Long-Term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data

T Jansen
K Kristensen
M Payne
et al

Let us know how access to this document benefits you
Long-Term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data

Jansen, T

http://hdl.handle.net/10026.1/15195

10.1371/journal.pone.0038758
PLoS ONE
Public Library of Science (PLoS)

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.
Long-Term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data

Teunis Jansen1,*, Kasper Kristensen1, Mark Payne1, Martin Edwards2, Corinna Schrum3, Sophie Pitois4

1 Technical University of Denmark (DTU) AQUA, National Institute of Aquatic Resources Charlottenlund, Charlottenlund, Denmark, 2 Sir Alister Hardy Foundation for Ocean Science (SAHFOS), Plymouth, United Kingdom, 3 Geophysical Institute, University of Bergen, Bergen, Norway, 4 Centre of Environment, Fisheries & Aquaculture Science (CEFAS), Suffolk, United Kingdom

Abstract

We present a unique view of mackerel (Scomber scombrus) in the North Sea based on a new time series of larvae caught by the Continuous Plankton Recorder (CPR) survey from 1948-2005, covering the period both before and after the collapse of the North Sea stock. Hydrographic backtrack modelling suggested that the effect of advection is very limited between spawning and larvae capture in the CPR survey. Using a statistical technique not previously applied to CPR data, we then generated a larval index that accounts for both catchability as well as spatial and temporal autocorrelation. The resulting time series documents the significant decrease of spawning from before 1970 to recent depleted levels. Spatial distributions of the larvae, and thus the spawning area, showed a shift from early to recent decades, suggesting that the central North Sea is no longer as important as the areas further west and south. These results provide a consistent and unique perspective on the dynamics of mackerel in this region and can potentially resolve many of the unresolved questions about this stock.

Introduction

Mackerel (Scomber scombrus) is one of the most abundant and widely distributed fish species in the North East Atlantic [1]. Mackerel plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks [2]. Mackerel is furthermore caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes [1]. Large changes in mackerel abundance and distribution have therefore significant effects on ecosystems as well as economics. The ecological impact through altered predation pressures on secondary production and fish recruits are likely large, but currently not assessed [2]. More easily observed are the political and economic consequences [3,4].

Radical changes in abundance and distribution have been observed throughout the north-east Atlantic during the last century of developing mackerel science and fisheries [1] especially in the North Sea. The North Sea mackerel is considered to be a distinct stock that, unlike the western mackerel stock spawns inside the North Sea (Figure 1). The North Sea spawning stock was large and lightly fished up to the late 1960s, where the development of modern sonars, power blocks and single-vessel purse seining led to a ten-fold increase in mackerel landings [5]. This fishery was unsustainable and resulted in a collapse of the stock in the 1970s. Despite subsequent regulations of the fishery designed specifically to protect this stock, it never rebuilt to its former level. In the last decade the spawning stock biomass has been 150-230 kt [1], compared to over 2 500 kt in the beginning of the 1960s [6,7]. It is currently unknown why the North Sea stock has not rebuilt to former levels.

Unfortunately, documentation of the historic development is based on fragmented information sources that do not consistently cover the whole period from before to after the collapse. This is a hindrance for addressing key questions about the lack of stock rebuilding and the consequences of these changes in distribution and abundance. An internally-consistent time-series with broad temporal span would therefore greatly aid the understanding of the development of this stock.

One such potential time series stems from the Continuous Plankton Recorder (CPR) survey in the North Sea. The CPR is a self-contained automatic plankton recorder that collects plankton continuously while being pulled by route-vessels of opportunity e.g. ferries. The monthly deployment on a variety of routes through 8 decades have resulted in a unique time series that have the former levels.

Recently the analysis of fish larvae in the CPR samples has been completed up to 2005. This offer a unique opportunity to investigate long term changes in abundance and distribution of mackerel larvae.

Citation: Jansen T, Kristensen K, Payne M, Edwards M, Schrum C, et al. (2012) Long-Term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data. PLoS ONE 7(6): e38758. doi:10.1371/journal.pone.0038758

Editor: Inés Álvarez, University of Vigo, Spain

Received January 12, 2012; Accepted May 10, 2012; Published June 21, 2012

Copyright: © 2012 Jansen et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: Research was funded by EURO-BASIN (FP7 #264933) and Department of Environment, Fisheries and Rural Affairs (Defra) who funded the analysis of fish larvae samples from 1979 to 2005 through project MF1101. The long-term ECOSMO model simulation was funded by the projects EU-MEECE (FP7 # 212085) and the Norwegian Research Council (MarinEra project ECODRIVE. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: Tej@aqua.dtu.dk
We present here the new time series of mackerel abundance in the North Sea based upon larvae caught by the CPR from 1948 to 2005, spanning both the period prior to the development of the intensive fishing in the late 1960s and modern times. We verify the spatial origin of the larvae through use of a hydrographic backtracking model for all sampled larvae. Using a technique not previously applied to CPR data, we then construct a larvae index considering catchability as well as spatial and temporal autocorrelation. Considering the larvae abundance as a proxy for number of spawned eggs and spawner biomass, we compare it with existing egg survey data and fisheries-based assessments with a focus on the decline around the 1970’s. We review the possible applications of this time series, including supplementing or improving the mackerel stock assessment and the international mackerel egg survey with data from the CPR survey. Finally, we provide recommendations regarding calculation procedures for CPR data.

**Materials and Methods**

Mackerel Larvae Data
Mackerel larvae from Continuous Plankton Recorder (CPR) surveys in 1948 to 2005 in the region 51–61°N and 3.5°W–9.5°E were obtained from the SAHFOS database. The details of the CPR survey are described elsewhere [9,10]. Briefly, the CPR are towed by ships of opportunity at speeds in the range of 10–15 knots and at an approximate depth of 7 m [9,11]. Water enters the recorder through an aperture of 1.62 cm², and is filtered through a continuously moving band of silk with an average mesh size of 270 μm. The captured plankton is fixed in formalin. The silk band is divided into samples representing 10 miles of tow for analysis, equivalent to approximately 3 m³ of filtered seawater. Methods of counting and data processing are described by [9,10].

Thermocline Data
Thermocline depth data for the period 1948–2005 were processed from a long-term ECOSMO model run [12,13]. The model is a coupled physical-biological 3-d deterministic model. It simulates the time varying hydrodynamic and lower trophic level conditions in the region North Sea and Baltic Sea as a function of atmospheric, oceanic and terrestrial time varying boundary conditions. The thermocline data are provided on the spherical model grid (0.1° lat × 1/6° lon) as monthly averages. Similar data from an earlier model simulation [14] are available via the ICES WGOOFE website (www.wgoofe.org) or directly from the University of Bergen (ftp://ftp.gfi.uib.no/pub/gfi/corinna/...
Effect of Larval Drift

The positions of mackerel larvae captured by the CPR survey do not necessarily correspond to the actual location where spawning took place. Ichthyoplankton can, in some regions of the North Sea, be rapidly advected away from their spawning location: the magnitude and direction of this drift can vary appreciably between years (e.g. [15,16]). As a first step in the analysis of the larval dataset, we attempted to estimate the magnitude of this advection, and thereby check for a potential bias introduced by drift processes.

As the basis for these calculations we applied an established hydrographic backtracking technique [17,18]. The backtracking calculation was performed using the IBMlib library [17], forced with hourly physical fields (currents, temperature and turbulence) derived from the NORWECOM model [19,20]. These fields were available from 1970 to 2005. Larval observations outside this period were not modelled. For each location (in time and space) where Mackerel larvae were observed in the CPR survey, 100 particles representing mackerel “larvae” were released in the model, uniformly distributed throughout the water column. Time in the model was then run backwards to determine a range of possible trajectories along which the larvae could have originated. No active-behaviour was applied to the particles – the “larvae” were mixed throughout the water column following the modelled turbulence as passive tracers. No explicit attempt was made to account for ontogenetic changes during this time (e.g. changes in egg buoyancy, hatching of eggs, changes from endogenous to exogenous feeding of larvae).

The duration of the backwards-advection scheme was based upon an estimate of time-since-spawning. Mackerel larvae in the CPR survey have a mean length of 4.8 mm (s.d. 2.0 mm) [21]. Under good temperature and food conditions, mackerel larvae grow from a typical hatch size of 3 mm to 4.8 mm in approximately 2.4 days [22]. Mackerel eggs are pelagic and therefore drift of the eggs also needs to be accounted for: typically 50% of mackerel eggs have hatched after 6.7 days at 11°C [23]. We therefore estimate that, on average, approximately 10 days have passed since the larvae captured by the CPR were spawned.

The simulated mackerel particles were therefore advected backwards in time for 10 days. At the completion of this period the geographical distance between the site of capture and the end point was calculated was calculated for each particle and the median of the distance distribution calculated. The process was then repeated for all larval observations in the CPR and the median of the distance distribution calculated. The process was then used to assess the magnitude and importance of advection processes in shaping the distribution of larvae.

Mackerel Larvae Model

The log gaussian cox model. The distribution of larvae captured in the CPR survey were analysed using the so-called “log-gaussian cox process” (LGCP) model [24]. This model assumes that observed larvae counts are Poisson distributed with a multivariate log-normal mean and a spatio-temporal correlation structure. Denote by \( i \) the id of the CPR sample and let \( N_i \) be the number of larvae caught in the sample. The model then states that given an unobserved/latent log-intensity in \( i \) we have:

\[
N_i \sim \text{Pois}(e^{\eta_i})
\]

Note that exponentiating the random variable \( \eta \) introduces overdispersion in the distribution [24] and that the latent vector \( \eta \) is assumed to be multivariate Gaussian:

\[
\eta \sim \mathcal{N}(\mu, \Sigma)
\]

with a mean vector \( \mu \) and covariance matrix \( \Sigma \). The \( \mu \) parameter describes the systematic effects while the covariance matrix models the random effects. Each sample unit \( i \) is associated with a set of covariates; position (cells of 0.3° latitude×0.6° longitude), year, day of year, thermocline depth and hour of day.

The random versus systematic effects. The spatio-temporal distribution of larvae is not completely random: aggregation in both space (“patches”) and time can be expected. Also, some degree of continuity from day to day and from year to year would be expected because the abundance of larvae are expected to be related to the stock size of the mackerel and mackerel lives and spawns for multiple years. We therefore consider the distribution of larvae as a so-called space-time separable random field with exponential correlation structure

\[
\rho(\Delta x, \Delta t) = \exp(-2|\Delta x|)\exp(-|\Delta t|)
\]

to define the covariance matrix \( \Sigma \) by

\[
\Sigma_{ij} = \sigma^2 \rho(x_i - x_i, t_i - t_i)
\]

In words this means that if we consider two samples \( i \) and \( j \) then the correlation between the two log-abundances depends in an exponentially-decaying manner on the spatial distance between the samples \( (\Delta x) \) and the temporal distance between the samples \( (\Delta t) \), where larger distances have smaller correlations. The decay of the correlation in space and time is described by the model parameters \( \alpha \) and \( \beta \). The variance parameter \( \sigma^2 \) describes the variations from the high abundance to low abundance areas.

In reality, even if a sample is taken in an area with high abundance, it is not guaranteed that the catch will be high. This is because individual samples from the sea generally show a high level of small scale variability. We can account for this by adding a further level of variance at the sample level. This local noise effect is also referred to as the “nugget effect” \( \eta_{\text{nugget}}(\cdot) \) [24].

It is assumed that spawning and hence larvae abundance follows a fixed seasonal pattern within the year, modelled here as a gaussian. However, the yearly level is considered as a random effect:

\[
\log r(y,d) = p_{\text{spawn}}(d) + \eta_{\text{spawn}}(y)
\]

where \( r(y,d) \) is the number of larvae on day number \( d \) in year \( y \). The seasonal log-abundance pattern is the 2nd order polynomial \( p_{\text{spawn}}(d) \). Note that a 2nd order polynomial is the logarithm of a gaussian density. The yearly log-level of the abundance is the random variable \( \eta_{\text{year}}(y) \) which is assumed to be normal distributed with mean zero and variance \( \sigma^2 \). A year to year correlation of this process is incorporated as exponentially decaying with the distance between years.
Due to the fact that the CPR operates horizontally in a fixed depth of approximately 7 m [9,11], the catchability (the relationship between the number of larvae present in the water column and the number of larvae caught) of the recorder can be expected to be sensitive to changes in vertical distribution of the larva. Small mackerel larvae, such as those caught by CPR, have been observed to stay above the thermocline where they migrate towards the surface at night [25,26]. However, the water immediately behind a large, fast-moving vessel is likely to be mixed and homogenized well below the CPR towing depth [9]. To test and account for any systematic effects from changes in vertical distribution, we included diurnal migration ($\mu(h)$) and thermocline depth ($h_{thcl}$) in the model. Non-significant ($p>0.05$) parameters were removed from the model. Furthermore, active avoidance of the sampling gear can also potentially affect catchability. This is more pronounced for larger larvae [26], but since the larvae caught by the CPR are small, we assumed that this effect was negligible.

**Model summary.** The log-intensity of individuals for sample number $i$ taken at position $x$, year $y$, day number $d$, hour $h$ is

$$\eta = \eta_{space \times time}(x,y) + \eta_{migr}(h) + \eta_{time}(y) + p_{time}(d) + p_{thcl}(h_{thcl})$$

$$+ \mu(h)$$

where

- $\eta_{space \times time}(x,y)$ is a mean zero gaussian stochastic process with covariance matrix

$$\left(\sigma^2 \rho(x_i-x_j,y_i-y_j)\right)_{ij}$$

- $\eta_{migr}(h)$ is mean zero gaussian noise with variance $\sigma^2_{\mu}$.
- $\eta_{time}(y)$ is a mean zero stochastic process with covariance matrix $\sigma^2 \exp(-|y_i-y_j|)$$\ni$.
- $p_{time}(d)$ is a second order polynomial ($a_{dpan1}d + a_{dpan2}d^2$) in the day number, $d$.
- $p_{thcl}(h_{thcl})$ is a second order polynomial ($a_{thcl1}h_{thcl} + a_{thcl2}h_{thcl}^2$) where $h_{thcl}$ is the thermocline depths at sample $i$.
- $\mu(h)$ is a parameter vector with one level for every hour of the day.

**Fitting the model.** The model was fitted as in [24] by the maximum likelihood method using the Laplace approximation. It is an important feature of the approach that it can deal consistently with missing data: latent variables (no direct observation) are integrated out of the likelihood function. Furthermore a “best guess” of any latent variable can be reconstructed based on the likelihood function. More precisely we used the conditional expectation of the variable given the data. This estimator has the property of being unbiased and having smaller variance than any other unbiased estimator [24].

The fitted model was used to predict the larvae concentration at any point in the North Sea, through each day in the period 1948–2005. From this dataset we produced yearly distribution maps and a time series of yearly indices of larvae abundance, by calculating the posterior mean of the spatially integrated intensity for each year. The hypothesis of a change in abundance from before 1970 to after 1990 was tested by a likelihood-ratio hypothesis test.

The model was run in R v.2.13.1 with the package “lge”. This package was developed in R and C and is available on request to kask@aquadtu.dk.

The annual larvae abundance index was compared to estimates of egg numbers and spawning stock size taken from the ICES WGWIDE reports and following publications [6,27–29].

**Results**

The CPR dataset consisted of 129,764 samples with 4,642 larvae observations. The samples are broadly distributed throughout the North Sea region (Figure 2a) and fairly equally distributed over the years (Figure 2b), within each year (Figure 2c) and day (Figure 2d). However, the sampling effort was poor in the central North Sea in the last decade of the time series (Figure S1).

Hydrographic drift simulations showed that advection of the larvae between the estimated spawning time and capture by the CPR was generally minor (Figure 3a). 90% of the larvae caught by the CPR had drifted less than 60 km from the spawning site and 75% have drifted less than 35 km (Figure 3b). Advection of mackerel eggs and larvae between spawning and capture in the CPR, and therefore any interannual variability associated with it, can reasonably be assumed not to induce a significant bias in the spawning distribution when looking for changes at the scale of the North Sea basin. The CPR larval observations can therefore be used as proxies for the spawning distribution of North Sea mackerel.

Larvae abundance model parameters are given in Table 1. Spatial correlation was found to be 0.65 on a 100 km distance ($\exp(-100z)$). Temporal correlation between adjacent years was estimated to be 0.74 ($\exp(-1.0\beta$). The “nugget effect” was found to be highly significant ($p<0.001$).

Of the two catchability effects; thermocline depth was found to be significant ($p<0.001$) whilst the diurnal catchability pattern (hour effect) was not ($p=0.75$). Consequently only thermocline depth was retained in the final model. Catchability peaked in areas where the CPR was sampling just above the thermocline. Larvae were rarely caught when the thermocline was below 45 m (Figure 4). Having corrected for catchability effects, we assume that the CPR catches represents the true larvae concentration plus random sampling error.

The seasonal peak of the larvae abundance was found to be in mid-July (day number 193, see Figure 5). Since we estimated mean larval age to be approximately 10 days, this corresponds to a peak in spawning at the start of July. This is comparable to egg survey based estimates from 1982–2008, where the peak spawning were found to be 8–20 days earlier [30]. A difference in this direction were expected because our study period includes cooler decades than the period from 1982 to 2008 and spawning is known to be earlier in warm years [30].

Annual larvae abundance index is illustrated for the whole study period in Figure 6. We found a significant ($p<0.001$) shift in the mean larval index of 6.1 from before 1970 to 1.6 after 1990 (Figure 6). There is unfortunately too much variability in the CPR larval index to precisely pinpoint the onset and completion of this decline (Figure 6; Figure 7a). Nevertheless, the broad pattern of a systematic decline in abundance between 1970 and the mid-1980s is shown here agrees with data from other independent sources e.g. standardized catch rates in the Dutch commercial spring fishery and catch/tagging based assessments indicate a decline beginning in the late 1960s (Figure 7b,c). The decline continues through the 1970s, as also indicated by the catch/tagging based ICES assessment and early mackerel egg surveys (Figure 7d,e), ending the decline in the mid 1980’s. The CPR larval index is therefore in
broad agreement with the piecewise picture available from other data sources: however, it also has the clear advantage of covering the entire time-span of interest.

Spatial distributions obtained from the model showed a shift in spawning area from early to recent decades (Figure 8 and S2), suggesting that the central North Sea is no longer as important as the areas further west and south. This change is in line with the results from the international mackerel egg surveys; although these surveys do not cover the extreme south and southeast (Figure 1) (ICES WGMEGS reports and pers. comm. S. Iversen, 13 Oct. 2011). Spawning in the north-western North Sea was, as also observed in the egg surveys, at a very low level in all periods.

**Discussion**

In this work we present a unique time series describing the dynamics of the North Sea mackerel. For the first time for this stock, a single unbroken time series, based on a consistent sampling methodology with broad spatial and temporal coverage, has been presented. The time series covers the full time span of
interest, from 1948, through the 1970s and 1980s stock collapse, all the way up to 2005. This index is based on a novel analysis of Continuous Plankton Recorder observations, using powerful modern statistical techniques. The resulting perspective is both unique and gives a broad view of the dynamics of this population where previously only brief glimpses were available.

Our results confirmed the long-term development of the North Sea stock, previously based on assessments of spawning stock size

**Figure 3. Backtracking simulations.** a) Examples of backtracked trajectories for six observations of larval in the CPR distributed across the North Sea. Red circles mark capture points in the CPR, blue circles the end points of particles after 10 days of backtracking. Black lines connect the two points for visual reference. Text denotes the CPR label code. b) Distribution of particle displacements after 10 days drift. Left axis (grey bars) depict the frequency (number of CPR observations containing larvae) for each 10km class bin. Black-line with black dot (right axis) shows the empirical cumulative distribution function.

doi:10.1371/journal.pone.0038758.g003

**Table 1. Larvae model parameter estimates.**

| Parameter | Estimate | s.d. |
|-----------|----------|------|
| $s_0^2$   | 2.36     | 0.17 |
| $s_1^2$   | 6.43     | 2.08 |
| Log(a)    | -5.45    | 0.19 |
| Log(b)    | -1.22    | 0.22 |
| $a_{spawn}$ | $2.41 \times 10^{-1}$ | $2.44 \times 10^{-2}$ |
| $a_{trash}$ | $6.21 \times 10^{-4}$ | $2.77 \times 10^{-5}$ |
| $a_{trash}$ | $8.33 \times 10^{-2}$ | $2.46 \times 10^{-2}$ |
| $a_{trash}$ | $2.71 \times 10^{-3}$ | $7.48 \times 10^{-4}$ |

doi:10.1371/journal.pone.0038758.t001

**Figure 4. Catchability effect of thermocline depth on CPR larvae index.**

doi:10.1371/journal.pone.0038758.g004
and egg abundance covering part of the time span. Furthermore, we found a spatial shift corresponding to a similar observation in egg distribution. This provides some validation for all approaches and suggests that the larvae index, at least on longer time scales, is a usable proxy for egg abundance and spawning stock size in the North Sea.

It is noteworthy that the uncertainty and interannual variability in the CPR index was very high. Several sources of variability seem possible: i) high statistical uncertainty such as random sampling error that increase due to the few larvae being captured in the later years, ii) variation in fecundity, iii) variation in mortality during the approximately 7 days of egg phase and 2 days of larval phase, iv) poor spatial sampling coverage in the central North Sea in later years, v) lack of sampling in Skagerrak/Kattegat.

However, our conclusion on the decline from before 1970 to after 1990 seems robust to these uncertainties. Even though sampling intensity in the central North Sea has been reduced in the later decades, the sampling that did take place in this area did not result in catch rates comparable to those in the earlier decades. Furthermore, analysis of the spatial patterns (Figure 8) also suggests that the central North Sea is no longer as important as the areas further west and south. However, a spatial shift back towards the central North Sea in the future might not readily be detected with the present survey design. Improved spatial coverage in this region would therefore improve the precision of the CPR larval index and further increase the value of this time series for the scientific community as well as stock advice and management.

Spawning is also known to take place in Skagerrak/Kattegat. The importance of this area is possibly limited to approximately 5% of the North Sea mackerel spawning [31]. However, this estimate is highly uncertain as the area has never been properly covered by the CPR or egg survey.

The CPR survey covered parts of the North Sea outside the egg survey area, providing an opportunity to evaluate the spatial coverage of the North Sea egg survey (Figure 1 and 8). Modelled distribution of larvae in the whole North Sea showed that the Southern North Sea has been a relatively important spawning area in the North Sea through the last decades. This result suggests that the area covered by the mackerel egg survey does not cover the entire spawning distribution, and may need to be expanded.

The described incomplete spatial coverage of both egg and larvae surveys, combined with the relatively high signal-to-noise ratio in the latter decades of low stock size, prevents us from validating the low level variation in SSB in the latter decades as suggested by the egg survey data (figure 7).

The new time series developed herein has the potential to address several outstanding problems regarding the mackerel stock in the North Sea. The most significant of these is: “Why has the North Sea spawning stock not rebuilt despite decades of protection from commercial fisheries?” We propose four hypothesis that may explain this observation: i) Changes in environment or predation pressure have reduced the productivity of the stock; ii) The fishing pressure is still too high due to by-catches in herring fisheries and/or in the large fishery for western mackerel in the northern North Sea; iii) The North Sea mackerel is not a separate natal homing stock and the observed collapse was merely a change in distribution of a single large north eastern Atlantic panmictic mackerel population; or iv) The North Sea mackerel was a separate natal homing stock up to the collapse where after modification of the genotype and behaviour happened as a result of intermixture between the small North Sea stock and the larger western stock [32]. Whilst it was not possible to address these questions directly here, further analysis of the CPR larval index have made a valuable contribution to testing hypothesis 3 by comparing the large interannual fluctuations with similar fluctuations in the western spawning area [33]. Furthermore, time series analysis relating the presented index with environmental factors has given indications on causal relationships between biological/physical drivers and migration [33].

Finally, phyto-, zoo- and ichyoplankton data from the CPR survey have repeatedly been used by scientists because of the unique spatiotemporal coverage over the last 8 decades. Typical methods for compiling time series have been deterministic algorithms raising the organism count in the samples to monthly averages in designated spatial rectangles, that are then aggregated over months or rectangles to provide time series or maps [8].
Figure 7. Long term mackerel trends in the North Sea [6,27–29]. Loess smoothed trend lines with span = 0.5.
doi:10.1371/journal.pone.0038758.g007
Present day’s improvement in computer power has made it possible to apply advanced statistical models to large high resolution datasets, such as CPR plankton samples. Applying state-of-the-art statistical models such as the present log-gaussian cox process model provides numerous advantages over the more simple deterministic raising algorithms. Organisms as well as the CPR samples are often patchily distributed in time and space. Any analysis of CPR data should consistently deal with these challenges, estimate the uncertainty that stem from these sources and propagate it into the final result. To deal with vertical patchiness and migration, that can have great effect on the variance of the relation between densities in CPR samples at 7 m and the whole water column [9,11], we considered two factors with potential to affect vertical distribution. By means of hypothesis testing, we could build the final model using only the significant parameter. The horizontal distribution issues were considered by using the exact sample positions (midpoints) and accounting for the spatial correlations between samples. This allowed for a more informed estimation of larvae densities in unsampled areas what could have been obtained through simple interpolations. Furthermore, it added to the uncertainty estimation procedure. Similarly, we could model temporal autocorrelation with i) a year-to-year correlation and ii) a seasonal day-to-day correlation. All model features were accounted for when maximizing likelihood of the model-observation fit. With this model we were able to provide the most likely estimate of larval density at any position and at any time – sampled or unsampled and present maps and time series in any resolution accompanied with uncertainty estimates.

We recommend the usage of such models for analyses of CPR data and encourage revisiting previously published studies with the aim of expansion and improvement.

Supporting Information

Figure S1 Maps of continuous plankton recorder sample locations in the spawning season May-July. a) 1948–1959. b) 1960–1974. c) 1975–1989. d) 1990–2005.

Figure S2 Animation of modeled annual spatial distribution of mackerel larvae caught by CPR. Color scale from white (low abundance) to red (high abundance).

Acknowledgments

Henrik Gislason (DTU Aqua, Denmark) for constructive comments, past and present SAHFOS staff for larvae data and Morten Skogen (Institute of Marine Research, Bergen, Norway) for providing access to the NORWE-COM flow fields.

Author Contributions

Conceived and designed the experiments: TJ. Analyzed the data: TJ KK MP. Contributed reagents/materials/analysis tools: TJ KK MP. Wrote the paper: TJ KK MP. Project leader on the reanalysis of CPR samples: SP Lead lab-team reanalysing the CPR samples: ME Modelled the thermocline dataset: CS.

References

1. ICES (2011) Report of the Working Group on Widely Distributed Stocks (WGWD), ICES CM 2011/ACOM:15.
2. Trenkel VM, Huse G, MacKenzie B, Alvarez P, Arizabalaga H, et al. (2012) Comparative ecology of widely-distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Prog Oceanogr : in press.
3. Bazilchuk N (2010) Mackerel wars. Frontiers in Ecol and the Environment 8: 397–397.
4. Cendrowicz L (2010) The Mackerel Wars: Europe’s Fish Tiff With Iceland. Time Mag 27: Aug.: 1–1.
5. Lockwood SJ (1988) The Mackerel - Its biology, assessment and the management of a fishery. Fishing News Books Ltd 181 p.
6. Hamre J (1978) The effect of recent changes in the North Sea mackerel fishery on stock and yield. Rapp p-v Reun (CIEM) 172: 197–210.
7. ICES (2010) Report of the Working Group on Widely Distributed Stocks (WGWIDE). ICES CM 2010/ACOM:15.
8. Richardson AJ, Walne AW, John AWG, Jonas TD, Lindley JA, et al. (2006) Using continuous plankton recorder data. Prog Oceanogr 68: 27–74.
9. Batten SD, Clark R, Flinkman J, Hays G, John E, et al. (2003) CPR sampling: the technical background, materials and methods, consistency and comparability. Prog Oceanogr 58: 193–215.
10. Colebrook JM (1975) The continuous plankton recorder survey: automatic data processing methods. Bull Mar Ecol 8: 123–142.
11. Hays GC, Warner AJ (1993) Consistency of Towing Speed and Sampling Depth for the Continuous Plankton Recorder. J Mar Biol Assoc U K 73: 967–970.
12. Schrum C, Alekseeva I, St John M (2006) Development of a coupled physical-biological ecosystem model ECOSMO - Part I: Model description and validation for the North Sea. J Mar Syst 61: 79–99.
13. Schrum C, Backhaus JO (1999) Sensitivity of atmosphere-ocean heat exchange and heat content in the North Sea and the Baltic Sea. Tellus A 51: 526–549.
14. Schrum C, Siegsmund F, St. John M (2003) Decadal Variations in the stratification and circulation patterns of the North Sea. Are the 90’s unusual. ICES J Mar Sci, Symp Ser 219: 129–131.
15. Bartsch J, Brander K, Heath M, Munk P, Richardson K, et al. (1989) Modeling the Advection of Herring Larvae in the North-Sea. Nature 340: 632–636.
16. Dickey-Collas M, Bolle LJ, van Beek JKL, Erftemeijer PLA (2009) Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of Downs herring larvae. Mar Ecol Prog Ser 390: 183–194.
17. Christensen A, Jensen H, Mosegaard H, John MS, Schrum C (2006) Sanderel (Ammodytes marinus), larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. Can J Fish Aquat Sci 63: 1498–1511.
18. Christensen A, Daewel U, Jensen H, Mosegaard H, St. John M, et al. (2007) Hydrodynamic backtracking of fish larvae by individual-based modelling. Mar Ecol Prog Ser 347: 221–232.
19. Skogen M, Søiland H (1998) A users guide to NORWECOM v.2. The NORGwegian ECOlogical Model system. Fisk Havet 18: 1–42.
20. Skogen MD, Swenden F, Bernsen J, Aksnes D, Urestad KB (1995) Modeling the Primary Production in the North-Sea using a Coupled 3-Dimensional Physical-Chemical-Biological Ocean Model. Estuar Coast Shelf Sci 41: 545–565.
21. Coombis SH, Mitchell CE (1981) Long-term trends in the distribution, abundance and seasonal occurrence of larvae of mackerel (Scomber scombrus L.) around the British Isles 1948–1978. J Mar Biol Ass UK 61: 343–350.
22. Bartsch J (2002) Modelling the temperature modulation of growth in larval fish. Fish Oceanogr 11: 310–314.
23. Mendida D, Alvarez P, Cotano U, Ezebeche E, De Murga AM (2006) Effects of temperature on development and mortality of Atlantic mackerel fish eggs. Fish Res 80: 156–168.
24. Lewy P, Kristensen K (2009) Modelling the distribution of fish accounting for spatial correlation and overdispersion. Can J Fish Aquat Sci 66: 1809–1820.
25. Hüllergruber N, Köppmann M (2001) Small-scale patterns in distribution and feeding of Atlantic mackerel (Scomber scombrus L.), larvae in the Celtic Sea with special regard to intra-cohort cannibalism. Helgel Mar Res : 149.
26. Röpke A (1989) Small-scale vertical distribution of ichthyoplankton in the Celtic Sea in April 1986. Meeresforsch 32: 192–203.
27. Postuma KH (1972) On the abundance of mackerel (Scomber scombrus L.) in the north-eastern North Sea in the period 1959–1969. J Cons Int Explor Mer 34: 453–465.
28. ICES (1979) Report of the mackerel working group. ICES CM 1979/H:5.
29. Iversen SA (1981) Spawning and trends in spawning stock size of the North Sea mackerel during the period 1973–1980. ICES CM 1981/H:16.
30. Jansen T, Gislasson H (2011) Temperature affects the timing of spawning and migration of North Sea mackerel. Cont Shelf Res 31: 64–72.
31. Iversen SA, Elinak A (1983) Spawning egg production and stock size of North Sea mackerel in 1982. ICES CM 1983/H:46.
32. Iversen SA, Skagen DW (1989) Migration of western mackerel to the North Sea 1973–1988. ICES CM 1989/H:20.
33. Jensen T (In prep) Mixing Between Metapopulations of Mackerel (Scomber scombrus L.) in the Northern Spawning Areas.
34. ICES (2008) Report of the Working Group on Widely Distributed Stocks (WGWIDE). ICES CM 2008/ACOM:13.
35. ICES (2005) Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA). ICES CM 2005/ACFM:08.