

Lophelia pertusa in Norwegian waters. What have we learned since 2008?

Johanna Järnegren
Tina Kutti



NINA Publications

NINA Report (NINA Rapport)

This is an electronic series beginning in 2005, which replaces the earlier series NINA commissioned reports and NINA project reports. This will be NINA's usual form of reporting completed research, monitoring or review work to clients. In addition, the series will include much of the institute's other reporting, for example from seminars and conferences, results of internal research and review work and literature studies, etc. NINA report may also be issued in a second language where appropriate.

NINA Special Report (NINA Temahefte)

As the name suggests, special reports deal with special subjects. Special reports are produced as required and the series ranges widely: from systematic identification keys to information on important problem areas in society. NINA special reports are usually given a popular scientific form with more weight on illustrations than a NINA report.

NINA Factsheet (NINA Fakta)

Factsheets have as their goal to make NINA's research results quickly and easily accessible to the general public. They are sent to the press, civil society organisations, nature management at all levels, politicians, and other special interests. Fact sheets give a short presentation of some of our most important research themes.

Other publishing

In addition to reporting in NINA's own series, the institute's employees publish a large proportion of their scientific results in international journals, popular science books and magazines.

Lophelia pertusa in Norwegian waters. What have we learned since 2008?

Johanna Järnegren
Tina Kutti



Järnegren, J. & Kutti, T. 2014. *Lophelia pertusa* in Norwegian waters. What have we learned since 2008? - NINA Report 1028. 40 pp.

Trondheim, March, 2014

ISSN: 1504-3312

ISBN: 978-82-426-2640-0

COPYRIGHT

© Norwegian Institute for Nature Research

The publication may be freely cited where the source is acknowledged

AVAILABILITY

Open

PUBLICATION TYPE

Digital document (pdf)

EDITION

Johanna Järnegren

QUALITY CONTROLLED BY

Elisabet Forsgren

SIGNATURE OF RESPONSIBLE PERSON

Research director Kjetil Hindar (sign.)

CLIENT(S)/SUBSCRIBER(S)

Norwegian Environment Agency

CLIENTS/SUBSCRIBER CONTACT PERSON(S)

Elisabet Rosendal

COVER PICTURE

Lophelia pertusa reef. Photo courtesy: Institute for Marine Research

KEY WORDS

Norway

Lophelia pertusa

Review

Climate change

Ocean acidification

Ocean warming

Reproduction

Fisheries

Trawling

Multiple stressors

Distribution

Mining

Aquaculture

CONTACT DETAILS

NINA head office

Postboks 5685 Sluppen

NO-7485 Trondheim

Norway

Phone: +47 73 80 14 00

NINA Oslo

Gaustadalléen 21

NO-0349 Oslo

Norway

Phone: +47 73 80 14 00

NINA Tromsø

Framsenteret

NO-9296 Tromsø

Norway

Phone: +47 77 75 04 00

NINA Lillehammer

Fakkelgården

NO-2624 Lillehammer

Norway

Phone: +47 73 80 14 00

www.nina.no

Abstract

Järnegren, J. & Kutti, T. 2014. *Lophelia pertusa* in Norwegian waters. What have we learned since 2008? – NINA Report 1028. 40 pp.

This report was requested by the Norwegian Environment Agency as a platform of knowledge to evaluate *Lophelia pertusa* as a possible “selected nature type” (utvalgt naturtype). It is a literature review that summarizes available knowledge since 2008 on *Lophelia pertusa* biology, ecosystem structure and functioning. In addition, existing knowledge on the response of *Lophelia* to the effects of increased ocean temperature and acidification and expanding industrial activities are described.

Lophelia pertusa (Linné, 1758) is a common stony coral, which forms extensive reefs in deep waters around the world. It has a wide range of tolerance, but is most abundant where bottom water temperatures range between 6-9°C, salinity is around 35, and with oxygen levels of 6.0-6.2 ml/L. “High quality” coral sites, such as most of the Norwegian *Lophelia* habitats, are associated with bottom waters with Dissolved Inorganic Carbon (DIC) values <2170 µmol/kg and within a seawater density envelope of 27.35-27.65 kg/m³. *Lophelia* does not contain photosynthetic symbionts but feeds on zooplankton, phytoplankton, bacteria and Dissolved Organic Material (DOM), depending on their availability. Most Norwegian *Lophelia* reefs seem to depend mainly on zooplankton for feed.

The occurrence of *Lophelia* varies from scattered colonies or groups of colonies to vast reef complexes (such as the Røst and Sula reefs). *Lophelia* is distributed along most of the Norwegian coast, with the highest densities occurring on the continental shelf north of Stadt up to Lofoten and along the coasts and fjords of Møre og Romsdal and Trøndelag. *Lophelia* has a linear polyp extension rate of approximately 10 mm year⁻¹ and the growth of a reef can amount to 5 mm year⁻¹. All reefs in Norwegian fjords and on the shelf have been formed after the retreat of the ice-sheet and the oldest reefs are around 8000 years.

The *Lophelia* reefs are regarded as hot spots for biodiversity and carbon cycling. The reefs are inhabited by a high number of invertebrates and seem to act as preferred habitat also for some common demersal fish. In the reefs carbon remineralization can be elevated by up to 25% compared to “normal” shelf sediments. Thus, *Lophelia* plays a key role in benthic ecosystems in Norwegian waters.

Lophelia ecosystems have come under increasing anthropogenic pressure due to releases of suspended particles from the aquaculture-, oil and gas-, mining- and bottom trawling industry. Changes in ocean temperature and the ongoing acidification will act as additional stressors on *Lophelia* ecosystems. Ocean acidification is considered the most serious threat. *Lophelia* appears to cope quite well with moderate sedimentation events. Laboratory studies have shown that the short-term cost of this appears to be low on adults but appears highly detrimental for larvae. Further, laboratory studies have shown that *Lophelia* resists realistic near-future increases in pCO₂ levels reasonably well.

However, there might be substantial negative effects on the reef structure. Although studies indicate that *Lophelia* appears to handle single stressors over short time periods quite well, additional effects could be detrimental. It is considered urgent to learn more on the effects of multiple stress factors and long-term exposure to stressful conditions. Of all known *Lophelia* occurrences in the world, 30% are from the Norwegian shelf giving Norway a special responsibility in managing this species and the ecosystem it creates.

Johanna Järnegren, Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, 7485 Trondheim, Norway. Johanna.Jarnegren@nina.no
Tina Kutti, Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway. Tina.Kutti@imr.no

Sammendrag

Järnegren, J. & Kutti, T. 2014. *Lophelia pertusa* in Norwegian waters. What have we learned since 2008? – NINA Report 1028. 40 pp.

Denne rapporten er bestilt av Miljødirektoratet og skal være et kunnskapsgrunnlag for å evaluere *Lophelia pertusa* som en mulig utvalgt naturtype. Den består av en litteraturgjennomgang som oppsummerer tilgjengelig kunnskap siden 2008, om biologi, økosystemstruktur og funksjon hos *Lophelia*. I tillegg beskriver rapporten eksisterende kunnskap om artens respons til økt temperatur og forsuring av havet og økt industriaktivitet.

Lophelia pertusa (Linné, 1758) er en vanlig steinkorall, som danner utstrakte rev på dypt vann overalt i verden. Den har bred toleranse, men er mest utbredt i områder der vanntemperaturen på bunn ligger mellom 6-9°C, saliniteten rundt 35 og oksygennivået er 6.0-6.2 ml/L. Korallområder med «høy kvalitet», sånn som mesteparten av de norske *Lophelia* habitatene, er karakterisert av bunnvann med konsentrasjoner av løst uorganisk karbon på <2170 µmol/kg og tetthet mellom 27.35-27.65 kg/m³. *Lophelia* inneholder ikke fotosyntetiserende symbionter, men lever av zooplankton, fytoplankton, bakterier og løst organisk materiale, avhengig av hva som er tilgjengelig. De fleste norske revene av *Lophelia* ser ut til å hovedsakelig leve av zooplankton.

Utbredelsen av *Lophelia* varierer fra spredte kolonier eller grupper av kolonier til vidstrakte revkomplekser (som revene på Røst og Sula). *Lophelia* finnes langs mesteparten av norskekysten, med de høyeste tetthetene på kontinentalsokkelen nord for Stadt og opp til Lofoten, og langs kysten og fjordene i Møre og Romsdal og Trøndelag. *Lophelia* har en lineær vekst på omtrent 10 mm per år og veksten av et rev kan utgjøre omtrent 5 mm per år. Alle rev i norske fjorder og på sokkelen har blitt dannet etter tilbaketrekningen av isen etter siste istid og de eldste revene er omtrent 8000 år gamle.

Lophelia-revene er ansett for å være «hotspots» for biodiversitet og karbonomsetning. Revene er bebodd av et høyt antall virvelløse dyr og ser ut til å være det foretrukne habitatet for noen av de vanlige artene av bunnlevende fisk. På revene kan karbonomsetningen være forhøyet med inntil 25 % sammenliknet med «normale» sokkelsedimenter, derfor spiller *Lophelia* en nøkkelrolle i bentiske økosystemer i norske farvann.

Lophelia-økosystemer har blitt utsatt for økt menneskelig påvirkning på grunn av utslipp av suspenderte partikler fra havbruksnæringa, olje- og gassutvinning, gruvedrift og bunntråling. Endringene i vanntemperatur og pågående havforsuring vil bety en ekstra belastning på *Lophelia*. Havforsuring er ansett som det største trussel. *Lophelia* ser ut til å håndtere moderate sedimenteringshendelser rimelig bra. Laboratorieforsøk har vist at korttidskostnadene av dette er lave for voksne individ, men øke sedimentering ser ut til å være meget skadelig for larver. Videre har laboratorieforsøk vist at *Lophelia* kan tåle realistiske økninger i pCO₂-nivåer relativt bra. Imidlertid kan det være vesentlig negativ effekt på rev-strukturen hvis det døde skjelettet løses opp.

Selv om undersøkelser indikerer at *Lophelia* kan håndtere en enkelt stressfaktor over kortere tidsperioder bra, kan påvirkning fra flere faktorer samtidig likevel være skadelige. Det anses som nødvendig å lære mer om effektene av flere påvirkningsfaktorer og langtidseffekter av stressende miljøforhold. Av alle kjente forekomster av *Lophelia* i verden er 30 % å finne på den norske kontinentalsokkelen, noe som gir Norge et spesielt ansvar for å forvalte denne arten og økosystemene den skaper.

Johanna Järnegren, Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, 7485 Trondheim, Norway. Johanna.Jarnegren@nina.no

Tina Kutti, Institute of Marine Research, P.O. Box 1870 Nordnes 5817, Bergen, Norway. Tina.Kutti@imr.no

Contents

Abstract	3
Sammendrag	4
Contents	5
Foreword	6
1 Introduction	7
2 Biology	8
2.1 Environmental factors	8
2.2 Reproduction	8
2.2.1 Asexual reproduction	8
2.2.2 Sexual reproduction	8
2.3 Population genetics	9
2.4 Distribution	10
3 Ecology	14
3.1 The formation of reefs	14
3.1.1 Developed coral reef forms	14
3.1.2 Inherited coral reef forms	14
3.1.3 Wall Reefs	15
3.2 Ecological function of <i>Lophelia</i> reefs	16
3.2.1 Invertebrate biodiversity	16
3.2.2 Fish habitats	17
3.2.2.1 Habitat preference of fish	17
3.2.2.2 Functional role of <i>Lophelia</i> reefs as fish habitats	18
3.2.3 Hot spots for carbon cycling	19
4 Anthropogenic impacts	21
4.1 Mechanical damage	21
4.2 Increased particle loads	22
4.2.1 Oil related activities	22
4.2.2 Bottom trawling	23
4.2.3 Mining and salmon farming	23
4.3 Ocean warming	24
4.4 Ocean acidification	25
4.4.1 OA and growth	25
4.4.2 OA and reproduction	25
4.4.3 OA and habitat	26
4.5 Multiple stressors	26
5 New knowledge, future research and monitoring	28
5.1 Knowledge gaps in 2008	28
5.2 Attained knowledge since 2008	28
5.3 Future research needs	29
6 References	30

Foreword

This report was requested by the Norwegian Environment Agency as a platform of knowledge to evaluate *Lophelia pertusa* as a possible “selected nature type” (utvalgt naturtype). It is a literature review on the cold-water coral *Lophelia pertusa* in Norwegian waters, summarizing ecosystem structure and functioning as well as knowledge of the response of the ecosystem to the effects of ocean acidification, temperature increase and expanding industrial activities on the Norwegian shelf and fjords (bottom trawling, oil and gas production and deposition of mine tailings). The report is intended to supplement the DN report 2008-4 “Utredning om behov for tiltak for koraller og svampsamfund” from 2008 with the most recent knowledge.

The authors wishes to thank Jan Helge Fosså for valuable comments on the report and Elisabet Forsgren for the final finish.

Trondheim, March 2014

Johanna Järnegren

Tina Kutti

1 Introduction

Lophelia pertusa (Linné, 1758) (hereafter called *Lophelia*) is a common scleractinian (stony coral), which forms extensive reefs in deep waters around the world. The species belongs to the family Caryophyllidae (Gray, 1846), is a pseudocolonial species, and similar to other deep-water scleractinians it does not contain photosynthetic symbionts (azooxanthellate). Colonies grow asexually via replication of polyps, forming a branching skeleton. As the branches become denser they frequently fuse together creating one of the most three-dimensionally complex habitats in the deep ocean, providing niches for many species. In the NE Atlantic, more than 1300 species have been found living on *Lophelia* reefs (Roberts et al. 2006) and this species diversity is in the same order of magnitude as the invertebrate fauna in tropical shallow water coral reefs.

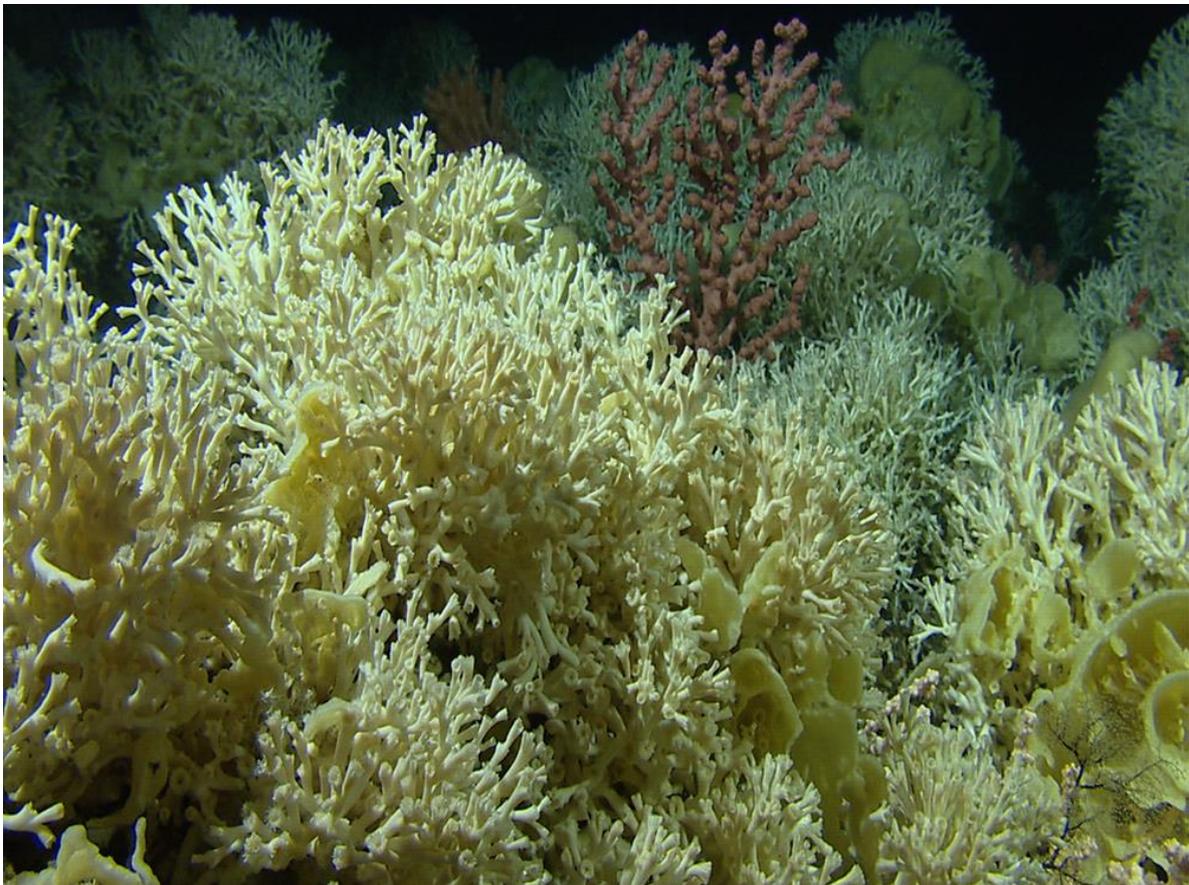


Figure 1. Flourishing colonies of *Lophelia pertusa*. Photo courtesy: IMR

2 Biology

2.1 Environmental factors

In general, *Lophelia* can be found where a constant food supply is present, in areas with strong currents and high productivity, often on topographical heights or steeply sloping bathymetry. It is naturally exposed to a wide range of temperatures (4-14°C) (Brooke et al. 2013 and references therein), salinity levels (32-38.8) (Findlay et al. 2014 and references therein) and oxygen levels (3.8-7.2 ml/L) (Roberts et al. 2009) in its distribution. Although it appears to have a wide range of tolerance, it is most abundant in temperatures between 6-9°C, salinity around 35 and oxygen levels of 6.0-6.2 ml/L (Roberts et al. 2009).

Other physical factors that recently have been suggested to be of importance to coral growth and distribution are the amount of Dissolved Inorganic Carbon (DIC) (Flögel et al. 2014) and seawater density range (Dullo et al. 2008, Flögel et al. 2014). "High quality" coral sites are associated with bottom waters with DIC values <2170 µmol/kg and within a seawater density envelope of 27.35-27.65 kg/m³, while "low quality" reefs are exposed to water with DIC levels higher than 2170 µmol/kg and fall out of the density envelope range. The coral reefs in Norwegian waters mainly fall into the category "high quality" sites (Flögel et al. 2014).

2.2 Reproduction

Lophelia reproduces both sexually and asexually. The relative contribution of each mode is important, as type of reproduction is one of the most significant life history traits due to its effect on demography (Abrahamson 1980, Eriksson 1986) and population genetic structure (Chung and Epperson 1999, Cepitis 2001). All sites sampled along the Norwegian coast with adequate sample size showed a high genotypic diversity, which indicates a balance between the two reproductive modes (Dahl 2013).

2.2.1 Asexual reproduction

Pieces of established colonies of *Lophelia* (genet) frequently break off and continue to grow and establish new colonies that are genetically identical to the parents (ramet). Reproduction is usually thought of as the mechanism that give rise to a genetically new offspring, and spatial increase through asexual reproduction is growth rather than reproduction. It can be argued that asexually produced polyps are no more offspring than new branches produced by a tree. But unlike branches on a tree, asexual coral colonies are capable of independent life that upon the death of the parental colony can continue to spread the parental genes in time and space, which is the definition of reproduction.

Asexual reproduction is important in the formation of *Lophelia* reefs. But it is not necessarily so that the number of ramets on a reef reflects the number of genets it contains. The relationship between them provides an index of clonal extension in a population. There have been very few studies on the concept of asexual reproduction but it has been shown that *Lophelia* have higher rates of clonal reproduction than previously thought and individual clones can be several thousands of years old (Dahl 2013). Reefs are created by a relatively low number of genetically different individuals and there are a small number of large clones and numerous small clones (Dahl 2013).

2.2.2 Sexual reproduction

While the asexual reproduction of *Lophelia* contributes to reef growth, sexual reproduction is necessary for genetic diversity and colonisation of new habitats. Coral ecosystems likely exist

for long periods without sexual reproduction, thus becoming more and more genetically similar making them vulnerable to environmental change and disease.

Larvae produced by external fertilization can often disperse over great distances, as the embryonic stages and larvae are carried passively with the currents. Analysis of dispersal potential, local reseeded and retention, constraints on dispersal imposed by near-bottom flows, and ability to colonize distant habitats all depend on a basic knowledge of reproductive biology and larval development.

Lophelia have separate sexes, it is either a male or a female. Spawning takes place by ejection of sperm and eggs into the water column for external fertilization. Depending on geographical location, this occurs in January to March in Norway (Brooke and Järnegren 2013). The southernmost reef in Norway, the Tisler reef at Hvaler, starts spawning in mid-January while the reefs in the Trondheim fjord in mid-Norway, starts mid-February (Larsson et al. in review). The time of onset further north is not known. Unlike tropical corals, *Lophelia* does not have one big spawning event but rather a prolonged spawning period lasting about a month. The fertilized eggs turn into embryos with a rather slow embryonic development and a late onset of competency. The larvae are likely planktotrophic, meaning that they feed while in the water column, and start searching for a suitable substrate to settle on at 3-5 weeks of age (Larsson et al. in review). They can remain in the water column for up to eight weeks under laboratory conditions, consequently having potential to spread far (Larsson et al. in review). The settling and metamorphosis of *Lophelia* have not yet been observed.

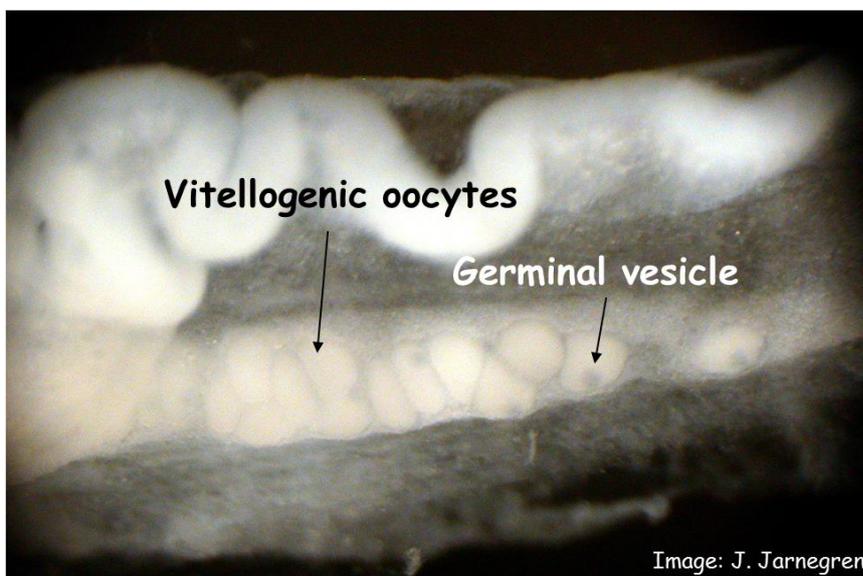


Figure 2. Gonad of female *Lophelia* showing the eggs ready to be ejected into the water mass. Photo courtesy: Johanna Järnegren

2.3 Population genetics

Dispersal is a key component of an organism's life history. Identifying routes and scales of connection is fundamental for our understanding and the implementation of marine reserves. Information on gene flow is a key objective in the planning of networks of marine protected areas.

Eastern and western Atlantic *Lophelia* populations are clearly distinctive from each other (Morrison et al. 2011). Low genetic differentiation among geographically close reef localities in NE Atlantic are most likely due to a common source of origin rather than gene flow among localities

(Dahl 2013). It is suggested that that one of the sources to the North Atlantic cold-water corals is the Mediterranean (Freiwald et al. 1999, De Mol et al. 2002; 2005, Dahl 2013).

In 2004, LeGoff-Vitry et al. reported that populations in the NE Atlantic forms highly distinct offshore and fjord populations. However, this is not strongly supported in more recent studies (Morrison et al. 2011, Dahl 2013). Fjord populations show signs of more isolation in relation to offshore sites but not higher genetic distances. The isolation is more likely caused by a low level of founders and restricted export of larvae to other localities due to oceanographic conditions (Dahl 2013).



Figure 3. *Lophelia* colonies from the Tautra ridge in Trondheimsfjorden. A large *Paragorgia aborea* thrives in the same conditions. Sponges can be seen among the *Lophelia* branches. Photo courtesy: Johanna Järnegren

2.4 Distribution

The Institute of Marine Research has collected, revised and quality assured available data on *Lophelia* occurrences during the last 15 years. The database is composed of records from scientific literature, observations by fishermen and video mapping carried out at IMR and by the oil industry (in particular by Statoil). The database is continuously updated with new information generated from the Mareano mapping program and other scientific cruises or through video surveys carried out in association with oil drilling operations. The Norwegian Marine Data Centre (NMD) at IMR manages the database that to date contains in excess of 600 records. The distribution records are thought to represent only a proportion of the actual *Lophelia* occurrences in Norway. The distribution as shown on the maps (Figure 4-6) therefore possibly reflects both sampling effort and underlying biological and ecological factors such as larvae supply and habitat suitability. Maps presented in this report, however, represent the most updated knowledge of *Lophelia* distribution in Norwegian waters. The distribution of *Lophelia* is partitioned into three different geographical zones in Norway; 1) from the coastline to 1 nautical mile off the baseline, 2) from 1 nautical to 12 nautical mile off the baseline and 3) from 12 to 200 nautical miles off the baseline. Within these three zones different sets of national legal instruments can be applied in the management of coral reefs, i.e. the Planning and Building Act can be applied out to 1 nm off the baseline while the Nature Diversity Act can be applied out to 12 nm off the baseline. The Pollution Control Act and the Marine Resources Act apply irrespective of distance to baseline.

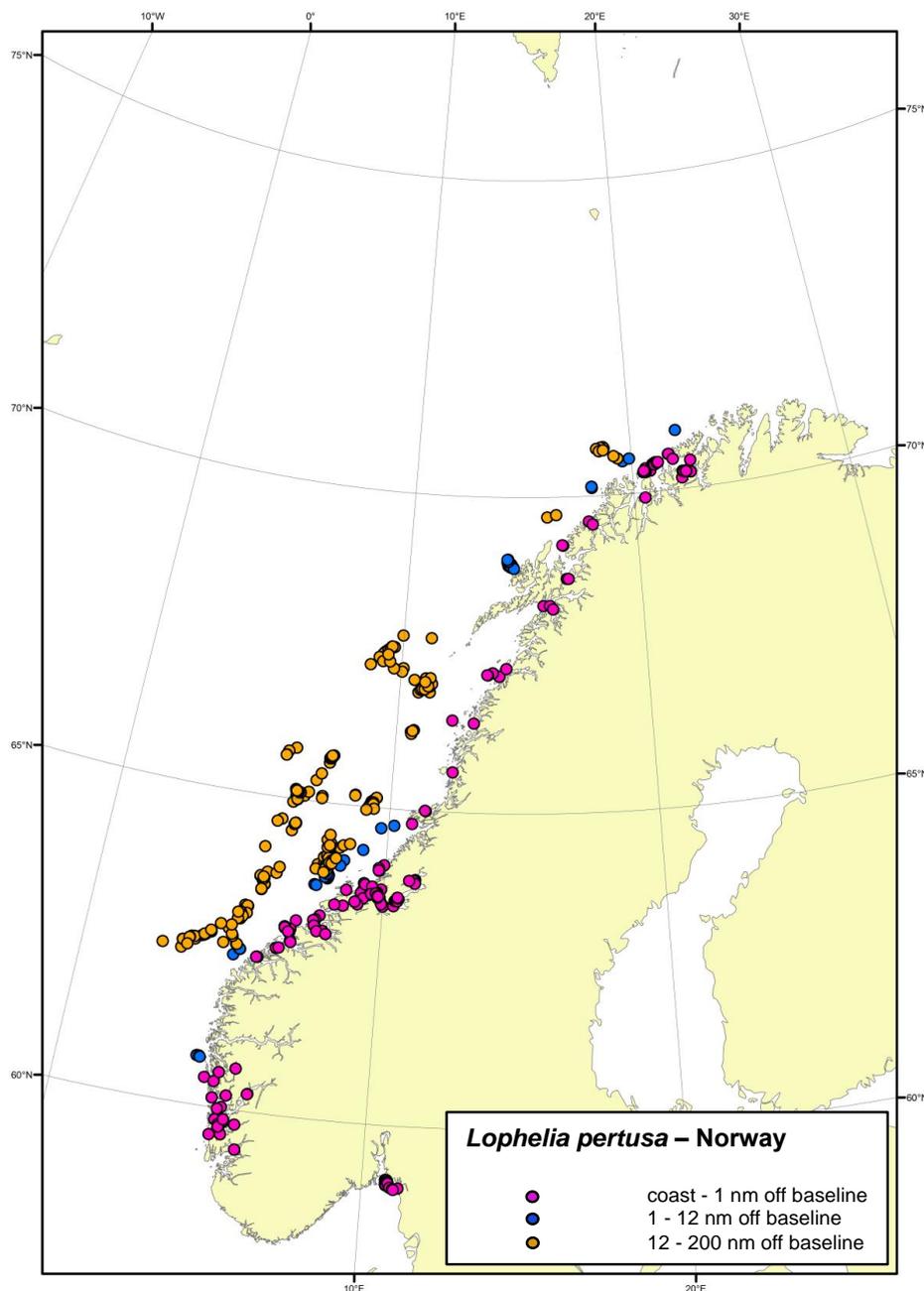


Figure 4. Distribution of *Lophelia pertusa* in Norwegian fjords, along the coast and on the continental shelf. The *Lophelia* records are from the database of the Norwegian Marine Data Centre, December 2013.

Scattered occurrences of *Lophelia* are found along most of the Norwegian continental shelf, along the coast and in the fjords (Figure 4). The world's most shallow *Lophelia* reef known is found at 39 m depth in Trondheimsfjorden. The largest in-shore reef is the Tisler reef in Oslofjorden. The northernmost known *Lophelia* reef, Korallen, is found southwest of Sørøya in Finnmark county and the world's largest known *Lophelia* reef, the Røst reef complex is found southwest of the Lofoten archipelago. Four larger regions apparently lack *Lophelia* records. On the coast of southern Norway from Østfold to Rogaland there is only one record, which is in the fjordsystem of Ryfylke (Figure 5). There are no *Lophelia* records on the coast of Sogn og Fjordane and none on the continental shelf south of Stadt (Figure 4). This could be due to a lack of sampling effort in the region. However, it appears that at least some of the explanation could be ecological and

due to factors such as a lack of larvae supply or unsuitable environment (Jan Helge Fosså pers. comm.). Even though there is fishing effort along the whole coast there are no scientific records of *Lophelia* nor observations from fishermen in these regions.

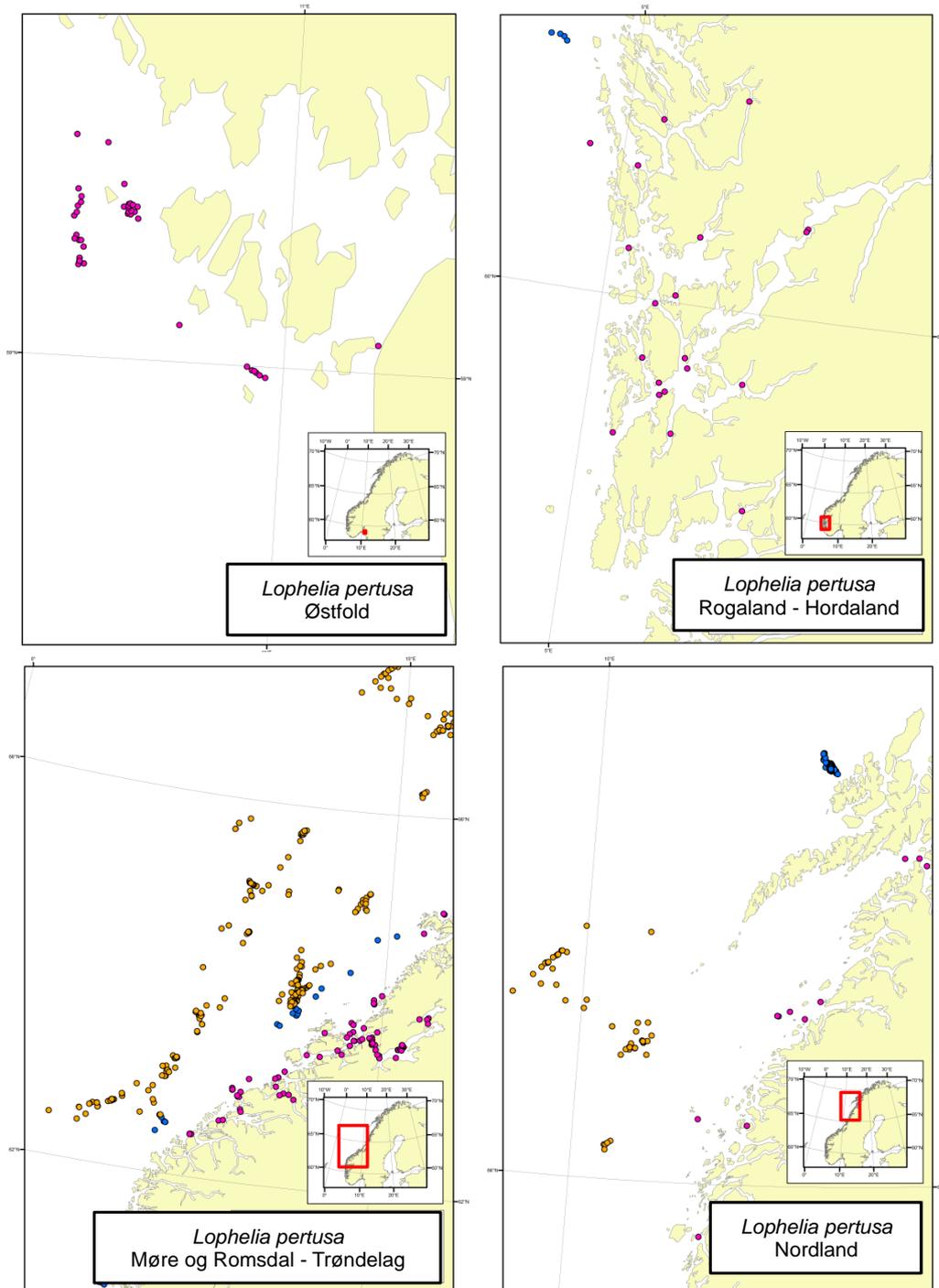


Figure 5. Distribution of *Lophelia pertusa* in and off the coasts of Østfold, Rogaland, Hordaland, Møre og Romsdal, Trøndelag and Nordland. *Lophelia* occurrences are partitioned into *Lophelia* found within the zone from the coastline to 1 nautical mile off the baseline (pink), occurrences from 1 nautical to 12 nautical mile off the baseline (blue) and occurrences from 12 to 200 nautical miles off the baseline (orange). The *Lophelia* records are from the database of the Norwegian Marine Data Centre, December 2013.

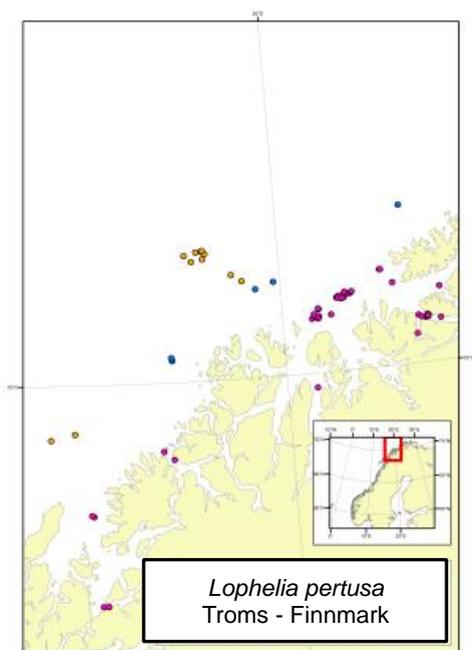


Figure 6. Distribution of *Lophelia pertusa* in and off the coasts of Troms and Finnmark. *Lophelia* occurrences are partitioned into *Lophelia* found within the zone from the coastline to 1 nautical mile off the baseline (pink), occurrences from 1 nautical to 12 nautical mile off the baseline (blue) and occurrences from 12 to 200 nautical miles off the baseline (orange). The *Lophelia* records are from the database of the Norwegian Marine Data Centre, December 2013.

The lack of substantial *Lophelia* occurrences north of Korallen could be changing water mass properties (temperature and perhaps carbon chemistry), however, the reason behind why *Lophelia* is not found further east has not been systematically analysed. Overall, it appears that the Norwegian shelf offers exceptionally good conditions for the settlement and continued growth of this species. Of all global registrations of *Lophelia* occurrences, 30% are from Norwegian waters.



Figure 7. Close up of the polyps of white *Lophelia* with the tentacles outstretched. Photo courtesy: Johanna Järnegren

3 Ecology

3.1 The formation of reefs

The occurrence of *Lophelia* varies from scattered colonies or groups of colonies to vast reef complexes. The term reef is used for *Lophelia* structures large enough to alter patterns of sediment deposition, which provide structural complexity and are subjected to both the process of growth and of bioerosion (Davies et al. 2009). Reefs are formed under complex interactions between biological and geological processes under suitable environmental conditions for hundreds to millions of years. While *Lophelia* has been reported to have a linear polyp extension rate of approximately 10 mm year⁻¹ the growth of a reef can amount to 5 mm year⁻¹ (Lindberg 2004). All reefs in Norwegian fjords and on the shelf have been formed after the retreat of the ice-sheet, e.g. the Sula reef complex and the Haltenpipe reefs have been aged to around 8000 years (Freiwald et al. 2002, Hovland et al. 2002, Hovland 2008).

Wheeler et al. (2007) defined two types of gross morphological forms of deep-water coral reefs, i.e. inherited forms and developed forms. In the inherited forms the substrate has a strong influence on the gross morphology of the reef while in developed forms the reef has a shape that has developed independently from the topographic shape of the original colonization site. Both types of reef forms are well represented on the Norwegian shelf.

3.1.1 Developed coral reef forms

Typical examples of a developed reef type are the small, elongated reefs found in the Træna Deep, the Hola Trough and at the Morvin field (Lindberg 2004, Ottesen et al. 2005, Mortensen and Lepland 2007, Boe et al. 2009, Hovland 2008, Hovland et al. 2012). In all three locations *Lophelia* larvae appear to have settled on topographical highs and with the local, largely unidirectional bottom current, having had a strong influence on the further growth of the coral colonies and thereby the resulting morphology of the reefs. These reefs all appear aligned parallel to the main current direction with a steep head-part containing large young, lobes of live *Lophelia* colonies facing the current and a less steep lee-side containing sediment in-filled older, dead coral framework and a coral rubble tail. Individual reefs are 100-200 m long and 25-55 m wide and with an elevation above the surrounding seabed of up to 20 m, with the Træna, Hola and Morvin reef fields containing hundreds to thousands of small reefs. At Træna the coral reefs can cover up to 10% of the sea-bed in the areas with the greatest density. In addition to these three reef fields that have been rather well described in the scientific literature also other areas with aggregations of small, elongated *Lophelia* reefs exists. Among those is the Kristin reef field where 120 slightly elongated or circular reefs have been mapped using multi beam techniques (Hovland 2008). The morphology of the Stjærnsund sill reefs clearly indicates a strong hydrodynamic control also on these reefs (Rüggeberg et al. 2011).

3.1.2 Inherited coral reef forms

The largest and the most well studied reefs on the Norwegian shelf, the Røst and the Sula reef complexes, have forms that are largely inherited from the morphology of the sea-bed (Freiwald et al. 1999, Fosså et al. 2000, Freiwald et al. 2002, Thorsnes et al. 2004, Nordgulen et al. 2006, Wheeler et al. 2007, Wehrmann et al. 2009, Mol et al. 2009). These reef complexes consists of hundreds to thousands of individual *Lophelia* mounds forming a more or less continuous structure that extends 14 km along the Sula ridge and 30 km along the headwall of the giant submarine Trænadjupet slide. Mounds of live *Lophelia* are most often located to topographic highs; on top of the elongated ridges of the Sula ridge moraine and on top of the dissected ridges of the Trænadjupet slide and on the flanks of iceberg plough marks on the shelf-part of the Røst reef. Such topographically elevated areas offer both a suitable substrate for the settlement of the

Lophelia larvae and favourable conditions for further growth. Another well-known reef complex of the inherited form is the Korallen reef complex, northwest of Sørøya, in Finnmark County.

On the mid-Norway continental shelf smaller, stand-alone, circular reefs are also abundant. These reefs have a summit with live *Lophelia* framework, which is surrounded by dead *Lophelia* framework and an outer lowermost zone of coral rubble. The 10 Haltenpipe reefs, which are about 5-30 m high and up to 50 m wide, are typical examples of this (Hovland et al. 2002, Hovland 2008). Also the Fugløya reefs could be examples of this reef type (Lindberg 2004). Coral reefs in Hardangerfjorden differ from this and appear to be composed of colonies of live *Lophelia* patchily distributed on a base of dead coral framework and coral rubble (Buhl-Mortensen & Buhl-Mortensen 2014). It is suggested that this may be due to a more complex sea-bed topography giving rise to more complex hydrodynamics.

3.1.3 Wall Reefs

In fjords *Lophelia* reefs often occur along the sides of the fjord in addition to the sills, on walls that are vertical or with overhang. Røberg and Stokkbergneset in Trondheimsfjorden and Hornaneset in Hardangerfjorden are examples of such localities. At Stokkbergneset, *Lophelia* is found from about 100 m and down to the bottom of the wall at 500 m (Järnegren pers. obs.). The coral grows preferably underneath overhangs where it creates “stalactite”-like structures that can measure several meters in both width and length, attached to the wall and hanging down. In the larger structures the coral attached to the wall are old and dead while the living outer parts flourish. Several smaller and larger colonies can also be seen attached to the walls. It appears that the distribution of *Lophelia* is connected to the inclination of the wall, the steeper the more corals are found (Järnegren pers. obs.). In addition to *Lophelia*, these localities have a very rich associated fauna of many different species of soft corals, *Acesta excavata*, bryozoans, sponges and anemones. Eventually the coral colonies grow too large and fall of the wall. On the soft sediment at the foot of the wall, piles of corals, bivalve shells and debris can be found, sometimes clearly visible on an eco sounder, as can be seen in Figure 8. Similar structures are described from the Whittard Canyon (Huvenne et al. 2011). Structures like this occur in many fjords and are potentially a large part of the Norwegian *Lophelia* populations that has been overlooked.

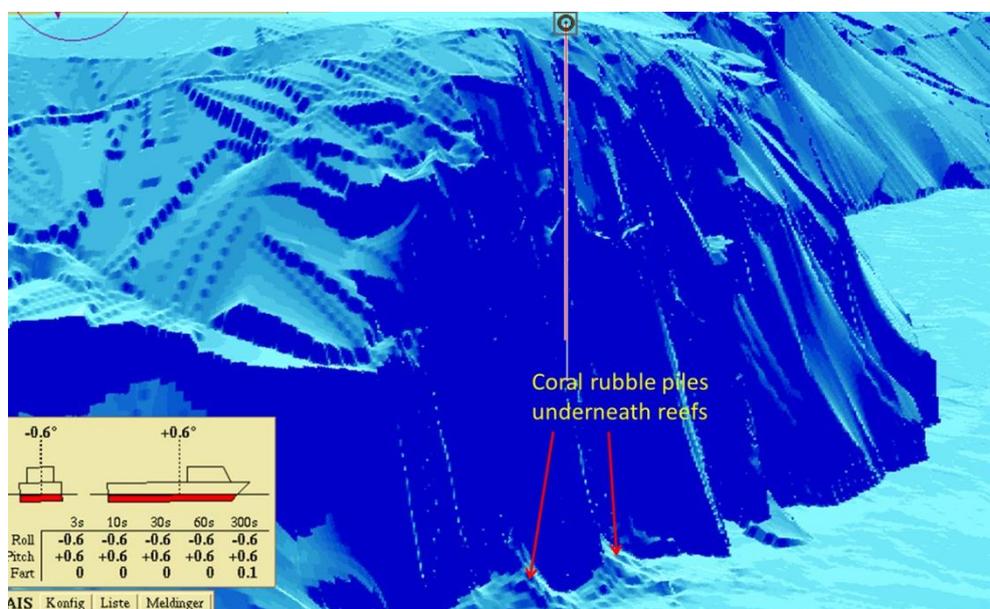


Figure 8. 3D-image from OLEX taken at Stokkbergneset in Trondheimsfjorden, showing coral rubble piles underneath the steep vertical wall. Photo courtesy: Johanna Järnegren

3.2 Ecological function of *Lophelia* reefs

The growth of *Lophelia* results in a distinct vertical zonation pattern of the reef. Four major macro habitat types have been discriminated. These include 1) the live coral framework, 2) the sediment-clogged dead-coral framework, 3) the coral rubble and 4) the underlying sediment (Mortensen et al. 1995). The coral reef ecosystems presents a mosaic of these habitat types each having distinct physical and biological characteristics.

3.2.1 Invertebrate biodiversity

Several studies have emphasized the fact that *Lophelia* ecosystems are biodiversity hotspots inhabited by a higher number of both sedentary and mobile invertebrates and fish compared to unstructured sea-bed (reviewed in Buhl-Mortensen et al. 2010). Among the most conspicuous sedentary invertebrates found in the framework of live *Lophelia* are the polychaete *Eunice norvegica*, the sponge *Mycale lingua*, the bivalve *Acesta excavata*, and the soft corals *Paragorgia arborea*, *Paramuricea placomus* and *Primnoa resedaeformis*. The scleractinian coral *Madrepora oculata* can sometimes constitute small parts of the reef framework. Other conspicuous species that are associated with the live *Lophelia* framework but that occur much more rarely are the soft coral *Clavularia borealis* and the basket star *Gorgonocephalus* sp. (Jensen et al. 2012; <https://love.statoil.com>, www.mareano.no). Mobile crustaceans such as shrimps (Purser et al. 2013) and the squat lobster *Munida* sp. are also commonly found in association with live *Lophelia* colonies. Other less characteristic species associated with the live *Lophelia* branches are the bivalve *Delectopecten vitreus* and the parasitic foraminifer *Hyrrokkin sarcophagi* (Freiwald & Schönfeld 1996).

The highest number of associated fauna is found in and among the dead coral framework. The dead coral framework is at times heavily colonised by the same set of soft corals as the live coral zone. The dead coral framework also forms a substrate for a range of smaller organisms that attach themselves to the dead coral skeleton (including bacteria, foraminifera, sponges, hydroids, bryozoans, bivalves and anemones) while small polychaetes and meiofauna are often found living on or in between dead coral branches (Freiwald et al. 2004; Mortensen and Fosså 2006). The least number of taxa appears in the coral rubble (Johnsson et al. 2004). Although the *Lophelia* habitat has sharp borders when it comes to substrate there appears to be a spill over effect with increase in local invertebrate biodiversity as far as 100-200 m away from the reef zone (Johnsson et al. 2004).

In an extensive study comparing samples collected on the Sula reef on the shelf and smaller coastal reefs in mid-Norway Mortensen and Fosså (2006) described in total 361 taxa living in association with *Lophelia*, with coastal reef being the most species rich of the coral ecosystems. Jensen et al. (2008) identified a total of 13 different bacteria phyla from one of the small isolated mounds on the mid-Norwegian shelf thereby giving an indication of the enormous microbial diversity that exists in these ecosystems. Bacterial diversity is high both in the sediment and in sponges associated with the coral reefs (Schötter et al. 2013). Microbial diversity and activity also appears to be elevated (up to 10 times) in the water masses surrounding cold-water coral reefs as evidenced from the Røst reef complex and the Morvin coral reefs field (Wild et al. 2008, Jensen et al. 2012).

There are no common species that are endemic to the *Lophelia* reefs. However, the recently discovered and rare polychaete *Notophyllum crypticum* n. sp. has only been described from *Lophelia* habitats (Nygren et al. 2010) and could thus represent a species endemic to *Lophelia* habitats. There are several examples of species that are common in coral habitats but appear to be rare in other habitats, such as the squat lobster *Munidopsis serricornis* and the bivalve *Bathyarca pectunculoides* (Mortensen and Fosså 2006, Lavaleye et al. 2009). Fosså et al. (2002) also list the brittle star *Ophiacantha* sp. and polychaetes *Eunice* sp. as such species.

The density and the composition of the fauna living in association with *Lophelia* will vary between locations. The file clam *Acesta excavata* is for example highly abundant within the live coral lobes of the Træna reefs and at Sotbakken reef but does not occur in high numbers at the Røst reef (Purser et al. 2013). The sponge *Mycale lingua* is highly abundant within the complex framework of live *Lophelia* in Trondheimsfjorden, at the Røst reef and at Korallen but has not been registered in similar biomasses within the live *Lophelia* lobes of the Træna Reefs (Purser et al. 2013) although the species is highly abundant on cobbles and boulders in between the small elongated reefs present at Træna (Kutti et al. 2013). Variations in associated species between different reefs are likely dependant on a combination of both abiotic- and biotic factors (such as competitive interactions between species or larvae supply).

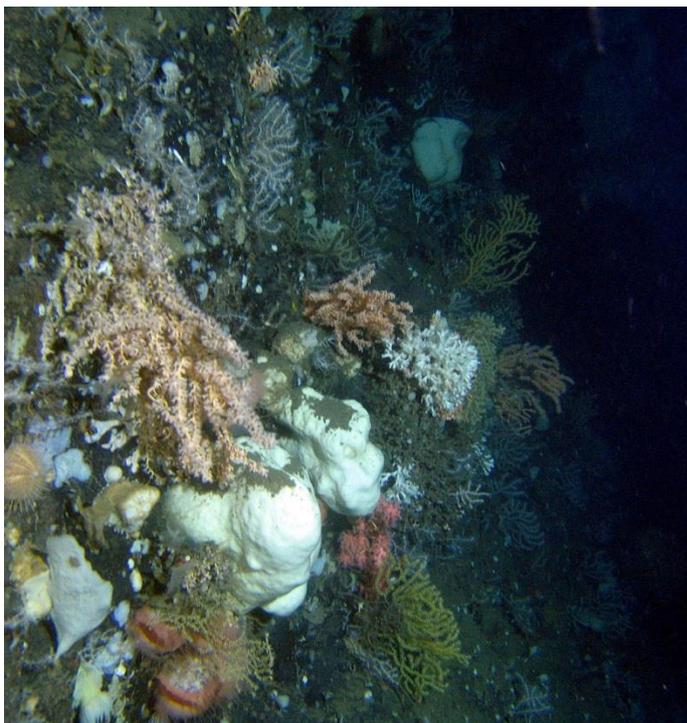


Figure 9. The occurrence of suitable substrate as well as beneficial abiotic conditions creates high species diversity on the walls of the fjords. *Geodia* sp. *Acesta excavata*, *Lophelia*, *Paramuricea placomus*, *Paragorgia aborea*, *Swiftia* sp. *Primnoa resedaeformis* and *Phakellia* sp. are amongst the species that can be seen. Photo courtesy: Johanna Järnegren

3.2.2 Fish habitats

It has been suggested that *Lophelia* reefs may function as nurseries, breeding and spawning areas for fish. If this is true they would as such be coined *essential fish habitats*, i.e. waters and benthic habitats necessary to fish either for spawning, breeding, feeding or growth to maturity (see e.g. Rosenberg et al. 2000). *Lophelia* reefs could also serve as important habitats for fish if they contain significant proportions of a fish population (see Auster 2005). There are several reasons why *Lophelia* reefs could be important habitats for fish, for one they may offer protection from predators and as the reef-associated invertebrate abundance is high (Mortensen & Fosså 2006) *Lophelia* reefs may serve as an attractive foraging area.

3.2.2.1 Habitat preference of fish

Underwater video surveys have shown that Norwegian *Lophelia* ecosystems tend to support comparatively many species of demersal fish with *Gadus morhua*, *Pollachius virens*, *Melanogrammus aeglefinus*, *Brosme brosme*, *Molva molva*, *Sebastes norvegicus* and *S. viviparus* being among the demersal fish species most often recorded in and in the near vicinity of *Lophelia*

habitats (Freiwald et al. 2002, Costello et al. 2005). Quantitative fishing experiments using long-lines and gill-nets at Aktiv- and Sørmannaneset, the mid Norwegian shelf break (Husebø et al. 2002) and at the Træna reefs, Northern Norwegian shelf (Kutti et al. 2014) have shown that *Lophelia* reefs seem to be a preferred habitat mainly for the red-fishes *S. norvegicus* and *S. viviparus* and for *B. brosme*. These species can be found with up to 5 times higher local abundances among the coral reefs that in other non-complex habitats. Long-line fishing at Træna showed that *Lophelia* reefs appear to be a preferred habitat also for *Galeus melastomus* and *Chimaera monstrosa* that occurred with 2-4 times higher abundances among the coral reefs than on unstructured sea-bed (Kutti et al. 2014).

Regional scale investigations of fish distributions performed using hull-mounted eco-sounders on the northern Norwegian shelf have indicated that large populations of fish detectable with acoustics are not particularly associated with *Lophelia* reefs (Kutti et al. 2012). Although *Sebastes* often forms smaller, loose aggregations around and above coral mounds, it is equally often found on flat seabed that lack habitat-forming species such as corals and sponges. Similar small shoals and aggregations of *G. morhua* and *P. virens* can be observed around coral reefs. However, from acoustics run across the Korallen reef, the Træna reefs, Røstbanken, the Røst Reef and the shelf break north of the Røst reef it appears that on a larger spatial scale these fish species are not associated with either the corals or any other large-scale topographical features, as the largest echo registrations are found on the banks. This is as expected because *G. morhua* and *P. virens* are widely distributed in the region and are only partly associated with the benthic system (Olsen et al. 2010, Bergstad 1991). Data from the Hermes acoustic lander monitoring one of the small, elongated Hola reefs confirmed that *Lophelia* habitats support a very low biomass of demersal fish detectable using acoustics (Godø et al. 2012).

3.2.2.2 Functional role of *Lophelia* reefs as fish habitats

Fosså et al. (2002) observed presumably gravid females of *Sebastes norvegicus* while Costello et al. (2005) reported to have observed gravid female *Sebastes viviparus* in close association with the corals at the Sula reef complex. Both authors suggested that the *Lophelia* habitats might serve as spawning areas for these species. A recent study from the Canadian shelf (Baillon et al. 2012) documented larvae of two other red-fish species, i.e. *S. fasciatus* and *S. mentella*, within the structure of sea-pens suggesting that sea-pen fields may serve as an essential habitat for these species. The lack of additional observations of gravid female red-fish within *Lophelia* ecosystems since the studies of Fosså et al. (2002) and Costello et al. (2005) indicates that *Lophelia* reefs are not extensively used as nursery area for red-fish in Norway although they might be locally important. Recent studies have indicated that *Lophelia* reefs may be used as nursery areas for local populations of also other fish species, e.g. Kutti et al. (2014) suggested that one explanation for the positive correlation between *Galeus melastomus* and *Chimaera monstrosa* abundance and the density of *Lophelia* reefs within the Træna region of the shelf could be that these species are using the complex structure of the coral framework as a shelter and protection against predators for its egg and young. This was based on the fact that shark or ray egg cases have previously been observed on video from the Sula reef and among the *Lophelia* framework in Mingulay Reef, Scotland (Freiwald et al. 2002, Henry et al. 2013). For *G. melastomus* and *C. monstrosa* no population declines have been observed during the last 10 years (Williams et al. 2008). However, all Chondrichthyans (that produce relatively few numbers of eggs or young) are considered to be particularly vulnerable to exploitation (Gordon 1999). Therefore further investigation of the use of *Lophelia* reefs as nurseries by targeted sampling of live coral framework and surrounding unstructured sediment at the time of spawning should be carried out. At no time-point during more than 5 months of acoustic records at the Hola reef with the Hermes lander were aggregations of larvae or juvenile fish detected on the echograms (Godø et al. 2012). However, the time-laps data generated by the LoVe platform (<https://love.statoil.com>) offers a good opportunity to study occurrences of scattered fish larvae and juveniles within the *Lophelia* framework in the future.

Brosme brosme is a widely distributed top predator that feeds mainly on benthic megafauna and

fish (Bergstad 1991, Husebø et al. 2002). It has a widespread spawning and epipelagic eggs (Bjørke 1981). The positive relationship between tusk abundance and the presence of *Lophelia* reefs appears to be related to higher food availability within the coral ecosystem. The main prey item squat lobster *Munida sarsii* is known to be abundant in coral rubble (Mortensen et al. 1995). Dense clusters of amphipods, krill and shrimps are frequently observed on underwater video from around cold-water coral reefs (Ross and Quattrini 2007, Costello et al. 2005) and in a recent study from the Røst reef Purser et al. (2013) described shrimp abundances being 10 times higher near corals than in non-biogenic habitats. Higher prey availability could be an important incentive for the species of pelagic fish that appear to have a preference for inhabiting coral habitats, such as *G. melastomus*, *S. norvegicus* and *S. viviparus*.

The demersal fish species most often recorded in the Norwegian *Lophelia* habitats are all widely distributed in the NE Atlantic and occur all along the Norwegian shelf, shelf break and fjords north of 62°N. Research performed so far indicates that these species exhibit a facultative use of the *Lophelia* habitat and that the habitat may be preferred but not essential for any populations of demersal fish on the Norwegian continental shelf (Husebø et al. 2002, Kutti et al. 2014).



Figure 10. *Lophelia* colony visited by a Redfish, *Sebastes viviparus*. Photo courtesy: IMR

3.2.3 Hot spots for carbon cycling

The establishment of *Lophelia* colonies and the further development of the reefs is hypothesised to be strongly regulated by hydrodynamics and food supply (Gass & Roberts 2006, Thiem et al. 2006, Davies et al. 2009, Mienis et al. 2009). Suspended particulate matter concentrations have been found to range between 10-50 $\mu\text{g C l}^{-1}$ in *Lophelia* ecosystems along the Atlantic continental margin (Kiriakoulakis et al. 2007, Lavaleye et al. 2009) and with sedimentation rates around 400 mg particulate organic carbon $\text{m}^{-2} \text{day}^{-1}$ except from during the spring bloom when larger fluxes can be measured (Lavaleye et al. 2009, Kutti unpublished data). Whether this represents optimum food ranges for *Lophelia* is not known.

There are few published studies from the NE Atlantic Ocean assessing the importance of food quality for the establishment and viability of *Lophelia* ecosystems. Tracing studies (using stable isotope and fatty acid signatures) have suggested that *Lophelia* rely on fresh phytodetritus (Duineveld et al. 2007), zooplankton faecal pellets (Duineveld et al. 2004, Duineveld et al. 2007) and zooplankton (Kiriakoulakis et al. 2005) for food. Recent laboratory studies have shown that *Lophelia* is an opportunistic feeder that can feed on different food types such as zooplankton, phytoplankton, bacteria and dissolved organic matter depending on their availability (Mueller et al. 2014). Some *Lophelia* reef systems are known to occur in areas with enhanced phytoplankton productivity (White et al. 2005, Duineveld et al. 2007). The only published study from Norway

relating to CWC feeding are the observations from Freiwald et al. (1998) that described video observations from the Sula ridge of *Lophelia* catching live prey, i.e. calanoid copepods. The LoVe observatory offers a unique chance to bridge this knowledge gap in Norway and quantify the link between coral feeding activity and food availability (phytoplankton and zooplankton).

Rates of carbon assimilation into the tissue of *Lophelia* in the lab have been estimated to $2 \mu\text{g POC g}^{-1} \text{ DW coral tissue}$ and with zooplankton capture rates of $50\text{-}350 \mu\text{g POC polyp}^{-1} \text{ day}^{-1}$ (Purser et al. 2010, Mueller et al. 2014). Estimated growth rates of *Lophelia* ranges from 8 mm year^{-1} at the Røst Reef with the formation of 1 new polyp every 2-3 years to 1 cm year^{-1} at the Morvin coral reef field and Nakken reef in the Hardanger fjord (Hovland et al. 2012, Sabatier et al. 2012, Kutti unpublished data). The addition of new polyps in Nakken was 1 new polyp on each 3 polyp coral fragment during summer (authors personal data). Respiration rates of *Lophelia* fragments are generally low $0.15\text{-}0.30 \mu\text{mol O}_2 \text{ g}^{-1} \text{ (dry weight) hour}^{-1}$ (Larsson et al. 2013). Respiration and carbon turn-over within the complete coral reef ecosystem (i.e. the live and dead *Lophelia* framework together with its associated fauna) is substantial (van Oevelen et al. 2009; Wehrmann et al. 2009). It has further been demonstrated that POC is being depleted from the up-current to the down-current part of the reef during periods of stable current directions at Tisler reef (Wagner et al. 2011).

Measurements of total community respiration from the Tisler Reef by White et al. (2012) showed that during summer oxygen consumption rates of the reef ecosystem varied between 50 and $90 \text{ mmol O}_2 \text{ m}^{-2}$ exceeding that of shelf sediment oxygen consumption by up to 9 times. They further suggested that in areas densely populated by *Lophelia* up to 25% of the total carbon processing will occur in the reef ecosystem, thus, *Lophelia* ecosystems are not only biodiversity hot spots but they are also hot spots for carbon cycling on the shelf (van Oevelen et al. 2009, White et al. 2012).

In all, studies suggest that *Lophelia* reefs support both fauna and ecosystem processes over a larger area than the habitat itself as defined by the area covered by live coral framework, dead-coral framework and coral rubble.

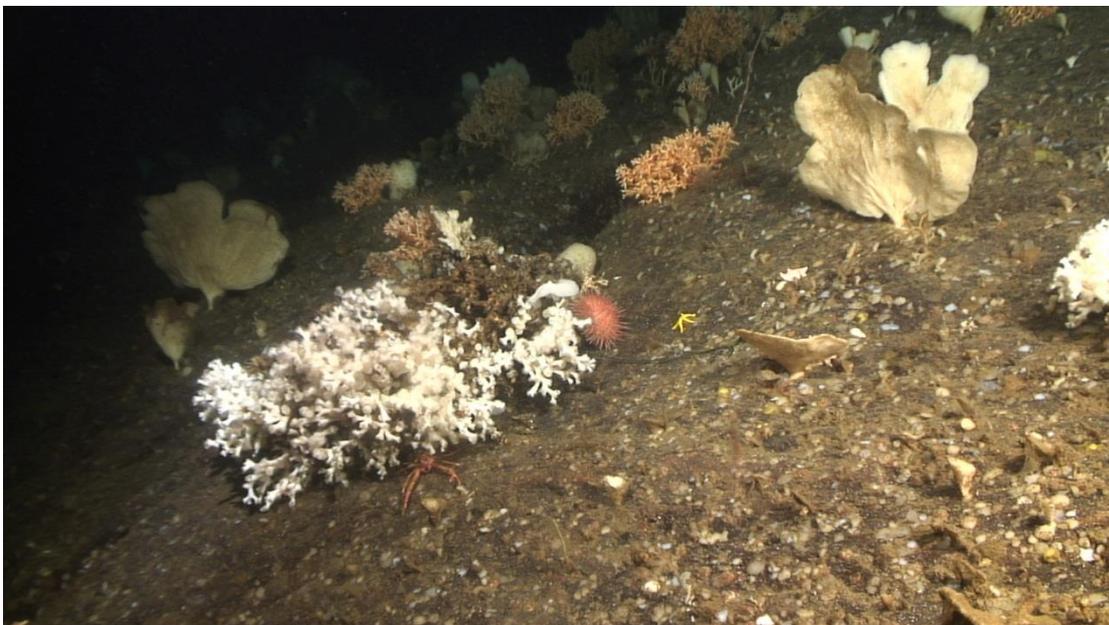


Figure 11. Small colonies of *Lophelia*, sponges, urchin, squat lobster and starfish are also seen. Photo courtesy: IMR

4 Anthropogenic impacts

4.1 Mechanical damage

All bottom touching fishing gears have the potential to negatively impact cold-water coral reefs with the degree of harm depending both on the force of the gear on the bottom substrate and on the extent of usage. The detrimental effects of bottom trawling on cold-water coral reefs are well documented, with the physical impact including crushing of the *Lophelia* framework and overturning of soft corals (Fosså et al. 2002, Fosså & Skjoldal 2009). Effects of bottom long-lining and gill netting are much more benign and involves mainly the taking of corals as by-catch. Invertebrate by-catch rates of long-line fishing were estimated in the Trænadjupet coral area to 1 coral and 2 sponge pieces per 2000 hooks set with the coral by-catch being composed mainly of small fragments of *Lophelia* (85%) and *Primnoa reseadeformis* (15%). Sponge by-catch was mainly composed of the fan-shaped sponge *Phakellia ventilabrum* (CoralFISH report D54). Using data from a range of underwater video surveys carried out in the late 1990ties Fosså et al. (2002) estimated that 30-50% of the *Lophelia* reefs occurring on the Norwegian shelf were either impacted or destroyed by bottom trawling. To prevent further damage caused by fishing activity Norwegian national regulations of 1999 prohibit intentional destruction of coral reefs and require precaution when fishing in the vicinity of known coral locations. The regulation also gives special protection to specified areas by totally banning the use of fishing gear that are dragged along the bottom and that might come in contact with the corals, i.e. mainly bottom trawling (Fosså & Skjoldal 2009). In 2010, 8 reefs or reef aggregations had received this special protection, i.e. the Sula Reef, Korallen, Iverryggen Reef, Breisunddypet, Røst Reef, Træna Reefs, Tisler Reef and Fjellknausene Reef, representing the largest reefs and reef aggregations. Fishing with static gear, such as bottom long lines and gill nets, is still allowed. Iverryggen, one of the reefs where Fosså et al. (2002) reported large damage from bottom trawling and gillnetting was in 2009 established as one of the new coral protections zone in Norway.



Figur 12. Gorgonians *Paramuricea placomus*, *Paragorgia aborea* growing on old *Lophelia* skeleton. The Redfish *Sebastes* mingling among them. Photo courtesy: IMR

New data generated by the MAREANO mapping program has shown that the general trend appears to be that coral reefs in fjords (e.g. Stjernesund and Andfjorden) and near the coast show relatively few indications of fishing induced damage while many reefs located far offshore still

show signs of trawl impact (Buhl-Mortensen et al. 2013). This appears to cohere with the general disallowance to use bottom fish trawls within 12 nautical miles of the shore. Buhl-Mortensen et al. (2013) quantified the impact at some selected reefs near the coast in Troms and found that in LoppHAVet and west of Sørøya 1-2% of the area designated as reef showed signs of damage while at Korallen 6% of the reef was damaged as an effect of bottom trawling. Most of the damage caused to the Korallen coral reef, however, appeared to date back to the time before 1999 and there are clear signs of regeneration of the *Lophelia* colonies in damaged areas (Buhl-Mortensen et al. 2013). In the Trænadjupet coral area very few signs of anthropogenic impact were observed on the sea-bed during CoralFISH cruises in 2009 and 2010. Only what appeared to be 3 trawl tracks and 5 lost long-lines were observed on a total of 130 000 m² of sea-bed surveyed. From late 2009 also this area has been protected from bottom trawling. Due to the low fishing pressure in the area (as evidenced from Vessel Monitoring System (VMS) data and fisheries statistics) and the relatively low by-catch rates the risk of future adverse impact of the fishing industry on the Trænadjupet cold-water coral ecosystem was considered low (CoralFISH report D31). Inspection of VMS data indicates that this also holds true for the other *Lophelia* areas protected from bottom trawling on the shelf. However, small patches with clusters of a few small reefs on the shelf are expected to continue to decline due to ongoing bottom trawling.

Mechanical damage to *Lophelia* reefs can occur also during the anchoring operations of rigs, installation of subsea templates and during the laying down of new pipelines and cables on the sea-floor in locations containing clusters of small *Lophelia* reefs. However, these activities require impact assessments and with a thorough mapping and video inspections such activities should be carried out with the aim of causing minimal impact on corals.

4.2 Increased particle loads

Sediment resuspension and sedimentation are naturally occurring processes regulating the concentration of suspended particles in the benthic boundary layer. Human activities can cause changes to the quantity and/or quality of suspended particles encountered by benthic suspension feeding fauna with the potential to impact organisms at an individual and population level. Off-shore *Lophelia* ecosystems are expected to be susceptible mainly to the release of suspended particles from exploration drilling and to suspended bottom sediments caused by bottom trawling. Coral ecosystems along the coast and within the fjords are susceptible mainly to impact by aquaculture activity and through submarine disposals of mine tailings.

4.2.1 Oil related activities

Benthic releases from oil drilling operations mainly occur during exploration drilling when large amounts of crushed rock and drill-mud are deposited on the sea floor and with a subsequent resuspension of the fine particles into the water masses around the drilling sites. Currently 45-55 exploration wells are drilled on the Norwegian shelf annually and with each well discharging approximately 1000 tonnes of drill cuttings (Anon. 2013, Neff 2005). Laboratory studies have shown that *Lophelia* appears to be adapted to cope with temporarily elevated suspended sediment loads. The coral efficiently removes accumulated sediment particles from the polyps by producing a mucus sheet that is subsequently rejected (Larsson et al. 2011, Larsson et al. 2013). Sediment seems to accumulate only on branches or areas on branches that are not covered by live tissue. In corals that are continuously exposed to suspended sediments the mucus-producing cells are larger than in unexposed corals, possibly due to an increase in mucus production in the exposed corals (Baussant 2012). Mucus production and the short-term cost of the production are difficult to measure, however, exposure to elevated suspended particles of drill cuttings <30 mg l⁻¹ in laboratory resulted in reduced growth of *Lophelia* after 12 weeks (Larsson et al. 2013). No effects on respiratory activity or energy storage in the coral were detected. The study further showed that *Lophelia* larvae appear to be highly sensitive to exposure to suspended fine particles of drill cuttings, which could have an indirect effect on *Lophelia* health and survival (Larsson et al. 2013). Exposure to very high loads of suspended sediment and complete burial

in sediment can be detrimental also for established colonies of *Lophelia*. Exposure to suspended natural bottom sediments of 100 mg l⁻¹ for two weeks resulted in a 50% polyp mortality (Brooks et al. 2009). As an effect of oxygen deficiency complete burial of both natural bottom sediment and drill cuttings will result in a polyp mortality of nearly 100% within 2-4 days (Allers et al. 2013, Brooks et al. 2009).

Investigating the effects of the release of drill cuttings and mud after the drilling of an exploration well in Trændjupet Mortensen and Lepland (2007) found traces of barite in the sediment up to 4 km away from the drill site. Corals as far as 600 m down-current from the drill site had incorporated barite particles into their calices. There were, however, no indications of reduced health of the corals exposed to increased suspended particle loads. In-situ monitoring of *Lophelia* reefs during exploration drilling has been attempted at Morvin and Pumbaa (Tenningen 2011, Møskeland et al. 2012). These studies conclusively show that suspended drill cuttings are dispersed several hundred meters away from the discharge point, but that the concentrations were often lower than what can be encountered naturally in these habitats as an effect of resuspension of bottom sediments.

Effects of weeks of slightly elevated suspended sediment loads on *Lophelia* (as evidenced by the amount of energy storages) appear to be low, however, long-term or delayed effects have not been thoroughly assessed. The combined results from the abovementioned studies support the view that the release of cuttings in the near vicinity of *Lophelia* reefs should be avoided. Further, the indications that coral larvae appear to be especially sensitive to suspended drill cuttings suggest that drilling operations in coral areas should be avoided during the spawning season, i.e. February to April. Effects of chronic exposure to low concentrations of dispersed hydrocarbons on sessile suspension feeders (such as corals) around oil producing platforms have not been assessed. It is therefore recommended that the release of produced water as well as drill cuttings should be avoided in areas with dense aggregations of corals.

4.2.2 Bottom trawling

Resuspension induced by bottom trawling is expected to be the main driver of sediment dynamics on the heavily trawled fishing grounds where suspended sediment loads can be up to 10-100 times normal background concentrations following a trawl passage (Martín et al. 2014, Bradshaw et al. 2012). However, small particles (<10 µm) that remain in suspension for days can propagate to areas beyond the fishing grounds by down slope gravity flow or bottom currents and thereby affecting *Lophelia* reefs that are protected from the mechanical destruction of bottom trawling through the regulations of fishing activity. Korallen and Iverryggen MPAs both lie in the near vicinity of heavily trawled areas and could potentially be affected by continuous, long-term slightly elevated suspended sediment loads. No studies have targeted impacts of suspended natural bottom sediments on *Lophelia* health.

4.2.3 Mining and salmon farming

Releases from the mining industry occur through the disposal of mineral waste particles into fjords by submarine tailings disposals (STD)(Cornwall 2013). STD sites are often active for decades, depositing anything between 300 000 and 4 million tons annually. The level of suspended sediments in the benthic boundary layer can be elevated up to ten times 1-2 kilometers away from the designated dump site (Berge et al. 2011). During the production of salmon in open net-cages large amounts of nutrients and particulate organic waste is released into surrounding ecosystems. In regions with multiple farms (such as Hardangerfjorden) the supply of organic matter to the sea-bed can be increased by 25-40% due to releases from the aquaculture industry (Kutti et al. 2008). Buhl-Mortensen & Buhl-Mortensen (2014) noticed that patches of fine particulate sediments appeared to be more common on *Lophelia* colonies Hardangerfjorden than on off-shore colonies. Whether this could be due to natural condition in the fjord e.g. siltation from

glaciers or caused by organic input from industries (agriculture, sewage and fish-farming) remains unclear. There are no published studies investigating impacts of particulate organic matter or mine tailings on *Lophelia* health.

There are several national and international legislations regulating the usage of the marine environment, however, there are no standard monitoring programs to assess the impact of the release of particulate waste from industrial activities on sessile filter feeders in Norway. Recently guidelines suggesting best practice procedures when drilling in coral areas and how to monitor impacts on *Lophelia* have been developed (Ulfsnes et al. 2013, Anon. 2012).

4.3 Ocean warming

Anthropogenic CO₂ emissions are causing climate change, with global warming as a consequence. Temperature and other variables have been observed since the mid-19th century but it is from the period 1950 and onward that more comprehensive sets of observations have been available. The temperature in the atmosphere has increased with almost 1°C, over the period 1880 to 2012 (IPCC 2013). Each of the last three decades has been successively warmer than any preceding decade since 1850 (IPCC 2013). The upper ocean (0-700m) store more than 60% of the net energy increase in the climate system, and about 30% is stored in the ocean below 700m. The last 40 years this has resulted in an increase in the ocean temperature (IPCC 2013). Ocean surface temperatures are predicted to rise between 1.4 and 5.8°C in the next hundred years. Increasing surface temperatures may affect the formation of cold oxygenated deep water and modify global ocean circulation. Warming decrease oxygen solubility and increases stratification of seawater which reduces vertical mixing and oxygen input. Less availability of dissolved oxygen in the deep-water masses might increase the existing natural Oxygen Minimum Zones (OMZ) (Ramirez-Llodra et al. 2011).

Evolved tolerance to a wide range of environmental variables is more common in fauna that lives in a variable environment, as compared to species living under stable environmental conditions. It has long been assumed that the conditions in the deep sea are relatively uniform, but this does not apply to slope depths and topographic features where corals are found. Recent long term data from in situ instruments close to cold water coral reefs indicate that the conditions are more variable at these sites than previously thought (Flögel et al. 2013, Findlay et al. 2014). Natural physiochemical conditions fluctuate (oxygen, carbon nutrients and food supply), driven by large-scale hydrodynamics, creating variability not accounted for by cruises that only sample once per station. This may provide flexibility to the corals, giving them increased adaptation potential for surviving a range of conditions (Findlay et al. 2014).

Lophelia can tolerate a wide range of temperatures as well as natural variation over time within the same site. It seems unlikely that they are found in habitats that have extended periods of 15°C or higher but it is difficult to set a single temperature as the upper lethal limit as it probably is a combination of duration and magnitude of temperature fluctuations. Lower thermal limit is still not determined (Brooke et al. 2013).

A temperature change will likely have a larger effect on those coral already living near the tolerance threshold. Although a temperature increase in seawater does not appear to be a great threat to *Lophelia* as a single stressor, it must be seen in combination with other factors changing in the environment and also how different genotypes may have different responses (Ramirez-Llodra et al. 2011, Hennige et al. 2014).

4.4 Ocean acidification

Ocean acidification (OA), often referred to as the “other CO₂ problem” or the “evil twin of global warming”, is caused by CO₂ dissolving into the oceans. Since preindustrial times the concentration of CO₂ in the atmosphere has risen with 40% (from 280 to 392 ppm). These concentrations are the highest recorded the past 800 000 years. As atmospheric CO₂ levels increase, more CO₂ dissolves into the oceans and forms carbonic acid, which dissociates to form hydrogen and bicarbonate ions. Since the beginning of the industrial era, the pH of ocean surface waters has decreased with 0.1 pH units, corresponding to a 26% increase in hydrogen ion concentration, and is predicted to further decline by about another 0.4 pH units until the end of the century (RCP8.5, IPCC 2013).

The shift in seawater carbonate chemistry associated with ocean acidification also reduces the saturation state of aragonite, which is the form of calcium carbonate from which *Lophelia* builds its skeleton. The aragonite saturation horizon (ASH) is predicted to become shallower, making it more difficult for calcifying organisms near this depth to maintain their skeleton and thereby affecting reef growth. A habitat suitable for stony corals, such as *Lophelia*, is predicted to be particularly reduced in the North Atlantic (Ramirez-Llodra et al. 2011).

4.4.1 OA and growth

The study of ocean acidification is a field that is growing strongly but there are still few studies reporting the effects on *Lophelia*. However, the studies done indicate that contrary to what has been assumed, the growth of *Lophelia* does not seem to be strongly affected by moderately rising levels of pCO₂ (Form and Riebesell 2012, Maier et al. 2013, Hennige et al. 2014). The living polyps appear to have the capacity to compensate for the lower pH and the calcification rate is not prominently affected by the pCO₂ level projected at the end of the century (1000 µatm) (Maier et al. 2013).

It is yet unclear how the corals are able to resist increasing levels of pCO₂ and how they maintain their calcification rates constant. It is suggested that *Lophelia* have the ability to maintain a high pH at the internal site where calcification takes place (Maier et al. 2013). Another suggestion is that the naturally fluctuating environment that *Lophelia* is exposed to makes them tolerant to a wide range of conditions (Findlay et al. 2014). This could also help to explain the variability of results from reported experiments.

But even if ocean acidification does not appear to affect the growth of the coral at first, it does affect the metabolism. A recent study showed that even though the calcification rates did not change, the respiration rate decreased (Hennige et al. 2013). This suggests an energetic imbalance where *Lophelia* may be forced to use energetic reserves to maintain calcification. In the long run, this is potentially detrimental as energetic reserves are not infinite.

4.4.2 OA and reproduction

It is only recently that the embryonic and larval biology of *Lophelia* has been described (Brooke and Järnegren 2013, Larsson et al. in review). The settlement and benthic juvenile stages have not been observed. Knowledge on the possible effects of ocean acidification on coral reproduction so far comes from tropical corals but it is reasonable to believe that there are many similarities (Albright 2013).

OA has the potential to affect sexual reproduction and multiple early life history stages of corals that are critical to reef persistence and resilience. Affected processes may include sperm motility and fertilization success, larval metabolism, larval settlement, and post settlement growth and calcification (Albright 2013 and references therein). These effects might occur via both direct pathways (e.g. depressed sperm motility, fertilization, larval respiration, growth and calcification) and indirect pathways (e.g. changes in substrate conditions that favour settlement). Implications

of these effects include reduced larval supply and depressed recruitment, which will likely compromise the ability of reefs to recover from disturbance (Albright 2013 and references therein). Slowed growth may trigger a number of effects, such as elevated juvenile mortality and shifts in population size structure (Albright 2013 and references therein).

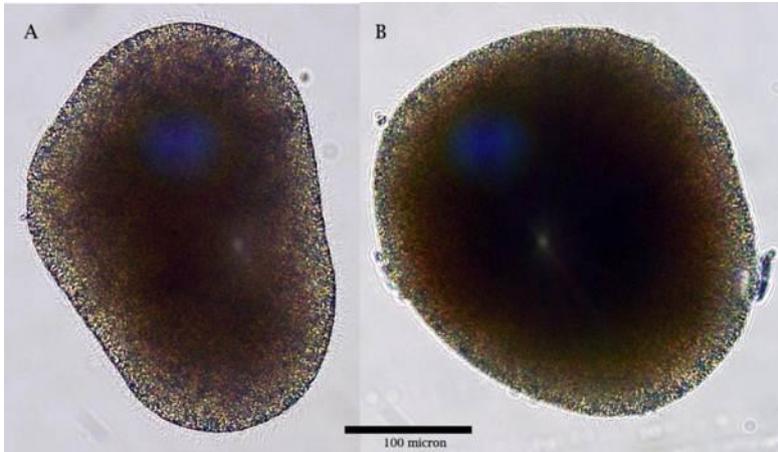


Figure 13. *Lophelia* larvae. Photo courtesy: Johanna Järnegren

Coral spat survivorship, the first year is extremely low, generally reported to be 0.2-6% (Albright 2013 and references therein). Chronic stressors and stochastic events that further reduce survivorship during these critical stages have the potential to significantly alter future population sizes. Increasing $p\text{CO}_2$ has the potential to impact several life stages of corals, also critical processes independent of calcification (Albright 2013 and references therein). Negative impact of successive life history stages may accumulate in such a way that the overall effect on recruitment is severe. Although early life history stages are sensitive, the most sensitive life stage might differ amongst species, and variation in life history characteristics may prove some species more resilient than others (Albright 2013 and references therein).

4.4.3 OA and habitat

The living polyps of *Lophelia* appear to be able to counteract moderately decreasing pH (Form and Riebesell 2012, Maier et al. 2013, Hennige et al. 2014). This is not necessarily true for the old, dead part of the reef. The dead coral is the fundament of the reef and is also the area that creates the important habitats for other species, housing the main part of the great species diversity. When $p\text{CO}_2$ level rises, the exposed and unprotected calcium carbonate of the dead skeleton of the reef is likely to start to dissolve. But not only will the acidification in itself affect the reef, also the efficiency of chemical bioerosion processes, mainly caused by sponges, are predicted to increase (Wisshak et al. 2012). The weakening of the framework might eventually cause the reef structure to collapse. The complex three-dimensional framework is the fundament for the high biodiversity occupying the coral reefs that then might diminish. The loss of structure will likely also affect the living *Lophelia* by e.g. reduction of flow, thereby lessening the food supply, less elevated position for feeding and less suitable habitat for juvenile settlement.

4.5 Multiple stressors

The main stressors for *Lophelia* are caused by ocean acidification and temperature increase (Ramirez-Llodra et al 2011). They will affect the reefs through direct effects on the coral, the habitat and associated fauna as well as through synergies with other human activities. Ocean acidification is considered the main threat (Ramirez-Llodra et al 2011).

Lophelia is resisting realistic (end of the century) increases in pCO₂ levels seemingly well and maintains constant calcification and growth (Form and Riebesell 2012, Hennige et al. 2013, Maier et al. 2013). This process likely requires energy. The warming of the oceans induces increasing stratification of the water masses, which decreases nutrient availability and surface productivity, in addition to diminishing the flux to the ocean seabed. An increasing pCO₂ level may cause a transfer in fauna from diatoms and large zooplankton to picoplankton and microzooplankton, leading to a different diet for the corals (Ramirez-Llodra et al 2011). These factors would likely to lead to a poorer food supply for *Lophelia*.

While *Lophelia* apparently can calcify and grow under moderately increasing pCO₂ levels, it shows lowered oxygen consumption (Hennige et al. 2013). This metabolic suppression is generally achieved by halting energy expensive processes, such as protein synthesis, and may lead to reduced growth and reproductive potential, if sustained (Albright 2011).

Lophelia removes settled particles from the body surface by producing a mucus layer, which it subsequently sheds off. The short-term cost of this appears to be low. However, exposure to elevated suspended particles (<30 mg l⁻¹) of drill cuttings in laboratory caused detectable reductions in growth of *Lophelia* fragments and a high mortality of *Lophelia* larvae. The effect response of *Lophelia* exposed to drill cuttings appears to be stronger when simultaneously exposed to reduced pH levels (Baussant 2012). Complete burial in sediment results in nearly 100% mortality of polyps after 2-4 days.

Apart from increasing suspended sediment loads bottom trawling can also damage *Lophelia* reefs upon contact resulting in the crushing of the coral framework. If abiotic conditions remain stable there is evidence that *Lophelia* will recover and re-establish with new colonies in the area with crushed corals, however, the process of establishing a new reef is slow and will likely take hundreds of years.

Although *Lophelia* appear to handle single stressors reasonably well separately, at least over short time periods (Larsson et al. 2011, Form and Riebesell 2012, Brooke et al. 2013, Larsson et al. 2013, Maier et al. 2013, Hennige et al. 2014), it is very likely that additional stressor are detrimental. We do not have enough knowledge and it is considered urgent to learn more on the effects of multiple stress factors.

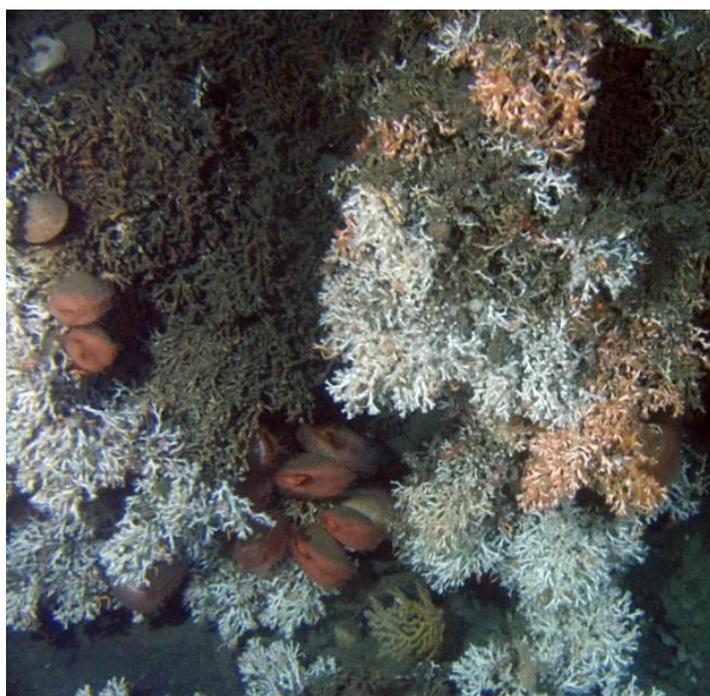


Figure 14. Wall reef of *Lophelia pertusa* at Stokkberghneset. The File clam *Acesta excavata* is also present as well as a small gorgonian *Paramuricia placomus*. Photo courtesy: Johanna Järnegren.

5 New knowledge, future research and monitoring

The DN report 2008-4 “Utredning om behov for tiltak for koraller og svamperamfund” from 2008 summarized the most recent knowledge on *Lophelia* ecosystem biology and function and listed several areas pin pointed by new research projects or where new knowledge was urgently needed. Much has been gained since then, however, there are still areas where new knowledge is urgently needed.

5.1 Knowledge gaps in 2008

Basic research:

- Studies directed at uncoiling the functional role of corals as habitats for fish and other invertebrates
- The potential of re-establishment of coral after damage
- Genetic diversity (within and between reefs)
- Reproduction of *Lophelia*
- The functional role of *Lophelia* reefs in the carbon cycling
- Finding what constitutes suitable habitat

Methodology development:

- New mapping and monitoring techniques
- Habitat suitability models
- Selection criteria for protection

Impact studies:

- Effects of reduced pH on calcification rates
- Effects of reduced pH on reproduction and larvae stages
- Impacts of passive bottom fishing gear
- Effects of accidental oil spills
- Effects of the release of drill mud and added chemicals
- Effects of the release of waste feed and faeces from salmon farms
- Effects of the release of chemicals and pharmaceuticals used in the aquaculture industry
- Assessing the extent and effects of coral rubble harvesting

5.2 Attained knowledge since 2008

Basic research:

- New knowledge on the functional role of *Lophelia* framework as habitat for invertebrates and fish and its role in carbon cycling has been described (Wild et al. 2008, Jensen et al. 2008, 2012, Lavaleye et al. 2009, Nygren et al. 2010, Godø et al. 2012, White et al. 2012, Henry et al. 2013, Purser et al. 2013, Schötter et al. 2013, Kutti et al. 2014).
- Sexual reproduction of *L. pertusa* has been described, as has the genetic diversity of some reefs and reef areas (Dahl 2013, Brooke and Järnegren 2013, Larsson et al. in review).

Methodology development:

- Sea-floor mapping is continuously being carried out with new and improved techniques, predictive habitat models have been developed and several new areas have been protected from bottom fishing (Davies et al. 2008, Mortensen et al. 2009, Rengstorf et al. 2013, MAREANO).

Impact studies:

- The effects of mineral particle release (i.e. drill cuttings and natural bottom sediment) on *Lophelia* health have been assessed in the laboratory (Brooke et al. 2009, Larsson et al. 2011, Larsson et al. 2013, Allers et al. in press)
- The effects of bottom trawling on *Lophelia* habitat on the shelf have been assessed (Kutti et al. 2014, D31-CoralFISH).
- Effects of reduced pH on *Lophelia* growth and calcification rates have been assessed (Form and Riebesell 2012, Hennige et al. 2013, Maier et al. 2013).

5.3 Future research needs

More research is urgently needed relating to the effects of ocean acidification on *Lophelia* larvae, juveniles, live colonies and on the dead coral framework (i.e. the reef structure) especially in combination with other stressors such as increased temperature, inorganic and organic particle releases. For coastal and fjord reefs the most relevant effluents to test would be organic waste from the aquaculture industry, release of mine tailings through submarine tailings disposal. For offshore reefs the most relevant effluents to test would be drill cutting and drill mud released during drilling of exploration wells and the effects on resuspension of natural sediments during bottom trawling. There is a clear need for long-term studies (months to years) to assess the effects of multiple stressors.

Genetic connectivity between fjord-, coastal- and offshore reefs and along a longitudinal gradient needs to be quantified to fully assess the vulnerability of these ecosystems and potential for recuperation. It appears highly relevant to investigate the clonal diversity on reefs both in fjords, coastal populations as well as offshore. Mapping of the occurrence of *Lophelia* inside the fjords are also needed to gain a better understanding of the distribution and ecological importance of the species in Norwegian waters.

With the ongoing acidification of the ocean and increased human activities on the shelf and in the fjords the health status of *Lophelia* ecosystems should be assessed regularly. Such monitoring has been initiated with the establishment of the Ocean Observatory Vesterålen within the Hola coral reefs field in 2013 (<https://love.statoil.com>). In addition, IMR has had regular cruises to the Træna coral reef area since 2003. However, there is a need expand on this and to develop a routine monitoring of a few selected *Lophelia* ecosystems. This monitoring should include sampling of physical and chemical data (such as aragonite saturation state) as well as an assessment of the health status of the coral ecosystem (including *Lophelia* and other key species). Non-intrusive assessments of the health status of *Lophelia* could include visual inspections to quantify the linear extension of selected branches, addition of new polyps, the proportion of live and dead coral at reefs and measuring the community respiration of the reef using the eddy correlation systems. Collection of live fragments of *Lophelia* would be necessary to allow a periodic assessment of calcification rates, energy storages and general biomarkers of physiological stress. There is a great need to develop suitable tools for measurement of health of the reefs. Reproductive output can be assessed through histological investigations of fecundity, development stage and size as well as lipid content of gonads. Genotypic richness should be determined for a number of representative reefs both within fjord, on the coast and offshore. Bio-erosion could be quantified by the deployment and collection of pre-weighed fragments of dead coral skeleton. Sites selected for monitoring should include both fjords, coastal and offshore sites. Monitoring of *Lophelia* reefs systems appears especially relevant considering the important ecological functions of the reef systems both as habitat for other species and for carbon remineralization.

6 References

- Abrahamson, W.G. 1980. Demography and vegetative reproduction. In: Solbright OT (ed) Demography and evolution in plant populations. Blackwell Scientific Publications, Oxford, pp. 89-106
- Albright, R. 2011. Reviewing the Effects of Ocean Acidification on Sexual Reproduction and Early Life History Stages of Reef-Building Corals. *Journal of Marine Biology*, vol. 2011, Article ID 473615, 14 pages. doi:10.1155/2011/473615
- Allers, E., Abed, R.M.M., Wehrmann, L.M., Wang, T., Larsson, A.I., Purser, A., de Beer, D. Resistance of *Lophelia pertusa* to coverage by sediment and petroleum drill cuttings. *Marine Pollution Bulletin*. *In press*.
- Anon. 2012. Drilling in sensitive areas. A guideline of "best practices" keeping focus on the seabed environment. Det Norske Veritas AS. 12-2012. 24 pp.
- Anon. 2013. Petroleum resources on the Norwegian continental shelf 2013 Exploration. Report from the Norwegian Petroleum Directorate. www.npd.no 63 pp.
- Auster, P.J. 2005. Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts JM (eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin Heidelberg, p 747-760
- Baillon, S., Hamel, J.F., Wareham, V.E., Mercier, A. 2012. Deep coral-water corals as nurseries for fish larvae. *Front Ecol Environ* 10:352-356.
- Baussant, T. 2012. Skader oljeletingen i nord viktige korallrev? Fakta fra Havet og Kysten. Norges forskningsråd. <http://www.forskningsradet.no/servlet/Satellite?blobcol=urldata&blobheader=application%2Fpdf&blobheadername1=Content-Disposition%3A&blobheadervalue1=+attachment%3B+filename%3DImpactofwater.pdf&blobkey=id&blobtable=MungoBlobs&blobwhere=1274494074305&ssbinary=true>
- Bergstad, O.A. 1991. Distribution and trophic ecology of some gadoid fish of the Norwegian Deep. 1. Accounts of individual species. *Sarsia* 75:269-313.
- Boe, R., V. K. Bellec, M. F. J. Dolan, P. Buhl-Mortensen, L. Buhl-Mortensen, D. Slagstad, and L. Rise. 2009. Giant sandwaves in the Høla glacial trough off Vesterålen, North Norway. *Marine Geology* 267:36-54.
- Bradshaw, C., Tjensvoll, I., Sköld, M., Molvær, J., Magnusson, J., Naes, K., Nilsson, H.C. 2012. Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. *Environmental Pollution* 170:232-241.
- Brooke, S.D., Holmes, M.W., Young, C.M. 2009. Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. *Marine Ecology Progress Series*. 390:137-144.
- Brooke, S., Järnegren, J. 2013. Reproductive periodicity of the deep-water scleractinian coral, *Lophelia pertusa* from the Trondheim Fjord, Norway. *Mar. Biol.*160:139-153
- Brooke S, Ross, S.W., Young, C.M. 2013. Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. *Deep Sea Research Part II: Topical Studies in Oceanography*. <http://dx.doi.org/10.1016/j.dsr2.2012.12.001>
- Buhl-Mortensen, P., Buhl-Mortensen, L., 2014. Diverse and vulnerable deep-water biotopes in the Hardangerfjord. *Marine Biology Research*. 10:253-267.
- Buhl-Mortensen, L., Aglen, A., Breen, M., Buhl-Mortensen, P., Ervik, A., Husa, V., Løkkeborg, L., Røttingen, I., Stockhausen, H.H., 2013. Impacts of fisheries and aquaculture on sediments and benthic fauna: suggestions for new management approaches. *Fisken og Havet* 2/2013.
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* 31:21-50.
- Chung, M.G., Epperson, B.K. 1999. Spatial genetic structure of clonal and sexual reproduction in populations of *Adenophora grandiflora* (Campanulaceae). *Evolution*, 53, 1068-1078

- Ceplitis, A. 2001. The importance of sexual and asexual reproduction in the recent evolution of *Allium vineale*. *Evolution*, 55, 1581-1591
- Cornwall, N. 2013. Submarine tailings disposal in Norway's fjords – is it the best option. Master Thesis. Environmental Management and Policy. University of Lund. IIIIEE Theses 2013:14.
- Costello, M.J., McCrea, M., Freiwald, A., Lundälv, T., Jonsson, L., Bett, B.J., van Weering, T.C.E., de Haas, H., Roberts, M.J., Allen, D. 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald A, Roberts JM (eds) *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin Heidelberg, p 771-799
- Dahl, M. 2013. Conservation genetics of the cold water coral *Lophelia pertusa* (Scleractinia). Doctoral thesis, Univ. of Gothenburg. <http://hdl.handle.net/2077/31819>
- Davies, A. J., Wisshak, M., Orr, J.C., Roberts, J.M. 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep Sea Research I* 55: 1048-1062.
- Davies, A.J., Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., van Haren, H., Roberts, J.M. 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. *Limnol. Oceanogr.* 54:620–629.
- De Mol, B., Van Rensbergen, P., Pillen, S., Van Herreweghe, K., Van Rooij, D., McDonnell, A., Huvenne, V., Ivanov, M., Swennen, R., Henriët, J.P. 2002. Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. *Marine Geology*. 188:193-231
- De Mol, B., Henriët, J-P., Canals, M. 2005. Development of coral banks in Porcupine Seabight: do they have Mediterranean ancestors? In: Freiwald A, Roberts JM (eds) *Cold-water corals and ecosystems*. Springer Verlag, Berlin Heidelberg pp 515-533
- Duineveld, G. C. A., M. S. S. Lavaleye, and E. M. Berghuis. 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Marine Ecology-Progress Series* 277:13-23.
- Duineveld, G. C. A., M. S. S. Lavaleye, M. I. N. Bergman, H. De Stigter, and F. Mienis. 2007. Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. *Bulletin of Marine Science* 81:449-467.
- Dullo, W.-C., Flögel, S., Rüggenberg, A. 2008. Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. *Marine Ecology Progress Series*. 371:165-176.
- Eriksson, O. 1986. Survivorship, reproduction and dynamics of ramets of *Potentilla anserina* on a Baltic seashore meadow. *Vegetatio*, 67, 17-25.
- Fosså, J.H., Skjoldal, H.R. 2009. Conservation of cold-water coral reefs in Norway. In: Grafton, R.Q., Hilborn, R., Squires, D., Tait, M., Williams, M. (eds). *Handbook of Marine Fisheries and Management*. p 215-230.
- Fosså, J.H., Mortensen, P.B., Furevik, D. 2000. *Lophelia* korallrev langs Norskekysten - forekomst og tilstand. *Fisken og Havet 2-2000*. Institute of Marine Research, Norway
- Fosså, J.H., Mortensen, P.B., Furevik, D.M. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* 471:1-12.
- Findlay, H. S., S. J. Hennige, et al. (2014). Fine-scale nutrient and carbonate system dynamics around cold-water coral reefs in the northeast Atlantic. *Scientific Reports*. 4. Article number: 3671. doi:10.1038/srep03671
- Flögel, S., W. C. Dullo, et al. (2014). Geochemical and physical constraints for the occurrence of living cold-water corals. *Deep Sea Research Part II: Topical Studies in Oceanography* 99(0): 19-26.
- Form, A.U., Riebesell, U. 2012. Acclimation to ocean acidification during longterm CO₂ exposure in the cold-water coral *Lophelia pertusa*. *Global Change Biol* 18: 843–853, doi: 10.1111/j.1365-2486.2011.02583.x.

- Freiwald, A., Schönfled, J. 1996. Substrate pitting and boring pattern of *Hyrrokkin sarcophaga* Cederhagen, 1995 (Foraminifera) in a modern deep-water coral reef mound. *Marine Micropaleontology* 28:199-207.
- Freiwald, A. 1998. Geobiology of *Lophelia pertusa* (Scleractinia) reefs in the north Atlantic. Habilitation thesis, Univ. Bremen, 116 pp.
- Freiwald, A., Wilson, J.B., Henrich, R. 1999. Grounding Pleistocene icebergs shape recent deep-water coral reefs. *Sedimentary Geology*. 125:1-8
- Freiwald, A., Hühnerbach, V., Lindberg, B., Wilson, J.B., Campbell, J. 2002. The Sula reef complex, Norwegian shelf. *Facies* 47:179-200.
- Freiwald, A., J. H. Fosså, A. Grehan, T. Koslow, and J. M. Roberts. 2004. Cold-water coral reefs. Out of sight no longer out of mind. UNEP-WCMC. Page 84, Cambridge, UK.
- Gass, S. E., Roberts, J.M. 2006. The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: Colony growth, recruitment and environmental controls on distribution. *Marine Pollution Bulletin* 52:549-559.
- Godø, O.R., Tenningen, E., Ostrowski, M., Kubilius, R., Kutti, T., Korneliussen, R., Fosså, J.H. 2012. The Hermes Lander project – the technology, the data and the evaluation of the concept & results. *Fisken og Havet* 3/2012. 64 pp.
- Gordon, J.D.M., 1999. Considerations of deep-water shark fishes. in: Shotton, R. (Eds.), Case studies of the Managements of elasmobranch fisheries. FAO Fisheries Technical Paper 378/1. Rome.
- Hennige, S. J., L. C. Wicks, et al. (2014). Short-term metabolic and growth responses of the cold-water coral *Lophelia pertusa* to ocean acidification. *Deep Sea Research Part II: Topical Studies in Oceanography* 99(0): 27-35.
- Henry, A.-L., Navas, J.M., Hennige, S.J., Wixks, L.C., Vad, J., Roberts, J.M. 2013. Cold-water coral reef habitats benefit recreationally valuable sharks. *Biological Conservation* 161: 67-70.
- Hovland, M. 2008. Deep-water coral reefs: unique biodiversity hotspots. Springer Praxis, Chichester
- Hovland, M., Jensen, S., Indreiten, T. 2012. Unit pockmarks associated with *Lophelia pertusa* reefs off mid-Norway – more evidence of control by “fertilizing” bottom currents. *Geo-Mar Lett* 32: 545-554.
- Hovland, M., Vasshus, S., Indreeide, A., Austdal, L., Nilsen, Ø. 2002. Mapping and imaging deep-sea coral reefs off Norway, 1982–2000. *Hydrobiologia* 471: 13–17
- Husebø Å, Nøttestad L, Fosså JH, Furevik D, Jørgensen SB (2002) Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471:91-99
- Huvenne VAI, Tyler PA, Masson DG, Fisher EH, Hauton C, et al. 2011. A Picture on the Wall: Innovative Mapping Reveals Cold-Water Coral Refuge in Submarine Canyon. *PLoS ONE* 6(12): e28755. doi:10.1371/journal.pone.0028755
- IPCC. 2013. Summary for Policymakers. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jensen, S., Neufeld, J.D., Birkeland, N.-K., Hovland, M., Murrell, J.C. 2008. Insight into the microbial community structure of a Norwegian deep-water coral reef environment. *Deep-Sea Research I* 55:1554-1563.
- Jensen, S., Bourne, D.G., Hovland, M., Murell, J.C. 2012. High diversity of microplankton surrounds deep-water coral reef in the Norwegian Sea. *FEMS Microbiol Ecol* 82:75-89.
- Jonsson, L. G., Nilsson, P.G., Floruta, F., Lundälv, T. 2004. Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Marine Ecology Progress Series* 284: 163-171

- Kiriakoulakis, K., E. Fisher, G. Wolff, A. Freiwald, A. Grehan, Roberts, M.J. 2005. Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition. In A. R. Freiwald, J.M., editor. *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin.
- Kiriakoulakis, K., Freiwald, A.E., Fisher, E., Wolff, G.A. 2007. Organic matter quality and supply to deep-water coral/mound systems of the NW European Continental Margin. *Int. J. Earth Sci.* 96: 159–170.
- Kutti, T., Bannister, R.J., Fosså, J.H. 2013. Community structure and ecological function of deep-water sponge grounds in the Traena dypet MPA-Northern Norwegian continental shelf. *Continental Shelf Research* 69: 21-30.
- Kutti T, Bergstad OA, Fosså JH, Helle K (2014) Cold-water corals mound and sponge-beds as habitats for demersal fish on the Norwegian shelf. *Deep Sea Research II* 99:122-133.
- Kutti, T., J. H. Fosså, I. Svellingen, O. A. Bergstad, J. Burgos, and S. A. Ragnarsson. 2012. Acoustic assessments of the distribution of fish and zooplankton in relation to cold water coral reefs on the Icelandic and Norwegian continental shelves. Deliverable 20 to the EU FP7 CoralFISH project. pp 31.
- Larsson, A., Purser, A. 2011. Sedimentation on the cold-water coral *Lophelia pertusa*: cleaning efficiency from natural sediments and drill cuttings. *Marine Pollution Bulletin* 62: 1159-1168.
- Larsson, A.I., van Oevelen, D., Purser, A., Thomsen, L. 2013. Tolerance to long-term exposure to suspended benthic sediments and drill cuttings in the cold-water coral *Lophelia pertusa*. *Marine Pollution Bulletin* 70: 176-188.
- Larsson, A.I., Järnegren, J., Strömberg, S.M., Dahl, M.P., Lundälv, T., Brooke, S.D. 2013. Embryogenesis and larval biology of the cold water coral *Lophelia pertusa*. Submitted to *PLoS One*
- Lavaleye, M., Duineveld, G., White, M., Guihen, D., Kirikoulakis, K., Wolff, G.A. 2009. Cold-water coral of the Tisler Reef – Preliminary observations on the dynamic reef environment. *Oceanography* 22: 76-84.
- Le Goff-Vitry, M.C., Pybus, O.G., Rogers, A.D. 2004. Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. *Mol Ecol*,13, 537-549
- Lindberg B (2004) Cold-water coral reefs on the Norwegian shelf - acoustic signature, geological, geomorphological and environmental setting. PhD-Thesis. Department of Geology, University of Tromsø
- Maier C, Schubert A, Berzunza Sánchez MM, Weinbauer MG, Watremez P, et al. 2013. End of the Century pCO₂ Levels Do Not Impact Calcification in Mediterranean Cold-Water Corals. *PLoS ONE* 8(4):e62655.doi:10.1371/journal.pone.0062655
- Martín, J., Puig, P., Palanques, A., Ribó, M. Trawling induced daily sediment resuspension in the flank of a Mediterranean submarine canyon. *Deep-Sea Research II* in press.
- Mienis, F., de Stigter, H.C., de Haas, H., van Weering, T.C.E. 2009. Near-bed particle deposition and resuspension in a cold-water coral mound area at the Southwest Rockall Trough margin, NE Atlantic. *Deep-Sea Research Part I - Oceanographic Research Papers* 56:1026-1038.
- Morrison, C., Ross, S., Nizinski, M., Brooke, S., Järnegren, J., Waller, R., Johnson, R., King, T. 2011. Genetic discontinuity among regional populations of *Lophelia pertusa* in the North Atlantic Ocean. *Conservation Genetics* 12(3): 713-729.
- Mortensen, P.B., Lepland, A. 2007. Ecological consequences of exploration drilling on coral reefs in the Træna Deep. *Fisken og Havet* 7/2007. 39 pp.
- Mortensen, P.B., Fosså, J.H. 2006. Species diversity and spatial distribution of invertebrates on *Lophelia* reefs in Norway. In: Suzuki Y, Nakamori T, Hidaka M, Kayanne H, Casareto BE, Nadaoka K, Yamano H, Tsuchiya M (eds) *Proc 10th Int Coral Reef Symp. Okinawa*, p 1849-1868

- Mortensen, P.B., Hovland, M., Brattegrad, T., Farestveit, R. 1995. Deep-water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64°N on the Norwegian shelf: structure and associated megafauna. *Sarsia* 80:145-158.
- Mortensen, P.B., Dolan, M., Buhl-Mortensen, L. 2009. Prediction of benthic biotopes on a Norwegian offshore bank using a combination of multivariate analysis and GIS classification. *ICES J Mar Sci* 66:2026-2032
- Mueller, C.E., Larsson, A.I., Veuger, B., Middelburg, J.J., van Oevelen, D. 2014. Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. *Biogeosciences* 11: 123-133.
- Møskeland, T., Ulfsnes, A., Sverdrup, L., Moe, J.A., Løkken, M. 2012. Monitoring of a drilling operation within a coral sensitive area - Case Pumbaa (Norway). SPE/APPEA International Conference on Health, Safety, and Environment in Oil and Gas Exploration and Production, Perth, Australia, 11-13 September 2012.
- Neff, J.M. 2005. Composition, environmental fates, and biological effects of water based muds & cuttings discharges to the marine environment: A synthesis and annotated bibliography. Prepared for Petroleum Environmental Research Forum (PERF) and American Petroleum Institute. 73 pp.
- Nordgulen, Ø., Bargel, T.H., Longva, O., Olesen, O., Ottesen, D. 2006. A preliminary study of Lofoten as a potential World Heritage Site basen of natural criteria. NGU Report 2005-086. 27 pp.
- Nygren, A., Eklöf, J., Pleijel, F. 2010. Cryptic species of *Notophyllum* (Polychaeta: Phyllodocidae) in Scandinavian waters. *Org. Divers. Evol.* 10:193-204.
- Olsen, E., Aanes, S., Mehl, S., Holstm J.C., Aglen, A, Gjøsæter, H. 2009. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES J Mar Sci* 67:87-101.
- Ottersen, D., Rise, L., Kneis, J., Olsen, L., Henriksen, S. 2005. The Vestfjorden-Trænadjupet palaeo-ice stream drainage system, mid-Norwegian continental shelf. *Marinr Geology* 218:175-189.
- Purser, A., Larsson, A.I., Thomsen, L., van Oevelen, D. 2010. The influence of flow velocity and food concentration on *Lophelia pertusa* (Scleractinia) zooplankton capture rates. *Journal of Experimental Marine Biology and Ecology* 395: 55-62.
- Purser, A., Ontrup, J., Schoening, T., Thomsen, L., Tong, R., Unnithan, V., Nattkemper, T.W. 2013. Microhabitat and shrimp abundance within a Norwegian cold-water coral ecosystem. *Biogeosciences Discuss.*, 10:3365-3396.
- Purser, A., Orejas, C., Gori, A., 2013. Local variation in the distribution of benthic mega fauna species associated with cold-water coral reefs on the Norwegian margin. *Continental Shelf Research*. 54: 37-51.
- Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, et al. (2011) Man and the Last Great Wilderness: Human Impact on the Deep Sea. *PLoS ONE* 6(8):e22588.doi:10.1371/journal.pone.0022588
- Rengstorf, A.M. Yesson, C., Brown, C., Grehan, A. J. 2013 High resolution habitat suitability modeling can improve conservation of vulnerable marine ecosystems in the deep sea. *Journal of Biogeography* 40: 1702-1714.
- Roberts-Murray J, Wheeler AJ, Freiwald A. 2006. Reefs of the deep: the biology and geology of cold water coral ecosystems. *Science magazine* 321:543-547
- Roberts, J.M., Wheeler, A.J., Freiwald, A., Cairns, S.D. 2009. *Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats*. Cambridge University Press, Cambridge, p.334.
- Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L., Bickers, K. 2000. Ecosystem approaches to fishery management through essential fish habitats. *Bull Mar Sci* 66:535-542
- Ross, S., Quattrini, A.M. 2007. The fish fauna associated with deep coral banks off the southeastern Unites States. *Deep-Sea Research I* 54:975-1007.

- Rüggeberg, A., Flögel, S., Dullo, W.-C., Hissmann, K., Freiwald, A. 2011. Water mass characteristics and sill dynamics in a subpolar cold-water coral reef setting at Stjersund, northern Norway. *Marine Geology* 282: 5-12.
- Sabatier, P., Reyss, J.-L., Hall-Spencer, J.M., Colin, C., Frank, N., Tisnérat-Laborde, N., Bordier, L., Douville, E. 2012. ^{210}Pb - ^{226}Ra chronology reveals rapid growth rate of *Madrepora oculata* and *Lophelia pertusa* on world's largest cold-water coral reef. *Biogeosciences*. 9: 1253–1265
- Schötter, S., Hoffmann, F., Cárdenas, P., Rapp, H.T., Boetius, A., Ramette, A. 2013. Relationships between host phylogeny, host type and bacterial community diversity in cold-water coral reef sponges. *PLOS ONE* 8(2)e5505. doi:10.1371/journal.pone.0055505
- Thiem, Ø., Ravagnan, E., Fosa, J.H., Bernstern, J. 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. *Journal of Marine Systems* 60:207-219.
- Thorsnes, T., Fosså, J.H., Christensen, O. 2004. Deep-water coral reefs. Acoustic recognition and geological setting, *Hydro International*, 8: 26–29
- Tenningen, E. E. 2011. Morvin environmental monitoring report 2009-2010 (Statoil). Institute of Marine Research, Bergen. 125 pp. http://www.imr.no/filarkiv/2010/10/morvin_environmental_monitoring_report_2_.pdf/nb-no
- Ulfesnes, A., Haugland, J.K., Weltzien, R. 2013. Monitoring of drilling activities in areas with presence of cold water corals. Det Norske Veritas AS. 2012-1691. 27 pp.
- Van Oevelen, D., GCA Duineveld, MSS Lavaleye, F Mienis, K Soetaert and CHR Heip 2009. The cold-water coral community as hotspot of carbon cycling on continental margins: a food web analysis from Rockall Bank (northeast Atlantic). *Limnology and Oceanography* 54:1829–1844
- Wagner, A., Purser, A., Thomsen, L., Jesus, C.C., Lundälv, T. 2011. Particulate organic matter fluxes and hydrodynamics at the Tisler cold-water coral reef *Journal of Marine Systems* 85: 19–29
- Wehrmann, L.M., Knab, N.J., Pirllet, H., Unnithan, V., Wild, C., Ferdelman, T.G. 2009. Carbon mineralization and carbonate preservations in modern cold-water corals reef sediments on the Norwegian shelf. *Biogeosciences* 6: 663-680.
- Wheeler, A.J., Beyer, A., Freiwald, A., de Haas, H., Huvenne, V.A.I., Kozachenko, M., Roy, K.O.-L., Operbecke, J. 2007. Morphology and environment of cold-water carbonate mounds on the NW European margin. *Int. J. Earth. Sci. (Geol. Rundsch.)* 96:37-56.
- White, M., Mohn, C., de Stigter, H., Mottram, G. 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald A, Roberts JM (eds) *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin Heidelberg, p 503-514
- White, M., Wolff, G.A., Lundälv, T., Guihen, D., Kiriakoulakis, K., Lavaleye, M., Duineveld, G., 2012. Cold-water coral ecosystem (Tisler Reef, Norwegian Shelf) may be a hotspot for carbon cycling. *Marine Ecology Progress Series* 465: 11-23.
- Wild, C., Mayr, C., Wehrmann, L., Schötter, S., Naumann, M., Hoffmann, F., Rapp, H.T. 2008. Organic matter release by cold-water corals and its implication for fauna-microbe interactions. *Marine Ecology Progress Series*. 372:67-75.
- Williams, T., Helle, K., Aschan, M., 2008. The distribution of chondrichthyans along the northern coast of Norway. *ICES J. Mar. Sci.* 65, 1161-1174.
- Wisshak, M., Schönberg, C.H.L., Form, A., Freiwald, A. 2012. Ocean Acidification Accelerates Reef Bioerosion. *PLoS ONE* 7(9): e45124. doi:10.1371/journal.pone.0045124



The Norwegian Institute for Nature Research (NINA) is Norway's leading institution for applied ecological research.

NINA is responsible for long-term strategic research and commissioned applied research to facilitate the implementation of international conventions, decision-support systems and management tools, as well as to enhance public awareness and promote conflict resolution.

ISSN: 1504-3312
ISBN: 978-82-426-2640-0

Norwegian Institute for Nature Research

NINA head office

Postal address: P.O. Box 5685 Sluppen, NO-7485 Trondheim, NORWAY

Visiting address: Høgskoleringen 9, 7034 Trondheim

Phone: +47 73 80 14 00

E-mail: firmapost@nina.no

Organization Number: 9500 37 687

<http://www.nina.no>

Cooperation and expertise for a sustainable future