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Half a century of high-latitude fisheries oceanography research on the "recruitment problem" in Northeast Arctic cod (*Gadus morhua*)

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Predicting recruitment in a reliable fashion is a great challenge within operational fisheries advice. Here, we consulted the unique but under-communicated IMR Cod Larva Project (1975–1990), its spin-offs, placed in an international era of advancements over the last 50 years to glance into the future. Few initiatives of this kind have applied such extensive research approaches, spanning from laboratory, mesocosm, tank, and field studies to process modelling. The "critical period" concept appeared misleading, covering months rather than days of the early life history stages (ELHS) of Northeast Arctic cod. Larval feeding success was strongly modified by improved encounter rates from wind-induced turbulence. In addition, the following maternal effect studies evidenced that the dynamics of stock demography prior to spawning should be upheld to promote recruitment success. Although we now have lower-trophic level models as well as ELHS individual-based models, such models are still insufficiently reflecting the needed spatiotemporal resolution. The same problem applies to climate/circulation models. Nevertheless, this long-lasting research has significantly improved the mechanistic understanding of ELHS dynamics but also of the more predictable adult reproductive parameters. Based on a "to-list list," we suggest research avenues that should be pursued to further improve our ability predicting recruitment strength in marine fish stocks.

Keywords: climate, egg survey, eggs, fecundity, larvae, marine history, maternal effects, plankton, turbulence, year class.

1 Rationale behind exploring recruitment mechanisms

Annual fluctuations of European fisheries have historically resulted in major economic impacts, and the need to better understand factors driving these fluctuations led to the establishment of The International Council for the Exploration of the Sea (ICES) at the beginning of the 20th century (Schwach, 2002). Johan Hjort, who was in the international group of the founders, primarily focused on the adult stages caught in the fishery, and from measuring variability in the strength of year classes, he hypothesized that this strength was set very early in life, corresponding to the first-feeding stage (Hjort, 1914). Nonetheless, it took 60 years before Norwegian colleagues established in-depth studies of the ideas of Hjort's seminal work.

In these respects, the recruitment-related findings from the unique Cod Larva Project (CLP 1975–1990) (Figure 1) stand out as particularly important but seem largely undercommunicated as the regular outlet was different types of documents. In addition to newer and older topical articles, we reviewed earlier progress and final reports (to grant providers) and ICES Council Meeting (CM) reports. Within the CLP consortium the collective rather than the individual contribution was the overriding principle implying that the authors typically were listed in an alphabetical order. The achieved results (and data sets) of CLP form an interesting reference point in a climate perspective, as this research initiative was accomplished prior to the increasing notification of anthropogenic global climate change effects (Shu *et al.*, 2022), although the role of inter-

annual climate variability as such has been on the agenda of the Northeast Atlantic scientific community since the beginning of the 20th century (Helland-Hansen & Nansen, 1909; Hjort, 1914).

While "the recruitment problem" (Houde, 2016) still largely remains unresolved in the sense that one is unable to reliably predict year-class strength, and probably never will be fully so, this interdisciplinary research effort has markedly advanced fisheries oceanography through world-leading pioneers and laboratories (Rothschild, 2015; Houde, 2016). Despite this, we feel that these progresses should be even further emphasized today—and extended with new accomplishments—as eggs and larvae are particularly vulnerable during on-going climate change (Alix *et al.*, 2020; Dahlke *et al.*, 2020; Servili *et al.*, 2020). Not only so, recruitment variability essentially relates to survival rates of ELHS (Hjort, 1914; Houde, 1987; Pepin, 1991) but also during the juvenile stage, at least for "cod-like or herring-like species" at higher latitudes characterized by relatively slow larval growth and small size at metamorphosis (Houde, 1987).
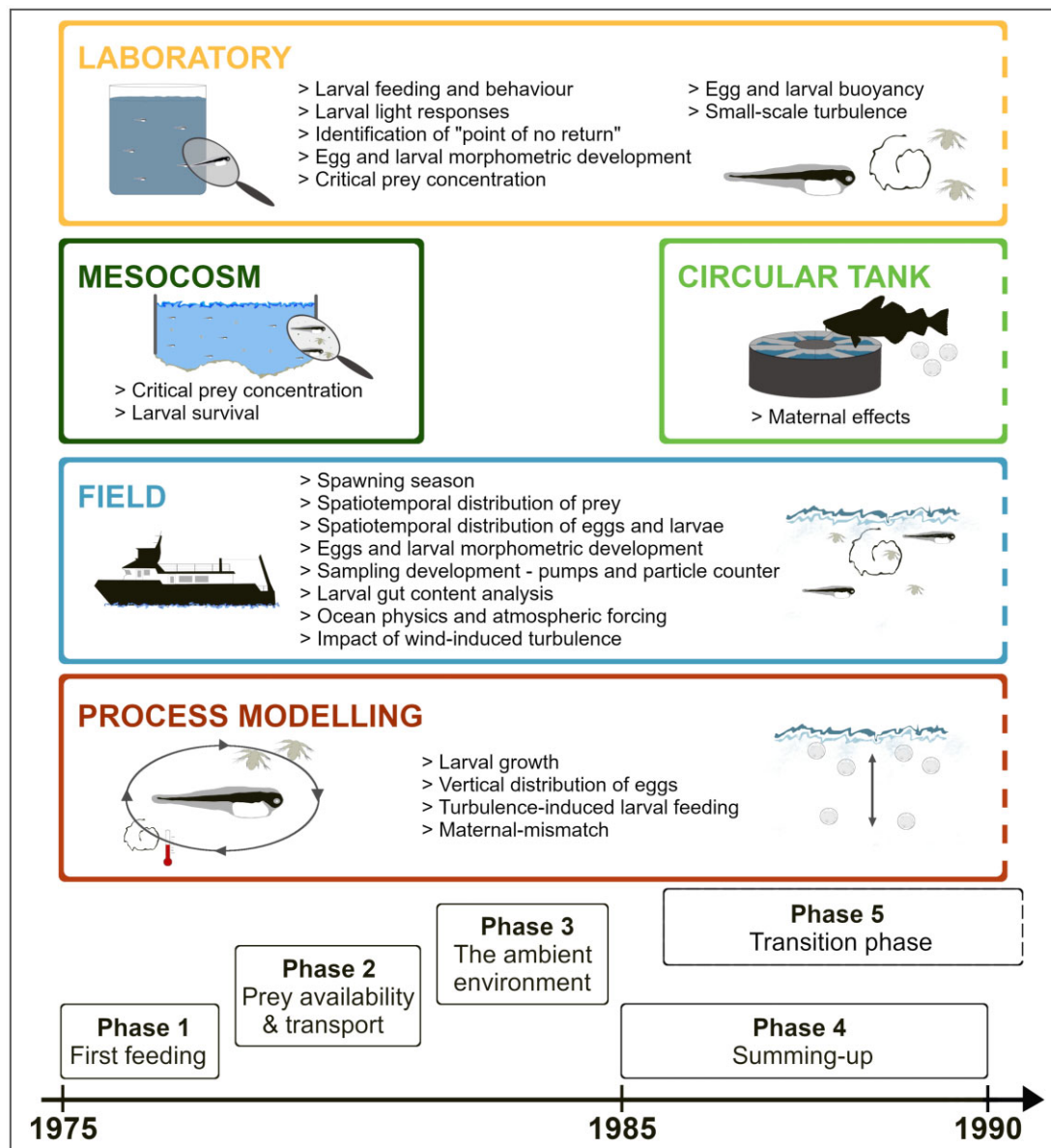
2 A retrospective view of the Cod Larva Project

2.1 Sources of inspiration

In todays' vocabulary, CLP unquestionably qualifies as a research program; the research interest was exceedingly broad, focusing on various life history traits of a series of Atlantic cod (*Gadus morhua*) stocks. A special focus was laid on the

Figure 1. Research phases, including associated method approaches and research topics, of the Institute of Marine Research Cod Larva Project (1975–1990). Open-ended box: continued investigations.

clearly biggest one in terms of biomass, the Northeast Arctic (NEA) cod (Gullestad *et al.*, 2020), backed-up by an exceptionally long population dynamics time series of >120 years (Hylen *et al.*, 2008).

CLP was inspired by Johan Hjort's seminal work *Fluctuations in the great fisheries of northern Europe viewed in the light of biological research* (Hjort, 1914). The scope and complexity of CLP were exceptional for the 1970–80s in terms of research questions, methodology, and the combination of laboratory, mesocosm (semi-natural enclosure), tank, and field studies (Figure 1). CLP was launched in 1975 by an informal group of IMR researchers: marine (fishery) biologist Per Solemdal, Snorre Tilseth, and Victor Øiestad. The main objective was comprehensive in nature: to better understand the mechanisms behind the noticed large variability in year-class strength. The more specific motivation came with that Hjort

in his field and experimental investigations indirectly observed an enormous mortality during early larval stages and realized that small variations in mortality could accumulate to large differences in the subsequent year-class strength (Hjort, 1914), for NEA cod referring to age 3 years (Hylen, 2002). Hjort (1914) primarily suggested two causal explanations behind this large mortality: (1) variation in the degree of spatiotemporal synchrony between planktonic prey and larvae, i.e. the critical period (or starvation) hypothesis (or the match-mismatch hypothesis (Cushing, 1990)); and (2) transport of the free-drifting offspring outside the natural habitat, i.e. the advection (aberrant drift) hypothesis. So, predation on eggs and larvae, i.e. the predation hypothesis (3), was missing from Hjort's ideas on the causes of the variability in year-class strength (Houde, 2016). CLP started off with Recruitment Hypothesis 1, thus, adopting that the most critical stage for the formation
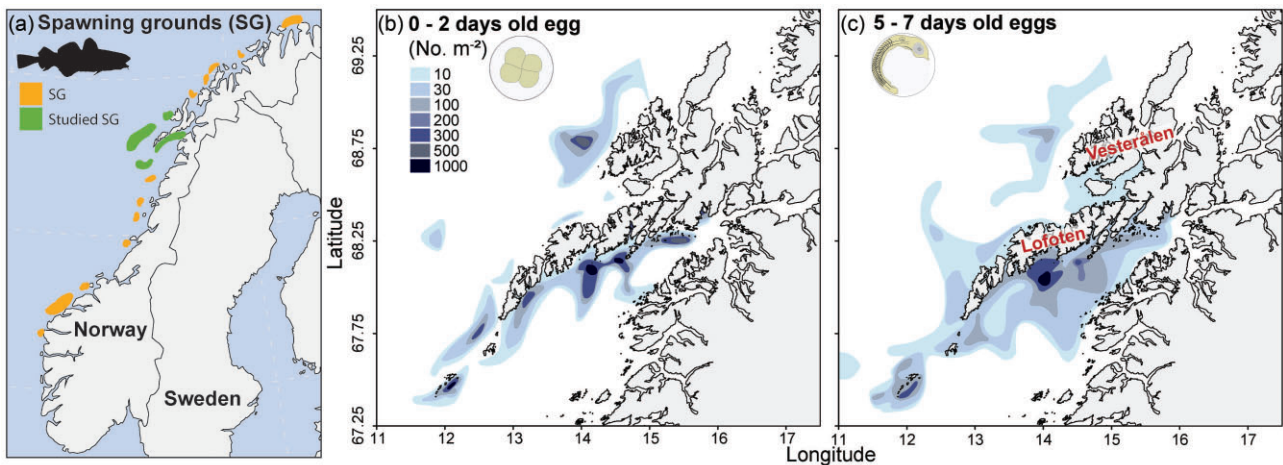
Figure 2. NEA cod spawning grounds, and pelagic research survey data on cod egg distributions in Lofoten-Vesterålen, Norway, 2–9 April 1984. (a) Geographical location of the studied as well as other reported spawning grounds of NEA cod; (b) distribution of 0–2 days old eggs in Lofoten-Vesterålen; (c) distribution of 5–7 days old eggs in Lofoten-Vesterålen. The distribution maps in (b) and (c) were produced by digitalization of Figures 23 and 24, respectively, in Sundby and Bratland (1987), whereas spawning ground locations in (a) are based on Sundby and Bratland (1987) and Sundby and Nakken (2008).

of a new year class was during the first days after completed larval start feeding (depleted yolk sac).

2.2 Organization of research phases and objectives

CLP successively built an increasing knowledge platform, organized into five phases (Solemdal, 1989) (Figure 1):

- Phase 1 *First feeding of cod larvae* (1975–1978) aimed at learning more about the biology of cod larvae, especially about their interaction with prey (including critical prey density) under different biophysical conditions using the whole toolbox of laboratory, mesocosm and field approaches.
- Phase 2 *Prey availability and transport of fish larvae in the coastal current* (1979–1981) intensified the focus on *in-situ* studies—supported by method developments—to examine spatiotemporal distribution and transport of eggs, larvae, and prey.
- During Phase 3 *Larval growth conditions in the coastal current* (1982–1984), synoptic surveys in the key study area Lofoten and Vesterålen off northern Norway were prioritized to investigate spawning ground locations and associated dynamics of ELHS (Figure 2).
- A summing-up phase, Phase 4, ended with an extensive project report to the Research Council (Solemdal, 1989).
- Based on this collation of results within Phase 1–3, major remaining gaps in the understanding behind ELHS-based recruitment variability were put forward (in parallel with Phase 4) and tested in Phase 5 (1985–1990) to quantify mortality (survival) of eggs and larvae from different spawning grounds. Moreover, the research was designed to identify additional recruitment factors, such as the effect of small-scale turbulence on larval feeding as well as maternal effects on egg and larval viability (Figure 1).

The resulting findings are exemplified below.

2.3 Phases 1-3–establishing a method-mechanistic framework, 1975–1984

CLP encompassed a mechanistic approach, encouraged by contemporary recruitment studies by Californian fishery biologists on "small pelagics" under the creative leadership of Reuben Lasker (Lasker *et al*., 1970; Hunter, 1972; May, 1974; Lasker, 1985). For IMR, related studies benefitted from hands-on experience with mesocosm experiments (Øiestad, 1983), but also the fact that the main NEA cod spawning ground in Lofoten showed exceptional high egg and larvae concentrations (Figure 2). In addition, the so-called 0-group time series (∼5-month-old juveniles) in the Barents Sea was coming into place (see Section 2.4.2), which, at least in principle, provided the opportunity to track the number of survivors to the following autumn.

Following these feasibility studies, CLP adopted the following investigative procedure: (i) Mimic, as far as possible, natural environmental conditions (light intensity, temperature, salinity, and oxygen content) of cod larvae in controlled laboratory and mesocosm settings; (ii) add prey particles (at seemingly natural variation in density), and measure larval feeding success and body traits to depict critical prey levels for larval survival; (iii) compare laboratory and mesocosm results with natural environmental conditions to assess the survival potential of the offspring in the field; and, finally, (iv) contrast proxies of recruitment success, i.e. survey estimates of 2- and 5-month-olds, with observed recruitment strength at age 3 years.

2.3.1 Lofoten—a unique spawning site

Because of the extraordinary dense aggregations of spawning cod along the east side of the Lofoten archipelago (Rollefsen, 1932; Wiborg, 1950; Sundby & Bratland, 1987)—confined to March and April (Pedersen, 1984)—the concentrations of cod eggs and larvae exceed by far most marine fish spawning areas in the world oceans. In extreme good spawning years (such as 2011–2013) peak concentrations have exceeded 30 000 eggs m^{-2} (Anders Thorsen, IMR, personal observation). Consequently, the major part of the CLP field studies was undertaken at the traditional Lofoten spawning grounds

(Figure 2). A fixed grid system was set up alongside the Lofoten archipelago in March–May, where the distance between stations was reduced to 1 km around the most intensive spawning grounds, providing detailed quantitative information on seasonal changes in egg and larval distributions (Ellertsen *et al.*, 1978).

2.3.2 The introduction of the salinity-gradient column for egg density measurements

Steve H. Coombs at the Plymouth Marine Laboratory revolutionized the measurement of ELHS buoyancy when he introduced a way to precisely measure the floating ability of single eggs (or sedated larvae) by establishing linear salinity gradients in temperature-controlled glass tubes (Coombs, 1981). CLP immediately applied this method on cod eggs sampled in Lofoten, finding that the vertical distribution in the field varied not only with egg buoyancy *per se* but also with wind conditions in the upper mixed layer (UML) (Solemdal & Sundby, 1981). These new understandings promoted the establishment of a generic model for the vertical distribution of buoyant eggs (Sundby, 1983). The model was subsequently presented in a numerical format (Westgård, 1989).

2.3.3 Larval feeding—the first synthesis, backed up by preliminary model runs

The detected influence of light intensity and prey density on cod larval feeding success was first presented at the ICES Annual Science Conference 1976 (Ellertsen *et al.*, 1976). This combined laboratory-mesocosm approach rendered it possible to observe the response of an entire cohort of larvae to the applied environmental situation. Phytoplankton, together with copepod nauplii, constituted a major part of the particles consumed. The larger phytoplankton was actively grazed, whereas relatively smaller phytoplankton were taken up passively because of their extraordinary high concentration; in the order of 10^3 particles ml^{-1}. It also became evident that cod larvae were obligatory visual feeders, with a minimum light threshold of 0.1 lux. Thus, already towards the end of CLP Phase 1 comprehensive results on larval feeding incidence and behaviour in relation to phytoplankton, zooplankton, and physical conditions were available (Ellertsen *et al.*, 1980).

To define the so-called "point of no return," i.e. when the starving larva is unable to retrieve viable health even if plentiful of prey is provided (Blaxter & Hempel, 1963), a mathematical model was constructed (Ellertsen, Moksness, *et al.*, 1981). The anticipated larval growth and survival in this first-generation model were set as the function of prey abundance and size fraction at different temperatures. The model outputs were thereafter contrasted with corresponding information from cod larvae reared in a 4400 m^3 mesocosm (Figure 1) for a 2-week period in the absence of predators (Ellertsen, Moksness, *et al.*, 1981). Overall, the modelled growth rates compared well with mesocosm observations, whereas the parametrization of survival rate resulted in underestimates as mesocosm larvae apparently coped better with negative trends in body growth rate than laboratory larvae (Ellertsen, Moksness, *et al.*, 1981; Øiestad, 1990). In parallel with these simulations, basic studies on the morphometric development of cod eggs and larvae were undertaken, finding that starvation of first-feeding larvae negatively affected their buoyancy (Strømme, 1977). Oppositely, a positive relationship existed between larval growth and daily increments in otoliths (Gjøsæter & Tilseth, 1981; Bergstad, 1984).
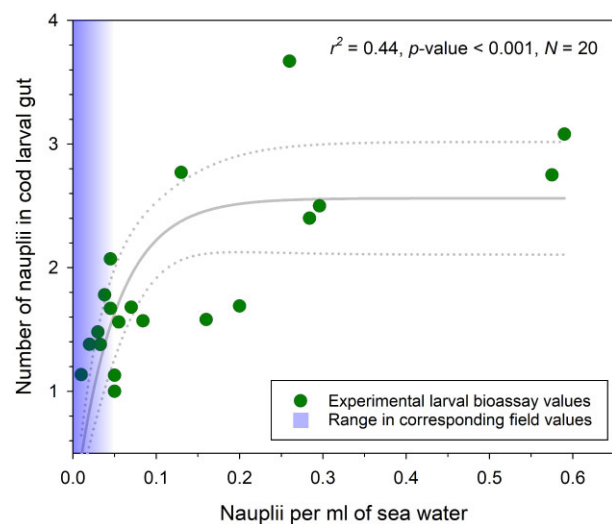
Figure 3. "Larval bioassay" on the relationship between number of copepod nauplii in the gut of first-feeding, reared larval cod (cf. field hatchery) and the density of nauplii in the sea water pumped onboard R/V Johan Ruud from various depths in Austnesfjorden, Lofoten in April 1977. The plotted larval bioassay data in Fig. 19 in Ellertsen *et al.* (1979) were digitalized and related statistically (with 95% confidence interval), using Ivlev's functional response equation (Ivlev, 1961). The corresponding range in field-observed values were given from Sundby and Fossum (1990).

2.3.4 Searching for prey micro-patchiness—inspirators abroad and method adjustments

The "troika" that initially defined the research aims of CLP consulted methods developed by the above-mentioned larval experimentalists in the California Co-operative Oceanic Fisheries Investigations (CalCOFI) programme (Lasker, 1974) (Section 2.3). Especially, their use of laboratory-reared larvae—in this case of Northern anchovy (*Engraulis mordax*)—attracted attention to explore which field conditions could possibly provide high enough concentrations of prey for successful larval survival (Lasker, 1975). During a National Oceanic and Atmospheric Administration (NOAA) colloquium on larval fish mortality in 1975, this kind of bioassay was specified as "shipboard feeding experiments designed to determine if water from a particular location and depth in the sea is suitable for larval survival" (Hunter, 1975). The researchers of CLP adjusted this method to the ideal working situation in the coastal region of Lofoten (Section 2.3.1), establishing a land-based laboratory ("field hatchery") in the close vicinity of where the echosounder of the research vessel was detecting high concentrations of spawning cod (Figure 2). Thus, reared cod larvae at the stage of first feeding could be quickly and regularly provided onboard. In line with the original protocol (Lasker, 1975), water at depths with different prey densities were pumped up to subsequently test larval feeding ability. The number of nauplii in the cod larval gut grew exponentially to a maximum—reaching an asymptote—with increasing nauplii concentration, though with an overall large variability (Ellertsen *et al.*, 1979) (Figure 3). Despite this, the same level of feeding success was also seen in the field, i.e. under more than one-order-of-magnitude lower nauplii concentrations (Sundby & Fossum, 1990), indicating that additional key factors were in operation in the natural environment. This interpretation was further underlined by that the

gut content in field larvae could be relatively high even at extremely low nauplii concentrations (Figure 3). So, there were strong reasons to believe that the reported laboratory nauplii concentrations did not properly reflect the natural microenvironment or feeding opportunities encountered by each prey-searching larva (Øiestad, 1990). One issue that partly spoke against this argument was the striking finding that the digestion time in question turned out to be exceedingly fast, seemingly ∼30 min, even at 5°C (Ellertsen *et al.*, 1979).

To properly contrast laboratory and mesocosm results with those from the field (Ellertsen *et al.*, 1978), one key task was the advancement of adequate equipment to collect these types of biological samples in an undamaged, representative way at or near the spawning grounds. Since traditional plankton nets were averaging over too large sea-water volumes to get a detailed enough spatial resolution, several plankton pumps were developed to obtain the small-scale vertical distribution resolution of copepod nauplii, and cod eggs and larvae (Ellertsen *et al.*, 1984). For larvae, the pump capacity had to be considerable since concentrations rarely exceeded 1 m^{-3}, even at the high-concentration Lofoten study sites; the selected pumps had capacities of 0.5–1.0 m^3 s^{-1} (Solemdal & Ellertsen, 1984). Hence, by pumping for 30 seconds at each depth quite a few larvae could be sampled.

In addition to the vertical profiling of nauplii, cod eggs, and larvae by a variety of pumps, an *in-situ* (Coulter) particle counter was adapted to reflect the concentration of nauplii-sized particles throughout the water column (Tilseth & Ellertsen, 1984a). This mode of action explicitly searched for any microlayers of high enough concentrations of nauplii for cod larvae to survive, i.e. patches undetected by plankton pumps that normally profiled discrete depths at 5 m intervals. However, the particle counter only showed small differences compared with the given nauplii counts from plankton pumps (Tilseth & Ellertsen, 1984a). Hence, microlayers with very high prey concentration were unlikely prevailing in the UML at the nursery grounds in Lofoten. This result became an enigma during the first two research phases as nauplii concentrations high enough for larval survival seldom were found in the field in view of the results from the above-mentioned larval bioassays (Figure 3) and related laboratory studies conducted at that time (Solberg & Tilseth, 1984), or today (Folkvord *et al.*, 2015).

2.3.5 Tracking prey-ELHS interactions—the weather issue

To resolve the physics behind the above-mentioned vertical variations in nauplii, cod eggs and larvae abundances (Section 2.3.4), detailed hydrography data were needed. In 1976, IMR charted the new coastal research vessel R/V Johan Ruud, owned by the University of Tromsø—the Arctic University of Norway, to be operated by CLP in 25 out of 50 cruises from 1977 to 1987 (Gulliksen, 2020). Although relatively small (30.5 m long and 335 tonnes), the vessel was well equipped with state-of-the-art acoustics, a precise CTD (conductivity-temperature-depth) (Brown, 1974), a functional plankton laboratory and a trawl deck to manage the plankton pump systems. In short, the vessel was ideal to dedicatedly circle in patches of high concentrations of cod eggs and larvae and then target a site for repeated biophysical sampling over a 24-hour period, or longer.

To address the consequences of mesoscale eddies and temporal weather events on ELHS location and drift patterns, a synoptic survey experiment in the Lofoten-Vesterålen region

in April 1977 was coordinated from R/V Johan Ruud as part of the Norwegian Coastal Current Project (Mork & Sætre, 1981). During this joint effort by three research vessels, 35 Aanderaa Current meters were deployed in Lofoten giving the first overview of short-time (hour-to-hour) changes in currents and hydrography before, during, and after the passing of an atmospheric low (Furnes & Sundby, 1981). This storm imposed an immediate response in the spawning location and transport of cod eggs (Ellertsen, Solemdal, *et al.*, 1981). The data demonstrated a close association between abundance of pelagic offspring and water mass properties but also the important influence of bottom topography on the steering of circulation features of water masses (Sundby, 1984).

The consequences of the encountered weather situation for the survival of ELHS attracted further interest as it became clear early on in CLP that wind force played a crucial role in defining the vertical mixing and distribution of nauplii, eggs, and larvae, as well as the horizontal drag and advection of the pelagic offspring. Concurrently, methods to measure the actual dynamic activity in the UML were developed in USA, with the first estimates on the relation between turbulent energy dissipation rates (Osborn & Crawford, 1980)—based on air foil probe measurements (Osborn, 1974)—and atmospheric wind forcing being presented (Oakey & Elliott, 1982). These advances clarified that wind measurements, both onboard and land-based, could be taken as proxies for the degree of turbulence in the UML.

2.4 Phases 4-5–both expanding and detailing the mechanistic framework, 1985–1990

2.4.1 Effect of small-scale turbulence on larval feeding—a major factor to consider

The main directional change to better explain why wild larvae showed markedly higher gut content than experimental larvae at similar prey concentrations (Figure 3) came with the introduction of the influence of small-scale turbulence on plankton contact rates by Rothschild and Osborn (1988). This novel theory opposed the argument presented by Lasker (1975) but also by Peterman and Bradford (1987) that turbulent mixing is detrimental for larval feeding because of the diluting impact on the plankton concentration as such. Owing to the comprehensive field sampling efforts within CLP, it became possible to explore how wind-induced turbulence contributed to the encounter rate between cod larvae and prey. This reanalysis documented that only a modest increase in wind speed from 2 to 6 m s^{-1} tripled the encounter rate (Sundby & Fossum, 1990), and by a factor of 7 from 2 to 10 m s^{-1} (Sundby *et al.*, 1994).

2.4.2 The critical period—much more extended than previously thought

From the mid-1980s, CLP studies increasingly suggested that the critical period was significantly longer than just a few days around larval first feeding. Furthermore, egg mortality rates were apparently substantial. Thus, CLP went from adopting to questioning Hjort's Recruitment Hypothesis 1, as did many other marine laboratories "late in the 20th century" (Houde, 2008). These newer insights arose from carefully surveying and staging patches of eggs and larvae in the study area (1983–1985) (Sundby & Bratland, 1987; Fossum, 1988) (Figure 2). Based on the total abundance of newly fertilized

eggs in the field, only 10% survived to hatching ∼20 days later (Fossum, 1988). Getting also access to time series of post-larval abundance (Bjørke & Sundby, 1987), segmented calculations of mortality rates from egg stages via larval and post-larval stages to the 0-group (juvenile) stage could for the first time be undertaken (Sundby et al., 1989). This study clarified that the mortality rate decreased exponentially after the newly fertilized egg stage, and, importantly, that the overall level of NEA cod recruitment success at age 3 years was largely predetermined by the number of ∼70-day-old offspring, i.e. postlarvae on the transition to becoming juveniles. Prior to this post-larval stage, mortality was found to be density independent, while afterwards density dependent (Sundby et al., 1989). Consequently, both starvation and predation turned out to be essential in defining year-class strength, and the critical period ranged from the egg stage to the pelagic juvenile stage, fitting into the conceptual mortality (M) vs. growth (G) ELHS framework made for various fish species by Houde (1987) in his review at that time (Section 1).

So, when CLP was finalized (Figure 1), the conclusions were considerably more complex compared to the initial hypothesis that year-class strength was determined subsequent to yolk sac absorption during larval first feeding. In essence, the understanding of the feeding ecology of cod larvae in view of recruitment dynamics, particularly for NEA cod, became highly complex as also other key variables had to be counted in, such as temperature, light conditions, and turbulence, thus, climate variability in the broad sense (Ellertsen et al., 1989). Although strong year-classes of cod typically occurred during warm periods in the Barents Sea (Sætersdal & Loeng, 1987), a high temperature during the spawning season was not sufficient: during years of low temperatures strong year classes did not occur, but in warm years both strong and weak year classes could be formed (Ellertsen et al., 1989). Hence, several diverse physical and biological conditions need to be met to produce strong year classes, but these conditions were more likely to coincide in warm years. In this way, temperature *per se* was not a direct factor of good recruitment but reflecting optimal ecosystem conditions, in cases.

2.4.3 Quantifying reproductive output

In 1983, CLP was asked to test the applicability of what became generally named the Annual Egg Production Method (AEPM) (Armstrong et al., 2001) on cod in Lofoten, encouraged by indications of a positive relationship between total number of pelagic eggs (Figure 2) and biomass of spawners in this area, the latter estimate given in that event from acoustics (Sundby & Bratland, 1987). To run the AEPM, these comprehensive egg survey data (1983–1985) had to be combined with individual fecundities to get the resultant spawning stock biomass (SSB), assuming a female sex ratio of 0.5. The first established potential fecundity curve (F_{pot}) for NEA cod (Kjesbu, 1988)—$F_{pot} = 1.25 \times 10^{-2} \times TL^{4.27}$ ($r^2 = 0.931$, $p < 0.001$, N = 100)—told that an individual of 80 cm (TL) typically showed 89% higher fecundity than the single estimate extracted from the historic literature (Sorokin, 1957); a general characteristic of fecundity data is the considerable body size-specific variation (Bagenal, 1978). However, the accompanying interests in applying egg production methods lost momentum due to the obvious benefits of using acoustics as abundance indicator, where IMR was an international leader

in close co-operation with the Norwegian company Simrad (Kongsberg Marine) (Nakken, 2008).

To progress further with cod reproductive ecology in more general terms, contacts with external experts were made. Instrumental in this respect were anatomist Harald Kryvi at University of Bergen (Kjesbu & Kryvi, 1989) and reproductive biologists Michael Greer Walker and Peter R. Witthames at Fisheries Laboratory [today Centre for Environment, Fisheries and Aquaculture Science (Cefas)], Lowestoft (Kjesbu et al., 1991). This UK laboratory was world-class, together with the similar laboratory of John R. Hunter at the Southwest Fisheries Science Center, NOAA, La Jolla, California. Both laboratories worked, however, primarily on small pelagics. The automated laboratory "fish egg counter" in Lowestoft was exceptional for its time (Witthames & Greer Walker, 1987), and attracted special interest to identify "the stage of spawning" in this multiple egg batch spawner (Kjesbu et al., 1990) used as standardization criterion in the ongoing field-based maternal effect studies (Solemdal, 1997).

Although maternal effect studies, at least at IMR, were still in their infancy, the fact that the exponent (b) in the above-given fecundity-total length power function was clearly allometric (b = 4.27) (Kjesbu, 1988) helped pushing the research curiosity in that direction, hypothesizing that bigger females contribute disproportionally more to the reproductive and thereby recruitment potential. To assess individual reproductive effort, one female and male ("pair") were held in experimental tanks (Figure 1), i.e. in the so-called "Circular Tank" divided into ten 20-m³ spawning chambers. Under this spacious experimental condition, each female spawned ∼15–20 times per season, releasing an egg batches every second or third day, with the resulting batch fecundity following a dome-shaped curve, whereas the corresponding egg size more or less steadily declined (Kjesbu, 1989). Such detailed tracking at the individual level on a marine multiple spawner could only be found in the investigations undertaken on haddock (*Melanogrammus aeglefinus*) at the Marine Laboratory, Aberdeen (Hislop et al., 1978), although serial spawning as such had already been noticed across many teleost species (Bagenal & Braum, 1978).

3 Joining forces internationally and broadening the research horizon, early 1990s—today

3.1 The trade-off between M and G

The interest in the establishment of conceptual ELHS M vs. G models peaked in the late 1980s-early 1990s (Houde, 1987; Miller et al., 1988; Pepin, 1991). These frequently consulted relationships should be considered as advanced null hypotheses, i.e. to be specifically tested for the species (stock) and organizational level in question (Pepin & Miller, 1993). This caution seems particularly valid for NEA cod, which apparently does not fit into the typical teleost pattern of an increased M of eggs, larvae and postlarvae with higher temperature (Pepin, 1991) (Section 2.4.2); no such testable M data for G. morhua appear in Pepin (1991).

3.2 The "blooming" and adopted framework of maternal effect studies

Maternal effects, i.e. the impact of the maternal phenotype on the offspring's phenotype independent of the offspring's
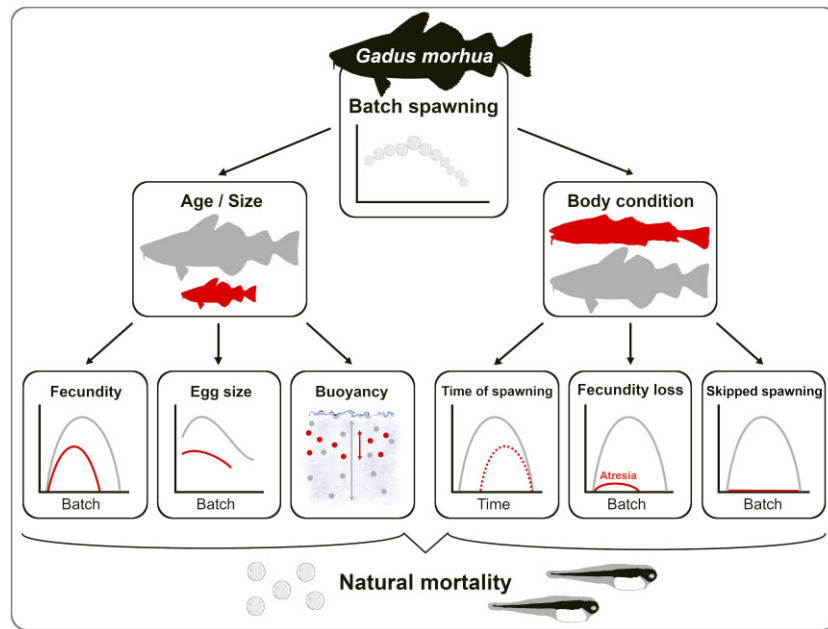
Figure 4. Examples of reproductive traits addressed for captive cod, held in the Institute of Marine Research Circular tank (Figure 1), as part of the maternal effect studies, focusing on the implications of alterations in age/size and body condition of this multiple batch spawner. The maternal effect is indicted by comparing trait responses of small or poor-condition specimens (red) vs. larger or good-condition specimens (grey).

genotype (Bernardo, 1996), captured renewed interests at IMR towards the early 1990s (Figure 1). Particularly, the well-back-in-time book of the Soviet–Russian ichthyologist Georgii V. Nikolskii (Nikolskii, 1969) on population dynamics was a source of inspiration, specifying that age/size and body condition—as effectors—were central within such studies. Body growth came as an additional important factor, well-known to be influenced by the imposed harvest regime (Trippel et al., 1997). This link to stock advice and management likely explains why this research topic was fronted by marine laboratories, as exemplified below. A common ambition in these investigations was that they should be quantitative in nature, e.g. in terms of fecundity, egg size, and spawning period.

3.2.1 Spawning activity—uncovering the individual day-to-day performance and output

The IMR Circular Tank studies mentioned in Section 2.4.3 were designed to track in detail the spawning activity of pairs of cod of different body size and condition (Figure 4), but, in cases, also of different stock origin. In 1992, the fishing moratorium for the major 2J3KL Northern cod came into place, persisting up today, except for a small stewardship fishery (DFO, 2020). Moreover, cod mariculture had seen its breakthrough (Øiestad et al., 1985). These backdrops probably contributed to the great interest by the marine science community in any relevant articles on cod reproduction (Kjesbu et al., 1991; Kjesbu et al., 1996). To be expected, the same attention was also given to such articles originating from investigations in Eastern Canada (Trippel, 1998; Lambert & Dutil, 2000; Ouellet et al., 2001) and in Iceland (Marteinsdottir & Steinarsson, 1998).

These research initiatives—spanning from experimental to field studies, or a mixture—resulted in significant advancements in the understanding of cod reproduction. The St. Andrews Biological Station differed methodologically from the

other laboratories, paying special attention to paternal effects, concluding that male body size (cf. demographic truncation) was not necessarily a key feature in terms of reproductive success (Rakitin et al., 1999). In terms of energetics (cf. harsh environmental impacts), the research from Maurice Lamontagne Institute advocated that the existence of a critical lower threshold for post-spawning (spent) body condition principally restricts how much a female can invest in reproduction without suffering subsequent death (Lambert & Dutil, 1997, 2000). Hence, the prespawning condition very much defines the subsequently realized reproductive investment. Associated larval development aspects were explored at the Icelandic Marine & Freshwater Research Institute in close association with the University of Iceland, demonstrating that egg size from females stripped in the field positively affected experimental larval feeding success, specific growth rate and swim bladder development (Marteinsdottir & Steinarsson, 1998). Related investigations were organized through IMR by Per Solemdal, transporting eggs from Lofoten to IMR Bergen for mortality studies. Additionally, at the IMR Austevoll advanced studies of larval swimming kinematics in Howard Browman's laboratory were conducted, noting that offspring from repeat spawners generally did better than recruit spawners in such tests (Solemdal et al., 1992). Embryologist Valeri Makhotin at Moscow State University joined this long-lasting research effort assessing the degree of egg (embryonic) malformation from direct field observations in Lofoten and Vesterålen (Figure 2) along with daily recordings of the resulting fate of single eggs incubated in NUNC wells (70% sea water, 4°C) (Makhotin et al., 2001). Although these data sets strengthened the common message that a repeat spawner contributes relatively more to the stock's reproductive potential than a (small) recruit spawner, this latter "stress test" caused markedly higher levels of lethal malformations (20%–49%) compared to the field situation (1%–7%) (Makhotin et al.,

2001). So, caution should be made if this information is to be entered in a population dynamics model, although referring to cumulative and instantaneous mortality, respectively. Nonetheless, "egg quality" could also be indicated through a series of physiological criteria, according to a well-cited review produced at that time (Kjørsvik et al., 1990). Today, molecular techniques and "omics" tools allow obtaining e.g. transcriptomic or proteomic data and identifying molecular pathways potentially involved in egg quality, showing unlimited prospects for fundamental insights, e.g. Lubzens et al. (2017).

3.2.2 Egg and larval buoyancy—addressing the basic determinants

The egg dry weight vs. egg diameter relationship turned out to be characteristic for a given specimen of cod, seen by following its egg releases over three consecutive seasons (Kjesbu et al., 1996). This systematic residual from the general regression line signifies that the egg water content is an inherited trait (Thorsen et al., 1996). Principally, egg buoyancy is positively affected by egg diameter, provided the other influential factors—such as eggshell mass—are held constant (Kjesbu et al., 1992; Jung et al., 2014). Consequently, bigger females exhibit a larger variance in buoyancy during the spawning period, explained by the corresponding larger variance in egg size (Kjesbu et al., 1992) (Figure 4). Probably related to these intrinsic patterns seen for egg buoyancy, larvae produced late in the season are generally less buoyant too (Saborido-Rey et al., 2003). In terms of the eggs, these insights led to the conclusion that the particularly advanced degree of yolk (vitellogenin) proteolysis (Sullivan & Yilmaz, 2018) seen for Baltic cod eggs underlies their extraordinary high water content and thereby the ability to float at remarkably low salinities (Nissling & Westin, 1991; Thorsen et al., 1996). Although this osmotic principle is well-established across phyla, this finding demonstrates that the reproductive physiology of Baltic cod deviates, at least in this respect, fundamentally from marine cod stocks.

### 3.2.3 Individual spawning time—a highly complex issue

The subject matter of size-specific spawning time—i.e. to which extent individuals of a given body size or age may commence spawning at a different time in the season than co-specifics differing in these traits—was extensively debated among colleagues in the 1990s. The main reasons were (1) lack of accurate data and (2) the "maternal—match-mismatch hypothesis" of Per Solemdal (Solemdal, 1997), using David Cushing's match-mismatch hypothesis as outset (Cushing, 1990). A prerequisite in Solemdal's conceptual framework was that older females—producing plentiful of big larvae—commence spawning first, leading to a more extensive overlap with the prey (nauplii) in a warm year (Kjesbu et al., 1996; Solemdal, 1997). These arguments were backed up by generally better recruitment of NEA cod in relatively warmer water (Ellertsen et al., 1989) (Section 2.4.2.). However, few facets within cod reproductive ecology are associated with such high levels of uncertainties as size-specific spawning time. This circumstance is particularly true for NEA cod migrating over exceeding long distances to different spawning grounds (Sundby & Nakken, 2008), making representative sampling at that time in the season a formidable task, on top of the high demographic dynamics seen at the spawning ground as such (Rollefsen, 1953).

The case that the cod is a multiple-batch spawner releasing gametes over several weeks (Figure 4) implies that the commonly used practice of estimating the proportion of adults being either spawning or spent is only indicative of the time of commencement of spawning. Development and application of better tools—foremost the first day of spawning as a function of leading cohort (LC) oocyte diameter, total length and the experienced temperature up to spawning (Kjesbu, 1994)—indicated that size dependency in spawning time might be present in one year but absent in another for NEA cod (Kjesbu, Righton, et al., 2010). Such techniques demonstrated, however, earlier spawning of larger specimens of North Sea cod (Kjesbu, Righton, et al., 2010), agreeing with corresponding estimates on proportion spawning-spent (Morgan et al., 2013). Offspring birth date information (Wright & Trippel, 2009) might be a way to proceed but then the link to any underlying reproductive trait is expected to be evasive in a field situation, e.g. a small larva may originate from a late batch of a big female or from an early batch of a small female (Figure 4). In either case, LC oocyte growth rate is generally accelerated in warmer water and thereby giving earlier spawning time, though with substantial individual variation (Kjesbu, Righton, et al., 2010). Under similar experimental conditions, daughters seem to spawn within the same part of the season as their mothers (Otterå et al., 2012), though any heritability factor involved should be towards the low side numerically speaking as traits coupled to fitness (cf. match-mismatch) cannot be too strictly steered genetically under highly fluctuating environmental conditions (Law, 2007).

3.3 Research networks, supercomputers, and climate impacts

Two circumstances especially pushed this research front on cod further ahead: the dedicated building of international networks through ICES, and access to significantly faster computers. In 1989, the *ICES Study Group on Cod Stocks Fluctuations* convened in Bergen. This initiative subsequently resulted in the *ICES Working Group on Cod and Climate Change* which ultimately became the *North Atlantic Regional GLOBEC Programme CCC* (1990–2008) (Brander, 2019). A key milestone and source of further inspiration was the arrangement of *ICES Symposium on Cod and Climate Change* held in Reykjavík in August 1993 (Jakobsson et al., 1994). In his summing up, Brander (2019) created an extensive matrix on the studied environmental factors × life history traits (× temporal scales) clarifying that highly different mechanistic processes might steer or influence local cod stock productivity. Despite that, this matrix provides plentiful of examples of missing (empty cells) or seemingly *ad hoc* research. In addition to these initiatives, the rapid increase in supercomputing capacity made it for the first time possible to combine ocean circulation model with individual-based models (IBMs) to simulate the performance of eggs, larvae, and pelagic juvenile as they were drifting along the current paths in the ocean model. This physical-biological coupling became the most comprehensive of the follow-up issues from CLP to today (Vikebø et al., 2021; Endo et al., 2022), though research vessel time for validation purposes—the trademark of CLP—often has become in shortage due to multiple, competing requests nowadays.
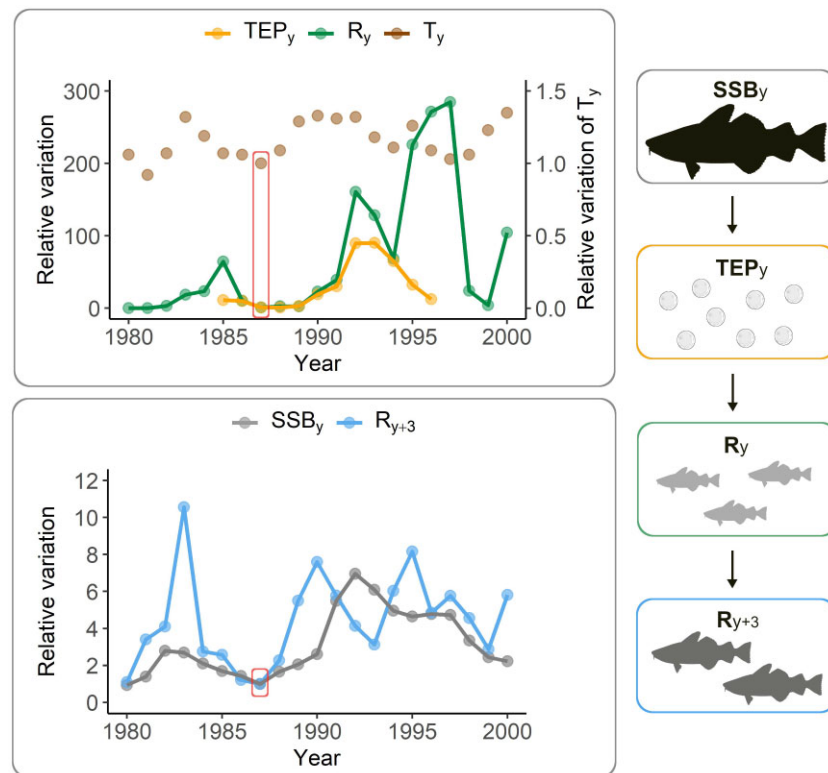
Figure 5. TEP_y, abundance of 0-group (R_y), and temperature (T_y) within a given year (upper panel) in view of the corresponding SSB_y and resulting recruitment three years later (R_{y+3}) (lower panel) for NEA cod. All data are relatively compared to 1987 (box), i.e. to the year with the lowest TEP_y in the time series from 1985 to 1996. The other time series displayed refer to 1980–2000. TEP_y data were given from Fig. 9 in Marshall *et al.* (1998), T_y from VNIRO, Russia (the Kola time series) (Boitsov *et al.*, 2012), whereas R_y, SSB_y and R_{y+3} were available via ICES (www.ices.dk) (ICES, 2021).

3.4 Scaling-up individual life-history traits to the stock level

Integrating life-history information—foremost on reproduction—into fisheries advice and management raised high up on the international marine research agenda after the mid-1990s, seeing for the next couple of decades two dedicated working groups, one within Northwest Atlantic Fisheries Organization (NAFO) and one within ICES, as well as an EU COST Action and several EU projects (Morgan *et al.*, 1999; Trippel, 2003; Hammer *et al.*, 2010; Kjesbu, Murua, *et al.*, 2010; Saborido-Rey, 2011). These managerial manoeuvres significantly contributed to creating an era of unprecedented progress within this sort of assessment- and advice-related studies (including methods) across species, stocks, countries, and contingent, as documented in the just mentioned references.

At IMR, this "push" to scale up individual reproductive information on NEA cod to the population level was foremost promoted by Øyvind Ulltang as "substantial work has been done on the problem of estimating fecundity as a function of age, size, and condition of the cod" (Ulltang, 1996). First, the standard assumption that SSB directly reflects total egg production (TEP) could be safely rejected (Marshall *et al.*, 1998). Second, total liver energy was a more precise proxy for TEP than SSB (Marshall *et al.*, 1999). Thus, in effect, TEP was significantly more variable than SSB and recruitment at age 3 years (R_{y+3}) (Figure 5). Third, this one-order-of-magnitude higher variability in TEP agreed better with the extent of variability seen in 0-group recruitment (R_y), supporting that year-

class formation is very much dependent upon the fate of ELHS (Section 2.4.2), but, obviously, also upon subsequent influential factors, and then in particular cannibalism (Holt *et al.*, 2019).

3.5 Current understanding of ELHS growth and distribution dynamics

3.5.1 Revisiting egg buoyancy and vertical distribution aspects

Just after the completion of CLP, Sundby (1991) expanded the model on vertical distributions on pelagic fish eggs to also include bathypelagic and demersal/bottom eggs. The latter kind was in this exploratory analysis restricted to those staying near the bottom due to their high specific gravity. Given that turbulent mixing in the halocline is several orders of magnitude lower than in the UML, the vertical spreading of a cohort of bathypelagic eggs was primarily determined by their variation in buoyancy. However, the vertical distribution of quasi-demersal eggs was influenced by same processes as for pelagic eggs in the UML, despite low mixing near or at the bottom. Additionally, it became important to consider how egg buoyancy varies throughout incubation, as buoyancy trajectory influences the actual drift route of the eggs and thereby their spatial distribution (Jung *et al.*, 2012). Egg specific gravity was reported to increase during the first days until the so-called "lens" stage, i.e. just before gastrulation, but thereafter decreased as the osmotic capacity of the embryo improved.

The earlier statement—based on cod data—that fish egg buoyancy is independent of ambient temperature and

determined by ambient salinity alone (Sundnes *et al.*, 1965) was a precondition behind the construction of Coombs apparatus (Coombs, 1981) (Section 2.3.2). Coombs *et al.* (1985) applied the new apparatus to re-explore the validity of the conclusion of Sundnes *et al.* (1965), conducting tests on sprat (*Sprattus sprattus*) and sardine (*Sardina pilchardus*) eggs. They detected only negligible changes in the buoyancy when the temperature was raised by as much as 10°C. Even so, experimentalists continued to express egg buoyancy measurements in terms of density which is a function of both temperature and salinity. Sundby & Kristiansen (2015) revisited the issue by principal physics and found that egg buoyancy indeed is practically independent of possible *in-situ* temperature changes because the volumetric thermal expansion of egg proteins and lipids constituents is compensated by a corresponding expansion of the ooplasm water content. This clarification enabled a further generalization of the model on vertical distribution of fish eggs in a halocline water column (Sundby, 1991), making it possible to apply the model also in off-shelf regions of the world's oceans where the temperature is the major determinant of specific gravity and where the vertical salinity gradient is opposite of in coastal regions. Based on these gathered insights, Sundby & Kristiansen (2015) hypothesized a critical spawning depth in regions with negative salinity gradient; spawning below this depth would result in eggs sinking out of the water column and thereby being lost to the population.

3.5.2 Validating the effect of small-scale turbulence on larval ingestion rates

Due to scepticism about the validity of the small-scale turbulence theory (Section 2.4.1), not only more field and laboratory data but also further theoretical considerations were arguably needed (Sundby *et al.*, 1994). This re-evaluation was in line with concurrent model works finding that the optimal level of turbulence for cod larvae feeding is at wind speeds above 11 m s^{-1}, probably around 14–15 m s^{-1} (MacKenzie *et al.*, 1994). However, as such wind strengths are seen in <2% of the time at first feeding (Sundby, 1982; Sundby, 1995), it seems reasonable to believe that cod larvae are adapted to frequent episodes of less wind-induced turbulence, an argument originating from the increased capacity of the larvae to swim as they grow in size (Sundby, 1995). This topical research was followed up by a series of articles, addressing the effect of turbulence on plankton distributions in general (Sundby, 1996, 1997; Stiansen & Sundby, 2001). Despite this, the earlier field observations were re-examined to give more complete insights into the role of turbulence on encounter rates. The Lofoten data from 1991 to 1992 on wind, hydrography, larval concentrations, and naupliar concentrations in the upper 40 m demonstrated that wind-induced turbulence is critical for larval feeding at all wind speeds and prey concentrations but especially below 5 nauplii l^{-1} (or 0.005 nauplii ml^{-1}; cf. Figure 3) (Kristiansen *et al.*, 2014).

3.5.3 Modelling transport and growth of pelagic offspring

Already in the beginning of the 1980s, CLP had developed a methodological approach to amalgamate process studies in field and laboratory (Ellertsen *et al.*, 1980; Ellertsen *et al.*, 1984; Solberg & Tilseth, 1984; Solemdal & Ellertsen, 1984; Tilseth & Ellertsen, 1984b) and to develop mathematical models of the observed processes (Ellertsen, Moksness, *et al.*, 1981; Sundby, 1983). However, to predict the recruit-

ment strength of a given year class, one should—in addition to assessing the foreseen key proximate factors, foremost SSB or TEP (Section 3.4)—ideally be able to track the encountered ambient conditions of different, successive life stages and their predators. At the beginning of the 1980s neither the state of trophic models nor the state of physical models made this achievable and at the completion of CLP, 10 years later, this task was still overwhelming.

By the end of the 1980s IMR had implemented the Princeton Ocean Model (POM) (Blumberg & Mellor, 1987) in the research on ocean climate and circulation. POM became the start of a series of studies on transport and spreading simulations of eggs, larvae, and pelagic juvenile fish. A Lagrangian particle tracking scheme was implemented in the model system to first of all handle transport of the pelagic offspring of cod from the main spawning areas in Lofoten into the feeding grounds in the Barents Sea (Ådlandsvik & Sundby, 1994). Comparison of these simulations with pelagic trawl surveys for a 10-year period (1977–1986) (Bjørke & Sundby, 1987; Sundby *et al.*, 1989) reproduced reasonably well the distribution of pelagic juvenile cod along the continental shelf and into the Barents Sea shelf, and partly the interannual variability. However, there was a tendency of too rapid ichthyoplankton transport along the shelf because the horizontal model grid size (20×20 km) did not sufficiently resolve the eddy-generating bank topography that reduced the long-shore advection of ichthyoplankton (Sundby, 1984).

In the following years, results on modelled transport and distribution of the pelagic juvenile cod gradually improved as computer capacity increased. By the early 2000s the next generation ocean model, the Regional Ocean Modelling System (ROMS) (Shchepetkin & McWilliams, 2005) was implemented at IMR (Ådlandsvik & Budgell, 2003). In addition, the particles were given "life" by running IBMs, where ambient food abundance, temperature, light, and turbulence were parts of the growth function for the particles (Fiksen *et al.*, 1998), resulting in improved drift modelling and larval and juvenile growth along the drift tracks (Vikebø *et al.*, 2005; Vikebø *et al.*, 2007). The new ROMS model had variable spatial resolution, allowing particularly high resolution where simulation of smaller-scale processes was critical, such as during initial transport at the spawning sites.

As pelagic offspring of cod are solely transported in the UML, it is particularly important that the numerical ocean model correctly represents the transport in this layer. The first-generation circulation models had a clear weakness in this respect, since they did not include the Stokes drift, which is the additional transport due to particles following the wave motion. In 2011, a field campaign was undertaken in Lofoten to evaluate the Stokes drift modelling by satellite positioned drifter. It turned out that the Stokes drift component was comparable to the pure traditionally modelled wind drift component and the model represented these two components well (Röhrs *et al.*, 2012). Hence, an improved method of the initial transport of eggs and larvae out from the spawning areas was thereby established. The Stokes drift model results were thereafter combined with the vertical distribution of eggs in Lofoten-Vestfjorden, detecting a stronger shoreward current component. The resulting up-concentrations of offspring closer to the coastline and a more stable longshore current direction along the Lofoten archipelago were in line with the observed egg and larval transport (Röhrs *et al.*, 2014). The often-observed sub-surface maximum in cod eggs at the core

spawning sites was explained by strong horizontal gradients in egg concentration combined with stronger current fluxes in the surface layer compared to in the layers below (Strand *et al.*, 2019).

3.5.4 Addressing connectivity mechanisms—NEA cod vs. Coastal (Local) cod

One remarkable feature of NEA and Coastal cod is the close distances among spawning sites of apparently separate stocks. Based on the knowledge on vertical distribution of eggs and larvae, it was hypothesized that differences in the coastal transport over small spatial scales during the initial transport of ELHS could lay the basis for the offspring to settle at the bottom at very different locations. Though egg specific gravity of NEA cod and Coastal cod are quite similar, the model results showed that coastal cod eggs were vertically distributed below the low-saline, out-flowing upper layers causing these eggs to be retained within the fjord system by the estuarine circulation (Myksvoll *et al.*, 2011). This retention increased throughout spring from mid-March to early May because the increasing spring freshwater discharge in May caused a more predominant low-saline upper layer. However, the seasonal cycle in freshwater discharge along the Norwegian coastline is in certain fjord systems also influenced by hydroelectric power regulation resulting in less-than-normal discharge during spring when coastal cod spawning occurs. Hence, the degree of retention of coastal cod eggs in a hydroelectric power-regulated fjord decreases because of the weaker low-saline upper layer causing the eggs to be distributed higher up in the water column and, in turn, resulting in larger offspring loss from the fjord habitat (Myksvoll, Sandvik, *et al.*, 2014). High-resolution wind forcing of the ocean circulation models—presenting thereby more realistic eddy activity—further contributed to explain the existence of these retention vs. advection areas (Myksvoll *et al.*, 2012). Finally, bank topography has strong impacts on the circulation pattern: fine-scale horizontal circulation is considered a major factor retaining offspring cod, contributing to dividing them into metapopulations along the Norwegian coast (Myksvoll, Jung, *et al.*, 2014). Hence, the model results clearly supported that minor differences in spawning sites and local salinity may result in very different settling locations for the offspring.

3.5.5 Contrasting larval and juvenile growth across the North Atlantic

The regional model advancements in Sections 3.5.3 and 3.5.4 were followed up by contrasting observational data on NEA (~68–71°N) and Nova Scotian cod (~42°N), finding that the offspring of the former grew twice as fast during summer as the daylight sufficient for feeding is 50% longer in the Barents Sea (24 hours compared to 16 hours) (Suthers & Sundby, 1996). Despite so, as 1-year-olds, the body growth of Nova Scotian cod juveniles caught up, apparently because the winter dark in the Barents Sea gave poorer food conditions compared to the lower-latitude Nova Scotian waters (Suthers & Sundby, 1996). Further to this, based on the modelled larval growth rates across latitudes, local spawning time seems an adaptation to optimal combinations of light, turbulence, and temperature, in addition to prey abundance (Kristiansen *et al.*, 2009). However, at least for Georges Bank, Icelandic, North Sea, and NEA cod, the duration of this match appears more important than a single peak (Kristiansen *et al.*, 2011), as suggested by CLP results several decades earlier (Section 2.4.2).

3.5.6 Revisiting Hjort's Recruitment Hypotheses 1 and 2

Regarding Hjort's Recruitment Hypothesis 1 (Section 2.2), parallel investigations on the Norwegian-spring spawning (*Clupea harengus*)—encouraged by access to high-resolution chlorophyll *a* and sea-surface wind data sets—revealed that about 60% of the variability in onset of spring bloom at its main spawning ground (62–63°N) is linked to atmospheric forcing (Vikebø *et al.*, 2019). Furthermore, this onset is typically delayed by 1 month from this location off western Norway to Lofoten (67–68°N), with the local variability halved over the same latitudes, implying that the time of the spring bloom is considerably more stable in Lofoten (Vikebø *et al.*, 2019). These insights are not only highly relevant concerning the seasonal prey field situation encountered by ELHS of (NEA) cod along the Norwegian coast (Sundby & Nakken, 2008) (Section 3.2.3) but also agree with the general conceptual framework that the spawning season is considerably shortened north of the "critical latitude" at ~64–66°N (Sundby *et al.*, 2016). So, the photoperiod constrains the seasonal life cycle of marine organisms due to its influence on spring bloom dynamics (Sundby *et al.*, 2016).

Modern biophysical modelling also opened for re-evaluating Hjort' Recruitment Hypothesis 2 (Section 2.2). Hjort rhetorically asked what would happen to those offspring of cod advected cross shelf into the deep Norwegian Sea instead of staying in the normal drift route on the coastal shelf to the Barents Sea (Hjort, 1914). The cross-shelf advection appeared related to the predominant wind direction: in years when southerly and westerly winds prevail the offspring are more frequently maintained on the shelf, whereas in years with more northerly wind a larger fraction ends up at the shelf break, in particular from the westernmost spawning areas (Strand *et al.*, 2017). Hjort (1914) could foresee two different destinies of the offshore fraction of the offspring: either death in the Norwegian Sea proper or return advection onto the shelf, where the offspring would contribute to recruitment of the Barents Sea component. However, a third option became evident from investigations during the present warm phase of the northern North Atlantic. One fraction, though small, of the offspring advected into the Norwegian Sea proper continued the drift towards north and west and ended up as 0-group cod onto the northeastern Greenland shelf (Strand *et al.*, 2017), considered inhospitable for cod settlement in the cool period during Hjort's work at the beginning of 20th century (Gullestad *et al.*, 2020). Any potential settling is, however, suggested by examples of young cod in trawl samples from this area being genetically classified as NEA cod (Christiansen *et al.*, 2016). It remains, however, to be documented whether these specimens will close their life cycle by migrating back to the Norwegian coast to spawn. Although this distance is no longer than from the traditional settling areas in northeastern Barents Sea, they would need to cross over deep oceanic basins. This said, fishable concentrations of spawning cod around Jan Mayen (71°N, 8–9°W), an island located on the Mid-Atlantic Ridge, have just been detected suggesting both an Icelandic and NEA cod origin (Bogstad, 2022).

3.6 Impacts of climate variability and change on recruitment strength

The above research achievements—with special reference to NEA cod—can in short be summarized by that egg production

and processes during pelagic early life stages, including specific wind conditions, apparently are contributing equally to year-class formation (Ottersen & Sundby, 1995), but where large-scale temperature variations act upon all influential factors (Ottersen & Sundby, 1995; Brander, 2019). In the Northeast Atlantic, the spring-spawning copepod *Calanus finmarchicus* plays a major role as prey for ELHS of cold-temperate species (Strand *et al.*, 2020; Kjesbu *et al.*, 2022) but also for adult pelagic fish, as Norwegian spring-spawning herring, Atlantic mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*) (Huse *et al.*, 2012; Bachiller *et al.*, 2016; Kjesbu *et al.*, 2022). In the case of the Barents Sea, an increased advection from the core production region of *C. finmarchicus* in the Norwegian Sea proper is associated with higher-than-average temperatures, whereas for the North Sea by lower-than-average temperatures (Sundby, 2000). Hence, the opposite recruitment response of Atlantic cod to warmer temperatures in these two ecosystems (Planque & Frédou, 1999) can possibly be a proxy for variations in advection of *C. finmarchicus*-rich water masses.

From the mid-1990s increased attention was given to the consequences of the interannual to decadal North Atlantic Oscillation (NAO) (Hurrell *et al.*, 2001; Stephenson *et al.*, 2003) on marine ecosystems. Less than a decade later, the larger-scale Atlantic Multidecadal Oscillation (AMO) likewise came into focus (Sutton & Hodson, 2005). The mechanisms behind the propagation of the great salinity anomalies of the northern North Atlantic Ocean during the 1970s, 1980s (Dickson *et al.*, 1988) and 1990s (Belkin, 2004) appeared due to the atmospheric action of NAO. This mode of action caused opposite volume fluxes: Atlantic water into the Arctic Ocean in the northeast Atlantic and Arctic water masses out of the Arctic Ocean in the northwest Atlantic (Sundby & Drinkwater, 2007). These salinity flux variations were also reflected in similar flux variations in the heat content of the water masses influencing local ecosystem and stock productivity (Sundby & Drinkwater, 2007).

The implications of these large-scale oceanic phenomena for spawning area displacements are important, particularly in considering impacts of climate change. The backdrop was that while the NAO impacts interannual variations in stock recruitment strength (Ellertsen *et al.*, 1989), the AMO with a cyclicity of 60–80 years (Sutton & Hodson, 2005) impacts the marine ecosystems more fundamentally by longer-term changes in species distribution (Drinkwater *et al.*, 2014). However, one necessary condition to support reproductive and recruitment success is that the altered spawning areas still upheld "the migration triangle" (Harden Jones, 1968): (1) the free (denatant) drift of the pelagic offspring from spawning area to settling area, (2) adult feeding migration, and (3) return (contranatant) migration to spawning area. The spawning areas of NEA cod are known to be displaced in concert with AMO oscillations; northwards during warm phases and southwards during cold phases (Sundby & Nakken, 2008). In contrast, shorter-term climate variability hardly affects spawning area location (Sundby & Nakken, 2008). In the late 1940s ICES participants became aware that the extensive poleward migrations of North Atlantic fish species seen from the 1920s coincided with long-term ocean warming (Rollefsen & Tåning, 1949; Drinkwater, 2006). At that time the science community did not, however, realize that this phenomenon was a glimpse of the AMO and thereby lost interest research-

wise when species moved equatorwards again during the cool 1960s and 1970s.

Today, long-term climate processes—like the AMO—have provided indispensable insights into how anthropogenic climate change might influence distribution and productivity of marine populations (Stenevik & Sundby, 2007; Hoegh-Guldberg *et al.*, 2014). In spite of this, extrapolation of poleward displacement into the future might be of questionable value at high latitudes where the timing of the spring bloom sets limits, especially north of the Artic Circle, where the spawning season of cold-temperate species is fine-tuned to match the production of prey for their larvae (Sundby *et al.*, 2016). In consequence, as fish species from lower latitudes are displaced polewards in response to climate change, they will encounter the critical latitude at around 64–66 ˚N (Sundby *et al.*, 2016) (Section 3.5.6). Farther displacement asks for a shift from a seasonally-extended (Rijnsdorp *et al.*, 2015) to a concentrated spring spawning behaviour (Sundby *et al.*, 2016). Although the recent record-high SSB of NEA cod is attributed to a warmer climate in combination with sustainable management (Kjesbu, Bogstad, *et al.*, 2014), history also tells that the warming period seen prior to the mid-20th century resulted in a parallel increase in both NEA cod and walleye pollock (*Gadus chalcogrammus*), the latter located in the Bering Sea (Hollowed & Sundby, 2014).

4 Legacy effects of CLP on present day management of NEA cod

4.1 Stock demography and maternal effects

The inclusion of maternal effects (Figure 4) was the first dedicated approach of the CLP network to establish a firmer link to the assessment of NEA cod (Marshall *et al.*, 1998) (Figure 5) in view of that stock demography is evidently strongly dependent upon the adopted exploitation pattern (Trippel *et al.*, 1997). Increased fishing mortality (F) typically leads to selective removal of the older and bigger specimens (Trippel *et al.*, 1997). Fortunately, this truncation is possible to reverse reasonably quickly if F is significantly lowered, as noticed for NEA cod following the effective implementation of a harvest control rule in the mid-2000s (Kjesbu, Bogstad, *et al.*, 2014; Rørvik *et al.*, 2022). The overall message from this lengthy research is that it is of paramount importance to maintain a rich demography to upheld the stock reproductive and recruitment potential (Trippel *et al.*, 1997; Scott *et al.*, 2006), and even more so today under climate change (Ohlberger *et al.*, 2022; Ottersen & Holt, 2023).

So far, the overall aim within the more quantitative side of maternal effects studies, considering in cases also parental effects (Nash *et al.*, 2008), has been "scaling up" (Section 3.4) instead of "scaling down," such as going from individual prespawning fecundity to TEP (Figure 5) rather than aiming at enumerating the reservoir of primary (previtellogenic) oocytes. The latter focus seems important too as these tiny oocytes are produced months ahead of the spawning season, as documented for European hake (*Merluccius merluccius*) (Serrat *et al.*, 2019) and Atlantic mackerel (dos Santos Schmidt *et al.*, 2021). This "quark" dynamics implies in the case of NEA cod that the underlying reason for the substantial variation in fecundity-at-body size (Section 2.4.3) might be much better understood by considering environmental influences in the autumn rather than as traditionally at or near spawning

grounds. Furthermore, the reality that this stock now inhabit an expanded area in the Barents Sea due to the retraction of the ice cover (Kjesbu, Bogstad, *et al.*, 2014) necessarily comes with longer spawning migrations to the Norwegian coast, especially for those individuals feedings in the northernmost subarea, potentially negatively influencing their fecundity (Kjesbu *et al.*, 2023).

The annual egg survey in Lofoten-Vesterålen, introduced by CLP (Section 2.4.2), has, with few exceptions, remained statutory up today providing a reasonably detailed spatiotemporal overview of the realized egg production (Höffle *et al.*, 2014). Such field efforts are important for detecting any trends or abrupt changes in reproductive phenology (Wieland *et al.*, 2000) and/or ELHS dynamics (Köster *et al.*, 2020).

4.2 The challenging issue of recruitment forecast

4.2.1 The impact of CLP on regional recruitment model building

CLP undoubtedly created an era of more advanced understanding of recruitment processes in the Northeast Atlantic, carried forward by later generations of marine researcher, many supervised by CLP members, in particular by Per Solemdal (Kjesbu & Sundby, 2016). ICES also played an important role (Section 3.3). This said, the first climate-related recruitment model employed in formal advice (ICES, 2008) on NEA cod, Norwegian spring-spawning herring and Barents Sea capelin (*Mallotus villosus*) was delivered by IMR (Stiansen *et al.*, 2005), very much following the lines of thoughts of CLP (Ottersen & Sundby, 1995). For NEA cod the recruitment predictors were Kola temperature, 1-year-old abundance (hence a 2-year prognosis) and capelin abundance (as anticannibalism factor) (Stiansen *et al.*, 2005). However, all these three stock-specific, multiple regression models collapsed after about 20 years and increasingly so when going from the capelin model to the NEA cod model and then to the herring model (Stiansen *et al.*, 2005), indicating that altered environmental conditions in Atlantic water masses were influential, and then in particular temperature (Kjesbu *et al.*, 2022). The loss in predictive power in the early 2000s coincided with the timepoint when Kola temperature exceeded the upper historic maximum (Kjesbu, Bogstad, *et al.*, 2014). This outline mirrors the situation seen for the documented, nearly 100-year close association between NEA cod liver index (liver weight over body weight) and Kola temperature breaking recently apart by displaying opposite trends (Kjesbu, Opdal, *et al.*, 2014).

4.2.2 Current status and tactical advice

The ICES Arctic Fisheries Working Group (AFWG) has introduced, discarded, re-introduced, and combined a series of recruitment prognosis models (1–4 years) over the last couple of decades, with an increasing use of advanced statistical modelling in R (ICES, 2021). For the time being, the selected explanatory factors are temperature, oxygen saturation, and ice coverage (Titov, 2021) (given high model weight) as well as recruitment indices (Shepherd, 1997) (given low model weight) to mimic the "true" recruitment at age 3 years (3y) from the state-space assessment model (SAM) (Tchetyrkin, 2021). In this multiple linear "hybrid" model, each separate model shows r > 0.5 (ICES, 2008). For the studied period 2008–2021, the model reflected well the trend in SAM3y (Tchetyrkin, 2021). Both ice coverage and oxygen saturation are,

however, function of temperature (given from the Kola Section), implying collinearity issues. Furthermore, the inclusion of oxygen saturation seemingly lacks causal explanation in this open, cold-water, oxygen-rich ocean basin (Pitcher *et al.*, 2021; Kjesbu *et al.*, 2022). Overall, this type of model constructs for NEA cod should, as recommended by Karp *et al.* (2020), consult "the large body of work focusing on understanding the biological processes," where CLP still stands out as one of the principal providers and ambassadors, as documented in earlier sections.

4.2.3 The forward-looking perspective

Despite that this review illustrates great leaps forward in the understanding of mechanisms ruling offspring survival rates of NEA cod, several of these findings should be revised, complemented, or generalized to further advance the accuracy and precision in recruitment forecasts. In our "to-do list" (Table 1), we summarize—based on this review—immediate to longer-term research initiatives that may help reducing the uncertainty in recruitment forecast of marine fish. The listed topical points span from "omics" to "number crunching" within the assessment working group in question, so going from truly basic to applied science. In the spirit of CLP, this work should be done in a coherent, step-wise, interdisciplinary fashion. Below, we go deeper into a few of the topical points, either because of the limited information at hand for now, or the extreme complexity involved (and thereby not specified in Table 1).

As Hjort (1914), CLP did not *de facto* investigate the extent of predation on eggs and larvae, although at some point during the life of this project acknowledged to be a key mechanism in recruitment regulation (Section 2.4.2). Neither did CLP address the predation pressure at the 0-group stage or, alternatively, the density-dependent *M* during the settling stage (Myers & Cadigan, 1993). Anyhow, to move forward, we would argue that proper tools need to be implemented to be able to *reliably quantity* the level of consumed ELHS by the predator (Table 1), exemplified by published cases of a high number of larval gene copies (herring) in visually empty (or "larvae-free") predator stomachs (mackerel) (Allan *et al.*, 2021). Associated digestion rates are, however, yet seemingly missing, or not relevant in the given situation, reducing the value of running consumption models (Allan *et al.*, 2021).

Overlying the given to-do list (Table 1) comes the need for improvement in ELHS modelling as such (Section 3.3 and 4.2.1), deserving extra comments due to the multifaced integration schemes, exciting perspectives but also open-ended research questions. For instance, would it be possible to instantaneously track offspring transport and growth based on weather forecasts from the time of NEA cod spawning in March and April along the Norwegian coast until near-bottom settlement in the Barents Sea during September? Essentially, by applying state-of-the-art IBMs embedded in ocean climate/circulation models, it might be feasible to accumulate discrete events on single grid-cell level critical for offspring survival and thereby integrating recruitment indices over time and space. However, such numerical upscaling is not necessarily reproduceable. The main problem apparently rests with that predator-prey relationships basically reflect particle encounters, but where the degree of patchiness is highly stochastic in nature and therefore, seemingly, unpredictable. This hurdle closely relates to lack of local insights in micro-patchiness and the consequences of small-scale turbulence on successful

Table 1. Proposed to-do list for improving the quality of tactical recruitment forecast for NEA cod, supplemented with more general aspects of relevance for the wider range of marine fishes. Arrows indicate the stepwise workflow in a life-history perspective, split into basic (yellow fill) and applied research (blue fill), along with the three different levels of priorities (immediate, shorter- and longer-term). This list should be considered as incomplete; new topics will emerge as science advanced but also with alterations in the strength of climate stressors.

Topic	Priority	Logic
predicting recruitment age 3 years	immediate to longer-term (depending upon resolution)	The modelling work in e.g. Stiansen *et al.* (2005) (Section 4.2.1) should be followed up by including any improvements in parameterization of the below-outlined topical explanatory factors (and conceptual framework). Regime shifts and non-linearity issues should be tested.
1–2 group	immediate	This survey information has so far been underutilized in tracking the fate from TEP to recruitment at age 3 years. The variability in abundance might be particularly high at age 1 year (Langangen *et al.*, 2013).
0-group	immediate	The most recently standardized time series on 0-group indices and 0-group length (Skjoldal *et al.*, 2022) should help deciphering the numerical level of survivors and their accumulated living conditions up to the end of the critical period.
larval predation	shorter-term	Due to the poleward migration of many planktivorous species like Atlantic mackerel (Nøttestad *et al.*, 2016), the prey field changes as well. Besides, molecular tools are today available to quantify predator gene copies in stomachs, although disintegration rates are seemingly yet missing (Allan *et al.*, 2021).
larval prey	longer-term (general)	Although the temperature conditions encountered by *C. finmarchicus* is still within the tolerable range in the Barents Sea (Strand *et al.*, 2020), the distribution of this copepod and thereby the nauplii prey for the cod larvae is today evidently displaced northwards, at least in the North Sea (Kjesbu *et al.*, 2023). Hence, zooplankton biogeography requires close attention.
$M \times G$	longer-term (general)	Mortality (*M*) vs. growth (*G*) inventories across species (Houde, 1987; Miller *et al.*, 1988; Pepin, 1991) should be i) updated and complemented, ii) grouped by tropical, cold-and warm-temperate and Arctic species (Kjesbu *et al.*, 2022), and, at least for cold-temperate species further sub-grouped by habitat, e.g. ELHS of North Sea cod performs very different than those of NEA cod under ocean warming (Kjesbu *et al.*, 2023).
egg mortality	shorter-term	The Russian ichthyoplankton time series (1959–1993) (Langangen *et al.*, 2013) should be merged with the IMR egg survey time series (1983-today) (Höffle *et al.*, 2014) to revise figures on annual egg mortality rates (Langangen *et al.*, 2013) back to fertilization.
TEP	immediate	The age diversity of NEA cod has largely recovered in the last decade implying that the TEP has increased for a given biomass due to positive maternal effects (Marshall *et al.*, 1998).
spawning phenology	shorter-term	Plans for NEA cod egg surveys and maturity monitoring should consider that the spawning phenology might be extended nowadays, as seen for Baltic cod since the 1990s (Wieland *et al.*, 2000).
fecundity	immediate	The generally longer and faster spawning migration seen currently for NEA cod is expected to lower the individual fecundity due to higher swimming costs (Kjesbu *et al.*, 2023).
maturity schedules	shorter-term	Age-at-50% maturity in NEA cod has underwent marked changes but this historic reaction norm is seemingly not backed-up by genomic changes (fisheries-induced evolution) (Pinsky *et al.*, 2021), suggesting other routes of adaptive changes (Rørvik *et al.*, 2022), or, potentially, sampling issues.
"omics"	longer-term	Growing evidence suggests that transgenerational effects are important for phenotypic adaption of the offspring to climate variability (Skjærven *et al.*, 2014).

larval feeding, although the paramount role of wind force in these respects is now firmly documented in general terms, both theoretically and operationally (Section 2.3.5, 2.4.1 and 3.5.2).

Additionally, for NEA cod, we would need to be able to forecast the weather during the half-year period of offspring denatant drift. Although seasonal weather forecasts have recently been issued with NAO as an important driver (Kol-

stad *et al.*, 2020), they do not—at least for now—display the needed spatiotemporal precision. In principle, however, it should be possible to mimic the real-time environmental conditions encountered by the larvae from consecutive weather forecasts, as illuminated for cod and herring (Vikebø *et al.*, 2011). A first step would be to link larval and pelagic juvenile trajectory models, cf. joint IBM-ocean circulation models, to models of distribution and abundance for prey. Secondary
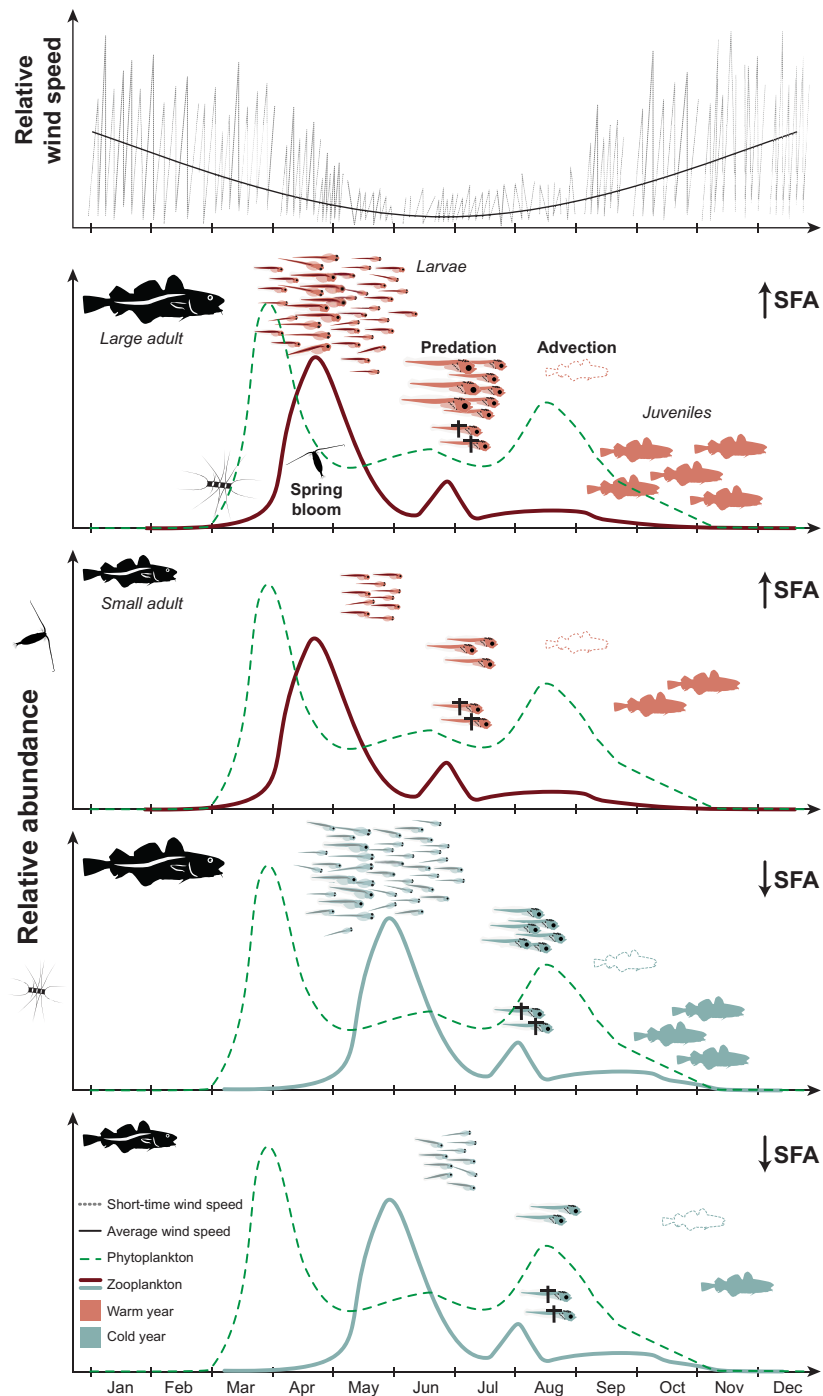
Figure 6. Schematic illustration of the above-reviewed key mechanisms affecting the survival potential of offspring of NEA cod, split into a relatively warm and cold year situation, with the wind speed superimposed. The cod spawning time is seemingly not only adapted to the appearance of the spring bloom and the following zooplankton (nauplii; larval prey) production but also optimal wind conditions (turbulence mixing) to enhance larval first-feeding success. Thus, the wind speed in winter is typically too strong and in summer too weak in this respect. The timing of the spring bloom is principally defined by the seasonal light cycle, whereas the appearance of the nauplii peak is significantly more variable due to varying temperature across years in the UML. In effect, sufficient concentrations of nauplii appear later in the season in a relatively colder coastal current. In contrast, the spawning phenology of NEA cod is remarkable stable, at least up today. This divergence implies that the larvae produced from a larger cod—spawning over a longer period than a smaller cod—will have an increased chance to match the prey peak. Provided that a larger female also generally spawns earlier, the markedly higher number of bigger larvae from this specimen will match the prey peak better than those of a smaller specimen, especially in a warm phase. On top of these size-specific trait differences comes that larvae from a larger female are likely more spread spatially due to their higher variation in buoyancy during the course of spawning, possibly increasing the chances to hit patches of nauplii. However, the critical period appears significantly longer than thought earlier due to the important effect of predation at a time when the larvae and postlarvae show little capacity to actively move themselves. Advection also contributes to reduce the number of offspring. When the adults return to the Barents Sea they will benefit from a more relaxed density-dependent effect in a warm ocean due to the significantly larger suitable feeding area (SFA) increasing stock productivity but not necessarily individual fecundity for the next season due to longer spawning migrations. The phytoplankton and zooplankton curves were reproduced from Falkenhaug et al. (2022) and Melle et al. (2004).

production models, with special reference to the key prey copepod *C. finmarchicus*, have already been run for one decade (Hjøllo *et al.*, 2012; Skaret *et al.*, 2014). Hence, it is certainly possible to link the model systems for secondary production and fish larval growth. However, as for the forecasts of ocean circulation, validation on zooplankton distribution and productivity on a smaller scale have not yet been done. Nevertheless, along this route of investigations one might ask the rhetorical question: What should then be considered as correct; the field observations or the model results?

So, predicting fish recruitment by building up quantitative biophysical models via SSB or even better TEP (Figure 5)—to make the necessary link to stock status in tactical advice—and thereafter integrate the foreseen deterministic processes (Table 1) is still out of reach more than 100 years after Johan Hjort outlined the grand challenge (Hjort, 1914). But the number of the pieces of the puzzle in place is steadily increasing, and from both the biological and physical perspective, we now know that some life-history traits (sensitivity attributes) and climate variables (exposures), respectively, are far more important than others for successful cod recruitment (Sundby, 2000; Drinkwater, 2005; Brander, 2019; Kjesbu *et al.*, 2022; Kjesbu *et al.*, 2023). Ocean temperature is a key overarching driver for ecosystem variability and change at high latitudes and has been broadly documented to impact marine life at all levels through the food web. Wind forcing and its mixing of the pelagic layer is key to local plankton production (Vikebø *et al.*, 2019) and is hence a more specific driver than ocean temperature as such; the impediment of the latter forcing is the difficulty to understand the mechanistic link between environmental temperature, either observed or modelled, and the specific marine population.

5 Conclusions

CLP was inspired by Hjort's seminal work of 1914 (Hjort, 1914) and commenced with the ambition of testing one single element of his ideas: Is year-class strength determined by starvation during the short period of larval life just after yolk-sac absorption? During the project it became clear that the determinants of recruitment variability of Atlantic cod are considerably more diverse. In fact, such variability can result from numerous processes (Houde, 2008), although the aspect of match-mismatch between abundance of fish larvae and their prey (Cushing, 1990), encompassing the outlined, influential maternal contribution (Solemdal, 1997), is still considered a particularly important recruitment process for fishes at high latitudes (Houde, 2016) (Figure 6). However, the surplus production of the entire stock of NEA cod is also steered by the accessibility to energetic food items (Holt *et al.*, 2019), including the size of the suitable feeding area (SFA, in km^2) in the Barents Sea, the latter significantly expanding in a warm climatic phase (Figure 6).

CLP succeeded in many of its goals to *understand* the central processes in reproduction and recruitment of Atlantic cod. Several of these fundamental findings are generally applicable to teleosts, such as biophysical and maternal factors influencing egg production, vertical distribution of ichthyoplankton, turbulence-induced encounter rates, and light responses in visual planktonic feeders. However, when these facets are integrated in today's IBMs, we are encountering great challenges when it comes to applying the outputs in prediction

exercises, primarily due to the stochasticity of the latter two factors. None of today's high-resolution ocean models have the capacity to reproduce ambient light and wind conditions for feeding offspring, even in hindcast modelling. Contrarily, sea temperature, salinity, and oxygen content influence ichthyoplankton on considerably lower spatiotemporal frequencies than *in-situ* wind and light. In consequence, the effects of the former three can be modelled with much higher precision than the latter two. Besides, long time series of sea temperature exist in the North Atlantic. Therefore, such ocean climate parameters, and then particularly temperature, are convenient to apply as effectors (Section 4.2.1 and 4.2.2). However, the intrinsic problem with applying sea temperature in predictive models is that it influences fish stocks *directly* as well as *indirectly* through other climate processes (Pepin, 2015) and, consequently, high correlations established for one period tend to collapse in other periods as the components within the ecosystem alter (Section 4.2.1). This circumstance demonstrates the need to better understand the functional mechanisms behind ecosystem changes.

Finally, it must be emphasized that the influence of long-term changes in population growth and distribution linked to natural multidecadal regional climate signals and to the longer-term global climate change goes far beyond strong recruitment success of single year classes. For iteroparous, multiple spawners, such as cod, we have in the past probably overfocussed on the importance of strong single year classes compared to the effect of year classes of modest strength repeatedly occurring year after year. Since the 1970s, the NEA cod has produced only a few, relatively strong year classes (ICES, 2021). In parallel, the number of recruits per tons of SSB has shown a declining trend (Rørvik *et al.*, 2022). Despite this, the SSB became record high in the beginning of the 2010s (ICES, 2021). Increased ocean temperature in the Barents Sea together with sustainable management are believed to be the overarching factors behind this substantial growth in the SSB (Kjesbu, Bogstad, *et al.*, 2014). Although the SBB thereafter went down, its current level is still high in a historic perspective (Hylen, 2002; ICES, 2021). So, under near-future climate change the NEA cod stock is foreseen to continue with a relatively high surplus production (Kjesbu *et al.*, 2022).

science issues from an entirely different angle. For that reason, he loved in-depth research discussions. In cases his forceful inputs—always well-intended—could be like "if you think you have a new idea, you have not read the literature well enough" (as communicated to the first author as PhD student). Such statements were rooted in a strong dedication to and recollection of marine history (Kjesbu & Sundby, 2016; Kjesbu *et al.*, 2021). Solemdal's rhetorical gifts helped open the door for significant funding schemes. Today, in the era of holistic ecosystem approaches, we can only imagine being granted single-stock, experimental research cruises with such long length and persistence in combination with plentiful of laboratory studies.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the article.

Author Contribution

Conceptualization: OSK, IT, and SS; activation of unpublished, historic information (at IMR): IT, AT, and OSK; reviews of already published articles: OSK, and SS; visualization: IT, MA, and OSK; first manuscript draft: OSK, SS, and IT; final manuscript draft: OSK, SS, MA, IT, and AT.

Data Availability

The presented data were extracted from the literature—as specified in each case in the main text—or from assessment expert reports (ICES, 2021), accessible via the ICES website (www.ices.dk).

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