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### Comment

# Towards a more balanced assessment of the dynamics of North Atlantic ecosystems—a comment on Drinkwater and Kristiansen (2018)

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Drinkwater and Kristiansen (hereafter D&K) (2018, A synthesis of the ecosystem responses to the late 20th century cold period in the northern North Atlantic, ICES Journal of Marine Science, 75: 2325–2341) examined multi-trophic level biological responses in relation to a 1960s–1980s "cold period" that they associated with the Atlantic Multidecadal Oscillation (AMO). They concluded that ocean temperature was a major driver of ecosystem changes throughout the North Atlantic during this interval and adversely affected the abundance, spawning stock biomass (SSB), recruitment, survival success of several species including cod in four North Atlantic ecosystems (NE Arctic, Iceland, West Greenland, and Labrador–northern Newfoundland). D&K further suggested that negative ocean temperature anomalies during this cold period occurred first in the Eastern Arctic and Barents Sea, propagated westward across the North Atlantic to the Labrador Sea and were potentially related to a sequential E–W collapse of the four cod stocks. We take issue with these conclusions and suggest that a more quantitative discussion of fisheries exploitation was in order.

Keywords: AMO, cod, exploitation, North Atlantic, top-down

#### Issues arising from D&K

In focusing mainly on ocean temperature D&K, in our view, did not adequately evaluate or acknowledge an extensive and growing literature documenting the reality that top—down restructuring linked to exploitation of top predators can penetrate to the base of the food chain and precipitate the multi-trophic level ecosystem responses. While D&K indicate that fishing can be another important driver, they do not provide any quantitative assessment of its importance. Here, we attempt to bring a more complete and balanced view of the dynamics of the late 20th century fishery declines. Specifically we raise the following issues arising from their paper: (i) their missing assessment of the role of fisheries exploitation in the four ecosystems featured beyond indicating it may be an important factor; (ii) the veracity of the assumption that AMO characterizes the local climate of these four regions

and that the ecosystem response can be interpreted on the basis of this characterization and compared to periods when the AMO was in a different state; (iii) the issue of east to west propagation of cooler ocean temperatures and its relationship with cod SSB declines raised and discussed by D&K and further addressed here.

#### Fisheries exploitation in the North Atlantic

Numerous studies, not considered by Drinkwater and Kristiansen (D&K), at regional scales have addressed the impacts of fisheries exploitation and top–down, multi-trophic level restructuring of ecosystems in the North Atlantic. Examples include Worm and Myers (2003), Johannesen *et al.* (2012), and Stige *et al.* (2014) for the Barents Sea (NE Arctic); Petrie *et al.* (2009), Fauchald (2010), Llope *et al.* (2012), and Lynam *et al.* (2017) for the North Sea; Molfese *et al.* (2014) for the English Channel; Worm and Myers

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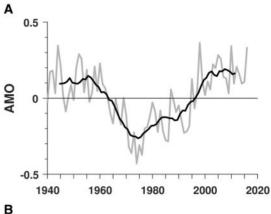
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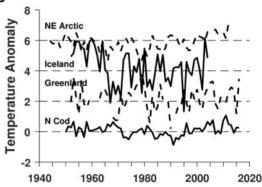
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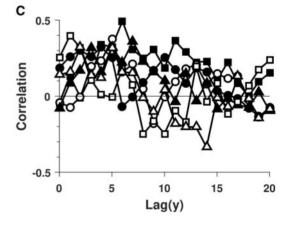
(2003), Carscadden et al. (2001), Frank et al. (2006), Petrie et al. (2009), and Boudreau et al. (2011) for Labrador/northern Newfoundland; Worm and Myers (2003), Frank et al. (2007), and Hedeholm et al. (2017) for West Greenland; Frank et al. (2007), Pálsson and Björnsson (2011), Björnsson et al. (2017), and Jónsdóttir (2017) for Iceland. Collectively, these studies provide empirical evidence of top-down control, involving not only direct effects (predator-prey), but also indirect, cascading effects influencing the dynamics of lower trophic levels (e.g. zooplankton and phytoplankton) which are often presumed to be largely driven by climatic factors alone rather than by trophic interactions coupled with climate. There are several comprehensive reviews of this general topic including examples from a variety of marine ecosystems beyond the North Atlantic and, in some cases, involving comparisons to freshwater, terrestrial, and experimental systems: Parsons (1992), Micheli (1999), Reid et al. (2000), Cury et al. (2003), Hunt and McKinnell (2006), Crowder et al. (2008), Baum and Worm (2009), Essington (2010), Strong and Frank (2010), Möllmann and Diekmann (2012), and Daewel et al. (2014). While D&K do mention the importance of exploitation, their statements are qualitative in nature and do not acknowledge the role of trophic dynamics in any of the case studies reviewed.

#### **AMO forcing**

D&K present the monthly detrended Atlantic Multidecadal Oscillation (AMO) index as their prime physical forcing and focus on its 10-year running average as the basis for defining the 1960s-1980s as a cold period (Figure 1a and Table 1A). To assess the validity of this approach, we investigated the relationship of the AMO to local observations of ocean temperature. Climatological time series compiled by ICES (https://ocean.ices. dk/iroc/) include depth-averaged temperatures for the four ecosystems of D&K (Figure 1b and Table 1A). The AMO features a broad period of negative anomalies with a decadal minimum in the 1970s; this feature is roughly seen in the four regional series, being strongest in the NE Arctic, with an average anomaly of -0.04°C (over four regions, 1960s–1980s; Table 1A). The temperature differences of these decadal averages during the cold period relative to the 1950s and the 1990s ranges from -0.5°C to +1.4°C and averages +0.2°C. The standard deviations of the annual temperature anomalies are small, varying from 0.4 to 1.2°C (Figure 1b and Table 1C) and decrease to 0.2 to 0.6 when the series are filtered with a 10-year running mean (RMF), the same filter used by D&K. The correlations among the annual temperature anomaly series for the four regions range from 0.12 to 0.68 and average 0.43 (Table 1B). Correlations of the in situ temperature series with the AMO vary from 0.2 to 0.52 for the annual and 0.39 to 0.77 for the 10-y RMF series (Table 1D). The standard deviation of the temperature anomaly coherent with the AMO is  $\sim$ 0.2°C for the annual and 10-y RMF series. There is no clear sign of the westward progression of the local temperature anomalies as implied by D&K; the correlations are low and generally noisy (Figure 1c). We conclude that there is little support for the use of the AMO as a strong proxy for in situ temperature series for the four regions discussed by D&K. The temperature differences in the 1960-1980 cold period relative to earlier and later decades are small, with a maximum contrast of  $\sim 1.5^{\circ}$ C (Iceland, 1950s vs. 1970s) but more typically <1°C. The physiological and population level impacts of a temperature change of this magnitude are judged to be negligible (Jobling, 1988; Myers et al., 1997; Rindorf et al., 2008).







**Figure 1.** (a) Time series of the annual (light line) and 10-year average (dark line) AMO (see Figure 1, D&K). (b) Temperature anomaly time series for: Northern cod (Labrador–northern Newfoundland), annual 0–176 m (Colbourne *et al.*, 2017); Greenland, Fyllas Banke, June/July 50 m Station 4 (Mortensen, 2018); northern Iceland Siglunes hydrographic section, five stations from 4 to 85 km offshore, late spring 0–200 m Astthorsson *et al.*, 2007); NE Arctic, Kola hydrographic section, stations 4–7, annual 0–200 m Hollowed and Sundby (2014). The Greenland, Iceland, and NE Arctic series are offset for clarity by 2, 4, and 6°C, respectively. (c) Lagged correlations among the four time series: NE Arctic–Iceland (filled circle); NE Arctic–Greenland (open circle); NE Arctic–Northern cod (filled square); Iceland–Greenland (open square); Iceland–Northern cod (filled triangle); and Greenland–Northern cod (open triangle).

#### Quantifying the impact of fishing

D&K preface their section headed **Fish and shellfish** by stating— "Fish and shellfish have long been known to respond to climate forcing (Hjort, 1914; Helland-Hansen and Nansen, 1920;

**Table 1.** Statistics of ocean temperature times series and the AMO (1940–2016).

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(A) Decadal averages of temperature and AMO anomalies							
Decade	L-nN	Greenland	Iceland	NE Arctic	АМО		
50s	0.17	0.22	1.40	-0.05	0.12		
60s	0.26	0.29	0.23	-0.46	-0.02		
70s	-0.07	0.42	-0.13	-0.42	-0.26		
80s	-0.11	-0.05	-0.06	-0.42	-0.12		
90s	-0.20	-0.26	-0.15	-0.13	-0.02		
00s	0.23	0.36	0.54	0.42	0.15		
(B) Correlatio	n matrix	for the tempe	rature time	e series			
	L-nN	Greenland	Iceland	NE Arctic			
N cod	1	_	-	_			
W Greenland	0.68	1	_	_			
Iceland	0.65	0.32	1	_			
NE Arctic	0.36	0.12	0.47	1			
(C) Standard	deviation	s of temperati	ıre anomal	ies			
Annual	0.36	0.84	1.2	0.5			
10-y RMF	0.21	0.31	0.56	0.29			
(D) Correlatio	ns of tem	perature serie	s with the	AMO			
Annual	0.52	0.20	0.24	0.33			
10-y RMF	0.65	0.39	0.69	0.77			

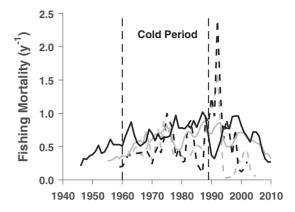
L-nN, Labrador-northern Newfoundland.

Shepherd et al., 1984), thus it is not surprising that with the downturn in temperatures during the 1960s to the 1980s strong responses resulted." Within this context, they discuss the declining trends of spawning stock biomass (SSB) among the NE Arctic, Iceland, West Greenland, and Labrador-northern Newfoundland (Northern cod) cod stocks which they attribute to the cold period. However, the 1960s-1980s period was also a time when exploitation was high, with an average instantaneous fishing mortality of 0.59, corresponding to 45% removal of the SSB annually (Figure 2). This direct, massive removal of biomass is completely independent of links to lower trophic levels through food availability as D&K hypothesize but did not quantify. In the Labrador-northern Newfoundland region, an extraordinary 11.3 Mt of cod was harvested between 1960 and 1989 (Lilly et al., 2006). During the same period, 4.1 Mt of cod was harvested from the Greenland fishery (ICES, 2016a, 2017). In the NE Arctic and Iceland, 18.9 and 11.4 Mt of cod were landed during the cold period (ICES, 2016b, 2018). These harvest levels are considered to be minimal estimates given their omission of discarded fish in either directed or non-directed (by-catch) fisheries (Crowder et al., 2008).

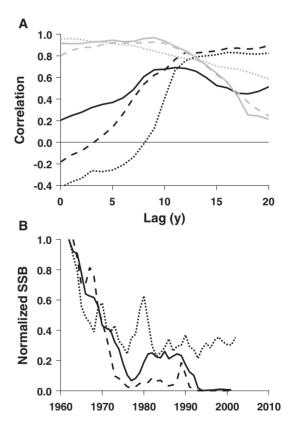
#### The spatial and temporal structure of SSB declines

D&K noted that during the cold period the four cod stocks seemed to decline at a similar rate and do so progressively from the northeast to the southwest (see D&K, Figure 6). In addition, they indicated that there was some evidence of a parallel progression of air temperature declines (Johannessen *et al.*, 2004) and of the intensity of the sea surface temperature cold pool from the Barents to the Labrador Sea (see D&K, Figure 3).

To evaluate these assertions, we quantified the decadal-scale rates of decline in cod SSB for the four areas referenced by D&K. We found that they differed by as much as a factor of  $\sim$ 2, from a low of 58 000 t/y (1959–1968) for the Icelandic cod stock to a high of 102 000 t/y (1962–1976) for Northern cod. NE Arctic cod declined at a rate of 68 000 t/y (1946–1958) and the cod stock at Greenland 77 000 t/y (1959–1974). This suggests that the cod SSB



**Figure 2.** Time series of instantaneous fishing mortality (F) for the four areas of D&K; NE Arctic, solid black line; Iceland, solid grey; Greenland, dashed black; Northern cod, dashed grey line. During the cold period of the 1960s–1980s, the average value of F was 0.59 with a standard deviation of 0.21.



**Figure 3.** (a) Lagged correlation between SSB for the four regions (NE Arctic–Iceland, solid black; Greenland, dashed black; Northern cod, dotted black; Iceland–Greenland, solid grey; Northern cod, dashed grey; Greenland–Northern cod, dotted grey). The lags are for the second region relative to the first. When the start of the second series was <15 years after the reference series, the number of pairs in the correlation calculation was reduced. All pairs were affected except NE Arctic–Northern cod. The reduction in the number of pairs began at ten y lag for NE Arctic with Iceland and Greenland, year 1 for Iceland–Greenland, and year 8 for Iceland and Greenland with Northern cod. (b) Normalized SSB = SSB(y)/SSB(1962), where y indicates the year from 1962 to the end of the series (Northern cod, solid line; Greenland, dashed line; Iceland, dotted line).

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**Table 2.** Correlation and per cent variance of SSB accounted for by F, the NAO, and the AMO in the multiple regression analysis.

	Correlatio		% Variance	:e
Variable	NEA	NWA	NEA	NWA
F	-0.77	-0.85	58.5	73.8
NAO	-0.05	-0.02	<1	8.4
AMO	0.16	0.22	<1	<1

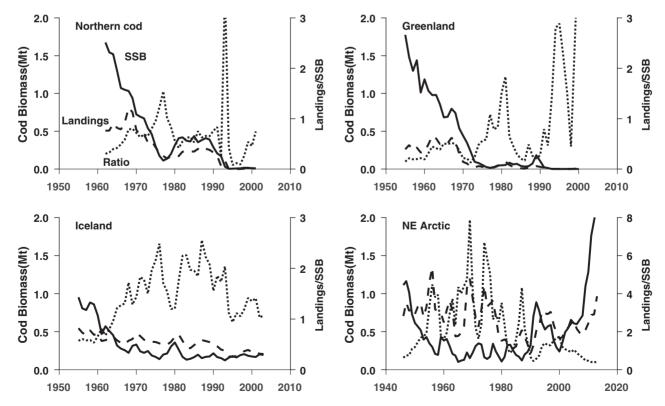
The Northeast Atlantic series (NEA) were from 1966 to 2012; the Northwest Atlantic series (NWA) were from 1970 to 1993; note that fishing moratoria on NWA cod were first initiated for several stocks in 1993 from Frank *et al.* (2016).

response to the AMO, if indeed it occurred, varied greatly over the North Atlantic. However, given the broad spatial scale of the AMO, it is not possible to determine whether the relationship between these rates of decline in cod SSB and the magnitude of the local climate variability is constant or variable from region to region.

We next addressed the east to west progression of the rate of decline of cod stocks implied by D&K using a lagged correlation analysis for all combinations of the four SSB time series. The analysis indicates that, based on the times when the correlations begin to asymptote, that the decline in SSB occurred first in the NE Arctic 7–11 years in advance of the decline in the three western regions (Figure 3a). Moreover, the correlations among the rates of decline in the three westernmost stocks were high at zero lag and remained relatively flat as the lag increased. This was also evident when these three SSB series were normalized by dividing by their 1962 SSB, the earliest common initial date for all three

series (Figure 3b). Thus, with the exception of a modest ~2 years lag of Northern cod behind Iceland (Figure 3a), the timing of the dynamics of these three western stocks was essentially synchronous. We conclude that the evidence supports a bimodal response, the NE Arctic stock constituting one node and the three western stocks a second that lagged the NE Arctic by about a decade. Therefore, the evidence supporting the propagation of the decline in cod SSB from east to west is weak. D&K further explored the link between the assumed propagation of the cod declines and the progression of sea surface temperatures but were unsuccessful. Based on this result they concluded it was unclear what role temperature played in the decline of the four cod stocks and in the temporal delay. However, we find little evidence of the progressive cooling and instead attribute the cod declines to shifts in exploitation.

A more plausible explanation for the differences in the timing of the declines of SSB between the eastern and western Atlantic is that it resulted from a shift in fishing effort, the cod stocks being first depleted in the eastern Atlantic which, in turn, led to a westward shift of effort by the European fishing fleet. Österblom and Folke (2015) provide a detailed description of the dominant impact of the Soviet fishing fleet on North Atlantic cod stocks during its westward transition during the 1960s. In support of this hypothesis, Garrod and Schumacher (1994) identified a peak in annual Northeast Atlantic cod landings of 2.2 Mt in 1956 which was followed by a steady decline. In the Northwest Atlantic, peak cod landings (1.3 Mt) occurred in 1968, again followed by a steady decline. This 12-year offset between peak landings in the eastern and western Atlantic is consistent with the results of our lagged correlation analysis (Figure 3a).



**Figure 4.** Time series of the estimates of SSB (solid line), recorded landings (dashed line), and the ratio of landings/SSB (dotted line) for Northern cod, Greenland, Iceland, and the NE Arctic cod stocks.

### The response of cod to AMO, NAO and exploitation

Frank et al. (2016) examined the dynamics of 22 North Atlantic cod stocks, including the four stocks featured in D&K [There are at least 22 cod stocks (independently assessed and managed) across the North Atlantic discussed by Frank et al. (2016). In addition to the four considered by D&K, there are annual time series of cod SSB available for thirteen stocks overlapping the "cold period" that could have been part of the overall analysis conducted by D&K. They include: Flemish Cap (1972), southern Grand Banks (1959), St. Pierre Bank (1959), southern Gulf of St. Lawrence (1950), eastern Scotian Shelf (1958), western Scotian Shelf (1950), northern Gulf of St. Lawrence (1974), Faroes (1961); Celtic Sea (1971), North Sea (1963), Kattegat (1971), western Baltic (1970), and central Baltic (1966) (starting year in parenthesis; see Kelly et al., 2009; Frank et al., 2016; ICES website, https:// www.ices.dk/ Pages/default.aspx).]. This analysis revealed that synchronous, coherent SSB variability occurred in 13 western Atlantic stocks that was distinct from a second pattern of synchronous variability in 9 eastern Atlantic stocks that included Iceland. They then investigated the relative contribution of AMO, NAO (North Atlantic Oscillation), and F (fishing mortality) to changes in these SSB patterns. Their results (reproduced here from their Supplementary Table S2) indicated that fishing mortality (F) was the major contributor to the observed variance in SSB (Table 2). In a related analysis, Vasilakopoulos et al. (2012) concluded that when ICES stocks are considered in aggregate, exploitation rate was the main driver of stock status trends through time.

These findings are consistent with the annual SSB and landings for the four regions assessed by D&K where the periods of strong decline of the cod fisheries align with high levels of harvesting of the stocks (Figure 4). Indeed, the ratio of landings to SSB varies from 0.39 (Greenland) to 2.8 (NE Arctic) indicating an extraordinary, high rate of removal from the stocks (Figure 4 and Table 3).

#### **Closing remarks**

We agree with the hypothesis advanced by D&K that climate variability can play a role in shaping the dynamics of marine ecosystems. However, in our view they have not adequately acknowledged the growing body of literature that points to the large-scale influence of exploitation in shaping these dynamics. This omission has become increasingly common in the literature examining the role of ocean climate in structuring the dynamics of exploited marine systems (Frank *et al.*, 2016, 2018). Our purpose in commenting here has been to illustrate the limitations inherent in such climate-centred approaches and to encourage a greater balance in future analyses of the important question of the factors that contribute to the shaping and stability of large marine ecosystems.

**Table 3.** Total landings, average SSB and average harvest rate (≡Landings/SSB) for the 1960−1989 period.

Cod stock	Landings (Mt)	SSB (average, kt)	Harvest rate
Labrador-northern Newfoundland	11.3	643	0.58
Greenland	4.1	351	0.39
Iceland	11.4	275	1.38
NE Arctic	18.9	226	2.78

#### References

- Astthorsson, O. S., Gislason, A., and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. Deep-Sea Research, 54: 2456–2477.
- Baum, J. K., and Worm, B. 2009. Cascading top–down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78: 699–714.
- Björnsson, B., Burgos, J. M., Sólmundsson, J., Ragnarsson, S. A., Jónsdóttir, I. G., and Skúladóttir, U. 2017. Effects of cod and haddock abundance on the distribution and abundance of northern shrimp. Marine Ecology Progress Series, 572: 209–221.
- Boudreau, S. A., Anderson, S. C., and Worm, B. 2011. Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean. Marine Ecology Progress Series, 429: 169–183.
- Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2001. Ecosystem changes and the effects on a major forage species, *Mallotus vil-losus*. Canadian Journal of Fisheries and Aquatic Sciences, 58: 73–85.
- Colbourne, E., Holden, J., Snook, S., Han, G., Lewis, S., Senciall, D., Bailey, W. *et al.* 2017. Physical oceanographic conditions on the Newfoundland and Labrador Shelf during 2016—erratum. DFO Canadian Science Advisory Secretariat Research Document 2017/079. v + 50 pp.
- Crowder, L. B., Hazen, E. L., Avissar, N., Bjorkland, R., Latanich, C., and Ogburn, M. B. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. Annual Reviews of Ecology, Evolution and Systematics, 39: 259–278.
- Cury, P., Shannon, L., and Shin, Y. J. 2003. The functioning of marine ecosystems: a fisheries perspective. *In* Responsible Fisheries in the Marine Ecosystem, pp. 103–141. Ed. by M. Sinclair and G. Valdimarsson. FAO, Rome, Italy.
- Daewel, U., Hjøllo, S. S., Huret, M., Ji, R., Maar, M., Niiranen, S., Travers. *et al.* 2014. Predation control of zooplankton dynamics: a review of observations and models. ICES Journal of Marine Science, 71: 254–271.
- Drinkwater, K. F., and Kristiansen, T. 2018. A synthesis of the ecosystem responses to the late 20th century cold period in the northern North Atlantic. ICES Journal of Marine Science, 75: 2325–2341.
- Essington, T. 2010. Trophic cascades in open ocean ecosystems. *In* Trophic Cascades: Predators, Prey, and Changing Dynamics of Nature, pp. 91–105. Ed. by J. Terborgh and J. A. Estes. Island Press, Washington, DC.
- Fauchald, P. 2010. Predator–prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology, 91: 2191–2197.
- Frank, K. T., Petrie, B., Leggett, W. C., and Boyce, D. B. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. Proceedings of the National Academy of Sciences of the United States of America, 113: 8248–8253.
- Frank, K. T., Petrie, B., Leggett, W. C., and Boyce, D. B. 2018. Exploitation drives an ontogenetic-like deepening in marine fish. Proceedings of the National Academy of Sciences of the United States of America, 115: 6422–6427.
- Frank, K. T., Petrie, B., and Shackell, N. L. 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends in Ecology and Evolution, 22: 236–242.
- Frank, K. T., Petrie, B., Shackell, N. L., and Choi, J. S. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecology Letters, 9: 1096–1105.
- Garrod, D. J., and Schumacher, A. 1994. North Atlantic cod: the broad canvas. ICES Marine Science Symposium, 198: 59–76.
- Hedeholm, R. B., Mikkelsen, J. H., Svendsen, S. M., Carl, J., and Jensen, K. T. 2017. Atlantic cod (*Gadus morhua*) diet and the interaction with northern shrimp (*Pandalus borealis*) in Greenland waters. Polar Biology, 40: 1335–1346.

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Helland-Hansen, B., and Nansen, F. 1920. Temperature variations in the North Atlantic Ocean and in the atmosphere. Smithsonian Miscellaneous Collections, 70: 480.

- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions/Conseil Permanent International pour l'Exploration de la Mer, 20: 1–228.
- Hollowed, A. S., and Sundby, S. 2014. Change is coming to the northern oceans. Science, 344: 1084–1085.
- Hunt, G. L., and McKinnell, S. 2006. Interplay between top-down, bottom-up, and wasp-waist control in control in marine ecosystems. Progress in Oceanography, 68: 115–124.
- ICES. 2016a. ICES Advice on fishing opportunities, catch, and effort Iceland Sea and Greenland Sea Ecoregions. Cod (*Gadus morhua*) in NAFO Subarea 1, inshore (West Greenland cod). ICES Advice 2016, Book 2. 6 pp.
- ICES. 2016b. ICES Advice on fishing opportunities, catch, and effort Iceland Sea and Greenland Sea Ecoregions. Cod (*Gadus morhua*) in Division 5.a (Iceland grounds). ICES Advice 2016, Book 2. 6 pp.
- ICES. 2017. ICES Advice on fishing opportunities, catch, and effort Arctic Ocean and Greenland Sea Ecoregions Published 13 June 2017 cod.21.1a-e. Cod (*Gadus morhua*) in NAFO divisions 1.A–E, offshore (West Greenland). 5 pp.
- ICES. 2018. ICES Advice on fishing opportunities, catch, and effort Arctic Ocean, Barents Sea, Faroes, Greenland Sea, Published 13 June 2018 Icelandic Waters, and Norwegian Sea ecoregions. doi:10.17895/ices.pub.4412 cod.27.1-2
- Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. Aquaculture, 70: 1–19.
- Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsaeter, H., Knutsen, T. et al. 2012. Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. ICES Journal of Marine Science, 69: 880–889.
- Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., Nagurnyi, A. P. et al. 2004. Arctic climate change: observed and modelled temperature and sea-ice variability. Tellus, 56A: 328–341.
- Jónsdóttir, I. G. 2017. Predation on northern shrimp (*Pandalus borealis*) by three gadoid species. Marine Biology Research, 13: 447–455.
- Kelly, J. E., Frank, K. T., and Leggett, W. C. 2009. Degraded recruitment synchrony in Northwest Atlantic cod stocks. Marine Ecology Progress Series, 393: 131–146.
- Lilly, G. R., Murphy, E. F., Healey, B. P., and Brattey, J. 2006. An Assessment of the Cod (*Gadus morhua*) Stock in NAFO Divisions 2J3KL in April 2006. Canadian Science Advisory Secretariat Research Document 2006/043. vi + 159 pp.
- Llope, M., Licandro, P., Chan, K. S., and Stenseth, N. C. 2012. Spatial variability of the plankton trophic interaction in the North Sea: a new feature after the early 1970s. Global Change Biology, 18: 106–117.

- Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., and Stenseth, N. C. 2017. Interaction between top-down and bottom-up control in marine food webs. Proceedings of the National Academy of Sciences of the United States of America, 114: 1952–1957.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer–resource dynamics in marine pelagic ecosystems. Science, 285: 1396–1398.
- Molfese, C., Beare, D., and Hall-Spencer, J. M. 2014. Overfishing and the replacement of demersal finfish by shellfish: an example from the English Channel. PLoS One, 9: e101506.
- Möllmann, C., and Diekmann, D. 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the northern hemisphere. Advances in Ecological Research, 47: 303347.
- Mortensen, J. 2018. Report on Hydrographic Conditions Off Southwest Greenland June/July 2017. NAFO SCR Doc. 18/005. 8 pp.
- Myers, R. A., Mertz, G., and andFowlow, P. S. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fisheries Bulletin, 95: 762–772.
- Österblom, H., and Folke, C. 2015. Globalization, marine regime shifts and the Soviet Union. Philosophical Transaction of the Royal Society B, 370: 20130278.
- Pálsson, O. K., and Björnsson, H. 2011. Long-term changes in trophic patterns of Iceland cod and linkages to main prey stock sizes. ICES Journal of Marine Science, 68: 1488–1499.
- Parsons, T. R. 1992. The removal of marine predators by fisheries and the impact of trophic structure. Marine Pollution Bulletin, 25: 51–53.
- Petrie, B., Frank, K. T., Shackell, N. L., and Leggett, W. C. 2009. Structure and stability in exploited marine ecosystems: quantifying critical transitions. Fisheries Oceanography, 18: 83–101.
- Reid, P. C., Battle, E. J. V., Batten, S. D., and Brander, K. M. 2000. Impacts of fisheries on plankton community structure. ICES Journal of Marine Science, 57: 495–502.
- Rindorf, A., Jensen, H., and Schrum, C. 2008. Growth, temperature and density relationships of North Sea cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 65: 456–470.
- Shepherd, J. G., Pope, J. G., and Cousens, R. D. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapports et Procès-Verbaux des Réunions/Conseil Permanent International pour l'Exploration de la Mer, 185: 255–267.
- Stige, L. C., Dalpadado, P., Orlova, E., Boulay, A. C., Durant, J. M., Ottersen, G., and Stenseth, N. C. 2014. Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in the Barents Sea. Progress in Oceanography, 120: 243–253.
- Strong, D., and Frank, K. T. 2010. Human involvement in food webs. Annual Review of Environment and Resources, 35: 1–23.
- Vasilakopoulos, P., O'Neill, F. G., and Marshall, C. T. 2012. Differential impacts of exploitation rate and juvenile exploitation on NE Atlantic fish stock dynamics over the past half century. Fisheries Research, 134–136: 21–28.
- Worm, B., and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology, 84: 162–173.

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