Fisheries and Oceans Science | Pêches et Océans Sciences

C S A S | **S C É S**

Canadian Stock Assessment Secretariat | **Secrétariat canadien pour l'évaluation des stocks**

Research Document 2000/147 | **Document de recherche 2000/147**

Not to be cited without permission of the authors [1]

Ne pas citer sans autorisation des auteurs [1]

Ecosystem effects on pre-recruit survival of cod in the southern Gulf of St. Lawrence

D. P. Swain[1], A. F. Sinclair[2], G. A. Chouinard[1] and K. F. Drinkwater[3]

[1]Department of Fisheries and Oceans, Gulf Fisheries Centre,
P.O. Box 5030, Moncton, NB, E1C 9B6

[2]Department of Fisheries and Oceans, Pacific Biological Station,
3190 Hammond Bay Road, Nanaimo, BC, v9R 5K6

[3]Department of Fisheries and Oceans, Bedford Institute of Oceanography,
P.O. Box 1006, Dartmouth, NS, B2Y 4A2

[1] This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

This document is available on the Internet at:

[1] La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

Ce document est disponible sur l'Internet à:

http://www.dfo-mpo.gc.ca/csas/

ISSN 1480-4883
Ottawa, 2000

Abstract

The recruitment rate of cod in the southern Gulf of St. Lawrence was remarkably high from the mid 1970s to the early 1980s. This high recruitment rate contributed to the rapid recovery of this stock from low levels of abundance in the mid 1970s. We sought an explanation for this unusually high recruitment rate by examining relationships between apparent pre-recruit survival of southern Gulf cod and ecosystem factors that might be expected to influence early survival, i.e. climate variables and potential predators of cod eggs and larvae (pelagic fishes) or cod juveniles (seals). We tested effects of these factors by including them as covariates in the stock-recruitment relationship of southern Gulf cod. The stock-recruit relationship was strongly compensatory, with a higher recruitment rate at low spawning stock biomass. A negative effect of pelagic fish biomass on cod recruitment rate was also highly significant for this stock. Cod recruitment rate was unrelated to the indices of seal abundance. With one exception, no significant effects of the climate variables were apparent after accounting for autocorrelation. The exception was a tendency for recruitment rate to be higher at intermediate dates for the last appearance of ice on the Magdalen Shallows, though this effect was relatively weak compared to the effects of pelagic fish biomass and cod spawning stock biomass on recruitment rate. The unusually high recruitment rate of southern Gulf cod in the mid to late 1970s can be explained by the low levels of both cod spawning biomass and pelagic fish biomass during this period.

Résumé

Le taux de recrutement de la morue dans le sud du golfe du Saint-Laurent, remarquablement élevé du milieu des années 70 au début des années 80, a contribué au rétablissement rapide de ce stock après qu'il ait affiché de faibles niveaux d'abondance au milieu des années 70. Nous avons cherché une explication de ce taux de recrutement exceptionnellement élevé en examinant les relations entre la survie apparente des pré-recrues de morue dans le sud du Golfe et des facteurs écosystémiques qui peuvent avoir eu une incidence sur la survie des premiers stades du cycle vital, c'est-à-dire des variables climatiques et des prédateurs potentiels des œufs et des larves (poissons pélagiques) et des juvéniles (phoques). Nous avons analysé les effets de ces facteurs en les incluant comme covariables dans la relation stock-recrutement pour la morue du sud du Golfe. Celle-ci était fortement compensatoire, donnant un taux de recrutement plus élevé lorsque la biomasse de reproducteurs était faible. Nous avons aussi observé un effet négatif très significatif de la biomasse de poissons pélagiques sur le taux de recrutement de la morue pour ce stock. Le taux de recrutement de la morue était sans rapport avec les indices de l'abondance des phoques. Aucun effet significatif des variables climatiques était évident après la prise en compte de l'autocorrélation, sauf pour la tendance du taux de recrutement à être plus élevé aux dates intermédiaires de la dernière manifestation des glaces sur les petits fonds des Îles de la Madeleine, bien que cet effet était relativement faible en comparaison des effets de la biomasse de poissons pélagiques et de la biomasse du stock reproducteur de morue sur le taux de recrutement. Les faibles niveaux de ces biomasses du milieu à la fin des années 70 peuvent être à l'origine du taux de recrutement exceptionnellement élevé de la morue du sud du Golfe pendant cette période.

Introduction

Like most other stocks of Atlantic cod (*Gadus morhua)* in the Northwest Atlantic, cod in the southern Gulf of St. Lawrence declined to a low level of abundance in the early 1990s. Recovery from this low level has been slow despite severe restrictions on fishing pressure. In contrast to this slow recovery, this population recovered rapidly from declines to low abundance in the mid 1970s (Fig. 1A), even though commercial fishing continued during the earlier period of low abundance.

Has recruitment during the recent period of low abundance been unusually low, or was it unusually high during the earlier low-abundance period? An index of juvenile or pre-recruit survival can be calculated by dividing *R*, the number of recruits, by *S*, the spawning stock biomass that produced them. We calculated this index for the southern Gulf of St. Lawrence cod stock. We used two independent time series of recruitment (defined here as abundance of 3 yr old cod) and spawning biomass, one based on the mean catch per tow in annual research vessel surveys and one estimated using sequential population analysis (SPA). Details are given in Chouinard et al. (1999). We present results from two SPAs, one calibrated with only the research survey catch rates (SPA rv) and one calibrated with research survey catch rates, fishery catch rates and five sentinel survey catch rate series (SPA all). Both the SPA- and survey-based indices indicate that *R* has not been unusually low in recent years given the recent low values of *S* (Fig. 1A). Instead, estimates of pre-recruit survival in the 1990s are comparable to or above those that persisted throughout the 1950s, 1960s and early 1970s (Fig. 1B). The period of unusual pre-recruit survival appears to be the earlier low-abundance period in the mid-1970s. Pre-recruit survival during this earlier period appeared to be remarkably high.

The purpose of this paper is to explore relationships between apparent pre-recruit survival of southern Gulf cod and ecosystem factors that might be expected to influence early survival of cod. In particular, an explanation is sought for the unusually high survival rates of pre-recruit cod from the mid 1970s to the early 1980s. The possibility that variation in characteristics of the spawning stock (e.g., age distribution, fish condition) contributes to apparent variation in pre-recruit survival will be considered in a second paper (Swain and Chouinard 2000*b*).

Hypotheses

1. Pelagic fishes

An effect of pelagic fish abundance on cod recruitment has often been suggested. Most studies have focussed on top-down control by pelagic fishes through predation on cod eggs and larvae, though bottom-up control through competition with early life history stages of cod is also a possibility (e.g., Bax and Eliasson, 1990). In the Baltic Sea, herring and sprat prey heavily on cod eggs (e.g., Köster and Möllmann, 2000), and Rudstam et al. (1994) suggested that cod recruitment may be depressed by increases in the abundance of these pelagic fishes. Likewise, herring have been reported as a heavy predator of cod eggs in the Lofoten area (Pálsson, 1994). Cod eggs have also been reported from herring stomachs in the North Sea (e.g., Daan et al., 1985), where an increase in the recruitment of cod and other gadoids coincided roughly with the collapse of herring and mackerel stocks due to overfishing (Daan et al., 1994). Lett (1980), noting that mackerel consume large quantities of fish eggs and larvae, proposed a negative effect of mackerel biomass on cod recruitment in the southern Gulf of St. Lawrence. Similarly, Paz and Larrañeta (1992) suggested that cod yearclass strength on the Grand Bank is influenced by mackerel predation on cod eggs and larvae. Herring and mackerel are the dominant pelagic fishes in the southern Gulf of St. Lawrence. We tested for an effect of their combined biomass on cod pre-recruit survival, predicting a negative relationship.

2. Seals

It has been suggested that exponential increases in seal abundance since the early 1970s have resulted in increased predation on cod, delaying cod stock recovery (e.g., FRCC, 1999). We tested for relationships between indices of harp and grey seal abundance and pre-recruit survival of southern Gulf cod, again predicting negative associations.

3. Climate

Climatic variability is expected to influence recruitment via a variety of mechanisms (Cushing 1982; Shepherd et al. 1984). We included the following environmental variables in this analysis: air temperatures at the Magdalen Islands, discharge from the St. Lawrence River system (RIVSUM), an index of the timing of ice-out on the Magdalen Shallows, and the North Atlantic Oscillation index (NAO index). Positive correlations have been reported between freshwater discharge from the St. Lawrence and fish catches (e.g., Sutcliffe 1972), leading to the hypothesis that high discharge promotes good recruitment by enhancing nutrient concentrations in upper water layers through mixing and entrainment processes. Water temperature in the upper layers may influence recruitment through effects on plankton production and larval growth rates. Lett et al. (1975) reported a positive association between sea surface temperature and cod egg survival and densities in the southern Gulf. Continuous longterm data on surface water temperatures are lacking in the southern Gulf; hence we used air temperatures as a proxy for this variable. We focussed on indices of conditions in spring and summer to cover the spawning season and the feeding season of pelagic 0-group cod. Indices of the timing of ice-out were included in the analysis because the migration of cod into the southern Gulf is delayed when ice-out is late (Sinclair and Currie 1994), presumably delaying the onset of spawning.Temperature in the cold intermediate layer (CIL) was included in the analysis as an indicator of general water temperature conditions over the Magdalen Shallows. The NAO index is a measure of the large-scale atmospheric circulation and has been shown to be related to numerous oceanographic and meteorological variables over an area extending from the Labrador Sea to the Middle Atlantic Bight (Colbourne et al., 1994; Drinkwater 1996).

Data

Cod Pre-recruit Survival

Calculation of the index of pre-recruit survival of southern Gulf cod is described by Swain and Chouinard (2000*a*). Most analyses presented here use the SPA-based index (to maximize time series length), using the formulation accepted in the most recent assessment of this stock (Chouinard et al., 1999) updated to include 1999 data. This SPA assumed an increase in M from 0.2 to 0.4 in 1986, and was calibrated using research survey catch rates, fishery catch rates and five sentinel survey catch rate series. Results were similar using estimates from the SPA calibrated using only the research survey catch rates. Some results are also shown using the survey-based survival index to demonstrate that the main conclusions are not sensitive to the assumptions made in the SPA (e.g., regarding M).

Pelagic Fish Biomass

We obtained estimates of herring and mackerel biomass in the southern Gulf of St. Lawrence from SPA. We used the biomass of southern Gulf herring aged 2 yr and older (2^+) given by Winters (1976) for 1958 to 1973, by Cleary (1982) for 1969 to 1981 and by Claytor and LeBlanc (1999) for 1978 to 1995. Estimates were for spring- and fall-spawning herring combined. Estimates from the different SPAs agreed well in the periods of overlap (1969-1973 and 1978-1981). We spliced the time series together between 1968 and 1969 and between 1977 and 1978, using the later SPA for each period of overlap. We used the estimates of mackerel spawning biomass given by Clark (1998). These estimates are for both the southern stock component spawning in waters off New England and the northern component spawning primarily in the southern Gulf. The two components are believed to be of similar size (F. Grégoire, IML, pers. comm.), and we constructed an index of pelagic fish biomass in the southern Gulf by adding the herring biomass to half the mackerel biomass.

Seal Abundance

We used estimates of the abundances of harp and grey seals. These are likely to be the most important seal predators in the southern Gulf due to their abundance (harp seals) or residency time and diet (grey seals) (Hammill et al., 1999). Estimates for harp seals were for the entire NW Atlantic population, kindly provided by G. Stenson (NWAFC, pers. comm.). Estimates for grey seals are the totals for both the Gulf and Sable Island herds (since seals from both herds enter the Gulf), kindly provided by M. Hammill (IML, pers. comm.). Tests using these indices are necessarily crude, since the proportions of these populations that enter the Gulf, their residency time there and the proportion of cod in their diets may vary from year to year.

Environmental Variables

Mean monthly air temperatures at the Magdalen Islands were averaged from May to July to provide an index of air temperature conditions in spring and early summer. The RIVSUM index was the combined discharges of the St. Lawrence, Ottawa and Saguenay Rivers during April, May and June. The CIL temperature index was the minimum CIL temperature index reported by Gilbert and Pettigrew (1997, Fig. 7). The ice index was the date of last appearance of ice in the spring, averaged over all grids in the southern Gulf. The NAO is the average pressure difference in mb between the Azores and Iceland in winter (December to February).

Time trends in potential explanatory variables

Time trends in pelagic fish biomass, seal abundance and environmental variables are shown in Figure 2.

Pelagic fish biomass declined precipitously from the late 1960s to the mid 1970s. This decline reflects sharp decreases in both herring and mackerel biomasses. Herring biomass declined when landings rose tenfold with the development of a new purse seine fishery in the mid to late 1960s (landings rose from an average annual level of 30,000 t to 270,000 t in 1970). Mackerel biomass declined following the development of a new distant-water trawl fishery in the late 1960s, with landings rising to 420,000 t in 1973, well above the 10,000-40,000 t level taken in coastal fisheries from the 1920s to the early 1960s (Anderson and Paciorkowski 1980). The period of exceptionally low herring and mackerel biomass that resulted from these population collapses coincided with the period of high pre-recruit survival of cod (Fig. 1B). These new fisheries were reduced considerably in the 1970s and the herring and mackerel populations recovered to relatively high biomasses in the mid- to late- 1980s, coinciding with a decline in pre-recruit survival of cod to levels typical of the 1960s.

Estimated abundance increased exponentially from the early 1970s to the mid 1990s for both harp and grey seals. Estimated harp seal abundance was at a minimum around 1970, though harp seal abundance was relatively low throughout the 1960s. Estimated grey seal abundance is available only since the late 1960s, though abundance throughout the 1960s is believed to have been at or below the low levels of the late 1960s (M. Hammill, pers. comm.). Thus, the unusually high pre-recruit survival of southern Gulf cod in the mid and late 1970s was during a period of increasing seal abundance while the lower survival levels of the 1960s was during a period of low seal abundance.

Discharge from the St. Lawrence River in spring and early summer generally declined throughout the 1950s to low levels in the early to mid 1960s, and then increased to high levels in the mid 1970s. Discharge has fluctuated around average levels since the late 1970s. Mean air temperature during the spring and early summer has fluctuated since 1950 without any strong trends except for a general tendency to increase over the time series. CIL temperature was at a low level in the early 1960s and mid 1970s and at a high level in the mid 1950s, 1970 and the early 1980s, declining steadily from 1985 to the mid 1990s. Spring breakup was especially late in 1967 and 1972, especially early in 1981, and tended to be late in the early to mid 1990s. High values of the NAO index, which tend to be associated with cold winters in the Northwest Atlantic, occurred in the early to mid 1970s, the early to mid 1980s and from the late 1980s to the mid 1990s.

Statistical Methods

We tested for ecosystem effects on the stock-recruitment relationship of southern Gulf cod. We assumed a Ricker relationship with lognormal error. We fit the relationship using linear regression, with $\log_e(R/S)$ as the dependent variable and S and the ecosystem variables as the independent variables (Walters 1987). We used the following procedure, recommended by Bence (1995), to account for autocorrelation (see Pyper and Peterman 1999). After fitting the regression using ordinary least squares, we tested for autocorrelation in the residuals using a Durbin-Watson test. In all cases, this test rejected the hypothesis of zero lag-1 autocorrelation (at $\alpha<0.1$). We thus simultaneously computed maximum likelihood estimates of the regression parameters and the first-order autoregressive parameter for the error. All independent variables were standardized to a mean of 0 and a standard deviation of 1 for these analyses, so that the magnitude of slope parameters is indicative of the relative strength of the ecosystem effects.

We also examined the possibility of nonlinear relationships between log survival and the environmental variables. These might be expected if environmental optima, at which survival is greatest, occur within the range of environmental conditions experienced by the population. We included quadratic terms for the environmental variables in models to allow for this possibility. In all but one case, there was no evidence for nonlinear relationships. We present results only for the environmental variable, timing of the spring breakup, that appeared to have an intermediate value producing greatest survival.

Results

Strong compensation is evident in the stock-recruit relationship of southern Gulf cod, with higher pre-recruit survival at low spawning stock biomass (Fig. 3, Table 4). A strong negative relationship is evident between pelagic fish biomass and residuals from the stock-recruit relationship (Fig. 4). No strong associations were evident between the residuals and any of the physical environmental variables (Fig. 4). There was a suggestion that residuals were highest at intermediate values for the last appearance of ice on the Magdalen Shallows (near about 105 days). Residuals showed an unusual pattern against the indices of seal abundance, increasing sharply to maximum values at intermediate levels of seal abundance, declining somewhat with further increases in seal abundance and appearing independent of seal abundance over a broad range of intermediate to high abundance levels.

The negative effect of pelagic fish biomass on cod pre-recruit survival was highly significant, both ignoring autocorrelation and after accounting for it by including a first-order autoregressive parameter for the error (Table 1). Pre-recruit survival was positively associated with RIVSUM ignoring autocorrelation, but there was no indication of an effect of this variable on survival after accounting for autocorrelation. There was no indication of an effect on pre-recruit survival for any of the other variables examined. In all cases, the tendency for log survival to be highest at low spawning stock biomass was highly significant.

Confounding among the various ecosystem variables could obscure effects on pre-recruit survival. We examined effects on pre-recruit survival testing all the ecosystem variables simultaneously (Table 2). Only a subset of the environmental variables was available for the entire 1950-1994 period. In the model that ignored autocorrelation, a positive effect of RIVSUM was significant and a negative effect of air temperature approached significance. However, no effects (except spawner biomass) were significant after accounting for autocorrelation. In the 1963-1994 period, when all variables were available, the negative effect of pelagic fish biomass was highly significant (P<0.0001) and the negative effect of air temperature was significant (P=0.028) ignoring autocorrelation, but only the effect of pelagic fish biomass remained significant (P=0.0005) accounting for autocorrelation.

There was some indication that pre-recruit survival was higher at intermediate values for the last appearance of ice on the Magdalen Shallows. This effect was not significant ignoring autocorrelation but the quadratic term for the ice index was significant (P=0.033) after accounting for autocorrelation, explaining an additional 12% of the variation in log survival (Table 3). This term remained significant (P=0.025) including pelagic fish biomass in the model, though the ice index accounted for only 5% of the variation in log survival compared to 27% for pelagic fish biomass and 24% for spawner biomass.

Effects of pelagic fish biomass were similar using results from either SPA calibration or using the survey data on their own (Table 4). In all cases, even the shorter survey-based time series, the negative effect of pelagic fish biomass on pre-recruit survival was highly significant. Adding pelagic fish biomass to the model doubled or tripled the R^2 value for the regression and substantially reduced the significance of autocorrelation in the error. In all cases, pre-recruit survival also tended to be higher when cod spawning biomass was lower, most significantly when pelagic fish biomass was included as a covariate.

Discussion

Our analyses suggest a strong negative effect of pelagic fish biomass on cod recruitment success in the southern Gulf of St. Lawrence, a hypothesis proposed by Lett (1980) some twenty years ago. In particular, the remarkable pre-recruit survival of cod between the mid-1970s and the early 1980s and the resulting rapid recovery of southern Gulf cod from low abundance in the mid-1970s can be accounted for by the coincident collapse of herring and mackerel stocks due to overfishing. Similar effects of pelagic fishes on cod recruitment have been proposed for the Baltic Sea (e.g., Rudstam et al. 1994), the North Sea (e.g., Daan et al. 1994), and the Grand Bank (Paz and Larrañeta 1992).

In analyses reported elsewhere (Swain and Sinclair 2000), we found that negative effects on cod pre-recruit survival were also highly significant for either herring or mackerel biomass alone in the 1971-1994 period, a period when general trends in biomass were similar between herring and mackerel. However, the effect of total pelagic fish biomass was much stronger than the effect of either herring or mackerel biomass alone in the longer 1963-1994 period. Trends in herring and mackerel biomass differed over this longer period, diverging sharply in the mid 1960s when mackerel biomass appeared to be low and herring biomass high. The much stronger effect of total pelagic fish biomass over the longer period suggests that it is the total biomass of herring and mackerel that is affecting cod recruitment success.

Biomass estimates for both cod and the two pelagic species must be viewed with some caution for the earlier years, particularly the 1950s and early 1960s, when sampling of the landings for size and age composition was less extensive (and entirely lacking in some years). Neither research survey nor fishery catch rate abundance indices are available for the earlier years. Extending SPA to these earlier years requires assumptions about the abundance of cohorts at the oldest ages (Winters 1976; Anderson and Paciorkowski 1980). These assumptions can have a substantial impact on biomass estimates. For example, different reasonable assumptions lead to relatively high estimates of mackerel abundance in the early 1960s (A. F. Sinclair, unpublished analyses). While the reliability of the low biomass estimates for herring and mackerel in the late 1950s or early 1960s is uncertain, these low estimates are consistent with an effect of the epizootic disease that infected pelagic fishes in the southern Gulf in the mid 1950s (Winters 1976).

The data since 1963, when biomass estimates are available for both pelagic fishes, support the hypothesis of a negative effect of pelagic fish biomass on cod recruitment success. The scant data available for earlier years do not provide additional support for this hypothesis. Cod pre-recruit survival appeared to be unremarkable in the late 1950s even though herring biomass appeared to be very low in 1958 and 1959 (Winters 1976). However, it is likely that many factors influence early survival of cod and it may be that other factors limited cod recruitment success in the late 1950s. For example, pre-recruit survival appears to be lower at high levels of cod spawning stock biomass (Fig. 3), and spawning stock biomass of cod was at a high level in the mid to late 1950s (Fig. 1).

Pre-recruit survival appeared to be unusually high for many Northwest Atlantic cod populations in the mid to late 1970s (Sinclair, 1996). Can reduced biomasses of pelagic fishes provide an explanation for the high recruitment success in these other populations during this period? Although spawning by the northern population of mackerel in the Northwest Atlantic is principally in the southern Gulf of St. Lawrence, these fish feed over a wider area, including the Scotian Shelf, northern Gulf of St. Lawrence and areas off Newfoundland. Thus, the collapse of this population in the mid to late 1970s may have contributed to the high pre-recruit survival of cod in these other areas during this period, as suggested by Paz and Larrañeta (1992) for the Grand Bank (though effects of mackerel on cod pre-recruit survival might be expected to be greatest in the southern Gulf where their residency time during the summer feeding season is greatest). Similarly, the rapid development of purse-seine fisheries for herring in the late 1960s resulted in declines in nearly all herring stocks in the Northwest Atlantic in the 1970s (Messieh, 1991). For example, herring were fished on the offshore banks of the Scotian Shelf in the 1960s, but appeared to be rare on these banks in the 1970s, increasing in abundance in the 1980s to relatively high levels throughout the 1990s (Stephenson et al. 1998).

Walters and Kitchell (2001) have recently suggested that the success of many of the large commercially important fishes depends on “cultivation” effects, in which the adults crop down forage fishes that are predators or competitors of their early life history stages. Our results suggest that this effect could be important for some populations of Atlantic cod. A consequence of these cultivation effects can be delayed depensatory decreases in juvenile survival when adult abundance is severely depleted by fishing. This can occur if reduced predation by adults results in increased abundance of the forage fishes that prey upon or compete with juveniles (or earlier life history stages). However, in our case, it would appear that the corollary may have been the case, i.e. that fisheries-induced collapses of both herring and mackerel may have improved cod pre-recruit survival and aided the recovery of cod in the late 1970s.

Our results also have implications for the recommendation that seal herds off Atlantic Canada should be culled to enhance cod production and promote stock recovery (FRCC 1999). It has been suggested that an exponential increase in seal abundance has resulted in increased predation on cod, thus delaying cod stock recovery. We were unable to detect an effect of seal abundance on pre-recruit survival of cod in the southern Gulf, though our tests, based on total abundance of the harp and grey seal herds, were crude and did not incorporate potential interannual variation in the proportions of these populations that enter the Gulf, their residency time there and the proportion of cod in their diets. Nonetheless, there is no indication that pre-recruit survival of cod in the southern Gulf has been lower in recent years of high seal abundance than in the 1960s when seal abundance was low (Fig. 1B). Furthermore, pelagic fishes like herring appear to be an important component of seal diets (e.g., Bowen et al. 1993). These results point to the possibility of a triangular food web involving cod, seals and pelagic fishes (Fig. 5). Manipulation of such food webs can lead to unexpected results (Bax, 1998). If seals consume more herring than they do cod, a seal cull could potentially result in decreased pre-recruit survival of cod (due to increased predation on cod eggs and larvae by herring) instead of the hoped-for increase in cod survival. Bax (1998) emphasizes the danger of concentrating only on direct (linear) predation interactions when there are indirect (triangular) interactions with the potential to reverse the effects of the direct interactions. Our results suggest that a better understanding of the interactions between cod, seals and pelagic fishes is needed before it will be possible to predict the effect of a seal cull on cod abundance.

Recruitment success also showed a strong negative relationship with spawning stock biomass, suggesting that mortality rates were strongly density-dependent or compensatory at pre-recruit stages in this population. Declines in pre-recruit survival at high levels of spawning stock biomass could result from a variaty of factors, such as cannibalism, density-dependent competition for food or space at the larval or juvenile stages, compensatory predation, etc.

The date of last appearance of ice on the Magdalen Shallows was the only environmental variable that was significantly related to recruitment success after acounting for autocorrelation. Recruitment tended to be highest in years when the spring break-up and disappearance of ice occurred at intermediate dates. The importance of this variable may be related to the timing of the spring pre-spawning migration into the southern Gulf. Timing of the spring migration into the Gulf is delayed when ice persists late on the Magdalen Shallows (Sinclair and Currie 1994). Intermediate (average) migration timing may result in spawning and larval production at the time of year when conditions are most favourable for survival of larvae. However, the effect of even this environmental variable was weak compared to the effects of cod spawning biomass and pelagic fish biomass on cod recruitment success.

The premise underlying the choice of environmental variables examined in this study was that variation in pre-recruit survival would depend most strongly on factors affecting the early life history stages (eggs, larvae and recently settled juveniles). Thus, measures of pre-recruit survival were related to environmental variables during a cohort’s first spring and summer. Alternatively, recruitment success may depend on cumulative effects of environmental conditions during the first two or three years of life. Such effects would not be detected by the analyses reported here.

Quadratic terms were considered for the environmental variables because of the possibility of environmental optima at intermediate levels of these variables. Optima at intermediate levels of environmental variables might be expected if cod are adapted to average environmental conditions. Quadratic terms were not considered for the indices of abundance of potential predators of cod (pelagic fishes and seals). Direct predatory effects would be expected to result in highest prey survival at low predator levels, not intermediate predator levels.

In conclusion, of the ecosystem variables that we examined, only the biomass of pelagic fishes (herring and mackerel) appeared to have a strong effect on pre-recruit survival of cod in the southern Gulf. This effect provides an explanation for the period of remarkable pre-recruit survival of cod in the southern Gulf from the mid 1970s to the early 1980s. As in any observational study, the possibility that this coincidence between high pre-recruit survival of cod and low pelagic fish biomass is spurious cannot be excluded. However, no other explanation for the period of high survival is provided by the ecosystem variables that we examined. Pre-recruit survival of southern Gulf cod also appears to be strongly compensatory, so the high survival during this period may also be partly attributable to low cod spawning biomass. Although we did not detect any strong effects of physical environmental variables on survival, favourable environmental conditions may have permitted the high survival during the mid to late 1970s. Survival showed a weak but significant tendency to be higher at intermediate dates for the last appearance of ice on the Magdalen Shallows, and this variable tended to be at intermediate levels in the mid 1970s.

Acknowledgements

We thank François Grégoire (DFO, MLI, Mont-Joli) for information on mackerel in the Northwest Atlantic and Garry Stenson (DFO, NWAFC, St. John's) and Mike Hammill (DFO, MLI, Mont-Joli) for indices of seal abundance.

References

Anderson, E. D., and Paciorkowski, A. J. 1980. A review of the Northwest Atlantic mackerel fishery. Rapp. P.-v. Réun. Cons. int. Explor. Mer **177:** 175-211.

Bax, N., and Eliassen, J.-E. 1990. Multispecies analysis in Balsfjord, northern Norway: solution and sensitivity analysis of a simple ecosystem model. J. Cons. int. Explor. Mer **47:** 175-204.

Bax, N. J. 1998. The significance and prediction of predation in marine fisheries. ICES J. mar. Sci. **55:** 997-1030.

Bence, J. R. 1995. Analysis of short time series: correcting for autocorrelation. Ecology **76:** 628-639.

Bowen, W. D., J. W. Lawson and B. Beck, 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 50: 1768-1778.

Chouinard, G. A., Sinclair, A., Currie, L., Poirier, G. and Swain, D. 1999. Assessment of Cod in the Southern Gulf of St. Lawrence, March 1999. CSAS Res. Doc. **99/23**.

Clark, S.H. [ed.] 1998. Status of the fishery resources off the northeastern United States. NOAA Technical Memorandum, NMFS-NE-115.

Claytor, R. R., and LeBlanc, C. 1999. Assessment of the NAFO Division 4T southern Gulf of St. Lawrence herring stocks in 1998. CSAS Res. Doc. 99/54 .

Cleary, L. 1982. Assessment of the 4T herring stock. CAFSAC Res. Doc. 82/47 .

Colbourne, E., S. Narayanan and S. Prinsenberg. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970-1993. ICES mar. Sci. Symp. 198: 311-322.

Cushing, D. H. 1982. Climate and Fisheries. Academic Press

Daan, N., Heessen, H. J. L. and Pope, J. G. 1994. Changes in the North Sea cod stock during the twentieth century. ICES mar. Sci. Symp. **198:** 229-243.

Daan, N., Rijnsdorp, A. D. and van Overbeeke, G. R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Trans. Am. Fish. Soc. **114:** 499-506.

Drinkwater, K.F. 1996. Climate and oceanographic variability in the Northwest Atlantic during the 1980s and early-1990s. J. Northw. Atl. Fish. Sci. 18: 77-97.

FRCC, 1999. 1999 conservation requirements for the Gulf of St. Lawrence groundfish stocks and cod stocks in Divisions 2GH and 3Ps. April 1999 report from the Fisheries Resource Conservation Coucil to the Minister of Fisheries and Oceans, Canada.

Gilbert, D., and B. Pettigrew. 1997. Interannual variability (1948-1994) of the CIL core temperature in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 54 (Suupl. 1): 57-67.

Hammill, M., J. F. Gosselin, F. Proust, and D. Chabot. 1999. A review of information relevant to the issue of consumption of Atlantic cod (*Gadus morhua*) by seal species in the southern Gulf of St. Lawrence. CSAS Res. Doc. 99/70.

Köster, F. W., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J. mar. Sci. 56: *in press*.

Lett, P. F. 1980. A comparative study of the recruitment mechanisms of cod and mackerel, their interaction, and its implication for dual stock assessment. Can. Tech. Rept. Fish. Aquat. Sci. No. 988.

Lett, P. F., A. C. Kohler, and D. N. Fitzgerald. 1975. The role of stock biomass and temperature in the recruitment of southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*). J. Fish. Res. Board Can. 32: 1613-1627.

Messieh, S. N. 1991. Fluctuations in Atlantic herring populations in the Northwestern Atlantic, with particular emphasis on the Gulf of St. Lawrence stocks. *In* Long-term variability of pelagic fish populations and their environment. *Edited by* T. Kawasaki, S. Tanaka, Y. Toba and A. Taniguchi. Pergamon, Oxford. pp. 155-163.

Pálsson, Ó. K. 1994. A review of the trophic interactions of cod stocks in the North Atlantic. ICES mar. Sci. Symp. **198:** 553-575.

Paz, J., and Larrañeta, M. G. 1992. Cod year-class variations and abundance of other commercial fish in NAFO Divisions 3NO. J. Northw. Atl. Fish. Sci. **14:** 129-134.

Pyper, B. J., and Peterman, R. M. 1999. Relationship among adult body length, abundance and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. Can. J. Fish. Aquat. Sci. **56:** 1716-1720.

Rudstam, L. G., Aneer, G. and Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. Dana **10:** 105-129.

Shepherd, J. G., Pope, J. G., and Cousens, R. D. 1984. VARIATIONS IN FISH STOCKS AND HYPOTHESES CONCERNING THEIR LINKS WITH CLIMATE. Rapp. P.-v. Réun. Cons. Int. Explor Mer 185: 255-267

Sinclair, A. 1996. Recent declines in cod species stocks in the Northwest Atlantic. NAFO Sci. Coun. Studies **24:** 41-52.

Sinclair, A. and L. Currie. 1994. Timing of cod migrations into and out of the Gulf of St. Lawrence based on commercial fisheries, 1986-1993. DFO Atl. Fish. Res. Doc. 94/47.

Stephenson, R. L., Power, M. J., Clark, K. J., Melvin, G. D., Fife, F. J., and Paul, S. D. 1998. 1998 evaluation of 4VWX herring. CSAS Res. Doc. 98/52.

Sutcliffe, W. H., Jr. 1972. Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian bays. J. Fish. Res. Board Can. 29: 357-362.
Swain, D. P., and G. A. Chouinard. 2000*a*. Background information on the southern Gulf of St. Lawrence cod stock for the Fisheries Oceanography Committee workshop on the cod recruitment dilemma. CSAS Res. Doc. 2000/142.
Swain, D. P., and G. A. Chouinard. 2000*b*. Spawning stock characteristics and cod recruitment success in the southern Gulf of St. Lawrence. CSAS Res. Doc. 2000/148.
Swain, D. P., and A. F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **57:** 1321-1325.
Walters, C.J. 1987. Nonstationarity of production relationships in exploited populations. Can. J. Fish. Aquat. Sci. 44: 156-165.
Walters, C. J., and Kitchell, J. F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: a serious flaw in the theory of fishing? Can. J. Fish. Aquat. Sci. **57:** in press.
Winters, G. H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence herring (*Clupea harengus harengus*). J. Fish. Res. Board Can. **33:** 1751-1763.

Table 1. Stock/recruitment analysis for southern Gulf of St. Lawrence cod, incorporating single ecosystem effects on recruitment success ($\log_e R/S$). b_S and b_C are the partial regression coefficients for *S*, cod spawning stock biomass, and for a covariate *C*. All independent variables were standardized to a mean of 0 and a standard deviation 1. *A*(1) is the first-order autoregressive parameter for the error. Results are shown both ignoring and accounting for autocorrelation. P_{DW} is the significance of autocorrelation in residuals from the model that ignores autocorrelation. R^2_{reg} gives the proportion of the variation explained by *S* and *C* after transformation to adjust for the estimated autocorrelation. R_T^2 gives the proportion of the variation accounted for by the full model, including the autoregressive error process. All *P*-values are from two-sided tests.

Covariate	Pelagic fish	Harp seals	Grey Seals	RIVSUM	Air Temp	CIL	Ice	NAO
Period	1963-94	1960-94	1968-94	1950-94	1950-94	1950-94	1963-94	1950-94
Ignoring aurocorrelation								
b_S	-0.3236	-0.3735	-0.3413	-0.4007	-0.4372	-0.4666	-0.3346	-0.4073
$P(b_S)$	0.0001	0.0008	0.0054	0.0001	0.0001	0.0001	0.0034	0.0001
b_C	**-0.4027**	0.0394	-0.0421	**0.1999**	-0.0500	0.0816	-0.0511	0.1217
$P(b_C)$	**0.0001**	0.70	0.71	**0.0138**	0.55	0.38	0.63	0.15
R^2	0.66	0.31	0.28	0.47	0.40	0.40	0.26	0.42
P_{DW}	0.0004	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Accounting for autocorrelation								
b_S	-0.3520	-0.4711	-0.4573	-0.4138	-0.4195	-0.4290	-0.4359	-0.3838
$P(b_S)$	0.0012	0.0047	0.0234	0.0052	0.0033	0.0034	0.0086	0.0068
b_C	**-0.4083**	-0.0991	-0.0971	-0.0585	-0.0745	0.0400	-0.0006	0.0649
$P(b_C)$	**0.0007**	0.71	0.66	0.36	0.12	0.51	0.99	0.27
A(1)	0.4769	0.7935	0.7376	0.7469	0.7317	0.7143	0.7455	0.7131
$P(A_{(1)})$	0.0087	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
R^2_{reg}	0.51	0.24	0.23	0.19	0.23	0.19	0.24	0.21
R_T^2	0.74	0.72	0.68	0.72	0.73	0.72	0.66	0.72

Table 2. Stock/recruitment analysis for southern Gulf of St. Lawrence cod, incorporating multiple ecosystem effects on recruitment success ($\log_e R/S$). Partial regression coefficients *b* and their significance level *P* are shown both ignoring and accounting for autocorrelation. Other symbols are as in Table 1. All independent variables were standardized to a mean of 0 and a standard deviation 1.

	S	Pelagic fish	Harp seals	RIVSUM	Air Temp.	CIL	Ice	NAO	*A*(1)
1950-94, Ignoring autocorrelation, P_{DW}=0.0001, R^2=0.52									
b	**-0.4374**	—	—	**0.2237**	-0.1458	0.0698	—	0.0616	—
P	**0.0001**	—	—	**0.018**	0.086	0.43	—	0.48	—
1950-94, Accounting for autocorrelation, R^2_{reg}=0.27, R^2_T=0.75									
b	**-0.4255**	—	—	-0.0497	-0.0721	0.0598	—	0.0776	**0.7529**
P	**0.0053**	—	—	0.44	0.14	0.32	—	0.19	**0.0001**
1963-94, Ignoring autocorrelation, P_{DW}=0.024, R^2=0.76									
b	**-0.2713**	**-0.5004**	0.1302	-0.0691	**-0.1674**	-0.0537	-0.0140	0.0330	—
P	**0.0022**	**0.0001**	0.14	0.51	**0.028**	0.55	0.86	0.73	—
1963-94, Accounting for autocorrelation, R^2_{reg}=0.63, R^2_T=0.78									
b	**-0.3154**	**-0.4785**	0.1351	-0.0677	-0.1008	0.0154	-0.0058	0.0371	0.3838
P	**0.0051**	**0.0005**	0.23	0.47	0.12	0.85	0.94	0.69	0.097

Table 3. Relationship between cod recruitment success and the date of the last appearance of ice on the Magdalen Shallows (Ice). Results are for regression analyses with $\log_e R/S$ as the dependent variable and S, Ice, Ice^2 and, in some analyses, pelagic fish biomass as independent variables. $A(1)$ is the first-order autoregressive parameter for the error. R is the number of recruits and S the spawning stock biomass that produced them. Partial regression coefficients b and their significance level P are shown.

	S	Ice	Ice^2	Pelagic fish	A(1)
A. Autocorrelation & pelagic fish ignored					
b	-0.3377	-0.0539	-0.0464	—	—
P	0.0035	0.61	0.48	—	—
B. Autocorrelation incorporated but pelagic fish ignored					
b	-0.4503	0.0087	-0.0732	—	0.7950
P	0.0053	0.88	0.033	—	0.0001
C. Autocorrelation & pelagic fish incorporated					
b	-0.3582	0.0188	-0.0761	-0.4303	0.5586
P	0.0017	0.74	0.025	0.0010	0.0029

Table 4. Stock/recruitment analysis for southern Gulf of St. Lawrence cod, incorporating effects of pelagic fish biomass on recruitment success ($\log_e R/S$). Results are shown using stock and recruitment estimates based on survey catch rates (Survey, 1971-1994) or on SPA (1963-1994), calibrated either with research survey catch rates, fishery catch rates and five sentineal survey catch rate series (SPAall) or with just the research survey catch rates (SPArv). b_S and b_C are the partial regression coefficients for S, cod spawning stock biomass, and for a covariate C, total pelagic fish biomass (herring and mackerel). Both S and C were standardized to a mean of 0 and a standard deviation 1. $A(1)$ is the first-order autoregressive parameter for the error. Significance levels are given in parentheses. R^2 gives the proportion of the variation explained by S and C after transformation to adjust for the estimated autocorrelation. R_T^2 gives the proportion of the variation accounted for by the full model, including the autoregressive error process.

	Independent Variables			
	S		*S* + *C*	
A. SPA all, 1963-1994				
b_S	-0.4358	(0.0073)	-0.3520	(0.0012)
b_C	—	—	-0.4083	(0.0007)
$A(1)$	0.7458	(0.0001)	0.4769	(0.0087)
R^2	0.24		0.51	
R_T^2	0.66		0.74	
B. SPA rv, 1963-1994				
b_S	-0.3770	(0.019)	-0.2558	(0.0071)
b_C	—	—	-0.4428	(0.0001)
$A(1)$	0.7648	(0.0001)	0.4090	(0.026)
R^2	0.18		0.54	
R_T^2	0.62		0.73	
C. Survey, 1971-1994				
b_S	-0.4626	(0.041)	-0.4532	(0.0053)
b_C	—	—	-0.6069	(0.0047)
$A(1)$	0.5272	(0.018)	0.1922	(0.39)
R^2	0.19		0.47	
R_T^2	0.41		0.55	

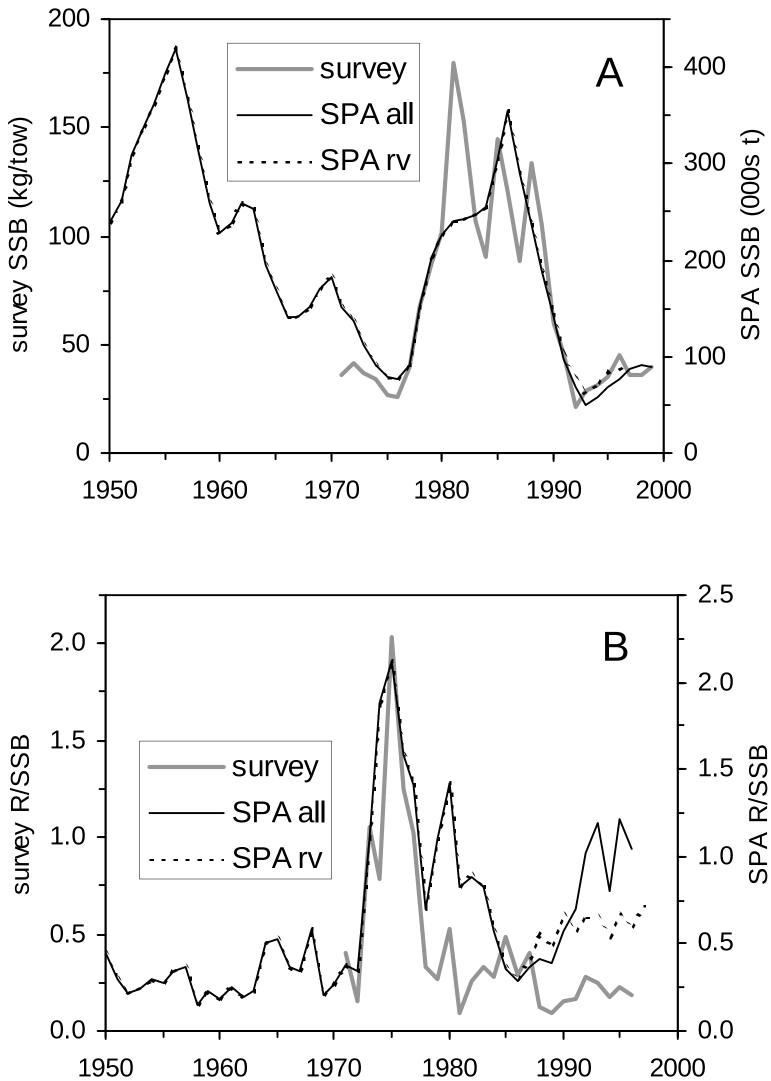

Figure 1. Time series of spawning stock biomass (A) and pre-recruit survival (B) for southern Gulf of St. Lawrence cod.

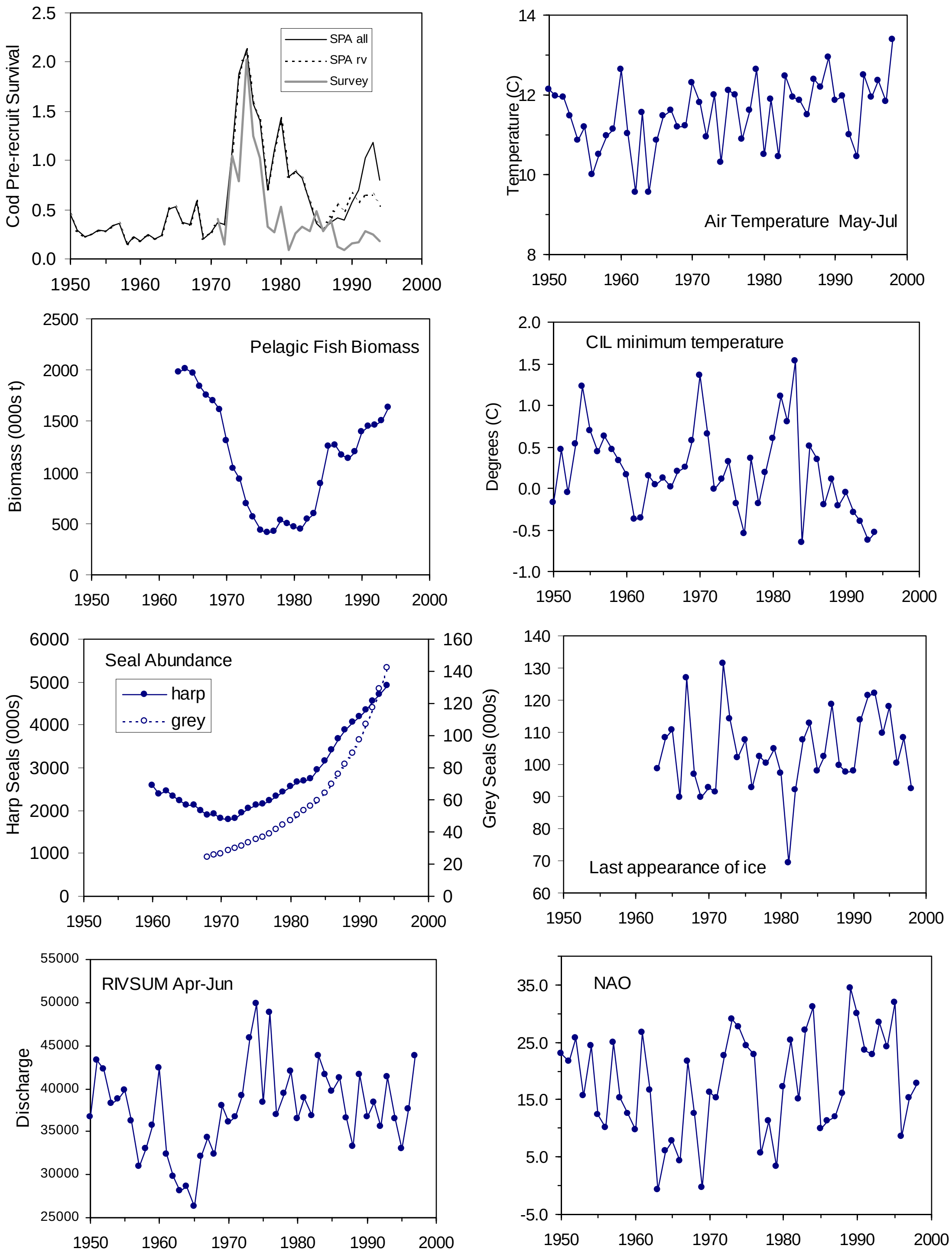

Figure 2. Time series of pelagic fish biomass (herring and mackerel) in the southern Gulf of St. Lawrence, harp and grey seal abundance, and physical environmental variables.

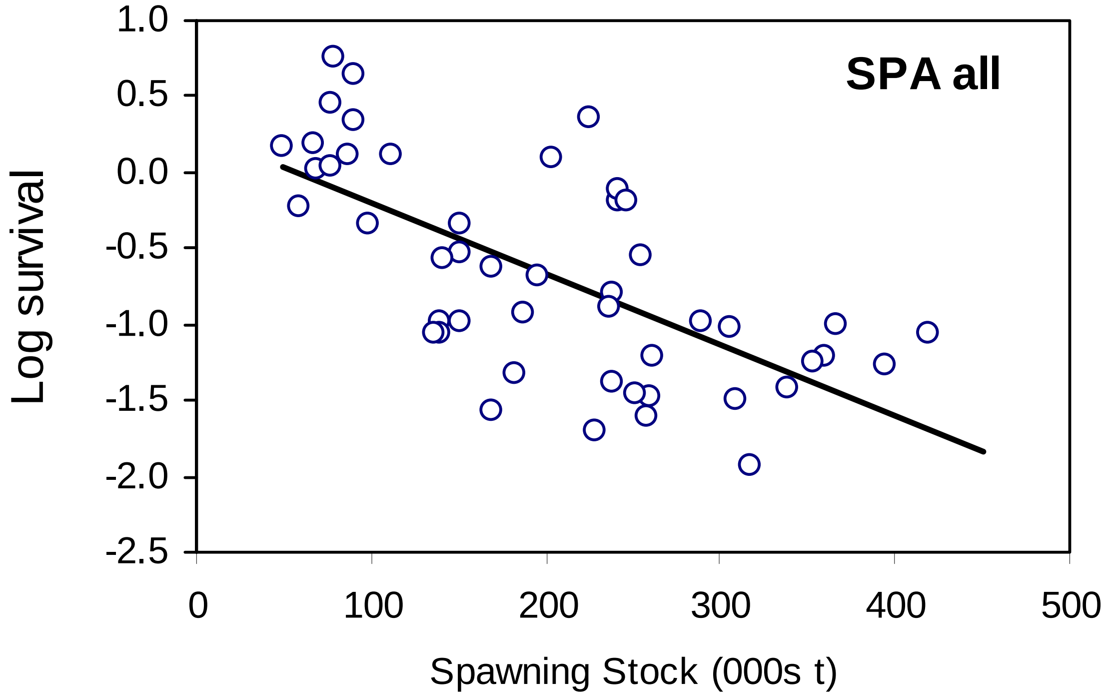

Figure 3. Relationship between log pre-recruit survival and spawning stock biomass for southern Gulf of St. Lawrence cod.

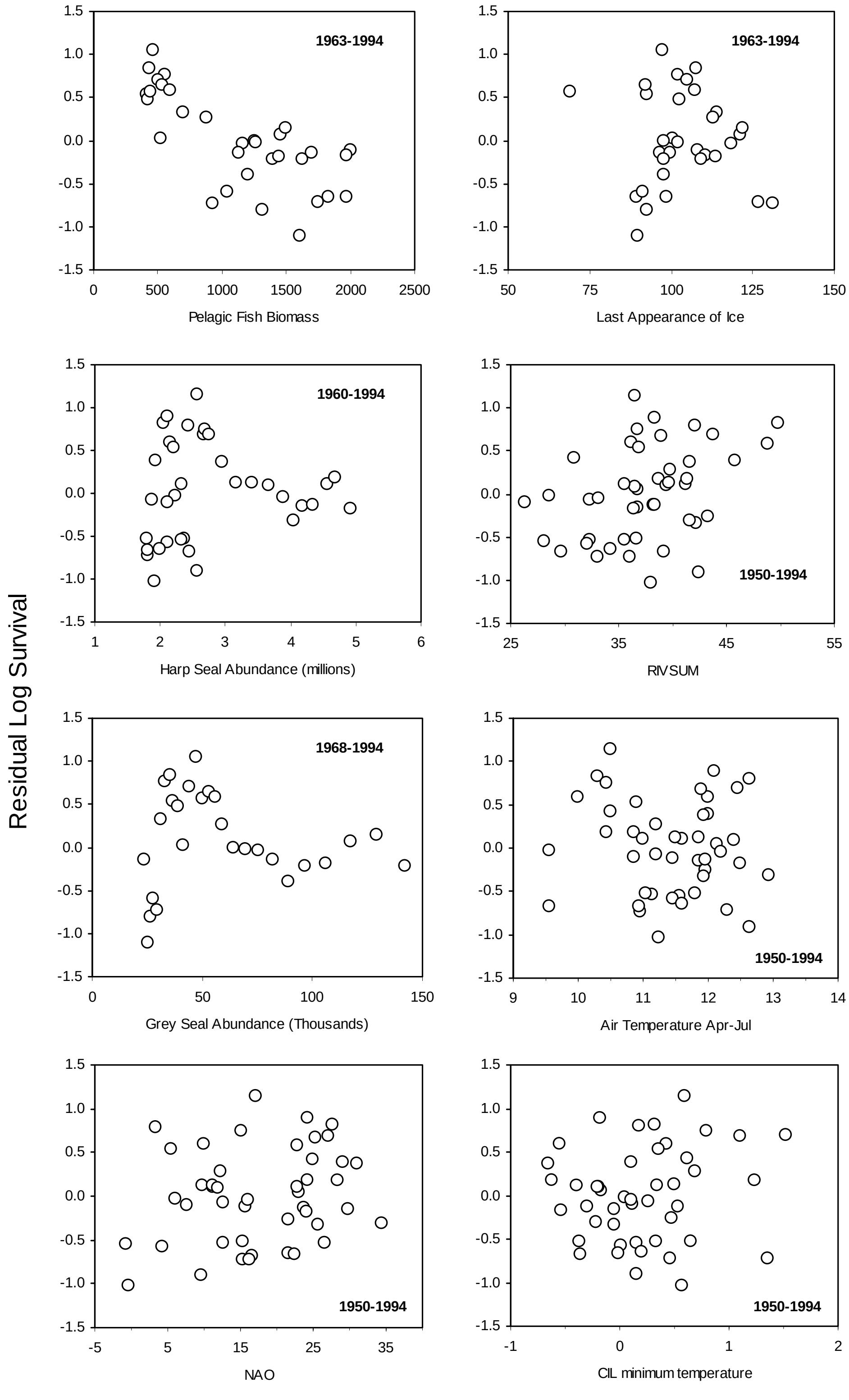

Figure 4. Relationships between ecosystem variables and residuals from the stock-recruit relationship for southern Gulf of St. Lawrence cod.

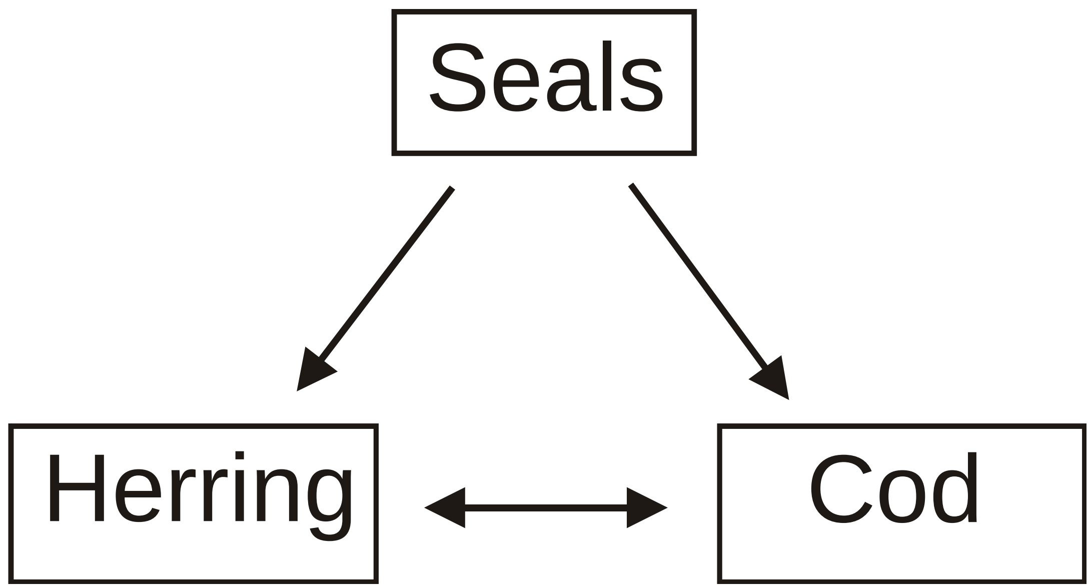

Figure 5. A triangular food web involving seals, cod and herring. Arrows point to prey species.