

CAN WE DETECT THE EFFECTS OF ENVIRONMENTAL VARIATIONS ON FISH POPULATIONS THROUGH VPA OUTPUTS? THE NORTH ATLANTIC ALBACORE CASE

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SUMMARY

Past studies have indicated that numbers-at-age 1 of albacore may be correlated with the winter NAO index in the previous year. Two main hypotheses have been stressed to explain such observation, i.e. an impact of the NAO on the recruitment or on migration patterns and consequently in the availability and catchability of specific age classes to the surface fishery. The objective of the present paper is to test whether such processes can be distinguished using VPA outputs. We first computed simple cross-correlations between the NAO at various lags, catches-at-age, Numbers-at-age and F-at-age estimated in the last assessment. Since results were inconclusive, simulations were undertaken. The results showed that the probability of detecting spurious correlations between a given environmental variable, such as the NAO, and VPA outputs appears to be strongly related to the level of errors due to the observation process and modelling assumptions made within the assessment procedure. We concluded that correlations based solely on VPA outputs should be interpreted with great care.

RÉSUMÉ

Des travaux antérieurs ont montré que l'abondance d'albacore d'âge 1 était corrélée à l'indice hivernal du NAO de l'année précédente. Deux hypothèses ont été avancées pour expliquer ce résultat, i.e., un impact du NAO sur le recrutement ou sur les routes migratoires et donc sur la capturabilité des différents âges aux engins de surface. L'objectif de ce travail est de voir si on peut distinguer ces deux types de processus. Nous avons tout d'abord calculé des corrélations croisées entre les abondances, captures et F aux différents âges avec le NAO, en considérant différents décalages, mais les résultats se sont avérés non concluants. Aussi, des simulations ont été entreprises. Les résultats montrent que la probabilité d'obtenir des corrélations spacieuses entre une variable environnementale, telle que la NAO, et des sorties de VPA est étroitement liée au niveau d'erreurs qui résultent du processus d'observation et des hypothèses faites dans les différents modèles utilisés pour la procédure d'évaluation. Nous concluons que les résultats des corrélations obtenus seulement sur des sorties de VPA doivent être en conséquence interprétés avec beaucoup de prudence.

RESUMEN

Estudios previos mostraron que la abundancia de atún blanco de edad 1 en un año dado podría estar correlacionada con el índice NAO invernal del año anterior. Se postularon dos hipótesis para explicar dicha observación: que la NAO influya sobre el reclutamiento o sobre los patrones de migración y por tanto la disponibilidad y capturabilidad de determinadas clases de edad en la pesquería de superficie. El objetivo del presente trabajo es ver si dichos procesos pueden ser distinguidos utilizando outputs del VPA. Primeramente se calculan las correlaciones cruzadas entre la NAO con varios lags temporales y la captura por edad, la abundancia por edad y la mortalidad por pesca por edad estimadas en la última evaluación. Los resultados resultaron poco concluyentes, por lo que se realizaron varias simulaciones. Los resultados mostraron que la probabilidad de detectar correlaciones espurias entre una variable ambiental como la NAO y los outputs del VPA está claramente relacionada con el nivel de error proveniente de los procesos de observación y de

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las asunciones realizadas en la evaluación. Concluimos que las correlaciones basadas solamente en outputs del VPA deben ser interpretadas con suma precaución.

KEYWORDS

Thunnus alalunga, North Atlantic Oscillation, simulation model, virtual population analysis, correlation coefficient, NAO

1. Introduction

The North Atlantic Oscillation (NAO) index measures the difference in normalised sea level pressures between the subtropical high pressures, centred on the Azores, and the sub-polar low surface pressures, centred on Iceland (Hurrell 1995). The speed and direction of the Westerlies across the North-Atlantic as well as temperatures on both sides of this ocean are correlated with the pressure difference between the Azores and Iceland. A positive NAO index is associated with a strong wind circulation in the North Atlantic, high temperatures in the western Europe and low temperatures in the East coast of Canada and *vice versa* Climatic oscillations as reflected by this dipole is known to impact ecological dynamics in both marine and terrestrial systems (see Ottersen *et al.* 2001 for a review).

Regarding albacore, estimated numbers-at-age 1 have been shown to be correlated with the winter NAO index in the previous year (**Figure 2**, ICCAT 2002). Two main hypotheses have been postulated to explain such observation (Bard and Santiago 1999, Bard 2001; Ortiz de Zárate *et al.* 1998)), i.e. impact of the NAO on: (1) the recruitment or (2) migration patterns and consequently, the availability and catchability of specific age classes to the surface fishery (**Figure 1**).

The objective of the present paper is to test whether such processes can be distinguished through Virtual Population Analysis (VPA) outputs. To do so, we first computed cross-correlations between catches, VPA estimates of numbers and fishing mortality-at-age and the NAO index. Then, we used a simulation framework (Kell *et al.* 2003) to model populations affected by the environment and their assessment, in order to confront observed and simulated results.

2. Results of cross-correlations

As expected under the recruitment hypothesis, cross-correlations between catches-at-age 1 and fishing mortality-at-age 1 and the NAO index with lag 1 (i.e., 1 year delayed) are high (**Table 1**). However, the relationship is not as clear when considering cross-correlations between numbers-at-age 1 and the NAO index. As expected under the migration/catchability hypothesis, strong correlations between N at ages 4 and 7 with the NAO with a lag of 0 can be detected. However, other strong cross-correlations are also observed. For example, there is an apparent cohort relationship between numbers-at-age 4 and the NAO at lag 0 up to numbers-at-age 7 and NAO at lag 3. There are also high correlations between catch-at-age 5 to 7 and the NAO at lag 3. These correlations remain difficult to explain under both hypotheses and could be simply spurious. Therefore a simulated framework was used to generate catch and CPUE data under the recruitment or catchability hypotheses. A VPA was then performed upon these data and the cross-correlations recomputed to see whether environmental signals could be detected.

3. Simulated model

Both the albacore population and the fishery upon it was simulated and catch and effort data generated for use in a calibrated VPA (equations and symbols used are given in the **Appendix**, see also Kell *et al.* 2003). Three scenarios corresponding to alternative hypotheses about how environmental processes act upon albacore biology were investigated:

- H₁: NAO affects recruitment
- H₂: NAO affects catchability of 1 and 4 year olds
- H₃: NAO affects catchability of 5 to 8 year olds.

Where, either recruitment (H_1), catchability at age 1 to 4 (H_2) or catchability at ages 5 to 8 (H_3) were correlated with the NAO ($R^2 = 0.5$). Otherwise uncertainty in recruitment and catchability was random, modelled by selecting from the recruitment or catchability residuals at random with replacement.

For each scenario (H_1 , H_2 , H_3) 5000 catch-at-age matrices and CPUE series were generated including due to sampling (log normal with a CV = 30%). VPA was then used to estimate population parameters and the cross-correlations recomputed. **Table 2** presents the median of the 5000 cross-correlations for each scenario, whereas **Table 3** presents the probability of getting a correlation > 0.25 for each scenario.

4. Results from the simulated data sets

- As expected under H_1 , higher correlations are found between the numbers-at-age 1 and 2 or the catch at age 2 and the NAO with a lag 1 and 2. However, these correlations are weaker than expected (considering solely a 50% of errors) and are not found when considering catch-at-age 1 and F.
- As expected under H_2 and H_3 , higher correlations between F and catch for specific ages and NAO with lag 0 can be detected, but without any cohort effects. However, there are no high correlations between N and NAO with lag 0, probably because of the algorithm of the VPA in which errors are cumulated for N but not for F.

Comparing this table to the original one (**Table 1**), one may see that we got a greater number of high correlations in **Table 1** than expected or found in **Table 2**, so that it is difficult to explain all the observed correlations in **Table 1**. We therefore looked at the probability of obtaining high correlations by calculating the number of times where a correlation was > 0.25 among the 5000 trials (**Table 3**):

- For H_1 , the picture resembles this of the **Table 2**, with the higher correlations between the numbers-at-age 1, 2 (and 3) or the catch at age 2 (and 3) and the NAO with a lag 1 and 2, but nothing appears clearly on the F matrix. However, the cohort effect is here more visible and the probability of obtaining spurious correlations is also large, especially for N and F at the older ages.
- For H_2 and H_3 , the same conclusion can be drawn. Expected correlations are found with the F and catch-at-age matrices, but not with the N matrices. Here also, spurious correlations can be easily detected for older ages within the 3 matrices (except for catch at age under H_2).

Short-time series (30 yrs), observation errors and autocorrelation in the NAO time series increase the probability of spurious correlations

5. Conclusion

The probability of detecting spurious correlations between a given environmental variable, such as the NAO, and VPA outputs appears to be strongly related to the level of error in the stock assessment, due to both the observations and assumptions made within the assessment procedure. VPA assumes that catch-at-age and natural mortality are known without error and that the data corresponds to a discrete stock. However in general, data used in VPA suffer from moderate to large observation errors (due to non random sampling strategies, approximations in length and age procedures etc.). Thus correlations based solely on VPA outputs may not be conclusive.

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Table 1. Cross correlations from VPA and catch data (ICCAT database) and NAO.

		<i>VPA Numbers-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lags	0	-0.03	-0.29	0.18	0.65	-0.08	-0.09	0.43	0.04
	1	-0.29	-0.10	-0.19	0.13	0.54	0.01	-0.05	0.31
	2	-0.05	-0.17	-0.17	0.07	0.01	0.42	-0.08	-0.16
	3	0.20	-0.01	-0.23	-0.25	0.06	0.02	0.43	-0.21
	4	0.05	0.26	0.00	-0.40	-0.12	-0.10	-0.19	0.14
	5	0.18	0.16	0.03	-0.06	-0.22	-0.11	-0.08	-0.12

		<i>VPA Fishing Mortality-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lags	0	0.09	0.06	0.15	-0.08	0.00	0.17	-0.10	-0.10
	1	-0.39	0.42	-0.21	0.02	-0.06	0.15	0.50	0.50
	2	0.10	0.01	-0.21	-0.06	0.45	-0.14	0.19	0.19
	3	0.00	-0.02	0.26	0.27	0.42	0.61	0.02	0.02
	4	-0.31	0.09	0.06	0.05	-0.03	-0.01	0.17	0.17
	5	0.26	0.08	0.13	-0.12	0.06	-0.06	-0.14	-0.14

		<i>Catch-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lags	0	0.11	-0.31	0.23	0.26	-0.08	0.12	0.26	-0.16
	1	-0.45	0.17	-0.28	0.08	0.29	0.22	0.40	0.56
	2	0.00	-0.13	-0.30	0.07	0.29	0.27	0.03	0.05
	3	0.05	-0.06	-0.05	0.29	0.42	0.55	0.54	0.07
	4	-0.29	0.36	0.04	-0.03	-0.02	-0.08	-0.19	0.39
	5	0.37	0.22	0.13	-0.05	-0.03	-0.09	-0.31	-0.24

Table 2. Cross correlations (Median value over the 5000 trials) from the simulated data sets according to hypotheses H_1 , H_2 and H_3 .

Numbers-at-age 1 correlated with NAO

		<i>VPA Numbers-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	-0.10	-0.01	0.10	0.13	0.01	0.00	0.01	-0.08
	1	-0.30	-0.10	0.00	0.06	0.10	0.01	0.02	-0.03
	2	0.04	-0.28	-0.06	-0.02	0.06	0.09	0.01	0.00
	3	0.14	0.03	-0.19	-0.08	-0.01	0.07	0.06	0.05
	4	0.04	0.05	-0.03	-0.11	-0.03	-0.01	0.02	0.11
	5	0.16	0.06	0.04	-0.04	-0.10	-0.02	0.00	0.11

		<i>VPA Fishing Mortality-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.18	0.14	0.10	0.14	0.17	0.16	0.16	0.16
	1	0.12	0.12	0.16	0.10	0.12	0.15	0.09	0.09
	2	0.12	0.03	0.18	0.15	0.09	0.09	0.05	0.05
	3	0.08	0.03	0.12	0.18	0.11	0.07	0.03	0.03
	4	0.12	0.10	0.15	0.13	0.10	0.12	0.10	0.10
	5	0.10	0.11	0.12	0.14	0.14	0.14	0.15	0.15

		<i>Catch-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	-0.03	0.01	0.07	0.10	0.05	0.03	0.00	-0.05
	1	-0.14	-0.08	0.06	0.03	0.07	0.01	0.01	-0.04
	2	0.01	-0.32	0.01	0.04	0.00	0.03	-0.06	-0.08
	3	0.06	-0.08	-0.21	-0.01	-0.03	-0.03	-0.01	-0.05
	4	0.01	0.03	-0.01	-0.11	-0.06	0.00	0.00	0.03
	5	0.05	0.03	0.03	-0.03	-0.08	-0.01	0.01	0.09

Catchability-at-ages 1 to 4 correlated with NAO

		<i>VPA Numbers-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	-0.01	-0.01	0.04	0.01	0.02	0.04	0.03	-0.02
	1	-0.01	-0.12	-0.14	-0.12	-0.07	0.02	0.04	0.03
	2	0.05	-0.04	-0.06	-0.10	-0.09	-0.05	0.03	0.06
	3	0.08	0.03	-0.02	-0.01	-0.08	-0.06	-0.03	0.09
	4	-0.02	0.01	0.03	0.02	-0.01	-0.07	-0.07	0.05
	5	-0.01	0.05	0.11	0.11	0.07	-0.02	-0.06	-0.01

		<i>VPA Fishing Mortality-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.67	0.46	0.44	0.49	0.16	0.16	0.16	0.16
	1	0.23	0.08	0.15	0.13	0.13	0.13	0.09	0.09
	2	0.03	0.07	0.09	0.05	0.10	0.11	0.04	0.04
	3	-0.07	-0.05	0.10	0.02	0.10	0.09	0.04	0.04
	4	-0.19	-0.14	-0.07	-0.11	0.12	0.11	0.07	0.07
	5	0.03	0.11	0.09	0.11	0.15	0.11	0.16	0.16

		<i>Catch-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.56	0.28	0.32	0.42	0.06	0.05	0.04	0.01
	1	0.11	-0.12	-0.12	-0.11	-0.07	0.01	0.01	-0.02
	2	-0.03	-0.08	-0.10	-0.16	-0.12	-0.07	-0.05	-0.04
	3	-0.10	-0.10	-0.03	-0.16	-0.10	-0.09	-0.12	-0.04
	4	-0.28	-0.20	-0.13	-0.21	-0.04	-0.07	-0.11	-0.01
	5	-0.05	0.03	0.10	0.12	0.07	-0.01	-0.04	0.02

Catchability-at-ages 5 to 8 correlated with NAO

		<i>VPA Numbers-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	-0.04	-0.01	0.04	0.03	0.04	-0.02	-0.02	0.03
	1	0.00	-0.03	0.00	0.00	0.02	-0.06	-0.14	-0.21
	2	0.06	-0.03	-0.04	-0.03	0.00	0.03	-0.07	-0.25
	3	0.06	0.03	-0.04	-0.05	-0.02	0.01	0.04	-0.10
	4	-0.03	0.00	0.02	-0.01	-0.03	0.00	0.02	0.01
	5	-0.01	0.00	0.00	0.01	-0.01	0.03	0.08	0.17

		<i>VPA Fishing Mortality-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.18	0.13	0.15	0.13	0.58	0.57	0.63	0.63
	1	0.17	0.15	0.19	0.16	0.15	0.17	0.18	0.18
	2	0.15	0.15	0.19	0.17	0.04	0.02	-0.07	-0.07
	3	0.10	0.09	0.20	0.18	0.00	-0.01	-0.14	-0.14
	4	0.13	0.11	0.13	0.14	-0.14	-0.18	-0.26	-0.26
	5	0.09	0.12	0.14	0.13	0.11	0.10	0.07	0.07

		<i>Catch-at-Age</i>							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.02	-0.01	0.05	0.03	0.45	0.45	0.30	0.45
	1	0.03	-0.02	0.05	0.03	0.06	0.00	-0.13	-0.12
	2	0.05	-0.03	0.05	0.03	-0.07	-0.06	-0.20	-0.31
	3	0.03	-0.02	0.01	0.01	-0.14	-0.14	-0.13	-0.31
	4	0.02	-0.01	0.00	0.00	-0.25	-0.26	-0.19	-0.27
	5	-0.02	-0.01	0.01	-0.01	-0.03	0.02	0.08	0.09

Table 3. Probabilities of getting an R value > 0.25 or < -0.25 over the 5000 trials. The intention is to show the probability of getting spurious correlations.

Numbers-at-age 1 correlated with NAO

		VPA Numbers-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.24	0.17	0.25	0.31	0.21	0.21	0.23	0.31
NAO Lag	1	0.61	0.22	0.15	0.22	0.28	0.21	0.23	0.31
NAO Lag	2	0.23	0.57	0.18	0.14	0.21	0.27	0.21	0.32
NAO Lag	3	0.34	0.24	0.39	0.23	0.18	0.23	0.25	0.32
NAO Lag	4	0.14	0.16	0.17	0.26	0.17	0.18	0.18	0.32
NAO Lag	5	0.28	0.16	0.18	0.16	0.24	0.17	0.16	0.35

		VPA Fishing Mortality-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.19	0.18	0.20	0.23	0.20	0.20	0.27	0.27
NAO Lag	1	0.19	0.18	0.20	0.20	0.21	0.21	0.24	0.24
NAO Lag	2	0.24	0.27	0.21	0.19	0.20	0.18	0.28	0.28
NAO Lag	3	0.22	0.27	0.20	0.22	0.19	0.22	0.30	0.30
NAO Lag	4	0.14	0.16	0.18	0.18	0.18	0.16	0.23	0.23
NAO Lag	5	0.17	0.16	0.18	0.18	0.17	0.19	0.18	0.18

		Catch-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.21	0.19	0.21	0.24	0.23	0.24	0.19	0.23
NAO Lag	1	0.30	0.22	0.22	0.20	0.23	0.22	0.19	0.21
NAO Lag	2	0.21	0.67	0.18	0.20	0.18	0.19	0.22	0.21
NAO Lag	3	0.27	0.23	0.42	0.21	0.18	0.22	0.21	0.22
NAO Lag	4	0.15	0.13	0.16	0.24	0.20	0.18	0.19	0.17
NAO Lag	5	0.19	0.15	0.16	0.18	0.22	0.16	0.16	0.21

Catchability-at-ages 1 to 4 correlated with NAO

		VPA Numbers-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.19	0.20	0.21	0.24	0.22	0.22	0.22	0.30
NAO Lag	1	0.17	0.25	0.28	0.25	0.25	0.19	0.20	0.33
NAO Lag	2	0.28	0.19	0.18	0.21	0.22	0.22	0.19	0.33
NAO Lag	3	0.29	0.26	0.19	0.19	0.20	0.20	0.23	0.33
NAO Lag	4	0.15	0.15	0.18	0.17	0.20	0.19	0.19	0.27
NAO Lag	5	0.12	0.18	0.23	0.24	0.19	0.19	0.17	0.27

		VPA Fishing Mortality-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.99	0.76	0.65	0.75	0.20	0.21	0.26	0.26
NAO Lag	1	0.21	0.15	0.16	0.16	0.20	0.20	0.23	0.23
NAO Lag	2	0.16	0.21	0.20	0.16	0.20	0.19	0.29	0.29
NAO Lag	3	0.32	0.34	0.20	0.25	0.19	0.22	0.29	0.29
NAO Lag	4	0.58	0.50	0.36	0.42	0.18	0.16	0.21	0.21
NAO Lag	5	0.10	0.13	0.17	0.15	0.20	0.17	0.20	0.20

		Catch-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.97	0.56	0.65	0.63	0.22	0.24	0.21	0.18
NAO Lag	1	0.21	0.27	0.26	0.22	0.22	0.19	0.19	0.21
NAO Lag	2	0.14	0.22	0.19	0.31	0.26	0.22	0.19	0.21
NAO Lag	3	0.24	0.29	0.19	0.31	0.25	0.25	0.30	0.22
NAO Lag	4	0.57	0.37	0.26	0.40	0.14	0.20	0.23	0.18
NAO Lag	5	0.13	0.15	0.21	0.22	0.21	0.16	0.18	0.18

Catchability-at-ages 5 to 8 correlated with NAO

		VPA Numbers-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.19	0.19	0.24	0.27	0.23	0.23	0.22	0.30
NAO Lag	1	0.19	0.17	0.18	0.22	0.24	0.24	0.31	0.45
NAO Lag	2	0.26	0.19	0.18	0.19	0.21	0.24	0.24	0.51
NAO Lag	3	0.27	0.24	0.25	0.22	0.21	0.24	0.23	0.37
NAO Lag	4	0.18	0.15	0.17	0.18	0.18	0.16	0.19	0.25
NAO Lag	5	0.13	0.16	0.15	0.17	0.17	0.19	0.21	0.38

		VPA Fishing Mortality-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.22	0.23	0.25	0.23	0.88	0.91	0.96	0.96
NAO Lag	1	0.22	0.21	0.22	0.20	0.15	0.16	0.20	0.20
NAO Lag	2	0.23	0.23	0.22	0.21	0.14	0.14	0.36	0.36
NAO Lag	3	0.19	0.24	0.23	0.24	0.26	0.25	0.50	0.50
NAO Lag	4	0.17	0.16	0.15	0.16	0.53	0.58	0.76	0.76
NAO Lag	5	0.20	0.18	0.16	0.18	0.16	0.16	0.16	0.16

		Catch-at-Age							
		1	2	3	4	5	6	7	8
NAO Lag	0	0.23	0.25	0.22	0.24	0.87	0.89	0.63	0.88
NAO Lag	1	0.24	0.20	0.22	0.20	0.16	0.14	0.26	0.18
NAO Lag	2	0.25	0.21	0.21	0.20	0.13	0.15	0.39	0.63
NAO Lag	3	0.24	0.22	0.21	0.22	0.27	0.27	0.27	0.64
NAO Lag	4	0.17	0.16	0.16	0.18	0.51	0.54	0.35	0.55
NAO Lag	5	0.19	0.17	0.18	0.15	0.14	0.13	0.18	0.17

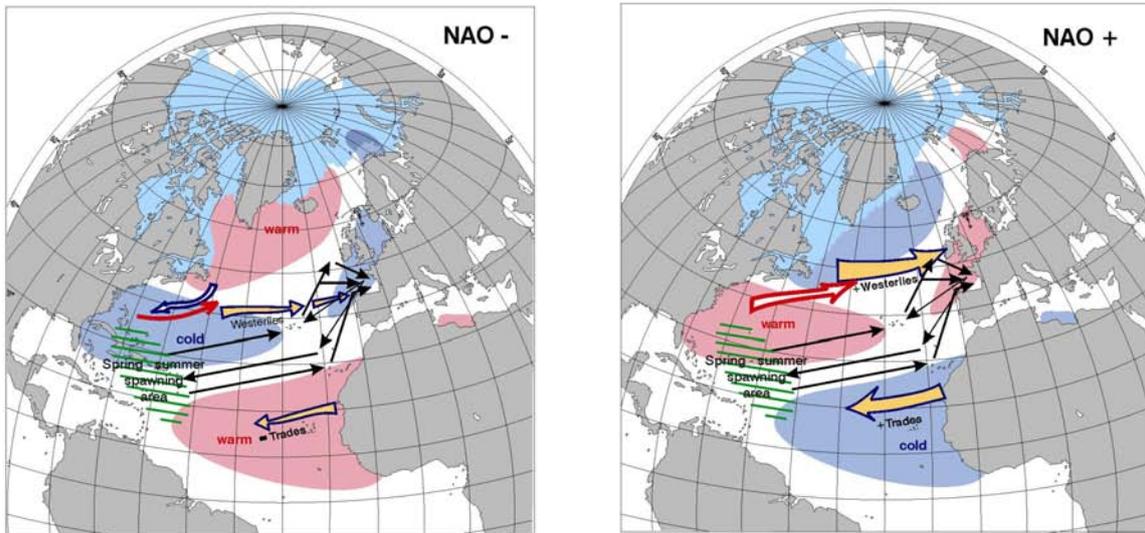


Figure 1. The Migratory behaviour of North Atlantic Albacore and the changes in large scale atmospheric and oceanographic factors associated with the negative and positive phases of the North Atlantic Oscillation (NAO), from Dickson (1997). The figure summarises wind circulation and temperatures in the in the North Atlantic and compares these to spawning and migratory behaviour.

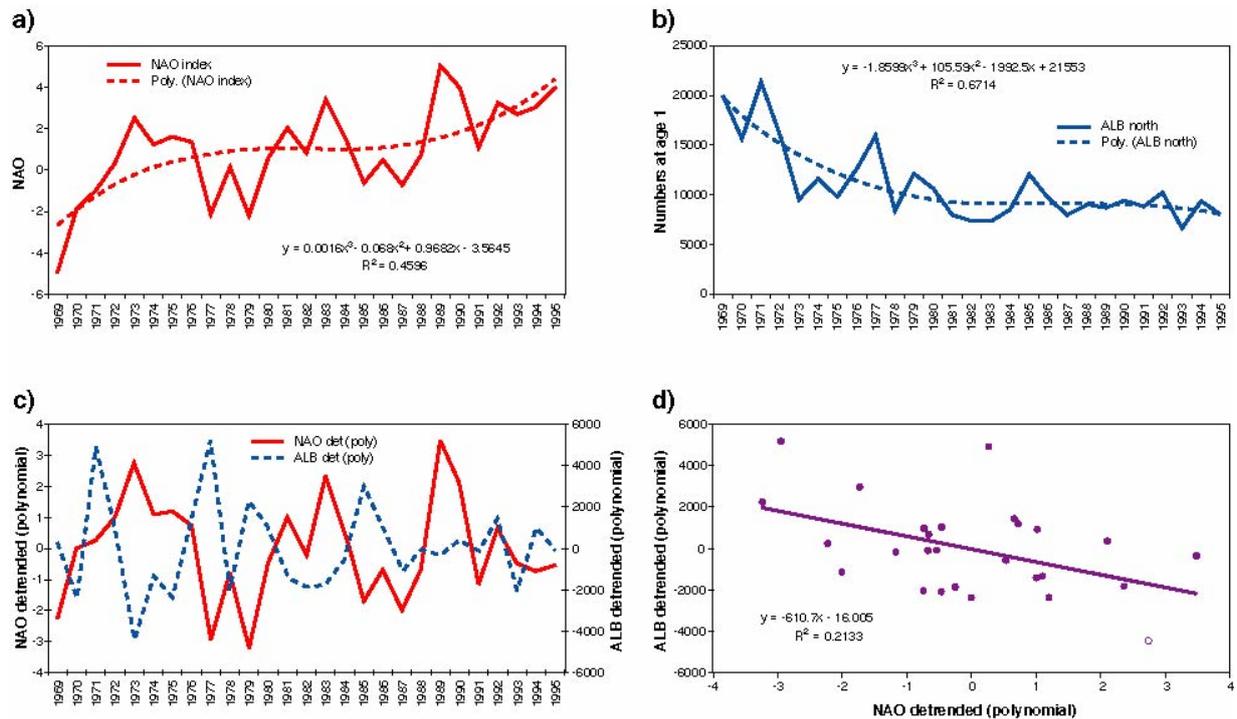


Figure 2. Correlation between North Atlantic Albacore numbers-at-age 1 and the winter NAO index. a: NAO and fitted trend. b: numbers-at-age 1 and fitted trend. c: detrended series of NAO and numbers-at-age 1. d: relationship between detrended series. From (ICCAT 2002).

Model Formulation

Equations used in simulation model

Population dynamics	$N_{a+1,y+1} = N_{a,y} e^{Z_{a,y}}$	1.
	$N_{p,y+1} = N_{p-1,y-1} e^{Z_{p-1,y-1}} + N_{p,y} e^{Z_{p,y}}$	2.
	$N_{r,y} = f(B_{y-r}) e^{\varepsilon}$	3.
Mortality rates	$Z_{a,y} = M_{a,y} + F_{a,y}$	4.
	$F_{a,y} = \sum_{i=1}^f S_{i,a,y} E_{i,y}$	5.
Catch equation	$C_{f,a,y} = N_{a,y} + \frac{F_{f,a,y}}{Z_{a,y}} (1 - e^{-Z_{a,y}})$	6.
Stock recruitment relationship Beverton and Holt	$N_{r,y} = \frac{B_{y-r}}{\alpha B_{y-r} + \beta}$	7.
Catch per unit effort	$U_{f,a,y} = q_{f,a,y} N_{a,y}$	8.
Yield	$Y_{f,y} = \sum_{i=r}^p C_{f,i,y} W_{f,i,y}$	9.
SSB	$B_y = \sum_{i=r}^p N_{i,y} W_{i,y} O_{i,y}$	10.

Symbols used in simulation model

INDICES

A	Age
Y	Year
F	Fleet
R	Recruit age
P	Plus group age

VARIABLES

N	Numbers-at-age
C	Catch-at-age
F	Fishing mortality-at-age
M	Natural mortality-at-age
Z	Total mortality-at-age
S	Selection-at-age
W	Weight-at-age
O	Proportion mature-at-age
E	Scaled effort
B	Spawning stock biomass
Y	Yield

PARAMETERS

α	Stock recruit parameter
β	Stock recruit parameter
ε	Recruitment residual
η	Selection-at-age residual

CORRELATION WITH NAO

Correlations were non-parametric, that is for a Spearman correlation of 1.0, residuals were ordered so the residual in a particular year fell in the same percentile as the NAO anomaly.

Noise was added by selecting at random with replacement from the original residuals i.e.

$$\varepsilon_y^* = \lambda \zeta_y + (1 - \lambda) \zeta^*$$

where ε_y^* is the residual used in the simulation

ζ_y is the residual from the same percentile as the NAO anomaly in year y

ζ^* is a residual randomly selected with replacement from the original residuals

and

λ is a weighting factor between 0.0 and 1.0; 0.0 gives no correlation and 1.0 perfect correlation with the NAO.