Seasonal abundance and distribution of gelatinous zooplankton in Oslofjorden, Norway

An ecological snapshot

Katrine Selsø

Master Thesis

Marine Biology Program, Department of Biology

UNIVERSITY OF OSLO

December 2012

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http://www.duo.uio.no

Print: Reprosentralen, Universitety of Oslo

Preface

This master thesis was carried out in 2010-2012 at the Marine Biology Program of the Department of Biology at the University of Oslo. The thesis was intended to be the beginning of a larger project on zooplankton in Oslofjorden, but due to unforeseen circumstances, this project is now in hibernation. Thus, the field and laboratory work performed is a much larger data set than the one included in the thesis. I hope that these data can be used in future research at the University of Oslo.

This thesis would not have been possible without help from a large number of people. First, I would like to thank my primary supervisor, Josefin Titelman (UiO) for giving me the opportunity to do a field study on gelatinous zooplankton. Thank you for all your guidance, a good collaboration, and especially for allowing me to take part in the course in gelatinous impact. I would also like to thank my co-supervisor Aino Hosia (IMR) for teaching me about jellyfish and taxonomy. Without you, I would still be in the lab trying to understand the identification literature. Thank you, as well, for helping me with finishing the writing process, and discovering the discrepancies in my thesis. Rita Amundsen, our Head engineer, you have been a tremendous help on cruises and in the laboratory. Your help and support was invaluable. Thank you, Senior engineer Sissel Brubak, for teaching me and helping me analyze the chlorophyll *a* samples. Karl Inne Ugland and Andreas Lindén, thank you both for saving the day and for your great help with the statistical analyses in the thesis. Your quick and thorough responses to questions and your support are what ultimately brought this thesis to its conclusion. Sindre Holm and the rest of the crew aboard Trygve Braarud, thank you so much for all your help and extra work, you made the cruises a great experience. I will never forget the efforts you went to so I could obtain all my samples, even giving me an extra cruise day.

Thank you to Asbjørn Vøllestad (UiO) Julie Døvle Johansen, Signe Røysland Sørlie and Christopher Hinchcliffe for taking the time to proofread and comment on my thesis. I also want to thank my fellow students for making these years unforgettable and for all the support.

Last, but not least, I want to thank my family and friends for supporting me and always being there. The biggest thank you goes to my boyfriend, Sigurd. You supported me every day, believed in me when I couldn´t and were incredibly patient with me throughout.

Abstract

Gelatinous zooplankters are thought to be important members of the pelagic ecosystem. Their abundance is known to vary with season, food availability and hydrographic conditions, sometimes forming massive blooms thought to be detrimental to socio-economic installations like aquaculture and power stations. There is, however, a severe lack of research on the gelatinous zooplankton community in Oslofjorden, Norway. In this study, three stations (Missingene, Elle and Steilene) along a geographical transect were sampled 10 times from January 2011 to January 2012. Environmental variables were analyzed to portray the hydrographic seasonal cycle during the year. A month was chosen to represent each of the four seasons. Gelatinous zooplankton was identified, measured and enumerated while non-gelatinous zooplankton was weighed, giving an estimate of biomass. These abundances were compared according to station and season, and showed that Missingene and Steilene were more similar in gelatinous community composition and abundance than Elle. The distribution of a formerly highly abundant hydromedusa in Oslofjorden, *Aglantha digitale*, was tentatively found to have decreased since the 1970´s. The abundance of six groups of gelatinous zooplankton (hydromedusae, siphonophores, ctenophores, chaetognaths, appendicularians, and holopelagic polychaetes, i.e., *Tomopteris helgolandica*) was modeled as a function of environmental variables using a new multivariate modeling-tool for ecological community research, "Mvabund". Significant variables were station, density, depth and fluorescence, while season did not appear to have any significant effect on the abundance of gelatinous zooplankton. The model had better fit for the groups hydromedusae, siphonophores and Chaetognatha than the groups Ctenophora, Appendicularia, and *Tomopteris*.

Table of contents

1 Introduction

Gelatinous zooplankton has a history of being overlooked and underrepresented in plankton research on a global scale due to their fragile nature and irregular life cycle pulses (Hamner et al. 1975, Arai 1992, Boero et al. 2008, Baxter 2012). Although generally not as abundant as crustaceans (Hamner et al. 1975, Arai 1992, Lenz 2000, Boero et al. 2008, Baxter 2012), gelatinous zooplankton can have a large effect on the ecosystem (Smedstad 1972, Haddock 2004, Hosia & Båmstedt 2007, Boero et al. 2008). Several studies have focused on the detrimental effect of coelenterates that are blamed, sometimes erroneously, for the collapse of ecosystems and fisheries alike as well as causes of regime shifts towards a more gelatinous ecosystem. Some examples of the effect of gelatinous blooms are: The invasive ctenophore *Mnemiopsis leidyi* in the Black Sea (Boero et al. 2008, Colin et al. 2010, Purcell 2012, Baxter et al. 2012). In Atlantic waters, examples are hydrozoans on both Norwegian and Irish farmed fish (Båmstedt et al. 1998, Baxter et al. 2011), and the crown jelly *Periphylla periphylla* in fjords of western Norway (Sornes et al. 2007, Dupont et al. 2009). However, gelatinous zooplankton are also key members of the ecosystem as predators of fish egg and crustacean zooplankton, by setting resources free for previously outcompeted species (for instance by grazing on predators), and as an integral part of the planktos-benthos network (Boero et al. 2008, Baxter et al. 2012). Although there have been no known mass occurrences in Oslofjorden, it is clearly important to map the gelatinous species abundance and diversity to gain an understanding of the ecosystem as a whole. In Oslofjorden there has not been a study of the gelatinous community since 1972 (Smedstad 1972), and that study only focused on one hydromedusan species (*Aglantha digitale)*. This study aims to rectify the situation by investigating the seasonal abundance and distribution of gelatinous zooplankton in Oslofjorden during one year.

1.1 Gelatinous zooplankton

1.1.1 Gelatinous terminology

Coelenterate is a common name for the non-taxonomic group encompassing the cnidarian and ctenophore phyla. It was used as a scientific term for many years and although no longer considered scientifically valid, it is still common in the literature (Arai 2001, Haddock 2004, Arai 2005). For the purpose of this study, coelenterate will be used as traditionally. Either gelatinous zooplankton or gelatinous plankters will be used as the term for all gelatinous organisms in the study. Hydromedusae will encompass all members of the taxonomic class Hydrozoa except siphonophores, which will be treated separately due to their different morphology and life cycles (Kirkpatrick & Pugh 1984).

The organisms included as gelatinous in the study are the phyla Cnidaria, Ctenophora, and Chaetognatha. In addition, a few organisms from the phylum Polychaeta and classes Gastropoda and Tunicata are termed gelatinous (Section 1.1.3 and Table 3.1). It is common to classify these organisms as gelatinous as they share key attributes like a transparent body that consist of >90% water (Hamner et al. 1975, Bone 2005, Baxter 2012). Scyphozoans are mostly excluded from analysis, as only one scyphozoan larva was collected, and the method used is not ideal for sampling scyphozoans. The remaining zooplankton is termed non-gelatinous zooplankton and mainly consists of various crustaceans and larvae from a plethora of taxa.

1.1.2 History of coelenterate research

Jellyfish have been studied for hundreds of years. Several influential biologists documented ctenophores and siphonophores during the 19th and 20th century, including Agassiz (1902), Leuckart (1853), Huxley (1859), Haeckel (1888), and Sars (1856). Many new species were discovered, which is mirrored in the scientific names of many cnidarians. Net collection methods were used even at these early times, and as these techniques were perfected, the collecting, preserving and describing of gelatinous zooplankton continued (Nansen 1915, Russell 1953, Totton & Bargmann 1965, Fraser 1968a). Net sampling of these fragile organisms is not ideal, however, and preservation can still be difficult (Purcell 1988, de Lafontaine & Leggett 1989, Sullivan & Gifford 2009). Several new, non-destructive methods have been used to rectify these problems, among them Scuba diving and video recording

from Remote Operated Vehicles (ROVs) (Hamner et al. 1975, Wiebe 2003, Hosia & Båmstedt 2008).

In recent years, focus in gelatinous research has shifted towards the ecological importance of gelatinous organisms (Purcell 1991, Hansson et al. 2005, Lynam et al. 2010, Hosia et al. 2011). The basic mapping of gelatinous species abundance and diversity, however, has to be answered before any effect of climate change, over-fishing or other anthropogenic disturbances can be discovered (Boero 2009). In Norway, research has mostly been done in the western fjords (Falkenhaug 1996, Pages et al. 1996, Båmstedt et al. 1998, Hosia 2007, Dupont et al. 2009). Except for a couple articles by Beyer (1968) and Smedstad (1972) very little gelatinous research has been done in Oslofjorden, however.

1.1.3 Gelatinous life history and ecologic role

The gelatinous organisms covered in this thesis are manifold and varied. Ctenophores, chaetognaths, appendicularians, *Tomopteris helgolandica*, and the hydrozoan trachymedusa and narcomedusa are all holopelagic organisms, completing their life cycles in the pelagic (Hosia 2007). Siphonophores (Hydrozoa) are also holopelagic, but they are polymorph organisms where the polyp and medusa stages together form one holopelagic, "colonial" organism (Baxter 2012). A single siphonophore colony contains both medusoid zooids, e.g. nectophores and gonozooids, and the polypoid gastrozooids zooids. Physonect siphonophores have no alternation of generations, while calycophore siphonophores alter between the sexual eudoxid stage and the asexual polygastric stage (Kirkpatrick & Pugh 1984). Other cnidarians, like anthomedusae and leptomedusae (class Hydrozoa*)* are meropelagic with a benthic, asexually reproducing polyp stage and a pelagic, sexually reproducing medusae stage (Graham et al. 2001, Baxter 2012). Coelenterates also differ in biogeographic distribution. Trachymedusae, narcomedusae and siphonophores are all considered oceanic groups. The remaining hydrozoans tend to have a coastal distribution due to their benthic stage (Kramp 1959, Kirkpatrick & Pugh 1984, Hosia 2007). Most ctenophores are also predominantly oceanic, except for instance the invasive species *Mnemiopsis leidyi* (Harbison et al. 1978, Oliveira 2007).

Gelatinous zooplankton often have life history strategies that cause dramatic fluctuations in their seasonal abundances (Arai 1992, Ballard & Myers 2000, Hosia & Båmstedt 2007, Boero et al. 2008). Chaetognaths have even been known to have such high abundances that the ocean turns grey (Bone 2005). These pulses are a rapid response to sudden occurrences of

abundant food sources and are the cause of their large impact, however momentary, on marine food webs (Behrends & Schneider 1995, Titelman & Hansson 2005, Boero et al. 2008). It has also been shown that coelenterates are able to survive in adverse environments for long periods of time (Lucas & Lawes 1998, Ishii 2003, Piraino et al. 2004), waiting for a food source to appear. Many of the coelenterates are capable of asexual budding (e.g., *Lizzia blondina*, *Rathkea octopuntata)* or have diapause stages that respond to often unknown environmental triggers (for instance the benthic stages of Hydrozoa) (Boero et al. 2008, Di Camillo et al. 2010). The four environmental variables that have the largest effect on gelatinous zooplankton communities are generally considered, though, to be water temperature, salinity, density, and fluorescence (Graham et al. 2001, Baxter 2012). Temperature and salinity, for instance, have a large impact on the life cycles of gelatinous zooplankton (Hansson 1997, Lucas & Lawes 1998, Ishii 2003, Jaspers et al. 2011). Fluorescence is a proximate measure of the amount of primary producers in the fjord, and the entire planktonic community is naturally influenced by the primary production (Skjoldal et al. 2000). Density is important for planktonic organisms, affecting their buoyancy (Graham et al. 2001, Bone 2005).

According to Mills (1995), ctenophores tend to be generalist predators, eating whatever species are currently available, although some species, like those from the *Beroe* genus are known to prefer other ctenophores as prey (Purcell 1991). Hydromedusae and siphonophores are predators that are more specialized. They often occur together in multispecies communities (Purcell 1991, Mills 1995, Pages et al. 1996) and are often sorted in two main groups according to their predation strategy; cruising predators and ambush-feeding predators (Hansson & Kiørboe 2006). These two groups may have different independent impact on the ecosystem. For the ecosystem as a whole, though, the trophic predation impact is caused by the co-occurring species of jellyfish *together* (Costello & Colin 2002), thus the total effect of hydromedusan and siphonophore predation on the community may share similarities with generalist predation, barring single-species massive blooms.

Gelatinous research often focuses on the detrimental effects of the organisms on the ecosystem. However, gelatinous zooplankton is also an integral part of the trophic food web. Coelenterates are well known predators in the marine ecosystem (Purcell 1991, Arai 2005). They are known to prey on crustaceans, phytoplankton and fish eggs (Mills 1995, Titelman & Hansson 2005, Regula et al. 2009, Colin et al. 2010) as well as other gelatinous organisms (Greve 1975, Mills 1995, Baxter 2012). Gelatinous animals have traditionally been less

recognized as important prey species, but this is changing. They are going from being regarded as dead-ends in the ecosystem to being important food sources for turtles, fish, other gelatinous animals, molluscs and even birds (Arai 2005). Chaetognaths are known prey organisms for all types of jellyfish (Purcell 1991) in addition to being a predator of zooplankton themselves (Øresland 1987, Kehayias 1996). *Tomopteris helgolandica* is from the only genus of holopelagic polychaetes and the species is interesting to include in the thesis for that reason alone. *T. helgolandica* is also a predator on other zooplankton, and is both a competitor and a predator to jellyfish. *Appendicularia* was the only completely filter-feeding taxonomic class in the study. They feed by excreting a mucus-like "house" around their body that filters and retains phytoplankton and detritus (Alldredge 1977), and are considered gelatinous because of this house (Lenz 2000). They are common in the pelagic environment and play a key role in the marine food web through grazing on small particles and contributing to vertical carbon flux (Alldredge 1977, Shiganova 2005).

Pulses in gelatinous zooplankton populations are common occurrences due to their life cycles (Boero et al. 2008, Condon et al. 2012). Gelatinous blooms are known to impact power stations, aquaculture, fisheries, fish stocks, and tourism (Purcell 2012) and seem to be increasing in recent years (Haddock 2004, Richardson & Gibbons 2008, Boero et al. 2008, Purcell 2012), although the evidence for this is conflicting (Condon et al. 2012, see Brotz et al. 2012). The gelatinous blooms influencing anthropogenic investments are one of the main foci of the scientific community today (Øresland 1987, Kehayias 1996, Haddock 2004, Richardson & Gibbons 2008, Boero et al. 2008, Lynam et al. 2010) and climate change, anthropogenic disturbances and removal of top predators are often given as causes (Colin et al. 2010, Jaspers et al. 2011, Purcell 2012). One of the more infamous examples of a regime shift thought to have been caused by jellyfish is the case of *Mnemiopsis leidyi* in the Black Sea. The ctenophore was introduced in the early 1980´s following two decades of increasing eutrophication and overfishing. The fisheries subsequently collapsed, along with the entire Black Sea ecosystem (Shiganova 2005). Although the causes were manifold, the collapse was blamed on the jellyfish, which gained it the misnomer "monster jellyfish". Yet another ctenophore, *Beroe ovata* was later introduced into the Black Sea and greatly reduced the abundance of *M. leidyi*. Shiganova (2005) investigated the effect of both these introductions on the appendicularian *Oikipleura dioica*. She found that the introduction of *M. leidyi* almost eradicated the *O. dioica* population, but that the population returned to the previous, high abundances once *B. ovata* was introduced. Although overfishing and eutrophication, not the

ctenophore, were the primary cause of the regime shift, it is clear that opportunistic gelatinous species can have a large impact on a changing ecosystem.

An understanding of what influences the abundance, diversity and life cycle patterns of gelatinous zooplankton is prerequisite to predicting their role in the changing oceans. Several studies has been done to close the gap in information (for instance Arai 2001, Graham et al. 2001, Arai 2008, Di Camillo et al. 2010, Prieto et al. 2010, Lucas et al. 2012), but further efforts are needed, especially in Norway.

1.2 Fjord ecosystems

1.2.1 Fjord hydrography

Fjord systems are found at higher latitudes in the temperate regions. In the northern hemisphere, fjords are found in countries like Norway and Canada. They were formed during glaciation periods, the last of which was more than 10,000 years ago (Brattegard 1979). Fjords are especially interesting for marine biologists for a number of reasons (Brattegard 1979), among them the (relatively) small size of the ecosystem, the special species composition likely to be found and the gradients of environmental variables from the outer to the inner fjord.

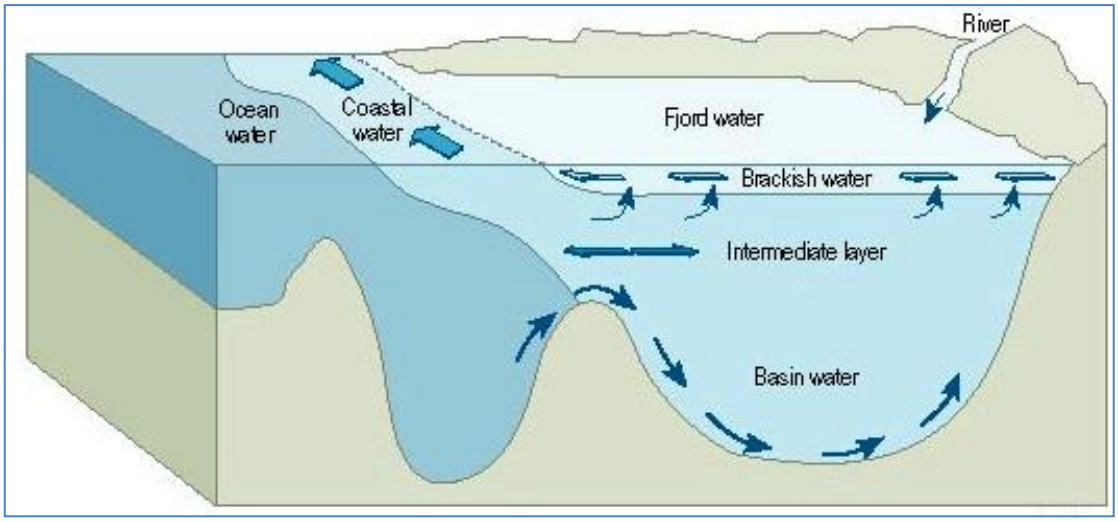

Figure 1.1 Schematic of hydrographic circulation in a fjord, after fig. 3.20 in AMAP assessment report (AMAP 1998, Lenz 2000)

The hydrography in a fjord stems from a combination of topography, hydrology of the adjacent water shed, the oceanographic conditions outside of the fjord and the weather patterns in the area (Brattegard 1979). The deep basins in the fjords are formed by shallow sills and act to keep the effects of the weather subdued, for seasons or even years – which is why the different water layers may have very differing properties (Brattegard 1979). A fjord system is roughly split into three water masses (Figure 1.1); the upper layer with estuarine circulation (brackish water from rain and river input), the middle part of intermediate water masses and the deep basins beneath the sill level(s) (Brattegard 1979). This was used to determine the different depth layers used in this study design (Table 2.1).

1.2.2 Fjord biology

Biologists have been studying the flora and fauna of fjords for at least 150 years (Brattegard 1979, Baalsrud & Magnusson 2002a). Researchers like Sars, Nansen, and Svendsen used Oslofjorden, among other fjords, in their scientific studies at the end of the 19th century (Baalsrud & Magnusson 2002a). Their research, along with a plethora of other researchers across the northern hemisphere, has shown that fjords usually have a large biological production and support a large biodiversity. In addition, their work showed that the species diversity and community structure may vary a lot between neighboring fjords and fjord arms (Brattegard 1979, Baalsrud & Magnusson 2002a, Hosia 2007).

The inner parts of fjords often act as bio-geographical enclaves of species surviving from the geographical history of the fjord (Brattegard 1979). Species in fjords can be divided into three groups: The occasionally present species that immigrate, but are unable to uphold a population; the species which are always present but need influx from outer areas to sustain the population, i.e., a "sink population"; and lastly the species that are always present in self-sustaining populations (Brattegard 1979). In this light, it is clear that the hydrodynamics of the fjord, the movement of the water masses, are crucial to the community structure.

1.2.3 Oslofjorden

Oslofjorden is a fjord on the South-East coast of Norway, reaching from Færder lighthouse and 100 kilometers into the eastern coastline (Baalsrud & Magnusson 2002b). It is a silled fjord, with an outer sill around the Søstrene islets, in the Hvaler archipelago of Østfold County, and an inner sill near Drøbak, Akershus. The outer sill is 150 meters deep and forms the Rauøy basin, but it is the inner sill at Drøbak, measuring only 19.5 meters which gives the fjord its characteristic properties (Baalsrud & Magnusson 2002c, Dragsund et al. 2006, Aure & Danielssen 2007).

The inner Oslofjord has a typical temperate weather pattern of warm summers and cold winters. During winter, the north winds prevail, while south-southwesterly winds dominate the summers (Baalsrud & Magnusson 2002c). The winter of 2011 was one of the few recent years where the ice covered the fjord out to Drøbak. This was much more common a few decades ago (Baalsrud & Magnusson 2002b).

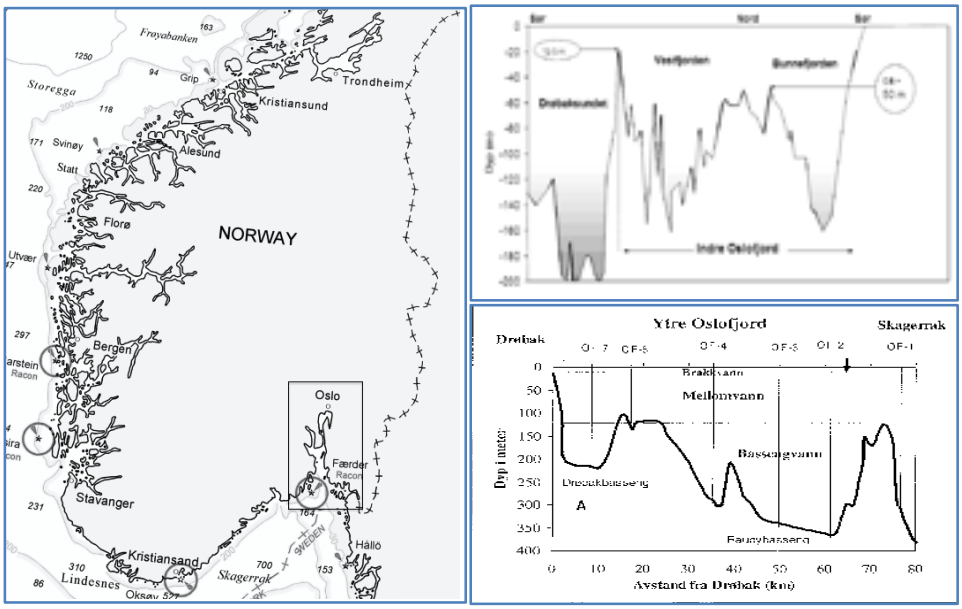

Figure 1.2 Left: map of southern Norway with Oslofjorden indicated (from the Norwegian Coastal administration). Top right: depth profile of the inner Oslofjorden (Baalsrud & Magnusson 2002c). Bottom right: depth profile of the outer Oslofjorden (Aure & Danielssen 2007).

Water in Oslofjorden enters from Skagerrak, which is heavily influenced by the Atlantic Ocean, the Baltic Sea and the Jylland current (Dragsund et al. 2006, Hostyeva 2011). Freshwater generally has very little influence in Oslofjorden because there are few rivers running out into the inner fjord (Baalsrud & Magnusson 2002d). Freshwater influence, whether from rivers or rain water is hydrographically important because it influences the stratification of the fjord (Brattegard 1979, AMAP 1998). In the inner parts of Oslofjorden, the only freshwater input generally comes from rain, while in the outer regions, two major rivers empty into the fjord; Glomma in Østfold, and Drammen River in Drammensfjorden, Vestfold (Dragsund et al. 2006, Aure & Danielssen 2007, Hostyeva 2011). This means that the salinity of surface layers is often lower (PSU < 25) at the outermost parts of the fjord than in the inner parts.

Oslofjorden, like many fjords, is thought to have a high biodiversity and species abundance (Baalsrud & Magnusson 2002c). However, increasing toxicity and eutrophication levels became a concern as early as 1930 as both are known to adversely affect biodiversity (Baalsrud & Magnusson 2002a). One of the results of the contamination was that the bio-geographical enclave in the inner Oslofjord was eradicated (Baalsrud & Magnusson 2002a). Even though the fjord is now recovering (Baalsrud & Magnusson 2002e), these species may never return. Knowing this history makes it especially important to compare different areas of Oslofjorden and discover which species are present, and their distribution.

1.3 Purpose of the master thesis

The purpose of this study is to remedy the lack of research done on gelatinous zooplankton in Oslofjorden. By choosing three stations along a geographical transect of the Oslofjord, this thesis aims to study the species distribution and abundance of gelatinous animals in relation to the concurrent environmental variables, in order to gain a better understanding of the potential impact of gelatinous zooplankton in Oslofjorden. Although this study is mostly descriptive, it can be used, with precaution, for predicting gelatinous abundances in Oslofjorden.

To answer this complex topic, the purpose of this study was split into four parts:

1) Map which species of Coelenterates (Cnidaria and Ctenophora) are present in Oslofjorden.

2) Quantify the abundance of gelatinous zooplankton at the three different stations.

3) Compare the concentration of gelatinous zooplankton (measured as individuals per $50m^3$ of water) with the biomass of non-gelatinous zooplankton.

4) Compare the composition of gelatinous community at the three stations throughout the year – in relation to the physio-chemical properties of the water column and seasonality of their life histories.

2 Materials and Methods

2.1 Sampling sites

Three sampling stations were chosen along a south-north gradient in the Oslofjord (Table 2.1). They were chosen because they were assumed to have different species abundance and distribution due to hydrographic differences.

Table 2.1 Overview of sampling sites, noting the station abbreviations, max depth of each station, their geographical position in Oslofjorden (see Figure 2.1) along with a short description of important factors influencing the hydrography at each station.

	Missingene	**Elle**	**Steilene**
Abbreviation	OF2	IM2	DK1d
Latitude	59 11.200N	59 37.322N	59 47.771N
Longitude	10 41.500N	10 37.693E	10 34.455E
Station depth (m)	358	200	129
Sampled depths (m)	345-100 100-50 50-0	195-100 100-50 50-0	N/A 125-50 50-0
Description	Hvaler archipelago Outer Oslofjord Deep station Skagerrak influence	Drøbak strait Bottleneck station Mid-depth station Near-shore	Vestfjorden Inner Oslofjord Shallow station Near Islands

2.1.1 Missingene

Missingene is the outermost station of this study. It is located in the Hvaler archipelago of Østfold County, close to the outermost sill in Oslofjorden. The station is the one most influenced by freshwater, it is located near the mouth of the largest river in Norway, Glomma (Baalsrud & Magnusson 2002c, Aure & Danielssen 2007). At the same time, the deeper layers are the sites with most influenced by the oceanic waters of Skagerak. Two factors combine to inhibit stratification at this station; the constant waves forming from Skagerrak, and the relative width of the fjord here (Aure & Danielssen 2007). The expectation is that these factors make the species community at Missingene more oceanic than the species communities at Elle and Steilene (Section 1.1.3).

2.1.2 Elle

Elle is right outside the innermost fjord sill in Drøbak and is in the bottleneck part of the Oslofjord itself – Drøbaksundet. The fjord width measures only a little above 1500 meters and the station is thus protected to a certain degree from the wind and waves (Baalsrud & Magnusson 2002c). There are no major river-runoffs in the area, making rainwater the primary freshwater influence, followed by influence from Drammensfjorden (Baalsrud & Magnusson 2002a). The species community is expected to be typically coastal (Section 1.1.3), comparable to fjords in western Norway, Ireland and the British Columbia region in Canada (Mills 1995, Ballard & Myers 2000).

2.1.1 Steilene

Steilene station is in the inner fjord, close to the Steilene islets of the Nesodden peninsula near Oslo. The true Steilene station (DK1) is slightly less than 100 meters deep, so the current site (DK1d) is a little south of the islets themselves to ensure a larger water column was sampled. Sampling a larger water volume is a common method to reduce the effect of patchiness (de Wolf 1989). The station is in the inner part of Vestfjorden, the innermost area chosen for this study. Any freshwater influence at this station is most likely from rainwater, it takes a long time for the freshwater from the outer fjord areas to penetrate this deeply into the fjord (Baalsrud & Magnusson 2002a). The species community is expected to be more similar to Elle than to Missingene, i.e., mostly coastal species (Section 1.1.3).

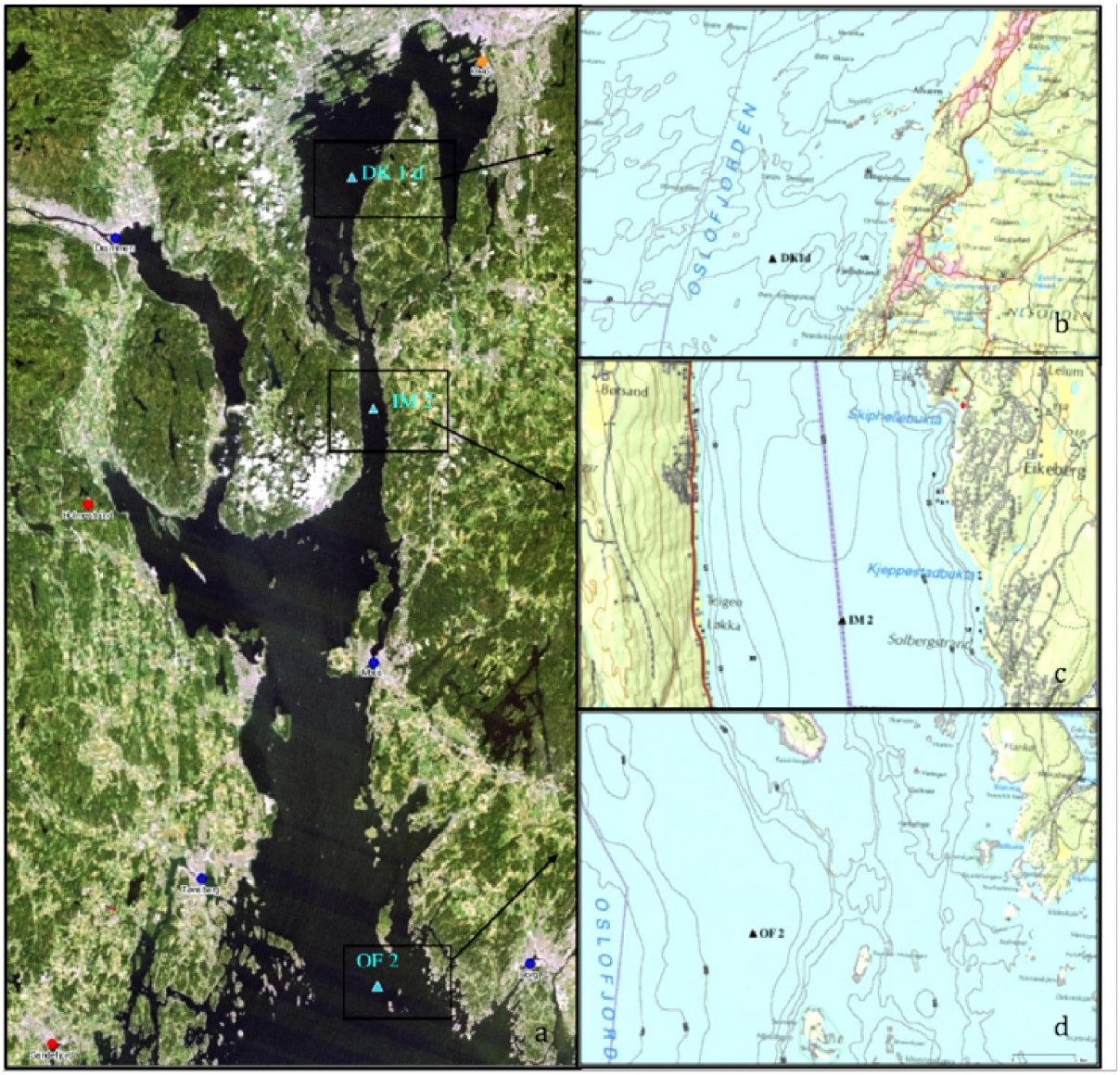

Figure 2.1 a: Map of Oslofjorden, Southeast Norway (Figure 1.2), b: Sampling station Steilene (DK1d), c: Sampling station Elle (IM2), d: Sampling station Missingene (OF2). All maps are from The Norwegian Coastal Administration.

2.2 Field and lab methods

All fieldwork was performed between January 2011 and January 2012. Ten cruises were taken aboard the 70 feet R/V Trygve Braarud. The three stations were sampled once a month and a complete overview of all sampling dates and samples taken is shown in the Appendix Table A.1. The four months of sampling that were chosen to represent the different seasons are shown in Table 2.2.

2.2.1 Environmental variables

A CTD instrument (Falmouth Scientific Inc., USA) measured temperature, salinity (calculated from conductivity) and fluorescence *in situ* as these variables are often thought to influence plankton communities directly or indirectly (Arai 1992, Graham et al. 2001, Purcell et al. 2010).

Table 2.2 Summary of sample dates and depths for the four months representing the different seasons. X marks which samples were taken for each depth layer and date. Gelatinous id indicates that all gelatinous organisms were identified and enumerated. Wet weight of non-gelatinous zooplankton. All light measurements were taken for the top 20 meters only.

Date	Station	Depth (m)	Sample name	Nansen net	Gelatinous id	Wet Weight	CTD	Chl *a*	Light
Spring									
11.04.11	DK1d	130-51	DK1d.4.2	x	x	x	x		
11.04.11	DK1d	51-0	DK1d.4.3	x	x	x	x	x	
11.04.11	IM2	200-104	IM2.4.1	x	x	x	x		
11.04.11	IM2	104-52	IM2.4.2	x	x	x	x		
11.04.11	IM2	52-0	IM2.4.3	x	x	x	x	x	x
11.04.11	OF2	350-104	OF2.4.1	x	x	x	x		
11.04.11	OF2	104-52	OF2.4.2	x	x	x	x		
11.04.11	OF2	52-0	OF2.4.3	x	x	x	x	x	x
Summer									
06.06.11	DK1d	125-52	DK1d.6.2	x	x	x	x		
06.06.11	DK1d	52-0	DK1d.6.3	x	x	x	x	x	x
06.06.11	IM2	195-104	IM2.6.1	x	x	x	x		
06.06.11	IM2	104-52	IM2.6.2	x	x	x	x		
06.06.11	IM2	52-0	IM2.6.3	x	x	x	x	x	
07.06.11	OF2	345-105	OF2.6.1	x	x	x	x		
07.06.11	OF2	105-52	OF2.6.2	x	x	x	x		
07.06.11	OF2	52-0	OF2.6.3	x	x	x	x	x	x
Fall									
20.09.11	OF2	345-106	OF2.9.1	x	x	x	x		
20.09.11	OF2	106-52	OF2.9.2	x	x	x	x		
20.09.11	OF2	52-0	OF2.9.3	x	x	x	x	x	x
21.09.11	IM2	196-105	IM2.9.1	x	x	x	x		
21.09.11	IM2	105-53	IM2.9.2	x	x	x	x		
21.09.11	IM2	53-0	IM2.9.3	x	x	x	x	x	
21.09.11	DK1d	125-55	DK1d.9.2	x	x	x	x		
21.09.11	DK1d	55-0	DK1d.9.3	x	x	x	x	x	x
Winter									
10.01.12	DK1d	125-51	DK1d.1.2	x	x	x	x		
10.01.12	DK1d	51-0	DK1d.1.3	x	x	x	x		
10.01.12	IM2	195-100	IM2.1.1	x	x	x	x		
10.01.12	IM2	100-52	IM2.1.2	x	x	x	x		
10.01.12	IM2	52-0	IM2.1.3	x	x	x	x	x	x
16.01.12	OF2	345-100	OF2.1.1	x	x	x			
16.01.12	OF2	100-53	OF2.1.2	x	x	x			
16.01.12	OF2	53-0	OF2.1.3	x	x	x			

* 11.01.2012 Nansen net ripped - samples retaken on the 16th.

2.2.2 Zooplankton net sampling

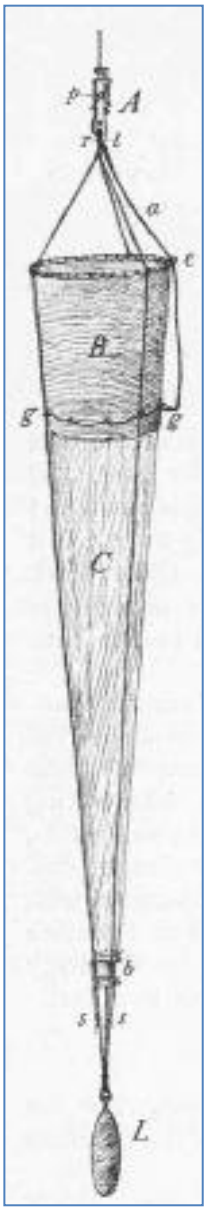

Figure 2.2 Open Nansen net, after fig.1 in Nansen (1915).

Zooplankton net sampling was performed once a month from January to October 2011 and in January 2012, 10 times total. Gelatinous zooplankton samples were collected with a Nansen net (Nansen 1915, Currie & Foxton 1956) with net opening diameter of 0.75 m, 500-µm mesh and a non-filtering cod-end. The samples were stratified vertically, in two or three strata dependent on depth of the station. A Nansen messenger was used to close the nets at the appropriate depths (Nansen 1915). The release depths were calculated from the upward net speed of 0.3 m s^{-1} and assuming terminal velocity (i.e., zero acceleration when the force of gravity is equal to the force of drag) of the messenger. Table 2.1 shows the approximate depth layers from the three stations, and figures 2.2 and 2.3 shows the net in open and closed position. The layers were not constant as the underlying waves and currents affected the angle of the wire through the water, varying the amount of friction between the messenger and the wire, i.e., the speed of the messenger was not constant at terminal velocity. This caused the net to close at different depths even when the messenger was released at the same depth. The closing depth was visible to the naked eye, as the wire ”jumped” when the net closed.

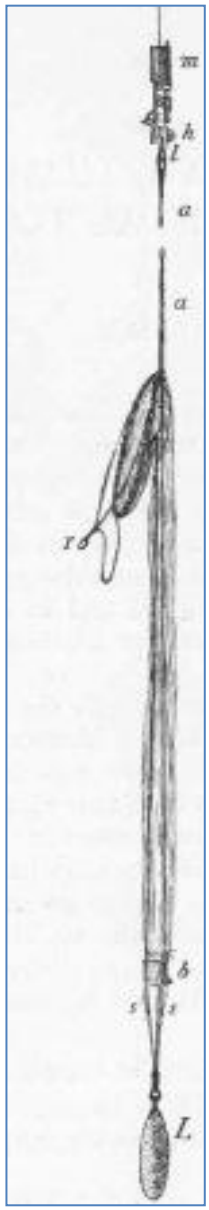

Figure 2.3 Closed Nansen net, after fig.2 in Nansen (1915).

2.2.3 Preliminary sample preparations and preservation

Nansen net samples were size fractioned on a 2 mm sieve. The organisms less than 2 mm were concentrated immediately through a 200 µm sieve and preserved in a plankton jar with borate-buffered 4% formalin. The organisms larger than 2 mm were immediately studied live on a light table (Figure 2.4) to enumerate, identify, and measure Ctenophores. After measuring, the Ctenophores were discarded, as they are difficult to preserve (Yip, 1982). The

remaining organisms were preserved in borate buffered 4% formalin in seawater, in separate plankton jars and identified later.

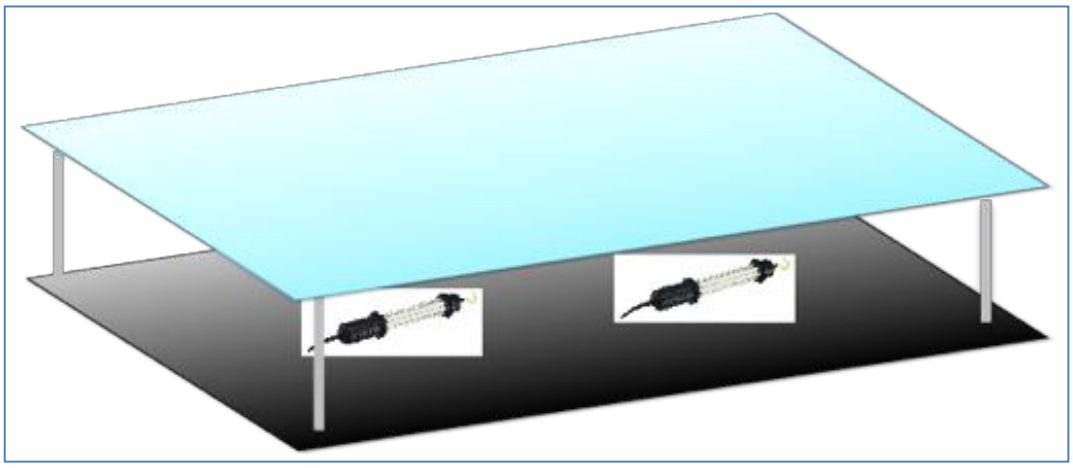

Figure 2.4 Illustration of light tables used to analyze Ctenophores aboard the boat. The top plate is a see-through Plexiglas where the Ctenophores were identified and measured using millimeter paper.

2.2.4 Zooplankton identification, enumerating, and measuring

Gelatinous animals from April, June and September 2011 and January 2012 were identified to species or lowest possible taxon and counted using a Nikon SMZ 745T stereomicroscope with C-W10xB/22 measuring ocular. Difficult specimens were fixed separately and later identified together with a taxonomy expert (A. Hosia) during two visits (October 2011 and June 2012) to the Institute of Marine Research (IMR) in Bergen. They were analyzed in a Leica MZ 7.5 double stereomicroscope in the IMR plankton lab. Table 2.3 shows how each group of zooplankton was analyzed.

At least the first 20 of each identified species, if present, were measured with the stereomicroscope. The remaining organisms were also counted, but not measured. Siphonophores were rarely collected intact; their numbers were calculated from the parts found in the samples. Each anterior nectophore or eudoxid bract counted as one individual of the calycophoran siphonophores. The presence of gonophores and posterior nectophores were noted, but not counted. The samples did not contain any intact physonect Siphonophores, thus 10 nectophores or one pneumatophore (rarely present) counted as one individual (Pugh 1984). When both parts were present, the nectophores decided the count, as the presence of pneumatophores was too uncertain. The presence of bracts, gastrozooids and papillae were noted, but not counted.

Table 2.3 Summary of methods and literature used for identification, enumerating and measuring zooplankton.

Organism group	Measurement	Definition of ind.	Identification literature
Leptomedusa	Diameter	Entire organism	The Hydromedusae of the Atlantic Ocean and adjacent waters (Kramp 1959) Fauna of the Mediterranean Hydrozoa (Bouillon et al. 2004) The medusae of the British Isles (Russell 1953) Synopsis of the medusae of the world (Kramp 1961) ICES zooplankton sheets, no. 100, 101, 102
Anthomedusa	Bell height	Entire organism	The Hydromedusae of the Atlantic Ocean and adjacent waters (Kramp 1959) Fauna of the Mediterranean Hydrozoa (Bouillon et al. 2004) The Medusae of the British Isles (Russell 1953) Synopsis of the medusae of the world (Kramp 1961) ICES zooplankton sheets, no. 2, 28, 29, 51, 54
Trachymedusa	Bell height	Entire organism	The Hydromedusae of the Atlantic Ocean and adjacent waters (Kramp 1959) ICES zooplankton sheets, no. 165 (Russell 1981)
Calycophore siphonophore	Eudoxid bract length Anterior nectophore length	Eudoxid bract or Anterior nectophore	Siphonophores and Vellelids (Kirkpatrick & Pugh 1984) Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters (Mapstone 2009) ICES zooplankton sheets, no. 55, 56 (Totton & Fraser 1955b, c)
Physonect siphonophore	Not measured	10 nectophores and/or 1 pneumatophore	ICES Zooplankton sheets, no. 61 (Totton & Fraser 1955a) Siphonophores and Vellelids (Kirkpatrick & Pugh 1984) Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters (Mapstone 2009)
Ctenophore	Aboral - oral length	Entire organism	ICES zooplankton sheets, no. 146 (Greve 1975)
Chaetognatha	Length	Entire organism	Coastal Marine Zooplankton (Todd et al. 1996) Coastal Plankton (Larink & Westheide 2006)
Appendicularia	Head and complete organism	Entire organism	Coastal Marine Zooplankton (Todd et al. 1996) Coastal Plankton (Larink & Westheide 2006)
Non-gelatinous zooplankton, >2mm	Wet weight	Not defined	ICES zooplankton methodology manual (Postel et al. 2000)
Non-gelatinous zooplankton, <2mm	Wet weight	Not defined	ICES zooplankton methodology manual (Postel et al. 2000)

Different morphological measurements were applied to the different classes of organisms (Table 2.3). Physonect Siphonophores were not measured to body size as only some of the parts constituting a colony were recovered in the samples.

The wet weights of the remaining formalin-fixed samples (non-gelatinous zooplankton) were weighed using small sieves (mesh < 30µm) in May 2012. The count of gelatinous plankton (ind. in *x* m^3) and non-gelatinous zooplankton (gram in *x* m^3) in each sample were then compared (*x* is the water volume filtered in a given sample). The water volume was calculated from the diameter of the net opening (0.75 m) and the length (h) of the haul assuming 100% filtration efficiency, using the formula for the volume of a cylinder (Equation 2.1). The counts and wet weights were then divided by volume sampled and multiplied by $50m^3$, giving the abundances of both gelatinous and non-gelatinous zooplankton. Abundance is thus defined as individuals pr. $50m^3$ the remainder of the thesis.

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$$\boldsymbol{Volume = \pi r^2 * h}$$

Equation 2.1

2.3 Statistical analysis

All analyses and statistical modeling were done using Microsoft Excel for Mac 2011, version 14.0.2 and R version 2.15.1 in R Studio, version 0.96.331.

2.3.1 Environmental variables

It may be expected that environmental factors play a substantial part in structuring the community of gelatinous zooplankton in Oslofjorden. The measurements of the four environmental variables (salinity, density, fluorescence, and temperature) for all 10 months of sampling were used to create seasonal contour plots in R, separated by station. These contour plots give a picture of the hydrographic conditions during the year of sampling. A more detailed salinity plot of the top 25 meters was later added to underscore the differences in freshwater influence between the stations.

In the statistical analysis, only density and fluorescence were used as explanatory variables to keep the number of explanatory variables sufficiently low. This is also because density is largely determined by temperature and salinity. In this way, one can circumvent possible problems of collinearity between the variables and poor identifiability of their separate effects.

2.3.2 Zooplankton statistical analysis

Species overview

A preliminary analysis was performed to describe the abundance of the 11 most abundant species according to the station and season sampled. First, the total abundance of all four months was plotted against the station where they were sampled. This portrays the differences in species composition at the three parts of Oslofjorden, disregarding the other explanatory variables. Next, the abundance data of each station was plotted against month, giving a snapshot of the abundance for each season. Visual inspection of these four plots gives a graphic indication of whether there were any differences in species community in the different regions of Oslofjorden.

All of the gelatinous zooplankton was then divided into six groups according to their differing ecology for further statistical analysis: Hydromedusae (1), Siphonophores (2), Ctenophores (3), Chaetognaths (4), Appendicularia (5) and Tomopteris (6). The remaining

gelatinous zooplankters (Table 3.1) were excluded from further analysis, as their presences were rare and abundances were extremely low.

Multivariate abundance analyses

Multivariate abundance analysis was used to investigate how the logarithmic abundance of the different groups of species varied in space and time, and to relate the abundances to environmental covariates. Multivariate abundance models and plots were done using the "mvabund" package in R (Wang et al. 2012a). The model fitting function used was the "manyglm", which is based on Generalized Linear Models (GLM), with a few adaptations to negate some of the assumptions in GLMs (Wang et al. 2012b).

The multivariate abundance model analysis was split into two subsets to obtain an orthogonal, balanced design. Both models based on these two subsets had month as an explanatory factor with four levels. The explanatory factors station and depth had different levels, in the two models:

- Zoo_1: Missingene (OF2) and Elle (IM2) with all three depth layers and four months.
- Zoo_2: Missingene (OF2), Elle (IM2) and Steilene (DK1d) with the topmost two depth layers and four months.

Following the multivariate model proposed by Wang et al. (2012a), it was assumed that the logarithmic abundance N_{kjdt} of the k^{th} zooplankton group (k = 1, 2,…, 6) found at station j (j = 1, 2, 3) at depth d (d = 1, 2, 3) in month t (t = 1, 2, 3, 4) has a negative binomial distribution where the mean is related to the factors by a log-linear relationship. In other words, the categorical explanatory factors station, depth and month, and the continuous explanatory variables density and fluorescence, influence the response variable – the abundance of gelatinous zooplankton (ind. pr. 50 m^3) in a multiplicative manner. The full model, with all variables included is:

$$N_{kjdt} \sim NegBin\left(m_{kjdt}\right)$$

$$\ln\left(m_{kjdt}\right) = intercept_k + a_{kj} * station_j + d_{kd} * depth_d + m_{kt} * month_m + s_k * density_{jdt} + f_k * fluorescence_{jdt}$$

Equation 2.2 a

This type of model can be written in a more compact form as:

$$Zoo \sim station\ (a) + depth(d) + month(m) + density(s) + fluorescence(F)$$

Equation 2.2 b

Interactions between the explanatory variables are not included in the model because the data set is too small. In addition to the obvious risk of over fitting, the resulting models would run out of degrees of freedom, making such an approach technically impossible.

Following the purpose of this study, the multivariate abundance was first modeled as a function of variability in time (month) and space (stations and depths).

$$Zoo \sim station\ (a) + depth(d) + month(m)$$

Equation 2.3

Next, the multivariate abundance was modeled with the environmental variables alone as explanatory variables. As explained earlier, only density and fluorescence were added as explanatory variables. Density is mostly determined by salinity, with temperature usually having a smaller effect (Baalsrud & Magnusson 2002c). Temperature is to a varying degree dependent on season and depth, so using both season and depth together with temperature was assumed redundant, especially as density was the other environmental variable. Fluorescence was included as a rough measure of primary production.

$$Zoo \sim density\ (s) + fluorescence(F)$$

Equation 2.3

Finally, the complete model (Equation 2.2 a) was fitted, using all the explanatory variables involved.

A comparison of the two categories of variables, however, did not answer which specific variables were most significant. Therefore, a more thorough analysis was performed (Table 3.2 – 3.3 and 3.6 – 3.7), looking at a combination of all explanatory variables, disregarding their categories.

Model comparison and parameter testing

The choice of the three areas in the Oslofjord and the sampling design with respect to depth and month allows the tentative assumption that the zooplankton counts are independent. For all models we assume a negative binomial error term, which is a common way to model

count data with larger dispersion than implied by a pure Poisson distribution (de Wolf 1989, Wang et al. 2012b). The quadratic mean–variance relationship of this model corresponds to a situation where there are unknown environmental variables affecting the response multiplicatively (Lindén & Mäntyniemi 2011), exactly as was assumed for all included explanatory variables here. Plotting the Pearson residuals against the fitted residuals of the optimal model tested these assumptions (Figure 3.8 and Figure 3.10).

The Akaike Information Criterion (AIC) was used for model selection and to summarize the relative fit of the models in relation to their complexity. In other words, AIC was used to answer which of the models *given* was best. It does *not* test how good the fit itself is (Akaike 1974). This explains why comparing more models than the primary three can be useful. AIC was calculated assuming independence among species groups, i.e., the values of the different species groups were simply summed together. The Akaike weights were then calculated to obtain a more intuitive measure of the relative supports for the different models. The Akaike weights sum to 1 (or 100%) for all models tested, analogous to probabilities. To ascertain that the results indicated by AIC held true, in particular in the light of assumption of species group independence, Wald tests were performed to test whether the model coefficients (or groups of coefficients) differ from zero. The Wald test gives the significance of each level of explanatory factor – giving a more nuanced picture than AIC. In addition, in the program used here, the Wald test accounts for dependence among species groups (Wang et al. 2012b), a more likely scenario in this study (Section 1.1.3).

Predictive powers of the optimal model

After the optimal model was reached, predicted and observed values for each species group was plotted separately to visualize the predictive power and model fit of the optimal model for the different groups. The intercept model for Zoo_1 described the situation for the deepest depth layer (1) at Missingene in April, as this was presumed as close to oceanic conditions possible. April was the intercept month as this was the beginning of the seasonal cycle of sampling. The intercept model for Zoo_2 was depth layer 2 (approximately 100-50 m), as depth layer 1 was excluded. The intercept month was April and the intercept station Missingene.

3 Results

3.1 Environmental variables

The environmental variables varied with season and depth, and the contour plots of the variables salinity, density, temperature, and fluorescence give an overview of the hydrographic conditions during the year of sampling (Figure 3.1 – Figure 3.4). Some of the resulting figures show a somewhat atypical scenario for Oslofjorden. For instance, there was complete convection of the water column of Missingene (OF2) and Steilene (DK1d) in April, a month when stratification is normally observed (Section 1.2.3).

Salinity

The salinity (termed Practical Salinity Units, or PSU, although actually unit-less) at Steilene (DK1d) was 16-34, with the lowest salinities generally found in the upper 10 meters. The salinity at Elle (IM2) and Missingene (OF2) had a larger range, reaching from 14-36. The contour plot of salinity (Figure 3.1) shows that the deep water at all three stations had a higher salinity than surface water from May through January and that the deepest water (>100 m depth) had a more stable salinity profile at Missingene than Elle in the same period. However, both Missingene and Steilene experienced complete convection of the water column in April, while Elle did not. In January of 2012, however, Missingene did not have convection of the water column, while the two other stations did. The figure also indicates that the salinity regime was different from the expectation that Missingene was the station with lowest surface salinity. To investigate this difference, a plot of the surface layer is given (Figure 3.5). This shows that from January through April, the salinity was lower at Missingene (with approx. 1-9 PSU), but from May on, the salinity was higher (with approx. 1-9 PSU) than at both Elle and Steilene.

Density

The water density (termed δT, although density is also unit-less) was between 11 and 28 at Steilene (DK1d), between 10 and 29 at Elle (IM2) and between 9 and 30 at Missingene (OF2). The higher densities (δT >27) were generally found at the lower depths at each station (>70 meters) and although it appears that Steilene had lower densities, this is simply because the station is not as deep as the other two stations (Figure 3.2). When comparing the density values for the same depths, it becomes clear that the depths below approximately 50 meters

had δT >27 at all stations. The exceptions are the month of April 2011 and January 2012, like in the salinity plots. Comparing salinity and density plots, (Figure 3.1 and Figure 3.2) it is clear that there was strong collinearity between these variables.

Temperature

The temperature regime was similar at all three stations (Figure 3.3) — ranging from approximately –1°C in January through March to 19°C at all stations (18°C at Steilene) during the summer months. The warmest water (>15°C) was in the upper layers during the months June through September, but the thermocline was different at the three stations. At Steilene (DK1d), the thermocline was at approximately 20 meters, at Elle (IM2) it started at 20 meters in June, but descended to around 60 meters in September, while at Missingene (OF2) the thermocline reached 100 meters depth in October. The three plots show that the surface layers were heated during the summer season, before the water started sinking and mixing with the deeper water (temperatures <5°C) as fall progressed and a more uniform range of temperatures were reached in January 2012 (approx. 6-10°C). The water column in January 2012 was both warmer and more layered than the water in January 2011, however.

Fluorescence

Fluorescence is a unit-less measure of phytoplankton presence. The three plots (Figure 3.4) clearly show that fluorescence was mostly present in the uppermost layer of the water masses. Taking into regard the differing scales of the three plots, we see that the higher levels of fluorescence (>1.5) reached down to approximately 20 meters at all three stations. Steilene (DK1d) had three periods when the fluorescence was higher than average in February (5 fluorescence units), June (3.1) and late September (3.2). The same seasonal trend was present at Elle (IM2), although the largest peak was in October (4.0) while the earlier peaks were only at about two fluorescence units. Missingene does not show any surface peaks in fluorescence. In addition, Missingene had a generally lower concentration of fluorescence (<2) than the other stations. The month with the highest concentration of fluorescence at Missingene was April, and the peak was found at 160 meters depth (Figure 3.4).

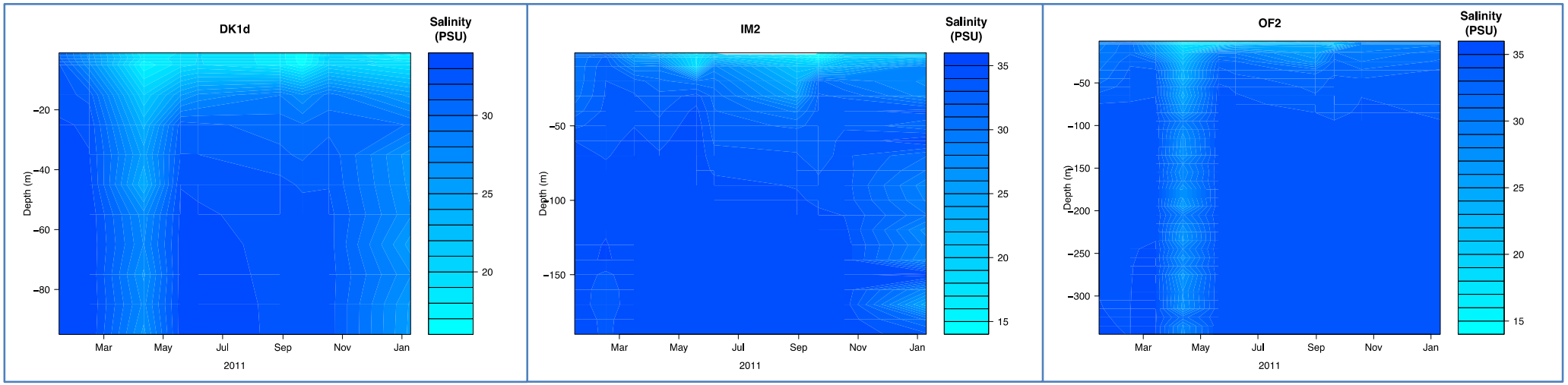

Figure 3.1 Seasonal contour plots of salinity profiles at Steilene (DK1d), Elle (IM2), and Missingene (OF2). The x-axis is time. The y-axis is depth (m) from the surface to 100, 190 and 340 m. The key label is color coded to PSU levels, the lighter color indicates lower PSU. Note that DK1d has a lower range of salinities (PSU =16-34) than IM2 and OF2 (PSU=14-36).

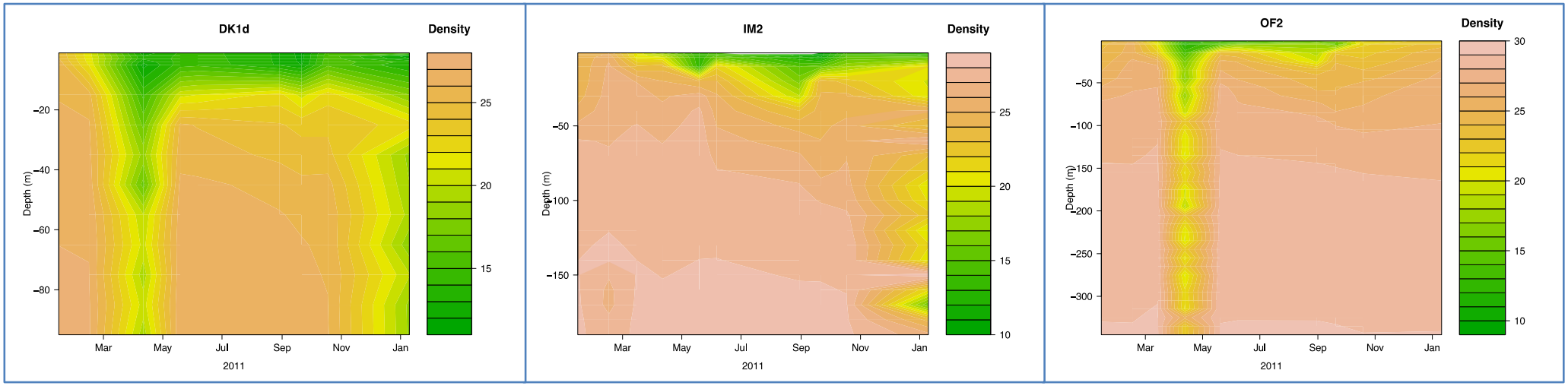

Figure 3.2 Seasonal contour plots of density (δT) profiles at Steilene (DK1d), Elle (IM2), and Missingene (OF2). The x-axis is time. The y-axis is depth (m). Green colors denote lower δT, while tan areas have higher δT. Note that the density range of DK1d is smaller (11-28) than that of IM2 and OF2 (10-30).

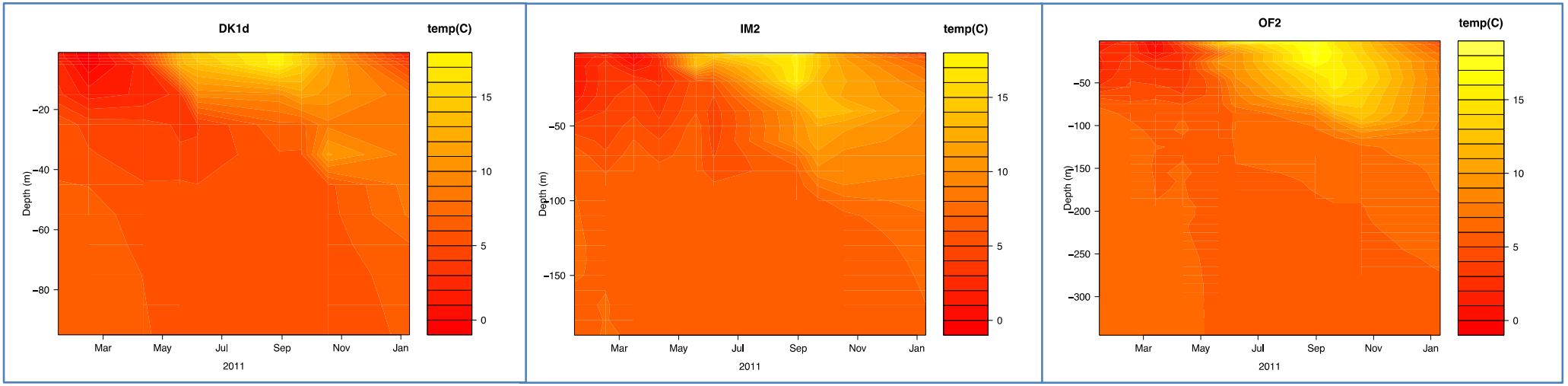

Figure 3.3 Seasonal contour plots of temperature profiles at Steilene (DK1d), Elle (IM2) and Missingene (OF2). X- and y-axes like figures 3.1/3.2 Red color is colder water, the brighter yellow, the warmer temperature. The range of temperatures is the same for all three stations.

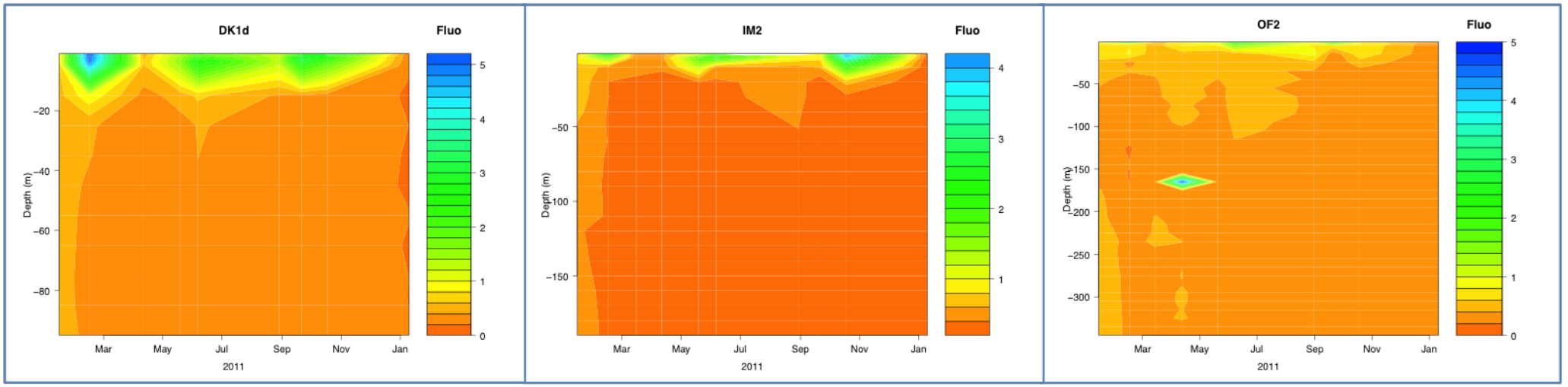

Figure 3.4 Seasonal contour plots of fluorescence profiles at Steilene (DK1d), Elle (IM2), and Missingene (OF2). X- and y-axes are the same as previous figures. Note that IM2 is the station with a lower range of fluorescence – with larger increments between color codes. Orange denotes low fluorescence, blue higher values. OF2 shows generally little fluorescence but has an interesting peak in April at about 160 meters.

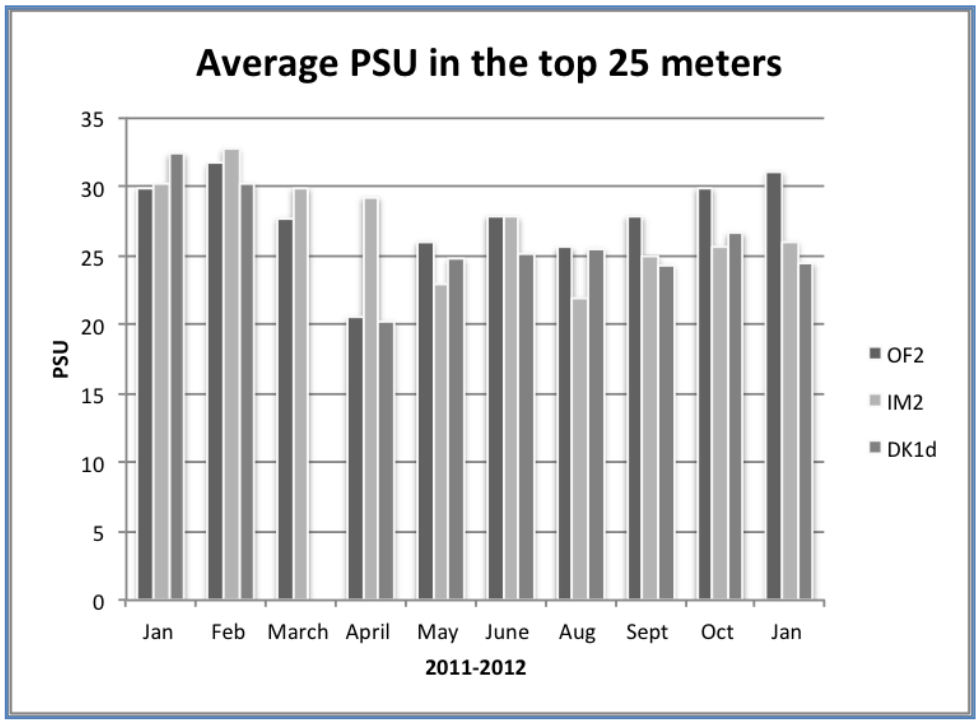

Figure 3.5 Average salinity (PSU) of the top 25 meters at each station in all months. Missingene (OF2) is the first column, Elle (IM2) the middle and Steilene (DK1d) the last column in each cluster. Note the change in May, where OF2 becomes the station with highest salinities.

3.2 Zooplankton analyses

3.2.1 Gelatinous identification and enumeration

A total of 5798 gelatinous zooplankters were identified and enumerated and are listed in Table 3.1. The list sorted by sample date and depth can be found in Appendix Table A. 5. The count at Elle (IM2) was the highest at 2892 individuals, followed by 1707 at Missingene (OF2), while at Steilene (DK1d) 1199 were counted. The most abundant organism was appendicularia, but Figure 3.6 shows that this was likely due to the extreme counts found in September at Elle and Steilene (~ 2700 individuals). In the other months, appendicularia was rarely found, and then only in low numbers. Clearly, appendicularia had very different population sizes at different sampling times.

Twelve species of hydromedusae were identified to species, the rest where either too damaged to identify (Cf. *Eirene* and Hydromedusae sp.) or juvenile (*Pandeidae* sp.). *Obelia* spp. is usually not identified to species in the medusae stage, only in the hydroid stage (Bouillon et al. 2004). Three species of the calycophore siphonophore genus *Lensia* were identified, however *Dimophyes arctica* was the most abundant siphonophore (130 specimens). The only physonect siphonophore positively identified was *Nanomia cara* as many of the physonect organisms were poorly preserved.

Chaetognaths were generally present in all samples. The large number of specimens only identified to phylum is due to poorly preserved specimens and juveniles. The largest abundances of chaetognaths were at Missingene and Elle. Comparing the two most common genera at these sites, it is clear that *Eukrohnia hamata* had larger presences at Missingene (count of 671 and 206 respectively), while *Sagitta* sp. had approximately the same populations size at the two stations (count of 459 and 417 respectively). There seemed to be little seasonality (in numbers) at Missingene, but larger differences at Elle (count approx. 4–90) and for *Sagitta* sp. at Steilene (count approx. 7–1000).

Another species that was present in most samples was *Tomopteris helgolandica*. It showed a similar pattern to *E. hamata*, with the largest presence at the outermost station, less at Elle and only two specimens found at Steilene. Season did not seem to be a contributing factor in determining their numbers; they were present in small quantities throughout the year.

The counts of ctenophores are likely to be underestimates, as many of the larger specimens were destroyed in the net and were not identifiable. Accounting for this, stations Missingene and Elle had a similar number of ctenophores identified (37 and 57 respectively). The only Ctenophore species other than *Beroe cucumis* were a single *Bolinopsis infendibulum* and two to three *Cydippid* sp. They were all found at Missingene.

Table 3.1 List of taxa identified, count per station of each species and total count. All specimens are identified to the lowest possible taxon and grouped to the most relevant taxonomic level.

Species	**No. specimens collected**			
	Steilene	Elle	Missingene	Total
Hydromedusae				
Aglantha digitale	2	32	190	224
Anthomedusa sp.	3	1	1	5
Cf *Eirene* sp.	-	-	1	1
Clytia hemisphaerica	3	4	5	12
Eirene viridula	-	-	2	2
Euphysa aurata	1	11	7	19
Homoeonema platygon	1	1	6	8
Hydromedusa sp.	4	2	2	8
Leukartiara octona	-	1	-	1
Lizzia blondina	66	114	1	181
Margelopsis hartlaubi	-	24	-	24
Mitrocomella polydiademata	-	1	2	3
Obelia spp.	3	16	19	38
Pandeidae sp.	-	-	2	2
Rathkea octopunctata	12	-	1	13
Sarsia gemmifera	1	2	-	3
Tiaropsis multicirrata	-	2	5	7
Siphonophora				
Calycophore siphonophore	-	3	-	3
Dimophyes arctica	-	51	79	130
Diphyidae sp.	1	1	5	7
Lensia Cf *subtilis*	-	-	2	2
Lensia conoidea	38	-	3	41
Lensia fowleri	-	1	-	1
Lensia sp.	1	8	-	9
Nanomia cara	-	9	9	18
Physonect siphonophore	-	4	3	7
Ctenophora				
Beroe cucumis	-	43	25	68
Bolinopsis infendibulum	-	-	1	1
Cf *Beroe* sp.	-	1	-	1
Cyddipid sp.	-	-	3	3
Ctenophore sp.	1	13	8	22
Chaetognatha				
Chaetognatha sp.	19	155	140	314

Species	**No. specimens collected**			
	Steilene	Elle	Missingene	Total
Eukrohnia hamata	4	206	671	881
Sagitta sp.	89	417	458	964
Tunicata				
Appendicularia	947	1757	30	2734
Ascidacea sp. (larvae)	-	2	-	2
Polychaeta				
Tomopteris helgolandica	2	8	19	29
Miscellaneous				
Clione limacina	1	-	3	4
Cyanea capillata	-	-	1	1
Limacina retroversa	-	2	-	2
Station total	**1199**	**2892**	**1707**	**5798**
Mean abundance (ind. pr. 50 m^3)	**268.71**	**417.48**	**139.69**	**245.58**

As the 11 most abundant taxa were roughly the same for all stations and seasons, these were plotted (Figure 3.6) against the stations (top left plot) and then against season (remaining plots).

3.2.2 Gelatinous zooplankton vs. non-gelatinous zooplankton

A trend analysis of the abundance (ind. pr. $50m^3$) of gelatinous zooplankton and the biomass (gram pr. $50m^3$) of non-gelatinous zooplankton is given in Figure 3.7. The plots give an estimation of the trend in biomass over time, although the numbers are not directly comparable, as the measurements used are different. To give directly comparable trends, biomass would have to be calculated for both types of organisms. However, the plots are used to find the seasonal pattern of both gelatinous and non-gelatinous zooplankton. They show that the two types of zooplankton were not following the same seasonal pattern. Only two organisms, the tunicate appendicularia and hydrozoan *Lizzia blondina*, caused the peak in September at Elle and Steilene. The peak in gelatinous zooplankton at Missingene in April was caused by *Aglantha digitale*.

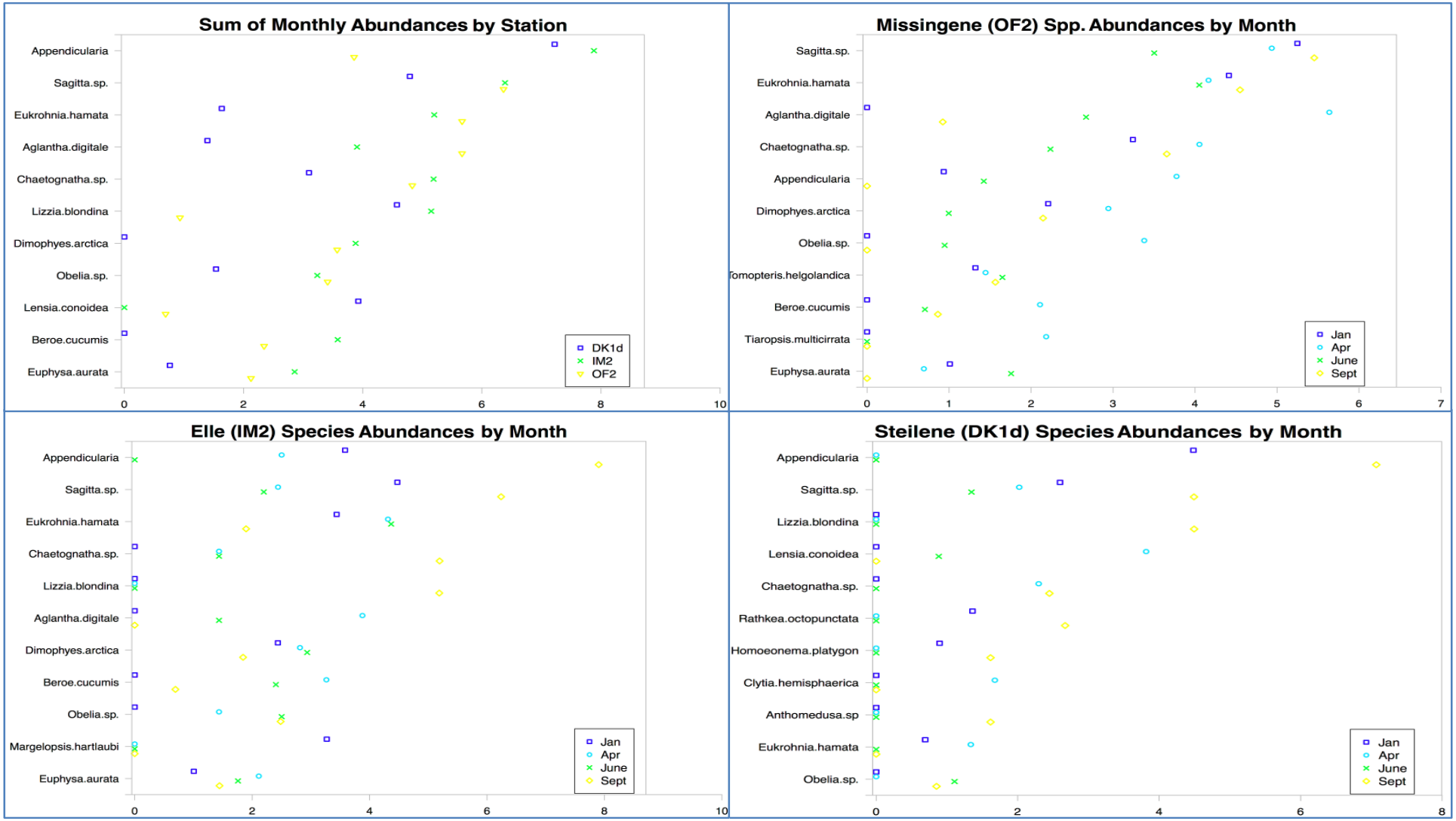

Figure 3.6 Abundance plot of the 11 most abundant organisms. X-axis is the abundances on the log-scale. Abundances from each month are the sum of the abundances from all depth layers of that station.

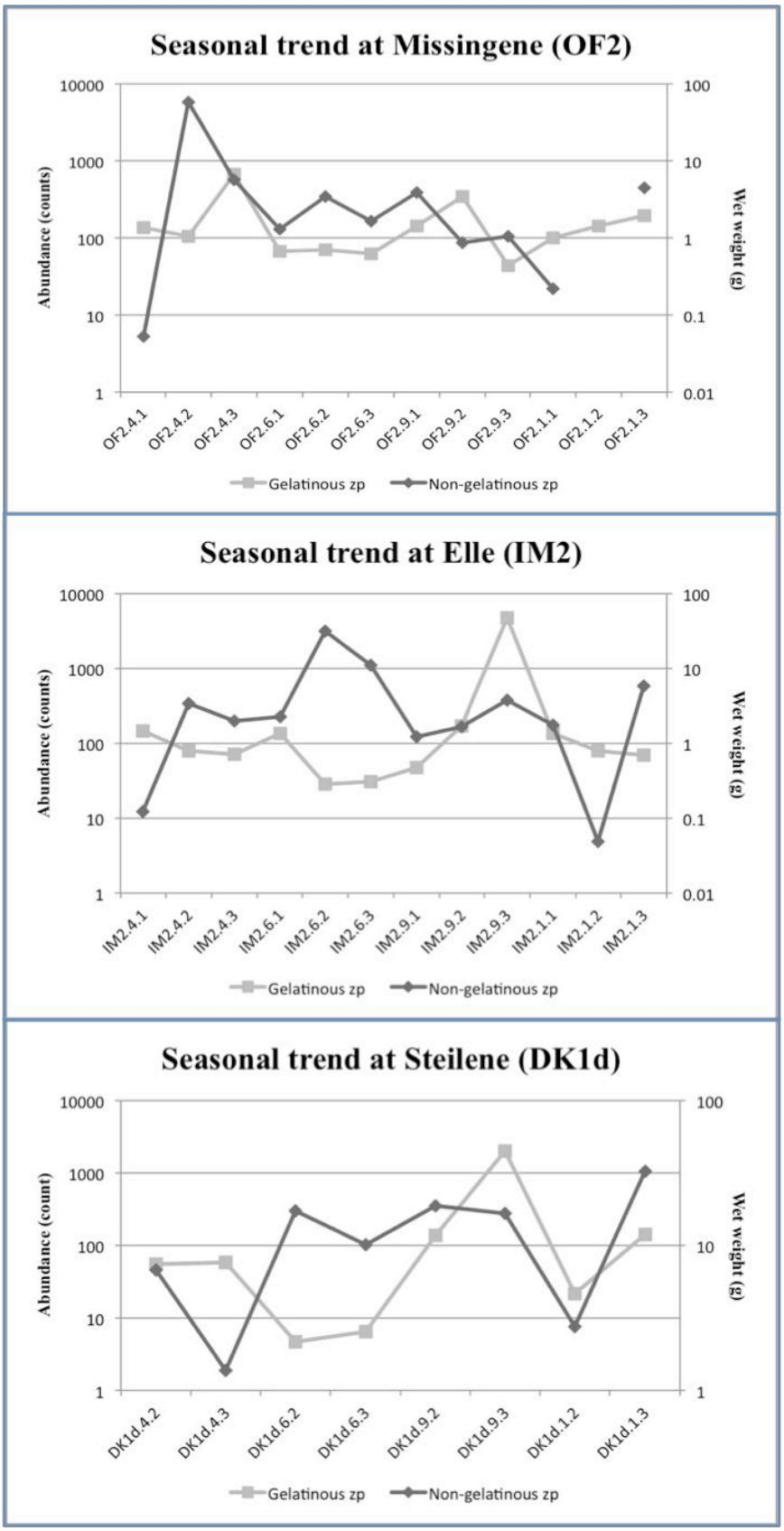

Figure 3.7 Abundances of gelatinous zooplankton (light grey, left y-axis), plotted against wet weight in grams (dark grey, right y-axis) of non-gelatinous zooplankton. Both measurements are given on a log-scale and for a water volume of 50m³. Each point is one sample, see Table 2.2 for sample names. Depth 1 is the deepest layer (>100m). Note the different scales of the y-axes.

3.3 Multivariate abundance analyses

The two subsets (Zoo_1 and Zoo_2) of the abundance data were analyzed using multivariate abundance modeling (hereafter referred to as mvabund) in the mvabund-package. The abundances were the ln-transformed sum of all specimens into the six groups (hydromedusae, siphonophores, ctenophores, chaetognaths, appendicularians, and *Tomopteris helgolandica*).

3.3.1 Mvabund for all depth layers at Missingene and Elle (Zoo_1)

The first multinomial test for Zoo_1 gave the Akaike Information Criterion for three different models (Equation 2.2 – 2.5), summarized in Table 3.2. The test showed that the model containing all variables, both categorical and continuous, was the optimal model (Zoo_1 ~ admsF). As explained (Section 2.3.2), however, the environmental variables were then separated in simpler models. This analysis showed that the complete model was not the optimal model after all. The seven, sorted models separating out the effect of each variable are shown, with their AIC values, in Table 3.3. The AIC values for all models can be found in Appendix Table A.3.

Table 3.2 AIC of the spatio-temporal model (adm), the environmental model (sF) and the complete model (admsF) in Subset 1. Notations: a = station, d = depth layer, m = month, s = density, F = fluorescence. ΔAIC is the difference in AIC between that model and the optimal model and indicates if the models are almost equal in fit or if the fit is substantially different. The column $e^{-0.5*\Delta AIC}$ is a step in the calculations to obtain the Akaike weight – moving from the ln-scale to the normal scale. The Akaike weight indicates the relative support of the model more intuitively than the ΔAIC (on a scale from 0 to 1).

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_1 ~ adm	1026.8	18.1	0.000119016	0.000
Zoo_1 ~ sF	1162.0	153.2	5.3997E-34	0.000
Zoo_1 ~ admsF	*1008.8*	*0.0*	*1*	*1.000*

Table 3.3 AIC values of the seven models with best fit - using different combinations of the two categories of factors in the Subset 1 dataset. See Table 3.2 for explanation of the different columns.

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_1 ~ ads	*990.5*	*0.0*	*1.00 E+00*	*0.966*
Zoo_1 ~ admF	997.2	6.8	3.38 E-02	0.033
Zoo_1 ~ adms	1003.5	13.0	1.50 E-03	0.001
Zoo_1 ~ admsF	1008.8	18.3	1.06 E-04	0.000
Zoo_1 ~ adsF	1010.3	19.9	4.82 E-05	0.000
Zoo_1 ~ adm	1026.8	36.4	1.26 E-08	0.000
Zoo_1 ~ adF	1028.4	38.0	5.66 E-09	0.000

It is seen from these tables that the best model for Zoo_1 is provided by the three factors station (a), depth (d) & density (s). This can be written as:

$$Zoo_1 \sim station\ (a)\ +\ depth\ (d) +\ density\ (s)$$

Equation 3.1

The model was selected because choosing area, depth and density as explanatory variables decreased AIC to its lowest value. The Akaike weight (0.966) reveals that the relative support for this model was large, in comparison to the other alternatives. Adding month and fluorescence did not improve the model fit enough to justify the added complexity of the model.

Coefficient testing

The individual coefficients, describing the effect sizes of the explanatory variables, were tested for the null hypothesis of zero value using Wald tests. The summary of the Wald test of the optimal model for Zoo_1 is given in Table 3.4. It shows that all factor levels in the optimal model for Missingene and Elle were significant. In effect, all depths are significantly different from the deepest layer at Missingene, and Elle is significantly different from Missingene.

Table 3.4 Summary of the optimal model for Subset 1 with station (a), depth (d) and density (s). Depth 2 is approx. 100-50 m. Depth 3 is approx. 50-0 m. * = p<0.05, ** = p<0.01.

Summary Zoo_1 ~ ads	Wald value	*p*-value	Sign. level
(Intercept)	6.671	0.013	*
Elle (a)	9.31	0.006	**
Depth 2	6.215	0.005	**
Depth 3	6.582	0.008	**
Density	5.934	0.016	*

A key assumption in this multivariate model was the log-linear response. As there is no tendency of a distinct shape, for instance a "U-shape", in the plot (Figure 3.8) of the Pearson residuals against the fitted values, the log-linearity assumption seems reasonable.

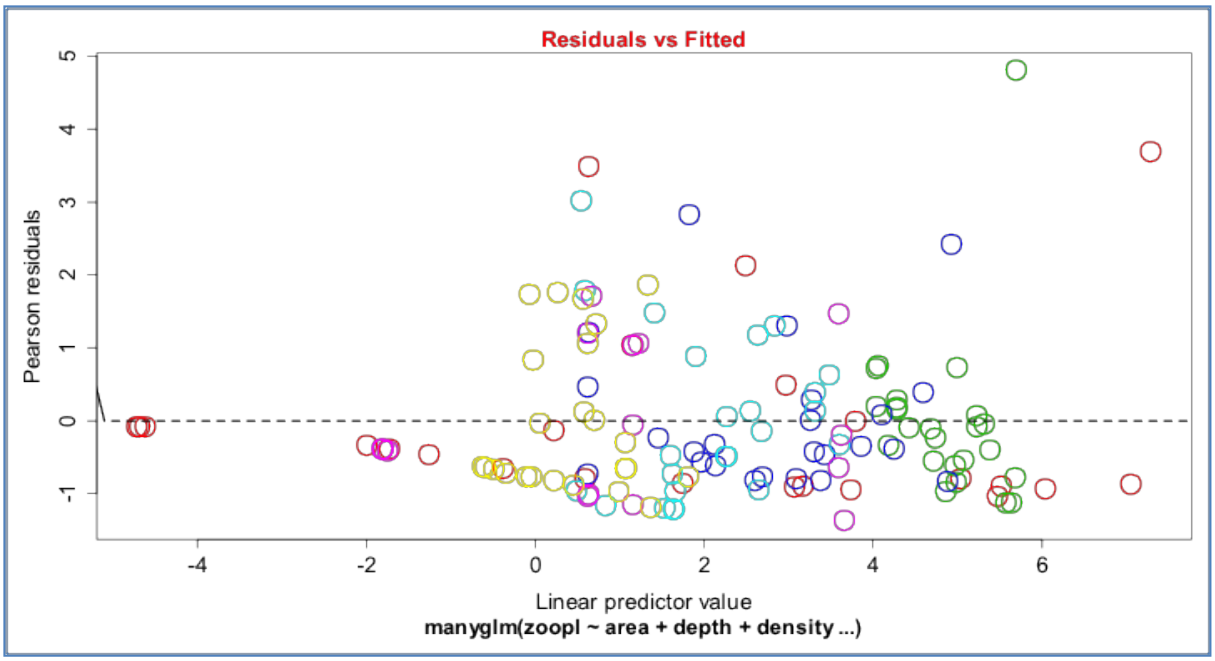

Figure 3.8 Pearson residuals vs. the fitted values of the optimal model for Subset 1. The colors indicate the different species groups. Note that the explanatory variables are area (station), depth and density with a negative binomial error term.

Predictive powers of the optimal Zoo_1 model

Although the Zoo_1 ~ ads model had the optimal fit for the data set as a whole, the picture was not as clear for each species group separately. The analysis that tested this is shown in Table 3.5. The coefficients of each group species in the model are given together with the corresponding standard errors, 95% confidence intervals and the multiplicative change in the response variable, corresponding to one unit of change in the explanatory variable (in categorical variables, the change compared to intercept). For example, for hydromedusae, Elle shows on average a density that is 430.6% of the density at Missingene, i.e., 330.6 % higher abundance at Elle than Missingene.

The table clearly shows that the model had different accuracy depending on the species group. For instance, the standard error for ctenophores going from the intercept to depth 3 is 106.21, while the remaining standard errors are in the range of 0.06 to 2.3. The effect of decreasing one increment of density was similar for all groups except appendicularia, where the effect was about half of the other effects. The effect of going from Missingene to Elle was large for all species group, although Tomopteris had the smallest change in predicted abundance (abundance at Elle was 58.3% of abundance at Missingene).

Table 3.5 Coefficients, standard errors (S.E.), 95 % confidence intervals (95% C.I.) and stepwise change in response variable for the six groups of organisms in the optimal model of all depths.

	Hydromedusae				**Siphonophores**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	3.66	2.22	{-0.78, 8.10}	-	3.32	1.46	{0.4, 6.24}	-
Elle (a)	1.46	0.55	{0.36, 2.56}	430.6	1.03	0.36	{0.31, 1.75}	280.1
Depth 2	1.08	0.69	{-0.3, 2.46}	294.5	-0.7	0.42	{-1.54, 0.14}	49.7
Depth 3	2.13	0.71	{0.71, 3.55}	841.5	-1.9	0.48	{-2.86, -0.94}	15.0
Density	-0.11	0.09	{-0.29, 0.07}	89.6	-0.04	0.06	{-0.16, 0.08}	96.1
	Ctenophores				**Chaetognaths**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	1.4	2.29	{-3.18, 5.98}	-	4.82	1.62	{1.58, 8.06}	-
Elle (a)	2.43	0.6	{1.23, 3.63}	1135.9	0.94	0.4	{0.14, 1.74}	256.0
Depth 2	-2.98	0.62	{-4.22, -1.74}	5.1	-0.27	0.49	{-1.25, 0.71}	76.3
Depth 3	-14.95	106.21	{-227, 197}	0.0	0.35	0.51	{-0.67, 1.37}	141.9
Density	-0.01	0.09	{-0.19, 0.17}	99.0	-0.02	0.06	{-0.14, 0.1}	98.0
	Appendicularia				**Tomopteris**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	11.01	2.26	{6.49, 15.53}	-	3.77	1.95	{-0.13, 7.67}	-
Elle (a)	5.05	0.72	{3.61, 6.49}	15602.2	-0.54	0.52	{-1.58, 0.5}	58.3
Depth 2	2.03	0.82	{0.39, 3.67}	761.4	-1.26	0.65	{-2.56, 0.04}	28.4
Depth 3	3.18	0.79	{1.6, 4.76}	2404.7	-0.91	0.64	{-2.19, 0.37}	40.3
Density	-0.55	0.1	{-0.75, -0.35}	57.7	-0.1	0.07	{-0.24, 0.04}	90.5

To illustrate the multivariate model fit for each species group, the observed abundances of the groups were plotted together with the predicted abundances from the optimal model (Figure 3.9). The abundance is log-scaled and each sample number has its own column. Of particular interest is the large difference in the model's predictive powers between the different groups. For hydromedusae, the model is reasonably well fitted to the samples, except for samples *OF2.9.1*, *OF2.9.3*, and *IM2.1.3*. The siphonophore plot shows a similar pattern where only a few samples are not predicted by the model. Ctenophores, appendicularia and tomopteris abundances seem to be quite badly predicted by the current model, as only a few predictions are in the range of the actual sample abundance. Chaetognaths, however, was the group of organisms that were best predicted by the model, the prediction line closely followed the sample abundance columns.

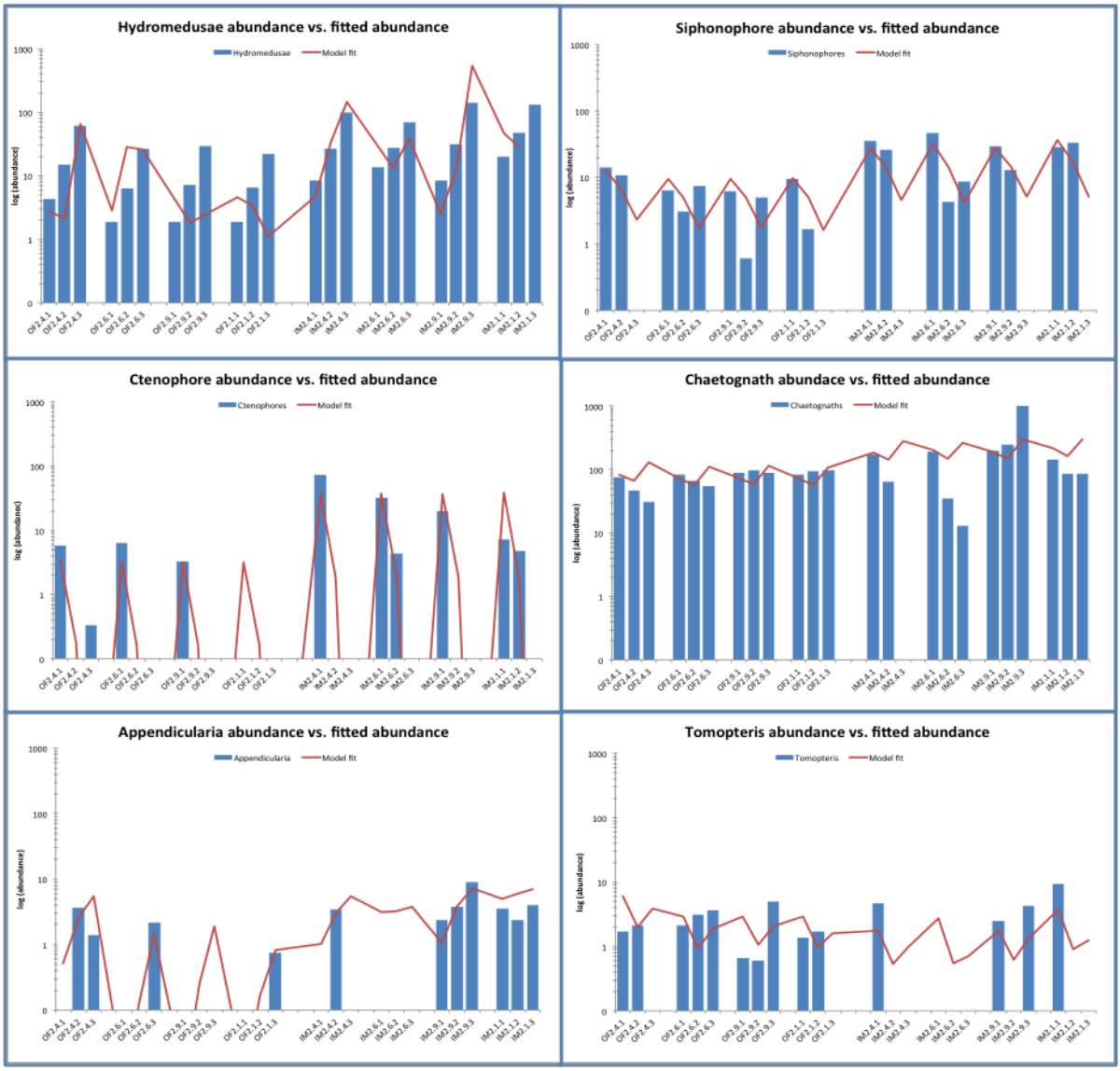

Figure 3.9 Visualization of log (abundance) of each group of organism vs. the corresponding optimal Zoo_1 model fit. The samples are in order from April 2011 through January 2012, with 3 depth layers for each month - going from deep (>100m) to shallow (50-0 m) depths. See Table 2.2 for further explanation of sample names. Missing columns indicate zero counts.

3.3.2 Mvabund model of all stations, two upper strata (Zoo_2)

The multivariate tests for Zoo_2 followed the same procedure as Zoo_1. Table 3.6 gives the AIC summary for the three primary models (Equation 2.2 a – 2.5). Note that the Akaike weight was a little lower in this subset than the first. The seven, sorted models separating out the effect of each variable are shown, with their AIC values, in Table 3.7. The AIC values for all models can be found in Appendix Table A.4.

Table 3.6 AIC of the spatio-temporal model (adm), the environmental model (sF) and the complete model (admsF) of Subset 2. Notations: a = station, d = depth layer, m = month, s = density, F = fluorescence. See Table 3.2 for explanations of columns

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_2 ~ adm	976.0532	6.4	0.040292094	0.039
Zoo_2 ~ sF	1136.895	167.3	4.77383E-37	0.000
Zoo_2 ~ admsF	969.63	0.0	1	0.961

Table 3.7 AIC values of the seven models with best fit using different combinations of the categories of factors in the Subset 2 dataset. See Table 3.2 for explanations of columns

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_2 ~ adsF	901.0321	0.0	1	1.000
Zoo_2 ~ ams	944.2102	43.2	4.20722E-10	0.000
Zoo_2 ~ amsF	945.9338	44.9	1.77713E-10	0.000
Zoo_2 ~ adms	965.8853	64.9	8.26621E-15	0.000
Zoo_2 ~ admsF	969.63	68.6	1.27103E-15	0.000
Zoo_2 ~ dm	975.0575	74.0	8.42536E-17	0.000
Zoo_2 ~ adm	976.0532	75.0	5.12124E-17	0.000

Interestingly, the model with best fit for Zoo_2 was the model including station (a), depth (d), density (s) and fluorescence (F).

$$Zoo_2 \sim station\ (\mathrm{a}) + depth(d) + density(s) + fluorescence(F)$$

Equation 3.2

The model was selected because adding month to the optimal model increased the complexity more than it improved the model fit according to AIC.

Coefficient testing

The summary of the Wald test for the optimal model is given in Table 3.8. It shows that all levels in the optimal model for all stations are significant if we use a significance level of 0.1, but not if using a significance level of 0.05. It does seem like Steilene is only marginally significantly different (p = 0.09) from Missingene and Depth 3 only marginally different from depth two (p = 0.079).

The plot of Pearson residuals against the fitted values (Figure 3.10) shows no distinct shape, so the log-linearity assumption was not violated.

Table 3.8 Summary of the optimal model for Subset 2 with station (a), depth (d), density (s) and fluorescence (F). Depth 3 is approx. 50-0m. The two factor levels with least significance (p<0.1) are in italic. * = p<0.05, ** = p<0.01.

Sum.adsF	Wald value	*p*-value	Sign.level
(Intercept)	5.885	0.042	*
Elle (a)	8.167	0.004	**
Steilene (a)	*4.8*	*0.09*	.
Depth 3	*4.91*	*0.079*	.
Density	7.07	0.012	*
Fluorescence	5.832	0.048	*

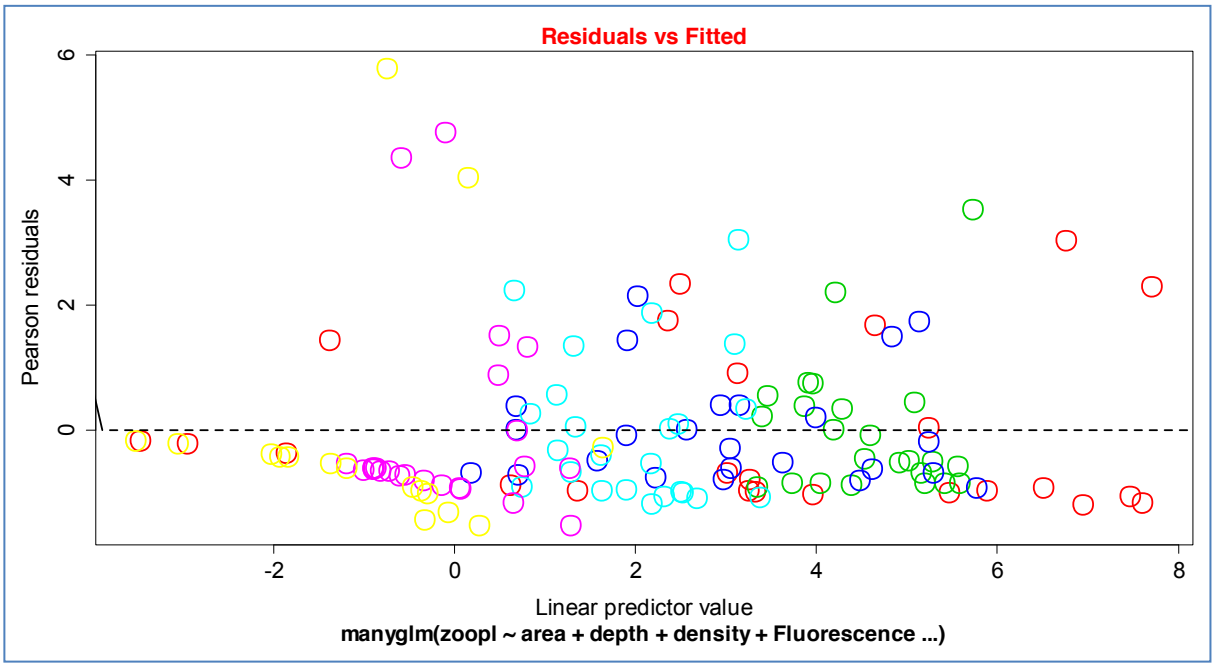

Figure 3.10 Pearson residuals vs. fitted values of the optimal Zoo_2 model. The colors indicate the different species groups Note that the explanatory variables are area (station), depth, density and fluorescence with a negative binomial error term.

The coefficients of each group of species in the optimal model for Zoo_2 are given in Table 3.9 together with the corresponding standard errors, 95% confidence intervals and stepwise change in response variable (i.e., group abundance).

Table 3.9 Coefficients, standard errors (S.E.), 95% confidence intervals (95% C.I.) and stepwise change (%Δ) in response variable for the six groups of organisms in the optimal Zoo_2 model. The table shows the effect, i.e., the change in abundance, of changing one unit (quantitative or qualitative) of each variable listed from the Intercept, i.e., Missingene in April at depth 2 (100-50m). Variables of particular interest are written in italic.

	Hydromedusae				**Siphonophores**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	-2.66	2.48	{-7.62, 2.3}	-	6.5	2	{2.5, 10.5}	-
Elle (a)	2.24	0.75	{0.74, 3.74}	939.3	1.2	0.63	{-0.06, 2.46}	332.0
Steilene (a)	0.29	0.76	{-1.23, 1.81}	133.6	0.63	0.62	{-0.61, 1.87}	187.8
Depth 3	*1.78*	*0.63*	*{0.52, 3.04}*	*593.0*	*-0.69*	*0.52*	*{-1.73, 0.35}*	*50.2*
Density	0.07	0.1	{-0.13, 0.27}	107.3	-0.19	0.08	{-0.35, -0.03}	82.7
Fluorescence	*6.26*	*2.03*	*{2.2, 10.32}*	*5.23E+04*	*-1*	*1.68*	*{-4.36, 2.36}*	*36.8*
	Ctenophores				**Chaetognaths**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	1.27	16.85	{-32.43, 34.97}	-	4.61	2.25	{0.11, 9.11}	-
Elle (a)	10.14	16.69	{-23.24, 43.52}	2.53E+06	1.1	0.68	{-0.26, 2.46}	300.4
Steilene (a)	7.09	16.66	{-26.23, 40.41}	1.20E+05	-0.78	0.68	{-2.14, 0.58}	45.8
Depth 3	*-1.69*	*0.67*	*{-3.03, -0.35}*	*18.5*	*0.34*	*0.58*	*{-0.82, 1.5}*	*140.5*
Density	-0.49	0.16	{-0.81, -0.17}	61.3	-0.04	0.09	{-0.22, 0.14}	96.1
Fluorescence	*3.33*	*3.17*	*{-3.01, 9.67}*	*2793.8*	*1.42*	*1.85*	*{-2.28, 5.12}*	*413.7*
	Appendicularia				**Tomopteris**			
	Coef.	S.E.	95% C.I.	% Δ	Coef.	S.E.	95% C.I.	% Δ
(Intercept)	8.23	2.04	{4.15, 12.31}	-	3.55	2.31	{-1.07, 8.17}	-
Elle (a)	5.88	0.86	{4.16, 7.6}	3.58E+04	-1.48	0.73	{-2.94, -0.02}	22.8
Steilene (a)	2.75	0.69	{1.37, 4.13}	1564.3	-1.48	0.69	{-2.86, -0.1}	22.8
Depth 3	*1.51*	*0.55*	*{0.41, 2.61}*	*452.7*	*-0.21*	*0.58*	*{-1.37, 0.95}*	*81.1*
Density	-0.51	0.09	{-0.69, -0.33}	60.0	-0.1	0.08	{-0.26, 0.06}	90.5
Fluorescence	*8.84*	*1.87*	*{5.1, 12.58}*	*6.90E+05*	*-0.79*	*1.91*	*{-4.61, 3.03}*	*45.4*

The species group with the largest standard errors was ctenophores in this subset as well, but these were not of the same magnitude as for Zoo_2. The extremely large differences between groups in effect of increasing fluorescence by one unit can be seen in Table 3.9. The table clearly shows that the response in abundance of appendicularia, ctenophores and hydromedusae to an increase in fluorescence was several magnitudes higher than the response in abundance of tomopteris, chaetognaths and siphonophores. For instance, the appendicularian abundance increased by $6.90 * 10^5$ % when increasing fluorescence by one unit, while for tomopteris the change in abundance was negative, i.e., it decreased by 45.4%. The same pattern can be seen in the effect of going from depth 2 (the intercept depth of 100 – 50 m) to depth 3 (surface layer).

An illustration of the model fit for each species group is shown in Figure 3.11. The abundance is log-scaled and each sample number has its own column. The figure shows that

the predictive powers of the optimal Zoo_2 model vary in a similar manner as that of the optimal Zoo_1 model (see Figure 3.9).

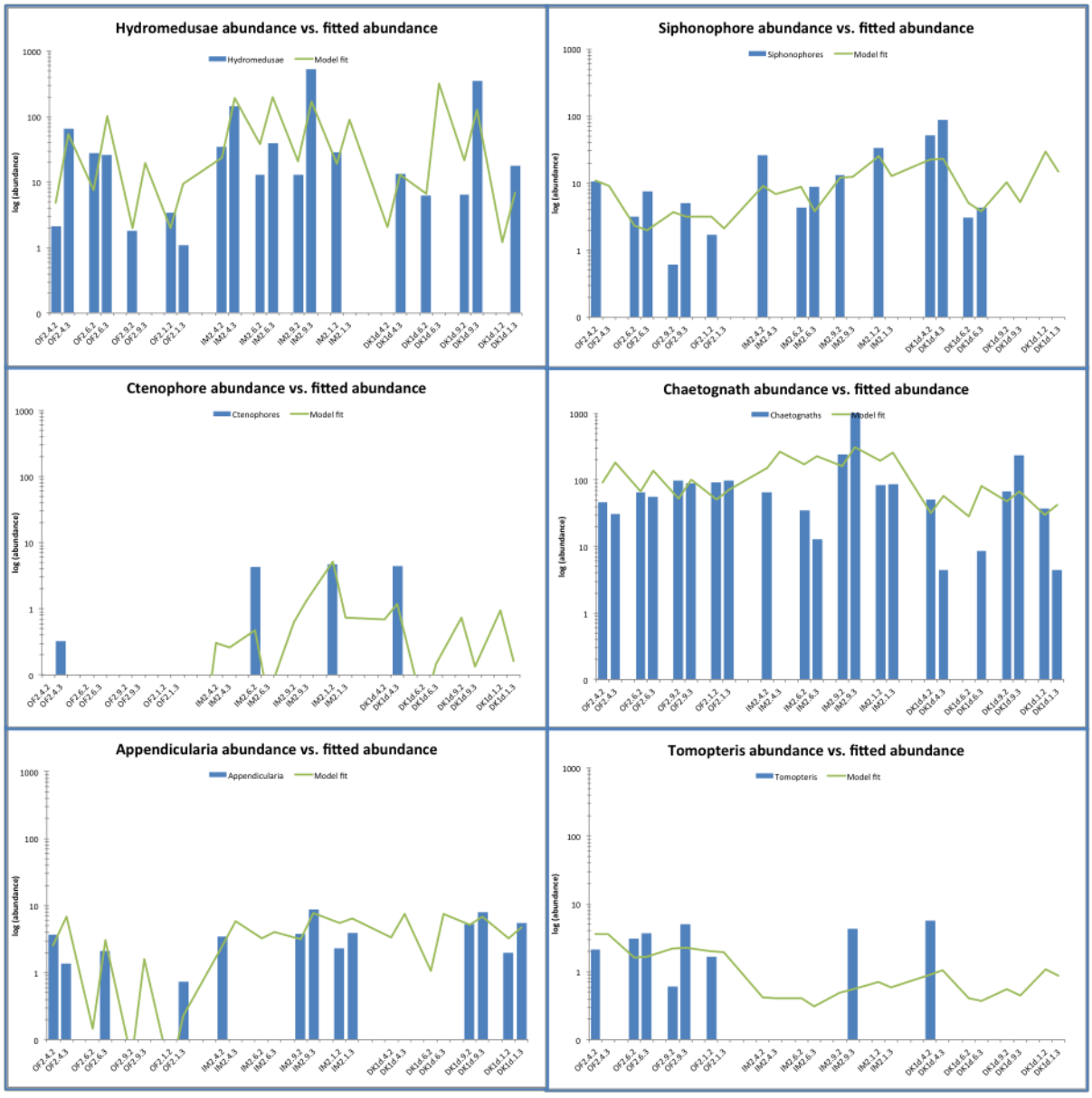

Figure 3.11 Visualization of the log (abundance) of each group of organism vs. the corresponding model fit using the optimal Zoo_2 model. The samples are in order from April 2011 through January 2012, with depth layers 2 (100–50m) and 3 (50–0m) for each station. See Table 2.2 for further explanation on sample names. Missing columns indicate zero counts.

4 Discussion

4.1 Gelatinous zooplankton

4.1.1 Abundances and gelatinous community composition

Because species diversity and abundance is often high in fjords (Smedstad 1972, Brattegard 1979, Baalsrud & Magnusson 2002d), the assumption was that Elle and Steilene would have larger abundances and diversity than Missingene, the "oceanic" station (Section 1.2.2). Looking at the counts of specimens sampled (Table 3.1) the total number of specimens counted at Elle was 2.4 times higher than the abundance at Steilene, and the count at Missingene was 1.4 times higher. This seems at odds with the presumption that Oslofjord has an outer to inner fjord transect of increasing species abundances. However, those counts are *not* adjusted for the differences in volume of water sampled at the different sites. As Missingene is a much deeper station, the deepest layer there had a much larger volume (>100 m^3) than the corresponding deep layer at Elle (~ 42 m^3), giving a bias towards higher abundance at Missingene.

In the same table (Table 3.1), the volume-adjusted gelatinous zooplankton concentration per 50 m^3 for each station is given, and these concentrations corresponded better with the hypothesis (Section 1.3). The abundance at Elle was 2.7 times higher, and the abundance at Steilene was 1.2 times higher than the abundance at Missingene. It is, however, somewhat surprising that the difference between the outermost and innermost station concentration was small (2073 and 2412 individuals, respectively). Clearly, there are other factors influencing the species abundance at Steilene than the ones considered in this thesis. One possible factor is the composition of available prey species, but the prey species were not identified, only weighed. Gelatinous animals show a clear specificity in prey selection (Costello & Colin 2002, Regula et al. 2009) but as this study analyzed the gelatinous animals pooled, the effect of prey selectivity *could* have been countered (Section 1.1.3). If so, the biomass of non-gelatinous zooplankton could have been added as an explanatory variable in the statistical models. However, the models were already in danger of oversaturation and the extra explanatory variable would have reduced the degrees of freedom even more. The differences in prey availability were thus considered too inaccurate a measurement (statistically) to include in the models.

The species composition at the three stations mostly followed the expectations. Appendicularians were found in extremely large abundances at both Steilene and Elle while very few were found at Missingene. The tunicates are herbivore, feeding on smaller phytoplankton and bacteria, and as Missingene had generally low fluorescence (and thus phytoplankton), it is logical that there was lower abundance there. In addition, the highest abundances of appendicularia corresponded with peaks in fluorescence at the two inner stations, further supporting the connection between phytoplankton and herbivore (although no correlation was statistically tested). Another species that peaked in September was *Lizzia blondina*. The hydromedusae is capable of asexual reproduction in favorable conditions by producing medusae buds, and many of the specimens identified in this study contained several medusae buds each. Clearly, the ability to quickly respond to a changing environment, whether that is caused by hydrography or a food source, is shared by the tunicate and the cnidarian. Ctenophora, Siphonophora, *Eukrohnia hamata*, and *Tomopteris helgolandica* were found to have decreasing abundances from the outer fjord (Missingene) to the inner fjord (Steilene). They are all oceanic species and were expected to be most abundant at the oceanic station. There was one exception, though; the diphyid siphonophore *Lensia conoidea* was found in high abundances at Steilene, while only three specimens were positively identified to the species at Missingene (Table 3.1). Another surprising find was the relatively high abundances of the anthomedusa *Margelopsis hartlaubi* (Figure 3.6). The species has, as far as I know, not been previously reported in Oslofjorden. Hosia (2007) found that the species had only been found in the vicinity of Bergen, but suggested that was due to a lack of research in other areas. Although the evidence is not conclusive, the findings of this study support the hypothesis. These findings together clearly illustrate the lack of knowledge of gelatinous plankton in Norwegian waters.

4.1.2 The curious case of *Aglantha digitale*

Aglantha digitale has long been recognized as one of the most widespread and abundant coelenterates in the North Atlantic (Kramp 1959, Williams & Conway 1981, Pages et al. 1996). It is generally considered an oceanic species, as are most trachymedusae. In spite of this it has had a self-sufficient population in Oslofjorden, that actually increased (from 30 to 1600 specimens in 100 m^3 water) towards the inner parts of the fjord (Smedstad 1972). Only two specimens of *A. digitale* were collected in the samples from the innermost station at Steilene in this study, however. One specimen was found in September and one specimen in January (an abundance of 4.1 and 4.4 specimens in 100 m^3, respectively). Clearly, it is no

longer the most abundant species in the inner Oslofjord. Possible explanations for this are the extreme patchiness of the pelagic environment, or large inter-annual fluctuations in the species abundance, but it is unlikely to be the entire explanation. Another hypothesis concerns the eutrophication level in the inner fjord. *A. digitale* is one of the few coelenterates that increase in abundance with eutrophication level (Arai 2001). Following this logic, it is quite possible that the species abundance is decreasing as the eutrophication level in Oslofjorden improves (Baalsrud & Magnusson 2002e). If the latter is the case, it can be argued that a decreasing population of *A. digitale* is a positive sign of an improving ecosystem. The different type of species populations that are found in a fjord were discussed in Section 1.2.2 and, if the picture from this study holds true, it is likely that *A. digitale* has changed from being a self-sustaining population to a sink population that needs influx of organisms from outside the community. In Oslofjorden, the deep-water is renewed approximately every third year (Baalsrud & Magnusson 2002c), potentially transporting more *A. digitale* into the inner fjord. As the abundance of *A. digitale* was high at Missingene, the source population is most likely rich enough to support the inner fjord population. It is not possible to conclude if the population has indeed changed from this study alone, but it clearly shows the importance of long-term studies of population abundances and variation of gelatinous zooplankton. There is so little knowledge on the gelatinous community in Oslofjorden that giving any predictions from this study alone is impossible.

4.2 Environmental variables

4.2.1 Seasonality

Expectations

Previous investigations (Baalsrud & Magnusson 2002c, Dragsund et al. 2006, Aure & Danielssen 2007, Hostyeva 2011), have found the hydrographical cycle in Oslofjorden to follow a general pattern. That is, a complete mixture of the water column during the winter months of 2011, then complete stratification in February/March lasting through summer, and finally gradually increasing water mixing in the fall months until complete convection was reached in November/December. This convection is caused in two ways. First, the prevailing north winds common in the winter season can cause a complete convection (Section 1.2.3) by cooling the upper water until it becomes so dense that it sinks and mixes with the lower strata. Secondly, ice cover acts to prevent wind and waves from influencing the water temperature, and the temperature, salinity and density of the water become uniform throughout the column as a result (Baalsrud & Magnusson 2002c). The water was regarded as mixed when the temperature, salinity and density were approximately equal from surface to bottom.

Compared to the deeper layers, the temperature, salinity and density were expected to show larger seasonal variability in the surface layers (AMAP 1998, Baalsrud & Magnusson 2002c), as wind, air temperature and rain fall have an immediate effect on the upper surface (Section 1.2.1). Fluorescence, as proxy for phytoplankton concentration, was expected to influence the surface layer positively, i.e., increased zooplankton abundance and the deeper strata negatively (due to its absence). This dual effect of primary production was expected to have a large impact on the community composition. In this study, however, fluorescence was only significant in the Zoo_2 model, which only compared the two upper strata. The reason it was not significant in the Zoo_1 model, which compared all three strata may be due to strong collinearity with depth (which was significant). It is more likely, though, that the negative influence on abundance in the two deeper strata was more similar than the difference between the positive and negative influence between the two upper layers. In other words, the low change in effect of fluorescence between the middle and bottom layers may have cancelled the effect of the change between the middle and upper layer. An additional confounding

factor was the large differences in fluorescence concentration at the three stations. This will be discussed under Section 4.2.2.

The seasonal cycle of 2011

A complete mixing of the water masses, and thus lack of stratification, occurred in April of 2011 at Steilene (Figure 3.1 and Figure 3.2). A possible cause is that the entire inner fjord was completely covered with ice in March (including Steilene). This was one to two months after the water is normally stratified, and there was indeed beginning stratification of the water before the advection in April. The water quickly re-stratified in May 2011, and the situation lasted until winter (Section 3.1). The temperature of both deep and surface water followed the normal cycle for Steilene, indicating that salinity, not temperature, had the largest influence on density during the sampling period. The fluorescence plot (Figure 3.4) showed that phytoplankton spring bloom started in February/March, followed by a reduction in fluorescence concentration in April/May before the fluorescence increased again. This was likely an effect of the ice cover inhibiting phytoplankton production by decreasing light. Primary production is important for all zooplankton (Lenz 2000), and a lack of phytoplankton in a normally highly productive period would likely have negative consequences on the gelatinous community, both indirectly for carnivorous organisms like chaetognaths and directly for filter feeders like appendicularians (Section 1.1.3). However, as there are *no* other studies on the gelatinous zooplankton community in Oslofjorden, no comparison between years is possible and this is only speculative.

The water at Elle was stratified from March and through summer, before it returned to being mixed in winter (Figure 3.1 and Figure 3.2). The seasonal cycle followed the expectation from previous investigations. The stratification was allowed to continue through April, as the fjord was not completely covered by ice. The temperature trend followed the expected pattern. The fluorescence plot, however, did show a decrease in phytoplankton concentration in April. A zooplankton bloom often follows the spring bloom, decreasing the phytoplankton abundance drastically by grazing (Lenz 2000), and this is likely the scenario seen in the plot (Figure 3.4).

At Missingene, the hydrographic cycle seen at Steilene was repeated. A beginning stratification pattern was interrupted in April by convection that reached the bottom at 350 meters. There was no ice at Missingene, though, so the more likely cause for this convection was that the prevailing wind/wave direction was stable for a long enough period that the

entire water column was replaced with water from outside the outer sill (Aure & Danielssen 2007). This water is both colder and more saline than the water in the inner fjord, possibly causing the vertical circulation. Unfortunately, this is only speculation, although the wind patterns can be found online (for instance at the weather service "Yr" by the Metrological Institute) and seem to follow this pattern during most of March and beginning of April. Whether this weather was enough to cause the advection from outside the sill would have to be analyzed by a physical oceanographer to be conclusive.

Temperature again followed the expected pattern, although the surface warmth lasted somewhat longer than normal, until October/November (Figure 3.3).

4.2.2 Station differences

Due to the influence of the two main rivers emptying into Oslofjorden, Glomma and Drammen River, the norm is that the surface layer at Missingene is fresher than the corresponding layer at Elle and Steilene. The deeper layers at Missingene are generally more saline than the other stations, due to the influence of Atlantic water from Skagerrak (Dragsund et al. 2006, Aure & Danielssen 2007). From May 2011, however, surface water at Missingene was more saline than the other stations (Figure 3.5 and Table A.2). Salinities of the surface layer at Missingene were generally high throughout the year (PSU between 25-32) except in April (PSU at 20). This adds merit to the theory proposed above, that new water from Skagerrak, at higher salinities and colder temperatures entered the Rauøy basin (e.g. Missingene station) in April, and changed the expected salinity pattern for the remainder of the year.

Elle also had high surface salinities for most of the year, as expected for an area of the fjord with little freshwater influence. Steilene had high values in the two first months (PSU of 32 and 30, respectively), but then had PSU in the low- to mid-twenties the remainder of the year. The most likely cause for the low surface salinity is that there was more rain throughout the sampling period than the average rainfall. However, a change in rainwater influence would be even more likely to show at Elle, where the fjord is narrower and runoff from both coasts more prominent. The data sampled in this study offer no adequate reason for this discrepancy.

Temperature and fluorescence patterns both followed the expectations (Sections 1.2.1, 2.1 and 3.1).

4.3 Sampling method and study design

Doing a study attempting to describe a seasonal and geographical trend in abundance has many pitfalls. The abundance of the different species that are caught is, in fact, only a snapshot of the ecosystem as a whole. A patchy distribution (spatial) of zooplankton is not only common, it is the rule (de Wolf 1989, Mills 1995, Titelman & Hansson 2005, Regula et al. 2009, Colin et al. 2010). This is especially true for gelatinous zooplankton (Arai 1992, Graham et al. 2001). Gelatinous zooplankton also has a patchy temporal distribution. A net haul that only samples a water column the size of the net opening at a given time will always sample fewer organisms than are present. In addition, many organisms are able to swim fast enough to escape the net, even if they are still considered planktonic, and the net never has a filtration efficiency of 100%, but often clog during longer hauls (Hernroth 1987, Sameoto et al. 2000, Skjoldal et al. 2000).

Replicate net hauls are one way to counter the shortcomings of net hauls (Currie & Foxton 1956, Fraser 1968b, Wiebe 2003). Replicate hauls are extremely time consuming with a Nansen net, though, even in a(s) shallow (an) area as Oslofjorden. There are several types of multiple net samplers that can sample several samples on the same haul, using much the same principle as the Nansen net (Wiebe 2003). The wire time would then be greatly reduced, as all strata are sampled in one net haul, making time for replicate samples. However, this equipment was not available at the University of Oslo and making replicate hauls was not feasible.

Video monitoring is useful for observing the gelatinous plankters in the vertical plane and also counters for the patchy distribution of plankton (Hamner et al. 1975, de Wolf 1989, Haddock 2004, Richardson & Gibbons 2008, Boero et al. 2008, Hosia & Båmstedt 2008, Purcell 2012). However, to correctly identify and quantify the species in the area, studying the organisms in the stereomicroscope is necessary, video monitoring is not sufficient. With other equipment, it would be possible to do both underwater video monitoring and net hauls (Hosia & Båmstedt 2008, Condon et al. 2012, Brotz et al. 2012), to give a more complete picture of the zooplankton community, but if only one method is feasible, sampling with a suitable net is adequate, especially for smaller species (Hosia et al. 2008). In addition, to completely counter the effect of patchiness, the video recording would have to be continuous

over long periods and the following video analysis would be more time consuming than practical.

Although the methods used have several shortcomings, the problems are the same for all the sites sampled, so the comparison between sites is still valid. Comparisons to other ecosystems must be done with caution, though, and reaching a conclusion from only one study is not possible.

4.4 Multivariate models

4.4.1 Ecological interpretation of the model results

Three variables were included in the optimal model of both subsets of multivariate data: station (a), depth (d) and density (s). In addition, fluorescence (F) was included in the Zoo_2 model, which included only the two upper depth strata. Depth is likely always significant ($p < 0.05$) because of the different water masses in the fjord that generally have differing properties in density, temperature, salinity (and light). As explained in the introduction, the upper stratum is the one directly influenced by current weather conditions and has the largest variability of environmental variables. For instance, temperature varies between approximately –1°C and 18°C in the upper 25 meters at Steilene (Figure 3.3), while it only varies between 5°C and 7°C in the bottom 50 meters or so. The middle layer is clearly a mixing area between the top and bottom layer. This trend is clear for all the other environmental variables as well (Figure 3.1, Figure 3.2, and Figure 3.4). In other words, depth may express many of the significant factors contributing to gelatinous abundance and this is one reason it was always significant in the models.

The presumption that the three stations are different seems to hold true, given their significance in both models (Zoo_1 and Zoo_2). It is important to remember that the stations were placed at strategic areas of Oslofjorden, i.e., the outer region (Missingene), the bottleneck (Elle) and the inner fjord (Steilene). In other words, the difference in abundance that is caused by station is likely an effect of the three different water masses at the three sites, the different geographic parameters, and the corresponding different stratification profiles. The species abundance and community composition is naturally influenced by the water masses of the station, so when these differ between the three stations, so does the species composition and their abundance. That the community is related to the water masses is one factor that may explain why month was not significant in the models.

Intuitively, month should have been included as an explanatory factor, as the study investigated the *seasonal* variability. Figure 3.7 even shows a definite seasonal trend in both gelatinous and non-gelatinous zooplankton. However, there are several reasons why month was not significant for the abundance of gelatinous zooplankton in this study. The first is that there was only four months included in the models. The months were selected as snapshot representatives of the four seasons in a year, beginning with spring 2011. It is possible that

excluding the months between the selected four months masked a seasonal effect. Most gelatinous zooplankters have short presences in the pelagic due to their short generation times (a few weeks to months). Thus, if a given species is present some time during the spring months, (late February to April), only analyzing one of these months would miss changes in the abundance from early to late spring. This becomes especially likely when grouping the different types of organisms together, as the group community is even more likely to miss changes of species composition within the season.

The second reason is more complex, and possibly more biologically relevant. It contains the aspect of the different water masses and stratification profiles of the different stations. The density included in the model is a measure of the stratification of the water masses at the three stations. As explained in the introduction, the presence or absence of stratification is closely correlated with season. Thus, the multivariate model may have judged the factor month superfluous as long as the factor depth was included. In other words, the distribution of organisms is correlated with the different water masses, not the month itself (according to the model). In addition, it is important to remember that the data used in the statistical analyses was pooled. It is likely that month plays a larger role for the individual species than for the pooled species group of the models. Thus, redoing the analysis where all species (or the lowest possible taxon) are separate may have shown that month was significant.

Gelatinous zooplankton are thought to be less affected by a possible trophic mismatch caused by climate change than for instance crustaceans due, in part, to their rapid responses to changes in the environment (Haddock 2004, Richardson & Gibbons 2008, Lynam et al. 2010). In the classification literature (Kramp 1959, Bouillon et al. 2004), it is common to note the seasonality of a species to aid in the identification process. However, not all studies find any seasonal effect on cnidarian abundances at all. Chapter four of the review article by Mackie et al. (1987) is devoted to the distribution and migration of Siphonophores. They reviewed several studies that showed that there was no seasonality in species populations, and that changes in populations by local winds, currents and changing hydrographic conditions could be falsely interpreted as seasonality (Mackie et al. 1987 and references therein). However, comparing between ecosystems that are in different regions is difficult, and any result should be treated with extreme caution, especially in this study due to the few data points and short sampling time. Several studies on the distribution of gelatinous zooplankton in concurrence with major water masses have been done (Baalsrud & Magnusson 2002a, Hosia & Båmstedt 2008, Purcell et al. 2010, Lynam et al. 2010), but the

majority of field studies focus on seasonality as the main explanatory factor (Ballard & Myers 2000, Cooney et al. 2001, Hosia & Båmstedt 2007). The results of this study show that the different water masses are significant, while season is not. Although no conclusion can be reached, it would be interesting to do more research into the different aspects influencing the gelatinous seasonality. Gelatinous plankton has been shown to react to a number of hydrographic changes, including (but not only) thermoclines, haloclines, Langmuir circulation, and even light (Arai 1992). These variables influence the aggregation and patchiness of zooplankton, both gelatinous and non-gelatinous through advection and convection processes. More work is needed to understand how these variables correlate with season, though, as season often encompass several of these variables. As gelatinous zooplankton has life history strategies that allow them to quickly respond to changes in water temperature, food sources and hydrography (Section 1.1.3), they may have a competitive edge over non-gelatinous zooplankton when they are advected into a new area with the water masses. Clearly, more focused research than this study is needed to predict how the gelatinous community will change with a warming, more acidic ocean. Note that the life cycle and seasonality of most scyphozoans are better known than the hydrozoans, ctenophores and other gelatinous organisms included in this thesis (Ballard & Myers 2000, Baxter 2012), and are thus exempt from the discussion.

Predictions

Both the optimal models for the two subsets (Zoo_1 and Zoo_2) had good fits for hydromedusae, siphonophores and chaetognaths. None of them had good fits for ctenophores, tomopteris or appendicularia. A likely explanation is that the distribution pattern (negative binomial) of the abundance was not a good fit for the species group (Section 4.5).

Appendicularians had the largest discrepancy in pattern with counts of 700 in one and 1650 in another sample from September, while the remainder of the year, they were present in very low numbers, if at all (Figure 3.7, Figure 3.9, and Appendix Table A. 5). Their life history is very different from the other organisms in the study and they are not strictly gelatinous (Section 1.1.3). For instance, they are filter feeder whose main prey are microscopic phytoplankton, bacteria and detritus. One of these aspects may be what gave them a massive increase in abundance at Steilene and Elle in September. At the time there was a bloom in phytoplankton which was clearly visible in the fluorescence contour plot (Figure 3.4), and given that small phytoplankton is one of the main prey groups of appendicularians, this could

be an explanatory factor. However, it is outside the scope of this investigation to identify the causal relationships for this bloom.

Ctenophores are another discrepancy in the model fit analyses. Ctenophores were most abundant at Elle and Missingene, while there was only one specimen found at Steilene. The ctenophore counts were in the range of 1 to 40 per sample, and if we look at Figure 3.9, they show an emerging pattern. The model is remarkably accurate for the deepest layer of water at both stations (samples *OF2.4.1, OF2.6.1, OF2.9.1, IM2.4.1, IM2.6.1, IM2.9.1*), less accurate for the middle layer, and completely inadequate for the surface layer. One possible cause for this is that the Ctenophores were more abundant and had less variation in the deepest layer. The same pattern is formed and confirmed in Figure 3.11, as the model for this subset only included the two upper layers. The first eight columns in the figure are the samples from Missingene, where there are no ctenophores present. This shows that, for Missingene at least, the ctenophores are all in the deepest layer – not in the two upper layers. Ctenophores are tactile predators, and may not need the lighter environment of the surface layer to feed. At the same time, they are more likely to remain unnoticed by visual predators in the deeper layers – this gives an added benefit to remaining at large depths for an organism as large as the ctenophores in this study. Most of the ctenophores found in this study were *Beroe*, a genus known for preying on other ctenophores. Thus, even though the ctenophores were pooled, since almost all ctenophores identified were one species, the detrimental effect of pooling may actually be smaller for ctenophores than for the other species groups. Likely, the preferred prey species of *Beroe cucumis* in Oslofjorden is *Pleurobrachia pileus*, a species that prefers to inhabit the bentho-pelagic region on the ocean floor. Although no *P.pileus* were collected with the Nansen net during this study, several specimens were collected using the WP2-net, and one specimen was even collected with a sediment core sampler by Elisabeth Alve at the Geology department, during one of the cruises at Missingene.

The reason why the model did not have a good fit for *Tomopteris helgolandica* might simply be that it was always present in low numbers of one or two individuals per sample. It also had a decrease in presence from the outer to inner station (of a total of 29 *Tomopteris*, 19 were found at Missingene, 8 at Elle and only 2 at Steilene). Low abundances could make model predictions more difficult. If the models were used separately at each station, we would likely have seen a better result, with a different pattern.

4.5 Choice of model and model tests

Wang et al. developed the mvabund package in R (Wang et al. 2012a) to analyze multivariate abundance data in relation to environmental variables, as they considered distance-based ordination methods ineffective (Wang et al. 2012b). Distance-based ordination methods are widely used to analyze multivariate abundance data in the ecological community (Shiganova 2005, Hosia 2007, Hosia et al. 2011, Oksanen 2011, Haraldsson et al. 2012). However, there are two problems with that type of method for this study. The first is that ordination is largely descriptive and does not identify which species (or species group) express the effect of the variables (Wang et al. 2012b). In other words, it can identify that there are differences between species compositions, but is not efficient at recognizing which factors influence these differences and how. Neither is it efficient at *predicting* the abundance of each species given different environmental conditions or geographical areas (Wang et al. 2012b).

Care is needed when predicting between ecosystems as all ecosystems are different, but prediction may still be used to map the response to specific changes within one ecosystem. In this case, the model predictions were used to determine to what extent the environmental variables together with the categorical factors of station and depth influenced the abundance of gelatinous zooplankton. It predicted changes in abundance given changes in density, fluorescence, station and depth. Given that premise, it was important to be able to determine which of the variables affected each species group. The model fitting function in the mvabund package is “manyglm”, which is based on fitting Generalized Linear Models (GLM) to all species groups separately. However, the package makes use of a resampling method, which takes into account the correlation between species when estimating the uncertainty of the parameters (Wang et al. 2012b). These factors together made the mvabund package more useful than ordination methods.

A key assumption in the mvabund models used (Zoo_1 and Zoo_2) was the distribution pattern of the response variable, i.e., the abundance of gelatinous zooplankton (Wang et al. 2012b). The negative binomial family is often chosen for data sets where zero values are common and there is large variability in the count (de Wolf 1989, Wang et al. 2012b). The assumption was tested on the model with best fit (

Equation 3.1 and Equation 3.2), and as no pattern was found in the residuals in either model (Figure 3.8 Figure 3.10), the assumption was validated. However, it is clear that the different

species groups (represented by different colors in the figures) had different residual values, and the distribution pattern may differ between groups.

When examining the predictive powers of the two models (Figure 3.9 and Figure 3.11), it seems that a standard logistic regression model, with presence-absence as the response variable, might have fitted better for ctenophores or appendicularians. These had either large presences or none at all (only 1 ctenophore in total at Steilene, for instance). An even better model might have been a zero-inflated negative binomial model. That is a combination of logistic and negative binomial regression, i.e., if a species group is present, (one part of the model) its abundance has a negative binomial distribution (another part of the model). According to that model, a zero count can be due to both true absence of the species and the sampling process. However, such a model is highly complex and requires far more data to discover the different effects on presence and abundance.

4.5.1 Different aspects of model evaluation

Two methods were chosen to evaluate which explanatory variables were important in the GLM-based models used (

Equation 3.1 and Equation 3.2). The first, AIC, was chosen to determine which of the given models was the best (Section 2.3.2). There are a few shortcomings with using AIC, one of which is that it only compares the models with each other, it does not analyze the *fit* of the best model to the data set (Akaike 1974). However, as most different combinations of factors (Appendix Table A.3) were tested in this study, it is reasonably safe to assume that the optimal model for the complete data was found by AIC. Another discussion would be if any variables or factors not included could improve the model, like the wet weight of zooplankton. However, a bigger dataset is needed to avoid saturating the model. The other shortcoming with AIC, as calculated in the mvabund package, is that is does not account for the dependence between the species groups in the study. This can indeed be a large drawback, as it is highly likely that there is some interdependence between the species groups (Section 1.1.3). Fortunately, the procedure for estimating parameter uncertainty accounts for this dependency, as does the Wald tests used to test the significances of individual coefficients. Thus, it is only when choosing between models that interdependencies are excluded, not when determining factor significance or predicting abundances.

5 Conclusions and future directions

The study answered some of the questions posed before it was started. It gave a reasonable preliminary mapping of the distribution of gelatinous zooplankton in Oslofjorden. The abundance of the one, well-studied species of Hydrozoa in Oslofjorden, *Aglantha digitale*, was discovered to have changed since the species was last investigated. The study also showed that the three stations representing the areas of the fjord likely have different contributions of the gelatinous groups and that these differences are a function of area and depth, density and fluorescence. This indicates that it is the different water masses in the fjord, caused by the stratification patterns, that is the largest cause for the differences in abundances, not the individual environmental variables. However, the samples included in the models were too few and sampled over too short a time to be conclusive, and further studies are needed.

Many of the samples taken in this study were not analyzed due to time restraint (Appendix Table A.1). Zooplankton was sampled using both a Nansen net and a WP2 net for all of the 10 cruise dates in the study. These samples are stored at the University of Oslo and should be the first step in further investigations of gelatinous zooplankton in Oslofjorden. Organisms from both net types should be identified to the species level, and the *species* abundance used as a response variable in statistical analyses to avoid any detrimental effect of data pooling. As the two net types have different diameters of the net opening and different filtration efficiencies, they are likely to have caught different species of gelatinous zooplankton, giving a more thorough investigation. They were taken in the same area at the same time and although not strictly replicates, they *would* counter some of the effects of patchiness of the plankton discussed above. The next step would be to also identify all the non-gelatinous zooplankton species in all samples. This would provide more insight into the entire predator-prey community. During lab analysis, the first 20 of each gelatinous species were measured. These measurements could be added to the statistical models to increase the likelihood of discovering a seasonal effect. In addition, adding measurements of both gelatinous- and non-gelatinous zooplankton could possibly be used to see if there is any effect of size on predation impact. The measurements could also be used to convert the abundance of gelatinous zooplankton into biomass – for better comparison with biomass of non-gelatinous zooplankton. The last suggestion for further research is to sample gelatinous zooplankton for several more years of to understand the underlying pattern better. When conducting future

sampling, I would suggest mounting an underwater camera to the net to observe the vertical distribution of species *in situ* and any behavior to avoid the net. This camera footage would also be helpful in identifying and enumerating siphonophores, especially the physonect species.

After these above steps have been taken, I recommend using the model prediction tools in the mvabund package to investigate how a changing environment in Oslofjorden is likely to affect the gelatinous community. In this instance, the statistical analysis developed by Wang et al. seems a better tool than distance based ordination methods. Although season was not discovered by the analysis in this study, that is likely due to the study design and data pooling, and not the statistical method. There are few studies on how the environment in Oslofjorden will change with a changing climate, but there is continuous monitoring of the hydrographic conditions in the fjord by NIVA (Norwegian Institute of Water Research) and DNV (Det Norske Veritas) among others. This could then be used to predict the likely hydrographic changes. The data from this study could be used as a baseline for the gelatinous community, or pilot project, because it indicates which species groups are best predicted by the models. With a clearly larger data set, it would be interesting and more informative to fit zero-inflated negative binomial models to the data.

Internet resources

The Norwegian Coastal Administration online Map service:

http://kart.kystverket.no/default.aspx?gui=1&lang=2#

Climate data of Færder lighthouse from the Metrological Institute:
http://www.yr.no/sted/Norge/Vestfold/Tjøme/Færder_fyr_målestasjon/almanakk.html?dato=2011-04-11

Scientific names of identified taxa and species (accessed throughout the study):

http://www.marinespecies.org/

http://biology.duke.edu/hydrodb/biblio.html

Assorted literature from 18-1900 (accessed throughout the study):

http://www.biodiversitylibrary.org/Default.aspx

The Cnidaria Newsgroup (e-mail service in the gelatinous research community)

https://maillists.uci.edu/mailman/listinfo/cnidaria

References

Agassiz A, Mayer AG (1902) Reports on the scientific results of the expedition to the tropical Pacific. III. Medusae. Memoirs of the Museum of Comparative Zoology, Cambridge, USA

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723

Alldredge AL (1977) House morphology and mechanisms of feeding in the Oikopleuridae (Tunicata, Appendicularia). Journal of Zoology 181:175–188

AMAP (1998) AMAP Assesment report. Arctic Pollution Issues, Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway

Arai MN (1992) Active and passive factors affecting aggregations of hydromedusae: A review. Sci Mar 56:99–108

Arai MN (2001) Pelagic coelenterates and eutrophication: a review. Hydrobiologia 451:69–87

Arai MN (2005) Predation on pelagic coelenterates: a review. J Mar Biol Ass 85:523–536

Arai MN (2008) The potential importance of podocysts to the formation of scyphozoan blooms: a review. Hydrobiologia 616:241–246

Aure J, Danielssen D (2007) Ytre Oslofjord: Hydrografi og næringssalter over terskeldyp 1995-1998, 6th edn. Statlig program for forurensningsovervåking, Bergen

Baalsrud K, Magnusson J (2002a) Oslofjordens forurensningsproblem. In: Indre Oslofjord. Fagrådet for vann- og abløpsteknisk samarbeid i indre Oslofjord, p 55–94

Baalsrud K, Magnusson J (2002b) Innledning. In: Indre Oslofjord. Fagrådet for vann- og abløpsteknisk samarbeid i indre Oslofjord, p 7–14

Baalsrud K, Magnusson J (2002c) Oslofjordens naturforhold. In: Indre Oslofjord. Fagrådet for vann- og abløpsteknisk samarbeid i indre Oslofjord, p 15–48

Baalsrud K, Magnusson J (2002d) Indre Oslofjord. Fagrådet for vann- og abløpsteknisk samarbeid i indre Oslofjord

Baalsrud K, Magnusson J (2002e) Fjorden friskner til. In: Indre Oslofjord. Fagrådet for vann- og abløpsteknisk samarbeid i indre Oslofjord, p 113–126

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

Baxter E (2012) Gelatinous zooplankton in Irish waters:. University College Cork, Ireland, Cork

Baxter E, Rodger H, McAllen R, Doyle T (2011) Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. Aquacult Environ Interact 1:245–257

Baxter EJ, McAllen R, Allcock AL, Doyle TK (2012) Abundance, distribution and community composition of small gelatinous zooplankton in southern irish coastal waters. Biology & Environment: Proceedings of the Royal Irish Academy 112:1–13

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

Behrends G, Schneider G (1995) Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). Mar Ecol Prog Ser 127:39–45

Beyer F (1968) Zooplankton, zoobenthos, and bottom sediments as related to pollution and water exchange in the Oslofjord. Helgoland Marine Research 17:496–509

Boero F (2009) Recent innovations in marine biology. Marine Ecology 30:1–12

Boero F, Bouillon J, Gravili C, Miglietta M, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Bone Q (2005) Gelatinous animals and physiology. J Mar Biol Ass 85:641–653

Bouillon J, Medel M, Pages F, Gili J, Boero F, Gravili C (2004) Fauna of the Mediterranean Hydrozoa. Sci Mar 68:5–449

Brattegard T (1979) Why biologists are interested in fjords. In: Freeland HJ, Farmer DM, Levings CD (eds) Fjord oceanography. Plenum Press, New York, p 53–66

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690:3–20

Colin SP, Costello JH, Hansson LJ, Titelman J, Dabiri JO (2010) Stealth predation and the predatory success of the invasive ctenophore *Mnemiopsis leidyi*. Proceedings of the National Academy of Sciences 107:17223–17227

Condon RH, Graham WM, Duarte CM, Pitt KA, Lucas CH, Haddock SHD, Sutherland KR, Robinson KL, Dawson MN, Decker MB (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience 62:160–169

Cooney R, Coyle K, Stockmar E, Stark C (2001) Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. Fish Oceanogr 10:97–109

Costello JH, Colin SP (2002) Prey resource use by coexistent hydromedusae from Friday Harbor, Washington. Limnol Oceanogr:934–942

Currie RI, Foxton P (1956) The Nansen closing method with vertical plankton nets. J Mar Biol Ass 35:483–&

de Lafontaine Y, Leggett WC (1989) Changes in size and weight of hydromedusae during formalin preservation. B Mar Sci 44:1129–1137

de Wolf P (1989) The price of patchiness. In: p 263–273

Di Camillo CG, Betti F, Bo M, Martinelli M, Puce S, Bavestrello G (2010) Contribution to the understanding of seasonal cycle of Aurelia aurita (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. J Mar Biol Ass 90:1105–1110

Dragsund E, Aspholm O, Tangen K, Bakke SM, Heier L, Jensen T (2006) Overvåking av eutrofitilstanden i ytre Oslofjord. Det Norske Veritas

Dupont N, Klevjer TA, Kaartvedt S, Aksnes DL (2009) Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. Limnol Oceanogr 54:1765–1775

Falkenhaug T (1996) Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. Mar Ecol Prog Ser 140:59–70

Fraser JH (1968a) The history of plankton sampling. In: UNESCO (ed) Zooplankton sampling. Monographs on Oceanographic Methodology

Fraser JH (1968b) Part II Standardization of zooplankton sampling methods of the sea. In: Fraser JH (ed) Zooplankton sampling. United Nations Educational, p 147–174

Graham WM, Pages F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212

Greve W (1975) Ctenophora. Fiches d'identification du zooplancton 146

Haddock SHD (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. Hydrobiologia 530:549–556

Haeckel E (1888) Report on the Siphonophorae collected during the voyage of H.M.S. Challenger during 1873-76 (CW Thomson, Ed.). Her Majesty's Stationary Office

Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol Oceanogr 20:907–917

Hansson LJ (1997) Effect of temperature on growth rate of Aurelia aurita (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. Mar Ecol Prog Ser 161:145–153

Hansson LJ, Kiørboe T (2006) Prey-specific encounter rates and handling efficiencies as causes of prey selectivity in ambush-feeding hydromedusae. Limnol Oceanogr 51:1849–1858

Hansson LJ, Moeslund O, Kiørboe T, Riisgård HU (2005) Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Mar Ecol Prog Ser 304:117–131

Haraldsson M, Jaspers C, Tiselius P, Aksnes DL, Andersen T, Titelman J (2012) Environmental constraints of the invasive *Mnemiopsis leidyi* in Scandinavian waters. Limnol Oceanogr 58

Harbison GR, Madin LP, Swanberg NR (1978) On the natural history and distribution of oceanic ctenophores. Deep-Sea Res 25:233–256

Hernroth L (1987) Sampling and filtration efficiency of two commonly used plankton nets. A comparative study of the Nansen net and the Unesco WP 2 net. Journal of Plankton Research 9:719–728

Hosia A (2007) Gelatinous zooplankton in western Norwegian fjords. The University of Bergen

Hosia A, Båmstedt U (2007) Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. Mar Ecol Prog Ser 351:113–127

Hosia A, Båmstedt U (2008) Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. Journal of Plankton Research 30:951–962

Hosia A, Stemmann L, 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

Hosia A, Titelman J, Hansson L, Haraldsson M (2011) Interactions between native and alien ctenophores: Beroe gracilis and Mnemiopsis leidyi in Gullmarsfjorden. Mar Ecol Prog Ser 422:129–138

Hostyeva V (2011) Seasonal cycle of phytoplankton in outer Oslofjorden with emphasis on *Pseudo-nitzschia* species. The University of Oslo

Huxley TH (1859) The oceanic Hydrozoa; A description of the calycophorid and physophorid observed during the voyage of H.M.S. "Rattlesnake," in the years 1846-1850. The Ray Society, London

Ishii H (2003) Development time of planula larvae on the oral arms of the scyphomedusa Aurelia aurita. Journal of Plankton Research 25:1447–1450

Jaspers C, Titelman J, Johan Hansson L, Haraldsson M, Røllike Ditlefsen C (2011) The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. Limnol Oceanogr 56:431

Kehayias GEA (1996) The diets of the chaetognaths *Sagitta enflata*, *S. serratodentata atlantica* and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. ICES Journal of Marine Science 53:837–846

Kirkpatrick P, Pugh P (1984) Siphonophores and velellids: (DM Kermack and RSK Barnes, Eds.). Brill Academic Pub

Kramp PL (1959) The hydromedusae of the Atlantic Ocean and adjacent waters. The Carlsberg Foundation

Kramp PL (1961) Synopsis of the medusae of the world. J Mar Biol Ass 40:7–382

Larink O, Westheide W (2006) Coastal Plankton (KH Wiltshire and M Boersma, Eds.).

Verlag Dr. Friedrich Pfeil, München

Lenz J (2000) Introduction. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, Calif., p 1–33

Leuckart R (1853) Zoologische Untersuchungen: Die Siphonophoren. J. Rickersche Buchandlung, Giessen

Lindén A, Mäntyniemi S (2011) Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92:1414–1421

Lucas CH, Lawes S (1998) Sexual reproduction of the scyphomedusa Aurelia aurita in relation to temperature and variable food supply. Mar Biol 131:629–638

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: Role of polyps in forming and maintaining Scyphomedusa populations. Advances in Marine Biology

Lynam CP, Lilley MKS, Bastian T, Doyle TK, Beggs SE, Hays GC (2010) Have jellyfish in the Irish Sea benefited from climate change and overfishing? Global Change Biology 17:767–782

Mackie G, Pugh P, Purcell J (1987) Siphonophore biology. Advances in Marine Biology

Mapstone GM (2009) Siphonophora (Cnidaria, Hydrozoa) of Canadian Pacific Waters. Canadian Science Publishing (NRC Research Press)

Mills CE (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. Journal du Conseil 52:575–581

Nansen F (1915) Closing-nets for vertical hauls and for horizontal towing. Journal du Conseil 1:3–8

Oksanen J (2011) Multivariate Analysis of Ecological Communities in R: vegan tutorial. ccoulufi:1–43

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. Aquatic Invasions 2:185–189

Pages F, Gonzalez H, Gonzalez S (1996) Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by Aglantha digitale (Trachymedusae). Mar Ecol Prog Ser 139:69–77

Piraino S, De Vito D, Schmich J, Bouillon J, Boero F (2004) Reverse development in Cnidaria. Can J Zool 82:1748–1754

Postel L, Fock H, Hagen W (2000) Biomass and abundance. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, Calif., p 82–192

Prieto L, Astorga D, Navarro G, Ruiz J (2010) Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish (SJ Goldstien, Ed.). PLoS ONE

5:e13793

Pugh PR (1984) The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 7. Siphonophores. Progress In Oceanography 13:461–489

Purcell JE (1988) Quantification of Mnemiopsis leidyi(Ctenophora, Lobata) from formalin-preserved plankton samples. Mar Ecol Prog Ser 45:197–200

Purcell JE (1991) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216:335–342

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Marine Sci 4:209–235

Purcell JE, Hopcroft RR, Kosobokova KN, Whitledge TE (2010) Distribution, abundance, and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 57:127–135

Regula C, Colin S, Costello J, Kordula H (2009) Prey selection mechanism of ambush-foraging hydromedusae. Mar Ecol Prog Ser 374:135–144

Richardson AJ, Gibbons MJ (2008) Are jellyfish increasing in response to ocean acidification? Limnol Oceanogr 53:2040–2045

Russell F (1981) Trachymedusae, Family: Rhopalonematidae. Fiches d'identification du zooplancton

Russell FS (1953) The Medusae of the British Isles. Cambridge University Press

Sameoto D, Wiebe P, Runge J, Postel L, Dunn J, Miller C, Coombs S (2000) Collecting zooplankton. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, Calif., p 55–82

Sars M, Koren J, Danielssen DC (1856) Fauna littoralis Norvegiae; oder, Beschreibung und abbildungen neuer oder wenig bekannten seethiere, nebst beobachtungen über die organisation, lebensweise u. entwickelung derselben.

Shiganova T (2005) Changes in appendicularian Oikopleura dioica abundance caused by invasion of alien ctenophores in the Black Sea. J Mar Biol Ass 85:477–494

Skjoldal HR, Wiebe PH, Foote KG (2000) Sampling and experimental design. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, Calif., p 33–55

Smedstad O (1972) On the biology of Aglantha digitale rosea (Forbes)(Coelenterata: Trachymedusae) in the inner Oslofjord. Norwegian Journal of Zoology 20:111–135

Sornes TA, Aksnes DL, Båmstedt U, Youngbluth MJ (2007) Causes for mass occurrences of the jellyfish *Periphylla periphylla*: a hypothesis that involves optically conditioned retention. Journal of Plankton Research 29:157–167

Sullivan LJ, Gifford DJ (2009) Preservation of the larval ctenophore Mnemiopsis leidyi A.

Agassiz (Ctenophora, Lobata). Journal of Plankton Research 31:921–926

Titelman J, Hansson LJ (2005) Feeding rates of the jellyfish Aurelia aurita on fish larvae. Mar Biol 149:297–306

Todd CD, Laverack MS, Boxshall GA (1996) Coastal Marine Zooplankton. Cambridge University Press

Totton A, Fraser J (1955a) Siphonophora. Sub-Order: Physonectae, Families various. Fiches d'identification du zooplancton 62

Totton AK, Bargmann HE (1965) A synopsis of the Siphonophora. Natural History, British Museum

Totton AK, Fraser JH (1955b) Siphonophora. Sub-order: Calycophorae. Family: Diphyidae. Genera: Dimophyes, Muggiaea, Sulculeolaria, Chelophyes, Eudoxoides.

Totton AK, Fraser JH (1955c) Siphonophora. Sub-order: Calycophorae. Family: Diphyidae. Genus: Lensia.

Wang Y, Naumann U, Wright ST, Warton DI (2012a) Package "mvabund."

Wang Y, Naumann U, Wright ST, Warton DI (2012b) mvabund–an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution

Wiebe P (2003) From the Hensen net toward four-dimensional biological oceanography. Progress In Oceanography 56:7–136

Williams R, 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

Øresland V (1987) Feeding of the chaetognaths Sagitta elegans and S. setosa at different seasons in Gullmarsfjorden, Sweden. Mar Ecol Prog Ser 39:69–79

Appendix

Table A.1 Summary of all sampling performed. X indicates which type of sample has been collected for that date, and at which depths they were collected. The CTD sampled conductivity, temperature and depth together with fluorescence. Chl *a* was filtered from water samples and Light measured for the top 20 meters of water.

Date	Station	Depth (m)	Nansen net	Gelatinous id	Wet Weight	CTD	Chl *a*	Light
13.01.11	OF2	350-0 *	x			x	x	x
14.01.11	IM2	190-105	x			x		
14.01.11	IM2	105-52	x			x		
14.01.11	IM2	52-0	x			x	x	x
14.01.11	DK1d	110-52	x			x		
14.01.11	DK1d	52-0	x			x	x	
15.02.11	OF2	350-103	x			x		
15.02.11	OF2	103-50	x			x		
15.02.11	OF2	50-0	x			x	x	x
16.02.11	IM2	198-104	x			x		
16.02.11	IM2	104-51	x			x		
16.02.11	IM2	51-0	x			x	x	x
17.02.11	DK1d	110-51	x			x		
17.02.11	DK1d	51-0	x			x	x	x
14.03.11	OF2	350-98	x			x		
14.03.11	OF2	98-48	x			x		
14.03.11	OF2	48-0	x			x	x	x
15.03.11	IM2	195-98	x			x		
15.03.11	IM2	98-48	x			x		
15.03.11	IM2	48-0	x			x	x	x
11.04.11	DK1d	130-51	x	x	x	x		
11.04.11	DK1d	51-0	x	x	x	x	x	
11.04.11	IM2	200-104	x	x	x	x		
11.04.11	IM2	104-52	x	x	x	x		
11.04.11	IM2	52-0	x	x	x	x	x	x
11.04.11	OF2	350-104	x	x	x	x		
11.04.11	OF2	104-52	x	x	x	x		
11.04.11	OF2	52-0	x	x	x	x	x	x
19.05.11	DK1d	125-52	x			x		
19.05.11	DK1d	52-0	x			x	x	**
19.05.11	IM2	195-104	x			x		
19.05.11	IM2	104-52	x			x		
19.05.11	IM2	52-0	x			x	x	*
20.05.11	OF2	350-105	x			x		
20.05.11	OF2	104-52	x			x		
20.05.11	OF2	52-0	x			x	x	x
06.06.11	DK1d	125-52	x	x	x	x		
06.06.11	DK1d	52-0	x	x	x	x	x	x
06.06.11	IM2	195-104	x	x	x	x		

Date	Station	Depth (m)	Nansen net	Gelatinous id	Wet Weight	CTD	Chl *a*	Light
06.06.11	IM2	104-52	x	x	x	x		
06.06.11	IM2	52-0	x	x	x	x	x	
07.06.11	OF2	345-105	x	x	x	x		
07.06.11	OF2	105-52	x	x	x	x		
07.06.11	OF2	52-0	x	x	x	x	x	x
30.08.11	DK1d	125-51	x			x		
30.08.11	DK1d	51-0	x			x	x	
30.08.11	IM2	195-104	x			x		
30.08.11	IM2	104-52	x			x		
30.08.11	IM2	52-0	x			x	x	x
31.08.11	OF2	350-105	x			x		
31.08.11	OF2	105-52	x			x		
31.08.11	OF2	52-0	x			x	x	x
20.09.11	OF2	345-106	x	x	x	x		
20.09.11	OF2	106-52	x	x	x	x		
20.09.11	OF2	52-0	x	x	x	x	x	x
21.09.11	IM2	196-105	x	x	x	x		
21.09.11	IM2	105-53	x	x	x	x		
21.09.11	IM2	53-0	x	x	x	x	x	
21.09.11	DK1d	125-55	x	x	x	x		
21.09.11	DK1d	55-0	x	x	x	x	x	x
18.10.11	DK1d	125-53	x			x		
18.10.11	DK1d	53-0	x			x	x	x
18.10.11	IM2	195-104	x			x		
18.10.11	IM2	104-50	x			x		
18.10.11	IM2	50-0	x			x	x	
19.10.11	OF2	345-105	x			x		
19.10.11	OF2	105-51	x			x		
19.10.11	OF2	51-0	x			x	x	x
15.11.11	OF2	350-0	x			x		x
20.12.11	OF2	350-0	x			x		x
10.01.12	DK1d	125-51	x	x	x	x		
10.01.12	DK1d	51-0	x	x	x	x		
10.01.12	IM2	195-100	x	x	x	x		
10.01.12	IM2	100-52	x	x	x	x		
10.01.12	IM2	52-0	x	x	x	x	x	x
11.01.12	OF2	350-0	***			x	x	x
16.01.12	OF2	345-100	x	x	x			
16.01.12	OF2	100-53	x	x	x			
16.01.12	OF2	53-0	x	x	x			

* 13.01.11 not stratified due to equipment malfunction

** 19.05.11 light not measured

*** 11.01.2012 Nansen net not working - those samples taken on the 16th.

Table A.2 Average PSU of the top 25 meters for every month of CTD sampling. A clear shift is visible in May (in italic), when the surface salinity at Missingene (OF2) becomes more saline than that of Elle (IM2) and Steilene (DK1d). There is no value for March at Steilene due to ice that made sampling impossible.

	OF2	IM2	DK1d
Jan	29.92	30.12	32.36
Feb	31.64	32.70	30.19
March	27.73	29.88	-
April	20.52	29.22	20.21
May	*25.98*	*22.83*	*24.76*
June	27.86	27.79	25.07
Aug	25.55	21.91	25.50
Sept	27.81	24.96	24.29
Oct	29.88	25.65	26.61
Jan	31.05	25.98	24.42

Table A.3 Akaike Information Criterion for the multinomial models of Zoo_1, i.e., three depth layers at Missingene and Elle. Notations: a = station, d = depth, m = month, s = density, F = fluorescence.

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_1 ~ a	1134.1	143.7	6.36 E-32	0.000
Zoo_1 ~ d	1084.3	93.9	4.10 E-21	0.000
Zoo_1 ~ m	1133.4	143.0	9.03 E-32	0.000
Zoo_1 ~ s	1171.8	181.3	4.27 E-40	0.000
Zoo_1 ~ F	1246.9	256.5	2.05 E-56	0.000
Zoo_1 ~ ad	1034.5	44.0	2.74 E-10	0.000
Zoo_1 ~ am	1103.0	112.5	3.72 E-25	0.000
Zoo_1 ~ dm	1055.1	64.7	8.96 E-15	0.000
Zoo_1 ~ as	1068.4	78.0	1.16 E-17	0.000
Zoo_1 ~ ds	1060.8	70.3	5.36 E-16	0.000
Zoo_1 ~ ms	1102.6	112.1	4.53 E-25	0.000
Zoo_1 ~ aF	1102.2	111.7	5.46 E-25	0.000
Zoo_1 ~ mF	1114.5	124.1	1.14 E-27	0.000
Zoo_1 ~ dF	1088.8	98.4	4.35 E-22	0.000
Zoo_1 ~ sF	1162.0	171.5	5.72 E-38	0.000
Zoo_1 ~ adm	1026.8	36.4	1.26 E-08	0.000
Zoo_1 ~ ads	990.5	0.0	1.00 E+00	0.966
Zoo_1 ~ adF	1028.4	38.0	5.66 E-09	0.000
Zoo_1 ~ ams	1059.3	68.8	1.13 E-15	0.000
Zoo_1 ~ amF	1053.0	62.6	2.56 E-14	0.000
Zoo_1 ~ asF	1066.1	75.7	3.71 E-17	0.000
Zoo_1 ~ dms	1081.1	90.6	2.12 E-20	0.000
Zoo_1 ~ dmF	1064.3	73.8	9.30 E-17	0.000
Zoo_1 ~ dsF	1060.4	69.9	6.51 E-16	0.000
Zoo_1 ~ msF	1128.0	137.6	1.34 E-30	0.000
Zoo_1 ~ adms	1003.5	13.0	1.50 E-03	0.001
Zoo_1 ~ admF	997.2	6.8	3.38 E-02	0.033
Zoo_1 ~ adsF	1010.3	19.9	4.82 E-05	0.000

Zoo_1 ~ amsF	1059.4	68.9	1.09 E-15	0.000
Zoo_1 ~ admsF	1008.8	18.3	1.06 E-04	0.000

Table A.4 Akaike Information Criterion for the multinomial models of Zoo_2, i.e., two depth layers at Missingene, Elle, and Steilene. Notations: a = station, d = depth, m = month, s = density, F = fluorescence.

Model	AIC	ΔAIC	$e^{-0.5*\Delta AIC}$	Akaike weight
Zoo_2 ~ a	1075.9833	175.0	1.02 E-38	0.000
Zoo_2 ~ ad	1025.7855	124.8	8.13 E-28	0.000
Zoo_2 ~ adF	1039.3986	138.4	9.00 E-31	0.000
Zoo_2 ~ adm	976.0532	75.0	5.12 E-17	0.000
Zoo_2 ~ admF	1015.0327	114.0	1.76 E-25	0.000
Zoo_2 ~ adms	965.8853	64.9	8.27 E-15	0.000
Zoo_2 ~ admsF	969.63	68.6	1.27 E-15	0.000
Zoo_2 ~ ads	1017.492	116.5	5.14 E-26	0.000
Zoo_2 ~ adsF	901.0321	0.0	1.00 E+00	1.000
Zoo_2 ~ aF	1007.1874	106.2	8.89 E-24	0.000
Zoo_2 ~ am	984.4031	83.4	7.87 E-19	0.000
Zoo_2 ~ amF	980.457	79.4	5.66 E-18	0.000
Zoo_2 ~ ams	944.2102	43.2	4.21 E-10	0.000
Zoo_2 ~ amsF	945.9338	44.9	1.78 E-10	0.000
Zoo_2 ~ as	1046.1446	145.1	3.08 E-32	0.000
Zoo_2 ~ asF	1011.6461	110.6	9.56 E-25	0.000
Zoo_2 ~ d	1088.6135	187.6	1.85 E-41	0.000
Zoo_2 ~ dF	1054.4835	153.5	4.77 E-34	0.000
Zoo_2 ~ dm	975.0575	74.0	8.43 E-17	0.000
Zoo_2 ~ dmF	979.0887	78.1	1.12 E-17	0.000
Zoo_2 ~ dms	987.5968	86.6	1.59 E-19	0.000
Zoo_2 ~ ds	1064.7149	163.7	2.86 E-36	0.000
Zoo_2 ~ dsF	1084.7807	183.7	1.26 E-40	0.000
Zoo_2 ~ F	1160.0039	259.0	5.82 E-57	0.000
Zoo_2 ~ m	997.5533	96.5	1.10 E-21	0.000
Zoo_2 ~ mF	978.3899	77.4	1.59 E-17	0.000
Zoo_2 ~ ms	1004.649	103.6	3.16 E-23	0.000
Zoo_2 ~ msF	1009.4989	108.5	2.80 E-24	0.000
Zoo_2 ~ s	1141.3437	240.3	6.56 E-53	0.000
Zoo_2 ~ sF	1136.895	235.9	6.07 E-52	0.000

Table A. 5 Abundances of organisms included in the thesis. The abundances are individuals pr. 50m3 at stations Steilene (DK1d), Elle (IM2), and Missingene (OF2) for each season and depth.

TAXA	DEPTH	STATIONS											
		DK1d				IM2				OF2			
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Aglantha digitale													
	> 100	N/A	N/A	N/A	N/A	1.18	0.00	0.00	0.00	0.92	0.94	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	11.10	2.10	0.00
	50-0	0.00	0.00	2.06	2.22	63.12	4.35	0.00	0.00	383.06	6.53	0.00	0.00
Anthomedusa sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.46	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	6.17	0.00	0.00	0.00	2.14	0.00	0.00	0.00	0.00	0.00
Appendicularia													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	4.97	16.68	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	98.63	3.06	15.24	0.00	22.64	4.72	39.18	0.00	0.00	0.00
	50-0	0.00	0.00	1697.65	130.93	0.00	0.00	3647.28	26.12	19.59	4.35	0.00	2.14
Ascidacea sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	4.53	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Beroe cucumis													
	> 100	N/A	N/A	N/A	N/A	34.19	13.68	3.73	0.00	7.82	1.41	1.89	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00	0.00
Bolinopsis infendibulum													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calycophore siphonophore													
	> 100	N/A	N/A	N/A	N/A	0.00	2.49	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.36	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cf Beroe													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TAXA	DEPTH	STATIONS											
		DK1d				IM2				OF2			
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Cf Eirene sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00
Chaetognatha sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	63.43	0.00	28.06	2.83	3.79	0.00
	100-50	11.46	0.00	16.17	0.00	4.35	4.35	113.18	0.00	30.47	0.00	48.20	16.86
	50-0	2.22	0.00	0.00	0.00	0.00	0.00	106.77	0.00	19.59	8.71	0.00	17.08
Clione limacina													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.46
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	2.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clytia hemisphaerica													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.39
	100-50	0.00	0.00	0.00	0.00	6.53	0.00	0.00	0.00	0.00	0.00	0.00	2.41
	50-0	6.66	0.00	0.00	0.00	0.00	0.00	2.14	0.00	0.00	0.00	0.00	2.14
Ctenophore sp.													
	> 100	N/A	N/A	N/A	N/A	2.36	2.49	4.97	3.57	0.00	1.89	1.89	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	2.18	0.00	2.36	0.00	0.00	0.00	0.00
	50-0	2.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cyanea capillata													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dimophyes arctica													
	> 100	N/A	N/A	N/A	N/A	8.25	19.90	13.68	4.77	16.10	2.36	6.16	8.78
	100-50	0.00	0.00	0.00	0.00	13.06	0.00	2.26	9.43	8.71	0.00	2.10	2.41
	50-0	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	2.18	0.00
Diphyidae sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	1.84	0.00	0.00	0.46
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	2.26	0.00	0.00	0.00	0.00	0.00
	50-0	2.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eirene viridula													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TAXA	DEPTH	STATIONS											
		DK1d				**IM2**				**OF2**			
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eukrohnia hamata													
	> 100	N/A	N/A	N/A	N/A	84.88	97.01	21.14	25.02	72.23	51.40	103.71	61.90
	100-50	4.30	0.00	0.00	1.53	15.24	6.53	0.00	9.43	10.88	24.41	18.86	50.57
	50-0	0.00	0.00	0.00	0.00	0.00	2.18	0.00	6.53	4.35	2.18	6.53	0.00
Euphysa aurata													
	> 100	N/A	N/A	N/A	N/A	1.18	0.00	0.00	0.00	1.38	0.00	0.00	0.00
	100-50	0.00	0.00	1.62	0.00	8.71	6.53	2.26	2.36	0.00	4.44	0.00	2.41
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	2.14	0.00	0.00	2.18	0.00	0.00
Homoeonema platygon													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	1.19	0.00	0.00	0.00	2.77
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	2.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydromedusa sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	4.53	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	6.17	2.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lensia cf subtilis													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lensia conoidea													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.46
	100-50	25.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	42.16	2.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lensia fowleri													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lensia sp.													
	> 100	N/A	N/A	N/A	N/A	9.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	1.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leukartiara octona													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TAXA	DEPTH	STATIONS											
		DK1d				IM2				OF2			
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	2.14	0.00	0.00	0.00	0.00	0.00
Limacina retroversa													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	4.53	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lizzia blondina													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	1.24	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	1.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	133.75	0.00	0.00	0.00	241.30	0.00	0.00	2.18	0.00	0.00
Margelopsis hartlaubi													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	22.64	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.79	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cyddipid sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.47	0.95	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mitrocomella polydiademata													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	2.18	0.00	0.00	0.00	0.00	4.44	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nanomia cara													
	> 100	N/A	N/A	N/A	N/A	0.00	1.24	1.24	8.34	0.00	1.89	1.89	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00
Obelia sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	3.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	2.06	0.00	4.35	15.24	14.95	0.00	39.18	2.18	0.00	0.00
Pandeidae sp.													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.19	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Physonect siphonophore													

TAXA	DEPTH	STATIONS											
		DK1d				**IM2**				**OF2**			
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	1.19	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	2.26	4.72	2.18	2.22	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	0.00
Rathkea octopunctata													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	20.58	4.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sagitta sp.													
	> 100	N/A	N/A	N/A	N/A	1.18	0.00	13.68	47.65	1.38	0.47	22.26	23.10
	100-50	10.03	0.00	17.78	16.82	13.06	6.53	13.58	33.01	6.53	22.19	266.18	65.02
	50-0	0.00	4.35	117.29	2.22	0.00	4.35	676.93	37.00	182.82	21.76	32.65	172.97
Sarsia gemmifera													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	2.06	0.00	0.00	0.00	4.27	0.00	0.00	0.00	0.00	0.00
Tiaropsis multicirrata													
	> 100	N/A	N/A	N/A	N/A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	100-50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	50-0	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	10.88	0.00	0.00	0.00
Tomopteris helgolandica													
	> 100	N/A	N/A	N/A	N/A	2.36	0.00	1.24	4.77	2.30	1.41	0.95	1.39
	100-50	2.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18	2.22	2.10	2.41
	50-0	0.00	0.00	0.00	0.00	0.00	0.00	2.14	0.00	0.00	2.18	2.18	0.00