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Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic

D.P. Swain and A.F. Sinclair

Abstract: Like most other stocks of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic, cod in the southern Gulf of St. Lawrence declined to low abundance in the early 1990s. Recovery has been slow in contrast with the rapid recovery from similar levels of abundance in the mid-1970s. This difference reflects remarkably high prerecruit survival of cod in the earlier period of low abundance rather than unusually poor survival in the 1990s. The period of high prerecruit survival of cod coincided with the collapse of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks resulting from overfishing. These pelagic fishes are potential predators or competitors of the early life history stages of cod. We report a strong negative relationship between the biomass of these pelagic fishes and recruitment rate of southern Gulf cod. This is consistent with the recent suggestion that the success of large predatory fishes may depend on "cultivation" effects in which the adults crop down forage fishes that are predators or competitors of their young. Our results also point to the possibility of a triangular food web involving cod, seals, and pelagic fishes, making it difficult to predict the effect of a proposed cull of seals on the recovery of cod.

Résumé : Comme la plupart des autres stocks de morue (*Gadus morhua*) de l'Atlantique Nord-Ouest, le stock de morue du sud du golfe du Saint-Laurent a atteint un faible niveau au début des années 90. Son rétablissement a été lent comparativement au rétablissement rapide qui s'est produit à partir de niveaux d'abondance similaires au milieu des années 70. Cette différence s'explique par le taux de survie remarquablement élevé des pré-recrues dans la période antérieure de faible abondance plutôt que par le taux de survie inhabituellement bas dans les années 90. La période de fort taux de survie des pré-recrues a coïncidé avec l'effondrement des stocks de hareng (*Clupea harengus*) et de maquereau (*Scomber scombrus*) dû à la surpêche. Ces poissons pélagiques sont des prédateurs ou des compétiteurs potentiels de la morue dans les premiers stades de sa vie. Nous avons relevé une forte relation négative entre la biomasse de ces poissons pélagiques et le taux de recrutement de la morue du sud du golfe. Cette observation va dans le sens de l'idée récemment avancée suivant laquelle le succès des grands poissons prédateurs peut dépendre d'un « effet cultural », dû au fait que les adultes prélèvent des poissons fourrage qui sont des prédateurs ou des compétiteurs de leurs jeunes. Nos résultats suggèrent aussi l'existence possible d'un réseau alimentaire triangulaire impliquant la morue, les phoques et des poissons pélagiques, ce qui rend difficile la prévision de l'effet d'une moisson sélective des phoques envisagée sur le rétablissement de la morue.

[Traduit par la Rédaction]

Introduction

Abundance of many Northwest Atlantic cod (*Gadus morhua*) populations declined to low levels in the early 1990s, resulting in moratoria on directed fishing for these stocks. Recovery of these stocks has been slow despite severe restrictions on fishing pressure. In contrast with this slow recovery, these cod populations recovered rapidly from declines to low abundance in the mid-1970s (Sinclair 1996), even though commercial fishing continued during the earlier period of low abundance. The recent failure of depressed cod stocks to recover from low abundance despite restricted fishing mortality has been termed a "recruitment dilemma" (FRCC 1999).

In this report, we describe a strong negative relationship between pelagic fish biomass and recruitment rate of cod in the southern Gulf of St. Lawrence. We suggest that an effect of pelagic fishes on cod recruitment success may be one cause of the apparent dilemma. We also discuss implications of such an effect for management action that has been proposed to accelerate the recovery of cod in the Northwest Atlantic, namely a cull of seal populations in this area.

What is the dilemma?

Has recruitment during the recent period of low abundance been unusually low, or was it unusually high during

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D.P. Swain.[1] Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.
A.F. Sinclair. Department of Fisheries and Oceans, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9R 5K6, Canada.

[1]Author to whom all correspondence should be addressed. e-mail: swaind@dfo-mpo.gc.ca

the earlier low-abundance period? An index of juvenile or prerecruit 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 and spawning biomass, one based on the mean catch per tow in annual research vessel surveys and one estimated using sequential population analysis (SPA)[2]. The survey recruitment index was based on catches of 2- and 3-year-old cod; the SPA index was the estimated abundance of 3-year-old cod. 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), with estimates of prerecruit survival in the 1990s comparable with or above those that persisted throughout the 1950s, 1960s, and early 1970s (Fig. 1B). Instead, prerecruit survival was remarkably high from the mid-1970s to the early 1980s. Thus, at least for southern Gulf cod, the dilemma is not posed by unusually low recruitment in recent years but rather by the unusually high recruitment rate in the earlier period of low abundance. A similar pattern of remarkable prerecruit survival in the mid- to late 1970s is also evident in most other cod stocks in the Northwest Atlantic (Sinclair 1996).

Pelagic fishes and cod recruitment

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. Heavy predation on cod eggs by herring and sprat has been demonstrated in the Baltic Sea, leading to the suggestion that the recovery of the Baltic cod stock from low population sizes may be hampered by recent increases in the abundance of these pelagic fishes (e.g., Köster and Möllmann 2000). Cod eggs have also been reported from herring stomachs in the North Sea, where an increase in the recruitment of cod and other gadoids coincided roughly with the collapse of herring (*Clupea harengus*) and mackerel stocks (*Scomber scombrus*) resulting from 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 year-class strength on the Grand Bank is influenced by mackerel predation on cod eggs and larvae.

To develop a better understanding of the factors influencing cod spawning success in the southern Gulf of St. Lawrence, we have examined a variety of biotic and abiotic factors that may affect cod recruitment. On the basis of these preliminary analyses, the unusually high recruitment rate of southern Gulf cod from the mid-1970s to the early 1980s did not appear to be attributable to climatic forcing or characteristics of the spawning stock but could be accounted for by a negative effect of herring and mackerel on cod spawning success.

Evidence that herring and mackerel have affected cod recruitment in the southern Gulf of St. Lawrence

Herring and mackerel comprise the major portion of the pelagic fish biomass in the southern Gulf of St. Lawrence (Winters 1976). We used estimates of the biomass of spring- and fall-spawning herring aged 2 years and older (Fig. 1C) and of mackerel spawning biomass (Fig. 1D) based on SPA[2]. Estimates of mackerel biomass were 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, Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, 800 route de la Mer, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada, personal communication), and we constructed an index of pelagic fish biomass in the southern Gulf by adding the herring biomass to half the mackerel biomass.

Estimated herring biomass in the southern Gulf exceeded 1 000 000 t throughout the 1960s but declined precipitously in the late 1960s and early 1970s (Fig. 1C) when landings rose tenfold with the development of a new purse-seine fishery (Messieh 1991). Mackerel biomass was also high in the late 1960s and early 1970s (Fig. 1D) but then also declined sharply following the rapid expansion of a new distant-water trawl fishery in the late 1960s (Anderson and Paciorkowski 1980). The period of exceptionally low herring and mackerel biomass that resulted from these population collapses coincided closely with the period of remarkable prerecruit survival of cod (Fig. 1).

We tested for an effect of herring and mackerel biomass 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 estimates of herring and mackerel biomass in the year of spawning as the independent variables. Durbin-Watson tests rejected the hypothesis of zero lag-1 autocorrelation in the residuals from the ordinary least squares regressions in all cases (at $\alpha < 0.1$). Thus we simultaneously computed maximum likelihood estimates of the regression parameters and the first-order autoregressive parameter for the error. Analyses were conducted for two time periods: 1971–1994, when both survey and SPA estimates of *S* and *R* were available and biomass estimates are likely to be the most reliable for all three species, and 1963–1994, the entire period with SPA estimates for all three species.

The recruitment rate of southern Gulf cod was highest when both *S* and pelagic fish biomass were low (Fig. 2). Regressions of recruitment rate on *S* were improved substantially by the addition of herring, mackerel, or total pelagic biomass as a covariate, with parameter estimates for the covariate in the predicted negative direction (Table 1). Fits of regression models including *S* alone were relatively weak, with strongly autocorrelated error terms (suggesting the action of factors not included in the models). In both the SPA and survey analyses for the 1971–1994 period, addition of either herring, mackerel, or total pelagic biomass increased

[2] Data are from various stock assessment documents (and Winters (1976) for herring before 1969), a list of which may be obtained from the authors upon request.

Fig. 1. Cod stock and recruitment and pelagic fish biomass in the southern Gulf of St. Lawrence. (A) Cod spawning stock biomass, estimated by SPA (sequental population analysis, solid line) or based on catch per tow in the annual research vessel survey (dotted line). (B) Indices of cod prerecruit survival, calculated as the ratio of recruits (*R*) divided by spawning stock biomass (*S*), estimated by SPA (solid line) or survey catch per tow (dotted line). (C) Herring biomass for ages 2 years and older. (D) Mackerel spawning stock biomass.

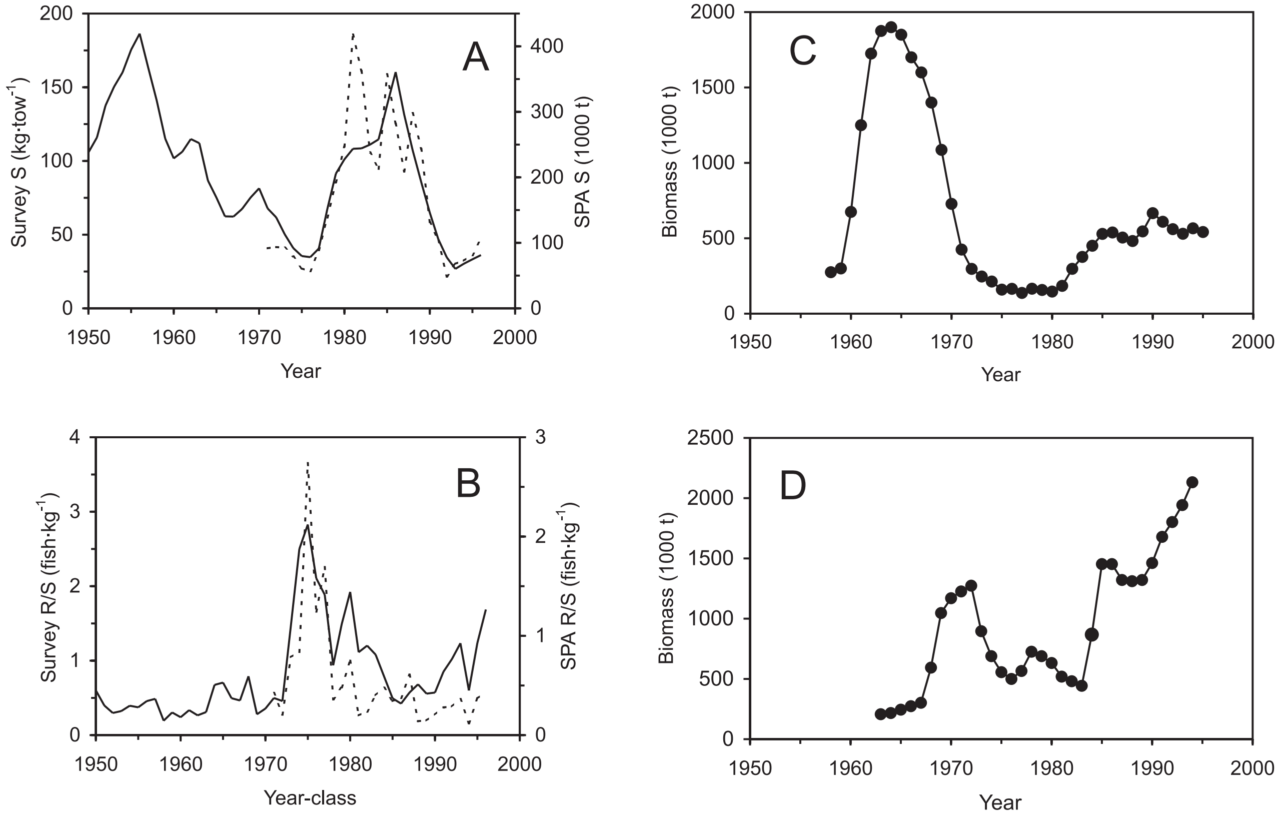


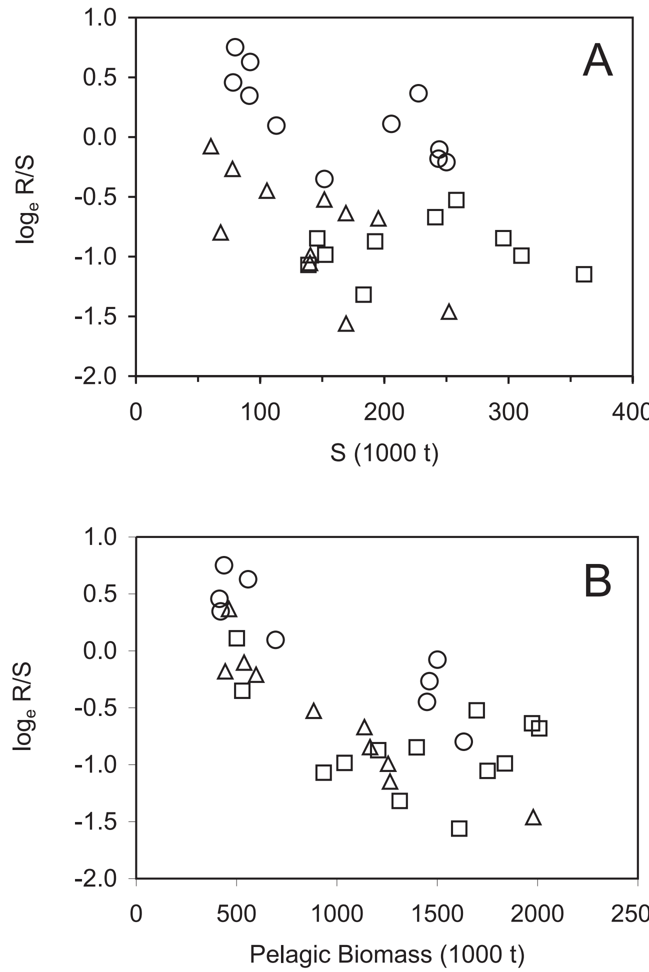
Table 1. Stock–recruitment analysis for southern Gulf of St. Lawrence cod, incorporating effects of herring and mackerel biomass on recruitment success ($\log_e R/S$).

Covariate	None		Herring		Mackerel		Total pelagic	
(A) Survey, 1971–1994								
b_S	–0.5544	(0.068)	–0.4025	(0.042)	–0.5522	(0.0042)	–0.4891	(0.0091)
b_C	—	—	–0.6076	(0.0051)	–0.6940	(0.0007)	–0.6827	(0.0009)
$A(1)$	0.6015	(0.013)	0.2209	(0.37)	0.1863	(0.43)	0.1887	(0.43)
R^2	0.18		0.43		0.53		0.52	
R_T^2	0.39		0.52		0.60		0.59	
(B) SPA, 1971–1994								
b_S	–0.5998	(0.094)	–0.3833	(0.054)	–0.5720	(0.0038)	–0.4969	(0.0094)
b_C	—	—	–0.7195	(0.0017)	–0.7435	(0.0003)	–0.7816	(0.0003)
$A(1)$	0.7471	(0.0002)	0.4168	(0.064)	0.4160	(0.053)	0.4286	(0.051)
R^2	0.15		0.50		0.57		0.58	
R_T^2	0.58		0.71		0.75		0.75	
(C) SPA, 1963–1994								
b_S	–0.6052	(0.028)	–0.4504	(0.045)	–0.6247	(0.017)	–0.4221	(0.0085)
b_C	—	—	–0.4925	(0.048)	–0.5700	(0.039)	–0.7393	(0.0001)
$A(1)$	0.7503	(0.0001)	0.5763	(0.0017)	0.7961	(0.0001)	0.4006	(0.032)
R^2	0.17		0.27		0.29		0.53	
R_T^2	0.59		0.62		0.65		0.72	

Note: b_S and b_C are the standard partial regression coefficients for *S* (cod spawning stock biomass) and for a covariate *C* (either herring, mackerel, or total pelagic biomass). $A(1)$ 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.

R^2 values by a factor of 2–4 and greatly reduced autocorrelation in the error term. For the 1963–1994 period, model improvement resulting from the addition of a term for either herring or mackerel biomass was less substantial, though either effect remained significant (two-sided $P < 0.05$). The effect of total pelagic biomass remained highly significant ($P < 0.0001$) for the 1963–1994 period, tripling the R^2 value for the regression and substantially reducing the significance of autocorrelation in the error. In all cases, addition of pelagic fish biomass to the stock–recruitment model revealed that the density dependence of prerecruit survival was also highly significant, with high survival at low spawning stock biomass. However, in most analyses, prerecruit survival was even more strongly related to measures of pelagic fish biomass than to cod spawning stock biomass (Table 1, Fig. 2).

Fig. 2. Relationships between cod recruitment rate and (A) cod spawning stock biomass *S* or (B) pelagic fish biomass in the southern Gulf of St. Lawrence. Different symbols are used for different levels of pelagic fish biomass (A) or cod spawning stock biomass (B) (low, circles; medium, squares; high, triangles). Data are for 1963–1994 and are estimated by SPA.



Discussion

Our analyses suggest a strong negative effect of pelagic fish biomass on cod recruitment success in the southern Gulf of St. Lawrence, an hypothesis proposed by Lett (1980) some 20 years ago. As in any observational study, we cannot exclude the possibility that this correlation between cod prerecruit survival and pelagic fish biomass is spurious. However, it provides a reasonable explanation (and the only explanation yet apparent) for the remarkable recruitment rate of southern Gulf cod between the mid-1970s and the early 1980s. Similar effects of pelagic fishes on cod recruitment have been proposed for the Baltic Sea (e.g., Köster and Möllmann 2000), the North Sea (e.g., Daan et al. 1994), and the Grand Bank (Paz and Larrañeta 1992). Lett's (1980) original proposal for the southern Gulf was based on data for the 1954–1972 period. Our analyses provide independent support for this proposal based on more recent data, making this one of few cases where a correlation with recruitment rate has stood the test of time.

Although predation by pelagic fishes on cod eggs and larvae has been demonstrated in other areas (e.g., Köster and Möllmann 2000), there are no data available to examine the extent of such predation in the southern Gulf. However, the opportunity for significant predation by herring and mackerel on eggs and larvae of southern Gulf cod clearly exists. Spawning by cod in the southern Gulf occurs from May to early July, and eggs and larvae are widely distributed throughout the southern Gulf in June and July. This is a period of heavy feeding by herring and mackerel in the southern Gulf, following spawning in spring and early summer. In the Baltic Sea, where predation by pelagic fishes on cod eggs has been intensively studied, estimated consumption of cod eggs by herring and sprat often exceeded estimated egg abundance (Köster and Möllmann 2000). In the southern Gulf, the ratio of pelagic fish biomass to cod spawning stock biomass exceeds that reported for the Baltic (D. P. Swain, unpublished data), suggesting that the potential for a substantial impact of pelagic fish predation on cod eggs exists in this area also.

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 (though biomass estimates from SPA must be viewed with caution for these earlier years, when sampling of the landings was less extensive and the abundance indices needed to verify SPA assumptions are lacking). Cod prerecruit survival appeared to be unremarkable in the late 1950s even though herring biomass appeared to be very low in 1958 and 1959 (Fig. 1). 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, prerecruit survival appears to be lower at high levels of cod biomass (Table 1), and cod biomass was at a high level in the mid- to late 1950s (Fig. 1). Thus, the exceptional recruitment rate of southern Gulf cod in the mid-1970s appears to reflect the combined effects of very low biomasses for both cod and pelagic fishes. Recruitment rates were lower in the early 1990s when cod biomass was low but pelagic fish biomass was high and in the late 1950s when pelagic fish biomass appeared to be low but cod biomass was high.

Recruitment rate 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, and the collapse of this population in the mid- to late 1970s may have contributed to high prerecruit survival of cod in other areas during this period, as suggested by Paz and Larrañeta (1992) for the Grand Bank. Similarly, the rapid development of purse-seine fisheries for herring in the late 1960s resulted in declines in many Northwest Atlantic herring stocks in the 1970s (Messieh 1991).

Our results are consistent with the suggestion by Walters and Kitchell (2000) 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. A consequence of these cultivation effects can be delayed depensatory decreases in juvenile survival when adult abundance is severely depleted by fishing. However, in our case, it would appear that the corollary may have been the case, with fisheries-induced collapses of pelagic fishes improving cod prerecruit survival and aiding the recovery of cod in the late 1970s.

Our results could also have implications for the recommendation that seal herds off Atlantic Canada should be reduced to promote cod stock recovery (FRCC 1999). It has been suggested that large increases in seal abundance have resulted in increased predation on cod, thus delaying stock recovery. However, 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. Manipulation of such food webs can lead to unexpected results (Bax 1998). Seals may have a direct negative effect on cod recruitment through predation on prerecruit cod. They also may have an indirect positive effect through predation on pelagic fishes, possible predators of early life history stages of cod, so that reductions in the seal herds may not lead to improved recruitment of cod. Bax (1998) emphasizes the danger of concentrating only on direct predation interactions when there are indirect interactions with the potential to reverse the direct effects. 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.

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