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Possible adverse impact of contaminants on Atlantic cod population dynamics in coastal ecosystems

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Abstract

While many in-lab ecotoxicological studies have shown the adverse impact of pollutants to the fitness of an individual, direct evidence from the field on the population dynamics of wildlife animals has been lacking. Here, we provide empirical support for a negative effect of pollution on Atlantic cod (*Gadus morhua*) population dynamics in coastal waters of Norway. We combine unique time series of juvenile cod abundance, body size, environmental concentration of toxic contaminants, and a spatially structured population dynamics model. Mercury concentration appeared to have decreased the reproductive potential of the cod populations in the region despite the general decline in environmental concentration of mercury, cadmium, and hexachlorobenzene since the implementation of national environmental laws. However, some cod populations appeared more resistant to mercury pollution than others and the strength and shape of mercury effect on cod reproductive potential was fjord-specific. Additionally, cod growth rate changed at scales smaller than fjords with a gradient related to the exposure to the open ocean and offshore cod. These spatial differences in life history traits emphasize the importance of local adaptation in shaping the dynamics of local wildlife populations. Finally, this study highlighted the possibility to mitigate pollution effects on natural population by reducing the overall pollution level but also revealed that pollution reduction alone was not enough to rebuild local cod populations. Cod population recovery probably requires complimentary efforts on fishing regulation.

Introduction

Increase in urbanization and anthropogenic pressure on coastal areas e.g. degradation/loss of natural habitat and pollution, has now become a global phenomenon and has changed the face of many coastal ecosystems [1,2]. Yet, awareness of these environmental problems did not grow in synchrony. The environmental movement slowly grew after World War II, when vast environmental challenges (oil spills, nuclear testing, smog) as well as cases of human health problems (e.g. the "itai itai" and the Minamata disease) started to burgeon and spread all around the globe, in parallel with the economic and industrial expansion. Environmental regulations and treaties were not implemented until the 60s and 70s (e.g. Clean Air Act (1963) and National Environmental Policy Act (1969) in the USA, Water Pollution Control Act (1970) in Norway, Stockholm Declaration (1972) by the United Nations) to regulate point source of contamination and their release to the natural environment. In Norway, for example, coastal area faced a strong demographic and industrial demand after World War II. Many heavy industries and agricultural areas have been zoned in major cities such as Kristiansand, Porsgrunn, and Fredrikstad. As a consequence, environmental contaminants, e.g. industrial chemicals and byproducts (e.g. HCB, a persistent organic pollutant) and toxic heavy metals (e.g. cadmium (Cd) or mercury (Hg)) have been discharged in coastal waters until 1970 when the Water Pollution (Control) Act was first introduced (then enacted in 1981 as Pollution Control Act).

Despite the wealth of information on the above pollutants at the individual level (from molecular to organism level), few studies have attempted to link pollution to direct population effects, in the natural environment [3,4]. Some studies have tried to extrapolate the individual-level contaminant effects observed in laboratory condition to the population level by creating individual based models or theoretical (no fit to empirical data) population level models (e.g. Leslie matrix models) but such approaches were not always successful and hard to validate. Others have performed a before-after-control-impact type analysis to evaluate the effect of pollution on natural population (often associated with cases of severe pollution e.g. oil spill [5]) or a correlative analysis comparing time series of population growth rates, or abundance with pollutant concentration [6]. However, examples of empirical, population-level, mechanistic ecotoxicological models applied to natural population remain limited [3,7,8]. Therefore, a study that directly incorporates and estimates the pathways and effect of environmental pollutant to the natural population dynamics, based on empirical fit to the data, could help fill in the gap and reveal potential hidden large-scale effects of pollution on natural population.

Here, we used Atlantic cod – a species with both cultural and economic importance in Norway; and one of the world's most economically important species – as a case study to examine whether HCB, Cd, and Hg environmental concentration history along the Norwegian coast may have impacted these populations. We specifically chose these three contaminants as they have the best spatial and temporal resolution within the available data and have been shown to have detrimental effects to living organisms (see Supplementary material, Appendix S1). Additionally, we evaluated whether the Pollution Control Act of 1981 might have played any role in mitigating the pollution impacts to this iconic species.

Material and method

Study system: species and location

The Atlantic cod – hereafter named cod - plays an important role in many of the world's ecosystems [9] including Norway where it has been a central species both culturally (back to the Viking era [10]) and economically (>6 billion NOK in value in 2017, which is more than a third of the total value of the fishery, https://www.ssb.no/en/fiskeri). The focus of this study is on the southern stock where two genetically distinct cod ecotypes co-exist (Fig. 1): an oceanic type and a coastal type. While the oceanic ecotype is more mobile [11], the coastal ecotype – the main focus of this study – is more local and is structured into many small locally genetically distinct populations regulated by water circulation pattern within fjords (which limits gene flow and favors local adaptation) [12,13] and high site fidelity and/or movement range of both juveniles and adults [14–16].

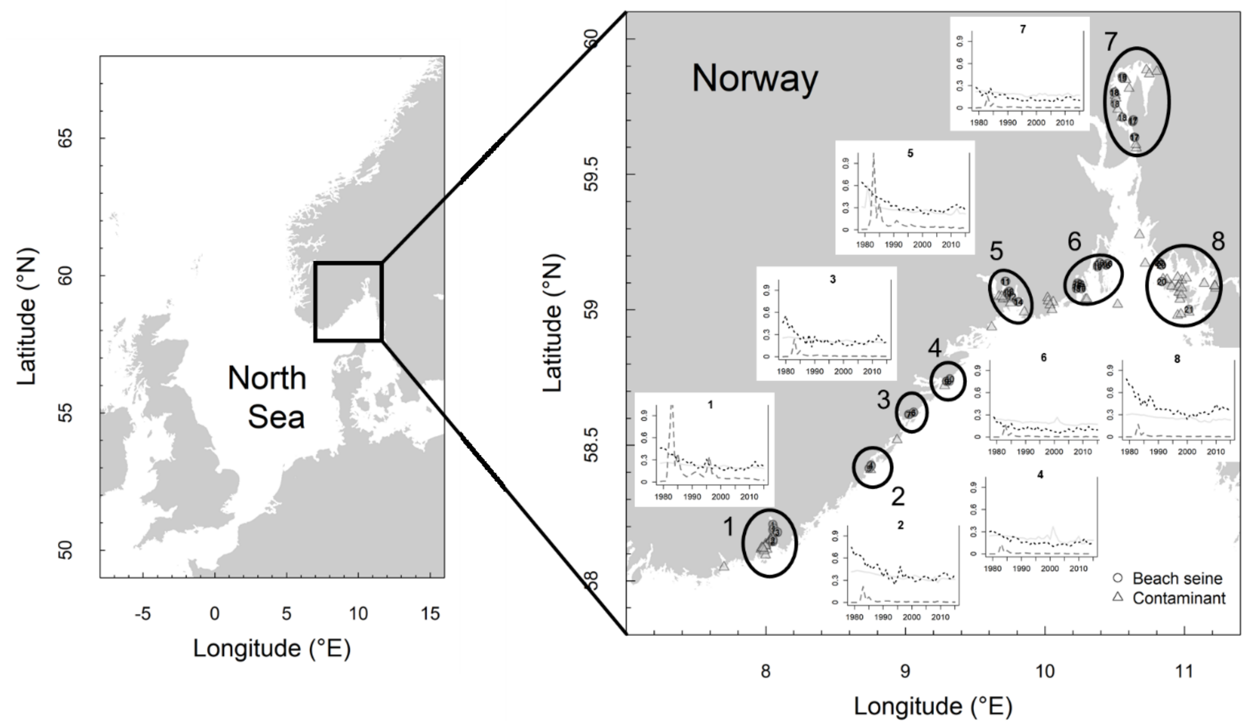

Figure 1: Map of the study region with the locations of the beach seine survey (empty circle) and contaminant data collection points (empty triangle). The beach seine survey locations are grouped into fjords as follows: 1. Torvefjord, 2. Flødevigen, 3. Lyngor, 4. Risør Skerries, 5. Langesund, 6. Tjøme – Sandefjord, 7. Oslofjord, 8. Hvaler. The number within each empty circle indicates the geographic unit each beach seine site belongs to. The numbered graph next to each fjord shows the Hg (dotted), Cd (solid), and HCB (dash) time series in mg/kg. Concentrations of Hg and HCB have been multiplied by 10 and 100 respectively to be in similar unit as Cd.

Time series data

Every year since 1919, from mid-September to early October, researchers at the Institute of Marine Research (IMR) have been conducting an extensive standardized beach seine survey along the Norwegian Skagerrak coast (Fig. 1). The survey provides a remarkable dataset containing information on catch but also length composition for cod and many other commercially and ecologically important species living in the Skagerrak coastal waters. The beach seine haul covers an area up to 700 m^2 and mostly captures age-0 and 1 cod with a few older fish. In this study, only stations with at least 10 years of observations (n = 162) between 1980 and 2015 were included in the analysis.

In parallel, contaminant data (in water, sediment, mussels and fish) have been regularly collected by NIVA since the 1980s throughout Norway, including the Skagerrak region, through various environmental monitoring activities. The blue mussel, in particular, has been getting increasing attention over the last decades and is becoming the sentinel for monitoring the pollution level in the coastal area. This filter feeder organism of practical size is able to reflect changes in the concentration of contaminants in the surrounding environment, accumulate and tolerate wide range of contaminant types and concentrations, while being generally abundant and easy to sample and transplant in cages [17,18]. Readers are referred to [17] for pollution data monitoring using blue mussels. Moreover, contaminant information from mussel has the longest spatial and temporal coverage than any other organisms collected by NIVA, in the region (Fig. 1).

Therefore, it is the perfect candidate to estimate potential contaminant exposure on locally residing cod populations. Several contaminants are measured in the mussel tissue by NIVA but the focus in this study is on Cd, Hg, and HCB concentrations in blue mussel for the period 1979-2016.

Building the cod population dynamics model that includes the effect of pollution

There are several challenges to build a spatially structured cod population dynamics model that is capable of incorporating and evaluating potential pollution effects, at the appropriate scale. These challenges include i) how to choose the spatio-temporal scale of analysis, ii) how to combine data collected across different temporal and spatial scales, iii) how to include (choice of pollutant(s), functional form of their effect, timing, and spatial scale) and choose the pollution effect that best explains changes in population dynamics.

Beach seine data were collected at specific site level. Data from of 162 sites were used in this study, some of which have only few catch and length measurements. [19] showed the importance of considering spatial structure in modeling the Skagerrak coastal cod dynamics and that a single coastwide population model missed important regional (fjord) scale dynamics. Running the model at the site level was not possible as some sites did not have enough information to reconstruct their abundance time series. Therefore, data needed to be aggregated and/or a hierarchical structure built into the model to inform sites with poorer data. [19] for example, have conducted the analysis at – what they call – fjord scale. However, some fjords spanned dozens of kilometers and included some sites that widely differed in exposure to the outer ocean. These sites, subsequently, could experience different environmental condition as well as inputs from the oceanic cod population [20,21] which might lead to contrasting population dynamics over time. We therefore sub-divided observations within a fjord into subgroups (strata) based on their geographic proximity, data availability, similarity in exposure to the outer coast and hydrographic conditions (Fig. S1). We called them "geographical units" or simply "units".

In addition to choosing the scale of analysis for the beach seine data, we also needed to choose the scale of the pollution data in order to jointly evaluate the potential effect of pollution to the cod population dynamics (Fig. 1). As the beach seine data was the main source of information to inform about the cod population dynamics, we decided to scale the contaminant data to the beach seine data. To do so, we fitted an autoregressive hierarchical Bayesian model (site within fjord nesting structure) to the pollution data then extrapolated the pollution level for each beach seine site from 1979-2015 (Supplementary information Appendix S2 and Table S1 eq1).

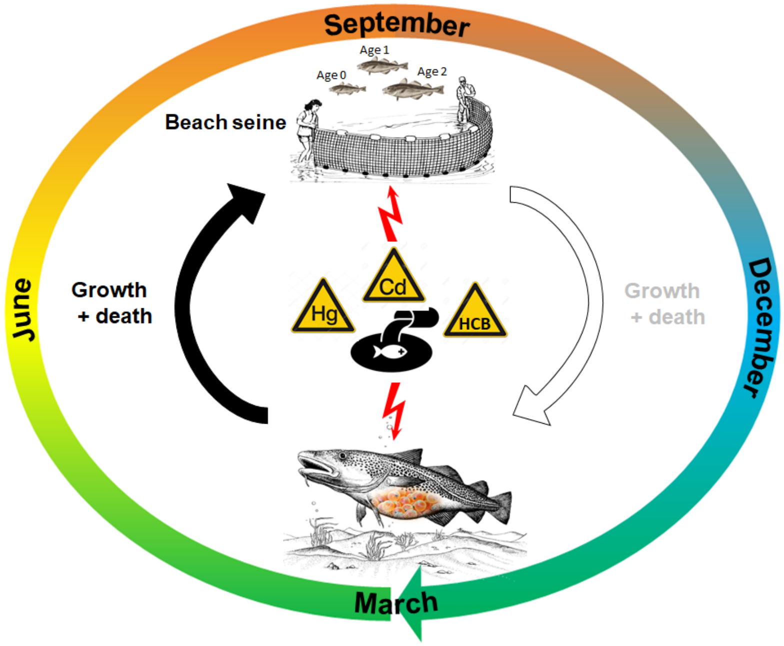

Figure 2: Schematic of cod population dynamics (annual cycle starts from April 1st and ends in March 31st) and possible pathways of pollution effect on cod. The potential pathways are indicated in red filled electric arrows.

Coastal cod spawns around March in Skagerrak and the beach seine survey is conducted around September (Fig. 2). This means that the annual cycle for the population dynamics model starts in April and ends in March and what we call age-0 recruits hereon are actually age 6-month fish, and age-1 cod are actually 1.5-year-old cod (and so on for all age classes) (Fig. S2). Therefore, when we write that age-0 recruits from year *y* depend on the spawners from year *y-1*, it actually means in that the 6-month-old cod caught in September come from the spawners in March from the same year. Similarly*,* when we formulate that pollution in year *y* affected spawners in year *y*, it actually means that the pollution in current year *y* affected March spawners in year *y+1*. If we now formulate that pollution in year *y* affected recruitment in year *y*, it actually means that pollution in current year *y* affected recruitment (the 6-month-old in September) in current year *y*. All the above are important distinctions to remember in this study.

<u>Cod population dynamics (Table S1 eq2)</u>

We parametrized the cod population dynamics using an age-structured model, starting from the recruits to age 5+ individuals (we aggregated individuals older than 5 years of age as they were rare and made up less than 1% of the population). It receives some portion of eggs and larvae from the North Sea depending on the inflow of North Sea waters [21] and environmental and biogenic condition (e.g. habitat, temperature, prey, and predator field) affect their survival [22]. We therefore parameterized coastal cod recruitment so that it depended on the local spawning stock biomass (SSB) with few additions: i) a location-based productivity parameter, α_i, that represented the average productivity of the spawners at the geographical unit, *i*. This could reflect the habitat effect for example, ii) an annual random effect term, b_y, to represent the influence of year to year change in general environmental and biogenic condition, iii) the pollution effect and iv) a residual term, $\varepsilon_{i,y}$ to model the potential effect of any other external forcing on local geographical unit level annual recruitment (e.g. larval drift from the offshore population). Survival to age 1 depended on stochastic error term $d_{i,y}$ that varies locally and annually and assumed to be centered around a grand mean $\bar{d}$ with variance σ_d^2. We included this stochasticity to account for the influence of various local environmental and biogenic factors. Total mortality rate for age 2 and above (Z) was assumed to be constant at Z = 0.916, corresponding to an annual survival rate of 40% [19,23]. We tested the sensitivity of the model to the choice of alternate annual survival rates (Z=1.3 leading to an annual survival rate close to 27% based on the values from [24,25] and a time varying Z which was reconstructed based on gillnet survey data from another study (See Supplementary material Appendix S3 on the Z time series reconstruction and limits) but the results were qualitatively the same as the most parsimonious model (Fig. S5). SSB depended on the number of individuals $N_{a,i,y}$, mass (Wa), and maturation probability (Ma) in each age class, a. Maturation probabilities (Ma) and body mass-at-age (Wa), were assumed to be fixed in this study as in [19]. All equations are summarized in Table S1.

Cod growth (Table S1 eq3)

We assumed that cod grew following the Von Bertalanffy growth curve with differences in mean growth trajectories at the geographical unit level [14,26]. We did this by estimating a separate growth coefficient for each geographical unit *i*, K_i, while sharing the same asymptotic length L_∞ (it is juvenile growth that matters the most in this study as we have most data on age 0 or 1 individuals). Additionally, we accounted for individual differences in growth trajectory by adding variability around the growth curve (assuming a normal distribution around the Von Bertalanffy growth curve), σ_{La}^2. We also accounted for the 6-month lag for each age class definition (i.e. what we called age 0 is actually a 6 month-old fish) by adjusting by 0.5yr the growth equation. σ_{La}^2 was fixed to 5 based on exploration of the length composition data in this study and expert knowledge. Values from 5-7 were tested but did not qualitatively change the results (Fig. S6).

From age to length: the age-length transition probability function (Table S1 eq4)

One novelty in this study is the direct use of an age-length transition probability function. Previous studies assigned fixed age categories to length measurement [27] but such approach failed to account for the inherent uncertainty associated with age-length assignment (or required extensive sensitivity tests as in [27]). However, by explicitly using the age-length transition probability function, we can directly account for the inherent uncertainty associated with age-length categorization.

The survey selectivity function (Table S1 eq5)

Not all fish are equally available to the beach seine sampling. We introduced this concept in this study by including a length-based selectivity function that combined both the idea of availability (whether fish lived at the beach seine sites) and full gear selectivity (the selectivity of the gear assuming species were all present at the sites). We modeled it using an inverse logistic function based on the observation that young and small individuals (age 1 or younger) mostly inhabit inshore whereas older individuals were more widely distributed (Table S1). However, for parameter estimability reason, we had to fix both $L_{50} = 30$ and $L_{diff} = 10$ based on expert knowledge. Sensitivity test to other L_{50} (25 and 35) and L_{diff} (8-12) values were also tested but it did not qualitatively change the results (Fig S7-8).

How to make use of the length composition data to inform population age structure? (Table S1 eq6)

By combining the selectivity equation and the age-length transition function above, one can convert from population age composition at the geographical unit *i* to population length composition at unit *i*.

Linking the population dynamics with cod catches (Table S1 eq7)

The observation model that translates from population to catch was based on over-dispersed lognormal Poisson process as in [19] or [28] to account for occasional high catches. Catchability, q_i, were fixed at 1 for all geographical units in this study because this parameter could not be estimated due to its confounding effects with the numbers at age and the selectivity function. Therefore, the estimated numbers at age, $N_{a,i,y}$, are in a relative scale.

How to include and model the pollution effects to the cod population dynamics (Table S1 eq8)

We hypothesized two potential pathways of pollution effect on cod population dynamics, both acting in a multiplicative way. i) pollution affected the survival rate of the offspring (recruits). We focused on recruits and not on subsequent age classes as we had the most information on age 0 recruits. ii) pollution affected the reproductive output by reducing the numbers of effective/successful spawners or the number of viable offsprings. The above two pathways could actually be modelled the same way due to their multiplicative effect e.g. saying that pollution in year *y-1* affected recruitment in year *y* was the same as saying that pollution in year *y-1* affected SSB in year *y-1.* Therefore, we only modeled the effect of pollution on recruitment in this study (Table S1 eq2). Moreover, we did not know which contaminant(s) time series or combinations might best explain changes in cod population dynamics. Therefore, all possible combinations of contaminants time series have been tested as chemicals with similar modes of action can increase their effect on the organisms [29]. However, before combining (arithmetic mean) the time series into a single pollution index, we first standardized each contaminant time series with its maximum value so that they all ranged from 0 to 1. Such transformation was necessary as the scale of pollution concentration differed between pollutants. Additionally, we did not know the functional form of the effect of pollution to the recruitment success. We therefore tested for a linear, exponential, and sigmoidal decrease of recruitment success with pollutant concentration (Table S1 eq8). We also tested for any potential time lag in pollution effect to the population i.e. no lag (pollution affect recruitment survival), one-year lag (pollution affect spawning potential) and two-year lags (pollution affect spawning potential). Finally, we tested if all local populations (at the geographical unit level) responded to the pollution the same way. We expected that local populations, with different pollution and environmental history, would show a different response to pollution. As testing all possible combinations of pollution effect was impractical, we decided to test the most plausible scenarios in a sequential way (Table S2-4).

Parameter estimation, model selection and validation.

All models were fitted using template model builder (TMB) [30]. We combined four different approaches to determine the most parsimonious cod population dynamic model as the sole use of a single information criterion such as AIC or BIC is often not sufficient [31]. The criteria we used are AIC, model convergence issue (i.e. non-invertible hessian), parameter identifiability problems, and goodness of fit to catch and length composition data (based on visual inspection of model fits to data). The model which showed the best combined performance (i.e. the lowest AIC without any problem for the other criteria) were chosen in the end as the most parsimonious model. Additionally, we decided to take a step-wise approach in choosing the most parsimonious model as it was practically impossible to test all possible combination of parameters and hypothesis. We therefore did the following. i) test all combinations of pollution time series (Cd, Hg, and HCB), functional form, time lag, and local pollution effect (i.e. same for all fjords or different for each fjord). ii) for each pollutant and functional form combination, find the time lag with the lowest AIC. If the above model includes a fjord-specific pollution effect, further refine the model to eliminate non-significant fjord-level pollution effects (if any) and lower AIC, iii) select the most parsimonious model from the above selection (Table S4-5).

Moreover, while state-space models are usually regarded as more accurate and reliable than observation or process error models [32], it is important to test and understand the limits and reliability of each developed model. In order to do this, we investigated i) if the model estimates (e.g. the time series of SSB) are reliable. To do this, we used a simulation-estimation approach to simulate data (100 sets) using the most parsimonious model (catch and length composition data were generated with the same sample size as the original dataset), re-fitted the same model to these data, and examined how similar these estimates were compared to the one used to generate the data. If the parameter estimates (with their 95% confidence interval) from simulated data (n=100) comprised the true value (used for simulation) less than 50% of the time, we deemed it was “unreliable”. ii) if model results were sensitive to the reconstructed pollution time series. We examined this as the reconstructed pollution trajectories were uncertain and showed variability between fjords. To do this, we generated 100 MCMC samples of pollution time series and refitted the most parsimonious model to each sample and examined model sensitivities.

Results

Reconstructed pollution time series

The average reconstructed pollution time series for Cd, Hg, and HCB, showed a generally declining trend since 1980 (Fig. 1 and S2-4). While, Cd and Hg in all eight regions experienced a steady decline over time (there was a mean correlation level of 0.65 between these two time series), HCB concentration fluctuated more episodically with few large peaks in the early 1980s (the mean correlation with the other two time series was 0.33 and 0.25 for Cd and Hg respectively). However, all three pollution time series came with large uncertainty that varied over time depending on the regions (Fig. S2-4). Reconstruction of the Hg time series was the least uncertain of the three, followed by Cd and HCB. Hg concentration was the most uncertain in Flødevigen, while Cd level was the least certain for Langesund fjord. HCB time series was the least reliable of the three with the largest credible interval for some years and fjords.

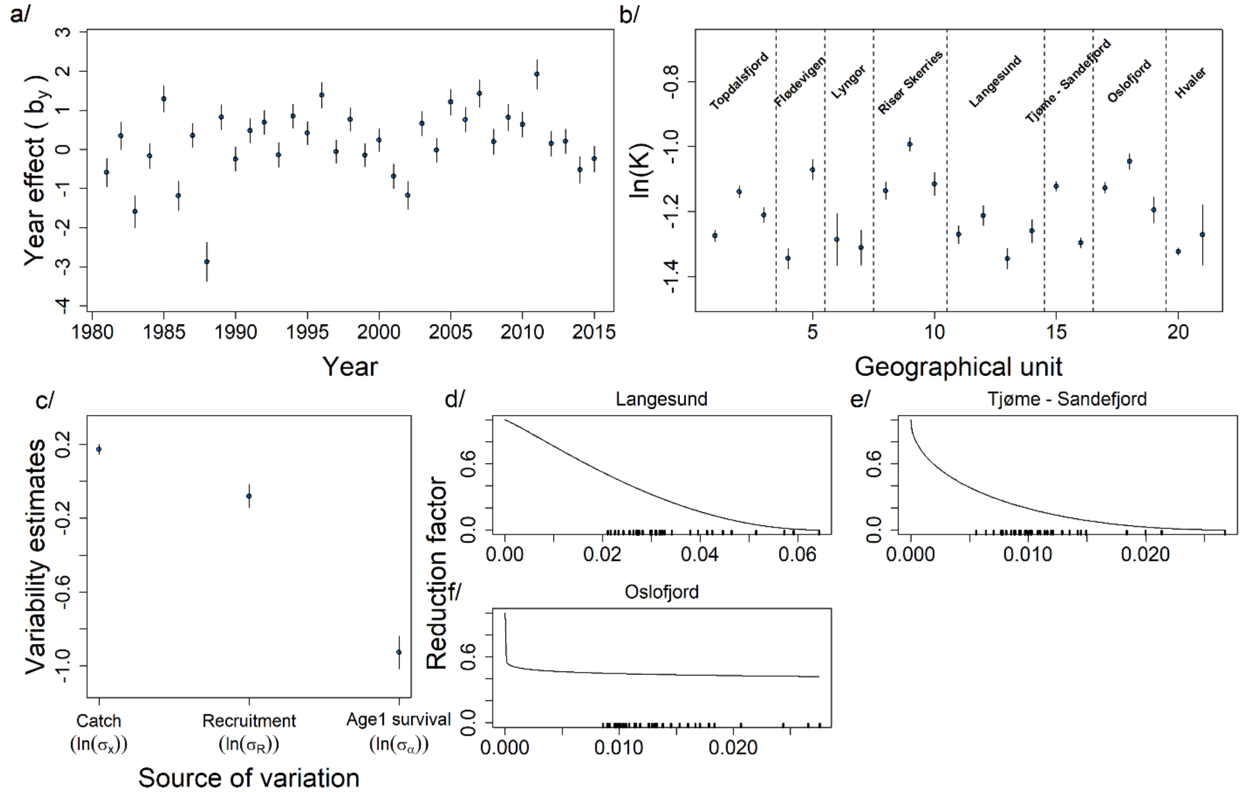

Figure 3: a/ Estimated year effect from 1980 to 2015. b/ Estimated cod growth speed for each geographical unit. c/ Estimated variability in cod catch, recruitment, and survival rate for age 1 fish. In a-c/, filled circles represent the mean and error bars the standard deviation. d-f/ Estimated mercury effect on cod spawning potential from the most parsimonious model. The rug plot on the x-axis shows the "observed" (technically, it is model derived) mercury concentration level in respective fjords.

Model selection results

The most parsimonious cod population dynamic model included Hg as a single pollution covariate (Table S3-5) acting on recruitment success through an inverse logistics shaped curve with a 2year-lag (equivalent to a year lag on SSB i.e. the environmental condition preceding the spawning period) (Fig. 3d-f). The two other pollutants (including all other combinations of pollutant time series) and the null model without pollution effect led to a poorer fit to the data (Table S3-4 and Fig. S9). The most parsimonious model only included the Hg effect in Langesund, Tjøme - Sandelfjord, and Oslo fjords (all located in the northern part of the study area). For the remaining five fjords (four of them located in the southern part of the study area i.e. Topdalsfjord, Flødevigen, Lyngor, and Risør Skerries), ambient Hg concentration in mussel did not show significant effect (decrease) on recruitment success. In Langesund and Tjøme – Sandelfjord, recruitment was reduced to very low level at the highest observed mercury concentration while in the Oslo fjord, recruitment level was not reduced below 50% even at their highest observed Hg level (Fig. 3d-f). However, the functional forms of the Hg effect on cod reproductive potential are to be interpreted with care. Sensitivity analysis based on 100 MCMC reconstructed Hg time series revealed some variability in the shape of estimated pollution effect (Fig. S10). This is especially true at low Hg concentration where data is missing and the estimated effect is simply based on extrapolation. Nonetheless, these apparent uncertainties in Hg effect did not necessarily lead to large changes in SSB time series estimates (Fig. S11). The biggest difference between the most parsimonious model and the MCMC samples were observed for years with large confidence interval around SSB estimates (Fig. 4 *vs.* S11).

Parameter estimates from the most parsimonious model

The estimated annual random year-effect, b_y, from the most parsimonious model varied from –2 to 2 except for 1988 when its effect was close to –3 (Fig. 3a). The model also estimated a large variability in juvenile growth potential between fjords and even within fjord (Fig. 3b). For example, cod growth potential was highest in Risør Skerries whereas it was much slower in nearby fjords such as Lyngor and Langesund. In the case of Flødevigen, there was even a large difference in growth potential between its two units (Fig. 3b). Despite this discrepancy in estimated growth potential, the simulation-estimation exercise showed that these estimates were generally reliable (Fig. S12).

Furthermore, there was some disparity in the amount of variability associated with different processes driving the cod population dynamics. The observation error associated with the catch data was the largest source of variability in the model suggesting a high degree of noise associated with the beach seine sampling. Additionally, recruitment variability was estimated to be higher than the variability around the age 1 survival suggesting a stronger influence of local factors to the recruitment success (Fig. 3c).

Changes in cod population over time

Cod SSB has generally been declining in six out of the eight fjords since 1980 but with a lot of inter-annual variability (Fig. 4). Lyngor and Risør Skerries were the two exceptions with a slightly increasing SSB over time despite the inter-annual variability. In addition to the differences in trend between fjords, geographical units within fjord also showed some contrasts. For example, while units 1 and 3 in Topdalsfjord showed a similar decreasing SSB trend (average correlation level of 0.62), unit 2 followed a different pattern (average correlation of 0.48 and 0.04 with unit 1 and 3 respectively). However, the simulation-estimation exercise indicated poor reliability for a few estimates (the vertical shaded bars in Fig. 4) e.g. the slight increase in SSB in unit 18 within Oslo fjord in the mid-2010s might only be an artefact. Nonetheless, these unreliable estimates were generally scarce and limited to a few years in unit 11 (in Langesund) and unit 18 and 19 (in Oslo fjord). The rest of the fjords including Topdalsfjord, Lyngor, Risør, Tjøme - Sandelfjord, and Hvaler showed a more reliable estimation performance. Finally, none of the units shared the same SSB trend except maybe an increase in SSB in the late 1990s (Fig. 4).

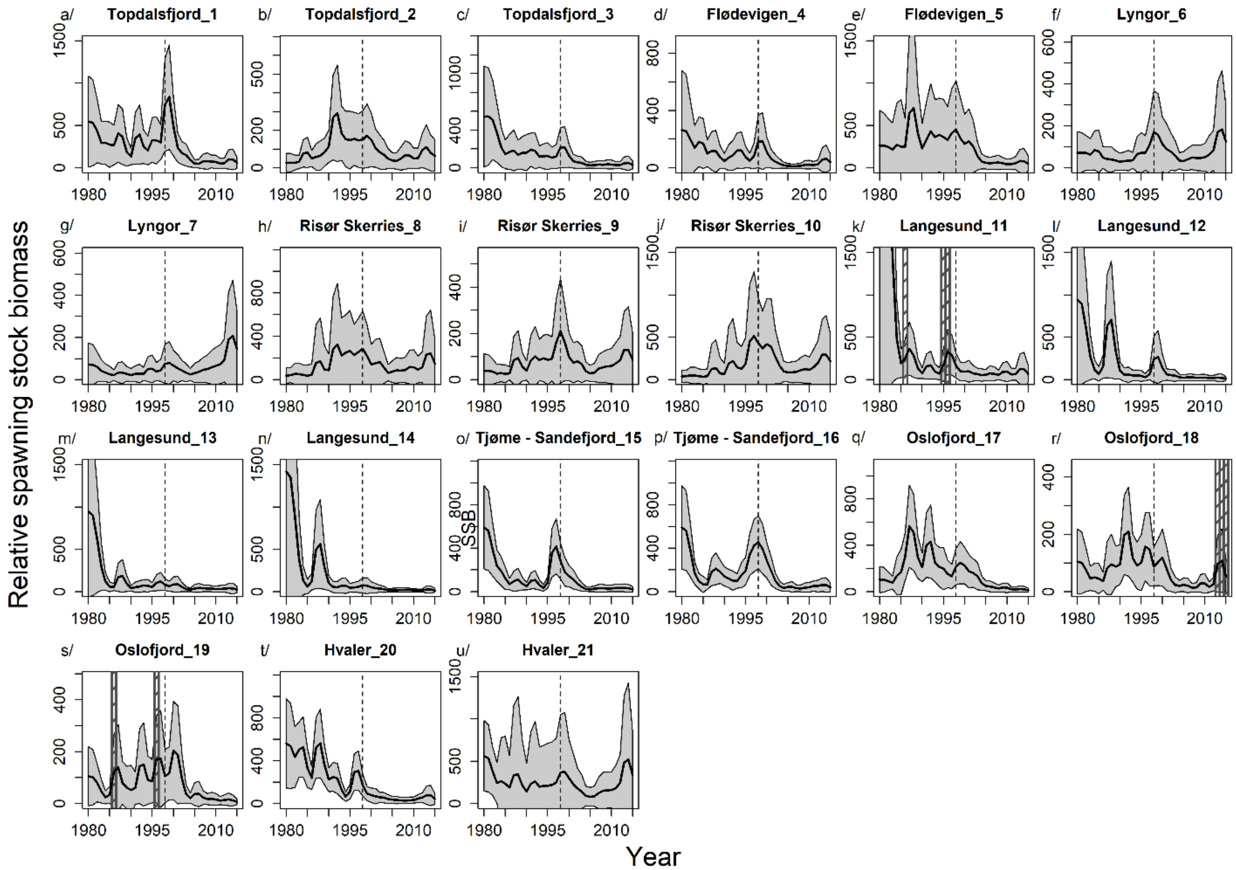

Figure 4: The average estimated SSB trajectory (a-u) and their 95% confidence interval by geographic units within different fjords. Thick black lines are the average and the shaded area represent the 95% confidence interval. Vertically shaded area with diagonal bars indicates years for which estimates are “unrealiable”.

Discussion

By combining unique time series of juvenile cod abundance, body size, environmental concentration of toxic contaminants, and a spatially structured population dynamics model, we were able to shed light on several aspects of Skagerrak coastal cod population dynamics, their life history, and their sensitivity to Hg, Cd, and HCB concentration in the environment.

Cod population dynamics over the last four decades

Many local cod populations appeared to have been declining since 1980 as was suggested in many other studies [19,33] but these patterns were not shared among all locations. In fact, some local cod populations in Lyngor or Risør Skerries, for example, were slightly increasing since 1980. Nevertheless, some patterns were common to all fjords. One example is the recruitment failure in 1988 that was caused by large toxic algae bloom that hit the coast of Skagerrak [34]. Alternatively, local cod populations shared several peak recruitment events e.g. 1985, 1989, 1996, 1998, and 2011 with a few (1985 and 1996) overlapping those of the oceanic cod from the North Sea, Skagerrak and Kattegat region [33] (Fig. S13); which observation strengthens the possibility that oceanic cod population influences coastal cod populations and that its magnitude depends partly on the connectivity with the North Sea [21].

Local scale variation in life history parameters

We also confirmed the importance of local scale dynamics in shaping natural populations as in many other studies (e.g. [19]). Cod growth were changing at scales smaller than fjords (Fig. 3) – called geographical unit in this study – leading to large differences in SSB (Fig. 4) and recruitment (Fig. S13) trend over time even between units within fjords such as in Topdalsfjord. Some of these dynamics could be related to the ocean exposure as sheltered sites showed a slower juvenile growth than exposed sites (e.g. unit 2 *vs.* 1&3, Fig. 3&S1) [35]. These exposed sites might be experiencing more favorable growth condition owing to an increased influence of the outer ocean and/or due to their genetic difference (small but significant) [15]. We also found some surprising results that juvenile cod growth was above average in the Oslo fjord area despite its history of pollution and anoxia [36]. This is probably due to the above average exchange of North Sea waters transporting faster growing cod compared to other areas in the Skagerrak [35].

Pollution history in Skagerrak and its possible effect on coastal cod

We found that the concentration of Hg, Cd and HCB in mussel tissue have all been declining (while there is a large variability around estimated pollution time series) since the early 1980s, suggesting a possible mitigation effect from the pollution control act of March 13th, 1981 and other environmental laws (e.g. Stockholm convention http://www.pops.int/). However, the declining trend in Hg concentration inside the fjords – the contaminant that showed the largest impact on cod populations dynamics in this study – might not have been enough to rebuild cod stocks in certain fjords. Indeed, despite the reduction in contaminant concentration and the presence of several large recruitment events, local cod population were still declining over time in six out of the eight fjords examined in this study. This would suggest that the local population decline was not only due to pollution but also to other factors such as fishing pressure, changes in environmental condition, other environmental pollutants (which all combined, slowed down population recovery). Furthermore, it must be kept in mind that cod may have been exposed to other xenobiotics or environmental stressors (e.g. anoxia), not examined by this study, which could have been covarying with Hg concentration. The causal relationship discussed here must therefore be seen as possible explanations.

Moreover, we found that Hg concentration experienced by cod before spawning (chosen by model selection) may have reduced the reproductive potential of cod in the region. This is in line with the well-known adverse effect of Hg (especially, its methylated form) on the reproductive success of wildlife (e.g. reduced embryo development, offspring numbers, and juvenile survival rates) [37]. Additionally, there was some local difference in cod sensitivity to Hg concentration: pollution effect was the most visible in the northern region than in the southern region despite having a similar range of Hg concentration. These fjord-level differences in pollution effect could, for example, be attributed to local adaptations [13,38]. However, we have to keep in mind that the estimated functional form of pollution effect was sensitive to the reconstructed pollution history, thus care must be taken in interpreting this result. Nevertheless, this source of uncertainty did not affect much the resulting value and trend in the SSB which was generally quite robust (Fig. 4&S11).

Challenge of scales in ecological analysis

Like in any ecological study, scientists must adequately choose the scale of analysis. Past studies have shown that a mischoice of scale can mask important variations and trends in local populations [19]. In this work, we reduced the scale of analysis from fjords (as in past studies such as [19,27]) to "geographical units" in the attempt to maximize the value of information. By doing so, we found out that all units within fjords did not follow the same population trend over time. However, the choice was not easy and a careful examination of residual pattern, parameter estimates, and a simulation-estimation exercise was required to confirm modeling choices. We also had to choose the geographic scale for reconstructing the pollution history. We were only able to model pollution at the fjord scale (i.e. assuming all units within a fjord had the same pollution history) as data availability was prohibitive. However, there are probably local differences in pollution concentration within a fjord based on proximity to the pollution source or localized water circulation pattern. Additionally, we ignored possible seasonal pollution dynamics (some information were collected at different time of the year), but other studies indicated that concentration changes through the seasons are small relative to differences among locations (e.g., [18]). Therefore, the overall annual pollution concentration and trend would still be generally representative for the geographical units. Moreover, unit-level pollution information might not even be useful especially that the pollution effect was best modeled on the spawners (and their reproductive outputs) which have higher mobility than juveniles with a range of dozens of km^2 [14,16]. More accurate information could be obtained by sampling pollutants on individual cod but such data were limited. Similarly, we do not know nor trying to know the precise period of the year when pollution most affected cod dynamics. Therefore, summarizing pollution information at an annual level was a good start to investigate the effect of pollution to the cod population dynamics (See Supplementary material Appendix S2 for more discussion).

Conclusion

In this study, we provided one of the first direct empirical indication of an adverse effect of contaminants on coastal cod population dynamics. Despite the overall decrease in Hg, Cd, and HCB concentration in the Southern Norwegian coastal waters since the 1980s, Hg appeared to have had a negative impact on cod reproductive success, with the reservation of confounding factors. In general, cod in the northern region showed a stronger sensitivity to Hg than the southern population and the populations showed a large variability in growth at scales smaller than fjords. Both observations suggest the importance of local adaptation in shaping the population dynamics of the natural resources in coastal waters. Nonetheless, many local cod populations are still in bad shape and only a few are doing good. This highlights that pollution reduction alone is not sufficient to rebuild cod populations and that complementary actions on fishing regulation, habitat improvement, and understanding on fish biology are needed to ensure a sustainable use and conservation of coastal natural resources.

Data, code and materials

The applied code and data are available on Dryad.

Competing interests

The authors declare no conflict of interest.

Authors' contributions

All authors have substantially contributed to the conception, design, acquisition of data, analysis, interpretation of the data, drafting, revising, and approving the final version of the manuscript.

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