

UiT

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## Chondrichthyan fishes in the Arctic Ocean and adjacent seas

- *do we know our species?*

—  
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*A dissertation for the degree of Philosophiae Doctor – June 2014*



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## List of papers

**Paper I:** Lynghammar, A., Christiansen, J.S., Mecklenburg, C.W., Karamushko, O.V., Møller, P.R. & Gallucci, V.F. (2013). Species richness and distribution of chondrichthyan fishes in the Arctic Ocean and adjacent seas. *Biodiversity* 14(1): 57-66.

**Paper II:** Lynghammar, A., Christiansen, J.S., Griffiths, A.M., Fevolden, S-E., Hop, H. & Bakken, T. (accepted 2014). DNA barcoding of the northern Northeast Atlantic skates (Chondrichthyes, Rajidae), with remarks on the widely distributed starry ray. *Zoologica Scripta* 00: 000-000.

**Paper III:** Lynghammar, A., Præbel, K., Fevolden, S-E. & Christiansen, J.S. (manuscript). Population genetic structure of an abundant skate (*Amblyraja radiata*) in the North Atlantic Ocean. Formatted to the standards of *Marine Ecology Progress Series*.

**Appendix:** Identification guide for skates (Chondrichthyes, Rajiformes) in Norwegian waters, for both sexes and all sizes.

## Summary in Norwegian

Fundamentet ein treng for å forvalte og forstå eit økosystem er korrekt artsbestemming og kunnskap om populasjonane. Utan å kjenne artane, er det ikkje mogleg å oppdage endringar i utbreiing eller talrikheit på grunn av klima-endringar, fiskeri, sjukdomar eller andre påverknader. Denne avhandlinga gjev den fyrste komplette oversikta over bruskfisk (hai, skater, rokker og havmus) som er funne i Det arktiske havet og dei kringliggjande havområda. Heile 49 artar har ein eller annan gong vore her, og dei mest artsrike områda er Beringhavet, Norskehavet og Barentshavet. Desse tre blir også kalla 'Arctic Gateways', altså inngangsportane til Arktis. Beringstredet er ein barriere som skil stillehavsartane frå atlantehavsartane. Når det gjeld feilbestemming av artar, står skatene i ei særstilling. Ulike artar blir behandla som éin (artskompleks), og både vitskapelege artiklar og fiskeria samlar gjerne skatene i ein sekk som blir kalla 'skater og rokker'. Med bruk av DNA-strek-koding blei det sett nærare på skateartane som har blitt registrerte i det nordlege Nordaust-Atlanterhavet. Tolv artar blei funne, og tre av desse var nye for området. Skater er ikkje sjeldne i området, men kring 95 % av dei er den småvaksne kloskata. Større skater blir stundom landa i fiskeria. Desse må nødvendigvis vere ei blanding av dei resterande 11 artane, og nokre av desse er truga. Det var sterke indikasjonar på at nebbskata har forsvunne, og det som tidlegare blei kalla storskate ser ut til å vere overrapportert. Kloskata kunne tenkjast å vere eit døme på eit artskompleks fordi ho i nokre område kjønnsognar seint og veks seg stor, medan det er motsett i andre område. DNA-strek-kodinga tydde ikkje på at kloskata i realiteten bestod av fleire artar. Difor blei det forsøkt ein annan metode som kan gje eit meir detaljert bilete av gensamansetjinga. Resultatet synte at det kan vere tre ulike grupperingar i Nord-Atlanteren: Nordvest-Atlanteren, Midt-Atlanteren (Grønland) og Nordaust-Atlanteren. Biletet var likevel ikkje heilt klart, fordi resultatata også synte at den same kombinasjonen av gener kunne opptre på begge sider av Nord-Atlanteren. Heller ikkje denne metoden støtta teorien om at kloskata kunne bestå av fleire artar. Sjølv om ikkje genene til kloskata kunne forklarast i detalj, har det blitt etablert grunnliner for utbreiinga av bruskfisk, og ein ny identifikasjonsnøkkel for skater er presentert. Vonleg vil dette føre til betre forvaltning av skatene ved at grunnleggjande data er meir korrekte.

## Summary

The basal prerequisite for managing species and understanding ecosystems is correct species and population identification. Without knowing the species, we cannot with accuracy detect changes in distribution or abundance due to climate change, fisheries, diseases or any other types of impact. This thesis gives the first complete overview of chondrichthyan fishes (sharks, skates, rays and chimaeras), recorded in the Arctic Ocean and adjacent seas. A total of 49 species were found to occur, and the most speciose regions were the Bering Sea, the Norwegian Sea and the Barents Sea, also known as the Arctic Gateways. The Bering Strait is an effective zoogeographic barrier, separating the Pacific from the Atlantic species. In particular, skates are prone to misidentifications. Species complexes are known to occur, and the group is commonly lumped as “Skates & Rays” in fishery statistics or in scientific publications. By use of genetic methods (DNA barcoding), the skate species reported from the northern Northeast (nNE) Atlantic was investigated. A total of 12 species were found to occur in the area, and three of those were new for the region. Skates are commonly encountered in the nNE Atlantic, but ~95 % are the smaller-sized *Amblyraja radiata*. Larger skates may be landed and they are necessarily a mix of the remaining 11 species, some of which are considered threatened. There were strong indications of the disappearance of *Leucoraja fullonica*, as well as over-reporting of the critically endangered common skate complex formerly known as *Dipturus batis*. *Amblyraja radiata* was suspected to be cryptic due to large differences in size-at-maturity across its distributional range. However, the mitochondrial gene cytochrome c oxidase subunit 1 (COI) did not support this hypothesis. To further elucidate this question, a higher resolution method was applied, and 10 microsatellite markers were investigated from specimens across the North (N) Atlantic. Pairwise fixation indexes ( $F_{ST}$ ) indicated that there may be three major clusters in the N Atlantic: Northwest Atlantic, Mid Atlantic (Greenland) and NE Atlantic. However, more rigorous tests revealed high physical mixing of individuals over a large geographical area. The microsatellite results did not support the hypothesis of *A. radiata* being cryptic. Although the population structure of *A. radiata* could not be fully explained, baselines for occurrence of chondrichthyan fishes are established, and a new identification guide for skates in the nNE Atlantic is provided. Hopefully, this will pave the way for a better management of the skates by improving data quality.

## Aims

The overall aim of this thesis is to highlight the importance of species identification in a heavily fished region, which is now facing climate change. The aims of the different papers are as follows:

### *Paper I:*

Investigate the distribution, zoogeographic affiliation and current red list status for chondrichthyans in the Arctic Ocean and adjacent seas.

### *Paper II:*

Assess DNA barcoding's ability to distinguish between skates reported from the northern Northeast Atlantic, and provide an updated species list for the region. Furthermore, the genetic structure of the widely distributed *Amblyraja radiata* was investigated using the same genetic marker.

### *Paper III:*

Investigate potential population genetic structuring in the widely distributed *Amblyraja radiata*, and look for a genetic basis for the highly variable life history traits observed between neighbouring sample sites.

### *Appendix:*

Provide an illustrated, easy-to-use guide for skate identification in the field.

# Introduction

## Systematics and taxonomy

The Chondrichthyes is a class of fishes with a fossil record dating at least back to the Devonian, 400 million years ago (Maisey 2012). It comprises the subclasses Holocephalii (chimaeras) and Elasmobranchii (sharks, skates and rays) (Nelson 2006), counting 1226 valid species (Eschmeyer & Fong 2014). Several characters define the chondrichthyans, the most prominent being a skeleton made up of cartilage, a spiral valved intestine, no swim bladder or lung, and internal fertilization by use of male claspers. A variety of phylogenetic interrelationships has been suggested (for a short summary, see Naylor et al. 2005 and references therein), and it is still debated. However, this is gradually improving with the use of molecular methods (Aschliman et al. 2012).

Skates (Elasmobranchii: order Rajiformes) are the main group of study in this thesis, comprising 363 valid species worldwide (Eschmeyer & Fong 2014). Skates have undergone significant taxonomic revisions, and Clark (1926) made a thorough revision of the European skates that is largely valid even today (but see Box 1). All skates were until then assigned to genus *Raia* (*Raja*), and subdivisions into the genera in current use were not made until McEachran & Dunn (1998) revised the taxon based on morphology. The most recent phylogenetic hypothesis of the family Rajidae interrelationships, based on genetic markers, is found in Chiquillo et al. (2014, Fig. 1). Problematic interrelationships are revealed and new genera names are being suggested therein, showing that basal issues regarding skate phylogeny still exist.



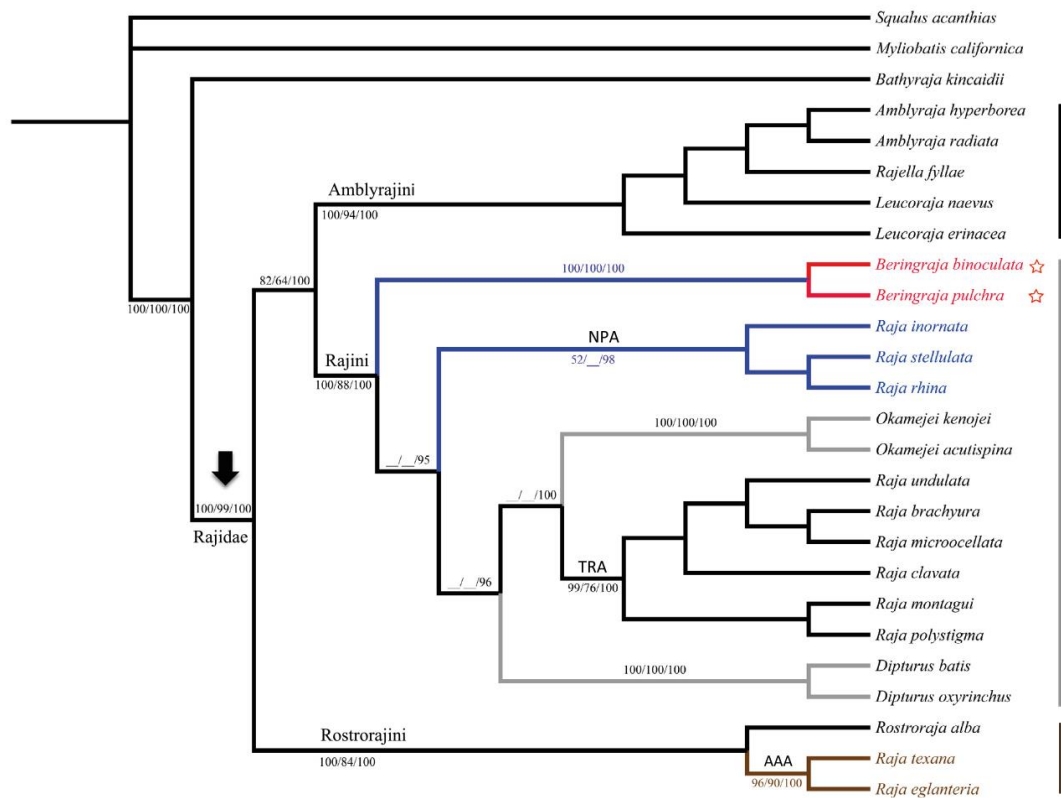


Figure 1. The most recent phylogenetic hypothesis of skates (Rajidae, black arrow) based on three mitochondrial genes. Numbers on the nodes are branch support for Neighbour joining, Maximum parsimony and Bayesian inference, respectively. Species with a star are assigned to a new genus, *Beringraja*, and share the character of having multiple embryos per egg capsule. Black, grey and red indicate clades where no nominal change is recommended, whereas blue and brown represents lineages in need of nominal revision. The bars on the right reflect tribes within the Rajidae: Amblyrajini (black), Rajini (grey) and Rostrorajini (brown). Reprinted by permission from Elsevier: *Molecular Phylogenetics and Evolution*, Chiquillo et al. 2014 (Fig. 1).

## Life history

Compared to bony fishes, which generally spawn thousands of eggs and milt with sperm in the water column (Helfman et al. 2009), chondrichthyans invest more energy in each of their offspring. Chondrichthyans as such have a wide range of strategies for ensuring an advantageous start for their young (Musick & Ellis 2005), but skates are solely egg-laying. The skates' leathery egg cases (Mermaid's purses) provide protection for the embryo and a large yolk sac provides nutrition. Laboratory experiments on temperate species have shown that the development time between egg deposition and hatching depends on species and

temperature (Clark 1922). Berestovskii (1994) reported hatching experiments of *Amblyraja radiata* in cold water. When incubating at ambient water temperatures ranging from -0.3 to 9.5°C, the embryos were developing for two and a half years. A single *Bathyraja spinicauda* specimen was included in the experiment, and after one year of incubation the embryo was considered dead. When the egg capsule was opened it turned out that the embryo was alive, and at an early stage of development. Less is known about *in situ* development, but skate species in the Bering Sea are found to deposit eggs at nursery grounds and may develop on the sea floor for up to three years (Hoff 2008, 2010). A similar nursery ground for *Amblyraja hyperborea* was found in 2009, off Bear Island in the Barents Sea (own pers. obs.). All stages from hatched eggs to undeveloped larvae and juveniles were found (Fig. 2). Berestovskii (1994) hypothesised the development time for this species to be 5-6 years based on preferred temperature and size of the egg capsule.



Figure 2. *Amblyraja hyperborea* juveniles found off Bear Island, Barents Sea (own pers. obs).

#### Box 1. The skate that would not die

The common skate has been regarded as one species since Clark (1926) revised the European skates. For almost a century, the species was called *Dipturus (Raja) batis*. In a *Nature* article, Brander (1981) claimed the species to be on the brink of extinction. Almost twenty years later, Dulvy et al. (2000) noted a relative (among skates) population decrease from 2 % to 0.2 %. Recently, both Iglésias et al. (2010) and Griffiths et al. (2010) found that *D. batis* in fact comprised two species: one larger and one smaller. Back in 1926, Clark did notice that males of the same size could have either underdeveloped or fully developed claspers, but attributed that to differences in food availability. A ‘Critically Endangered’ skate suddenly became two even more critically endangered species. Nevertheless, despite longstanding claims of a decline in abundance, specimens are still being caught.

## Biogeographic scope and methods

Paper I covers the seas from the temperate Norwegian Sea across the Arctic Central Basin to the temperate Bering Sea (Fig. 3). The taxonomic scope is wide, and includes all chondrichthyan species found in the area. Published literature and museum collections were assessed, and respective species were associated to respective regions (n = 16) by presence/absence. Red List (<http://www.iucnredlist.org>) and zoogeographic status were identified for all species.



Figure 3. Geographical scope of Paper I (shaded areas). Abbreviations are as follows: The Arctic Central Basin (ACB), the Norwegian Sea (NOR), the Barents Sea (BAR), the White Sea (WHI), the Kara Sea (KAR), the Laptev Sea (LAP), the East Siberian Sea (SIB), the Bering Sea (BER), the Chukchi Sea (CHU), the Beaufort Sea (BEA), the Canadian Arctic Archipelago (CAN), Baffin Bay (BAF), Hudson Bay (HUD, including the Labrador coast), coastal Greenland south of the Arctic Circle (west (CGW) and east (CGE)) and the Greenland Sea (GRS).

The geographic and taxonomic range was narrowed down in Paper II, and limited to order Rajiformes inhabiting the northern Northeast (nNE) Atlantic – more specifically Norwegian waters. All species that have previously been reported from the region was included in the

study. However, some species could not be found there and were obtained from UK waters. Up to ten specimens of each species were collected, with a total of 105 specimens from 15 putative species (Fig. 4). Additionally 70 *A. radiata* specimens covering a wider part of its distributional range were included to further explore potential genetic subdivision (Fig. 8). Samples were collected by commercial fishermen and recreational anglers, but the main bulk of materials came from scientific cruises. The mitochondrial gene cytochrome *c* oxidase subunit I (COI) was sequenced from all individuals. Genetic data, station data, images, and basic biological data as well as catalogue numbers for archived specimens are publicly available under the project ‘DNA barcoding of the northern Northeast Atlantic skates’ at the Barcode of Life Datasystems (<http://www.boldsystems.org>, Ratnasingham & Hebert 2007).

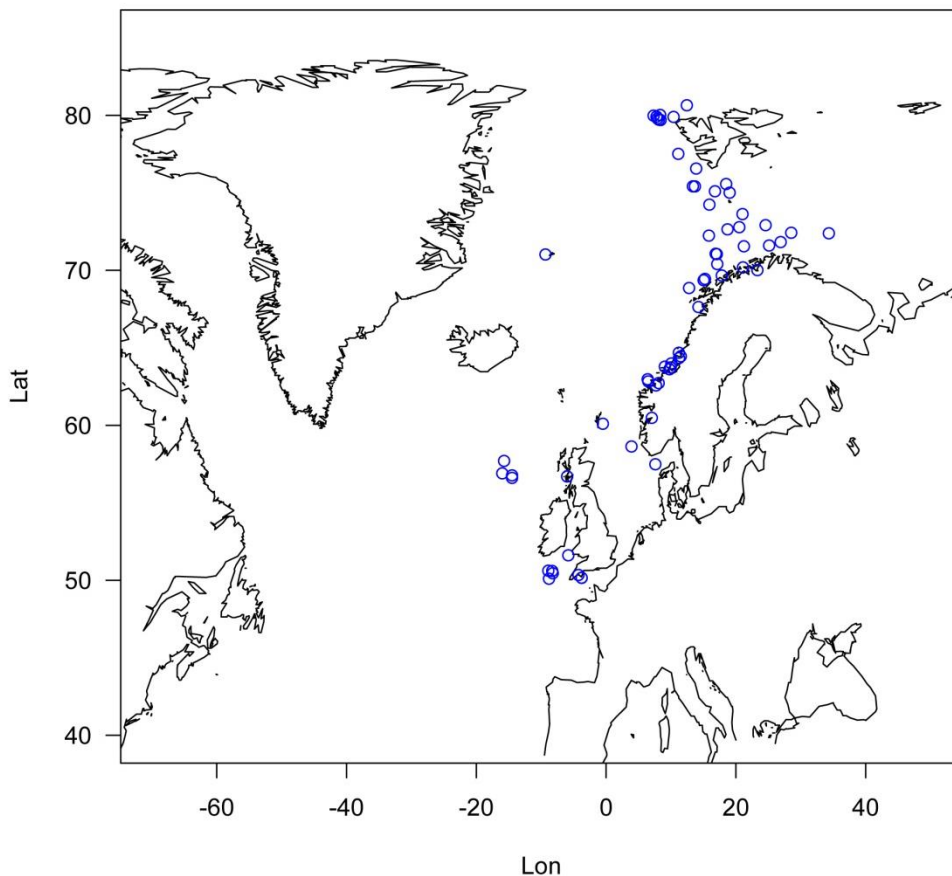


Figure 4. Map of 105 skate specimens analysed in Paper II. One point may represent several individuals. See Fig. 8 the for the additional 70 *A. radiata* samples.

In Paper III, the taxonomic range was limited to *A. radiata*, and the number of specimens was increased. A total of 656 specimens from both sides of the North Atlantic, including Greenland, were sampled as in Paper II. A total of 10 microsatellite loci in three multiplexes were analysed. Individuals from the NW Atlantic were assigned to two groups according to life history (early or late attainment to sexual maturation), whereas the Greenland and NE Atlantic specimens were separated by geography. In total, there were 11 groups with sample sizes ranging from  $n = 5$  (NEGr) to  $n = 189$  (BaE) and an average of  $n = 60$  individuals per group (Fig. 5).

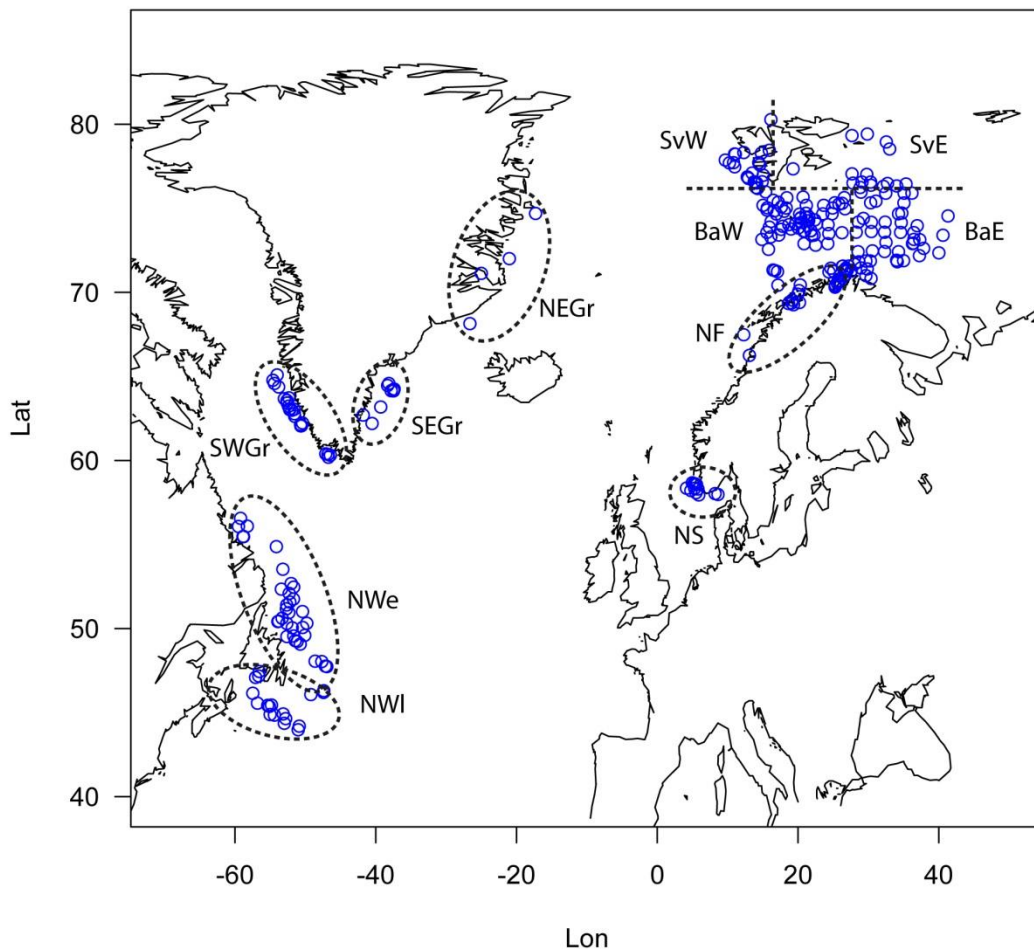


Figure 5: *Amblyraja radiata* samples grouped by life history or geography. Northwest Atlantic late maturing (NWI), Northwest Atlantic early maturing (NWe), Southwest Greenland (SWGr), Southeast Greenland (SEGr), Northeast Greenland (NEGr), Svalbard west (SvW), Svalbard east (SvE), the Barents Sea west (BaW), the Barents Sea east (BaE), Norwegian fjords (NF) and the North Sea (NS).

# Main results

## Paper I

A total of 49 chondrichthyan species were found in the Arctic Ocean and adjacent seas (AOAS). This constitutes 7.8% of the total number of fish species in the area (unpubl. database) and corresponds to the global proportion of chondrichthyan fishes (Nelson 2006). The most species-rich group was the skates ( $n = 27$ ), followed by sharks ( $n = 20$ ), while only one dasyatid and one chimaera were found. The most species-rich regions (Fig. 6) were the Norwegian Sea (28 species in 15 families), the Barents Sea (19 species in 11 families) and the Bering Sea (18 species in 4 families). The remaining regions that are less influenced by currents from warmer regions, only held one to six species. The Barents and Norwegian Seas have about equal numbers of sharks and skates, whereas the Bering Sea is dominated by skates, accounting for 83 % of the species. The Bering Strait appears to be an effective barrier to chondrichthyans, and with the exception of a single record of the Pacific *Squalus suckleyi*, there are no species occurring on both sides of the strait. Hence, all species in the AOAS north of the Bering Strait are of Atlantic Origin.

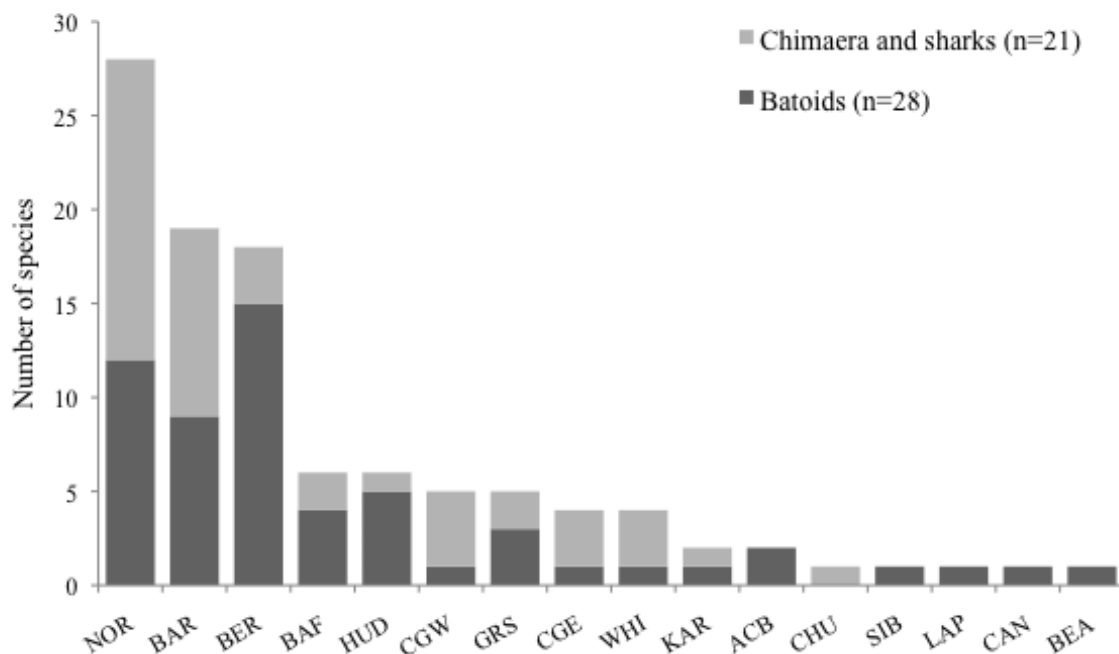


Figure 6. Number of chondrichthyan species in the 16 regions, 'Batoids' includes both skates and rays. For regional abbreviations, see Fig. 3.

The Arctic skate *A. hyperborea* occurs in 11 of the 16 regions and has thus the widest geographical distribution. This is also the only true ‘Arctic’ species (Fig. 7). The large Greenland sleeper shark *Somniosus microcephalus* and the abundant (at least in temperate regions) *A. radiata* occupy nine regions. Eight species have been caught only once, most of those are categorised as ‘Widely Distributed’.

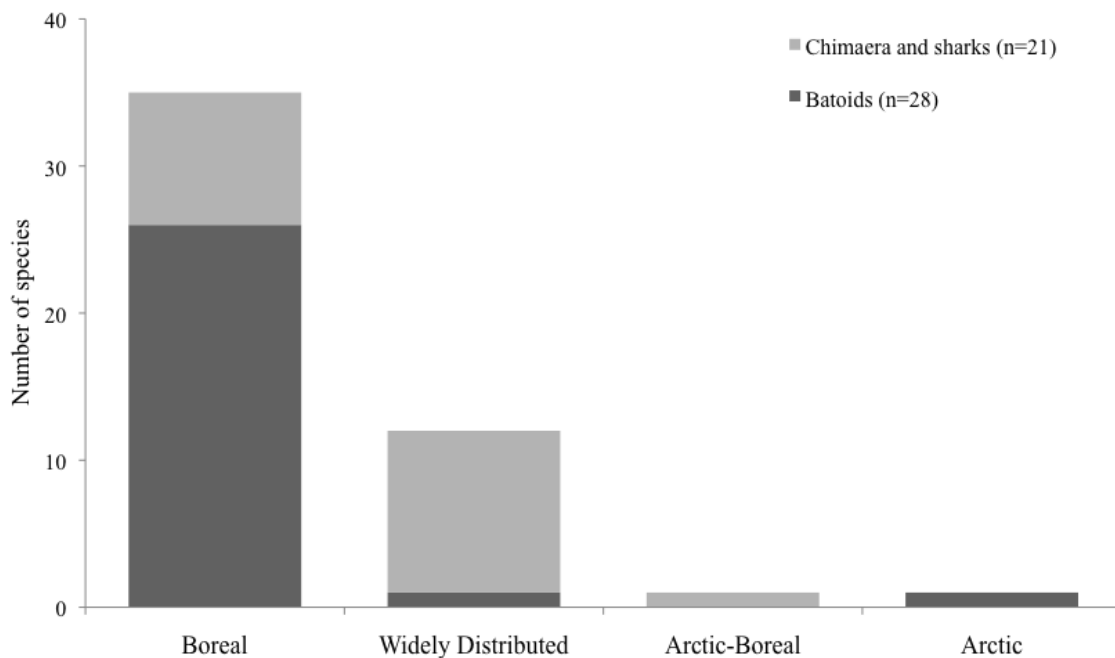


Figure 7. Zoogeographic affiliation of chondrichthyans in the Arctic Ocean and adjacent seas. Most are boreal, and sharks constitute the majority of the ‘Widely Distributed’ species. ‘Batoids’ includes both skates and rays.

## Paper II

In the North Atlantic, narrowing down to skates, DNA barcoding results were in concordance with morphological identification. A total of 15 species in 6 genera and 2 families were unambiguously identified. The intraspecific variation was surprisingly low, as two or less



haplotypes were found for 13 species. On the other hand, *A. radiata* and *Rajella fyllae* expressed significantly higher diversities (8 and 4 haplotypes, respectively).

Previous papers have reported signs of cryptic diversity in *A. radiata* (e.g. Templeman 1984a, 1987). This, and the large intraspecific variation, led us to include more specimens as well as expanding the study area. Four groups were formed: 1) a large, late maturing type from the NW Atlantic, 2) a small, early maturing type from the NW Atlantic, 3) East Greenland and 4) the Norwegian and Barents Sea (Fig. 8). As the denotation implies, the first group matures late and may attain significantly higher maximum total lengths, than the three remaining groups which matures early. A significant  $F_{ST} = 0.133$  ( $p < 0.001$ ) was found between the nNE Atlantic and the late maturing group in the NW Atlantic. A lower, but significant  $F_{ST} = 0.066$  ( $p = 0.009$ ) separated the early maturing group in the NW Atlantic from the nNE Atlantic group. On the contrary, a small and non-significant fixation index ( $F_{ST} = 0.017$ ) was found between the early and late maturing group in the NW Atlantic.

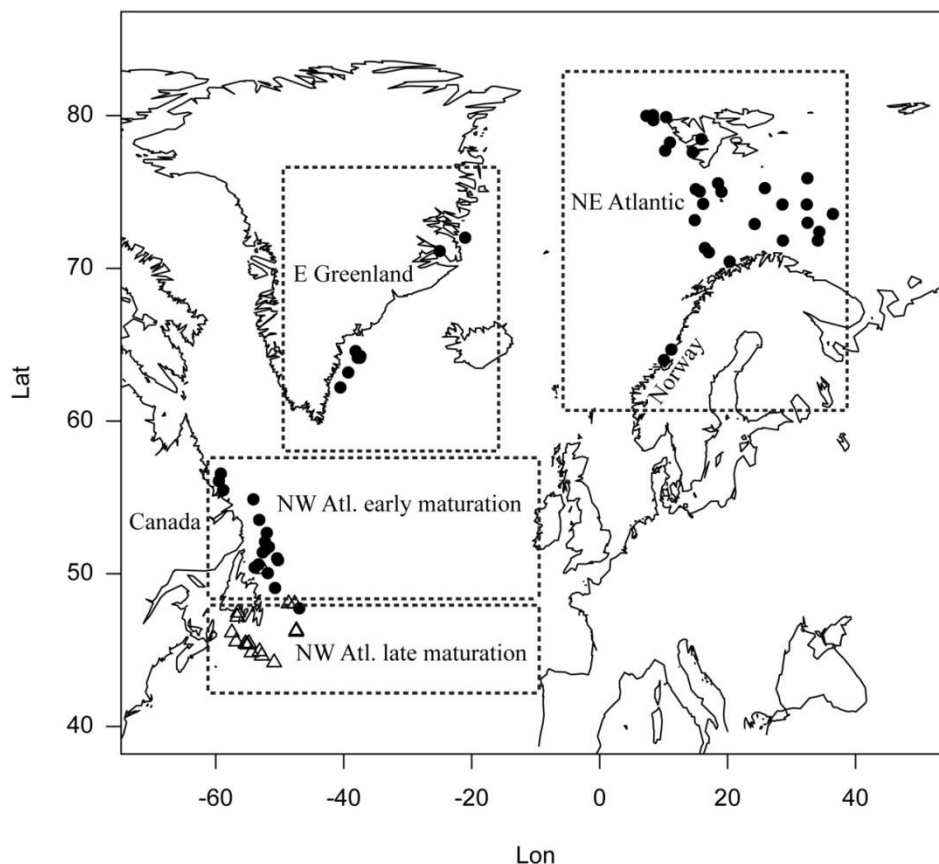


Figure 8. Four groups of *Amblyraja radiata* by geography and size-at-maturity (n=80). One dot may represent several specimens.

### Paper III

A total of 656 *A. radiata* specimens were divided into 11 groups (Fig. 5). The global  $F_{ST}$  was 0.019, and significant  $F_{ST}$  values ranged from 0.01 (SWGr vs. SvW) to 0.100 (NWI vs. NS). The  $F_{ST}$  values are visualised in Fig. 9.  $F_{ST}$  values are highly dependent on the assignment of samples to locality, which in this case was done by geography (NE Atlantic and Greenland samples) or life history characteristics (NW Atlantic).

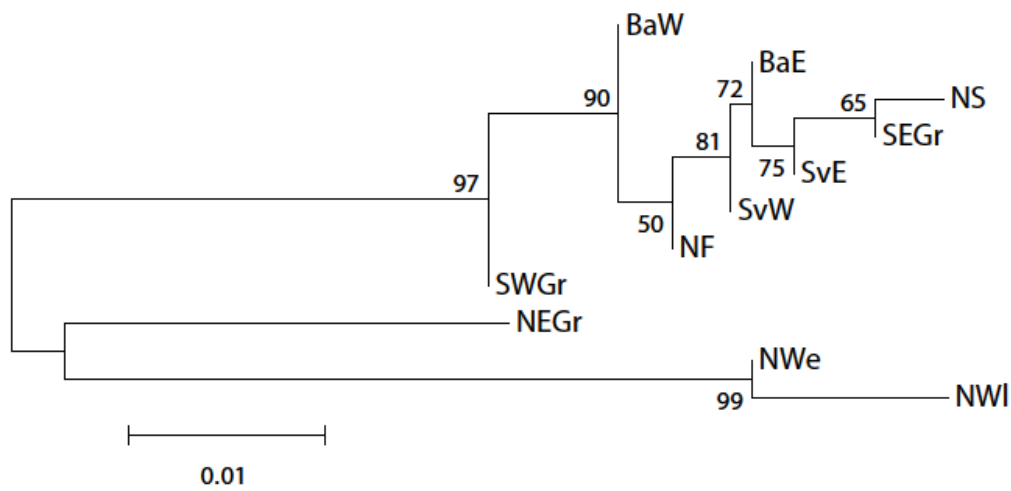


Figure 9. Neighbour joining tree of *Amblyraja radiata* samples, using corrected  $F_{ST}$  distances. Numbers at the nodes are bootstrap values with 1000 iterations. Northwest Atlantic late maturing (NWI), Northwest Atlantic early maturing (NWe), Southwest Greenland (SWGr), Southeast Greenland (SEGr), Northeast Greenland (NEGr), Svalbard west (SvW), Svalbard east (SvE), the Barents Sea west (BaW), the Barents Sea east (BaE), Norwegian fjords (NF) and the North Sea (NS). The clustering of NEGr with NWe and NWI must be interpreted with caution, as the number of NEGr individuals is only five.

To avoid the bias from prior assignment to sampling sites, the software STRUCTURE was used in order to find the number of potential populations ( $\Delta K$ ) in the dataset. The first run resulted in  $\Delta K = 2$ , and as evident from Fig. 10A, the geographic origin of the samples was not reflected, with a possible exception of the NW Atlantic samples (NWe & NWI). The proportion of membership to each cluster for each individual was set using  $q$  value thresholds of 0.3/0.7 (Fig. 10B). The majority of NW Atlantic samples were found in the second cluster (Fig. 10C). Each of the two clusters and the unassigned cluster were run again separately, resulting in  $\Delta K = 2, 3$  and 2, respectively (Fig. 10D). The individual memberships to the

clusters (Fig. 10E) suggest a high physical mixing of *A. radiata* throughout its range, but the analysis also suggest a finer scaled structure within the N Atlantic. Lastly, the STRUCTURE analysis did not provide evidence for any underlying genetic component to the observed pattern of different size-at-maturity in the NW Atlantic.

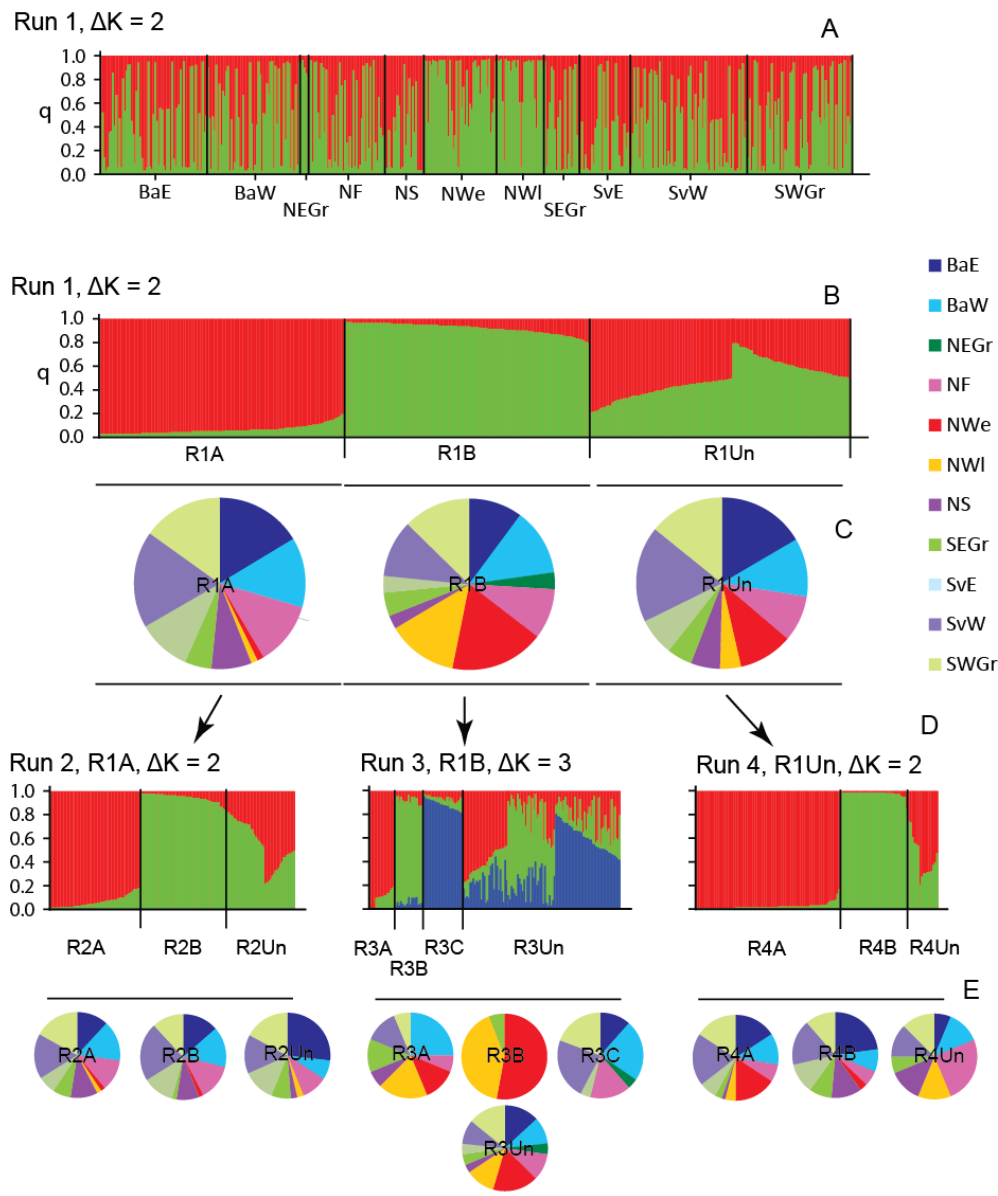


Figure 10. STRUCTURE output for *Amblyraja radiata*. Each bar represents the genotype of one individual in A, B and D. The pie charts (C & E) show the relative proportion of individuals from each locality in the inferred clusters. Black lines separate the sampling locations (A), or the clusters (B & D). With the exception of the two NW Atlantic groups, there is no apparent geographical structure (A).

## Discussion

For centuries, the northern and polar regions of the world have been, and are, of great interest for humans in terms of resource exploitation such as hunting for marine mammals, fisheries, mining and oil extraction. Activities will continue in the future, but possibly with a different impact. With increasing prospects for global warming (IPPC 2014a) and prospecting for fossil resources such as oil and gas (Huntington 2013), the Arctic has become more interesting for scientists, governments and other stakeholders. It is therefore imperative to gather existing and new data to establish baselines of which organisms are present in the region (Wassmann et al. 2011, Christiansen et al. 2014).

The Arctic Ocean and adjacent seas (AOAS, Fig. 3, Paper I) are diverse in many perspectives, from the shallow shelves in the Barents Sea, the Kara Sea, the Laptev Sea, the East Siberian Sea and the Chukchi Sea, to the deeper Arctic Central Basin, the Greenland Sea and the Norwegian Sea (Jakobsson et al. 2003, Blindheim 2004). This, and especially the shallow Bering Strait, has shaped the distribution of chondrichthyan fishes in the AOAS. Water-flow is an important factor for the dominance of Atlantic species north of the Bering Strait, as 90 % of the overall water-flow comes from the Atlantic whereas only 10 % has a Pacific origin (Roach et al. 1995, Blindheim 2004). This may explain why there is an abrupt change in species composition (Paper I), but the shallow water in the Bering Strait may contribute, as many of the Bering Sea chondrichthyans are skates which prefer deeper water. *Amblyraja hyperborea* may occur in the north, close to the Bering Strait, but a range expansion southwards into warmer and shallower water seems unlikely.

### **Does climate change affect chondrichthyan fishes?**

Poloczanska et al. (2013) reviewed range shifts for a variety of taxa (Fig. 11), and the results are also published in the latest Intergovernmental Panel on Climate Change report (IPPC 2014b). According to this report, nearly all taxa show a positive shift towards the poles, except for ‘non-bony fish’. Non-bony fishes seem to have an overall distribution shift into warmer water, opposite from what is hypothesised (Chen et al. 2011, Poloczanska et al. 2013). It must be noted that the number of observations in this category is low. A closer look into the background data reveals the difficulties of extracting data from different sources. First

of all, the opah *Lampris guttatus* (Francour et al. 2010) is a bony fish and should not be included in the analysis. *Leucoraja naevus* seems to have shifted its distribution into deeper waters, but two of the cited papers use the same background data (Perry et al. 2005 and Dulvy et al. 2008, respectively) and should be considered as one observation. Skates as a group have shifted northwards in the Bering Sea (Mueter & Litzow 2008), and four chondrichthyan species in the Southeast Australia has shifted southwards, most likely due to climate change (Last et al. 2011). Two skates, however, seem to have a range shift in the opposite direction – away from the pole. Using data from the Spring Bottom Trawl Survey (Northeast Fisheries Science Center, <http://nefsc.noaa.gov>), Nye et al. (2009) found that the centre of biomass of *Leucoraja erinacea* and *Leucoraja ocellata* had moved southwards. There are, however, considerable uncertainties in skate identification in these surveys (NEFSC 2007). Additionally, these two species are very difficult to identify at sizes <30 cm, and genetic methods are required (Bremer et al. 2005). Also, taking into account that the actual range of these two species is larger than the area covered by the Spring Bottom Survey (Nye et al. 2009), it is difficult to conclude that chondrichthyan species are moving away from the poles with increasing sea temperatures, or if the shift is caused by something else. To sum up, chondrichthyans do seem to respond to climate change as predicted.

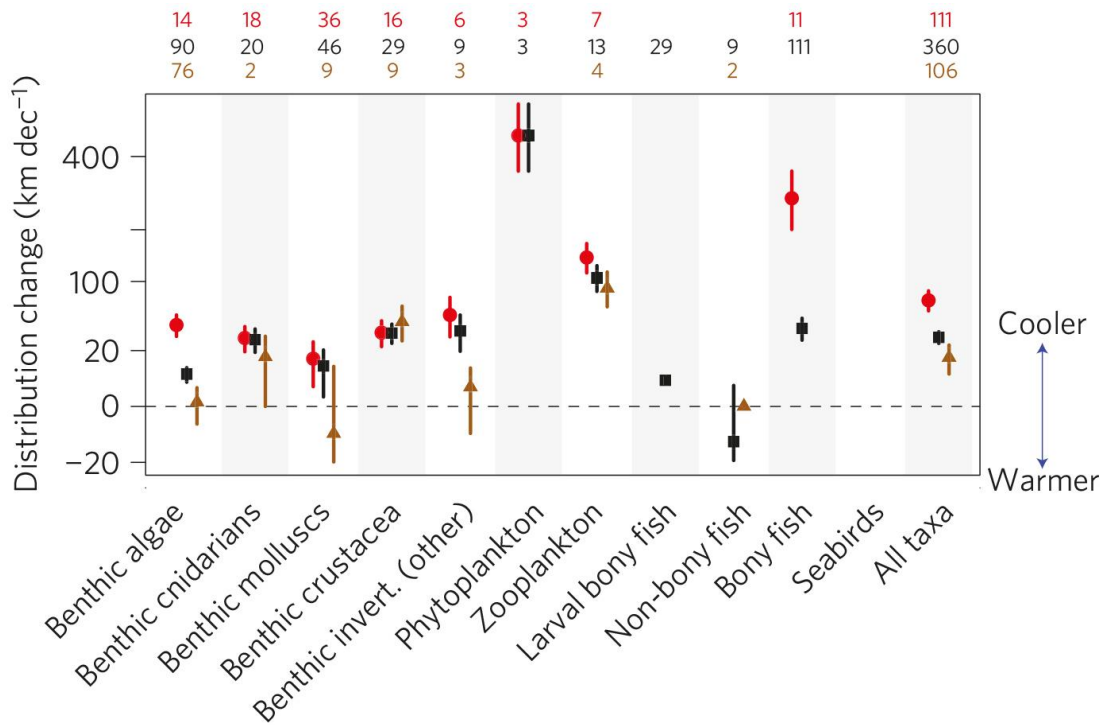


Figure 11. Range shifts given in kilometres per decade. Number of observations are given on top, with leading (red) and trailing edges (brown). Black squares are the average distributional shift regardless of range location by use of all data. Reprinted by permission from Macmillan Publishers Ltd: *Nature Climate Change*, Poloczanska et al. 2013 (Fig. 2a).

## Misidentifications

As evident from the examples given above, species identification may occasionally be questionable. Most records in Paper I originated from the literature, and as the work progressed in Paper II, some doubt was raised concerning the *D. batis* complex. This species complex has earlier been mixed up with another, large-bodied skate, the more frequently occurring *B. spinicauda*. A strong indication of misidentification is found in Dolgov et al. (2005), where given depth occurrence for the two species in the Barents Sea appears to be similar and is ranging from 300-750 m. According to the literature, preferred depths for the *D. batis* complex and *B. spinicauda* are 100-200 m and 200-800 m, respectively (Ebert & Stehmann 2013). To my knowledge, the *D. batis* complex has not been observed in the Barents Sea, but that does not mean it is totally absent.

DNA barcoding is a standardised method for identifying species by using the mitochondrial cytochrome *c* oxidase subunit I (COI, Hebert et al. 2003, Ward et al. 2009). The criterion for separating species is that the intraspecific variation needs to be lower than the interspecific variation. However, defining a species is often an utmost complex task (Hey 2006), and additional genetic markers as well as morphology and ecology need to be taken into consideration. An important prerequisite for identifying an unknown species by DNA barcoding is that the species boundary and the genetic sequence (COI) must be characterised in advance. In other words, trained taxonomists are needed for building up the database, to ensure the correct connection between genotype, phenotype and species name. The rationale for choosing the mitochondrial COI marker in Paper II was, besides its ability to discriminate between species, that it is widely in use and to date there are millions of barcode sequences available in the Barcode of Life Datasystems (BOLD, <http://www.boldsystems.org>, Ratnasingham & Hebert 2007). Previously, DNA barcoding of skates has been published from Canada (Coulson et al. 2011) and the southern North Atlantic (Serra-Pereira et al. 2011) and in Paper II one of the knowledge gaps for skates in the North Atlantic is being closed. One practical implication of the accomplishments is that skinned skate wings, that are difficult to identify by morphology, may be sequenced and checked against the database. This could reveal threatened species at fish markets (Griffiths et al. 2013).

Although the Norwegian and Barents Seas are well investigated (Skjoldal 2004, Sakshaug et al. 2009), the occurrence of skate species is unclear due to misidentifications. Low commercial interest and equal pricing for all species may contribute to this. A total of 15 species are previously reported from the area, and all are easily distinguished by use of DNA barcoding (Paper II). During the course of this study, three species, *Leucoraja circularis*, *Leucoraja naevus* and *Raja montagui* were formally documented for the first time in Norway and vouchered in natural history museums. Only one of each of the two latter was recorded, thus representing the only known specimens of these species in Norwegian waters. *Leucoraja fullonica*, which had previously been considered common (e.g. Storm 1880), may according to Paper II have disappeared. After publication of that paper, however, one record of *L. fullonica* off central Norway in July 2010 has been personally communicated by O. Bjelland, Institute of Marine Research (IMR).

As mentioned above, the critically endangered common skate has been split in two (Box 1). A single specimen of the larger species (*Dipturus cf. intermedia*) was found in Paper II, but no

evidence of the smaller. The latter has been recorded in Icelandic waters, and we cannot exclude its existence in Norwegian waters. Lastly, *Raja brachyura* has been reported (Williams et al. 2008), but all records are most likely misidentifications. Paper II herein provides the first published COI sequences that confirm both the splitting of the *D. batis* complex (Griffiths et al. 2010, Iglésias et al. 2010) and the recent reallocation of *Dipturus linteus* to *Rajella lintea* (Stehmann 2012). In summary, there are 13 species in Norwegian waters that with certainty have been encountered, and how to identify those species by morphology is described in a new identification guide (Appendix).

### **Vulnerability and fisheries**

Global landings of chondrichthyans peaked in 2003 (Dulvy et al. 2014), and is currently declining. Landings and actual abundance are not comparable (e.g. discards due to low commercial value), and it is estimated that about half of the global chondrichthyan catch is discarded (Stevens et al. 2000). Being large at the time of birth implies a higher susceptibility for being caught in fishery gear, and even egg cases are caught in trawls (own pers. obs.) The presence of spines and a wide body in skates make them prone to entanglement in gillnet and trawl, and a large mouth literally opens up for swallowing baited long-lines. A typical chondrichthyan fishery is rarely sustainable over time, and there are numerous examples of fishery-induced collapses such as for four skate species off the eastern coast of Canada (McPhie & Campana 2009), and the sharks *Lamna nasus* (Campana et al. 2008) and *Squalus acanthias* (Fordham et al. 2006). However, low fecundity *per se* is not the most significant factor for low resilience to fisheries. Dulvy & Reynolds (2002) evaluated the risk of local extinction for skates worldwide, and found body size to be the best predictor, larger skates faced a higher risk of extinction (see also Stevens et al. 2000, Hutchings et al. 2012).

### **Skate landings in Norway**

The total landings from Norwegian vessels (Statistics Norway, <http://www.ssb.no>) show an overall negative trend (Fig. 12). The reason for this is not known, and besides a true decline, skates might have become less profitable for the fish industry. It could also be due to modernisation of the fishing fleet, with automated filet machines which are not configured for skates. Most of the catch is delivered for consumption, but the category ‘feeding stuff or bait’



seems to increase and in 2013 this proportion was 25 % (Statistics Norway, <http://www.ssb.no>). Interestingly, *A. radiata* has been retained in Icelandic waters since the 1990ies (Icelandic Fisheries 2014). The *D. batis* complex has been depleted there, and *A. radiata* is now filling the market demand.

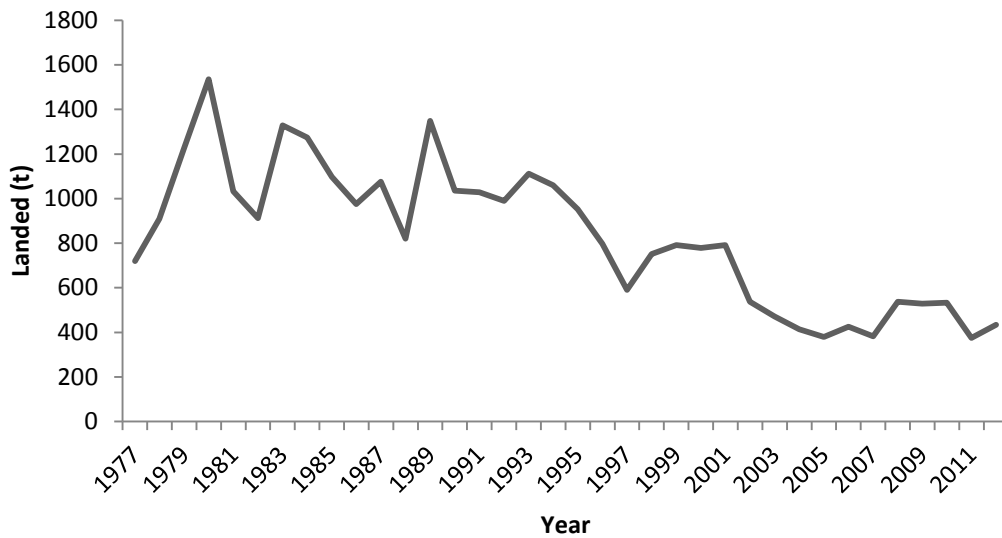


Figure 12. Total landings (tonnes) of “Skates & Rays” from Norwegian vessels. Catches from other countries than Norway are included. Data from Statistics Norway (<http://www.ssb.no>).

The fundamental problem of assessing landings and abundances of skates is the lack of species-specific data. In Norway, scientific catch data from the IMR can generally not be trusted prior to 2007 (R. Wienerroither, IMR, pers. comm.). In recent years, more emphasis has been given to proper species identification (e.g. workshops with trained taxonomists, myself included), and this has improved the data quality. In the commercial fishery industry, the identification is still poor. Skates are grouped into ‘Skates & Rays’, or simply misidentified. Part of the problem could be a confusing report system which is based on species codes from the Norwegian Directorate of Fisheries (NDF) and the Food and Agricultural Organization of the United Nations (FAO). As Tab. 1 shows, there are five categories for essentially the same group. *Rajella lintea*, a relatively large species frequently occurring in fish markets, is missing. Codes for a number of species not occurring in Norwegian waters are included, and this is because the Norwegian fishing fleet also operates

in other regions of the North Atlantic. Unfortunately, more options create more room for misidentification. Identification issues are not restricted to Norway, but it is a general problem for skates (Stevens et al. 2000, Tinti et al. 2003, ICES 2007, Stevenson et al. 2007, 2008, Iglésias et al. 2010). Commercial fishermen are using a variety of gears, different from scientific vessels. They have an invaluable capacity for recognising species by habitus, and they are occasionally catching rare species. However, they may not realise that their knowledge is unknown to the scientific community. Technological advances such as cameras (on e.g. mobile telephones) are helpful, and fishermen should be encouraged to take pictures and send them to experts for verification. The single *D. cf. intermedia* found in Paper II, was provided by a fisherman.

Table 1. Species codes and names from the Norwegian Directorate of Fisheries (NDF) and the Food and Agriculture Organization of the United Nations (FAO), available to the Norwegian fishing fleet (skates and rays only). There are five aggregative categories (in bold), and *Rajella lintea* is missing.

NDF code	Vernacular name	Scientific name	FAO code
<b>5</b>		<b>RAJIFORMES</b>	
<b>51</b>		<b>Rajidae</b>	
511	Blue skate	<i>Dipturus (Raja) batis</i>	RJB
512	Thornback ray	<i>Raja clavata</i>	RJC
513	Spotted ray	<i>Raja montagui</i>	RJM
514	Shagreen ray	<i>Leucoraja (Raja) fullonica</i>	RJF
515	Cuckoo ray	<i>Leucoraja (Raja) naevus</i>	RJN
516	Longnose skate	<i>Dipturus (Raja) oxyrinchus</i>	RJO
517	Little skate	<i>Leucoraja (Raja) erinacea</i>	RJD
518	Barndoor skate	<i>Dipturus (Raja) laevis</i>	RJL
519	Winter skate	<i>Leucoraja (Raja) ocellata</i>	RJT
520	Thorny skate/ Starry ray	<i>Amblyraja (Raja) radiata</i>	RJR
521	Smooth skate	<i>Malacoraja senta</i>	RJS
522	Spinytail skate	<i>Bathyraja spinicauda</i>	RJQ
523	Blonde ray	<i>Raja brachyura</i>	RJH
524	Sandy ray	<i>Leucoraja (Raja) circularis</i>	RJI
525	Round ray	<i>Rajella (Raja) fyllae</i>	RJY
526	Small-eyed ray	<i>Raja microocellata</i>	RJE
527	Undulate ray	<i>Raja undulata</i>	RJU
528	White skate	<i>Rostroraja (Raja) alba</i>	RJA
<b>529</b>	<b>Raja rays nei</b>	<b>Raja spp.</b>	<b>SKA</b>
53		Myliobatidae	
531	Eagle rays	<i>Myliobatidae</i>	EAG
54		Torpedinidae	
541	Torpedos	<i>Torpedo</i> spp.	TOE
55		Rajidae	
551	Norwegian skate	<i>Dipturus (Raja) nidarosiensis</i>	JAD
552	Arctic skate	<i>Amblyraja (Raja) hyperborea</i>	RJG
<b>559</b>	<b>Rays and skates nei</b>	<b>Rajidae</b>	<b>RAJ</b>
<b>599</b>	<b>Skates and rays, nei.</b>	<b>Rajiformes</b>	<b>SRX</b>

Statistics received from the NDF (G. A. Kuhnle, pers comm.), show that approximately 330 tonnes of skate have been landed annually from 2007-2012. The numbers are somewhat lower than from Statistics Norway because only catches from Norwegian waters are considered

(including landings from foreign vessels). In the years from 2007-2012, more than 90 % of the landings were skate wings only. Less than 10 % of the landings are reported to species level, and many of those are probably misidentified (Paper II). The fishery is small compared to other species, such as the Atlantic cod *Gadus morhua*, for which about 280 *thousand* tonnes were landed annually in the corresponding years.

Discarding is prohibited according to Norwegian law (Fiskeri- og kystdepartementet 2007). However, an analysis by Vollen (2010) revealed a discrepancy in catches from a reference fleet and the regular fleet, indicating that discarding is still an issue. Size matters in the fisheries and only specimens above a certain total length (TL) are retained. In UK waters, 50 % retention size (the size where 50 % of the catch is retained) for skates is about 49-50 cm TL (Silva et al. 2012) and this retention size could be valid in Norwegian waters as well.

### **International and national red lists**

The Convention on Biological Diversity was signed in Rio de Janeiro in 1992 (<http://www.cbd.int>), aiming to ensure sustainable development and provide a healthy and viable world for future generations. World leaders agreed that conservation of biological diversity and sustainable use of its components are of high importance. There are many good arguments for maintaining high diversity, such as more stability in fisheries (Worm et al. 2006), or increased production and buffer capacity to disturbance (Duarte 2000). A frequently occurring term is ‘ecosystem services’, where ecosystems are linked to human well-being (Millennium Ecosystem Assessment 2005). This is examples of anthropocentric arguments, but just as important is the moral aspect for conserving biodiversity. Biocentrism is the belief that the rights of humans are not more important than other living things (<http://www.oxforddictionaries.com>), and should in my opinion be weighted equally to the significance of ecosystem services. The IUCN Red List of Threatened species (<http://www.iucnredlist.org>) and the Norwegian Red List (<http://www.artsdatabanken.no>) aim to determine the extinction risk for species. The two red lists have different geographical limitations, with international and national focus, respectively. Species are living in dynamic environments, and the red list assessments are therefore updated annually or every fourth year. Due to identification issues as mentioned above, the lists are somewhat subjective and proper catch statistics are lacking from most countries. Nevertheless, it gives an idea of the

status for most species. Species are grouped into categories from ‘Not Evaluated’ to ‘Extinct’, and only three categories are considered threatened (Fig. 13).

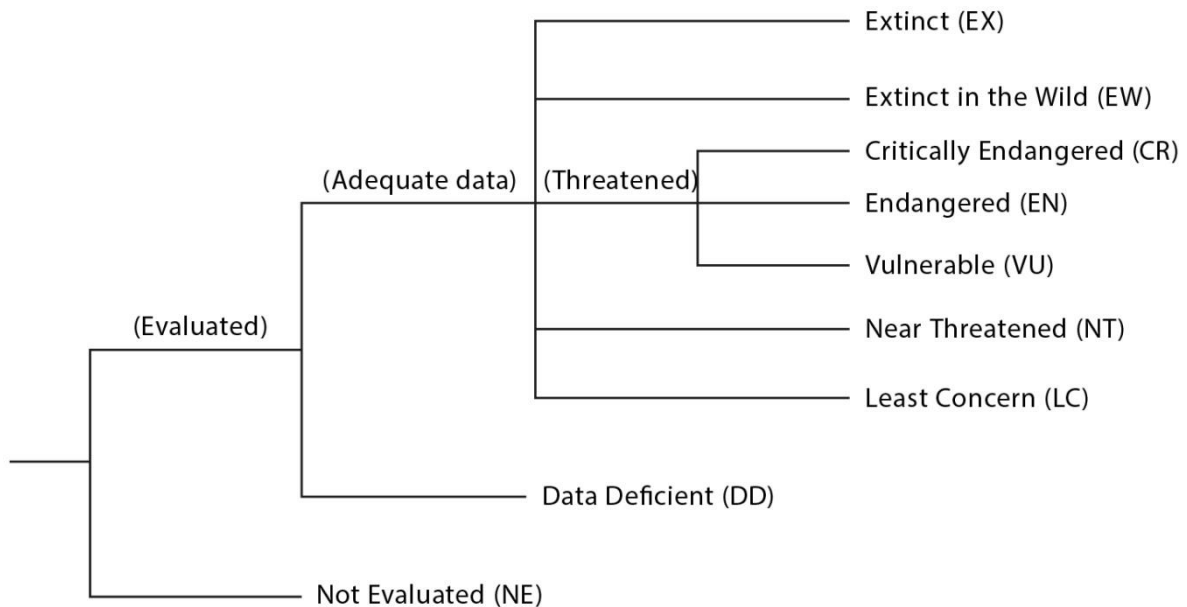


Figure 13. Red list categories. Redrawn from <http://www.iucnredlist.org>.

National and international red lists are not necessarily similar due to local populations (Tab. 2, Paper III). One example is *Amblyraja radiata*, which is considered ‘Vulnerable’ as a whole and in Canadian waters, ‘Least Concern’ in the Northeast Atlantic, but is ‘Critically Endangered’ and declining in US waters (Kulka et al. 2009). Species are not included in national lists if < 2 % of the global populations is thought to be present in the respective waters. *Leucoraja circularis*, *L. naevus* and *R. montagui* are known from few specimens only (Paper II), and are thus not considered in the Norwegian Red List (Tab. 2).

Table 2. Skate species recorded from Norwegian waters with associated international and national red list status.

Species	IUCN Red List	Norwegian Red List
<i>Bathyraja spinicauda</i>	Near Threatened	Near Threatened
<i>Amblyraja hyperborea</i>	Least Concern	Least Concern
<i>Amblyraja radiata</i>	Vulnerable	Least Concern
<i>Dipturus batis</i> *	Critically Endangered	Critically Endangered
<i>Dipturus nidarosiensis</i>	Near Threatened	Near Threatened
<i>Dipturus oxyrinchus</i>	Near Threatened	Least Concern
<i>Leucoraja circularis</i>	Vulnerable	Not Evaluated
<i>Leucoraja fullonica</i> **	Near Threatened	Near Threatened
<i>Leucoraja naevus</i>	Least Concern	Not Evaluated
<i>Raja clavata</i>	Near Threatened	Least Concern
<i>Raja montagui</i>	Least Concern	Not Evaluated
<i>Rajella fyllae</i>	Least Concern	Least Concern
<i>Rajella lintea</i>	Least Concern	Least Concern

\*The red lists do not yet consider this complex as two distinct species.

\*\*Paper II suggests that this species could be close to extinction in Norwegian waters.

Skate management in the North Atlantic is based on inconsistent reporting of species (Clarke 2009), which is even worse than reporting the catch as ‘Skates and rays’. This issue was addressed already in Dulvy et al. (2000), but without any significant improvement since then. Skates were generally recorded as ‘Other species’ in the Bering Sea until 2011, but are now reported at species level and fisheries observers have been thoroughly trained (Ormseth et al. 2010). The relatively small-sized *A. radiata* is the most common species in the North Sea (Walker & Heessen 1996, Skjæraasen & Bergstad 2000) and it comprises about 95 % of the skates caught by number in the Barents Sea (Dolgov et al. 2005). Mostly large specimens are landed, and a major concern is that the remaining 12 species comprise only ~5 % of the skates by number. These species may be at risk (Paper II), but it must be noted that some species do have natural low abundance or are occasional visitors. Egg cases from seven skate species have been found in the study area (Paper II). This is a strong indication of local spawning and thereby gives Norway a special responsibility to reduce the risk of local extinction.

### **Conservational actions**

Regardless of the data quality in red list assessments, measures must be taken based on what we know, and the precautionary principle should be taken into account (O'Riordan & Cameron 1994). Most skates are caught as by-catch and could be released alive. The survival rate, however, would depend on the condition of the animal when they are brought on board. This again depends on species, towing time and cod end weight, and survival rates were 95 % for skates expressing 'good health' (Enever et al. 2009). The European Union has now banned directed fishery or landings of the *D. batis* complex for their fishing fleet, and accidentally captured specimens should be released immediately (EU 2011). Regulations could thus be useful, but require correct species identification by the fishermen. Skates are not distributed evenly (Serra-Pereira et al. 2014), and more precise identification lead to better distribution maps. Restricted areas may hold rare species such as *L. circularis* (Williams et al. 2008), or they may be nursery grounds, as observed for *A. hyperborea* off Bear Island (own pers. obs.). To protect such regions might be a possible action. Barnett et al. (2013) suggest some changes for the eastern Bering Sea, such as reducing fisheries within certain depths, or avoid nursery sites. This is something to consider also in the nNE Atlantic, but better background data are needed. Even depth preference for different species is subject to uncertainties, as systematic misidentification has been an issue, such as for the *Raja clavata/A. radiata* (Williams et al. 2008) and *B. spinicauda/D. batis* complex (Dolgov et al. 2005), four species with highly different depth preferences.

### **Population genetic structure in *Ambyraja radiata***

As shown in Tab. 2, species may face different trends in abundance throughout their range. If the populations are considered panmictic, a declining population may be assigned to a less critical red list category if migrations from a nearby area are thought to counteract the decline. However, this assumption may be critical if the genetic structuring is higher than anticipated (Dudgeon et al. 2009). It is therefore important to investigate the population structure of a species and the potential for a cryptic species complex. The results from the COI marker (Paper II) indicated a slight differentiation between the NW Atlantic (combined) and the nNE Atlantic group ( $F_{ST} = 0.085$ ,  $p < 0.001$ ). The highest  $F_{ST}$ -value was found between the NW Atlantic late maturing group and the nNE Atlantic group ( $F_{ST} = 0.133$ ,  $p < 0.001$ ). The hypothesis that the early and late maturing group in the NW Atlantic displayed genetic

divergence could not be accepted, as the pairwise  $F_{ST} = 0.017$  was not significant. Geographic distance is thus a greater structuring factor than life-history traits according to this single genetic marker.

Microsatellites, as used in Paper III, are short, repeated sequences that have high mutation rates and are therefore widely used for investigating population structure (Ellegren 2004). Interestingly, the results of Paper III, using 10 microsatellite loci, are very similar to those of Paper II, using a single mitochondrial marker. We hypothesised that long term migration of *A. radiata* from the NE Atlantic to the NW Atlantic was possible, but only via the Norwegian continental shelf and the submarine ridges from Scotland to Greenland (see Paper III). The genetic difference should thus be larger between Svalbard samples and NW Atlantic samples, and this was generally confirmed when looking at pairwise  $F_{ST}$  distances. According to the pairwise  $F_{ST}$  distances, three major clusters are suggested for the N Atlantic: NW Atlantic, Mid Atlantic (Greenland) and NE Atlantic. However, a test of isolation by distance proved to be non-significant, and the STRUCTURE analysis could not find any conclusive pattern that relates the individuals to sampling locality. Moreover, the STRUCTURE analyses suggest some fine scaled structure in the N Atlantic that supports the  $F_{ST}$  estimates. One explanation to the physical mixing of individuals in the N Atlantic could be migration. However, skates do not have any planktonic larval stages and cannot take advantage of ocean currents for dispersal. Tagging studies of *A. radiata* so far indicate generally little migration (Templeman 1984b, Walker et al. 1997). Conversely, the skates of the N Atlantic may have been forced into a refuge in glacial periods. Assortative mating may have contributed to maintain the genetic signature of the individuals, and after re-colonising the N Atlantic, assortative mating may have continued promoting the individual genetic signature. Finally, as for the single mitochondrial marker, the microsatellites gave no indication of genetic isolation between late and early maturing individuals, and the hypothesis of *A. radiata* being cryptic has not been supported. However, neutral loci, as used here, require long time to differentiate between diverging populations. Adaptive genomic differences occur faster, and future studies should consider both neutral and adaptive loci.



## Conclusions

A baseline is here presented for the occurrence of species in the Arctic Ocean and adjacent seas (Paper I & II). Substantial misidentification of skates is revealed (Paper II), meaning that data on abundance, distribution and physical preferences for the respective species may be inaccurate or wrong. In light of the given examples of species mix-ups, scientists are urged to be critical in their use of data. Correct species identification forms the basis for ecosystem management, and without accurate data, red list status cannot be assessed or biodiversity loss be detected. A practical tool for identifying skates in the field is provided (Appendix), and this will hopefully improve the data collection and proper species identification in the future. Rare species, found only once (Paper I & II), may currently have a low ecological impact on the ecosystem, but they give an indication of which species to expect with environmental change. Skates are not commercially valuable in the nNE Atlantic today, but this may change in the future, as seen in Iceland (Icelandic Fisheries 2014) and in the NW Atlantic (Link 2007). The results of Paper II and III agreed to reject the hypothesis of *A. radiata* being a cryptic species, but the spatial distribution and genetic structure of *A. radiata* could not be fully explained. In other words, for every knowledge gap being closed, a new gap is opened on each side.

## Future perspectives

Large data sets have been collected during the last years, and with the taxonomical issues largely solved, ecological knowledge gaps may also be examined. A list of actions and potential studies follows below:

1. The identification guide will be distributed widely. The Norwegian Directorate of Fisheries has received the latest edition and will make it available for fishermen. The guide will be published in *Zootaxa*, after a peer review process.
2. The microsatellites used on *A. radiata* also fit *A. hyperborea*. A total of 130 specimens from the Barents Sea and a few from NE Greenland are sampled and run on the fragment analyser, ready for genotyping. More specimens could be obtained from across its range, and potential genetic structure is especially interesting when considering study number 3 below.
3. The nursery ground of *A. hyperborea* off Bear Island should be investigated, and the Mareano project (<http://www.mareano.no>) has been contacted since they are doing underwater filming and mapping of the seascape. They have not yet investigated the area off Bear Island, but may do so in the future (B. Holte, IMR, pers. comm.). This will give us important insight of the site, without invasive trawl sampling (although tissue samples for genetic analyses would be very welcome).
4. In cooperation with IMR, we have collected egg cases from the Barents Sea. Measurements are finished, but analyses are yet to be done. DNA barcoding of the egg cases failed, but an identification guide will be made, based on morphology. When this is accomplished, we may be able to pinpoint areas where respective species deposit eggs.
5. About 800 skates of different species are measured and tissue samples are taken for genetic and stable isotope analyses. Stomachs are kept frozen, and we are thus able to compare stomach contents with the stable isotopes in order to determine their trophic level. Maturity status has been determined, and is ready for analysis. This is in cooperation with IMR, who also have an aging lab, where spines and vertebrae can be used for age determination.

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