TOP-DOWN VERSUS BOTTOM-UP CONTROL IN OCEANIC FOOD WEBS: A

META-ANALYSIS OF COD-SHRIMP INTERACTIONS IN THE NORTH ATLANTIC

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Abstract

Predator control of lower trophic levels, or "top-down control" has been recognized as an important structuring force in terrestrial, freshwater and coastal marine food webs. Because offshore marine webs can typically not be studied using experimental techniques, there is only weak and isolated evidence that top-down control is important in the open ocean. Consequently, many marine scientists believe that environmental fluctuations that regulate productivity ("bottom-up control") represent the predominant structuring force in the open ocean.

Here we present a meta-analytic approach to analyze species interactions across the North Atlantic Ocean. We assembled all available biomass time series for a well-documented predator-prey couple, cod (*Gadus morhua*) and Northern shrimp (*Pandalus borealis*) to test whether the temporal dynamics of these populations are consistent with the "top-down" or "bottom-up" hypothesis. Eight out of nine regions showed inverse correlations of cod and shrimp biomass, supporting the top-down view. Inverse correlations were weak or absent only close to the southern range limit of both species. Meta-analysis of shrimp versus cod and shrimp versus temperature series showed that increased cod abundance (weighted mean effect size: r=-0.5) and warm ocean temperatures (r=-0.29) both limit shrimp biomass in the North Atlantic Ocean, but that cod had stronger effects overall. The effects of cod predation decreased with increasing mean ocean temperature, suggesting that these effects are not independent.

Based on these results we propose that reductions in predator populations, such as in the case of overfished cod stocks can have strong indirect effects on prey populations

in oceanic food webs. In order to further investigate this hypothesis, we establish a methodological framework to analyse species interactions from time series data.

Key words: *climate, bottom-up versus top-down control, ecosystem effects of fishing, meta-analysis, predation*

Introduction

Aquatic food webs have been studied intensively with respect to the interaction of resource ("bottom-up") and consumer ("top-down") effects on species composition and abundance. Experimental work in lakes, streams and coastal marine systems in particular showed that variations in predator populations often have cascading effects across the food web, with implications for community structure and ecosystem functioning (Carpenter and Kitchell 1985, Mazumder et al. 1990, Power 1990, Brett and Goldman 1997, Estes et al. 1998, Worm et al. 2000, Jackson et al. 2001). Unfortunately, it is not clear how the concepts that emerged from these studies can be applied to the continental shelves and the open ocean, which cover more than two-thirds of earth's surface. It has been argued that the diversity of species, and stochasticity of environmental controls in the open ocean may counter strong top-down effects (Strong 1992, Jennings and Kaiser 1998). Others argue that there is convincing evidence that predation can structure open marine as well as inshore webs (Verity and Smetacek 1996, Pace et al. 1998). This question is not only of academic interests, since oceanic food webs support most of the world's fisheries. So far, simulation models have been used as the main tool to study the ecosystem effects of fishing in the world's oceans. These have revealed that predictions

are very sensitive to the assumed balance of consumer and resource control (Walters et al. 1997, Cury et al. 2000, Bundy 2001). Consumer-controlled webs react strongly to fishing, as prey populations react rapidly to the removal of predators. Resource-controlled webs in contrast are relatively insensitive to overfishing of higher trophic levels (Walters et al. 1997). Clearly, there is a lack of empirical studies that tests these ideas and evaluates the role of species interactions in oceanic food webs. One major reason for this lack is that these systems typically cannot be studied using powerful experimental techniques such as whole lake manipulations, caging or mesocosm studies in lakes, streams or coastal marine systems.

Our approach here is to estimate the effects of species interactions using meta-analysis of time series data. The rationale is that a prevailing bottom-up regime should result in a positive correlation between predator and prey abundance, because both ultimately depend on factors that regulate productivity. In contrast, strong top-down effects should result in a consistent negative correlation among predator and prey populations (McQueen et al. 1989). A weak interaction should result in no correlation at all. In addition, strong environmental controls should result in significant correlations between population abundance and ocean temperature.

As an example, we use time series of cod (*Gadus morhua*), which has historically been a very abundant predator on forage fishes and benthic invertebrates in the North Atlantic. In the last two to three decades, cod abundance in the North Atlantic has shown strong fluctuations and rapid declines, as a result of overfishing (Myers et al. 1996, 1997). Today, many stocks are at historically low levels. We suggest that each cod stock may be viewed as the replicated realization of a large-scale, albeit unintended, predator

removal experiment. If analyzed properly, this can teach us something about how large marine ecosystems work. Observations indicate that while cod stocks declined, benthic crustaceans such as Northern shrimp (*Pandalus borealis*), crabs (*Chionocetes opilio*) and lobster (*Homarus americanus*) have increased in catches and abundance (see results). Analyses of single stocks have yielded inconsistent results on the causes of the increase in benthic prey species. Typically the increase was attributed to changes in ocean temperature, release from cod predation or both (Magnússon & Pálsson 1991, Berenboim et al. 2000, Koeller 2000, Lilly et al. 2000). In this paper, we focus on the interaction between cod and Northern shrimp, because both species occur on both sides of Atlantic, the amount and quality of available data is much better than for crab, lobster or pelagic prey species. Also, there is good direct evidence from stomach content analysis that shrimp is an important prey species of cod (Lilly 1991, Lilly and Parsons 1991, Magnússon & Pálsson 1991, Berenboim et al. 2000, Torres et al. 2000). Here, we use biomass time series of the two species as compiled by stock assessment scientists and temperature time series as compiled by physical oceanographers to estimate the interaction between shrimp, cod, and temperature. We use meta-analysis to determine if any reliable generalizations can be drawn from the available data.

There are several difficulties in carrying out a meta-analysis of population interactions from observational time-series data. First, the assumption of independence among data sets may be compromised by spatial correlation. For example, in marine fish, the recruitment between populations is correlated on a scale of approximately 500 kilometers (Myers et al. 1997). A related problem is the temporal autocorrelation within time series, which effectively reduce the true degrees of freedom that are available to test

hypotheses (Bence 1995, Pyper and Peterman 1998). This problem is commonly ignored, because most time series are short, and loss of degrees of freedom strongly reduces the power of the significance test (Pyper and Peterman 1998). We deal with this problem, by adjusting the degrees of freedom, and then combining time series from many datasets using random-effects meta-analysis, which increases the power of our analysis. Finally, measurement error is well known to attenuate correlation coefficients. Quantifying measurement error and adjusting correlation coefficients, also increases the power of the test. In this study we attempt to combine these techniques with two purposes in mind (1) To evaluate the generality of strong predator versus environmental controls of shrimp populations in the North Atlantic, (2) To develop a powerful, methodological framework which allows to analyze the strength of species interactions from time-series data.

Methods

Species

Northern shrimp (*Pandalus borealis*) is a medium-sized benthic decapod (carapace length up to 30 mm), which is most abundant in deeper (200 - 500 m), muddy habitats on the continental shelves in the North Atlantic and Pacific Oceans. This distribution is believed to be linked to a preference for cooler temperatures (1-6 ^{o}C) and soft, muddy sediments which contain large amounts of organic material on which the animals feed (Shumway et al. 1985, Ramseier et al. 2000). Maximum age is approximately 8 yr. Cod (*Gadus morhua*) is a large (up to 130 cm) and formerly very abundant demersal fish which occurs throughout the North Atlantic Ocean at depths ranging from 1 - 600 m. Maximum

age is in excess of 20 yr, although young fish (ages 2-5) constitute the bulk of the biomass in most stocks today. Cod feeds mostly on benthic crustaceans such as shrimp and crabs and smaller fish like herring or capelin. Crustaceans comprise between 30 – 90% of stomach contents in small cod (<20 cm), but usually <40% in large cod (>60 cm), which feed mainly on small forage fishes like capelin (Pálsson 1994). The ranges of Northern shrimp and cod are largely overlapping and Northern shrimp is an important diet component for cod in most regions (Table 1).

Data sources

As an initial step we used the existing NAFO (Northwest Atlantic Fisheries Organization, Dartmouth, Nova Scotia, Canada) database to look for patterns in the catches of cod and some benthic prey species, Northern shrimp, snow crab, and American Lobster. Then we collected all available time series of cod and Northern shrimp biomass from those areas in the Atlantic Ocean with substantial populations of both species (Fig. 1, Table 1). We had to exclude those time series where observations covered less than 10 years, because after treatment for autocorrelation the true sample size in those series was reduced below n=3 (see below). Whenever possible, we used research trawl survey estimates of biomass, which represent the highest quality information available. All research trawl surveys were designed incorporating a random stratified sampling strategy, although for some surveys (e.g., English Groundfish Survey), the stations were not re-randomized each year. For all data sets we collected estimates of uncertainty (when available) and details of the survey used. This information, along with the original data is available at *<www.fish.dal.ca/codshrimp.html>*. Where multiple research surveys had been

conducted within one region, we averaged across these data sets. Long-term research trawl survey data were not available for five of the northern shrimp populations, because existing research surveys were not originally designed to monitor shrimp abundance. In these cases we used a combination of biomass estimates from short-term trawl surveys and published commercial catch per unit effort (CPUE) estimates, but only if those were standardized to correct for changes in gear technology and vessel characteristics. Standardized CPUE estimates were scaled up to biomass using the point estimates produced by the trawl surveys.

Measurement error and autocorrelation

It is well known that measurement error will bias our individual estimates of the correlations towards zero. Suppose that instead of measuring the variables U and V, we measure

Equ 1 $X=U+\eta,$ $Y=V+\zeta$

Where η and ζ are measurement errors. If errors are normally distributed and independent of U and V, the relationship between the correlations $\rho(U,V)$ and $\rho(X,Y)$ can be calculated (Hedges and Olkin 1985, p.228). If estimates of the measurement error variance (σ^2_η, σ^2_ζ) can be obtained it is possible to correct for this bias using

Equ 2 $\hat{\rho}(U,V) = r_{xy} / \sqrt{\sigma_u^2 /(\sigma_u^2 + \sigma_\eta^2) \cdot \sigma_v^2 /(\sigma_v^2 + \sigma_\zeta^2)}$

We used published estimates of the estimation error variance (σ^2_η, σ^2_ζ) for research trawl surveys in the North Atlantic (Myers XXX) and for CPUE time series (Harley and Myers 2001). We took a conservative approach by assuming error variances ranging at the lower end of reported values ($\sigma^2_{error} = 0.1$ and 0.03 for cod and shrimp, respectively).

A second well-known problem in time series analysis is strong autocorrelation in many data sets, especially those dominated by low-frequency variability (Bence 1995, Pyper and Peterman 1998). This problem is similar to spatial pseudoreplication because it violates the assumption of independence among observations, which is required for most classical inference tests (Hurlbert 1984). In general, this means that a sample correlation between two autocorrelated time series has fewer degrees of freedom than assumed by the significance test. If the problem is ignored, as commonly seen in ecological papers, the test will have a Type I error rate greater than the specified α, and a significant correlation may be detected when in fact none is present. Recently, a robust method has been suggested to adjust the degrees of freedom for the sample correlation ("modified Chelton method", Pyper and Peterman 1998), which has the advantage conserving both Type I and Type II error rates. This advantage is not shared by some alternative methods, which remove autocorrelation from the data (e.g. "first-differencing", "prewhitening"), but tend to inflate Type II error rates and thus decrease the power of the hypothesis test (Pyper and Peterman 1998).

We tested for autocorrelation by correlating log-transformed population abundance in each year with abundance in years n+1, …, n+5 (lag-1 to lag-5). This revealed moderate to high autocorrelation in both cod and shrimp time series ranging

from 0.5 to 0.96 at lag-1. We adjusted degrees of freedom accordingly using the "modified Chelton" method proposed by Pyper and Peterman (1998).

Data analysis

Shrimp and cod times series were log-transformed and correlated using Pearson's correlation coefficient. Let d_i be the magnitude parameter, i.e. the "effect size", for the meta-analysis (Hedges and Olkin 1985, Cooper and Hedges 1994). The effect size in our case will be the variance stabilizing z transform of the correlation coefficient r_i. That is, our estimate of d_i is

Equ 3 $$d_i = 0.5 \cdot [\ln(1 + r_i)/(1 - r_i)]$$

If the underlying data are bivariate normal, the conditional variance of d_i is

Equ 4 $$v_i = 1/(n_i - 3)$$

where n_i is the effective sample size of the *i*th correlation. Note that this variance depends only on within-study sample size, not on the correlation parameter itself, which is a desirable property.

Now let d be the vector of estimates of effect size for each of the populations. The errors in the estimate are assumed to approximately follow a multivariate normal distribution with mean 0 and variance-covariance Σ. To test heterogeneity of the effect sizes, i.e. all d_i are equal we use the test statistic

Equ5

(Hedges and Olkin 1985, page 211) where **M** is the matrix

Equ 6

where **e** is a p-dimensional column vector of ones and M^ is the estimate of **M**. If the p

populations have the same coefficient, then the test statistic Q has an asymptotic chi-

squared distribution with p-1 degrees of freedom (Hedges and Olkin 1985, page 211). If

the values of Q are small or statistically non-significant, the estimates of the components

of **d** may be pooled.

Random effects meta-analysis

Under a random effects model the effects size d_i is not assumed to be fixed, but is itself a

random variable. This relaxes the assumption of homogenous effects sizes. When

comparing studies that were conducted in different ecosystems, this is likely more

realistic than assuming that the underlying true effect size is precisely equal across all

regions. Under a random effects model the total observed variability in the effect size

estimate d_i, contains the conditional variation v_i around each d_i, and random variation,

σ^2_δ , of the individual d_i around the mean population effect size. The unconditional

variance used in the analysis is

Equ 7 $\qquad v_i^* = \sigma^2_\delta + v_i$

We can use the Q estimated above, as an estimate of the weighted sample

estimate of the unconditional variance (Cooper and Hedges 1994, p. 275).

Spatial correlation

A final problem in combining data from various regions is that some regions may be

spatially correlated, and therefore not completely independent. This is equivalent to an

experimental situation where plots are so close to one another that they influence each

other. For many fish including cod, it has been shown that recruitment between stocks is

correlated on a scale of <500 km (Myers et al. 1997). This suggests that data sets in

regions which are <500km away may not be entirely independent. Unfortunately, to date

there is no established methodology that solves this common problem in meta-analysis,

for example by adjusting the weightings given to particular studies. Therefore, we had to

use a less powerful approach: we report both the results of the complete analysis, and

those from an analysis where those regions which were <500km from neighboring ones

were excluded from the analysis.

Testing alternative hypotheses

Using the same framework as outlined above, we analyzed correlations among cod

biomass and bottom temperature and shrimp biomass and temperature respectively. The

rationale was that cod recruitment is thought to decrease at lower temperatures (XXX),

but shrimp recruitment may be sensitive to high temperatures (Shumway et al. 1985).

Increases in temperature could send cod and shrimp on opposite trajectories, which could

be falsely interpreted as an indication of top-down effects. To test this hypothesis we

assembled long-term ocean temperature series for the depth regions that shrimp and cod distributions overlap (ca. 100 – 300 m). Data were retrieved from published oceanographic time series or oceanographic databases. In cases were only raw data were available we recalculated mean annual temperatures for 200 m depth using generalized linear modeling (RAM, DO WE HAVE A REF FOR THIS?).

Then we correlated temperature series with the log-transform of cod and shrimp biomass respectively, at a time lag of 3 years. Changes in temperature are thought to affect larval processes and recruitment in particular (Myers 1998). Under this assumption changes in adult abundance would lag several years behind temperature series. We chose a lag of three years because at this age, both cod and shrimp mature in most regions.

We were interested to test whether there are any consistent trends in the relationship between shrimp and cod and shrimp and temperature with increasing mean temperature in the study regions. We hypothesized that temperature effects may become stronger and species interactions weaker at extreme temperatures (northern or southern range limits, Myers 1998). To test this we correlated mean temperature as averaged from the temperature time series in the various study regions with the correlation coefficients r_i of the cod-shrimp and the shrimp-temperature analyses. Mean temperature was log-transformed for the analysis.

Results

Across all NAFO regions combined catches of cod showed strong inverse trends to catches of benthic prey species such as shrimp, snow crab and lobster over the last 40

years (Fig. 2). Biomass time series of 9 cod populations in the North Atlantic show order of magnitude declines of cod in the Northwest Atlantic, and fluctuating but overall more stable populations in the NE Atlantic (Fig. 3). Shrimp populations in the same areas were also fluctuating, but generally increasing over most of the time series (Fig. 3). Correlations between cod and shrimp biomass time series revealed strong negative relationships in all populations with the exception of Gulf of Maine (weak negative) and Skagerrak (strong positive) (Fig 3). These two exceptions represent also the southernmost populations of Northern shrimp in the West and East Atlantic respectively (Fig. 1, Table 2).

When we corrected for measurement error and autocorrelation in the data, correlation coefficients increased, but effective sample size decreased dramatically in all data sets (Table 3). Due to very low effective sample sizes, only one (Barents Sea data set) remained significant on its own (Table 3). When data sets were combined in a random-effects meta-analysis, the weighted mean correlation coefficient for the cod – shrimp correlation indicated a strong negative relationship ($r_{weighted}$= -0.50) which was significantly different from zero (Fig. 5a, Table 4). Meta-analysis of cod versus ocean temperature revealed a weak positive correlation ($r_{weighted}$= 0.21), which was not significantly different from zero (Fig. 5b, Table 4). In contrast, the shrimp versus temperature correlation was negative ($r_{weighted}$= -0.29) and significantly different from zero (Fig. 5c, Table 4). These results were corroborated in a subsequent analysis where the Northern Newfoundland and Northern Gulf of St. Lawrence data sets were excluded to avoid potential problems of spatial correlation (Table 5).

When we correlated shrimp-cod and shrimp-temperature correlation coefficients for each area with the mean temperature in the study region we found a non-significant trend for the shrimp-cod correlation (r=0.59, P=0.094, Fig. 6a) and no trend for the shrimp-temperature correlation (r=-0.08, P=0.833, Fig. 6b). If the analysis is restricted to those data sets that show a negative correlation between cod and shrimp (excluding the Skagerrak), the correlation between mean temperature and the shrimp-cod correlation is significant (r=0.77, P=0.025)

Discussion

Our meta-analysis suggests co-limitation of shrimp populations by predator abundance and ocean temperature. The mean effect size of cod abundance was substantially higher than the effects size for temperature. Thus may suggest that predator effects on biomass are stronger than temperature controls. This is probably the case because predation directly affects shrimp biomass whereas temperature affects recruitment (Richards et al. 1996, Myers 1998), and hence only indirectly biomass. This evidence adds generality to the notion that predators can suppress lower trophic levels in oceanic food webs, as they do in lakes, streams, and coastal waters (McQueen et al. 1989, Power 1990, Paine 1994).

Strong predation effects of Atlantic cod on invertebrates and forage fishes have been described before (Pálsson 1994, and references therein). The problem with most studies is that only single stocks were analyzed and there was usually not sufficient power to test for the significance of hypothesized relationships. Thus the evidence remained largely observational and subject to many alternative interpretations. In contrast

the combination of data sets from various regions possesses the power to detect general patterns (Myers and Mertz 1998). There is only one other study that we know of which utilized meta-analysis to detect species interactions in oceanic ecosystems (Micheli 1999). Her elegant analysis of small-scale mesocosm and large-scale time-series data arrived at similar conclusions as this study: marine pelagic food webs are structured simultaneously by strong bottom-up and top-down forces (Micheli 1999). In her analysis nutrient availability and planktivore biomass were the driving factors, whereas we focused on ocean temperature and cod biomass. Taken together, these results reconfirm that an isolated focus on primary production and abiotic controls (commonly found in biological oceanography) or on species interactions (commonly found in marine ecology) is artificial and counterproductive (Verity and Smetacek 1996). We strongly suggest that these approaches need to be combined to look at marine ecosystems in a comprehensive way. In coastal food webs this can be achieved by factorial experimentation (Menge et al. 1997, 1999, Worm et al. 1999, 2000, 2001, Lotze et al. 2001). In offshore food webs, however, we rely on the analysis of time-series data and between-system comparisons.

We recommend the following formal procedure to detect general patterns in species interactions in the ocean. (1) Use diet composition, or behavioral data to establish food-web interactions (predation on particular species or functional groups, competition among predators for similar resources), (2) assemble biomass time series for species that are likely to interact based on the diet data, (3) correct for measurement error and autocorrelation, using established methods, (4) correlate time series, and use random-effects meta-analysis to combine estimates of effect size (z-transformed correlation coefficients), (5) Examine data sets for possibility of spatial correlation, and if necessary

perform sensitivity analysis, where data sets that are spatially correlated are eliminated, finally (6) test alternative hypotheses using the same framework. We also urge scientists to make the raw data on which the analysis is based widely accessible, in order to facilitate re-evaluation and further synthesis by others.

Like all scientific methodologies, this approach has some important limitations. Meta-analysis cannot cope with fundamental inadequacies and biases in the data. As with any analysis the data must be carefully examined for inconsistencies in the methodology, violations of assumptions and influential outliers (Cooper and Hedges 1994). Finally, combining correlation coefficients cannot reveal mechanisms. This type of data analysis must be grounded in solid biological evidence that documents a link between two populations.

We feel that some important questions could be answered with this methodology. With respect to the effects of overfishing of cod, increases in other prey species should be addressed. Catch plots, such as those presented in Fig. 2, suggest that entire guilds of species may be affected by the collapse of cod stocks. Also, the effects on forage fishes such as capelin (Lilly 1991, Magnússon and Pálsson 1991) should be analyzed to gain a more comprehensive view of how the ecosystem has changed. Proposed feedback effects that inhibit recovery of cod, such as predation by forage fishes on cod eggs and larvae (Köster and Möllmann 2000, Walters and Kitchell 2001), could be analyzed. The effects of depletion of large megafauna such as sharks or turtles need to be addressed in a quantitative way (Jackson et al. 2001, Jackson and Sala 2001). Finally, interactions between changes in predation and changes in the abiotic environment have been hypothesized but remain largely unexplored so far (Sanford 1999). For example, in the

case of the classic keystone predator, upwelling-related decreases in water temperature greatly reduce predation by *Pisaster* on mussels (Sanford 1999). In this paper, we detected a trend towards decreased importance of cod predation with increasing mean ocean temperature (Fig. 6 a). we hypothesize that in warmer climates, such as the Gulf of Maine for example, the diversity of potential predators is increased and the effects of a single keystone such as cod may weaken. A comprehensive understanding of the relative roles of climate and species interactions is needed, in order to predict cumulative human effects on food-web structure and ocean climate.

Acknowledgements

References

To be added

Tables

Table 1. Summary of direct information on cod predation on *Pandalus*. Percent diet refers to the mean percentage (range in brackets) of *Pandalus* in cod stomachs by volume or weight.

Region	Percent diet	Data	Reference
Northern Newfoundland	6.7 (2.0-25.2)	1981-94	Lilly et al. 2000
Flemish Cap	5.6 (1.3-14.5)	1993-98	Rodríguez-Marín & del Río 1999
Barents Sea	7.2 (1.9-12.8)	1984-96	Berenboim et al. 2000
Flemish Cap	9.6 (ND)	1993-2000	Torres et al. 2000
Iceland	5.5 (0.6-13.3)	1980-90	Magnússon and Pálsson 1991
Skagerrak	<2 (ND)	1981	Boerje et al. 1987

Table 2. Study regions, geographical positions, mean ocean temperatures, and assessment methods for cod and shrimp biomass estimates. RS=Research survey, CPUE=Catch per unit effort, XSA=Extended Survival Analysis, SPA=???.

Region	Latitude	Longitude	Temperature	Cod	Shrimp
Labrador	55 00	-58 00	2.77	RS	CPUE, RS
Northern Newfoundland	52 30	-53 00	3.06	RS	CPUE, RS
Flemish Cap	47 30	-45 40	9.34	XSA	RS
Northern Gulf of St. Lawrence	49 50	-64 00	4.55	SPA	CPUE, RS
Eastern Scotian Shelf	44 50	-60 00	2.91	SPA	CPUE, RS
Gulf of Maine	43 30	-70 00	8.96	RS	RS
Iceland	66 30	-23 00	3.47	SPA	CPUE, RS
Barents Sea	74 00	25 00	3.92	XSA	RS
Skagerrak	57 40	7 20	6.58	SPA	XSA

Table 3. Pearson's correlation coefficients, *P*-values and sample sizes for time series correlations of shrimp and cod biomass indices. Asterisks indicate parameters that were corrected for measurement error and autocorrelation.

Region	*r*	*N*	*P*	*r**	*N**	*P**
Labrador	-0.746	23	0.000	-0.827	4.8	0.173
N. Newfoundland	-0.911	13	0.000	-0.976	3.3	0.140
Flemish Cap	-0.526	12	0.079	-0.607	6.3	0.201
N.Gulf of St. Lawrence	-0.708	19	0.001	-0.827	3.4	0.438
Eastern Scotian Shelf	-0.856	21	0.000	-0.982	3.5	0.121
Gulf of Maine	-0.131	31	0.483	-0.147	9.3	0.706
Iceland	-0.459	33	0.007	-0.630	8.2	0.094
Barents Sea	-0.412	18	0.090	-0.635	11.7	0.036
Skagerrak	0.788	11	0.004	0.808	5.0	0.192

Table 4. Random-effects meta-analysis of the full data set. Results are given for weighted mean correlations of cod versus shrimp, cod versus temperature and shrimp versus temperature. The Q statistic tests for heterogeneity of effect sizes, the z statistic tests whether the correlation coefficient is significantly different from zero.

Correlation	Q	df	P	r	z	P
Cod - shrimp	10.23	8	0.249	-0.502	-2.40	0.017
Cod - temperature	14.77	8	0.063	0.208	1.56	0.117
Shrimp - temperature	13.53	8	0.095	-0.288	-2.04	0.041

Table 5. Random-effects meta-analysis of the reduced data set. The Newfoundland and Gulf of St. Lawrence data sets were eliminated to correct for the possibility of spatial correlation.

Correlation	Q	df	P	r	z	P
Cod - shrimp	9.40	6	0.152	-0.475	-2.03	0.042
Cod - temperature	14.25	6	0.026	0.199	1.16	0.246
Shrimp - temperature	11.35	6	0.089	-0.317	-1.95	0.051

Figures and Legends

ADD MAP

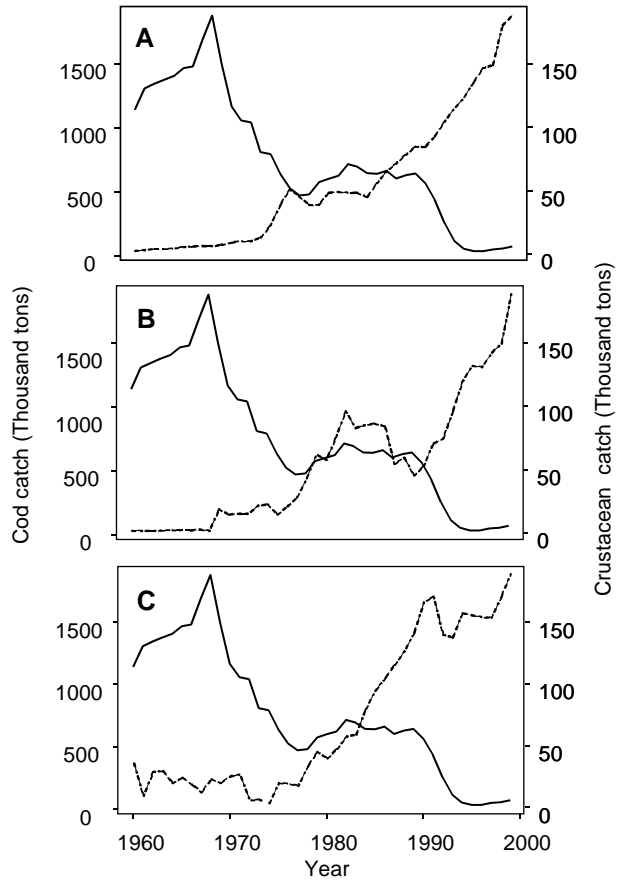Fig. 1. Study regions in the North Atlantic Ocean.

Fig. 2. Catch statistics of cod (*Gadus morhua,* continuous line) versus crustacean prey species (broken lines) in the NW Atlantic. A. Cod versus Northern shrimp (*Pandalus* sp.) and B. Cod versus snow crab (*Chionocetes opilio*), C. Cod versus American lobster (*Hommarus americanus*).
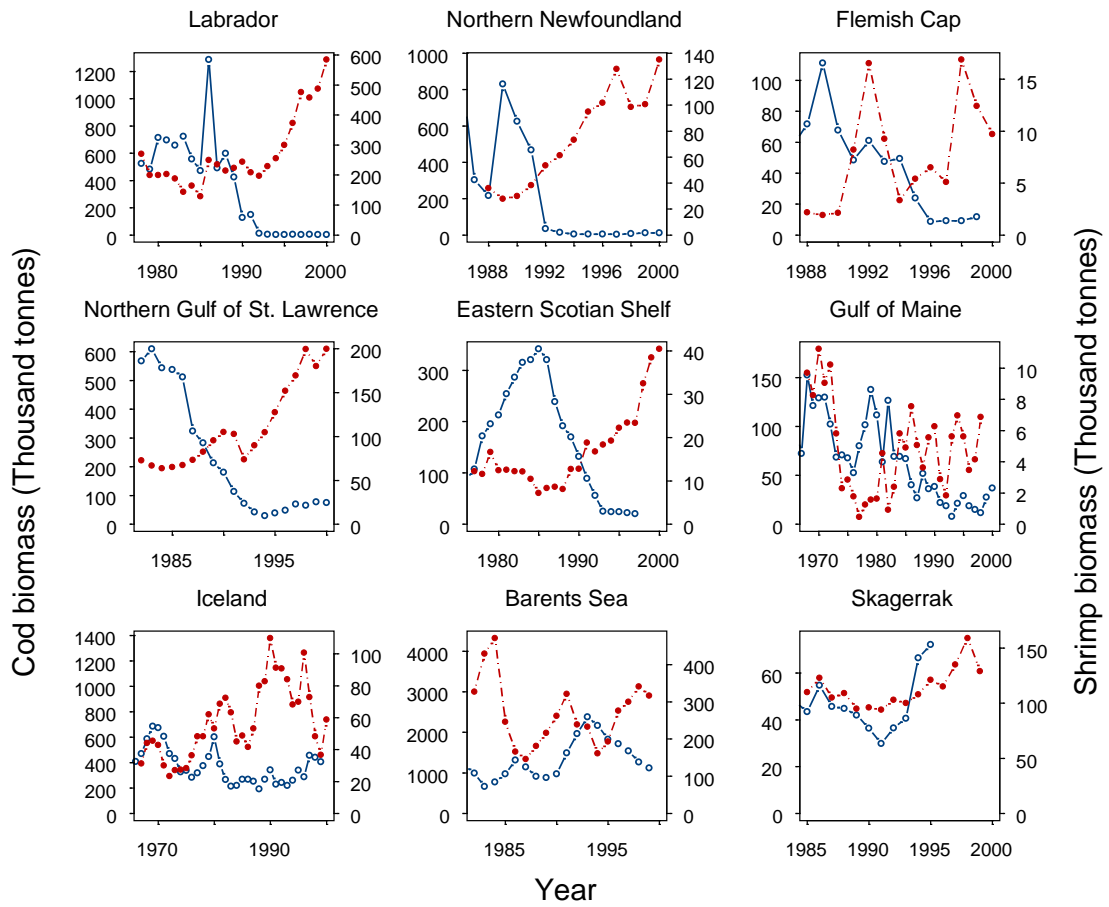
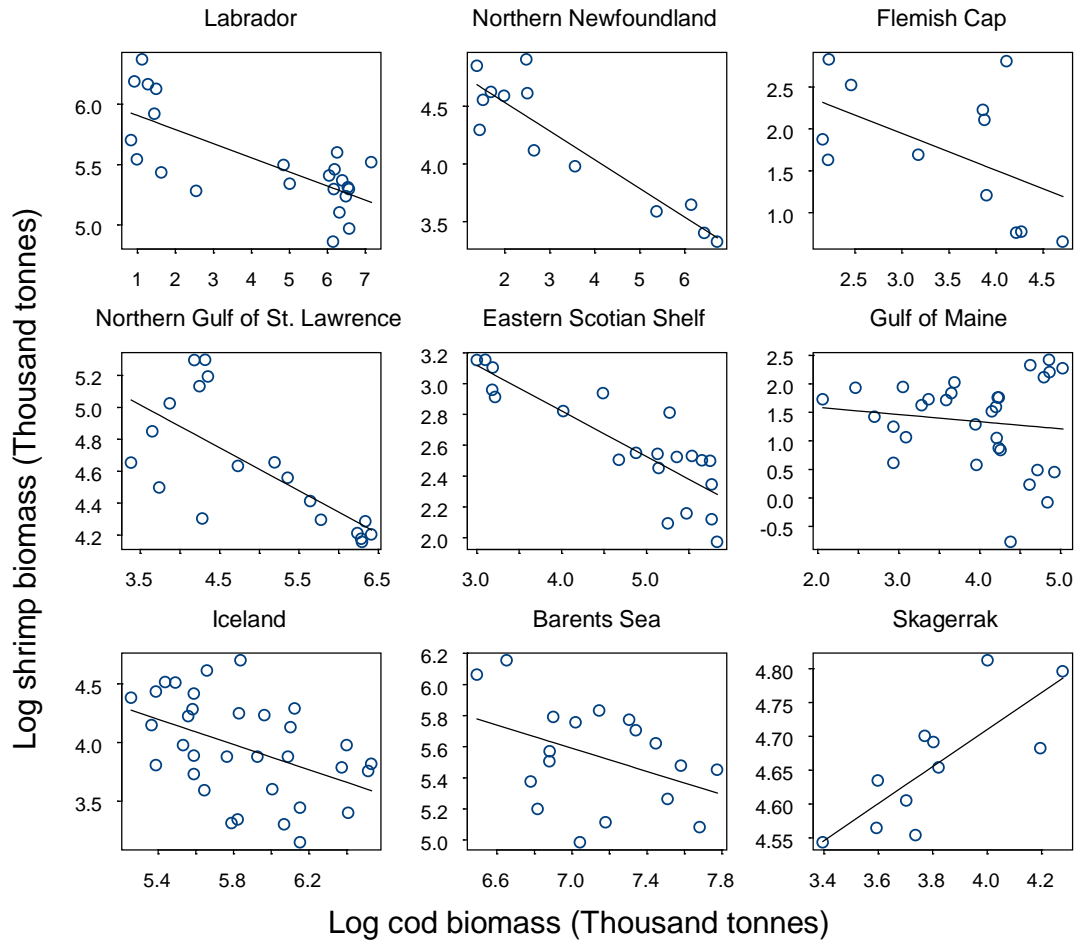Fig. 3. Cod (open symbols) and shrimp (closed symbols) biomass time series in nine regions of the North Atlantic.

Fig. 4. Linear correlation of cod and shrimp biomass time series. For analysis refer to Table 3.
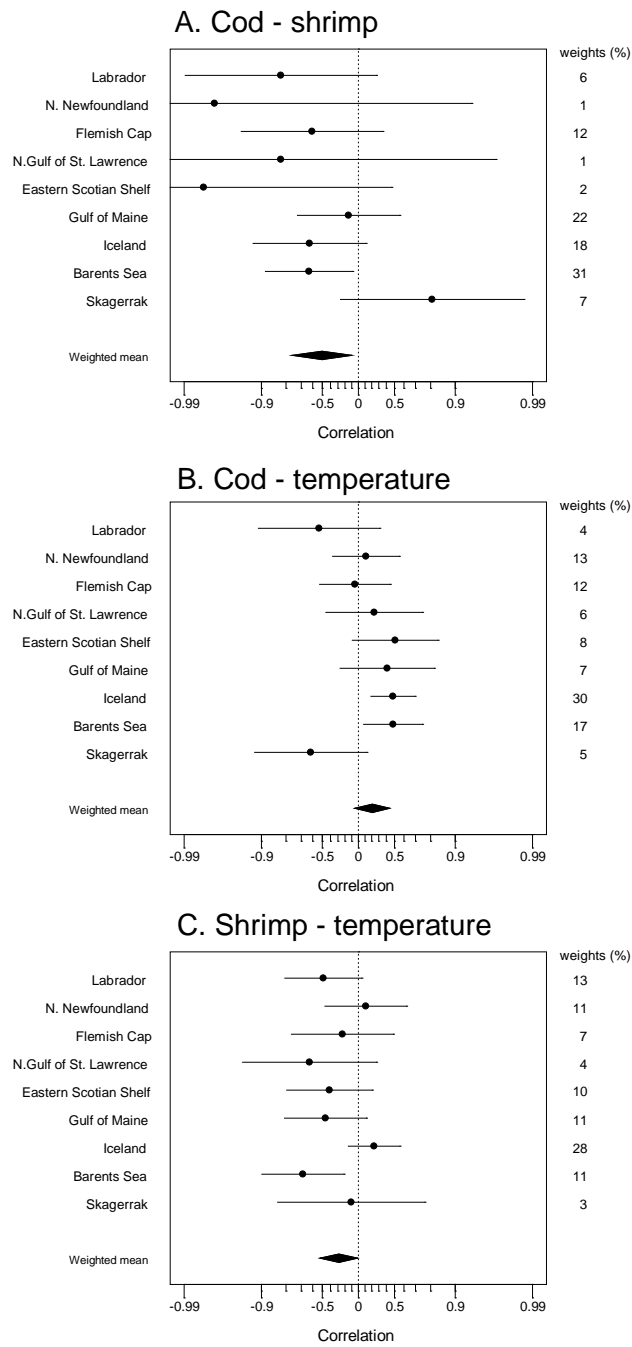
Fig. 5. Random-effects meta-analysis. (A) Cod versus shrimp, (B) Cod versus temperature, (C) Shrimp versus temperature. Also see Table 4 and 5 for analysis.
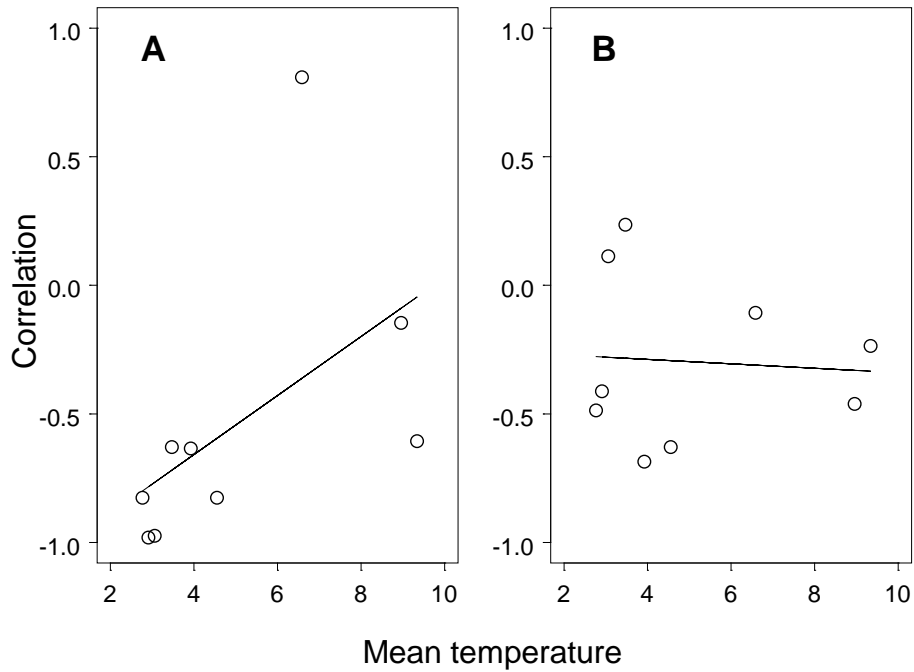
Fig. 6. Relationships between the mean temperature in the study region and (A) shrimp-cod (r=0.59, P=0.094) and (B) shrimp-temperature correlation coefficients (r=-0.08, P=0.833). Points represent individual regions, lines represent least-square linear regression fits.