

Inferring genetic connectivity in real populations, exemplified by coastal and oceanic Atlantic cod

SI Appendix

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## SI Appendix

### *Details of the individual-based model*

For each simulation, microsatellite alleles were randomly generated at 13 independent loci under the stepwise mutational model (1), based on characteristics of microsatellite loci in Atlantic cod and other marine fish species. Allele distributions were simulated with average heterozygosity characteristic of Atlantic cod and other marine fish; typically 0.79 ( $\sigma = 0.26$ ), with 19 ( $\sigma = 6.6$ ) alleles per locus on average (2). A survey of 18 microsatellite loci developed for Atlantic cod indicated a similar level of heterozygosity; 21 alleles per locus on average ( $\sigma = 11.1$ ; 3). Alleles were randomly assigned to individuals in two modeled age-structured populations (North Sea and inner fjord or North Sea and outer coast), whose size reflected actual population sizes as closely as possible. Models were run for an initial 600-year burn-in to achieve migration-drift equilibrium, because the populations are likely to be approximately in migration-drift equilibrium (4, 5). Migration-drift equilibrium was achieved in fished, rather than unfished, populations for computational efficiency. The trajectory of  $F_{ST}$  values calculated over the 700-year simulation period is shown in Fig. S1 for two base cases with 100 simulation runs each, between the North Sea and the inner fjord populations with 55 age-0 migrants per year (Fig. S1a), and between North Sea the outer coast with 1,400 age-0 migrants per year (Fig. S1b).

Simulated fishing took place in each year at fishing mortality rates consistent with estimates used for management (6), and mutation was applied during the 600-year burn-in and the 100-year simulation period at the same rate. The mutation rates for each locus and simulation were drawn from a beta distribution parameterized to provide expected levels of heterozygosity,  $\mu = 0.375$ ,  $\sigma = 0.300$ . The beta distribution provides values between 0 and 1; mutation rates were therefore scaled down by a factor of 100 to provide mutation rates in the range of those expected for microsatellites in marine fish ( $10^{-4}$ - $10^{-2}$ ), and a maximum value of  $10^{-2}$ . The genotype of the new recruit was selected by Mendelian inheritance from the parental genotypes (described in the main body of the paper). During a 100-year simulation period, following the 600-year burn-in,  $F_{ST}$  was computed every twenty years. We assumed that the estimates of  $F_{ST}$  based on 100 samples in (7) were accurate, and considered sampling bias to be outside the scope of the paper; therefore  $F_{ST}$  was calculated based on all fish in each population rather than a sample. Each simulation scenario was replicated 100 times.  $F_{ST}$  results reflect the mean over 100 simulations over the last 100 years of each simulation (five measurements per simulation).

### *Parameterizing the model*

Estimates of the inner fjord and outer coast population sizes used in the model were based on field surveys of those populations (7). The census size estimate for the inner fjord (Søndeled) is 1,847 fish, excluding age-0s (7). Using estimates of survival-at-age from (7), the extrapolated total number, including age-0s is 5,380. Census numbers refer to the number of individuals observed during November research surveys, while spawning takes place in February-March. The number of fish in the outer coast (Risør) was extrapolated from its estimated effective population size ( $N_e$ ) of 542 (95% CI: 269 -  $\infty$ ; 7). The upper bound of infinity highlights uncertainty in population structure; it is

uncertain whether the Risør outer coast comprises a distinct population, or whether it is a component of the North Sea population. The  $N_e/N_s$  ratio, where  $N_s$  represents the number of spawners, is 0.14 (7). The  $N_e/N$  ratio, or effective to census size ratio, is 0.037 in the inner fjord, given the census size estimate of 5,380 and the estimate of effective population size of 198. If the  $N_e/N$  ratio is similar for Søndeled and Risør, this would result in an estimate of 14,971, roughly 15,000 (2.5% and 97.5% CI: 7,430 –  $\infty$ ) total individuals in the Risør outer coast. Stochasticity in population dynamics model led to minor variation in population sizes among simulations; the estimated true population sizes were the target values and actual mean population sizes (over all simulations) are provided in Table S1. These mean values were used when calculating migration rate ( $m$ ), which was calculated as the proportion of migrants in the age-0 category.

The North Sea Atlantic cod stock was estimated at 54,721 t in 2012 (ICES 2012), or approximately  $7.6 \times 10^7$  fish. If the estimate of 15,000 fish in the outer coast population is correct, then the North Sea stock is approximately 5,000 times larger than the outer coast population. Tagging, genetics, and other studies have revealed significant differentiation of cod populations within the North Sea, suggesting a metapopulation structure with various rates of mixing among the sub-populations (8, 9, 10, 11). Therefore, some components of the North Sea may interact with the Skagerrak coast while others may not. To capture this uncertainty in our simulations, we used two samples from different positions in the North Sea (main paper, Table 1: the German Bight in 2002 and off Hirtshals in 2000 and 2001). However, the North Sea cod stock was treated as a single large panmictic population in the simulations. Simulations could not be conducted with the total census size of the North Sea cod, given its large size and because of computational limitations. Therefore, most runs were performed with a large, but feasible value, approximately  $6.4 \times 10^4$  fish and sensitivity to population size was tested. The code for running the model is available at: <https://github.com/31ingrid/Acod>.

### *Specifications of the age-based population dynamics model*

The population dynamics of each population were simulated using an age-structured model with parameters given in Tables S1 and S2. The initial spawning biomass in each population ( $I$ ) was  $\tilde{S}_0^I$ . The initial number of recruits in each population ( $I$ ) in the absence of fishing,  $R_0^I$ , was calculated using the equation:

$$(1) \quad R_0^I = 2\tilde{S}_0^I / \sum_a W_a \tilde{N}_{init,a}^I Q_a,$$

where  $a$  indexed age class,  $W_a$  was weight-at-age,  $Q_a$  was maturity-at-age, and  $\tilde{N}_{init,a}^I$  was the number of fish in each age class prior to exploitation relative to the number of age-0 fish. The latter quantity was calculated under the assumption that the population was in unfished equilibrium, given an instantaneous rate of natural mortality for animals of age  $a$ ,  $M_a$ , and  $x$  represents the plus group, ages 6 and older:

$$(2) \quad \tilde{N}_{init,a}^I = \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{init,a-1}^I e^{-M_{a-1}} & \text{if } 1 \leq a \leq x-1 \\ \tilde{N}_{init,x-1}^I e^{-M_{x-1}} / (1 - e^{-M_{x-1}}) & \text{if } a = x. \end{cases}$$

The numbers in each age class in each true population ( $l$ ) were then scaled to the population size that would result from  $R_0^l$  recruits:

$$(3) \quad N_{init,a}^l = R_0^l \tilde{N}_{init,a}^l.$$

For years  $init+1$ ,  $init+2$ , etc., the numbers-at-age were computed allowing for fishing and a Beverton-Holt stock recruitment relationship (12):

$$(4) \quad N_{y+1,a}^l = \begin{cases} \frac{4hR_0^l \tilde{S}_y^l}{\tilde{S}_0^l(1-h) + \tilde{S}_y^l(5h-1)} e^{\delta_R - \sigma_R^2/2} & \text{if } a = 0 \\ N_{y,a-1}^l e^{-(S_a^l F_y^l + M_{a-1})} & \text{if } 1 \leq a \leq x-1 \\ N_{y,x-1}^l e^{-(S_{x-1}^l F_y^l + M_{x-1})} + N_{y,x}^l e^{-(S_x^l F_y^l + M_x)} & \text{if } a = x, \end{cases}$$

where  $N_{y,a}^l$  was the number of fish of age  $a$  in population  $l$  at the start of year  $y$ ,  $S_a^l$  was the selectivity-at-age for the fishing gear,  $h$  was steepness,  $\tilde{S}_y^l$  was spawning biomass in population  $l$  at the start of year  $y$ , and  $F_y^l$  was the instantaneous fully-selected fishing mortality rate during year  $y$  for population  $l$ . Variation with bias-corrected lognormal error was applied to the recruitment in each population in each year, i.e.,  $\delta_R \sim N(0; \sigma_R^2)$ , and  $\sigma_R^2$  was determined from the CV of recruitment (Table S3), using the equation

$$(5) \quad \sigma_R^2 = \log(CV_R^2 + 1).$$

$\tilde{S}_y^l$  was calculated subsequent to the initial year, using:

$$(6) \quad \tilde{S}_y^l = 0.5 \sum_a W_a N_y^l Q_a.$$

The number of spawning males in each population was set equal to the number of spawning females, and was based on the proportion of individuals in each age group that were expected to be mature that year:

$$(7) \quad SP_{y,a}^l = 0.5 N_y^l Q_a.$$

Catch in numbers of fish of age  $a$  in population  $l$  during year  $y$ ,  $C_{y,a}^l$ , was a function of  $S_a$ , fishing mortality rate, natural mortality, and numbers-at-age,

$$(8) \quad C_{y,a}^l = \frac{S_a F_y^l}{S_a F_y^l + M_a} (1 - e^{-(S_a F_y^l + M_a)}) N_{y,a}^l.$$

Finally, the total catch in weight from population  $l$  during year  $y$ ,  $C_y^l$ , was calculated as:

$$(9) \quad C_y^l = \sum_a W_a C_{y,a}^l.$$

Age was converted to weight for the North Sea population using a von Bertalanffy growth function (13):

$$(10) \quad W_a = \psi [L_\infty (1 - e^{-Ka})]^\gamma,$$

where  $L_\infty$  was the mean maximum length,  $K$  was a rate constant ( $\text{year}^{-1}$ ), and  $\psi$  and  $\gamma$  determined the relationship between length and weight (Table S3). Weight-at-age of Skagerrak cod was a linear function of age, with slope 0.5508 (7). The model included

seven ages, from zero to 6, with the oldest age inclusive of all ages 6 and above, consistent with age categories in the ICES North Sea cod assessment (6). Natural mortalities-at-age and maturity-at-age were also set to estimates from the ICES assessment (6; Table S2). Skagerrak maturity-at-age was based on previous studies (7). Fishing gear selectivity-at-age estimates (mean and interquartile range over time) were computed from the annual fishing mortality-at-age ( $F_{age}$ ) estimates over the years 1963-2011 by dividing all fishing mortality-at-age values for a given year by the highest  $F_{age}$  (the fully-selected fishing mortality rate,  $F_{Full}$ ) in that year (6; Table S2). Selectivity is applied in the model as a multiplier that adjusts fishing mortality based on the effectiveness of the fishing gear on fish at each age and the relative availability of fish of different ages to the fishery (Eqn. 4).

In the model,  $F_{Full}$  for both populations was randomly generated in each year from a lognormal distribution with variance equal to the assessment estimate,  $\sigma^2 = 0.023 \text{ yr}^{-2}$  (6). The assessment tends to overestimate fishing mortality (6); therefore, the mean fishing pressure for the simulated North Sea population was adjusted from  $\mu = 0.896 \text{ yr}^{-1}$  to  $\mu = 0.75 \text{ yr}^{-1}$  so that age structure in the simulation model would be consistent with empirical estimates of age structure (Table A1 in reference 7, truncated at age 6, corresponding to their age class 7). Reports of fishing mortality are unavailable for the Skagerrak coast; for this component, the  $F_{Full}$  was tuned so that the age distribution was similar to that observed for the simulated fjord and coastal populations (7; Fig. S2). This estimate was also  $\mu = 0.75 \text{ yr}^{-1}$ . Estimates of variability in recruitment were calculated from recruitment estimates in the ICES assessment; the coefficient of variation (CV) of recruitment from 1963-2011 was 0.75 (Table S3).

The value for the steepness of the stock-recruitment relationship ( $h$ ), the fraction of unfished recruits produced when spawning biomass is 20% of its unfished state (14), was chosen based on the estimate of steepness for Atlantic cod (15). This meta-analysis produced estimates of steepness from several Atlantic cod populations ( $h=0.84$ ; 0.76, 0.9 – 20<sup>th</sup> and 80<sup>th</sup> percentiles, respectively; 15). Steepness affects the number of recruits produced at a given stock size; high steepness allows for more recruits despite low stock size. A range of steepness values was considered in initial model runs. The observed age structure could not be matched with steepness values of 0.84 or less because the high fishing mortality rate resulted in too few recruits to sustain the population. Therefore, the value 0.9 was chosen because it was within the range of the distribution for steepness derived by (15), and allowed for the observed age distribution to be matched using the model (Fig. S3).

The model did not account for higher fecundity in older fish, as would be expected for Atlantic cod and other species (16). If older fish had higher fecundity, then more migrants would be required to achieve the same fixed levels of genetic differentiation because older fish would spawn the majority of offspring, and not all migrants would live to older ages. The increase in the number of migrants would not have a direct effect on the effective number of migrants,  $M_e = N_e m$ , because the shift toward spawning at older ages would reduce the effective population size, balancing the increase in migration to some extent.

We calculated effective population size and generation length under the assumption that the variance was equal to the mean reproductive success for individuals who were mature (17). This did not imply that  $\phi_x$  (the variance divided by the mean lifetime

reproductive success of individuals age x) was equal to one because only a proportion of individuals were mature in each age class ( $Q$ ). Therefore, we calculated  $\phi_x$  as follows:

$$\phi_x = \frac{V_{k_x}}{\bar{k}_x} = \frac{E[k_x^2] - E[k_x]^2}{b'_{xmat}}, \text{ where } V_{k_x} \text{ is the mean reproductive success of all individuals in}$$

age class x,  $k_x$  is the reproductive success of individuals age x,  $b'_{xmat}$  is the standardized mean number of newborns produced by a mature individual age x, and  $\bar{k}_x$  is the mean reproductive success. The variance in the numerator can be expressed as

$$V_{k_x} = \frac{N_x [b_x (\bar{k}_x + \bar{k}_x^2) + (1 - b_x) * 0]}{N_x} - (b_x^2 + 0), \text{ where } * \text{ indicates multiplication, because}$$

we assume that  $V_{k_x} = \bar{k}_x$ , and the sum of squared number of offspring age x,  $SS = N_x b_x (V_{k_x} + \bar{k}_x^2) = N_x b_x (\bar{k}_x + \bar{k}_x^2)$ . Note that individuals that were not mature produced zero offspring. The mean number of newborns produced by an individual age x and the probability of survival from age x to x+1 were projected to age 15, because effective population size calculations are not amenable to plus groups (17).

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Table S1. The number of age zero migrants per year from the North Sea to the Skagerrak (either inner fjord, IF, or outer coast, OC) required in simulations to achieve low and high empirical levels of  $F_{ST}$  ( $M_{0low}$  and  $M_{0high}$ ; inner fjord  $F_{ST}=0.0039, 0.0051$ ; outer coast  $F_{ST}=0.0001, 0.0003$ ). The effective to census size ratio, ( $N_e/N_t$ ), generation length ( $L$ ), census population size ( $N_t$ ), and the number of age-0 individuals ( $N_0$ ), and are shown for each sensitivity test, and results are averaged over 100 simulations. Migration rate ( $m_{0high}$ ,  $m_{0low}$ ) is the number of age zero migrants divided by the number of age zero fish in the recipient Skagerrak population (e.g.  $m_{0low}=M_{0low}/N_0$ ). The population to which each sensitivity test was applied is shown in parentheses: IF, OC, or North Sea (NS).

Sensitivity test	Skagerrak Population				North Sea				$M_{0high}$	$M_{0low}$	$m_{0high}$	$m_{0low}$
	$N_e/N_t$	$L$	$N_t$	$N_0$	$N_e/N_t$	$L$	$N_t$	$N_0$				
Migration from the North Sea to the inner fjord												
Base case (IF)	0.195	2.91	5,444	3,438	0.115	3.52	65,064	39,196	55	80	0.016	0.023
Half pop. size (IF)	0.194	2.90	2,872	1,815	0.115	3.53	67,819	42,836	58	79	0.032	0.044
Double pop. size (IF)	0.195	2.90	10,957	6,924	0.116	3.53	70,378	44,459	51	74	0.007	0.011
Lower selectivity (NS)	0.195	2.90	5,448	3,442	0.147	4.33	65,446	38,934	55	74	0.016	0.021
Higher selectivity (NS)	0.195	2.90	5,426	3,429	0.112	3.48	49,786	31,636	67	94	0.020	0.027
Lower fishing mortality (NS)	0.195	2.90	5,405	3,415	0.218	6.01	65,788	33,510	49	69	0.014	0.020
Higher maturity (IF)	0.212	2.78	5,413	3,420	0.116	3.54	67,034	42,320	50	73	0.015	0.021
Migration from the North Sea to the outer coast												
Base case (OC)	0.195	2.91	15,035	9,492	0.115	3.51	65,756	41,550	1,400	2,925	0.147	0.308
Half pop. size (OC)	0.195	2.91	7,322	4,627	0.115	3.53	66,214	41,813	1,000	1,800	0.218	0.392
Double pop. size (OC)	0.197	2.91	29,785	18,808	0.115	3.52	66,854	42,220	2,000	5,000	0.106	0.266
Lower selectivity (NS)	0.195	2.90	14,818	9,362	0.147	4.33	64,661	38,491	1,150	2,500	0.123	0.267
Higher selectivity (NS)	0.195	2.91	14,930	9,430	0.112	3.47	51,050	32,421	1,700	3,700	0.180	0.392
Lower fishing mortality (NS)	0.195	2.91	14,915	9,420	0.218	6.02	65,890	33,537	1,030	2,300	0.109	0.244
Higher maturity (OC)	0.212	2.79	14,997	9,468	0.115	3.53	65,920	42,095	1,350	2,750	0.143	0.290
2x NS size	0.195	2.91	15,057	9,511	0.115	3.52	136,344	86,154	1,200	2,600	0.126	0.273
5x NS size	0.195	2.90	14,889	9,410	0.115	3.52	313,987	198,570	1,060	2,500	0.113	0.266

Table S2. Age-specific parameters used in the model; North Sea parameters are annotated by an \* (6), and Skagerrak parameters by † (7). Quantile values used in sensitivity testing are shown in parentheses. Age 0 selectivity is set to zero in the model.

Age	Maturity* (Q)	Maturity† (Q) (5% and 95%)	Fishing gear Selectivity* (5% and 60%)	Natural Mortality (yr <sup>-1</sup> )*
0	0.01	0.032 (0.019, 0.046)	0.220 (0.201, 0.226)	1.038
1	0.05	0.149 (0.135, 0.164)	0.818 (0.656, 0.876)	0.698
2	0.23	0.482 (0.451, 0.514)	0.974 (0.891, 1.000)	0.490
3	0.62	0.831 (0.768, 0.895)	0.895 (0.783, 0.919)	0.233
4	0.86	0.963 (0.919, 1.000)	0.847 (0.742, 0.846)	0.2
5	1	0.992 (0.917, 1.000)	0.848 (0.743, 0.850)	0.2
6	1	0.999 (0.999, 1.000)	0.848 (0.743, 0.850)	0.2

Table S3. Parameter values used in the model.

Parameter	Application	Parameter value	Reference
$\psi$	Weight-at-age	$1.75 \times 10^{-5}$	(8)
$\gamma$	Weight-at-age	2.8571	(8)
$L_\infty$	Length-at-age	197 cm	(8)
$K$	Length-at-age	$0.1030 \text{ yr}^{-1}$	(8)
$CV_R$	Recruitment CV	0.75	(6)
$\delta_R$	Recruitment error	$\sim N(0; \sigma_R^2)$	

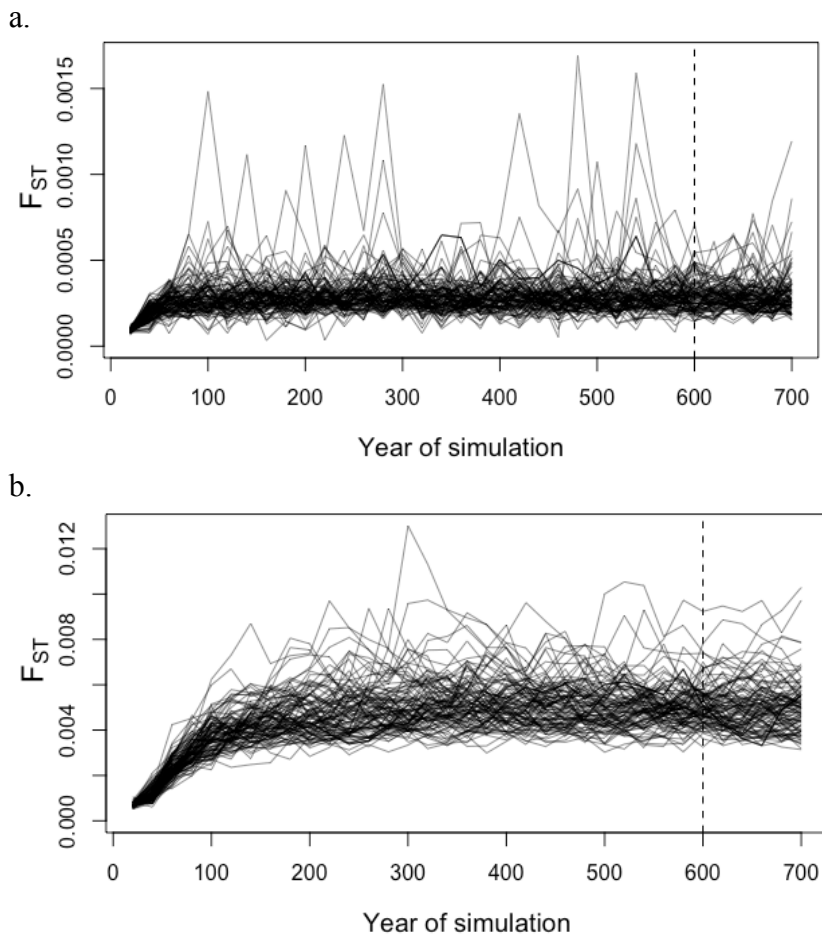


Figure S1.  $F_{ST}$  measured every 20 years over the 700-year simulation period between the North Sea population and the inner fjord (a.) and outer coast (b.). Simulations were repeated 100 times and represented base case parameterizations with 55 age-0 migrants per year from the North Sea to the inner fjord and 1,400 age-0 migrants per year from the North Sea to the outer coast. Vertical horizontal line represents the end of the burn-in period and the beginning of the 100-year simulation period.

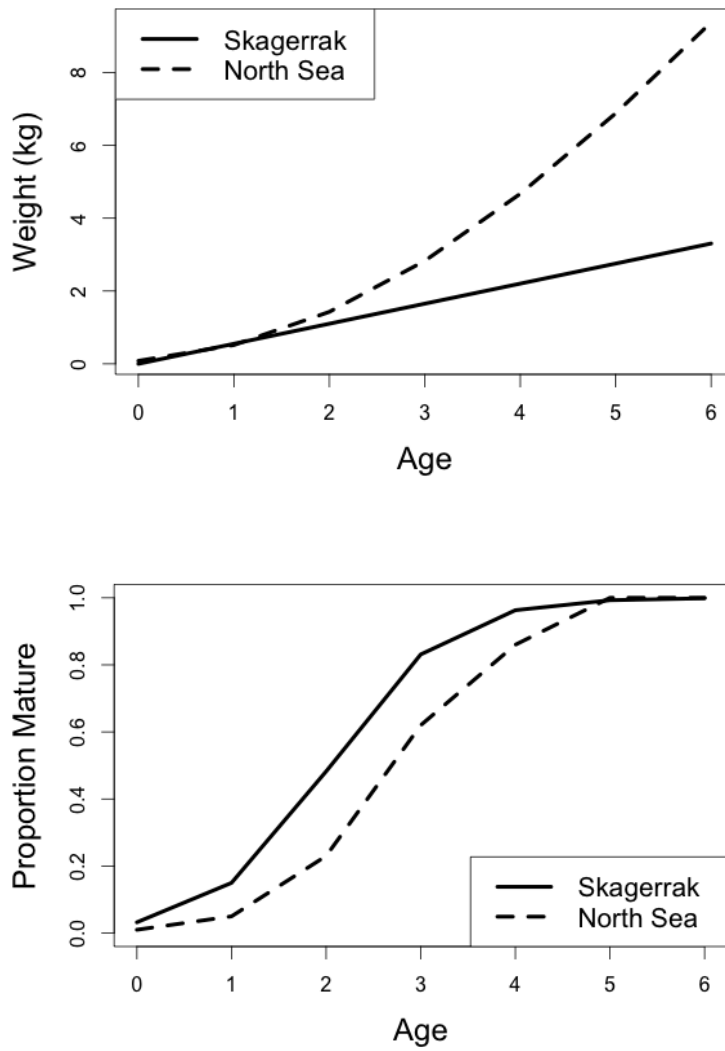


Figure S2. Weight-at-age and maturity-at-age for Atlantic cod in the North Sea and Skagerrak. Upper panel: average weight-at-age estimated for the North Sea stock of Atlantic cod (8) and the Skagerrak coast (7). Lower panel: maturity-at-age estimated for the North Sea (6) and the Skagerrak coast (7).

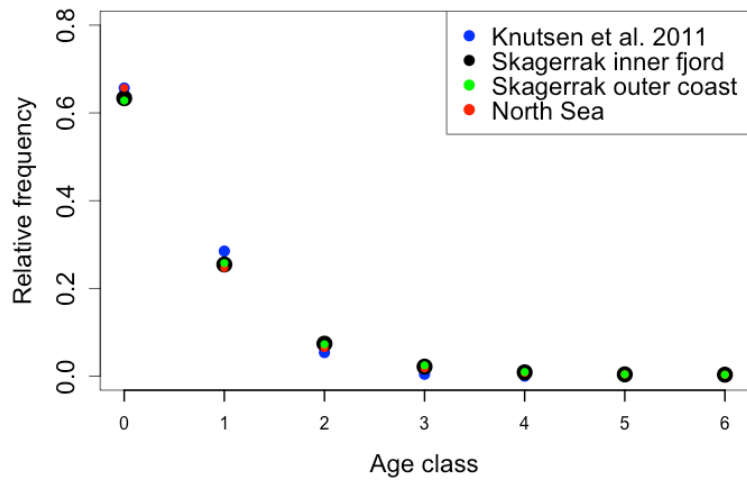


Figure S3. Age structure of the Skagerrak and North Sea modeled populations, compared to observed age structure reported by (7).