

Adjusting Hjort’s “critical period” hypothesis to the southern range of cod

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Abstract. Hjort put forward the availability of food to first feeding larvae of Arcto-Norwegian cod (*Gadus morhua*) as the primary driver of recruitment variability in the Barents Sea, later known as the “critical period” hypothesis. However, given the large latitudinal range of the Atlantic cod and the boreal affinity of its most important prey during the larval stage, the copepod *Calanus finmarchicus*, the challenges of matching larval development with the seasonal dynamics of *C. finmarchicus* is expected to vary. In this study we set out to apply Hjort’s widely acclaimed critical period hypothesis to the recruitment of cod (*Gadus morhua*) in Skagerrak nursing grounds, which according to recent surveys is among the most southern nursery grounds of significance for the species on the east side of the Atlantic. Our investigation was designed to discern the environmental and biological factors that contributed to a good year class for recruitment of cod in the Skagerrak, including potential drift of pelagic juveniles from the North Sea validated by field sampling and genetic assignment of settled juveniles. We put special attention in our analyses to the year of 2011, as this was by far the best year class for cod in the Skagerrak throughout the past decade. The only significant deviation from a normal year found in the physical environment was that the Norwegian coastal water was colder than usual in winter. We hypothesis that the colder winter temperatures may have slowed down the seasonal development of the zooplankton, leading to a later peak as well as stably high availability of *C. finmarchicus* copepodites to cod larvae throughout the settlement period. Thus, in contrast to the popular interpretation of Hjort’s hypothesis, that proclaims the end of the yolk sac stage to be the crux point for the year class of cod, we hypothesise that the period from settlement to the transition to benthic feeding is the decisive period in Skagerrak nursing grounds. The rationale being that during this time period when metabolic requirement is at it’s highest, as this coincides with peak temperatures, any variability in the zooplankton that the larvae still are dependent on could prove fatal.

Introduction

One of the oldest conundrums in fisheries biology is the determinants of year class strength. In his treatise on “Fluctuations In The Great Fisheries Of Northern Europe” (1914), Hjort put forward the availability of food to pelagic larvae as the primary driver of recruitment success. He observed that at the time of spawning of the Arcto-Norwegian cod (*Gadus morhua*) the water around Lofoten was devoid of zooplankton and remarked that the cod probably spawned at that particular time in anticipation of the spring bloom, to ensure that larvae hatched when the availability of food would be at its peak. His rationale was that the presence or absence of food at the time when the larvae had absorbed their yolk sac would largely decide the year class strength. Cushing (1990) later generalised this notion that a coinciding (or separate) peak in prey abundance with the extent of the larval phase would prevent (or induce) bottlenecks in population numbers, and termed it the Match-Mismatch hypothesis. However, in for example the North Sea, high recruitment of cod has been found to be dependent on high abundance of zooplankton throughout the early phases of life, and even more so at the end of the larval stage (Cushing 1984, Rothschild 1998). This by no means discredit the “critical period” as a concept, because it was already loosely coined in the first place, as we can read under the header *Origin of the fluctuations in renewal of the stock* (Hjort 1914, p.202), where Hjort summarises his thoughts on the causality of the variability of the great fisheries of herring, cod, and haddock in the Nordic Seas: “It ... appear most probable that the renewal of the fish stock ... is dependent upon many factors, all necessary, and all more or less variable. Thus in each individual instance, the *missing factor* will appear to be that which *determines the ultimate result*”. Given the large latitudinal range of the Atlantic cod (spawning from 50°N to 70°N on eastern side of Atlantic) and the boreal affinity of its main pelagic prey during the early stages of life, the copepod *Calanus finmarchicus* (Heath & Lough 2007, Melle et al. 2014), the challenges of matching larval development with the

seasonality of *C. finmarchicus* is expected to vary along their range (Sundby 2000). For example, in the Skagerrak the abundance of *C. finmarchicus* usually build up from next to nothing in early February towards a peak in April, upon almost disappearing from the upper water column in summer. This in contrast to the main spawning ground of the Arcto-Norwegian cod in the Lofoten archipelago, which has a comparably vast abundance almost year round, except a short period of absence in February to March (Melle et al. 2014). Since the mean hatching date of cod throughout its east Atlantic range is quite conservative, with a peak hatching rate around 1st of April in the Skagerrak and 10th of May north of Lofoten (Suthers & Sundby 1993, Øresland & Andre 2008), the challenge for larval cod in their southern range is rather that the bloom of *C. finmarchicus* is already over before the larvae have time to capitalise on them, unlike dying of starvation before the bloom. If we also take into account that summer temperatures are at least ten degrees warmer in the littoral nursery habitat in the Skagerrak than in the Barents sea, and knowing that metabolic requirement of fish increases exponentially with temperature (e.g. Clarke & Johnston 1999), any variability in *C. finmarchicus* abundance during that critical summer period may prove sharply defining to the year class strength.

Since the restructuring of the survey program of the North Sea cod stock in 1992, the international bottom trawl survey (IBTS) now encompasses the entire North Sea as well as the southern Skagerrak (ICES 2015). Recent surveys suggest that most of the one year old recruits of the North Sea cod stock are found in the southern Skagerrak nursery areas (Hjermann et al. 2013, Nicolas et al. 2014, ICES 2015). Northern Skagerrak nursery habitats have also been surveyed along the Norwegian coast since the dawn of the 19th century, and together these two data sets offer a unique perspective on long-term as well as short-term recruitment patterns in the Skagerrak. The variability in recruitment to Skagerrak nursery areas is large, and typically has a series of mediocre and bad years, interrupted by a good year

94 now and then. The good years of the past three decades are by far the seasons of 1996, 1998,
95 and 2011, and in these years we find good recruitment across the entire Skagerrak.
96 Explanations have been many on what creates the variation in cod recruitment to Skagerrak
97 nursing grounds, from overfishing (Cardinale & Svedäng 2004), inter -and intra cohort
98 competition (e.g. Fromentin et al. 2001), variable import from the North Sea (Stenseth et al.
99 2006), to variability in the prevalent wind field and large scale climatic phenomena (Lekve et
100 al. 2002). However, more similar to the match-mismatch hypothesis of Cushing and critical
101 period hypothesis of Hjort, Johannessen (2014) put forward an interesting hypothesis
102 regarding recruitment of cod in Skagerrak. His studies suggest that recruitment in general is
103 decoupled between the pelagic to benthic phase, largely because the number of cod larvae
104 surviving the settlement phase is dependant on food conditions in terms of quantity and/or
105 quality during summer. In short, the answer to this question remains many-faceted. The scope
106 of this study was thus quite simply to evaluate the leading hypothesis on what drives
107 recruitment of cod in Skagerrak. Our primary objective was to apply the “critical period”
108 hypothesis of Hjort to nursery habitat in the southern range of cod, where challenges to the
109 development of larvae may be fundamentally different than were the concept first was coined.
110 Our secondary objectives was to investigate the possible drift routes taken by North Sea cod
111 larvae that have frequently been reported settling into coastal Skagerrak nursery grounds
112 (Knutsen et al. 2004, 2011, Stenseth et al. 2006) as well as to evaluate the impact climatic
113 variables may have on recruitment in Skagerrak littoral nursing areas (Lekve et al. 2002,
114 Rogers et al. 2011). Our investigation was designed to discern the environmental and
115 biological factors that contributed to a good year class for recruitment of cod in Skagerrak and
116 contrast it to a mediocre year. We put special attention to the year of 2011, as this was by far
117 the best year class for cod in these waters throughout the past decade. To evaluate the impact
118 of food availability on recruitment, we analyse the phenology of the copepod community

sampled bimonthly over the two years. In our analyses we focused on the species of copepods that has been shown to be important food items of cod larvae, in decreasing order of importance: *Calanus spp.*, *Paracalanus/Pseudocalanus*, and *Oithona sp.* (Heath & Lough 2007). Our queries on the role of import of larvae and pelagic juveniles from the North Sea to Skagerrak nursing grounds were addressed by the deployment of a biophysical dispersal model of the Skagerrak and the northern North Sea, coupled with empirical data on the distribution of potential cod egg production. We validated our modelled drift trajectories and settlement distribution with recruitment data of half-year old cod collected in the Skagerrak as well as genetic assignment of the recruits. And lastly, to evaluate the climatic impact on recruitment, we analysed empirical data on the physical environment experienced by eggs and larvae over the two contrasting years, both the early pelagic habitat and the later benthic nursery areas.

Materials and methods

The biophysical dispersal model of cod early life stages

To derive an estimate of the potential spawning distribution in the northern North Sea, we extrapolated potential egg production from the annual ICES international bottom trawl survey (IBTS, quarter 1). This survey is run between January and March every year, and is designed, among other things, to assess the spawning stock biomass of cod. We used the coordinates of the survey hauls as release points in our drift simulations, and the number of eggs released was calculated from the number of fish of different size classes caught at that location (see Fig. 1 for spatial distribution of calculated egg production within model domain). The potential egg production at each location was calculated using a simple equation for fecundity of cod: $F = 5.4 \times L^3 - 13000$ (eqv. [3] in Oosthuizen & Daan 1974), where F is number of eggs, and L is length class of cod binned into 10 cm intervals. The long-term average fraction (i.e.

over the last decade) of potential North Sea egg production that was within our model's domain was 58%. The modelled egg production at a given site was then portioned out over the spawning season typical of the North Sea cod in a normal distribution, from February 2nd to May 9th (Brander 1994). To simulate spawning behaviour observed in the wild (e.g. Rose 1993), the eggs were released uniformly from one meter above the sea bottom, up to 40% of bottom depth (e.g. up to 20 m when total depth was 50 m) at each release site.

At the initiation of each drift simulation, eggs were assigned an individual buoyancy value measured in practical salinity units. As no studies has quantified buoyancy of North Sea cod eggs, we used values typical of Arcto-Norwegian cod, between 33 and 34 (Sundby 1997). Density of eggs was then calculated as a function of its pre-set salinity equivalent and the eggs' in-situ sea temperature (Coombs et al. 1981). At each time step of ten minutes, the egg was then pushed either upwards or downwards depending on the hydrostatic pressure acting on it. Egg incubation time was calculated as a function of temperature (Peterson et al. 2004), and larvae experienced temperature dependent growth (Folkvord 2005). In the wild, young cod larvae are generally found within or immediately below the pycnocline (Munk 2014), while older larvae are found deeper (Lough & Potter 1993). Cod larvae are also known to display a vertical movement of up to 10 m over the course of 24 hours (Höffle et al. 2013, Munk 2014), indicating some active movement in the water column. However, during episodes of high wind-induced turbulence, smaller larvae have been shown to be mixed homogenously in the water column indicating that their vertical position is not maintained if convectional forces are too high (Ellertsen et al. 1984). Thus, from hatching until time of first feeding our modelled larva had little swimming capability (max 10 cm per 10-minutes), vertical position was mainly regulated by their density (Saborido-Rey et al. 2003), and they were programmed to attract towards the pycnocline. After the time of first feeding, we hypothesised that vertical position was regulated by larva's behaviour in response to light.

169 The rationale is that a certain amount of light is needed to feed, while too much light would
170 increase predator exposure. Thus, the feeding larvae were programmed to swim upwards if
171 situated below the isolume of 1 W/m^2 , downwards if above the isolume of 10 W/m^2 , and
172 remain and remain at their vertical level at onset of total darkness. Maximum swimming
173 speed of feeding larva smaller than 10 mm was set to 0.5 m per 10 min, while bigger larvae
174 were allowed to swim up to 1 m per 10-minute time step. The potential integrated vertical
175 swimming distances used in the model was well below critical swimming speeds observed in
176 laboratory experiments (Guan et al. 2008), as there is no empirical evidence that the
177 maximum swimming ability is realised in the wild. To account for vertical mixing
178 experienced by eggs and larvae, a pre-set vertical perturbation component was added at each
179 time step. If mixed downward into the transition layer with higher density and when situated
180 below the upper mixing layer, one tenth of the mixing coefficient was used. The mixed layer
181 depth was calculated from the hydrodynamic model as the depth where the vertical gradient in
182 water density was highest. Particle advection in the horizontal plane was modelled using a
183 fourth-order Runge-Kutta scheme with the velocity field arrays from the hydrodynamic
184 model. We included no horizontal swimming behaviour to larvae in our model. When larvae
185 reached a size between 25 mm and 50 mm they were defined as ready to settle (this size class
186 of larvae is henceforth termed the pelagic juvenile stage), as this is the size range of newly
187 settled cod observed along the Skagerrak coast, down to no deeper than 40 m (Johannessen *et*
188 *al.* 2014). To quantify the spatial distribution of settlement along the coast, we integrated the
189 number of days spent by pelagic juveniles in proximity of each grid point of our hydro-
190 dynamical model that was shallower than 40 m. The bottom areas of our model constrained
191 by the upper 40 m were thus defined as nursery habitat of the cod along the Norwegian
192 Skagerrak coast.

The circulation model used was the Regional Ocean Modelling System (ROMS, <http://myroms.org>), a free-surface, hydrostatic, primitive equation ocean model (e.g. Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). The circulation model was run with 800m resolution in the horizontal and using 35 topography-following levels in the vertical over a time period of 2×180 days (from February 1st to August 1st in addition to spin-up) for two consecutive years (2011 and 2012), and was forced using daily averages of currents and hydrography along the open boundaries from a large-scale 4km-model covering the Nordic Seas (Lien et al., 2014), high-resolution wind fields (Weather Research and Forecasting model, WRF, using 3km horizontal resolution, see Skamarock et al. [2008]) and realistic freshwater discharge from all rivers in the model domain (provided by the Norwegian Water Resources and Energy Directorate, see Beldring et al. [2003]). The time-varying arrays from the ROMS model had a temporal resolution of two hours and contained horizontal current fields and hydrographic variables covering a total area of 880×850 grid points, giving a total model area of approximately $704 \text{ km} \times 680 \text{ km}$. More technical details on the ROMS simulation can be found in Albretsen et al. (2011). To validate the ocean model, we compared its physical output variables (salinity and temperature) with hydrographical data routinely sampled within the model domain. Overall, the model compared well with observations, with no significant biases in predicted salinity or temperature, equivalent to former and more comprehensive validation analysis of the same modelling system shown in e.g. Myksvoll *et al.* (2013).

Field sampling and statistical analyses

Every year since 1919, with a few exceptions during WWII, there has been an annual collection of half-year-old juvenile cod along the Norwegian Skagerrak coast using a standardised beach seine-sampling regime. Average catches vary substantially among years in

218 this survey, and there is considerable spatial variation in abundance both within and between
219 years at the ca. 135 stations sampled today. To be able to directly compare the modelled
220 distribution of settlement from the northern North Sea with the abundance of the half-year-old
221 cod sampled in nursery habitat in September, we projected both of the geo-located spatial
222 abundances onto a new axis running parallel to the southern Norwegian coast, corresponding
223 to the horizontal axis of the ocean model (rotated $\approx 45^\circ$ relative to true north), binned into 800
224 m intervals corresponding to the resolution of the model. Prior to a correlation test, we
225 applied a mild smoother to the spatial abundance projected on the new axis, effectively
226 averaging the 800 m bins that had several observations between each grid point, and giving
227 the grid points along the new axis with no sampling coverage an interpolated value. We thus
228 imposed a spatial autocorrelation on the raw data; however this is already a common feature
229 in the data set, with significant spatial auto-correlation out to more than 30 km (Rogers et al.
230 2014). Note that cod found along the Skagerrak coast belongs to at least two genetic groups
231 where one is similar to the North Sea cod and dominates the outer parts of the coast, while the
232 Norwegian coastal cod is more prevalent in more sheltered locations (Knutsen et al. 2011).
233 Thus to validate the origin of the half-year-old cod collected by beach seine along the
234 Norwegian coast in 2011 (i.e. North Sea like or local origin), a total of 815 individuals from
235 11 locations were scored for genetic origin, identified by 26 single nucleotide polymorphisms
236 unique to either the North Sea or Norwegian coastal cod. Because genetic assignment of
237 individuals only had two possible outcomes applying this method and that origin-estimates
238 from larger beach seine hauls (up to 800 individuals per haul) were sub-samples of what was
239 actually caught, we deemed the Wilson interval as appropriate for estimating the confidence
240 interval of the true proportions present in the area (Brown et al. 2001). To compare
241 recruitment level on the Norwegian Skagerrak coast with recruitment in southern Skagerrak,
242 we used the data from the ICES IBTS for the third quarter. This sampling cruise is done in

autumn and is designed (among many things) to survey the abundance of half-year-old cod in the North Sea and southern Skagerrak. We thus tested for a correlation between mean yearly abundance per trawling hour in the Skagerrak division of the IBTS with the mean annual abundance in beach seine hauls along the Norwegian Skagerrak coast, which had a temporal overlap of 21 years, from 1992 to 2013.

The environmental variables analysed in this study were collected along a regular transect with ten fixed, nearly equidistant stations running across Skagerrak, between Torungen (Norway) and Hirtshals (Denmark). The variables collected were: salinity, temperature, chlorophyll, nitrogen, phosphorous, and oxygen; all measured at 0, 5, 10, 20, and 50 m. These measurements have been taken approximately once a month from 1988 until 2012. Coarsely we can divide the sampling stations into three groups based on what water mass they are sampling: (1) the stations closest to the Danish coast sample the water coming from the southern North Sea, high in nutrients and with a noticeable freshwater content coming from the major rivers of continental Europe; (2) the stations in mid Skagerrak has a thin layer of fresher water on top with a mixed origin but mostly samples the Skagerrak mid and deep waters, which is similar to the water found in the northern North Sea; and (3) the stations closest to the Norwegian coast usually samples the Norwegian coastal water and the coastal current, with a high influence of freshwater from the Baltic and the major Norwegian rivers running out in Skagerrak (Kristiansen & Aas 2015). To get an overview of the primary modes of variability of the sampled physical environment in the period winter to early summer (i.e. encompassing the period from spawning to settlement), we did a principal component analyses on the physical variables. To give each of the variables equal weight in the analyses, we did a Hellinger transformation of the raw data (i.e. the data was standardised and square-root transformed). Additionally, to get a more detailed overview of how the temperature in 2011 developed compared to the normal the past three decades, we fitted a

generalised additive mixed model (GAMM) to the \approx monthly measured temperature at 20 m, at the ten stations across Skagerrak; as this is the closest depth segment sampled that the cod larvae are usually found (e.g. Munk 2014). A random intercept was also included in the temperature model, allowing the yearly intercept at each station to vary according to normal distribution (i.e. a random intercept mixed model). Moreover, to evaluate the impact temperature in the littoral zone may have on recruitment, which is the primary nursery habitat for cod along the Norwegian Skagerrak coast; we also measured temperatures daily at 1 m, from 2009 to 2012. These temperature measurements were done at two different locations, in the Flødevigen bay, just inshore of Torungen, and in Drøbak situated in the mid-Oslofjord (roughly 175 km apart). To quantify the anomalies in summer temperature, we fitted a GAMM to the daily mean temperature, also here allowing the yearly intercept at each location to vary according to the normal distribution.

Approximately one nautical mile offshore from Torungen (at the second sampling station of the hydrography transect 58°23'N 8°49'W, see figure 1) we collected zooplankton samples bimonthly, from January 2011 to December 2012. Zooplankton sampling was done by vertical hauls with a WP2 net (180 μ m mesh, 0.25 m² mouth opening), from 50 m to the surface. The zooplankton vertical hauls were thus sampling the coastal water and coastal current for the most part, and a small part of the deeper Skagerrak water. Samples were preserved in 4% borax buffered formaldehyde-seawater solution for species identification and enumeration. To determine the contribution of the single-most important food item (i.e. *Calanus spp.*) to the biomass of the zooplankton samples, we multiplied developmental stage counts with stage-specific weight estimates from the literature (Heath et al. 2000). Note that for the early developmental stages of *Calanus spp.*, from nauplii to stage IV, *C. finmarchicus* and *C. helgolandicus* were pooled together. And although *C. finmarchicus* is frequently cited as the most preferred species for cod larvae, traditionally there appears to have been put little

293 effort into distinguishing *C. finmarchicus* from sister species *C. helgolandicus* (Heath &
294 Lough 2007)—but for most practical comparisons they are identical, where for example
295 differences in size and mass of lipid storage is more variable among geographical populations
296 within the species range than between the two species (Wilson et al. 2015).

Results

Oceanographic conditions

The physical conditions in the pelagic habitat experienced by eggs and larval stages, sampled across Skagerrak throughout winter and spring, showed little deviance from the typical pattern since 1988. This can be deduced from the principal components analysis where observations in 2011 does not occupy a distinct area in the diagram but are distributed more or less evenly around the average measurement (i.e. the centre of the diagram). However, there were a few measurements of unusually high oxygen and chlorophyll concentrations in the Norwegian coastal water in February 2011, along with colder temperatures than normal (Fig. 2A). On closer inspection, this low temperature in the Norwegian coastal water in February 2011 was not sustained for long, but the cold bliss could be measured in all depths down to 20 m. However, this mid-water-mass warmed up unusually fast this year, and ended up being warmer than normal in the subsequent summer (Fig. 2B, C). Temperature in the littoral zone in late spring, summer, and autumn however, did not deviate from the normal since 2009, neither in the measurements taken inshore of Torungen nor in the Oslofjord (Fig. 2D).

Drift, settlement and recruitment

Of all pelagic juveniles produced in the model domain 1.3% and 1.6% spent their “settlement window” in Norwegian Skagerrak coast nursery habitat in the 2011 and 2012 spawning seasons. However, 4.6% and 5.5% of all the modelled pelagic juveniles spent at least one of their settlement days in Norwegian Skagerrak nursery habitat, whereas 7.4% and 9.5% of all the individual propagules (integrated over all pelagic stages) spent at least one day in Norwegian Skagerrak nursery habitat; these percentages being for 2011 and 2012 respectively. In both years the bulk of the modelled settlement was distributed west of the

322 Oslofjord, yielding few settlers to the Hvaler archipelago and leaving the Oslofjord almost
323 devoid of North Sea import. There was a clear regional maximum in modelled settlement
324 within and outside the Grenlandfjords and Kragerø area in both years. In 2011 three lesser
325 maxima were found outside Arendal, Kristiansand, and Mandal. In 2012, there were two
326 lesser maxima, found south of Arendal and outside Mandal. The majority of larvae settling
327 along the Norwegian Skagerrak coast in 2011 were spawned either west of the Viking bank,
328 over the Ling bank, the Fisher banks, or north of Skagen. In 2012, the major sources of
329 settling larvae were similar to 2011, although with a larger supply coming from north of
330 Skagen, reflecting the high number of eggs released there that year (Fig. 3). Comparing the
331 alongshore distribution of modelled settlement with alongshore spatial abundance of half-
332 year-old cod in beach seine hauls, there was a significant positive correlation in 2011 ($r = 0.4$,
333 $t = 7.95$, $p < 0.001$). In 2012 however, there was no correlation between modelled settlement
334 and observed abundance ($r = 0.1$, $t = 1.66$, $p = 0.09$). The highest relative difference in
335 modelled settlement to observed abundance in autumn was found within and outside the
336 Grenlandfjords in both years (large peak at $x_i \approx 400$ in Fig. 4A, B). Moreover, of the 815 half-
337 year-old cod screened for genetic origin in the 2011 beach seine hauls, 86% were classified as
338 North Sea-like, in distinction to Norwegian coastal cod. There was no large-scale
339 geographical trend in prevalence of North Sea genotype juveniles, besides a slightly lower
340 percentage in the samples taken inside the Oslofjord. However, this was also the region with
341 the lowest sample sizes screened for genetic origin (as reflected in the wide interval estimates
342 for the proportions), as well as having the lowest abundance of juveniles in beach seine hauls.
343 The highest densities of juvenile cod were found in the Kristiansand area, and here North Sea
344 originating juveniles dominated (Fig. 4A). The annual mean abundance of half-year-old cod
345 found in the Skagerrak division of the IBTS in autumn was significantly correlated with the
346 mean abundance of half-year-old cod found in the annual beach seine survey along the

Norwegian Skagerrak coast ($r = 0.42$, $t = 2.1$, $df = 21$, $p < 0.05$, see figure 4C for average yearly abundance in the two nursery areas).

Copepod phenology and biomass

The phenology of our selected copepod species assemblage started with a peak in calanoid nauplii abundance on the 28th of February 2011 (87 552 ind/m²), coinciding with the modelled end of the yolk sac stage of the earliest hatched larvae that year. Further into the 2011-season the subsequent peaks of the later developmental stages of *Calanus spp.* closely followed the development of the cod larvae. The peak abundance of *Calanus spp.* copepodites was sampled on the 9th of June (3712 ind/m²), which coincided with the start of the settlement period, as 23% of the total number of settlement days spent in the nursery habitat had already accumulated at this point. After the settlement period was over in 2011 (i.e. when all modelled juveniles had grown past 50 mm), there was a high abundance of *Oithona sp.* and Paracalanus/Pseudocalanus (87 552 ind/m² and 79 626 ind/m²) present in the zooplankton of (Figure 5A). Despite the low numerical abundance of *Calanus spp.* copepodites compared to the higher numbers of *Oithona sp.* and Paracalanus/Pseudocalanus, *Calanus spp.* contribution to the overall biomass of the zooplankton outweighed all the other zooplankton species during spring and early summer of 2011 (Figure 5B). In spring 2012 the succession of the zooplankton was more sporadic, and no peak in favoured food items coincided with the modelled settlement period. However, on 27th of August and 19th of September, both dates well beyond the settlement period in 2012, we found the highest abundance of Paracalanus/Pseudocalanus and *Oithona sp.* in the two-year zooplankton sampling record of 120 832 ind/m² and 119 296 ind/m² (Figure 5A).

Discussion

Here we presented a case study that covered all the relevant aspects of the drift, development, settlement, and food availability of North Sea and Skagerrak cod larvae during the most recent good year of recruitment (2011). We compared the oceanic conditions in Skagerrak in the winter and spring of 2011 with the normal the past three decades and found few systematic deviations. Neither was the temperature in the littoral zone in summer significantly different from the normal of the past decade. The modelled onshore drift of North Sea originating pelagic juveniles to the coast was also remarkably consistent between years. However, one thing that stood out in our analysis was the phenology of the important prey copepod species in 2011, where especially the succession of the developmental stages of *Calanus spp.* was close to the theoretical optimum for cod larvae. At a first glance, our data thus lends support to the notion that availability of food to larvae determines year class strength of cod in coastal Skagerrak, in distinction to physical variables as for example temperature and drifting routes. In the following sections we will try to generalise our findings to further capsule the driving forces for recruitment of North Sea cod in Skagerrak.

Inter-annual consistency in drift and settlement patterns

The large scale flow pattern of water masses between the northern North Sea and Skagerrak is highly robust among years, and has been relatively unchanged since the beginning of the “modern” observational record, i.e. since the 1950s. We do note that there are alternative flow patterns, but these have been relatively uncommon the past decades because of the contemporary state of the North Atlantic Oscillation (Winther & Johannessen 2006, Hjøllø et al. 2009, Mathis et al. 2015). In detail, the majority of the upper water masses flowing through the North Sea and Skagerrak during spring is advected from the North Sea over the open northern boundary between Shetland and the Viking bank (Hjøllø et al. 2009), and the

395 inflowing Atlantic water is extremely stable in temperature, ranging from 7 °C in February to
396 9 °C at end of May (Furnes et al. 1986). The usual wind direction over the North Sea in spring
397 is westerly (i.e. wind coming from between south-southwest and north-northwest, Heath et al.
398 1999), which means that by Ekman drift the upper water masses of the northern North Sea is
399 advected along the Norwegian trench and subsequently into Skagerrak (Furnes 1980, Furnes
400 et al. 1986). Along the south-western slopes of the trench elevated densities of newly
401 spawned cod eggs are found, released by the high densities of cod congregating along the
402 slopes of the Trench (Fox et al. 2008). Most likely this happens over a fixed season every year
403 with peaks of very little inter-annual variability, which is common for cod in these waters
404 (Cushing 1990, Brander 1994). Upon entering the Skagerrak, this egg-enriched northern
405 North Sea water mass gets wedged between the westwards flowing Norwegian coastal current
406 and the intermittent West-Jutland coastal current. In the convergence zone of these three
407 water masses a more or less continuous front is sustained, traversing almost the entire
408 Skagerrak. Within this front high concentrations of cod larvae of all sizes is a typical feature
409 in spring and early summer (Munk 2007, 2014). Although this front is present year-round, the
410 half-life of the water masses contained within it is quite short. This is because of the intense
411 mixing of the northern North Sea water with the fresher German bight water and the Baltic
412 outflow. The resulting water mass of intermediate density created by this mixing subsequently
413 has to float out of Skagerrak, and does so in a counter clock-wise motion, piling up along the
414 Norwegian Skagerrak coast (Gustafsson & Stigebrandt 1996). Concurrent with the results
415 from our dispersal model, field studies suggest that high abundances of drifting larvae are still
416 present in the continuum of the frontal water mass flowing along the Norwegian Skagerrak
417 coast (Munk et al. 1995, 1999). Moreover, beach seine hauls performed throughout spring and
418 summer along the Norwegian Skagerrak coast suggest a consistent settlement period between
419 May to August, peaking in June with a similar magnitude among years (Johannessen *et al.*

2014), a time frame that is identical with our modelled settlement period. In light of earlier population genetic studies on larvae and juvenile cod Skagerrak (Knutsen et al. 2004, 2011, Øresland & Andre 2008), and given the high densities of mature cod found along the Norwegian Trench the past decade (Engelhard et al. 2014, Holmes 2014), we can thus safely conclude that a large portion of the North Sea originating juveniles repeatedly found in the Skagerrak nursery grounds follow the drift route sketched out above. However, we can also from the first part of our discussion agree that a high number of cod larvae drifting into Skagerrak from the North Sea is probably not an uncommon phenomena that in itself guarantee a great year for recruitment, since both years modelled here had almost equal import of North Sea settlers, but yielded very different year class strength.

In both of the years we ran the biophysical model there was a distinct maximum in predicted settlement outside the Grenlandfjords not reflected in the observed recruitment in that area, followed by minor peaks further down the coast. We note that ichthyoplankton surveys done in spring/summer in the Skagerrak have identified a peak abundance of cod larvae outside the Grenlandfjords, with a minor peak further south (Munk et al. 1995, 1999). However, the high level of modelled settlement here may also be an artefact from the model. More specifically, in the deep gorge pointing into the Grenlandfjords, topographic steering of the coastal current onto the coast could be overrepresented compared to areas with smaller gorges actually present along the coast not represented well in the model. On the other hand, this may also be the kind of macro scale topographic structures that induces settlement by disrupting the continuity in flow of the coastal current, effectively creating pockets of retention. The Grenlandfjords have also been an area along the Norwegian Skagerrak coast that have historically had consistently high recruitment, but saw collapse in the 80s most likely due to changes in the zooplankton community (Johannessen & Sollie 1994, Johannessen et al. 2012). Thus, although the settlement patterns predicted by our biophysical

dispersal model compared fairly well with field observations, the relatively coarse resolution of our model compared to the detailed topography of the coast could bias the results.

Is there a critical period for cod larvae in Skagerrak?

In light of the acclaimed critical period hypothesis that we set out to test, where the theory suggest that year class strength of cod is determined in the period immediately following the time of first feeding—how does this compare with what we observed in the Skagerrak? As was discussed in the introduction a major difference to nursery habitat in more northern latitudes compared to southern nursery grounds may be the challenges related to metabolic activity and food availability during pelagic juvenile stage. The rationale was that as the phenology of the zooplankton usually ‘matures’ earlier and faster in the south, reducing the chance for larval cod to capitalise on their most favoured food item (i.e. *C. finmarchicus*)—and at the same time the higher temperatures increases the chance of starvation if the right food is lacking. To further ground our hypothesis we will briefly review the feeding ecology of cod larvae and the challenges they face in the first few months of development. When cod larvae are small several food items can fill the “feeding niche” that is mainly constrained by availability and the gape size of the larvae (i.e. the max size of prey a larva can ingest), whereas when the cod larvae grow larger they prefer the later stages of *C. finmarchicus* (Economou 1991, Munk 1997, Heath & Lough 2007). The first pelagic juveniles of the season observed along the Norwegian Skagerrak coast usually arrive in late April at a mean size of ≈ 3 cm (Johannessen *et al.* 2014), which compares well with our modelled progression of the settlement period, starting at 17th in 2011 and 14th of April in 2012. Now, the diet of newly settled larvae/juveniles smaller than 3 cm is exclusively pelagic; at 3 cm 75% is pelagic prey; at 5 cm 50% is still pelagic prey; but at 7 cm the transition to benthic feeding is almost total (Bastrikin *et al.* 2014). And as shown by Johannessen *et al.* (2014), the presence of *Calanus* during that

early benthic phase makes a huge difference in condition and survival of the settled juveniles in Skagerrak nursing grounds. In our zooplankton record we observed a peak in biomass of *Calanus* and peak abundance of *Calanus* copepodites at the start of settlement period of 2011; this in contrast to the settlement period of 2012 when much lower biomass of preferred prey was found. Knowing that the energetic requirement of newly settled juveniles most likely skyrocket as response to the increasing summer temperatures in the littoral zone (estimated to 7.8°C, 12.7°C, 16.4°C, and 18.5°C from May through August when temperature peaks), we can safely argue that any variability in food availability during this period can prove fatal, as may have been the case in 2012 when few of the preferred *Calanus* copepodites were present. Thus, in the period from settlement until at least reaching ≈ 5 cm, when a sustainable range of benthic prey start being eatable/available to the settlers (Demain et al. 2011, Bastrikin et al. 2014), acquiring the proper pelagic prey is crucial. But at the same time, the abundance of *C. finmarchicus* in these waters usually peak in April and thus a deviation from the normal is needed for adequate availability to cod in this critical period. A displacement in *C. finmarchicus* peak abundance could for example be caused by variability in environmental factors such as primary productivity or predation (Head et al. 2000), as well as more stochastic effects as for example advection (Aksnes et al. 1989, Salvanes et al. 1995). However, the most parsimonious explanation for the delayed peak in *C. finmarchicus* biomass in 2011 may be the lower than normal temperatures observed in the coastal water in winter and spring, given the mechanistic relationship that exists between temperatures and the phenology of *C. finmarchicus* (Kvile et al. 2014).

To conclude, our findings suggest that there indeed is a critical period that could determine year class strength of cod in Skagerrak. However, in contrast to the traditional interpretation of Hjort's hypothesis, that exemplifies the end of the yolk sac stage as the crux point, we argue that the period from settlement to the transition to benthic feeding is the

495 decisive period in southern latitudes. Our rationale being that during this time period when
496 metabolic requirement is at it's highest, as this coincides with peak summer temperatures, any
497 variability in the zooplankton that the larvae still are dependent on could prove fatal to the
498 year class. It appears most probable that what determines the fate of the cod year class in
499 Skagerrak, as in Lofoten, is that *missing factor*. However, in the case of Skagerrak nursing
500 grounds, the *critical period* is not the start of larval development but at the end.

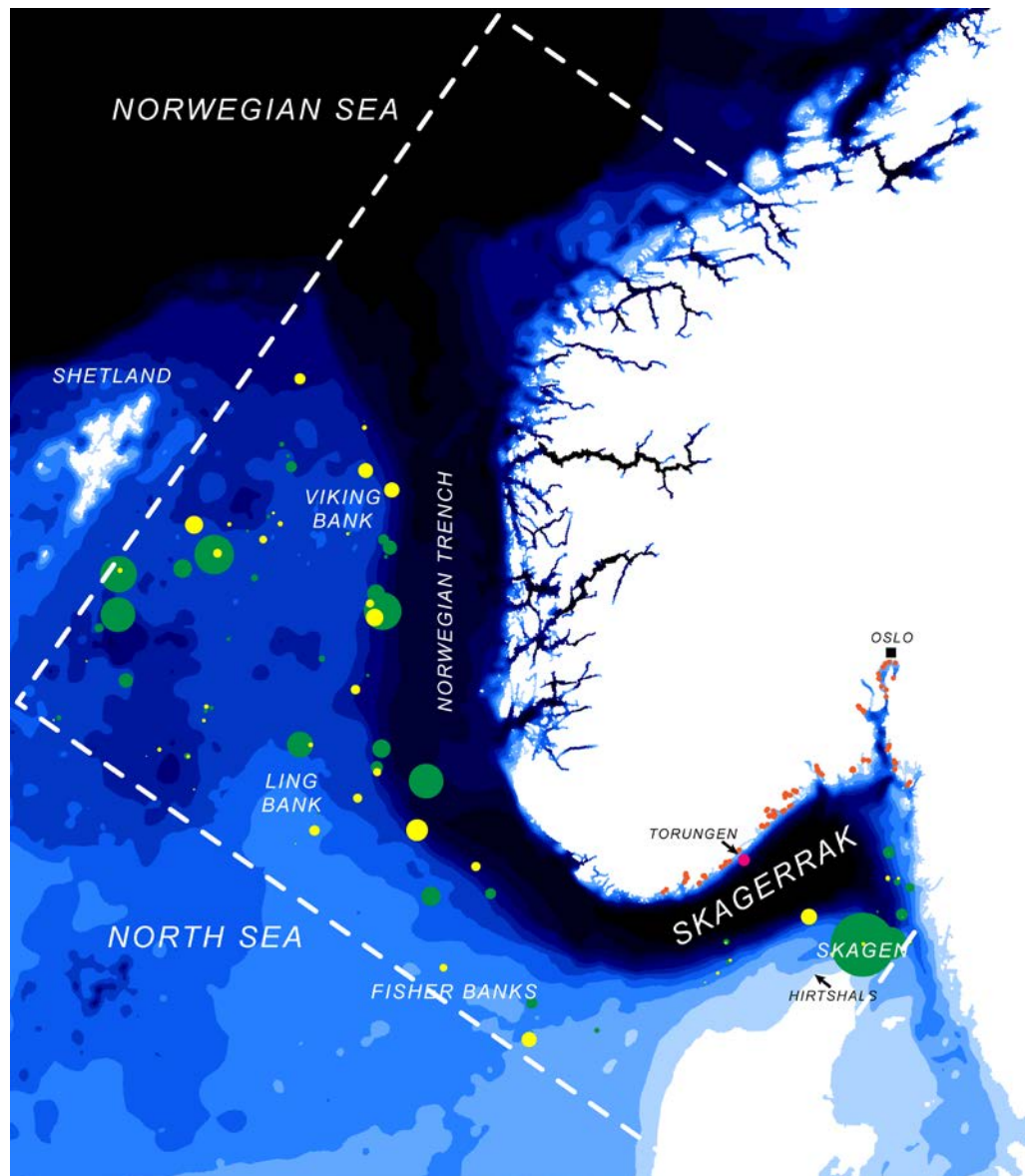
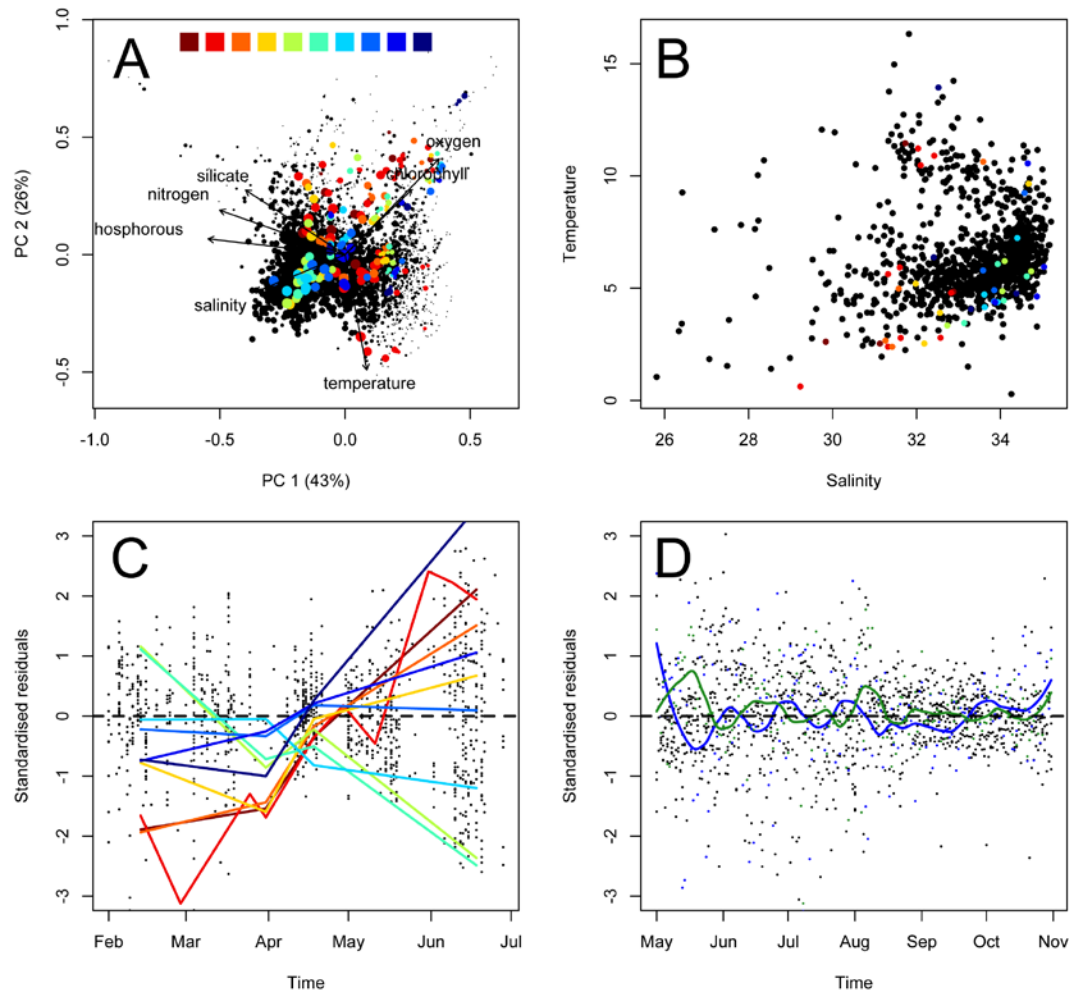
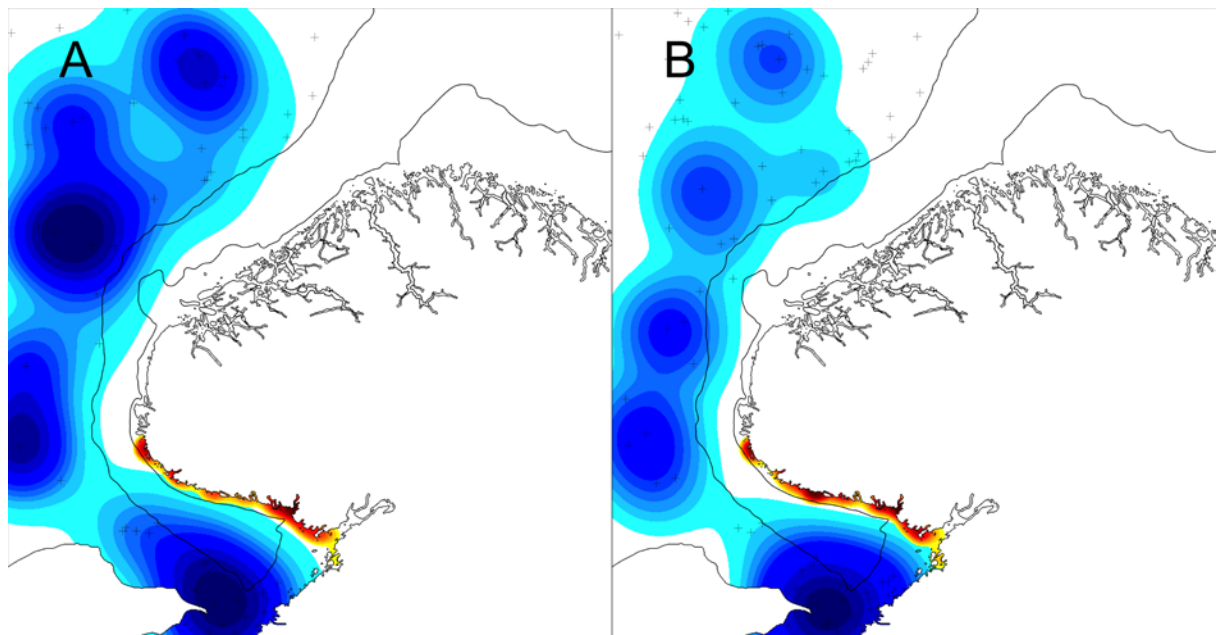


Figure 1. Bathymetry of Skagerrak and the North Sea. Yellow and green circles represent the spatial distribution and estimated egg production in 2011 and 2012, extrapolated from the ICES IBTS survey. Orange circles represent beach seine sampling locations for half-year-old cod in autumn, and the purple circle just south-east of Torungen represents the zooplankton sampling station.



507

508 Figure 2. (A) Principal components analyses on environmental variables sampled bimonthly
 509 between February and May in years from 1988 to 2013 across the Torungen-Hirtshals
 510 transect. Highlighted in colours are the samples from spring 2011, where the sequence of
 511 coloured squares in the inset represents the geographical sequence of stations across the
 512 transect. Here red parts of the colour spectre represent samples from Norwegian coastal
 513 waters, greens the Skagerrak/northern North Sea water, and blues the southern North Sea
 514 water. (B) Physical characteristics of water masses sampled at 20 m across the transect,
 515 sampled between February and June. (C and D) Anomalies in temperature in the pelagic (20
 516 m) and littoral zone (1 m), scaled to unit standard deviations. Colours in panel C represents
 517 the same stations as in panel A. Green and blue points and lines in panel D are measurements
 518 taken in Flødevigen and mid Oslofjord in 2011, respectively.



519

520 Figure 3. Density distributions of pelagic juvenile settlement days spent in Norwegian

521 Skagerrak nursery habitat (warm colours) and starting positions of individual particle

522 trajectories spending settlement days in Norwegian Skagerrak nursery habitat in 2011 (A) and

523 2012 (B).

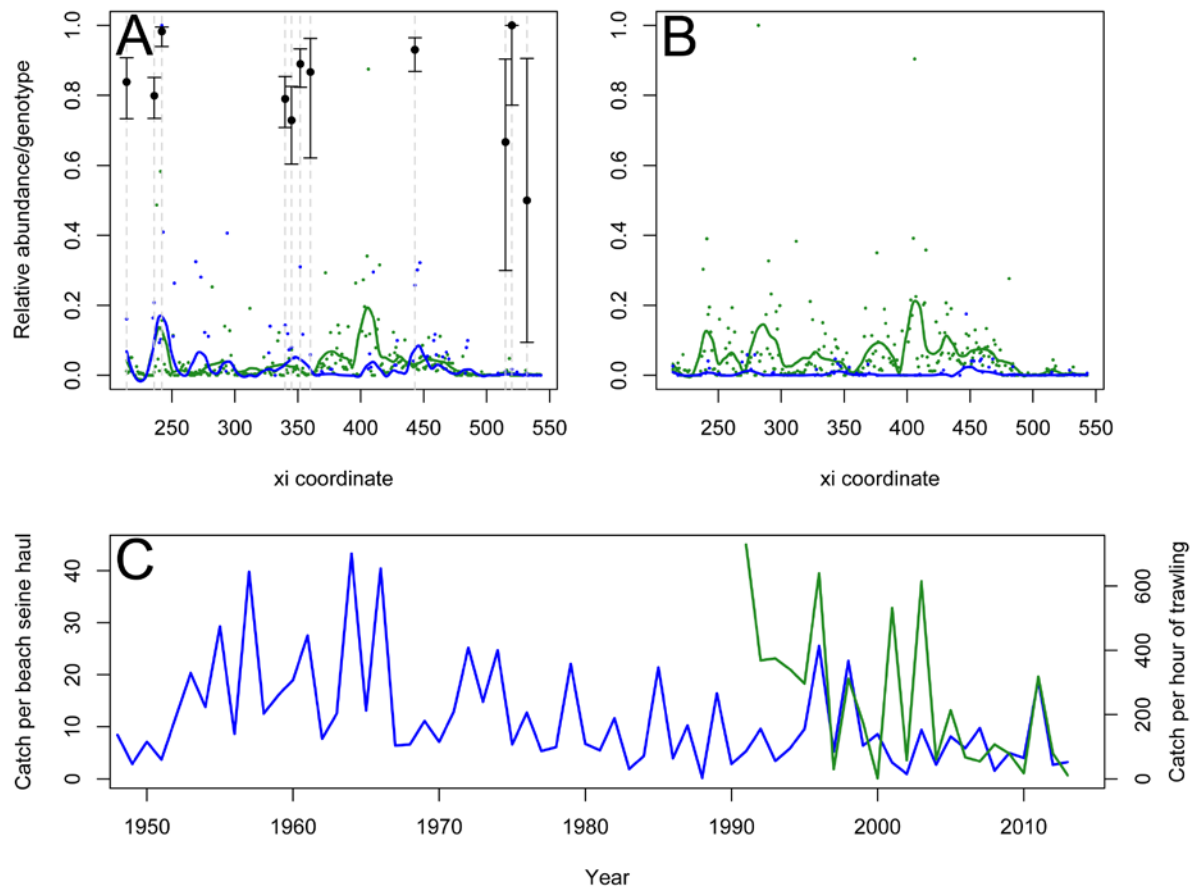


Figure 4. One-dimensional representation of the modelled settlement of pelagic juveniles on the Norwegian Skagerrak coast (green circles and smoothed lines), compared to sampled densities of half-year-old cod in beach seine hauls (blue circles and smoothed lines) of 2011 (A) and 2012 (B). The black circles and confidence intervals in panel A refers to the proportion of individuals sampled at a particular location of North Sea origin. (C) Average abundance of half-year-old cod caught in the annual beach seine survey along the Norwegian Skagerrak coast (blue line) and average number of half-year-old cod caught per hour of trawling in the Skagerrak division of the international bottom trawl survey (green line).

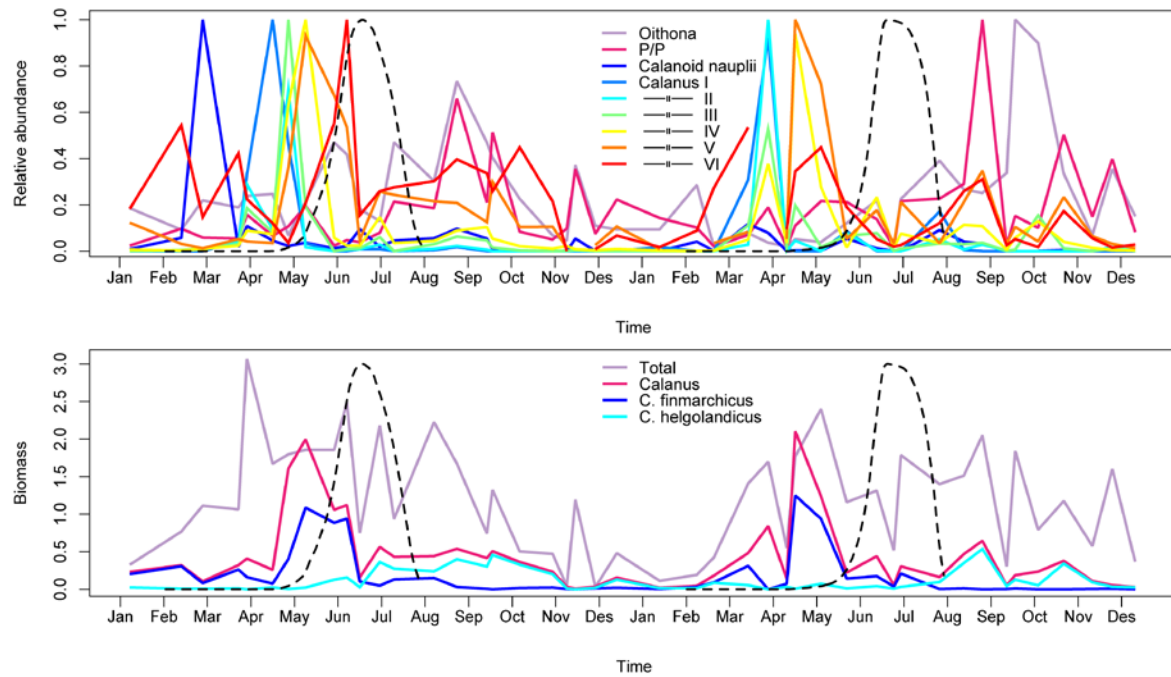


Figure 5. (A) Relative abundance of the three most favoured copepod species/groups throughout pelagic and early settlement stage of cod larvae, scaled by the peak abundance of each species/stage (see text for peak abundances). Note that all the developmental stages of *Calanus* spp. are represented, from nauplii to adults. (B) Total biomass of zooplankton samples and calculated total biomass of *Calanus* spp (integrated over all stages). Note that in biomass estimates only stages CV and CVI was separated down to species level between *C. finmarchicus* and *C. helgolandicus*.

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