A novel approach to assess distribution trends from fisheries survey data

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Abstract

Climate change and fishery impacts modify the spatial distribution of marine species. Understanding and predicting changes in distribution is important for adaptation by fishers and the management of fishery resources and biodiversity. However, identifying such trends is challenging given the variability inherent in trawl survey data. We apply a novel two-step approach to identify fish distribution trends from trawl surveys. First, species-specific average locations (mean latitude and longitude centre of gravity) and extent (effective area occupied) were estimated within a spatio-temporal delta modelling framework. The resulting time series and associated variance estimates were then passed to a multivariate Bayesian state-space model to estimate average trends over the study period. We applied this two-stage approach to three decades (1986-2016) of demersal trawl research survey data from the Agulhas Bank of South Africa to quantify distributional changes in 44 commonly caught fishes (chondrichthyans and teleosts). Across the entire assemblage, average trends showed a westward (alongshore) shift in location and a reduction in the extent of populations. At the species level, six taxa showed a location trend towards the west or south-west, and three shifted towards the east or north-east. The area occupied by species showed two taxa that had a decreasing trend in spatial extent and one species that was expanding. The mean westward and contracting trends of the assemblage were interpreted as likely signals of climate forcing, whereas the eastward shift of three species may be linked to fishing impacts. A lack of knowledge of subsurface oceanographic changes in the region challenges interpretation of the distribution changes and is identified as a research priority. We recommend additional research regarding causal drivers of distribution shifts, specifically to attribute observed changes to climate, fishing, and inter-annual environmental variability.

Keywords

Distribution trend, spatio-temporal model, trawl surveys, South Africa

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1. Introduction

A common theme in marine ecology is the dynamic nature of populations in space and time. Distribution changes, persistent beyond seasonal or short-term population variability, could modify gene flow, species interactions and ecosystem functions and result in socio-economic impacts (Barange et al., 2014; Blamey et al., 2015; Ortega-Cisneros et al., 2018; Pecl et al., 2017). Spatial management of fisheries and biodiversity has become a common approach because impacts and potential interventions tend to be spatially structured. Therefore, identifying and understanding shifts in the distribution of marine fauna can contribute important information to resource and biodiversity management, as well as helping to address climate change adaptation and mitigation in fishing communities.

Fishing pressure and anthropogenic climate change are expected to be amongst the dominant drivers of spatial changes in marine populations (Bell et al., 2015; Genner et al., 2010; Hilborn et al., 2003). Fishing impacts may translate to changes in distribution via localised density reduction or extirpation (Ferretti et al., 2013; Hilborn et al., 2003), via range contraction/expansion from/towards modified habitats (Bell et al., 2015; Thorson et al., 2016b), or via the truncation of ages in species that have age-specific distributions (Bell et al., 2015). The effects of anthropogenic climate change may be more gradual than many fishing impacts, yet are often widespread and most likely difficult to reverse. Marine species have responded to temperature changes by adjusting their location, depth, or both (e.g., Dulvy et al., 2008; Edwards and Richardson, 2004; Engelhard et al., 2011; Pinsky et al., 2013). Besides their direct effects, both fishing and climate may influence distributions indirectly via species interactions or changing habitats (Doney et al., 2012; Kaiser et al., 2000).

Demersal trawl surveys are a feature of long-term fisheries research and monitoring in many marine jurisdictions. The accumulation of decades of comparable data across regional spatial scales and near-annual frequencies invites interrogation of multi-year or decadal changes in species distributions with increasingly effective statistical tools and computational powers. For example, previous research has calculated the centroid of sampling data and compared the relationship between this centroid and proposed mechanisms for distribution shifts (Engelhard et al., 2011; e.g. Pinsky et al., 2013). Recent progress in geostatistical models has enabled estimation of population centroids while controlling for random variation in sampling location and characterizing uncertainty in the centroid estimates (Thorson et al., 2016a). These advances help discriminate between sampling variation and biological variation in distributions.

In South Africa, government-led trawl surveys have supported a wide range of demersal research (e.g., Atkinson et al., 2011; Kirkman et al., 2013; Payne et al., 1987; Rademeyer et al., 2008; Roel and Butterworth, 2000; Yemane et al., 2010, 2005). The distributions of species and assemblages have been characterised from these data (e.g., Badenhorst and Smale, 1991; Pecquerie et al., 2004; Smale et al., 1993). However, few studies have examined temporal changes in spatial distributions, although Yemane et al. (2014) investigated changes in the spatial and depth distributions of trawl-caught species on the west coasts of Angola, Namibia and South Africa. Their results suggest that over half of the 54 species assessed on the South African west coast have modified their distribution. Regional distribution changes of key ecosystem components were also studied by Watermeyer et al. (2016), who found evidence that some species appeared to follow a late-1990s eastward shift of small pelagic fish (Fairweather et al., 2006; van der Lingen et al., 2006). Using trawl survey data from 1998 to 2012, Jansen et al. (2016) detailed the stock structure, distribution and migration patterns of shallow-water hake (*Merluccius capensis*) across the south coast Agulhas Bank and the west coasts of South Africa and Namibia. Despite these efforts, much further work is needed to identify and understand potential distribution changes of demersal fauna, to provide meaningful advice to fishers and managers of marine resources and biodiversity.

The Agulhas Bank has supported trawl fisheries for 120 years (Lees, 1969). However, distribution changes of demersal fish have received almost no attention there. The bank consists of a broad shelf that extends up to 250 km beyond Africa's southernmost coastline. Warm Agulhas

Current waters bound its eastern and southern edge, while the cool Benguela upwelling region stretches northwards from the Bank's western side. One might, therefore, expect a warming signal in demersal waters to result in species shifting westwards. However, the oceanography of the bank is complex, with characteristics of both an upwelling system and a temperate shallow shelf (Hutchings et al., 2009). The depth contours over much of the Bank orientate predominantly south-west to north-east. If loyal to a depth stratum, species shifting westwards would likely shift southwards and those moving eastwards would tend to shift northwards.

In this work, we used a novel combination of statistical methods to estimate distributional trends of species and assemblages from three decades of trawl survey data on the Agulhas Bank. The two metrics investigated were 'centre of gravity' as a measure of a population's average location and 'effective area occupied' as a measure of its extent. These were predicted using a species distribution function that was estimated within a geostatistical model (Thorson et al., 2015b). The underlying model can efficiently reconstruct variation in population density given highly-variable biomass sampling data and account for variation arising from changes in survey design or random variation in sampled locations (Thorson et al., 2016a, 2015b). Given the predicted metric time series, univariate and multivariate state-space models were applied to estimate trend components for individual species and assemblages of demersal taxa. The state-space models effectively identify longer-term signals while dealing with autocorrelation and the year-to-year 'process error' typical of annual trawl surveys. This framework was employed using three decades of research trawl survey data from the Agulhas Bank to identify and quantify distributional changes of demersal fish. Although comparable (resolution and period) fishing effort and hydrographic data were not available to include in the statistical framework, their potential role is discussed with interpretations of observed distributional changes.

2. Material and methods

2.1. Study area and data preparation

The Agulhas Bank forms the shelf extension of the southern tip of Africa. It narrows abruptly on the western side and more gradually to the east, following the shape of the coastline curving northward (Fig. 1). Although resembling a temperate shallow shelf, the influence of oceanic forcing from the Agulhas Current, seasonal coastal upwelling and South Atlantic waters on its western margins complicate its hydrographic structure (Hutchings et al., 2009). Waters over the Bank tend to be well stratified (Largier et al., 1992; Swart and Largier, 1987), decoupling surface temperature dynamics from subsurface signals. Demersal waters tend to be well oxygenated, except for central inshore areas where seasonal coastal upwelling can drive high productivity and result in lower dissolved oxygen concentrations (Roberts, 2005). A high turbidity 'nepheloid layer' is characteristic of inshore bottom waters that overlie muddy sediments (Zoutendyk and Duvenage, 1989). The central and eastern parts of the Bank are covered by the south-coast surveys employed here.

Demersal trawl survey data and commercial trawl effort data for the Agulhas Bank were obtained from the South Africa's Department of Agriculture, Forestry and Fisheries (DAFF). The survey data were collected during annual stratified random surveys on the continental shelf. Initially both autumn and spring surveys were conducted. However, the spring surveys were effectively discontinued after 2008. The data used here span the period 1986-2016 and were bounded by longitudes 20° and 27° E. Prior to 2011, the latitudinal bounds of the survey area were from the coastline to the 500 m isobath, whereas sampling was occasionally extended to 1,000 m depth thereafter. Trawl stations beyond 500 m depth were omitted from these analyses. A summary of data used in analyses is provided in Table A1 (Appendix A).

Commonly caught taxa were chosen for analyses by summing occurrences by taxon, ranking them from highest to lowest and selecting 80% of cumulative occurrence records. Small pelagic fish (*Engraulis encrasicolus, Etrumeus whiteheadi, Sardinops sagax*) were removed as they are unlikely to be effectively sampled by demersal trawl surveys. Invertebrate catches were also excluded, focussing analyses on the remaining 44 teleost and chondrichthyan taxa. Trawl samples retained for analyses had a duration between 20 and 35 minutes, a towing speed of 3-3.5 knots and did not suffer net damage or other disruptions that may have influenced the catch.

Most of the survey data were collected by the government research vessel, RS *Africana*. However, in 2000 the survey was performed using the RV *Dr Fridtjof Nansen* and in 2014-2016 commercial trawl vessels were used to conduct the annual research surveys. During the survey period a change in trawl gear also took place, as detailed by Leslie (2008) and Atkinson et al. (2011). In 2004, the old trawl gear was replaced with a new net, trawl doors and foot-rope. However, the old gear was again employed in 2006 and 2010 (Table A1, Appendix A). Although they were of similar design and size, these gear changes likely affected the selectivity for some species (Leslie, 2008). The trawl gear used on board the RV *Dr Fridtjof Nansen* (in 2000) provides a third set of gear that likely had different selectivity to both other sets (Axelsen and Johnsen, 2015). In addition to the potential effect of gear changes, there were some inconsistencies in the depth (and therefore spatial) coverage of surveys. Whereas most surveys extended to depths of 500 m or more, the spring surveys of 1990 to 1995 were limited to ≤200 m. The impact of such spatial and gear changes were considered in analyses as described below.

2.2. Measures of mean location and extent

Potential changes in the distribution of trawl-caught fauna were assessed using their mean centre of distribution, hereafter referred to as 'centre of gravity'. This has commonly been calculated as an abundance-weighted average of sample coordinates (e.g. Engelhard et al., 2011; Fairweather et al., 2006; Hiddink et al., 2015; Perry et al., 2005; Pinsky et al., 2013). Thorson et al. (2016a) showcased a method that calculates the centre of gravity from a species distribution function that is estimated within a geostatistical model framework. One of the main advantages of doing so, rather than using catch rates to calculate spatial metrics, is that results benefit from the underlying statistical model's ability to account for changes in sampling design (Thorson et al., 2016a). Unbalanced sampling effort in space and time, or changes in sampling gear or strategy, can for example be accounted for in the design of the model (Grüss et al., 2017; Thorson et al., 2016a).

Using the species distribution function, the weighted centre of gravity was calculated at model-predicted locations. For example, the calculation of latitudinal centre of gravity for each year t was:

$$\overline{Latitude}(t) = \frac{\sum_{s=1}^{n_s} a(s) * \hat{d}(s,t) * Latitude(s)}{\sum_{s=1}^{n_s} a(s) * \hat{d}(s,t)} \tag{1}$$

where n_s was the number of grid cells defined in the model, abundance at grid cell s was a product of its area $a(s)$ and its predicted density for that year $\hat{d}(s,t)$, while $Latitude(s)$ represented the corresponding cell latitude. The same calculation was applied to longitudes to gain the east-west centre of gravity.

The spatial extent of a population was investigated using a measure of 'effective area occupied' (Thorson et al., 2016b). Calculated for each year t, it represents the geographic area (h_t; km^2) that would be required to contain the total population biomass (b_t; kg) at its average population density (m_t; kg·km^{-2}), as predicted from the species distribution function:

$$h_t = \frac{b_t}{m_t} \tag{2}$$

This simple measure of area occupied does not require parameters to be defined a priori (e.g. $X\%$ of the population), the value of which could affect results (Thorson et al., 2016b supplementary material). It is also not biased by sampling areas of zero or very low density (Thorson et al., 2016b supplementary material).

We estimated the species distribution function using a geostatistical delta-generalised linear mixed model (geoGLMM) from Thorson et al. (2016a). Developed to estimate abundance indices from trawl surveys (Thorson et al., 2015b), it models fish catches as a function of location and time. This is achieved using a delta approach, whereby the probability of encounters (non-zero catch) and the expected density when encountered, are modelled separately (Aitchison, 1955; Lo et al., 1992). Spatially correlated errors are assumed for both parts of the model and the spatial variation is decomposed into two components; one that is constant among years and another that varies, thereby accounting for changes in spatial distribution over time (Thorson et al., 2016a). As the centre of gravity and effective area metrics are estimated within the geoGLMM, their standard error incorporates estimation uncertainty of model parameters. The mathematical structure of the geoGLMM is documented by Thorson et al. (2015b).

We modelled the positive catches (kg) using a gamma distribution, whereas the probability of encounters assumed a Bernoulli process. Swept area, calculated as the drag distance multiplied by the width of the trawl net, was included as an offset in the model. The geoGLMM was based on a 2.5 by 2.5 minute spatial grid. A spatial resolution of 500 'knots' was specified to define the localities within the polygon mesh at which spatio-temporal functions were solved.

The geoGLMM with outputs of effective area and centre of gravity were calculated using the R package SpatialDeltaGLMM (Thorson et al., 2015b; https://github.com/nwfsc-assess/geostatistical_delta-GLMM). It uses the Template Model Builder package (TMB; Kristensen et al., 2016) to implement the Laplace approximation of marginal likelihoods of fixed effects while integrating across all random effects (Skaug and Fournier, 2006). Potential bias in the calculation of nonlinear functions of fixed and random effects was avoided by applying the 'epsilon' bias-correction in TMB (Thorson and Kristensen, 2016).

The geoGLMM framework did not estimate a depth covariate within the model. Although considered, this was not done due to the fact that depths may vary substantially within areas resolved by the model grid cells (approximately 17.5 km^2 per grid cell in the study area). Johnson et al. (this issue) show that failing to include covariates that account for spatial variation in the geoGLMM (e.g., depth) results in little degradation of estimates of abundance indices or spatial distribution metrics. Estimation of mean depths external to the model was attempted, using standardised catch samples and their depth measurements (as in Dulvy et al., 2008; Engelhard et al., 2011; Yemane et al., 2014). However, substantial bias (including a deepening trend in the autumn time series) was present in the survey data (Fig. A1, Appendix A), precluding such methods.

2.3. Trend estimates by state-space models

Trends were estimated from the centre of gravity and effective area time series using a Bayesian state-space model framework (Winker et al., 2018). This involved composing the series of observations into two parts: 1) a state process which models the dynamics of unobserved state variables (e.g., the 'true' centre of gravity) and 2) a stochastic observation process or error that is conditional on the underlying state (Simmons et al., 2015).

The unknown 'true' population-level response was treated as the state variable that follows a Markovian process (Gilks et al., 1995). The value of the current year ($\mu_{t,i}$) was assumed to be dependent on its value in the previous year ($\mu_{t-1,i}$), an underlying trend component (β) and a process error term ($\eta_{t,i}$) that incorporates variation among years via a random normal walk with mean zero and an estimable variance σ_i^2. The state process equation was defined as

$$log(\mu_{t,i}) = log(\mu_{t-1,i}) + \beta + \eta_{t,i}\,, \qquad \eta_{t,i} \sim N(0, \sigma_i^2) \tag{3}$$

and the observation error equation as

$$log(\hat{y}_{t,i}) = log(\mu_{t,i}) + \epsilon_{t,i}\,, \qquad \epsilon_{t,i} \sim N(0, SE_{t,i}^2) \tag{4}$$

where $\hat{y}_{t,i}$ represents the centre of gravity or effective area values predicted using the species distribution function and $\epsilon_{t,i}$ is the observation error that is normally distributed with mean zero and variance equal to the square of the standard error ($SE_{t,i}$) from the predictions of the species distribution function. The subscripts denote years t and species i, where $i = 1$ for a single species or $i = \{1,2,\ldots N\}$ for the combined set of N species. In this way, the underlying trend β represents an estimate of the average rate of change over the time series, accounting for both observation error (the variance associated with the centre of gravity or effective area estimate) and process error (a measure of the year-to-year variability among estimates).

Before being passed to the state-space model, time series were normalised by their mean value for the entire period. In the case of single-species trend estimates, both spring and autumn values were normalised by the mean of autumn, so as to preserve differences between the seasons when combined on one plot.

Non-informative priors were used for model parameters so that inference would be based primarily on information contained in the data. An inverse-gamma distribution with scale and shape parameters set to 0.001 was used as a prior for the process variance (Chaloupka and Balazs, 2007). Expected values for the first year ($\mu_{1,i}$) were drawn from a flat normal distribution with mean equal to $\hat{y}_{t,i}$ and standard deviation of 10^6. The prior used for the trend (β) was a flat normal distribution with a mean of zero and a standard deviation of 10^6.

The joint posterior probability distributions were estimated using Markov Chain Monte Carlo (MCMC) simulations implemented in the JAGS software (Plummer, 2003). The model formulation was passed to JAGS using the R package 'jagsUI' (Kellner, 2016), which uses functions from the 'rjags' package (Plummer et al., 2016).

Each state-space model was run using 50,000 MCMC iterations, removing the first 5,000 iterations as 'burn-in' and thereafter sampling every fifth iteration to construct the posterior distribution. The median and 95% credibility intervals (2.5th and 97.5th percentiles) were used to visualise the model prediction in plots. To assess the probability that the estimated trend component was different from zero (i.e., had a positive or negative slope), its posterior distribution was used as a bootstrap sample to calculate equal-tail p-values as per MacKinnon (2009). A positive longitudinal centre of gravity trend indicated an eastward movement, while for latitudes it signified a northward shift. Negative centre of gravity trends signified westward and southward shifts, respectively.

Analyses were repeated on subsets of data that excluded changes in sampling methods to assess whether emerging trends might be affected by potential sampling bias. A set of analyses was repeated on the spring survey data while omitting samples with mean depth >200 m to examine whether a potential depth bias might affect results. Analyses were also repeated on data restricted to the 'old trawl gear' and the RS *Africana* to examine whether observed trends might be caused by changes in vessel or gear. As this curtailed time series contained far fewer data than the original analysis, a loss of statistical power was expected and trends were visually assessed rather than using the statistical thresholds applied to the entire dataset.

2.*4 Changes in commercial trawl effort*

Spatial and temporal changes in commercial trawling effort were investigated to provide context of demersal fisheries impacts for the interpretation of distributional changes. These data consisted of the number of trawl hauls reported annually on a grid with 20 minute spatial resolution. Although coordinates of trawls were recorded from 2004 onwards, previously only the grid cell was recorded and analyses were therefore applied at the grid resolution. Data were available from 1983 to 2015.

The spatial distribution of cumulative commercial trawl pressure in recent decades was mapped as the mean number of trawl hauls recorded in each commercial trawl grid cell between 1983 and 2015. Change in effort over time was assessed by regressing the number of trawl tows against years in each grid cell. To reduce the chances of type II errors in applying linear fits to potentially non-linear patterns and to reduce the influence of isolated years with unusually large effort records, we binned the data into averages of 5-year periods before applying the regression. A slope different from zero ($p \leq 0.05$) was inferred as evidence of an increase (positive slope) or decrease (negative slope) in commercial effort over time.

Trawl effort (number of trawls over time) was also examined for the entire study area, covering most of the Agulhas Bank, and two smaller areas in the western and eastern inshore parts of the study area respectively. The inshore areas were chosen as six commercial grid cells covering areas adjacent to the coastline. The western inshore area stretches between Cape Infanta and the first grid cell to the east of Mossel Bay. The eastern inshore area extended from Port Alfred westward to between Cape St. Francis and Port Elizabeth.

3. Results

A multivariate trend estimated for the full 44-taxa fish assemblage identified a westward longitudinal shift in the mean location in the autumn survey time series (Table 1; Fig. 2). Although the trend was significant ($p<0.01$), the median effect was small (-0.26 $\mathrm{km \cdot year^{-1}}$). The spring survey series and the latitudinal centre of gravity changes were also negative (westwards and southwards, respectively), but lacked statistical evidence to suggest they were different from zero.

The mean extent (effective area) of the trawl-caught fish assemblage indicated a significant reduction for both autumn and spring survey series (Table 1; Fig. 3). The estimated reduction in spatial extent was similar for both seasons (close to -60 $\mathrm{km^2 \cdot year^{-1}}$), even though the periods covered by the autumn and spring surveys differed (Table A1, Appendix A). The mean shift in the trawl-caught assemblage is the integrated signal of different responses from individual taxa, which are outlined below.

Ten of the 44 investigated taxa showed evidence of a trend in distribution during the three decades assessed. Nine taxa shifted their average location, while three changed their spatial extent (Table 1). The remaining 34 species did not show statistical evidence of a trend in their spatial distribution, even though some shorter-term variations and non-significant trajectories were visually apparent. The latitude and longitude centre of gravity estimates were in most cases highly correlated, with a tendency for greater variability (and trend estimates) in the east-west longitude axis. Due to the orientation of the coastline and the tendency for species to maintain their depth, westward centre of gravity changes were usually associated with southward shifts and eastward changes with northward shifts.

Of the nine taxa that indicated a trend in their centre of gravity ($p \leq 0.1$), six shifted towards the west or south over time and three towards the east or north. Several remaining taxa showed westward trajectories that were not significant, likely contributing towards the assemblage-wide trend reported above. For ease of interpretation and display, three different response patterns were identified from the species trends in average location:

1. The first group of taxa showed evidence of a trend towards the west (and/or south). This response is illustrated by the example of slime skate (*Dipturus pullopunctatus*; Fig. 4), but also included Agulhas sole (*Austroglossus pectoralis*), thornback skate (*Raja straeleni*) and ribbon fish (*Lepidopus caudatus*).
2. The second response pattern consisted of taxa that showed an eastward (or northward) shift in location. This group consisted of white stumpnose (*Rhabdosargus globiceps*; Fig. 5), lesser sandshark (*Acroteriobatus annulatus*) and kob (*Argyrosomus* spp.).
3. The third response pattern represented a trend along one axis (e.g. north-south) but lacked evidence of a corresponding trajectory in the orthogonal axis (e.g. east-west). Such distributional changes indicate directional shifts that likely crossed depth contours, which are predominantly southwest-to-northeast in direction. Bluntnose spiny dogfish (*Squalus acutipinnis*) showed a southward shift without a corresponding westward movement (Fig. 6) and Cape horse mackerel (*Trachurus capensis*) showed a westward, but no southward, trend in their average location. The former suggests an increase in the population's depth distribution and the latter a decrease.

Only three taxa showed statistical evidence of a trend in effective area, of which one was increasing (*Gonorynchus gonorynchus*) and two were decreasing (*Dipturus pullopunctatus, Trachurus capensis*; Table 1; Fig. 4).

The distribution of commercial trawling pressure and its change over time were investigated as a potential explanation of observed distribution changes. Certain shallow grounds (≤100 m) experienced relatively high trawling pressure over the study period, including Cape Infanta to Mossel Bay, the central Agulhas Bank and an inshore area between Port Elizabeth and Port Alfred

(Fig. 7). Deeper offshore grounds where effort was concentrated includes the Chalk Line grounds south of Port Elizabeth and Cape St. Francis, and the southern and southwestern edge of the Agulhas Bank (Fig. 7). These deeper margins have experienced an increase in the number of commercial trawls per year, with an exception of the southwestern edge of the Bank. In contrast, many of the remaining areas of the Bank, including some of the heavily-fished inshore grounds, showed decreasing numbers of commercial trawls per year (Fig. 7).

The number of trawls recorded over the entire survey area declined during the study period, most notably from 2008 onwards (Fig. 8a). In the western inshore areas (Cape Infanta to Mossel Bay), effort remained relatively high between the 1980s and 2004, after which it sharply declined (Fig. 8b). In eastern inshore areas (near Port Elizabeth and Bird Island), effort levels were notably lower than aforementioned western areas and were in decline during most of the assessed period, reaching lowest effort values in 2014 and 2015.

The same centre of gravity and effective area analyses were repeated on subsets of the data. The first was a restriction on depths ≤200 m for the spring survey. The results (not shown) were qualitatively the same as those of the full dataset. The second subset of data restricted to trawls sampled with the old DAFF trawl gear (see Methods) gave mixed results. The general westward (and southward) location trend seen for the full dataset was not evident (Fig. A3, Appendix A). However, the decreasing effective area trends seen in the full dataset remained, even though statistical evidence of a trend different from zero remained only in the autumn time series. Of the distributional trends identified for 10 species in the full dataset, non-significant trajectories of similar direction were seen in the single-gear time series for all except two skate species (*D. pullopunctatus* and *R. straeleni*). The ‘old gear’ equivalent plots of Figs. 2-6 are provided in Appendix A (Figs. A3-A7).

4. Discussion

The combined use of geostatistical and Bayesian state-space models offered a robust and reproducible framework to identify and quantify multi-year to decadal-scale trends from fishery surveys. These methods propagate uncertainty throughout the joint estimation process and account for properties of spatially stratified time series data that can be challenging to address with design-based statistical approaches. These include potential spatial bias in sampling intensity, spatial and spatio-temporal dependence in the trawl survey data, and temporal autocorrelation and random, interannual process ‘noise’ during trend estimation from the predicted means. We anticipate that our approach might be applicable for similar analyses of other marine survey datasets, including physical and chemical hydrographic fields.

Of the trawl-caught fishes assessed on South Africa's Agulhas Bank, 23% showed evidence of distribution trends over the three decades studied. The multivariate trends identified a mean westward shift in location and decreasing extent for the assemblage as a whole (Table 1; Figs. 2, 3). The magnitude of estimated trends appeared to be relatively modest in several cases, for example, leading to 30-year location shifts of between 10 and 102 km. While some of the figures may seem small, they need to be interpreted in terms of a population of many individuals over a large geographic area, with many factors influencing movements and abundance fluctuations at local scales. Some of the noted shifts might have little immediate ecological impact, but they represent a directional signal for the sampled population (assemblage) as a whole, which may result in ecological and socio-economic consequences if it continues. The small magnitude of the integrated assemblage trends are not surprising, considering that shifts from individual taxa are frequently in opposing directions and many species may not be changing their distribution. Besides suggesting there may be a common driver among several taxa, further ecological interpretations of the assemblage trends would likely require additional analysis.

Despite the highly significant assemblage-wide trends, relatively few species showed individual trends. We have no evidence of meaningful bottom water changes in this region and perhaps seasonal or interannual variability dominate longer-term trends. The complex oceanographic setting of the Agulhas Bank, as well as its predominantly east-west (as opposed to poleward) orientation may provide additional reasons for a lack of coherent distribution trends in the surveyed demersal ecosystem. Many of the species appeared to have distributional 'trajectories' that lacked statistical power to be considered significant ($p>0.1$). As the power to detect a trend is strongly dependent on the length of its time series (Schlegel and Smit, 2016), the detection of species-level distribution trends may increase as the survey dataset lengthens in future.

4.1 Fishing and climate as potential drivers

Disentangling the impact of climate change and fisheries on marine ecosystems is important to building predictions of fishery responses and informing biodiversity or resource management interventions. However, separating the influence of these two pressures on distribution changes involves complexity, much of which may not have been measured. Ideally, relationships between distributional changes and metrics of fishing intensity and climate should be assessed within the statistical framework (e.g., Bell et al., 2015; Engelhard et al., 2014). In this case, fishing effort and hydrographic data were not available at a comparable resolution for a substantial part of the study period. Without their inclusion as covariates in the models, a start would be to understand their spatio-temporal changes during the study period to guide interpretation of observed distribution changes.

Whether (or how) the hydrography of Agulhas Bank demersal-zone waters might have changed over recent decades has not been adequately addressed. Global trends and satellite measurements of offshore surface waters indicate warming (Levitus et al., 2005; Rouault et al., 2009; Wu et al., 2012). However, evidence from surface temperatures (Rouault et al., 2010; Schlegel et al., 2017), current observations (Beal and Elipot, 2016) and distribution changes of coastal species (Blamey et al., 2015; Bolton et al., 2012; Cockcroft et al., 2008) support the hypothesis of greater coastal or shelf-edge upwelling on eastern and inshore parts of the Bank, implying cooler subsurface temperatures there. Hydrographic changes in the bottom waters of this area require investigation. Without such knowledge, interpretation of potential environmental drivers of observed distribution shifts is hampered, highlighting this research gap.

The evolution of fishing pressures may have influenced distribution changes, for which there is more information available (than demersal hydrographic changes). Trawling started on the Agulhas Bank at the turn of the 20th century, escalated in the 1950s and peaked in the 1960s and 1970s as catch rates declined (Griffiths et al., 2004; Payne and Punt, 1995). A notable reduction in fishing effort ensued when South Africa declared a 200-nautical-mile exclusive fishing zone in 1977 and phased out access by foreign fleets, but considerable impact had by then been exerted on Agulhas Bank resources (Japp et al., 1994). While the annual number of trawl hauls has declined on the Agulhas Bank during the study period, especially in some of the most heavily fished grounds closer to shore (Figs. 7, 8), these areas remain exploited by trawling and other fishing sectors. It is not clear whether the reduced trawl effort over shallower parts of the Agulhas Bank may have allowed a measurable recovery of fished populations in those areas. Had the fish assemblage showed an increase in spatial extent, its westward shift might have been interpreted as a recovery of populations on the central Agulhas Bank, following declining trawl effort during the period examined (Fig. 8) and reduced international trawl pressure in the years prior (Japp et al., 1994). The mean decreasing spatial extent observed for the assemblage is not consistent with such an explanation, however.

The evidence of a community-wide average westward trend in mean location, together with a generally decreasing spatial extent, yet easing commercial trawl pressure over much of the sampled domain (Figs. 7, 8), suggests a climate (environmental) rather than a fisheries driver. The areas that showed an increase of trawl effort over the study period are deeper trawl grounds near the outer edges of the Agulhas Bank (Fig. 8). Had observed distribution trends been concentrated (or exaggerated) among species inhabiting those deeper areas, it might have implicated fishing pressure as a driver, but this was not the case. Pinsky et al. (2013) found that climate velocity explained distribution changes in demersal fish more effectively than taxonomic or biological characteristics. Although not formally tested, our distributional trends did not appear to group species with similar taxonomy or life-history strategies.

Contraction of the area occupied by populations likely implicates a stress acting on them (Mace et al., 2008). Multiple scenarios might lead to a reducing population extent, including retraction from a changing environment (e.g., Jones et al., 2010), contraction of population size towards core habitat (MacCall, 1990) and excessive exploitation reducing density in certain areas (e.g., Shackell et al., 2005). While trawl effort may have been easing on many parts of the Agulhas Bank, cumulative impacts from other fishing sectors and climate changes may have persisted or increased. Studies examining indices of fish length, population sizes, community composition or ecosystem states over periods similar to that assessed here, have pointed towards increasing pressures on the Agulhas Bank (Yemane et al., 2008) or the broader southern Benguela region (Blamey et al., 2015; Coll et al., 2009; Shannon et al., 2009).

4.2. Species-level changes

Species showed a variety of distributional changes, many quite different to the assemblage-wide mean signal. The interpretation of such responses from individual species requires consideration of several factors, which might include geographic and depth ranges, temporal changes in their abundance indices, life history, behaviour, vulnerability to fishing gears and environmental or habitat preferences. The discussions below highlight key findings, while we refer to the Appendix and Currie (2017) for greater detail on species responses within the context of regional knowledge.

Contrary to the average assemblage trend, *R. globiceps*, *Argyrosomus* spp. and *A. annulatus* showed distributions shifting towards the east (and north). All three taxa inhabit relatively shallow coastal waters, although *R. globiceps* extends onto the central Agulhas Bank (Fig. A8, Appendix A). Abundance indices and maps of their predicted density from the geoGLMM (not shown) suggested that *Argyrosomus* spp. and *A. annulatus* populations have decreased in western parts of the survey area, leading to the eastward trends. Conversely, the eastward location shift seen for *R. globiceps* appears to be driven by an expansion that has been pronounced in the eastern areas near Port Elizabeth (Fig. A8, Appendix A).

Although oceanographic forcing cannot be excluded as a causal factor, fishing pressures are thought to be a more likely driver of these eastward shifts. Trawling in areas immediately east of the survey domain (Port Alfred) reportedly ceased in the early 1980s and was declining before then (Booth and Hecht, 1998). In addition, trawling intensity has been lower in the eastern coastal areas (around Port Elizabeth) than in western inshore grounds (near Mossel Bay and Cape Infanta) and has been mostly in decline since the 1990s (Fig. 8b), when the majority of the Port Elizabeth fleet moved to Mossel Bay (Booth and Hecht, 1998). The western trawl grounds near Mossel Bay and Cape Infanta also experienced a decrease in trawl effort, but only from the mid-2000s onwards, before which trawling pressure appears to have been substantially higher than in the eastern inshore areas (Fig. 8b). Thereby trawling pressures appear consistent with the eastward shift in mean location of these populations. It is important to note, however, that these species are also caught by line fishers, the impact of which could be contributing to observed distributional changes.

The strong correlations between latitudinal and longitudinal variability seen amongst the majority of taxa are not surprising, considering the predominantly south-west to north-east depth contours over most of the study area. A trend in average latitude, without evidence of a longitudinal change, points to a changing depth distribution. This pattern was seen for *S. acutipinnis*. A bias in sampling depths over time (Fig. A1, Appendix A) precluded estimation of a depth trend directly. However, peak *S. acutipinnis* catches appeared to shift deeper by about 30 m between the first and last five years of trawl survey data (Fig. A2, Appendix A), supporting the geographic evidence of a population moving into deeper water. Yemane et al. (2014) documented this species (then referred to as *S. megalops*; Viana and de Carvalho, 2016) shifting to greater depths on the South African west coast. Although species identification issues could affect results (Appendix A), we expect the majority of Agulhas Bank catches to have been *S. acutipinnis* (Viana et al., 2017) and that the deepening trend may be true for this species.

4.3. Future work

The identification of trends leads to many hypotheses and potential expansions of this work. As the spatial resolution of the geoGLMM models increase, the inclusion of a depth covariate may provide additional insight to spatial responses of species. When available, an obvious next step to isolating potential drivers of distribution shifts would be to incorporate fishing effort and hydrographic data into the statistical framework (e.g., Bell et al., 2015). Models that integrate such information when estimating densities (e.g., Kristensen et al., 2014; Thorson et al., 2017, 2015a) may provide valuable tools to understand and attribute causal impacts. Exploring species traits and which parts of the assemblage have responded in similar ways (Kleisner et al., 2016) might help understand the causes and where the most pronounced changes have taken place. The use of the recently developed multivariate VAST package (Thorson and Barnett, 2017) could also help understand the dynamics of certain species or groups of taxa better by taking into account the correlation among their size classes or individual species.

Another improvement might be to add a seasonal component to the geoGLMM, allowing the use of all data within one model. Although not implemented at the time of this work, seasonal models would enable explicit assessment of differences in distribution between or among seasons. The substantial proportion (25%) of taxa that appeared to have disparate distributions between the two survey seasons points to the importance of considering seasonal variation in studies and management decisions. Another benefit of a seasonal model would be to estimate distributions for seasons in which surveys were not conducted. Seasonal models might also be useful when integrating fishery and survey data into a single spatio-temporal model, especially in cases where surveys are conducted predominantly during a single season, yet fisheries operate over a broader period in each year.

5. Conclusions

Understanding the distributional dynamics of marine species is important to inform management of ocean spaces. This is especially pertinent as the ocean become more crowded with new industries looking to harness the blue economy and when climate change and/or fishing impacts influence where marine taxa live. Our approach to identify potential distributional trends from trawl surveys provides an improved statistical framework over methods typically used in the past. We hope it will stimulate further development of methods that characterise trends and patterns within the spatio-temporal structure and variability typical of such datasets.

The identification of ecological trends and development of their climate impact predictions hinges on the availability of multi-decadal, ecological time series such as the trawl surveys analysed here. Such time series enable increasingly powerful (distributional and abundance) assessments of species and ecosystems, allowing their trajectories to be measured against historically-informed targets. The continuation of such standardised surveys is vital to improved understanding and management of ocean spaces in South Africa and globally.

Acknowledgements

Kristin Kleisner, Lewis Barnett and two anonymous reviewers are thanked for useful comments that improved the manuscript. The Department of Agriculture, Forestry and Fisheries: Branch: Fisheries Management are acknowledged for the use of their data. Funding support is acknowledged from the Claude Leon Foundation, the National Research Foundation, including its Professional Development Programme, SAEON (South African Environmental Observation Network), the African Coelacanth Ecosystem Programme (ACEP) Deep Secrets Project, and from the Climate Change Division at SANBI (South African National Biodiversity Institute). The funders had no role in the study design, analysis, interpretation, writing or submission process. Computations were performed using facilities provided by the University of Cape Town's ICTS High Performance Computing team (http://hpc.uct.ac.za).

Declarations of interest: none

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Tables

Table 1. Centre of gravity (COG) and effective area results for 44 species and all taxa combined. The first six columns show trend estimates (km.year^{-1} or km^2.year^{-1}). Bold figures indicate evidence of trends different from zero ($p\leq0.1$). Underlined figures identify those with $p\leq0.05$. Bold r^2 values in right-most columns identify species lacking significant correlation ($p>0.05$) between longitudinal and latitudinal COG time series.

Taxa	**Longitudinal COG**		**Latitudinal COG**		**Effective area**		**Correlation r^2 E-N**	
	Autumn	**Spring**	**Autumn**	**Spring**	**Autumn**	**Spring**	**Autumn**	**Spring**
All taxa	**-0.26**	-0.16	-0.04	-0.01	**-61.87**	**-58.35**	NA	NA
Acroteriobatus annulatus	0.95	-0.05	**0.35**	0.00	-151.67	-173.73	1.00	0.87
Argyrosomus spp.	1.32	1.78	**0.32**	0.37	-140.86	-119.81	0.97	0.53
Argyrozona argyrozona	-0.03	-1.15	-0.12	-0.54	58.70	-52.85	0.51	**0.22**
Arnoglossus capensis	0.12	0.26	0.10	0.23	-274.45	-277.47	**0.16**	0.77
Austroglossus pectoralis	-0.71	**-2.61**	-0.04	**-0.50**	-89.24	-207.65	0.42	0.84
Callorhinchus capensis	0.52	-0.25	0.07	-0.17	53.95	97.02	0.61	0.37
Chelidonichthys capensis	-0.56	-0.14	-0.13	-0.06	-112.28	-34.31	0.67	**0.25**
Chelidonichthys queketti	0.43	0.20	-0.06	0.11	-59.21	-20.82	0.73	0.87
Congiopodus spinifer	-0.28	-0.11	-0.25	0.04	23.95	-259.45	0.78	0.78
Congiopodus torvus	-0.10	-0.18	-0.09	-0.25	-51.91	-377.07	1.00	0.97
Cynoglossus zanzibarensis	-0.68	0.43	-0.48	0.23	-276.16	-213.97	0.67	0.61
Dasyatis chrysonota	1.25	0.26	0.17	0.07	-71.18	-40.12	0.98	0.95
Dipturus pullopunctatus	**-0.68**	-0.30	**-0.38**	-0.24	**-634.69**	-136.54	1.00	1.00
Galeichthys feliceps	-0.56	1.52	-0.02	0.15	-18.22	-36.14	0.85	0.78
Galeorhinus galeus	-0.45	-0.12	-0.26	-0.11	-279.77	-60.09	0.54	**0.03**
Genypterus capensis	-0.49	0.88	-0.45	0.25	-109.08	-69.64	0.89	0.92
Gonorynchus gonorynchus	1.08	0.21	0.42	0.06	**430.38**	657.28	0.78	0.58
Halaelurus natalensis	0.25	0.29	0.19	0.16	-171.11	-141.17	0.73	0.94
Haploblepharus edwardsii	-0.26	-0.26	0.00	0.11	-115.35	-253.34	0.39	0.49
Helicolenus dactylopterus	-0.12	-0.03	-0.10	-0.02	1.03	-8.12	0.85	1.00
Holohalaelurus regani	-0.52	-0.06	-0.17	-0.07	-168.45	-27.72	0.62	0.98
Lepidopus caudatus	**-3.02**	-1.00	-1.26	-0.26	-246.54	-135.27	0.84	0.70
Leucoraja wallacei	-0.27	-0.33	-0.19	-0.33	-376.24	-120.79	1.00	0.90
Lophius vomerinus	-0.86	-0.43	-0.80	-0.30	-164.92	-116.48	0.89	0.98
Merluccius capensis	-0.33	-0.41	0.11	-0.28	-90.70	-19.47	**0.10**	0.50
Merluccius paradoxus	-1.64	-0.30	-0.87	-0.19	17.13	-84.53	0.99	0.99
Mustelus mustelus	0.70	-0.05	0.28	-0.01	-97.41	4.65	0.90	0.99
Mustelus palumbes	0.07	-0.10	-0.16	0.00	-66.52	107.66	0.55	**0.12**
Myliobatis aquila	-0.10	-1.57	-0.09	-0.57	3.69	263.06	0.89	0.75
Pagellus natalensis	0.61	-1.87	0.13	-0.43	-22.77	3.55	0.99	0.92
Paracallionymus costatus	-0.39	-0.73	-0.23	0.09	-68.37	13.23	0.91	0.83
Pterogymnus laniarius	-0.48	-0.31	-0.17	-0.09	-40.53	0.51	0.93	0.88
Raja miraletus	-0.86	0.52	0.14	0.24	-125.44	-166.00	0.16	0.97
Raja straeleni	**-0.94**	-0.87	**-0.51**	-0.29	-537.23	-134.12	0.78	0.53
Rhabdosargus globiceps	1.11	**1.94**	0.23	0.31	139.20	157.33	0.66	0.77
Rostroraja alba	0.21	0.64	0.45	0.45	-310.94	-460.80	0.55	0.99
Scomber japonicus	-1.60	-2.20	0.31	-0.05	1204.13	388.61	**0.08**	0.57
Scyliorhinus capensis	-0.58	-0.03	-0.60	0.03	-250.88	103.55	0.84	0.50
Sphoeroides pachygaster	0.31	0.01	0.11	0.01	6.74	52.67	0.95	0.98
Spondyliosoma emarginatum	0.38	0.47	0.03	-0.01	-251.94	-51.64	0.91	0.74
Squalus acutipinnis	-0.31	-0.46	**-0.76**	-0.53	-57.63	12.00	0.47	0.88
Thyrsites atun	0.14	-1.12	0.29	-1.23	-9.07	-362.84	0.75	0.76
Trachurus capensis	**-2.61**	**-3.41**	0.88	-1.03	**-487.56**	-314.99	**0.10**	0.73
Zeus capensis	0.26	0.63	-0.07	0.23	-56.61	-88.06	0.90	0.76

Figure captions

Figure 1. Map indicating the western and eastern bounds of the study area, and place names referred to in text. Shelf edge approximated by the 200 m isobath. Inset shows regional location of the map.

Figure 2. A single trend (black line) with 95% confidence intervals (grey shading) estimated from the longitude centre of gravity time series of all 44 taxa (thin blue lines) in the autumn survey. Inset shows the density distribution of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles shaded. The median trend value and the probability that zero fell within the trend distribution are shown.

Figure 3. A single trend with 95% confidence intervals (shading) estimated from the effective area time series of all 44 taxa (thin lines) in the autumn survey. Inset shows the density distribution of trend estimates, with the origin (zero) marked by a vertical line and the tails beyond 5th and 95th percentiles shaded. The median trend value and the probability that zero fell within the trend distribution are shown.

Figure 4. Estimates of longitudinal (left) and latitudinal (centre) centre of gravity, and effective area (right), shown for autumn (black/grey) and spring (blue) time series for slime skate (*Dipturus pullopunctatus*). Error bars represent standard error. Trend line and shaded 95% confidence intervals estimated by the state-space model are overlaid. Inset graphs are density distributions of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles shaded. Median trend values and the probability that zero fell within the trend distributions are shown.

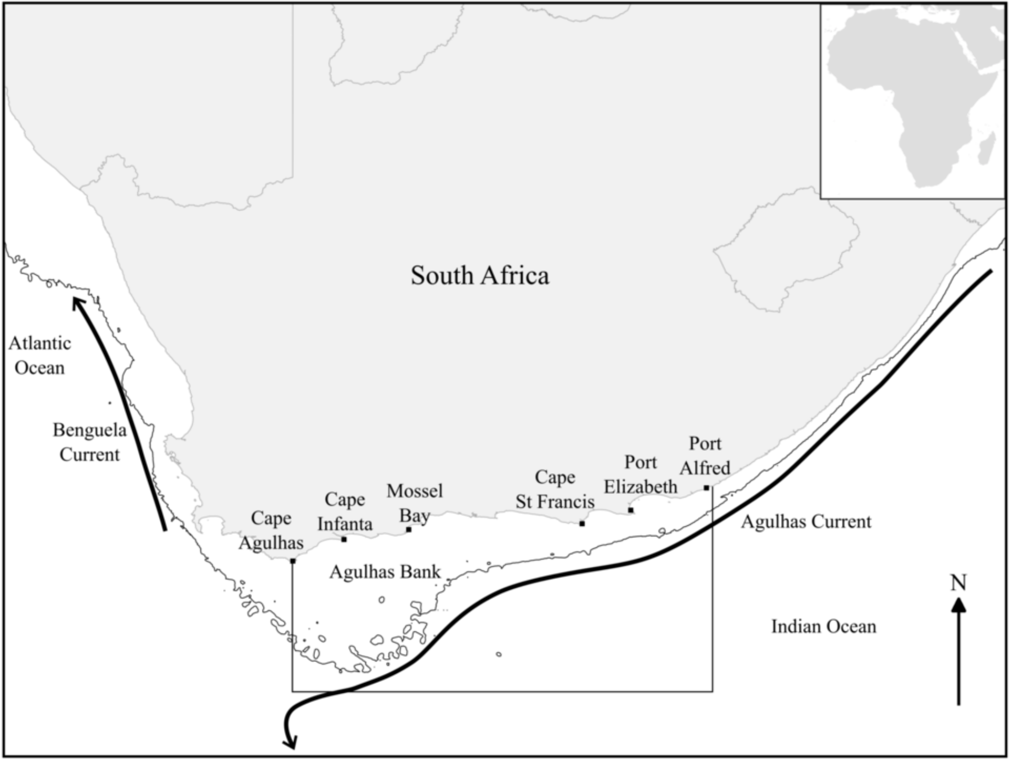
Figure 5. Estimates of longitudinal (left) and latitudinal (centre) centre of gravity, and effective area (right), shown for autumn (black/grey) and spring (blue) time series for white stumpnose (*Rhabdosargus globiceps*). Error bars represent standard error. Trend line and shaded 95% confidence intervals estimated by the state-space model are overlaid. Inset graphs are density distributions of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles shaded. Median trend values and the probability that zero fell within the trend distributions are shown.

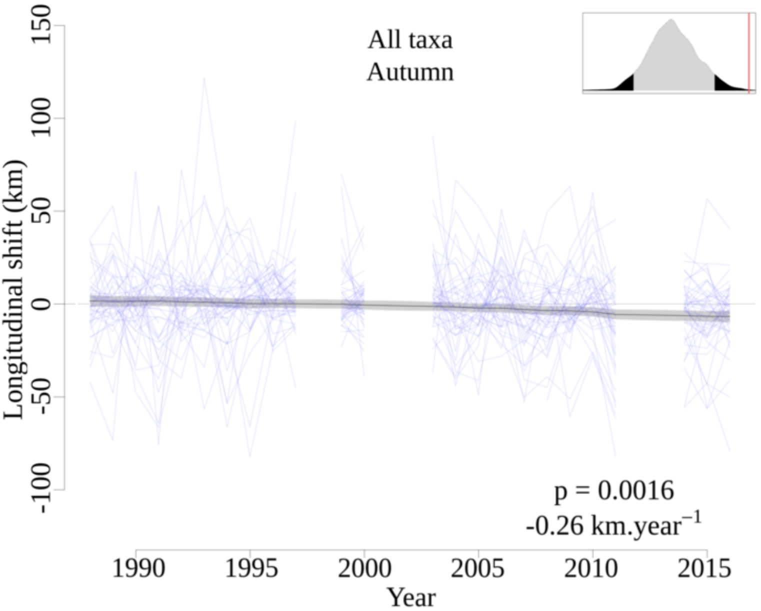
Figure 6. Estimates of longitudinal (left) and latitudinal (centre) centre of gravity, and effective area (right), shown for autumn (black/grey) and spring (blue) time series for bluntnose spiny dogfish (*Squalus acutipinnis*). Error bars represent standard error. Trend line and shaded 95% confidence intervals estimated by the state-space model are overlaid. Inset graphs are density distributions of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles shaded. Median trend values and the probability that zero fell within the trend distributions are shown.

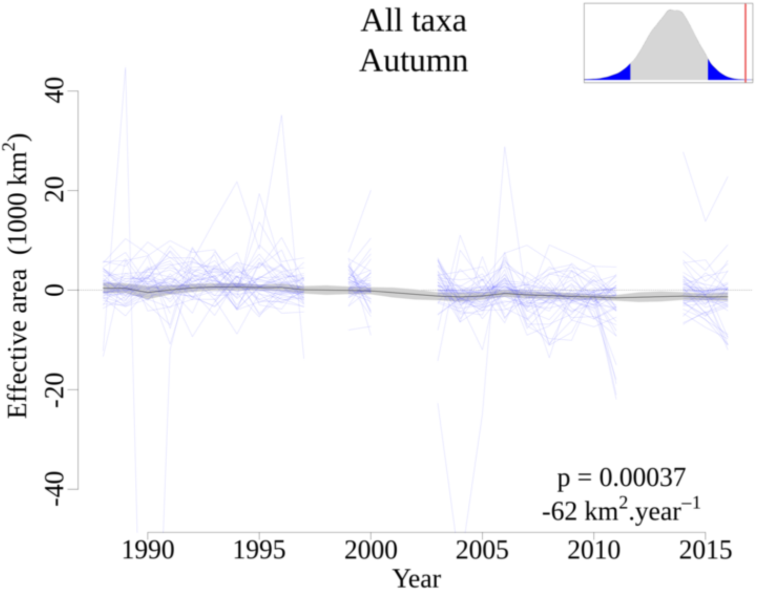
Figure 7. Agulhas Bank commercial trawl effort for the period 1983-2015 as recorded on a 20' by 20' resolution grid. Annual mean number of trawl drags are shown (shades of grey), together with

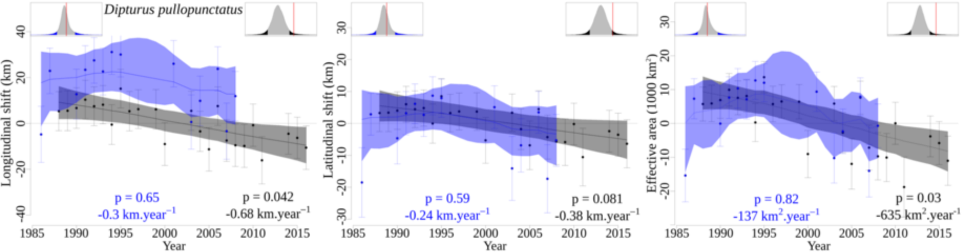
linear slopes different from zero (*p*≤0.05) indicating an increase (red) or decrease (blue) over time. Depth contours of -100 m, -200 m and -500 m are shown, as well as locations mentioned in the text.

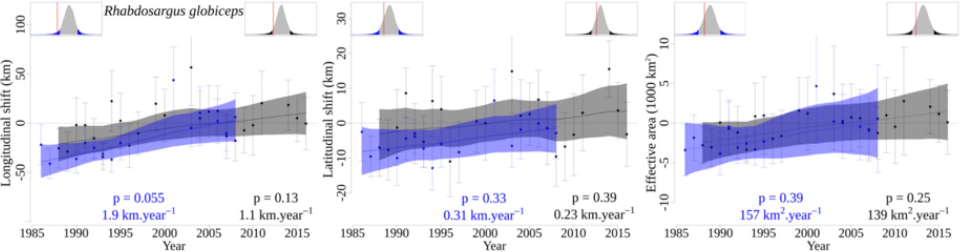
Figure 8. Commercial trawl effort recorded on the Agulhas Bank, summed for a) the entire south coast trawl survey area, and b) for six inshore grid cells in the western area (Cape Infanta to Mossel Bay) and the eastern area (Port Elizabeth to Port Alfred). Non-linear LOESS fits are included.

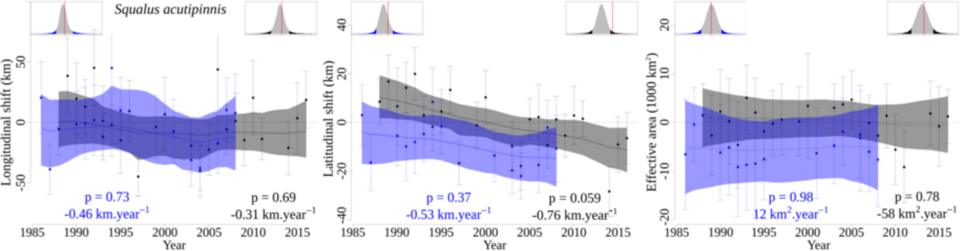

South Africa
Atlantic Ocean
Benguela Current
Cape Agulhas
Cape Infanta
Mossel Bay
Cape St Francis
Port Elizabeth
Port Alfred
Agulhas Bank
Agulhas Current
Indian Ocean
N

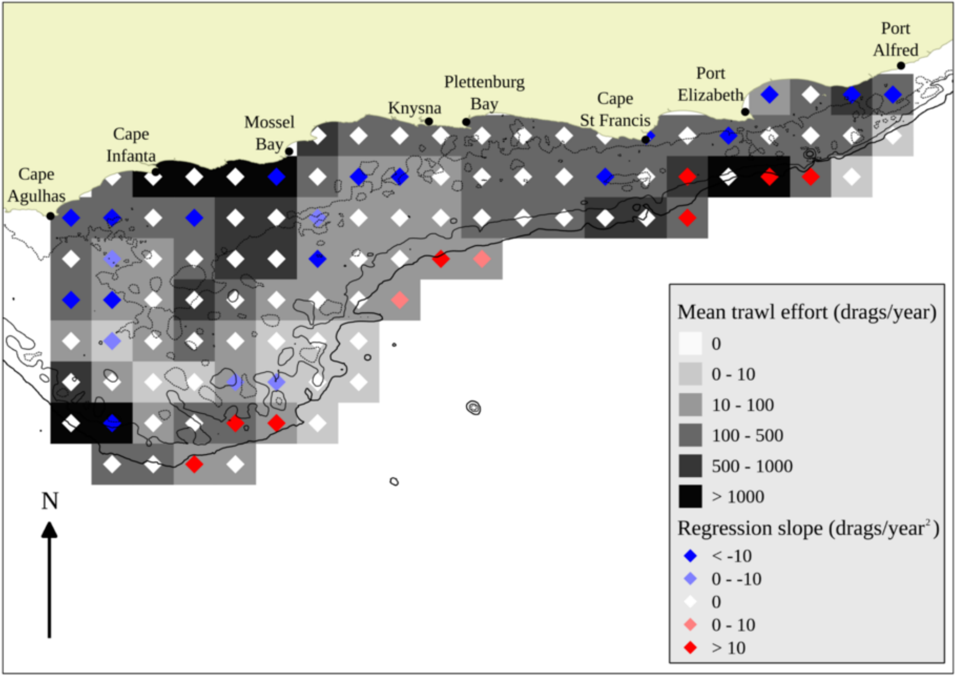

All taxa
Autumn
Longitudinal shift (km)
150
100
50
0
-50
-100
1990
1995
2000
2005
2010
2015
Year
p = 0.0016
-0.26 km.year^{-1}

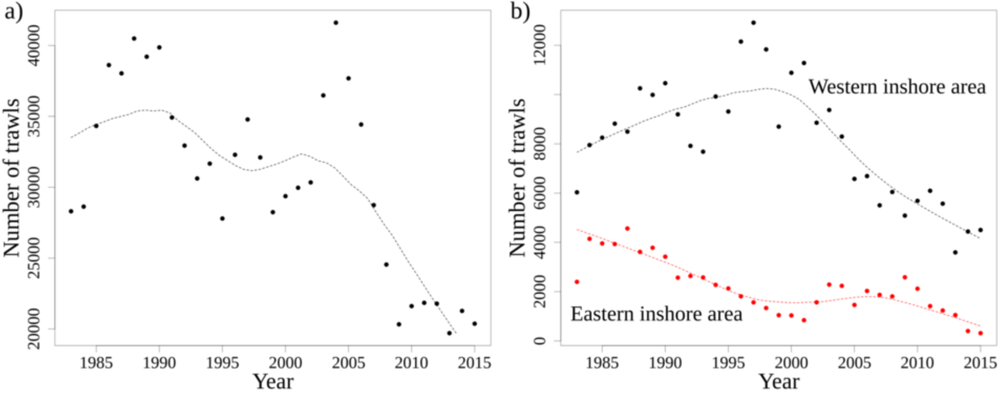

All taxa
Autumn
Effective area (1000 km^2)
40
20
0
-20
-40
1990
1995
2000
2005
2010
2015
Year
p = 0.00037
-62 km^2.year^{-1}


Dipturus pullopunctatus
Longitudinal shift (km)
40
20
0
-20
-40
p = 0.65
-0.3 km.year^{-1}
p = 0.042
-0.68 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Latitudinal shift (km)
30
20
10
0
-10
-20
-30
p = 0.59
-0.24 km.year^{-1}
p = 0.081
-0.38 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Effective area (1000 km^2)
30
20
10
0
-10
-20
p = 0.82
-137 km^2.year^{-1}
p = 0.03
-635 km^2.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year


Rhabdosargus globiceps
Longitudinal shift (km)
100
50
0
-50
p = 0.055
1.9 km.year^{-1}
p = 0.13
1.1 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Latitudinal shift (km)
30
20
10
0
-10
-20
p = 0.33
0.31 km.year^{-1}
p = 0.39
0.23 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Effective area (1000 km^2)
10
5
0
-5
-10
p = 0.39
157 km^2.year^{-1}
p = 0.25
139 km^2.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year


Squalus acutipinnis
Longitudinal shift (km)
50
0
-50
p = 0.73
-0.46 km.year^{-1}
p = 0.69
-0.31 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Latitudinal shift (km)
40
20
0
-20
-40
p = 0.37
-0.53 km.year^{-1}
p = 0.059
-0.76 km.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year
Effective area (1000 km^2)
20
10
0
-10
-20
p = 0.98
12 km^2.year^{-1}
p = 0.78
-58 km^2.year^{-1}
1985
1990
1995
2000
2005
2010
2015
Year


Port Alfred
Port Elizabeth
Cape St Francis
Plettenburg Bay
Knysna
Mossel Bay
Cape Infanta
Cape Agulhas
N
Mean trawl effort (drags/year)
0
0 - 10
10 - 100
100 - 500
500 - 1000
> 1000
Regression slope (drags/year²)
< -10
0 - -10
0
0 - 10
> 10


a)
Number of trawls
20000
25000
30000
35000
40000
Year
1985
1990
1995
2000
2005
2010
2015
b)
Number of trawls
0
2000
4000
6000
8000
12000
Western inshore area
Eastern inshore area
Year
1985
1990
1995
2000
2005
2010
2015