

Environmental drivers of pelagic fish stocks in the NW Atlantic Ocean

(3924 words)

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Abstract (201 words)

Ecosystem-based approaches to fisheries management are becoming increasingly popular and account for the effects of ecological and environmental factors on fish stocks in addition to the impact of fishing itself. To identify and quantify such bottom-up environmental effects on nine NW Atlantic fish stocks across four species, we employed a tiered statistical modelling approach to link fish stock metrics (*i.e.*, condition, abundance, recruitment) to dominant modes of environmental variability. An analysis of optimal models describing these metrics revealed that condition is chiefly dictated by predictors related to phenology and zooplankton community composition, while abundance is modulated by physical factors and zooplankton. Models of recruitment featured predictors relating to all aspects of the environment. These results are consistent with a strong influence of food quality and quantity on condition and with the influence of suitable habitat (*e.g.*, temperature, prey) on abundance, while successful recruitment is the outcome of a complex combination of biotic and abiotic processes. The dominant driver of variability in our models of fish stocks was a long-term shift in the zooplankton community, which represented two important factors in fish ecology – prey abundance and thermal conditions – and demonstrates the key role zooplankton can play as a predictor of fish stocks.

1 Introduction

Variability in the physical environment and in lower trophic levels influences the dynamics of fish stocks by altering the distribution and abundance of prey, and the extent of suitable habitat. While it is often difficult to link individual environmental variables (e.g., sea-surface temperature, copepod biomass) directly to fish stock indices, recent studies have been successful in relating modes of variability in the environment to fluctuations in fish populations (e.g., Plourde et al. 2015, Reed et al. 2019). Establishing these relationships provides an improved understanding of how fish stocks respond to changes in ecosystem characteristics and, in the future, may allow management strategies to be adjusted in light of anticipated shifts in environmental conditions (Pikitch et al. 2004).

The NW Atlantic is currently experiencing a long-term shift in oceanographic and biological conditions manifested by a decline in dominant phytoplankton and zooplankton species and total zooplankton biomass (Johnson et al. 2017), warming of shelf waters, and increased stratification due to both warming and freshening (Hebert et al. 2016). Nonlinear relationships and ecological interactions mean that such changes do not necessarily elicit straightforward responses in fish stocks. Nevertheless, statistical modelling provides a means addressing these issues by characterising the behaviour of complex systems under changing conditions without having to specify the details of ecosystem dynamics *a priori*.

By undertaking a comparative statistical modelling study of pelagic fish stocks in the NW Atlantic, we sought to identify overarching drivers of key stock metrics – condition, abundance, and recruitment – during this period of environmental change. Here, we consider pelagic fish stocks on the Scotian Shelf, in the Gulf of St. Lawrence, and on the Newfoundland Shelf that fill similar ecological niches – including herring, mackerel, silver hake, and capelin – and, consequently, were expected to exhibit similar responses to environmental variability. Based on previous work, we hypothesized that condition would be dictated by food, abundance determined by water temperature and other physical factors, and recruitment controlled by both thermal conditions and food (Reed et al. 2019).

2 Methods

2.1 Analysis

The approach adopted here directly follows Reed et al. (2019), based on the approach adopted by Plourde et al. (2015). Briefly, data sets were constructed that represent three key aspects of the pelagic habitat: physical environment, zooplankton community composition, and timing of annual biological events (referred to as physical, zooplankton, and phenology, hereafter). Regional data sets were constructed for the Newfoundland Shelf (NLS), Gulf of St. Lawrence (GSL), and Scotian Shelf (SS), regions which host the nine fish stocks considered here. The dominant modes of variability in these data sets were characterised using Principal Component Analysis (PCA). The first three principal components (PCs) explained the majority of variance in the data sets and were used as predictors in Generalised Additive Models (GAMs) of fish stock metrics – condition, abundance, and recruitment. Adult abundance and/or biomass was also used a predictor for condition and recruitment. For these GAMs, we adopted the following generic formulation:

$$g(E(y)) = \eta = \beta_0 + \sum_{i=1}^n f_i(x_i) + \epsilon$$

where y is the dependent variable (*i.e.*, fish stock metric) and x_i represents the i^{th} independent variable (*e.g.*, PCs), f_i is a smoothing function for covariate x_i , β_0 is the intercept of the model, n is the number of covariates, and η is the predictor, which is associated with the expected value of y through a link function, g . Here, we use an identity link function and Gaussian distribution of the response variable ($\epsilon \sim N(0, \sigma^2)$). All possible GAMs with a maximum of three terms per model were fitted to the data sets and those with excessive concurvity – a nonlinear analog of multicollinearity – were discarded. Models were limited to three terms with a basis dimension of three to prevent overfitting. All remaining models were ranked by Akaike information criterion (AIC), which quantifies the goodness of fit while accounting for the

complexity of the model. The top ranking models for each stock-metric combination – termed the *optimal* model hereafter – were then selected.

2.2 Data assembly

Data sets describing the environmental conditions for the three regions were constructed from data products of the Atlantic Zone Monitoring Program (AZMP; Therriault et al. 1998, Mitchell et al. 2002). For the Scotian Shelf, we use the data set previously assembled by Reed et al. (2019) and analogous data sets were constructed for the Gulf of St. Lawrence and Newfoundland Shelf (see Supplementary tables). All data sets included deep (or bottom) temperatures, sea-surface temperatures, and indices of large-scale climate variability (*i.e.*, North Atlantic Oscillation, Atlantic Multidecadal Oscillation). The SS and GSL data set also include the St. Lawrence River flux to represent fresh water input (omitted for NLS, which is upstream of the St. Lawrence River). Data sets also include metrics representative of winter conditions, as these conditions define the initial state for the production cycle in spring. In all regions, cold surface waters of Arctic origins are mixed downwards to intermediate depths during winter. Surface waters are subsequently warmed in summer months resulting in a three layer system: warm, saline deep waters; cold, fresh intermediate waters, termed the Cold Intermediate Layer (CIL); and warm, fresh surface waters. All data sets include a metric of the CIL. In addition, the Scotian Shelf data set includes an index of stratification between 0 and 50 m.

Data sets were constructed representing the abundance of dominant and subdominant copepod taxa, as well as the dominant non-copepod zooplankton, using standard scores. For the GSL data set, sampling took place at several sections – Central GSL, Cabot Strait, Southwest Anticosti, Bonne Bay, Sept-Îles, St. Lawrence Estuary, and Magdalen Islands – and two high-frequency stations at Shediac and Rimouski. For the NL data set, data were collected at four sections – Southeast Grand Banks, Flemish Cap, Seal Island, and Bonavista Bay – and one high-frequency station, Station 27 (S27). For the SS data set, sampling took place at three sections – Browns Bank Line, Halifax Line, and Louisbourg Line – and at one high-frequency station, Halifax 2 (HL2), located on the inshore central Scotian Shelf. Anomalies were

calculated for log transformed abundances (NLS and GSL reference period 1999-2016; SS reference period 1999-2010).

Data sets were constructed to quantify the timing of key biological processes. The rate of surface warming was determined by fitting a linear model to sea-surface temperatures (SST) for March, April, and May using bimonthly means for SST from NOAA's Advanced Very High Resolution Radiometer and estimating the slope of the regression. This metric was calculated for standard boxes: St. Anthony Basin, Northeast NLS, Hibernia, Flemish Pass, and Southeast Shoal for the NLS; Northeast GSL, Northwest GSL, Magdalen Shallows, and Cabot Strait for the GSL; West, Central, and East Scotian Shelf for the SS. A $0.1^\circ \times 0.1^\circ$ grid covering the area between 65°W to 40°W and 43°N to 55°N was used to calculate the final day of sea ice. The SS and GSL were combined into a single region for this metric, while a separate region was used for the NLS. Mean ice area over January, February, and March was also included in these data sets for these regions.

Development of the zooplankton community on the SS and NLS was characterised with the timing of the maximum zooplankton biomass, as well as the peaks in total *Calanus finmarchicus* abundance and *C. finmarchicus* life stages CI-III. In the NW Atlantic, *C. finmarchicus* is often the biomass dominant zooplankton and, consequently, an important component of the food web. For the GSL, there are two peaks in *C. finmarchicus* life stages CI-III within a year representing two generations (G1, G2), and timing of these peaks and of the ratio of the two were used to characterise zooplankton development rate after Plourde et al. (2015). Like *C. finmarchicus* elsewhere, *C. hyperboreus* plays a key role in the zooplankton community on the NLS. Therefore, the timing of peaks in total *C. hyperboreus* and life stages CI-III were used in the NLS data set. The start day and duration of the spring phytoplankton bloom in each of the regions was determined using Sea-viewing Wide Field-of-View Sensor (SeaWiFS) data (1999-2008) and Moderate-resolution Imaging Spectroradiometer (MODIS) data (2009-2016) for the same standard boxes as SST warming.

Abundance of Newfoundland capelin was derived from spring acoustic surveys in NAFO regions 3KL. Surveys took place annually between 1999 and 2017 in May with the exception of 2006 and 2016 when surveys did not take place. While there have been changes in technology, sampling gear, calibration techniques, et cetera over this period, these sources of variability have been accounted for in the data (Mowbray 2012). Acoustic surveys were complemented by targeted fishing sets from which condition and recruitment could be determined. Abundance was estimated from the mean number adults per standard tow (1.75 nautical miles), while condition was represented by the mean weight at 15 cm – the most abundant length of adults. Recruitment was estimated as the mean abundance of two-year-olds with a two year lag.

Six herring stocks were modelled for the Gulf of St. Lawrence corresponding to spring and autumn spawners across three NAFO divisions: 4R, 4S, and 4T. Spring and autumn spawners are genetically distinct and could be differentiated from one another as herring consistently return to the same feeding, spawning, and overwintering sites (Brophy et al. 2006, Lamichhaney et al. 2017). Data for spawning-stock biomass (SSB) and recruitment (abundance of two-year olds) were estimated using virtual population analysis (VPA) based on commercial fisheries data (Brosset et al. 2018). Condition, represented by Fulton's condition factor, was similarly determined from commercially-caught herring.

Data for GSL mackerel were taken from Plourde et al. (2015) and extended to 2016. Spawning stock biomass, abundance, and recruitment were all determined using Sequential Population Analysis performed on commercial landings data. To calculate recruitment, the natural log of one year-olds divided by the abundance of adults in the previous year. Condition was estimated using fisheries data to calculate Fulton's coefficient, which was averaged across all cohorts. Similarly, condition of GSL capelin was estimated using the mean annual Fulton's coefficient for fish caught commercially in NAFO regions 4R, 4S, and 4T.

Data for Scotian Shelf silver hake were produced by Fisheries and Oceans Canada's (DFO) summer research vessel surveys, which are stratified random bottom trawl surveys. Data for condition, adult abundance, and recruitment were used from strata 440-483 and were previously compiled by Reed et al. (2019). To quantify condition, we used stratified mean weight at 25 cm (i.e., adults). Abundance was estimated as the stratified mean abundance of adults, while recruitment was estimated as the stratified mean abundance of fish with a total length of 10-18 cm, which represents fish that will be recruited within the next year, lagged by 1 year (Reed et al. 2019).

Like silver hake, data for Scotian Shelf herring were produced by DFO's summer research surveys on the Scotian Shelf and Bay of Fundy. Condition and abundance were estimated using data from strata 440-495. Condition was calculated as the stratified mean weight at 28 cm – the average length of adults – while abundance was estimated as the stratified mean abundance. Recruitment was estimated as the annual difference in acoustically-determined spawning biomass from surveys of German Bank and Scots Bay.

3 Results

The 26 optimal models that were determined for fish metrics across nine stocks and three regions (Fig. 1) explained between 44% and 95% of the deviance with a mean value of 71%, although the vast majority of optimal models (77%) could explain at least 60% of the deviance. Top-ranking models of condition were largely a function of the timing of biological events and composition of the zooplankton community with phenology and zooplankton PCs accounting for 47% and 35% of significant predictors, respectively (Fig. 2a). Optimal models of abundance only featured zooplankton and physical PCs (58% and 42% of significant predictors, respectively; Fig. 2b), whereas recruitment models showed a fairly even distribution of predictors across the variable groupings (Fig. 2c). The most common predictor was zooplankton PC1 featuring in 11 of 26 optimal models (42%) including models from all regions and species.

4 Discussion

Optimal models for condition, abundance, and recruitment were broadly consistent with our previous analyses of Scotian Shelf silver hake (Fig. 2; Reed et al., 2019). Condition was chiefly a function of phenology and, to a lesser degree, zooplankton community composition (Fig. 2a). These variables largely represent system productivity and prey availability, suggesting that condition is chiefly dictated by food. Optimal models of abundance, however, comprised mainly physical and zooplankton variables (Fig. 2b), which influence the distribution of fish stocks by defining the extent and location of suitable habitat in terms of temperature and prey. Recruitment was shown to be a function of all groups of predictors (Fig. 2c) suggesting that food availability, thermal conditions, abundance of spawning adults, and composition of the zooplankton community all factor into the production of larval fish and their survival to adulthood.

4.1 Condition

Condition of fish is affected both by the abundance of prey (*e.g.*, Lloret et al. 2014) as well as the quality of their diet (*e.g.*, Orlova et al. 2010, Paul et al. 2018). In the northwest Atlantic, fish biomass (*i.e.*, annual long-term mean landings) is strongly correlated with mean chlorophyll concentration (Frank et al. 2006) illustrating the link between fish stocks and abundance of lower trophic levels. Our results were broadly consistent with this trend, as optimal models of condition frequently contained phenology PCs (Fig. 1a; 8 of 17 significant terms), which incorporated variables that represent the productivity of the system (*e.g.*, onset and duration of the phytoplankton bloom; Reed et al., 2019). Furthermore, these models often included zooplankton PCs, which reflects both the abundance (*i.e.*, quantity) of zooplankton and the composition (*i.e.*, quality) of the community. This is in agreement with the established link between fish condition and the content of their diet.

Fish condition may also be affected by ambient temperature, both directly through physiological effects and indirectly through factors such as food availability (*e.g.*, Brander 1995, Krohn et al. 1997, Rätz and Lloret 2003, Pardoe et al. 2008). Only two models of condition included physical PCs explicitly;

however, zooplankton PCs may account for both the direct and indirect impacts of temperature fluctuations (Runge 1988). For example, zooplankton PC1 was correlated with physical PC1 in both the GSL and on the SS (Pearson's correlation coefficients of 0.59 and 0.77, respectively; results not shown), but had a weaker relationship on the NLS (Pearson's correlation coefficient of 0.26; results not shown). In all regions, physical PC1 represented an overall shift in the temperature of the system: loadings for surface and deep temperatures generally had the same sign. For the NLS physical PCA, deep temperatures for 3LNO in spring and 3Ps were an exception to this trend, as they showed opposite loadings to other deep temperatures and surface temperatures. In all regions, CIL and sea ice indices showed opposite loadings to surface and deep temperatures with the exception of the CIL index for the GSL, which had the same sign as surface- and deep-water temperatures. Effects of food and temperature are thus conflated in zooplankton PC1, which represents a useful metric of system dynamics.

Spawning-stock biomass was selected as a significant predictor in only one optimal model of condition, suggesting that density-dependent affects appear to be less important than those related to food and physical environment. This model referred to Gulf of St. Lawrence mackerel, which has previously been shown to have density-dependent condition (Plourde et al. 2015).

4.2 Abundance

It is well-established that fluctuations in the physical environment alter the distribution of marine fish (Hela and Laevastu 1961 and references therein). The models fit here describe this variability in spatial distribution and availability to be caught, as we used unlagged predictors and related abundances to current conditions. Optimal models of abundance only featured significant predictors from physical and zooplankton PCAs (Fig. 2b) with seven of the eight models containing either zooplankton PC1 or physical PC1 as a significant predictor (Fig. 1b). These PCs – which are correlated, although to lesser degree on the NLS – describe an overarching change in the temperature and an associated shift in the zooplankton, respectively. Their prominent role in optimal models of abundance is consistent with observations that temperature is central in modulating the distributions of fish species considered here

(Rikhter et al. 2001, Trenkel et al. 2014). In addition to temperature, these predictors may also reflect variability due to other known physical drivers included in the analysis, such as sea ice dynamics for capelin (Gjøsæter 1998) and large-scale climate indices for silver hake (Nye et al. 2011). Fish landings are also influenced by the abundance of prey (*e.g.*, Ogawa and Nakahara 1979) and zooplankton PC1 thus accounts for shifts in distribution associated with both physical properties and food availability (*i.e.*, quantity and quality). Broadly, these results are consistent with known drivers of fish abundance; however, some important drivers of abundance – such as predation (*e.g.*, Swain et al. 2015), inter- or intraspecific competition (*e.g.*, Ward et al. 2006), and fishing (*e.g.*, Fogarty and Murawski 1998) – were not included in our analysis and, consequently, the explanatory power of these factors cannot be compared to those selected by the optimal models.

4.3 Recruitment

Many theories have been put forward to explain variability in recruitment (Hjort 1914, Cushing 1969, Lasker 1978, Sale 1978, Iles and Sinclair 1982, Cury and Roy 1989). Nonetheless, it is now generally accepted that there is no single driver of recruitment, but rather recruitment is the result of “complex trophodynamic and physical processes acting over many temporal and spatial scales and throughout pre-recruit life” (Houde 2008). Our results are broadly consistent with this assertion, as all possible predictors except for phenology PC2 were included as significant terms in optimal models of recruitment (Fig. 1c). Moreover, predictors are fairly evenly distributed between variable groups (Fig. 2c).

Half of all optimal models for recruitment included at least one significant physical predictor, reflecting the importance of the physical environment in regulating recruitment. For example, recruitment has been shown to be modulated by physical factors such as temperature (*e.g.*, Francis 1993), large-scale climate dynamics (*e.g.*, Brander 2005), and other physical processes (*e.g.*, Brickman et al. 2001). Predictors for phenology and zooplankton also featured prominently in these models, as recruitment has been linked to various biotic factors such as food availability (*e.g.*, Zenitani et al. 2007) and congruent life cycles between larvae and prey (*e.g.*, Cushing 1990). Spawning-stock biomass also featured as a significant term

in 3 of 8 models (Fig. 1c). This is consistent with an analysis of 211 fish stocks, which revealed a persistent stock-recruitment relationship but with a limited explanatory power (Cury et al. 2014). In short, these results support the hypothesis that recruitment is ultimately a complex combination of abiotic and biotic processes.

4.4 Implications of long-term shifts in the zooplankton community

A marked long-term shift in the zooplankton community, as quantified by zooplankton PC1, featured prominently in optimal models for GSL stocks (Fig 1). Almost all of these models showed a decrease in the response variable with increasing principal component score, regardless of the metric they describe (results not shown). One exception is for the abundance of autumn-spawning 4R herring, which showed a strong increase with increasing zooplankton PC1. These results suggested that if the long-term zooplankton trend continues, GSL fish stocks will decline as a result, in terms of condition (4R & 4S autumn-spawning herring), abundance (mackerel, 4R & 4T spring-spawning herring) and recruitment (4R autumn-spawning herring). In contrast, abundance of silver hake on the SS and recruitment of capelin on the NLS both showed positive trends with respect to zooplankton PC1, suggesting improvements if the trend persists. The key role played by this long-term, composite signal of suitable habitat (*e.g.*, food quality and quantity, thermal conditions) demonstrated that zooplankton community composition is a potentially valuable index of system state when quantitatively modelling fish stock dynamics.

4.5 Conclusions

GAMs describing fish metrics revealed broad trends in drivers across various stocks of the NW Atlantic. Condition was primarily affected by PCs related to food quantity (*i.e.*, system productivity) and quality (*i.e.*, composition of the zooplankton community), whereas abundance was chiefly a function of zooplankton and physical PCs, which define suitable habitat in terms of availability of prey and temperature. Models of recruitment featured almost all possible predictors, reflecting the complex combination of processes involved. These results are consistent with observations, although there are other biotic and abiotic factors that potentially affect fish stock metrics that were not considered in our

analysis, such as parasites, inter- and intraspecies competition, predation, and oxygen saturation. As a result, the contribution of these factors cannot be assessed. Nonetheless, models presented here are able to explain on average 71% of the deviance with the predictors included in our analysis, suggesting that key processes are represented. In particular, the prominence of zooplankton PC1 across optimal models suggests zooplankton abundances are promising indices of both biotic and abiotic processes that influence fish stocks and should be considered in future ecosystem-based approaches to fisheries management.

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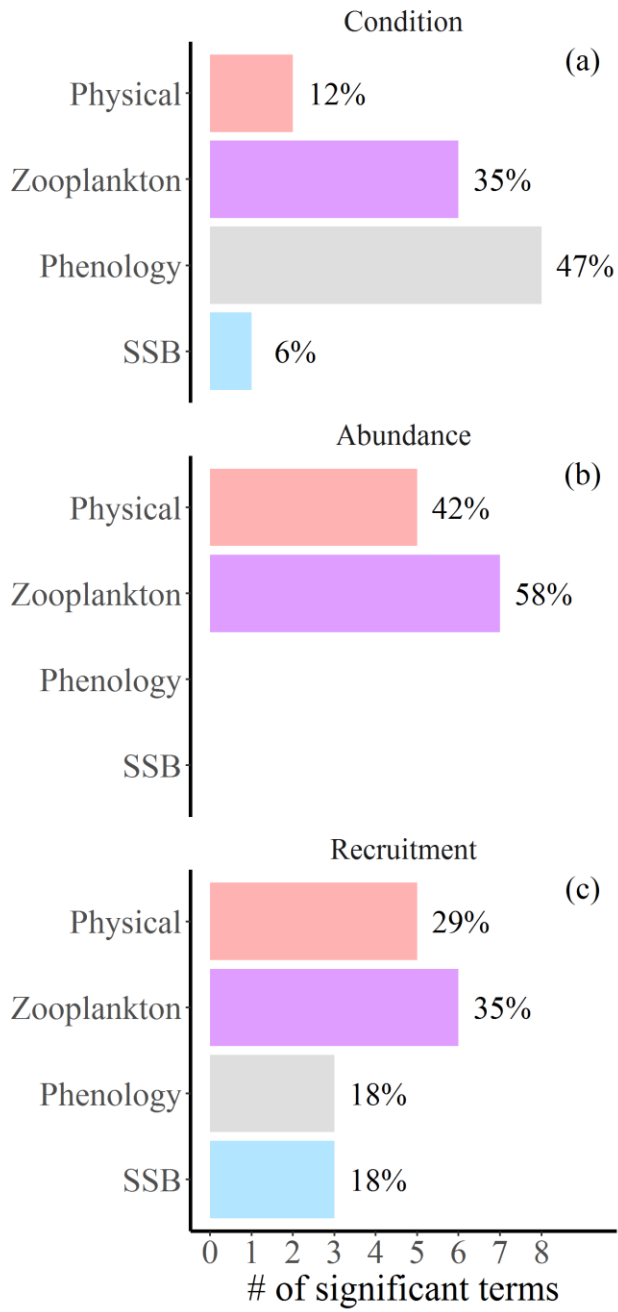
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Figure 1: Optimal Generalised Additive Models for each stock/metric. Panels (a), (b), and (c) represent models of condition, abundance, and recruitment, respectively. Each row represents an optimal model with symbols indicating which terms featured in the optimal model and their significance. Model terms appear on the x -axis. Pink, purple, and grey symbols represent physical (Phy), zooplankton (Zoo), and phenology (Phe) principal components, respectively, while blue symbols denote spawning stock biomass (SSB). Labels on the left indicate fish species modelled with the region in brackets (NL = Newfoundland Shelf; GSL = Gulf of St. Lawrence; SS = Scotian Shelf). Labels on the right indicate the percent deviance explained by each model.



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367 Figure 2: Number of significant terms in each variable group (physical, zooplankton, phenology,
368 spawning stock biomass) that appear in optimal models for (a) condition, (b) abundance, and (c)
369 recruitment. Numbers on each bar represent the number of significant terms as a percentage of total for
370 that fish metric (i.e., condition, abundance, or recruitment).