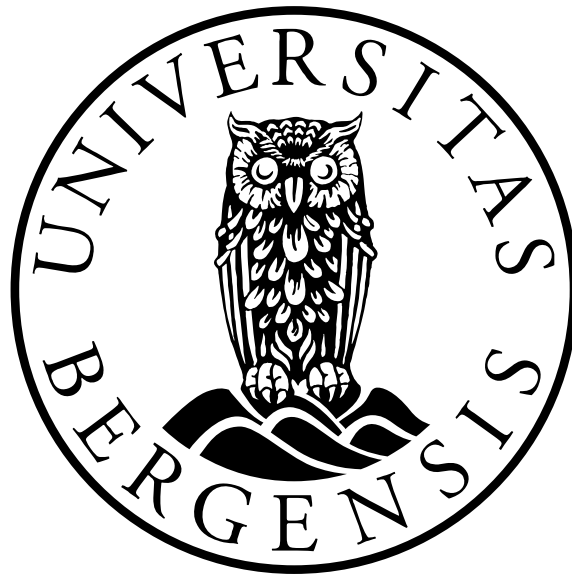


# **Gelatinous zooplankton in western Norwegian fjords**

*Ecology, systematics and comparisons with adjacent waters*

**Aino Hosia**



Dissertation for the degree philosophiae doctor (PhD)

University of Bergen

May 2007



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## Scientific environment

This thesis forms part of the project *Gelatinous zooplankton in fjords and coastal waters of Norway*, financed by The Research Council of Norway (project no. 146994/S40). Further funding for the thesis has been granted by The Finnish Cultural Foundation. The work has been conducted at the Department of Biology, University of Bergen, under the supervision of Professor Christoffer Schander and Professor Ulf Båmstedt (Department of Ecology and Environmental Sciences, Umeå University).

The candidate has also been involved in the Census of Marine Life project Mar-Eco. Results from the collaboration are presented in paper V.

During doctoral studies the candidate has visited Dr. Marsh Youngbluth at the Harbor Branch Oceanographic Institution, Florida, and Dr. Francesc Pagès at the Institut de Ciències del Mar, Barcelona, Spain.



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The input of all of my co-authors is greatly appreciated. It has been a privilege to work with Francesc Pagès, a jelly taxonomist *par excellence*. Marsh Youngbluth has had a significant impact on my view of the gelatinous denizens of the oceans, not least of all through offering me the chance of a lifetime to dive into the deep to see them first hand. I have thoroughly enjoyed my stays with Marsh in Florida and Francesc in Barcelona. Working together with Tom Sørnes has been a welcome change to my normally rather solitary toiling in Bergen. All three have also endured weeks at sea with me. They and other colleagues on board have made cruises not only productive but also socially rewarding.

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Friends and family have provided a welcome escape from work. They have been forever supportive and never expressed doubt, although it must have occasionally crept into their minds - especially so when I started expecting Iida. Fortunately, Iida has proven to be a positive force for my work. She has put things into perspective and made writing a thesis seem a less daunting task. I am looking forward to spending more time with her once this thesis is out of my hands!

Finally, I want to thank my husband Heikki for his love and commitment. His moral support and practical help have been invaluable. I could not have done this without you.

Bergen, February 2007

A handwritten signature in black ink, appearing to read 'Aino Hosia', with a long horizontal flourish extending to the right.

Aino Hosia

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## Summary

Gelatinous zooplankters, also known as jellies, are ubiquitous in the marine pelagic. Medusae, siphonophores and ctenophores are voracious predators that can, when abundant, have significant structuring effects on the pelagic community. Many jellies exhibit opportunistic life history characteristics such as short generation times, asexual reproduction or hermaphroditism, high fecundity, rapid growth, and ability to exploit high food concentrations effectively. While siphonophores and ctenophores are generally holoplanktonic, most scypho- and hydromedusae are meroplanktonic with a benthic polypoid stage. These characteristics contribute to the naturally pulsed occurrence of jellies in the plankton. In order to assess the role of jellies in the fjord ecosystems, information on the identity, seasonal abundance, distribution and behaviour of the species constituting the gelatinous community is necessary. This thesis attempts to fill in several gaps in knowledge regarding the systematics and ecology of gelatinous zooplankton in western Norwegian fjords. In order to do so, both net based sampling and remotely operated vehicles (ROVs) have been utilized.

Seasonal changes in the gelatinous community as a whole as well as the abundances of the individual species in Korsfjord and Fanafjord, western Norway, were examined. The gelatinous communities showed a clear seasonal succession, with maximum diversity and abundance occurring in April-June. *Aglantha digitale* was numerically dominant in both fjords. Meroplanktonic hydromedusa species appeared sequentially and were most common during the summer months. During the winter, the siphonophores *Nanomia cara*, *Lensia conoidea* and *Dimophyes arctica* formed the bulk of the community especially in Korsfjord. While the two fjords had rather similar faunas, they differed in terms of the relative importance of the observed groups. Siphonophores were prominent in the more oceanic Korsfjord, while Fanafjord was characterized by meroplanktonic hydromedusae. A community of deep-water hydromedusae was found at the deeper stations at Korsfjord. Two new

species presumed to be members of this deep-water community, *Foersteria quadrata* and *Parateclaia norvegica*, are described in this thesis.

The vertical distribution of animals in a fjord has relevance in terms of degree of overlap with prey and predator distributions as well as the likelihood of being advected from the fjord. Exchange of fjord water is most pronounced in the layers occurring above sill depth, while the sill promotes the retention of basin water. The holoplanktonic *Aglantha digitale* and *Nanomia cara* both seem to facilitate their retention in the fjords by residing below sill depth when mature. Younger stages of both species are known to have a shallower distribution, and may thus be more susceptible to advective transport.

Comparison with results from the northern portions of the Mid-Atlantic Ridge (MAR) show that the same species of planktonic cnidarians (*A. digitale*, *N. cara*, *L. conoidea* and *D. arctica*) dominated the epipelagic both in Korsfjord and the corresponding latitudes at the MAR. However, the mesopelagic siphonophores and medusae common at the MAR (e.g. *Chuniphyes multidentata*, *Gilia reticulata*, *Pantachogon haeckeli* and *Aeginura grimaldii*) seem to have been unable to colonize the fjords.

The notable exception to the above rule is *Periphylla periphylla*, a coronate mid-water scyphomedusa with abundant populations in certain west Norwegian fjords. Large *P. periphylla* in Lurefjord were shown to feed primarily on *Calanus* spp., but also on krill and ostracods. They behaved as ramming predators, approaching their prey tentacles first in order to minimize fluid disturbance, and were found to have clearance rates comparable with other gelatinous predators of similar size. The horizontal and vertical distributions of siphonophores were found to be negatively correlated with *P. periphylla* distribution.

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## List of papers

### **I Aino Hosia and Ulf Båmstedt**

Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway

*Submitted manuscript*

### **II Aino Hosia and Ulf Båmstedt**

Seasonal abundance and vertical distribution of siphonophores in Norwegian fjords

*Manuscript*

### **III Aino Hosia and Francesc Pagès**

Unexpected new species of deep-water Hydroidomedusae from Korsfjorden, Norway

*in press, Marine Biology* online first DOI: 10.1007/s00227-006-0466-2

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### **IV Tom A. Sørnes, Aino Hosia, Ulf Båmstedt and Dag L. Aksnes**

Swimming and feeding in the stealth predator *Periphylla periphylla* (Scyphozoa, Coronatae)

*Manuscript conditionally accepted in Marine Biology*

### **V Aino Hosia, Lars Stemmann and Marsh Youngbluth**

Distribution of net-collected planktonic cnidarians at the northern Mid-Atlantic Ridge and their associations with the main water masses

*Manuscript accepted in Deep-Sea Research II*

The papers are referred to by their roman numerals in the text.



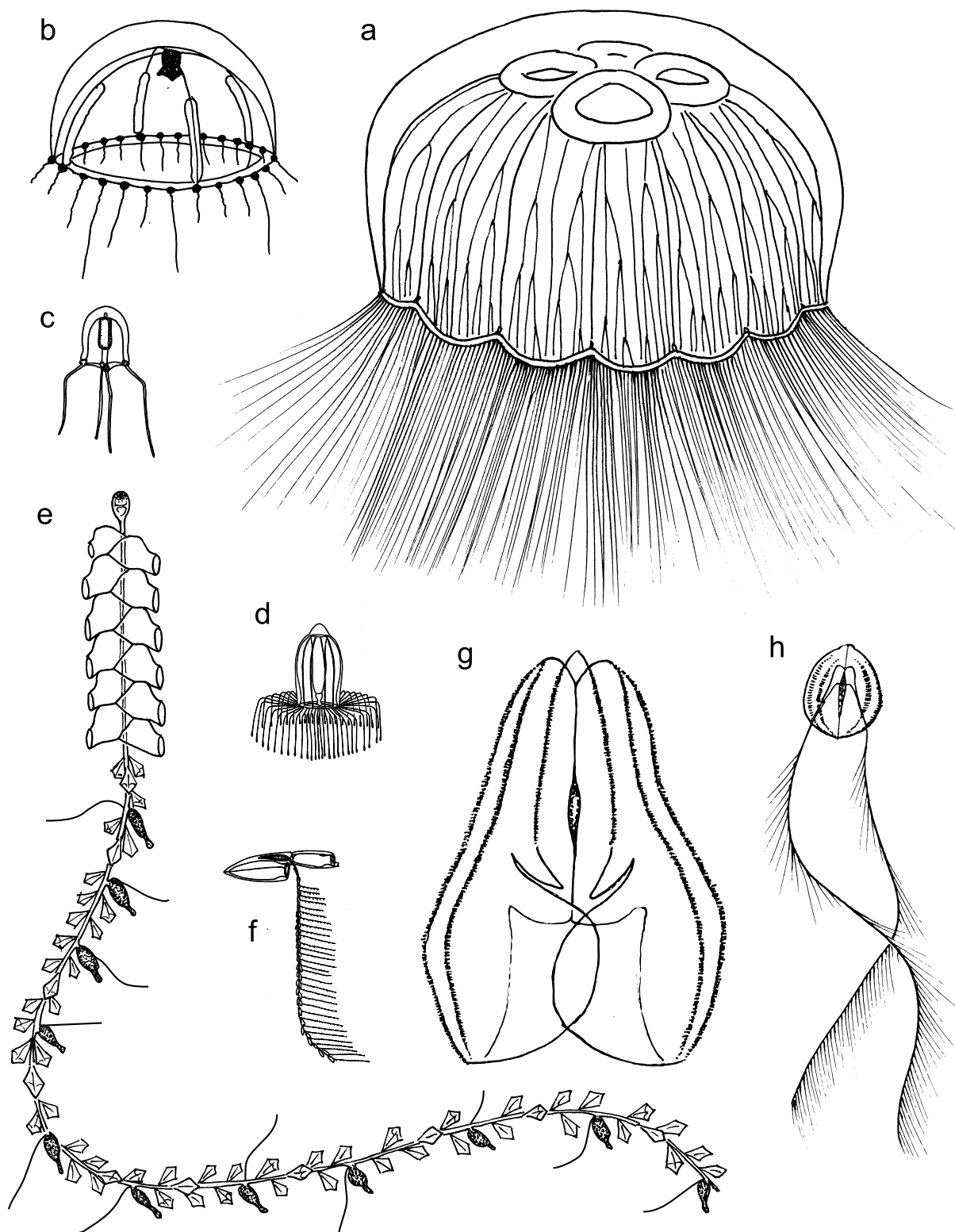
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## 1. Introduction

Gelatinous zooplankton, also known as jellies, is a taxonomically diverse group of organisms whose soft bodies consist of at least 95% water. They are often (but not always) transparent, and close to neutrally buoyant. Many jellies are macroplanktonic, i.e. >2 cm. The high water content facilitates growth with a minimal investment in organic matter, and large size increases predation efficiency through higher encounter rates with prey (Harbison 1992, Acuña 2001) as well as protects from predation by smaller species (Nival & Gorsky 2001). Gelatinous zooplankton encompasses, but is not limited to, cnidarians, ctenophores, heteropods, pteropods, salps, doliolids, appendicularians, as well as several types of meroplanktonic larvae. The organisms dealt with in this study are the planktonic members of the group that for historical reasons is jointly referred to as coelenterates: the phyla Cnidaria and Ctenophora (Fig. 1).

Cnidarians and ctenophores are among the major planktonic predators of the pelagic. They prey on other zooplankton as well as on fish eggs and larvae, and can have a structuring effect on the pelagic community through direct predation as well as by competition for food (Alldredge 1984, Purcell 1985, Matsakis & Conover 1991, Behrends & Schneider 1995, Purcell 1997, Nicholas & Frid 1999). Abundant gelatinous predators have also been implicated in phytoplankton blooms through trophic cascading (Lindahl & Hernroth 1983, Verity & Smetacek 1996, Schneider & Behrends 1998). Furthermore, the release of nutrients and dissolved organic carbon (DOC) by jellyfish may stimulate bacterial production (Hansson & Norrman 1995, Riemann *et al.* 2006, Titelman *et al.* 2006).

Many jellies are able to quickly react to changes in resource availability. Short generation times, high fecundity, and rapid growth typical of many gelatinous zooplankters allow fast population growth under favourable conditions (Alldredge 1984, Graham *et al.* 2001). Gelatinous planktivores are also able to maintain feeding rates proportional to food concentration over a wide range, allowing them to



**Fig. 1.** Common groups of ctenophores and cnidarians occurring in Norwegian fjords: a) scyphomedusa, b) leptomedusa, c) anthomedusa, d) trachymedusa, e) physonect siphonophore, f) diphyid siphonophore (polygastric stage), g) lobate ctenophore, h) cydippid ctenophore. Note that figures are not drawn to scale.

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efficiently exploit high prey densities (e.g. Alldredge 1984, Båmstedt 1990, Båmstedt 1998, Sørnes & Aksnes 2004). These life history characteristics may at times result in a competitive edge in resource utilization with respect to other, slower growing consumers of zooplankton, e.g. many crustaceans and fish (Alldredge 1984), and contribute to the naturally pulsed occurrence of many species of gelatinous predators in the plankton as well as the extraordinary blooms of jellies frequently observed (Arai 1992, Boero *et al.* 2001, Boero 2002).

Gelatinous zooplankton has often been considered a cul-de-sac of pelagic food webs, channelling energy away from the economically important fish (Verity & Smetacek 1996). One hypothesis proposes that two major pathways exist in the marine pelagic food web: a low energy pathway characterized by small zooplankton feeding on small phytoplankton and terminating in gelatinous planktivores, and a high energy pathway moving from large phytoplankton, through large zooplankton, to fish (Greve & Parsons 1977, Parsons and Lalli 2002, criticized by Longhurst 1995, Mills 1995). However, the view of jellies as trophic dead-ends may not be entirely justified. While the watery composition of gelatinous animals has been thought to render them unattractive to predators (Verity & Smetacek 1996, Robison 2004), jellies may in fact be more nutritious than their reputation, with the high water content compensated for by higher rates of digestion and assimilation by their predators (Arai 2005). Due to rapid digestion and deterioration during fixation processes, the extent of gelatinous content in fish stomachs may have been consistently underestimated (Arai 2005). A number of fish and other animals are known consumers of gelatinous zooplankton (e.g. Davenport 1998, Purcell & Arai 2001, Arai 2005).

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“Working with net-caught specimens is akin to trying to construct a snowball after it has hit a wall.”

Peter Herring, 2002

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The feature unifying the several taxa encompassed by the term ‘gelatinous zooplankton’ is their jelly-like consistency. Consequently, traditional plankton nets are generally poorly suited for collecting jellies. Unless special precautions are taken,

the animals caught in the net tend to disintegrate and pass through the mesh, fall to pieces, or be damaged beyond recognition (Hamner *et al.* 1975, Larson *et al.* 1991). The emphasis given to net based quantitative zooplankton studies in the 20<sup>th</sup> century has therefore been a major setback for research on gelatinous zooplankton, and has led to consistent underestimation of the abundance as well as diversity of gelatinous animals (Raskoff *et al.* 2003, Haddock 2004).

During recent decades, advances in undersea technology have made *in situ* work feasible. Blue-water scuba diving techniques developed in the 60's and 70's (Hamner 1975, Hamner *et al.* 1975) and the subsequent development of human occupied vehicles (HOVs), remotely operated vehicles (ROVs) and other optical methods such as under water video profilers (UVPs) for research purposes has presented scientists with an unprecedented opportunity to delve ever deeper to observe pelagic life first hand. The ability to observe the animals in their natural environment and to collect specimens in good condition has greatly improved our understanding of the ecology of gelatinous zooplankton in the midwater realm. One of the main findings has been that jellies are more diverse and account for a larger proportion of the mesopelagic biomass than previously assumed (Haddock 2004, Robison 2004). It has also become possible to observe the detailed vertical distribution (e.g. Mackie 1985, Larson *et al.* 1991, paper III), behaviour (e.g. Matsumoto & Harbison 1993, Raskoff 2002, paper IV) and species associations (e.g. Drazen & Robison 2004, Gasca & Haddock 2004, Raskoff & Robison 2005) of gelatinous zooplankters, impossible to deduct from net samples. The ability to capture and bring to surface relatively unharmed specimens has allowed scientists to conduct controlled experiments on jellies (e.g. Biggs 1977, Bailey *et al.* 1995). These new techniques have also resulted in a renaissance of descriptive taxonomic work, especially for the fragile siphonophores and ctenophores (Raskoff *et al.* 2003, Haddock 2004; e.g. Madin & Harbison 1978, Hissmann *et al.* 1995, Matsumoto *et al.* 2003, Dunn *et al.* 2005).



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## 2. Scope of the thesis

This thesis attempts to fill in several gaps in the knowledge regarding the systematics and ecology of gelatinous zooplankton in Norwegian fjords. In order to assess the role of jellies in the fjord ecosystems, information on the identity, seasonal abundance, distribution and behaviour of the species constituting the gelatinous community is necessary. A one-year study examining the species composition, seasonal abundance and succession of the gelatinous fauna in Korsfjord and Fanafjord, western Norway, was conducted in order to provide such necessary baseline information (Papers I and II). As a by-product of this study, two new species of hydromedusae, *Foersteria quadrata* and *Parateclaia norvegica*, were described from Korsfjord (Paper III). The vertical distribution of animals in a fjord has relevance in terms of degree of overlap with prey and predator distributions as well as the likelihood of being advected from the fjord. An ROV was used to study the vertical distributions of *Aglantha digitale* and physonect siphonophores in western Norwegian fjords (Papers I and II). The ROV was also utilized for an *in situ* study on the feeding ecology of *Periphylla periphylla*, a coronate midwater medusa extraordinarily abundant in certain western Norwegian fjords (Paper IV). Finally, a paper on the distribution of cnidarian fauna at the Mid-Atlantic Ridge (MAR) is presented for comparison with the western Norwegian fjord fauna (Paper V).

The rest of this synthesis will focus on gelatinous zooplankton residing in the fjords of western Norway and attempt to integrate results from the constituent papers in this context. I will first summarize some of the hydrological characteristics of west Norwegian fjords relevant to plankton populations residing in fjords (section 3.1), as well as give a short overview of prior research on gelatinous zooplankton in Norwegian fjords (section 3.2). In a section on the gelatinous fauna of fjords (3.3), the biogeographic influences shaping the west Norwegian fjord fauna are outlined (section 3.3.1). The differences in the species composition and abundance of gelatinous zooplankton between fjords and oceanic North Atlantic (section 3.3.2), as

well as the implications of the observed vertical distribution of some of the dominant gelatinous carnivores in the fjords (section 3.3.3) are discussed. There is also a short section on *Periphylla periphylla* (3.3.4). Finally, concluding remarks on anthropogenic influences on the gelatinous fauna and emerging further questions are made (section 4).

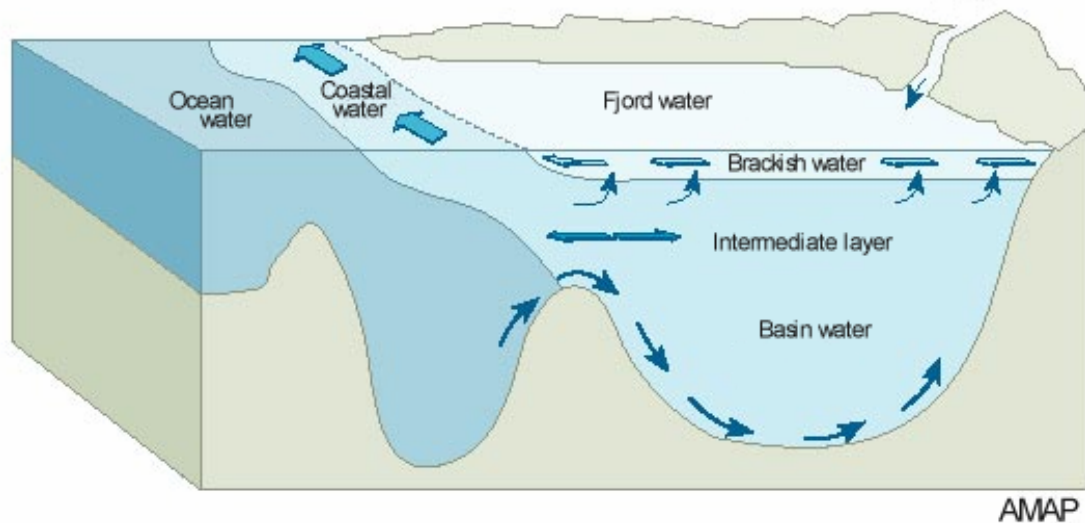
## **3. Gelatinous zooplankton in west Norwegian fjords**

### **3.1 Fjord hydrology**

As advective processes may be significant in transporting plankton in and out of fjords (Aksnes *et al.* 1989, Salvanes *et al.* 1995), it is useful to shortly review basic features of fjord circulation. Modifications to the simplified scheme presented below can occur due to local characteristics such as the topography of the fjord and prevailing winds and tides (Aksnes *et al.* 1989).

Fjords in western Norway are often long, narrow and much deeper than the continental shelf outside, from which they are separated by a sill of varying depth. The fjord waters can, from the surface down, be divided into several distinct layers: a few meters thick layer of brackish surface water, a layer of intermediate water below this and down to the sill level, and basin water found below sill level (Stigebrandt 2001, Tande 2001) (Fig. 2). The surface layer of fjords is characterized by an estuarine circulation, where fresh water runoff into the fjord drives net transport of brackish surface water out of the fjord. Entrainment of the more saline water underneath leads to increased salinity of the surface waters towards the mouth of the fjord and the formation of a compensation current moving in the opposite direction.

Water transport in the intermediate layer of fjords along the west coast of Norway is primarily wind driven. Southerly winds generate coastal downwelling and inflow of water in the upper intermediate layer, while northerly winds result in upwelling and



**Fig. 2.** Longitudinal section of an idealized fjord (modified from AMAP 1998)

the flushing of the upper intermediate waters out of the fjord, with compensatory counter currents forming below (Asplin *et al.* 1999, Tande 2001). The relative importance of water transport in the intermediate layer increases together with sill depth and is often dominant (Stigebrandt 2001).

The exchange of basin water in the fjords is limited by the presence of the sill. However, frequent renewal generally does take place as coastal upwelling due to north wind causes dense water to rise above the sill depth, often in late winter. Basin waters thus generally remain oxygenated (Tande 2001).

Advection can be an important factor regulating zooplankton abundances especially above sill depth. The amount of advected mesozooplankton may at times significantly exceed local production, especially in relatively open fjords (Aksnes *et al.* 1989, Salvanes *et al.* 1995). The deep fjord basins, in contrast, are rather conservative environments (Brattegard 1979) and may act as refuges for zooplankton populations local to the fjord (Aksnes *et al.* 1989, Gorsky *et al.* 2000, Sørnes *et al.* in press).

### ***BOX: Note on systematics and nomenclature***

The systematics of Hydrozoa are in a state of change and can appear somewhat confusing (Fautin 2002, Collins *et al.* 2006; the latter provide a comparison of suggested hypotheses regarding the phylogeny of medusozoan Cnidaria published since 1940). While there is an intuitive division into siphonophores and medusae, the latter of which are often referred to as hydromedusae or hydroidomedusae (Bouillon *et al.* 1992), such a dichotomy does not correctly reflect the current understanding of the phylogeny of these groups (Marques 2001). Instead, it has been suggested that Hydrozoa should be divided into two clades: clade Trachylina, consisting of the groups Limnomedusae, Trachymedusae and Narcomedusae (and possibly Actinulidae), and clade Hydroidolina, containing the groups Capitata and Filifera (previously jointly considered Anthomedusae), Hydridae, Leptomedusae, Laingiomedusae and Siphonophora (Collins 2000, 2002, Collins *et al.* 2006). Molecular phylogenetics have also challenged the traditional classification within Siphonophora (Dunn & Wagner 2005). Nevertheless, although not phylogenetically sound, Hydrozoa is in my thesis for practical reasons divided into the conceptual groups siphonophores and hydromedusae.

The systematic and nomenclatural situation is particularly difficult within the non-siphonophoran hydrozoans, many of which have a medusoid as well as a hydroid phase. Since most researchers have only concentrated on one of the two life stages, two parallel taxonomies exist (Bouillon *et al.* 1992). To further complicate the situation, the corresponding hydroids and medusae have in many cases not been matched.

While it is very exciting that new species of gelatinous zooplankton are frequently described, it also presents an extra challenge for those working with these groups: with the exception of the recent *Fauna of the Mediterranean Hydrozoa* (Bouillon *et al.* 2004), little of the ensuing new literature has been collected into comprehensive faunistic accounts or identification keys. The situation is especially frustrating with ctenophores, for which no good account of diversity exists (but see *Phylum Ctenophora: list of all valid species names*, Mills 1998-present). There are also at least two dozen known but as of yet undescribed species of ctenophores, mostly in new genera (Haddock 2004). Indeed, readers well versed in the subject will probably go ‘Aha!’ upon reading the description of the unidentified cydippid in Paper I.

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## 3.2 Overview of research from Norwegian fjords

Early research on gelatinous zooplankton in Norway focused mostly on faunistics of medusae. Studies dating from 1776 to 1921 are reviewed in *Les Méduses de la Norvège* by Kramp and Damas (1925). As well as presenting extensive original material covering most of the Norwegian coast, including the description of the deep-water hydromedusae *Calyropsis simplex* and *Ptychogena crocea* from west Norwegian fjords, the paper lists the records of medusae from Norwegian waters prior to its publication. While not specifically focusing on Norway, several later works by Kramp (e.g. 1937, 1947, 1959, 1961) are also significant in describing the Norwegian hydromedusan fauna. The coelenterate fauna of Herdla-, Hjelte- and Mangerfjord in the vicinity of Bergen has been studied by Runnström (1931) and Rees (1938, 1952). Rees (1938) also includes a description of a new species of anthomedusa, *Thamnostoma russeli*, from Herdla-fjord. The cnidarian fauna of Korsfjord, with emphasis on the seasonal biology of *Aglantha digitale*, has been previously examined by Rasmussen (1971), but his study suffered from instrumentation poorly suited for sampling small or fragile gelatinous zooplankton.

Relatively little work has been done on siphonophores in Norwegian waters. In his work *Fauna Littoralis Norvegiae* Sars (1846) described three new species of siphonophores from the vicinity of Florø, western Norway: *Diphyes truncata*, now known as *Lensia conoidea* (Keferstein & Ehlers, 1860)<sup>1</sup>; *Diphyes biloba*, now *Sulculeolaria biloba* (Sars, 1846); and *Agalmopsis elegans*. The latter was a compound species; While tricornuate tentilla belonging to the species now called *Agalma elegans* (Sars, 1846) were also described, the majority of the description pertained to what is now known as *Nanomia cara* Agassiz, 1865 (Totton 1965). This may have caused confusion with later identifications of agalmid physonects from

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<sup>1</sup> Despite the apparently conflicting priority of these names, the European Register of Marine Species (ERMS; <http://www.marbef.org/data/erms.php>) gives *Lensia conoidea* (Keferstein & Ehlers, 1860) as the accepted name for this species, while *Diphyes truncata* Sars, 1846 is given as its unaccepted basionym. The reasons for this are beyond the scope of this thesis.

Norwegian waters. Runnström's (1931) study from Herdla- and Hjeltefjord included siphonophores, and Kramp (1937) also included notes on the distribution of siphonophores in Norwegian waters. In recent years, invasions of the southern siphonophores *Apolemia uvaria* and *Muggiaea atlantica* have been observed in western Norway; both species caused great problems for fish aquaculture during their mass occurrences (Båmstedt *et al.* 1998, Fosså *et al.* 2003).

During the last decades research has been geared towards the ecology of gelatinous zooplankton. The biology of *Aglantha digitale* has been studied in Oslofjord (Smedstad 1972) and Korsfjord (Rasmussen 1971). The composition and diet of cnidarian zooplankton as well as the potential predatory effect of *A. digitale* close to what was assumed to be its annual maximum abundance in Hardangerfjord were studied by Pagès *et al.* (1996). They concluded that while the predatory effect of *A. digitale* on the copepods (up to 5.7 % and 8.7 % of the total population of *Temora longicornis* and *Oithona similis*, respectively, removed daily) may not have been enough to reduce the standing stocks, the combined predatory effect of the total cnidarian zooplankton may have been significant, and that the abundant *Obelia* spp. could have an impact on the microplankton community. Gorsky *et al.* (2000) utilized an underwater video profiler (UVP) to compare the vertical distribution of macrozooplankton in Sognefjord, Lurefjord, Herdla fjord and Korsfjord in western Norway, finding significant differences between fjords in the relative abundances and vertical distribution of six main groups including ctenophores, siphonophores and the scyphomedusa *Periphylla periphylla*. The latter species has in some western Norwegian fjords developed extraordinarily abundant, persistent populations, which have been subject to several investigations in recent years (see section 3.3.4). Other research on scyphozoans includes several studies on the distribution and trophic biology of the jellyfishes *Aurelia aurita* and *Cyanea capillata* in Norwegian waters (e.g. Matsakis *et al.* 1993, Båmstedt *et al.* 1994, Berstad *et al.* 1995, Martinussen & Båmstedt 1995). Several papers have also examined the trophic and functional ecology of the ctenophores *Pleurobrachia pileus* and *Bolinopsis infundibulum*

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(Falkenhaug 1996, Båmstedt 1998, Sørnes & Aksnes 2004, Båmstedt *et al.* submitted).

### 3.3 Fjord fauna

#### 3.3.1 Biogeography

The western coast of Norway belongs to the East Atlantic boreal biogeographic region. The hydromedusan fauna within this region is relatively uniform, with the North Sea containing the highest number of species and diversity decreasing towards the north (Kramp 1959). The hydromedusan fauna of the North Sea is a mixture of northern and southern species, but with a predominance of southern species and only a few primarily Arctic ones (e.g. *Bougainvillia superciliaris* and *Euphysa tentaculata*, the latter of which is an Arctic survivor in the Baltic and Kattegat (possibly also Korsfjord, paper I). Further north along the Norwegian coast, in the Barents Sea region, there is a clear influence of Arctic species (Kramp 1959).

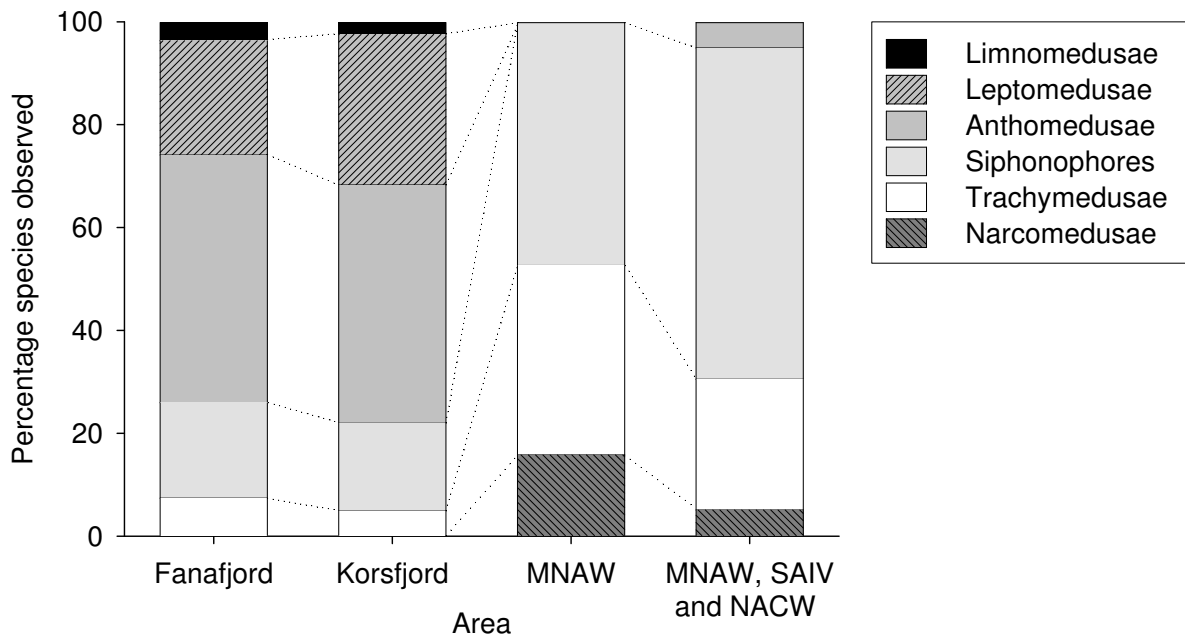
Cataloguing of benthic organisms found on the Norwegian coast has shown that Bergen is situated in a region of high diversity (Brattegard & Holthe 1997). Several species of hydromedusae have the northern limits of their distribution around Bergen (Kramp 1959). There are also some hydromedusa species that have only been found in the vicinity of Bergen, e.g. *Thamnostoma russeli* and *Margelopsis hartlaubi* (Kramp 1959), as well as *Foersteria quadrata* and *Paratecliaia norvegica* (paper III), although this might be an artefact due to the town historically being a centre for marine research.

In addition to the permanent fauna of the region, several southern visitors are carried up to the Norwegian west coast by the North Atlantic Drift (NAD). In recent years, these have included the siphonophores *Apolemia uvaria* and *Muggiae atlantica* as well as the hydromedusa *Pandea* sp. (Båmstedt *et al.* 1998, Fosså *et al.* 2003, Fosså quoted in Hansen 2004). *Sulculeolaria biloba* described from waters close to Florø in western Norway by Sars in 1894 may represent a historical example, as *S. biloba* in fact is a warm water species rarely encountered in temperate waters (Kirkpatrick &

Pugh 1984). The sporadic appearance of such visiting species is probably dependant on variations in the flux of Atlantic water to the Norwegian coast (Båmstedt *et al.* 1998, Edwards *et al.* 1999).

### 3.3.2 Species composition and abundance

Holopelagic trachy- and narcomedusae tend to be more oceanic in distribution than hydromedusae with a benthic stage (Kramp 1959, Goy 1991) and siphonophores are also considered to be a predominantly oceanic group (Kirkpatrick & Pugh 1984). Even though Korsfjord and Fanafjord were rather similar in terms of their faunas, the relative importance of the observed groups differed between the two fjords. Korsfjord was clearly the more oceanic of the two fjords, with siphonophores accounting for a significant portion of the gelatinous zooplankton, while Fanafjord, located further in in the fjord system, was more characterized by meroplanktonic hydromedusae (Paper I). Although the same species – *Aglantha digitale*, *Lensia conoidea*, *Dimophyes*



**Fig. 3.** Percentage of observed species belonging to the different hydrozoan groups in Fanafjord and Korsfjord (Paper I) and the different water masses along the northern Mid-Atlantic Ridge (Paper V). MNAW = Modified North Atlantic Water, SAIV = Sub-Arctic Intermediate Water, NACW = North Atlantic Central Water. The two MNAW stations were located at ca. 60° N, i.e. approximately same latitude as Bergen.



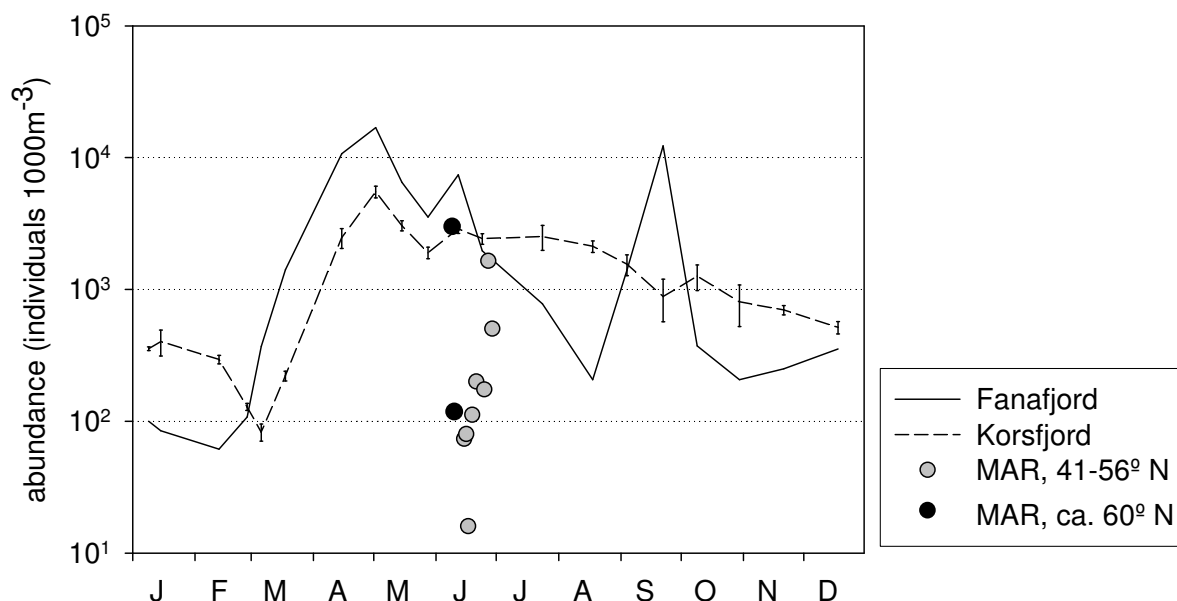
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*arctica* and *Nanomia cara* – were numerically dominant both in Korsfjord (Papers I and II) and at the Mid-Atlantic Ridge (MAR) stations located at corresponding latitude (ca. 60° N) (Paper V), the rest of the fauna was rather different in its composition (Fig. 3). These differences in the species composition were especially noticeable when considering mesopelagic animals. Mid-water depths at the MAR sites were numerically dominated by siphonophores, including *Chuniphyes multidentata* and *Gilia reticulata* in addition to the above mentioned primarily epipelagic species. Mesopelagic hydromedusae found at the MAR mostly belonged to trachy- and narcomedusae. These mesopelagic siphonophores, narcomedusae and trachymedusae observed at the MAR were generally not encountered in the fjords (with the exception of *A. digitale*). Instead, primarily meroplanktonic deep-water hydromedusae inhabited the deeper stations of Korsfjord, and presumably form an important component of the mesopelagic community there (Papers I and III). Similar observations exist from other west Norwegian fjords<sup>2</sup> (Kramp & Damas 1925, Kramp 1959). The differences in the deep faunas probably partly arise from the sill acting as a barrier for the movement of mesopelagic species, as well as the lack of substrate for the benthic stages of the meroplanktonic medusae at oceanic sites.

Gelatinous carnivores are generally more common in neritic than oceanic waters (Alldredge 1984). The average density of planktonic cnidaria in the upper 500 m at the Mid-Atlantic Ridge (Paper V) varied between 16-3006 individuals 1000m<sup>-3</sup> in June 2004 (Fig. 4). The concentrations at the two northernmost stations located at ca. 60° N were 3006 and 118 individuals 1000m<sup>-3</sup>. The higher of these values is comparable with the levels observed in Korsfjord at the same time of the year in 2003. However, the majority of the MAR abundances were an order of magnitude lower than those observed from the fjords in June. Sampling at the MAR took place

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<sup>2</sup> Kramp (1959) included these species of hydromedusae in so called slope species, or "species which occur in the deep water layers, but near the coast" and are presumably meroplanktonic. It is interesting to note that he also points out that several of these species have been found in the deep strata of the Norwegian fjords but *not* in the off-shore waters.



**Fig. 4.** Seasonal changes in the total abundance of gelatinous zooplankton in Korsfjord and Fanafjord in 2003 (paper I), with gelatinous zooplankton abundances observed in June 2004 at the MAR (Paper V) superimposed. Average and se shown for the Korsfjord stations.

at a time when gelatinous zooplankton concentrations there may have been close to their annual maxima (Stemmann *et al.* submitted). The maximum concentrations of gelatinous zooplankton in the fjords were, however, observed already in early May, and the difference in the peak abundances may thus be even higher.

### 3.3.3 Vertical distribution

Examination of the vertical distribution of a few dominant groups of gelatinous zooplankton in the fjords revealed that the bulk of mature *Aglantha digitale* and physonect siphonophores resided below sill depth, thus reducing their risk of advection from the fjord and enabling the formation of resident populations (Papers I and II). However, due to the lower size limit for ROV observations (ca. 1 cm) the data is primarily on large, mature specimens. Both younger *A. digitale* (Russell 1938, Smedstad 1972, Williams & Conway 1981, Pertsova *et al.* 2006) and *Nanomia* spp. (Barham 1963, Rogers *et al.* 1978, Mackie 1985, Benfield *et al.* 2003) are known to reside at shallower depths than their larger conspecifics. Advective transport during earlier ontogenic stages could thus be important in structuring the populations of *A.*

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*digitale* and *N. cara*. Such transport of larvae would also contribute to geneflow between fjord and shelf populations of *A. digitale* and *N. cara*.

Preliminary results (paper II) indicate that the vertical distribution of physonect siphonophores in west Norwegian fjords may be affected by the presence of the mid-water scyphomedusa *Periphylla periphylla*.

### 3.3.4 *Periphylla periphylla*

No work on the gelatinous fauna of west Norwegian fjords would be complete without mentioning *Periphylla periphylla*. This beautiful coronate scyphomedusa is a cosmopolitan mid-water species that occurs in extraordinary numbers in some western Norwegian fjords (Sneli 1984, Fosså 1992, Youngbluth & Båmstedt 2001, Sørnes 2005), assuming the position of top predator (Sötje *et al.* 2007). One hypothesis suggests that poor light conditions in certain fjords, e.g. Lurefjord, may favour tactile predators like *P. periphylla* over visual predators such as fish (Eiane *et al.* 1997, Eiane *et al.* 1999, Sørnes 2005, Sørnes & Aksnes 2006). The persistence, easy access and uniqueness of these populations have prompted large amounts of research. Our study showed that *P. periphylla* in Lurefjord were feeding primarily on *Calanus* spp., but also on krill and ostracods (paper IV). The large *P. periphylla* behaved as ramming predators, approaching their prey tentacles first in order to minimize fluid disturbance that could elicit an escape response, and had clearance rates comparable with other gelatinous predators of similar size (Paper IV, Sørnes 2005). Recent calculations based on the metabolic demand of *P. periphylla* and observed zooplankton biomass suggest that *P. periphylla* may be able to exert control on its prey populations in Lurefjord (Sötje *et al.* 2007). Preliminary results suggest that *P. periphylla* has a significant structuring effect on zooplankton composition and distribution in the fjords it abounds in (Paper III, Youngbluth & Båmstedt 2001, Sötje *et al.* 2007, Båmstedt *et al.* submitted).

## 4. Concluding remarks

The future may well be more gelatinous. In recent years, there have been reports of several, presumably anthropogenic changes in gelatinous faunas from around the world. One phenomenon observed in many places is the apparent increase in the numbers of jellies (Mills 2001, Purcell 2005). Such increases are generally considered detrimental due to their adverse effects on fish stocks and fisheries, tourism and their tendency to block seawater intakes (CIESM 2001, Boero 2002, Lynam *et al.* 2005, Purcell 2005 and references therein, Attrill *et al.* 2007). Several mechanisms accounting for population increases of gelatinous zooplankton have been proposed (see e.g. CIESM 2001). Eutrophication often results in reduced diversity but increased biomass of coelenterates (Arai 2001). Increased turbidity reduces light and may give tactile gelatinous predators a competitive edge over visual predators (Eiane *et al.* 1999, Aksnes *et al.* 2004, Sørnes & Aksnes 2004). It has been suggested that overfishing may promote increased abundances of jellies through redirection of the available energy to gelatinous predators (Mills 1995, Daskalov 2002, Parsons & Lalli 2002) as well as a reduction on predation pressure exerted on jellies by fish (Purcell & Arai 2001). A variety of environmental changes resulting in a shift in the composition of mesozooplankton prey towards smaller size ranges have also been indicated, with the so called “low energy food chains” characterized by small flagellates and small zooplankton at the lower trophic levels favouring jellies over fish predators (Greve & Parsons 1977, Parsons & Lalli 2002).

A warming climate may have an effect on the size as well as the composition of the gelatinous community. For many temperate species, a warmer climate may lead to larger populations and wider distributions (Purcell 2005). Furthermore, the opportunistic life history characteristics of many gelatinous predators could mean that the predicted increase in phenological mismatch between trophic groups due to climate change (Edwards & Richardson 2004) will have less adverse effects on them than on organisms with less flexible life cycles. A trend of poleward movement has

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been detected for copepod communities of the northeastern Atlantic (Beaugrand *et al.* 2002) and it has been predicted that a more positive North Atlantic Oscillation (NAO) index due to global warming will generally increase gelatinous zooplankton abundances in the North Sea (Attrill *et al.* 2007). Southern visitors may in the future be able to establish permanent populations in Norwegian fjords.

Invasive gelatinous species should also be mentioned. Notorious examples include *Mnemiopsis leidyi* in the Black Sea (e.g. Daskalov 2002, Gucu 2002, Kideys 2002), but several less dramatic cases are also known (Purcell *et al.* 1999, Mills & Rees 2000, Mills 2001, Väinola & Oulasvirta 2001, Graham *et al.* 2003, Genzano *et al.* 2006). In 2006, while I was putting the finishing touches to this thesis, worrisome reports regarding *Mnemiopsis leidyi* observations from the North Sea and the Baltic started streaming in (Faasse & Bayha 2006, Hansson 2006, Javidpour *et al.* 2006). The species was also observed along the southern and western coast of Norway, up to the level of Bergen (T. Falkenhaus, pers.com.). Future will show whether *M. leidyi* will become a permanent member of the gelatinous fauna of Northern European waters, and with what consequences.

Potential changes outlined above are likely to be reflected in the future species composition and abundance of gelatinous zooplankton in Norwegian waters. Although Norwegian fjords are far from pristine, this study contains some of the best available baseline information on the coelenterate fauna of Norwegian fjords. However, the seasonal studies presented in this thesis only cover a single year, and further research is needed to establish how representative this is. Also, this study only examined the fauna of a part of a single fjord system in detail, and it is well known that species composition can be surprisingly different even in neighbouring fjords (Brattegard 1979, Tande 2001). Knowledge on the life history and functional biology of several key species of gelatinous zooplankton, e.g. the siphonophores *Nanomia cara*, *Lensia conoidea* and *Dimophyes arctica*, in the fjords is also lacking.

The surprising finding of two new species of presumably deep-water medusae from the well-studied Korsfjord (paper III) makes one wonder what might be lurking in the

depths of other fjords. The benthopelagic gelatinous fauna and its biology has been poorly studied due to methodological constraints (Larson *et al.* 1992, Robison 2004), and represents great potential for new discoveries.

Finally, of course, there is *Periphylla periphylla*. Will it persist, will it spread, or will it subside and become a queer historic bloom mentioned in a few papers of its time? Significant changes in the population structure of *P. periphylla* have been observed in some of the fjords it dominates, indicating that the populations may not be at equilibrium (Jarms *et al.* 1999, Sötje *et al.* 2007). A recent hypothesis suggests that the persistent *P. periphylla* populations of Lurefjord and Halsafjord may be the result of anthropogenically mediated increase in light attenuation (Sørnes *et al.* in press), and *P. periphylla* populations have lately been discovered from several fjords in which it was not observed before (C. Schander and J. Titelman, pers.com.). Also, the mechanisms structuring the pelagic community in the *Periphylla*-dominated fjords are far from clarified.

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