Ecology of Planktonic Atlantic Cod (*Gadus morhua*)

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Abstract

Atlantic cod larvae surviving the first weeks after hatching settle next years juvenile recruitment on Georges Bank (USA). It probably supports Hjort's critical period hypothesis that effects of climate on marine biological productivity control early-life history processes and recruitment in fish populations. Climate also regulates local ultraviolet sea surface radiation, which may potentially kill microbes pathogenic to planktonic cod eggs. Survival capacities of cod larvae depend on maternal effects on egg qualities attained during oogenesis, influenced by variable food sources for female cod. Actual survival of first-feeding cod larvae requires proper abundance of preferred prey, copepod nauplii, produced by fertile females. Temporal and spatial mismatch between cod larvae and prey is normal, extensive and lethal, counteracted by opportunistic behavior that optimizes encounters. In spawning habitats of Northeast Arctic cod, the abundance of *Calanus finmarchicus* nauplii possibly results from coastal biological productivity in the previous year, which may explain time lags in positive correlations between vernal river discharge and NEA cod recruitment. Extensive meltwater storage for year-round hydroelectric production probably limits food web productivity, survival of NEA cod larvae and stock recruitment. Global climate change and stock management interact ecologically with other anthropogenic influences concerning sustainability of Atlantic cod population systems.

Keywords: Norwegian Sea, Barents Sea, Gulf of St. Lawrence, Lofoten Islands, North Atlantic Current, Norwegian Coastal Current, Arctic Mediterranean Ecosystem, hydrological cycle, NAO, AO, UVR

1. Introduction

Like many other bony fish, Atlantic cod (*Gadus morhua*) emerges from its egg as a very tiny larva that spends its first juvenile life span in planktonic communities. The species inhabits the North Atlantic, from the eastern coasts of the United States of America and Canada to the Baltic and Barents Seas in Northwestern Europe. The species segregates into population systems ranging from local units inshore to extensive units that occupy wide continental shelf systems.

Atlantic cod is a socio-economic commodity traded in international markets for nearly a millennium, which created wealth that built nations and financed wars [1]. Harbors and communities for landing, processing and marketing cod products expanded when cod migrated in abundance for annual reproduction in known spawning grounds. Migrations failed in other periods, leaving starving families, bankrupt companies and weak local and national economies. Despite being subject to intensive scientific investigations from fisheries biologists for more than a century, the ecological causes for fluctuations in the economy of cod fisheries are still an ecological enigma.

About 150 years ago, a pioneer in Norwegian marine science, Georg Ossian Sars, was the first to observe fish to spawn pelagic eggs. He reported that fertilized eggs of cod spawning at the Lofoten Islands in Northern Norway (**Figure 1**) were buoyant, accumulating just beneath the sea surface in calm weather. He studied the embryonal development and kept eggs in aquaria until the hatching of cod larvae. By doing that, he developed criteria for identification of different stages in the morphological development of juvenile cod. He organized marine research expeditions in Arctic waters and found that adult cod spawning at Lofoten spent their summers in the northern Barents Sea, which established its status as one population. Sars understood the life history of Atlantic cod and discovered the population structure and migratory nature of Northeast Arctic Cod (NEA cod), which became his legacy as founder of international fisheries biology.

Today, bilateral research and management organized by Russia and Norway have succeeded in maintaining NEA cod at a sustainable level. Comprehensive research develops understanding of how the population interacts with other species in different habitats within its population system. Several planktivorous fish fall prey in habitats for somatic growth of juvenile and

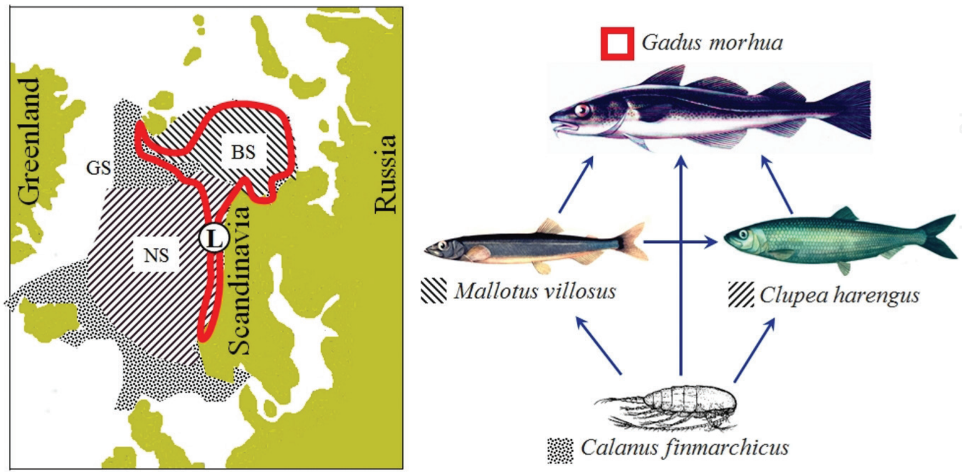

Figure 1. Main geographic distribution of NEA cod (*G. morhua*), Barents Sea capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*) and *C. finmarchicus* in the Norwegian, Greenland and Barents Seas (NS, GS and BS, respectively). (**L**) Main spawning habitat of NEA cod in the Lofoten archipelago. (Arrows) Directions of trophic energy flow.

adult cod in the Barents Sea (**Figure 1**). A single planktonic copepod species (*Calanus finmarchicus*) is the preferred prey of NEA cod larvae, and it produces much of the biomass that directly and indirectly fuels the entire food web of NEA cod. Sars did not know this, and he could not explain how an abundance of cod migrated to Lofoten in some years and were missing in others. Decades later, his successor as leader of the Norwegian fisheries science, Johan Hjort, concluded at the end of his service that fluctuations in the yield from fisheries in general were possibly due to environmental variability in population systems of fish [2, 3]. He suggested a concept of trophic causality in marine food webs, where primary production of phytoplankton was subject to interannual fluctuations, which regulated the reproduction and growth of zooplankton being food for juvenile fish. Hjort even hypothesized that the first encounter between larva and its prey was a critical period when starvation and mortality regulated the proportion of larvae that would live until the age of recruitment to the exploited stock.

For scientists who joined Hjort's paradigm, *C. finmarchicus* stood out as a key to understanding survival of fish larvae in the North Atlantic, being the most abundant metazoan species in Arcto-boreal waters [4]. Therefore, the scene for scientific testing of Hjort's critical period hypothesis has frequently been habitats that feature a short planktonic food chain, established by Atlantic cod and *C. finmarchicus* that reproduce in concert.

Unfortunately, Hjort left fisheries science after World War I. His interdisciplinary research group in fisheries ecology dissolved when the Norwegian government would no longer finance the operation of a seagoing research vessel, but his legacy survived. For more than a century, his critical period concept was a beacon for the international community of fish population ecologists and fisheries biologists, but they now question its general validity [5]. The current understanding is that interannual variability in recruitment of NEA cod can result from many sources acting throughout pre-recruit life, one of the most important being cannibalism from older year-classes [6]. Some even concluded 'the quest for solving the Recruitment Problem has been called off' [7]. However, maybe Hjort and modern fellow scientists did not study the same population system, meaning that its state has changed along the course of a century and that Hjort was correct in his time. Ecological conditions ruling then may still work but overshadowed by man-made variables in modern times.

2. Geographic distribution, genetic variability and early ontogeny

Atlantic cod belongs to the family of Gadidae, a circumpolar taxon on the northern hemisphere. It is also true for the genus of *Gadus* that contains several species. Mackie and Richie [8] suggested that *G. morhua* has evolved into two closely related subspecies, the Pacific cod *G. morhua macrocephalus* and the Atlantic cod *G. morhua morhua*. In this paper, information referring to cod and *G. morhua* addresses only Atlantic cod.

Atlantic cod establishes populations on the continental shelves on both sides of the North Atlantic. It occurs from North Carolina to the Labrador Sea on the eastern shelf of North America and occurs periodically in southern Greenland depending on sea temperatures. In European waters, it exists from the Bay of Biscay to the Svalbard archipelago at N80° and from Iceland at W20° to Novaya Zemlya at E50°. It may live for considerably more than 20 years and grow into large size, exceeding 55 kg and a total length >1.8 m, which is not common today due to extensive commercial exploitation.

Atlantic cod displays a variety of ecotypes adapted to particular environmental conditions. Some are stationary in coastal waters, and others migrate to spawn at a distance from where they forage and grow between spawning seasons. Cod wintering in Newfoundland bays at subzero temperatures produces antifreeze glycoproteins that prevent formation of ice crystals in their plasma [9]. The plasticity of physiological and biochemical processes that allow short-term adaptation in cod are not known, but epigenetic changes caused by methylation of DNA seems to be a promising field of research.

New genomic research on Atlantic cod revealed that two distinct ecotypes of homozygotes occur [10, 11]. One is an original ecotype that adjusts rapid changes in swim-bladder volume resulting from vertical migration close to the surface. The other has evolved from the original, having the same genome except for some inverted DNA regions. The inverted genome changes the swim-bladder function and causes cod to forage and migrate in deep water. The two ecotypes occur on both sides of the Atlantic.

In Europe, the original genome dominates from the British waters to the Baltic and White Seas, which includes Norwegian Coastal (NC) cod [11]. The inverted genome occurs in NEA cod that forage and grow in Barents Sea habitats, except when adults migrate to spawn in March-April along the Norwegian shelf even as far south as below N62°. NEA cod are homozygous for the genomic inversions, while NC cod are homozygous for the ancestral non-inverted genome. Experimental crossing of the two homozygotes produces heterozygotes. Such heterozygous cod are common in coastal waters north of Lofoten and less common at the southern spawning habitats of NEA cod. It is rare in the White Sea and the Skagerrak coast of southern Norway [11]. In the theory, mating by two heterozygous cod in Norwegian waters may result in heterozygous offspring as well as homozygous siblings being either NEA cod or original NC cod, but scientific evidence remains unobserved in nature.

No information exists about differences in the early ontogeny from fertilization to hatching of eggs in the three ecotypes. Variability in ontogeny probably rather depends on environmental effects during ripening of eggs in female ovaries and ambient temperature on embryonic development before eggs hatch. In general, embryonic ontogeny lasts for a couple of weeks, being inversely related with temperature, in Northern Norway typically lasting about 3 weeks at 3°C [12].

Cod larvae emerging from the egg carry a yolk sac that supports further development of organs necessary for subsequent intake and digestion of prey. At this stage, the larva has no functional jaw but an opening to the mouth cavity that allows it to drink seawater, which causes passive accumulation of small microalga (1–4 μm) in the gut. However, cod larvae may actively filter larger microalgae (6–10 μm) at rates 500–7000 times the drinking rate, facilitated by flagella on the visceral arches [13]. The larger algae may constitute nearly 40% of the gut content in larvae 7 days old but decreases in older larvae requiring animal protein to grow.

Marine microalgae accumulate orthophosphate (PO_4-P) from seawater and store intracellular polyphosphate [14], which may be imperative for somatic development and survival of cod larvae. They use phosphate for synthesis of adenosine triphosphate (ATP) that transfer energy to all intracellular life processes, and for bio-syntheses building skeletal calcium phosphate (aragonite), phospholipids in every cellular membrane and nucleotides building DNA and RNA in all cells. Thus, feeding on phytoplankton seems essential to develop organs and morphological capacities necessary to hunt and digest prey. NEA cod larva is about 4.5–5.1 mm long when the yolk sac is empty [15], and they need animal protein to grow. Van der Meeren and Næss [16] observed that cod larvae reared in mesocosms stayed alive feeding unselectively on protozoans but increased their specific growth rate from 2.8 to 21.7% when changing to their preferred prey, the nauplius of copepods.

3. Coastal ecotypes distinguished by egg retention in northern Norway

Based on numerical modeling, Myksvoll et al. [17] identified three categories of spawning strategies of Atlantic cod in Norwegian waters. The categories represent oceanic cod, migratory coastal cod and fjord cod. Oceanic cod is equivalent to NEA cod spawning in habitats from where the eggs drift offshore into the Norwegian Coastal Current (NCC). It runs northwards outside the official Norwegian coastal baseline that encloses all islands and headlands along the coast, transporting the progeny of NEA cod to nursery habitats in the Barents Sea. Coastal cod spawn among islands inside the baseline but outside fjords. Their eggs are temporarily retained by eddies and backwaters between shallow archipelagos, which causes the eggs from several spawning habitats to hatch within the region of a common population system. Fjord cod spawn at the head of fjords, and the retention of eggs supposedly lasts long enough to cause hatching within the fjords.

An empirical study in 20 Norwegian fjords south of the Lofoten Islands as far as to the eastern North Sea demonstrated retention of cod eggs particularly in fjords with shallow sills [18]. In a large fjord at about N70°, and with no sill that separated it from the Barents Sea, cod eggs spawned in March-April did not accumulate at the fjord's head. Most were probably buoyant in high-salinity surface water (≥33 psu) advected by predominant wind drift to hatching habitats outside the fjord [12]. Retention of locally spawned eggs only appeared to occur in a small side fjord with shallow sill, after the vernal freshwater discharge had started in May. Coastal cod in the main fjord grow faster than cod in the side fjord, but both mature at the same age, while earlier than NEA cod [19]. The two stocks perhaps fit the distinction between coastal and fjord cod suggested by Myksvoll [17].

Fevolden and Pogson [20] concluded that genetic heterogeneity exists among resident populations of cod in different fjords. Thus, the gene flow among fjord populations throughout Northern Norway may be considerably lower than previously believed. However, Myksvoll et al. [21] observed that parts of the eggs spawned by fjord cod left the local fjord at rates that depended on local estuarine circulation and winds during the main spawning season (March-April). Few eggs and larvae seem to drift from one fjord to another, but the rates are possibly sufficient to establish genetic connectivity that makes neighboring fjords unite into metapopulations ('population of populations').

4. Plankton ecology of cod spawning habitats in fjords

Every fjord in Norway is probably a spawning habitat for Atlantic cod. The typical fjord is an estuarine system where freshwater is discharged to the fjord's head, its inner part. The discharge may occur naturally as vernal meltwater from rivers in May–July or from hydroelectric power plants governed to produce in other seasons. Discharged freshwater mixes with seawater imported from the open sea, which produces brackish surface water that contains far more seawater than freshwater when it leaves a fjord. The brackish outflow causes a salter compensation current to flow in opposite direction underneath, which tends to retain cod eggs by transporting them toward the head. However, retention depends on how buoyant eggs spawned during runoff are and the amount of freshwater discharged.

Most Norwegian cod spawn their eggs before the maximum vernal freshwater run-off season in May–June. Cod eggs sink in brackish fjord water (salinity <30 psu), and all are buoyant at 34 psu which is classified as coastal water [22]. Thus, the eggs do not ascend into a brackish surface current flowing out of a fjord. Physical modeling support that they normally attain neutral buoyancy in more saline coastal water advected by the compensation current, which retains the eggs at the fjord's head [21]. However, a proportion of cod eggs spawned in years with exceptionally low discharge or in locations that receive little freshwater from small drainage areas may be subject to seaward transport by wind-driven surface advection. Heavier eggs may remain neutrally buoyant at larger depths and stay retained by inward advection, and their proportion varies with the salinity gradient between the surface outflow and the compensation current.

Little information exists on the first feeding and growth of fjord cod larvae into metamorphosis and subsequent recruitment to fjord stocks. However, the estuarine biota of fjords differs from habitats for first-feeding larvae in Lofoten, which is evident in one of the regions modeled by Myksvoll et al. [17]. There, a permanent fjord stock of Atlantic cod recruited juveniles <1 year old every autumn or winter [23]. The habitat is a typical fjord characterized by a 156 m deep basin separated from a deeper fjord system by its 60 m deep sill. Today, its two rivers receive regulated freshwater outflow from hydroelectric production. In its previous natural state, the vernal meltwater discharge generated strong estuarine circulation that started in May and reached maximum in June [24]. A characteristic spring bloom of diatoms, dinoflagellates, euglenophytes and about 6-μm-long nannoflagellates develop in April [25]. The production of diatoms decreased in May, while the production of other phytoplankton proceeded. Nannoflagellates dominated in a year with moderate freshwater supply, and euglenophytes dominated when the discharge was stronger. The dominating nannoflagellate species probably originated from freshwater habitats [25] and possibly continued to grow in the fjord's oligohaline surface water. Euglenophytes are large flagellates about 50 μm long that may also live in freshwater. They may be both phototrophic and phagotrophic that feed on bacteria and small flagellates. Thus, the brackish water biota of Norwegian fjords forms food webs that in general deviate from what occurs in the euhaline habitats (>30 psu) of cod larvae in Lofoten.

Fjord stocks of *C. finmarchicus* in juvenile ontogenetic stages (nauplii and immature copeodids) tend to be abundant during moderate freshwater discharge in May-June and practically absent when the discharge was strong [26]. However, Bucklin et al. [27] observed that *Calanus* in fjords often consists of three species, *C. finmarchicus*, *C. glacialis* and *C. helgolandicus*. They are difficult to distinguish by morphological characters, and it is probable that copepods previously identified as *C. finmarchicus* in Norwegian fjords may be a mixture of these. In any circumstance, if estuarine circulation retains cod larvae in fjords, it seems that they would have richer diets of microalgae and nauplii and a better scope for survival in years with reduced estuarine circulation.

5. The population system of Northeast Arctic cod

NEA cod is one of the most thoroughly studied fish stocks worldwide [6], which covers all levels of its life history and all parts of its geographically extensive and ecologically complex population system. Commercial fishing has occasionally caught adult NEA cod in Spitsbergen waters at about N80°, and their spawning occurs in Norwegian coastal waters from about N60° to about N70° at the entrance of the Barents Sea. Adult cod >6 years old repeat annual upstream spawning migrations in Atlantic water flowing northwards along the continental shelf break, termed the Norwegian Atlantic Current (NAC). They return to the banks of the Barents Sea to forage between each spawning and mainly occupy western habitats influenced by warm Atlantic water. Immature cod mainly occupy the colder eastern parts, north of the Russian coast. While adults prefer temperatures >1°C, the juveniles tolerate −1.8°C in the northern Barents Sea [28].

Eighty years of research have tried to settle whether NEA cod and a variety of local stocks in Norwegian coastal waters effectively make up one large population or >1 non-interbreeding groups [29]. Important steps made lately [10, 11] indicate that some interbreeding may occur, possibly mainly in Lofoten where most NEA cod spawn. The Lofoten fishery lands mostly NEA cod, but it traditionally starts with the arrival of NC cod that assumedly migrate from banks on the continental shelf. Some of the NC cod possibly pass by, destined to spawn in habitats on the mainland coast. Other NC cod spawn in concert with NEA cod in Lofoten, which opens for some interbreeding. However, it has been suggested that the mating of cod involves lekking, starting when females ready to spawn seek aggregations of males that compete for female attention. Male courting involves dancing, fin postures and noisy muscular drumming on their swim bladders [30]. NC cod and NEA cod possibly have different courtship displays that discourage mating. However, ripe NEA cod and NC cod may occur simultaneously in close spawning habitats and even be caught in the same catch at spawning grounds off the Lofoten Islands [29]. This suggests that some interbreeding between NEA and coastal cod may occur, at least by chance in seawater where gametes from both kinds of cod are mixed. If both parents may be homozygous, one with original genome and one with the inverted NEA cod genome, the offspring will be heterozygous.

Normally, the massive immigration of NEA cod from the Barents Sea is likely to outnumber NC cod in Lofoten. That may not be true in years when NEA cod failed to migrate into some of the traditional spawning habitats in Lofoten, while NC cod perhaps occurred in normal abundance. Thus, some scientific results reported on cod eggs and larvae from Lofoten may not strictly represent NEA cod. In any circumstance, cod larvae of either kind probably do not behave very differently to local environmental conditions in a common habitat and represent Atlantic cod in general.

In the main spawning habitat of NEA cod in the Lofoten archipelago, Wiborg [15] observed that larvae <6 mm long had stomachs containing mainly copepod eggs and nauplii of *C. finmarchicus* and *Metridia* spp. *C. finmarchicus* that was most abundant in Lofoten is widely distributed in the North Atlantic [4]. During copulation with males, the females of *C. finmarchicus* store semen in their spermatecs, i.e., small organs keeping spermatozoa alive for fertilization of eggs on later occasions. The females are batch spawners, meaning that they produce eggs repeatedly in numbers and at frequencies that depend on the amount of feasible food. Their diet is mainly autotrophic microalgae and to some extent ciliates and other heterotrophic microorganisms. The females produce their first egg batches during the phytoplankton spring bloom, which in boreal habitats lasts for about 1 month, starting after spring equinox at 20–21 March. NEA cod in Lofoten has by then started their spawning season that peaks in the late March or early April, and the abundance of their first-feeding larvae culminate during a period from the late April to the middle of May [31].

The eggs of *C. finmarchicus* hatch in 1 or a few days depending on ambient seawater temperature. The emerging nauplius stage one (NI) molts into a succession of stages (NII–NVI) before the individual grows through six copepodid stages (CI–CVI), the last being sexually mature adults. The mouth of cod larvae ≤6 mm can possibly handle any nauplius stage and even *C. finmarchicus* CI [15]. Thus, an understanding of how reproduction success correlates with recruitment to an exploited cod stock depends on variables that regulate the abundance of proper food.

Wiborg [15] supposed that adult *Pseudocalanus* spp. and *C. finmarchicus* CII were appropriate prey for >6 mm cod larvae. Lynch et al. [32] used data from Georges Bank to develop a conceptual model for larval cod feeding on stage-structured prey populations. The model suggested that *C. finmarchicus* alone was not a sufficient prey for 6 mm and larger cod larvae. They needed a supplement of *Pseudocalanus* spp. for their survival and growth. However, Lynch et al. [32] had no information on prey smaller than *C. finmarchicus* CI and could not address dietary requirements for smaller cod larvae.

As they grow, new generations of NEA cod larvae drift northwards from the spawning habitats. Their habitat is now the NCC where the sea surface temperature may be about 10°C during summer [33]. Cod larvae grown at this temperature in experimental culture metamorphose into juveniles at a total length of <35 mm [34]. Metamorphosis is gradual, starting with changes related to swimming performance [35]. At 20 mm length, the spine displays a complete set of visible vertebrae, and a full set of functional fins have developed. At 35 mm length, the upper jaw is nearly as long as the lower, and the stomach digests the exoskeleton of copepods, which combined make the juvenile successfully feed on *C. finmarchicus* CIII–CV. However, its typical external morphology of older cod showing an upper jaw longer than the lower appears only when the juvenile cod is about 65 mm long.

NEA juveniles that enter the southwestern Barents Sea in August-September 5 months after spawning have total lengths 5.5–8 cm long, their size being directly proportional with sea temperatures ranging from 4.8 to 6.3°C [36]. They are then nektonic, forming schools foraging on zooplankton in depths down to about 100 m. They still feed on *C. finmarchicus* that gradually molt into stage CV copepodids that enter diapause, which means that they no longer perform diurnal vertical migration (DVM). They sink toward the bottom, which possibly stimulates both carnivorous zooplankton and juvenile cod to enter hyper-benthic habitats of the Barents Sea.

In terms of fisheries science, the abundance of juveniles of the year is termed 0-group fish until the end of the calendar year [6], when the generation becomes 1-group fish. Every year in August-September, Norwegian and Russian scientists survey the abundance of juvenile fish in the Barents Sea, using advanced acoustic instruments and trawls. They also monitor older fish and their predators and prey, which paint a comprehensive picture of the Barents Sea as a large habitat system for commercial fish stocks.

The Barents Sea is often described as an ecosystem [37, 38], which is not strictly true according to the theory of systems ecology [39]. A true ecosystem should conserve biogenic energy that flows through the system's complete food web, at least containing populations that are the most influential producers of biomass. The Barents Sea is different, being extremely open regarding exchange of biomass with the Norwegian Sea.

Only parts of the population system of NEA cod occupy the Barents Sea. Most of its spawning habitats occur along half of Norway's coastline (**Figure 1**). They overlap the population systems of *C. finmarchicus* and the Norwegian spring spawning herring (*Clupea harengus*), both having population systems that occupy the Norwegian Sea. NEA cod also overlaps with parts of the population system of Barents Sea capelin (*Mallotus villosus*) that extends farther north. Both herring and capelin migrate to spawn eggs deposited in benthic habitats along the Norwegian coast. Their meroplanktonic larvae feed on *C. finmarchicus* nauplii and copepodids while transported by the NCC. 0-group juveniles of herring and capelin compete for planktonic food in the Barents Sea, and older than 0-group juvenile herring are predators on capelin larvae.

0-group herring and capelin are essential for chick survival in colonies of cliff-breeding seabirds along the Norwegian coast. The adult seabirds do not compete with their offspring, some foraging rather on juveniles of cod and other Gadidae that spawn along the Norwegian coast. A number of seals and whales prey on Atlantic gadoids and compete with human exploitation, which combined accounts for most of the mortality in NEA cod after recruitment to the exploited stock.

When herring start to mature sexually, they leave the Barents Sea for their first spawning along the Norwegian coast. After each annual spawning, adult herring migrate to the western Norwegian Sea to feed during summer, mainly on *Calanus hyperboreus*, a copepod that reproduces in the Greenland Sea [40]. It may have a multiannual life cycle in high-Arctic water, which possibly maintains a pan-Arctic population system. Another copepod, *Calanus glacialis*, has a circumpolar distribution associated with polar sea ice and the Arctic continental shelves of Eurasia and North America. The polar production of *C. glacialis* is important to the growth of capelin, which establishes a major food chain for NEA cod.

Many benthic invertebrates that fall prey to cod in the Barents Sea reproduce by meroplanktonic larvae. The deep-sea prawn *Pandalus borealis* is an important demersal food source for NEA cod and widely distributed in the Barents Sea. Its larvae may live in pelagic habitats for 2–3 months before they settle as epibenthic juveniles. The species occurs along the entire coast of Norway, and some of the recruitment of juveniles to the Barents Sea stock is due to dispersal of larvae by advection of Atlantic water from reproduction habitats in Norwegian coastal waters [41].

NEA cod is a very opportunistic predator in the Barents Sea. It is omnivorous on every stage in its life history. The animal diet of juveniles changes gradually from mesozooplankton (0.2–2 cm) like copepods to macrozooplankton (>2 cm) like decapods, and to planktivorous fish. They eventually turn to predation on a variety of epibenthic invertebrates and demersal fish living at or on the bottom. It is also cannibalistic, a behavior it expresses even as a larva [34]. 1-group NEA cod is a major predator on 0-group cod when there is little capelin in the Barents Sea, and cannibalism on older cod increases with increasing size of the cod spawning stock [6]. Cannibalism is an investment in the ecological resilience of the population, because it shortcuts and increases the trophic flow of biomass to the spawning stock, which buffers effects of predation and fishing on adult cod.

The versatile trophic roles of NEA cod couple its population to an interspecific multitude of population systems that differ in geographic extension, which makes the Barents Sea a very complex habitat system. It interacts with the Norwegian Sea and other large systems situated between the Eurasian and North American continents. Drainage of freshwater from continental watersheds forces the haline circulation of the Arctic seas (**Figure 2**), which shapes the hydrology of the Arctic Mediterranean Ecosystem (AME). The river systems are habitats

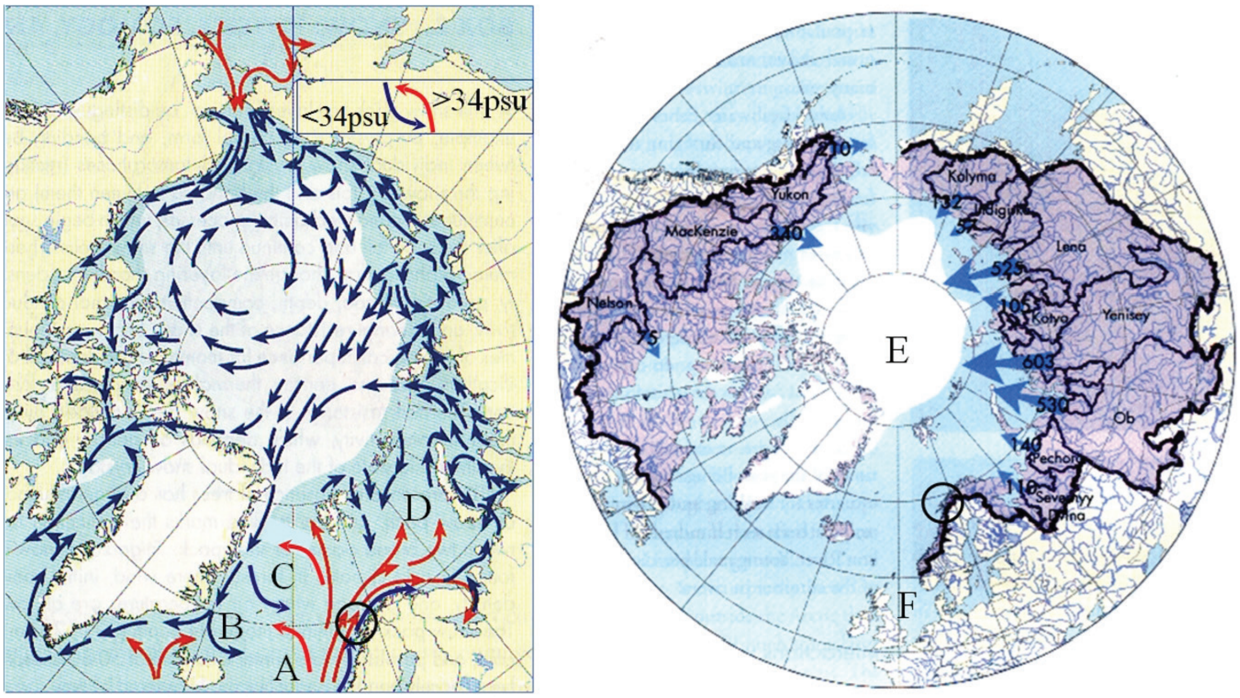

Figure 2. Polar projections of the Arctic Mediterranean Ecosystem, showing catchment areas for drainage of freshwater (right) and main circulation of sea surface water (left) distinguished by salinity (psu). (A) Norwegian Sea. (B) Icelandic Sea. (C) Greenland Sea. (D) Barents Sea. (E) Polar Sea. (F) North Sea. (Circle) Vestfjord, Lofoten Archipelago and offshore habitats of planktonic Northeast Arctic cod (*G. morhua*) (modified from imr.no (left) and caff.is (right)).

for diadromous fish that live parts of their life cycle in brackish and marine habitats. Several of them fall prey to Atlantic cod and other marine species within the AME. All are subject to ecological changes caused by hemispheric climate variability that causes bottom-up forcing of food webs based on the ecosystem's plankton production [42].

6. Variable female fecundity and egg mortality in NEA cod

The number of spawning NEA cod has varied much since World War II (**Figure 3**). Naval warfare prevented trawl fishing in the Barents Sea during 1940–1945, and shortage of fuel reduced traditional coastal fishing with hand-line, longline and gillnets. The reduced exploitation of NEA cod allowed the spawning stock biomass (SSB) to recover from prewar fishing mortality. After the war, technological development resulting from warfare gave rise to considerable modernizing of the international fishing fleet that commenced fishing for Atlantic cod in the Barents Sea and on banks along the Norwegian coast.

Post-war SSB declined to about 20% in 1958, not only because of legal landings of fish. International competition in the fishing industry, inadequate reporting of catches and landings, as well as weak public management bodies, opened for fishing with illegal trawls and unreported discarding of dead or dying juvenile fish. Increased public awareness about illegal practices, jurisdictional improvements and increased research on resources started about 1970. The political process gradually improved the national and international fisheries management, which to some extent explains how the NEA cod SSB recovered during the last decade. However, it may also result from global warming. Advection of warmer water by the Norwegian Atlantic Current (NAC) and the NCC has increased the area of benthic foraging habitats of NEA cod, which promotes the growth of adult cod and their production of eggs.

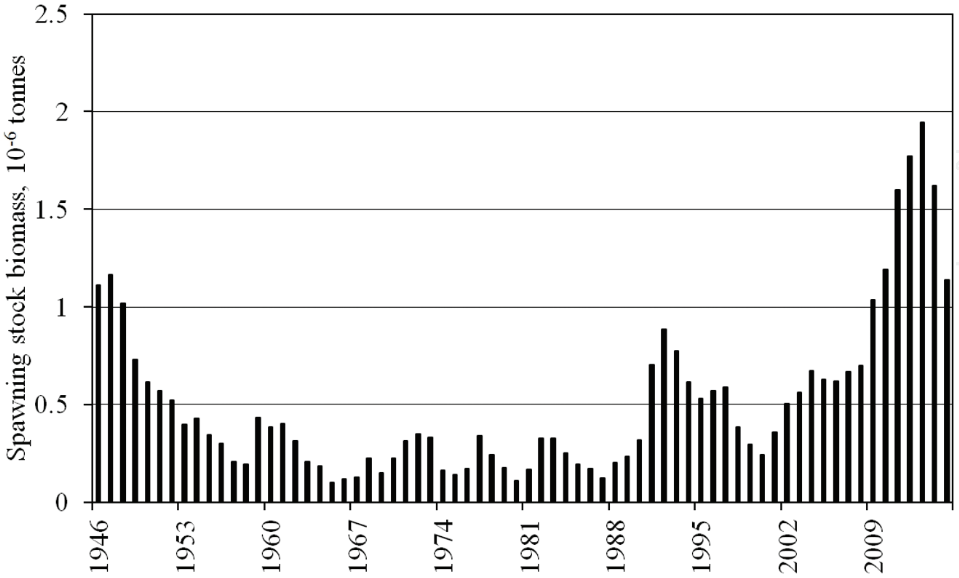

Figure 3. NEA cod (*G. morhua*) spawning stock biomass (tonnes) during 1946-2015 (data from ICES Arctic Fisheries Working Group 2015).

Atlantic cod is very fecund and iteroparous, spawning many eggs usually every year throughout its life, which perhaps could last >30 years before the introduction of industrial fishing. Then, some first-spawning NEA cod could be as old as 14 years, while they today mature at an age of 6–9 years. Cod in Icelandic waters, and the Irish and North Seas spawn at an earlier age and smaller size but have higher size-specific fecundity [43].

Old NEA cod tend to have more eggs than younger fish at the same size [44], but the egg production varies with amount and quality of food available between each spawning season. The amount of fat stored in the female liver during gonad development influences the quality of the eggs in terms of size and yolk content. Old cod grown large emerge in the spawning habitats earlier than smaller fish, and their larger eggs have maternal qualities that increase the potential for survival of their eggs and larvae. However, low sea temperatures may delay zooplankton reproduction and cause temporal mismatch between first-feeding cod larvae and their prey [45].

About 90% of the NEA cod eggs die before hatching [46], but little knowledge exists about egg predation by carnivorous zooplankton, planktivorous fish and seabirds. During peak spawning by NEA cod in Lofoten, an abundance of their eggs may float just underneath the sea surface film when there is no wind but disperse in the upper mixed layer when there is wind stress and turbulence. In any circumstance, predation on the enormous amount of eggs normally spawned by NEA cod in Lofoten may not be of major importance to the mortality of eggs and larvae and recruitment to the population.

Canadian scientists expressed concern that ultraviolet radiation (UVR) might harm survival in eggs of cod and *C. finmarchicus* in the Gulf of St. Lawrence. Laboratory experiments confirmed that exposure to UVR was harmful to both [47], but modeling suggests that events of UVR mortality in Lofoten have only minor direct influence on the overall mortality of cod eggs and larvae [48]. The modeling experiment applied hydrographical time series and UVR doses calculated from satellite data, ozone measurements, meteorological data and in situ diffuse extinction coefficients. Only when thin ozone layer and slack winds coincide with meager phytoplankton stocks would UVR induce mortality harmful to cod eggs and larvae in Lofoten.

Contrary to being detrimental, UVR in Lofoten possibly initiates ecological processes that protect eggs of cod and *C. finmarchicus*. In August-September of 1973–2000, 0-group abundance of NEA cod was positively correlated with average 11-day maximum doses of UVR in two periods earlier in the same year, one around 1 April (**Figure 4**) and one around 1 May. The first coincided with the spawning period of cod and the other when most larvae have normally hatched. Skreslet et al. [49] suggested that ultraviolet radiation (UVR) probably counteracted mortality caused by harmful marine bacteria. The rationale for the assumption was that bacteria frequently infest fertilized cod eggs incubated in cultures with natural seawater [50]. Infestation may start 2 hours after fertilization and cause eggs overgrown by various coccoid, rod-shaped, vibrioid and filamentous bacteria many days before hatching. To prevent mortality in cultures of marine fish eggs and larvae, the aquaculture industry now usually sterilizes seawater by UVR and ozone.

In Lofoten, large amounts of ovarian fluids from females and semen from males mix and probably provide a rich growth medium for bacteria naturally occurring in seawater. UVR

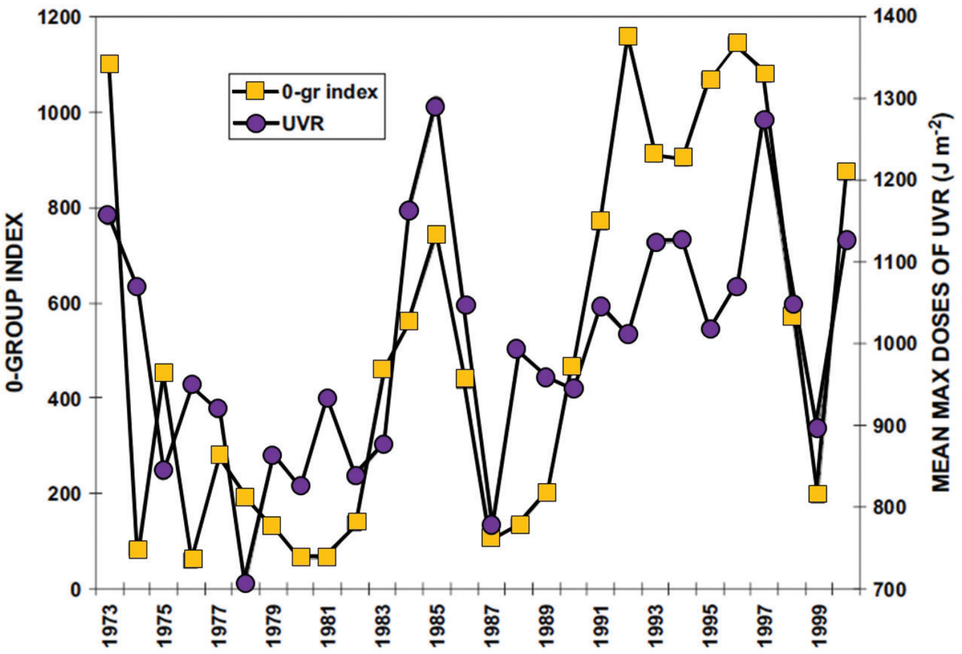

Figure 4. Interannual variation in 0-group abundance of NEA cod (*G. morhua*) in the Barents Sea during August-September and average maximum doses of UVR in Lofoten during April of the same year ($p = 0.01$) (modified from Ref. [49]).

may directly kill bacteria growing on cod eggs accumulating underneath the sea surface film during calm weather, but the eggs then risk detrimental effects of UVR exposure [47]. When there is wind, the eggs disperse in the upper mixed layer and escape lethal UVR because of its high extinction coefficient in coastal seawater. However, the eggs may experience brief doses as they circulate near the surface. Thus, the important effect of UVR may not be the duration of exposure but the dose that eggs are exposed to when close to the surface. The intensity of UVR in Lofoten depends on ozone layer thickness and local conditions regarding cloud cover and albedo caused by snow cover on the alpine landscape.

There is a possibility that high UVR doses do not effectively kill bacteria on large numbers of infested cod eggs, but rather disinfect the circulating seawater itself, killing germs that are potentially infectious. Another and more intriguing explanation is an indirect ecological relationship with cod eggs, caused by viruses that turn virulent by UVR and reproduce by lysis of bacteria [51].

7. Mortality and survival strategy of cod larvae

Fisheries biologists calculate the abundance of NEA cod that enter the exploited stock each year, by virtual population analysis (VPA) made on commercial catches. They are still juveniles, being 3-group cod in their third year after hatching. An early VPA [52] attempted to establish a theoretical relationship between the number of NEA cod eggs spawned per year and the subsequent abundance of recruits. Recruitment tended to decrease when the stock fecundity was $>10^{15}$ eggs, and the best recruitments in 1942–1968 occurred when the fecundity was lower (**Figure 5A**). Extremely low recruitment usually followed years with very low egg production, except for 1 year that resulted in the strongest recruitment of all. Details from the study show that the recruitment declined as the fecundity increased from 1942 to 1945 (**Figure 5B**). The recruitment increased after the war ended, even while fishing reduced the spawning stock biomass. The relationship may indicate that larvae were subject to density-dependent mortality, meaning that the number of larvae hatched from a large number of eggs exceeded the habitat's carrying capacity for production of prey.

Wiborg [15] reported a plankton sample taken in Lofoten in April 1930. It contained an extraordinary abundance of cod larvae dead before capture. Their body had decayed and only heads remained, indicating death at sea from starvation, probably showing a rare evidence of density-dependent mortality. Offspring from very fecund oviparous fish must in general tolerate extremely high rates of mortality depending on density-dependent regulatory mechanisms. Most of this mortality occurs during a critical pelagic larval stage, concentrated during a relatively short period in early development [53].

Not before 1977, did the US Northeast Fisheries Center organize MARMAP, an investigation that came forward with results that support Hjort's critical period concept. After 11 years of extensive data acquisition on the Georges Bank Morse [54] observed that their scientific production index of ≤6 mm long Atlantic cod larvae correlated positively with the abundance of age 1 recruits next year (**Figure 6**). Newly hatched cod larvae were slightly longer than 4 mm, which means that the establishment of cod year-class strength during 1997–1987 occurred during the first weeks of life after hatching.

The genome of cod larvae has evolved some strategic capacities that optimize their ability to locate, observe and attack prey. The yolk-sac larva is rather passive in the first days after hatching. At 5°C, it may each minute make about five short bursts of swimming at a speed of 5 cm min^{-1} [55].

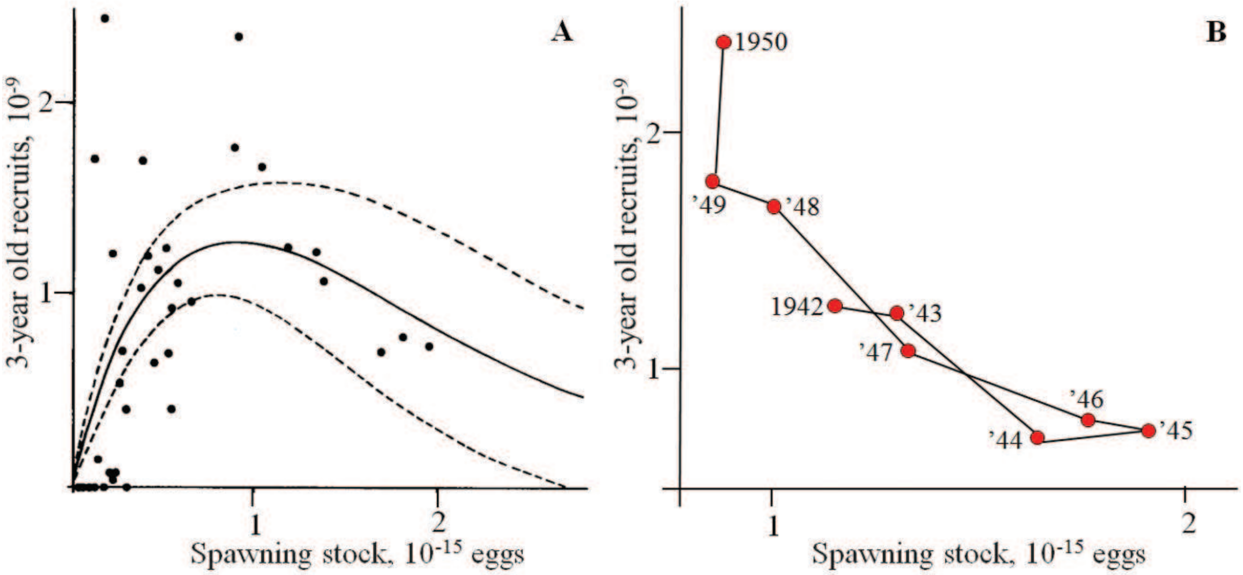

Figure 5. Ricker stock and recruitment equation fitted to data for NEA cod (*G. morhua*) (1942–1968). Number of 3-year-old recruits of NEA cod plotted against total stock fecundity. (A) Stock-recruitment curve with 95% confidence limits. (B) Details from 1942 to 1950 (extracted from Garrod and Jones [52] and presented by permission of the authors).

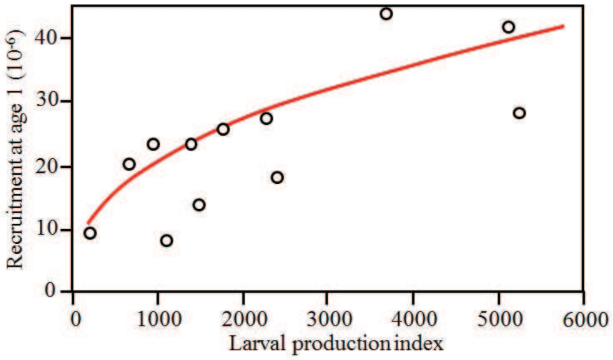

Figure 6. Production index of ≤6 mm Atlantic cod larvae (*G. morhua*) on Georges Bank 1977–1987 related to subsequent recruitment at age 1 (redrawn from Ref. [54]).

The swimming activity culminated 6 days after hatching, 1–2 days before the yolk reserves were exhausted. Two to three weeks after hatching the larva had developed a saltatory search pattern. Starved larvae swam in bursts for 0.2 seconds, stopping to reposition for 0.8 seconds by using their pectoral fins, while larvae having fed on nauplii lowered both duration and frequency of their burst swimming [56]. At encounters with prey, the larva stopped and positioned itself while curling its tail for the swift attack and when successful sucking the prey into its mouth cavity. The larvae accepted nauplii 120–360 μm long but selected 200 μm when prey densities >50 l^{-1}. In a natural environment with few copepod nauplii, the cod larvae may forage on small prey like tintinnids and oligotrich ciliates but then experience slow growth and lower survival rates [16].

Swarming is a normal survival behavior in zooplankton [57] but also provides options for predators. The abundance of cod larvae and nauplii of *C. finmarchicus* in Lofoten may correlate positively when the sea is calm (**Figure 7**). The cod larvae probably navigate successfully in marginal gradients of prey in the periphery of swarms or patches. The capacity results from bilateral vision, which makes it statistically probable that the next sighting of prey occurs in the direction of higher prey abundance. When the larva succeeds to see prey at both sides after each attack, it is likely to remain in a position with optimal prey density for some time.

Newly hatched nauplii in stage NI have slow locomotion in the viscous medium of cold seawater. They are small and hardly sink according to Stokes' law. Every ecdysis into a higher stage of development increases the locomotion and capacity to swarm. Onset of turbulence probably dissolves patches where nauplii and cod larvae occur together [58] but offer other options. Wind mixing forces micro-turbulence that moves nauplii toward cod larvae in ways that increases the rate of encounters between cod larvae and their prey. Microturbulence at winds stronger than 4 m s^{-1} even exceeds contact rates obtained by swimming [59].

Strong and steady wind causes small and neutrally buoyant particles to disperse, while particles with other properties may be subject to sorting by Langmuir circulation that generates vortices aligned with the wind [60]. Every vortice rotates opposite of the next, which causes bands of upwelling separated by bands where surface water sinks and causes accumulation of foam and floating debris (**Figure 8**). NEA cod eggs are positively buoyant in the upper mixed layer in Lofoten and possibly accumulate at the surface below the flotsam. Negatively phototactic organisms perhaps accumulate in up-welling bands during daytime. During a period of

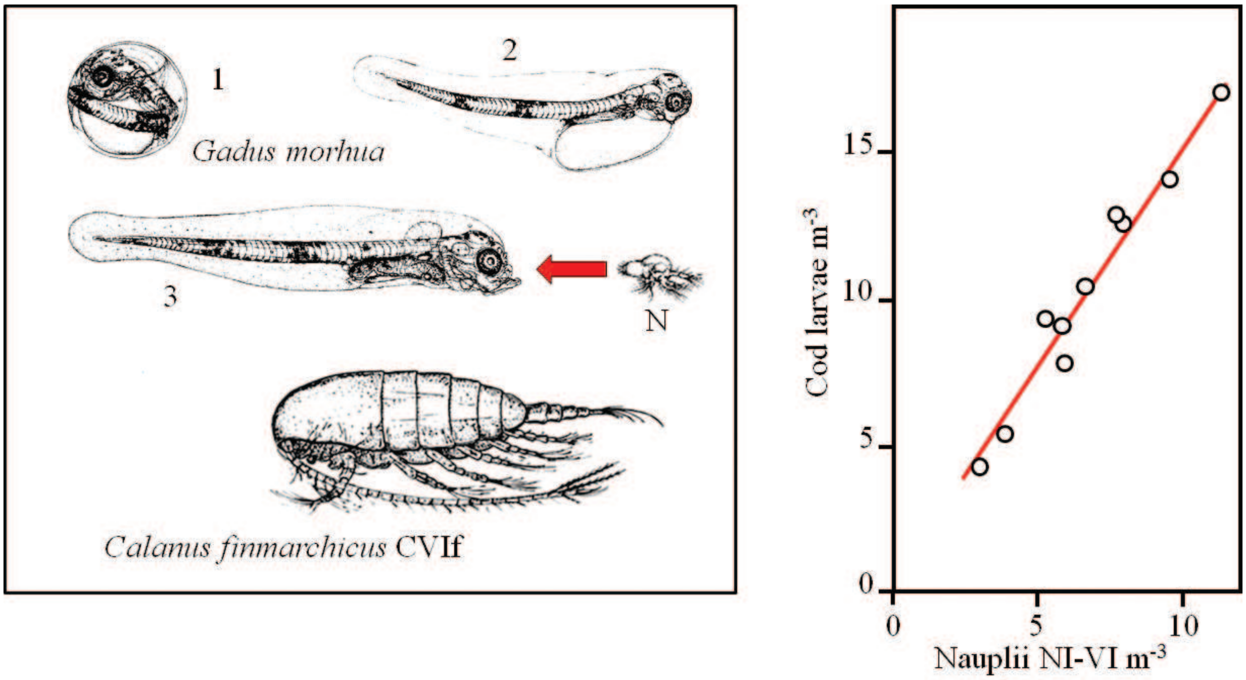

Figure 7. Planktonic Atlantic cod (*G. morhua*): fully developed embryo (1), newly hatched larva with yolk sac (2) and larva with fully developed digestive system (3). Female (CVIf) and nauplius (N) of *C. finmarchicus* (left). (Right) Correlation ($p = 0.01$) between abundance of cod larvae (total length >4.8 mm) and nauplius I–VI of *C. finmarchicus* in Lofoten (graph redrawn from Ref. [58]).

moderate gale (15 m s^{-1}) decreasing to fresh breeze (9 m s^{-1}) during sampling at noon, abundance of cod larvae in Lofoten correlated positively with the abundance of female *C. finmarchicus* [58]. The copepod was possibly foraging on phytoplankton and producing eggs, while cod larvae foraged on nauplii. The micro-turbulence was possibly optimal in a kind of 'bottle neck' between two vortices where upwelling occurred (**Figure 8**), allowing cod larvae

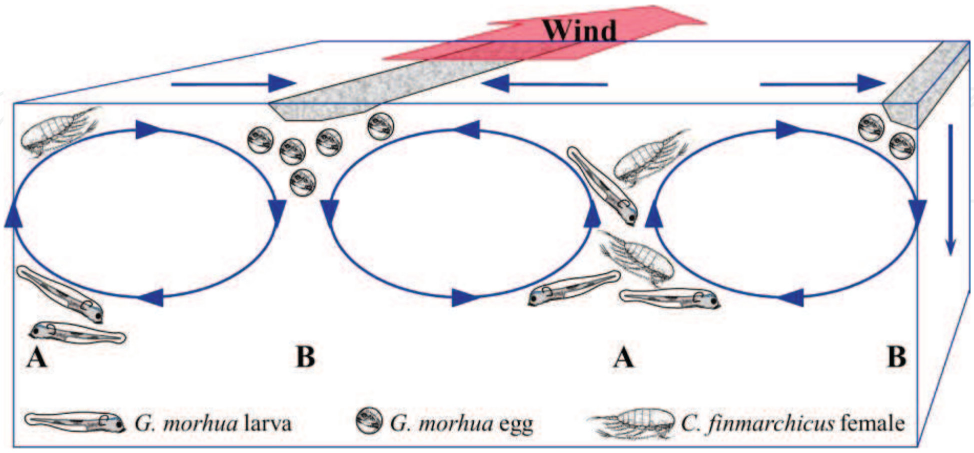

Figure 8. Langmuir circulation according to Ref. [60] showing how NEA cod larvae (*G. morhua*) possibly correlate positively with female *C. finmarchicus* during strong wind at noon in Lofoten, supposedly due to (A) up-welling and negative phototaxis [58]. Buoyant eggs of NEA cod possibly accumulate under stripes of flotsam floating on the surface where down-welling occurs (B). Nauplii of *C. finmarchicus* and microalgae (not shown) disperse in the mixed layer.

to change tactics from stalking to ambush on prey. However, in calming weather, patches with cod larvae possibly contain spawning females of *C. finmarchicus* producing eggs developing into feasible prey for resumed stalking.

8. History of variable NEA cod recruitment

The number of NEA cod that enter fisheries as 3-year old juveniles (3-group cod) varied from 1946 to 2015, showing a shift in abundance after 1973 (**Figure 9**). For the next 42 years, there were only four year-classes with more than 1 billion 3-group recruits. During the 28 preceding years, 14 year-classes were stronger than 1 billion. Seven were stronger than 1.5 billion, which has not happened after 1973. Taking the entire period, there seems to be an inverse relationship between recruitment and SSB (**Figure 3**). However, the increase in SSB since 1990 seems to have improved and stabilized the recruitment at a level that on average has exceeded 0.5 billion 3-group cod, compared with the previous period when recruitment was very weak in many years during 1968–1992. Before, a series of years with mostly strong recruitment occurred in 1956–1967, despite the SSB was in general low in the period 1953–1964. Three extremely strong year-classes, exceeding 2 billion 3-gr cod, were recruited to the fisheries in 1951–1953 (**Figure 9**), following reproduction by comparatively strong SSB in 1948-50 (**Figure 5**).

Increase in stock fecundity of NEA cod in 1942-45 (**Figure 5**) caused comparably low stock recruitment in the first post-war years (**Figure 9**), possibly resulting from density-dependent mortality. It indicates that the abundance of cod larvae exceeded the carrying capacity of their habitats, i.e., the production of copepod nauplii. By 1948, the spawning stock fecundity had decreased to ~10^{-15} eggs (**Figure 5**) which reduced density-dependent mortality and possibly allowed the >2 × 10^9 recruits of 3-gr cod in 1951–1953 (**Figure 9**). The SSB and the spawning

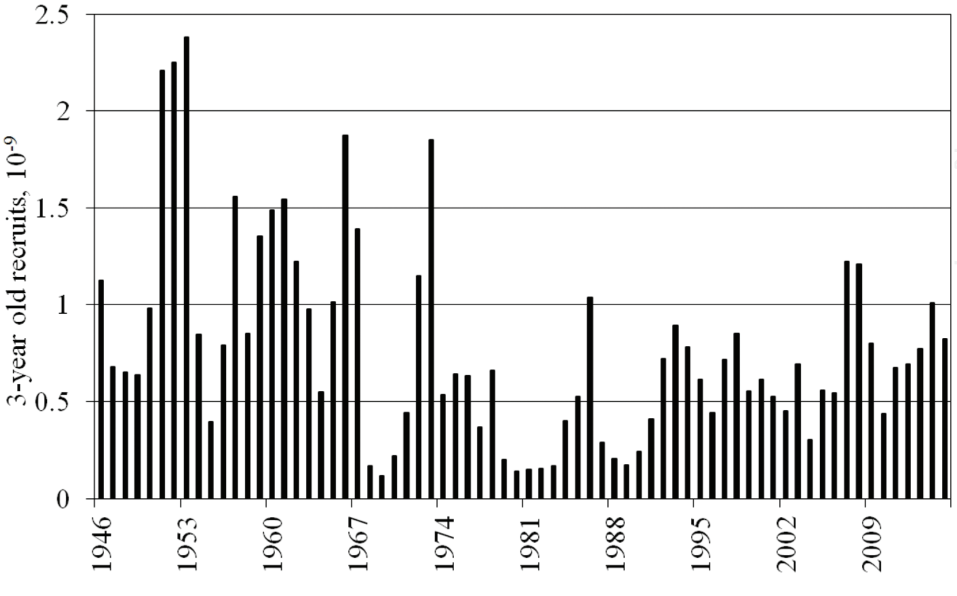

Figure 9. Abundance of 3-group Northeast Arctic cod (*G. morhua*) in the Barents Sea (1946–2015) (data from ICES Arctic Fisheries Working Group 2015).

stock fecundity continued to decrease (**Figures 3** and **5**) but still resulted in strong recruitment until 1967 and the last year-class that exceeded 1.5 billion 3-group cod in 1973 (**Figure 9**). In all following years, no comparable recruitment has occurred.

The causal relationships behind differences between NEA cod recruitment in 1946–1973 and 1974–2015 (**Figure 9**) are obscure and certainly complex. They call for an approach based on multiple variables [61], including variability in natural processes, socio-economic relationships regarding exploitation and other anthropogenic influences. It is possible that the historic maximum in SSB at the end of the period (**Figure 3**) results from a combination of successful management of the NEA cod stock and global climate change.

9. Plankton links cod recruitment to global climate?

Klyashtorin and Lyubushin [62] drew attention to how many fish populations vary with the annual global temperature anomaly (global dT) which is based on air temperature at the surface of the planet. Global dT is characterized by a sinusoidal 60-year cycle that is in phase with sea temperature in the Barents Sea observed in the Kola meridian. Recruitment to the NEA cod stock lagged about a decade after both global dT and Barents Sea temperatures. Global dT was also in phase with annual North Atlantic Oscillation (NAO) from the 1930s to the early 2000s. NAO represents the difference in barometric pressure between the Azores and Iceland. The index is positive when the difference is higher than the average and negative when lower.

The abundance of *C. finmarchicus* immigrating to a fjord habitat near Lofoten during September-October correlated positively with average NAO in March-July (**Figure 10**), resulting from variable precipitation in Norwegian alpine landscapes [42]. It forces meltwater discharge from rivers to the NCC on the mid-Norwegian shelf during May-August. The discharge initiates vertical turbulence in the frontal jet current that marks the transition between NCC and offshore shelf waters (**Figure 11**). Inorganic nutrients brought to the euphotic zone generate primary production that makes female *C. finmarchicus* ripen batches of eggs repeatedly in June-August. The species spawns vigorously during June-July in the marginally stratified frontal zone of the NCC [63]. The abundance of nauplii correlates negatively with salinity along the NCC jet [49, 64], resulting from freshwater discharge stimulating biological production. The new generation drifts northwards, some of it into the Vestfjord during autumn [65] when freshwater outflow decreases and the NCC obtains a landward vector due to decreased stability [66].

The outer part of Vestfjord is wide and has a sill about 200 m deep between the mainland and the Lofoten Islands (**Figure 11**). A series of >600 m deep basins inside the sill serve as the wintering habitat for a large wintering stock of *C. finmarchicus*. The copepods mature and mate after midwinter, and the females produce nauplii while transported by a seaward current running along the south shores of Lofoten [67, 68]. NEA cod traditionally spawn at 5–6°C in a gradient between this current and warmer water underneath.

The reported abundance of *C. finmarchicus* wintering in a side fjord (**Figure 10**) did not correlate significantly with 0-group NEA cod [49]. Observations in 1997–1998 revealed that *Calanus helgolandicus* and *Calanus glacialis* contaminated the sampled time series. Although

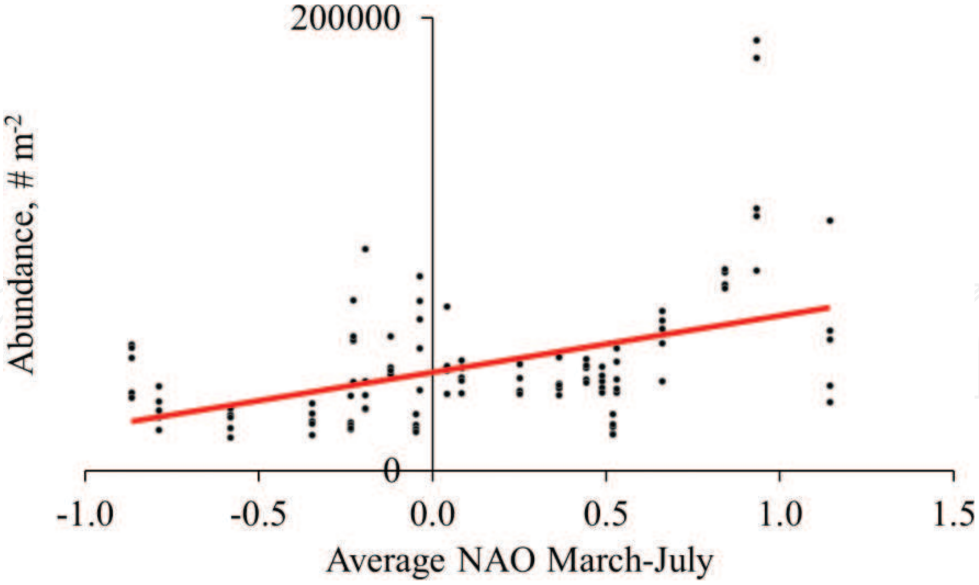

Figure 10. Abundance of *C. finmarchicus* during October as the function of North Atlantic Oscillation (NAO) in March-July of the same year, sampled 1983–2005 in 382 m deep fjord basin storing Atlantic water advected from the Norwegian Sea [42].

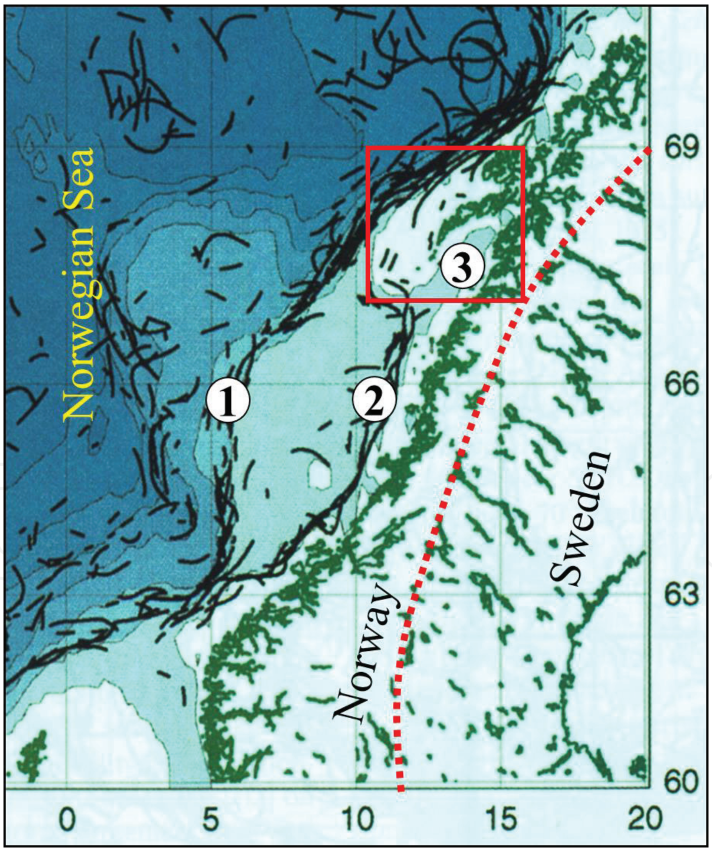

Figure 11. Norwegian Sea shelf break jet (1) and NCC jet (2) as indicated by Argo drifter tracks showing surface velocities >40 cm s^{-1} (from Ref. [64]). (3) Vestfjord wintering habitat for *C. finmarchicus*. (Rectangle) Habitat for joint reproduction of NEA cod and *C. finmarchicus* in April. (Stippling) Watershed between Norway and Sweden. (Right margin scale) Latitude. (Bottom margin scale) Longitude.

C. finmarchicus may usually dominate over other *Calanus* spp. in the time series, genomic work on *Calanus* spp. in Norway shows that *C. glacialis* in fjords may be more abundant than previously experienced [27]. The interannual variability in abundance of *C. glacialis* and *C. helgolandicus* is unknown. At present practical considerations and costs of genomic work prevent samples of *C. finmarchicus* to be cleaned from contamination by other *Calanus* spp. Thus, proportionality between abundance of *C. finmarchicus* in Vestfjord and survival rate of NEA cod larvae in Lofoten remains a missing part in the complete ecological puzzle about climate variability and stock recruitment.

10. The role of freshwater discharge in marine fish reproduction

Helland-Hansen and Nansen [69] were among Johan Hjort's contemporary colleagues in oceanography and the first to discuss whether interannual differences in marine fish recruitment resulted from climate variability and freshwater discharge. They observed that 1-year-old sprat (*Sprattus sprattus*) and herring (*C. harengus*) were abundant 1 and 2 years after rainy years, respectively. The interesting proposal did not materialize in comprehensive empirical research, not before the International Geosphere-Biosphere Program in Canada (1964–1974) addressed effects of St. Lawrence River discharge on marine ecology in the Gulf of St. Lawrence.

A paper by Sutcliffe [70] initiated a series of publications that documented landings of fish and shellfish from the Gulf of St. Lawrence to vary with freshwater discharge, most correlations being positive while some negative. For a period after 1949, a modeled survival index for NEA cod correlated positively with natural meltwater discharge from rivers along the Norwegian coastline [71]. The correlation was highest with run-off from Møre (**Figure 12**), a region south of the mid-Norwegian shelf (cf. **Figure 11**). It broke down after 1960, possibly because increasing fishing

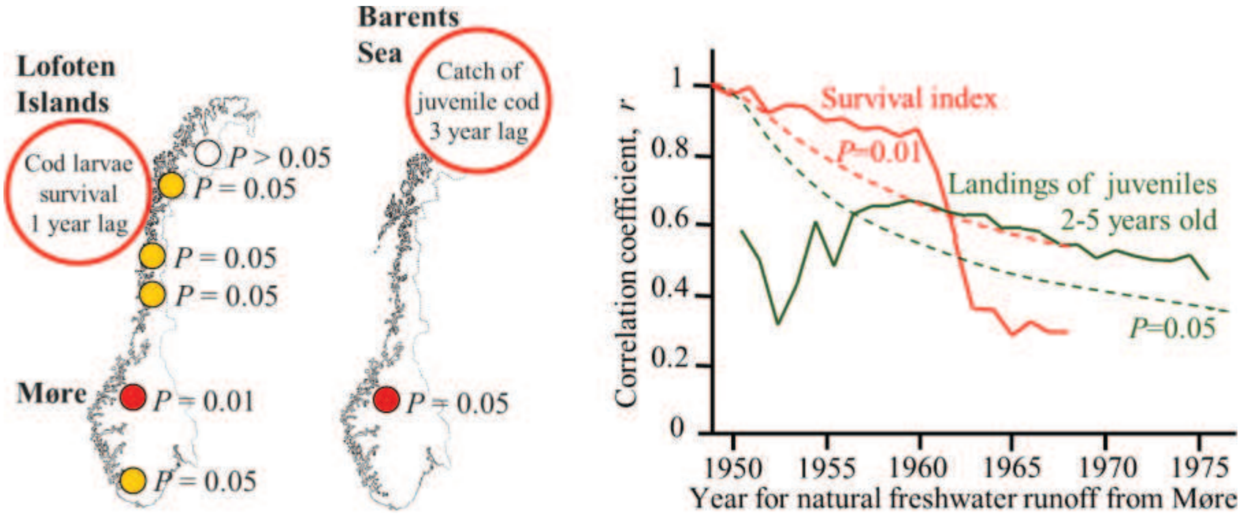

Figure 12. Maps of Norway showing positions (dots) of locations for 30 days of maximum freshwater discharge correlating positively with survival of NEA cod larvae (*G. morhua*) 1 year later and Norwegian landings of juvenile NEA cod 2–5 years old from the southern Barents Sea 3 years later. Graph shows stepwise calculation of correlation coefficients with population variables from the NEA cod stock as the function of freshwater discharge at Møre. (Stippled curves) Critical values for *p* (redrawn from [71, 72]).

efforts decreased the stock fecundity below 10^{15} eggs (**Figure 5**). It is possible that decreasing SSB (**Figure 3**) eventually obliterated density-dependent mortality of cod larvae as a forcing factor in the causal relationship between larval prey abundance and recruitment to the exploited stock.

Positive correlation observed between natural vernal discharge and landings of juvenile NEA cod to ports on the Norwegian Barents Sea coast [72] existed until 1975 (**Figure 12**). Occasional recruitment stronger than 1.5 billion 3-group cod occurred until 1973 (**Figure 9**), which has never happened again. After 1975, river flow used in the correlation had regulated flow due to hydroelectric production, which obstructed options for continued testing of correlations.

Time lags in the Canadian and Norwegian correlations with freshwater discharge indicate causal relationships occurring on extensive spatial and temporal scales, exemplified by Steven [73]. He summarized research on plankton ecology in the Canadian IBP, stating that entrainment in the St. Lawrence Estuary fed inorganic nutrients into a geostrophic brackish plume flowing along the southern coast. It stimulated primary production >100 mgC m^{-2} h^{-1} from April to July over several hundreds of km downstream, which resulted in zooplankton production with biomass maxima 600–700 km away. Estimated time for particles to drift from the estuary to the Cabot Strait where the Gulf meets the open Atlantic was 80–90 days.

The phenology in plankton development along the Norwegian coast probably shows similar scales in time and space. Freshwater outflow from any section of the coast probably stimulates primary production in the marginal frontal zone of NCC and reproduction of *C. finmarchicus* during summer [49]. Increased shear stress between NCC water and the underlying salter layer results in lateral advection of a thin layer transporting coastal plankton offshore into the Norwegian Sea [74, 75]. Helland Hansen and Nansen [69] suggested that the seaward vector changes to landward advection during autumn, later confirmed by physical modeling [66]. Thus, *C. finmarchicus* that starts ontogeny in coastal habitats may continue growing in the Norwegian Sea and return to complete the life cycle in Norwegian coastal waters farther north.

During autumn, advection of Atlantic water by the NAC transports zooplankton from the deep Norwegian Sea to the shallow Barents Sea, to be foraged by pelagic 0-group cod. Few cod larvae from Lofoten are transported into the Norwegian Sea [76], which may be different for fractions hatched in coastal habitats farther south in Norway. The fate may not be detrimental to this fraction, considering that they may benefit from rich zooplankton production in the central Norwegian Sea [77].

11. Conceptual model for reproduction ecology of NEA cod

More than one hundred years of information from research on Atlantic cod make it possible to suggest a conceptual model for the reproduction and recruitment ecology of NEA cod (**Figure 13**). Ecological premises for successful first feeding of NEA cod occur in Year 0, 1 year in advance of the actual spawning. Then, a spring generation of *C. finmarchicus* produced in the North Sea [78], and in Norwegian fjords [75, 79], migrates onto the mid-Norwegian shelf in early summer. Their food source is planktonic primary production that occurs along the NCC jet (**Figure 11**). It continues through summer like a chemostat process, depending on

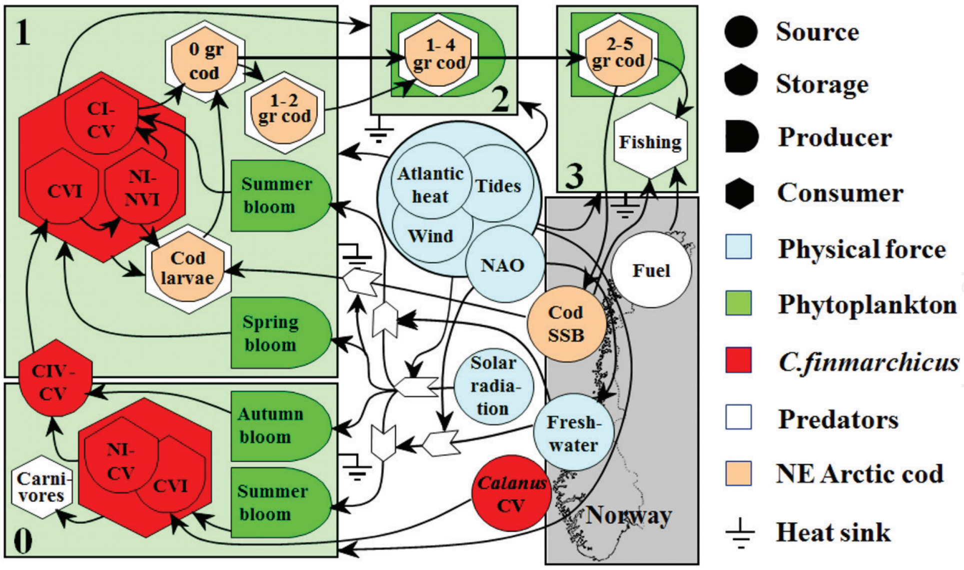

Figure 13. Transfer of trophic energy within and between population systems of *C. finmarchicus* and NEA cod (*G. morhua*) as influenced by sources of forcing (circles). (Year 0) Primary production on the mid-Norwegian shelf and growth of summer generation reproduced by source generation of *C. finmarchicus* imported from the North Sea. (Year 1) Spawning of NEA cod in Lofoten during spring bloom in April and reproduction of *C. finmarchicus* having wintered in the Vestfjord, followed by export of plankton community from the Norwegian to the Barents Sea and cannibalism on 0-gr cod. (Years 2–3) Growth of juvenile NEA cod, predation by older juveniles and recruitment to exploited stock three years after initial forcing by vernal freshwater discharge. (Cod SSB) Spawning stock of cod >6 years old. (NI–NVI) Nauplii. (CI–CVI) copepodids (Figure modified from [65, 74, 85]) (symbols: adopted from Odum [39]).

the strength and duration of vernal freshwater discharge from rivers. NAO and precipitation over Norway in March-July regulate freshwater drainage from alpine landscapes in May–August, which initiates extensive eddy formation and fluxes of inorganic nutrients to the euphotic zone of the NCC frontal system. *C. finmarchicus* reproduces in this habitat increasingly with declining surface salinity, but the progeny does not remain in the NCC summer habitat [49]. The new generation is probably subject to flushing onto the mid-Norwegian shelf where it grows into copepodid stages CIV–CV [80], before being transported by advection into the Vestfjord for overwintering (**Figure 11**).

During Year 1 in the Vestfjord and its numerous branches (**Figure 13**), the spring bloom in April occurs as a batch culture, assimilating nutrients made available by vertical convection to depths of 150–200 m by the end of winter. Within a couple of weeks, microalgae consume nutrients accumulated in the euphotic zone. Female *C. finmarchicus* (CVI) forage on the biomass and produce eggs and nauplii (NI–NVI) that promote survival and growth of cod larvae as they are transported by the NCC along the narrow shelf to the north of Lofoten [76]. They forage on the summer production of plankton that results when plumes of brackish water from fjords export phytoplankton and zooplankton that continue reproduction on the shelf [81]. During this period, the cod larvae metamorphose into 0-group juveniles that continue feeding on zooplankton. Some suffer cannibalism from older juveniles when other prey is lacking [6]. Cannibalism varies in the following years, finally adjusting the number of cod recruiting as 3-group juveniles to fisheries statistics. However, fast-growing 2-group as well as slow-growing 4–5 group cod may recruit simultaneously in real fisheries.

Figure 13 is a very simplified presentation of what happens in nature. Tidal and wind mixing of seawater forces turbulent diffusion of heat and inorganic nutrients, which directly or indirectly regulate growth and biological productivity in a multitude of organisms from microbes to fish. The spectrum of solar radiation ranges from infrared (IR) to photosynthetic active radiation (PAR) and UVR, all being coupled to recruitment of NEA cod in various ways.

Compared with coastal and fjord cod, the NEA cod population system is particular in terms of large spatial and temporal life history scales. Its genomic constitution is not compatible with vertical migration near sea surface because of restricted swim-bladder functions [11]. It is possibly the cause for juveniles to leave epipelagic habitats after completion of full metamorphosis at a size of ~6 cm, and later in life preferably migrate horizontally within an extensive mesopelagic habitat.

Successful reproduction and recruitment to exploited cod stocks depend on the fate of the individual under influence of many ecological variables. The combination of modern fishing and management of Atlantic cod is a major anthropogenic variable that regulates spawning stocks. Out-fished stocks produce few eggs with little chance of causing stock recovery, which is evident in North American waters where populations show few signs of recovery. Adequate management of NEA cod made it recover from overfishing before 1990 to reaching a historic maximum after 2010 (**Figure 3**). Inadequate management may explain decline in stocks of NC cod, which at present is enigmatic, and require increased scientific attention to recover and improve stocks. However, it may be futile if unfortunate anthropogenic manipulation of climate and habitat systems remains unchecked.

12. Assessment of anthropogenic production of hydropower

Seasonal variability in run-off from land is typical of coastal regions, interacting with many marine habitats and population systems globally. Marine systems in the northern hemisphere respond seasonally to accumulation of snow on land during winter, followed by snow-thaw during spring and early summer. The quest for electric energy has caused construction of large power plants of great socio-economic importance. The production of electricity occurs the year-round which causes freshwater discharge to increase during winter, at the expense of natural vernal outflow from rivers. In Norway for the period 1969-73, the average peak flood in May was reduced to 52% in the most developed region, while the average reduction for all regions was 16% [82].

Human regulation of freshwater flow on the marine environment gives very enigmatic effects, and there is little empirical evidence available for solving the problem. However, the understanding of processes involved is sufficient for building and testing of numerical models. Myksvoll et al. [83] modeled a fjord system subject to regulated discharge from a hydroelectric plant. They observed that larger proportions of fertilized eggs drifted out of the fjord than during natural winter discharge, suggesting that decreased retention of eggs in regulated fjords may impair recruitment of juveniles. Taking into account that the national capacity for storage of freshwater in reservoirs increased from 11% in 1972 to 21.2% in 2009, the observed decline in populations of coastal and fjord cod along the Norwegian coast may be a result.

After completion of the Canadian IBP in the Gulf of St. Lawrence, Steven [73] stated ‘It seems safe to conclude that the force of the river flow, which depends on the amount of fresh water discharged, determines the amount of nutrients brought to the surface and carried seawards into the Gulf and this in turn determines the size of the annual crops of phytoplankton and zooplankton, on which depend survival and growth of the young stages of fish and other animals at higher trophic levels.’ He and other oceanographers [84, 85] argued on scientific evidence that hydroelectric production with seasonal regulation of river flow may reduce biological production and ecological carrying capacity for commercial exploitation of marine resources.

Concern about effects of regulated river flow raised discussions in dedicated scientific meetings with international participants [86, 87]. Both these meetings and a committee established by the Government of Canada [88] concluded that the concern was relevant, but the scientific knowledge was insufficient to reach conclusions. A review by Drinkwater and Frank [89] concluded that decline in some coastal fisheries with an overall negative impact on the biota is generally associated with reductions in freshwater flow. However, none of these assessments took into full account the complexity and scales of time and space of ecological processes involved in reproduction and growth of marine resources.

13. Trophodynamic framework of the Arctic Mediterranean Ecosystem

The fluxes of energy and biomass in true marine ecosystems occur within food webs of basin-scale prototypes large enough to conserve energy produced by the system’s primary production. Bucklin et al. [90] proposed that *C. finmarchicus* has established a population system contained in the Northeast Atlantic, genetically different from two other populations, one south of Iceland and one in the western North Atlantic. It circulates anticlockwise in the Norwegian Sea, between the coasts of Norway, East Greenland and northern Iceland. However, it also occupies fjords and coastal waters in Norway and parts of the North Sea [78] and exports biomass into the Barents and Polar Seas by advection of Atlantic water (**Figure 2**). *C. hyperboreus* and *C. glacialis* have population systems associated with less-saline polar water (<34 psu). Carnivorous macrozooplankton and planktivorous fish including herring, capelin and 0-group Atlantic cod that feed on *Calanus* spp. disperse assimilated biomass over extensive time and space scales within the Arctic Mediterranean Ecosystem (**Figure 1**), by a food web that even includes diadromous populations. With 90% reduction of energy by entropy on each trophic level, <1% of the annual marine primary production would remain as biomass on trophic levels higher than *Calanus* spp. Thus, the Arctic Mediterranean Ecosystem seems to be the prototype of a closed ecosystem that circulates and conserves most of the biogenic energy fluxes within its food web. Hemispheric climate variability as indicated by tropospheric NAO and stratospheric Arctic Oscillation [42] seems to force bottom-up control of biological production from primary production to the trophic levels of Atlantic cod (**Figure 13**). Roles of seabirds, seals, whales and human fisheries exert top-down control, which also NEA cod older than 0-group do by being cannibalistic. Understanding the intricacies of marine ecosystem control requires methods that are now at hand.

Sophisticated and very promising modeling that couples geophysical and hydro-chemical parameters in the Norwegian Sea computes production of microalgae and reproduction and growth of *C. finmarchicus* in neritic and oceanic habitats [80, 81, 91]. However, model results based on average seasonal run-off from unregulated rivers in 1931–1960 [91] do obviously not represent interannual variability in plankton production in Norwegian shelf waters today.

Comprehensive hydroelectric development in Norway started decades before World War II and escalated during post-war decades [82] until most large rivers were regulated by the end of the previous century. Hydrological data that summarize discharge from undeveloped as well as regulated catchment areas are in general unavailable and hard to get for scientific purposes. Thus, the full potential for the scientific use of existing high-quality geophysical and ecological models depends on future cooperation between national water resource authorities, academic institutions and managers of marine resources.

Progress in marine ecological science aimed at understanding how complex basin-scale marine ecosystems respond on extensive time scales to global climate variability requires conceptual closing of gaps between plankton ecology and fisheries research [92]. Interdisciplinary nesting of geophysical and plankton production models with multispecies population models under development by fisheries biologists would pay adequate tribute to pioneering scientific generalists like Johan Hjort and his contemporary oceanographers.

14. Conclusions on planktonic forcing of Atlantic cod recruitment

Empirical US research on Georges Bank cod in 1977–1987 observed positive correlation between abundance of cod larvae and recruitment to the stock of juvenile Atlantic cod in the following year. Larvae growing from 4 mm length to 6 mm in a couple of weeks had evidently finished the critical period of first feeding, which supports Johan Hjort’s classical critical period concept in fisheries science.

Seasonal river flow from eastern Canada correlated with landings of fish from the Gulf of St. Lawrence. Similarly, interannual variability in natural meltwater discharge from Norway correlated positively with abundance of recruits to the NEA cod stock for decades after World War II. Time lags suggested that river flow initiated geophysical forcing of planktonic primary and secondary production in mid-Norwegian shelf waters during summer, on spatial and temporal scales similar to production forced by St. Lawrence River flow. This probably explains trophic coupling of produced copepod biomass to food chains of first-feeding larvae of NEA cod 1 year later.

In the spawning habitats of NEA cod, stock fecundity and effects of UVR on pathological microbes probably control hatching success and abundance of first-feeding cod larvae. Abundance of preferred prey and changes in ambient physical processes influence patchiness, prey gradients and encounters with prey, which make cod larvae shift between tactics for stalking and ambush. Successful foraging on phytoplankton and copepod nauplii during the first weeks after hatching promotes growth to a size >6 mm which probably makes cod larvae escape the critical period of extreme mortality. Mortality at lower rates occurs during the following months of meroplanktonic growth until the end of metamorphosis at a size of ~6 cm. By then, advection of coastal water has transported the 0-group to their juvenile habitat in the Barents Sea.

Extensive industrial fishing of Atlantic cod and modern stock management regulations in our times exert strong influence on spawning stock size and fecundity, which influences egg production and abundance of first-feeding cod larvae. The density of their prey results from local stock abundance of reproducing female copepods emerging from their overwintering habitats. Their abundance results from biological productivity in the previous summer and climate forcing exerted by a range of energy sources, including effects of natural and regulated freshwater outflow.

The population system of NEA cod and the marine food web of the Arctic Mediterranean Ecosystem are no longer pristine. It was in the times of Johan Hjort, before World War I, when fishing for cod relied on artisan methods and climate maintained a natural hydrological cycle. The population system was probably close to pristine for some years after World War II when NEA cod had recovered after prewar trawling efforts. River flow to the mid-Norwegian shelf was mostly natural, which probably caused its planktonic production to be richer and support recruitment of many year-classes of NEA cod stronger than 10^9 juveniles until 1973. After that, reduced recruitment coincided with technological development in fisheries and production of hydroelectric energy.

Johan Hjort's critical period concept is still valid but can probably only predict recruitment to pristine fish stocks. It may not be useful in extensively regulated modern management of highly industrialized fisheries, but is still a relevant theory in general ichthyoplankton science.

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