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The distribution of chondrichthyans along the northern coast of Norway

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The relationship between temperature, latitude, and depth, and the distribution and relative abundance of chondrichthyans along the northern coast of Norway was examined on the basis of catches made in scientific trawls north of 62°N from 1992 to 2005. It appears that *Chimaera monstrosa, Etmopterus spinax, Squalus acanthias*, and *Galeus melastomus* were more abundant in the south, and *Amblyraja radiata* more common in the north. Between 1992 and 2005, the distribution and relative abundance did not appear to change significantly even though average water temperatures rose during the period. Current fishing levels do not appear to be impacting the populations of the more common species, but the status of species rarely found in the survey catches is unclear.

Keywords: abundance, bottom trawl survey, Chondrichthyes, distribution, elasmobranchs, Norway, shark, skate.

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Introduction

There is increased awareness that stocks of chondrichthyans are particularly susceptible to overexploitation as either target or bycatch species. As large-bodied species with few natural predators when fully mature, they have not evolved strategies to withstand rapid changes in mortality (Stevens *et al.*, 2000). To varying degrees, all these species are slow-growing, have a long lifespan and low fecundity, and attain sexual maturity at a late age (Holden, 1977; Walker and Heessen, 1996). Population growth is influenced by juvenile survivorship and age at maturity (Sosebee, 2005). Although theoretical mechanisms of density-dependence have been looked at, empirical evidence for chondrichthyans (elasmobranchs) is limited and often confounded by methodological issues (Ellis *et al.*, 2008). Their limited ability to compensate for being depleted has often been exemplified by the poor record of sustainability by fisheries that have targeted them (Stevens *et al*., 2000), and by elasmobranch stocks that have declined either unnoticed or unchecked. The reasons for these stock declines have been described by a number of authors (Bonfil, 1994; Dulvy *et al.*, 2000; Stevens *et al.*, 2000; ICES, 2006).

Fisheries research has traditionally focused on the more commercially important teleost and shellfish species, and little research has been undertaken on chondrichthyans. Catch and landings data from commercial fisheries are often poor because of a general lack of species-specific recording (Johnston *et al.*, 2005), and bycatch data only became moré available recently. As a result, even the most basic data are unavailable for quantitative studies of the stock status of most chondrichthyans, including those in the Northeast Atlantic (ICES, 2006). The uncertainties in historical total landings and bycatch data attributable to the common practice of recording catches generically, e.g. as “dogfish and hounds”, rather than by species, makes fishery-independent data from surveys an important source for studying the distribution and relative abundance of chondrichthyans. To varying degrees, research has been undertaken throughout much of the ICES area (Walker and Hislop, 1998; Daan *et al.*, 2005; Ellis *et al.*, 2005a), and studies have been conducted along the coast of southwestern Norway (Skjæraasen and Bergstad, 2000, 2001), and northwards into the Barents Sea (Dolgov, 1997, 2006; Dolgov *et al.*, 2004, 2005a). However, the chondrichthyan species along the northern coast of Norway have received little attention and are poorly understood.

Norwegian fisheries targeted Greenland shark (*Somniosus microcephalus*) until 1960 and basking shark (*Cetorhinus maximus*) until 2006 (ICES, 2006). Other chondrichthyans have not been and are not currently targeted by commercial fisheries operating along the northern coast of Norway, but are taken as bycatch in the coastal fishery. The coastal fleet consists of vessels using a variety of gears, including gillnet, longline, trawl, Danish seine, handline, and pots. Gillnet and longline fisheries targeting demersal fish (e.g. cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*) generate the bulk of the chondrichthyan bycatch (Table 1), and management strategies are in place to minimize the bycatch of undersized commercial species, though not relating directly to chondrichthyans (Nakken, 2003). The introduction of sorting grids (Nordmøre grid) in the shrimp fishery in 1992 reduced the bycatch significantly, and only juvenile chondrichthyans (generally <25 cm) have been caught since (Reithe and Aschan, 2004).

Climate may also play a part in determining the biogeographical distribution of the group. Therefore, studies on the distribution and movement of elasmobranchs should examine environmental parameters associated with the distribution of the various species (Pawson and Ellis, 2005). Dolgov *et al.* (2005a) suggested that the distribution of various skate species in the Barents Sea appeared to be related to sea temperature. Since the 1990s, there has been a marked increase in sea temperature, particularly in the southern part of the coast of northern Norway (Pawson and Ellis, 2005). Many chondrichthyans found along this coast are close to their geographical limits, so changes in environmental conditions may be expected to affect their local abundance.

The aim of this study is (i) to identify species present along the northern coast of Norway between 1992 and 2005, (ii) to describe their distribution and abundance, (iii) to identify significant spatial or temporal differences between species, and (iv) to evaluate whether changes observed in distribution and abundance over time are affected by sea temperature. Such information will, we believe. help to resolve the issue of identifying appropriate stock units for management.

Material and methods

The study area consists of fjords and offshore banks along the northern coast of Norway from south of Ålesund (62°00'N 4°50'E) to the Russian border near Kirkenes (69°50'N 30°50'E) (Figure 1). Fjords north of 68°N are mainly shallower than 300 m, though those to the south are generally deeper. The coastal banks outside the fjords range in depth from 50 to 400 m (Berg and Albert, 2003). Despite the high latitude, sea temperatures are generally warmer than in other northern coastal areas because of the influence of the Norwegian Current, a branch of the Gulf Stream that flows northeastwards along the coast. As the current passes through higher latitudes, there is an overall reduction in sea temperature. Temperatures are not constant and fluctuate in short- and long-term intervals (Gyory *et al.*, 2005), and average sea temperatures have increased over the past century (Berstad *et al.*, 2003).

Temperature data

During the period 1935–1947, several permanent hydrographical sampling stations were established along the Norwegian coast by the Institute of Marine Research (IMR, 2007). Temperature data from four stations, Bud (62°56'N 6°47'E), Eggum (68°22'N 13°38'E), Ingøy (71°08'N 24°01'E), and Vardø (70°45'N 31°03'E), were used in this study (Figure 1). Water temperature and salinity were measured using CTD sensors deployed from research vessels. Approximate bottom temperatures were measured as close to the seabed as the equipment would allow (generally within 10 m) and registered to an accuracy of 0.01°C. Annual temperatures at each station were calculated as the mean of quarter-year values.

Survey data

The survey data were from the annual combined trawl and acoustic surveys conducted each autumn by the Norwegian Institute of Fisheries and Aquaculture Research (Fiskeriforskning) from 1992 to 2001, and by IMR during the period 2002–2005 (Table 2). The main aim of these coastal surveys was to investigate commercial species such as coastal cod, haddock, saithe (*Pollachius virens*), and juvenile herring (*Clupea harengus*).

At the start of the survey in 1992, the intended survey area was divided into three sections, to determine the feasibility of the survey and to facilitate the development of a practical design. One section was intensely sampled each year, the northern section in 1992, the central section in 1993, and the southern section in 1994 (Table 2). Since 1995, the entire area has been sampled annually. The surveys then began at the northeastern limit of the area, covered the Norwegian coast to 62ºN, and lasted approximately 30 d (Figure 1). Sampling was evenly distributed along the coast, and included fjords and offshore areas near the coast (Figure 1). Sampling stations were not selected randomly, because the seabed in fjords and over the shelf is often too rough to permit trawling (Berg and Albert, 2003). The same stations were approximately fixed for each survey from 1995 to 2005, although poor weather conditions or technical difficulties resulted in some stations occasionally being omitted. Catches were considered reasonably representative of substrata suitable for trawling at 30–700 m. The deepest average depth trawled was around 65ºN (Figure 2).

The sampling trawl was a Campelen 1800 shrimp trawl with a 30-m headline, 19-m groundrope, 80–42-mm knot-to-knot stretched mesh in the body, and 20-mm standard mesh size in the inner net (Table 2) (Aschan and Sunnanå, 1997). The gear had 40-m bridles and rock-hopper groundgear, with eight steel spacers between 14 rubber discs. Sensors monitored trawl geometry, and strapping constrained the distance between doors to approximately 47 m while trawling (Aschan and Sunnanå, 1997). At this door spread, the silt plume was directed towards the trawl wings and considered to maximize the herding effect between doors and net.

Species identification

All species were identified, counted, and weighed. In 14 of the trawl samples taken between 1997 and 2004, all the skate species (Rajidae) were grouped and recorded generically, so these observations were excluded from this study. Originally, the names were in Norwegian, according to the species list in the IMR quality control system (Mjanger *et al*., 2004), but the species list of 2004 included Latin names. These names have been monitored and, where appropriate, updated to valid scientific names according to the Integrated Taxonomic Information System (ITIS, 2008).

The reliability of the results from this study depends on the species identifications being accurate and consistent. Unfortunately, no voucher specimens were collected because the main target of the survey was the commercially important teleosts. Therefore, uncertainties in species identification were analysed during the 2006 survey. Participating scientists were observed sorting and identifying fish, then interviewed to understand better the limitations of the identification procedures, especially for skates, which are a problematic taxonomic group (e.g. *Raja montagui* is sometimes confused with *Raja brachyuran*, according to J. R. Ellis, pers. comm., and *Raja clavata* and *Amblyraja radiata* are often confused – Daan, 2001). Because of the uncertainties involved in modifying the raw data, changes in identification (described by Williams, 2007) were limited to clear inconsistencies that were demnstrated between personnel shifts during some surveys. Individual *Amblyraja radiata* may have been misidentified as *Raja clavata* during the 1990s, but *Raja clavata* has rarely been taken and then mainly south of 68ºN (W. Richardsen, pers. comm.). However, we cannot confirm these recordings, so have excluded *Raja clavata* from our analyses.

Abundance and distribution mapping

The estimated spatial distribution for a species was based on data from the entire survey period (1992–2005). Abundance was expressed as the number of individuals per km^2 at each station. Abundance was estimated based on the area trawled at each station using the method of Jakobsen *et al.* (1997):

$$\rho_s = \frac{f_s}{a_s}, \qquad (1)$$

where ρ_s denotes the abundance in number of fish per km^2 at sample station *s*, f_s the number captured (frequency) at sample station *s*, and a_s is the area swept (km^2) at sample station *s* (nautical miles trawled × 1.852 × 0.047 km).

The door spread of 47 m was assumed to be the upper limit of the mean effective catching width of the gear. A more precise estimate of catch efficiency was beyond the scope of this study.

The annual mean catch (number per km^2) was used to compare species abundance. Species with an annual mean catch >5 animals per km^2 were grouped as common species, and included for further statistical analysis. Species with lower catch rates were either grouped as infrequent, if previously recorded in the survey area, or rare if not recorded previously.

Pethon (2005) and FishBase (Froese and Pauly, 2007) give previously estimated distributions. The two sources were generally consistent, although they differed for *Dipturus batis*, *Leucoraja fullonica*, *Dipturus linteus*, *Bathyraja spinicauda*, and *Galeus melastomus*. All five of these species are described by Pethon (2005) as having a more northerly distribution than given in FishBase (Froese and Pauly, 2007). In our opinion, the species distributions of Pethon (2005), which are updated based on recent data, were more accurate than those in FishBase, so were taken as the standard distributions for the present study.

Statistical analysis

For seven common species, the relative abundance (number km^{-2}) in each trawl sample was used to assess the statistical significance of temporal and spatial variation in abundance. Year, depth, and area were the independent variables. The survey area was divided into seven subareas by degree latitude from 62 to 69°N, and a northern region (from 69 to 71°N) was divided into two subareas east and west of 25°E (Figure 1). Samples were identified by 50-m depth interval, encompassing the depth range covered by the survey. Average abundance for each species was calculated, and differences in abundance were tested against the three variables, depth, latitude, and year, using one-way single factor ANOVA. The significance level was set at $p = 0.05$.

A constrained (canonical) correspondence analysis (CCA) was run in R 2.5.0 (R Development Core Team, 2007) using the vegan package (Oksanen, 2007). As the species data contained many zeros, they were analysed using unimodal methods (ter Braak and Verdonschot, 1995). The ten most common species were included in the analysis, and their abundance estimates were log(x+1)-transformed. Potential explanatory variables were longitude, latitude, depth, and year of sampling. Shifts in abundance of each species were shown as percentages of deviation from the average abundance within the total survey area and presented with respect to the strongest explanatory variable.

Correlations were tested for all species with distributions significantly correlated with latitude. The locations of the four temperature stations determined the areas 63°N, 68°N, West (69–71°N), and East (69–71°N) (Figure 1) used for assessing correlations between abundance and temperature. Spearman's rank-order correlation (ρ) was used to test whether latitudinal or annual differences in temperature significantly influenced the distribution of nine common species.

Results

Abundance and distribution

During the survey period 1992–2005, 18 species Chondrichthyes were recorded at 1932 stations (Table 3). The most diverse orders observed were skates (Rajiformes, 13 species) and dogfish sharks (Squaliformes, three species). In contrast, only one species of catshark (Scyliorhinidae) and rabbitfish (Holocephali) were identified in the samples. Six species were observed across the entire latitudinal range (62–71ºN), and many species seemed to have a boundary in the north (Figures 3 and 4). Mean annual catch rates and frequency of occurrence for each species reveal that *Chimaera monstrosa*, *Etmopterus spinax*, *Galeus melastomus*, *Amblyraja radiata*, *Squalus acanthias*, and *Dipturus oxyrinchus* were the main species (Table 4). For many species, abundance sometimes varied greatly between years, but there were no obvious negative or positive trends, indicating no recent changes in abundance of the more common species (Figure 5). One exception was *R. fyllae,* which exhibited an increasing trend in the data. Annual changes in abundance were only significant ($p < 0.05$) for *A. radiata* (Table 5), which increased significantly between 2002 and 2003, decreased by the same extent between 2004 and 2005, but had no apparent long-term trend (Figure 5). Latitude was a significant factor (ANOVA, $p < 0.05$) affecting the abundance of all common species (Table 6).

C. *monstrosa* and *E. spinax* (Figure 3a, b) were observed in all areas except in the far northeast (East 69–70ºN). Abundance was greatest in the south, where catch rates were occasionally >2000 fish per haul, suggesting an aggregating behaviour by the two species. Distributions of *G. melastomus, S. acanthias*, and *D. oxyrinchus* (Figure 3c, e, f) appeared to be constrained to areas south of 68ºN, with most catches south of 65ºN. Catches of *G. melastomus* of >200 animals in each of 10 hauls highlights the aggregating nature of this species. *A. radiata* was the dominant skate species and was caught throughout the survey area, but in greater abundance in the north. The distribution of *R. fyllae* was similar (Figure 3d, g).

Abundance appeared to be greatest for *C. monstrosa* at 450–550 m, for *G. melastomus* deeper than 150 m, for *A. radiata* at 600–650 m, and for *R. fyllae* and *D. batis* shallower than 500 m (Table 4; Figure 6). However, differences in depth-dependent abundance were only statistically significant for *G. melastomus* (Table 7), with greatest abundance in the 500-m interval. The three other common species were more evenly distributed with respect to depth (Figure 6).

The constrained correspondence biplot shows the species scores that may be taken as the optimal location for nine species in the environment field spanned by the site scores (Figure 7). The constrained axis CCA1 (eigenvalue 0.457, 88%) has a much larger explanatory value than CCA2 (eigenvalue 0.049, 9%). Latitude seemed to structure the chondrichthyan assemblage into three groups (Figure 7), a northern component consisting of *A. radiata* and *R. fyllae*, a central component with *C. monstrosa*, *D. batis*, *E. spinax*, and *L. fullonica*, and a southern component consisting of *D. oxyrinchus*, *G. melastomus*, and *S. acanthias*. The relative abundance along the latitude shows the same pattern for species of each group (Figure 8). Depth and year were of little importance in defining species distribution (Figure 7).

Of the four species ranked as infrequent, *D. batis* was observed along the entire coast at depths of 85–425 m, and *L. fullonica* from 77–512 m in all areas except the eastern sector of 69–70ºN (Table 4; Figure 4). *D. nidarosiensis* was found as far north as 68ºN at depths of 140–590 m, whereas its known distribution was primarily south of 65ºN (Pethon, 2005). A single *S. microcephalus* was caught 480 m deep at 69º10´N 16º19´E in 1993.

From 1992 to 2005, six rare species were reported, extending the distributions given by Pethon (2005). *R. brachyura*, *R. montagui*, and *L. circularis* were all caught south of 64ºN, but at higher latitudes than previously documented (Pethon, 2005). Of these three, *L. circularis* was caught most frequently and in greatest number, 23 animals in six trawls. The depths of capture for *L. circularis* were 88–244 m, and for *R. montagui* 63–120 m, and four *R. brachyura* were caught at 99 m. Totals of 11 *B. spinicauda* and nine *A. hyperborea* were caught in trawls north of 67ºN at depth ranges of 48–410 m and 125–620 m, respectively, and one *D. linteus* was caught at 588 m off Lofoten at 68ºN.

Abundance and temperature

With the exception of the eastern sector at 69–71°N, all areas appeared to show an overall increase in sea temperature between 1992 and 2005 (Figure 9). With the exception of *R. fyllae*, the abundance of chondrichthyans showed no obvious trend during the study period (Figure 5). Therefore, the Spearman rank analysis showed no significant correlations between annual sea temperature and abundance for each species in the areas 63°N, 68°N, 69–71°N (West), and 69–71°N (East). Bottom temperature decreased in a northward direction along the coast. Latitudinal shifts in abundance for *C. monstrosa*, *E. spinax*, *G. melastomus*, and *S. acanthias* showed positive correlations ($\rho > 0.9$) with bottom temperature, whereas *A. radiata* abundance showed a negative correlation ($\rho > -0.9$) with temperature.

Discussion

Survey data uncertainty

The surveys were designed primarily to assess the commercially important teleosts, so chondrichthyans were not taken into account in the design. Consequently, it is uncertain how accurately the catch rates reflect the relative abundance of the various species (Kotwicki and Weinberg, 2005). As trawl catchability varies with bottom type and species, there is little information available for estimating absolute stock size (Bonfil, 1994; Abella and Serena, 2005; Daan *et al.*, 2005; Dolgov *et al.*, 2005a). Moreover, species that favour hard rocky substrata (e.g. *D. batis*) are likely to be under-represented because most trawling was conducted on seabed that could be trawled, i.e. was fairly smooth.

Species identification issues are important, although this was corrected where possible (Williams, 2007). Misidentification of skates is common (Daan, 2001), and with the exception of the more visually distinct species such as *D. nidarosiensis*, there is still concern regarding the validity of the skate identifications. The main uncertainty in our results is the soundness of the estimated distribution of the infrequent and rare species such as *Raja clavata* (which was excluded from the analyses). For the common species, the data are considered to be valid for describing their relative abundance and distribution.

An update on chondrichthyan distributions

The porbeagle (*Lamna nasus*), which is recorded as a bycatch in the area (Table 1), was not caught at all during the coastal surveys, because the species is rarely taken by trawl (Daan *et al.*, 2005). Basking sharks (*Cetorhinus maximus*) are caught as a bycatch in pelagic fisheries, but were not in our survey data.

From 1992 to 2005, the distribution and abundance of the common species appeared to remain stable (Figure 5). Latitudinal trends in distribution correlated well with previous distributions given by Pethon (2005). Shark species and *C. monstrosa* were clearly more abundant south of 65°N. *C. monstrosa* and *E. spinax* appeared to be the most abundant species, including north of 70°N (Figure 3). *C. monstrosa* has recently also been observed in the southern Barents Sea (Dolgov, 2006; Byrkjedal and Høines, 2007). *A. radiata* is uniformly and widely distributed, and was the dominant skate, followed by *R. fyllae*. The dominance of these two species agrees with studies undertaken in the neighbouring Barents Sea, northeastern North Sea, and Norwegian Sea (Skjaeraasen and Bergstad, 2001; Dolgov *et al.*, 2005a; Dolgov, 2006; Byrkjedal and Høines, 2007). In the south, *D. oxyrinchus* appeared to be more abundant than *R. fyllae*. This may be a fairly localized population, because *D. linteus* replaces *D. oxyrinchus* in the skate assemblage that dominates the neighbouring northeastern North Sea and Norwegian Sea (Skjaeraasen and Bergstad, 2001). *R. clavata* has been recorded as far north as the Barents Sea (Hognestad and Vader, 1979; Fossheim *et al.*, 2006; Byrkjedal and Høines, 2007), but was not observed during Russian surveys from 1996 to 2007 (A. V. Dolgov, pers. comm.). We believe that this species may be a sporadic visitor to the whole northern coast of Norway and may also be taken occasionally in the southwestern Barents Sea. However, the real distribution of *R. clavata* needs further clarification because identification of this species in our data seems to have been biased; voucher specimens are required to confirm its occurrence in northern Norwegian waters.

Because of a lack of knowledge and infrequency of recordings of the rare and infrequent species, it is impossible to be certain of any distribution shifts. Our observations show that *R. brachyura*, *L. circularis*, and *R. montagui*, commonly associated with the North Sea and Atlantic areas south of 62°N (Dulvy *et al.*, 2000; Pethon, 2005; Froese and Pauly, 2007), may all be present as far north as 64°N. This is probably not attributable to a change in distribution, but rather because of poor data historically. *A. hyperborea* and *B. spinicauda* are associated with offshore areas (Mahon *et al.*, 1998; Pethon, 2005; Fossheim *et al.*, 2006; Byrkjedal and Høines, 2007), but were found closer to the coast in our study.

Spatial distribution

A. radiata has a wide and uniform distribution throughout the study area, tough with biomass increasing to the north, and is found also in the Barents Sea (Dolgov *et al.*, 2005a; Byrkjedal and Høines, 2007). Annual distribution maps show that the distributions of *C. monstrosa, E. spinax*, *G. melastomus*, and *S. acanthias* are patchy (Williams, 2007). The large catches (>500 animals in a single haul) underscore the aggregating behaviour of these species. *S. acanthias* often in shoals of the same sex and/or size (Ellis *et al.*, 2005b; Stenberg, 2005), similar to *G. melastomus*, for which there are also bathymetric patterns (Massuti and Moranta, 2003; Calis *et al.*, 2005; Coelho *et al.*, 2005). These uneven distributions can be linked to the availability of suitable bottom substrata or food availability, as has been suggested to explain similar distribution patterns in the neighbouring North Sea and Skagerrak (Skjæraasen and Bergstad, 2000). Tagging studies indicate little mixing of *S. acanthias* between northern and southern areas of the North Sea (Aasen, 1962; Holden, 1967), and Holden (1968) claimed that the Norwegian–Scottish and Channel populations are separate stocks. Despite assertions of transatlantic migration (Holden, 1967; Tempelman, 1984), recent analysis of tag returns indicates that Northeast and Northwest Atlantic stocks should be managed independently. No decline over time was observed for *S. acanthias* in our study area, but declines have been documented for the North Sea, Celtic Sea, and off Northwest Scotland (Daan *et al.*, 2005; Dobby *et al.*, 2005; Ellis *et al.*, 2005a; ICES, 2007). Those studies, however, were based on surveys that started in the 1970s and 1980s. The few large catches (7–19 fish) indicate that, although *D. oxyrinchus* is relatively scarce, local aggregations may occur.

The abundance of some species appeared to be depth-dependent. *D. batis* and R. *fyllae* were confined to water shallower than 500 m (Table 4). However, *R. fyllae* probably exits over a wider depth range (Dolgov *et al.*, 2005a; Jørgensen *et al.*, 2005; Pethon, 2005) and probably prefers deeper waters in the south (Skjaeraasen and Bergstad, 2001). As observed in other areas, *G. melastomus* preferred depths deeper than 150 m (Magnussen, 2002; Massuti and Moranta, 2003; Rey *et al.*, 2004; Costa *et al.*, 2005; Serena *et al.*, 2006). *C. monstrosa* was found mainly in deeper water (>400 m), but may migrate to shallower water in spring and summer to deposit egg capsules (Bristow, 1992; Pethon, 2005). *E. spinax* was found in both deep and shallow water in the north and the south of the survey area, and the depth range was not clearly dependant on latitude in the survey area, as suggested by Pethon (2005). *A. radiata* and *D. oxyrinchus* were present at all depths.

Formatert: Engelsk (Storbritannia)

Feltkode endret

Formatert: Engelsk (Storbritannia)

Formatert: Engelsk (Storbritannia)

Species assemblages

The northern, central, and southern species assemblages shown by the constrained correspondence biplot revealed that factors linked to latitude play an important role in determining species distribution and abundance. The sharp decline in abundance north of 65°N for species in the southern and central group was particularly noteworthy because it suggests a latitudinal change in conditions, resulting in a shift in biodiversity. The 65°N region is, on average, deeper than the other areas surveyed, and the deep trench may function as a biogeographical barrier (Figure 2). However, depth alone does not appear to explain this trend, and the Lofoten Peninsula may function as a physical barrier.

Temporal and spatial shifts with regard to sea temperature

Because of the small number of stations with temperature measurements, sea temperature had limited ability to explain shifts in abundance in our data. Skate distribution in the Barents Sea has been linked to changes in bottom temperature (Dolgov *et al*., 2005a). In some areas of the Northeast Atlantic, the increase in sea temperature in recent years has coincided with a gradual northward shift in the distribution of some species (Perry *et al.*, 2005; Dolgov, 2006). So far, though, there appear to have been no such shifts along the northern coast of Norway. Demersal fish species such as cod seem to be able to adapt to moderate changes in their ambient temperature and do not necessarily respond to it with a change in distribution (Ottersen *et al.*, 1998), at least to the same extent as do pelagic fish, such as blue whiting (*Micromesistius poutassou*), capelin (*Mallotus villosus*), and herring (Bergstad *et al.*, 1999; Toresen and Østvedt, 2000; Fossheim *et al.*, 2006). Depth and temperature are unlikely to be the only factors involved in determining the apparent trends in distribution and general stability in abundance of each chondrichthyan listed here. As the distributions of the southern and central species assemblages have not expanded north in response to ocean warming, other factors may be playing a role in determining abundance and distribution.

Little is known about how fisheries have impacted chondrichthyan populations along the northern coast of Norway. However, we know that they provide a significant and probably underestimated bycatch in gillnet and longline fisheries (Table 1). It is therefore reasonable to assume that the demersal fisheries in particular have a negative impact on chondrichthyan stocks (Bonfil, 1994; Stevens *et al.*, 2000; Dolgov *et al.*, 2005b; Drevetnyak *et al.*, 2005). Any major changes in population structure in response to fishing probably took place in the survey area before 1992, when the most significant development in the fisheries there took place. As mentioned, the introduction of sorting grids in the shrimp fishery reduced bycatch to include only juveniles. This has not resulted in an obvious increase in chondrichthyan abundance, but may be one reason why the stocks are not decreasing. The populations of *A. radiata* and *R. fyllae* in the neighbouring Barents Sea appear to be stable at current fishing levels (Drevetnyak *et al*., 2005), so both species are probably similarly tolerant to current fishing pressure within our study area.

The processes influencing the population dynamics of the chondrichthyans described here are undoubtedly complex. Geographical barriers, particularly the deep trenches in the region of 67°N (Vestfjord) and the Lofoten Peninsula, could restrict passage and inhibit an expansion in the distribution of a species. Also, chondrichthyans are generally long-lived, and their distribution may to some degree be the consequence of territorial behaviour and a slow rate of migration. For example, some skates do not migrate great distances (Hunter *et al.*, 2005) and may show clear gaps between areas of high concentration, perhaps indicating that they may form local stock units (Daan *et al.*, 2005). However, *A. radiata* seems to be an exception, because the continental shelf edge apparently does not present a barrier to its migration, and there are no significant population gaps in the North Atlantic generally (Chevolot *et al.*, 2007). This is one explanation for the uniform distribution of *A. radiata* in the study area and in the Barents Sea.

Although chondrichthyans are potentially vulnerable to fisheries (Stevens *et al.*, 2000; Priede *et al.*, 2006), the current populations in the study area of the more common species appear not to be adversely affected by bycatch at the current levels of fishing activity (although historical estimates of abundance are not available). Stocks of *Chimaera monostrosa*, *Etmopterus spinax*, *Somniosus microcephalus*, *Galeus melastomus*, *Squalus acanthias*, *Dipturus batis*, and recently also *Amblyraja radiata* have declined in the North Sea (Daan *et al.*, 2005; Ellis *et al.*, 2005a; Jones *et al.*, 2005; ICES, 2007), but there has been no such decline in our area of interest. This may be due to the lower effort in the demersal fishery in general and in the elasmobranch fishery in particular along the northern coast of Norway over the period 1992–2005. However, because of the limitations of our data, we cannot be certain that this is the case for the less frequently caught species, especially given the comparatively short period covered by the study. For example, species such as *S. microcephalus* are reported to have had longer term declines in Norwegian waters (Ruud, 1968).

As species identification is currently difficult and potentially inaccurate, effort should be put into quality controlling available taxonomic keys for northern areas, especially for skates, which are known to have high morphological interspecific variability (Serena *et al.*, 2005). To address the distribution of skate species in Norwegian waters, future surveys should place more emphasis on species identification, including the collection of voucher specimens, and the development of appropriate field identification guides should be given high priority. Knowledge of chondrichthyan species along the coast of Norway remains limited compared with that for the neighbouring North Sea (ICES, 2007) and further work is required.

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Figure 1. Survey area and strata along the northern coast of Norway. Positions of permanent hydrographic stations are marked with circles.

Figure 2. Average bottom depth with standard deviation of trawl stations taken in each area along the northern coast of Norway during the coastal surveys of 1992–2005.

Figure 3. Distribution and abundance of (a) *Chimaera monstrosa*, (b) *Etmopterus spinax*, (c) *Galeus melastomus*, (d) *Amblyraja radiata*, (e) *Squalus acanthias*, (f) *Dipturus oxyrinchus*, (g) *Rajella fyllae*, and (h) *Dipturus batis* along the northern coast of Norway from the coastal surveys of 1992–2005. Note that the abundance scales differ between panels. The shaded area is the distribution according to Pethon (2005).

Figure 4. Distribution and abundance of (a) *Leucoraja fullonica*, (b) *Leucoraja circularis* and *Bathyraja spinicauda*, (c) *Amblyraja hyperborea*, (d) *Dipturus nidarosiensis*, (e) *Raja montagui* and *Raja brachyura*, and (f) *Dipturus linteus* and *Somniosus microcephalus* along the northern coast of Norway from the coastal surveys of 1992–2005. Note that the abundance scales differ between panels. The shaded area is the distribution according to Pethon (2005). **Figure 5**. Mean abundance of all chondrichthyan species along the northern coast of Norway from the coastal surveys of 1992–2005. Note that the abundance scales differ between panels. **Figure 6**. Mean abundance and standard error for the common species in each depth zone along the northern coast of Norway from the coastal surveys of 1992–2005. Note that the abundance scales differ between panels.**Figure 7**. Ordination bi-plot of constrained correspondence analysis (CCA) relating the abundance of the ten most abundant chondrichthyan species along the northern Norwegian coast to the potential explanatory variables, longitude, latitude, depth, and year of sampling. Am_rad = *Amblyraja radiata*, Ch_mon = *Chimaera monstrosa*, Dip_batis = *Dipturus batis*, Di_oxy = *Dipturus oxyrinchus*, En_spin = *Etmopterus spinax*, Ga_mel = *Galeus melastomus*, Le_ful = *Leucoraja fullonica*, Ra_fyl = *Rajella fyllae*, and Sq_aca = *Squalus acanthias*.

Figure 8. Shifts in abundance, given as percentages of deviation from mean abundance (number km^{-2}) within the total survey area, with respect to latitude area for species grouped as (a) northern, (b) central, and (c) southern assemblages.

Figure 9. Mean annual temperature at the hydrological stations along the northern coast of Norway at Vardø, Ingøy, Bud, and Eggum.

Running headings

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Distribution of chondrichthyans along the northern coast of Norway

Table 1. Average bycatch (kg) and standard deviation (s.d.) by gear type, and the number of reported landings (*n*) of chondrichthyan species along the northern coast of Norway during the period 2000–2005, based on official landings data provided by the Norwegian Directorate of Fisheries. Some of the landings are reported in aggregated categories: "Dogfish and hounds" and "Rajidae". Such records landings may contain landings of the main species and other species not identified when caught or delivered.

	Gillnet		**Longline**		**Other**		**Total**		***n***
Taxon	**Average**	**s.d.**	**Average**	**s.d.**	**Average**	**s.d.**	**Average**	**s.d.**	
Chimaera monstrosa	7	6	3 501	7 305	0	–	3 239	7 080	40
Lamna nasus	190	454	79	99	68	64	177	431	339
Squalus acanthias	6 020	15 626	1 383	3 751	1845	452	2 735	9 998	1 188
Dogfish and hounds	20	12	952	2 001	13	9	485	1 444	14
Dipturus batis	212	337	73	97	19	22	143	273	121
Rajidae	656	946	468	1 181	272	461	465	946	1 441
Total	2 357	9 548	926	2 937	225	449	1 315	6 338	3 143

Table 2. Survey period, vessel, statistical areas (Directorate of Fisheries), trawl gear specifications, and number of stations for each coastal survey conducted along the Norwegian coast from 62ºN to 70ºN during the period 1992–2005.

Survey period	**Vessel**	**Statistical areas**	**Inner net mesh size**	**Strapping**	**Number of stations**
25 August – 3 October 1992	RV "Johan Ruud"	03, 04 and northern sector of 05	20 mm	Yes	127
1 August – 8 September 1993	RV "Mikael Sars"	05 and eastern limit of 37	20 mm	Yes	163
22 September – 19 October 1994	RV "Mikael Sars"	06, 07 and eastern limit of 37	35 mm	No	106
13 September – 11 October 1995	RV "Mikael Sars"	00, 03, 04, 05, 06 and 07	35 mm	No	129
11 September – 6 October 1996	RV "Mikael Sars"	As above	35 mm	No	130
20 August – 23 September 1997	RV "Mikael Sars"	As above	20 mm	For most	159
26 October – 19 November 1998	RV "Jan Mayen"	As above	20 mm	Yes	132
22 October – 19 November 1999	RV "Jan Mayen"	As above	20 mm	Yes	154
23 October –16 November 2000	RV "Jan Mayen"	As above	20 mm	Yes	154
23 October – 17 November 2001	RV "Jan Mayen"	As above	20 mm	Yes	125
29 October – 26 November 2002	RV "Jan Mayen"	As above	20 mm	Yes	168
11 October - 14 November 2003	RV "Jan Mayen" RV "Johan Hjort"	As above	20 mm	For most	133
13 October – 9 November 2004	RV "Jan Mayen" RV "Johan Hjort"	As above	20 mm	For most	128
11 October – 8 November 2005	RV "Jan Mayen" RV "Johan Hjort"	As above	20 mm	For most	124

Table 3. Chondrichthyan species identified along the northern Norwegian coast during the coastal surveys of 1992–2005. Are you sure that the describers of each species should be in parenthesis? I am no taxonomist, but my gutfeel says that it is very unlikely that all should be in parenthesis – parenthesis and non-parenthesis around the describers means different things, relating to whether it is the original or a subsequent description. If you aren't sure and cannot find out, err on the safe side and delete all describers (it doesn't add a lot here anyway)

Scientific name	**Family**	**Common name**	**Norwegian Red List ***
Chimaera monstrosa (Linnaeus, 1758)	Chimaeridae	Rabbitfish	No
Etmopterus spinax (Linnaeus, 1758)	Dalatiidae	Velvet belly	No
Somniosus microcephalus (Bloch & Schneider, 1801)	Dalatiidae	Greenland shark	Near-threatened
Galeus melastomus (Rafinesque, 1810)	Scyliorhinidae	Blackmouth catshark	No
Squalus acanthias (Linnaeus, 1758)	Squalidae	Spurdog	Critically endangered
Amblyraja hyperborea (Collett, 1879)	Rajidae	Arctic skate	Data-deficient
Amblyraja radiata (Donovan, 1808)	Rajidae	Thorny skate	No
Bathyraja spinicauda (Jensen, 1914)	Rajidae	Spinetail ray	Data-deficient
Dipturus batis (Linnaeus, 1758)	Rajidae	Blue skate	Data-deficient
Dipturus linteus (Fries,1838)	Rajidae	Sailray	Data-deficient
Dipturus nidarosiensis (Storm, 1881)	Rajidae	Norwegian skate	Data-deficient
Dipturus oxyrinchus (Linnaeus, 1758)	Rajidae	Longnosed skate	Data-deficient
Leucoraja circularis (Couch, 1838)	Rajidae	Sandy ray	No
Leucoraja fullonica (Linnaeus, 1758)	Rajidae	Shagreen ray	Data-deficient
Raja brachyura (Lafont, 1873)	Rajidae	Blonde ray	No
Raja clavata (Linnaeus, 1758)	Rajidae	Thornback ray	No
Raja montagui (Fowler, 1910)	Rajidae	Spotted ray	Data-deficient
Rajella fyllae (Lütken, 1887)	Rajidae	Round skate	No

* Species entry in the 2006 Norwegian Red List – Artsdatabanken Norwegian Biodiversity Information Centre

Table 4. Average annual catch rates and standard deviations, proportion of trawl stations where the species was observed in the coastal surveys of 1992–2005, qualitative abundance category, and latitude and depth ranges.

Species	**Mean catch (number per km^2)**	**s.d.**	**Proportion of stations at which observed (%)**	**Abundance**	**Latitude (ºN)**	**Depth (m)**
Chimaera monstrosa	2 586.2	3 250.7	29.5	Common	62–71	42–665
Etmopterus spinax	2 078.4	2 234.0	17.7	Common	62–71	47–730
Galeus melastomus	605.7	598.0	13.2	Common	62–68	51–665
Amblyraja radiata	55.2	20.7	19.6	Common	62–72	30–635
Squalus acanthias	49.3	49.3	4.5	Common	62–69	42–515
Dipturus oxyrinchus	7.7	15.6	2.0	Common	62–68	45–665
Rajella fyllae	5.5	8.3	2.2	Common	62–72	83–415
Dipturus batis	2.2	2.2	1.0	Infrequent	62–71	85–425
Leucoraja fullonica	1.8	2.7	1.0	Infrequent	62–71	77–512
Leucoraja circularis	1.7	3.2	0.4	Rare	62	88–244
Bathyraja spinicauda	1.1	1.4	0.5	Rare	67–72	48–410
Amblyraja hyperborea	0.6	1.9	0.3	Rare	67–71	125–620
Dipturus nidarosiensis	0.5	0.9	0.3	Infrequent	62–69	132–588
Raja montagui	0.4	0.6	0.3	Rare	62	63–120
Raja brachyura	0.3	1.1	0.02	Rare	62–63	99
Dipturus linteus	0.1	0.3	0.1	Rare	68	588
Somniosus microcephalus	0.1	0.3	0.02	Infrequent	69	480

Table 5. One-way single factor ANOVA schemes for determining the significance of temporal differences in abundance of the main species caught during the coastal surveys of 1992–2005.

Species	**Sum of squares**	**d.f.**	**Mean square**	***F***	***p***	F_{crit}
Chimaera monstrosa	3 717 741.6	11	337 976.5	0.98	0.473	1.88
Etmopterus spinax	893 976.4	11	81 270.6	0.58	0.840	1.88
Galeus melastomus	231 510.3	11	21 046.4	0.68	0.751	1.88
Squalus acanthias	5 282.6	11	480.2	0.76	0.675	1.88
Amblyraja radiata	184.2	11	16.7	1.92	**0.044**	1.88
Dipturus oxyrinchus	52.4	11	4.8	1.00	0.449	1.88
Rajella fyllae	14.0	11	1.3	1.61	0.107	1.88

Significant differences ($p = 0.05$) emboldened.

Table 6. One-way single factor ANOVA schemes for determining the significance of latitudinal differences in abundance of the main species caught during the coastal surveys of 1992–2005.

Species	**Sum of squares**	**d.f.**	**Mean square**	***F***	***p***	F_{crit}
Chimaera monstrosa	7 537 614.7	8	942 201.8	2.8	**0.007**	2.03
Etmopterus spinax	5 141 623.0	8	642 702.9	6.0	**<0.001**	2.03
Galeus melastomus	1 078 162.9	8	134 770.4	5.5	**<0.001**	2.03
Squalus acanthias	13 594.7	8	1 699.3	2.8	**0.007**	2.03
Amblyraja radiata	294.3	8	36.8	5.3	**<0.001**	2.03
Dipturus oxyrinchus	162.5	8	20.3	5.0	**<0.001**	2.03
Rajella fyllae	10.3	8	1.3	2.8	**0.008**	2.03

Significant differences ($p = 0.05$) emboldened.

Table 7. One-way single factor ANOVA schemes for determining the significance of depth-dependent differences in abundance of the main species caught during the coastal surveys of 1992–2005.

Species	**Sum of squares**	**d.f.**	**Mean square**	***F***	***p***	F_{crit}
Chimaera monstrosa	40 047 077	9	4 449 675.2	1.46	0.170	1.95
Etmopterus spinax	1 386 782	9	154 086.9	1.69	0.098	1.95
Galeus melastomus	352 063	9	39 118.1	3.23	**0.001**	1.95
Squalus acanthias	4 807	9	534.1	1.65	0.107	1.95
Amblyraja radiata	155	9	17.2	1.21	0.297	1.95
Dipturus oxyrinchus	135	9	15.0	0.97	0.469	1.95
Rajella fyllae	5	9	0.6	1.81	0.072	1.95

Significant differences ($p = 0.05$) emboldened.

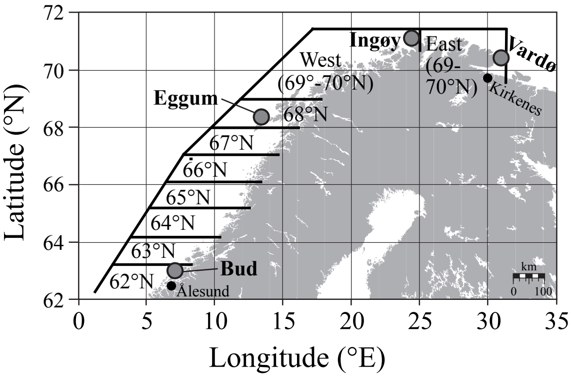

Latitude (°N)
Longitude (°E)
72
70
68
66
64
62
0
5
10
15
20
25
30
35
Ingøy
Vardø
West
(69°-70°N)
East
(69-
70°N)
Kirkenes
Eggum
68°N
67°N
66°N
65°N
64°N
63°N
62°N
Bud
Ålesund
km
0
100

Figure 1

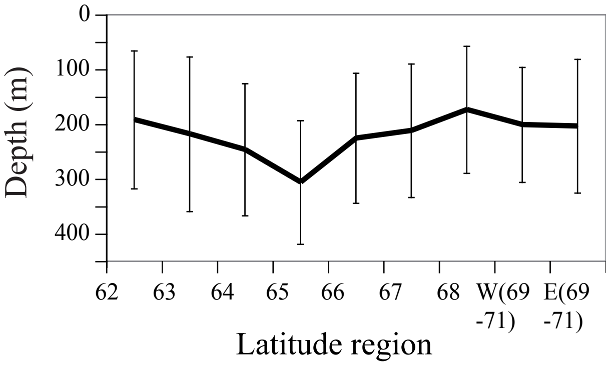

0
100
200
300
400
Depth (m)
62
63
64
65
66
67
68
W(69 -71)
E(69 -71)
Latitude region

Figure 2

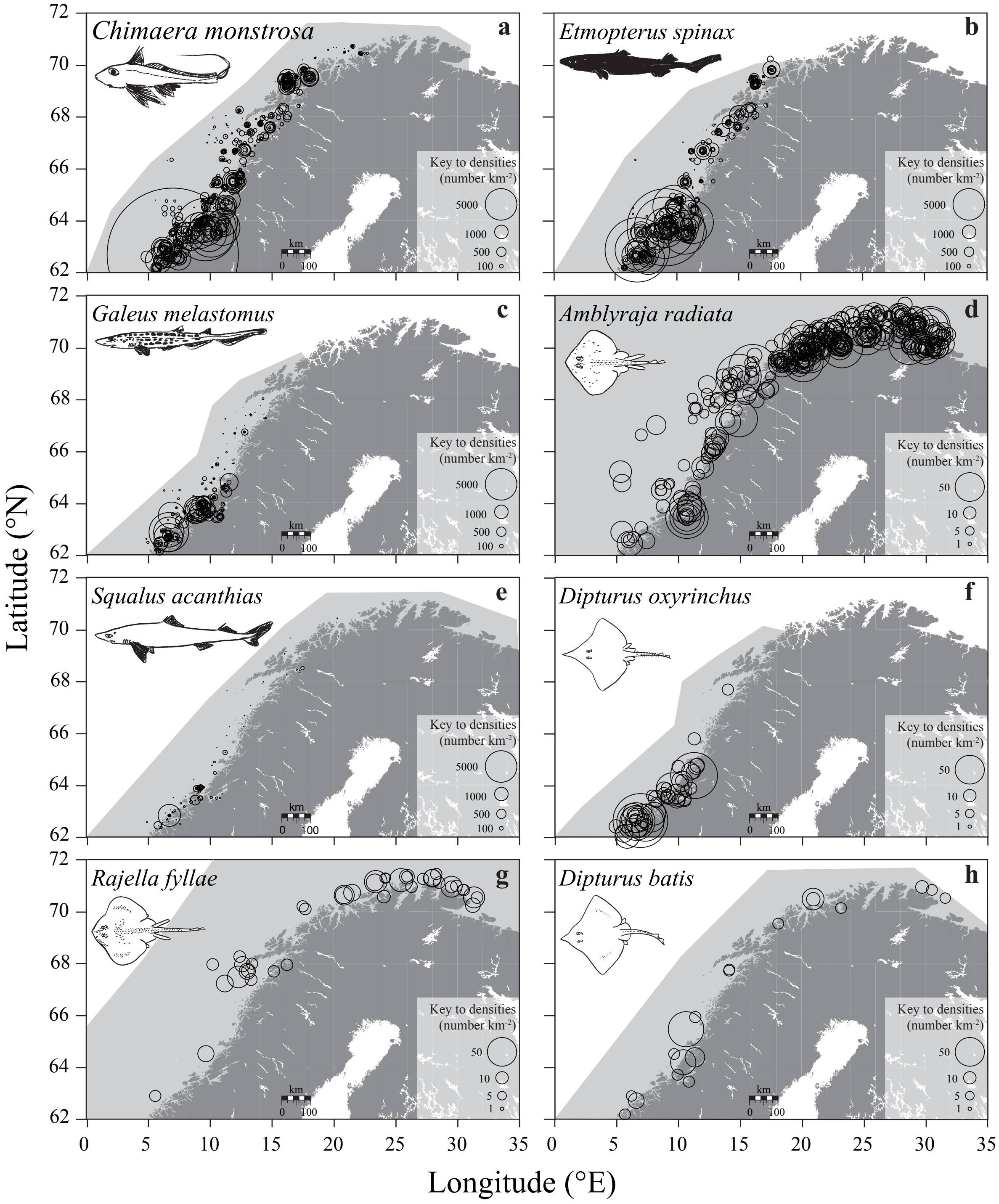
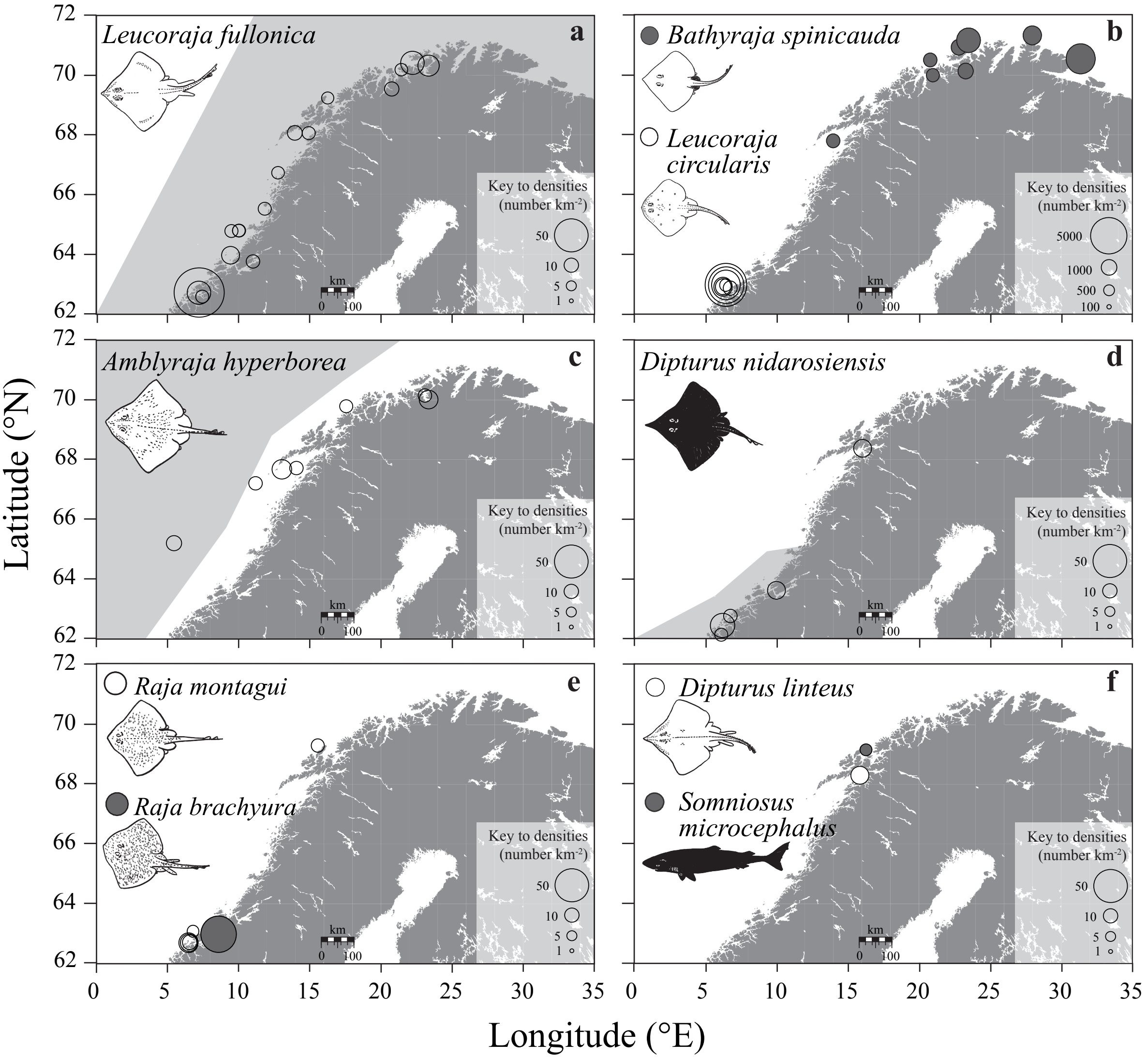

Chimaera monstrosa
a
Etmopterus spinax
b
Galeus melastomus
c
Amblyraja radiata
d
Squalus acanthias
e
Dipturus oxyrinchus
f
Rajella fyllae
g
Dipturus batis
h
Key to densities (number km^{-2})
5000
1000
500
100
50
10
5
1
km
0 100
Latitude (°N)
72
70
68
66
64
62
Longitude (°E)
0
5
10
15
20
25
30
35

Figure 3



a
Leucoraja fullonica
b
Bathyraja spinicauda
Leucoraja circularis
c
Amblyraja hyperborea
d
Dipturus nidarosiensis
e
Raja montagui
Raja brachyura
f
Dipturus linteus
Somniosus microcephalus
Key to densities (number km^{-2})
50
10
5
1
5000
1000
500
100
km
0
100
Latitude (°N)
Longitude (°E)
72
70
68
66
64
62
0
5
10
15
20
25
30
35

Figure 4

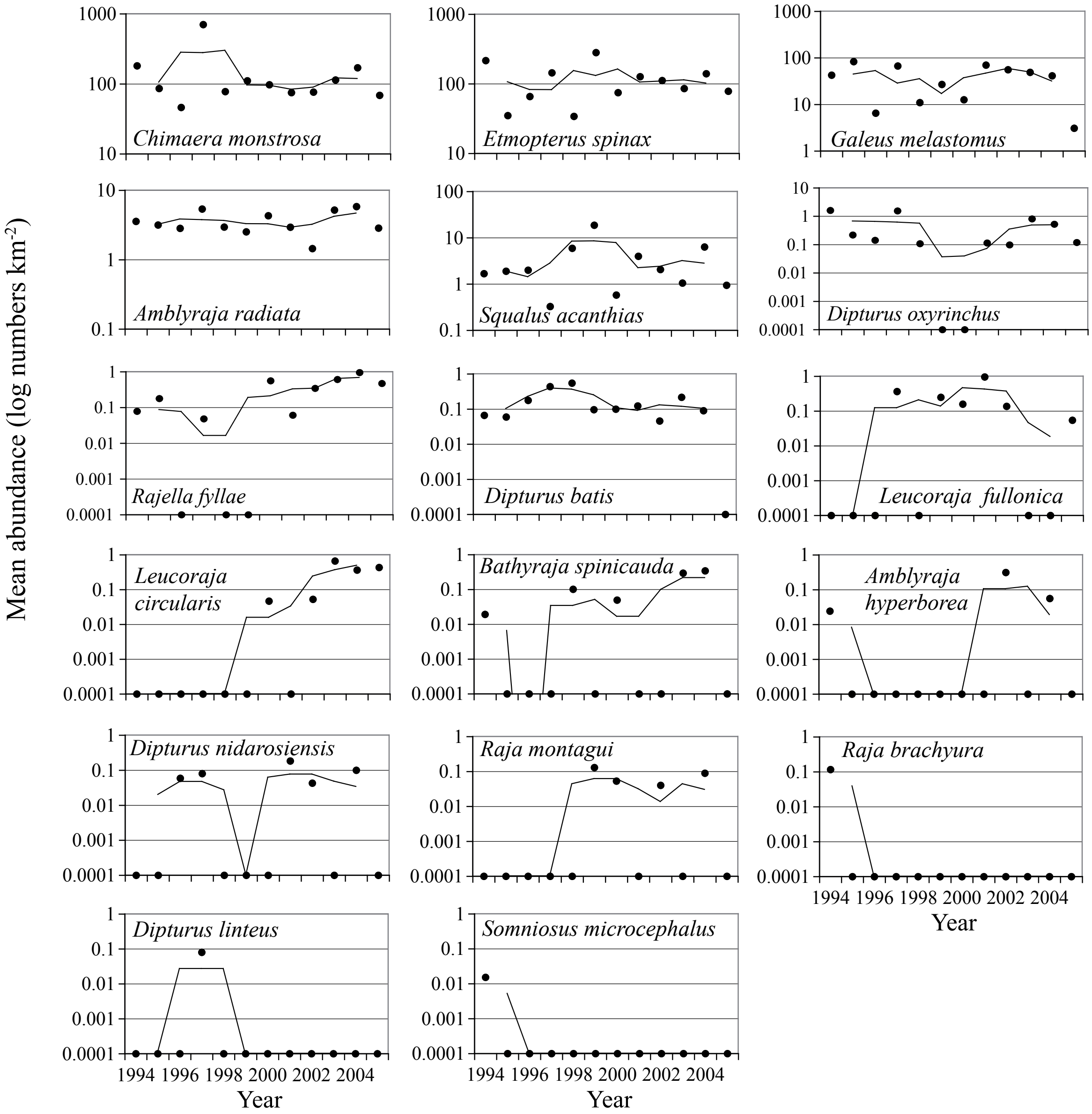

Mean abundance (log numbers km^{-2})
Chimaera monstrosa
Etmopterus spinax
Galeus melastomus
Amblyraja radiata
Squalus acanthias
Dipturus oxyrinchus
Rajella fyllae
Dipturus batis
Leucoraja fullonica
Leucoraja circularis
Bathyraja spinicauda
Amblyraja hyperborea
Dipturus nidarosiensis
Raja montagui
Raja brachyura
Dipturus linteus
Somniosus microcephalus
1000
100
10
1
0.1
0.01
0.001
0.0001
1994
1996
1998
2000
2002
2004
Year

Figure 5

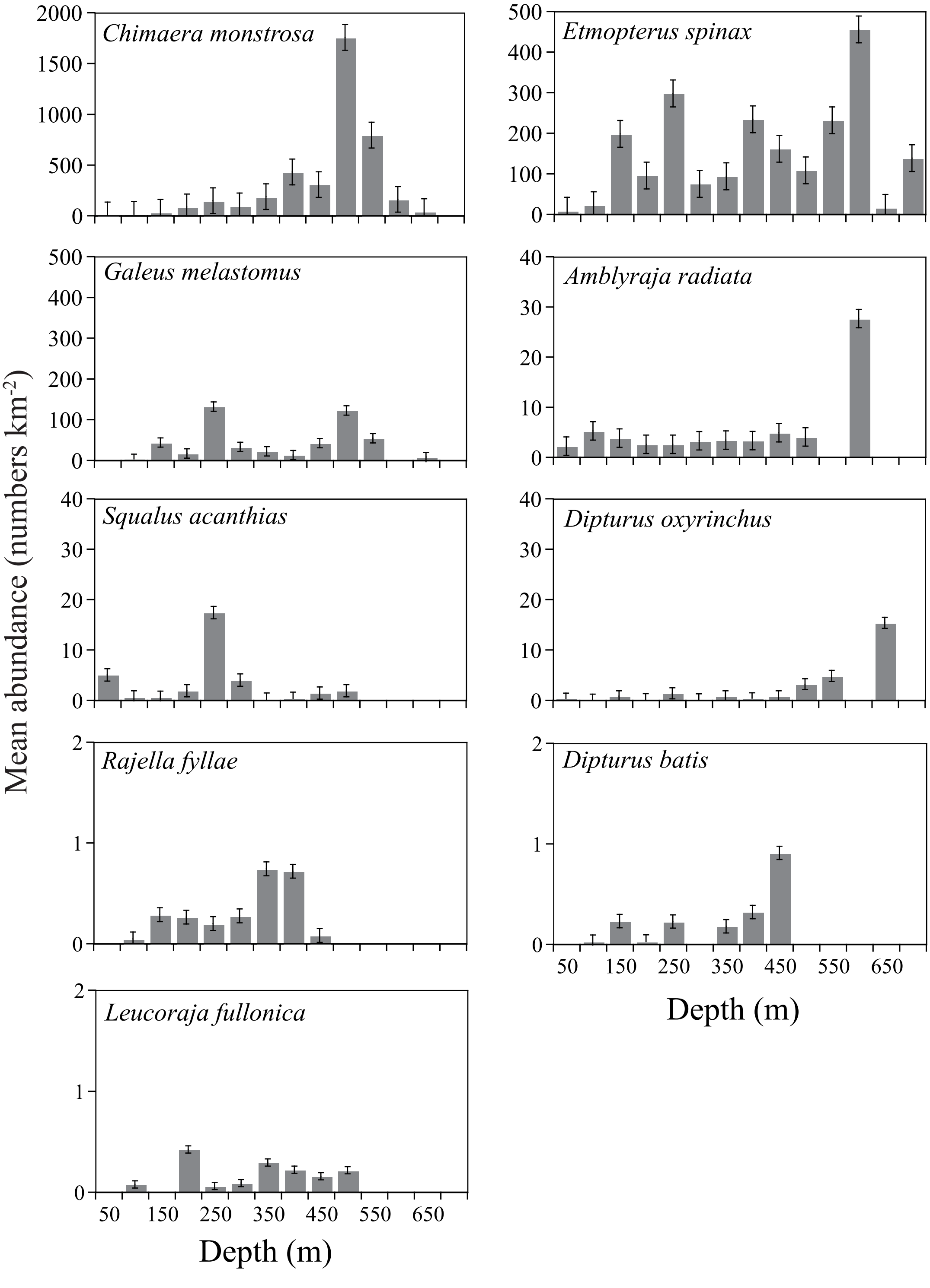

Mean abundance (numbers km^{-2})
Chimaera monstrosa
0
500
1000
1500
2000
Etmopterus spinax
0
100
200
300
400
500
Galeus melastomus
0
100
200
300
400
500
Amblyraja radiata
0
10
20
30
40
Squalus acanthias
0
10
20
30
40
Dipturus oxyrinchus
0
10
20
30
40
Rajella fyllae
0
1
2
Dipturus batis
0
1
2
Leucoraja fullonica
0
1
2
50
150
250
350
450
550
650
Depth (m)
50
150
250
350
450
550
650
Depth (m)

Figure 6

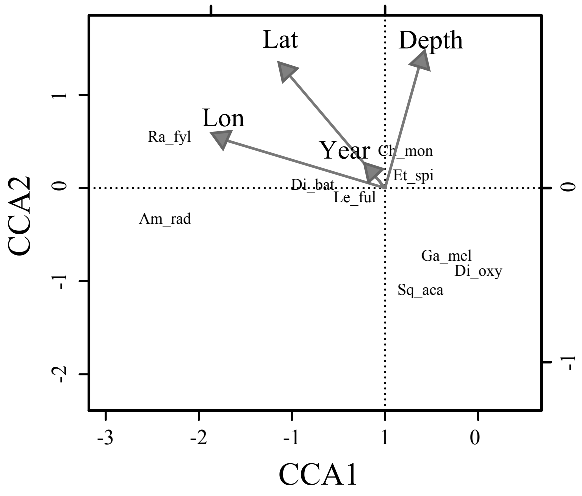

Lat
Depth
Lon
Year
Ra_fyl
Ch_mon
Et_spi
Di_bat
Le_ful
Am_rad
Ga_mel
Di_oxy
Sq_aca
CCA2
1
0
-1
-2
0
-1
-3
-2
-1
1
0
CCA1

Figure 7

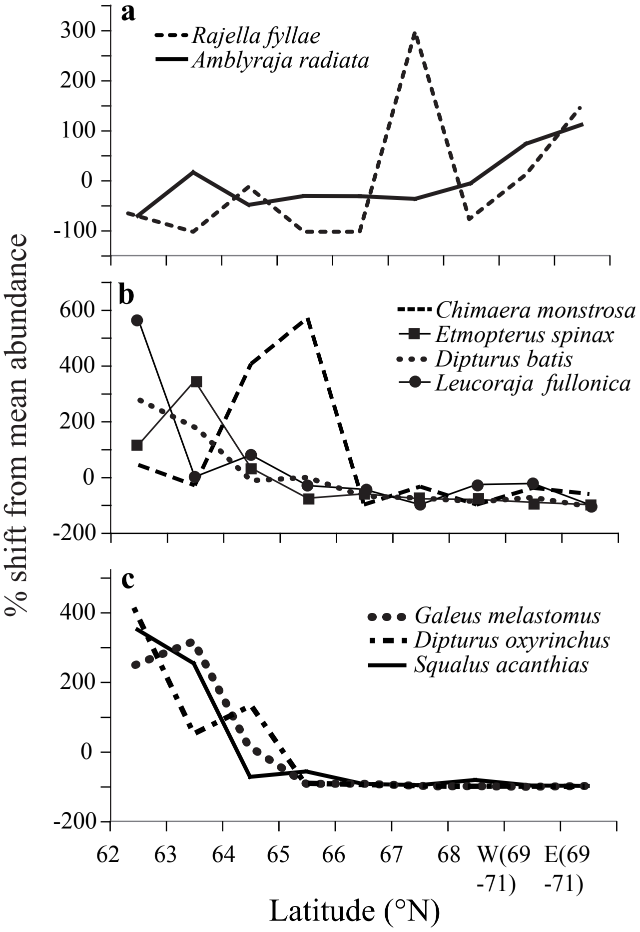
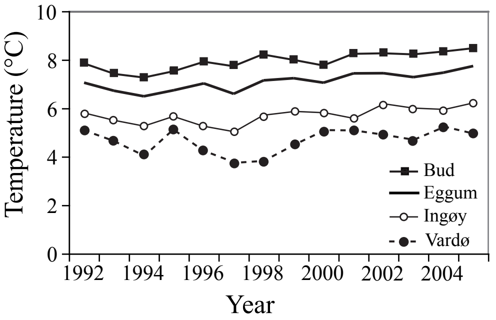

a
Rajella fyllae
Amblyraja radiata
300
200
100
0
-100
b
Chimaera monstrosa
Etmopterus spinax
Dipturus batis
Leucoraja fullonica
600
400
200
0
-200
c
Galeus melastomus
Dipturus oxyrinchus
Squalus acanthias
400
200
0
-200
% shift from mean abundance
62
63
64
65
66
67
68
W(69 -71)
E(69 -71)
Latitude (°N)

Figure 8



Temperature (°C)
10
8
6
4
2
0
1992
1994
1996
1998
2000
2002
2004
Year
Bud
Eggum
Ingøy
Vardø

Figure 9