

# Are negative intra-specific interactions important for recruitment dynamics? A case study of Atlantic fish stocks

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**ABSTRACT:** In fishes, strong year classes can suppress survival of the following year class because of interactions such as cannibalism and between-cohort competition. The incidence of such negative intra-specific interactions in recruitment dynamics was investigated for commercially relevant fish stocks in the Atlantic Ocean using residuals from the Ricker stock-recruitment model. The autocorrelation of recruitment residuals at lags ranging from 1 to 5 yr were computed and examined. The number of stocks that exhibited positive autocorrelation in recruitment residuals decreased with increased lag length. Negative autocorrelation of recruitment residuals at lags were found in a number of stocks from 3 to 5 yr and were interpreted as evidence of cannibalism or intra-specific competition. Autocorrelation analysis of recruitment time-series provides an easy and generally accessible method of detecting negative intra-specific interactions. However, it is a conservative method, especially when stocks have undergone periods of low abundance or are subject to other strong density-dependent or -independent influences. While the majority of stocks studied here did not exhibit evidence for negative intra-specific interactions, our findings nonetheless suggest that cannibalism and competition at high stock levels can have important consequences on the determination of sustainable biomass and harvest levels.

**KEY WORDS:** Cannibalism · Intra-specific competition · Recruitment · Population dynamics · Atlantic Ocean

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## INTRODUCTION

Cannibalism is believed to be common among fish (Smith & Reay 1991). Inter-cohort cannibalism, where an abundant cohort suppresses later cohort(s), is potentially an important mechanism influencing recruitment (Claessen et al. 2000, Walters & Martell 2004); inter-cohort cannibalism is one of the mechanisms leading to over-compensatory, Ricker-type stock-recruitment relationships (Hilborn & Walters 1992). Inter-cohort cannibalism is expected to lead to negative autocorrelation between abundance of successive cohorts, which can be used to detect canni-

balism in recruitment data (Myers & Cadigan 1993, Fogarty et al. 2001). Using this method, negative autocorrelations suggestive of cannibalism have been detected in a number of demersal stocks in the North Atlantic, but these correlations were not statistically significant (Myers & Cadigan 1993), or their significance was not reported (Fogarty et al. 2001).

Correlation in inter-cohort abundance is also affected by factors or processes other than cannibalism. Competition is another negative inter-cohort interaction (Claessen et al. 2000), acting on the correlation similarly to cannibalism. In contrast, both environmental forcing and aging errors tend to make the cor-

relation more positive (Myers & Cadigan 1993). Environmental forcing in marine systems is often believed to be dominated by long-term fluctuations (Steele 1985, Cyr & Cyr 2003, Vasseur & Yodzis 2004), which would tend to lead to increased autocorrelation at short to moderate time lags. Aging errors will lead large cohort to 'spill' over to adjacent cohorts, thus introducing a positive bias to autocorrelation at short time lags; this effect is probably minor if recruitment is directly estimated from survey or catch data on recruits, but may be large if recruitment is obtained by back-projection with cohort-analysis-type methods. Therefore, the autocorrelation approach will be conservative in detecting cannibalism and other negative intra-specific interactions.

An important limitation of earlier studies (Myers & Cadigan 1993, Fogarty et al. 2001) is that they have only investigated autocorrelations with a lag of 1 yr. This puts emphasis on immediately adjacent cohorts only, whereas negative intra-specific interactions could be important across a wider span of age differences. Indeed, neither Fogarty et al. (2001) nor Myers & Cadigan (1993) found evidence of cannibalism for stocks like Northeast Arctic cod *Gadus morhua*, despite the fact that cannibalism is known to be common and important in this stock (Bogstad et al. 1994, Hjermann et al. 2004, Yaragina et al. 2009), and mortality from cannibalism is even included in the stock assessment (ICES 2014a). Quite the contrary, both studies found relatively strong positive autocorrelation for this stock. We suggest that considering time lags longer than 1 yr will facilitate detecting cannibalism because most aging errors are small and because environmental autocorrelations will decay over time.

In this paper, we use autocorrelation analysis of stock-recruitment data to assess the presence of inter-cohort cannibalism and competition for a large number of fish stocks from the North Atlantic. Our analysis allows for time lags longer than 1 yr, which we expected to facilitate detection of negative inter-cohort interactions. Furthermore, we take advantage of much longer time-series than were available for earlier studies that used similar methods to detect cannibalism in a subset of stocks included here.

## METHODS

### Stock and recruitment data

We collated all publicly available stock assessments from the Atlantic Ocean that used cohort analysis type methodology (e.g. virtual population

analysis). We focused on this methodology since the estimated recruitment time-series do not depend on an assumed underlying stock-recruitment relationship, unlike closed life cycle statistical catch-at-age/length methods. The stock assessments came from fish stocks managed by the International Council for the Exploration of the Sea (ICES) in the eastern North Atlantic, by Fisheries and Oceans Canada and the United States Marine Fisheries Service in the western North Atlantic, by the International Commission for the Conservation of Atlantic Tuna (ICCAT) in the High Seas of the Atlantic and by the Consejo Federal Pesquero in Argentina. Recent ICES stock assessment data were obtained for a total of 43 different stocks from the Baltic Sea (ICES 2014b), Barents Sea and Norwegian Sea (ICES 2014a), Celtic Sea and the area west of Scotland, North Sea, the Channel and Skagerrak (ICES 2013a), and widely distributed stocks (ICES 2013b) and 69 other assessments from the Atlantic Ocean were extracted from the RAM Legacy Stock Assessment Database (Ricard et al. 2012). In total, we obtained data for 112 stocks, with time-series varying in length from 10 to 116 yr. The data used are summarized in Tables S1 & S2 in the Supplement at [www.int-res.com/articles/suppl/m547p211\\_supp.pdf](http://www.int-res.com/articles/suppl/m547p211_supp.pdf).

### Statistical analyses

To detect autocorrelations potentially caused by negative inter-cohort interactions, it is important to first remove the effects of other known sources of autocorrelation. Therefore, we remove the effect of stock on recruitment by first fitting a stock-recruitment model to the data and then using the residuals from this fit for further analysis. We use the Ricker stock-recruitment model because it can fit compensatory and over-compensatory relationships. Our approach is similar to the one used by Fogarty et al. (2001).

In order to appropriately capture the relationship between spawning stock and its associated recruitment, the recruitment time-series were offset by the age of recruitment ( $a$ ) for each stock ( $s$ ). For each stock, the Ricker stock-recruitment model was then fitted to each available time-series of spawning stock ( $S_s \in \{S_{s,1}, S_{s,2}, \dots, S_{s,n-a}\}$ ) and recruitment ( $R_s \in \{R_{s,1+a}, R_{s,2+a}, \dots, R_{s,n}\}$ ):

$$R_{s,y+a} = \alpha_s S_{s,y} \exp(-\beta_s S_{s,y}) \quad (1)$$

We used the  $n-a$  years of available information to estimate the  $\alpha_s$  and  $\beta_s$  parameters of the model by minimising a likelihood function using a gamma

error and identity link. The autocorrelations of the residuals from Eq. (1) were then computed for lags ranging from 1 to 5 yr. Fig. 1 graphically shows the methodological details.

The stock assessments used in the analyses covered a total of 34 finfish species from 12 taxonomic families (Table S1). The Ricker stock-recruitment model was successfully fitted, and recruitment residuals could be evaluated for all 112 stocks under scrutiny. While the diagnostics of some model fits were indicative of poor fit, the fits were biologically reasonable, and we kept them since the autocorrelation results were similar to those obtained directly from stock and recruitment data. All analyses were conducted using R version 3.1.3 (R Core Team 2015).

### RESULTS

At short time lags (1 to 2 yr), autocorrelations were significantly positive, or most often, not different

from zero (Fig. 1, Table S1). Significant negative autocorrelations were present at lags between 3 and 5 yr (Lags 3 to 5), specifically, for 6 stocks at Lag 3 (Norwegian spring spawning herring *Clupea harengus*, Irish Sea cod, North-East Arctic cod, Atlantic cod in ICES Division VIIa, Argentine hake *Merluccius hubbsi* in southern Argentina, and sole *Solea solea* in ICES Division VIIa) and for 6 stocks at Lag 4 (Atlantic cod in NAFO Divisions 3Pn4RS, Georges Bank, and ICES Division VIa; whiting *Merlangius merlangus* in ICES Subarea IV and Division VIId; Argentine hake in southern Argentina; sole in ICES Division VIIa; Fig. 2). At Lag 5, only one stock, Argentine hake in southern Argentina, showed negative autocorrelation. Argentine hake and sole in ICES Division VIIa were negatively autocorrelated at lags over 3 and 2 yr, respectively, while all other negative autocorrelations were found for 8 different stocks (4 stocks at Lag 3 yr and 4 stocks at Lag 4 yr).

A substantial proportion of stocks had significantly positive Ricker residuals autocorrelation, with the

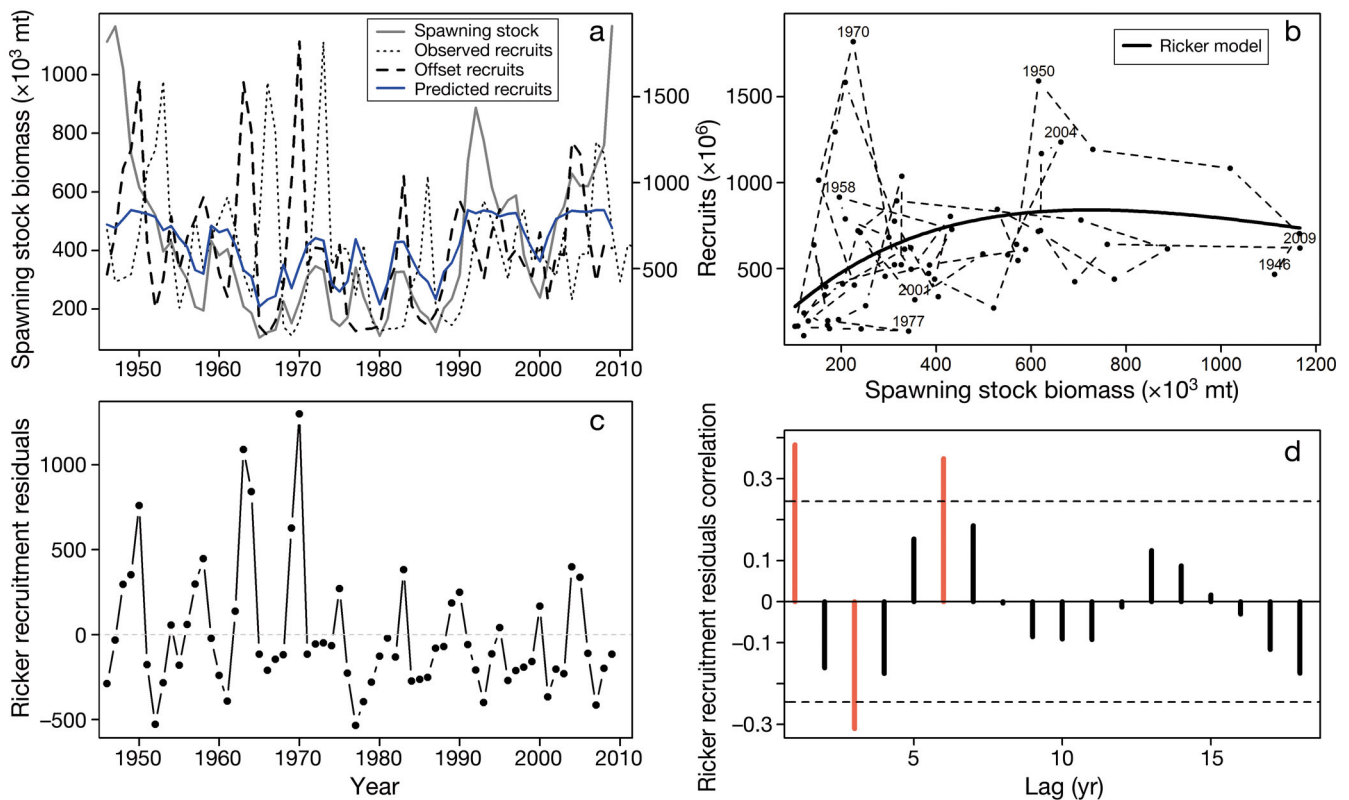


Fig. 1. Flow of the analysis illustrated for Northeast Arctic cod *Gadus morhua*. (a) Time-series of virtual population analysis (VPA)-derived spawning stock biomass and recruitment. Recruitment time-series offset by the age at recruitment (= 3 yr) and recruitment predicted by the fitted Ricker model are also shown. (b) Relationship between spawning stock biomass and offset recruitment. Fitted Ricker model also shown. (c) Recruitment residuals from the Ricker model. (d) Value of the autocorrelation function of the recruitment residuals at various lags. Significance level ( $p < 0.05$ ) identified by a dashed line; significant autocorrelations shown in red

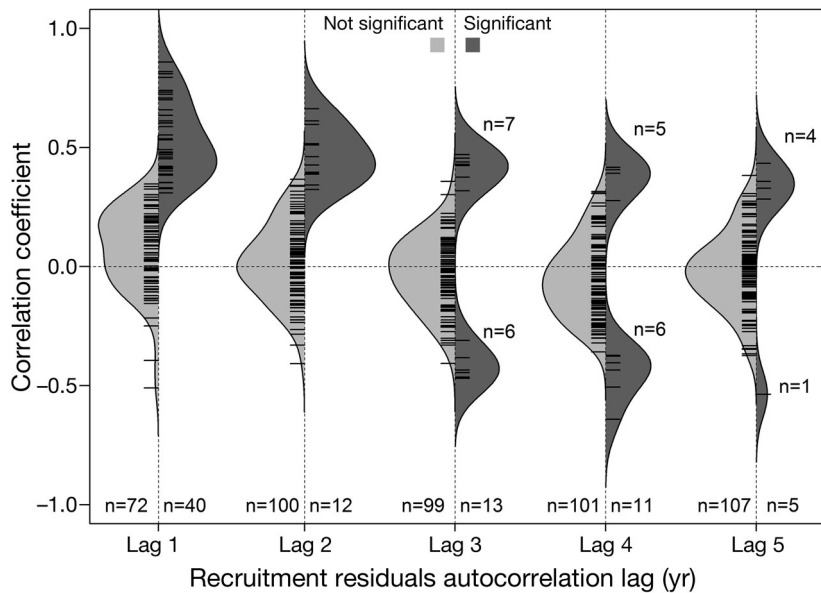


Fig. 2. Autocorrelation of recruitment residuals computed using fitted Ricker model. For each time lag for 1 to 5 yr, the value of the autocorrelation function for each available stock is shown as a thin horizontal bar; a Gaussian density kernel shows the overall distribution for both non-significant (light grey kernel, left) and significant ( $p < 0.05$ ; dark grey kernel, right) values. Number of non-significant and significant autocorrelations at each time lag appear at the bottom of plot

highest number of 40 stocks at Lag 1 and 12 stocks at Lag 2. Significantly positive autocorrelations decreased to 7, 5, and 4 at Lag 3, 4, and 5, respectively. For a total of 11 stocks, significantly positive autocorrelations were detected at 2 or more lags. Of those, cod in Subdivision 25–32 and Greenland halibut *Reinhardtius hippoglossoides* showed significantly positive autocorrelation over the whole range of 5 yr.

## DISCUSSION

Our results show that at all time lags the majority of autocorrelations in recruitment residuals were of moderate magnitude ( $|r| < 0.3$ ) and not significantly different from zero. The strongest positive correlations occurred at shortest time lags. Our results thus show that recruitment dynamics, after removing the effect of spawning stock, predominantly behave like white or red noise (Halley 1996).

Negative autocorrelation in recruitment residuals can indicate the existence of inter-cohort interactions and identify cases where cannibalism or competition is an important factor in explaining recruitment dynamics. Our results reveal only a relatively small fraction of cases showing significantly negative autocorrelations, thus suggesting that cannibalism and

intra-specific competition do not play a predominant role in the dynamics of most Atlantic fish stocks. Yet, negative intra-specific interactions can be important for recruitment dynamics for a handful of stocks. In particular, the gadoid species Atlantic cod, Argentine hake and whiting exhibited negative recruitment residuals autocorrelation at Lags 3 and 4. Additionally, one herring stock and one sole stock exhibited evidence of cannibalism and/or competition.

The largest proportion of significantly positive autocorrelations occurred at a lag of 1 yr (36%), followed by a lag of 2 yr (11%); no significantly negative autocorrelations were found at these lags. At lags of 3 and 4 yr, however, significantly negative and positive lags occurred at low but approximately equal frequencies (~5%). At a lag of 5 yr, few significant autocorrelations survive. This pattern is consistent with aging errors and environmental forcing being important drivers of the autocorrelation

pattern in recruitment: these factors are expected to shift autocorrelation in a positive direction but with a declining impact with increasing lag length. Most aging errors are small and therefore introduce positive bias at short time lags only (i.e. 1–2 yr). Positively auto-correlated environmental forcing will also cause a positive bias that is strongest at short time lags, although general predictions are difficult for how fast this bias should decline with increasing lag length.

We suggest that our results underestimate the occurrence of cannibalism and intra-specific competition. The weakness of our approach is that autocorrelation in recruitment residuals is influenced by many other mechanisms that can overshadow the effect of cannibalism. In particular, as discussed above, at short lags, the effects of aging errors and environmental forcing are likely to mask the effect of cannibalism, if present. There are also types of cannibalism, such as egg cannibalism by the adult stock, that are less likely to show up as negative recruitment residuals. For example, egg cannibalism is known to occur in Argentine anchovy *Engraulis anchoita*, but this did not show up in our analysis.

Detection of negative interactions becomes more likely at longer time lags when the effects of aging errors and environmental forcing are reduced. All

positive detections of negative autocorrelations in our analysis occurred at longer lags. However, another potential challenge is that cannibalism and competition that happen after recruitment age will not be visible in recruitment residuals, unless recruits are an important part of the spawning stock. Thus, when recruitment is estimated at a very early age, our approach may again miss negative intra-specific interactions.

Stock-recruitment data are typically very noisy and rarely show a clear relationship. This is substantiated in the present study by highly variable quality of fits, even though we were able to fit the Ricker model to all stock and recruitment time-series. Some stocks displayed high recruitment variability without any apparent pattern, whereas others showed long-term patterns that had no relationship with the spawning stock. Poor fits are caused by data uncertainty and the presence of stock-independent drivers of recruitment. Uncertainty in stock-recruitment models originates from general model uncertainty as well as measurement errors of data that are themselves estimated from stock assessment (Patterson et al. 2001, Haddon 2010, Brooks & Deroba 2015). Secondly, besides stock size and cannibalism, various ecological and environmental factors may determine recruitment and therefore generate stochasticity in the data (Fogarty et al. 1991). In Norwegian spring-spawning herring, for instance, larval and juvenile survival is determined by specific hydrographic conditions and drift patterns along the Norwegian coast into the Barents Sea and their spatio-temporal overlap with the distribution of prey as well as adult herring and several predator species, leading to high year class variability (Sætre et al. 2002, Vikebø et al. 2012, Skagseth et al. 2015). Consequently, cannibalism as one specific cause of density-dependent recruitment may be difficult to detect within the available time-series.

Cannibalism is facilitated by high stock sizes in combination with insufficient food availability from other sources. For demographically significant levels of cannibalism to occur, population density must be above a certain threshold and include sufficient demographic diversity as well as spatial overlap, so that recruits and older age classes as their predators have a high chance of encountering each other. Depleted and collapsed stocks are unlikely to exhibit significant levels of cannibalism, and consequently time-series including high stocks sizes are probably necessary to detect signals of cannibalism. A majority of the commercial stocks in the North Atlantic, however, has a history of low stock sizes and depletion

(Cook et al. 1997, Christensen et al. 2003, Hutchings 2005, Savenkoff et al. 2007), which could explain why negative autocorrelations were mostly weak or absent. This is illustrated by examples such as the 2 Baltic cod stocks, where empiric evidence from stomach contents suggests cannibalism rates of up to 25% of diet weight during periods of high abundance (Neuenfeldt & Köster 2000) while no negative autocorrelations were found in our analysis. Moreover, recruitment of the eastern Baltic stock is known to be strongly influenced by hydrographic conditions and egg predation by clupeids (Köster et al. 2009), which we expect to increase autocorrelations. Spatial or temporal separation between adults and juveniles through shifts in currents, migration pattern, or distribution in the water column can complement or enhance low abundance effects, as shown for example in walleye pollock *Theragra chalcogramma* (Wespestad et al. 2000) or Baltic cod (Uzars & Plikshs 2000), and lead to temporal fluctuations in cannibalism that obliterate clear negative autocorrelations.

Furthermore, the density of prey species may play a role in the occurrence of cannibalism similar to the role played by the density of the population itself. For instance, low capelin density leads to more cannibalism in Northeast Arctic cod (Hjermann et al. 2007), and vice-versa. Occurrence and intensity of cannibalism may therefore not only be subject to population density but also to temporal patterns in food availability as a result of food web dynamics. This is also reflected in the occurrence of significantly positive autocorrelations. Besides ageing errors, positive autocorrelation can be caused by periods with favourable environmental conditions (Fogarty et al. 1991) and positive feedback cycles between recruitment and spawning stock during periods of population growth (Rothschild & Jiao 2009). It remains therefore challenging to distil specific density-dependent mechanisms from recruitment data that are subject to various density-independent effects as well as anthropogenic and non-anthropogenic drivers of stock fluctuations.

A limitation of our analyses is that each stock is analysed independently of its environmental and ecological context. In particular the distinction between predation and cannibalism is not trivial and would be difficult to disentangle. Predation mortality is the key driver of survival in juvenile fish and thus the abundance and spatial distribution of other species which may be potential predators of recruits (Minto & Worm 2012). For instance, predation by adult herring decreases recruitment in Norway pout *Trisopterus esmarkii* when their distributions spa-



tially overlap (Huse et al. 2008). Similarly, presence and abundance of adult Atlantic mackerel *Scomber scombrus* and herring decreases survival of young life stages in blue whiting *Micromesistius poutassou* and Norwegian spring-spawning herring, and therefore, recruitment (Skjoldal 2004, ICES 2013b). Furthermore, predation mortality itself is often positively density-dependent (Bailey 1994, Jennings et al. 2009), which means that predation mortality intensifies with larger stock size the same way as cannibalism is expected to do. Because predation from other species tends to be equally or more important than cannibalism, this implies that dynamics between recruits and their predators will easily overshadow cannibalism in the data, making it difficult or impossible to isolate cannibalistic effects.

Cannibalism and intra-specific competition reduce the benefits from increased stock size and are therefore relevant for fisheries management. Over-compensatory density dependence through cannibalism and competition decreases overall production and subsequently sustainable yield. Ignoring the occurrence of cannibalism may thus lead to management targets that overestimate the benefits of higher stock sizes for yield and risk mitigation. Since the management and state of many North Atlantic stocks has substantially improved over recent years, cannibalism is becoming increasingly important for management advice. Our study provides a general method of detecting potential cannibalism and intra-specific competition based on negative autocorrelations between year classes from standard stock assessment data. The method is easy to apply, but conservative. It can reveal stocks where cannibalism or intra-specific competition is important, but not where it is unimportant.

Our findings indicate significant cannibalism or intra-specific competition in several gadoid stocks, confirming previous evidence for common cannibalism in these stocks and consequently the performance of our approach. Additionally, the results reveal that cannibalism or intra-specific competition may be also present in species such as herring and sole, suggesting a potential relevance for the management of these stocks. Furthermore, a high number of non-significant negative autocorrelations indicates that significant cannibalism potentially occurs in more stocks than found here. Longer time-series that include more data points from high stock sizes will help to improve the quality of results in the future.

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