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An unintended experiment in fisheries science: a war mediated protected area in the North Sea results in Mexican waves in fish numbers-at-age

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Abstract

Marine protected areas (MPAs) will attain increasing importance in the management of marine ecosystems. They are effective for conservation in tropical and sub-tropical areas (mainly coral and rocky reefs) but it is debated whether they are useful in the management of migratory fish stocks in open temperate regions. World War II created a large marine area within which commercial fishing was prevented for six years. Here we analyse scientific trawl data for three important North Sea gadoids, collected between 1928 and 1958, and show the potential of MPAs for expediting the recovery of over-exploited fisheries in open temperate regions. Age-structured data and population models suggest that wild fish stocks will respond rapidly and positively to reductions in harvesting rates; and that the numbers of older fish in a population will react before, and in much greater proportion, than their younger counterparts in a kind of Mexican wave. The analyses demonstrate both the overall increase in survival due to the lack of harvesting in the War, and the form of the age-dependent wave in numbers. We conclude that large closed areas are useful in the conservation of migratory species from temperate areas, that older fish benefit fastest and in greater proportion, and, importantly, that a rise in spawning stock biomass may not immediately result in better recruitment, which might take longer to occur and to feed through to higher future harvestable biomass levels.

Introduction

In 1939 the North Sea was almost entirely closed to commercial fishing until 1945 due to the outbreak of World War II (WWII). Fishing vessel movements were severely restricted because of the dangers of mines, surface and submarine naval activity and potential aerial attacks, and many fishing vessels were sunk in the hostilities. Fishermen were called up, especially those at prime age, and most fishing vessels, including the most modern trawlers, were requisitioned for war service; in particular for deployment as mine sweepers (Beverton and Holt 1957; Gulland 1968; Hannesson 2007; Engelhard 2008). Thus fishing effort in the North Sea was very significantly reduced; for example, effort by British steam trawlers, the dominant fishing fleet at the time, fell by 97% between 1938 and 1941 [Note: there were 2 million hours fishing in 1938, see (Engelhard 2005)]. The War thus created, at 575,000 km^2, an extensive, 'accidental' marine protected area (MPA); or arguably a six-year temporary closure to fisheries. In comparison the world's largest network of no-take marine reserves on Australia's Great Barrier Reef covers a mere 115,000 km^2 (Russ, et al. 2008).

The effects of WWII on fish population dynamics have hardly been researched in recent years, in spite of the availability of data and their potential utility for addressing key problems in fisheries management. Although war-mediated effects on plaice *Pleuronectes platessa* populations in the southern North Sea have been examined (Graham 1949; Wimpenny 1953; Beverton and Holt 1957) only a few authors have explored such effects on the commercially important gadoid species in the northern North Sea, and no detailed information exists on changes in age-structure that occurred when fishing mortality ceased (Margetts and Holt 1948; Parrish 1948). Studies on the effects of WWII may, however, help to place in context the substantial population fluctuations that North Sea gadoids showed in the immediate post-war decades, including the 'Gadoid Outburst' of the 1960s–1980s (a period of especially favourable recruitment and high landings of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*) and the sharp population declines of these species thereafter (Hislop 1996; Bannister 2004).

MPAs have also become a major focus in fisheries management and marine ecology (Halpern and Warner

2003; Russ et al., 2008; White et al., 2008). The European Union is a signatory of the Johannesburg Declaration on sustainable development which calls for a network of MPAs to be established by 2012 (United Nations 2002). Of those MPAs that have been scientifically monitored, and shown to be effective, most are in the (sub-) tropics (mainly coral and rocky reefs) or in kelp forests: i.e. they are almost exclusively inshore. One reason often cited for the success of MPAs in lower latitudes is that their fish populations tend to live out their lives in more clearly defined habitats. In open, temperate marine regions where dispersal potential and gene flow in fish are higher there remains much debate over whether MPAs will be effective measures for conservation at all (Hilborn, et al., 2004; Worm et al.,, 2006; Blythe-Skyrme et al.,. 2006; Laurel and Bradbury 2006; Hölker et al., 2007) and it has been suggested that gadoid stocks typically fail to recover after population declines and moratoria on fishing activities (Hutchings 2000). There is, however, little quantitative information on how fish populations in temperate seas actually respond to the implementation of MPAs. The aim of this paper is to expose, quantitatively, the response of three fish populations to a temporary (six year) cessation in harvesting using fishery independent data. This is done with a simple statistical summary of trawl survey data analysed in the context of the available commercial data, a population model, and relevant environmental data.

Total instantaneous mortality (Z) on a fish population is the sum of fishing (F) and natural (M) mortality (Beverton and Holt 1957). Thus, the war-mediated MPA 'experiment' allows us to examine changes from an F + M state to an M state and back again to an F+M state. First principles suggest that a reduction in F: (a) cannot cause an immediate increase in recruitment, i.e. there may have to be a lag before increases in the numbers of sexually mature adults can feed forward into increased numbers of recruits (see theoretical age-structured population model described in S1); (b) will lead to an increase in the numbers of older fish in the population; and (c) will result in an age-dependent wave, the timing and magnitude of the response by each age-class following each other successively in a cascade. This phenomenon is comparable to '*Mexican waves'* which surge through rows of spectators at a football stadium (Farkas et al. 2002). These expectations were supported by the actual data available.

Material and Methods

Scientific trawl survey data in the form of length-frequencies and age-length keys were made available by Marine Science Scotland, Aberdeen for the entire northern North Sea, spanning the period between March 1925 and December 2007. After detailed examination of the data we opted to consider only area 'Buchan' (Figure 1) for the period between 1928 and 1958. Buchan was selected because there was consistent spatial coverage over time. The period 1928 to 1958 was chosen because it spanned the war, and because the research vessels and gears used to collect the data were consistent. The area is possibly also sufficiently small to be comparable to a realistic marine protected area in future. Numbers-at-age matrices for cod, haddock, and whiting were constructed from survey age-length keys and length-frequencies (see S2,S3, and S4 for data). These data were log-transformed and changes in age structures over time summarized using the following series of regression models:

1.) $ln(cpue) = 1$
2.) $ln(cpue) = year$
3.) $ln(cpue) = year + age$
4.) $ln(cpue) = smooth(year) + age$
5.) $ln(cpue) = smooth(year) * age$

Analyses of variance tests between these successively more complex, nested, models enabled us to find the 'best' model. In all cases model 5 was chosen as both the best statistically, and the most sensible scientifically, since it allows the abundance of each age group to change both non-linearly (smoothly) and independently with year. That is to say significant interactions between year and age mean that the shapes or trends of the modeled lines can be different for each age group.

Commercial data were obtained (or extracted) from hand-drawn maps and charts supplied by Cefas, Lowestoft, England (Engelhard 2005). Total landings, total numbers of hours fished by the commercial steam trawler fleet, and hence catch per unit effort were made available by year and ICES statistical rectangle.

Results

Stock dynamics

In haddock the abundance of all age groups fell steadily in the population between 1928 and 1939. The gradients of this decline, however, get flatter as age increases (Figure 2). Between 1939 and 1945 all age groups, except the age 0s (recruits), experienced a step-wise increase in abundance. In the younger fish (ages 2 and 3) this increase continued until the end of the series in 1958. Abundances of older fish (e.g. ages 4 to 8) dipped between 1947 and 1950, after when they again began to increase. It is interesting to note the similarities in time trend between the trawl survey numbers-per-unit-effort (Figure 2) and the commercial landings-per-unit-effort (Figure 3) data where the older fish from the trawl survey mirror the U-shaped pattern seen in the commercial data. In cod (see S5) there was a peak in abundance in 1935 followed by a dip into the war period and a strong recovery between 1939 and 1945. After the war when fishing recommenced, abundances fell just like haddock with the trough occurring in the early 1950s. Unlike haddock, recruitment (age 0s) in cod also increased during the war, although this appears to have been part of an overall long-term decline (1928-1958). The commercial data for cod show rising landings per unit effort between 1928 and 1938, an abrupt increase in 1947, followed by a fall and then recovery (see Figure 3). The trawl survey data for whiting (see S6) have parallel time-trends for ages 3-9: there is a peak in the early 1930s followed by abrupt increases between 1939 and 1945. After the war, increased fishing effort again caused a fall, followed by rising abundance into the late 1950s. Recruitment in whiting (age 0s) also appeared to 'dip' into the early part of the war period and increased thereafter. The commercial data (see Figure 3) suggest overall rising abundance between 1928 and 1958.

Consider the cohort trajectories (1928 to 1958) from the modeled indices from Buchan for the three gadoids plotted in Figures 4a, 4b, and 4c. The change in gradients between the pre, post and WWII periods has been extracted from linear models fitted to each cohort and plotted in Figure 5. The gradients of these lines represent a measure total mortality (Z). A component of Z is due to mortality by fishing (F) and another unknown component is due to mortality by predation and disease (natural mortality, M). Estimates of Z (see Figure 5) peaked for all species during the period immediately before WWII, mirroring the change in fishing effort (see Figure 3). The effect of the cessation of fishing during WWII was dramatic, with sharp increases in the rate of decline in total mortality (Z) being observed in all three of the gadoids examined. Lowest mortalities were observed in 1942 (haddock), 1944 (cod) and 1945 (whiting), after when Z began to rise again as fishing re-commenced in the post-war period. Mortality rates never again reached the high levels observed in the late 1920s and 1930s, presumably since similar levels of effort (300,000 hours) were not attained in the aftermath of WWII because much of the fleet capacity and its man-power had been negatively affected by the general war effort. In Figure 6 the indices for haddock have been re-scaled for each age category so that all previous and subsequent observations in the time-series reflect change relative to 1939, i.e. to the start of hostilities and to the cessation of commercial fishing.

The Mexican wave in the haddock population suggested by first principles is clear. The youngest fish (age 0s) responded negatively, levels falling by 83% between 1939 and 1945, whereas the older age categories all responded positively. The mean level of age 10 haddock in the population rocketed, increasing nearly 12 times between 1939 and 1945. Increases by the younger age groups were found to be arranged in an ordered sequence between these two extremes; for example age 8s increased by 747%, age 6s by 579%, age 4s by 427%, and age 2s by 170%. It should be noted that this wave is seen twice, but travelled in the reverse direction after 1945 when levels of older fish decreased further and fastest when fishing recommenced in the post-war period (Figure 6). A similar phenomenon was observed in both cod, *Gadus morhua*, and whiting, *Merlangius merlangus* although the numbers of younger fish in the population also rose in those species.

Both mean length and mean biomass have been suggested as useful indicators for assessing conservation and fisheries-related effects of MPAs (Pelletier et al.,. 2008) and this study supports that view. The mean length of haddock in the trawl survey sampled Buchan population was 24.8 cm in 1939 and 28.7 cm in 1945 while the catch-per-unit-effort (in weight) of haddock rose from 11 to 59 kg h^{-1} of fishing. Similarly, cod average length in the trawl catches rose from 45.8 cm just before the war to 51.2 cm just after, while average whiting lengths increased from 26.5 cm to 27.8 cm. The catch-per-unit-effort of cod increased nearly ten times from 4 kg h^{-1} in 1939 to 36 kg h^{-1} in 1945. Changes in whiting catch-per-unit-effort were more modest, trebling from 5 kg h^{-1} in 1939 to 16 kg h^{-1} in 1945. Substantial increases in the catch-per-unit effort were also seen in the commercial data.

Environmental effects on stock dynamics

We hypothesized that the changes observed in gadoid abundance in Buchan, between 1939 and 1945, might plausibly have been caused by environmental factors such as changes in temperature or the volume of Atlantic inflow, rather than by fishing. Above, we examined how the entire age structure of each of the three most important gadoids changed, between 1928 and 1959, using population abundance indices from trawl surveys. To examine the possible impact of changes due to the physical environmental, as opposed to those due to commercial fishing, we opted to simplify the problem by examining only 'recruits' (age 0s) and SSB (all the fish thought to be old enough to reproduce estimated using maturity-at-length data), comparing them to a range of environmental covariate data we were able to assemble.

Tables 1, 2, and 3 show pair-wise correlations (1928-1958) between two indices (*i.e.* R_age0 = numbers of age 0 fish which is also known as ‘recruitment’ and SSB = numbers of sexually mature fish) representing changes in the haddock, cod and whiting populations and some potentially explanatory oceanographic variables: temperature, salinity and the North Atlantic Oscillation Index. [Note: some sea surface temperature data are available for the war time period]. The haddock recruits (Table 1) were positively correlated with SSB (r=0.35) and negatively correlated with temperature in quarter 3 (r=-0.43). There was also a negative relationship between haddock SSB and salinity in quarter 3 (r=-0.36). Cod recruitment (Table 2) was negatively correlated (-0.41) with salinity in quarter 3 whereas SSB was not related to any of the variables we examined. Recruitment in whiting, on the other hand, was negatively related to salinity in quarter 1 (-0.46) while SSB was positively related to sea surface temperature in quarter 1 (Table 3). It should be noted here that there are also close connections between the oceanographic variables themselves: salinity and temperature being positively related.

These data have been plotted as time-series in Figure 7. Recruitment fell steadily between 1928 and 1939 in haddock, cod and whiting. In the case of haddock, recruitment fell further during the war, and then rose again between 1945 and 1958. In both cod and whiting, recruitment rose during the war and in cod continued to rise thereafter (Figure 7). Levels of recruitment in whiting, however, remained fairly stable after the war.

SSB in all three gadoids fell between 1928 and 1939. During the war SSB levels of all three species rose. Immediately after WWII, spawner abundance dipped again, presumably when fishing recommenced, after when spawner abundance rose again gradually.

In order to investigate these relationships in more detail we extended the simple pairwise correlation analysis (e.g. Tables 1, 2, and 3) by using a combination of multiple linear regression models on log-transformed data, together with traditional nonlinear stock-recruitment models (Ricker 1954). In both cod and whiting, spawning stock biomass was not clearly related to any of the environmental data: the best predictor being the SSB the year before (see Tables 2 and 3). In haddock there is an indication (r=-0.36, Table 1) that SSB might be negatively related to salinity during quarter 3 (SAL Q3). When this was tested with an analysis of variance (Table 4), however, it was not found to be statistically significant (p=0.1).

An examination of environmental factors (e.g. temperature, North Atlantic Oscillation Index) thus failed to convincingly explain the abrupt changes in either the abundance of sexually mature fish or their changing age-structure and we are confident that they can be attributed to the virtual absence of fishing mortality.

Stock-recruitment relationships

It is usually assumed that recruitment (R_age0) is directly related either to SSB in year *t,* or to SSB the year before (SSB_{t-1}). To explore these relationships we fitted R_age0 to the abundance of spawners, together with a range of environmental variables, using linear models and compared the output using nested analysis of variance tests. In haddock, spawner abundance the year before (SSB_{t-1}) was quickly eliminated; recruitment (R_age0) being more strongly related to SSB in the same year. S7 shows that both SSB and temperature during quarter 3 (given that SSB is in the model) are related significantly to recruitment. The coefficients from model 3 are the following: intercept = 4.2, SSB = 0.5, and SST Q3 = -0.64. Hence rising late summer temperatures will result in falling recruitment. Between 1939 and 1945 average quarter 3 temperatures rose (see also Figure 7) indicating that temperature *could* have caused the fall in recruitment that we see during the war. The authors also fitted a Ricker stock-recruitment curve to these data, adding quarter 3 temperature data as a covariate, according to the methods outlined in the FLR package (Kell et al., 2007). In this formulation, temperature in quarter 3 was not significant.

In the case of cod, neither SSB nor SSB_{t-1} were useful for predicting cod recruitment in Buchan between 1928 and 1958 (see S8). Salinity in quarter 3 had a negative affect (p=0.06) on cod recruitment, when SSB was also included in the model. Quarter 3 salinity fell between 1939 and 1946 (Figure 7) and *could*, therefore, have been a factor in the increasing recruitment we observed during the war.

The patterns observed in haddock and cod was similar for whiting. Again, neither SSB nor SSB the year before could explain the pattern in whiting recruitment in Buchan between 1928 and 1958. Salinity in quarter 1 had a positive effect (p=0.08) when SSB was also in the model (see S9) and so salinity in early spring *might*, therefore, have contributed to the increasing recruitment we observed during the war, since it fell quite sharply between 1938 and 1948 (Figure 7) although the exact mechanism cannot be deduced from this study.

Discussion

We have ‘tracked’ the response of the entire age-structure of three fish populations in a large temperate area through a complete closure to fishing, emphasising the important differential response by each age category. The first ‘*Mexican wave’* we see, between 1939 and 1945, is caused by the enhanced survival rates due to the cessation of fishing, the effects of which accumulated steadily over time as each cohort aged. This result might at first appear obvious but we have found no clear references to this effect (age-dependent cascade) in the literature. One reason might be that fishery science traditionally models the entire age-structure but then aggregates the sexually mature component (the spawning stock biomass) and only its relationship to the ‘recruits’, i.e. the juvenile part of the stock (Pope and Macer 1996; Jennings 2001) is typically considered. This obscures independent changes that can take place in separate age classes. Further, the majority of population models for marine reserve designs currently include no detailed age-structure for their resident populations (Gerber et al., 2003).

The fall in numbers of juvenile (age 0) haddock between 1939 and 1945 is interesting as it contrasts with increasing numbers of all older age classes. This appears to be due, either to density-dependent effects, or to the increase in late summer temperatures observed between 1939 and 1945 which may be directly or indirectly causative. Reduced mortality on older fish caused by zero harvesting raised levels of both inter- and intra-specific competition for resources, in addition to increasing mortality by both predation and cannibalism. In the case of haddock this effect was not ameliorated by enhanced recruitment from a much larger spawning stock biomass possibly due to the lag effect clear from our population model (see S1). (Note: recruitment in both cod and whiting increased between 1939 and 1945 so the situation is extremely complex and a detailed discussion is beyond the scope of this article). Interestingly, there are also parallels with human populations in which changes in mortality rates due, say, to better healthcare, lead to ‘complete demographic transitions’ from populations dominated by juveniles to those dominated by adults (Caldwell et al., 2006).

The reduction of mortality due to commercial fishing thus changed the entire structure of the gadoid populations in Buchan, reducing the relative numbers of younger fish and increasing the relative proportions of their older counterparts. Had fishing been prohibited for longer it would have resulted in a completely new population 'equilibrium', bearing in mind that the six-year duration of the war is far less than the longevity of all the gadoids examined, implying that none of the cohorts would have experienced an entire lifetime completely free from mortality due to fishing. This all has clear implications for the economics of the fishing industry; older fish generally being disproportionately more valuable. The maintenance of such populations would also reduce discarding of small non-marketable fish which is a current objective of the Common Fisheries Policy of the European Union (Council of the European Union 2002).

This work has the potential to enable 'managers' to quantify how the instigation of MPAs might affect fish stocks and to harvest them without damaging the resource. Predictions of the development of age structure in a population of migratory fish within a large open MPA can now be made. This has not been shown hitherto. In many cases, resource managers and stakeholders expect to see major benefits in the short term after the establishment of a marine protected area. Thus, an important question is the development of theoretical approaches that allow us to predict biologically reasonable time frames under which the effects of MPAs can be detected. We have shown how a reduction in fishing effort from 300,000 (the Buchan area) hours to practically zero over six years to around 100,000 hours in the immediate post-war period impacted the age structure of gadoid populations in the northern North Sea. Such imputations would be impossible to make confidently using more contemporary data (e.g. most fish stock data used currently typically extend back to the 1960s), during which fishing levels have been consistent and ubiquitous.

In conclusion, this work shows that large closed areas can be useful in the conservation of migratory species from temperate areas, that older fish benefit fastest and that better recruitment may not occur instantly as it is more dependent on factors other than fishing, and hence may take longer to feed through to higher biomass levels that can be harvested.

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Figure Legends

Figure 1. Map of the study area Buchan. Dots denote trawl haul locations (shooting) 1928-1958.

Figure 2. Haddock trawl survey index (ages 0, 2-8) in area Buchan for August-October (1928-1958). The thin broken lines represent the raw data, the thicker lines the fitted models. The two vertical solid lines delineate WWII

Figure 3. Total annual haddock, cod and whiting commercial landings (a), effort (b), and landings per unit effort (c) for the steam trawler fleet in Buchan 1928 to 1958.

Figure 4a. Haddock cohorts (ages 2 to 8) in area Buchan estimated from scientific trawl survey data.

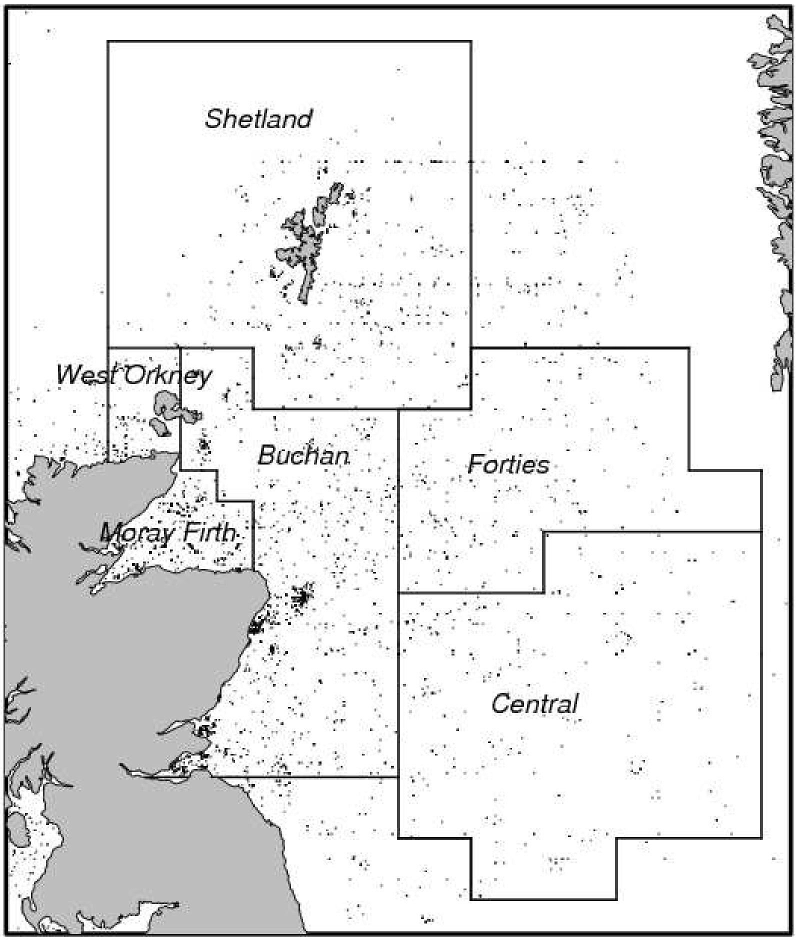
Figure 4b. Cod cohorts (ages 2 to 5) in area Buchan estimated from scientific trawl survey data.

Figure 4c. Whiting cohorts (ages 3 to 9) in area Buchan estimated from scientific trawl survey data.

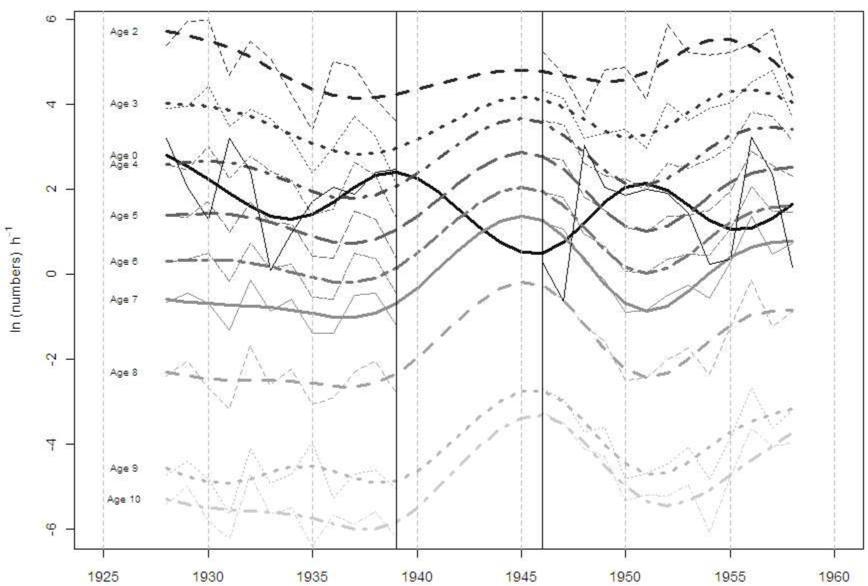
Figure 5. Total haddock, cod, and whiting mortality (Z) on ages 2-4 estimated from the trawl survey data 1928-1958.

Figure 6. The Mexican wave: haddock trawl survey abundance index for ages 0, 1, 2, 4, 6, 8, and 10 between 1928 and 1958. (Note: the series have been scaled to equal one in 1939).

Figure 7. Time-series summarizing change in the haddock, cod and whiting abundance together with five environmental variables in Buchan between 1928 and 1958.



Map of the study area Buchan. Dots denote trawl haul locations (shooting) 1928-1958.
215x279mm (72 x 72 DPI)



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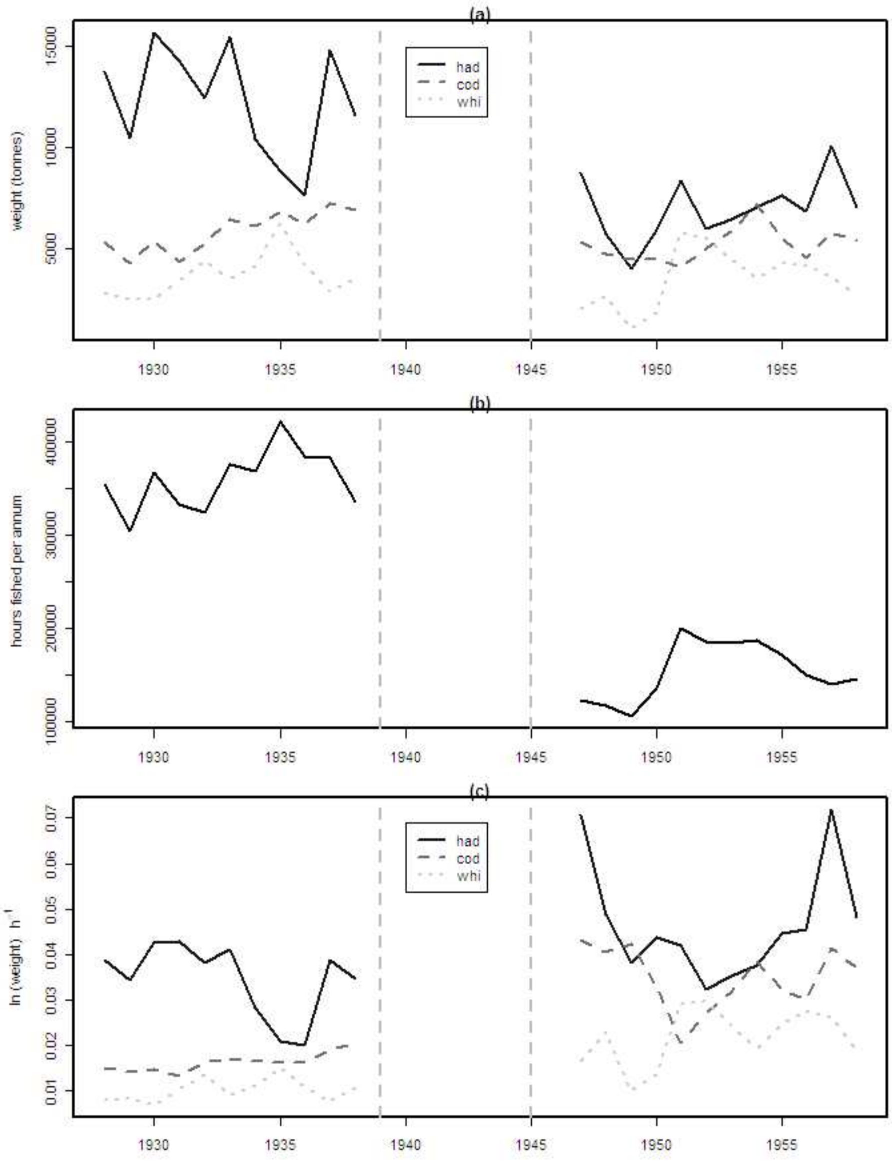
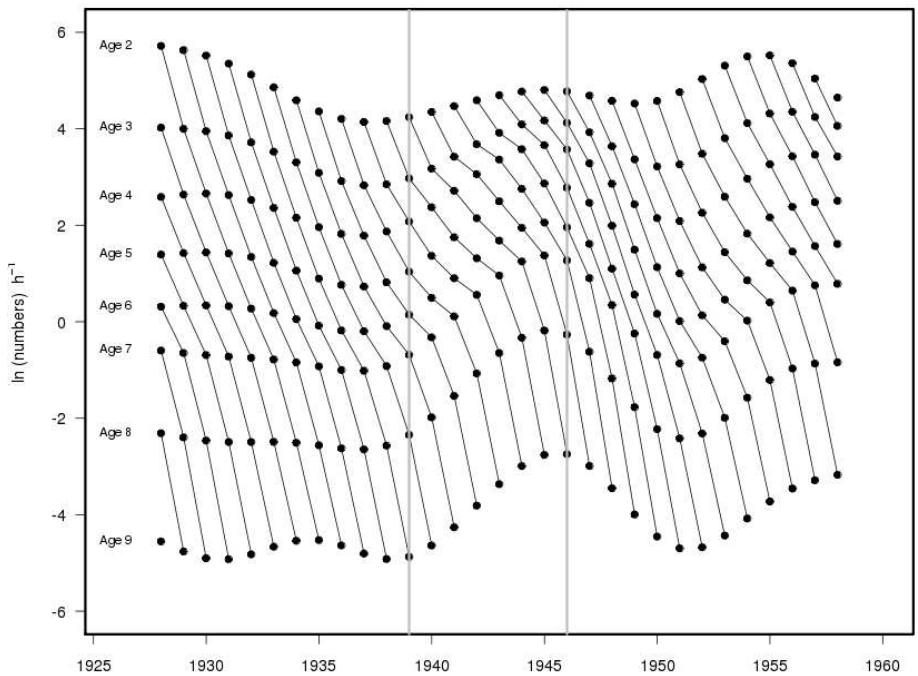
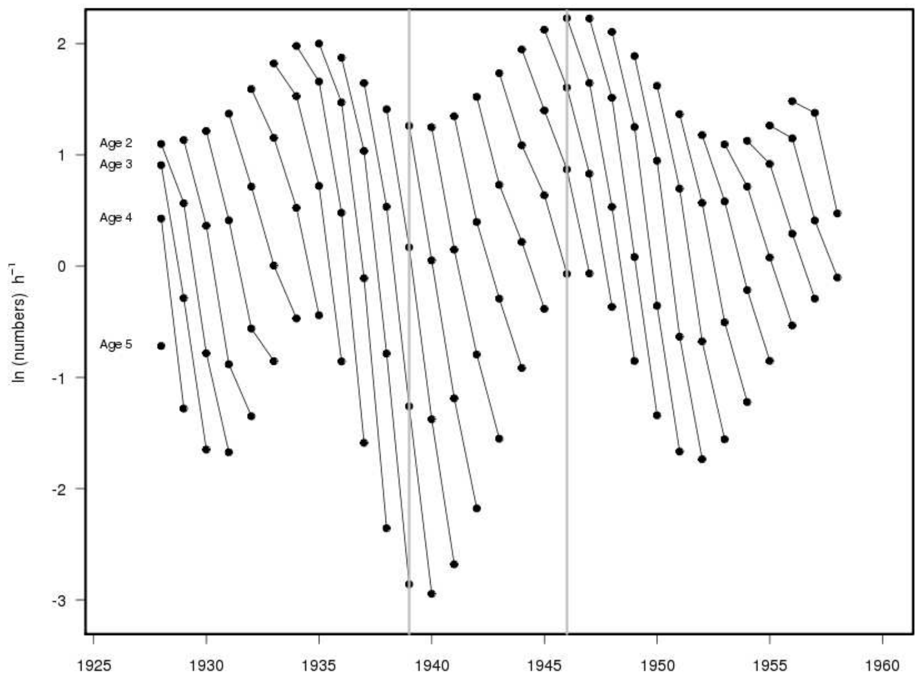


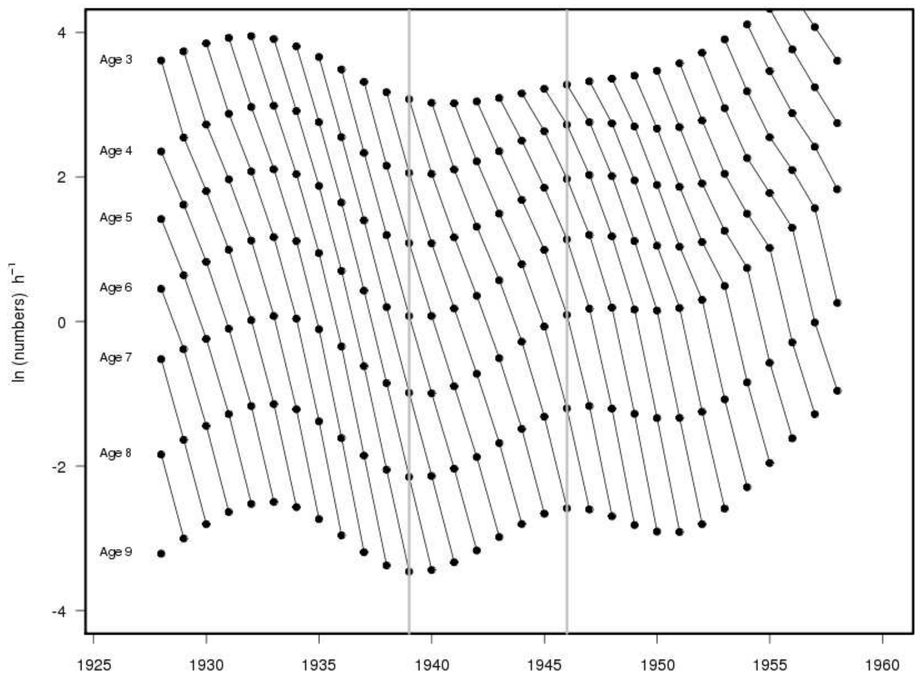
Total annual haddock, cod and whiting commercial landings (a), effort (b), and landings per unit effort (c) for the steam trawler fleet in Buchan 1928 to 1958.



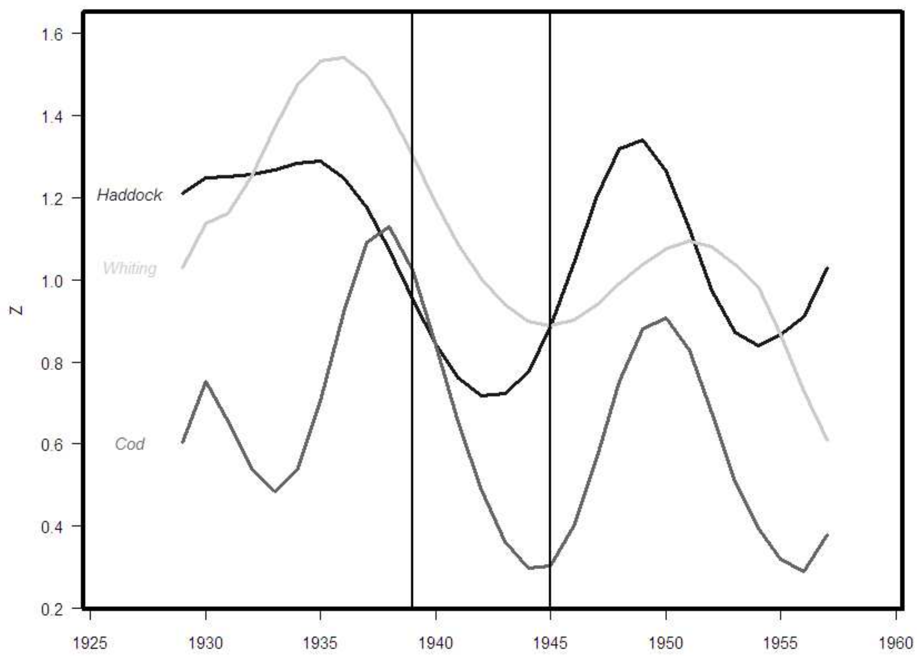
Haddock cohorts (ages 2 to 8) in area Buchan estimated from scientific trawl survey data
317x246mm (72 x 72 DPI)



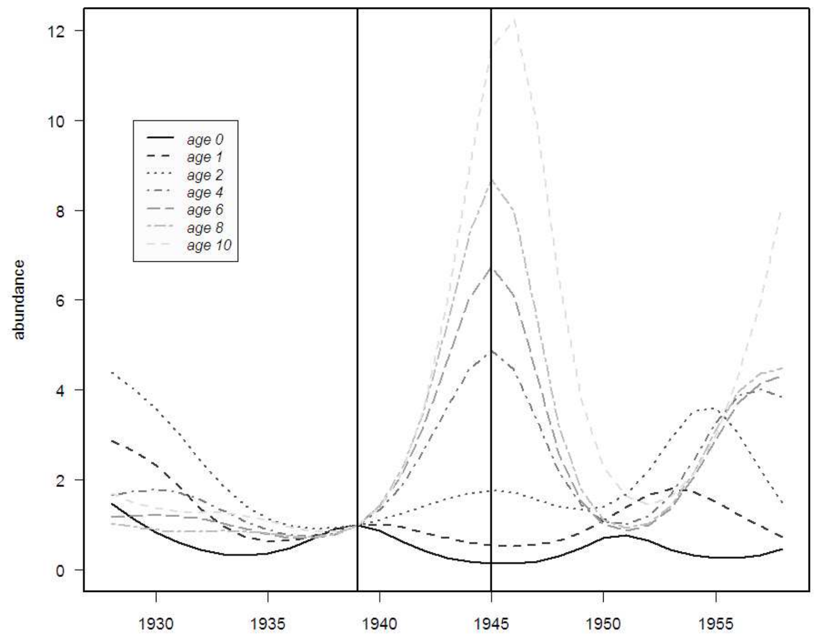
Cod cohorts (ages 2 to 5) in area Buchan estimated from scientific trawl survey data.
317x246mm (72 x 72 DPI)



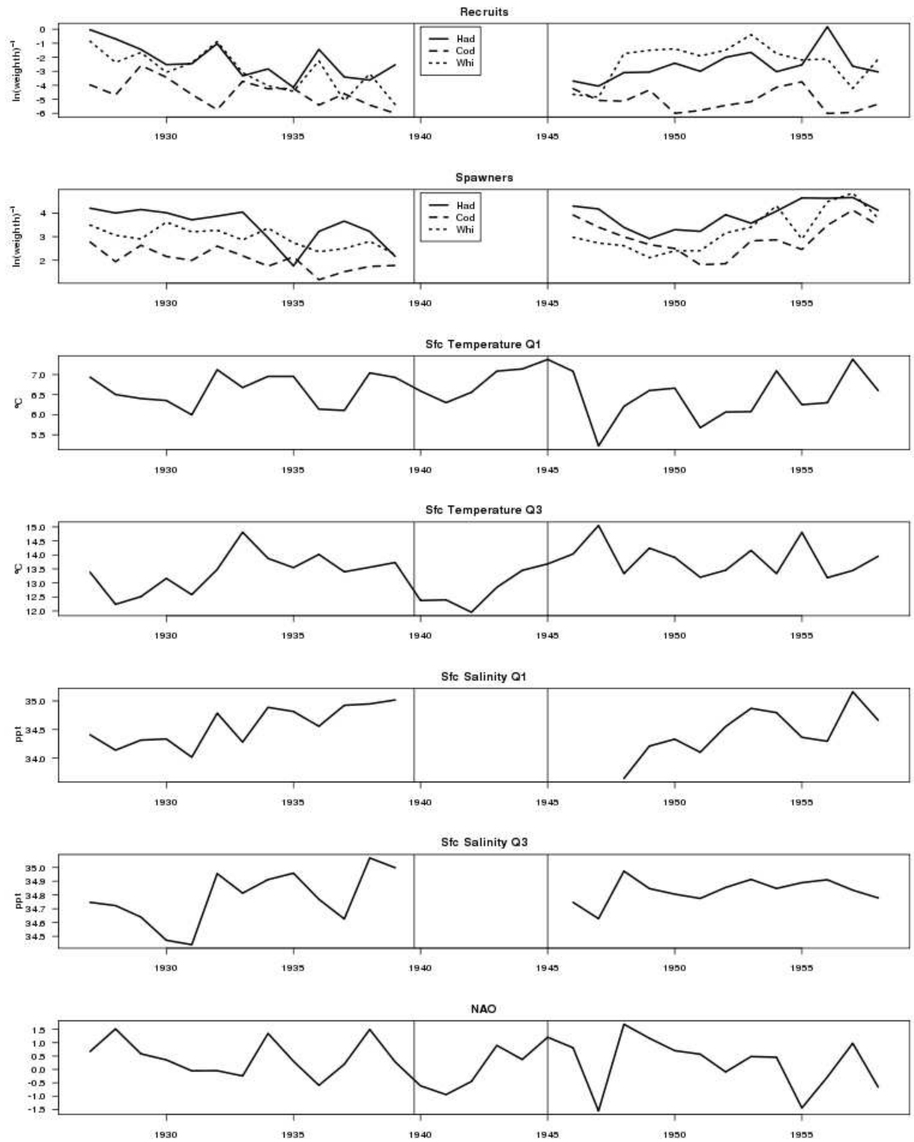
Whiting cohorts (ages 3 to 9) in area Buchan estimated from scientific trawl survey data.
317x246mm (72 x 72 DPI)



Total haddock, cod, and whiting mortality (Z) on ages 2-4 estimated from the trawl survey data 1928-1958.



The Mexican wave: haddock trawl survey abundance index for ages 0, 1, 2, 4, 6, 8, and 10 between 1928 and 1958. (Note: the series have been scaled to equal one in 1939).



Time-series summarizing change in the haddock, cod and whiting abundance together with five environmental variables in Buchan between 1928 and 1958.
282x352mm (72 x 72 DPI)

Table 1. Haddock: correlation coefficients between Recruits, Spawning stock biomass (SSB) the year before, sea surface temperature (SST), salinity (SAL) and the North Atlantic Oscillation index (NAO). Q1 and Q3 denote that the data were calculated for quarters 1 (January, February, March) and Quarter 3 (July, August, September).

	R_age 0	SSB	SSB_{t-1}	SST Q3	SST Q1	SAL Q3	SAL Q1	NAO
R	1.00	0.35	0.10	-0.43	0.03	-0.02	-0.18	0.02
SSB	0.35	1.00	0.61	-0.01	-0.10	-0.36	-0.17	-0.30
SST Q3	-0.43	-0.01	0.07	1.00	-0.09	0.26	0.23	-0.18
SST Q1	0.03	-0.10	0.01	-0.09	1.00	0.44	0.57	0.48
SAL Q3	-0.02	-0.36	-0.12	0.26	0.44	1.00	0.35	0.24
SAL Q1	-0.18	-0.17	-0.12	0.23	0.57	0.35	1.00	-0.06
NAO	0.02	-0.30	0.11	-0.18	0.48	0.24	-0.06	1.00

Table 2. Cod: correlation coefficients between Recruits, Spawning Stock Biomass (SSB) the year before, sea surface temperature (SST), salinity (SAL) and the North Atlantic Oscillation index (NAO). Q1 and Q3 denote that the data were calculated for quarters 1 (January, February, March) and Quarter 3 (July, August, September).

	R_age 0	**SSB**	**SSB_{t-1}**	**SST Q3**	**SST Q1**	**SAL Q3**	**SAL Q1**	**NAO**
R	1.00	-0.06	-0.06	-0.04	0.04	-0.41	-0.21	0.01
SSB	-0.06	1.00	0.7	0.18	0.2	0.03	0	-0.06
SST Q3	-0.04	0.18	0.33	1.00	-0.09	0.26	0.23	-0.18
SST Q1	0.04	0.2	-0.13	-0.09	1.00	0.44	0.57	0.48
SAL Q3	-0.41	0.03	-0.14	0.26	0.44	1.00	0.35	0.24
SAL Q1	-0.21	0	-0.34	0.23	0.57	0.35	1.00	-0.06
NAO	0.01	-0.06	-0.14	-0.18	0.48	0.24	-0.06	1.00

Table 3. Whiting: correlation coefficients between Recruits, Spawing Stock Biomass (SSB) the year before, sea surface temperature (SST), salinity (SAL) and the North Atlantic Oscillation index (NAO). Q1 and Q3 denote that the data were calculated for quarters 1 (January, February, March) and Quarter 3 (July, August, September).

	R_age 0	**SSB**	**SSB_{t-1}**	**SST Q3**	**SST Q1**	**SAL Q3**	**SAL Q1**	**NAO**
R	1.00	0.12	-0.03	-0.19	-0.1	0.08	-0.46	0.07
SSB	0.12	1.00	0.56	-0.23	0.33	-0.03	0.27	-0.02
SST Q3	-0.19	-0.23	0.24	1.00	-0.09	0.26	0.23	-0.18
SST Q1	-0.1	0.33	-0.07	-0.09	1.00	0.44	0.57	0.48
SAL Q3	0.08	-0.03	0.16	0.26	0.44	1.00	0.35	0.24
SAL Q1	-0.46	0.27	-0.24	0.23	0.57	0.35	1.00	-0.06
NAO	0.07	-0.02	0.33	-0.18	0.48	0.24	-0.06	1.00

Table 4: Haddock: analysis of variance summarising the relationship between spawners and salinity in Buchan during quarter 3.

Model	Res. Df	RSS	Df	Sum of Sq	F	Pr(>F)
1. SSB = 1	23	12				
2. SSB = SAL Q3	22	10.6	1	1.4	2.9	0.1