

META-ANALYSIS OF COD–SHRIMP INTERACTIONS REVEALS TOP-DOWN CONTROL IN OCEANIC FOOD WEBS

BORIS WORM¹ AND RANSOM A. MYERS

Biology Department, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

Abstract. Here we present a meta-analytic approach to analyzing population interactions across the North Atlantic Ocean. We assembled all available biomass time series for a well-documented predator–prey couple, Atlantic cod (*Gadus morhua*) and northern shrimp (*Pandalus borealis*), to test whether the temporal dynamics of these populations are consistent with the “top-down” or the “bottom-up” hypothesis. Eight out of nine regions showed inverse correlations of cod and shrimp biomass supporting the “top-down” view. Exceptions occurred only close to the southern range limits of both species. Random-effects meta-analysis showed that shrimp biomass was strongly negatively related to cod biomass, but not to ocean temperature in the North Atlantic Ocean. In contrast, cod biomass was positively related to ocean temperature. The strength of the cod–shrimp relationship, however, declined with increasing mean temperature.

These results show that changes in predator populations can have strong effects on prey populations in oceanic food webs, and that the strength of these interactions may be sensitive to changes in mean ocean temperature. This means that the effects of overfishing in the ocean cascade down to lower trophic levels, as has been shown previously for lakes and coastal seas. In order to further investigate these processes, we establish a methodological framework to analyze species interactions from time series data.

Key words: Atlantic cod; bottom-up vs. top-down; climate; *Gadus morhua*; marine food webs; meta-analysis; North Atlantic; northern shrimp; overfishing; *Pandalus borealis*; predator–prey interaction; temperature.

INTRODUCTION

Aquatic food webs have been studied intensively with respect to the interaction of consumer (“top-down”) and resource (“bottom-up”) effects on species composition and abundance. Experimental work in lakes, streams, and coastal marine systems, in particular, have shown that variations in predator populations often have cascading effects across the food web, with implications for community structure and ecosystem functioning (Carpenter et al. 1985, Mazumder et al. 1990, Power 1990, Estes et al. 1998, Worm et al. 2000, 2002, Jackson et al. 2001). Unfortunately, it is not clear how the concepts that emerged from these studies can be applied to the vast continental shelves and open oceans, which cover more than two-thirds of Earth’s surface. It has been argued that high diversity of species and stochasticity of environmental controls in the ocean may counter strong “top-down” effects (Strong 1992, Jennings and Kaiser 1998). Others argue that there is convincing evidence that predation can structure oceanic as well as coastal food webs (Verity and Smetacek 1996, Pace et al. 1999). This topic is also of applied interest, because oceanic food webs support most of the world’s fisheries (Pauly and Christensen 1995). Some simulation models suggest that predictions about the ecosystem effects of fishing are very sensitive to

the assumed balance of “bottom-up” vs. “top-down” control (Walters et al. 1997, Cury et al. 2000, Bundy 2001). In these models, consumer-controlled webs respond strongly, whereas resource-controlled webs appear to be relatively insensitive to overfishing of higher trophic levels (Walters et al. 1997). Clearly, there is a lack of empirical studies that test these ideas and evaluate the role of population interactions in oceanic food webs (Jennings and Kaiser 1998).

In this paper, we focus on the trophic role of Atlantic cod (*Gadus morhua*), which has historically been a very abundant predator on smaller fishes and benthic invertebrates in the North Atlantic Ocean (Jackson et al. 2001). In the last two to three decades, cod abundance in the North Atlantic has shown violent fluctuations and rapid declines, mostly due to overfishing (Myers et al. 1996, 1997b). Today, many stocks are at historically low levels. Here we suggest that each cod stock may be viewed as a replicated realization of a large-scale, unintended predator removal experiment, which 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*), snow crabs (*Chionocetes opilio*), and American lobster (*Homarus americanus*) have increased in catches and abundance (see *Results*). Analyses of single stocks have suggested various factors that may explain the increase in benthic prey species, including changes in ocean temperature (which

Manuscript received 7 December 2001; revised 17 May 2002; accepted 26 May 2002. Corresponding Editor: O. J. Schmitz.

¹ E-mail: Boris.Worm@dal.ca

TABLE 1. Atlantic cod (*Gadus morhua*) predation on northern shrimp (*Pandalus borealis*), based on percentages of shrimp, by mass or volume, in cod stomachs.

Region	Percentage of diet			Data	Reference
	Mean	1 SE	Range		
Northern Newfoundland	6.7	1.70	2.0–25.2	1981–1994	Lilly et al. (2000)
Flemish Cap	5.8	1.90	1.3–14.5	1993–1998	Rodríguez-Marín and del Río (1999)
Flemish Cap	9.3	1993–2000	Torres et al. (2000)
Gulf of Maine	4.0	1973–1998	Link and Garrison (2002)
Barents Sea	7.2	...	1.9–12.8	1984–1996	Berenbiom et al. (2000)
Iceland	5.0	0.57	1.0–7.5	1980–1990	Magnússon and Pálsson (1991b)

Note: Data were pooled over all size classes of cod and shrimp.

might affect cod and crustaceans independently), release from cod predation, or both (Berenbiom et al. 2000, Koeller 2000, Lilly et al. 2000). The problem with single-stock studies is that true samples size and, thus, statistical power, are very low, and therefore it is often impossible to distinguish among competing hypotheses.

Our approach here is to combine all available data and analyze population interactions across the North Atlantic using meta-analysis of time series data. We focus on the interaction between Atlantic cod and northern shrimp because the amount and quality of available data are much better than for other species. Also, analyses of stomach contents confirm that northern shrimp is an important prey species of cod on both sides of the Atlantic Ocean (see Table 1). We correlate biomass time series of northern shrimp and cod, compiled by stock assessment scientists, and temperature time series, compiled by physical oceanographers, to estimate the relationships between shrimp, cod, and temperature, respectively. We distinguish among four competing predictions. (1) Strong “bottom-up” control should result in a positive correlation between predator and prey abundance because both populations depend on factors that regulate productivity. Such bottom-up control is predicted by ratio-dependent predator–prey models (Arditi and Ginzburg 1989) and some prey-dependent models (Abrams 1994), if the dominant source of variability comes from the lowest trophic levels. (2) Strong “top-down” effects should result in a negative correlation between predator and prey because predators suppress prey abundance (McQueen et al. 1989). Most predator–prey models, other than donor-controlled models (Pimm 1991), predict such a relationship if strong predator–prey relationships are assumed. (3) Weak interactions should result in weak or no correlation between populations. Many ecologists believe that this is the most common and important form of ecological interactions (Polis and Strong 1996). However, weak correlations between predator and prey are also predicted by certain prey-dependent models (e.g., Oksanen et al. 1981), if we assume that shrimp represent the second level and cod are the top predators in a tritrophic food web. (4) Strong “climate control” should result in significant correlations between pop-

ulation abundance and environmental variables, e.g., ocean temperature. Among biological oceanographers and fisheries biologists, this is the most widely accepted hypothesis to explain interannual variability in the abundance of marine species (Anderson and Piatt 1999, Hare and Mantua 2000, Myers 2002).

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 among populations is correlated on a spatial scale of ~500 km (Myers et al. 1997c). A related problem is temporal autocorrelation within time series, which effectively reduces the true degrees of freedom that are available to test hypotheses (Bence 1995, Pyper and Peterman 1998). This problem is ignored in most studies of ocean food webs (e.g., Shiomoto et al. 1997, Stefánsson et al. 1998, Reid et al. 2000) because most time series are short, and loss of degrees of freedom strongly reduces the power of the hypothesis test (Pyper and Peterman 1998). We deal with this problem by first adjusting the degrees of freedom and then combining time series from many data sets 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 accordingly further 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 vs. environmental controls of shrimp populations in the North Atlantic, and (2) to develop a powerful, methodological framework, which allows us to analyze population interactions from time series data.

METHODS

Species

The northern shrimp (*Pandalus borealis*) is a medium-sized decapod crustacean (carapace length up to 30 mm) that is most abundant in deeper (100–500 m), muddy habitats on the continental shelves in the North Atlantic and Pacific Oceans. The northern shrimp is

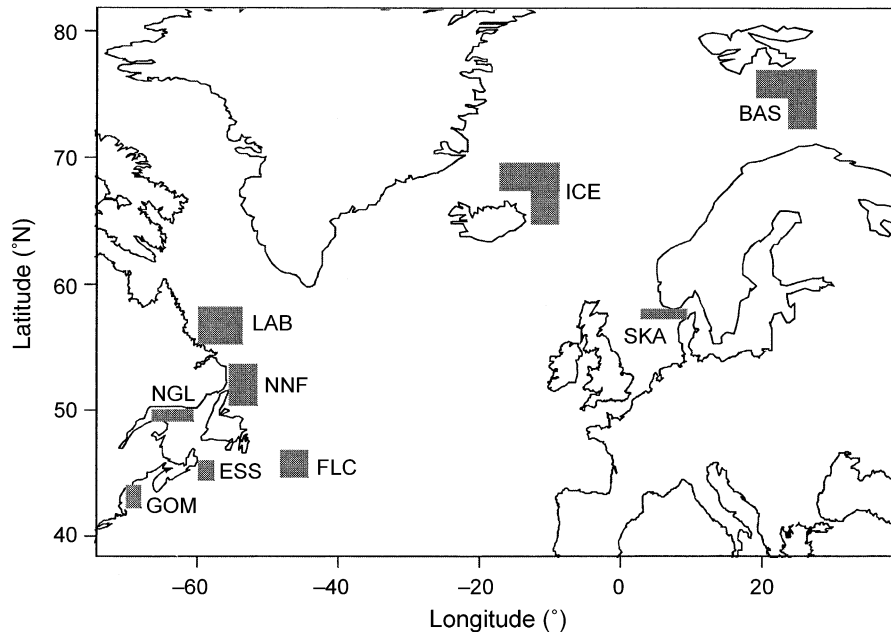


FIG. 1. Study regions in the North Atlantic Ocean. Dark gray areas represent the approximate range of shrimp stocks: BAS, Barents Sea; ICE, Iceland; SKA, Skagerrak; LAB, Labrador; NNF, northern Newfoundland; NGL, northern Gulf of St. Lawrence; FLC, Flemish Cap; ESS, eastern Scotian Shelf; GOM, Gulf of Maine.

believed to prefer cooler temperatures (1–6°C) and soft, muddy sediments containing large amounts of organic material on which it feeds (Shumway et al. 1985, Ramseier et al. 2000). Its maximum age is ~8 yr. The Atlantic cod (*Gadus morhua*, simply “cod” hereafter) is a large (up to 150 cm) and formerly very abundant demersal fish that occurs throughout the North Atlantic Ocean at depths ranging from 1 m to 600 m. Its maximum age is in excess of 20 yr, although young fish (ages 2–5 yr) constitute the bulk of the biomass in most stocks today. Cod are opportunistic feeders, but most their diet consists of benthic crustaceans such as shrimp and crabs and smaller fish such as herring (*Clupea harengus*) or capelin (*Mallotus villosus*). Crustaceans comprise 30–90% of stomach contents in small (<20 cm) cod but usually <40% in large (>60 cm) cod, which feed mainly on small pelagic fishes such as capelin (Pálsson 1994). The geographical distributions of northern shrimp and cod are largely overlapping, with the exception of Northwest Greenland and Baffin Bay (no cod), and Georges Bank, southern North Sea, and English Channel (no northern shrimp). Where the two species co-occur, northern shrimp represents an important diet component for cod (Table 1).

Data sources

As an initial step, we used the existing NAFO (Northwest Atlantic Fisheries Organization, Dartmouth, Nova Scotia, Canada) database to search for patterns in the catches of cod and some benthic prey species, northern shrimp, snow crab, and American lobster. We recognize that catch data are partly confounded

by changes in fishing effort, and therefore use catch data only to generate hypotheses about the relative abundance of populations.

To test hypotheses, we collected all available time series of cod and northern shrimp biomass estimates from areas with substantial populations of both species (Fig. 1, Table 2). We excluded those time series in which observations covered <10 yr, because after treatment for autocorrelation, the true sample size for those data was reduced below $n = 3$. We used three standard sources of abundance data: biomass estimates derived from research survey (RS) or from sequential population analysis (SPA), and catch per unit effort (CPUE) data. Whenever possible, we used research trawl survey estimates of biomass, which represent the highest quality information available. All research trawl surveys used a random stratified-sampling strategy. SPA estimates of abundance were derived from commercial catch at age data, which were standardized using research trawl survey data (Hilborn and Walters 1992). 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 published CPUE estimates, but only if those were standardized to correct for changes in gear technology and vessel characteristics. Standardized CPUE estimates were converted to biomass using the most recent biomass estimate produced by the research trawl surveys. The data set can be accessed online.²

² URL: <www.fish.dal.ca/~myers/papers.html>

TABLE 2. Study regions, geographical positions, mean temperature (1970–2000), standard error for temperature series, and assessment methods for cod and shrimp biomass estimates.

Region	Latitude	Longitude	Temperature		Assessment [†]	
			Mean	1 SE	Cod	Shrimp
Labrador	55°00'	–58°00'	0.40	0.14	RS	CPUE, RS
Northern Newfoundland	52°30'	–53°00'	1.29	0.10	RS	CPUE, RS
Flemish Cap	47°30'	–45°40'	3.07	0.12	SPA	RS
Northern Gulf of St. Lawrence	49°50'	–64°00'	4.68	0.07	SPA	CPUE, RS
Eastern Scotian Shelf	44°50'	–60°00'	2.91	0.14	SPA	CPUE, RS
Gulf of Maine	43°30'	–70°00'	8.97	0.22	RS	RS
Iceland	66°30'	–23°00'	3.15	0.18	SPA	CPUE, RS
Barents Sea	74°00'	25°00'	3.92	0.09	SPA	RS
Skagerrak	57°40'	7°20'	6.50	0.10	SPA	SPA

[†] Abbreviations for methods: RS, research survey, CPUE, catch per unit effort; SPA, sequential population analysis.

Measurement error and autocorrelation

Shrimp and cod biomass time series data from all nine regions were log-transformed and correlated using r_i , which is the Pearson’s correlation coefficient of the i th correlation. No time lags were used because we reasoned that cod predation would have an immediate effect on shrimp populations. Correlation coefficients were corrected for measurement error. It is well known that measurement error will bias our individual estimates of the correlation coefficients toward zero (Hedges and Olkin 1985:228). Instead of measuring the variables U and V , we measure

$$X = U + \eta, Y = V + \zeta \tag{1}$$

where η and ζ are measurement errors. If errors are normally distributed and independent of U and V , it is possible to correct for measurement error using

$$r'_i = r_i / \sqrt{[\sigma_u^2(\sigma_u^2 + \sigma_\eta^2)][\sigma_v^2/(\sigma_v^2 + \sigma_\zeta^2)]} \tag{2}$$

where r'_i is an estimator of the true correlation and σ_η^2 and σ_ζ^2 are estimates of measurement error variance. Here, we used published estimates of measurement error variance for North Atlantic research trawl surveys (Myers and Cadigan 1993) and CPUE time series (Harley et al. 2001). We took a conservative approach by assuming error variances ranging at the lower end of reported variances ($\sigma_\eta^2 = 0.1$ for cod and $\sigma_\zeta^2 = 0.03$ shrimp, respectively).

A second problem is caused by significant 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 (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 this is ignored, 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 Chel-

ton method”; Pyper and Peterman 1998), which has the advantage of conserving both Type I and Type II error rates. This advantage is not shared by methods that 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 $n + 1, \dots, n + 5$ (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 as described by Pyper and Peterman (1998).

In the following, we simply denote correlation coefficients corrected for measurement error and sample sizes corrected for autocorrelation with prime symbols (r'_i, n'_i).

Data analysis

Corrected correlation coefficients r'_i were combined using fixed- and random-effects meta-analysis, respectively. 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 normalizing and variance-stabilizing Fisher’s z transform of r'_i . That is, our estimate of d_i is

$$d_i = 0.5 \left[\ln \left(\frac{1 + r'_i}{1 - r'_i} \right) \right] \tag{3}$$

If the z -transformed data are bivariate normal, the conditional variance estimate of d_i is approximately

$$v_i = \frac{1}{(n_i'^2 - 1)} + \frac{4 - r_i'^2}{2(n_i' - 1)^2} \tag{4}$$

where n'_i is the effective sample size of the i th correlation (Stuart and Ord 1987:533). We recommend using this estimate rather than its commonly used approximation $v_i = 1/(n - 3)$, which greatly inflates the variance estimate at low sample sizes.

Because we combine data from multiple populations, we have k estimates (from $k = 9$ regions) of the effect size d_i and associated variances v_i , respectively. We use these to calculate an estimated weighted mean effect size \bar{d} with a confidence interval. Fixed-effect meta-analysis assumes that there is only one true value of \bar{d} , which is estimated by

$$\bar{d} = \frac{\sum_{i=1}^k w_i d_i}{\sum_{i=1}^k w_i} \quad (5)$$

where w_i represents the weight assigned to the i th study. These weights are inversely proportional to the variance in each study, i.e., $w_i = 1/v_i$. The average effect size \bar{d} has conditional variance v , which is a function of the conditional variances of each effect size being combined:

$$v = \frac{1}{\sum_{i=1}^k (1/v_i)}. \quad (6)$$

The square root of v is the standard error of estimate of the combined effect size \bar{d} . Multiplying the standard error by an appropriate critical value C_α (commonly the unit normal $C_\alpha = 1.96$, the Z statistic for a two-tailed test at $\alpha = 0.05$) and adding and subtracting the resulting product to \bar{d} yields the 95% CI for \bar{d} (Cooper and Hedges 1994:266). If the confidence interval does not contain zero, we reject the null hypothesis. Equivalently, we can test the null hypothesis with the statistic

$$Z = \frac{|\bar{d}|}{v^{0.5}}. \quad (7)$$

The null hypothesis is rejected if Z exceeds 1.96, the 95% two-tailed critical value of the standard normal distribution.

Interpretation of the results is facilitated by converting the estimates for the mean effect size \bar{d} back to the metric of a correlation \bar{r} , using the inverse of the z transform:

$$\bar{r} = (e^{2\bar{d}} - 1)/(e^{2\bar{d}} + 1). \quad (8)$$

Finally, we need to test the assumption of homogeneity of effect sizes among the different regions. Under the fixed-effects model we have presented, it is assumed that all d_i are equal and all of the observed variation in the individual d_i is due to estimation error. To test this assumption, we use the test statistic Q as given by

$$Q = \sum_{i=1}^k w_i d_i^2 - \frac{\left(\sum_{i=1}^k w_i d_i\right)^2}{\sum_{i=1}^k w_i}. \quad (9)$$

If the values of Q are small or statistically nonsignif-

icant, the estimates of effect size may be pooled. When the assumption of homogenous effect sizes is violated, one should incorporate this heterogeneity among effect sizes into a random-effects model (Cooper and Hedges 1994).

Random-effects meta-analysis

Under a random-effects model, the effect size d_i is not assumed to be fixed, but is a normal random variable. This relaxes the assumption of homogenous effects sizes. When comparing populations from many different ecosystems, this is probably a more realistic model than assuming that the true effect size is precisely the same across all populations. Under a random-effects model, the total observed variability in the effect size estimate d_i contains the conditional estimation error variance v_i and an estimate of the random variation σ_δ^2 . The unconditional variance estimate used in the analysis is

$$v'_i = \sigma_\delta^2 + v_i. \quad (10)$$

We can use the estimated Q to derive an estimate of the weighted-sample estimate of the unconditional variance (Cooper and Hedges 1994:275):

$$\sigma_\delta^2 = \frac{Q - (k - 1)}{\sum_{i=1}^k w_i - \frac{\sum_{i=1}^k w_i^2}{\sum_{i=1}^k w_i}}. \quad (11)$$

The estimates of v'_i are used to calculate the weights $w'_i = 1/v'_i$. The analysis then proceeds equivalent to the fixed-effects model as previously outlined.

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 in which plots are so close that they influence each other. For marine fish including cod, it has been shown that recruitment between stocks is often correlated on a scale of <500 km (Myers et al. 1997c). This suggests that data sets in regions that are <500 km away may not be entirely independent. Unfortunately, our data set was too small to accurately estimate the covariation among stocks and use this as a measure of spatial independence (Myers et al. 1997a). Therefore, we report both the results of the complete analysis and those from an analysis in which the regions that were <500 km from neighboring ones were excluded. Then we examine whether the results are sensitive to these manipulations.

Testing alternative hypotheses

It is widely believed that community changes in the ocean are often related to changes in ocean temperature that may cause abrupt "regime shifts" (Anderson and

Piatt 1999, Hare and Mantua 2000). As for cod and shrimp, a positive correlation among these populations could be due to similar, but independent, responses to changes in ocean temperature. A negative correlation could be due to opposite responses to changes in ocean temperature. To test these alternative hypotheses, we analyzed correlations among cod biomass and bottom temperature and among shrimp biomass and temperature, respectively. We assembled temperature time series for depth regions where shrimp and cod distributions overlap (usually 200–250 m). Data were retrieved from published oceanographic time series and the Canadian Department of Fisheries and Oceans Oceanographic Database.³ From these data, we recalculated mean annual temperatures using generalized linear modeling, with year and month as the independent variables. Then we correlated temperature series with the log-transform of cod and shrimp biomass, respectively, at a time lag of three years. Changes in temperature are thought to affect larval processes and recruitment in particular (Myers 1998). Under this assumption, changes in adult abundance will lag several years behind temperature series. We a priori chose a lag of three years because, beginning at this age, both cod and shrimp contribute to the overall biomass estimate as derived from the research survey and catch per unit effort data.

Finally, we were interested in testing whether there are any consistent trends in the relationships between cod, shrimp, and temperature with the mean temperature among study regions. We hypothesized that temperature effects may become stronger and species interactions weaker at the northern or southern range limits of species (Myers 1998). To test this hypothesis, we correlated mean temperature, as averaged from the temperature time series in the various study regions, with the correlation coefficients of the cod–shrimp, cod–temperature, and shrimp–temperature analyses, respectively.

RESULTS

Across all NAFO regions combined, commercial catches of cod showed strong inverse trends with catches of benthic prey species such as shrimp, snow crab, and lobster over the last 40 yr (Fig. 2). We hypothesize that these inverse trends indicate changes in true abundance, in addition to changes in commercial fishing effort. Biomass time series of nine cod populations in the North Atlantic showed order of magnitude declines of cod in the Northwest Atlantic, and fluctuating, but overall more stable, populations in the Northeast 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

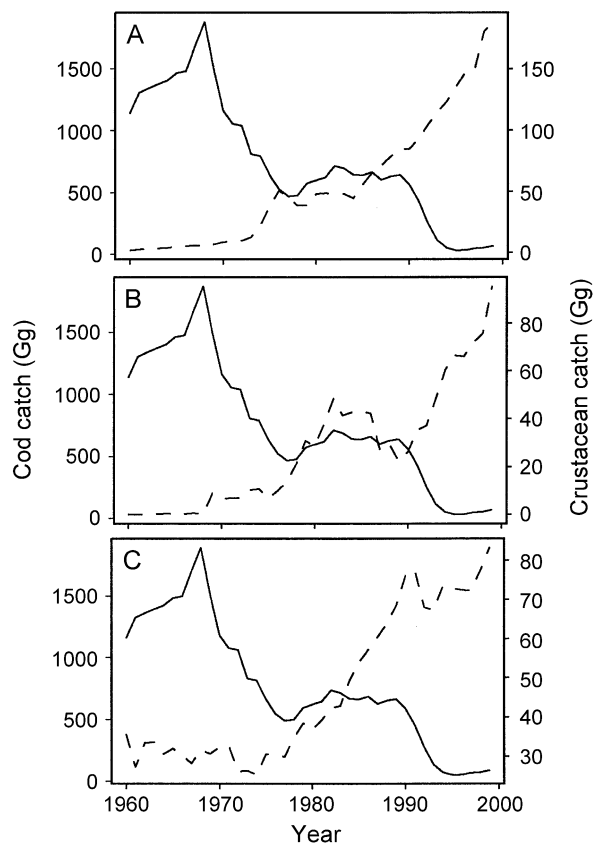


FIG. 2. Catch statistics from 1960 to 2000 for cod (*Gadus morhua*, solid line) vs. three crustacean prey species (dotted lines) in the northwest Atlantic. (A) Cod vs. northern shrimp (*Pandalus* sp.); (B) cod vs. snow crab (*Chionocetes opilio*); and (C) cod vs. American lobster (*Homarus americanus*); 1000 metric tons = 1 Gg.

negative relationships in all populations, with the exception of Gulf of Maine (weak negative) and Skagerrak (strong positive; Fig. 4, Table 3). These two exceptions also represent 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, correlation coefficients increased, but effective sample size decreased dramatically in all data sets (Table 3). Because of low effective sample sizes, only three correlation coefficients remained significant at the $\alpha = 0.05$ level (Table 3). When we combined data sets in a meta-analysis, the Q statistic indicated that the fixed-effects model was inappropriate for the cod–shrimp ($P < 0.05$) and possibly the shrimp–temperature analysis ($P < 0.2$), but not for the cod–temperature analysis ($P > 0.5$; Table 4). Because the results were not sensitive to the choice of the model (Fig. 5), we report test statistics for the more conservative random-effects model only (Table 4). The weighted mean correlation coefficients for the cod–shrimp correlation indicated a strong negative relationship ($\bar{r} = -0.64$),

³ URL: (http://www.mar.dfo-mpo.gc.ca/science/ocean/database/data_query.html)

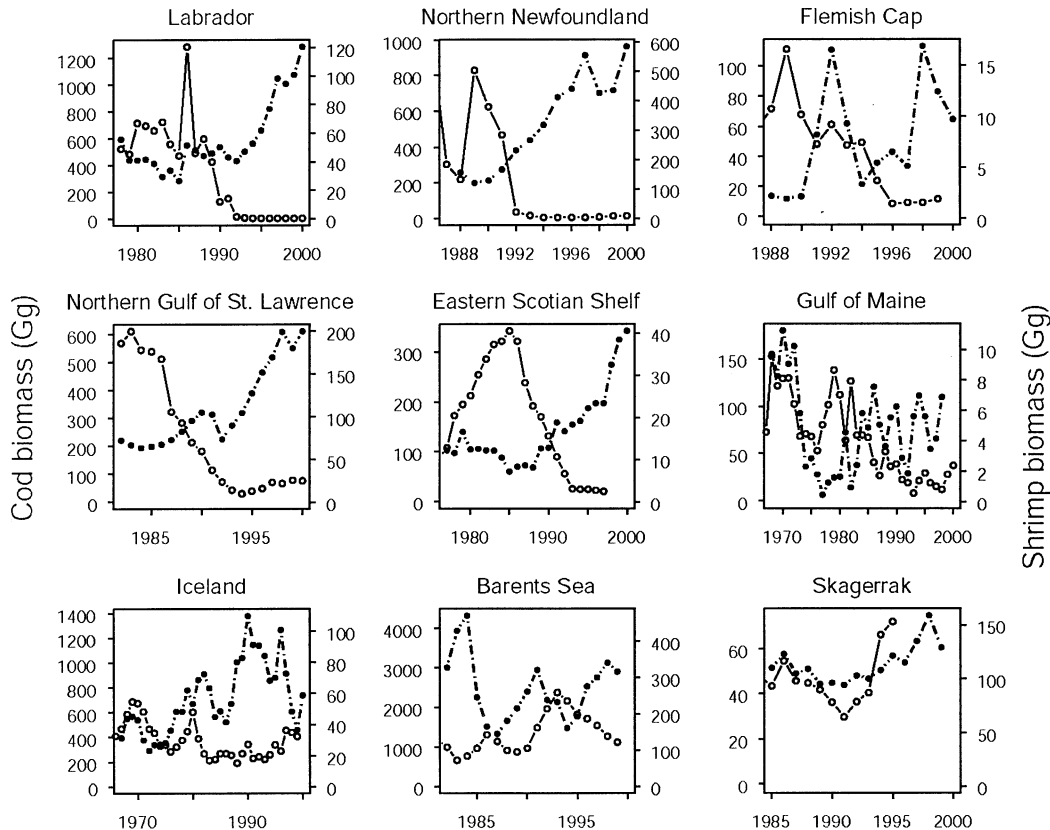


FIG. 3. Cod (open symbols, solid line) and shrimp (closed symbols, dotted line) biomass time series in the North Atlantic Ocean.

and analysis of cod–temperature revealed a strong positive relationship ($\bar{r} = 0.49$; Fig. 5A,B, Table 4a). The shrimp–temperature correlation ($\bar{r} = -0.24$) was not significantly different from zero (Fig. 5C, Table 4a). These results were corroborated in a subsequent analysis in which the northern Newfoundland and northern Gulf of St. Lawrence data sets were excluded to avoid potential problems of spatial correlation (Table 4b). The same results were obtained when the Newfoundland and Scotian Shelf data sets were eliminated.

When we correlated correlation coefficients for each area with the mean temperature in the study region, we found a significant trend for the shrimp–cod correlation, which may indicate that the relationship between cod and shrimp weakens with increasing temperature (Fig. 6A). No significant trend was found for the cod–temperature and shrimp–temperature correlations (Fig. 6B,C).

DISCUSSION

Our analysis suggests that shrimp populations across the North Atlantic Ocean are strongly inversely related to predator abundance, but not to ocean temperature. Observed strong increases in shrimp populations following the decrease in cod stocks are in accordance with a “top-down” view of marine food webs. Simi-

larly, catches of crabs and lobsters continue to increase despite high fishing pressures (Fig. 2). This may suggest that other benthic prey species respond in a similar manner to unprecedented declines in cod stocks. These results support the generalization 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). Moreover, it implies that overfishing of oceanic predators can have cascading effects on lower trophic levels. This should be of concern to fishery managers, who often adhere to single-species management, ignoring species interactions and the indirect effects of fishing (Botsford et al. 1997).

The alternative models of strong bottom-up or climate control were not supported by our meta-analysis. Predominant bottom-up control would lead to positive or weak correlations between predator and prey (depending on whether one assumes prey- or ratio-dependent predation; Arditì and Ginzburg 1989). This was only seen in two shrimp stocks at the southern end of the range (Gulf of Maine, and Skagerrak; Figs. 1 and 4). In these warmer regions, the strong dynamics shown by other stocks may be weakened by the fact that shrimp tend to hide in deep holes and trenches, and that cod are partially replaced by “southern” species

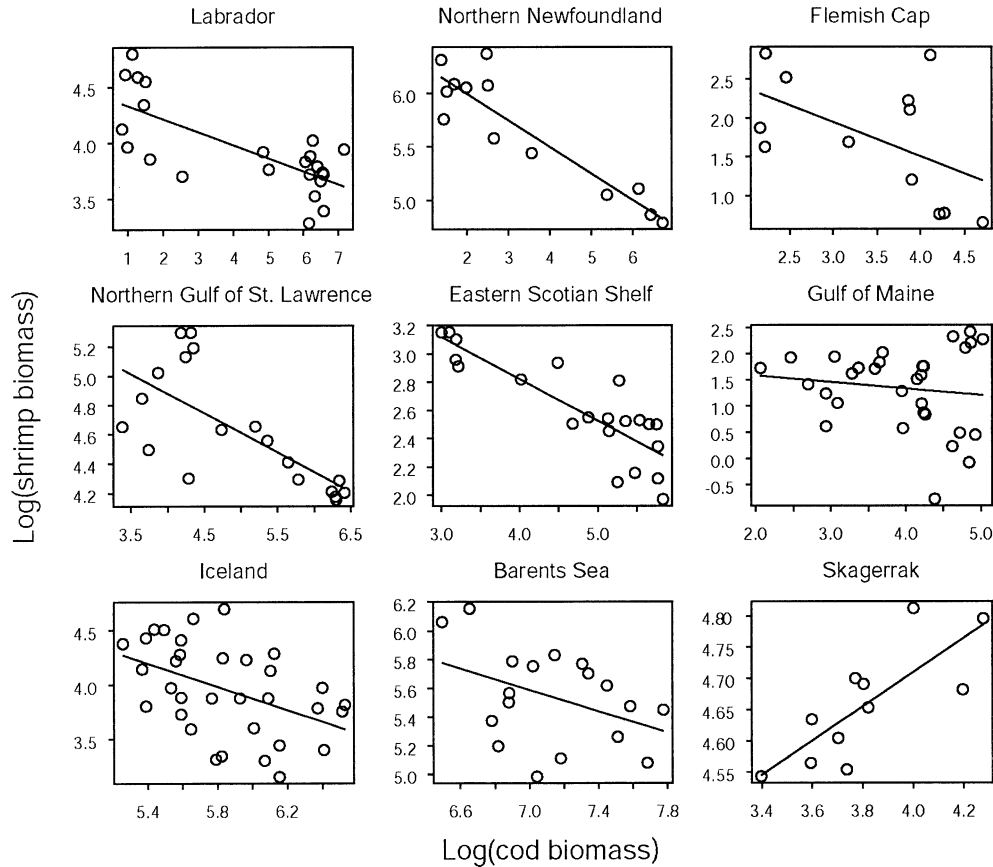


FIG. 4. Linear correlation of log-transformed cod and shrimp biomass time series. Biomass was originally measured in gigagrams. For analysis, refer to Table 3.

such as hakes. We hypothesized that the strength of top-down control by cod on shrimp is inversely related to the mean temperature in the region. Our analysis supports this hypothesis, showing a general trend of decreasing correlation between cod and shrimp with increasing mean temperature in each region (Fig. 6A). Cod biomass within each region, however, was positively correlated with temperature. This may be explained by the fact that recruitment, at least in northern stocks (Myers 1998, Planque and Frédou 1999), and somatic growth of cod (Brander 1995) increase with

temperature. Across all regions, we found no relationship between the cod-temperature correlation with mean temperature, which contrasts a more extensive analysis that demonstrated such a relationship when considering the entire range of cod in the North Atlantic (Myers 1998). Neither shrimp biomass within each region nor between regions was significantly related to temperature. This leads to rejection of the “regime-shift” hypothesis (Anderson and Piatt 1999) that the inverse trends in cod and shrimp may be caused by independent responses to climate variability. We con-

TABLE 3. Pearson’s correlation coefficients, sample sizes, and *P* values for time series correlations of shrimp and cod biomass indices.

Region	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i> †	<i>n</i> †	<i>P</i> †
Labrador	-0.746	23	0.000	-0.827	4.80	0.054
Northern Newfoundland	-0.911	13	0.000	-0.976	3.30	0.012
Flemish Cap	-0.526	12	0.073	-0.607	6.30	0.161
Northern Gulf of St. Lawrence	-0.708	19	0.000	-0.827	3.40	0.165
Eastern Scotian Shelf	-0.856	21	0.000	-0.982	3.50	0.004
Gulf of Maine	-0.131	31	0.485	-0.147	9.30	0.701
Iceland	-0.459	33	0.006	-0.630	8.20	0.075
Barents Sea	-0.412	18	0.087	-0.635	11.70	0.023
Skagerrak	0.788	11	0.002	0.808	5.00	0.061

† Parameters that were corrected for measurement error and autocorrelation.

TABLE 4. Random-effects meta-analysis, reporting the weighted mean correlation coefficients \bar{r} and the estimated random effects variance σ^2 .

Correlation	df	Q^\dagger	P	σ^2	\bar{r}	Z^\ddagger	P
a) Full data set							
Cod–shrimp	8	19.35	0.013	0.382	-0.636	-2.68	0.007
Cod–temperature	8	5.25	0.730	0.000	0.494	3.86	0.000
Shrimp–temperature	8	12.66	0.123	0.066	-0.240	-1.67	0.094
b) Modified data set§							
Cod–shrimp	6	15.58	0.016	0.360	-0.534	-2.01	0.043
Cod–temperature	6	4.16	0.654	0.000	0.375	3.94	0.000
Shrimp–temperature	6	11.07	0.086	0.082	-0.224	-1.40	0.162

† The Q statistic tests for heterogeneity of effect sizes.

‡ The Z statistic tests whether \bar{r} is significantly different from zero.

§ Newfoundland and Gulf of St. Lawrence data were removed to correct for the possibility of spatial correlation.

clude that local climate may affect the strength of the cod–shrimp relationship through its effects on cod biomass, but does not generally override these interactions.

Strong predation effects of Atlantic cod on invertebrates and forage fishes have been hypothesized before (Pálsson 1994, and references therein). The problem with these former 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 alternative interpretations. In contrast, the combination of data sets from various regions possesses the power to detect general patterns (Myers and Mertz 1998). We know only of one other study, that of Micheli (1999), utilizing meta-analysis to detect general patterns of food web interactions in the ocean. She found that phytoplankton biomass was primarily related to “bottom-up” and zooplankton biomass to “top-down” forcing in marine pelagic webs. If we assume that shrimp have a similar trophic position as zooplankton, these conclusions could be extended to benthic food webs by our analysis.

To further test this and related hypotheses for other species and ecosystems, we propose the following formal procedure: (1) Use diet composition or behavioral data to establish possible food web linkages (e.g., predation on particular species or functional groups); (2) assemble biomass time series for species that are believed to interact; (3) correct for measurement error and autocorrelation; (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 spatial correlation (Myers et al. 1997c) and adjust weightings accordingly (Myers et al. 1997a), or, alternatively, perform a sensitivity analysis in which potentially correlated data sets are eliminated; (6) test alternative hypotheses using the same framework; and (7) fit alternative models. We admit that log–log correlations represent a very simplistic mathematical model of population interactions, equivalent to a power model of the form $s = \alpha/c^\beta$, where s and c

represent shrimp and cod biomass and α and β are parameters. Although we found that this relationship worked well in our case, fitting more advanced models to the data may, in many cases, provide additional insights and predictive power (Hilborn and Mangel 1997). For example, Ives et al. (1999) fitted autoregressive models to time series data from whole-lake manipulations in order to construct pelagic interaction webs. Their approach could be made even more powerful by combining data sets through meta-analysis of time series models in which parameters are shared among populations. However, this has not been attempted yet.

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). Also, combining correlation coefficients cannot reveal mechanisms. This type of data analysis must be grounded in solid biological evidence that documents the linkages between two populations. Meta-analysis can only test for the generality of this linkage.

Despite these limitations, we feel that some important questions could be answered using the approach just outlined. With respect to the effects of overfishing of cod, trajectories of other prey species should be analyzed. Catch plots such as those presented in Fig. 2 suggest that entire guilds of species could be affected by the collapse of cod stocks. Although some of the observed pattern in Fig. 2 might be attributed to changes in effort, the magnitude, timing, and generality of the observed changes also suggest substantial increases in prey species biomass. Similar biomass increases after release from cod predation have been observed in small pelagic fishes such as capelin (*Mallotus villosus*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) (Lilly 1991, Magnússon and Pálsson 1991a, Garrison and Link 2000, Köster and Möllmann 2000, Köster et al. 2001). These changes may trigger feedback effects such as increased predation on cod eggs and

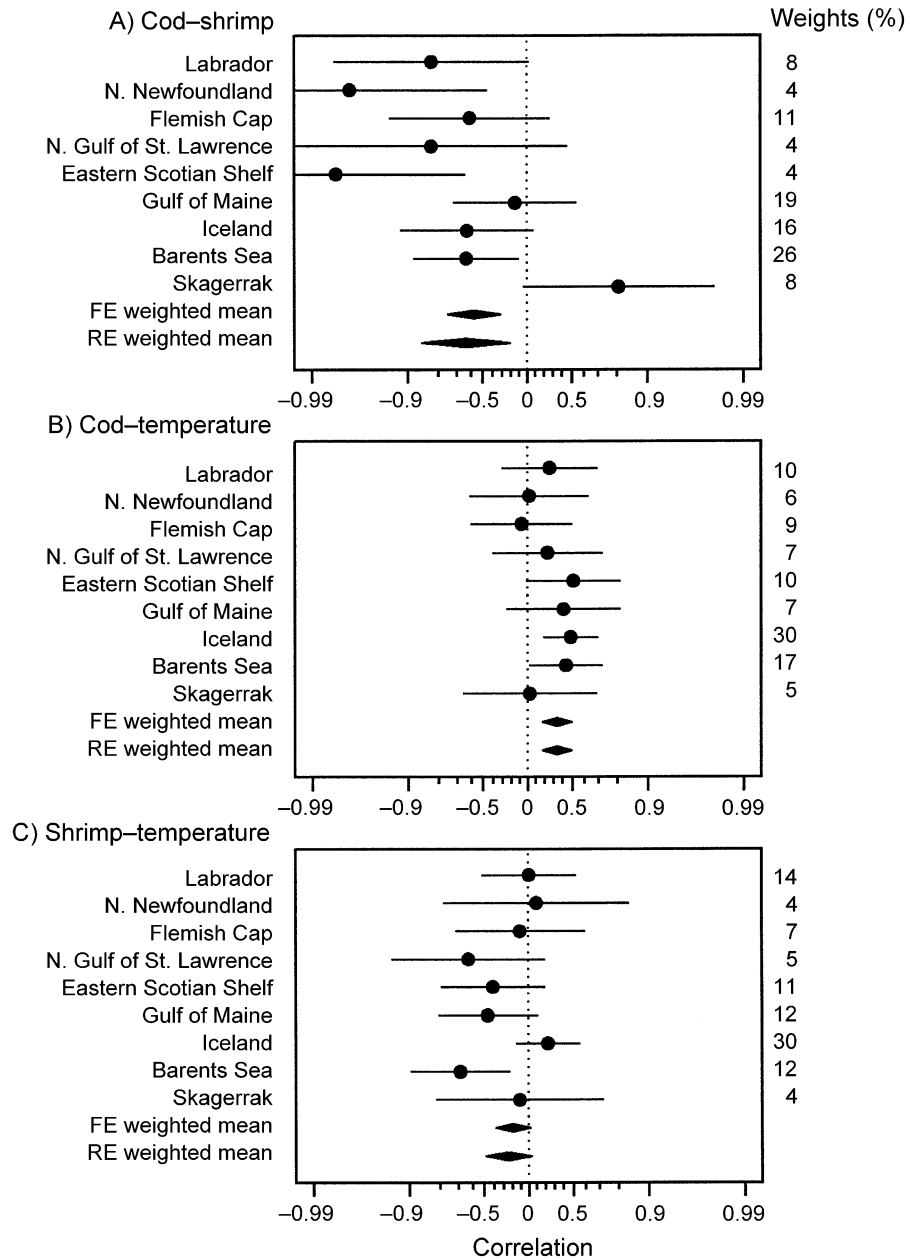


FIG. 5. Meta-analysis: (A) effects of cod on shrimp; (B) effects of ocean temperature on cod; and (C) effects of temperature on shrimp. Circles and bars represent correlation coefficients and 95% confidence intervals, respectively. The weighted mean correlations (\bar{r}) with 95% confidence limits are shown as diamonds and were calculated using a fixed-effects (FE) and random-effects (RE) model, respectively. Relative weights of individual data sets in the analysis are shown. All data were plotted on a Fisher's z scale for easier interpretation. See Table 4 for test statistics.

larvae that could inhibit recovery of cod, resulting in a permanently changed food web (Köster and Möllmann 2000, Walters and Kitchell 2001). Likewise, the ecosystem effects of overfishing large megafauna such as sharks or turtles need to be addressed in a quantitative way (Jackson et al. 2001).

In conclusion, we believe that meta-analysis of time series data provides a powerful tool to explore food

web interactions in ecosystems that are not amenable to controlled experimentation. Our present analysis exemplifies this potential by demonstrating that, despite substantial physical and biological variability in marine ecosystems, alterations of predator abundance through overfishing result in strong and general patterns of community change, and that predation appears to be a strong structuring force in the North Atlantic Ocean.

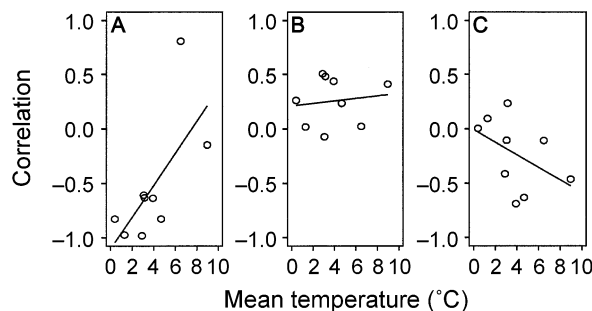


FIG. 6. Relationships between the mean temperature in the study region and (A) shrimp–cod ($r = 0.68$, $P = 0.044$), (B) cod–temperature ($r = 0.14$, $P = 0.726$), and (C) shrimp–temperature ($r = -0.46$, $P = 0.219$) correlation coefficients. Points represent individual regions, and lines represent least-square linear regression fits.

ACKNOWLEDGMENTS

We thank Nick Barrowman, Wade Blanchard, and Sonja Teichert for help with the programming, and Sean Cox, Paul Fanning, Mike Fogarty, Alain Fréchet, Lotta Fyrberg, Shelton Harley, Josef Idoine, Dan Kehler, Peter Koeller, George Lilly, Jason Link, Heike Lotze, Steve Martell, Ralph Mayo, David Orr, Vladimir Ozhigin, Don Parsons, Unnur Skúladóttir, and Carl Walters for data, discussion, and insights. Special thanks to Brian Pypers for providing the autocorrelation function. B. Worm gratefully acknowledges funding from the German Research Council (DFG Wo 818/1-1).

LITERATURE CITED

- Abrams, P. A. 1994. The fallacies of ratio-dependent predation. *Ecology* **75**:995–1004.
- Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* **189**:117–123.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator–prey dynamics: ratio dependence. *Journal of Theoretical Biology* **139**:311–326.
- Bence, J. R. 1995. Analysis of short time series: correcting for autocorrelation. *Ecology* **76**:628–639.
- Berenboim, B. I., A. V. Dolgov, V. A. Korzhev, and N. A. Yaragina. 2000. The impact of cod on the dynamics of Barents Sea shrimp (*Pandalus borealis*) as determined by multispecies models. *Journal of Northwest Atlantic Fisheries Science* **27**:69–75.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* **277**:509–515.
- Brander, K. M. 1995. The effect of temperature on growth of Atlantic cod *Gadus morhua* (L.). *Canadian Journal of Fisheries and Aquatic Sciences* **52**:1–10.
- Bundy, A. 2001. Fishing on ecosystems: the interplay of fishing and predation in Newfoundland–Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1153–1167.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**:634–639.
- Cooper, H., and L. V. Hedges. 1994. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quinones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. ICES [International Council for the Exploration of the Sea] *Journal of Marine Science* **57**:603–618.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**:473–476.
- Garrison, L. P., and J. S. Link. 2000. Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. ICES [International Council for the Exploration of the Sea] *Journal of Marine Science* **57**:723–730.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* **47**:103–145.
- Harley, S. J., R. A. Myers, and A. Dunn. 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1705–1772.
- Hedges, L. V., and I. Olkin. 1985. *Statistical methods for meta-analysis*. Academic Press, San Diego, California, USA.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, New York, New York, USA.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of field experiments. *Ecological Monographs* **54**:187–211.
- Ives, A. R., S. R. Carpenter, and B. Dennis. 1999. Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology* **80**:1405–1422.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34**:201–352.
- Koeller, P. 2000. Relative importance of abiotic and biotic factors to the management of the Northern shrimp (*Pandalus borealis*) fishery on the Scotian Shelf. *Journal of Northwest Atlantic Fisheries Science* **27**:37–50.
- Köster, F. W., H.-H. Hinrichsen, M. A. St. John, D. Schnack, B. R. MacKenzie, J. Tomkiewicz, and M. Plikshs. 2001. Developing Baltic cod recruitment models. I. Incorporation of environmental variability and species interactions. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1534–1556.
- Köster, F. W., and C. Möllmann. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES [International Council for the Exploration of the Sea] *Journal of Marine Science* **57**:310–323.
- Lilly, G. R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES [International Council for the Exploration of the Sea] *Marine Science Symposium* **193**:133–146.
- Lilly, G. R., D. G. Parsons, and D. W. Kulka. 2000. Was the increase in shrimp biomass on the Northeast Newfoundland Shelf a consequence of a release in predation pressure from cod? *Journal of Northwest Atlantic Fisheries Science* **27**:45–61.
- Link, J. S., and L. P. Garrison. 2002. The trophic ecology of Atlantic cod in the Northeast United States continental shelf ecosystem: prey distribution, prey reference and diet composition across three dynamic decades. *Marine Ecology Progress Series* **227**:109–123.
- Magnússon, K. G., and Ó. K. Pálsson. 1991a. Predator–prey interaction of cod and capelin in Icelandic waters. ICES [International Council for the Exploration of the Sea] *Marine Science Symposium* **193**:153–170.

- Magnússon, K. G., and Ó. K. Pálsson. 1991*b*. The predatory impact of cod on shrimps in Icelandic waters. ICES [International Council for the Exploration of the Sea] Council Meetings **1991/K**:31.
- Mazumder, A., W. D. Taylor, D. J. McQueen, and D. R. S. Lean. 1990. Effects of fish and plankton on lake temperature and mixing depth. *Science* **247**:312–315.
- McQueen, D. J., M. R. S. Johannes, J. R. Post, D. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecological Monographs* **59**:289–309.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* **285**:1396–1398.
- Myers, R. A. 1998. When do environment–recruitment relationships work? *Reviews in Fish Biology and Fisheries* **8**:285–305.
- Myers, R. A. 2002. Recruitment: understanding density-dependence in fish populations. In P. Hart and J. D. Reynolds, editors. *Fish and fisheries handbook*. Blackwell Scientific, London, UK, in press.
- Myers, R. A., M. J. Bradford, J. M. Bridson, and G. Mertz. 1997*a*. Estimating delayed density-dependent mortality in sockeye salmon, *Oncorhynchus nerka*; a meta-analytic approach. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2449–2463.
- Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:1576–1590.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series* **138**:293–308.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997*b*. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* **7**:91–106.
- Myers, R. A., and G. Mertz. 1998. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. *Fisheries Research* **37**:51–60.
- Myers, R. A., G. Mertz, and J. M. Bridson. 1997*c*. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1400–1407.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**:483–488.
- Paine, R. T. 1994. Marine rocky shores and community ecology: an experimentalist's perspective. Ecology Institute, Oldendorf, Germany.
- Pálsson, Ó. K. 1994. A review of the trophic interactions of cod stocks in the North Atlantic. ICES [International Council for the Exploration of the Sea] *Marine Science Symposia* **198**:553–575.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* **374**:255–257.
- Pimm, S. L. 1991. *The balance of nature?* University of Chicago Press, Chicago, Illinois, USA.
- Planque, B., and T. Frédo. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **56**:2069–2077.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* **250**:411–415.
- Pyper, B. J., and R. M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analysis of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:2127–2140.
- Ramseier, R. O., C. Garrity, D. G. Parsons, and P. Koeller. 2000. The influence of particulate organic carbon sedimentation within the seasonal sea-ice regime on the catch distribution of northern shrimp (*Pandalus borealis*). *Journal of Northwest Atlantic Fisheries Science* **27**:25–47.
- Reid, P. C., E. J. V. Battle, S. D. Batten, and K. M. Brander. 2000. Impacts of fisheries on plankton community structure. ICES [International Council for the Exploration of the Sea] *Journal of Marine Science* **57**:495–502.
- Rodríguez-Marín, E., and J. L. del Río. 1999. Length distributions and recruitment index of northern shrimp (*Pandalus borealis*) in Flemish Cap (Division 3M) in 1993–1998, as inferred from stomach contents analysis of cod (*Gadus morhua*), Greenland halibut (*Reinhardtius hippoglossoides*) and thorny skate (*Raja radiata*). NAFO SCR [Northwest Atlantic Fisheries Organization Scientific Council Research] Document **99/73**:1–14.
- Shiomoto, A., K. Tadokoro, K. Nagasawa, and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding links from pink salmon. *Marine Ecology Progress Series* **150**:75–85.
- Shumway, S. E., H. C. Perkins, D. F. Schick, and A. P. Stickney. 1985. Synopsis of biological data on the pink shrimp *Pandalus borealis* Kroyer, 1834. FAO [Food and Agriculture Organization of the United Nations] *Fisheries Synopsis* **144**:1–57.
- Stefánsson, G., U. Skúladóttir, and B. Æ. Steinarsson. 1998. Aspects of the ecology of a boreal system. ICES [International Council for the Exploration of the Sea] *Journal of Marine Science* **55**:859–862.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**:747–754.
- Stuart, A., and J. K. Ord. 1987. *Kendall's advanced theory of statistics. Volume 1. Distribution theory*. Oxford University Press, New York, New York, USA.
- Torres, P., E. Rodríguez-Marín, and I. Loureíro. 2000. Preliminary results from feeding analysis for the most abundant demersal fishes in Flemish Cap during summer (1993–2000). NAFO SCR [Northwest Atlantic Fisheries Organization Scientific Council Research] Document **0/60**:1–9.
- Verity, P. G., and V. Smetacek. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* **130**:277–293.
- Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass–balance assessments. *Reviews in Fish Biology and Fisheries* **7**:139–172.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/densification effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1–12.
- Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**:848–851.
- Worm, B., H. K. Lotze, and U. Sommer. 2000. Coastal food-web structure, carbon storage and nitrogen retention regulated by consumer pressure and nutrient loading. *Limnology and Oceanography* **45**:339–349.

Erratum

In our article, Worm, B., and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**:162-173, minor typesetting errors occurred on page 165 in Equation 3 and 4, respectively. The correct form is given below:

Our estimate of d_i is

Equation 3 $d_i = 0.5 \cdot \left[\ln \frac{(1+r_i')}{(1-r_i')} \right].$

If the z -transformed data are bivariate normal, the conditional variance estimate of d_i is approximately

Equation 4 $v_i = \frac{1}{(n_i'-1)} + \frac{4-r_i'^2}{2(n_i'-1)^2},$

Where n_i' is the effective sample size of the i th correlation (Stuart and Ord 1987, p. 533).