris* sp. and *S. elegans*. The dissimilarity between the Celtic Sea and Irish Sea community was driven by copepods (68%), *Clione* sp. (8%), decapod larvae (8%) and *Tomopteris* sp. (5%), however, only decapod larvae, *A. digitale* (0.02%) and *Limacina* sp. (<0.001%) were indicated as significant (p = <0.001). The dissimilarity between Celtic Sea and Celtic Deep was also driven by copepods (72%), *Clione* sp. (7%),

Tomopteris (5%) and decapod larvae (5%). Of those taxa, *Clione* sp. and *Tomopteris* were significant (p = <0.001), as were *S. elegans, B. infundibulum, A. digitale, Beroe* sp., *M. atlantica, C. hemisphaerica,* polychaete larvae and *Limacina* sp. (Figs. 3.8 & 3.9). The dissimilarity between the Irish Sea and Celtic Deep was driven by copepods (82%) and decapod larvae (10%), of which, decapod larvae were significant. In addition, *M. atlantica, C. hemisphaerica,* polychaete larvae, ichthyoplankton, *Sagitta setosa* and *Lepeophtheirus* sp. were significant. The mean biomass in the Celtic Sea (55054 ± 45390 mg C 1000 m^{-3}) was greater than the Celtic Deep (45855 ± 42563 mg C 1000 m^{-3}) and the Irish Sea (41428 ± 24885 mg C 1000 m^{-3}), but the differences were not significant (ANOVA, $F_{2,46}$ = 0.97, p > 0.05). Analysis of the community biomass with the ENVFIT and BIOENV gave virtually identical results to the previous analysis of abundance, achieving the best correlation between the environmental and community NMDS ordinations by retaining only bottom temperature (i.e. 50 m depth) and bathymetry (Mantel, r = 0.51, p < 0.001).

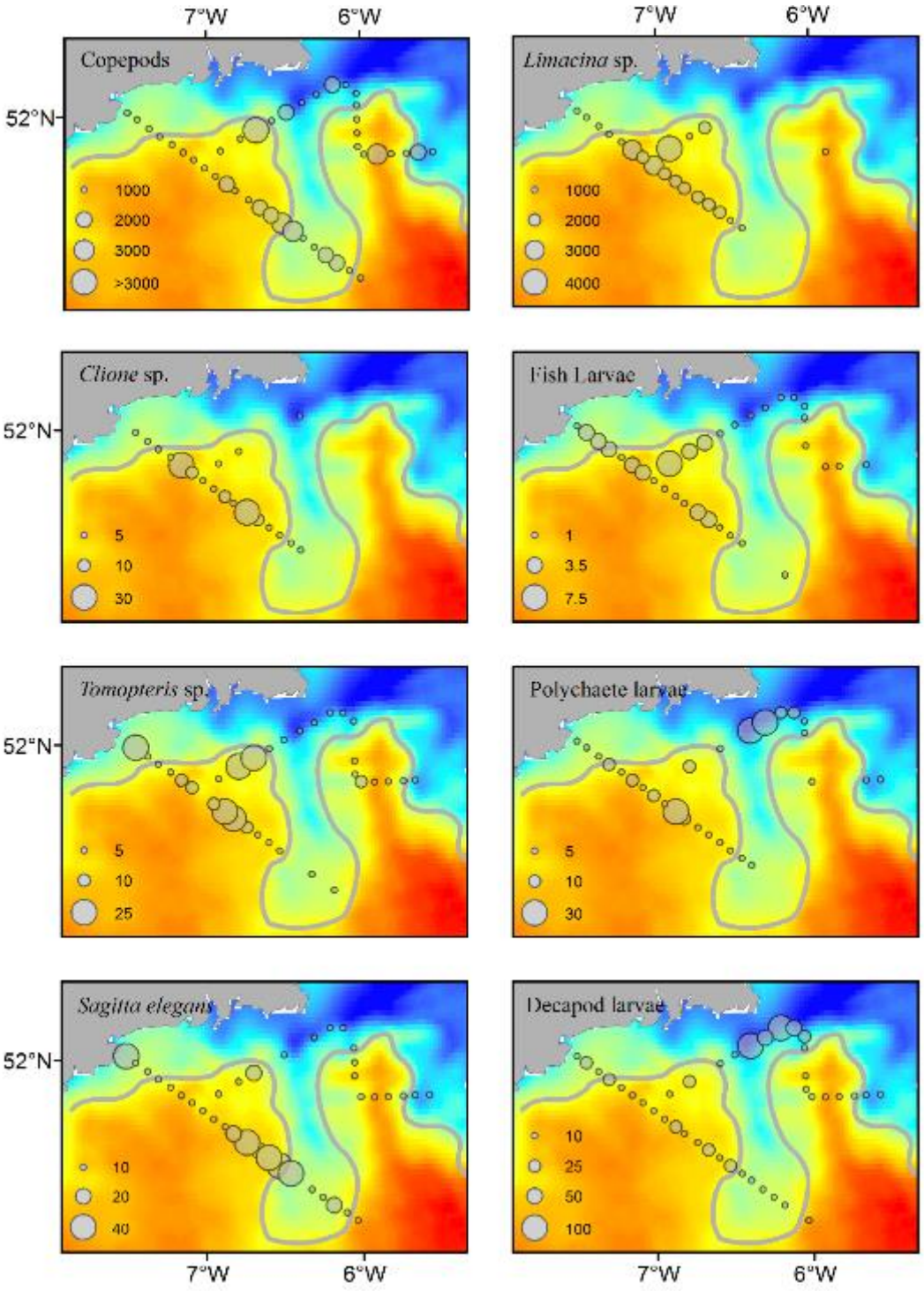


Figure 3.8: Abundance (indiv. m^{-3}) and distribution of the non-gelatinous zooplankton that primarily drove the community dissimilarities. The Celtic Sea community was characterised by oceanic species, e.g. *Tomopteris* & *Limacina* sp., whereas the Irish Sea community was characterised by meroplanktonic polychaete and decapod larvae. Note, the legend for each species is different.

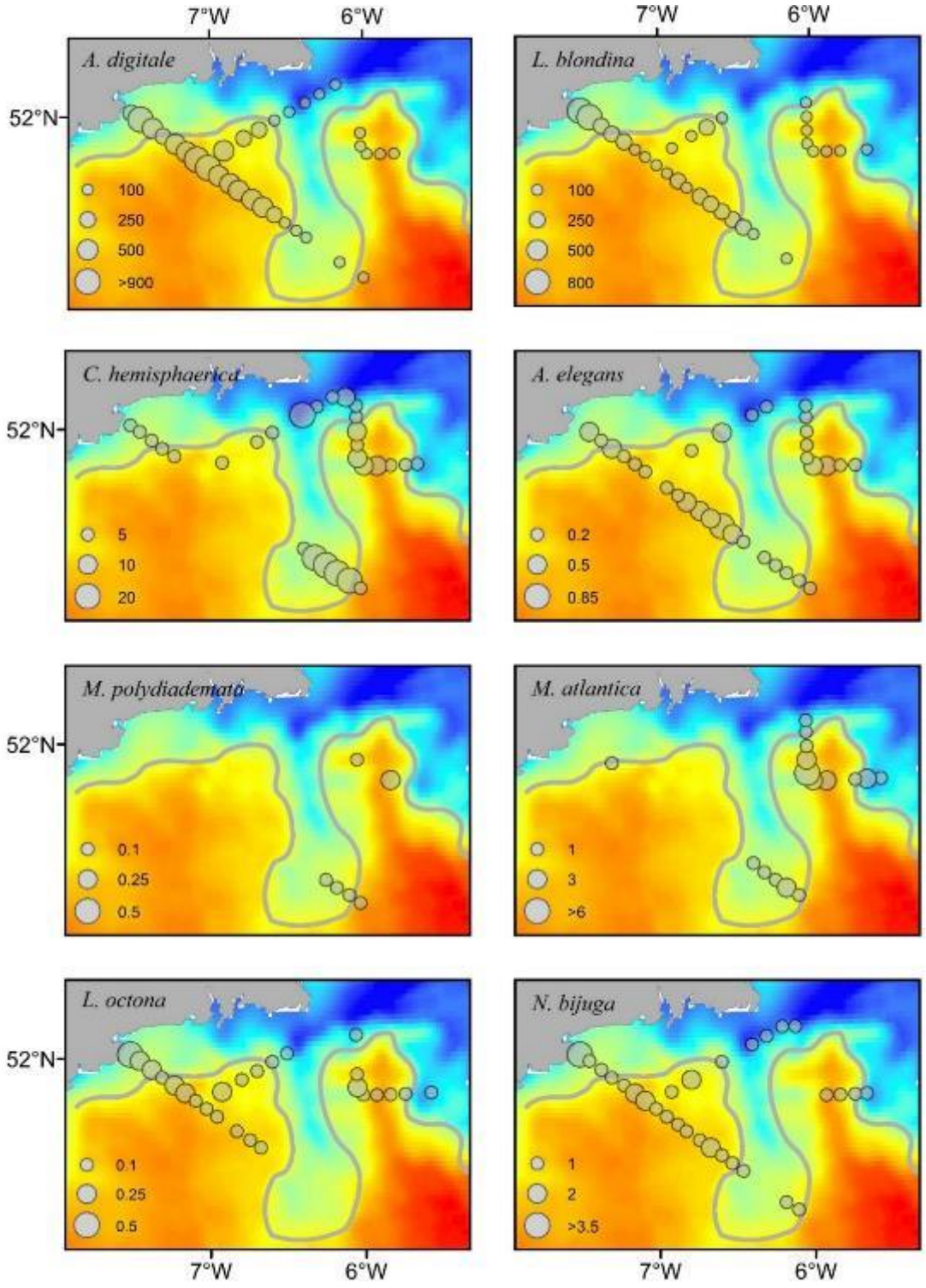


Figure 3.9: Abundance (indiv. m^{-3}) and distribution of the dominant gelatinous zooplankton that primarily drove the community dissimilarities. The majority of species were far more abundant in the Celtic Sea, with the exception of *C. hemisphaerica*. In addition, the Celtic Sea Front (CSF) appears to partition meroplanktonic hydromedusae. Note, the legend for each species is different.

Gelatinous zooplankton biomass

Community analysis of only the gelatinous zooplankton (scyphomedusae, hydromedusae, siphonophores and ctenophores) abundance and biomass indicated that there were two distinct communities across the survey area (Fig. 3.10). The stations defined as the Celtic Sea community (cluster 1 in Fig. 3.7) in the previous analysis of abundance remained clustered together, while the remaining stations defined as the Irish Sea and Celtic Deep communities clustered together in a single community (Fig. 3.10). Analysis of similarity confirmed the changes in community were significant (ANOSIM, $r = 0.72$, $p < 0.001$). The dissimilarity between the two communities was driven by *A. digitale* (24%), *N. bijuga* (23%), *Bolinopsis infundibulum* (16%) *L. blondina* (8%) and *C. hemisphaerica* (5%) (Fig. 3.9) and all were indicated as significant except for *B. infundibulum.*

Further species specific analysis of variance showed that *P. pileus* biomass increased significantly in Irish Sea/Celtic Deep water, whereas the increase in *B. infundibulum* biomass was not significant (Table 3.2). Total gelatinous biomass was significantly higher in the Celtic Sea (2085 ± 1718 mg C 1000 m^{-3}) compared with Irish Sea/Celtic Deep (1328 ± 1189 mg C 1000 m^{-3}) (Table 3.2). Of the 14 gelatinous zooplankton species analysed, only four (*B. infundibulum, P. pileus, C. hemisphaerica* and *M. polydiademata*) had a higher biomass in the Irish Sea/Celtic Deep (Table 2.2). Gelatinous zooplankton biomass as a percentage of the total zooplankton biomass ranged from 0.005 – 16.8%; the mean percentage in the Celtic Sea (6 ± 4%) was significantly higher than the mean percentage in the Irish Sea/Celtic Deep (4 ± 4.3%), (ANOVA, $F_{1,47} = 4.19$, $p = 0.046$).

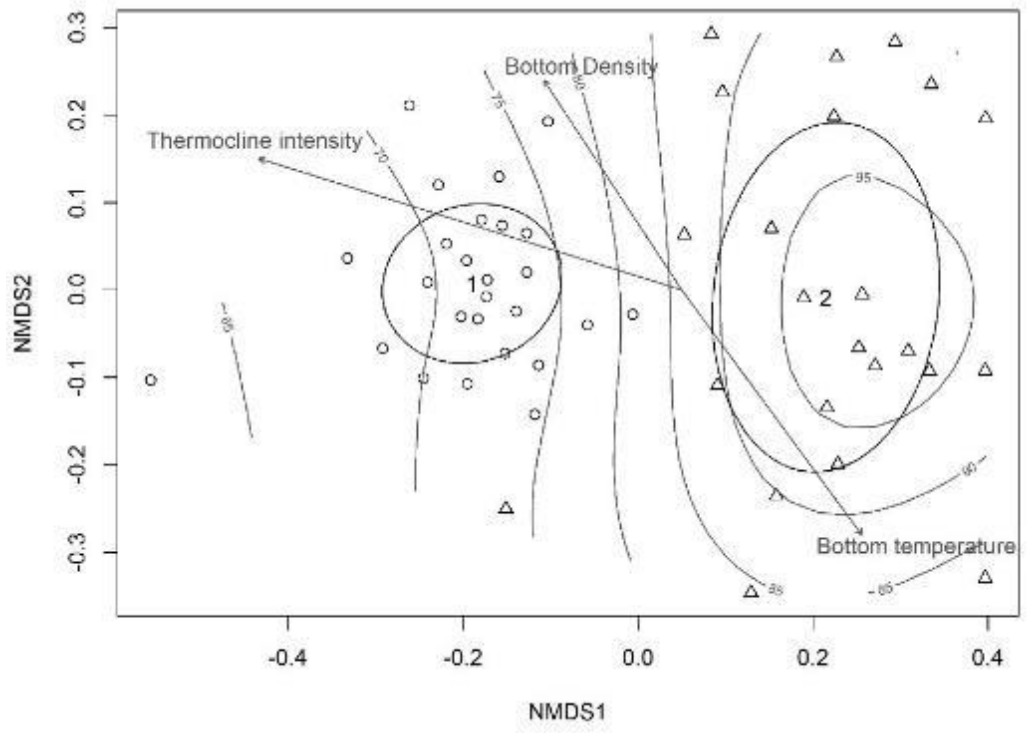


Figure 3.10: Two dimensional non-metric MDS plot (Stress = 0.15) of gelatinous zooplankton biomass (mg C 1000 m^{-3}). The most significant environmental parameters are displayed on the plot, with depth as a fitted surface and the remaining variables displayed as a vector with direction and length indicating the direction and magnitude of influence. The stations are coded by symbols according to the cluster analysis, open circles are Celtic Sea community and open triangles are Irish Sea/Celtic Deep communities.

The contribution of individual species to the gelatinous biomass at each station varied substantially. The mean contribution of *A. digitale* in the Celtic Sea community was 33 ± 23% (max 96%) and then declined to 1.1 ± 4.9% (max 24%) in the Irish Sea/Celtic Deep. Siphonophores were an important component of the biomass in both the Celtic Sea and the Irish Sea/Celtic Deep communities, representing 36.4 ± 20% (max 78%) and 26.8 ± 21% (max of 63%) respectively. Nonetheless, some stations in both communities had no siphonophore presence. This siphonophore biomass was

dominated by *N. bijuga* with a mean contribution of 30.1 ± 19.7% (max 73%) and 9.5 ± 16.3% (max 58%) in the Celtic Sea and Irish Sea/Celtic Deep respectively. The contribution of *A. elegans* did not change significantly across the survey region (Table 3.2), reaching a maximum of 42%, however, the mean contribution was generally low at 5.9 ± 8.8 % (Fig. 3.8). *Muggiaea atlantica* was recorded almost exclusively over the Celtic Deep, contributing 58.6% of the gelatinous biomass at one station (Fig. 3.9), with a mean contribution of 11.6 ± 15.8% across the Irish Sea/Celtic Deep community. *Muggiaea atlantica* was present at one station in the Celtic Sea and its contribution to the total biomass was negligible.

The ENVFIT function indicated that numerous environmental parameters were significantly correlated with the gelatinous zooplankton biomass NMDS ordination. Thermocline intensity (r^2 = 0.35, p=0.001), bathymetry (r^2 = 0.33, p=0.001), bottom salinity (r^2 = 0.18, p=0.013), bottom density (r^2 = 0.24, p=0.003), bottom temperature (r^2 = 0.24, p=0.004) and pycnocline intensity (r^2 = 0.24, p=0.002) all had a significant and positive correlation with the NMDS ordination, however, the r^2 values suggest that some of the correlations are weak. Lastly, there was a significant, though weak correlation between distance to the front and the NMDS ordination (r^2 = 0.14, p=0.027), which would suggest that gelatinous zooplankton biomass was not greater near the front.

Table 3.2: Mean biomass ± SD (mg C 1000 m^{-3}) of the gelatinous species which drove the dissimilarity between the two different communities according to the SIMPER analysis, and the results of ANOVA or Mann Whitney tests for individual species showing where between group differences in biomass were significant.

	Biomass mg C 1000 m^{-3}		
Species	**Celtic Sea**	**Irish Sea & Celtic Deep**	**ANOVA/Mann Whitney**
*A. **digitale***	587 ± 365	12 ± 52	U = 589, p = < 0.001
N. bijuga	771 ± 1266	110 ± 231	U = 516, p = < 0.001
B. infundibulum	150 ± 560	572 ± 958	U = 241, p = > 0.1
L. blondina	238 ± 305	21 ± 52	U = 533, p = < 0.001
P. pileus	137 ± 167	229 ± 149	U = 159, p = 0.005
Beroe sp.	61 ± 142	153 ± 324	U = 241, p = > 0.1
C. hemisphaerica	1.7 ± 5.5	119 ± 110	U = 25, p = < 0.001
A. elegans	117 ± 147	52 ± 68	U = 391, p = > 0.05
Obelia sp.	4.5 ± 8.3	1.4 ± 3.6	U = 356, p = > 0.2
M. polydiademata	0.1 ± 0.36	2.1 ± 6.3	U = 227, p = < 0.05
L. octona	0.5 ± 0.69	0.50 ± 0.23	U = 398, p = > 0.05
L. undulata	0.41 ± 0.71	0.15 ± 0.23	U = 304, p = > 0.8
E. gracilis	0.1 ± 0..3	0..05 ± 0..14	U = 317, p = > 0.58
M. atlantica	0.2 ± 1.0	104 ± 193	U = 96, p = < 0.001
Total biomass	2085 ± 1718	1328 ± 1189	U = 411, p = <0.05

To explore biotic drivers of the gelatinous zooplankton community, the biomass of potential prey taxa was included in the ENVFIT analysis. The following taxa, *Sagitta elegans* (r^2 = 0.31, p=0.001), *Tomopteris* sp. (r^2 = 0.24, p=0.002), polychaete larvae (r^2 = 0.19, p=0.01) and ichthyoplankton (r^2 = 0.17, p=0.015) were revealed to have a significant correlation with the NMDS ordination. However, the subset of environmental and biotic parameters with the best correlation, with the gelatinous zooplankton biomass NMDS ordination (using BIOENV) excluded all potential prey taxa and retained only the bottom temperature and bathymetry (Mantel, $R = 0.53$, $p < 0.001$). Multivariate analysis with community clustering as a factor found additional parameters were significant in shaping the gelatinous community, including the distance to the SST front (Table. 3.3). However, once again the bathymetry and bottom temperature demonstrated the strongest relationship.

Table 3.3: Results of multivariate permutational analysis (ADONIS) of the gelatinous biomass.

	Df	**Sums Sqs.**	**Mean Sqs.**	**F**	**r^2**	**Sig.**
Bathymetry	1	1.9887	1.9886	11.005	0.14853	0.001
Bottom temperature	1	2.1808	2.18078	17.2005	0.16288	0.002
Thermocline gradient	1	0.5460	0.54599	3.0215	0.04078	0.03
Distance to front	1	0.473	0.473	2.6176	0.03533	0.016
Copepod biomass	2	0.4306	0.43065	2.3832	0.03216	0.031
Residuals	43	7.7701	0.18070		0.58033	
Total	48	13.3891			1.00000	

Influence of the front on gelatinous biomass

To investigate the relationship between gelatinous zooplankton and the SST front further, the abundance and biomass were modelled against distance to the front while excluding T1 stations which were *ca.* 40 km form the SST front. For all stations, the gelatinous carbon biomass increased significantly with distance to the front (r^2 = 0.16, p = 0.007) (Fig. 3.11A). However, the increase in biomass with distance to the front was significant only in the Irish Sea/Celtic Deep stations (r^2 = 0.38, p = 0.002), and not in the Celtic Sea stations (r^2 = 0.02, p = 0.58). Investigation of the raw data suggested that the presence of relatively rare large bodied ctenophores in the Irish Sea/Celtic Deep stations may have increased the r^2 value. Removing the ctenophores resulted in similar linear trends across both communities (Fig. 3.11B), and the trend in the Irish Sea/Celtic Deep became weak and insignificant (r^2 = 0.08, p = 0.18).

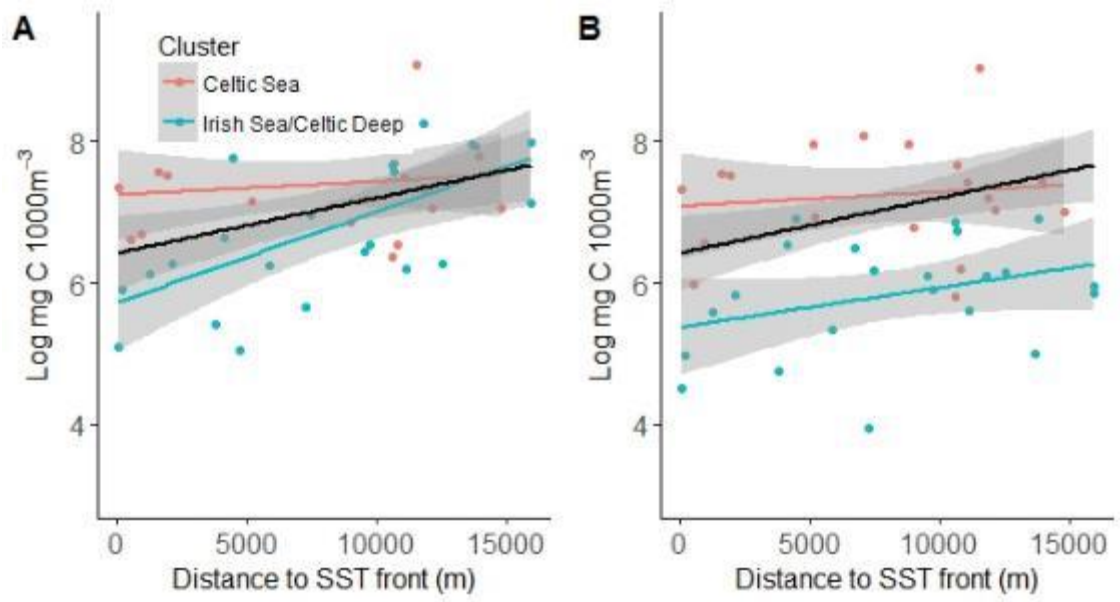


Figure 3.11: Relationship between the distance to the Celtic Sea Front (CSF) and A; gelatinous zooplankton biomass (log mg C 1000 m^{-3}) and B; gelatinous zooplankton biomass excluding ctenophores. The black line is the linear trend for all data points,

the red and blue lines are the trends for the two communities identified during MDS and cluster analysis. The grey shading are the 95% confidence interval.

Discussion

The importance of fronts and other mesoscale oceanic features in physical, biological and biogeochemical interactions has been recognised since the 1960s (Owen, 1981; McGillicuddy, 2016). The influence of thermohaline fronts on phytoplankton (Hill et al., 2008; Belkin et al., 2009; Raine, 2014) and to a lesser extent zooplankton (Schultes et al., 2013; McGinty et al., 2014) has advanced substantially in recent years. However, knowledge gaps remain with regards to gelatinous zooplankton and thermohaline fronts (Graham et al., 2001; Purcell, 2009). The results in this study indicated that gelatinous zooplankton are not aggregated by the Celtic Sea Front, but the front does partition gelatinous zooplankton into two distinct communities. However, there was a slight trend of increasing biomass moving away from the front in both communities, but this is more likely a result of an increase in gelatinous zooplankton biomass as the sampling moved into warmer and more stratified waters. In the Celtic Sea community, there was consistently high biomass of *A. digitale, N. bijuga* and *L. blondina* along the T2 transect (Fig. 3.10), and within the Irish Sea/Celtic Deep community it was clear that *M. atlantica* and *C. hemisphaerica* were more abundant over the deep stratified regions between segments of the front (Fig. 3.10). Previous work in the Celtic Sea has revealed strong associations between the frontal dynamics and primary productivity (Pingree and Griffiths, 1978; Le Fèvre, 1987; Raine, 2014). This pattern was consistent with the significant positive correlation between the sub-surface chlorophyll-*a* maximum and the pycnocline found here, however, neither parameter was found to have a significant relationship with the gelatinous biomass, suggesting that there is not a strong relationship between the front

and gelatinous taxa recorded here. In addition, multivariate analysis of both the gelatinous and the total zooplankton community consistently selected bathymetry and the bottom temperature as most the influential parameters, suggesting that physical rather than biological processes controlled the shifting community.

A similar disassociation between frontal dynamics and the zooplankton biomass was observed in 2009, at the Celtic Sea Front (McGinty et al., 2014) and the Ushant Front (Schultes et al., 2013). The spatial variation in the zooplankton community across the Celtic Sea Front in 2015 was consistent with the observations of McGinty et al. (2014) during 2009. McGinty et al. (2014) also recorded the highest zooplankton and hydromedusae abundance in the Celtic Sea and physical parameters were to the fore in explaining the community variation. Although those parameters differed from this study, SST, dissolved oxygen and water column stability were most influential (McGinty et al., 2014), they nonetheless point to water column structure as the primary influence. In contrast to the Celtic Sea Front, the Ushant Front had little apparent influence over the zooplankton or cnidarian community in 2009, with a gradual neritic to oceanic variation moving east to west (Schultes et al., 2013). However, like the Celtic Sea Front, the highest zooplankton abundance was recorded in the warm stratified oceanic side of the front. In terms of gelatinous zooplankton abundance, both studies (Schultes et al., 2013; McGinty et al., 2014) found much lower densities that the present study, < 2 indiv. m^{-2} (McGinty et al., 2014) and < 50 indiv. m^{-3} (Schultes et al., 2013) compared with > 1300 indiv. m^{-3} during this study in 2015. This similarity would suggest that the numerically dominant medusae here, *Aglantha digitale*, was not abundant in 2009. Furthermore, the high relative abundance of oceanic taxa, including the pelagic molluscs *Clione* sp. and *Limacina* sp., *Tomopteris* sp., *Agalma elegans* and *Sagitta elegans* were also not evident in 2009

(Schultes et al., 2013; McGinty et al., 2014). These taxa are indicative of colder oceanic water (Russell, 1935; Southward et al., 1995) and long-term fluctuations of these species in the Celtic Sea is strongly linked to large scale oceanographic processes, rather than localised bottom up processes (Southward, 1980; Southward et al., 1995).

High gelatinous biomass and diversity has been recorded on the warm stratified oceanic side of frontal systems off the Benguela coast, South Africa (Hutchings et al., 1986; Pagès and Gili, 1992), and off the South American coast (Brazil, Uruguay, & Argentina) (Mianzan and Guerrero, 2000). Powerful frontal jets (*ca.* 1 m^{-s}) are present along the Benguela front and form a distinct barrier between the offshore region and the upwelling crustacean rich inshore region (Hutchings et al., 1986). There is some evidence that prolonged upwelling and enhanced primary productivity can enhance the copepod abundance along the front edge, however, the gelatinous community appear to be driven by longer term seasonal and/or oceanographic changes rather than localised trophic changes (Hutchings et al., 1986; Pagès and Gili, 1992). A front as a barrier was also evident along the Catalan shelf slope front, where the dominant cnidarians species were retained on the inshore side of the front (Guerrero et al., 2016). Guerrero et al. (2016) also found that the distribution of cnidarians was coupled to physical parameters, i.e. bathymetry and salinity, rather than primary productivity. Interestingly, despite a much lower current velocity along the Catalan Front (*ca.* 0.3 m^{-s}) (Font et al., 1995), compared with current velocity along the Benguela Front, both were found to be discrete barriers between communities (Pagès and Gili, 1992; Guerrero et al., 2016). The Celtic Sea Front by comparison has a dual character; while the Celtic Sea community ends abruptly along the western edge of the front, the homogenous Irish Sea/Celtic Deep gelatinous

community and the broad similarity in the Irish Sea and Celtic Deep zooplankton communities indicate mixing between the two. A further indication of mixing in this region was that the high fluorescence values in the Irish Sea were also present over the Celtic Deep.

The intense physical gradients around the cold dense water at the Celtic Deep create some of the highest current velocities (~1 m^{-s}) measured at the Celtic Sea Front, which in turn creates cyclonic instabilities along the boundary of the front (Brown et al., 2003). These near surface features are unlikely to extend more than 30 m deep (Horsburgh et al., 1998) and are a potential mechanism for transferring nutrients and plankton across the front. These types of interactions between a frontal system and the benthic topography are not unusual and thought to enhance cross-frontal exchange in other systems (Belkin et al., 2009). It is probable that the Benguela and Catalan Fronts, which are situated in much deeper water (> 300 m depth), are not as tightly coupled to the underlying topography and therefore the front is less likely to form instabilities. The Celtic Sea also experiences some of the world's largest tides (> 5 m amplitude) and spring tides in particular can cause cross frontal exchange (Le Fèvre, 1987). It is possible the zooplankton biomass recorded in the Celtic Deep here was anomalous and due to a periodic and short lived exchange, as sampling in 2009 and evidence from the Continuous Plankton Recorder indicate a long term trend of low biomass over the Celtic Deep (McGinty et al., 2014).

The occurrence of *Muggiaea atlantica* over the Celtic Deep was of particular interest and the distribution would indicate a Celtic Sea origin. The abundance was very low compared with previous work in the region (Baxter et al., 2012b), and the predominance of polygastric nectophores suggests negligible *in situ* reproduction. The distribution here would suggest an association with the frontal jet, however, the

absence of *M. atlantica* across most of the survey area meant that there was little explanatory power in the data. *Muggiaea atlantica* has long been considered an indicator species, associated with the presence of warm Atlantic water of southerly origin in the Western English Channel (WEC) (Russell, 1935; Southward, 1980; Southward et al., 1995). However, more recent analysis shows that *M. atlantica* is resident in the WEC and the cold-water versus warm-water paradigm no longer offers a complete explanation of the population dynamics in the WEC (Blackett et al., 2014; Blackett et al., 2015). Temperature and the phenology of prey species, predominantly but not exclusively copepods, are the primary determinants of *M. atlantica* population dynamics, and the late autumn population is highly dependent on early spring population (Blackett et al., 2015). As the WEC population is the most northerly self-sustaining *M. atlantica* population (Blackett et al., 2014; Blackett et al., 2015), and there is no indication of self-sustaining *M. atlantica* in Irish waters, it is reasonable to suggest that the *M. atlantica* in Irish coastal water originates in the WEC (Haberlin et al., 2016). The thermohaline circulation around the Celtic Sea (Hill et al., 2008; Raine, 2014) provides a mechanism which can advect *M. atlantica* into Irish coastal waters. Furthermore, the predominantly late seasonal occurrence of *M. atlantica* in Irish waters (Haberlin et al., 2016) would be coincident with the seasonal weakening of the fronts as temperature gradients decline (Hill et al., 2008), thereby releasing zooplankton from the WEC into the Celtic Sea circulation. Although the data here did not reveal any local relationship between the Celtic Sea Front and *M. atlantica*, there is substantial evidence indicating that the front is part of a much larger system that does influence the occurrence of *M. atlantica* in the Celtic Sea and in Irish waters.

One of the more notable findings of the study was the substantial contribution of physonect siphonophores to the gelatinous biomass (Table 3.2), contributing >36%

in the Celtic Sea. An inshore survey in 2009, found *N. bijuga* at *ca.* 50% of stations along the south and southwest coasts, with *A. elegans* at a single station (Baxter et al., 2012b), whereas here, both species were found at >60% of stations. Historically, surveys that identify and enumerate physonects in shelf regions are sparse and it is difficult to determine the importance of these observations against a poor baseline. The data here would suggest that these species are ecologically more important in the Celtic Sea than previously thought, with a possible predatory impact on the larvae of important commercial species (Purcell, 1981; Mills, 1995). Physonect siphonophores consume a variety of prey including chaetognaths, decapod larvae, larval fish, although copepods tend to be the dominant prey (Purcell, 1981; Purcell, 1997). Interestingly, the physonects and the two hydromedusae *L. blondina* and *A. digitale,* were all spatially coincident with the highest abundance of potential prey taxa, yet only copepods were significant in explaining the gelatinous community and this correlation was very weak. The substantial changes in gelatinous zooplankton community across a largely unchanging copepod abundance/biomass (Table 3.1) would suggest weak links between these gelatinous predators and their prey and perhaps weak links between the oceanic holoplanktonic taxa and the neritic meroplanktionic taxa. The numerically dominant *A. digitale* was largely composed of immature medusae < 2.5 mm in height which are too small to prey on the copepods present (Williams and Conway, 1981). Likewise, the *L. blondina* were minute in size (*ca.* 1 mm diameter) and also possibly unable to consume the copepods present. The mollusc *Limacina* sp., while numerically extremely abundant, is a suspension feeder and is the sole prey species of the other abundant mollusc *Clione* sp., which means that neither species would have a direct a trophic impact on other zooplankton (Boer et al., 2005).

Despite the significant shift in communities across the survey area, the mean biomass did not change significantly, and this would suggest that the gelatinous community is less important than the copepod community that clearly dominate the standing biomass. However, cnidarians turn over large quantities of carbon and ammonia which alter trophic structures in less direct ways (Biggs, 1977; Pitt et al., 2013). Cnidarians acquire excess carbon which is not needed due to an extremely low metabolic demand and the excess is shed as dissolved organic matter (DOM) and mucus (Pitt et al., 2013). The discarded nutrients become available to microbes and phytoplankton therefore a substantial proportion of the nutrients consumed by cnidarians are shunted away from higher trophic levels (Biggs, 1977; Condon et al., 2011). Increased nutrient levels in the presence of cnidarians, allied to predations on copepods, has been shown to enhance heterotrophic dinoflagellate abundance in mesocosm experiments (Pitt et al., 2007). Therefore, an increase in gelatinous zooplankton may favour harmful algal blooms which are known to originate in the Celtic Sea (Raine and McMahon, 1998; O'Boyle and Raine, 2007; Raine, 2014).

It is clear that while local dynamics at the Celtic Sea Front influence the distribution of the gelatinous and zooplankton communities, there is little to suggest that the front physically aggregates or promotes the biomass of either community through bottom up processes. It is known that tidal pulses create heterogeneity along Celtic Sea fronts at low trophic levels, however, the same intense dynamics creating those pulses are likely to dissipate nutrients and prey before predator species can utilise them (Le Fèvre, 1987; Schultes et al., 2013). Although no potential prey taxa were correlated with the gelatinous community, it is likely that integrated vertical sampling is simply too coarse to reveal trophic relationships (Benoit-Bird et al., 2013). High resolution vertical sampling in a front in the Southern California Bight did reveal

interesting trophic relationships, and in fact, was also able to detect several hydromedusae species aggregated at the front (Luo et al., 2014). The influx of oceanic cold-water species into the Celtic Sea is a common phenomenon (Southward, 1980; Southward et al., 1995), and almost certainly driven in part by the greater thermohaline circulation of which the Celtic Sea Front is a part. The same mechanism is likely to be a key driver of *M. atlantica* in Irish Waters, however, investigating this will require a higher frequency of dedicated gelatinous surveys in the Celtic Sea.



Chapter 4

Warm core eddies create a patchy gelatinous landscape

Abstract

Mesoscale eddies are increasingly recognised are important drivers of physical and biological heterogeneity across pelagic ecosystems. Gelatinous zooplankton can respond rapidly to eddies, increasing or decreasing in abundance, however, detailed descriptions of the community composition are rare. To investigate the influence of mesoscale eddies on gelatinous zooplankton, a research cruise crossing the north Atlantic during April 2015 carried out plankton sampling across a warm core (anticyclonic) eddy, which was identified prior to the cruise using satellite data. Quantitative estimates of abundance using stratified multinet sampling identified a 12-fold decrease in the abundance of gelatinous taxa within the eddy core, decreasing from 660 ± 349 to 49 ± 54 indiv.1000 m^{-3}. Diphyid siphonophores dominated the gelatinous taxa and were virtually absent from the eddy core, which was taken to be everything inside the 10°C isotherm. Qualitative observations indicated some larger calycophoran genera were present in the eddy core, nonetheless, these were rare by comparison with the outside. Most zooplankton taxa had a negligible presence in the eddy core, and only large predatory amphipod taxa increased in abundance inside the eddy. There was no evidence of exchange across the high velocity (> 1 m^{-s}) boundary zone, however, higher resolution sampling is needed to fully describe the community across the eddy boundary.

Introduction

During the past few decades there has been considerable research effort investigating the ecology of gelatinous zooplankton in neritic habitats. Much of this effort has been directed towards understanding the population dynamics (Including trends in abundance) of jellyfish species that interact negatively with tourism and marine industries, e.g. aquaculture, fisheries and power generation (CIESM, 2001; Purcell et al., 2007; Doyle et al., 2008a; Canepa et al., 2014; Haberlin et al., 2016). In contrast, there has been comparatively less research on the ecology of gelatinous zooplankton in oceanic habitats. Some of this disparity is due to the difficulty in sampling oceanic environments, which requires larger and more expensive vessels, and there are far fewer 'ships of opportunity' providing the necessary platform for targeted research or bycatch data (Bastian et al., 2010; Bastian et al., 2011; Lynam et al., 2011). Furthermore, without the same societal imperatives driving research in the oceanic domain, progress has been slower, however, the advent of direct observation and capture techniques in the 1970s revealed that diversity and biomass have generally been underestimated (Barham, 1963; Hamner, 1975; Haddock, 2004; Vinogradov, 2004).

The oceanic gelatinous community is composed of many taxonomic groups (Robison, 2004), however, this study is mainly concerned with the scyphomedusae, hydromedusae, ctenophores, and pelagic tunicates. Numerically, siphonophores (Pugh, 1984; Mackie et al., 1987), and pelagic tunicates (Alldredge and Madin, 1982; Anderson, 1998) are often the most abundant taxa, particularly in the epipelagic zone. Nonetheless, both groups are found in the mesopelagic zone and there is substantial evidence of vertical niche separation (Pugh, 1984; Roe et al., 1984; Mackie et al., 1987; Hosia et al., 2008). Members of the Trachymedusae and Narcomedusae and the

coronate scyphomedusae are also evident across broad oceanic regions (Kramp, 1959; Larson et al., 1991; Hosia et al., 2008), however, the vertical distribution of many species is not well described. The pelagic tunicates are predominantly found in the epipelagic (Ruppert and Barnes, 1994), although some species extend their range well into the mesopelagic (Anderson, 1998; Hopcroft and Robison, 1999). A common characteristic amongst all the deeper living taxa (in the mesopelagic and bathypelagic) is a more cosmopolitan distribution, most likely due to a more homogeneous environment below the euphotic zone (Robison, 2004; Doyle et al., 2013). The geographic distribution of siphonophores is broadly aligned with hydrographic water masses and broad trends in latitude and longitude are evident (Pugh, 1977; Mackie et al., 1987; Hosia et al., 2008). Temperature, salinity, light level, oxygen concentration and primary productivity are key drivers of these broad scale trends over 1000s km (Mackie et al., 1987; Lucas et al., 2014). However, it is increasingly clear that mesoscale features such as eddies and frontal systems create an extremely patchy oceanic ecosystem (Stommel, 1958; Chelton et al., 2011; McGillicuddy, 2016), and the influence of this patchiness on gelatinous zooplankton remains poorly understood (Arai, 1992; Graham et al., 2001).

Mesoscale eddies permeate the entire pelagic ecosystem and influence horizontal and vertical mixing of nutrients, energy, plankton and micronekton (Owen, 1981; Wiebe et al., 1985; Zhang et al., 2014; Dufois et al., 2016; McGillicuddy, 2016). They range in size from 25 – 250 km in diameter, can reach depths of up to 2500 m (Mittelstaedt, 1987), and their occurrence is predominantly associated with instabilities or meanders which break away from oceanic currents to form a rotating ring, essentially an enclosed frontal system (Stommel, 1958; Owen, 1981). The Warm Core Rings (WCRs) project in the early 1980s established that macrozooplankton

biomass can increase inside Gulf Stream eddies, and that eddy structure could change rapidly in response to season, weather and interactions with boundary currents (Joyce, 1984; Davis and Wiebe, 1985; Roman et al., 1985; Wiebe et al., 1985; Hitchcock et al., 1987). Crustacean and fish communities within warm core eddies are shown to be distinct from the exterior cold water communities, and can be transported substantial distances within the eddy (Cox and Wiebe, 1979; Brandt, 1981; Tranter et al., 1983). Whether the same patterns hold true for gelatinous zooplankton is unknown, and work on non-eddy frontal systems indicates substantial variation in their influence; on occasion representing a barrier and on other occasions having no apparent effect (Pagès and Gili, 1992; Mianzan and Guerrero, 2000; Luo et al., 2014; Guerrero et al., 2016). Graham et al. (2001) suggested the influence of fronts is scale dependent, with localised systems more likely to aggregate gelatinous zooplankton, while large scale features, e.g. the Antarctic Polar Front (Pages et al., 1996), serve as a partition between communities.

How mesoscale eddies influence gelatinous zooplankton has important implications for oceanic trophic ecology and biogeochemical cycling. Leatherback turtles *Dermochelys coriacea* and sunfish *Mola mola* are primary consumers of gelatinous taxa (Arai, 2005; Doyle et al., 2013), and recent satellite biotelemetry suggests extended foraging of both species along frontal systems (Doyle et al., 2008b; Sousa et al., 2016). Furthermore, it is increasingly apparent that a large number of oceanic vertebrate predators consume gelatinous taxa, including fish, turtle and bird species (Arai, 2005; Doyle et al., 2014), and all of these groups demonstrated spatial distributions coherent with frontal systems (Brandt, 1981; McGillicuddy, 2016). Cnidarians and ctenophores are voracious predators with the capacity to exert considerable top down pressure on the zooplankton community (Greve, 1994; Purcell,

1997; Shiganova, 1998), but equally provide prey (including parasitism) for a range of invertebrate predators including other hyperiid amphipods (Fleming et al., 2014), several genera of pelagic molluscs and other gelatinous taxa, e.g. the siphonophore *Apolemia uvaria* is recorded preying on a variety of other gelatinous taxa (Choy et al., 2018). Gelatinous zooplankton can influence carbon and nutrient cycling at the base of the food web: the excretion of labile carbon and nitrogen (in the form of ammonium) can benefit primary producers (Biggs, 1977; Pitt et al., 2013) and members of the microbial community (Condon et al., 2011), potentially retaining biomass in the euphotic zone. Equally, blooms of pelagic tunicates can divert biomass and nutrient from the base of the food web to the sea bed (Anderson, 1998; Robison et al., 2005).

New advances in oceanographic modelling, bio-acoustics and remote sensing have led to a reappraisal of the importance of mesoscale eddies in structuring primary productivity, micronekton and oceanic circulation (Chelton et al., 2011; Godø et al., 2012; Zhang et al., 2014; Fennell and Rose, 2015), however, their influence over mid-trophic gelatinous zooplankton represents a substantial knowledge gap in the literature. With this in mind, the aim of this study was to describe the changes in abundance, vertical distribution and community structure of gelatinous zooplankton across a warm core eddy boundary in the North Atlantic Current.

Material and Methods

Study region

During a trans-Atlantic crossing between Ireland and Newfoundland (April/May 2015), the Irish research vessel *R.V. Celtic Explorer* collected hydrographic data and biological samples in a warm core eddy situated *ca.* 400 km east of the Flemish Cap or *ca.* 1000 km east of Newfoundland (Fig. 4.1). In the north west Atlantic warm core eddies regularly form and spin off the northern boundary of the North Atlantic Current (NAC) and move eastward, in the general direction of the NAC, carrying parcels of warm water into the cooler surrounding water (Stommel, 1958; Rossby, 1996). The eddy region is vast, encompassing a band 1500 km wide, exchanging water across the subarctic front, mixing subtropical and polar waters (Krauss, 1986; Rossby, 1996).

Hydrographic data collection

Prior to departure, sea surface height (altimetry) maps, downloaded from the Colorado Center for Astrodynamics Research (CCAR), were used to locate a probable warm core eddy west of the Mid Atlantic Ridge within the North Atlantic Current eddy field. The eddy was chosen before departure from Ireland, and near real time satellite updates were used to stay on target. With respect to a mean sea level height, positive or negative values are indicative, but not diagnostic of cyclonic and anticyclonic rotations or eddies. Therefore, while the satellite data guided the vessel towards the suspected eddy location, confirmation of an actual warm core eddy and definition of the limits of the eddy required *in situ* data collection. The aim was to transit through the eddy, from east to west. This was provided by Sippican T5 eXpendable Bathy Thermograph (XBT) probes which were released at approximately 50 km intervals

throughout the cruise to a depth of 1800 m. When the vessel approached the positive sea level anomaly, XBT probes were released at 2.5 – 10 km intervals and a Conductivity, Temperature and Depth (CTD) sensor (Seabird 911) was deployed to *ca.* 1800 m to properly define the eddy boundary.

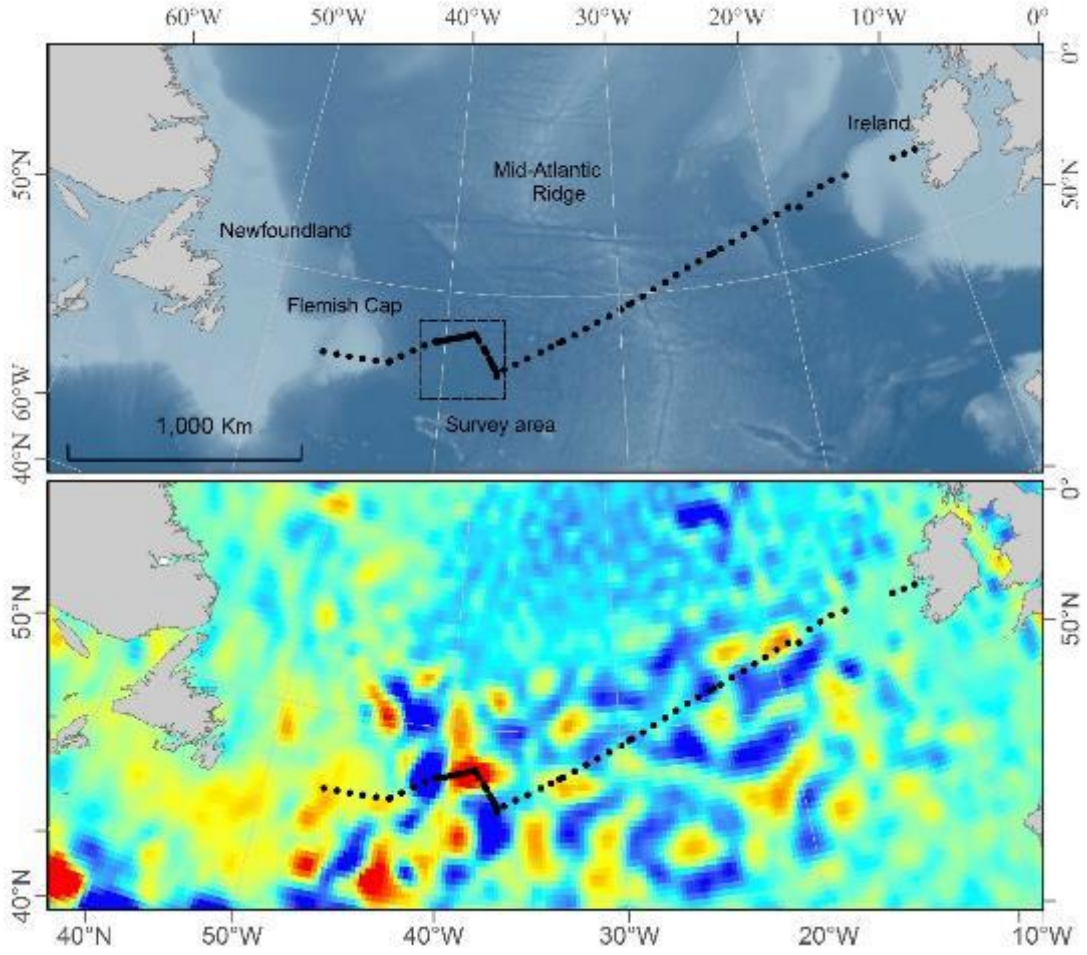


Figure 4.1: Map of North Atlantic region with; A) the location of the study area along the vessel track and; B) the sea surface height anomaly, red being positive and blue being negative. Positive and negative anomalies are indicative of anticyclonic (clockwise) and cyclonic (anticlockwise) rotation, respectively. Each black dot is the position of an expendable bathythermograph (XBT) release.

Back scatter coefficient data were recorded continuously using Simrad EK60 echo sounder operating at 18, 38, 120 and 200 Hz mounted on a drop down keel which extends 8.8 m below sea level. At each sampling station a 75 KHz Ocean Surveyor Acoustic Doppler Current Profiler (ADCP) was used to record the current speed throughout the top *ca.* 750 m of the water column and an additional CTD sensor on the multinet (described in the following section) recorded data to *ca.* 600 m.

Zooplankton sampling

Three gear types were used to collect zooplankton samples; a Grand Overture Trawl with a 20 mm small mesh liner in the cod end (Reid et al., 2012), a 1 m plankton net (270 µm mesh) and a five bag multinet (Hydro-Bios) with 180 µm mesh and 0.25 m^2 opening (Table 4.). Trawl nets were deployed at two depths at each station, also determined by backscatter coefficient values, primarily to capture mesopelagic fish and micronekton, i.e. 2-10 cm. Trawls samples were not replicated due to time constraints. The plankton net was hauled vertically from 200 m depth to the surface at 1 ms^{-1}, with two replicates at each station. The multinet was hauled vertically from 600 m to the surface and the nets were closed at 120 m intervals, with two replicates at each station. The sample depth intervals were based on the distribution of the deep scattering layer (DSL) depths, as determined by backscatter coefficient. All large (>1 cm) gelatinous zooplankton were extracted from plankton and trawl samples with the aid of a light box and fixed in a buffered 4% formalin and seawater solution for later study. The multinet samples were likewise inspected for large zooplankton, their presence noted and the samples were fixed for later study. All gelatinous zooplankton and the multinet samples were identified to the lowest taxonomic level (Russell, 1953; Totton and Bargmann, 1965; Kirkpatrick and Pugh, 1984; Mapstone, 2009) and enumerated using a stereomicroscope in the laboratory, approximately 6-9 months

after collection. The large scyphozoan species, *Periphylla periphylla* and *Atolla wyvillei* were counted and weighed on board the vessel immediately after sampling and then discarded.

Some of the calycophoran nectophores captured in the multinet were crushed, probably by the side of the nets when the bag closed. This made subsequent identification impossible although some specimens could be identified as belonging to the family Diphyidae. Where the anterior and posterior nectophore were present for a species, the greater number was taken as the polygastric count. Eudoxids or eudoxid bracts were counted separately to polygastric stages, and the total quantity for a given species was a combination of polygastric and eudoxid counts. Surprisingly, some of the larger calycophorans in the Hippoppdidae and Prayidae families came up reasonably intact in the trawl nets and were identifiable as single colonies. Where nectophores from either family were found in the plankton or multinet samples, the number was always less than 10, implying one colony, and therefore was recorded as one colony (Totton and Bargmann, 1965).

Table 4.1: Sampling gear used at each station (see fig. 4.2 & fig. 4.3) during the eddy survey. The x represents where a gear type was not used.

	GEAR TYPE		
STATION	Trawl	Plankton net	Multinet
9	✓	✓	✓
10	x	✓	✓
11	✓	✓	✓
12	x	✓	✓
13	✓	✓	✓
14	✓	x	x

Data analysis

The community composition and distribution was analysed using non-metric multidimensional scaled (nMDS) ordinations and cluster analysis based on Bray-Curtiss dissimilarity matrices (Clarke and Warwick, 2001). Various multivariate tools (Bioenv, Anosim and Adonis) within the 'Vegan' package (Oksanen et al., 2017), were used to analyse the influence of the eddy structure over the zooplankton community. All statistical analysis was conducted using R 3.2.5 (R Core Team, 2017). The oceanographic data were analysed using the 'Oce' package (Kelley and Richards, 2017). The XBT and CTD profiles were smoothed using a 10 m rolling mean, and the sections are based on 10 m depth intervals. The ADCP data were extracted using WinADCP (Ver. 1.14 Teledyne RD Instruments). Data were binned according to hourly means, and the most proximate bin by location and depth of samples was used during further analysis. In order to analyse the environmental data with the community matrix, all of the environmental parameters, (i.e. back scatter coefficient, temperature, salinity, density, vertical current and horizontal current), were averaged over every 120 m vertical layer from 0 – 600 m depth.

The sea level anomaly data were downloaded from the Copernicus marine environment monitoring service (www.marine.copernicus.eu) and is a 0.25-degree gridded data set, based on subtracting the 12 week mean sea surface height from the sea surface height. This data varied slightly from the sea surface height data used to locate the eddy initially, with the processing involved giving greater precision, and therefore it was preferred for retrospective viewing and analysis. The sea surface anomaly satellite data were analysed in ArcGIS (version 10.2).

Results

Sampling the eddy

Initially the survey was designed to sample outside, on the boundary and inside the eddy, using a combination of satellite data, XBT, CTD and EK60 back scatter to identify these positions. Finding a distinct 'outside' eddy station proved difficult because of the deep layer of warm water on the south side of the eddy. Nonetheless, where the lowest temperature was found and the satellite data indicated a position well outside the eddy, this became Station 9 (26th Apr, 2015) (200 km from St. 13) (Fig. 4.2). Station 10 was closer to the eddy, but still outside (160 km from St. 13). The vessel subsequently steamed towards the eddy centre and when back scatter readings indicated that a substantial change had taken place, this location was taken to be the eddy boundary and became station 11 (27th Apr, 2015) (84 km from St. 13). Station 12 was approximately 13 km closer to station 13, but the back scatter still indicated the vessel was on the eddy boundary. Station 13 (28th Apr, 2015) was initially located at the eddy centre using the best available satellite update at the time, however, subsequent analysis of satellite and physical data indicated that station 13 was actually nearer the northern boundary of the eddy (Fig. 4.2).

The vessel then steamed west and carried out trawl samples at station 14. Further XBT probes were deployed along the same course to locate the western boundary of the eddy, however, during the early hours of April 29th the weather deteriorated badly and sampling activities had to cease. Subsequent analysis of the station positions with more precise sea surface height anomaly data and a complete analysis of the XBT sections (Fig. 4.3) revealed the true position of the station relative to the eddy. While station 9 and 10 were outside the central core, stations 11, 12 and 13 were all situated inside the central core. Station 14 was likewise inside the core,

however it appeared to be close to a sharp isotherm (Fig. 4.3A) which suggests that the core was elongating and dispersing. It was apparent that the satellite data and the actual eddy dimensions were not well aligned and this was possibly due to the relatively coarse resolution (0.25 degrees) of the satellite data.

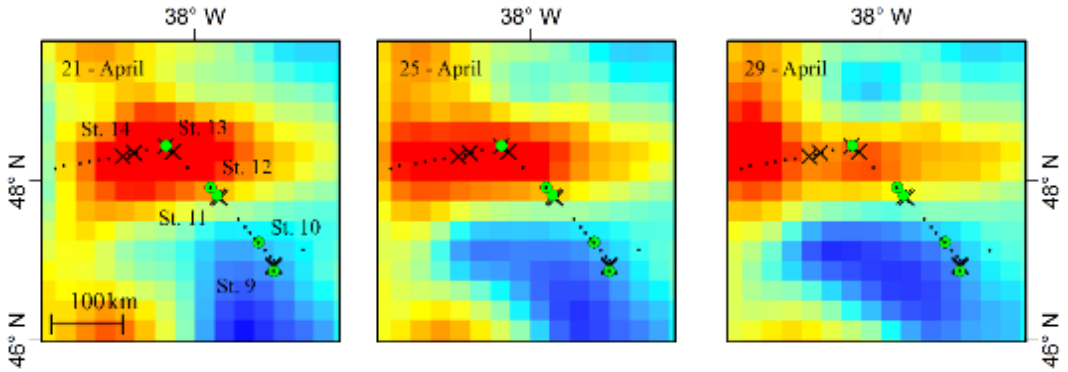


Figure 4.2: Change in the sea surface height anomaly at the eddy from April 21st to April 29th, 2015. The green markers represent plankton and multinet stations and the x markers represent trawl stations.

The combination of XBT and CTD profiles resulted in a high resolution section through part of the eddy, revealing a central core of > 14°C from the surface to *ca.* 300 m depth, and a 10°C isotherm reaching from *ca.* 300 m (37.45W) to *ca.* 800 m depth (39.93W) (Fig. 4.3). Below 600 m depth, the temperature continued to decrease from 10 to < 4°C, although the eddy appeared asymmetric in shape with 8°C penetrating to *ca.* 930 m at 39.56W in the western section. On the south side of the eddy, warm surface water penetrated down to more than 300 m (Fig. 4.3B), however, on the north side the 10°C isotherm ascended at a sharp angle to the surface, and the surface water beyond the isotherm rapidly cooled below 8°C moving west (Fig. 4.3A).

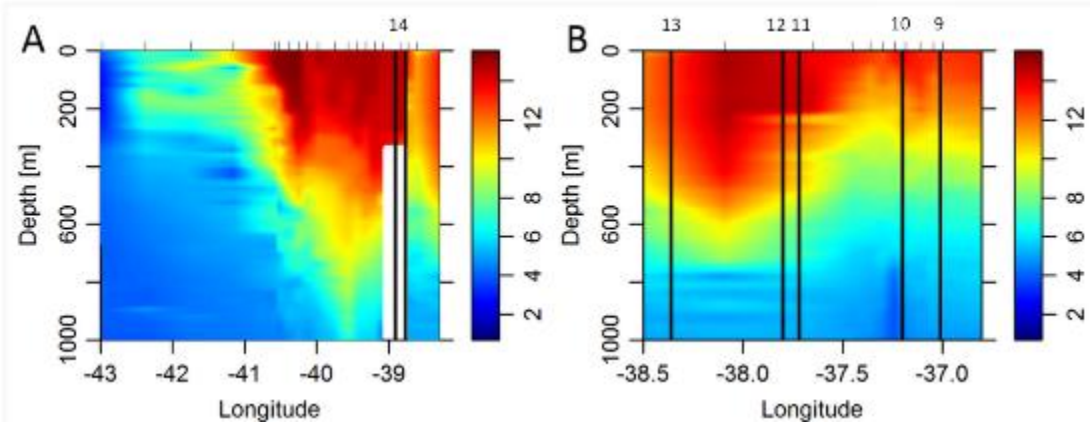


Figure 4.3: Temperature profile of the; A) western and; B) eastern sections of the eddy. The black vertical lines indicate the stations, which are numbered on the top x axis. The tick marks on the top x axis indicate where XBT and CTD sensors were deployed.

The movement apparent in the sea surface anomaly data (Fig. 4.2) is indicative of the constant movement in the region. A time lapse of the region from January to December 2015 reveals constantly shifting positive and negative sea surface anomalies, with a slight progression to the northwest. On occasion, there was no obvious propagation of the anomalies in a particular direction, but positive and negative anomalies appeared to rotate around each other. In addition, features appeared and disappeared over relatively short periods, i.e. < 1 month. During our survey the mean horizontal current velocities ranged from 0.32 m^{-s} to 0.86 m^{-s}, with the highest current velocities measured at station 11 and 13 in the 0 -120 m and 120 – 240 m depths. The lowest velocities were measured at stations 9 and 10, with little variation between the depths. The mean vertical current ranged from -0.08 to 0.02 m^{-s}, with a mean downward current at all depths at stations 11 and 12, where the highest values were measured.

G

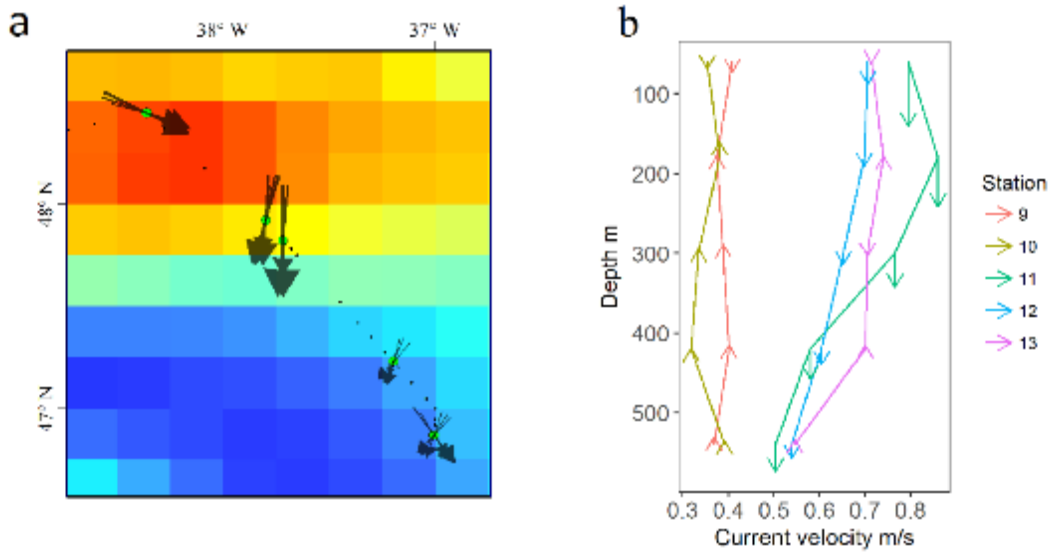


Figure 4.4: A) horizontal current direction at 5 sample depths from station 9 to station 13 and; B) the average current velocity in each sample depth, with the vertical component of the current displayed by the vertical arrows, with magnitude mapped to arrow length.

Community composition, abundance and distribution

In total, 54 zooplankton taxa were identified from the samples taken across the warm core eddy. This included 41 gelatinous species or genera; 25 siphonophores, 6 hydromedusae, 3 scyphomedusae, 2 ctenophores and 5 tunicates. These total counts are likely to be underestimates, as the unidentified hydromedusae and scyphomedusae were excluded from total counts, and it is likely that the large number of unidentifiable diphyid nectophores would have contained additional species. The remaining taxa belonged to Crustacea, Polychaeta, Chaetognatha, Foraminifera and Mollusca (Table 4.2). Data from the plankton and trawl samples are presented here and discussed later, however, only the quantitative data from the multinet sampler were used for multivariate analysis.

Table 4.2: Presence/absence table of meso-zooplankton across the warm core eddy during April 2015. Stations marked with * denote where trawls were also carried out, the station marked with ** denotes where only trawl samples were carried out. Taxa in **bold** print were captured by trawl net only. Taxa with † superscript were captured by plankton net only.

Station	9*	10	11*	12	13*	14**
Hydrozoa						
***Aequorea* sp.**						x
Aglantha digitale†		x			x	
Hydromedusae	x	x	x		x	
Leuckartiara species	x	x				
Cunissa alderi†		x				
Phialopsis diegensis†	x	x	x	x		
Rhopalonema velatum	x	x		x	x	
Scyphozoa						
Pelagia noctiluca	x				x	x
Periphylla periphylla	x		x		x	x
Scyphomedusae unidentified	x	x	x	x	x	
Atolla wyvillei			x			x
Siphonophora						
Abylopsis tetragona†		x		x		
Crystallophyes amygdalina		x	x			
Chuniphyes mulitdentata	x	x	x		x	x
Ampicaryon acaule			x			
Agalma elegans†			x			
Ceratocymba sagittata†			x			
Desmophyes annectens†		x				
Dimophyes arctica	x	x	x	x	x	
Diphyes dispar						x
Diphyidae	x	x	x	x	x	x
Hippopodius hippopus	x	x	x			x

Table 4.2 continued

Station	9*	10	11*	12	13*	14**
Lensia achillies	x	x			x	
Lensia conoidea	x	x				
Lensia fowleri		x				
Lensia hotspur†				x		
Lensia multicristata	x			x		
Lensia subtilis	x	x	x	x		
Nanomia cara			x			
Praya dubia			x			
Physonectae	x		x	x		
Prayidae	x	x	x	x		
Sphaeronectidae†		x		x		
Vogtia glabra	x		x		x	
Vogtia serrato			x	x		
Vogtia spinosa	x		x			
Ctenophora						
Pleurobrachia pileus	x					x
Beroe species	x	x	x	x	x	
Mollusca						
Cavoliniidae	x	x	x	x		
Cephelapoda	x					
Clionidae	x	x	x	x		
Pterotracheoidea	x	x	x	x	x	x
Crustacea						
Hyperiidea	x	x	x	x	x	
Euphausiacea	x	x	x	x	x	
Ostracoda	x	x	x	x	x	
Phronimia spp.	x		x	x	x	
Copepoda	x	x	x	x	x	
Tunicata						
Appendicularia	x	x				
Dolioletta gegenbauri		x				
Doliolidae species	x	x			x	
Salpa fusiformis	x	x	x		x	
Salpa species	x		x	x	x	x
Thalia democractica†	x					
Polychaeta						
Tomopteris species	x	x		x	x	
Fish larvae	x	x	x		x	
Chaetognatha	x	x	x	x	x	
Foraminifera	x	x	x	x	x	

Multinet samples

Thirty-one zooplankton taxa were recorded in the multinet samples. This included 19 gelatinous species or genera; 13 siphonophores, 2 hydromedusae, 3 tunicates and an unidentified scyphomedusae. The total abundance of the gelatinous taxa ranged from 0 – 38310 indiv.1000 m^{-3}, however, the appendicularians accounted for the majority of that number and excluding them resulted in an abundance ranging from 0 – 1677 indiv.1000 m^{-3}. The mean gelatinous abundance (excluding appendicularians) across all depths and stations was 456 ± 410 indiv.1000 m^{-3}. The mean gelatinous abundance outside and inside the eddy was 660 ± 349 and 49 ± 54 indiv.1000 m^{-3}, respectively (Fig. 4.5A). The highest abundance and diversity was outside the eddy at stations 9 and 10, in the 300 and 420 m depth layers (Figs. 4.5A & 4.5B). The dominant species were *Salpa fusiformis* and *Chuniphyes multidentata*, reaching maximum abundances of 677 and 452 indiv.1000 m^{-3} respectively, outside the eddy at station 9. Collectively, diphyid siphonophores were highly abundant reaching a maximum of >900 indiv.1000 m^{-3}, outside the eddy at station 10 (Fig. 4.5A). A non-metric dimensional scaled (nMDS) ordination of the community assemblage indicated 2 clusters of samples (Fig. 4.6), the first containing the samples from stations 9-10 and the second containing samples from stations 11-13., ANOSIM tests indicated the differences in the community between stations was significant (r = 0.43, $p < 0.001$), and the difference between stations grouped as ‘outside’ or ‘inside’ were significant (r = 0.64, $p < 0.001$). Depth was not significant (r = 0.099, p = 0.15).

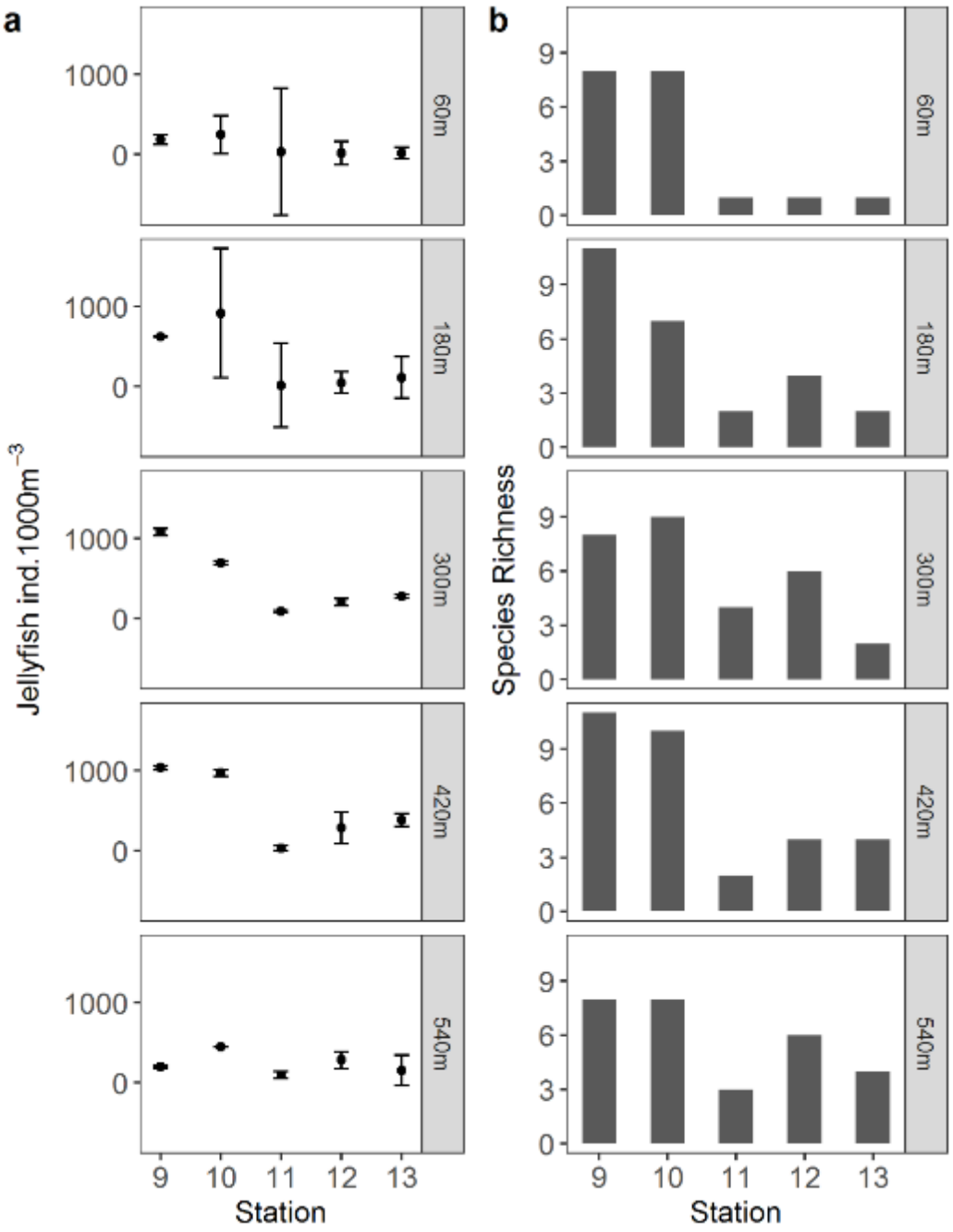


Figure 4.5: The (A) mean gelatinous abundance ± SD (N=2) at each sample depth (excluding appendicularians) and (B) the total number of gelatinous taxa at each sample depth. The displayed depth is the central depth of the sampled water column.

Including all zooplankton (Fig. 4.7), the dominant taxa were copepods (range 223 – 112200 indiv.1000 m^{-3}), foraminiferans (range 0 – 47170 indiv.1000 m^{-3}) and appendicularians (range 0 – 26260 indiv.1000 m^{-3}). Notably, the abundance of copepod exuvia (range 2023 – 139400 indiv.1000 m^{-3}) often exceeded the number of live copepods. Appendicularians were only recorded in the top 120 m at stations 9 and 10, being completely absent from all other samples.

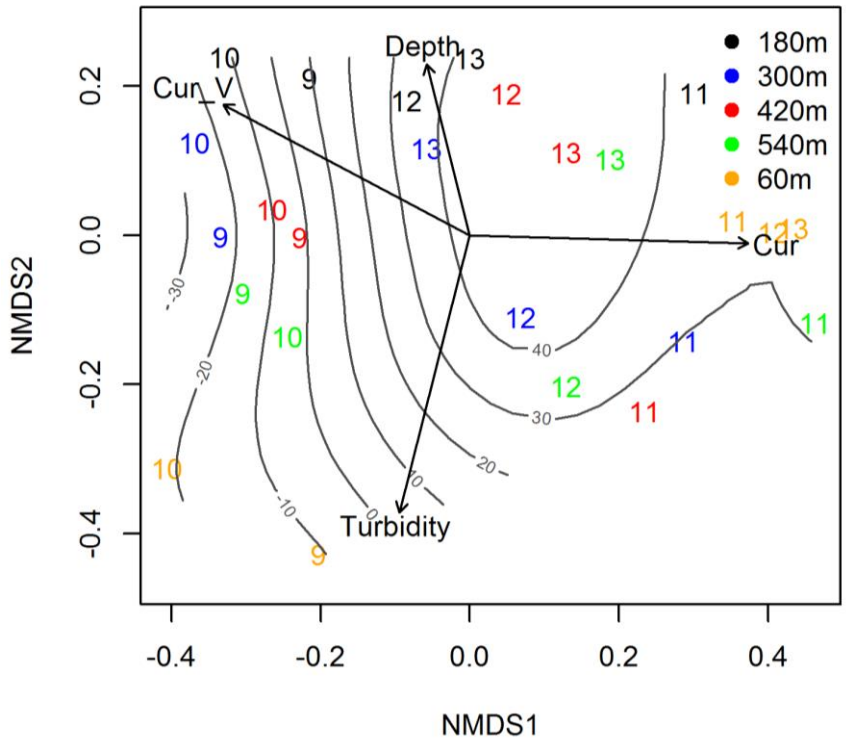


Figure 4.6. Non-metric dimensional scaled ordination of the gelatinous community from stations 9-13. The contours are the sea surface height anomaly displayed as a fitted surface with the dissimilarity matrix, and the arrows indicates environmental parameters fitted to the dissimilarity matrix, with the direction and magnitude indicating the respective influence of each parameter over the community. Cur_V = Vertical current, Cur = Horizontal current.

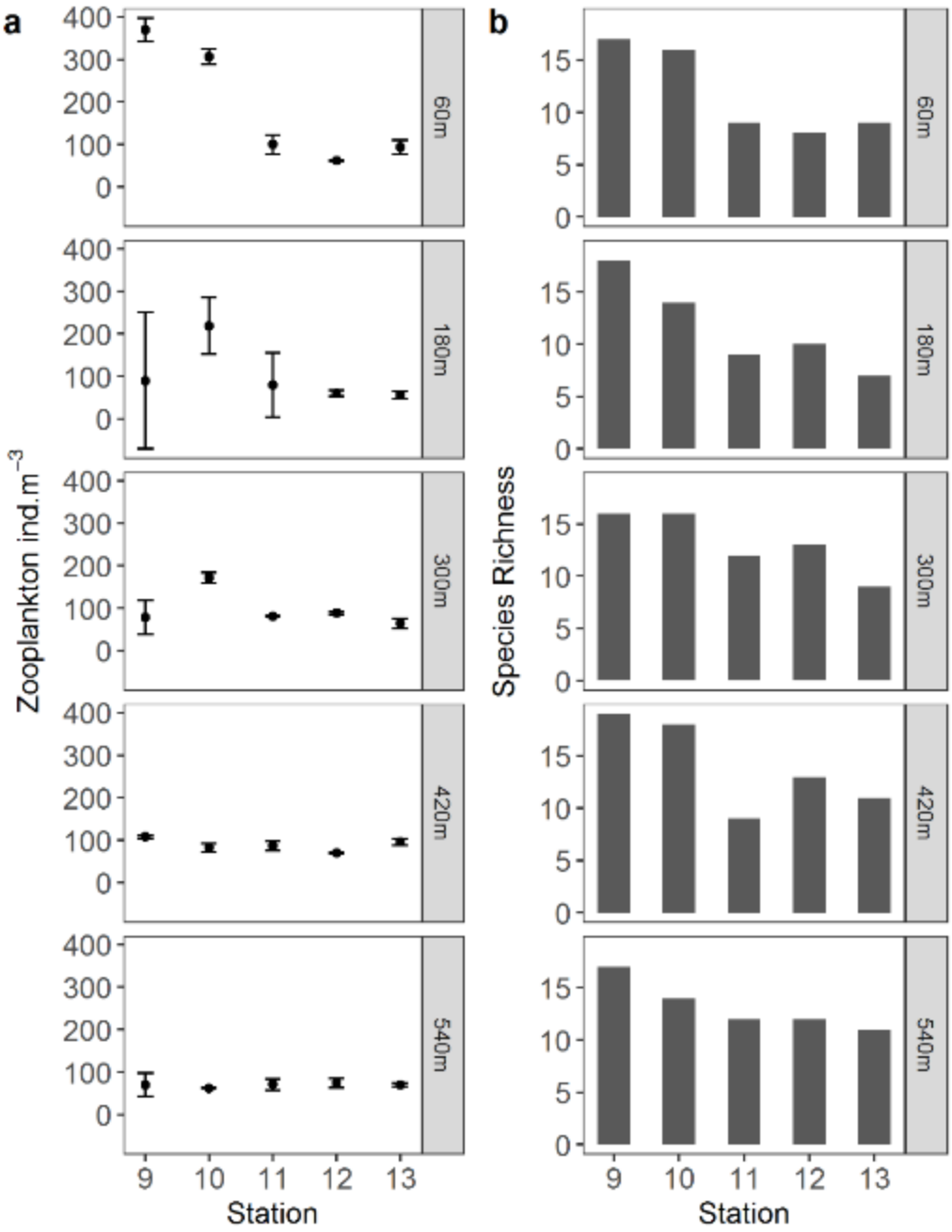


Figure 4.7: The (A) mean zooplankton abundance ± SD (N=2) at each sample depth and (B) the total number of zooplankton taxa at each sample depth. The displayed depth is the central depth of the sampled water column.

In addition, the copepods, foraminifera, chaetognaths, polychaetes and molluscs reached their maximum abundance at stations 9 and 10, in the two upper most layers, i.e. 60 m and 180 m (Fig. 4.7A). Ostracods were also most abundant at stations 9 and 10, but were concentrated at 300 and 420 m. The larger macro-zooplankton like *Phronemia* spp., euphausiids and hyperiids were more inclined to be found inside the eddy. *Phronemia* reached their highest abundance at station 13, at 180 m; both the euphausiids and hyperiids shared a similar distribution, being found in all the surface samples, and predominantly inside the eddy in the deeper samples (Fig. 4.7). ANOSIM tests indicated the differences in the community between stations was significant ($r = 0.52$, $p < 0.001$), and the difference between stations grouped as 'outside' or 'inside' were significant ($r = 0.85$, $p < 0.001$). Differences in community composition with respect to depth were not significant ($r = 0.048$, $p = 0.23$).

Environmental variables

The subset of environmental variables with the best correlation, with the gelatinous community NMDS ordination (Fig. 4.6) included temperature, current velocity and the northern component of the current velocity (Mantel, $r = 0.56$, $p < 0.001$). Further analysis of variance using ADONIS with eddy region as a grouping factor, indicated that temperature, current velocity and turbidity were the most influential variables (Table 4.3). When the potential prey species were included as environmental variables, none were identified as significant. When the total zooplankton community NMDS ordination was considered, the subset of environmental variables included temperature and current velocity (Mantel, $r = 0.54$, $p < 0.001$). Further analysis of variance using ADONIS with eddy region as a group

factor, indicated that temperature, current velocity, turbidity and backscatter were the most influential variables (Table 4.3).

Trawl nets

The trawl samples captured 21 species in total, 11 of which were exclusive to trawl samples. All of the taxa were jellyfish except for the large crustacean *Phronemia*, which resides in an empty salp body. In some samples the empty '*Phronemia* houses' outnumbered the number of actual *Phronemia*, e.g. at station 9, only houses were recorded.

Table 4.3: ADONIS multivariate permutational analysis of the zooplankton community and gelatinous community dissimilarity (Bray-Curtis) matrices. The eddy region, i.e. 'outside' and 'inside' was used as a grouping factor in the model. * Cur. Vel. is the maximum recorded current velocity.

Gelatinous zooplankton ADONIS output

	Df	Sums Sqs.	Mean Sqs.	*F*	r^2	Sig.
Temperature	1	0.8967	0.89665	6.6144	0.17350	0.001
Cur. Vel.*	1	1.1321	1.13206	8.3509	0.21905	0.016
Turbidity	1	0.2925	0.29247	2.1574	0.05659	0.034
Residuals	21	2.8468	0.13556		0.55085	
Total	24	5.168			1.00	

Zooplankton community ADONIS output

	Df	Sums Sqs.	Mean Sqs.	*F*	r^2	Sig.
Temperature	1	0.22564	0.22564	6.8851	0.14954	0.001
Cur. Vel.*	1	0.43729	0.43729	13.3433	0.28980	0.005
Turbidity	1	0.10758	0.10758	3.2827	0.07130	0.010
Back scatter	1	0.08296	0.08296	2.5314	0.05498	0.041
Residuals	20	0.65544	0.03277		0.43438	
Total	24	1.50891			1.00	

The large species, *Periphylla periphylla, Atolla wyvillei, Pelagia noctiluca* and *Praya dubia* were only captured by trawl samples and *P. periphylla* was substantially more abundant than the other species, with the highest numbers, at station 9 and 13. At those stations, the 350 m trawls captured greater numbers, 11 and 27 *P. periphylla*¸ respectively, compared with the 500 m trawl, 6 and 13 *P. periphylla*¸ respectively. The size and mean mass of *P. periphylla* medusae was substantially greater at station 13 (0.85 kg) compared with mean weight at station 9 (0.33 kg). *Atolla* was rare, with one medusa captured inside the eddy during the deep trawls (500 m) at stations 11 and 14. *Praya dubia* was only recorded at station 11, with nectophore numbers indicating two colonies at both depths.

Plankton nets

24 macrozooplankton taxa were recorded from the plankton nets, 10 of which were exclusive to plankton net samples. Taxa included 12 siphonophores, five hydromedusae, three tunicates and one ctenophore. Non-gelatinous taxa included *Phronemia* species, a large (>10 cm) gastropod mollusc of the pterotracheidae family and *Tomopteris* species. The majority of records were of single individuals in a sample, however, relatively high numbers of *Salpa fusiformis, Phialopsis diegensis* and *Beroe* species were found outside the eddy at stations 9 and 10, with a maximum of 38, 9 and 13 individuals, respectively. Inside the eddy, the maximum number recorded was 5, 5 and 3 individuals, respectively. *Rhopalonema velatum* was also found in relatively high numbers, however, the maximum was inside the eddy at station 11 and 12, where 6 and 12 individuals were recorded respectively. The maximum recorded outside the eddy was three individuals at station 9. Diphyid nectophores were rare, with a maximum of 1 in any one sample (mean vol. 1335 ± 471

sd m^{-3}), however, this is almost certainly an underestimate as plankton net samples were not enumerated using a microscope.

Discussion

Gelatinous zooplankton are ubiquitous throughout pelagic ecosystems and are considered important predators with the capacity to dominate ecosystems (Graham et al., 2001; Robison, 2004), and alter nutrient and biogeochemical cycling (Pitt et al., 2009; Pitt et al., 2013). While broad patterns in distribution and abundance are evident across ocean basins (Mackie et al., 1987; Gibbons and Richardson, 2008; Hosia et al., 2008; Arai, 1997), the mesoscale heterogeneity, which is widely reported for phytoplankton, micronekton and higher predators (Owen, 1981; Wiebe et al., 1985; McGillicuddy, 2016), has received little attention for gelatinous zooplankton. Considering that gelatinous zooplankton have the potential to transfer biomass upward or to divert it from higher tropic levels (Robison, 2004; Condon et al., 2011), it is important to understand how they associate with possibly the most widespread physical features in the pelagic environment (Chelton et al., 2011).

This study revealed a 12-fold decrease in the abundance of gelatinous zooplankton within a warm core eddy compared with the adjacent cold water, with the greatest abundance and diversity in the middle sample depths, outside the eddy (Fig. 4.5). This decline in abundance was evident for gelatinous taxa at all trophic levels, from the appendicularians to the larger calycophoran siphonophores (Fig. 4.8). The only group to show in increase inside the eddy were the Physonectae and due to the difficultly in interpreting the abundance of colonies from separate pieces (Totton and Bargmann, 1965) the apparent increase must be viewed with caution. The diphyid

siphonophores were, by some considerable margin, the most abundant group and their abundance across the eddy was broadly coherent with the 10°C isotherm, decreasing by an order of magnitude above the thermocline and within the eddy core (Fig. 4.8). The significant change in community composition is driven by decreases in all the zooplankton taxa, except for the large crustaceans, the euphausiids, hyperiids amphipods (Fig. 4.9) and suggests that the eddy core is a highly unfavourable habitat for most of the mesozooplankton and macrozooplankton recorded here. Pelagic tunicates, and especially appendicularians, can respond rapidly (in less than 24 hrs) to primary productivity (Anderson, 1998; Holland, 2016), and their virtual absence from the eddy core indicates an oligotrophic ecosystem. It follows then, that their greater abundance outside the eddy (Fig. 4.8) is a strong indication of higher primary production and microscopic particulate matter outside the eddy (Alldredge and Madin, 1982; Holland, 2016). Further evidence of the paucity of the eddy core was the almost complete absence of copepods, in point of fact, only four multinet samples inside the eddy found an abundance greater than 1 copepod m^{-3}. Consequently, it is highly unlikely that the diphyid siphonophores, which predominantly prey on copepods (Mackie et al., 1987; Purcell, 1997), could survive in the eddy core.

Interpreting distribution and abundance of the larger calycophoran siphonophores, like the physonects, must be carried out with a little more caution. Although the multinet samples indicated a negligible presence in the eddy core (Fig. 4.8), several genera were captured in the plankton and trawl samples (*Praya*, *Hippopodius* and *Vogtia* spp.), indicating the inaccuracy of the multinet estimates in assessing these rare taxa (Mackie et al., 1987). The increased abundance of the large amphipods in the eddy core (Fig. 4.9), which are known to feed upon and parasitize gelatinous taxa (Arai, 2005; Burridge et al., 2017) is possibly indirect evidence that

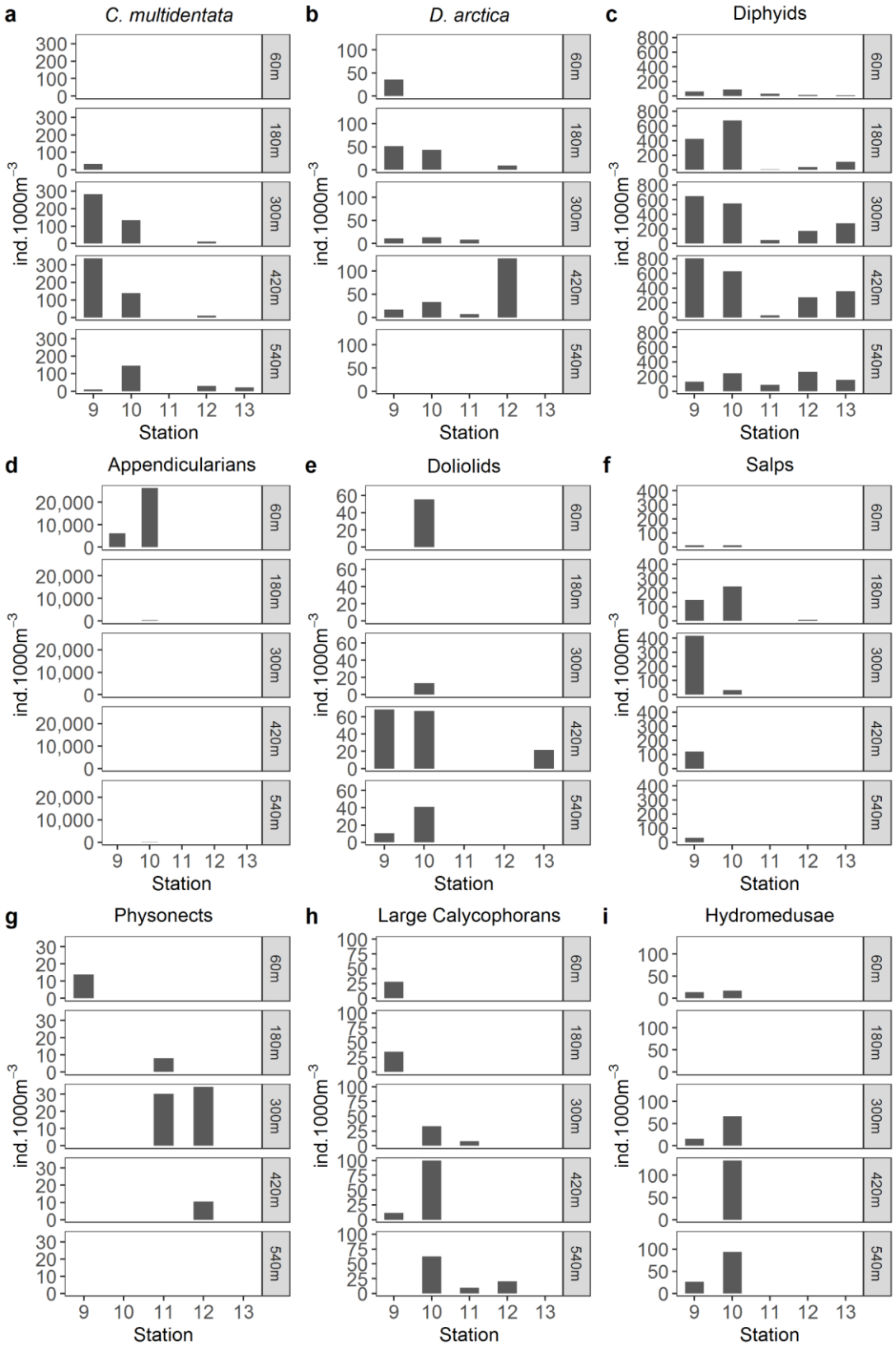


Figure 4.8. Abundance (individuals 1000 m^{-3}) of the major gelatinous taxa across the warm core eddy. Note the different scales on the y axis.

these larger genera are present in the core as well. This highlights the diverse ecological traits across the gelatinous taxa recorded here, and the inadequacy of relying on a single sampling method for quantitative estimates, nonetheless, it does not detract from the profound community differences already described.

These significant changes in the gelatinous community have important implications for biogeochemical cycling across mesoscales, as gelatinous taxa can divert biomass and nutrients away from the 'traditional' bottom to top trophic pathways (Condon et al., 2011; Pitt et al., 2013). The excess mucus excreted by gelatinous taxa contains carbon and nitrogen, which can be utilised by microbes and phytoplankton, thereby increasing biomass in the microbial foodweb (Biggs, 1977; Condon et al., 2011; Pitt et al., 2013). In addition, gelatinous predators can release the phytoplankton from copepod grazing, further enhancing primary productivity (Pitt et al., 2007), and potentially increasing biomass at the base of the food web. Conversely, where tunicate abundance increases they can increase the downward flow of carbon through the continuous shedding of their feeding apparatus which can sink rapidly (Robison et al., 2005). Therefore, depending on which gelatinous taxa are abundant at any one time, biomass might be concentrated or diverted from the base of the food web. Inside the eddy, the prevalence of higher level taxa, many of which are mutual predators, with longer generations times can retain biomass and nutrients in the mid-trophic levels, thereby reducing the turnover of biogenic carbon characteristic at lower trophic levels (Robison, 2004). However, when these longer lived taxa die, the resultant 'jelly-falls' can remove substantial biomass from the mid-trophic levels and deliver it to to the sea bed in short periodic pulses (Lebrato et al., 2012).

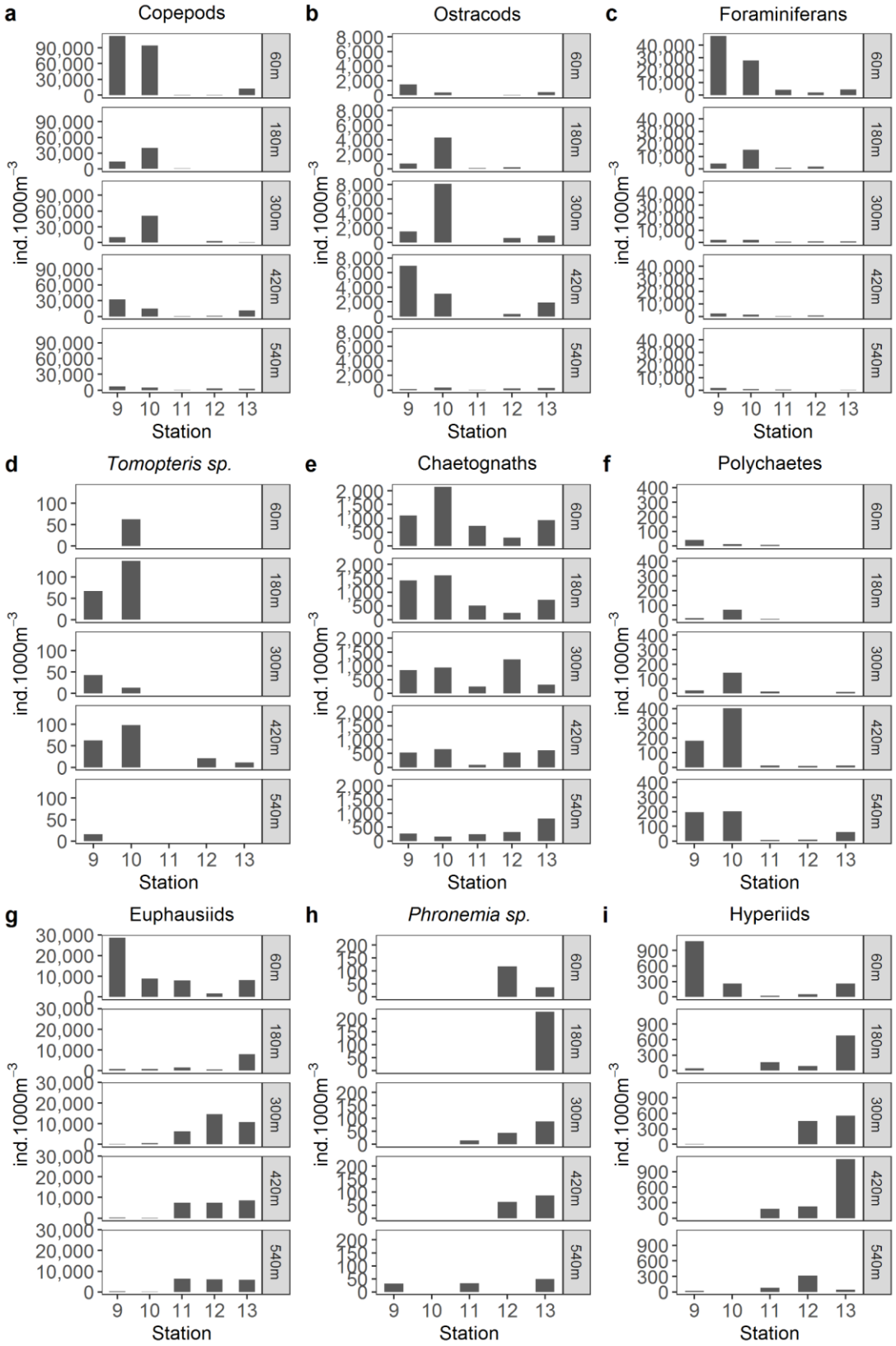


Figure 4.9. Abundance (individuals 1000 m^{-3}) of large macro-zooplankton across the warm core eddy. Note the different scales on the y axis.

A heterogeneous gelatinous distribution also has implications for a range of oceanic vertebrate predators including marine turtles (Hays et al., 2008; Hays et al., 2016), over 120 fish species (Purcell and Arai, 2001; Arai, 2005) and sea birds (Arai, 2005; Scales et al., 2014a). Indeed, there is good evidence that many of these gelatinous predators' forage along frontal zones (Scales et al., 2014a; Sousa et al., 2016), with satellite biotelemetry demonstrating substantial leatherback turtle foraging at an eddy in the north east Atlantic (Doyle et al., 2008b). While a single eddy is obviously transient, the most intense eddy regions such as the NAC eddy field are permanent (Stommel, 1958; Rossby, 1996) and potentially offers a reliable foraging zone to important migrating oceanic predators. Whether anticyclonic eddies physically aggregate gelatinous zooplankton remains an open question, one which the wide resolution of sampling here cannot address, however, there is little evidence of aggregation of zooplankton at other oceanic mesoscale features (Graham et al., 2001). Where gelatinous taxa have responded to dynamic boundary systems, it appears to be restricted to shallow shelf regions where upwelling and the resultant high primary productivity has enhanced local populations of pelagic tunicates (Deibel, 1985; Luo et al., 2014). Substantial changes in primary productivity are entirely possible in warm core eddies (McGillicuddy, 2016), and evident in previous research during the Warm Core Rings Project (Hitchcock et al., 1987), however, whether similar processes in the oceanic ecosystem provoke the same response from gelatinous taxa is unknown.

The higher abundance of pelagic tunicates found outside the eddy here, were *ca.* 75 km from the high velocity eddy boundary where the measured (ADCP) current velocities were low. This would suggest that the eddy had minimal effect at these stations and vertical mixing in the epipelagic zone was the likely driver of tunicate abundance (Deibel, 1985; Holland, 2016). Interestingly, within the boundary zone

where the horizontal currents were greatest, there were also substantial downward vertical currents (Figure 4.4B). Downwelling is a characteristic of warm core anticyclonic eddies (Gaube and McGillicuddy, 2017), removing organic matter and nutrients from the surface water and exacerbating the oligotrophic nature of the core water mass. This would suggest that the oligotrophic core water is maintained in an oligotrophic state by inherent eddy mechanisms, however, Ekman transport and eddy stirring can also enhance upward nutrient flux in eddies, having the opposite effect (Gaube and McGillicuddy, 2017). In this instance, the history of the eddy is unknown, thus it become difficult to speculate on which mechanism is in effect. The broad outcome of the Warm Core Rings project demonstrated that warm core eddies can be very isolated bodies of water (Wiebe et al., 1985), and more recent research modelling anticyclonic eddy dynamics has also demonstrated the propensity for eddies to retain particles (Samuelsen et al., 2012). While the sampling here cannot define the community transition outside the boundary with high resolution, the consistency of the community in the eddy core stations would suggest minimal exchange into the eddy.

Considering the changing zooplankton community composition, there appears to be three distinct groups: 1) a warm surface water group composed of copepods, ostracods, foraminiferans and appendicularians; 2) an eddy core group overlapping with group 1 but with vastly reduced numbers of most taxa, except the large predatory crustaceans; 3) a cold water group dominated by the siphonophores, but also including tunicates and rare hydromedusae (See figures S4.2 & S4.3 in supporting material). These groupings are not meant to imply a strict spatial separation of taxa, for example, *Salpa* species and *R. velatum* were recorded in plankton net samples, in the top 200 m, and clearly are present in the group 1. Nonetheless, the best quantitative estimates

from the multinet place these taxa in group 3. This community structure is not dissimilar to the mytophid fish community structure found across a warm core eddy off eastern Australia (Brandt, 1981). Brandt (1981) recorded five distinct groups; 'outside eddy cold water species', 'eddy species', 'warm water species', 'widespread species' and 'cold water species'. The increased number of communities identified by Brandt (1981) is possibly due to niche differentiation of the more diverse myctophid fish community, i.e. 250 species (Catul et al., 2011) compared with the predominantly siphonophore community here, i.e. 175 species, (Mapstone, 2015). However, one group was comprised of only a single species and this suggests that both myctophids and siphonophores potentially share traits in response to a warm core eddy.

Given the location of the eddy within the NAC, it is not surprising that the gelatinous community, in the main, reflected the southerly origin of the NAC water. The numerical dominance of calycophoran siphonophores, and the species present was consistent with previous surveys in the North Atlantic, with species typical of Sub-Arctic Intermediate Water (SAIW) and North Atlantic Central Water (NACW) (Pugh, 1977; Pugh, 1984; Hosia et al., 2008). The most abundant species, *Chuniphyes multidentata* and *Dimophyes arctica* have been found from 41°N - 60°N along the North Atlantic Ridge (Hosia et al., 2008), and *D. arctica* has been categorised as eurybiotic, i.e. living in all biogeographical regions (Mackie et al., 1987). Their distribution below the epipelagic here is typical for both species (Hosia et al., 2008; Mapstone, 2009) and neither are indicative of a particular hydrographic origin. The *Vogtia* species and small Diphyinea like *Lensia fowleri, Lensia subtilis* have been identified as having a predominantly southerly distribution, below 43°N in the north Atlantic (Hosia et al., 2008). The hydromedusae *Rhopalonema velatum* and *Phialopsis diegensis* are both widespread oceanic species, however *R. velatum* is considered a

distinctly warm water species generally found in tropical or subtropical regions, while *P. diegensis* is considered a cold northern species (Russell, 1953; Kramp, 1961). *Lensia conoidea* was present at station 9 and although in low numbers, it is considered typical only in surface waters north of the Sub-Polar Front (Mackie et al., 1987; Hosia et al., 2008), and in more southerly latitudes is generally found below 1000 m depth (Pugh, 1977).

The low abundance or absence of many of these southerly gelatinous taxa from the eddy core serves to illustrate the different origins of the eddy and the surrounding water. The differences in abundance between the eddy and the surrounding water are profound and highlight a heterogeneous gelatinous zooplankton distribution that is likely replicated across vast regions of the pelagic ecosystem (Chelton et al., 2011). The impact of this heterogeneity on important ecosystem functions, i.e. biogeochemical cycling, is probably underestimated at this point in time, and further studies at a much finer scale are needed. Also, because gelatinous zooplankton occupies a range of trophic levels, future studies must attempt to solidify the relationships between gelatinous prey/predator interactions and accurately assess the contribution of gelatinous taxa to oceanic ecosystems.



Chapter 5

Investigating the efficacy of bubble curtains as a barrier against jellyfish

Abstract

In recent years, salmon aquaculture has struggled to mitigate the impact of harmful jellyfish species in Northern Europe and beyond. Typically, large aggregations of jellyfish are carried by currents through salmon cages, leading to unsustainable mortality levels in some years. One potential solution is to create a bubble curtain barrier to exclude jellyfish from cages. This study investigated the efficacy of a bubble curtain as a jellyfish barrier in the context of key aquaculture locations in Ireland. Field tests on bubble curtains provided mixed results: a high air flow bubble curtain set at 5 m depth in S.W. Ireland effectively deflected large compass jellyfish, however, a low air flow bubble curtain set at 5 m depth in N.W. Ireland did not significantly impact the abundance of small hydromedusae on either side of the bubble curtain. Flume tank experiments demonstrated that increased wave height, and increased air flow, increased jellyfish transport through the curtain and the lateral movement was consistent with Stokes Drift, i.e. an elliptical motion that includes forward movement with each wave. These results suggest that sites with relatively high wave energy may be unsuitable for bubble curtain use, and that the variable size and shape of jellyfish may be an important factor in jellyfish – bubble curtain interactions.

Introduction

It is widely accepted that jellyfish blooms have become an important issue for the marine finfish aquaculture industry globally (Purcell et al., 2013; Bosch Belmar et al., 2014). However, the available literature is biased towards interactions between jellyfish and farmed Atlantic Salmon, *Salmo salar* Linnaeus 1758, in north west Europe (Doyle et al., 2008a; Ferguson et al., 2010; Hamish et al., 2010; Nickell et al., 2010; Baxter et al., 2011a; Baxter et al., 2011b; Rodger et al., 2011b), however, the problem is becoming increasingly apparent in other areas where jellyfish biomass and the incidence of blooms appear to be increasing (Brotz et al., 2012; Condon et al., 2013). The geographic bias in research and reporting is most likely a reflection of the long tradition and economic importance of salmon aquaculture in north western European countries with well-developed research structures, rather than a reflection of jellyfish ecology. Recent research in the Mediterranean has revealed the deleterious impact of jellyfish on farmed sea bass *Dicentrarchus labrax* and gilthead sea bream *Sparus aurata* (Bosch-Belmar et al., 2016a; Bosch-Belmar et al., 2016b), and demonstrates a much wider impact on marine finfish aquaculture.

Jellyfish can injure fish directly through contact with jellyfish stinging capsules called nematocysts, or indirectly by clogging cages and increasing the risk of hypoxia (Doyle et al., 2008; Bosch Belmar et al., 2014). Gill damage in several fish species has been demonstrated by laboratory experiments (Baxter et al., 2011b; Bosch-Belmar et al., 2016b) and in field studies (Baxter et al., 2011a; Bosch-Belmar et al., 2016a). The size of the jellyfish in relation to the cage mesh is largely irrelevant as the medusae are easily fragmented against cages and loose jellyfish pieces, loaded with nematocysts can easily enter cages. The accumulation of large jellies against the exterior wall of fish cages can reduce the flow of fresh oxygenated water through

cages, leading to stagnation and asphyxiation of the fish (Klebert et al., 2013). In fact, gill damage and decreased oxygen concentration can act synergistically, increasing the deleterious impact on the fish (Bosch-Belmar et al., 2016a). At lower jellyfish densities rapid mortality is unusual, however, the initial injury can lead to secondary bacterial infections and 'gill disease' (Rodger et al., 2011a). Furthermore, the presence of the bacteria *Tenacibaculum maritimum* on infected fish and on some jellyfish species, suggests that jellyfish may also be a source of secondary infection (Ferguson et al., 2010; Delannoy et al., 2011).

The economic cost of harmful jellyfish is highly variably from year to year, however, some figures from northern Europe indicate how serious this issue has become. Over a six-year period in Scotland (1999 - 2005), 60% of mortalities were attributed to harmful zooplankton (Rodger et al., 2011a). In Ireland, from 2003 – 2005, the majority of mortalities at farms were attributed to gill disease, averaging 12%, but reaching *ca.* 80% (Rodger, 2007). In some instances, catastrophic fish kills can happen when large smacks (aggregations) of the scyphomedusae *Pelagia noctiluca* are carried into shallow coastal waters (Fig. 5.1). *Pelagia noctiluca* has become a primary agent of gill disease in European countries, however, several other species are implicated, see Rodger et al. (2011a) for list of documented incidents. Elsewhere, gill damage has tentatively been assigned to *Aurelia aurita* in Tasmania (Adams et al., 2004), scyphomedusae and hydromedusae in Chile (Palma et al., 2007). Finfish aquaculture has become increasingly important, accounting for 49.8 million tonnes of annual aquaculture production globally, with an estimated US$99.2 billion (FAO, 2016). Considering projected increases of *ca.* 40% in finfish aquaculture globally (FAO, 2016), and changing pelagic ecosystems which may favour jellyfish species (Boero et

al., 2016), interactions between fish farms and jellyfish are likely to increase, with commensurate increases in economic cost.

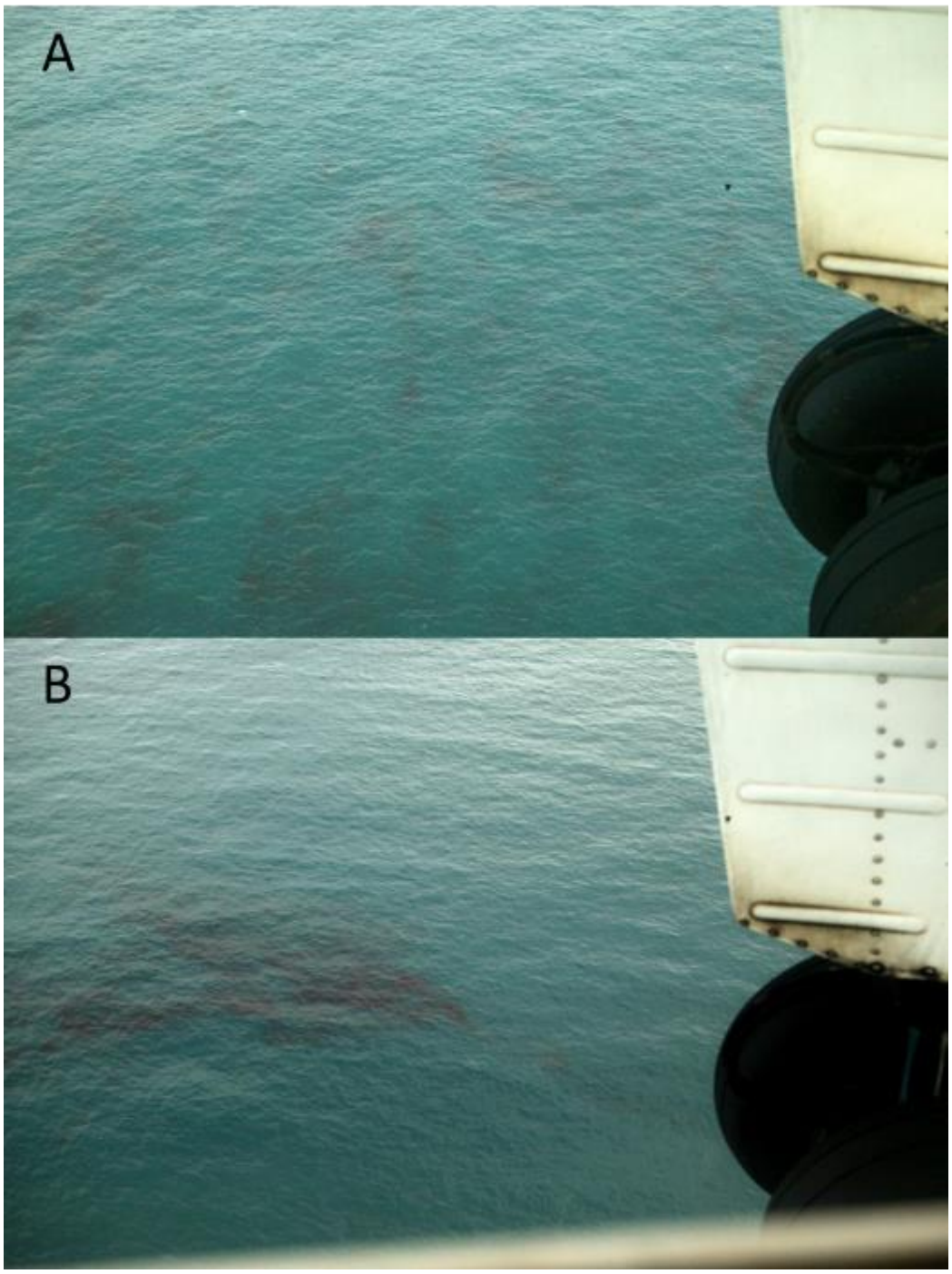


Figure 5.1: Photographs taken during aerial surveys (flying at 200m altitude) off Loop Head, Co Clare, west coast of Ireland, showing large smacks of *Pelagia noctiluca* near the surface. These smacks were distributed over an area of 10s km^2 and individual aggregations were estimated to reach over 100 m in length.

At the present time, mitigating against the impact of harmful jellyfish is extremely difficult and managers rarely have advanced warning. Mitigation measures to date include cessation of feeding, oxygenation of cages and making fish shoal deeper in order to avoid surface concentrations of jellyfish (Ruane et al., 2013). A more drastic measure is to harvest fish early to avoid damage, meaning that they have not achieved market size or value and is therefore economically expensive. In addition, evacuation of a large number of cages containing fish at different stages of maturity is simply not feasible.

The concept of a bubble curtain as a barrier to prevent jellyfish entering fish cages has been suggested as a potential mitigation measure (Rodger et al., 2011a; Ruane et al., 2013). In concept, a bubble curtain is simple; compressed air is pumped through a porous tube and the escaping air rises to the surface in a plume of expanding bubbles. The plume entrains water creating an upward current which is deflected horizontally at the surface. Objects which are carried into the bubble curtain are pushed to the surface, where they may be collected or flow around the 'protected' body of water. Bubble curtains are currently used in oil spill mitigation, effectively retaining surface oil, however, the current, wave energy, and wind speed can affect the efficacy of the barrier (Lo, 1996). Bubble curtains have been installed at power station coolant water intakes in several countries (e.g. Japan), to prevent jellyfish clogging intake pipes (Masilamoni et al., 2000). Unfortunately, details concerning the setup and efficacy of these systems have not been published and an objective assessment of their performance is lacking. A brief experiment, carried out in Mulroy Bay, Donegal, Ireland, during 2004, was hampered by the low abundance of jellyfish and produced equivocal results (Ratcliff, 2004). It did, however, highlight some of the logistical difficulties such as biofouling and power consumption which would need to

be addressed. Therefore, the aim of this study was to assess the efficacy of a bubble curtain as a barrier system to prevent jellyfish incursions into finfish aquaculture cages.

Material and Methods

Bubble curtain tests in Bantry Bay

In cooperation with Marine Harvest Ireland Ltd., a series of small scale experiments were undertaken in Bantry Bay, southwest Ireland (Fig. 5.2), during September 2014 and during June to September 2015 to test a small scale bubble curtain.

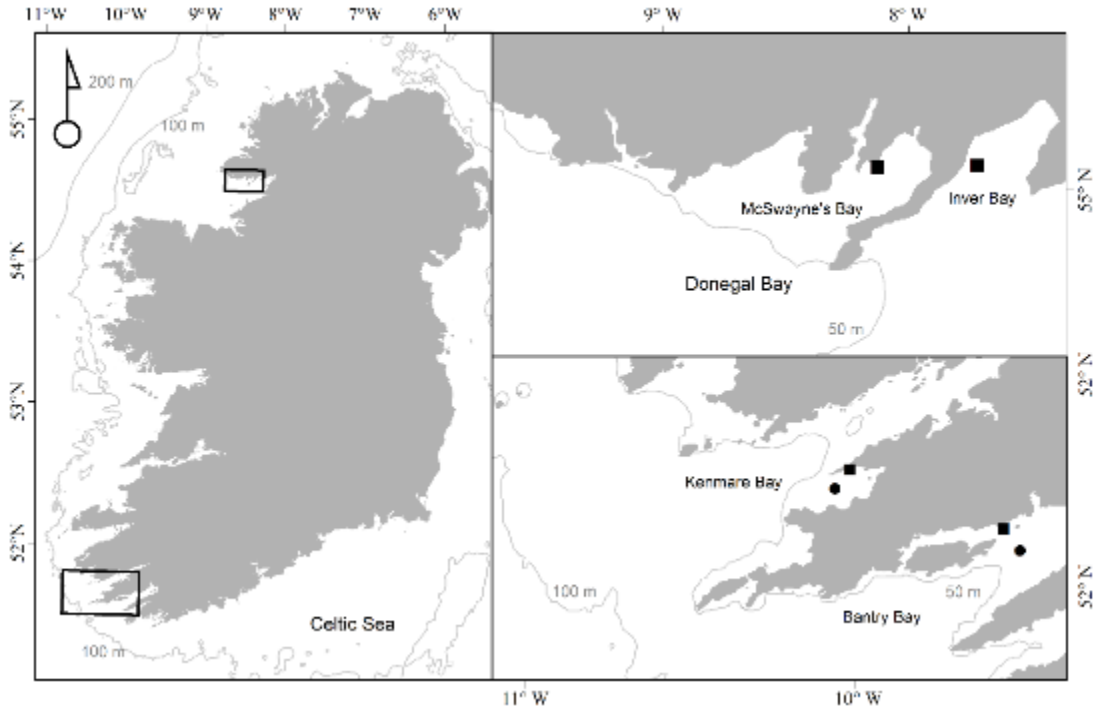


Figure 5.2: Location of bubble curtain field experiments, at Marine Harvest Ireland Ltd. farms in the southwest and Ocean Farm farms in the northwest of Ireland. Square symbols are salmon farms and the circles are the DVM sampling stations in the southwest.

Test 1; A bubble tube was made using 105 mm PVC tubing, with 1 mm holes drilled every 50 cm. The total tube was 8 m long, and compressed air was provided by an Atlas Copco XAS47 mobile compressor, capable of delivering 2.5 m^3 per minute at 7 bar. The tube was suspended at 5 m depth from a barge and two divers recorded any

interactions between jellyfish and the bubble curtain. Specifically; did jellyfish get entrained in the bubble curtain, at what distance from the curtain was an effect evident, how did the surface current effect the jellyfish, and what was their subsequent behaviour?

Test 2; A bubble tube was made using 25 mm HDPE tubing, with 1 mm holes drilled every 50 cm. This tube was 25 m long and supplied with air using the same compressor as test 1 above. During tests the tube was suspended at 5 m depth between the barge and a moored RIB and two snorkelers recorded the interaction between any jellyfish present and the bubble curtain.

Bubble curtain tests in Donegal Bay

During June – September, 2016, at the Ocean Farms farm in Inver Bay, a six cage array was encircled with perforated bubble tubing from Canadian Pond Ltd. The 2 cm diameter, *ca.* 800 m long tubing was supplied with air from a Compair C200TS compressor, capable of delivering 20 m^{-3} per minute of air at 14 bar (Fig. 5.3A). The tube was installed 5 m below the surface using the anchoring network around the cages as attachment points. This depth was chosen because plankton sampling indicated that hydromedusae were consistently aggregated in the top 5 m at the farm location (Haberlin. D., unpublished data). The main feedline from the compressor was split into eight feedlines (Fig. 5.3B) for the bubble tube in order to equalise the pressure throughout the tube as much as possible. This also allowed certain sections of the tube to receive greater airflow for experimentation. In order to test the effectiveness of the bubble curtain, during the period when it was in operation the daily plankton tows which were inside the bubble curtain were supplemented with another series of samples taken outside the bubble curtain perimeter. Sample analysis was as described, for Bantry samples.

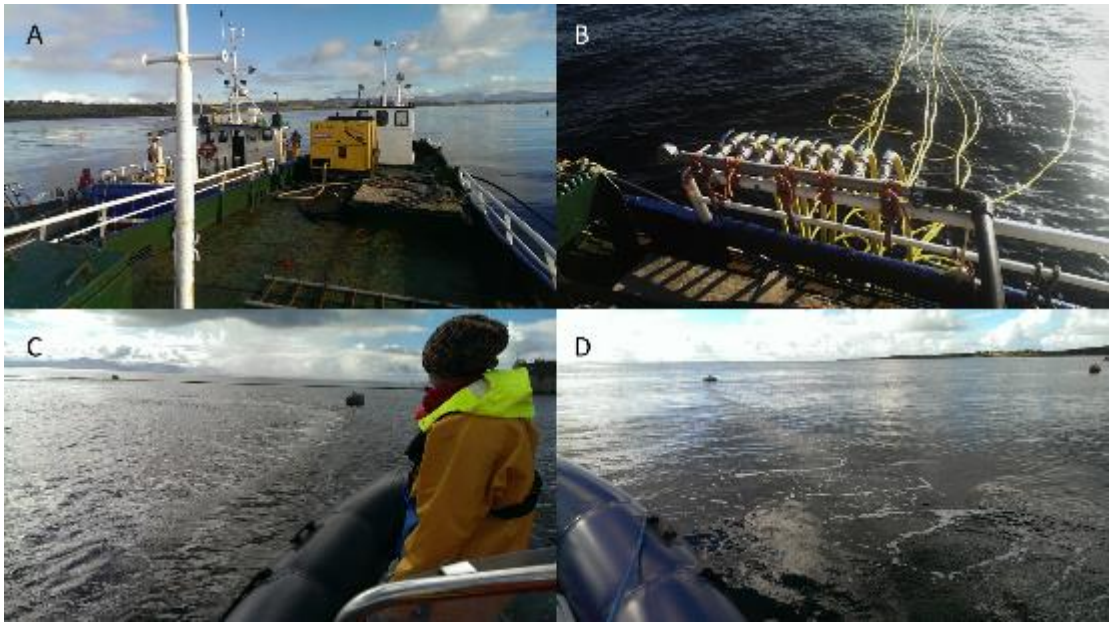


Figure 5.3: Bubble curtain set up at Inver Bay during 2016; (A) a portable turbo screw compressor; (B) manifold splitting the air delivery into 8 hoses; (C & D) fully established bubble curtain along the lesser fouled portions of the tubing.

Flume testing in LIR

During October 2017, experiments to test the efficacy of a bubble curtain as a barrier were carried out in the flume tank at LIR, the national ocean testing facility in County Cork, Ireland (Figs. 5.4A & 5.4B). The original schedule contained a combination of current and wave conditions, however, a malfunction in the tank meant that current was no longer available and the experiment was rewritten to investigate wave conditions only. In total, 140 tests were performed in the flume, using a 3-5 mm thick, 50 mm diameter silicone 'jellyfish'. Each set of wave conditions, i.e. simulation, was replicated six times, except for some simulations which were used to video what happened in the flume.

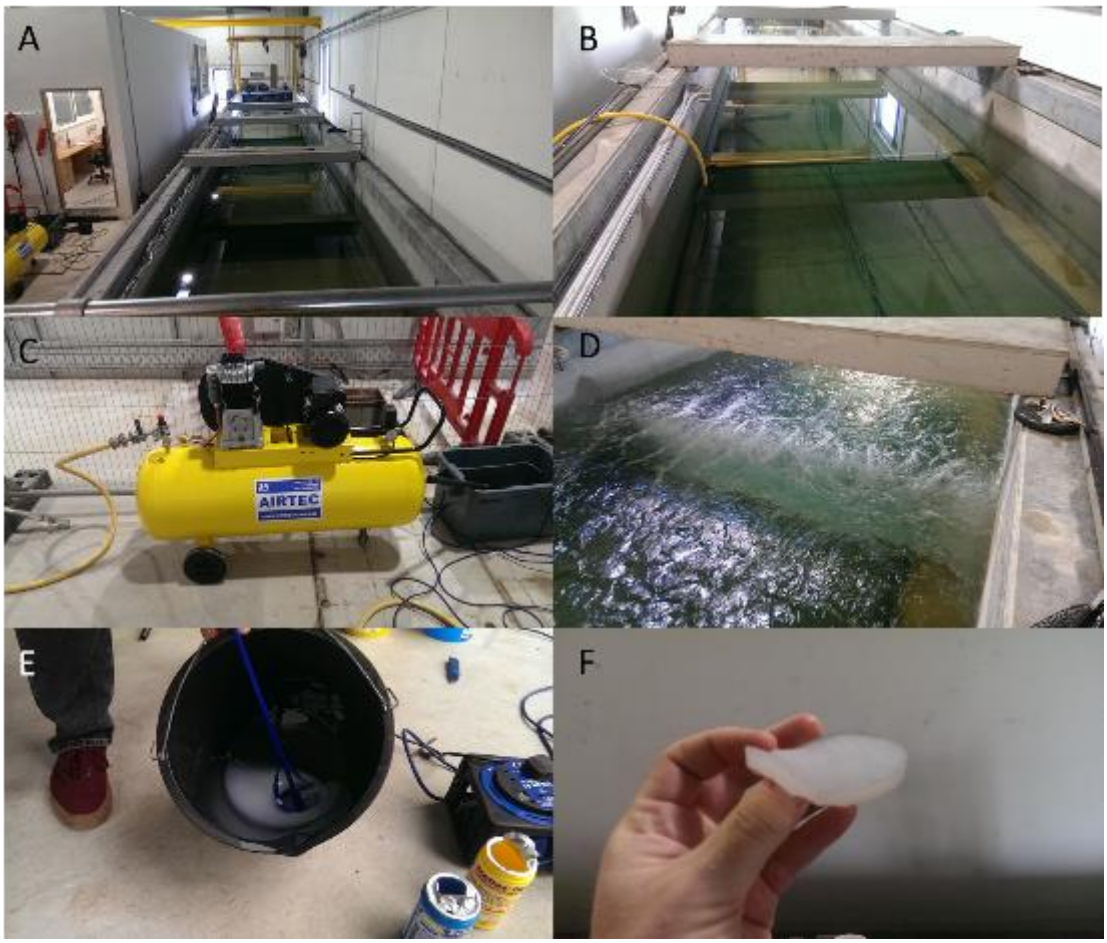


Figure 5.4: (A) 50 m flume tank (1 m deep) at the LIR facilities in MaREI; (B) the bubble tube was placed across the full width of the flume tank, cable tied to an aluminium bar to maintain a straight barrier; (C) a piston compressor supplied the air; (D) bubble curtain on at high air flow; (E) mixing the EcoFlex compound before casting the 'jellyfish'; (F) the final model jellyfish, 50 mm in diameter and *ca.* 5 mm in thickness.

Test were carried out using wave periods from 1 – 1.8 seconds, wave heights from 0.1 – 0.2 m and low and high air flow settings on the compressor. The bubble tubing was supplied by Canadian Pond Ltd. (Quebec, Canada) and the ballasted tubing was connected to a Stanley 3 hp piston compressor with 200 L reservoir, capable of delivering air at 330 L per minute, at up to 10 bar (Figs. 5.4C & 5.4D). During each test, the appropriate wave conditions were set in motion and once a regular wave pattern was established, 50 of the 50 mm 'jellies' were thrown into the water, 0.5 –

0.6 m in front of the bubble curtain. The test was timed from the moment the 'jellies' were introduced and wave and air were shut down after 30 or 120 seconds. The 'jellies' were then recovered using landing nets, recording the numbers recovered from either side of the bubble curtain. Finally, Go-Pro cameras were set up in the flume to record several tests and the video was reviewed to analyse the movement of the 'jellyfish' due to wave action and the bubble curtain.

Making silicone jellyfish

The model jellyfish used in the experiments was moulded using EcoFlex 00-20 which is a platinum cured silicone compound. It is extremely stretchy, soft and pliable, has a specific gravity close to water (1.07 g cc^{-1}) and is resistant to tearing. These properties made it ideal for repeated handling required for tank simulations. Moulding the jellyfish required mixing two viscous compound in a 1:1 ratio and casting in the required shape (Figs. 5.4E & 5.4F). In order to get the large number of jellyfish used here, a long cylindrical mould (50 mm PVC pipe) was used and the subsequent cast was cut into 5 mm disks (Fig. 5.4F) to create a 'jellyfish'.

Results

Bantry Bay pilot tests

These trials, although effective for ironing out the mechanical problems with running a bubble curtain continuously, were unable to generate quantitative data. The tidal currents in the vicinity of the farms are generally less than 0.2 m^{-s}, which made it difficult to design a small scale test with a discrete upstream and downstream side. In addition, for the test to be statistically testable, it would have had to run for an extended duration which was logistically not possible at the site, at that time. However, during test 2 with the longer tube, there were substantial numbers of compass jellyfish *Chrysaora hysoscella*, Linnaeus 1767, in the area and when they came into contact with the bubble curtain they were transported to the surface. At the surface, the jellyfish were driven horizontally away from the bubble curtain. In fact, the surface current generated by the curtain was sufficiently strong to push a diver up from a 5 m depth to the surface and then >10 m away from the curtain. It was concluded that the bubble curtain was acting as a barrier for the large medusae present at the time, however, the system was over powered and could not be realistically or economically scaled up to protect a full farm site.

Donegal Bay pilot tests, Inver Bay 2016

Because the weather at this time was poor with high wind and seas, the tests had to be postponed on several occasions, allowing the bubble tubing to develop substantial biofouling, dominated by mussels. As a result, once the tests were started, large gaps in the bubble curtain were apparent and it did not constitute a coherent and continuous barrier. Even when the maximum pressure was directed to a certain section of the tube, it was not sufficient to blow through the biofouling mussels. Where the tubing was less fouled, a consistent bubble curtain was established (Figs. 5.3C & 5.3D). In

addition, the constant weather fronts moving through the region resulted in breakages in the bubble tubing. In some ways, the setup of the system exacerbated these breakages. The bubble tubing was attached to the cage anchoring system and the constant abrasion against the heavily fouled (predominantly mussels) anchor lines and chains lead to failures. While some sampling was carried out with the bubble curtain running, the data are not presented here as there were too many flaws present to claim that this was a valid test of the system as a barrier. Logistical issues were not confined to the bubble tubing, the compressor (Fig. 5.3A) suffered overheating problems and would automatically shut down. This was possibly due to fouling creating excessive back-pressure which would increase the load on the compressor, however, adjusting the manifold (Fig. 5.3B) to divert airflow to the relatively un-fouled sections of the tubing did not prevent further shut-downs. Although the compressor and fuel supply were situated on an old barge which provided a substantial platform, the original deck mounted fuel tank was badly damaged during heavy weather and fuel was subsequently supplied from the vessel's internal fuel tanks. This has no bearing on the test *per se*, but does further demonstrate the challenge involved in operating in exposed Atlantic sites.

Donegal Bay full scale test, McSwyne's Bay 2017

To avoid the fouling issues of 2016, the tubing was installed rapidly over several days during 2017 and began operating on the 21st September. Because the 2016 sampling indicated that all jellyfish were aggregated in the top 5 m, the bubble curtain was installed at a depth of 6 m. *Muggiaea atlantica* and *Clytia hemisphaerica* accounted for the majority of the hydromedusae present during the test, contributing a mean of 48 ± 29 % and 31 ± 25 % respectively (Fig. 5.5A). The remaining percentage was contributed by *Obelia* spp. and the other gelatinous zooplankton present included

Sagitta spp., *Doliolum* spp., and *Pleurobrachia pileus*. A t-test was carried out to compare the total hydromedusae abundance inside and outside the bubble curtain during the experiment. There was no significant difference between the mean abundance inside (18 ± 12 indiv. m^{-3}) and outside (22 ± 11 indiv. m^{-3}) (t_{40} = -1.136, p = 0.26) (Fig. 5.5B). Similarly, a t-test revealed no significant difference between the mean total gelatinous zooplankton abundance inside (36 ± 19 indiv. m^{-3}) and outside (42 ± 18 indiv. m^{-3}) the bubble curtain (t_{40} = -1.047, p = 0.3).

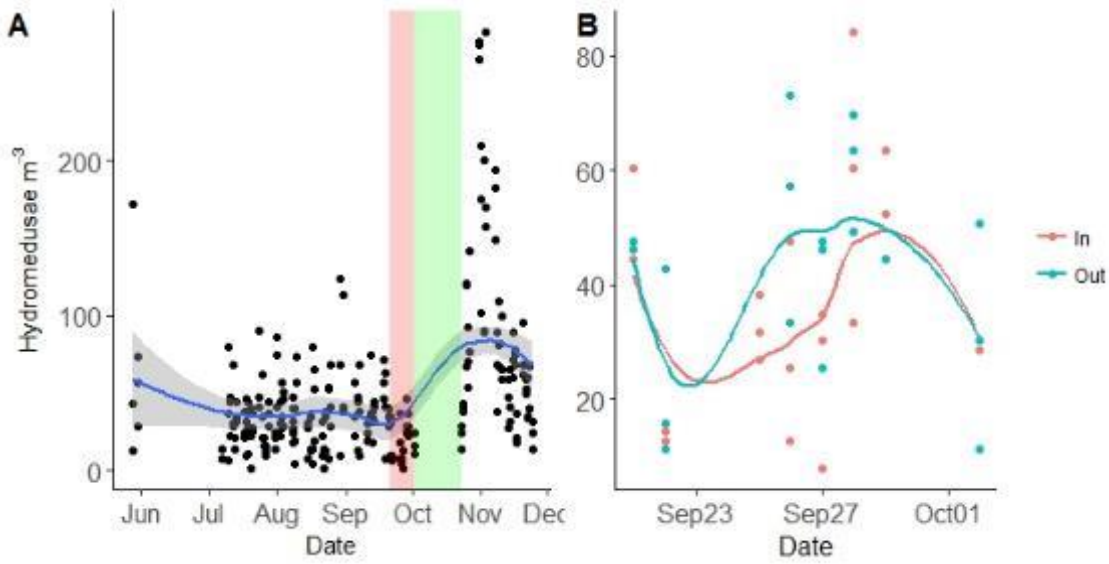


Figure 5.5: (A) Abundance of hydromedusae in the top 5 m throughout the sampled period in 2017 at McSwyne's Bay, with the duration of the bubble curtain test marked in red and a period of no sampling in green; (B) Abundance of hydromedusae (indiv. m^{-3}) inside and outside the bubble curtain, while the system was continually running. All the trend lines are polynomial regression lines fitted to the respective data. Note the different scales on the y axis.

These results suggest that the presence of the bubble curtain was not decreasing the abundance of gelatinous zooplankton. On the assumption that the two most abundant hydromedusae, having very different morphology, might respond differently to the bubble curtain, the mean abundance of *M. atlantica* and *C. hemisphaerica* inside and outside the bubble curtain were also compared. Mann-Whitney tests were carried out for both species, and there was no significant difference between *M. atlantica* or *C. hemisphaerica* abundance inside (9 ± 8 indiv. m^{-3} and 6 ± 7 indiv. m^{-3}, respectively) and outside (12 ± 8 indiv. m^{-3} and 7 ± 9 indiv. m^{-3}, respectively) the bubble curtain (U = 169, p = 0.23 and U = -221, p = 0.89, respectively).

Flume tank testing

The first series of tests were carried out to test the effect of wave period on the passage of 'jellyfish' through the curtain. When air flow (low) and wave height (0.1 m) were held constant, the greatest number of 'jellyfish' passed through with 1.4 and 1.6 second waves, 15 ± 7 and 14 ± 6.5 'jellyfish', respectively. The lowest number passed through with 1.2 second waves, 8.5 ± 7.2 (Fig. 5.6A), however there was no significant difference between wave periods. Turning off the waves reduced the number that passed through to 3.6 ± 3 'jellyfish', which was significantly lower than the number passing through at all other wave periods, except at 1.2 seconds (ANOVA, $F_{5,37}$ = 3.8, p = 0.007). Similarly, turning off the bubble curtain significantly lowered the number of jellyfish passing through the curtain (ANOVA, $F_{1,10}$ = 15.08, p = 0.003) (Fig. 5.6B). The second series of tests were carried out to test a reduction in wave height and an increase in air flow. As wave period was not influential, only 1 and 1.8 second periods were used in combination with the other factors.

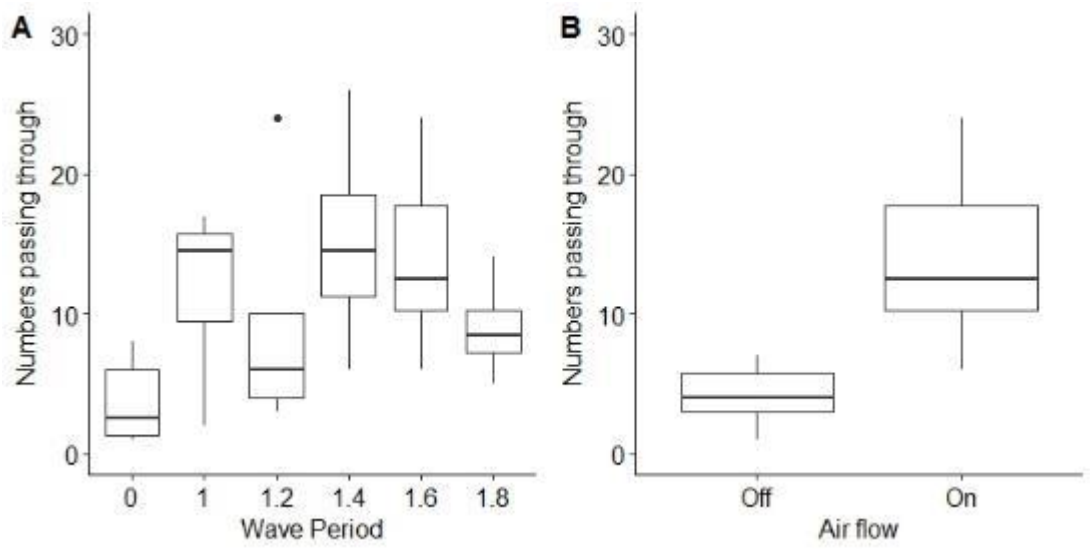


Figure 5.6: Number of 'jellyfish' passing through the bubble curtain; (A) with different wave periods set at 0.1 m wave height and low airflow; (B) with low airflow on/off, set at 1.4 m wave period and 0.1 m wave height.

These were retained so that any potential interaction between wave period and another factor would be captured in the data. Both wave height and air flow were significant factors in the second series of tests, but the model indicated the interaction between them was not significant (ANOVA, $F_{3,68}$ = 19.9, p = <0.001). Reducing the wave height from 0.1 m to 0.05 m significantly reduced the number of 'jellyfish' passing through the bubble curtain, while increasing the air flow significantly increased the number passing through the bubble curtain (Fig. 5.7A). A final series of tests were carried out for an extended duration at high air flow, and this clearly demonstrates that a longer test leads to a significantly higher number of 'jellyfish' passing the curtain (ANOVA, $F_{3,44}$ = 31.68, p = <0.001) (Fig. 5.7B). This test also indicated that during the longer test runs, wave height became less significant.

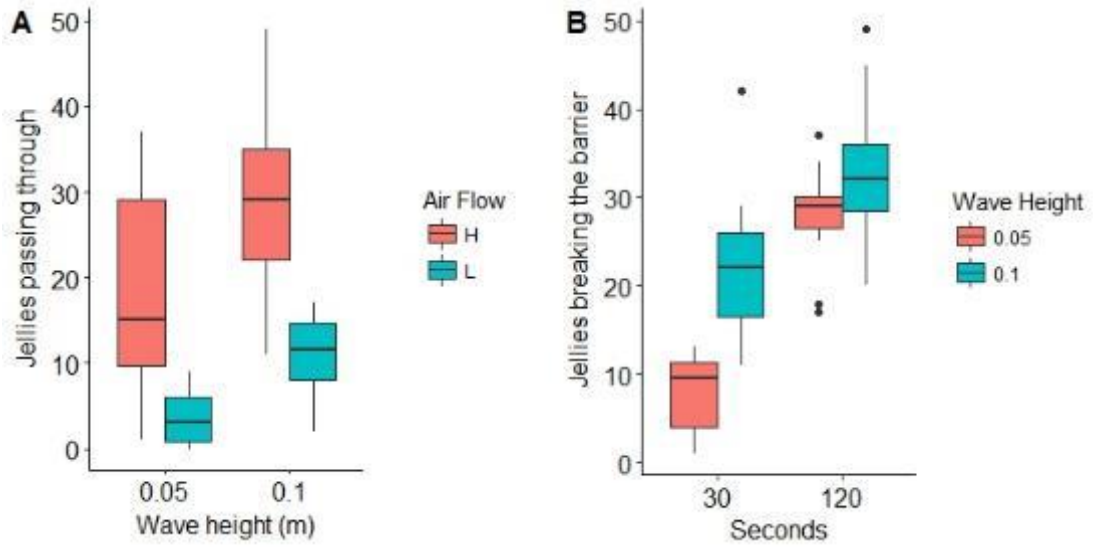


Figure 5.7: Number of 'jellyfish' which pass through the bubble curtain; (A) with different wave height and airflow; (B) with high airflow and changing duration.

Observations from the flume tank experiment

The different conditions had a marked effect on the extent to which the surface current pushed 'jellyfish' away from the bubble curtain. During longer wave periods, the surface current was observed to carry jellyfish 3 - 4 m horizontally away from the bubble curtain, however, when the wave period was shortened to 1 or 1.2 seconds the waves began to break against the surface current and 'jellyfish' were carried less than 1 m horizontally away from the bubble curtain. Once the 'jellyfish' sank below the surface current they started to move back towards the bubble curtain with the wave motion. Review of the Go-Pro video revealed that wave motion caused the 'jellyfish' to move in a circular pattern, moving incrementally forward with each passing wave (Fig. 5.8). This movement is known as Stokes drift, and describes the circular motion of a parcel of water with each passing wave, whereby the parcel of water ends the movement slightly forward from where it started, in the direction of the wave propagation (Tucker and Pitt, 2001) (Fig. 5.9). Further observations suggested that 'jellyfish' entering the bubble plume closer to the bottom were more likely to pass

through the plume, while ‘jellyfish’ entering the plume nearer the surface were more likely to be entrained in the vertical current and ejected horizontally at the surface (Fig. 5.9).

There were, nonetheless, ‘jellyfish’ which behaved in unpredictable ways and did not follow this simple dichotomy. What was certain however, was that inevitably the majority of ‘jellyfish’ would pass through the curtain, as can be seen in the video stills taken from a long 120 second test (Fig. 5.8). A final observation which was not documented quantitatively was the time elapsed before the first ‘jellyfish’ passed through the bubble curtain. At the higher wave height and shorter wave period, this time was much shorter, in the order of < 10 seconds. In contrast, at lower wave heights and longer wave periods the first ‘jellyfish’ did not pass through until after the 20 seconds or so.

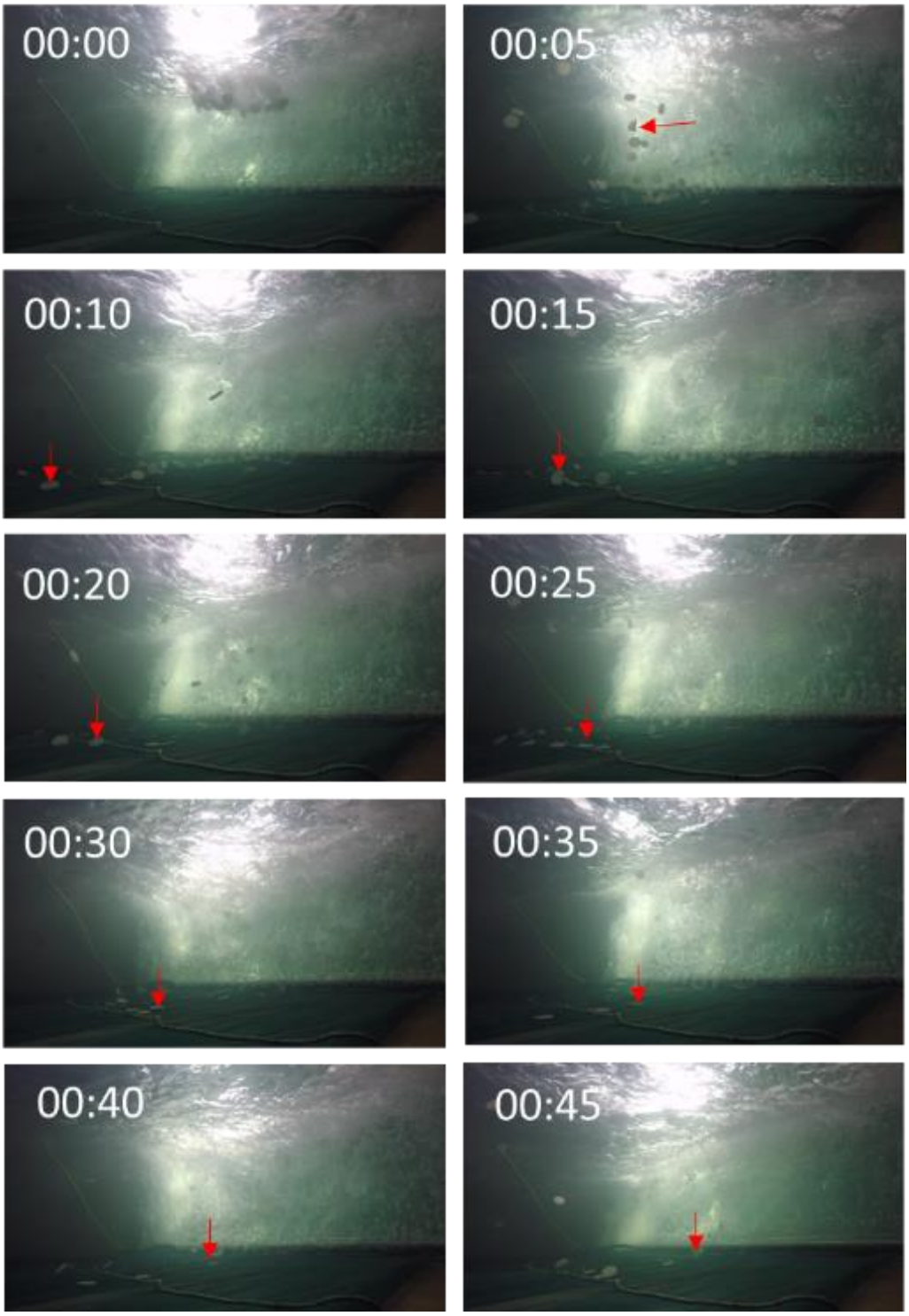


Figure 5.8: Snapshots of simulation with 0.1 cm wave height and 1 second wave period, demonstrating the progression of 'jellyfish' towards the bubble curtain. The red arrow tracks the movement of one selected 'jellyfish' through a 45 second simulation in a flume tank.

Discussion

Mitigation against jellyfish species that can harm finfish aquaculture is hampered by a lack of applied research. A bubble curtain as a barrier system typifies this, in that the concept is reported in the literature as a potential solution (Ruane et al., 2013), yet only a single experiment, with equivocal results, has been conducted to date (Ratcliff, 2004). Results in this study, from both the *in situ* experiments in Donegal Bay (NW Ireland) and the wave flume experiments suggest that a bubble curtain may not constitute an effective barrier to jellyfish. The flume experiments provided clear evidence that a model silicone 'jellyfish' can pass through the curtain in the presence of wave motion. In addition, changes in the wave characteristics have a significant effect on the rate at which jellies pass through the bubble curtain. Somewhat counterintuitively, at the higher air flow the rate of 'jellyfish' transport through the curtain increased (Figs. 5.7B & 5.6A), which suggested an interaction between the bubble curtain induced current and the wave motion.

Observations from the video confirmed that with each passing wave, the jellyfish moved incrementally towards the bubble curtain in accordance with 'Stokes Drift'. In shallow environments, where the wave interacts with the sea bed, the motion becomes elliptical and the forward drift with each wave is thus increased (Tucker and Pitt, 2001). Therefore, as wave height was increased in the flume, it is possible that the forward movement was increased with each wave, and secondly, as wave period decreased, the rate of forward movement is increased. This mechanism offers an explanation for the increase in 'jellyfish' passing through the barrier with increased wave height. However, the additional increase caused by the airflow needs further explanation. Previous studies have demonstrated that oil particles can pass through a bubble curtain below the surface current (Delvigne, 1987; Lo, 1996). Oil droplets

became entrained into the bubble plume and passed through the curtain in a process called ‘droplet shedding’, which increased with increased airflow through the bubble curtain (Delvigne, 1987). This observation would seem to be similar to the results here, and in fact, the numbers passing through the bubble curtain were lowest when the air was off (Fig. 5.6B). As a horizontal current will deflect a bubble curtain and the airflow must be increased to compensate (Lo, 1996), it is likely that were a current available during this study, then transport of ‘jellyfish’ through the curtain would have increased during simulations.

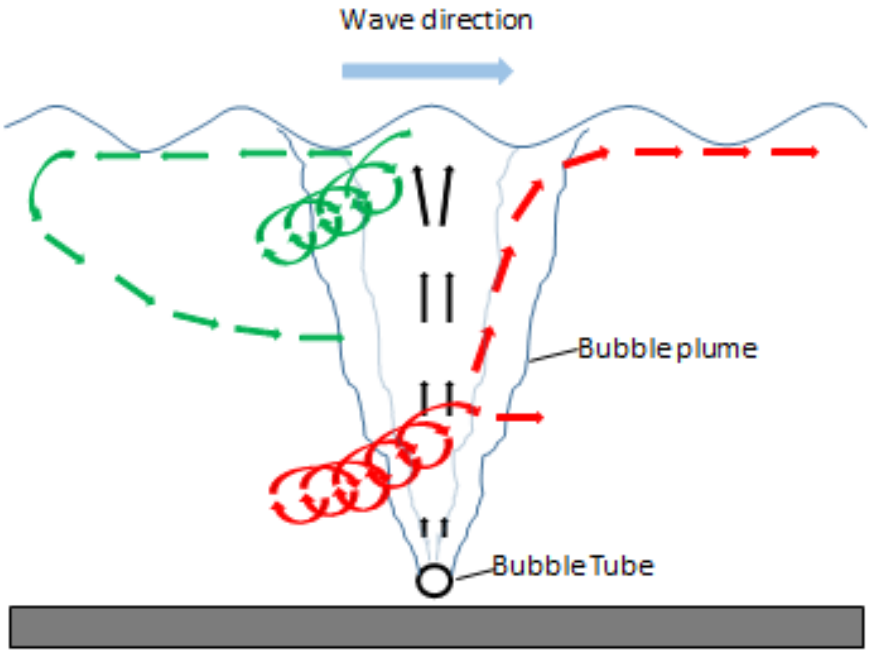


Figure 5.9: Schematic of ‘jellyfish’ movement at two different entry points into the bubble curtain during wave flume tests. The red movement experiences less vertical current and a narrower plume, whereas the green movement experiences increased vertical current and a wider plume and a horizontal current near the surface. The black arrows indicate vertical current velocity.

Qualitative observations from the Go-Pro video in conjunction with the quantitative 'jellyfish' counts revealed some important insights about the dynamics of the bubble curtain. The surface current generated by the bubble curtain was dissipated by higher and more frequent waves, meaning 'jellyfish' were circulated back into the bubble curtain faster. As with the droplet shedding, it seems logical that adding a current flow to the experiment would have increased this circulation further and lead to faster 'jellyfish' transmission through the curtain. Despite the droplet shedding in oil spill experiments, bubble curtains are still able to divert the majority of oil around a 'protected' area making them useful in oil spill mitigation (Lo, 1996). This partial success is predicated on the positive buoyancy of oil which is not the case with jellyfish. Observations from scyphomedusae tagging studies indicate that larger jellyfish species, when disturbed, often descend in the water column (Hays et al., 2008), which would take them out of the surface current and possibly back into the bubble curtain again.

The field tests here suggested that the bubble curtain had no effect on hydromedusae abundance, however, considering the technical problems with installing and maintaining the bubble curtain and the rough weather, the tests conditions were far from ideal and the results could not be considered unequivocal. Conditions during the tests in September were rough, with moderate to strong winds (12 – 20 Km h^{-1}), and therefore the top few metres of the water column would have experienced substantial wave movement which might explain the lack of effect. It is also possible that a build-up of jellyfish on one side of the bubble curtain, would eventually lead to jellies under-flowing the barrier, as happens when oil booms are too shallow (Lo, 1996). The model 'jellyfish' used in this study were based on the average bell diameter of *Pelagia noctiluca* (5 cm) measured on previous occasions, and

whether the observations from the flume tests can be extrapolated to the small hydromedusae present in Donegal during 2017 is unknown. The body form of *M. atlantica*, the dominant species here, has a different profile and drag characteristics compared with oblate forms (Costello et al., 2008), and it is possible they might interact with the vertical current in a different way. Furthermore, it has been show that Stokes Drift for oil particles diverges with variation in size and buoyancy (Golshan et al., 2018), and therefore the buoyancy of each species is also a factor in jellyfish bubble curtain interactions. Direct observations of compass jellyfish, *Chrysaora hysoscella*, in Bantry Bay (SW Ireland) suggested that large scyphomedusae would be consistently entrained into the bubble curtain, as no compass jellyfish were observed to pass through the curtain (Haberlin D., pers. comm.). In this instance it may well be that the bubbles were changing the buoyancy of these large medusae, by providing extra lift as they flowed over and around the animal. In the flume tests, small bubbles were observed to occasionally 'adhere' to a 'jellyfish' making them more buoyant. It is reasonable to suggest that a large compass jellyfish, with a concave umbrella and multiple irregularities in shape, and possessing tentacles would provide a substrate where bubbles can become trapped and provide a 'lift' force in addition to the vertical current. Observations at the Hunterston Nuclear power plant, in the Firth of Clyde Scotland, where coolant intakes are surrounded by a bubble curtain, would also support that the idea that larger scyphomedusae are lifted to the surface upon encountering the bubble curtain. While no quantitative data have been collected at Hunterston to date, the facility has employed the bubble curtain seasonally over the last 13 years and it is considered effective by management (Young B., Coastworks Ltd., pers. comm.). Notably, the Hunterston bubble curtain is set up in a diamond shape with the long axis perpendicular to the current which may well enhance its

efficacy as a jellyfish barrier. The barrier is relatively short (10s m), and jellyfish pushed to the surface are pushed along by the current and unlikely to come back into contact with the bubble curtain. Given the area covered by many fish farms, this type of set up is likely not possible, and the greater circumference of a fish farm bubble curtain means that jellyfish pushed to the surface are likely to be circulated back into the bubble curtain again, as in the flume tests.

In addition to considering the physical dimensions of any proposed bubble curtain, the ecology, particularly the vertical distribution, of target species must be considered. Diel variation has been recorded in the vertical distribution of *M. atlantica* in the Western English Channel (Southward and Barret, 1983), and substantial variation in the vertical distribution of hydromedusae between different locations has been observed in Ireland (Haberlin D., unpublished data). Moreover, the vertical distribution in SW Ireland appears to be highly variable, with a diel component (Haberlin D., unpublished data) and substantial oceanographic changes which may well alter the gelatinous zooplankton community (Raine et al., 2014; Haberlin et al., 2016). These changes in vertical distribution are likely to be important, as hydromedusae in the surface waters will experience greater Strokes Drift and might be more likely to pass through a bubble curtain. Equally, current strength and direction can change with depth, with wind driven surface currents and sub-surface flows in some locations (Raine et al., 2010). As air flow needs to be increased to counteract an increasing current (Lo, 1996), variable current conditions may well increase jellyfish transport through the curtain. In addition to the the physical factors that drive jellyfish distribution, behaviour is also a ley driver of distribution (Arai, 1992; Graham, 2001). Small hydromedusae, in particular, are osmoconformers and can aggregate along haloclines (Arai, 1992), and this combined with behavioural responses to prey

distribution (Folt and Burns, 1999) can influence distribution. Understanding both the physical and biological drivers of jellyfish blooms and incursions will undoubtedly lead to better mitigation measures.

Unfortunately, much of the evidence here indicates that a bubble curtain is a porous barrier for small jellyfish, nonetheless, it may prevent larger jellyfish from entering cages. Future field experiments should be reduced in scale, perhaps a bubble curtain around a single cage, allowing greater control of airflow and a simpler logistical challenge. Furthermore, the experiment needs to be moved to a sheltered location where wave energy is minimal. In addition, the ecology of problem species like *Muggiaea atlantica* and *Pelagia noctiluca* must be studied in greater detail, with the farms themselves involved in on-going temporal sampling. In particular, stratified vertical sampling is required to better understand hydromedusae ecology and refine any potential mitigation measures.



Chapter 6

Reducing Ectopleura larynx growth on salmon cages: efficacy of a novel non-toxic coating

Abstract

Biofouling on finfish cages presents a range of physical and biological challenges for the aquaculture industry. The hydroid *Ectopleura larynx* is often dominant on salmon cages and poses a direct risk to fish health via stinging tentacles. Traditional antifouling is reliant on toxic or biocidal coatings which carry an unacceptable environmental hazard and new non-toxic alternatives are needed. Here, the efficacy of a non-toxic aryldiazonium carbohydrate coatings to reduce biofouling on nylon salmon cage nets was examined at a salmon farm in southwest Ireland. The mean biomass reached 393 gm^{-2} after 31 days' immersion, and main macrofoulers were *Ectopleura larynx, Mytilus* sp. and *Jassa* sp., reaching mean densities of 58779, 601511 and 106399 indiv. m^{-2}, respectively. The coating did not reduce the density of *E. larynx* or the total fouling biomass, nor did it increase the clean-ability of the nets. However, adenosine-triphosphate (ATP) quantity retained on rinsed nets was lower, after 20 and 31 days' immersion, indicating a reduced density of microscopic fouling. Proximity to the farm enhanced the recruitment of *Mytilus* sp. and *Jassa* sp., but did not appear to affect the development *E. larynx*. It is likely that the complex surface structure of the nylon netting reduces the effectiveness of the coating here, and it may be more effective when bonded to a simpler single stranded netting.

Introduction

Biofouling on physical structures is ubiquitous in the marine environment where a great diversity of marine organisms attach to, and grow on a wide variety of natural and artificial surfaces. The rate of settlement and growth varies with species, location, hydrography, season, temperature and salinity (Braithwaite and McEvoy, 2004; Chambers et al., 2006; Blöcher et al., 2013a). For the majority of marine activities and industries biofouling is a major challenge and can weaken structures (Maréchal and Hellio, 2009) and impair vessel efficiency (Callow and Callow, 2011) and sensor functioning (Whelan and Regan, 2006). Biofouling is also a major issue for the marine finfish aquaculture that uses sea cages that accumulate very substantial biofouling communities (Hodson et al., 1997; Braithwaite and McEvoy, 2004; Greene and Grizzle, 2007; Fitridge et al., 2012; Kassah, 2012). Aquaculture farms are usually situated in areas with relatively low tidal currents, and sheltered from the high wave action, which further promotes biofouling, particularly of filter and suspension feeders, e.g., hydroids, mussels and ascidians which tend to dominate the cage fouling community in the northeast Atlantic (Boero, 1984; Gili and Hughes, 1995; Braithwaite et al., 2007; Carl et al., 2011; Fitridge et al., 2012). Heavy biofouling on these farm cages (sea pens) restricts water flow through the cages, thus creating hypoxic conditions inside the cage. Biofouling is also linked to the presence of fish pathogens (De Nys and Guenther, 2009; Floerl et al., 2016) and fouling hydroids can sting and injure fish directly (Baxter et al., 2012a). The costs associated with biofouling are substantial, with copper based antifouling coatings and high pressure washing being the two most common mitigation strategies (Floerl et al., 2016). It is conservatively estimated that 5-10% of production costs are spent on biofouling mitigation (Fitridge et al., 2012).

The hydroid *Ectopleura larynx* Ellis and Solander 1786, is a dominant fouling organism on salmon cages throughout the North Atlantic (Braithwaite and McEvoy, 2004; Greene and Grizzle, 2007; Baxter et al., 2012a; Kassah, 2012; Blöcher et al., 2013a), and its presence has been shown to inflict gill injury via nematocyst stinging capsules (Baxter et al., 2012a; Bosch-Belmar et al., 2017). Other hydroid species (*E. exxonia, Plumerlaria* spp., *Obelia* spp. and *Sarsia* spp.) are amongst the dominant fouling organisms in New Zealand, Tasmania and North America (Floerl et al., 2016). Furthermore, hypoxia and jellyfish stings can act synergistically and have an enhanced negative impact on fish health (Bosch-Belmar et al., 2016a). *Ectopleura larynx* is an early settler on new substrates and it is able to reproduce within 2-3 weeks (Pyefinch and Downing, 1949). Released actinula (larvae) settle on and fuse with existing hydroids producing tangled colonies (Nawrocki and Cartwright, 2012). *Ectopleura larynx* has, like *Mytilus* sp. and ascidian species, demonstrated resistant to copper coatings (Pyefinch and Downing, 1949; Greene and Grizzle, 2007). In addition, copper based coatings have a limited effective duration as pressure cleaning damages the coating (Braithwaite et al., 2007). *Ectopleura larynx* responds to high pressure cleaning by growing back faster and increasing the number of polyps (Guenther et al., 2010). High pressure cleaning also creates a plume of organic debris containing pathogens and fragments of *E. larynx*, potentially causing harm to fish through the initial injury and subsequent secondary infection (Floerl et al., 2016). The debris can contain viable gametes and larvae which can promote self-seeding, causing increased biofouling downstream of the cleaning site (Floerl et al., 2016). Hydroids in particular are adept at settling on new surfaces quickly (Pyefinch and Downing, 1949), and severing *E. larynx* polyps from the hydrocaulus promotes larval release (Carl et al.,

2011) and fouling rates within a farm site can be up to 49 fold greater than at a control site (Blöcher et al., 2015).

Given the banned use of tributyltin (TBT) since 2008 and evidence of the negative impact of many metal based biocidal compounds (Burridge et al., 2010), there is a strong incentive to create new non-toxic antifouling compounds. The cost of testing new biocidal compounds could potentially run into the €millions under the Biocidal Products Directive 98/8/EC (Maréchal and Hellio, 2009), and is an additional incentive to create non-biocidal compounds which do not leach into the environment. To this end, research has focused on creating antifouling (AF) surfaces which inhibit fouling organisms, or foul release (FR) surfaces which allow organisms to bind, but with reduced adhesion strength (Callow and Callow, 2011). The successful settling, adhesion and metamorphosis of organisms is dependent on a number of cues including surface chemistry, microtopography, the presence of con-specifics or competitors and prior microbial fouling, i.e. bacteria (Maréchal and Hellio, 2009; Callow and Callow, 2011). Zwitterionic coatings are effective at deterring barnacle cypris larvae from settling (Aldred et al., 2010) and also reduce settlement of *Ulva* algal spores and diatoms (Callow and Callow, 2011). Superhydrophobic nano rough surfaces also show some promise at deterring cyprid and bryozoan larval settlement (Scardino et al., 2009), although their hydrophobicity and thus their AF effect declines with immersion time, and manufacturing these surfaces at scale is expensive (Scardino et al., 2009; Callow and Callow, 2011). The low wettability of silicone has been utilised by mixing it with polymers to make effective FR coatings (Callow and Callow, 2011). Much of the above work is based on bioassays using flat surfaces which may be of limited use in the context of finfish aquaculture, however, a silicone based coating used on cage netting in Tasmania has demonstrated effective FR properties (Hodson et al., 2000).

Hydroids have received little attention in fouling studies and are rarely used in bioassays using novel surfaces or coatings. Where work has been carried out, *E. larynx* actinula showed no clear preference for hydrophobic or hydrophilic surfaces (Blöcher et al., 2013a), and bioassays using varied microtopography reveal contradictory results (Nellis and Bourget, 1996; Blöcher et al., 2013a). The presence of a biofilm seems to be both conducive (Huang and Hadfield, 2003; Huggett et al., 2006) and inhibitory to settling invertebrate larvae and algal spores (Dobretsov et al., 2006). Pyefinch and Downing (1949) showed enhanced *E. larynx* settlement on glass surfaces pre-conditioned with a biofilm, although the constituents of the biofilm were not elucidated. Bacteria, diatom and protozoa are amongst the first micro-foulers on netting (Hodson and Burke, 1994; Corner et al., 2007), and some hydroids appear to rely on bacterial films in order to settle (Müller et al., 1976). The extent to which microfouling can influence macrofouling on finfish cage netting is completely unknown.

The aim of this study was to investigate the effect of a novel non-toxic antifouling coating applied to nylon salmon cage netting and deployed on a salmon farm in the southwest of Ireland. The coating consists of a hydrophilic aryldiazonium saccharide molecule that bonds to a surface forming a thin conformal film, and can be applied via dip coating or spraying and is therefore easily scalable (Myles et al., 2017). This coating has proven to be effective at reducing protein adsorption at various surfaces (Angione et al., 2015; Esteban-Tejeda et al., 2016; Zen et al., 2016) and at reducing adhesion of marine foulants on topographically smooth coupons of nylon-6 (Myles et al., 2017)

Materials and Methods

During a 31-day period from August 8th to September 7th, 2015, a total of 30 (30 x 30cm) 15mm aperture nylon net panels were deployed at Roancarrig in Bantry Bay (51.657°N, 9.765°W), southwest Ireland (Fig. 6.1).

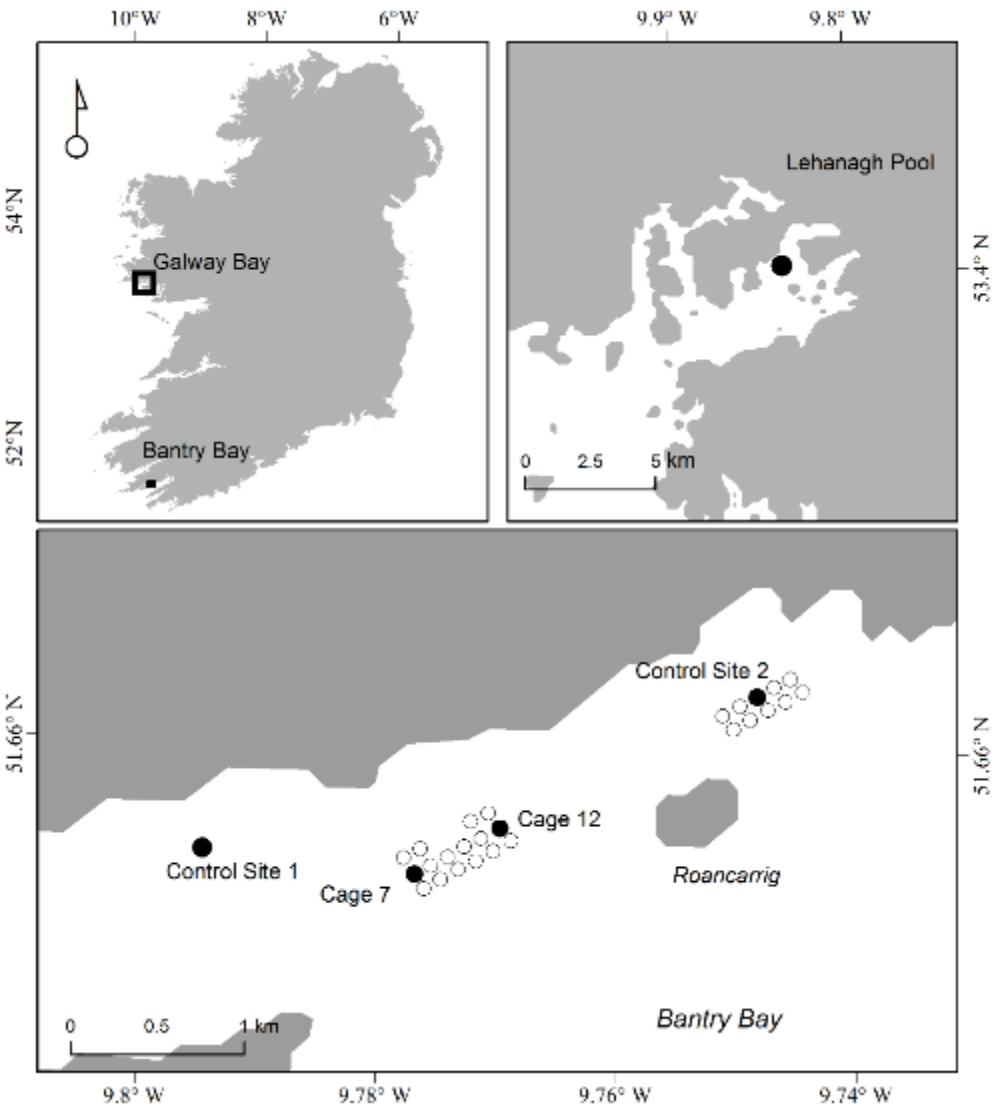


Figure 6.1: Location of study sites at Roancarrig situated in Bantry Bay, County Cork (bottom) and Lehanagh Pool (top right) situated within Kilkieran Bay, County Galway.

To investigate the effect of the antifouling coating, 24 panels were deployed at the Roancarrig salmon farm in two 12 panel arrays, with six treated and six untreated panels in each array (Fig. 6.2A). The two arrays were placed at the western and eastern extremity of the farm and were suspended from the collar of a cage (Fig. 6.1). A treated and untreated panel was removed from each array after 2, 4, 6, 11, 20 and 31 days of immersion.

To investigate the effect of the farm infrastructure on biofouling development, three untreated panels were placed at two control sites approximately 1000m east and west of the farm, with one net being removed from each array after 11, 20 and 31 days. The western control panels were suspended from a temporary mooring; the eastern control panels were suspended from a fallow floatation collar with no netting attached.

To investigate low and high pressure rinsing, a further 12 net panels were deployed at the Lehanaghpool aquaculture site in Bertraghboy Bay, Co. Galway (53.402°N, 9.830°W) on 24/08/2016. Two frames containing six randomly distributed net panels were suspended from a fallow salmon cage. There were three panels for each treatment: treated plus high pressure rinse, treated plus low pressure rinse, untreated plus high pressure rinse and untreated plus low pressure rinse. The low pressure rinse was considered the control as light rinsing was necessary for the ATP analysis (see below).

Preparation of treated panels

The nylon panels were immersed in deionised water and rinsed under agitation approximately 10 times to remove dust and debris prior to coating. The coating process was carried out as previously described Myles et al. (2017); briefly, netting panels were incubated in a formaldehyde solution, containing catalytic amounts of

hypophosphorous acid, at 30 °C overnight. Panels were rinsed thoroughly with deionised water and functionalised via immersion in freshly prepared 1.0 mM solutions of lactoside-bearing aryldiazonium cations generated *in situ* from the corresponding amine, 4-aminophenol-β-D-lactopyranose. Samples were incubated in the dark for 1 h in the diazonium salt solution, rinsed in deionised water and then stored wet in sealed Ziploc® bags until deployment at the salmon farm, which took place within 24 h of functionalisation. Coating on nylon-6 with lactoside-bearing aryldiazonium cations had previously been demonstrated to result in an increase in hydrophilicity, as confirmed by a reduction in the water contact angle of nylon surfaces from 80.6 ± 2.8° to 68.1 ± 2.3° (Myles et al., 2017).

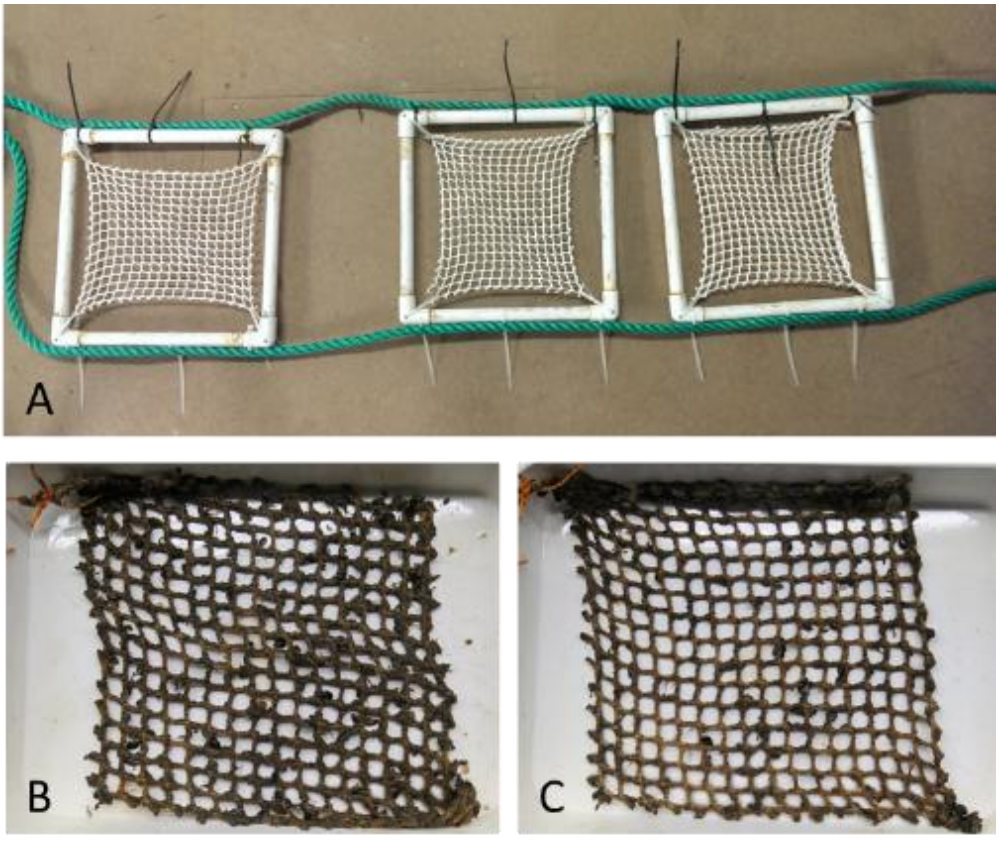


Figure 6.2: (A) PVC frames with untreated clean netting before immersion. (B) Sample net from cage 7 after 30 days' immersion before rinsing, and (C) sample net from cage 7 after 30 days' immersion after rinsing.

Sample analysis

Each panel was removed from the array and placed directly into a Ziploc® bag filled with ambient sea water and sealed. The panels were transported back to the lab (2-hour journey) in a cool box. To test whether the treatment made the nets easier to clean, each panel was rinsed using filtered (10 µm and UV filter) sea water. Each panel was rinsed under a pump feed hose, held 25 cm above the sample for 20 seconds, at a constant flowrate of 0.25 l^{-s}. The fouling material and organisms rinsed from the net panel was caught in a 180 µm sieve. A small subsample of each net panel was removed, placed in a sterile vial and sent for ATP analysis. The panels and rinsate were then stored in 4% formalin for later analysis. Two subsamples were taken from each panel, the first to analyse the macro fouling community and the second to calculate biomass. The macro fouling community was identified and enumerated using a Zeiss stereomicroscope (Stemi 2000). To calculate wet mass, each subsample was blotted dry on paper towels and then weighted to the nearest 0.01 g. The dry mass was taken after oven drying at 60°C for 48 hours. The mean wet and dry mass of 10 net pieces was subtracted from the subsample wet and dry mass to obtain actual biomass. The rinsate was treated in a similar manner to the net pieces. The macrofouling community was identified and enumerated and a subsample of the rinsate was used to calculate wet and dry biomass. Each subsample was filtered through 90 mm Whatman filter paper using a vacuum pump and the wet and dry mass was recorded.

For the Galway Bay rinsing experiment, the net panels were rinsed under low and high pressure using the same procedure as above. As this approach was used to

assess the clean-ability of the nets, only the biomass removed was recorded and no enumeration of the macrofouling community was carried out.

Bantry Bay Microfouling

The level of microfouling on samples was measured using the amount of adenosine triphosphate (ATP) as an indicator of the amount of microbes on the surface (Muthukumar et al., 2011). A commercial luciferase assay and luminometer were used (Aquasnap Total Water, Hygiena); the assay was first calibrated using standard solutions to obtain a conversion from relative luminescence units (RLU) to ATP concentrations. Approximately 1 cm long sections of netting were cut from three different locations in each netting panel; the cutting was suspended in 30 mL of deionised water in sterile centrifuge tubes and then sonicated for 10 min. The value of RLU was determined for each water sample and converted to ATP concentrations; water samples were diluted if needed to bring the ATP concentration within the linear range of the assay. Post sonication, the cuttings were dried under argon and their mass determined to normalise ATP determinations on individual cutting which is reported as nmol of ATP released per gram of dry netting ($nmol/g_{net}$).

Data Analysis

All of the data were standardised to give biomass in gm^{-2} and density in individuals m^{-2}. Biomass and abundances were investigated using t-tests, ANOVA, ANCOVA or linear regression. Due to the small sample size, tests for normality may be misleading (Quinn and Keough, 2002), however ANOVA is robust to a minor lack of normality (Underwood, 1981). In addition, residuals, QQ-norm plots, Cook's distance and scale-location plots were used to check model results. All analysis was carried out using R

3.2.3 (R Core Team, 2017). The majority of values are reported as means ± 1 standard error, unless specified otherwise.

Results

Biofouling on net panels

In total 10 taxa were identified on the panels and in the rinsate. The most abundant taxa on the net panels were *Mytilus edulis*, the amphipods *Jassa* sp. and caprellids, the hydroid *Ectopleura larynx* and the red algae *Polysiphonia* species (Fig. 6.3A – 6.3G). Green filamentous algae and *Obelia* hydroids were identified on some net panels, but because their presence was relatively rare they were noted but not quantified. Polychaetes, brachyurans and echinoderm species were present after longer immersion times, but were found only in the rinsate with none remaining on the nets after rinsing. The wet biomass on the nets increased from day 2 to day 31, however, between days 6 and 11 the biomass declined (Fig. 6.4A). A multiple linear regression was calculated to model the fouling biomass with respect to immersion time, cage number and treatment. A significant regression equation was found ($F_{3,20}$ = 23.96, p = <0.001), with an r^2 of 0.63. The increase in biomass was significant with respect to time and cage number, however, the treatment was not a significant factor in the model (Table 6.1).

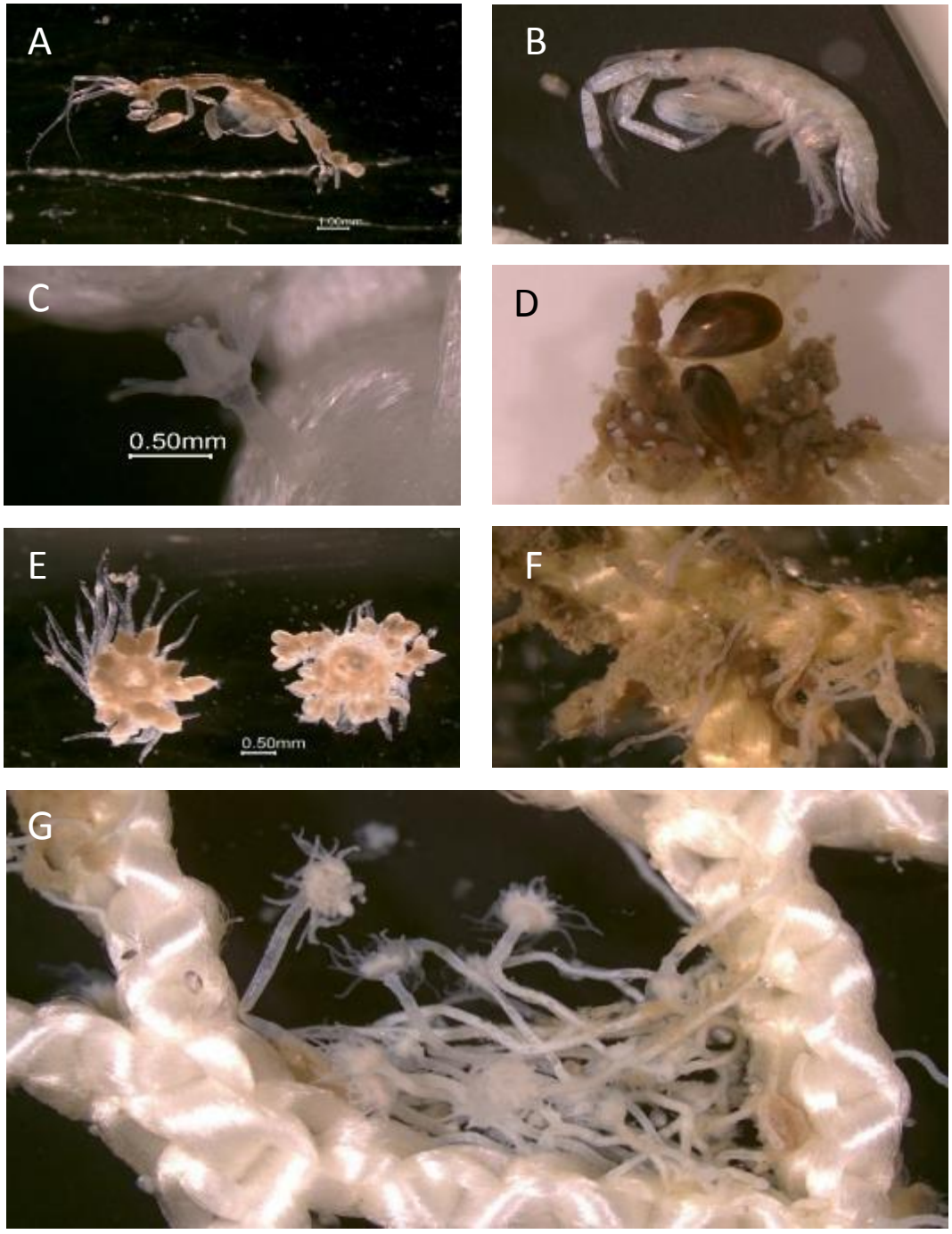


Figure 6.3: The dominant macrofouling invertebrates recorded on sample net panels; (A) large adult caprellid amphipod, (B) adult *Jassa* sp. amphipod, (C) *Ectopleura larynx* polyp after 4 days' immersion, (D) *Mytilus* sp. clustered around net junction, (E) loose *E. larynx* hydranths or polyp heads at an advanced stage of maturity, (F) section of net panel from cage 7 with heavy fouling after 31 days' immersion, (G) section of net panel from control site 1 after 21 days' immersion.

Table 6.1: Tabulated linear model output exploring changes in wet biomass against several variables, $\log_{10}$(biomass)~Cage + $\log_{10}$(Time) + treatment

	Estimate	**Std. Error**	***t* value**	***p***
Intercept	1.52803	0.12565	12.161	1.07×10^{-7}
Cage	0.24586	0.0882	2.787	0.0114
$\log_{10}$ Time	0.5554	0.10853	5.117	5.25×10^{-5}
Treatment	-0.04061	0.0882	-0.46	0.65

Pooling the treated and untreated net panels, the mean biomass increased from 84 ± 28 to 393 ± 68 gm^{-2}. The abundance of *Jassa* sp. (Fig. 6.3B) on the farm panels was notable, with a mean density of 12863 ± 2700 indiv. m^{-2} after two days, and reaching a mean density of 106399 ± 10767 indiv. m^{-2} after 31 days. The density had declined substantially by day 11, 5426 ± 2995 indiv. m^{-2}, before increasing again thereafter and most likely explains the decline in wet biomass at the same time. A multiple linear regression was calculated to model *Jassa* sp. density with respect to immersion time and cage number. A significant regression equation was found ($F_{2,21}$ = 7.44, p = <0.005), with an r^2 of 0.41. The increase in *Jassa* sp. density was significant with respect to immersion time, but insignificant with respect to cage number ($F_{2,21}$ = 7.44, p = <0.005). The density of *Mytilus* sp. (Fig. 6.3D) increased from 24241 ± 2504 indiv. m^{-2} after 2 days to 601511 ± 52134 indiv. m^{-2} after 31 days.

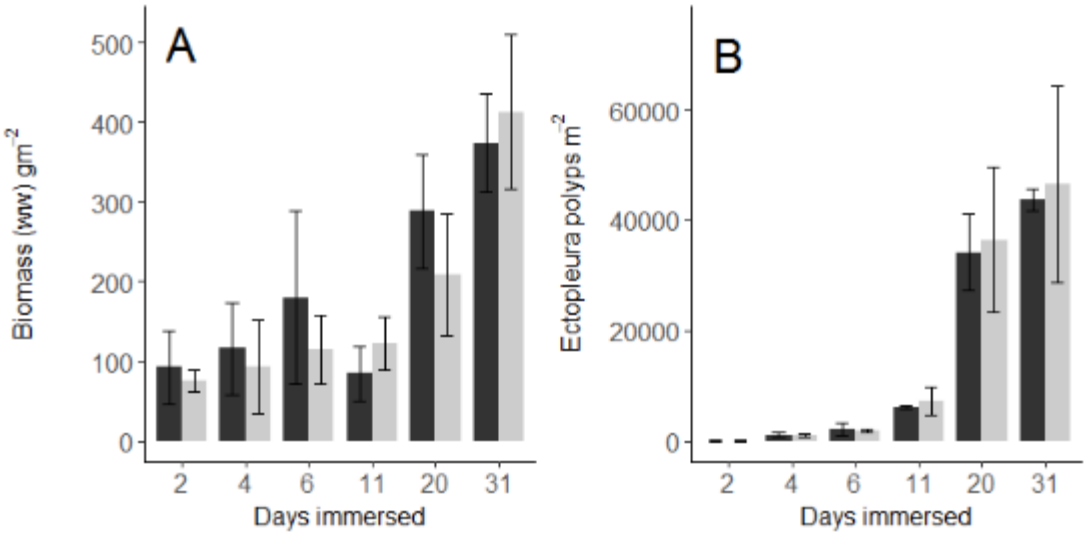


Figure 6.4: Mean wet biomass ± SE on net panels (A) and mean *Ectopleura larynx* polyp abundance ± SE on net panels. Figures include data from farm deployed net panels only. Black and grey bars represent treated (N=2) and untreated (N=2) net panels. Note the different scales on the y axis.

The decrease in total biomass and *Jassa* sp. between day 6 and 11 was not reflected in changes in *Mytilus* sp. density on the nets, although from day 4 to day 6 and from day 20 to day 31, there were substantial change in density. A multiple linear regression was calculated to model *Mytilus* sp. density with respect to immersion time and cage number. A significant regression equation was found ($F_{2,21}$ = 100.1, p = <0.001), with an r^2 of 0.9. The increase in *Mytilus* sp. density was significant with respect to immersion time, but not with respect to cage number or treatment.

Comparison between farm and control sites

The following comparison was carried out using only the data after 11, 20 and 31 days' immersion. Furthermore, as there was no difference between the treated and untreated panels at the farm, these data were pooled. The fouling biomass increased substantially

during the 20-day period and was greater at the farm compared with the control sites. There was a significant effect of site on fouling biomass after controlling for immersion time ($F_{2,15}$=31.33, P =< 0.001) (Fig. 6.5A). The same broad pattern of development was evident for *Mytilus* sp. and *Jassa* sp. (Figs. 6.5B & 6.5C), with models of $\log_{10}$ indiv. m^{-2} showing a significant effect of site after controlling for immersion time ($F_{2,15}$=37.29, P =< 0.001 & $F_{2,15}$=109.5, P =< 0.001, respectively). The maximum *Mytilus* abundance at the farm was 601511 ± 52134 m^{-2} compared with 133571 ± 77476 m^{-2} at the control sites. Likewise, the maximum mean abundance of *Jassa* sp. at the farm was 106399±10767 m^{-2} compared with 29468 ± 9504 m^{-2} at the control sites.

Ectopleura larynx fouling on net panels

Ectopleura polyps (Fig. 6.3C & 6.3G) were found on net panels after four days' immersion. The maximum of over 70000 polyps m^{-2} was found on net panels at one of the control sites. Polyp abundance increased dramatically between day 11 and day 20, and continued to increase up to day 31, at the farm and control sites (Fig. 6.4B & 6.4D). The number of polyps was greater at the farm during the initial 20 days' immersion, however, the mean number of polyps at the control site was greater after 31 days (Fig. 6.5D). The effect of the treatment was minimal; the mean number of polyps on treated and untreated nets after 4 days was 1139 ± 352 m^{-2} and 992 ± 294 m^{-2}, respectively. The mean number of polyps on treated and untreated nets after 31 days was 43705 ± 1960 m^{-2} and 46532 ± 17754 m^{-2}, respectively. A multiple linear regression was calculated to model *E. larynx* density with respect to immersion time, treatment and cage number. A significant regression equation was found ($F_{3,20}$ =

33.34, p = <0.001), with an r^2 of 0.83. The increase in *E. larynx* density was significant with respect to immersion time, but not with respect to cage number or treatment. Pooling the treated and untreated panels at the farm and comparing with the control sites, indicated there was little difference in rate of *E. larynx* development, or in the final density of polyps at either location (Fig. 6.5C). A significant regression equation was found ($F_{2,15}$ = 20.17, p = <0.001), with an r^2 of 0.73, indicating that the increase in *E. larynx* polyp density was significant with respect to immersion time, but not with respect to site.

Effect of the coating on net cleaning

The vast majority of *Jassa* sp., caprellids and *Mytilus* sp. were removed from panels during the rinsing, although some did remain on the panels and occasionally *Jassa* were found still inside their tube houses. The *E. larynx* colonies remained intact, although some some polyp heads were removed during rinsing. The wet biomass (gm^{-2}) that was removed by rinsing was consistent with the pattern of biomass accumulated on the nets, initially increasing up to day 6, was substantially reduced at day 11, and then increasing again at days 20 and 31 (Fig. 6.6A). A multiple linear regression was calculated to model wet biomass removed with respect to immersion time, cage number and treatment. A significant regression equation was found ($F_{3,20}$ = 4.992, P = < 0.001) with an r^2 of 0.43 (Table 6.2), indicating that biomass removed was significant with respect to immersion time, but not cage number or treatment. Substituting the proportion of wet biomass removed from nets during rinsing, for the actual wet biomass removed, resulted in an insignificant regression equation ($F_{3,20}$ = 0.944, P = ns) with an r^2 of 0.12. This suggested that the cleanability of the net panels was not improved by the treatment. Pooling the treated and untreated net panels, the proportion of biomass removed ranged from 19 – 93%, with the highest values

occurring at cage 7 after 2 – 6 days' immersion. It was clear during the rinsing experiments that *Jassa* sp. were the dominant component of the rinsed material.

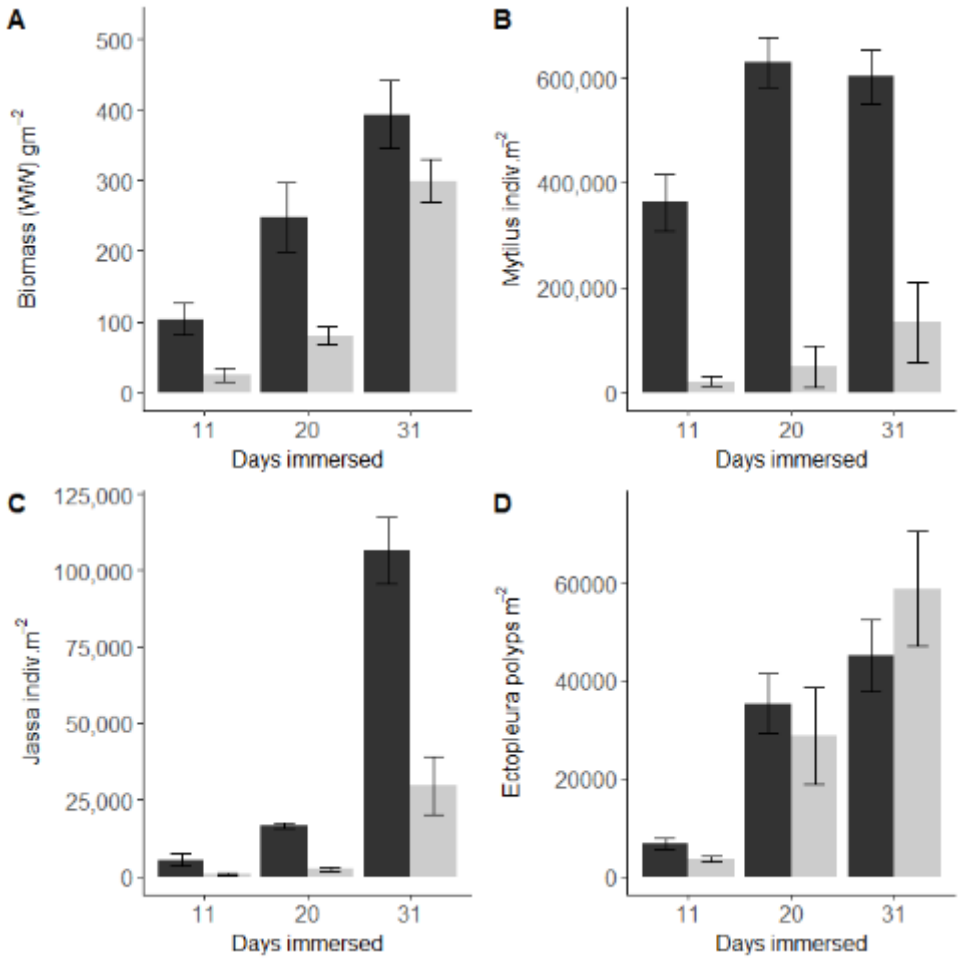


Figure 6.5: (A) Wet biomass on net panels, (B) *Mytilus* sp. density on net panels, (C) *Jassa* sp. density on net panels and (D) *Ectopleura larynx* polyp density on net panels. Black bars represent all net panels deployed at the farm (N=4) and and grey bars represent net panels at control sites (N=2). Note the different y axis.

Table 6.2: Tabulated linear model output exploring changes in wet weight biomass against several variables, Biomass removed ~ treatment + Time + Cage

	Estimate	**Std. Error**	***t* value**	***p***
(Intercept)	25.635	21.214	1.208	0.24099
Treatment	-10.225	20.091	-0.509	0.61638
Time	3.234	0.984	3.287	0.00369
Cage no.	39.761	20.091	1.979	0.06175

The mean biomass removed from treated and untreated nets by low pressure rinsing was 7.8±1.1 gm^{-2} and 8.54±0.5 gm^{-2} respectively. The mean biomass removed from treated and untreated nets by high pressure rinsing was 12.24±0.9 gm^{-2} and 12.72±0.9 gm^{-2} respectively. A two-way analysis of variance was conducted on the influence of treatment and rinsing pressure on the biomass removed. The main effect for treatment was not significant ($F_{1,21}$ = 0.72, p = 0.4), while the main effect for rinsing pressure was significant ($F_{1,21}$ = 36.24, p = < 0.001), increasing the mean biomass removed from 8.2±0.3 gm^{-2} to 12.5±0.6 gm^{-2}.

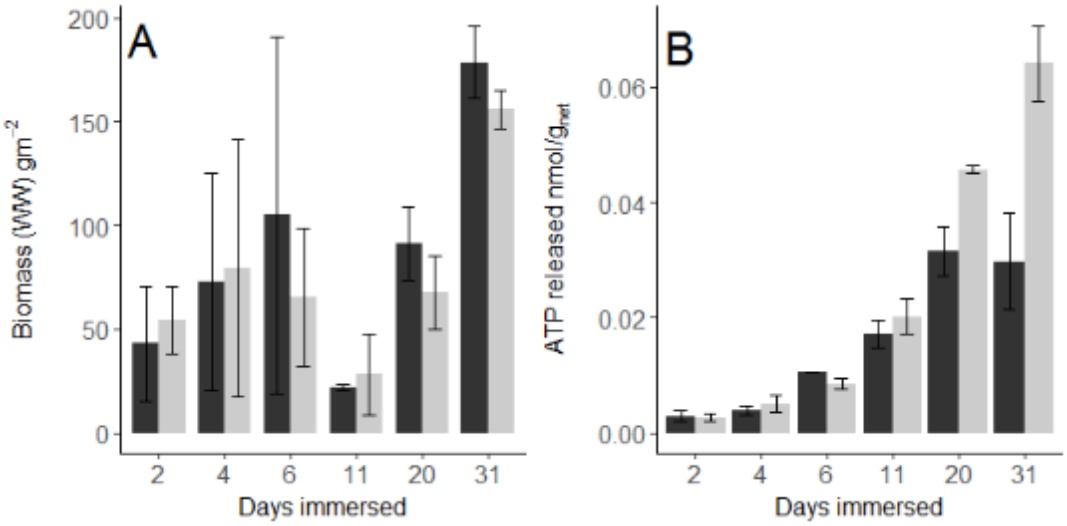


Figure 6.6: (A) Biomass (mean ± SE) removed from net panels (N=2) during the rinsing procedure. (B) Quantity of ATP released (mean ± SE) from 1 gram of netting (N=6) after rinsing procedure. Figure includes data from farm deployed net panels only. Black and grey bars represent treated and untreated net panels. Note the different y axis.

ATP released after cleaning

The quantity of ATP released per gram of netting (nmol ATP/g_{net}) increased with immersion time, and was positively correlated with total biomass (r =0.63, p = <0.001) (Fig. 6.6B). The treatment did not appear to influence the quantity of ATP released after 2, 4 or 6 days' immersion, however, after 11, 20 and 31 days' immersion the treated panels released lower quantities of ATP than untreated panels (Fig. 6.6B). After two days' immersion, treated and untreated panels released 0.0029 ± 0.001 and 0.0027 ± 0.0066 nmol ATP/g_{net}; in contrast after 31 days' immersion, treated and untreated panels released 0.03 ± 0.0084 and 0.064 ± 0.0065 nmol ATP/g_{net}. There was a significant effect of treatment on ATP released after controlling for time immersed (F =$_{2,21}$ 49.99, P=<0.001), which indicated that the treated panels had significantly less bound organic material after the longer immersion time.

Discussion

Biofouling in finfish aquaculture is difficult to manage, posing complex biological and physical challenges for the industry (Blöcher et al., 2013a; Klebert et al., 2013). A non-toxic coating or treatment is a primary goal of contemporary antifouling research which can be broadly separated into antifouling (AF) and fouling release (FR) coatings. Both strategies involve altering the physico-chemical or material properties of a surface (Maréchal and Hellio, 2009; Callow and Callow, 2011). The current study showed that a novel hydrophilic coating significantly lowered the quantity of ATP released after 20 and 31 days' immersion. There are several possible explanations for this observed difference in ATP released with respect to immersion time. The coating, by changing the surface chemistry, might have caused the microbial community to diverge after the initial stages of fouling, by impairing metabolism and growth or favouring particular species over others (Mieszkin et al., 2013). Depending on the point of divergence, this might explain the initial similarity in ATP released. Furthermore, microbial adhesion is a two-part process, beginning with weak reversible adhesion to a substrate and then transitioning to irreversible adhesion (Kumar and Anand, 1998). Irreversible adhesion involves the direct contact between microbe and substrate via surface appendages and crucially makes microbes much harder to remove (Kumar and Anand, 1998). Therefore, the coating may have had a negligible effect on the initial reversible attachment, while having a weakening effect on subsequent irreversible attachment. Different microbial communities can change surface chemistry and the palatability of a surface to subsequent foulers (Müller et al., 1976; Maréchal and Hellio, 2009; Callow and Callow, 2011), and therefore might explain the delayed effect on ATP released seen here. The delay in

effect is unlikely to be due to bacterial colonies with short generation times, however, diatom communities take 2-3 weeks to develop (Hodson and Burke, 1994; Corner et al., 2007) and an interaction between bacteria and diatoms has been shown (Grossart et al., 2005). Investigations of flat rectangular sheets (nylon and stainless steel) treated with the same coating used here, suggested a qualitative decrease in diatom attachment (Myles et al., 2017). Unfortunately, a characterisation of the microbial fauna on the panels was beyond the scope of this investigation.

Unlike, the microfouling community, there was no significant effect of the treatment on total fouling biomass, nor did it increase the biomass removed by rinsing. The biomass was dominated by *Jassa* sp., *Mytilus* sp. and *Ectopleura larynx*, which was broadly consistent with similar studies in Norway and north eastern U.S. coast (Greene and Grizzle, 2007; Guenther et al., 2010; Blöcher et al., 2015), but contrasts with studies in Scotland and Tasmania where initial fouling can be dominated by algae (Hodson et al., 2000; Braithwaite and McEvoy, 2004). The differences in *Jassa* sp, *Mytilus* sp. and *E. larynx* density between treated and untreated net panels was minimal and variable, indicating that the treatment did not affect the relative composition of the macrofouling community. It is possible that for these genera the complex topography of the multi-stranded nylon provides a surface that is easy to anchor to and settle on (Carl et al., 2011), and therefore if the thin conformal carbohydrate coating has no appreciable effect on that topography, it may not affect these foulers. There is some evidence that thick wax and silicone based coatings, which can fill in and smooth the topographic structure of netting, can affect the macro-fouling community (Hodson et al., 2000).

A silicone based coating tested on nets in Tasmania altered the composition of the fouling community, and proved to be an effective foul release coating (Hodson et

al., 2000). The reasons for the changes were most likely due to altered surface chemistry, altered topography and reduced surface free energy, however, the fouling community in Tasmania was dominated by algae which do not share the same mechanisms of attachment as many invertebrates (Hodson et al., 2000; Callow and Callow, 2011). Many algal spores attach to a surface by secretion of a basal disc and are able to attach to the low energy silicone surface, albeit with reduced adhesive strength (Hodson et al., 2000). Both *E. larynx* and *Mytilus* spp. larval stages have the ability to adhere to surfaces immediately, and are not dependent on the secretion of an adhesive disc or pad (Pyefinch and Downing, 1949; Silverman and Roberto, 2007). *Ectopleura larynx* actinulae can adhere to a surface using their nematocyst tipped tentacles when surface properties are not ideal or even toxic (Pyefinch and Downing, 1949). This mechanism may allow actinulae to break the surface tension at a hydrophilic surface by contracting of the tentacles and pushing the aboral end onto a surface, thereby allowing adhesion between the aboral end and the surface. *Mytilus* spp. also adhere immediately to surfaces via secretion of glue from a gland in the foot, which form the byssus threads (Silverman and Roberto, 2007). Hydrophilic surfaces such as the one being tested here have been shown to benefit *Mytilus* spp. adhesion (Silverman and Roberto, 2007; Carl et al., 2012), although no difference was evident here. It was notable that the *Mytilus* sp. and larger clumps of organic debris were clustered at net junction (Fig. 6.3D), rather than along the net bars, and this is perhaps a further indication that the corners, and depressions of the net enhance fouling (Carl et al., 2012). There are varying results of the effect of microtopography on *E. larynx* attachment; Blöcher et al. (2013a) found a lack of effect across varying microtopography and varying wettability, finding both hydrophilic and hydrophobic materials were amongst the materials with the lowest settlement of *E. larynx*. In

contrast, Nellis and Bourget (1996) found that *E. larynx* settled preferentially on 1000um granules compared with smaller sizes.

The ability of *E. larynx* to settle on a range of surfaces is matched by its ability remain attached to the nets. Very few polyps or pieces of colony were removed during rinsing and this is due to the ability of the colonies to grow a system of stolons that wrap around the net and attach to the net substrate at several point (Fig. 6.3F & 6.3G) (Carl et al., 2011). Although it was not obvious in this study, Carl et al. (2011) also showed that *E. larynx* could incorporate strands of netting into the perisarc, and is superbly adapted to benefit from this type of substrate.

A surprising result of this study was the lack of a difference between *E. larynx* development on farm deployed panels and control panels situated *ca.* 1 km from the farm. This is in contrast to previous work in Norway showing that recruitment on farms far exceeds recruitment at control sites 1.5 km from the farm (Blöcher et al., 2015). The limited mobility and rapid settling of actinulae (Pyefinch and Downing, 1949) and the reduced water movement within the cage array of a farm (Blöcher et al., 2015) would promote recruitment within the confines of a farm. Nonetheless, the farm deployed panels here were only *ca.* 1 metre from heavily fouled cages and there was no apparent difference. It is possible that ambient tidal movement and the continuous release of actinulae at this time of year created a region of dispersion that went beyond the 1 km radius. This finding has important implications for the placement of farms or indeed other structures in close proximity; multi-use platforms, e.g. combining aquaculture and renewable energy, and multi-trophic aquaculture would seek to place structures close to each other by design and potentially increase the density and risk from planktonic *E. larynx* actinulae (Bosch-Belmar et al., 2017). Recruitment of *Mytilus* sp. and *Jassa* sp. were clearly enhanced on the farm deployed panels compared

to the control sites (Fig. 6.4B & 6.4C). Why this is the case for those two species and not for *E. larynx* is difficult to understand at present, particularly in the case of *Mytilus* sp. which has non-motile spat similar to actinula.

The presence and abundance of *Jassa* sp. was remarkable, being found on 100% of the panels at both farm and control sites, reaching over 100,000 m^{-2} after 31 days. In contrast, Blöcher et al. (2015) only found *Jassa* spp. on *ca.* 50% of farm deployed experimental panels and *ca.* 5% on control panels. While mobile amphipods like *Jassa* sp. are not considered true foulers in the sense that they do not adhere to a substrate, they do construct tube houses from organic matter including diatoms (Nair and Anger, 1979). By doing so, they are creating an increasingly complex substrate for other fouling organisms and adding substantially to the biomass on nets. The bimodal increase in *Jassa* sp. density may indicate an interaction with other fouling organisms and possibly *E. larynx*. Caprellid amphipods have been positively correlated with hydroid presence on macro algae (Cunha et al., 2018), although here it is not clear that *E. larynx* would provide a surface that is easier to cling to compared with the nylon netting. Although *Jassa* spp. are recognised as an important fouling genus on salmon cages (Braithwaite and McEvoy, 2004; Greene and Grizzle, 2007; Blöcher et al., 2013b), and they appear to be unselective consumers with complex life cycles (Nair and Anger, 1979), the potential interactions with other fouling organisms is unknown.

Conclusions

Measurement of released ATP indicated that treated net panels immersed for 20 or more days were ‘cleaner’ than untreated panels after a light rinse. The taxa and mechanism behind this difference is not clear, and therefore it may be a foul deterrent

or foul release mechanism. *Ectopleura larynx* development and density was unaffected on treated nets, nor was it effected by being placed 1 km from the farm. Relatively few studies have focused on the development of fouling communities on aquaculture cage nets, and lab based assays on flat surfaces may be of limited relevance. Results here suggest that the micro and macro-topographic structure of the nylon netting might reduce the effectiveness of extremely thin antifouling coatings. New single stranded nets are being manufactured and these may work more effectively with the aryldiazonium saccharide coating. Future studies should include efforts to characterise the microbial fouling community and the interactions with subsequent macrofoulers; encouraging a particular fouling community, via manipulation of surface properties, that deters a specific pest species like *E. larynx* would be a cost effective and sustainable solution.



Chapter 7

General discussion

Gelatinous zooplankton are often identified as a nuisance in many regions, and by many sections of society, with the possible exception of regions where some species (mainly cnidarians) are valued as food. Although understandable, this characterisation is misleading and ignores the vital ecosystem functions that gelatinous zooplankton carries out in pelagic ecosystems (Boero et al., 2016; Graham et al., 2016). These functions include carbon sequestration (Madin et al., 2006; Lebrato et al., 2012), a source of shelter, refuge and food for multiple taxa (Graham et al., 2016), and potential prey for a large range of taxa (Arai, 2005). Nonetheless, the deleterious impact of some species on certain industries including fisheries, power generation, tourism and aquaculture has risen well beyond a 'nuisance' level and it is reasonable to suggest that the sustainability of some of these industries is threatened by blooms and aggregations of gelatinous zooplankton in certain regions (Purcell et al., 2007; Rodger et al., 2011a; Purcell, 2012). Our understanding of, and thus our ability to respond to, these impacts is hampered by a lack of knowledge at present, and to a large extent the field of gelatinous zooplankton ecology is playing catch up with other fields of plankton research (Haddock, 2004).

Gelatinous zooplankton are now recognised as a serious cause of injury and mortalities to farmed fish in a number of regions and on a number of species (Doyle et al., 2008a; Baxter et al., 2011a; Baxter et al., 2011b; Bosch-Belmar et al., 2014), and further studies are required to develop a greater understanding of the physical drivers that influence the ecology of gelatinous zooplankton. Chapters 2, 3 & 4 build on recent research in Ireland, developing a greater understanding of the physical drivers that influence the abundance and distribution of gelatinous zooplankton

(Chapters 2, 3 & 4). Mesoscale features are particularly influential over planktonic heterogeneity and understanding how they passively advect and aggregate gelatinous zooplankton (Chapter 3 & 4), and create sharp environmental boundaries which potentially enhance the populations of harmful gelatinous species (Chapter 2, 3 & 4), will provide a knowledge base with which to manage deleterious impacts. Finally, chapters 5 & 6 document the first attempt to quantify the efficacy of a bubble curtain as a barrier to jellyfish (Chapter 5) and the effect of a novel non-toxic antifouling coating on biofouling hydroids (Chapter 6).

Monthly sampling in collaboration with the salmon farming industry was continued during 2014 – 2016 in Bantry Bay, southwest Ireland, in order to build upon previous work carried out in the region (Baxter et al., 2011a; Baxter et al., 2012b). During 2014, the absence of *Muggiaea atlantica* and elevated presence of *Nanomia bijuga* was unusual in the context of recent and historic work in the region (Table 2.1) and suggested a physical mechanism was driving the changes. Periodic observations of oceanic gelatinous taxa, like *Agalma elegans* and *Liriope tetraphylla* for short periods, also suggested a physical mechanism. Such a mechanism exists in the form of a wind driven shelf/bay exchange that takes place periodically, and these exchanges are known to advect Harmful Algal Blooms (HABs) into southwest and west facing bays (Raine et al., 2010). Furthermore, this exchange mechanism interacts with a coastal jet (a narrow high velocity current) along the Irish south coast (Fernand et al., 2006; Hill et al., 2008) that is driven by the seasonal thermohaline front between the Irish and Celtic Seas. This coastal jet is known to advect HABs from the Celtic Sea westward, and given the striking similarity in the occurrence of *Muggiaea atlantica* in Bantry Bay and the Western English Channel (WEC), it is reasonable to suggest the WEC population, which is now a resident population surviving over winter (Blackett

et al., 2014; Blackett et al., 2015), might be a source for the Bantry Bay summer/autumn populations. While the data from Bantry Bay was insufficient to empirically establish a link with the WEC, research based on the PML zooplankton dataset has shown patterns in the zooplankton community which strongly imply a role for the Celtic Sea Front (Southward, 1980; Southward et al., 1995). Southward et al. (1995) categorically showed that warm or cold years had a temporal effect on the annual arrival of 'warm water' zooplankton into the Celtic Sea, although they did not invoke the Celtic Sea Front as the mechanism underlying these community changes. However, a fuller understanding of the front dynamics was not available at the time (Hill et al., 2008), and the pattern Southward et al. (1995) described would be explained by the effect of ambient temperature on front formation, intensity and eventual dissipation (Hill et al., 2008).

Thermohaline fronts: a potential edge over the jellyfish

Implicating the Celtic Sea Front as a seeding mechanism for *M. atlantica* populations north of the English Channel has important implications for salmon farming industry in Ireland and Scotland. The front driven coastal jet continues along the south and west Irish coastline and northward along the Scottish west coast, potentially advecting *M. atlantica* into many important salmon farming sites. Because the front is geographically stable and because it can now be monitored using satellite data (Fig. 3.1), this raises the possibility of an early warning system for the salmon farming industry and it would be a useful exercise to look for correlations between *M. atlantica* blooms and changes in the weather and satellite archival data. While accurate estimates of *M. atlantica* and indeed other harmful species are sparse for much of the operational history of salmon farms in Ireland (25 years plus), there is accurate mortality data for much of that time (Marine Harvest Ireland Ltd., pers. comm.) and

this could be used as a proxy for the presence of harmful species. Together with weather and satellite archives, which are now largely freely available, there are sufficient data to begin exploring a model combining the Celtic Sea Front dynamics – shelf/bay exchanges along the west – mortality data and jellyfish presence. Teasing apart the exact cause of mortalities will be difficult, as there is evidence that jellyfish may be the vector for injury and the subsequent secondary infections (Ferguson et al., 2010; Delannoy et al., 2011; Rodger et al., 2011a), and furthermore pathogens and environmental variables can interact synergistically to increase morbidity/mortalities (Bosch-Belmar et al., 2016a). Nonetheless, exploring these drivers in a theoretical model is likely to yield new lines of enquiry and investigating the statistical power of different variables could enhance monitoring techniques by refining when, where and how much sampling is required.

The investigation of the Celtic Sea Front during 2015 (Chapter 3) was a direct follow up to the study in Bantry Bay (Chapter 2), and a core aim of the work was to establish the distribution of *M. atlantica* with respect to the Celtic Sea Front. While *M. atlantica* was present in the vicinity of the front, the abundance was relatively low compared with other years (see Figs. 2.4 & 2.5) and testing an association with the front was not possible. Analysis of the gelatinous zooplankton community provided strong evidence that the front represents a barrier to gelatinous zooplankton. Previous work has demonstrated partitioning of large scyphozoan jellyfish at the Celtic Sea Front (Houghton et al., 2006; Doyle et al., 2007b; Bastian et al., 2011) and here the same pattern is demonstrated for predominantly hydromedusae community.

While there was little evidence that any gelatinous taxa were aggregated at the front, the lack of vertical resolution in the plankton sampling does impose restrictions on how one might interpret the data. Integrated vertical sampling, when standardised

to indiv. m^{-3}, gives an impression of homogeneity which is known to be unrepresentative of actual zooplankton distributions (Folt and Burns, 1999; Benoit-Bird et al., 2013). Although this is not a criticism of the methods in Chapter 3, integrated tows will likely obscure predator – prey relationships that might be detectable through stratified sampling. Vertical niche separation is commonly reported amongst gelatinous taxa (Williams and Conway, 1981; Mackie et al., 1987; Graham et al., 2001), and using sophisticated video profiling systems that account for vertical distribution has demonstrated specific trophic relationships at other frontal systems (Luo et al., 2014). Furthermore, Luo et al. (2014) was able to show aggregation of some gelatinous taxa within the frontal zone. These aggregations are likely to be the result of passive and behavioural factors (Folt and Burns, 1999; Graham et al., 2001), and are more probable for herbivorous filter feeding tunicates that are adapted to respond to relatively short pulses of productivity (Deibel, 1985; Holland, 2016). For example, prolonged upwelling might lead to a mature frontal community favouring mesotrophic gelatinous predators (Luo et al., 2014), but there is little evidence to suggest that prolonged upwelling occurs in the Celtic Sea (Cooper, 1967; Le Fèvre, 1987; Schultes et al., 2013).

Though there was no evidence that the Celtic Sea Front enhanced gelatinous zooplankton populations through passive and bottom up process, however, it may enhance gelatinous populations in a less direct manner. The warm stable stratified conditions in the Celtic Sea are thought to enhance gelatinous abundance in other frontal systems (Pagès and Gili, 1992), and if sufficient copepod prey were present, it would certainly represent a favourable environment for *M. atlantica* (Blackett et al., 2014; Blackett et al., 2015). Conversely, research on HABs suggests that the stratified conditions in the Celtic Sea support dinoflagellates rather than diatoms (Raine, 2014)

and this is likely to be detrimental for herbivorous copepods and possibly also for copepods predators like *M. atlantica* (Purcell, 1982). These are simplistic scenarios, and work in the WEC has shown that the high reproduction in the *M. atlantica* populations is predicted on a complex interaction between plankton phenology and variation of environmental variables (Blackett et al., 2015). At this time, more surveys with greater temporal resolution are needed to show whether *M. atlantica* reproduces in the Celtic Sea or not.

Fronts and Eddies: the same but different?

The study on the mid-Atlantic warm core (anticyclonic) eddy (Chapter 4) revealed the physical eddy structure had a profound influence over the distribution of the gelatinous zooplankton, with a 12-fold decline in gelatinous abundance within the eddy core. The faunal poverty of the eddy core was also evident across the entire zooplankton community with the exception of several large crustacean species that were more abundant in the eddy core. Previous work has documented the gelatinous zooplankton biomass in warm core eddies (Davis and Wiebe, 1985; Wiebe et al., 1985) and a more specific taxonomic description of the gelatinous taxa across a cold core eddy was provided by (Suárez-Morales et al., 2002). Nonetheless, this is possibly the first detailed description of gelatinous zooplankton across a warm core eddy and demonstrates that the mesoscale heterogeneity evident in primary productivity (McGillicuddy, 2016), macrozooplankton (Wiebe et al., 1985) and micronekton (Boyd et al., 1986) is also evident in gelatinous zooplankton. Perhaps the most important aspect of the eddy study is the impact of such biological heterogeneity on biogeochemical cycling within the top 1000 m or more of the oceanic ecosystem. In this instance the eddy contained no herbivorous plankton indicating an oligotrophic ecosystem with the biomass concentrated in a small number of mesotrophic predators,

and might be loosely described as a biological ‘hole’ in the ocean. Early research would suggest that this oligotrophic ecosystem is characteristic of anticyclonic eddies containing Gulf Stream or Sargasso Sea water, with a net downward flux of nutrients (Gaube and McGillicuddy, 2017). However, previous work has found quite the opposite: a Gulf Stream warm core eddy increased its macrozooplankton biomass, exceeding adjacent productive slope waters, and enabling a community shift to mesotrophic predatory zooplankton (Davis and Wiebe, 1985; Wiebe et al., 1985). An evolving understanding of eddy dynamics, which includes eddy pumping, Ekman induced vertical nutrient transport and lateral eddy stirring suggests that warm core eddies can exceed the chlorophyll levels of cold core eddies at times (Gaube and McGillicuddy, 2017).

In a sense, an eddy represents a contradiction: the physics of eddies enable the upward transfer of nutrient from deeper layers via eddy pumping (McGillicuddy, 2016), and lateral mixing (Joyce, 1984), yet, observations and modelling studies also indicate isolated core water masses that resist exchange (Davis and Wiebe, 1985; Samuelsen et al., 2012). In this respect the eddy and thermohaline boundaries are similar, in that they both enable mixing and enhanced primary productivity, but remain a barrier to gelatinous zooplankton and mesoplanktonic taxa (Chapter 3). But there are also profound differences: the thermohaline front being coupled to topography, remains stable, whereas eddies can potentially carry an isolated community considerable distances (Shoosmith et al., 2005). Pulses of productivity at the front are mediated through stochastic weather events and predictable tidal events, but are probably dispersed rapidly due to the open nature of the system (Le Fèvre, 1987). Pulses of productivity in eddies, except for a seasonal element, are likely to be entirely

stochastic (McGillicuddy et al., 2007) and each eddy will evolve in a variable manner, but crucially that productivity has the potential to reach the higher mesotrophic levels.

These fundamental differences change the way these features might be used by higher gelatinous predators, which includes reptiles, birds and fish species which are known to associate with frontal systems (Bakun, 2006; Block et al., 2011; Scales et al., 2014a). A stable system like the Celtic Sea Front could become a reliable foraging area as part of a calculated migration route (Barnard, 2004), whereas, eddy foraging is more likely to be the result of a random encounter. While the major eddy fields present a broadly stable eddy producing region (Stommel, 1958; Chelton et al., 2011) and are therefore also reliable, encountering the 'right' eddy at the right time would still be a random process due to the variation mentioned above. Biotelemetry of leatherback turtles in the north Atlantic does show a lack of pattern (Luschi et al., 2003; Ferraroli et al., 2004), however, upon encountering the 'right' eddy they have been shown to remain there for an extended period (Doyle et al., 2008b).

There remains a huge amount of work to be done in order to better understand the interaction between eddies and gelatinous zooplankton, and the similarities in the boundary dynamics of both eddies and thermohaline fronts might offer a cost effect way of studying some aspects of mesoscale eddy biology. Advances in satellite sensors have made it relatively easy to monitor certain aspects of frontal systems such as temperature, chlorophyll and spatial movement, yet the ground-truthing needed to relate these remotely sensed changes to biological changes above the lowest trophic levels is lagging behind. The Celtic Sea Front is a well described frontal system in the literature and offers a good model for studying "frontal- boundary/zooplankton interactions". Moreover, the substantial oceanic holoplanktonic community in the Celtic Sea during 2015, which is probably periodic (Southward, 1980; Southward et

al., 1995), provides an opportunity to study holoplanktonic oceanic taxa along a dynamic frontal boundary less than 20 km from the coastline. In the past, bycatch from trawl based fisheries surveys have provided adequate data with which to study the ecology of scyphozoans, however, for the smaller hydromedusae and ctenophores targeted surveys with specific sampling gear will be required to progress the field.

Mitigation against jellyfish incursions into fish farms

Throughout these studies and in conjunction with plankton sampling described in Chapters 2 and 5, investigations were carried out into the potential use of a bubble curtain as a barrier to harmful jellyfish species. The experiments in the LIR flume tank with a model silicone 'jellyfish' revealed some interesting insights into the interaction between waves and a slightly negatively buoyant jellyfish. At a greater wave height and shorter wave period, a greater number of 'jellyfish' passed through the bubble curtain, and likewise at greater airflow, a greater number of 'jellyfish' passed through the bubble curtain. In short, as the system became more turbulent, the 'jellyfish' passed through the bubble curtain at an accelerated rate, propagating forward in an elliptical movement known as Stokes Drift (Fig. 5.9). Stokes Drift is a second order movement imparted by waves and likely be exacerbated in the exposed energetic site around the Irish coast. The early qualitative observations in Bantry Bay suggested that the bubble curtain would be effective at stopping large *Chrysaora hysoscella*, Linnaeus 1767, however, these tests were carried out with a vastly overpowered system, creating a massive plume of bubbles, and replicating such a system over an entire farm would be economically untenable and impractical. Nonetheless, fine tuning the system to reduce power consumption might make it more feasible.

It is possible a bubble curtain system might have some application in very sheltered sites where wave energy is slight, and there are many such sites in Norway, Scotland and the Americas where sites are situated in fjord systems, or very enclosed bays and estuaries. However, it is crucial that a proposed system be accompanied by a physical characterisation of each site and an ecological characterisation of the problem species occurring there. Unpublished observations referenced in chapter 5 indicate variation in the vertical distribution of hydromedusae at different Irish sites, most likely driven by bathymetry, weather and oceanographic processes. However, these data represent snap shots of the hydromedusae abundance and distribution and there is a lack of detailed temporal studies which may well reveal important changes that are relevant to mitigation measures.

In addition to preventing harmful jellyfish from entering fish cages, the study in chapter 6 investigated the efficacy of a non-toxic coating which might reduce the harmful hydroids that resident on the cages (Baxter et al., 2012a; Blöcher et al., 2013b; Bosch-Belmar et al., 2016b). Despite a lack of effect on the hydroids and indeed the other macrofoulers, the evidence of an effect on the microscopic fouling organisms was encouraging. Teasing apart the physical and chemical properties which govern interactions between a substrate and a settling organism is complex, and it seems likely that the complex topographic structure of the net attenuates the intended hydrophilic effect of the coating. Although the field of biofouling is branching out in exciting directions, with an increasing focus on non-toxic antifouling and foul-release technologies, and on bio-engineering surfaces to take advantage of natural successional development and allelopathy (Callow and Callow, 2011). Unfortunately, much of the work is driven by the requirements of the shipping industry, which uses flat coupons and a restricted group of model fouling organisms (e.g. barnacles and

algae of the *Ulva* genera) more relevant to ship hull fouling, and does not include hydroids (Callow and Callow, 2011).

Early work on *E. larynx* has shown some preferences in terms of settlement (Pyefinch and Downing, 1949; Hawes, 1958) and other hydroid species do respond to microbes or their metabolites when settling (Müller et al., 1976), and a greater focus on the settlement behaviour, and chemical cues involved is likely to yield new strategies to reduce hydroid fouling. Future studies of biofouling should also place some emphasis on the phenology of fouling, cleaning regimes and fish health. Hydroids as a cause of injury has been established in several regions, but there are also potential links between biofouling and the transmission of pathogens to fish (De Nys and Guenther, 2009; Floerl et al., 2016). Interactions between fish and the biofouling community are likely to be influenced by seasonal and environmental components (Bosch-Belmar et al., 2016a), and the current level of data collection at farms precludes an in depth analysis of all the components.

Concluding Remarks and future research

The current research has contributed new insights into several aspects of gelatinous zooplankton ecology. While this knowledge has contributed to the investigation of mitigations measures tested in Chapters 5 and 6, it is clear that there are still considerable knowledge gaps in terms of gelatinous ecology and impacts on finfish aquaculture. The research presented here could be built upon in a number of ways, and the following are just some of the potential areas considered during the completion of this thesis.

- The potential link between *Muggiaea atlantica* in Irish coastal waters and the Western English Channel could be further investigated by combining oceanographic modelling, zooplankton data from L4 (WEC), zooplankton data and fish mortalities from Irish aquaculture sites. The short term predictive model of Raine et al., (2010) and the HABs monitoring programme in Ireland provide a good template to start this research. There may be adequate data to begin this research, however, the full potential of this type of modelling relies on large quantities of data and as yet, there is no long term zooplankton monitoring in Ireland.
- Following the above, there is enormous scope to turn Irish salmon farms into zooplankton monitoring stations, collecting data to address their own needs and providing a valuable long term data set for ecologist. Currently, different farms follow various protocols for gathering zooplankton data, and once archived the data appears to lie largely dormant. With relatively minor changes to daily routines and perhaps using a centralised cloud based IT system, the industry in Ireland could move towards a near real-time monitoring programme.
- Future research cruises at the Celtic Sea front should sample the front during September – October to maximise the chances of encountering *M. atlantica* in high abundance. The sampling regime should also include stratified vertical sampling and stable isotope analysis to investigate the actual vertical distribution of gelatinous taxa and their trophic position within the Celtic Sea ecosystem. The coastal jet that likely transports *M. atlantica* along the south coast lies several km off the coastline and it would be feasible to sample this feature manually from a small craft. Therefore, further preliminary work

investigating gelatinous zooplankton in the jet is feasible without a large research vessel.

- As with the Celtic Sea Front, and for the same reasons, future sampling of mesoscale eddies should also include stratified vertical sampling and stable isotope analysis. Mesoscale eddies occur off the shelf edge in the north east Atlantic and further research from the Celtic Explorer is eminently feasible and does not require an extended trans-Atlantic voyage. Eddies form off the northern shelf edge current and in combination with satellite tracking, presents an exciting opportunity to observe the evolution of a gelatinous community inside an isolated body of water.
- The shifting zooplankton community in the Celtic Sea is a fascinating topic, and the mechanism controlling these changes remains vague at present. Here again, oceanographic modelling may be able to provide some insight into the processes which drive the transition from a 'cold-water' to a 'warm-water' community (Southward et al., 1995). The influx of oceanic taxa (i.e. 'cold-water') revealed in chapter 3 is likely to alter the food web and modelling these changes using Ecopath and Ecosim would be a useful way of trying to understand these changes.
- Future research on a bubble curtain 'barrier' would benefit from reducing the scale of the Donegal experiment. A small scale experiment in a relatively shallow bay where *Pelagic noctiluca* occurs would be an ideal testing ground. In this respect, the dimensions and velocity of large *P. noctiluca* aggregations represents a knowledge gap, and could easily be gathered form small craft in coastal waters. For example, drop down cameras could be used to estimate the depth of aggregations and satellite tracked drogues used to track movement.

This type of basic ecological data is missing at present and is an important part of any potential mitigations strategy.

- The field of antifouling is progressing in exciting ways, and biomimetics or bioengineering hold a lot of potential in terms of developing non-toxic technology (Callow and Callow, 2011). The aquaculture industry would benefit from a wider perspective and further collaboration with chemistry, biochemical and even medical researchers which could likely progress antifouling mitigation on salmon farms.
- Aquaculture is likely to change and in fact will be forced to change in respond to environmental and legislative changes in the future. Moving cages to deeper offshore locations and/or having totally enclosed circulatory systems are just 2 possible changes. This means that farms will be exposed to different challenges and in turn changes the focus for applied research. To address these changes, it will be necessary to take a more integrated approach to aquaculture research, combining ecology, economics, policy and social sciences.

The above is not intended as an exhaustive list possible research ideas, but does summarise where perhaps substantial knowledge gaps still exist. One area not covered, but which is of considerable concern from both an ecological and aquaculture industry perspective is ocean warming. The potential consequences of ocean warming includes a wider reproductive period of some species and potential arrival of tropical species, which may mean a greater abundance of gelatinous zooplankton for longer periods annually. It may also mean the northward migration of cold water species (e.g. the lions mane *Cyanea capillata*) and unpredictable changes to polyp strobilation which may well reduce the abundance of some taxa. Ocean warming could deepen seasonal thermoclines affecting the formation of the Celtic Sea Front, and more intense thermal

gradients would lead to an intensification of the front with largely unknown consequences for sites in the southwest and further north. Similarly, ocean warming will change the stratification of the semi-enclosed bays in the southwest/west and potentially alter the vertical distribution of harmful species, and potentially alter the way shelf/bay exchanges occur at present. Any of these changes will have important consequences for the pelagic ecosystem around Ireland, and also for salmon aquaculture operating within that ecosystem. Understanding these changes and how aquaculture can respond to them remains a considerable challenge and it is hoped the studies presented here add to the knowledge base, with which some of these challenges can be addressed in the future.

References

Adams, M. B., Ellard, K., and Nowak, B. F. 2004. Gross pathology and its relationship with histopathology of amoebic gill disease (AGD) in farmed Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases,* 27: 151-161.

Agassiz, A. 1865. Contributions to the Natural History of the United States of America: North American Acalephae. *Illustrated Catalogue of the Museum Comparative Zoology at Harvard College,* II: 200-213.

Aldred, N., Li, G., Gao, Y., Clare, A. S., and Jiang, S. 2010. Modulation of barnacle (*Balanus amphitrite* Darwin) cyprid settlement behavior by sulfobetaine and carboxybetaine methacrylate polymer coatings. *Biofouling,* 26: 673-683.

Alvariño, A. 1971. Siphonophores of the Pacific with a review of the world distribution. *Bulletin of the Scripps Institution of Oceanography Technical Series,* 16: 432 pp.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26: 32-46.

Anderson, V. 1998. Salp and pyrosomid blooms and their importance in biogeochemical cycles. In *The Biology of Pelagic Tunicates*, pp. 125-137. Ed. by Q. Bone. Oxford University Press, New York.

Angel, M. V., and P. R. Pugh. "Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic." In *Island, Ocean and Deep-Sea Biology*, pp. 161-179. Springer, Dordrecht, 2000. Angione, M. D., Duff, T., Bell, A. P., Stamatin, S. N., Fay, C., Diamond, D., Scanlan, E. M., et al. 2015. Enhanced antifouling properties of carbohydrate coated poly (ether sulfone) membranes. *ACS applied materials & interfaces,* 7: 17238-17246.

Arai, M. N. 1992. Active and passive factors affecting aggregations of hydromedusae: A review. *Scientia Marina,* 56: 99-108.

Arai, M. N. 2005. Predation on pelagic coelenterates: a review. *Journal of the Marine Biological Association of the United Kingdom,* 85: 523-536.

Arai, M. N. 1997. *A functional biology of Scyphozoa,* Chapman & Hall, London.

Bakun, A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina,* 70: 105-122.

Ballard, L., and Myers, A. 2000. Observations on the seasonal occurrence and abundance of gelatinous zooplankton in Lough Hyne, Co. Cork, South-West Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy,* 100B: 75-83.

Båmstedt, U., Fosså, J. H., Martinussen, M. B., and Fosshagen, A. 1998. Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. *Sarsia,* 83: 79-85.

Banerjee, I., Pangule, R. C., and Kane, R. S. 2011. Antifouling coatings: recent developments in the design of surfaces that prevent fouling by proteins, bacteria, and marine organisms. *Advanced materials,* 23: 690-718.

Barham, E. G. 1963. Siphonophores and the deep scattering layer. *Science,* 140: 826-828.

Barnard, C. J. 2004. *Animal behaviour: mechanism, development, function and evolution,* Pearson Education Limited, London.

Bastian, T., Haberlin, D., Purcell, J. E., Hays, G. C., Davenport, J., McAllen, R., and Doyle, T. K. 2011. Large-scale sampling reveals the spatio-temporal

distributions of the jellyfish *Aurelia aurita* and *Cyanea capillata* in the Irish Sea. *Marine Biology,* 158: 2639-2652.

Bastian, T., Stokes, D., Kelleher, J. E., Hays, G. C., Davenport, J., and Doyle, T. K. 2010. Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. *ICES Journal of Marine Science,* 68: 436-443.

Baxter, E. 2011. *Gelatinous Zooplankton in Irish Waters: Ecology and Role in the Gill Disorders of Marine-farmed Salmon*. Thesis for the Degree of Doctor of Philosophy University College Cork, Ireland.

Baxter, E., Sturt, M., Ruane, N., Doyle, T., and McAllen, R. 2012a. Biofouling of the hydroid *Ectopleura larynx* on aquaculture nets in Ireland: implications for finfish health. *Fish Veterinary Journal,* 13: 17-29.

Baxter, E. J., McAllen, R., Allcock, A. L., and Doyle, T. K. 2012b. Abundance, Distribution and Community Composition of Small Gelatinous Zooplankton in Southern Irish Coastal Waters. *Biology and Environment: Proceedings of the Royal Irish Academy,* 112b: 91-103.

Baxter, E. J., Rodger, H. D., McAllen, R., and Doyle, T. K. 2011a. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. *Aquaculture Environment Interactions,* 1: 245-257.

Baxter, E. J., Sturt, M. M., Ruane, N. M., Doyle, T. K., McAllen, R., Harman, L., and Rodger, H. D. 2011b. Gill damage to Atlantic salmon (*Salmo salar*) caused by the common jellyfish (*Aurelia aurita*) under experimental challenge. *PLoS One,* 6: e18529.

Beaugrand, G., Ibanez, F., and Reid, P. C. 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series,* 200: 93-102.

Belkin, I. M., Cornillon, P. C., and Sherman, K. 2009. Fronts in Large Marine Ecosystems. *Progress in Oceanography,* 81: 223-236.

Benitez-Nelson, C. R., Bidigare, R. R., Dickey, T. D., Landry, M. R., Leonard, C. L., Brown, S. L., Nencioli, F., et al. 2007. Mesoscale eddies drive increased silica export in the subtropical Pacific Ocean. *Science,* 316: 1017-1021.

Benoit-Bird, K. J., Shroyer, E. L., and McManus, M. A. 2013. A critical scale in plankton aggregations across coastal ecosystems. *Geophysical Research Letters,* 40: 3968-3974.

Berntson, E. A., France, S. C., and Mullineaux, L. S. 1999. Phylogenetic relationships within the class Anthozoa (phylum Cnidaria) based on nuclear 18S rDNA sequences. *Molecular and Phylogenetics Evolution,* 13: 417-433.

Bigelow, H. 1911. The Siphonophorae. Report on the scientific research expedition Albatross to the tropical Pacific. 23. *Memoirs of the Museum of Comparative Zoology, Harvard College,* 38: 173-402.

Biggs, D. C. 1977. Respiration and Ammonium Excretion by Open Ocean Gelatinous Zooplankton. *Limnology and Oceanography,* 22: 108-117.

Blackett, M., Licandro, P., Coombs, S. H., and Lucas, C. H. 2014. Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel. *Progress in Oceanography,* 128: 1-14.

Blackett, M., Lucas, C. H., Harmer, R. A., and Licandro, P. 2015. Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. *Marine Ecology Progress Series,* 535: 129-144.

Blöcher, N., de Nys, R., Poole, A. J., and Guenther, J. 2013a. The fouling hydroid *Ectopleura larynx*: a lack of effect of next generation antifouling technologies. *Biofouling*, 29: 237-246.

Blöcher, N., Floerl, O., and Sunde, L. M. 2015. Amplified recruitment pressure of biofouling organisms in commercial salmon farms: potential causes and implications for farm management. *Biofouling*, 31: 163-172.

Blöcher, N., Olsen, Y., and Guenther, J. 2013b. Variability of biofouling communities on fish cage nets: A 1-year field study at a Norwegian salmon farm. *Aquaculture*, 416: 302-309.

Block, B., Jonsen, I., Jorgensen, S., Winship, A., Shaffer, S., Bograd, S., Hazen, E., et al. 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475: 86-90.

Boer, M., Gannefors, C., Kattner, G., Graeve, M., Hop, H., and Falk-Petersen, S. 2005. The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy. *Marine Biology*, 147: 707-717.

Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. *Marine Ecology*, 5: 93-118.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M. P., Parsons, T., and Piraino, S. 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, 356: 299-310.

Boero, F., Brotz, L., Gibbons, M. J., Piraino, S., and Zampardi, S. 2016. *Impacts and effects of ocean warming on jellyfish*. In: Laffoley, D., & Baxter, J.M. (editors). 2016. Explaining ocean warming: Causes, scale, effects and consequences. Full report. Gland, Switzerland: IUCN. pp. 213-238.

Bosch-Belmar, M., Giomi, F., Rinaldi, A., Mandich, A., Fuentes, V., Mirto, S., Sara, G. and Piraino, S. 2016a. Concurrent environmental stressors and jellyfish stings impair caged European sea bass (*Dicentrarchus labrax*) physiological performances. *Scientific Reports*, 6: 27929.

Bosch-Belmar, M., Kéfi-Daly Yahia, O., M'Rabet, C., Dhaouadi, R., Fuentes, V., Chalghaf, M., and Piraino, S. 2014. Effects of *Pelagia noctiluca* jellyfish swarms on caged gilthead sea bream. *ICES CM*, 3728.

Bosch-Belmar, M., M'Rabet, C., Dhaouadi, R., Chalghaf, M., Daly Yahia, M. N., Fuentes, V., Piraino, S. and Yahia, O. K. D.. 2016b. Jellyfish Stings Trigger Gill Disorders and Increased Mortality in Farmed *Sparus aurata* (Linnaeus, 1758) in the Mediterranean Sea. *PLoS One*, 11: e0154239.

Bosch-Belmar, M., Milisenda, G., Girons, A., Taurisano, V., Accoroni, S., Totti, C., Piraino, S., et al. 2017. Consequences of Stinging Plankton Blooms on Finfish Mariculture in the Mediterranean Sea. *Frontiers in Marine Science*, 4.

Bouillon, J., Gravili, C., Gili, J.-M., and Boero, F. 2006. *An introduction to Hydrozoa*, Baxkhuys Publishers BV, Mémoires Du Muséum National d'Histoire Naturelle. 1-591 pp.

Bouillon, J., and Mar, I. d. C. d. 2004. *Fauna of the Mediterranean Hydrozoa*, Institut de Ciències del Mar, CMIMA-CSIC.

Boyd, R., Ó Céidigh, P., and Wilkinson, A. 1973. Investigations of the Plankton of the West Coast of Ireland: VI. Pelagic Cnidaria of the Galway Bay Area 1956-72, with a Revision of Previous Records for These Species in Irish Inshore Waters. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, 73: 383-403.

Boyd, S. H., Wiebe, P. H., Backus, R. H., Craddock, J. E., and Daher, M. A. 1986. Biomass of the micronekton in Gulf Stream ring 82-B and environs: changes

with time. *Deep Sea Research Part A: Oceanographic Research Papers,* 33: 1885-1905.

Braithwaite, R., and McEvoy, L. 2004. Marine biofouling on fish farms and its remediation. *Advances in Marine Biology*, 47: 215-252.

Braithwaite, R. A., Carrascosa, M. C. C., and McEvoy, L. A. 2007. Biofouling of salmon cage netting and the efficacy of a typical copper-based antifoulant. *Aquaculture*, 262: 219-226.

Brandt, S. B. 1981. Effects of a warm-core eddy on fish distributions in the Tasman Sea off east Australia. *Marine Ecology Progress Series*: 19-33.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., and Pauly, D. 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia*, 690: 3-20.

Brown, J., Carrillo, L., Fernand, L., Horsburgh, K. J., Hill, A. E., Young, E. F., and Medler, K. J. 2003. Observations of the physical structure and seasonal jet-like circulation of the Celtic Sea and St. George's Channel of the Irish Sea. *Continental Shelf Research,* 23: 533-561.

Browne, E. T., Thompson, I. C., Gamble, F., Herdman, W., Cunningham, J., Beaumont, W., and Weiss, F. 1898. The fauna and flora of Valencia Harbour on the West Coast of Ireland. *Proceedings of the Royal Irish Academy*: 667-854.

Burridge, A. K., Tump, M., Vonk, R., Goetze, E., and Peijnenburg, K. T. C. A. 2017. Diversity and distribution of hyperiid amphipods along a latitudinal transect in the Atlantic Ocean. *Progress in Oceanography,* 158: 224-235.

Burridge, L., Weis, J. S., Cabello, F., Pizarro, J., and Bostick, K. 2010. Chemical use in salmon aquaculture: a review of current practices and possible environmental effects. *Aquaculture*, 306: 7-23.

Buskens, P., Wouters, M., Rentrop, C., and Vroon, Z. 2013. A brief review of environmentally benign antifouling and foul-release coatings for marine applications. *Journal of Coatings Technology and Research,* 10: 29-36.

Callow, J. A., and Callow, M. E. 2011. Trends in the development of environmentally friendly fouling-resistant marine coatings. *Nature communications,* 2: 244.

Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F., and Gili, J.-M. 2014. *Pelagia noctiluca in the Mediterranean Sea*. *In* Jellyfish Blooms, pp. 237-266. Ed. by K. A. Pitt, and C. H. Lucas. Springer Netherlands, Dordrecht.

Carl, C., Guenther, J., and Sunde, L. M. 2011. Larval release and attachment modes of the hydroid *Ectopleura larynx* on aquaculture nets in Norway. *Aquaculture Research,* 42: 1056-1060.

Carl, C., Poole, A., Sexton, B. A., Glenn, F., Vucko, M. J., Williams, M., Whalan, S., et al. 2012. Enhancing the settlement and attachment strength of pediveligers of *Mytilus galloprovincialis* bychanging surface wettability and microtopography. *Biofouling,* 28: 175-186.

Carré, C., and Carré, D. 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 334: 27-32.

Cartwright, P., Evans, N. M., Dunn, C. W., Marques, A. C., Miglietta, M. P., Schuchert, P., and Collins, A. G. 2008. Phylogenetics of Hydroidolina (Hydrozoa: Cnidaria). *Journal of the Marine Biological Association of the United Kingdom,* 88: 1663-1672.

Catul, V., Gauns, M., and Karuppasamy, P. K. 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Reviews in Fish Biology and Fisheries,* 21: 339-354.

Cayula, J. F., and Cornillon, P. 1992. Edge-Detection Algorithm for Sst Images. *Journal of Atmospheric and Oceanic Technology,* 9: 67-80.

Chambers, L. D., Stokes, K. R., Walsh, F. C., and Wood, R. J. 2006. Modern approaches to marine antifouling coatings. *Surface and Coatings Technology,* 201: 3642-3652.

Chelton, D. B., Schlax, M. G., and Samelson, R. M. 2011. Global observations of nonlinear mesoscale eddies. *Progress in Oceanography,* 91: 167-216.

Choy C. A., Haddock S. H. D., Robison B. H. 2017 Deep pelagic food web structure as revealed by in situ feeding observations. *Proceedings of the Royal Society B*, 284:

CIESM. 2001. Gelatinous zooplankton outbreaks: theory and practice. n°14. 122 pp.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecology,* 18: 117-143.

Clarke, K. R., and Warwick, R. M. 2001. *Changes in marine communities: an approach to statistical analysis and interpretation*, PRIMER-E Ltd, Plymouth.

Colombo, G. A., Mianzan, H., and Madirolas, A. 2003. Acoustic characterization of gelatinous-plankton aggregations: four case studies from the Argentine continental shelf. *ICES Journal of Marine Science,* 60: 650-657.

Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B. and Uye, S. I., 2013. Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences of the United States of America,* 110: 1000-1005.

Condon, R. H., Steinberg, D. K., del Giorgio, P. A., Bouvier, T. C., Bronk, D. A., Graham, W. M., and Ducklow, H. W. 2011. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences,* 108: 10225-10230.

Cooper, L. H. N. 1952. The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom,* 30: 465-510.

Cooper, L. H. N. 1960. Some theorems and procedures in shallow-water oceanography applied to the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom,* 39: 155-171.

Cooper, L. H. N. 1967. The physical oceanography of the Celtic Sea. *Oceanography and Marine Biology: An Annual Review,* 5: 99-110.

Corner, R. A., Ham, D., Bron, J. E., and Telfer, T. C. 2007. Qualitative assessment of initial biofouling on fish nets used in marine cage aquaculture. *Aquaculture Research,* 38: 660-663.

Costello, J. H., Colin, S. P., and Dabiri, J. O. 2008. Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. *Invertebrate Biology,* 127: 265-290.

Cox, J., and Wiebe, P. H. 1979. Origins of oceanic plankton in the Middle Atlantic Bight. *Estuarine and Coastal Marine Science,* 9: 509-527.

Cronin, M., Cusack, C., Geoghegan, F., Jackson, D., McGovern, E., McMahon, T., O'Beirn, F. X., O Cinneide, M. and Silke, J., 2004. Salmon Mortalities at Inver Bay and McSwyne's Bay Finfish farms, County Donegal, Ireland, during 2003. 15.

Cunha, A. F., Maruyama, P. K., and Jacobucci, G. B. 2018. Epiphytic hydroids (Cnidaria, Hydrozoa) contribute to a higher abundance of caprellid amphipods (Crustacea, Peracarida) on macroalgae. *Hydrobiologia,* 808: 251-264.

Cunningham, J. T., 1892. On a species of siphonophore observed at Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, *2*(3), pp. 212-215.

Daly, M., Brugler, M. R., Cartwright, P., Collins, A. G., Dawson, M. N., Fautin, D. G., France, S. C., Mc Fadden, C. S., Opresko, D. M., Rodriguez, E. and Romano, S. L., 2007. The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*: 127-182.

Davis, C. S., and Wiebe, P. H. 1985. Macrozooplankton biomass in a warm-core Gulf Stream ring: Time series changes in size structure, taxonomic composition, and vertical distribution. *Journal of Geophysical Research: Oceans,* 90: 8871-8884.

Dawson, M. N., and Hamner, W. M. 2009. A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. *Hydrobiologia,* 616: 193-215.

Deibel, D. 1985. Blooms of the pelagic tunicate, Dolioletta gegenbauri: Are they associated with Gulf Stream frontal eddies? *Journal of Marine Research,* 43: 211-236.

Deibel, D., and Paffenhofer, G. A. 2009. Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). *Journal of Plankton Research,* 31.

De Nys, R., and Guenther, J. 2009b. *The impact and control of biofouling in marine finfish aquaculture*. *In* Advances in marine antifouling coatings and technologies, pp. 177-221. Elsevier.

Delannoy, C. M. J., Houghton, J. D. R., Fleming, N. E. C., and Ferguson, H. W. 2011. Mauve Stingers (*Pelagia noctiluca*) as carriers of the bacterial fish pathogen *Tenacibaculum maritimum*. *Aquaculture,* 311: 255-257.

Delap, M., and Delap, C. 1905. Notes on the marine plankton of Valencia Harbour, 1899-1901. *Annual Report of Fisheries in Ireland (1902-3),* 2: 3-19.

Delap, M. J. 1924. Further notes on the plankton of Valentia Harbour. 1906-1923. *The Irish Naturalist,* 33: 1-6.

Delle Chiaje, S., 1844. Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore osservati vivi negli anni 1822–1830. Tomo Ottavo. Appendice, Osservazioni Critiche, Indice Generale. Stabilimento Tipografico di C. Batelli e Comp.: Napoli.

Delvigne, G. A. L. 1987. *Laboratory Experiments on Oil Spill Protection of a Water Intake*. *In* Oil in Freshwater: Chemistry, Biology, Countermeasure Technology, pp. 446-458. Ed. by S. E. Hrudey. Pergamon.

Denman, K. L., Mackas, D. L., Freeland, H. J., Austin, M. J., and Hill, S. H. 1981. *Persistent Upwelling and Mesoscale Zones of High Productivity off the West Coast of Vancouver Island, Canada*. *In* Coastal Upwelling, pp. 514-521. American Geophysical Union.

Dobretsov, S., Dahms, H.-U., and Qian, P.-Y. 2006. Inhibition of biofouling by marine microorganisms and their metabolites. *Biofouling,* 22: 43-54.

Doyle, T. K., De Haas, H., Cotton, D., Dorschel, B., Cummins, V., Houghton, J. D. R., Davenport, J. and Hays G. C., 2008a. Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research,* 30: 963-968.

Doyle, T. K., Georges, J.-Y., and Houghton, J. D. 2013. A leatherback turtle's guide to jellyfish in the North East Atlantic. *Munibe Monographs. Nature Series*, 1: 15-21.

Doyle, T. K., Hays, G. C., Harrod, C., and Houghton, J. D. R. 2014. *Ecological and Societal Benefits of Jellyfish*. *In* Jellyfish Blooms, pp. 105-127. Ed. by K. A. Pitt, and C. H. Lucas. Springer Netherlands, Dordrecht.

Doyle, T. K., Houghton, J. D., McDevitt, R., Davenport, J., and Hays, G. C. 2007a. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology*, 343: 239-252.

Doyle, T. K., Houghton, J. D., O'Súilleabháin, P. F., Hobson, V. J., Marnell, F., Davenport, J., and Hays, G. C. 2008b. Leatherback turtles satellite-tagged in European waters. *Endangered Species Research*, 4: 23-31.

Doyle, T. K., Houghton, J. D. R., Buckley, S. M., Hays, G. C., and Davenport, J. 2007b. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia*, 579: 29-39.

Dufois, F., Hardman-Mountford, N. J., Greenwood, J., Richardson, A. J., Feng, M., and Matear, R. J. 2016. Anticyclonic eddies are more productive than cyclonic eddies in subtropical gyres because of winter mixing. *Science Advances*, 2: e1600282.

Dunn, C. W., Leys, S. P., and Haddock, S. H. 2015. The hidden biology of sponges and ctenophores. *Trends in ecology & evolution*, 30: 282-291.

Dunn, C. W., Pugh, P. R., and Haddock, S. H. 2005. Molecular phylogenetics of the siphonophora (Cnidaria), with implications for the evolution of functional specialization. *Systematic Biology*, 54: 916-935.

Edwards, A., Jones, K., Graham, J.M., Griffiths, C.R.,MacDougall,N., Patching, J., Richard, J.M., Raine, R., 1996. Transient coastal upwelling and water circulation in Bantry Bay, a ria on the SWcoast of Ireland. *Estuarine, Coastal and Shelf Science* 42, 213–230.

Ellis, J., & Solander, D. C., (1786). *The natural history of many curious and uncommon zoophytes: collected from various parts of the globe*. Benjamin White and Peter Elmsly. London.

Esteban-Tejeda, L., Duff, T., Ciapetti, G., Angione, M. D., Myles, A., Vasconcelos, J. M., Scanlan, E. M., and Colavita, P. E.,. 2016. Stable hydrophilic poly (dimethylsiloxane) via glycan surface functionalization. *Polymer*, 106: 1-7.

Faghmous, J. H., Frenger, I., Yao, Y., Warmka, R., Lindell, A., and Kumar, V. 2015. A daily global mesoscale ocean eddy dataset from satellite altimetry. *Scientific Data*, 2: 150028.

FAO. 2016. The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all.

Farrell, H., Gentien, P., Fernand, L., Lunven, M., Reguera, B., Gonzalez-Gil, S., and Raine, R. 2012. Scales characterising a high density thin layer of *Dinophysis acuta* Ehrenberg and its transport within a coastal jet. *Harmful Algae*, 15: 36-46.

Fennell, S., and Rose, G. 2015. Oceanographic influences on Deep Scattering Layers across the North Atlantic. *Deep-Sea Research Part I: Oceanographic Research Papers*, 105: 132-141.

Ferguson, H. W., Christian, M. J. D., Hay, S., Nicolson, J., Sutherland, D., and Crumlish, M. 2010. Jellyfish as vectors of bacterial disease for farmed salmon (*Salmo salar*). *Journal of Veterinary Diagnostic Investigation*, 22: 376-382.

Fernand, L., Nolan, G. D., Raine, R., Chambers, C. E., Dye, S. R., White, M., and Brown, J. 2006. The Irish coastal current: A seasonal jet-like circulation. *Continental Shelf Research,* 26: 1775-1793.

Ferraroli, S., Georges, J.-Y., Gaspar, P., and Le Maho, Y. 2004. Endangered species: where leatherback turtles meet fisheries. *Nature,* 429: 521-522.

Fewkes, J. W. 1888. Studies from the Newport Marine Zoological Laboratory. On certain medusae from New England. *Bulletin of the museum of comparative zoology,* XIII: 209-240.

Fitridge, I., Dempster, T., Guenther, J., and de Nys, R. 2012. The impact and control of biofouling in marine aquaculture: a review. *Biofouling,* 28: 649-669.

Fives, J. M. 1971. Investigations of the Plankton of the West Coast of Ireland: V. Chaetognatha Recorded from the Inshore Plankton off Co. Galway. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*: 119-138.

Fleming, N. E., Harrod, C., Griffin, D. C., Newton, J. and Houghton, J. D., 2014. Scyphozoan jellyfish provide short-term reproductive habitat for hyperiid amphipods in a temperate near-shore environment. *Marine Ecology Progress Series*, 510: 229-240.

Fleming, J., 1823. *Gleanings of Natural History, Gathered on the Coast of Scotland, During a Voyage in 1821*. éditeur inconnu.

Floerl, O., Sunde, L. M., and Bloecher, N. 2016. Potential environmental risks associated with biofouling management in salmon aquaculture. *Aquaculture Environment Interactions,* 8: 407-417.

Folt, C. L., and Burns, C. W. 1999. Biological drivers of zooplankton patchiness. *Trends in Ecology and Evolution,* 14: 300-305.

Font, J., Garcialadona, E., and Gorriz, E. G. 1995. The Seasonality of Mesoscale Motion in the Northern Current of the Western Mediterranean - Several Years of Evidence. *Oceanologica Acta,* 18: 207-219.

Forbes, E. and Goodsir, J., 1853. XVIII.—On some remarkable Marine Invertebrata new to the British Seas. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *20*(2), pp.307-315.

Forbes, E., 1848. *A monograph of the British naked-eyed medusae: with figures of all the species* (Vol. 10). Printed for the Ray Society.

Fosså, J. H., Havforskningsintituttet, P. R. F., Bathyiologica, A. B. O., and Veterinaerinstituttet, F. J. 2003. Sm og usynlige, men plagsomme maneter av arten *Muggiaea atlantica*. *Fisken Havet,* 2: 99-103.

Gaube, P. and McGillicuddy Jr, D. J., 2017. The influence of Gulf Stream eddies and meanders on near-surface chlorophyll. *Deep Sea Research Part I: Oceanographic Research Papers*, *122*, pp.1-16.

Gibbons, M. J., and Richardson, A. J. 2008. Patterns of jellyfish abundance in the North Atlantic. *Hydrobiologia,* 616: 51-65.

Gili, J.-M., and Hughes, R. G. 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology,* 33: 351-426.

Giribet, G. 2016. Zoology: At Last an Exit for Ctenophores. *Current Biology,* 26: R918-R920.

Godø, O. R., Samuelsen, A., Macaulay, G. J., Patel, R., Hjøllo, S. S., Horne, J., Kaartvedt, S., et al. 2012. Mesoscale eddies are oases for higher trophic marine life. *PLoS One,* 7: e30161.

Golshan, R., Boufadel, M., Rodriguez, V., Geng, X., Gao, F., King, T., Robinson, B., et al. 2018. Oil Droplet Transport under Non-Breaking Waves: An Eulerian

RANS Approach Combined with a Lagrangian Particle Dispersion Model. *Journal of Marine Science and Engineering,* 6: 7.

Graham, W.M., Gelcich, S., Robinson, K.L., Duarte, C.M., Brotz, L., Purcell, J.E., Madin, L.P., Mianzan, H., Sutherland, K.R., Uye, S.I. and Pitt, K.A., 2014. Linking human well-being and jellyfish: ecosystem services, impacts, and societal responses. *Frontiers in Ecology and the Environment*, 12 (9): 515-523.

Graham, W. M., Pages, F., and Hamner, W. M. 2001. A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia,* 451: 199-212.

Greene, J. K., and Grizzle, R. E. 2007. Successional development of fouling communities on open ocean aquaculture fish cages in the western Gulf of Maine, USA. *Aquaculture,* 262: 289-301.

Greve, W. 1994. The 1989 german bight invasion of muggiaea atlantica. *ICES Journal of Marine Science,* 51: 355-358.

Grossart, H.-P., Levold, F., Allgaier, M., Simon, M., and Brinkhoff, T. 2005. Marine diatom species harbour distinct bacterial communities. *Environmental Microbiology,* 7: 860-873.

Guenther, J., Fitridge, I., and Misimi, E. 2011. Potential antifouling strategies for marine finfish aquaculture: the effects of physical and chemical treatments on the settlement and survival of the hydroid *Ectopleura larynx*. *Biofouling,* 27: 1033-1042.

Guenther, J., Misimi, E., and Sunde, L. M. 2010. The development of biofouling, particularly the hydroid *Ectopleura larynx*, on commercial salmon cage nets in Mid-Norway. *Aquaculture,* 300: 120-127.

Guerrero, E., Marrodan, A., Sabates, A., Orejas, C., and Gili, J. M. 2016. High spatial heterogeneity of two planktonic cnidarian species related to the variability of a shelf-slope front at short time scales. *Scientia Marina,* 80: 487-497.

Haberlin, D., Mapstone, G., McAllen, R., McEvoy, A. J., and Doyle, T. K. 2016. Diversity and Occurrence of Siphonophores in Irish Coastal Waters. *Biology and Environment: Proceedings of the Royal Irish Academy,* 116b: 119-129.

Haddock, S. H. D. 2004. A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia,* 530: 549-556.

Hamish, D. R., Louise, H., and Susan, O. M. 2010. Non-infectious gill disorders of marine salmonid fish. *Reviews in Fish Biology and Fisheries,* 21.

Hamilton, G., 2016. The secret lives of jellyfish: long regarded as minor players in ocean ecology, jellyfish are actually important parts of the marine food web. *Nature*, 531(7595): 432-435.

Hamner, W. M. 1975. Underwater Observations of Blue-Water Plankton - Logistics, Techniques, and Safety Procedures for Divers at Sea. *Limnology and Oceanography,* 20: 1045-1050.

Hamner, W. M., and Dawson, M. N. 2009. A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. *Hydrobiologia,* 616: 161-191.

Harbison, G. R., Madin, L. P., and Swanberg, N. R. 1978. On the natural history and distribution of oceanic ctenophores. *Deep Sea Research,* 25: 233-256.

Hawes, F. 1958. Preliminary observations on the settlement of the actinula larva of the *Tubularia larynx* (Ellis & Solander). *Journal of Natural History,* 1: 147-155.

Hays, G. C., Ferreira, L. C., Sequeira, A. M., Meekan, M. G., Duarte, C. M., Bailey, H., Bailleul, F., Bowen, W. D., Caley, M. J., Costa, D. P. and Eguíluz, V. M.,

2016. Key questions in marine megafauna movement ecology. *Trends in ecology & evolution*, 31(6): 463-475.

Hays, G.C., Doyle, T.K., Houghton, J.D., Lilley, M.K., Metcalfe, J.D. and Righton, D. 2008. Diving behaviour of jellyfish equipped with electronic tags. *Journal of Plankton Research*, *30*(3): 325-331.

Hill, A. E., Brown, J., Fernand, L., Holt, J., Horsburgh, K. J., Proctor, R., Raine, R. and Turrell, W. R., 2008. Thermohaline circulation of shallow tidal seas. *Geophysical Research Letters*, 35.

Hitchcock, G. L., Langdon, C., and Smayda, T. 1987. Short-term changes in the biology of a Gulf Stream warm-core ring: Phytoplankton biomass and productivity. *Limnology and Oceanography,* 32: 919-928.

Hodson, S., Burke, C., and Bissett, A. 2000. Biofouling of fish-cage netting: the efficacy of a silicone coating and the effect of netting colour. *Aquaculture,* 184: 277-290.

Hodson, S. L., and Burke, C. 1994. Microfouling of salmon-cage netting: A preliminary investigation. *Biofouling,* 8: 93-105.

Hodson, S. L., Lewis, T. E., and Burkea, C. M. 1997. Biofouling of fish-cage netting: efficacy and problems of in situ cleaning. *Aquaculture*, 152: 77-90.

Holland, L. Z. 2016. Tunicates. *Current Biology*, 26: R146-R152.

Holligan, P. M. 1981. Biological Implications of Fronts on the Northwest European Continental Shelf. *Philosophical Transactions of the Royal Society A Mathematical Physical and Engineering Sciences,* 302: 547-562.

Hopcroft, R. R., and Robison, B. H. 1999. A new mesopelagic larvacean, *Mesochordaeus erythrocephalus*, sp nov., from Monterey Bay, with a description of its filtering house. *Journal of Plankton Research,* 21: 1923-1937.

Horsburgh, K. J., Hill, A. E., and Brown, J. 1998. A summer jet in the St George's Channel of the Irish Sea. *Estuarine Coastal and Shelf Science,* 47: 285-294.

Hosia, A., and Båmstedt, U. 2008. Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. *Journal of Plankton Research*, 30.

Hosia, A., Falkenhaug, T., Baxter, E. J., and Pagès, F. 2017. Abundance, distribution and diversity of gelatinous predators along the northern Mid-Atlantic Ridge: A comparison of different sampling methodologies. *PLoS One,* 12: e0187491.

Hosia, A., Stemmann, L., and Youngbluth, M. 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55: 106-118.

Houghton, J.D., Doyle, T.K., Davenpor, J. and Hays, G.C., 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. *Marine Ecology Progress Series*, 314: 159-170.

Huang, S., and Hadfield, M. G. 2003. Composition and density of bacterial biofilms determine larval settlement of the polychaete *Hydroides elegans*. *Marine Ecology Progress Series,* 260: 161-172.

Huggett, M. J., Williamson, J. E., de Nys, R., Kjelleberg, S., and Steinberg, P. D. 2006. Larval settlement of the common Australian sea urchin *Heliocidaris erythrogramma* in response to bacteria from the surface of coralline algae. *Oecologia*, 149: 604-619.

Hutchings, L., Armstrong, D. A., and Mitchell-Innes, B. A. 1986. The Frontal Zone in the Southern Benguela Current. *Elsevier Oceanography Series*, 42: 67-94.

Hyndman, G. 1841. Note on the Occurrence of the Genus *Diphya* on the Coast of Ireland. *Journal of Natural History,* 7: 164-166.

Jager, M., and Manuel, M. 2016. Ctenophores: an evolutionary-developmental perspective. *Current Opinion in Genetics & Development,* 39: 85-92.

Jeal, F., and West, A. 1970. A Check List of Siphonophora from Irish Waters, with a Record of *Physophora hydrostatica* (Forskal) from the Irish Coast. *The Irish Naturalists' Journal,* 16: 338-342.

Joyce, T. M. 1984. Velocity and hydrographic structure of a Gulf Stream warm-core ring. *Journal of Physical Oceanography,* 14: 936-947.

Kaiser, M. J. 2011. *Marine ecology: processes, systems, and impacts,* Oxford University Press, Oxford, United Kingdom.

Kassah, J. E. 2012. *Development of biofouling on salmon cage nets and the effects of anti-fouling treatments on the survival of the hydroid (Ectopleura larynx)(Ellis & Solander, 1786). In* Biology. Trondheim; Norwegian University of Science and Technology.

Kelley, D., and Richards, C. 2017. *oce: Analysis of Oceanographic Data. R package version 0.9-22. https://CRAN.R-project.org/package=oce.*

Kirkpatrick, P., and Pugh, P. 1984. *Siphonophores and velellids: Keys and notes for the identification of the species,* Brill Archive, London.

Klebert, P., Lader, P., Gansel, L., and Oppedal, F. 2013. Hydrodynamic interactions on net panel and aquaculture fish cages: A review. *Ocean engineering,* 58: 260-274.

Kramp, P. L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report 46,* 1: 1-283.

Kramp, P. L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom,* 40: 7-382.

Krauss, W. 1986. The north Atlantic current. *Journal of Geophysical Research: Oceans,* 91: 5061-5074.

Kumar, C. G., and Anand, S. K. 1998. Significance of microbial biofilms in food industry: a review. *International Journal of Food Microbiology,* 42: 9-27.

Lara-Lopez, A. L., Davison, P., and Koslow, J. A. 2012. Abundance and community composition of micronekton across a front off Southern California. *Journal of Plankton Research,* 34: 828-848.

Larson, R. J., 1986. Water-content, organic content, and carbon and nitrogen composition of medusae from the Northeast Pacific. *Journal of Experimental Marine Biology and Ecology,* 99, 107–120.

Larson, R. J., Mills, C. E., and Harbison, G. R. 1991. Western Atlantic midwater hydrozoan and scyphozoan medusae: in situ studies using manned submersibles. *Hydrobiologia,* 216: 311-317.

Le Fèvre, J. 1987. Aspects of the Biology of Frontal Systems. *Advances in Marine Biology,* 23: 163-299.

Le Fèvre, J., Le Corre, P., Morin, P., and Birrien, J. 1983. The pelagic ecosystem in frontal zones and other environments off the west coast of Brittany. *Oceanologica Acta,* Special issue: 125-129.

Lebrato, M., Pitt, K. A., Sweetman, A. K., Jones, D. O. B., Cartes, J. E., Oschlies, A., Condon, R. H., Molinero, J. C., Adler, L., Gaillard, C. and Lloris, D., 2012. Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia,* 690: 227-245.

Lesueur, C. A., 1815. Voyage de découvertes aux terres australes. Histoire Naturelle. Partie iconographique et gravure.

Linnaeus, C. V. 1758. Systema Naturae, edition X, vol. 1 (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata). *Holmiae Salvii, 824*.

Linnaeus, C. V. 1767. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Vol. 1). Typis Ioannis Thomae.

Lo, J. 1996. Laboratory investigation of single floating booms a and series of booms in the prevention of oil slick and jellyfish movement. *Ocean engineering,* 23: 519-531.

Lucas, C., Williams, D., Wiliams, J., and Sheader, M. 1995. Seasonal dynamics and production of the hydromedusan *Clytia hemisphaerica* (Hydromedusa: Leptomedusa) in Southampton water. *Estuaries and Coasts,* 18: 362-372.

Lucas, C. H., Jones, D. O. B., Hollyhead, C. J., Condon, R. H., Duarte, C. M., Graham, W. M., Robinson, K. L., Pitt, K. A., Schildhauer, M. and Regetz, J., 2014. Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. *Global Ecology and Biogeography,* 23: 701-714.

Luo, J. Y., Grassian, B., Tang, D., Irisson, J. O., Greer, A. T., Guigand, C. M., McClatchie, S., et al. 2014. Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. *Marine Ecology Progress Series,* 510: 129-149.

Luschi, P., Hays, G. C., and Papi, F. 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos,* 103: 293-302.

Lynam, C., Lilley, M., Bastian, T., Doyle, T., Beggs, S., and Hays, G. 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology,* 17: 767-782.

Mackie, G. O., Pugh, P. R., and Purcell, J. E. 1987. *Siphonophore biology*. *In* Advances in Marine Biology, pp. 97-262. Academic press.

Madin, L. P., Kremer, P., Wiebe, P. H., Purcell, J. E., Horgan, E. H., and Nemazie, D. A. 2006. Periodic swarms of the salp Salpa aspera in the slope water off the NE United States: biovolume, vertical migration, grazing, and vertical flux. *Deep-Sea Res* **53**: 804–19.

Mapstone, G. M. 2009. *Siphonophora (Cnidaria, Hydrozoa) of Canadian Pacific waters,* NRC Research Press, Ottawa, Ontario, Canada. 302 pp.

Mapstone, G. M. 2014. Global diversity and review of Siphonophorae (Cnidaria: Hydrozoa). *PLoS One,* 9: e87737.

Mapstone, G. M. 2015. *Systematics of Siphonophores*. *In* Evolution of Venomous Animals and Their Toxins, pp. 1-37. Ed. by P. Gopalakrishnakone, and A. Malhotra. Springer Netherlands, Dordrecht.

Maréchal, J.-P., and Hellio, C. 2009. Challenges for the development of new non-toxic antifouling solutions. *International Journal of Molecular Sciences,* 10: 4623-4637.

Marques, S. C., Azeiteiro, U. M., Marques, J. C., Neto, J. M., and Pardal, M. Â. 2006. Zooplankton and ichthyoplankton communities in a temperate estuary: spatial and temporal patterns. *Journal of Plankton Research,* 28: 297-312.

Masilamoni, J. G., Jesudoss, K. S., Nandakumar, K., Satpathy, K. K., Nair, K. V. K., and Azariah, J. 2000. Jellyfish ingress: a threat to the smooth operation of coastal power plants. *Current Science,* 79: 567-569.

McGillicuddy, D. J. 2016. Mechanisms of Physical-Biological-Biogeochemical Interaction at the Oceanic Mesoscale. *Annual Review of Marine Science,* 8: 125-159.

McGillicuddy, D. J., Jr., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., Goldthwait, S. A. and Hansell, D. A., 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science,* 316: 1021-1026.

McGinty, N., Johnson, M. P., and Power, A. M. 2014. Spatial mismatch between phytoplankton and zooplankton biomass at the Celtic Boundary Front. *Journal of Plankton Research,* 36: 1446-1460.

McGowan, J. A., and Fraundorf, V. J. 1966. The relationship between size of net used and estimates of zooplankton diversity. *Limnology and Oceanography,* 11: 456-469.

Mianzan, H. W., and Guerrero, R. A. 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the South-western Atlantic Ocean. *Scientia Marina,* 64: 215-224.

Mieszkin, S., Callow, M. E., and Callow, J. A. 2013. Interactions between microbial biofilms and marine fouling algae: a mini review. *Biofouling,* 29: 1097-1113.

Mills, C. E. 1995. Medusae, Siphonophores, and Ctenophores as Planktivorous Predators in Changing Global Ecosystems. *ICES Journal of Marine Science,* 52: 575-581.

Mittelstaedt, E. 1987. Cyclonic cold-core eddy in the eastern North Atlantic. I. Physical description. *Marine Ecology Progress Series*, 39: 145-152.

Müller, W. A., Wieker, F., and Eiben, R. 1976. *Larval adhesion, releasing stimuli and metamorphosis*. *In* Coelenterate ecology and behavior, pp. 339-346. Ed. by G. O. Mackie. Springer, Boston, MA. Müller, O. F., 1776. Zoologiae Danicae prodromus: seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium. *Hafniae, Typiis Hallageriis.* 1-274.

Muthukumar, T., Aravinthan, A., Lakshmi, K., Venkatesan, R., Vedaprakash, L., and Doble, M. 2011. Fouling and stability of polymers and composites in marine environment. *International Biodeterioration & Biodegradation,* 65: 276-284.

Myles, A., Haberlin, D., Esteban-Tejeda, L., Angione, M. D., Browne, M. P., Hoque, M. K., Doyle, T. K., Scanlan, E. M. and Colavita, P.E., 2017. Bioinspired Aryldiazonium Carbohydrate Coatings: Reduced Adhesion of Foulants at Polymer and Stainless Steel Surfaces in a Marine Environment. *ACS Sustainable Chemistry & Engineering,* 6: 1141-1151.

Nair, K., and Anger, K. 1979. Experimental studies on the life cycle of Jassa falcata (Crustacea, Amphipoda). *Helgoländer wissenschaftliche Meeresuntersuchungen,* 32: 444.

Nawrocki, A. M., and Cartwright, P. 2012. A novel mode of colony formation in a hydrozoan through fusion of sexually generated individuals. *Current Biology,* 22: 825-829.

Nellis, P., and Bourget, E. 1996. Influence of physical and chemical factors on settlement and recruitment of the hydroid *Tubularia larynx*. *Marine Ecology Progress Series,* 140: 123-139.

Nickell, T., Davidson, K., Fox, C., Miller, P., and Hays, G. 2010. Developing the capacity to monitor the spatial and temporal distribution of jellyfish in western Scottish waters. *The Crown Estate*: 70.

O'Boyle, S., and Raine, R. 2007. The influence of local and regional oceanographic processes on phytoplankton distribution in continental shelf waters off north-western Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, 107b: 95-109.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., et al. 2017. *vegan: Community Ecology Package. R package version 2.4-5. https://CRAN.R-project.org/package=vegan.*

Olson, D. B., and Backus, R. H. 1985. The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. *Journal of Marine Research*, 43: 113-137.

Olson, D. B., Hitchcock, G. L., Mariano, A. J., Ashjian, C. J., Peng, G., Nero, R. W., and Podestá, G. P. 1994. Life on the edge: marine life and fronts. *Oceanography*, 7: 52-60.

Owen, R. W. 1981. *Fronts and eddies in the sea: mechanisms, interactions and biological effects*. *In* Analysis of marine ecosystems, pp. 197-233. Ed. by A. R. Longhurst. Academic Press, London and Orlando.

Pagès, F., Gili, J.M. and Bouillon, J., 1989. The siphonophores (Cnidaria, Hydrozoa) of Hansa Bay, Papua New Guinea. *Indo-Malayan Zoology*, 6: 133-140.

Pagès, F., and Gili, J. M. 1992. Influence of Agulhas waters on the population structure of planktonic cnidarians in the southern Benguela region. *Scientia Marina*, 56: 109-123.

Pagès, F., Gili, J. M., and Bouillon, J. 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina*, 56: 1-64.

Pages, F., Gonzalez, H. E., Ramon, M., Sobarzo, M., and Gili, J. M. 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora : Calycophorae). *Marine Ecology Progress Series*, 210: 13-24.

Pages, F., and Schnack-Schiel, S. B. 1996. Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). *Journal of Marine Systems*, 9: 231-248.

Pages, F., White, M. G., and Rodhouse, P. G. 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. *Marine Ecology Progress Series*, 141: 139-147.

Palma, S., Apablaza, P., and Soto, D. 2007. Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). *Investigaciones marinas*, 35.

Palma, S., Silva, N., Retamal, M. C., and Castro, L. 2011. Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile. *Continental Shelf Research*, 31: 260-271.

Pingree, R. D., and Griffiths, D. K. 1978. Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research*, 83: 4615.

Pingree, R. D., Holligan, P. M., and Mardell, G. T. 1979. Phytoplankton Growth and Cyclonic Eddies. *Nature*, 278: 245-247.

Pingree, R. D., and Le Cann, B. 1989. Celtic and Armorican slope and shelf residual currents. *Progress in Oceanography*, 23: 303-338.

Pingree, R. D., Sinha, B., and Griffiths, C. R. 1999. Seasonality of the European slope current (Goban Spur) and ocean margin exchange. *Continental Shelf Research*, 19: 929-975.

Pitt, K. A., Duarte, C. M., Lucas, C. H., Sutherland, K. R., Condon, R. H., Mianzan, H., Purcell, J. E., Robinson K. L. and Uye, S. I., 2013. Jellyfish body plans provide allometric advantages beyond low carbon content. *PLoS One,* 8: e72683.

Pitt, K. A., Kingsford, M. J., Rissik, D., and Koop, K. 2007. Jellyfish modify the response of planktonic assemblages to nutrient pulses. *Marine Ecology Progress Series*, 351: 1-13.

Pitt, K. A., Welsh, D. T., and Condon, R. H. 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. *Hydrobiologia*, 616: 133-149.

Poos, M. S., and Jackson, D. A. 2012. Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. *Ecological Indicators,* 18: 82-90.

Pugh, P. R. 1977. *Some observations on the vertical migration and geographical distribution of siphonophores in the warm waters of the North Atlantic Ocean*. *In* Proceedings of the symposium on warm water zooplankton. National Institute of Oceanography. Goa, India.

Pugh, P. R. 1984. The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Progress in Oceanography*, 13: 461-489.

Pugh, P. R., Pages, F., and Boorman, B. 1997. Vertical distribution and abundance of pelagic cnidarians in the eastern Weddell Sea, Antarctica. *Journal of the Marine Biological Association of the United Kingdom*, 77: 341-360.

Purcell, J. E. 1981. Dietary-Composition and Diel Feeding Patterns of Epipelagic Siphonophores. *Marine Biology*, 65: 83-90.

Purcell, J. E. 1982. Feeding and Growth of the Siphonophore *Muggiaea atlantica* (Cunningham 1893). *Journal of Experimental Marine Biology and Ecology,* 62: 39-54.

Purcell, J. E. 1991. A review of cnidarians and ctenophores feeding on competitors in the plankton. *Springer*: 335-342.

Purcell, J. E. 1997. Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. *Annales de Institut Océanographique,* 73: 125-137.

Purcell, J. E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom,* 85: 461-476.

Purcell, J. E. 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia,* 616: 23-50.

Purcell, J. E. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science,* 4: 209-235.

Purcell, J. E., and Arai, M. N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia,* 451: 27-44.

Purcell, J. E., Baxter, E. J., and Fuentes, V. L. 2013. *13 - Jellyfish as products and problems of aquaculture*. *In* Advances in Aquaculture Hatchery Technology, pp. 404-430. Woodhead Publishing.

Purcell, J. E., Uye, S., and Lo, W. T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series,* 350: 153-174.

Pyefinch, K., and Downing, F. 1949. Notes on the general biology of *Tubularia larynx* Ellis & Solander. *Journal of the Marine Biological Association of the United Kingdom,* 28: 21-43.

Quinn, G. P., and Keough, M. J. 2002. *Experimental design and data analysis for biologists,* Cambridge University Press, Cambridge, United Kingdom.

R Core Team 2017. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.* 3.4.3 edn. Ed. by R. F. f. S. Computing. Vienna, Austria.

Raine, R. 2014. A review of the biophysical interactions relevant to the promotion of HABs in stratified systems: The case study of Ireland. *Deep Sea Research Part II: Topical Studies in Oceanography,* 101: 21-31.

Raine, R., McDermott, G., Silke, J., Lyons, K., Nolan, G., and Cusack, C. 2010. A simple short range model for the prediction of harmful algal events in the bays of southwestern Ireland. *Journal of Marine Systems,* 83: 150-157.

Raine, R., and McMahon, T. 1998. Physical dynamics on the continental shelf off southwestern Ireland and their influence on coastal phytoplankton blooms. *Continental Shelf Research,* 18: 883-914.

Raine, R., McMahon, T., O'Mahony, J., Moloney, M., and Roden, C. 1990. Water circulation and phytoplankton populations in two estuaries on the west coast of Ireland. *Estuarine Ecotoxicology. JAPA, Wicklow*: 19-28.

Ratcliff, J. 2004. Mulroy Bay Plankton Monitoring 2004. 13 pp.

Reid, D., Kynoch, R., Penny, I., Summerbell, K., Edridge, A., and O'Neill, F. 2012. A comparison of the GOV survey trawl with a commercial whitefish trawl. *Fisheries Research,* 121: 136-143.

Reygondeau, G., and Beaugrand, G. 2010. Water column stability and *Calanus finmarchicus*. *Journal of Plankton Research,* 33: 119-136.

Roberts, J. J., Best, B. D., Dunn, D. C., Treml, E. A., and Halpin, P. N. 2010. Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C plus. *Environmental Modelling & Software,* 25: 1197-1207.

Robison, B. H. 2004. Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology,* 300: 253-272.

Robison, B. H., Reisenbichler, K. R., and Sherlock, R. E. 2005. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science,* 308: 1609-1611.

Rodger, H. D. 2007. Gill disorders: an emerging problem for farmed Atlantic salmon (*Salmo salar*) in the marine environment. *Fish Veterinary Journal,* 9: 38-48.

Rodger, H. D., Henry, L., and Mitchell, S. O. 2011a. Non-infectious gill disorders of marine salmonid fish. *Reviews in Fish Biology and Fisheries,* 21: 423-440.

Rodger, H. D., Murphy, K., Mitchell, S. O., and Henry, L. 2011b. Gill disease in marine farmed Atlantic salmon at four farms in Ireland. *The Veterinary record,* 168: 668.

Roe, H. S. J., Angel, M. V., Badcock, J., Domanski, P., James, P. T., Pugh, P. R., and Thurston, M. H. 1984. The diel migrations and distributions within a Mesopelagic community in the North East Atlantic. 1. Introduction and sampling procedures. *Progress in Oceanography,* 13: 245-268.

Rogers, C. A., Biggs, D. C., and Cooper, R. A. 1978. Aggregation of Siphonophore *Nanomia Cara* in Gulf of Maine - Observations from a Submersible. *Fishery Bulletin,* 76: 281-284.

Roman, M. R., Gauzens, A. L., and Cowles, T. J. 1985. Temporal and spatial changes in epipelagic microzooplankton and mesozooplankton biomass in warm-core

Gulf Stream ring 82-B. *Deep Sea Research Part A. Oceanographic Research Papers*, 32: 1007-1022.
Rossby, T. 1996. The North Atlantic Current and surrounding waters: At the crossroads. *Reviews of Geophysics*, 34: 463-481.
Ruane, N. M., Rodger, H., Mitchell, S., Doyle, T., Baxter, E., and Fringuelli, E. 2013. GILPAT: An Investigation into Gill Pathologies in Marine Reared Finfish.
Ruppert, E. E., and Barnes, R. D. 1994. *Invertebrate zoology*, Saunders College Publishing, Florida. 1056 pp.
Russell, F. S. 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 20: 309-332.
Russell, F. S. 1953. *The medusae of the British Isles. Volume I: anthomedusae, leptomedusae, limnomedusae, trachymedusae and narcomedusae*, Cambridge University Press, Cambridge, United Kingdom.
Russell, F. S. 1970. *The medusae of the British Isles. Volume II: Pelagic Scyphozoa*, Cambridge University Press, Cambridge, United Kingdom.
Ryan, T., Rodhouse, P., Roden, C., and Hensey, M. 1986. Zooplankton fauna of Killary Harbour: the seasonal cycle of abundance. *Journal of the Marine Biological Association of the United Kingdom*, 66: 731-748.
Sabatés, A., Pagès, F., Atienza, D., Fuentes, V., Purcell, J. E., and Gili, J.M. 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia*, 645: 153-165.
Samuelsen, A., Hjøllo, S. S., Johannessen, J. A., and Patel, R. 2012. Particle aggregation at the edges of anticyclonic eddies and implications for distribution of biomass. *Ocean Science*, 8: 389-400.
Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., and Votier, S. C. 2014a. Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of The Royal Society Interface*, 11: 20140679.
Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., and Votier, S. C. 2014b. On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51: 1575-1583.
Scardino, A. J., Zhang, H., Cookson, D. J., Lamb, R. N., and Nys, R. d. 2009. The role of nano-roughness in antifouling. *Biofouling*, 25: 757-767.
Schick, R. S., Goldstein, J., and Lutcavage, M. E. 2004. Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). *Fisheries Oceanography*, 13: 225-238.
Schultes, S., Sourisseau, M., Le Masson, E., Lunven, M., and Marie, L. 2013. Influence of physical forcing on mesozooplankton communities at the Ushant tidal front. *Journal of Marine Systems*, 109: S191-S202.
Shiganova, T. A. 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fisheries Oceanography*, 7: 305-310.
Shoosmith, D. R., Richardson, P. L., Bower, A. S., and Rossby, H. T. 2005. Discrete eddies in the northern North Atlantic as observed by looping RAFOS floats. *Deep Sea Research Part II: Topical Studies in Oceanography*, 52: 627-650.
Silverman, H. G., and Roberto, F. F. 2007. Understanding Marine Mussel Adhesion. *Marine Biotechnology*, 9: 661-681.

Simpson, J. H. 1981. The Shelf-Sea Fronts - Implications of Their Existence and Behavior. *Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences,* 302: 531-546.

Sousa, L. L., Queiroz, N., Mucientes, G., Humphries, N. E., and Sims, D. W. 2016. Environmental influence on the seasonal movements of satellite-tracked ocean sunfish *Mola mola* in the north-east Atlantic. *Animal Biotelemetry,* 4: 7.

Southward, A. J. 1980. The Western English Channel—an inconstant ecosystem? *Nature,* 285: 361-366.

Southward, A.J. and Barrett, R.L., 1983. Observations on the vertical distribution of zooplankton, including post-larval teleosts, off Plymouth in the presence of a thermocline and a chlorophyll-dense layer. *Journal of Plankton Research,* 5 (4): 599-618.

Southward, A. J., Hawkins, S. J., and Burrows, M. T. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology,* 20: 127-155.

Sparks, C., Buecher, E., Brierley, A. S., Axelsen, B. E., Boyer, H., & Gibbons, M. J. (2001). Observations on the distribution and relative abundance of the scyphomedusan *Chrysaora hysoscella* (Linné, 1766) and the hydrozoan Aequorea aequorea (Forskål, 1775) in the northern Benguela ecosystem. In *Jellyfish Blooms: Ecological and Societal Importance* (pp. 275-286). Springer, Dordrecht.

Stemmann, L., Youngbluth, M., Robert, K., Hosia, A., Picheral, M., Paterson, H., Ibanez, F., Guidi, L., Lombard, F. and Gorsky, G., 2008. Global zoogeography of fragile macrozooplankton in the upper 100–1000 m inferred from the underwater video profiler. *ICES Journal of Marine Science,* 65: 433-442.

Stephens, J. 1904. A List of Irish Coelenterata, including the Ctenophora. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science,* 25: 25-92.

Stommel, H. M. 1958. *The Gulf Stream: A Physical and Dynamical Description,* University of California Press, California.

Suárez-Morales, E., Gasca, R., Segura-Puertas, L., and Biggs, D. C. 2002. Planktonic cnidarians in a cold-core ring in the Gulf of Mexico. *Anales del Instituto de Biología. Serie Zoología,* 73: 19-36.

Suchman, C. L., and Brodeur, R. D. 2005. Abundance and distribution of large medusae in surface waters of the northern California Current. *Deep Sea Research Part II: Topical Studies in Oceanography,* 52: 51-72.

Totton, A. K. 1954. *Siphonophora of the Indian Ocean: together with systematic and biological notes on related specimens from other oceans,* University Press.

Totton, A. K., and Bargmann, H. E. 1965. *A Synopsis of the Siphonophora,* British Museum (Natural History).

Tranter, D., Tafe, D., and Sandland, R. 1983. Some zooplankton characteristics of warm-core eddies shed by the East Australian Current, with particular reference to copepods. *Marine and Freshwater Research,* 34: 587-607.

Tranter, D. J., Parker, R. R., and Cresswell, G. R. 1980. Are warm-core eddies unproductive? *Nature,* 284: 540-542.

Tucker, M. J., and Pitt, E. G. 2001. *Waves in ocean engineering,* Elsevier, Oxford.

Underwood, A. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Annual Reviews of Oceanography and Marine Biology,* 19: 513-605.

Vinogradov, G. M. 2004. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1". *Marine Biology,* 146: 325-331.

Walbaum, J.J., 1792. Petri Artedi sueci genera piscium. *quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis*. redactis speciebus 242 ad genera 52: Ichthyologiae pars 3. Ant. Ferdin. Röse: Grypeswaldiae. 723, 3 plates pp.

Whelan, A., and Regan, F. 2006. Antifouling strategies for marine and riverine sensors. *Journal of environmental monitoring,* 8: 880-886.

Wiebe, P. H., Flierl, G. R., Davis, C. S., Barber, V., and Boyd, S. H. 1985. Macrozooplankton biomass in Gulf Stream warm-core rings: Spatial distribution and temporal changes. *Journal of Geophysical Research: Oceans,* 90: 8885-8901.

Williams, R., and Conway, D. 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (OF Müller)(Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. *Journal of Plankton Research,* 3: 633-643.

Worm, B., Sandow, M., Oschlies, A., Lotze, H. K., and Myers, R. A. 2005. Global patterns of predator diversity in the open oceans. *Science,* 309: 1365-1369.

Wroblewski, J. 1989 A model of the spring bloom in the North Atlantic and its impact on ocean optics. *Limnology and Oceanography,* 34: 1563-1571.

Yebra, D. M., Kiil, S., and Dam-Johansen, K. 2004. Antifouling technology—past, present and future steps towards efficient and environmentally friendly antifouling coatings. *Progress in Organic Coatings,* 50: 75-104.

Zen, F., Angione, M. D., Behan, J. A., Cullen, R. J., Duff, T., Vasconcelos, J. M., Scanlan, E. M., et al. 2016. Modulation of Protein Fouling and Interfacial Properties at Carbon Surfaces via Immobilization of Glycans Using Aryldiazonium Chemistry. *Scientific Reports,* 6: 24840.

Zhang, Z., Wang, W., and Qiu, B. 2014. Oceanic mass transport by mesoscale eddies. *Science,* 345: 322-324.

Appendix A

Supporting Material for Chapter 3

Table S3.1. Presence/absence table for all zooplankton taxa identified from Celtic Sea samples (N=49).

Station	**2**	**4**	**6**	**8**	**10**	**12**	**14**	**16**	**18**	**20**	**22**	**24**	**26**	**28**	**30**	**32**	**34**	**36**	**38**	**40**	**42**	**44**	**46**	**48**	**50**	**52**	**54**	**56**	**58**	**60**	**62**	**64**	**66**	**68**	**70**	**72**	**74**	**76**	**78**	**80**	**82**	**84**	**86**	**88**	**90**	**92**	**94**	**96**	**98**
Hydromedusae																																																	
Aglantha digitalis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x		x				x	x	x	x	x					x	x	x	x	x	x	x	x
Amphinema rugosum														x																																				
Bougainvillia		x																																															
Clytia hemisphaerica		x		x		x	x	x	x	x	x	x												x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x									x
Cosmetria pilosella				x										x																																				
Cyanea species																									x																									
Euphysa aurata																x																	x																
Eutima gracilis					x				x		x						x						x								x					x											x		
Laodiciea undulata				x	x							x																		x			x															
Leuckartiara octona	x		x	x			x	x	x	x	x	x	x	x	x	x		x	x	x									x		x	x	x	x	x	x			x				x	x	x	x	x	x
Lizzia blondina	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x				x		x	x	x	x	x	x	x					x	x	x	x	x
Melicertum octocostatum				x																																													
Metrocomella polydiademata		x	x																							x	x	x	x				x			x	x													
Obelia sp.	x	x	x	x	x	x	x		x	x	x	x				x		x				x								x	x		x	x		x		x				x	x	x				
Podcoryne borealis				x	x																																												
Unidentified species							x									x				x	x	x	x	x																								x		x

Table S3.1 continued. Presence/absence table for all zooplankton taxa identified from Celtic Sea samples (N=49).

Station	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98
Siphonophora																																																		
Muggiaea atlantica											x													x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x									
Polygastric											x														x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x									
Eudoxid																								x	x		x	x			x	x	x		x	x	x	x	x	x									
Nanomia bijuga		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x				x	x			x	x	x	x							x	x	x	x		x			x
N. bijuga larvae											x		x	x	x		x	x	x	x	x	x																										x	x
Agalma elegans		x	x	x		x	x	x	x		x	x		x				x			x					x	x	x	x				x	x	x			x	x	x			x		x			
A. elegans larvae		x	x			x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x		x	x	x	x	x			x	x	x	x	x	x	x	x	x			x	x		x		x	
Ctenophora																																																		
Pleurobrachia pileus		x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Beroe sp.				x	x	x	x														x					x		x					x	x	x														
Bolinopsis infundibulm						x								x					x							x		x	x						x							x		x	x					
Tunicata																																																		
Appendicularia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
Chaetognatha																																																		
Sagitta elegans	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x		x		x	x	x
Sagitta setosa																																								x	x	x								
Echinodermata																																																	
Ophiuroidea larvae		x	x	x			x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	x	x	x				x	x	x	x	x	x	x	x	x	x	x		x		x	
Echinoidea larvae													x	x	x	x	x	x	x	x	x	x	x						x					x	x	x	x	x											
Phytoplankton																																																	
Ceratium sp.		x	x	x	x	x	x	x	x	x	x	x												x	x	x	x	x	x					x		x			x	x				x		x	
Noctiluca sp.								x																							x	x		x															

Table S3.1 continued. Presence/absence table for all zooplankton taxa identified from Celtic Sea samples (N=49).

Station	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98
Mollusca																																																		
Limacina sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x						x	x			x					x	x	x	x	x	x	x
Clione sp.	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			x				x	x	
Bivalve larvae			x	x											x							x							x	x													x	x	x		x	
Polychaeta																																																	
Tomopteris sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x			x		x				x	x	x	x	x	x	x			x	x	x		x	x	x	x	x	x
Syllidae																							x								x	x			x			x				x							
Poecilochaetidae		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x			x			x		x	x	x	x	x		x	x	x		x	
Polychaete larvae	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						x	x				x				x	x	x	x	x	x	x	x		x	
Magelonidae	x	x	x	x	x	x		x	x	x	x	x		x	x		x	x	x		x				x		x	x				x				x			x	x	x		x	x	x	x	x	x	x
Phoronid larvae								x	x	x	x		x	x																							x								x	x				
Polychaete larvae	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						x	x				x				x	x	x	x	x	x	x	x		x	
Crustacea																																																	
Copepods	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Euphausiid																																x	x																	
Megalops	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x	x		x					x	x	x						x	x	x	x	x	x	x	x			
Zoea	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x
Hyperiid	x	x	x	x	x	x	x					x																																					
Lepeophtheirus sp.												x	x									x	x						x	x				x		x	x	x	x	x	x	x						
Caprellid																																									x	x	x	x	x	x				

Table S3.1 continued. Presence/absence table for all zooplankton taxa identified from Celtic Sea samples (N=49).

Station	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98
Actinopterygii																																																		
Arnoglossus laterna					x	x				x	x		x		x			x	x	x	x		x																							x	x	x
Buglossidium luteum					x	x									x	x						x																				x							
Callionymus spp.		x	x	x	x	x	x		x	x			x	x	x		x	x	x	x	x															x		x		x	x	x		x	x	x
Chelidonichthys lucerna																x					x																			x				x					
Chelon labrosus																							x																x									
Ctenolabrus rupestris																						x																									x	
Echiodon drummondi	x	x	x		x																																											
Glyptocephalus cynoglossus	x	x	x	x												x																																	
Gobidae	x	x		x	x	x	x	x	x			x	x	x	x		x	x	x	x	x	x					x				x		x	x						x	x	x	x	x	x	x	x	x
Hippoglossoides platessoides						x																																										
Hyperoplus lanceolatus																																										x						
Labrus bergylta	x																																									x	x		x			
Limanda limanda				x																																												
Merluccius merluccius				x		x	x					x	x	x					x																													x
Microchirus variegatus					x	x				x	x	x	x				x			x	x														x									x		x	x	x
Microstomus kitt			x													x																																
Pollachius pollachius					x																																											

Table S3.1 continued. Presence/absence table for all zooplankton taxa identified from Celtic Sea samples (N=49).

Station	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98
Raniceps raninus	x											x									x																												
Sardina pilchardus				x	x	x	x							x		x	x	x	x	x	x																														x
Scomber scombrus						x				x		x	x		x		x	x	x	x	x	x	x																									x	x
Scophthalmus rhombus																															x						x												
Scorpionidae																																													x	x	x			
Trachinus draco																																											x			x	x	x	x	
Trachurus trachurus																		x																																
Trigladae			x		x	x				x		x	x		x																						x									x		x	
Unidentified species					x	x		x	x							x				x																											x		
Fish Eggs	x	x	x	x	x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																	x	x	x	x	x	x	x		x		

32 Table S3.2. Mass measurements of individual zooplankton species

Group	Species	Dry mass (mg)	C (mg)	Reference
Cnidaria	*Aglantha digitale*	0.0148826	0.0015899	7
Cnidaria	*Hydractina borealis*	0.02396	0.006009168	7
Cnidaria	*Lizzia blondina*	0.0003944	0.00005166	7
Cnidaria	*Leuckartiara octona*	0.06928	0.006503	7
Cnidaria	*Clytia hemisphaerica*	0.1522	0.018615	7
Cnidaria	*Eutimia gracilis*	0.085638	0.011218681	7
Cnidaria	*Laodicea undulata*	0.424274	0.0570523	7
Cnidaria	*Metrocomella polydiademata*	0.424274	0.0570523	7
Cnidaria	*Obelia* species	0.004316	0.001557	7
Cnidaria	*Muggiaea atlantica* (poly)	1.656	124.3656	10
Cnidaria	*Muggiaea atlantica* (Eu)	0.35	36.61	10
Cnidaria	*Nanomia bijuga*	12.404	1.7278772	Na
Cnidaria	*N. bijuga* larvae	0.6202	0.08639386	Na
Cnidaria	*Agalma elegans*	15.60344346	2.173559674	Na
Cnidaria	*A. elegans* larvae	1.560344346	0.217355967	na
Ctenophora	*Pleurobrachia pileus*	16.58405066	0.713114178	7
Ctenophora	*Beroe* species	157.2337832	11.32083239	7
Ctenophora	*Bolinopsis infundibulum*	1845.071195	27.67606792	7
Actinopterygii	*Glyptocephalus cynoglossus*	0.039623142	0.015849257	11
Actinopterygii	*Microchirus variegatus*	0.189095754	0.075638302	11
Actinopterygii	*Buglossidium luteum*	0.076244993	0.030497997	11
Actinopterygii	*Pollachius pollachius*	0.112463906	0.044985562	11
Actinopterygii	*Trachurus trachurus*	0.116637459	0.046654984	11
Actinopterygii	*Scomber scombrus*	0.327501441	0.131000576	11
Actinopterygii	*Pleuronectes platessa*	3.051112288	1.220444915	11
Actinopterygii	*Arnoglossus laterna*	0.07882	0.031528	11
Actinopterygii	Gobidae	0.088092908	0.035237163	11
Actinopterygii	*Chelon labrosus*	0.025219293	0.010087717	11
Actinopterygii	*Merluccius merluccius*	0.021760512	0.008704205	11
Actinopterygii	*Ctenolabrus rupestris*	2.837749393	1.135099757	11
Actinopterygii	*Raniceps raninus*	0.560535295	0.224214118	11
Actinopterygii	*Labrus bergylta*	0.116637459	0.046654984	11
Actinopterygii	*Callionymus* species	0.061449623	0.024579849	11
Actinopterygii	*Trachinus draco*	0.028716323	0.011486529	11
Actinopterygii	*Echiodon drummondi*	0.10989	0.043956	11
Actinopterygii	Trigladae Species	0.380616789	0.152246716	11
Actinopterygii	*Chelidonichthys lucerna*	0.380616789	0.152246716	11
Actinopterygii	Scorpionidae	0.298731964	0.119492786	11
Actinopterygii	*Scophthalmus rhombus*	0.062002125	0.02480085	11
Actinopterygii	*Hyperoplus lanceolatus*	0.041167176	0.016466871	11
Actinopterygii	*Microstomus kitt*	0.092042868	0.036817147	11
Actinopterygii	*Sardina pilchardus*	0.10989	0.043956	11
Actinopterygii	*Limanda limanda*	0.089431583	0.035772633	11

Table S3.2. continued.

Group	Species	Dry mass (mg)	C (mg)	Reference
Actinopterygii	Fish larvae	0.1483	0.05932	6
Actinopterygii	Fish egg	0.109	0.0436	5
Mollusca	*Limacina* species	0.03636	0.00803556	4
Mollusca	*Clione* species	1.741	0.384761	2
Copepoda	Copepods	0.112308	0.053319	8
Decapoda	Megalops	0.555	0.2202	1
Decapoda	Zoea	0.304	0.1332	1
Amphipoda	Hyperiidae	0.4295	0.1767	3
Copepoda	*Lepeophtheirus* species	0.4295	0.1767	8
Tunicata	Appendicularia	0.00349	0.00161	11
Chaetognatha	*Sagitta elegans*	0.1840772	0.074131024	11
Chaetognatha	*Sagitta setosa*	0.1840772	0.074131024	11
Polychaeta	*Tomopteris* species	0.51368812	0.27048	11
Polychaeta	Polychaete larvae	0.0113	0.00595	11
Echinodermata	Ophiuroidea	0.0216	0.00864	6
Echinodermata	Asteroidea	0.05839	0.023359	6

References for Table S3.2.

1. Anger, K., Laasch, N., Püschel, C., and Schorn, F. 1983. Changes in biomass and chemical composition of spider crab (*Hyas araneus*) larvae reared in the laboratory. *Marine Ecology Progress Series*: 91-101.
2. Böer, M., Gannefors, C., Kattner, G., Graeve, M., Hop, H., and Falk-Petersen, S. 2005. The Arctic pteropod *Clione limacina:* seasonal lipid dynamics and life-strategy. *Marine Biology*, 147: 707-717.
3. Donnelly, J., Kawall, H., Geiger, S. P., and Torres, J. J. 2004. Metabolism of Antarctic micronektonic crustacea across a summer ice-edge bloom: respiration, composition, and enzymatic activity. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51: 2225-2245.
4. Gannefors, C., Böer, M., Kattner, G., Graeve, M., Eiane, K., Gulliksen, B., Hop, H., et al. 2005. The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. *Marine Biology*, 147: 169-177.
5. Hislop, J. R. G., and Bell, M. A. 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. *Journal of Fish Biology*, 31: 1-20.
6. Laurence, G. 1979. Larval length-weight relations for 7 species of northwest Atlantic fishes reared in the laboratory. *Fishery Bulletin*, 76: 890-895.
7. Lucas, C. H., Pitt, K. A., Purcell, J. E., Lebrato, M., and Condon, R. H. 2011. What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. *ESA Ecology*, 92: 1704.
8. McGinty, N., Johnson, M. P., and Power, A. M. 2014. Spatial mismatch between phytoplankton and zooplankton biomass at the Celtic Boundary Front. *Journal of Plankton Research*, 36: 1446-1460.
9. Pepin, P. 1995. An analysis of the length-weight relationship of larval fish: limitations of the general allometric model. *Fishery Bulletin*, 93: 419-426.
10. Purcell, J. 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). Journal of Experimental Marine Biology and Ecology, 62: 39-54.
11. Uye, S. 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of Oceanography*, 38: 149-158.

Appendix B

Published papers resulting from thesis

Paper I

Diversity and occurrence of siphonophores in Irish coastal waters.

Haberlin, D., Mapstone, G., McAllen, R., McEvoy, A.J. and Doyle, T.K.

Published in *Biology and Environment: Proceedings of the Royal Irish Academy*, 2016, Vol. 116, No. 2, pp. 119-129

Paper II

First observations of the freshwater jellyfish Craspedacusta sowerbii Lankester, 1880 in Ireland coincides with unusually high water temperatures

Minchin, D., Caffrey, J.M., Haberlin, D., Germaine, D., Walsh, C., Boelens, R. and Doyle, T.K., 2016.

Published in *Bioinvasions Records*, 2016, 6 (2), 67-74

Paper III

Bioinspired Aryldiazonium Carbohydrate Coatings: Reduced Adhesion of Foulants at Polymer and Stainless Steel Surfaces in a Marine Environment.

Myles, A., Haberlin, D., Esteban-Tejeda, L., Angione, M.D., Browne, M.P., Hoque, M.K., Doyle, T.K., Scanlan, E.M. and Colavita, P.E.

ACS Sustainable Chemistry & Engineering, 2017, 6(1), pp.1141-1151.