Thesis for the Degree of Doctor of Philosophy

Conservation genetics of *Lophelia pertusa*

Mikael Dahl

UNIVERSITY OF GOTHENBURG

FACULTY OF SCIENCE
DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

Akademisk avhandling för filosofie doktorsexamen i Naturvetenskap med inriktning marin ekologi, som med tillstånd från Naturvetenskapliga fakulteten kommer att försvaras offentligt fredagen den 15:e mars 2013 kl. 14.00 i stora föreläsningssalen, Institutionen för Biologi och miljövetenskap, Lovéncentret – Tjärnö, Strömstad

Examinator: Professor Per Jonsson, Institutionen för Biologi och miljövetenskap, Göteborgs Universitet

Fakultetsopponent: Doktor Martin Taylor, School of Biological Sciences, Bangor University, Gwynedd, UK

ISBN: 91-89677-54-4

Conservation genetics of *Lophelia pertusa*

Cover illustration: The drawing of *Lophelia pertusa* is taken from the publication Gunnerus, J.E. – 1768. Om nogle Norske Coraller. *Det Kongelige Norske Videnskabers Selskab Skrifter*, 4, 38-73.

ISBN: 91-89677-54-4

Printed by Ale Tryckteam AB, Bohus, Sweden 2013

Too my family

“For too long, the world acted as if the oceans were somehow a realm apart – as areas owned by none, free for all, with little need for care or management... If at one time what happened on and beneath the seas was ‘out of sight, out of mind', that can no longer be the case.”

Kofi Annan, UN Secretary General, Mauritius, 2005

ABSTRACT

The cold-water coral *Lophelia pertusa* is the most important reef-building coral species in the NE Atlantic Ocean. The reef framework creates a complex structural habitat that sustains high species diversity in the deep-sea. During the last decades, powered by improvements in deep-sea research equipment, it has become clear that threats imposed by anthropogenic activities have caused considerable destruction of these cold-water coral ecosystems.

To assist cold-water coral management and conservation, this thesis aim to improve the understanding of *L. pertusa* biology, focusing on genetic population structure, larval development and restoration.

First, we investigated the fine-scale genetic structure within and among reefs in the NE Skagerrak using microsatellite markers. Clonal reproduction was common resulting in an aggregated distribution of genotypes within reefs. There was a significant genetic differentiation among reef localities at spatial scales of tens of km (paper I). On the scale of the NE Atlantic genetic structure could be explained in terms of holocene range expansion (paper II). Finally, we compared the whole mitochondrial genomes of two geographically separated individuals (Norway and Italy, respectively) and found virtually no sequence differences (paper III). This result corroborates previous findings of low diversity in Anthozoa mitochondrial DNA, but is also in line with the hypothesis of long-range gene flow and a Mediterranean origin of *L. pertusa* populations on the Scandinavian continental margin.

The larval stage is the only dispersal phase of corals and therefore tightly associated with connectivity among reefs. Using laboratory crossings and larval rearing we show for the first time that *L. pertusa* produce pelagic larvae that can live in the watercolumn for several weeks (paper IV).

Bottom trawling has caused extensive destruction of cold-water coral habitats worldwide. In Sweden only one of six reefs is still alive, but the risk that this reef also will be lost is imminent. We tested the possibility to restore a damaged reef by using transplants of *L. pertusa* from a healthy reef (paper V). More than three years after the deployment with transplanted coral the survival of fragments was 76%, and the mean size of fragments increased with 39 %, demonstrating the potential for active restoration of cold-water coral habitats.

Populärvetenskaplig sammanfattning på svenska

Korallrev är kända för den rika biologiska mångfald de ger upphov till, både i tropikerna likväl på högre breddgrader som i Skandinavien. I Sverige har vi endast en revbyggande korallart och det är en kallvattenkorall som heter ögonkorall (*Lophelia pertusa*). Denna kräver en fullt marin miljö med en stabil hög salthalt och låg vattentemperatur året om; i Sverige kan man bara hitta dessa förutsättningar i norra Bohuslän där djupvatten från Atlanten leds in genom den Norska rännan. Att det finns kallvattenkorallrev i Sverige har varit känt sedan mitten på 1920-talet. Då kunde man finna levande korall på ett antal lokaler i Kosterfjorden. Idag finns det bara ett levande rev kvar i svenska vatten, Säckenrevet som är i mycket dåligt skick, svårt sargat av direkt åverkan från trålning och dessutom utsatt för ökad sedimentering av partiklar p.g.a. övergödning och resuspension av bottensediment från trålning i närheten. Detta är dock inte endast ett lokalt problem utan är vanligt förekommande i alla hav. Det största och mest akuta hotet mot kallvattenkoraller utgörs just utav fiske med bottensläpande redskap som ”manglar” havsbotten. Bottentrålar kan inom loppet av minuter förstöra något som har tagit hundratals år att bygga upp.

Denna doktorsavhandling eftersträvar att öka kunskapen om kallvattenkorallers biologi som är viktig i ett bevarandeperspektiv. Med hjälp av genetiska markörer har jag beskrivit hur enskilda kloner fördelar sig över ett korallrev, och baserat på storleken av dessa kloner funnit att vissa individer av ögonkorall kan bli flera tusen år gamla. Den äldsta individen beräknas kunna vara upp mot 6000 år gammal. Vidare har vi beskrivit den relativa balansen av asexuell och sexuell förökning för att bättre förstå viktiga populationsprocesser.

Genetiska markörer kan även användas för att skatta graden utav migration och genflöde mellan olika revområden. Genflöde mellan rev sker via sexuellt reproducerade larver som driver med havsströmmar. Att tillståndet för Säckenrevet har varit dåligt och gradvis försämrats har gjort att förhoppningar har satts till att återetablering uv revet skulle kunna ske genom införsel av larver från andra rev som finns på relativt nära avstånd i nordöstra Skagerrak. Dessvärre visar våra resultat (artikel I) att Säckenrevet är genetiskt isolerat från de andra korallrev i nordöstra Skagerrak vilket betyder att sannolikheten för kolonisering av nya korallarver i Säcken är låg.

Ögonkoraller är även mycket vanligt förekommande utefter den Europeiska kontinentalsockeln på 200-400 meter djup, och stora områden utanför Norge har blivit förstörda utav trålning. I artikel II beskriver vi balansen mellan sexuell och asexuell reproduktion, samt spridningsmönstret baserat på prover insamlade från olika revområden längs den Europeiska kontinentalsockeln: Med genetiska markörer kunde det säkerställas att klonalitet utgör en mycket viktigt faktor för tillkomsten och fortbeståndet av dessa rev. Vi kunde även identifiera ett antal genetiska rev-kluster: Koraller från rev utanför Mauretaninen och medelhavet visade sig tillhöra separata genetiska kluster. Vidare visade det genetiska mönstret från två olika genetiska markörer (mikrosatellit DNA, artikel II och mitokondrie DNA, artikel III) att koraller från medelhavet har spridits ut till sydvästra brittiska öarna, och därifrån genom den nordatlantiska strömmen snabbt spridits vidare upp längs den skandinaviska kontinental sockeln och etablerat nya rev. Tillsammans med information från andra forskningsfält, t.ex. geologi, glaciologi, och paleoceanografi, så visar det genetiska spridningsmönstret hur dessa korallpopulationer etablerades snart efter att den Europeiska inlandsisen drog sig tillbaka från Skandinavien.

Det finns olika metoder för att få reda på hur geografiskt skilda populationer är kopplade till varandra (konnektivitet), kunskap som är väldigt viktigt vid planering av nätverk av skyddade områden. Ifall de områden som väljs ut inte har någon biologisk förankring kan skyddet bli verkningslöst. I de tidigare artiklarna (I-III) används genetiska markörer för att ta fram information om konnektivitet. Alternativt, kan man göra med oceanografiska modeller där simulerade larver visar hur områden är anslutna till varandra. Dessa modeller är beroende av adekvat information om larvstadiets längd o.d. I artikel IV beskriver vi hur ögonkorall larver utvecklas efter befruktning, samt deras beteende. Denna information kommer bli mycket viktig för att kunna utveckla modeller som på ett bra sätt kan simulera spridningsvägar. På detta sätt kan man även få information om områden man inte tidigare har prover ifrån.

Baserat på de resultat som har framkommit om Säckenrevet, vilket utgör en unik biotop i Sverige, beslutade vi att undersöka om det med aktiva metoder skulle vara möjligt att hjälpa revet att återhämta sig. I artikel V undersöks om det är möjligt att förflytta levande koraller från friskt rev till Säckenrevet. De koraller som hämtades karakteriserades genetiskt för att det ska vara möjligt att veta hur många genetiska individer som flyttas. Detta görs för att försäkra sig om att den genetiska mångfaldes bibehålls, och att materialet som används inte är från en och samma klon. Förhoppningen var att korallerna skulle överleva den behandling som krävs för att förflytta dem, och att de ska kunna hjälpa till med återetableringen, dels genom asexuell förökning (kloner) och dels genom sexuell reproduktion, med larver som kan etablera sig i populationen. Efter mer än tre års uppföljning kan vi se att korallerna klarar detta.

List of papers

This thesis is based on following publications/manuscripts. Publications will be referred to in the text by Roman numerals as follows:

I. Dahl M.P., Pereyra R. T., Lundälv T., André C. (2012) Fine-scale spatial genetic structure and clonal distribution of the cold-water coral *Lophelia pertusa*. *Coral Reefs*, 31, 1135-1148.

II. Dahl M.P., Pereyra R. T., Lundälv T., Järnegren J., Arnaud-Haond S., André C. (Manuscript) Genetic structure and the postglacial colonization process in the East Atlantic Ocean of the cold-water coral *Lophelia pertusa*.

III. Flot J.-F., Dahl M.P., André C. (In review) *Lophelia pertusa* from the Ionian and Barents seas share identical nuclear ITS2 and near-identical mitochondrial genome sequences. *BMC Research Notes*.

IV. Larsson A. I., Järnegren J., Strömberg S. S., Dahl M.P., Lundälv T., Brooke S. (Manuscript) Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*.

V. Jonsson L.G*., Dahl M.P*., Strömberg S.S., Lindegarth M., André C., Lundälv T. (Manuscript) In situ measurement of survival and growth of genotyped transplanted fragments of the cold-water coral reef *Lophelia pertusa*. *equal contribution

Paper I is reprinted with the kind permission from Springer Science and Business Media.

TABLE OF CONTENTS

Introduction

The deep-sea (>200 m) is the largest biome on Earth representing more than 65% of the surface and 95% of the global biosphere. The average depth of the oceans is 3800 meters and the deepest place on Earth is the Mariana Trench, 11 034 m deep. Human exploration has produced considerably more detailed and accurate maps of the Moon and the planet Mars than the bottoms of the deep sea. The deep-sea is truly the last great wilderness of our planet, and only a tiny amount of the deep seafloor has been subject to biological investigations.

Deep-sea research

During the 19th century there was a debate whether life occurred at depths below 300 fathoms (ca 550 m). Edward Forbes hypothesised in 1844 that no life could exist below that depth and the debate was the offset for modern deep-sea research and exploration. Sir John Ross provided the first evidence of a deep-sea species in 1818 when he found the ophiuroid *Gorgonocephalus caputmedusae* while sounding at 1600 m in the Northwest Passage, but Ross' evidence never got an airing. It was not until much later scientific evidence for deep-sea fauna was presented. Michael and Georg Ossian Sars, two pioneers in deep-sea research, found life in abyssal depths of Norwegian fjords. Michael Sars described the fauna of Norwegian fjords in a series of reports, and one of his dredging expeditions resulted in the description of the first stalked crinoid (*Rhizocrinus lofotensis*) in 1867-68. That publication spurred another famous pioneer within deep-sea exploration, the Scottish naturalist Charles Wyville-Thomson, who later led the worldwide HMS *Challenger* expedition (1872-1876), on which they found animals on all abyssal plains that were sampled. Decades of deep-sea research followed and the *Galatea* expedition (1950-52) showed that animals live at all depths, including the deepest parts of the sea. But even though life had been found at abyssal depths, the view on the deep-sea environment remained to be considered as a uniform, of low biodiversity, without seasonality, no primary production, constant temperature, shortage of food; tranquil and invariant. It was within this conception of the world the United Nations Convention on the Law of the Sea (UNCLOS) was written and signed in 1972. The high diversity of the deep-sea was not revealed until late 1960s (Hessler and Sanders

1967) but it took some years for evidence to accumulate to support a paradigm shift. Increasingly sophisticated advances in deep-sea submersibles, image- and sampling technologies changed the old view substantially. Today, we know that the bottoms of the sea is not flat but have hundred of thousands seamounts, giant underwater mountain chains, canyons and trenches. We also know that the deep-sea environment is a highly dynamic environment where tidal motions, thermohaline circulation, internal waves causing benthic storms, dense shelf water cascading etc create high habitat heterogeneity, which supports high biodiversity. The discovery of hydrothermal vents in the late 1970´s even changed the way we define life. Since then many exciting discoveries in the deep sea have been made, i.e. cold seeps, brine pools, chemosynthetic ecosystems on whale falls, and cold-water coral ecosystems, that has supported the presence of high biodiversity.

Cold-water corals

Corals are major habitat-forming organisms in the deep sea as well as in shallow areas. Corals is a diverse taxonomic group and may be defined as “Animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous, usually microscopic, individual sclerites, or that have a black, horn-like, proteinaceous axis” (Cairns 2007), which includes seven taxa (Scleractinia, Zoanthidea, Antipatharia, Octocorallia, Stylasteridae, Hydractiniidae, Milleporidae). Using this definition there are 5080 species of coral described and 1482 of those are extant species of scleractinian corals (Cairns 2007). The number of azooxanthellate and zooxanthellae is roughly equal. Most azooxanthellate corals are solitary, and of those that are colonial only a few have the potential to form reef frameworks.

Many names have been used to discriminate the corals not being warm-water shallow tropical species. Terms like ahermatypic- or azooxanthellate corals, deep-sea corals, deep-water corals, cold-water, cool-water corals are commonly used interchangeably and/or synonymously. This is clearly incorrect, but it is problematic to find a term that distinguishes a particular group of species from another since all species have different life-history strategies and there are no clear biological boundaries. The term zooxanthellate refers to whether a coral harbors symbiotic dinoflagellates or not. The term hermatypic refers to whether a coral species is capable of forming a reef structure or not. Furthermore, depth-based definitions are inadequate since “cold-water” corals occur over an extensive depth distribution, i.e. *Lophelia pertusa* lives from 39-3383 m depth. There are also facultative zooxanthellate corals (eg *Oculina varicosa*) that harbours zooxanthellae at shallow depths and are without in the deep. Zooxanthellate corals are restricted bathymetrically (0-50 m) and geographically (30°N - 30°S) by the one-celled algal symbionts that lives in their endodermal tissue. These restrictions limits these corals to occur along the shores of continents and islands in tropical shallow waters; optimal temperature for most tropical corals is 26–27°C, but there are reefs in the Persian Gulf adapted to temperatures of 13°C in winter and 38°C in summer. The deep-sea coral *Lophelia* have been found in water holding 13.8°C so there is also an overlap in temperature. Azooxanthellate corals that do not rely on symbiontic algae have a much broader range: from Barents Sea (71°N) to the Ross Sea (78°S) from the surface down to more than 6300 meters, the deepest reported at 6 328 m (Keller 1976). Azooxanthellate corals occurs also in a much wider temperature range from -1 up to 29°C. Even though it is difficult to find a proper name, the term cold-water corals are used in this thesis.

The term reef have also been controversy: a decade ago there was a debate whether the structures created by cold-water corals should be referred to as reefs or not. One definition of a reef commonly used in the tropical coral reef literature is that a reef is a structure just above or below the surface that can cause ships to run aground. However, the European Habitats Directive 92/43/EEC, define a reef as a biogenic concretions that arise from the sea floor in the littoral or sublittoral zone and according to this definition is there a some azooxanthellate hermatypic cold-water coral species that create proper reefs.

Tropical shallow-water coral reefs and cold-water coral reefs form a continuum of coral ecosystems that stretches from the surface down to several thousand meters depth. The range of reef ecosystems are similar in many aspects but fundamentally different in others: Tropical corals are dependent on their zooxanthellate symbionts and therefore utterly dependent on sunlight while cold-water corals are dependent on the supply of current-transported particulate organic matter and zooplankton. Another major difference is the number of species that creates the reef habitat. Typically tropical reefs is a mosaic composed of hundred of species that compete and interact with each other. In contrast, there are only six azooxanthellate reef framework-forming species worldwide (Cairns 2001), and in a single reefs are typically created by only one species with occasional minor contribution of other species. The six cold-water coral reef builders are *Lophelia pertusa*, *Madrepora oculata*, *Oculina varicosa*, *Goniocorella dumosa*, *Solenosmilia variabilis* and *Enallopsammia profunda* (Cairns 2001).

Importance of cold-water corals

Deep-water scleractinian corals constitute the foundation of diverse marine ecosystems worldwide (Freiwald *et al*. 2004). The reef framework forms a complex three-dimensional structure that provides habitat, feeding grounds, recruitment and nursery functions for thousands of other deep-water organism, including commercial fish species (Buhl-Mortensen *et al*. 2010). Cold-water reefs host highly diverse faunal communities characterised by high abundance and biomass, and more than 1300 species have been found on *Lophelia* reefs in NE Atlantic (Roberts *et al*. 2006), but that number of species is expected to be much higher since the fauna is incompletely sampled. Mortensen and Fosså (2006) compared the species they found from one study with the species found in five other published investigations. Most of the species (536 of 796) was only found in one study area while only 21 species was found in all studies. Hence, the variation in species composition between reef localities is extremely high and the total number of species that exists on cold-water corals reefs will increase dramatically as more studies will be performed.

Moreover, recent research has discovered that the deep-sea is an important area of speciation. Previously it has been assumed that corals evolved in shallow tropical waters and migrated down in the deep where they diversified. This view have recently been proven incorrect by Lindner *et al*. (2008) who showed that that the second most diverse group of scleractinian corals, the stylasterid corals, originated and diversified extensively in the deep sea, and subsequently invaded shallow-water ecosystems at least four times (three times in the tropics and one time in temperate North Pacific).

A comprehensive world-wide approximation of the diversity of deep-water (>50 meters depth) azooxanthellate corals showed that the diversity centers were remarkably similar to those described for shallow-water corals (Cairns 2007).

Bottom-line is that cold-water coral ecosystems are important biodiversity hotspots and constitute a biological resource with intrinsic and socio-economic value. Additionally, they serve as a storage bank of rich genetic resources for future human utilisation (Johansen *et al*. 2010).

Threats to cold-water corals

Corals are in serious decline world-wide (Carpenter *et al*. 2008; Freiwald *et al*. 2004). Since the mid-1980´s the deeper parts of the world´s oceans have been increasingly impacted by humans activities. Later technical advancement, i.e. Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUV) and benthic lander systems have made a major difference to deep-sea research. Ironically, when we have the technical means to discover and understand the incredible diversity and ecological importance of these ecosystems, we also realise it is time to act before they are gone.

Fig 1. The photo to the left show a trawl that is dragged across the bottom, and the photo to the right show a pair of trawldoors standing next to two cars. Photo: Mikael Dahl

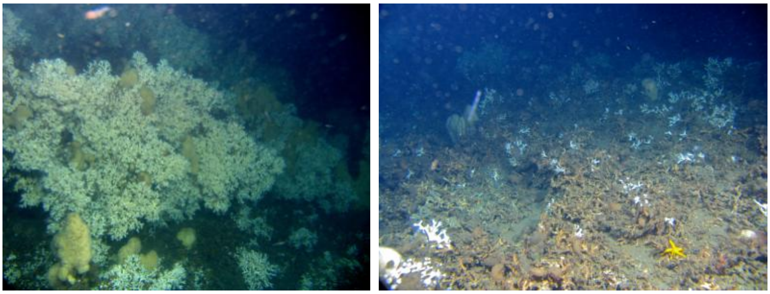

Fig 2. *Lophelia pertusa* colonies at the Tisler reef, NE Skagerrak. Left photo show an undisturbed area and the photo to the right show how it looks like a few years after a trawl have been dragged over the coral framework. Photo: Tomas Lundälv, Sven Lóven centra for marine sciences – Tjärnö

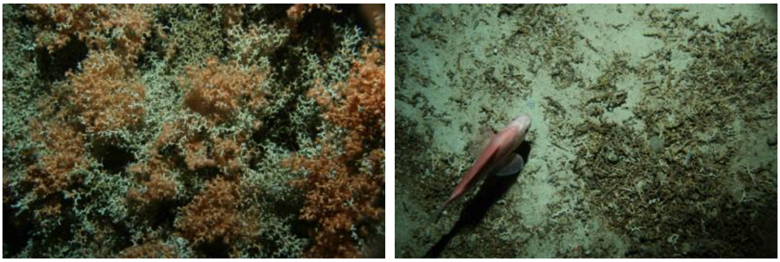

Fig 3. Untrawled *Madrepora oculata* (left) and trawled (right) seamounts in New Zealand area. Photos courtesy of Malcolm Clark, NIWA, Wellington, New Zealand.

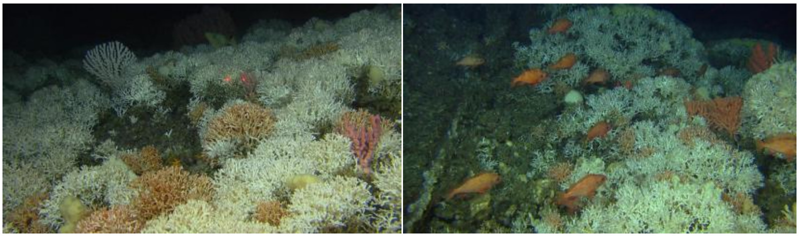

Fig 4. *Lophelia pertusa* colonies at Korallen. Photo: Pål Buhl-Mortensen, Intitute of Marine Research, Norway

There are many documented and potential sources of threats to cold-water corals, e.g. bottom-trawling, other fishing techniques with bottom-tending gear, hydrocarbon exploration and production, cable and pipeline placement, bioprospecting, scientific sampling, waste disposal and dumping, coral exploitation and trade, sub-seabed sequestration of CO_2, ocean acidification, and mineral exploration. The main threats to cold-water corals are attributed to bottom trawling and ocean acidification (Gianni 2004; Guinotte *et al*. 2006; Turley *et al*. 2007). Cold-water coral reefs have long been known as rich fishing grounds, attracting commercial fishing activities close to the coral habitat. Unfortunately, bottom-tending fishing gear has shown to cause major disturbance and destruction to deep-sea coral communities, in particular bottom-trawling which has been identified as one of the greatest threats to cold-water coral ecosystems (Rogers 1999, Freiwald 2004). Cold-water corals are slow growing and the calcium carbonate skeleton is brittle and fragile, characteristics that make them particularly vulnerable to physical damage. Damages from bottom-trawling have been identified all around the world including Australia (Koslow *et al.* 2000; Koslow *et al.* 2001) Ireland (Hall-Spencer *et al.* 2002; Grehan *et al*. 2005), USA (Stone 2006; Reed *et al*. 2007; Waller *et al.* 2007), England (Wheeler *et al.* 2005), New Zeeland (Probert 1997), and Canada (Gass and Willison 2005). Norway estimate their total coral distribution to cover 1500 - 2000 km^2, of which 30 - 50% have been destroyed or damaged by trawling (Fosså *et al.* 2000; Fosså *et al.* 2002).

One of the remaining misconceptions of the deep-sea is that it is too remote and too vast to be negatively affected by anthropogenic activities. Halpern *et al*. (2008) assembled a global map showing the cumulative human impact on marine ecosystems (Fig. 5) showing that there are nearly no places unaffected by human activities.

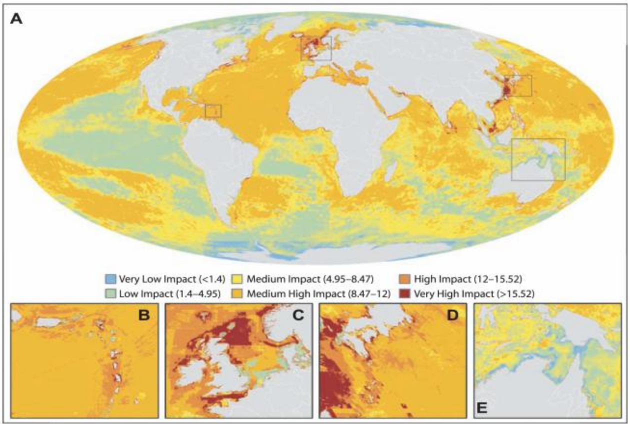

Fig 5. A) Global map from Halpern *et al*. (2008) showing cumulative human impact on marine ecosystems. Insets B) Caribbean C) the North Sea D) Japanese waters E) Torres strait. Reprinted with permission by Ben Halpern.

Biology of Lophelia pertusa
Taxonomic classification

The oldest known record of *Lophelia pertusa* is from the 1755 book *The Natural History of Norway* by the Right Reverend Erich Pontoppidan. Carl von Linné described the species 1758 and the systematic classification is the following according to Zibrowius (1980).
Phylum Cnidaria
Class Anthozoa
Subclass Hexacorallia
Order Scleractinia
Family Caryophyllidae (Gray 1846)
Subfamily Desmophyllinae (Vaughan and Wells 1943)
Genus *Lophelia* (Milne Edwards and Haime 1849)
Species *Lophelia pertusa* (Linnaeus 1758)

Etymology
The name is derived from the Greek *lophos* (crest) and *helios* (sun), and the Latin word *pertusus* (perforated), referring to the sun-like appearance created by the prominent polyp mouth with the many tentacles surrounding it.

Distribution of Lophelia pertusa

Even thought the existence of *Lophelia pertusa* have been known for more than 250 years biological and ecological knowledge about the species are still scarce. Hitherto, much of the research has been focused on distribution, mapping and habitat characterization. (Dons 1944; LeDanois 1948, Wilson 1979a, Fredriksen *et al*. 1992; Fosså *et al*. 2000; Mortensen *et al*. 2001; Orejas *et al*. 2009). The full extent of the geographic distribution is still unknown but it is clear that it has a wide geographic distribution (Fig 6). The occurrences of *Lophelia* cover an extensive depth-interval ranging from 39 m in the Trondheimsfjord (Rapp & Sneli 1999) to 3383 m at the New England seamount chain in the North Atlantic Ocean (Squires 1959). It is definitely the most important cold-water coral in the Northeast Atlantic Ocean (Freiwald 1998; Rogers 1999; Roberts *et al*. 2006), but it has been recorded from both sides of the Atlantic and from both hemispheres (ranging from 55°S to 70°N). It is important to bear in mind that there is a clear bias in research effort and seabed mapping from the NE Atlantic, and research expeditions at the continental shelves off the coast of Africa and South America continuously report new discoveries of *Lophelia* occurrences, i.e. outside Uruguay (Carranza *et al*. 2012), Brazil (Kitahara 2007), Angola (Le Guilloux 2009), and Mauritania (Eisele *et al*. 2011). Given the large distribution area and population density *Lophelia pertusa* is likely the most abundant scleractinian coral species on earth.

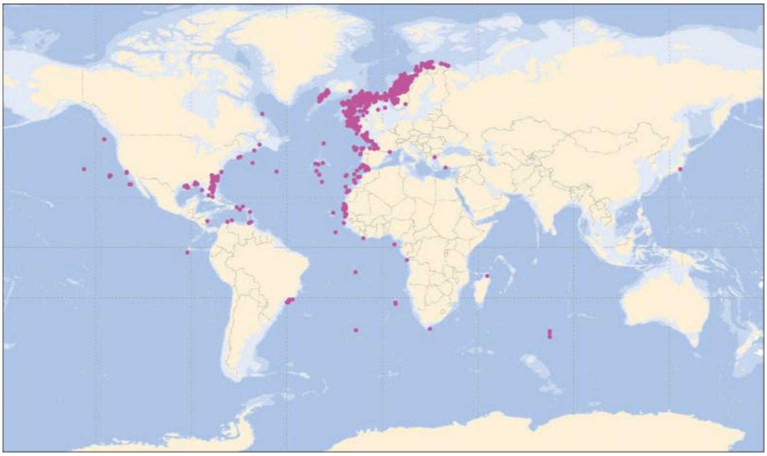

Fig 6. *Lophelia pertusa* distribution. From UNEP-WCMC

The physical requirement of Lophelia

Comparing the distribution map of *Lophelia* with similarities and variation among sites can help understanding of the factors limiting the distribution. *In situ* measurements of depth, temperature, salinity, water velocity, nitrate, phosphate, silicate, dissolved oxygen, dissolved inorganic carbon, etc. with landers during the last decade has considerable improved our understanding of the physical requirement for coral growth. *Lophelia* occurs in oceanic water masses in water temperatures ranging from 4-14°C and a salinity of 35-39 (Freiwald *et al*. 2002; Taviani *et al*. 2005). It is commonly found in areas with relatively low amount of dissolved oxygen (3-5 ml l^{-1} in the North East Atlantic)(Freiwald 2002), but have also been found in areas with both lower (2.6-3.2 ml l^{-1}) in the Gulf of Mexico, Schroeder 2002) and higher (4.8-6.7 ml l^{-1}) in the Swedish Kosterfjord, (Wisshak *et al.* 2005) amount of dissolved oxygen. Dullo *et al*. (2008) found that living corals occur in watermasses within a potential density envelope of sigma-theta, σ_θ, from 27.35-27.65 kg m^{-3}.

The knowledge of physical requirements has been used to develop high-resolution predictive models of habitat suitability for cold-water corals (Davies *et al*. 2008; Tittensor *et al*. 2009; Davies and Guinotte 2011). These studies lend support for existing distribution maps and clearly show that we can expect the highest concentration of *Lophelia pertusa* in the northeast Atlantic Ocean.

Reproduction

Scleractinian corals have two sexual reproductive systems (gonochoristic and hermaphroditic) with two modes of development (brooding and spawning). In addition at least five different mechanisms of asexual reproduction have been reported: fragmentation, polyp bail-out, polyp expulsion, polyp balls and asexual production of larvae.

Until recently neither spawning nor larvae had been described for *Lophelia*, and the actual time of spawning was not known. Waller and Taylor (2005) suggested that *Lophelia* had an annual gametogenic cycle with spawning around January/February based on the results from a histological study. From the histology they concluded that *Lophelia* is a gonochoristic species, that the larvae probably had a lecithotrophic larval phase, and that the fecundity was very high with an average of 3 300 oocytes per cm^2. Although *Lophelia* larva had never been observed occurrences on Oil platforms in the North Sea indicated that a planktonic stage must exist (Gass and Roberts 2006). Information on timing of spawning and larval behaviour is needed for the construction of predictive oceanographic models of connectivity.

Previously only one study has used molecular markers to investigate the genetic structure of *Lophelia* (LeGoff-Vitry *et al*. 2004). Based on six populations distributed from the northwest Iberian Peninsula to mid-Norway, samples from one oil platform in the North Sea, and three fjord populations, the authors concluded that populations in the NE Atlantic form highly distinct offshore and fjord populations. The high differentiation observed for the fjord populations' lead the authors to hypothesise that the partial isolation of fjord populations might represent incipient allopatric speciation sites. Furthermore, the offshore aggregations were significantly differentiated and did not form one panmictic population. Only three out of ten populations showed signs of asexual reproduction in their study.

The only known mechanism of asexual reproduction of *Lophelia* is through fragmentation. A model of *Lophelia* patch development was described in an early study from the Rockall Bank (Wilson 1979b). The model described the rise of circular-like shaped coral patches that are commonly seen on *Lophelia* reefs. The pattern arises from an initial settling event of a single larva, which will metamorphose and establish a coral colony that grow into a small irregular coralbush and later into a roughly hemispherical colony. The colony will continue to grow, but it is only the outer part that is alive. The base of the branches that are no longer alive is weakened over time by bioeroding animals, and at some point parts of the colony will fall off. Some of the polyps on the fragments that fall off will survive and continue to grow; eventually they form new distinct colonies that are genetically identical to the parental colony. As these fragments grow larger and merge they surround the central colony forming a Wilson ring or 'thickets' as described by Squires (1964). The central colony will eventually die due to the reduced water flow within the patch and be reduced to coral rubble, leaving a halo-shaped ring or 'coppice' of coral. Subsequent growth around the outside of the coppice results in concentric circles of growth forming a mature 'coppice'. Another typical reef structure is the elongated reef shape that is common along the Norwegian coast. These reefs only have one living side that form a ´head´ of the structure and a long dead ´tail´ giving the reef structure an elongated form. The shape comes from local terrain features that are exposed to a unidirectional current where the living part grows against the current.

Conservation genetics

The discipline of conservation biology is very recent; the term conservation biology was first used in 1978, and was born as a response to the worldwide mass extinction of species. The new discipline was set out to bridge the gap between theoretical ecology and population biology on one hand and conservation policy and practise on the other. Conservation biology and the concept of biodiversity emerged together to form modern conservation science and policy. Marine Conservation Biology was born for the same reasons as the terrestrial environment, awareness of collapsing fish stocks worldwide and that the world´s coral reefs were deteriorating, following the First Symposium on Marine Conservation Biology in 1997.

Conservation genetics is an interdisciplinary scientific field that apply genetic methods to the conservation and restoration of biodiversity. Molecular ecology and population genetics is two of the research fields that commonly are used, that also is the main approach in this thesis. Population genetics is the study of allele frequency distribution and change under the influence of the four main evolutionary processes: natural selection, mutation, migration, and genetic drift. ***Natural selection*** is the non-random process by which alleles become more or less common as a result of that some organisms are better adapted to their environment and will survive and produce more offspring. ***Mutation*** occurs commonly during meiosis and DNA replication, but mutations are also caused by radiation, viruses, mutagenic chemicals, and transposons. ***Migration*** (or gene flow) is the main mechanism of connectivity. With migration alleles are transferred from one population to another making them more similar to each other. ***Genetic drift*** is the change in the relative allele frequency over time. Drift occurs in a population due to random sampling and chance, i.e. alleles in the offspring are a random sample of those in the parent population. Chance also plays a role in determining whether a specific individual survives until it has the chance to reproduce. The random loss of genetic variation from generation to generation is inversely proportional to the effective population size. Thus, when a new population is established by a small number of colonising individuals genetic variation is greatly reduced (a founder effect). Small populations have low genetic variation, are more sensitive to genetic drift and have increased inbreeding.

In all wild populations these evolutionary forces are ongoing natural processes that acts to change the allele frequencies over the lifetimes of individuals, populations and species. Over time, populations can become differentiated from one another, which is commonly quantified with F-statistics. The parameter F_{ST} is the genetic measure of differentiation, or how genetic variation is distributed within and among populations. It is defined as $F_{ST} = (H_T - H_S)/H_T$, were H_S in the mean of expected heterozygosities over all subpopulations and H_T is expected heterozygosity in the total populations, ignoring subdivision. F_{ST} is also directly related to the variance in allele frequency among populations and the degree of resemblance among individuals within populations

The advent of molecular markers has greatly enhanced our ability to analyse the genetic variation within and among populations. Molecular markers target small fragments of the genome, representing either genome-wide processes such as drift and migration, or locus-specific differences such as selection and local adaptation (Allendorf and Luikart 2007).

Genetic biodiversity

Genetic diversity is one of the three forms of biodiversity (McNeely et al. 1990) that have been recognised to conserve; the other two are ecosystems and species. Genetic diversity is the raw material for evolution by natural selection; hence genetic factors are also import in the conservation of species and ecosystem diversity.

During the United Nations Conference on Environment and Development (UNCED) 1992 the Convention on Biologica1 Diversity (CBD; www.cbd.int) was signed by more than 150 countries, and is one of the most significant and far-reaching environmental treaties that ever have been developed. All nations agreed upon to stop and reverse the negative impact of human behaviour on the physical environment and biodiversity. In the convention biodiversity is recognized as a key component of the environment. As it states in the preamble: the Contracting Parties ‘are aware of the general lack of information and knowledge regarding biological diversity and of the urgent need to develop scientific, technical and institutional capacities to provide the basic understanding on which to plan and implement appropriate measures.’

In more recent years, the global community has set clear targets for sustainability and biodiversity conservation. At the 2002 World Summit on Sustainable Development, governments adopted a plan to significantly reduce the loss of biodiversity by 2010, with genetic diversity as an explicit goal of the CBD. The 2010-biodiversity target was passed without any of the 191 parties to the CBD have started to monitor gene-level diversity routinely (Laikre et al. 2010). Genetic diversity has been neglected in too many efforts to conserve species, quite surprising considering it is the fundamental force that shapes the biology of living organisms.

AIMS OF THE THESIS

At the beginning of the 00´s it was clear that coral ecosystem in the deep-sea was heavily impacted by bottom trawling. Both local and cold-water coral reefs around the world were seriously threatened and there was an urgent need for conservation measures to be taken.

The overall aim of this thesis was to improve the understanding of biological processes and identify important life-history traits relevant for conservation and management of cold-water coral ecosystems created by *Lophelia pertusa*.

In particular, observations from the Swedish Säcken reef showing that the reef was in a deteriorating state prompted the initiation of this project. Important gaps in knowledge for effective conservation were identified, and a number of scientific questions were formulated.

Three major goals were determined to be the most urgent for informed conservation: The first goal was to determine the distribution of genetic diversity of *Lophelia* at different spatial scales to elucidate patterns of larval dispersal (connectivity and gene-flow): First, one study at the scale of the entire European continental margin, for estimating large-scale gene flow pattern. Second, a small-scale that looked at the gene flow among the five known reef localities in NE Skagerrak, and lastly the distribution of clones within a reef to determine clonal architecture and prevailing reproductive strategies.

The second major goal was to provide information about mode and timing of larval development, information important for the planning of networks of marine protected areas. This goal was achieved owing to corals that were kept at the lab spawned in the aquariums, and hence showed the exact time of spawning. This further allowed us to observe development and behaviour larvae, and corroborate the genetic inheritance.

The third major goal was to test the possibility of transplanting living *Lophelia* fragments for the restoration of damaged and extinct reefs.

Methods

Sample collection

The majority of samples were collected with a Remotely Operated Vehicle (ROV) to minimise damage and to allow a precise geographic position of each sample. A few samples in the Mediterranean Sea were obtained by trawl. All samples from Skagerrak (paper I, paper IV, paper V) were taken with ROV (2003-2011) and the positions of the samples were obtained by means of a USBL underwater positioning system of type Simrad HPR 410 P in combination with a Furuno GPS gyro type SC 110 and a DGPS instrument type GBX Pro. Data were visualised and logged in the navigational software Olex. The accuracy of obtained positions was approximately ± 2 m. The samples of the large-scale studies (paper II and paper III) were collected in collaboration with partners in the European framework programs Hotspot Ecosystem Research along the Margins of European Seas (HERMES, FP6 program, 2005-2009) and Hotspot Ecosystem Research and Man´s Impact ON European Seas (HERMIONE, FP7 program, 2009-2012). All samples were preserved in ethanol (96%) prior to analysis.

Name of sampling locality	Abbre-viation	Ramets	Genets	R	A	H_E	H_O	F_{IS}
Korallen	Kor	25	14	0,54	8,07	0,79	0,61	0,22*
Lopphavet	Lop	30	15	0,48	8,89	0,84	0,72	0,14*
Stjärnsund	Stj	7	7	1,00		0,83	0,62	0,25
Röst reef	Ros	18	16	0,88	8,55	0,82	0,69	0,16*
Traena reef	Tra	26	20	0,76	8,07	0,80	0,68	0,15*
Osterfjord	Ost	12	3	0,18		0,46	0,89	-0,92*
Trondheimsfjord	**Tro**	66	45	0,68	8,36	0,81	0,63	0,22*
Tautra	Tau	12	9	0,73		0,72	0,60	0,17*
Stokkbergneset	Sto	38	29	0,76		0,82	0,62	0,25*
Rødberg	Rod	14	7	0,46		0,81	0,71	0,12*
Nord Leksa	Lek	2	2	1,00		0,80	0,61	0,23
NE Skagerrak (excl. Säcken)	**NES**	207	73	0,35	8,60	0,83	0,70	0,16*
Tisler reef	Tis	130	39	0,29		0,82	0,69	0,16*
Säcken	Sac	18	4	0,18		0,52	0,78	-0,50
Fjellknausene	Fje	19	9	0,44		0,76	0,68	0,11*
Väst Söstrene	Wso	12	4	0,27		0,87	0,78	0,11
Öst Söstrene	Eso	46	21	0,44		0,84	0,70	0,16*
Darwin Mounds	Dar	45	18	0,39	6,93	0,80	0,77	0,04*
Mingulay reef	Min	22	17	0,76	8,30	0,82	0,66	0,20*
Rockall Bank	Roc	11	11	1,00	8,22	0,80	0,63	0,21*
Porcupine Seabight	Por	41	15	0,35	8,21	0,82	0,63	0,22*
La Galicia Bank	Gal	32	22	0,68	8,29	0,82	0,64	0,22*
Aviles Canyon	Avi	13	13	1,00	8,13	0,79	0,66	0,16*
Mediterreaneam Sea	**Med**	29	21	0,71	8,17	0,78	0,68	0,13*
Cap de Creus Canyon	CCC	4	4	1,00		0,75	0,61	0,18
Strait of Sicily	SoS	8	3	0,29		0,66	0,57	0,13
Santa Maria di Leuca	SML	32	20	0,61		0,83	0,64	0,23*
Adriatic Sea	Adr	4	3	0,67		0,84	0,85	-0,02
Mauritania	Mau	19	16	0,83		0,52	0,74	0,27*
Platforms and low sample localities								
Platform - Beryl	Ber	10	6	0,56		0,76	0,67	0,12*
Platform - North Cormorant	NCo	4	4	1,00		0,79	0,64	0,19
Platform - NW Hutton	NHu	7	7	1,00		0,85	0,60	0,29*
Platform - Magnus	Mag	2	2	1,00		0,54	0,50	0,07
Platform - Tern Alpha	TAl	1	1	1,00		0,44	0,44	
Faroe Island	Far	2	2	1,00		0,65	0,44	0,31
Trönabanken	Trb	1	1	1,00		0,67	0,67	
Hjeltefjord	Hje	1	1	1,00		0,67	0,67	
Fugloybanken	Fug	2	2	1,00		0,72	0,56	0,23
Sponge garden	Spo	2	2	1,00		0,74	0,78	-0,05
Gulf of Cádiz	GoC	1	1	1,00		0,56	0,56	

Table 1. Sample localities of all *Lophelia pertusa* that were collected during this project. Number of ramets, number of genets, genotypic richness (R), allelic richness (mean number of alleles/loci) (A), expected heterozygosity, observed heterozygosity, the inbreeding coefficient F_{IS}. * Denotes significant values at $P < 0.05$

History of sampling areas

Due to the Fenno-Scandinavian inland ice, coral reef complexes distributed along the western European continental (see table x) margin do not share history. The reef localities in the north have a very different history than the localities in the south. Quaternary glaciations, particularly the last glacial period, which started about 116 ka and the last glacial maximum (LGM) occurred around 18 ka, greatly affected the distribution of temperate species as their ranges retreated southward to escape the ice sheets (Denton and Hughes 1981; Dawson 1992). The sea level changed regularly throughout the Pliocene and Pleistocene with lowest sea levels 140k (-130 m) and 30k (-120 m) years ago (Waelbroeck *et al*. 2002). The extent of the ice during the LGM reached as far south as the northern limit of Bay of Biscay, covering the British Islands (Svendsen *et al*. 2004). However, the precise extents of ice sheets are controversial (Sejrup *et al*. 2005). Postglacial colonization events in northern Europe have distinctly shaped the contemporary distribution of genetic variation in natural populations for both animals and plants (Taberlet *et al*. 1998; Avise 2000).

Scandinavia

The Fennoscandian icesheet retreated from the Mid-Norwegian shelf about 12 000 years ago and the modern oceanographic circulation pattern were established around 8000 years ago. Large scale modelling has shown that the general circulation pattern in the NE Atlantic during the last Glacial was not very different from the present-day state, although the flow strength was significantly reduced (Shäfer-Neth and Paul 2001). The last calving ice front in Skagerrak occupied the Oslofjord until the ice retreated on-shore around 10 700 yr BP and the modern circulation pattern in the eastern North Sea and Skagerrak was established at 8500 yr BP (Gyllencreutz 2006). Not long after suitable conditions for coral growth were established. All reefs on the Scandinavian shelf are of post-glacial origin and situated on top of post-glacial structures, e.g. iceberg plough-marks and moraines, (Freiwald *et al*. 1999). Isotopes studies where corals have been dated corroborate this. The earliest known coral growth from the Scandinavian shelf is from Stjernsund (~10.9 kyr BP, López Correa *et al*. 2012). Haltenpipe reefs off mid-Norway have been dated to 8.62 kyr BP (Hovland and Mortensen 1999) and the nearby-located Sula ridge 8.15 kyr

BP (Hovland *et al*. 1997). The oldest dated records of corals from the Oslofjord are 8.7-7.8 kyr BP (Mikkelsen *et al*. 1982).

The Mediterranean and southern Europe

The Mediterranean is a semi-enclosed basin, technically a part of the Atlantic Ocean, though often referred to as an independent body of water. It is an interesting region for cold-water coral research due to its long history of cold-water corals. From fossil archives the occurrence of extant cold-water corals in the Mediterranean is known since the Upper Miocene, and *Lophelia* is known to have existed since the Middle Miocence off Sardinia (Taviani *et al*. 2005 and references therein). To put this period of time in perspective, it can be mentioned that the Alps and Himalayas have been formed and the diversification of the primates, including the first apes has taken place meanwhile. It also says something about how well adapted these animals are to the environment they live in.

The Mediterranean basin was closed off from the Atlantic with the closure of the Rifean and Baetic gateways, 5.6 Ma ago, which led to the Messinian salinity crises (Duggen *et al*. 2003), whereby the Mediterranean Sea within a millenium was nearly completely desiccated through evaporation. The dry basin was at some places 5 km below the world ocean level, with a few hypersaline Dead-Sea-like pockets. The Messinian salinity crises ended with the opening of the Straight of Gibraltar (5.33 Ma) with the Zanclean flooding, which filled the Mediterranean basin in less than two years. Re-colonisation of the basin by cold-water corals in likely to have started with the Pliocene but little is known about this epoch in respect to deep coral biota.

Cold-water corals have persisted in the Mediterranean for over 480k years, and have been especially prolific during interstadial periods. The Mediterranean Outflow Water (MOW) flows northward and this watermass correlates well with the occurrences of coral banks in the Porcupine Seabight at 700-850 m depth where large mounds hundreds of meters high and several kilometres across exist (Wheeler *et al*. 2007). The carbonate mound (Challenger Mound) in Porcupine Seabight is entirely the result of coral growth since 2.6 Ma ago (Kano *et al*. 2007), hence corals in this area are much older than populations on the Scandinavian shelf.

Molecular markers

Clonality has previously caused a particular challenge for studies on population genetics due to the difficulty in discriminating between genetically distinct individuals and ramets that are clonal replicates. This is important for not violating the assumptions underlying the theoretical framework of population genetic models (Hey and Machado 2003). The problem has largely been overcome by the use of microsatellite DNA markers, where the high polymorphism facilitate easy discrimination between genetically distinct individuals and clonal replicates. Furthermore, microsatellites are usually co-dominantly inherited and non-coding, thus considered as selectively neutral molecular markers; the discrete allelic states can be used to quantify allelic diversity, allelic richness, genotypic richness, and the level of heterozygosity. This is important as many genetic models and softwares are based on the amount of heterozygosity (Excoffier and Heckel 2006).

Microsatellites have been a very important tool in this thesis and have been used **paper I**, **II**, **IV** and **V**. In the beginning I used the dinucleotide microsatellites loci (*Le*) developed by Marie LeGoff-Vitry and Alex Rogers (2002), but changed to the tri and tetra nucleotide microsatellite loci (*Lpe*) developed by Cheryl Morrison *et al*. (2008), because longer repeat units are easier to score and give more robust result. Furthermore, all *Lpe* loci amplify under the same chemical and PCR conditions, which improved the laboratory work considerably.

In contrast to nuclear DNA markers such as microsatellites, animal mitochondrial genomes are haploid, non-recombining and nearly exclusively maternally inherited. Hence, compared to nuclear DNA (ncDNA) the effective population size is four times smaller, which consequently have repercussions on the faster pace of lineage sorting (Birky *et al*. 1983). Another interesting feature of mitochondrial DNA (mtDNA) is that it has high rates of nucleotide substitution in animals. For these reasons mitochondrial genes have been used in numerous phylogenetic and phylogeographic studies.

The rate of mtDNA evolution is however variable among groups of organisms. In mammals, mtDNA is accumulating substitutions up to ten times faster than in single-copy ncDNA (Brown *et al*. 1979) while in some invertebrates the rate of substitutions have been shown to be equal in mtDNA and ncDNA. Furthermore, different regions evolve at different rates. Among the mitochondrial genes the genes encoding for rRNA and tRNA are the most conserved, and the control region (D-loop) generally evolves the fastest.

In the class Anthozoa (were Hexacorallia belong) the sequence diversity has been found to be unexpectedly low (Shearer *et al*. 2002). There is hardly any variation among conspecifics, not even in the third codon position in protein coding sequences. The evolutionary rate of the *Acropora* cytochrome b gene (*cob*) is approximately 10-20 times slower than the standard molecular clock rate of 2% per million years (Ma^{-1}) (van Oppen *et al*. 1999). It has been a long debate whether mitochondrial genes were useful for population-level studies in corals, and which gene that was best suitable for such. For that reason I decided to sequence the whole mitochondrial genome from two geographically distant individuals (**paper III**). Using the whole mitochondrial genome from a large number of individuals is now commonly used in phylogeographic and population genetic studies (e.g. Morin *et al*. 2010; Teacher *et al*. 2012).

Main results and discussion

Genetic structure

Genetic structure refers to any pattern in the spatial distribution of genetic diversity among populations or individuals within a population. Due to limited vagility, e.g. physical barriers to migration or natal philopatry, a genetic pattern develop; natural populations are very rarely panmictic. Hence, spatial genetic structure is primarily determined by limited dispersal of some kind, usually strongly influenced by the life-history traits related to reproduction. The larval phase is the only long-distance dispersal phase in the life cycle of sessile invertebrates (i.e. corals), and therefore a considerable focus is placed on this stage in addressing issues of population connectivity. If the dispersal capacity is smaller than the species geographic distribution range nearby populations will be genetically more similar to each other compared to populations located further away, a phenomenon termed isolation by distance.

Mixed mode of reproduction

Lophelia pertusa reproduce both sexually (**paper IV**) and asexually (**paper I, II**), and knowledge of the relative contribution of those modes is important because the mode of reproduction is one of the most important life-history characteristics of clonal populations due to its effects on demography (Abrahamson 1980; Eriksson 1986) and population genetic structure (Chung and Epperson 1999; Ceplitis 2001).

Species with a mixed mode of reproduction may exhibit high variation among locations in the relative contribution of sexual and asexual reproduction within populations (Eriksson 1986, 1993, 1996). This mixed life-history strategy can be evolutionary stable if the environment is variable and each of the reproductive modes is successful under different circumstances (Bengtsson and Ceplitis 2000). Empirical studies demonstrate that the relative contribution varies in response to biotic as well as abiotic factors, e.g. latitude and population density (Dorken and Eckert 2001; van Kleunen *et al*. 2001; Hoffman 1986). The degree of clonality in *Lophelia* was variable among localities at both small and large scales (**paper I**, **II**) and did not seem to be correlated with any other pattern.

Moreover, the frequency of clonality often increase at species' geographic distribution limit compared to central populations and with population age (Lesica and Allendorf 1995; Eckert 2002; Silvertown 2008). This was not the case for Lophelia: Korallen the most northerly known coral locality of *Lophelia* did not exhibit any higher level of clonality than other more "central" sites (**paper II**).

Genotypic diversity in clonally reproducing populations is expected to decrease over time due to elimination of genets by selection and stochastic effects (Eriksson 1989; Hartnett and Bazzaz 1985) but high genotypic diversity in asexually reproducing populations can be maintained at high levels if the life span of genets is long and sexual reproduction occurs occasionally. All sampled populations with adequate sample size (**paper I, II**) had high genotypic diversity, which confirms a life-history strategy with a balance between the reproductive modes.

Clonality

Asexual reproduction does not involve genetic recombination; hence all new polyps that are produced are genetically identical to the parental colony. In this respect, spatial increase through asexual reproduction is more akin to growth than to reproduction. The act or process of reproducing is usually thought of as a mechanism that gives rise to offspring that is a new generation in the demographic sense. Hence, it can be argued that asexually produced polyps are no more offspring than new branches produced by a tree, drones in a bee society or worker ants in an colony. But in contrast to these, asexual coral colonies are capable of independent life that upon the death of the parental colony can propagate the parental genes in time and space, which is the definition of reproduction.

Paper I and **paper II** highlights the importance of asexual reproduction in the formation of *Lophelia pertusa* reefs. One of the most obvious consequences of clonality for cold-water coral populations is that the number of ramets in a population does not reflect the number of genets it contains. The relationship between these two measurements provides an index of the extent of clonal propagation in a population (Genotypic richness or proportion of clonemates). The only two scientific studies that have approached the issue of clonality on *Lophelia* reefs previously (LeGoff-Vitry *et al*. 2004, Morrison *et al*. 2011) have most likely underestimated the extent of clonality. The main purpose of these studies were population genetics, typically aiming att maximising the number of different genetic individuals, hence collecting the individual samples at large distances from each other. This is unfortunate because knowledge of the amount of clonality is needed for proper interpretation of population genetic results.

The proportion of clonemates was zero in seven out of ten *Lophelia* populations in the LeGoff-Vitry *et al*. (2004) study, hence only three populations were reported to have asexual reproduction. La Galicia and Porcupine Seabight had relatively low levels of asexual reproduction (0.15 and 0.20 respectively) whereas the proportion of clonemates at Darwin Mounds was 0.49; this was attributed to the effect of bottom trawling resulting in higher fragmentation of clones and increased clonal spread. This may be correct since we know that the area have been severely damaged by trawling activity. However, the genetic samples for the study were collected with an agassiz trawl, which may have caused colonies fragmentation in the trawl resulting in an overestimation of the number of colonies and clonemates in the sampling. In a more recent study on Western Atlantic *Lophelia* reefs by Morrison *et al.* (2011) the proportion of clones varied from 0 to 0.33 with an average at 0.13. In that study 12 collection sites had zero proportion of clones.

The high variation of genotypic richness and proportion of clones among sample localities in those studies of *Lophelia pertusa* is most likely due to the variation in number of sampled individuals and sampling design. This is clearly also true for estimation of population structure in **paper I**, and **paper II**. Using the samples in table 1 shows that there is a negative correlation between the number of samples taken at a reef site and the estimated genotypic richness (Fig. 7, see also Fig 4. in **paper I**). The probability of sampling a previously sampled genet increases with the number of samples.

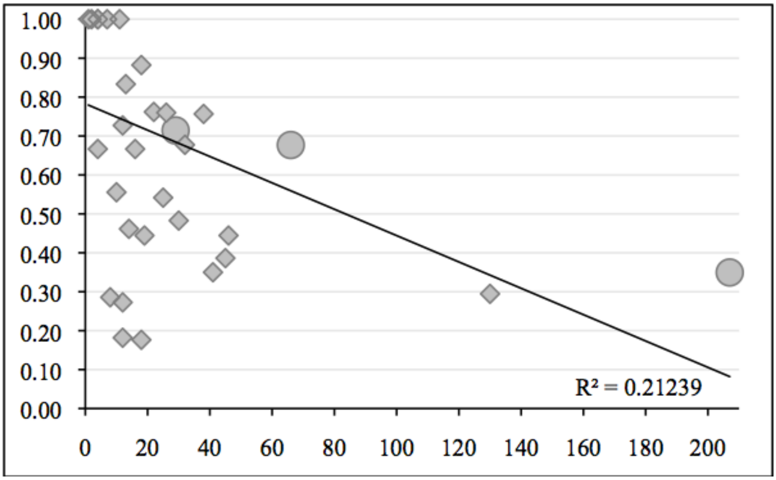

Fig 7. The correlation between number of sampled ramets and genotypic richness (R). The three circles represent pooled samples from the Mediterranean Sea, Trondheim fjord, and NE Skagerrak, from left to right, respectively. Y-axis is genotypic richness, x-axis is number of samples.

Results from the intrareef study at Tisler, explicitly focused on clonal distribution (**paper I**), suggest that clonality is important for development of *Lophelia* reefs. But the study was only on a single reef in Skagerrak and the generality of the result is unknown. With this in mind for the sampling design of the large-scale study (**paper II**, where population genetics also was a major aim and therefore required as many different genetic individuals as possible), samples were taken at slightly smaller distances than normal. The results from the large-scale study (**paper II**) corroborates the results from paper I and indicates that the importance of asexual reproduction is a general phenomenon and not an isolated effect caused by specific oceanographic circulation conditions in the Skagerrak.

Life span is a key demographic trait for understanding life history, population dynamics, and evolutionary fitness (Harper 1977) and is, by far, the most important trait influencing population persistence (Weiher *et al.* 1999). Demographic data of long-lived clonal organisms at the genet level is scarce, and life span in particular is one of the least accessible demographic traits (Menges 2000). Persistent clonal reproduction cause genets to increase in size as a function of time; hence size of genets divided by annual size increment yield an indirect estimate of genet age. The method has been commonly used in terrestrial systems for clonal herbs, shrubs, trees, grasses and sedges, and marine clonal organism (Witte and Stöcklin 2010). Using this method (**paper I)** we identified a number of clones that are a few thousands of years old; the largest clone may be over 6000 years old. From the spatial distribution of clones (**paper I)** it was possible to obtain some information about basic population demography and population dynamics. The distribution of ramets among genets was skewed, and there were a few large highly aggregated clones and several small clones, which indicate long life-spans with either a continuous inflow of migrants (overlapping generations) or an initial settlement all over the reef and subsequent competition among genets. However, based on observations of genet interaction in aquariums the former explanation is more likely. We also estimated that the total number of individuals at the Tisler reef was relatively low, approximately 100-200 individuals. This suggest that turnover rate of individuals in *Lophelia* populations are extremely slow.

Effect of trawling

Trawling on cold-water coral habitats has previously been identified to disrupt the three-dimensional structure of reefs, which alter the hydrodynamic, and sedimentary conditions around the reefs (Rogers 1999). Other studies have shown that loss of coral habitat causes a decline in richness, diversity and density of reef-associated megabenthos, but there are no studies that have looked at the effect on the corals species themselves, how the physical destruction may alter demographic structure in the population. Population structure and genotypic variation have been correlated with disturbance history in tropical corals (Coffroth and Lasker 1998; Hunter 1993), but as outlined in section X there is a fundamental difference how shallow and cold-water coral reef are composed and therefor also what the effect and consequences from physical disturbances will be. In tropical corals intraspecific competition and variation in different life-history strategies among species will cause a change in the relative abundance of species. Fast-growing species or species that are better adapted to survive fragmentation may benefit from the disturbance and increase in abundance, at least initially, and with time intraspecific competition may change the distribution of clones and species again. In contrast, *Lophelia* reefs are only created by a single species and hence there will be no change in species composition after the reef have been impacted by trawling. In **paper I** we show that the clonal subrange increased in areas impacted by trawling. That means that the clonal architecture and the distribution of clones are altered after trawling, since coral colonies are shattered and some coral fragments survive after have been dragged away by the trawl. An example of this can be seen in figure 2, where small living fragments are visible. Increased clonal subrange has also been observed in impacted seagrass meadows (also a clonal habitat-creating species) in the Mediterranean Sea (Diaz-Almela *et al*. 2007).

Changing the spatial distribution of clones may affect the relative contribution of sexual reproduction. *Lophelia* is a gonochoristic species (i.e. different clones have different sex) and fertilization occurs externally when gametes from the different individuals meet. Thus, the distance between individuals is critically important for successful fertilization, which means that changing the clonal architecture and spatial distribution of clones may reduce the level of fertilization. Experimental evidence on fertilization of echinoid eggs showed that increasing distance drastically reduced the level of fertilization (Pennington 1985).

Clones show high aggregation with limited distribution (**paper I, II**) and given the large areas trawls have the capacity to destroy (and have destroyed already), we can assume that in areas where the reef framework is completely destroyed, individuals with unique genetic composition (genotypic and possibly allelic diversity) may have been lost forever. This can lead to increased genetic drift and elevated inbreeding within the reef population (Young *et al*. 1996).

It is difficult to predict what impact bottom trawling have on *Lophelia* reefs but as with all kind of disturbances in natural systems the response of the ecosystem will depend on the magnitude and frequency of the disturbance. A completely levelled reef (like what have been observed on *Oculina varicosa* reefs outside Florida) is more likely to die completely than a reef that merely has been exposed for a few trawl hauls. Spatial rearrangement and destruction of genets may shift the natural dynamics of the system to an unstable state where processes related to recruitment, dispersal and survival of genets are negatively affected.

Population genetic structure

Dispersal is a key component of an organism's life history, and the rate of differentiation between subpopulations and the degree to which populations’ function as independent demographic units is governed by gene flow. Identifying routes and scales of connectivity is therefore fundamental for our understanding and the implementation of marine reserves (Cowen *et al*. 2006; Palumbi 2003), and consequently information about gene flow has been recognised as a key conservation objective in the planning of networks of marine protected areas (MPAs) (Roberts 2006, Salm 2006).

There has been a long-standing notion that marine populations are generally highly connected resulting in weak genetic structures, but this view has recently been challenged (Cowen *et al*. 2000; Hauser and Carvalho 2008), and corals indeed show a wide range of genetic structures, from panmixia over 7 000 km (Takabayashi *et al*. 2003) to locally subdivided populations (see van Oppen and Gates 2006 for a review; Underwood *et al*. 2007). We found significant genetic differentiation among reef localities at both large (**paper II**) and small scales (**paper I**).

In the small-scale study over populations in NE Skagerrak one reef (Säcken) was differentiated from the other four reef localities, that together formed one genetic cluster. The result was supported by a number of different statistical analyses (i.e. F_{ST}, Assignment test, Bayesian clustering, FCA), and the isolation of the Säcken reef is likely due to oceanographic isolation of the area. When looking at how the reef localities in NE Skagerrak is related to the populations located in the Atlantic they belong to the same genetic cluster as nearly all the Atlantic populations (see Fig. 7 in **paper II**). There is however a genetic differentiation (See Tab. 4 in **paper II**) among reef localities within that genetic cluster that most likely are attributed to differential dispersal and connectivity routes. Skagerrak was not with significantly differentiated from La Galicia Bank, Avilés Canyon, Rockall Bank, Mingulay reef, Darwin Mounds but significantly differentiated from all localities (except Sula reef complex) that are located further north along the Scandinavian continental margin. This indicate that Skagerrak is a “sink” locality with limited possibility to export coral larvae. There are some special circulation patterns in Skagerrak that could promote retention of locally produced larvae, in **paper I** ten individuals were predicted to be first generation migrants. The strongest connection by the network analysis connects Skagerrak with Avilés canyon, which could be an important founder site. The age the oldest dated records of corals from the Oslofjord corresponds nicely with the opening of English Channel that can be a potential migration route to the Skagerrak area.

Network theory has emerged as a powerful tool to improve the understanding of complex systems were many interacting units are involved (Albert and Barabási 2002). This method have been adapted to analyse the genetic relationships among populations (Dyer and Nason 2004) and individuals with clonal life-history characteristics (Rozenfeld *et al.* 2007). In contrast to traditional population genetic tools that summarize relationships in a pairwise fashion network analysis utilizes the high dimensional covariance relationships among all populations simultaneously. The visual output from a network analysis allow a very intuitive and information-rich image in a connectivity context. For identifying postglacial colonisation routes in the Atlantic (**paper II**) network analyses indeed proved that is is a valuable analysis method that allowed additional information not easily perceived by the results from *F*-statistics or Bayesian clustering.

Three different Bayesian clustering methods identified three distinct genetic clusters over the scale of Europe: Mauritania, Mediterranean Sea, and NE Atlantic Ocean. But, except for the Mauritanian, the clusters occasionally showed high levels of admixture. There is a clear signal that the Mediterranean Sea is in genetic contact with north Atlantic populations, corroborated by the oceanographic currents from the Mediterranean into the east Atlantic. There are some hypotheses about connectivity routes for *Lophelia* that have been proposed previously. The Mediterranean Outflow Water (MOW) entering the Atlantic Ocean, flows northward. This distinct watermass correlates well with the occurrences of coral banks in the Porcupine Seabight at 700-850 m depth. Based on this Ben De Mol formulated a hypothesis that coral larvae from the Mediterranean may be the ancestors to the Porcupine populations (De Mol *et al.* 2002; 2005), and Andre Freiwald suggested that the northern European continental slope was colonised by larvae carried away further north by the North Atlantic Current (Freiwald et al. 1999). The result from **paper II** is exactly in line with those two hypotheses. We found that two individuals from Italy and northern Norway respectively, shared nearly identical mitochondrial genomes (**paper III**). The result corroborate the result of a Mediteranean origin of North Atlantic cold-water corals. The North Atlantic Current flow from the Caribbean across the Atlantic, passing north of the British Isles and continiues north along the Norwegian coast. This current cause a asymmetrical dispersal of larvae in NE Atlantic and the probability that a <200um larvae (**paper IV**) is dispersed to the south is much less like likely than it will be swept to the north. The network analysis suggest that migrant have been transported long distances to the north from glacial refugia areas. The relatively homogenous admixed genetic cluster in the north Atlantic is exactely what is expected if coral larvae originate from a limited number of refugial areas (that harbours migrants from the Mediterreanean Sea and). It is important to note that the two coral localities in **paper** II that appears to be highly important for northern gene flow are the only two samples sites from these areas. They should be considered as representatives from the larger area that the northwest corner of the Iberian Peninsula and Bay of Biscay constitute, the region as a whole is most likely important for present day export of larvae to the Scandinavian margin, and for replenishment of new individuals that is required for recovery of the many trawl damged sites there.

The genetic structure and routes of connectivity predicted by the genetic analysis correlates well with findings of geological surveys where isotope measurement have predicted ages on the coral formations. Recently, evidence show that the area between ~50^{O}N and ~70^{O}N constitute the biogeographic limit of reef development during glacial-interglacial oscillations (Frank *et al.* 2011). These range contractions and expansions are likely the mechanism causing the genetic structure we see in **paper II**. The movement of coral distribution in response to changing environmental conditions has also been seen in the Mediterranean Sea and Gulf of Cádiz. The most recent prolific period for cold-water corals in the Mediterranean occurred within the Younger Dryas period from 12 900 to 11 700 yrs BP ending abruptly 10 900 yrs BP due to rising temperatures and high sedimentation that accompanied glacial meltwater pulses (McCulloch *et al.* 2010). West of the Straight of Gibraltar in the Gulf of Cádiz similar patterns have been found, and dating of cold-water corals in the area range from 400 ka to 9.2 ka BP, with prolific growth during glacial periods. No evidence for coral growth has been found for a period of 10 kyr, starting directly after the end of Younger Dryas. All *Lophelia* fragments from Gulf of Cádiz were dated to the last glacial (22-32 kyr BP), when bottom current strength in the area was enhanced, and the limited occurrences of live scleractinian corals were concentrated to the Moroccan margin (Wienberg et al. 2009; 2010). Decline of coral in Gulf of Cádiz during Younger Dryas correlates well with recent active coral mound formation on Rockall Bank and the Porcupine Seabight 11 ka (Frank *et al*. 2009). The latitudal shift with optimal growth conditions for cold-water corals changed over a few hundred years from Gulf of Cádiz to the Celtic margin located approximately 2500 km north. Very soon after, as the inland ice retreated, the rapid colonization of the entire 2000 km long Scandinavian continental margin (additional 1500-3000 km to the north) occured. Hence, the recent and quick range expansion to the north has shaped a distinct genetic pattern with low levels of differentiation among reef localities (**paper II**).

LeGoff-Vitry *et al*. (2004) found significant differentiation among all sampled locations in the NE Atlantic and interpreted this as "if some gene flow occurring along the continental slope, the recruitment of sexually produced larvae is likely to be strongly local". This conclusion is questionable. The fact that the Fennoscandian inland ice covered the whole Scandinavian shelf area until relatively recently and that the area quickly became colonised after the termination of Younger Dryas and now harbour one of the most abundant and widespread presence of cold-water corals in the world show that *Lophelia* is a successful and potent coloniser of newly available substrates and capable of long-range dispersal.

How clonality affects genetic diversity

In *L. pertusa*, populations are typically founded by a relatively low number of genetic individuals and the distribution of clonal replicates (or clone size) is skewed (**paper I, II**). There are a few large clones that extended over large geographic areas (hundred of square meters) and a much higher number of small clones (**paper I**). The combined effect of two separate facts may help explain the low level of genetic differentiation among reef localities: 1) Probability of a genet death decrease as a function of number of ramets. At a certain threshold the probability of genet death approaches zero. 2) Reproductive output increases as a function of size. This means that these old large clones will have an extremely high fecundity and that their reproductive output will contribute unproportionally to the genepool, and they will do that for a very long time. There will be an increased probability that any given egg will be fertilized by one of these dominating clones. Hence, the "swamping" of these alleles acts to homogenise the genepool and reduce the number of alleles. This increase the generation time and slow down the loss of genetic diversity through genetic drift, and consequently the evolutionary rate (Orive 1993, Potts 1984, Young *et al*. 1996, Lasker and Coffroth 1999).

Coral reef restoration

The Säcken reef is a Swedish national hotspot of marine diversity and harbours numerous species that do not exist anywhere else in Sweden. The deteriorated condition of the Säcken reef was one main reason for the initiation of this project. The reef site was protected already in 2001 but trawling scars were observed at several occasions after that. In 2009 did Sweden and Norway established two protected areas that together form a transboundary marine national park covering 751 square kilometres. The park encompasses all of the coral reef areas in **paper I**. In spite of the protective measures that have been established monitoring of the Säcken reef show that the condition of the reef is deteriorating further.

After the discovery of the Säcken reef, and the damages to the reef, it was hypothesised that larvae from nearby Norwegian reefs (e.g. Tisler) would repopulate the Säcken reef. Four settlement panels were deployed on the Säcken reef (between 2001 and 2006) to monitor the rate of natural coral replenishment at the site. When the panels were recovered and thoroughly examined after five years deployment not a single coral recruit was found (Strömberg 2007). The apparent lack of connectivity among reefs in Skagerrak was further corroborated in **paper I** that showed that Säcken reef is genetically isolated from the other known reefs in Skagerrak. The reef was also found to be genetically impoverished with extremely low levels of genetic diversity.

We know that the corals at the nearby Tisler reef produce gamets because corals that were collected at the reef spawned in the aquariums at the Tjärnö Marine Biology Lab. Eggs were fertilized and larvae development was observed during eight weeks (**paper IV**). Likely, this happens also at the reef, from where larvae theoretically have the capacity to be transported to Säcken. We also know that *Lophelia* settle on all different kind of structures (e.g. Cables, oilplattforms, warships), indicating that the larvae are not that picky about the substrate as long as the conditions are suitable for growth. The transplanted coral fragments in **paper V** are healthy and growing, indicating that the environmental condition at the Säcken reef site is suitable for coral growth. Hence, the Tisler reef produce larvae and Säcken reef have suitable conditions, but the apparent lack of recruits at the site and the genetic differentiation between the sites suggest that larvae are not transported between the sites.

The lack of larvae from elsewhere and continued deteriorating health trend of the Säcken reef indicate that recovery by only protecting the site against further bottom trawling would not be enough. The reef has possibly passed the tipping point where recovery by solely natural processes is highly unlikely. It has been shown that after particular severe, or long-term habitat deterioration, conservation actions such as MPA establishment, a "passive" management measure is not enough to reverse the deterioration (e.g. Huntington *et al*. 2011). Integrating "active" restoration may thus be necessary to alleviate rates of reef decline and assure that the structural integrity and ecosystem services of the reef framework will be continued as suggested by Rinkevich, (2005, 2008). Although active restoration can certainly enhance conservation, restoration is always poor second best to the preservation of the original habitats. Particularly for corals that live deep down in the ocean is the undertaking of reef restoration costly and technically challenging. Unfortunately the second best option is the only option sometimes. If the reef is too badly damaged for natural processes to stimulate a recovery the only option is either to try restore the reef or let it be lost. The Säcken reef site is the last known living reef in Sweden and truly a unique ecosystem for our national biota. For this reason we initiated a pilot project testing coral transplantation from a healthy reef with the hopes that reef restoration will be possible (**paper V)**.

We found that transplantation is a viable method for restoring *Lophelia* reefs. Coral fragments collected at a nearby reef survived the required handling to transfer them to the transplant site. The

survival at the new site was high and that the coral fragment increased in size. We identified 25 genetic individuals in the coral material collected for **paper V**, and tested if genetic diversity enhanced survival (see below).
We discovered that larger fragment of corals survive better than smaller transplanted fragment. Hence, large fragments are recommended to be used in future restoration projects of *Lophelia*. However, there is a clear trade-off with using larger fragments of corals because more material needs to be taken from the donor site. A potential solution is to use the extensive ability of corals to reproduce asexually. Corals in large quantities can be grown in nurseries from small fragments or from sexually produced larvae (if we manage to get them to settle). Culturing and growing coral fragments from larvae require more technical expertise than the asexual cultured fragments but gives higher genetic variation. Either way, culturing fragments in this way can give hundreds of times more material, but it will require a substantial amount of resources.

Rehabilitation of cold-water coral reefs is a long-term process. The deployed racks in our study will remain in Säcken and monitored annually for as long as possible in order to achieve the long-term results that are vital for a better understanding of the possibilities for active restoration of cold-water coral reefs.

Genetic diversity

An accumulating amount of evidence indicate that it is important to preserve genetic diversity within species in conservation and restoration efforts. Studies of eelgrass has show that genotypic diversity enhances resistance to disturbance (Hughes and Stachowicz 2004), parasites and pathogens (Booth and Grime 2003), as well as ecosystem recovery after extreme climatic events (Reusch *et al.* 2005). Additionally, studies has shown that reduced genetic diversity affects both population growth and individual fitness (Williams 2001).

In **paper V** we tested if high genotypic richness increased survival or transplantation success but no significant effect between plates of high diversity vs. low diversity could be detected. Neither was there any significant difference in growth rates between genotypes.

The high variation in numbers of clonal fragment between genotypes caused that the statistical power was very low. However, albeit not being statistical significant, there was some relation between growth rate of genets and heterozygosity. Similar correlations between growth and heterozygosity have been observed in a wide range of organisms previously (Koehn and Gaffney 1984; Pujolar et al. 2005 and the references therein). Heterozygosity has also been positively correlated with many other fitness-related traits such as survival, fecundity, or developmental stability. Reed and Frankham (2003) identified in a meta-analysis that heterozygosity levels are correlated with reduced population fitness via inbreeding depression.

Conclusions

- *Lophelia pertusa* have higher rates of clonal reproduction than previously thought. Individual clones can be several thousands of years old. Clonality affects the demography and spatial distribution of genetic diversity and is consequently one of the most important life-history characteristics for *L. pertusa*.

- Reefs are created by a relatively low number of genetic individuals, but the distribution of the number of ramets among genets is skewed. There are a small number of large clones and numerous small clones.

- *Lophelia pertusa* have sexual reproduction where larvae are capable for spending many weeks in the plankton, hence having potential for long-distance dispersal.

- Connectivity at the scale of the NE Atlantic Ocean is asymmetric and mainly driven by large-scale oceanographic currents; main connectivity is in a north-south direction, with most likely little local retention of larvae.

- South European reef localites have been important refugia during the last glacial maximum, and these reefs have in turn ancestry from the Mediterranean Sea, but possibly other unknown reef localities as well.

- Scandinavian fjord populations are not strongly isolated but export of larvae from theese reefs seems to be limited by the coastal current regime.

- Transplantation of *Lophelia pertusa* corals is possible and may be a viable method for reef restoration.

Acknowledgement

I would like to express my deepest gratitude to my advisor Carl André for his guidance and encouragement during my years as a Ph.D student. I have been incredibly fortunate to have an advisor who gave me the freedom to explore on my own. Many thanks also go to my co-supervisor Tomas Lundälv for his help and support in many ways throughout these years. Your knowledge and expertise of *Lophelia* stretches as deep and endless as your curiosity of the deep-sea ecosystems. You have been a true source of inspiration and a good companion on many fun and interesting travels around the globe.

I am grateful for the fantastic years I have been fortunate to spend at Tjärnö. The island and the lab was my home for many good years. And you, all colleagues at Tjärnö, thank you for making that time so good. I also want to thank all colleagues and friends at Kristineberg, I feel really privileged to have been able to learn to know you all. Workplaces with more knowledgeable, skilled, friendly and fantastic people that these two field stations do not exist. Thank you all!

Rick and Robin, I guess you guys also are colleagues, but I consider you more like good friends. Thanks for nice hanging out, diving, parties, pleasant dinners, beer drinking, tequila drinking, whiskey drinking, and other unhealthy stuff. I hope we will have many more chances for these kinds of activities during the years to come.

I would also like to thank my friends in Lysekil, it helps to have friends that can support and help out in all kind of various ways. Thank you!

I wish to thank professor Karin Rengefors, director of the graduate research school in genomic ecology (GENECO), and the students at the research school that offered a stimulating and friendly atmosphere.

And finally, and certainly the most importantly, I would like to thank Hannah and my two wonderful children. Hannah, It would not have been possible without you, you have been a great support, especially in the end of my thesis work. I hope I will be able to be as great support when it is your time.

This PhD project has been financed by Oscar and Lili Lamm, many thanks for that opportunity you gave me. Helge Ax:son Johnsons stiftelse, Wilhelm och Martina Lundgrens Vetenskaps- och Understödsfond, and Colliander have also been important sources of funding for this project. Valuable funding for sampling was supported by the two European projects: HERMES EC contract no GOCE-CT-2005-511234, funded by the European Commission's Sixth Framework Programme under the priority ‘Sustainable Development, Global Change and Ecosystems’ and the HERMIONE project, EC contract no 226354, funded by the European Commission´s 7th Framework Programme under the theme Environment (including climate change).

References

Abrahamson WG (1980) Demography and vegetative reproduction. In: Solbright OT (ed) Demography and evolution in plant populations. *Blackwell Scientific Publications, Oxford*, pp. 89-106

Albert R, Barabási AL (2002) Statistical mechanics of complex networks. *Review of Modern Physics*, 74, 47–97

Allendorf FW, Luikart G (2007) Conservation and the genetics of populations. *Wiley-Blackwell*, pp. 642

Avise, JC. (2000) *Phylogeography: the history and formation of species. Cambridge, Mass., Harvard University Press,* pp. 1–447

Bengtsson BO, Ceplitis A (2000) The balance between sexual and asexual reproduction in plants living in variable environments. *J. Evol. Biol.,* 13, 415-422

Birky CW, Maruyama T, Fuerst P (1983) An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplast, and some results. *Genetics*, 103, 513-527

Booth RE, Grime JP (2003) Effects of genetic impoverishment on plant community diversity. *J Ecol*, 91, 721-730

Brown WM, George M, Wilson AC (1979) Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences of the USA*, 76, 1967-1971

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology*, 31, 21-50

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science* 81, 311-322

Cairns SD (2001) A brief history of taxonomic research on azooxanthellate Scleractinia (Cnidaria: Anthozoa). *Bulletin of the Biological Society of Washington*, 10, 191-203

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodson G, Johan O, Licuanan WY, Livingston SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E

(2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, 321, 560–563

Carranza A, Recio AM, Kitahara M, Scarabino F, Ortega L, López G, Franco-Fraguas P, De Mello C, Acosta J, Fontan A (2012) Deep-water coral reefs from the Uruguayan outer shelf and slope. *Marine Biodiversity*, 42, 411-414

Chung MG, Epperson BK (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

Coffroth MA, Lasker HR (1998) Population structure of a clonal gorgonian coral: the interplay between clonal reproduction and disturbance. *Evolution* 52, 379–393

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: Open or closed? *Science* 287, 857-859

Le Danois E (1948) Les profondeurs de la mer. Trente ans de recherche sur la faune sous-marine au large des côtes de France. Paris: Payot. pp. 303

Davies AJ, M Wisshak, JC Orr, and JM Roberts (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Research Part I*, 55, 1048-1062

Davies AJ, Guinotte JM (2011) Global habitat suitability for framework-forming cold-water corals. *PloS ONE* 6, e18483

Dawson AG (1992) Ice age earth. *Late Quaternary Geology and Climate. Routledge, London, UK.*

Denton GH, Hughes TJ (1981) The last great ice sheets. *Wiley and Sons, New York, US.*

Diaz-Almela E, Arnaud-Haond S, Vliet MS, Álvarez E, Marbà N, Duarte CM, Serrão EA (2007) Feed-backs between genetic structure and pertubation-driven decline in seagrass (*Posidonia oceanica*) meadows. *Conservation Genetics*, 8, 1377-1391

Dons, C, (1944) Norges korallrev. *Det Kongelige Norske Videnskabers Selskabs Forhandlinger*, 16, 37-82. [In Norwegian]

Dorken ME, Eckert CG (2001) Severly reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *J Ecol.*, 89, 339-350

Duggen S, Hoernle K, van den Bogaard P, Rupke L, Phipps Morgan J (2003) Deep roots of the Messinian salinity crisis. *Nature*, 422, 602–606

Dullo W-C, Flögel S, Rüggeberg 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

Dyer RJ, Nason JD (2004) Population graphs: the graph theoretic shape of genetic structure. *Mol. Ecol.* 13, 1713–1727

Eckert CG (2002) The loss of sex in clonal plants. *Evol Ecol* 15, 501-520

Eisele M, Frank N, Wienberg C, Hebbeln D, López Correa M, Douville E, Freiwald A (2011) *Marine Geology*, 280, 143-149

Eriksson O (1986) Survivorship, reproduction and dynamics of ramets of *Potentillia anserina* on a Baltic seashore meadow. *Vegetatio*, 67, 17-25.

Eriksson O (1993) Dynamics of genets in clonal plants. *Trends in Ecology and Evolution* 8, 313-316

Eriksson O (1989) Seedling dynamics and life histories in clonal plants. *Oikos* 55, 231-238

Eriksson O (1996) Regional dynamics in plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, 77, 248-258

Excoffier L, Heckel G (2006) Computer programs for population genetics data analysis: a survival guide. *Nature reviews Genetics*, 6, 847-859

Fosså JH, Mortensen, PB, Furevik DM (2000) *Lophelia*-Korallrev langs norske kysten. Forekomst og tilstand. *Fisken og havet*, no. 2 [In Norwegian.]

Fosså JH, Mortensen PB, Furevic DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia,* 471, 1-12

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal mixing. *Sarsia*, 77, 157-171

Frank N, Ricard E, Lutringer-Paquet A, van der Land C, Colin C, Blamart D, Foubert A, Van Rooij D, Henriet J-P, de Haas H, van Weering T (2009) The Holocene occurrence of cold water corals in the NE Atlantic: implications for coral carbonate mound evolution. *Mar. Geol.,* 266, 129-142

Frank N, Freiwald A, López Correa M, Wienberg C, Eisele M, Hebbeln D, Van Rooij D, Henriet J-P, Colin C, van Weering T, de Haas H, Mortensen PB, Roberts JM, De Mol B, Douville E, Blamart D, Hatte

C (2011) Northeastern Atlantic cold-water coral reefs and climate. *Geology*, 39, 743-746

Freiwald A (1998) Geobiology of *Lophelia pertusa* (Scleractinia) reefs in the north Atlantic. *Habilitation thesis, Univ. Bremen*, 116 pp.

Freiwald A, Wilson JB, Henrich R (1999) Grounding Pleistocene icebergs shape recent deep-water coral reefs. *Sedimentary Geology*, 125, 1-8

Freiwald A (2002) Reef forming cold water corals. In: Ocean Margin Systems, ed. G Wefer D, Billett D, Hebbeln D, Jorgensen BB, Schluter M, van Weering T. Springer, pp. 365-385

Freiwald A, Fosså JH, Grehan A, Koslow JA, Roberts JM (2004) Cold-water coral reefs. UNEP-WCMC report, *Biodiversity Series*, vol. 22, pp. 1–84

Gass SE, Willison JH (2005) An assessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge. In: *Cold-water Corals and Ecosystems*. Springer-Verlag Berlin Heidelberg, pp, 223-245

Gass SE, Roberts JM (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

Gianni M (2004) High seas bottom trawl fisheries and their impacts on the biodiversity of vulnerable deep-sea ecosystems. Report for ICUN, NRDC, WWF, Conservation International

Grehan AJ, Unnithan V, Olu Le Roy K, Opderbecke J (2005) Fishing impacts on Irish deepwater coral reefs: making a case for coral conservation. In *Benthic Habitats and the Effects of Fishing*, ed PW Barnes and JP Thomas. *American Fisheries Society Symposium*, 41, 819-832

Guinotte J, Orr J, Cairns S, Freiwald A, Morgan L, George R (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Frontiers in Ecology and the Environment* 4, 141-146

Gyllencreutz R, Backman J, Jakobsson M, Kissel C, Arnold E (2006) Postglacial palaeoceanography in the Skagerrak. *The Holocene*, 16, 975-985

Hall-Spencer J, Allain V, Fosså JH (2002) Trawling damage to Northeast Atlantic ancient coral reefs. *Proceeding of the Royal Society of London Series B-Biological Sciences*, 269, 507-511

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C *et al.* (2008b) A global map of human impact on marine ecosystems. *Science*, 319, 948–952

Harper JL (1977) Population biology of plants. *Academic Press, London, England*

Hartnett DC, Bazzaz FA (1985) The genet and ramet population dynamics of *Solidago canadensis* in an abondoned field. *J Ecol.,* 73, 407-413

Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. *Fish and Fisheries*, 9, 333-362

Hessler RR, Sanders HL (1967) Faunal diversity in the deep sea. *Deep-Sea research I*, 14, 65-78

Hey J, Machado CA (2003) The study of structured populations - New hope for a difficult and divided science. *Nature Reviews Genetics*, 4, 535-543

Hoffmann RJ (1986) Variation in contributions of asexual reproduction to the genetic structure of populations of the sea anemone *Metridium senile*. *Evolution* 40, 357-365

Hovland M, Mortensen PB (1999) Norske korallrev og processer i havbunnen. John Grieg forlag, Bergen. [In Norwegian]

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc Natl Acad Sci* 101, 8998-9002

Hunter CL (1993) Genotypic variation and clonal structure in coral populations with different disturbance histories. *Evolution* 47, 1213-1228

Huntington BE, Karnauskas M, Lirman D (2011) Coral fail to recover at a Caribbean marine reserve despite ten years of reserve designation. *Coral Reefs*, 30, 1077-1085

Johansen SD, Emblem A, Karlsen BO, Okkenhaug S, Hansen H, Moum T, Coucheron DH, Sternes OM (2010) Approaching marine bioprospecting in hexacorals by RNA deep sequencing. N *Biotechnology*, 27, 267-275

Kano A, Ferdelman TG, Williams T, Henriet JP, Ishikawa T, Kawagoe N, Talkashima C, Kakizaki Y, Abe K, Sabai S, Browning EL, Li X (2007) Age constraints on the origin and growth history of a deep-water coral mound in the northeast Atlantic drilled during Integrated Ocean Drilling Program Expedition 307. *Geology*, 35, 1051–1054

Keller NB (1976) The deep-sea madreporarian corals of the genus Fungiacyathus from the Kurile-Kamchatka, Aleutian Trenches. Trudy Instituta Okeanologii, 99, pp. 31- 44

Kitahara MV (2007) Species richness and distribution of azooxanthellate Scleractinian in Brazil. *Bull Mar Sci*, 81, 497-518

van Kleunen M, Fisher M, Schmid B (2001) Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos,* 94, 5151-5524

Koehn RK, Gaffney PM (1984) Genetic heterozygosity and growth rate in *Mytilus edualis*. *Marine Biology*, 82, 1-7

Koslow JA, Boehlert GW, Gordon JDM *et al.* (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem, *ICES Journal of Marine Science*, 57, 548–557

Koslow JA, Gowlett-Holmes K, Lowry JK *et al.* (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology Progress Series*, 213, 111-125

Laikre L, Allendorf FW, Aroner LC, Baker CS, Gregovich DP, Hansen MM, Jackson JA, Kendall KC, McKelvey K, Neel M, Olivieri I, Ryman N, Schwartz MK, Bull RS, Stetz JB, Tallmon DA, Taylor BL, Vojta CD, Waller DM, Waples RS (2010) Neglect of genetic diversity in implementation of the convention on biological diversity. *Conservation Biology*, 24, 86-88

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? *Conserv Biol*, 9, 753-760

Le Guilloux E, Olu K, Bourillet JF, Savoye B, Iglésias SP, Sibuet M (2009) First observations of deep-sea coral reefs along the Angola margin. *Deep-Sea Research II*, 56, 2394-2403

Le Goff MC, Rogers AD (2002) Characterization of 10 microsatellite loci for the deep-sea coral *Lophelia pertusa* (Linnaeus 1758). *Molecular Ecology Notes*, 2, 164-166

Le Goff-Vitry MC, Pybus OG, Rogers AD (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

Lasker HR, Coffroth MA (1999) Responses of clonal reef taxa to environmental change. *Amer Zool*, 39, 92-103

Lindner A, Cairns SD, Cunningham CW (2008) From Offshore to Onshore: Multiple Origins of Shallow-Water Corals from Deep-Sea Ancestors. *PLoS ONE*, 3, e2429

López-Correa M, Montagna P, Joseph N, Rüggeberg A, Fietzke J, Flögel, Dorschel B, Goldstein SL, Wheeler A, Freiwald A (2012) Preboreal onset of cold-water coral growth beyond the Arctic Circle revealed by coupled radiocarbon and U-series dating and neodymium isotopes. *Quaternary Science Reviews*, 34, 24-43

McCulloch M, Taviani M, Montagna P, López Correa M, Remia A, Mortimer G (2010) Proliferation and demise of deep-sea corals in the Mediterranean during the Younger Dryas. *Earth and Planetary Science Letters*, 298, 143-152

McNeely JA, Miller KR, Reid WV, Mittermeier RA, Werner TB (1990) Conserving the world's biological diversity. IUCN, World Resources Institute, Conservation International, WWF-US and the World Bank, Washington DC

Menges ES (2000) Population viability analyses in plants: challenges and opportunities. *Trends in Ecology & Evolution*, 15, 51–56

Mikkelsen N, Erlenkeuser H, Killingley JS, Berger WH (1982) Norwegian corals: radiocarbon and stable isotops in *Lophelia pertusa*. Boreas, 11, 163-171

De Mol B, Van Rensbergen P, Pillen S, Van Herreweghe K, Van Rooij D, McDonnell A, Huvenne V, Ivanov M, Swennen R, Henriet JP 2002) Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. *Marine Geology*, 188, 193-231

De Mol B, Henriet 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

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Durban J, Parson K, Pitman R, Li L, Bouffard P, Abel Nielsen SC, Rasmussen M, Willerslev E, Gilbert MT, Harkins T (2010) Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research*, 20, 908-916

Morrison CL, Eackles MS, Johnson RL, King TL (2008) Characterization of 13 microsatellite loci for the deep-sea coral, *Lophelia pertusa* (Linnaeus 1758), from the western North Atlantic Ocean and Gulf of Mexico. *Molecular Ecology Resources*, 8, 1037-1039

Morrison CL, Ross SW, Nizinski MS, Brooke S, Järnegren J, Waller RG, Johnson RL, King TL (2011) Genetic discontinuity among regional populations of *Lophelia pertusa* in the North Atlantic Ocean. *Conserv Genet* 12, 713-729

Mortensen PB, Hovland MT, Fosså JH, Furevik DM (2001) Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. *J Mar Biol Assoc UK*, 81, 581–597

Mortensen PB, Fosså (2006) Species diversity and spatial distribution of invertebrates on *Lophelia* reefs in Norway. Proceeding of the 10th International Coral Reef Symposium. Okinawa, Japan, pp 1849-1868

van Oppen MJH, Willis BL, Miller DJ (1999) Atypical low rate of cytochrome *b* evolution in the scleractinian coral genus *Acropora*. *Proc. R. Soc. Lond*. B, 266, 179-183

van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, 15, 3863-3883

Orejas C, Gori A, Lo lacono C, Puig P, Gili JM, Dale MRT (2009) Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. *Mar Ecol Prog Ser*, 397, 37-51

Orive ME (1993) Effective population-size in organisms with complex life-histories. *Theoretical Population Biology*, 44, 316-340

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, 13, 146-158

Pennington JT (1985) The ecology of fertilization of echinoid eggs: The consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biol. Bull*, 169, 417-430

Potts DC (1984) Generation times and the quaternary evolution of reef-building corals. *Paleobiology*, 10, 48-58

Probert PK, McKnight DG, Grove SL (1997) Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 7, 27-40

Pujolar JM, Maes GE, Vancoillie C, Volvkaert FAM (2005) Growth rate correlates to individual heterozygosity in the European eel, *Anguilla Anguilla* L. *Evolution*, 59, 189-199

Rapp HT, Sneli JA (1999) Lophelia pertusa - Myths and realities - Poster, 2nd Nordic Marine Oceanographes conference, Hirtshals in Denmark 2.-4. April 1999

Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. *Conservation Biology*, 17, 230-237

Reed JK, Koenig CC, Shepard AN (2007) Impacts of bottom trawling on a deep-water *Oculina* coral ecosystem off Florida. *Bulletin of Marine Science*, 81, 481-496

Reusch TBH, Ehlers A, Hammerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *P Natl Acad Sci USA*, 102, 2826-2831

Rinkevich B (2005) Conservation of coral reefs through active restoration measures_ recent approaches and last decade progress. *Environmental Science & Technology*, 39, 4333-4342

Rinkevich B (2008) Management of coral reefs: We have gone wrong when neglecting active reef restoration. *Marine Pollution Bulletin,* 56, pp 1821-1824

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science,* 312, 543-547

Roberts CM, Reynolds JD, Cote IM, Hawkins JP (2006) Redesigning coral reef conservation. In: *Coral reef conservation*, pp. 515-537. Cambridge University Press, Cambridge.

Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, 84, 315-406

Rozenfeld AF, Arnaud-Haond S, Hernandez-Garcia E, Eguiluz VM, Matias MA, Serrao E, Duarte CM (2007) Spectrum of genetic diversity and networks of clonal organisms. *Journal of the Royal Society Interface*, 4, 1093-1102

Salm RV, Done T, McLeod E (2006) Marine protected area planning in a changing climate. In: *Coral reefs and climate change: science and mangement*, pp. 207-221. American Geophysical Union, Washington D.C.

Schroeder WW (2002) Observations of *Lophelia pertusa* and the surficial geology at a deep-water site in the northeastern Gulf of Mexico. *Hydrobiologia*, 471, 29-33

Sejrup HP, Hjelstuen BO, Dahlgren KIT, Haflidason H, Kuijpers A, Nygård A, Praeg D, Stoker MS, Vorren TO (2005) Pleistocene glacial history of the NW European continental margin. *Marine and Petroleum Geology*, 22, 1111–1129

Shearer TL, van Oppen MJH, Romano SL, Wörheide G (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology*, 11, 2475-2487.

Schäfer-Neth C, Paul A (2001) Circulation of the Glacial Atlantic: A synthesis of global and regional modelling. In: Schäfer P, Ritzrau W, Schlüter M, Thiede J (Eds.) The northern North Atlantic: a changing environment. Springer, Berlin: 441-462

Silvertown J (2008) The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. *Int J Plant Sci,* 169, 157-168

Squires DF (1959) Deep-sea corals collected by the Lamont Geological Observatory. 1. Atlantic corals. American Museum Novitates, n. 1965, 1-42.

Squires DF (1964) Fossil coral thickets in Wairarapa, New Zealand. *J. Palaeontol,* 38, 904-915

Stone RPP (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs,* 25, 229-238.

Strömberg S.M. (2007) A settling experiment to study the Benthic Fauna in association with the cold-water coral *Lophelia pertusa* at the reef site a-patch Säcken (NE Skagerrak). MSc thesis, Department of Marine Ecology, University of Gothenburg, pp 1-42

Svendsen JI, Alexanderson H, Astakhov VI, et al (2004) Late Quaternary ice sheet history of northern Eurasia. *Quat Sci Rev,* 23,1229–1271

Taberlet P, Fumagalli L, Wust-Saucy AG, and Cossons J-F (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology,* 7, 453–464

Takabayashi M, Carter DA, Lopez JV, Hoegh-Guldberg O (2003) Genetic variation of the scleractinian coral *Stylophora pistillata*, from western Pacific reefs. *Coral Reefs,* 22, 17-22

Taviani M, Remia A, Corselli C, Freiwald A and others (2005) First geo-marine survey of living cold-water Lophelia reefs in the Ionian Sea (Mediterranean basin). Facies 50: 409 – 417

Teacher AGF, André C, Merilä J, Wheat CW (2012) Whole mitochondrial genome scan for population structure and selection in the Atlantic herring. BMC Evolutionary Biology, 12, 248-

Tittensor DP, Baco AR, Brewin PE, Clark MR, Consalvey M, Hall-Spencer J, Rowden AS, Schlacher T, Stocks KI, Rogers A (2009) Predicting global habitat suitability for stony corals on seamounts. *Journal of Biogeography,* 36, 1111-1128

Turley CM, Roberts JM, Guinotte JM (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs,* 26, 445-448.

Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology,* 16, 771-784

Waelbroeck C, Labeyrie L, Michel E et al. (2002) Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews*, 21, 295–305

Waller RG, Tyler PA (2005) The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. *Coral Reefs*, 24, 514-522

Waller R, Watling L, Auster P, Shank T (2007) Anthropogenic impacts on the corner rise seamounts, north-west Atlantic ocean. *Journal of the Marine Biological Association of the United Kingdom*, 87, 1075-1076

Weiher EA, Van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, 10, 609 – 620

Wheeler AJ, Bett BJ, Billett DSM, Masson DG, Mayor D (2005) The impact of demersal trawling on the northeast Atlantic deepwater coral habitats: the case of the Darwin Mounds, United Kingdom. In *Benthic Habitats and the Effects of Fishing*, ed PW Barnes and JP Thomas. *American Fisheries Society Symposium*, 41, 807-817

Wheeler AJ, Beyer A, Freiwald A, de Hass H, Huvenne VAI, Kozachenko M, Olu-Le Roy K, Opderbecke J (2007) Morphology and environment of cold-water coral carbonate mounds on the NW European margin. *International Journal of Earth Sciences*, 96, 37-56

Wienberg C, Frank N, Mertens KN, Stuut J-B, Marchant M, Fietzke J, Mienis F, Hebblen D (2010) Glacial cold-water coral growth in the Gulf of Cádiz: implications of increased palaeo-productivity. *Earth and Planetary Science Letters*, 298, 405-416

Wienberg C, Hebbeln D, Fink HG, Mienis F, Dorschel B, Vertino A, López Correa M, Freiwald A (2009) Scleractinian cold-water corals in the Gulf of Cádiz – first clues about their spatial and temporal distribution. *Deep-Sea Research* I, 56, 1873-1893

Williams SL (2001) Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications*, 11, 1472-1488

Wilson JB (1979a) The distribution of the coral *Lophelia pertusa* (L.) [L. prolifera (Pallas)] in the northeast Atlantic. Journal of the Marine Biological Association of the United Kingdom, 59, 149-164

Wilson JB (1979b) `Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall bank. Journal of the Marine Biological Association of the United Kingdom, 59, 165-177

Wisshak M, Freiwald A, Lundalv T, Gektidis M (2005) The physical niche of the bathyal Lophelia pertusa in a non-bathyal setting: environmental controls and palaeoecological implications. In : Freiwald A, Roberts JM (eds), Cold-water corals and ecosystems. Springer Verlag, Berlin Heidelberg, pp 979-1001

Witte LC, Stöcklin J (2010) Longevity of clonal plants: why it matters and how to measure it. *Ann Bot*, 106, 859-870

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Oceanographique, Monaco*, 11, 1–227

Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. *Trends Ecol Evol*, 11, 413-418