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SHORT NOTE

Atlantic cod (*Gadus morhua*) feeding over deep water in the high Arctic

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Abstract The Atlantic cod (*Gadus morhua*) is a highly adaptive demersal, boreal species with a broad distribution on the continental shelves on both sides of the North Atlantic. However, whether the species also uses adjoining deeper water basins as feeding grounds or migration corridors remain unknown. In this study, we aimed to describe the vertical and horizontal distributions of Atlantic cod observed feeding over the northern Fram Strait, between Greenland and Svalbard, and relate this to the prey field and environmental conditions. During surveys in 2014 and 2015, we combined biological sampling of cod, caught in ten pelagic trawls, with environmental data and acoustic registrations. The findings reveal that cod leave the continental-shelf waters and migrate westwards into the deeper water (>2800 m) of Fram Strait, as they feed on a mesopelagic layer of krill, amphipods, and small fishes. We suggest that leaving the shelf waters to feed over deeper water is a mechanism for the cod to avoid competition for food on their normal feeding grounds over the shelf, or it may demonstrate the phenomenon of a high-risk taker exceeding the limits of its natural demersal environment. The observed migration behavior may be widespread or else linked to ecological features involving physical factors or competition for food, possibly in combination with a large stock of cod. Thus, although the permanent distributions of Atlantic cod are constrained by depth, migration across deeper straits or basins must be considered.

Keywords Cod (*Gadus morhua*) · Arctic Ocean · Pelagic distribution · Fram Strait

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Introduction

The Atlantic cod (*Gadus morhua*) is a highly adaptive boreal species with a broad geographic distribution spanning various ecosystems, from temperate seas at the southern limit of its range to subarctic waters at its northern limits (Righton et al. 2010). Cod are widely distributed over the continental shelves and banks on both sides of the North Atlantic. The environmental factors and the diet and population dynamics of this species vary enormously throughout this range, and the behavior of cod is known to be extremely plastic. Owing to its large body size (max. 200 cm TL), great migration potential (>1000 km), wide temperature tolerance (–1.5 to 19 °C), and broad diet, this species is able to exploit and influence a wide range of prey (cf. Johannesen et al. 2012a). However, the behavior of cod remains constrained by its physiology, such as linked to temperature tolerance, metabolism, or buoyancy control (for a discussion, see Neat et al. 2014).

The success of this highly exploited fish seems related to different life-history strategies of the multiple migratory and stationary populations (Kirubakaran et al. 2016). As a result of careful management in combination with favorable climate conditions, the Barents Sea cod stock (also known as Northeast Arctic or Arcto-Norwegian cod: Ottersen et al. 2014) is currently at its largest (Kjesbu et al. 2014). This stock is widely distributed in the Barents Sea and exists

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in periods in high concentrations west of Svalbard both in summer and winter (Johansen et al. 2013; Townhill et al. 2015).

Climate variation is a main driving forces influencing the abundance and geographical distribution of fish species in marine ecosystems (Thuiller 2004; Perry et al. 2005; Rose 2005). The climate in the Barents Sea region is characterized by strong variability, and over the last four decades, there has been an increase in annual temperatures, while the area covered by warmer Atlantic Water has simultaneously expanded (Johannesen et al. 2012b). Associated with these changes is a northward expansion in the distribution of Barents Sea cod (Drinkwater 2011; Kjesbu et al. 2014; Fossheim et al. 2015).

Even though Barents Sea cod are considered a demersal fish that usually stay close to the seabed, vertical migrations with more pelagic phases have been documented. For example, during foraging and spawning migrations, Barents Sea cod perform vertical movements down to depths of about 500 m, with frequent swimming descents and ascents spanning up to 250 m (Godø and Michalsen 2000). These pelagic movements may occur either within restricted periods in a diel cycle, as occasional ascents seemingly without rhythm, or for longer periods during long-distance horizontal migrations between the Barents Sea and the coast of Norway (Michalsen et al. 2014). Cod at Newfoundland have also been shown to dive into deeper waters (Rose 1993).

In 2014 and 2015, during surveys in the northern Fram Strait and the region north of Svalbard, we detected Atlantic cod in midwater over deep-water basins. Here, we combine the data of biological sampling of the cod and acoustic registrations of their depth distribution to describe and discuss the occurrence of Atlantic cod over deep waters in the high Arctic.

Materials and methods

Data were collected as part of the SI_ARCTIC 2014 and 2015 surveys (http://siarctic.imr.no/) conducted onboard the RV Helmer Hanssen, from 19 August to 9 September, 2014, and 17 August to 9 September, 2015. The focus area for the investigation was the northern Fram Strait and the region north of Svalbard (Fig. 1). More information on the project, surveys, and sampling can be found in Online Resource 1.

Biological sampling

Fish sampling was carried out using two types of trawls: Harstad trawl (Dingsør 2005) and Åkra trawl (Valdemarsen

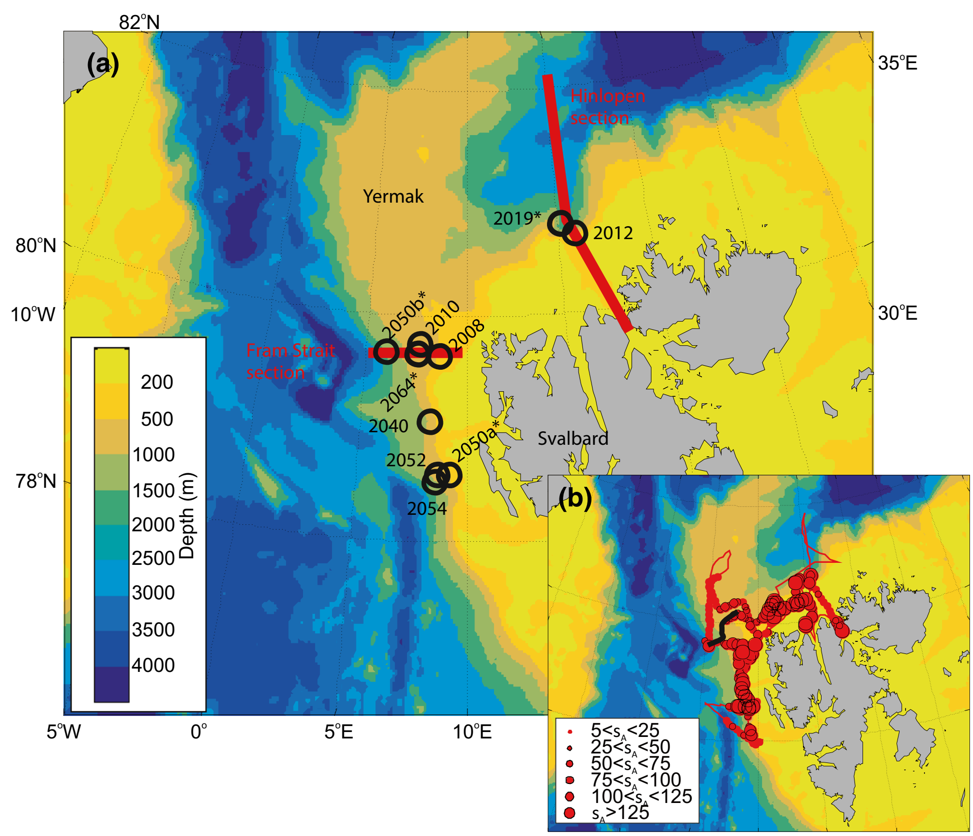

Fig. 1 Map showing study area and bathymetry. **a** Stations where Atlantic cod (*Gadus morhua*) were caught in pelagic trawls (*black circles*) and the Fram Strait and Hinlopen sections (*red lines*). **b** Acoustic registrations (s_A in m^2 nmi^{-2}) of Atlantic cod during the 2014 and 2015 surveys based on vertically integrated registrations across all depths. *Black line* shows location of echogram given in Online Resource 4. (Color figure online)

and Misund 1995). These small- and medium-sized trawls are designed for catching small pelagic species, such as capelin, herring, and blue whiting. The trawls were towed at a speed of 2.8–3.2 knots. Owing to their relatively small openings, both trawls types cover a limited volume even when being towed for several hours. Thus, the catch efficiency of adult cod is presumably limited when towing these small trawls pelagically at ~3 knots. However, although the recorded catches might not give a representative sample of the cod present, the fact that cod were caught corroborates the interpretation of the acoustic targets as cod. Length-stratified sub-sampling of weights, stomachs, and cod otoliths were conducted according to the standard protocols (Online Resource 1). For the purposes of this research, stomach samples from all cod specimens examined in a catch were added together, to represent typical stomach contents of the catch. Stomach contents are given as the subsample percentage (%) of the total weight of the contents. The Fulton's condition factor (K) was calculated using $K = 100\ (W/L^3)$, where W is the weight (g) and L is the total length (cm) of the fish (see Online Resource 1).

Acoustic data

Acoustic surveying was conducted with a Simrad EK60 split-beam Windows™-operated scientific echosounder, operated at three acoustic frequencies (18, 30, and 120 kHz), with transducers mounted on a drop keel. Multi-frequency scrutinizing and target-strength analysis were conducted with the Large-Scale Survey System post processing system (Korneliussen et al. 2016). The main tool for identifying plankton and fish was the frequency response and sequential thresholding so as to separate weak and strong targets, while trawl data were used to corroborate the interpretation of the acoustic data. The multi-frequency recordings were interpreted according to the standard procedures in which the total backscatter was split into different target categories. The low-noise level enabled measurements down to approximately 800 m, but for the analyses presented here, we used data to 700 m only, as no cod were observed below that depth. The total backscatter from cod is low compared to that from mesopelagic fishes and plankton. However, single, large cod targets with a target strength (TS) of −20 to −30 dB re 1 m^2 can be easily detected by hard amplitude thresholding of the echogram. The density of groups of cod was determined using the standard counting techniques.

Results

Biological samples

In total, 26 adult cod were caught in 10 pelagic hauls in 2014 and 2015 (Fig. 1a; Table 1). The depths of these catches varied from 315 to 449 m. The length of the cod sampled varied from 49 to 91 cm TL, and their age was 4–9 years. Mean length was 68.4 cm TL and mean weight was 2.7 kg, some specimens were immature, and others were mature. The overall average condition factor (Fulton's K) was 0.80 ± 0.07. The averaged K was nearly identical for the two sampling years, but varied among samples from 0.72 to 0.85.

Stomach samples were analyzed from cod collected at four of the ten stations (Fig. 2; Online Resource 3): two stations relatively close to the shelf break at the southern and northern reaches of the study area in 2014 (stations 2019 and 2050a, Fig. 1a) and two stations further offshore in the

Table 1 Catches of cod from pelagic trawl hauls

Station no	Latitude (°N)	Longitude (°E)	Bottom depth (m)	Fishing depth (m)	Catch (no)	Mean weight (kg)	Mean length (cm)	Length min–max (cm)	Age min–max (years)
2008[a]	79°40′	08°34′	477	357	4	1.60	57.5	51–62	–
2010[a]	79°40′	07°29′	804	411	1	2.08	64	64	–
2019[a,*]	80°48′	15°60′	1822	420	4	2.77	71	64–87	5–8
2040[a]	79°05′	08°10′	954	419	1	4.90	86	86	8
2050a[b,*]	78°36′	09°07′	525	449	5	3.27	72.6	64–86	5–8
2052[b]	78°37′	08°37′	823	446	4	2.64	65	49–91	4–9
2054[b]	78°33′	08°32′	983	429	2	2.76	70	55–85	4–7
2012[b]	80°42′	15°54′	480	370	2	2.80	72	68–76	6–7
2050b[b,*]	79°41′	05°54′	1395	350	1	2.35	65	65	7
2064[b,*]	79°45′	07°35′	755	315	2	1.87	61	58–64	6

[a]Harstad trawl and [b]Åkra trawl shows the trawl type used for the sampling. Stations with * in the station number have cod stomach content data, as shown in Fig. 2. More information about the hauls can be found in Online Resources 2 and 3

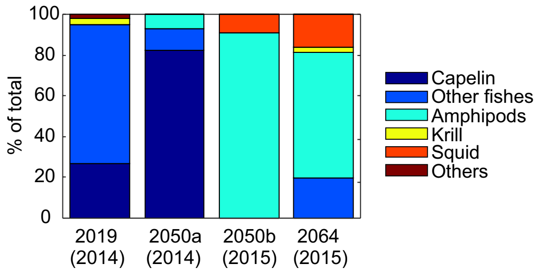

Fig. 2 Atlantic cod (*Gadus morhua*) stomach content from pelagic trawls in 2014 and 2015. More information about the stomach content can be found in Online Resource 3

northern Fram Strait in 2015 (2050b and 2064, Fig. 1a). These analyses showed that the cod had been eating various fishes, squids, and large plankton (krill and amphipods). Among the fish prey identified were capelin, various mesopelagic species, redfish, and sand eel (indicating predation both in the mesopelagic layer and near bottom); however, in some stomachs with partly digested contents, the fish prey could only be identified as "teleosts" or "other fish" (Online Resource 3). Capelin and other fish prey dominated in the two samples from 2014 (68.4–82.4% of total stomach contents), whereas amphipods dominated in the two samples from 2015 (61.7–90.8% of total stomach content).

Cod distribution based on acoustics

Vertically integrated acoustic registrations of cod in the two sampling years show that they were present in large parts of the study area (Fig. 1b). An example of the echogram obtained while moving along the ice edge from deep water towards the shelf on southern Yermak Plateau show cod in a 250–500 m deep layer, both off-shelf and on-shelf, although in substantially lower densities off-shelf (Online Resource 4). The highest concentrations of cod were found near depths of 400 m. Densities of cod determined from all the acoustic data plotted against bottom depths revealed that despite a substantial decrease in cod concentrations when reaching deep water, cod were also present in mid-water, where the bottom depth reached 2800 m (Fig. 3a). Mean densities of cod plotted against the observed depths indicated different patterns of vertical distribution on the shelf and in deeper waters: on the shelf, the highest concentrations of cod occurred at a depth of 180–200 m, probably corresponding to cod near the bottom (Fig. 3b), while over deeper water, the highest concentrations of cod were between 250 and 500 m depth (Fig. 3c).

The acoustic data from the northern Fram Strait section show cod present from about 150 m to deeper than 600 m above the continental slope and in a 300–500 m deep layer off the slope (Fig. 4a, b). This corresponds well with the location of the trawl stations, where cod were caught (represented by squares in Fig. 4a, b). In both sampling years, cod were present all the way to the westernmost boundary of the study area (approx. 4.8°E), although they were not continuously present from the shelf to the westernmost boundary in 2014. The vertical distribution of cod corresponded with the distribution of krill, amphipods, and mesopelagic fishes (Fig. 4c, d). The temperature in the depth layer where cod were detected was 2–4 °C (Fig. 4 a, b). Cod were also detected north of Svalbard, on the shelf and just off the shelf break, likewise overlapping with a mesopelagic prey field both, in 2014 and 2015 (Online Resource 5). However, unlike in Fram Strait, the cod there apparently did not migrate outwards to deeper water, despite seemingly similar (although somewhat poorer) food and temperature conditions.

The estimated density of cod in the 300–500 m deep layer above deep water in northern Fram Strait, using a mean cod length of 68.4 cm TL (see Table 1), varied between 120 and 2900 cod per nmi^2 (in the 200 m deep layer). Using total catch efficiency of the trawl (wherein all

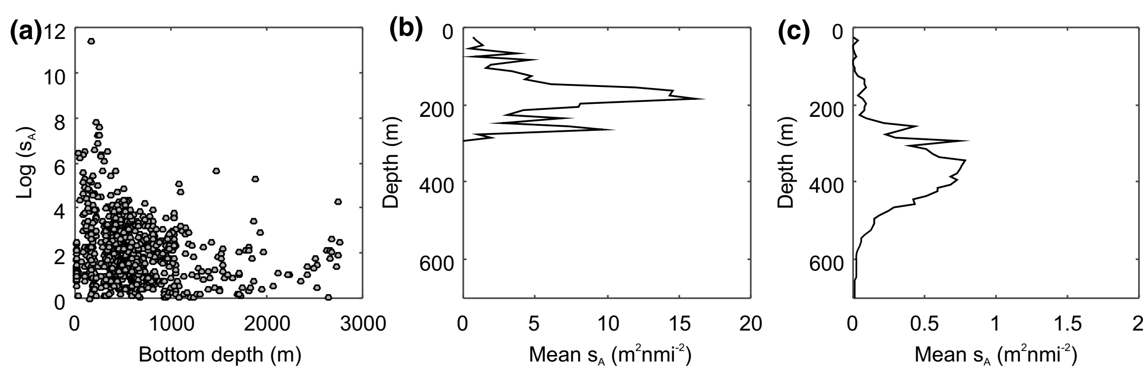

Fig. 3 Vertically integrated acoustic registrations (logarithm of s_A in m^2nmi^{-2}) of Atlantic cod (*Gadus morhua*) against bottom depth (**a**) and mean s_A (m^2nmi^{-2}) of cod against depth for bottom depths shallower than 300 m (**b**) and deeper than 300 m (**c**). Note that the single high maximum in (**a**) was not included when calculating the mean profiles in (**b**) and (**c**)

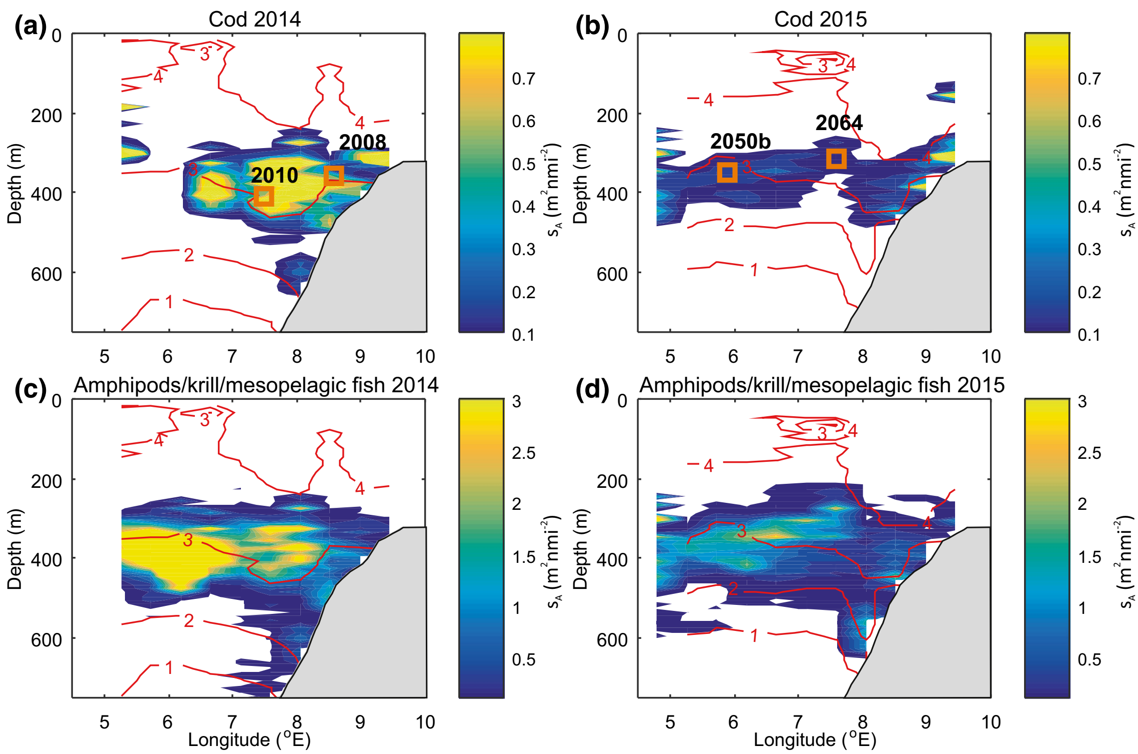

Fig. 4 Atlantic cod (*Gadus morhua*) and prey field in the northern Fram Strait section (for location, see Fig. 1a). *Upper panels* show acoustic registrations (*colors*) of cod in 2014 (**a**) and 2015 (**b**). *Orange squares* show location of pelagic trawl stations where cod were caught (Table 1). *Lower panels* show acoustic registrations of krill, amphipods, and mesopelagic fishes below 200 m depth in 2014 (**c**) and 2015 (**d**). *Red lines* show temperature measured with a Sea-Bird 911plus CTD during the surveys. Total length of the section is about 55 nautical miles. (Color figure online)

fish inside the mouth of the trawl net are caught), the densities corresponded to a catch of 0 to 5 cod per trawled nmi. The corresponding densities of cod caught just off the slope in Hinlopen was 4600 cod per nmi^2 in 2014 and 2900 cod per nmi^2 in 2015, reflecting a theoretical trawl catch of 5–7 cod per trawled nmi. The numbers of cod actually caught in the trawl hauls were somewhat lower. In several hauls where cod traces were detected acoustically, there was no catch of cod (data not shown), but 1–5 cod were caught in each of ten hauls (Online Resource 2); this indicates a low catch efficiency of this fast-swimming fish with these trawls.

Discussion

An overview of cod migration in European waters by Neuenfeldt et al. (2013) provides several examples of migrations that must have involved movement over deep waters. However, although the migration of cod into deep-water basins has been deduced from some studies, cod in waters with a depth exceeding several thousand meters have, to our knowledge, never before been documented. The findings presented here, based on trawl catches and acoustics, show that despite being a demersal fish, cod do migrate into the waters of deep basins. Thus, although permanent fish distributions may be constrained by depth (Rutterford et al. 2015), migration across deep straits or basins should be taken into account.

Barents Sea cod is an opportunistic feeder that preys on a number of species (Bogstad et al. 2000; Johannesen et al. 2012a). Our results show that cod close to the shelf break mostly preyed on capelin and other fishes (Fig. 2: stations 2019 and 2050a). However, the acoustics from Fram Strait show a vertical overlap with a mesopelagic layer of krill, amphipods, and mesopelagic fishes. Moreover, the samples of stomach contents from cod caught of this layer in northern Fram Strait confirmed predation on amphipods and krill as well as squid (Fig. 2: stations 2050b and 2064). Detailed sampling revealed that the mesopelagic layer was dominated by the northern krill *Meganyctiphanes norvegica*, the Arctic pelagic amphipod *Themisto libellula*, the glacier lantern fish *Benthosema glaciale*, and the squid *Gonatus sp*. (Ingvaldsen et al. 2016). These findings suggest that cod leave the shallower Barents Sea to enter deeper water in northern Fram Strait while feeding on a mesopelagic layer of small prey.

Fulton's *K* is a metric indicating feeding conditions during a recent period for an individual or group of fish (Online Resource 1). Mean values of *K* for the few individuals of cod caught in pelagic fish trawls during the two survey years was 0.80. To check if these values were atypical for cod in the area, *K* was calculated for 50 similarly sized cod (40–96 cm TL) caught in bottom trawl on the continental shelf at approximately the same latitudes, giving an average *K* of 0.81. Furthermore, the *K* values from the present study were compared to values for 36 cod (length 41–96 cm TL) collected during the same month from four randomly chosen stations in the central Barents Sea, wherein *K* was 0.83. The calculated *K* values also compare well with values from different age/length groups in the Barents Sea from the last 20 years as well from cod at Newfoundland (Online Resource 1). Hence, we may conclude that there is no major difference between the condition of the cod sampled pelagically and that caught demersally in the same area, or between the pelagic feeding cod and cod caught demersally in the central Barents Sea during the same period.

One major question posed by the research is why cod should leave the shallower water of the shelf to feed over deeper water. Possible explanations include density-dependent effects, as these have been shown to be important for cod migration (Kjesbu et al. 2014). Another possibility is that the cod observed over deep water may represent high-risk takers in the population exploiting the boundaries of their primary feeding area (Sih et al. 2004). Although, we cannot make a definitive conclusion on this topic based on the present investigation, we can deduce that both explanations would be appropriate in combination with suitable environmental conditions.

The environmental conditions in the survey region are strongly influenced by the West Spitsbergen Current, which carries Atlantic Water northwards on the western side of Svalbard (Online Resource 6). The current system is complex and consists of several branches, including the Return Atlantic Current that sends strands of Atlantic Water westwards across the northern Fram Strait, in the region where we observed cod over deep water (Online Resource 6). This flow carries heat and organisms providing cod with suitable thermal and feeding conditions into and possibly across the strait. In this region, cod on a northward feeding migration reach their north-westernmost demersal habitat; therefore, cod migrations in the pelagic zone could be most likely to occur here.

Several authors have discussed climate effects on the geographic distribution of marine invertebrates and fish (Thuiller 2004; Perry et al. 2005; Rose 2005). During the past decades, there has been a tremendous warming trend in Fram Strait (cf. Polyakov et al. 2012). This could indicate that cod feeding over the deep water of Fram Strait is a phenomenon linked to warming, since in the context of increasing ocean temperatures, the area with suitable temperatures and an adequate prey field for this species have probably expanded westwards. Alternatively, the low density of cod in the deeper waters surveyed, which made their detection with acoustics and trawling tedious, possibly suggests that cod may have long been present in this area although previously undetected. However, no firm conclusions on this topic are possible based on the current investigation.

Implications and future work

During a recent marine biological expedition, Christiansen et al. (2016) made the first discovery of Atlantic cod on the Northeast Greenland Shelf break on the western side of Fram Strait. The observed cod were juveniles, and Christiansen et al. (2016) found it conceivable that the individuals were advected with the Return Atlantic Current from the Barents Sea during their young pelagic phases. This is a reasonable assumption, especially given the long distance from our westernmost observation to the East Greenland Shelf (~270 km), yet we cannot speculate whether cod actually do migrate across the strait. Notably, however, the acoustic instruments revealed cod at the westernmost boundary of the study area, indicating that cod might also be found farther west. Nonetheless, our observations were made close to the minimum span from the Barents Sea westwards across the Norwegian Sea and Greenland Sea (Online Resource 6). Therefore, if Barents Sea cod migrate westwards searching for new habitat, this area appears a likely place for successful migration.

Given the interest in projecting future fish migrations and distributions, further investigations of cod feeding over deep water should be highly valuable. We suggest that future studies consider (1) investigation of the direction of cod migration using acoustic tracking of individual cod; (2) detailed examination of the vertical structure of the pelagic layer, including how it varies over deeper water as compared with over the continental shelf; and (3) comparisons of the environmental conditions (especially temperature and currents) and prey availability in Fram Strait with that of the area north of Svalbard. The last point in particular could clarify why cod were observed to feed over the deep waters of Fram Strait but not the deep waters north of Svalbard.

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