

Top-down and bottom-up forces interact at thermal range extremes on American lobster

Stephanie A. Boudreau^{1*}, Sean C. Anderson² and Boris Worm¹

¹Department of Biology, Dalhousie University, 1355 Oxford Street, P.O. Box 15000, Halifax, NS B3H 4R2, Canada; and ²Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

Summary

1. Exploited marine populations are thought to be regulated by the effects of fishing, species interactions and climate. Yet, it is unclear how these forces interact and vary across a species' range.

2. We conducted a meta-analysis of American lobster (*Homarus americanus*) abundance data throughout the entirety of the species' range, testing competing hypotheses about bottom-up (climate, temperature) vs. top-down (predation, fishing) regulation along a strong thermal gradient.

3. Our results suggest an interaction between predation and thermal range – predation effects dominated at the cold and warm extremes, but not at the centre of the species' range. Similarly, there was consistent support for a positive climate effect on lobster recruitment at warm range extremes. In contrast, fishing effort followed, rather than led changes in lobster abundance over time.

4. Our analysis suggests that the relative effects of top-down and bottom-up forcing in regulating marine populations may intensify at thermal range boundaries and weaken at the core of a species' range.

Key-words: American lobster, Atlantic cod, climate, meta-analysis, North Atlantic Oscillation Index, Northwest Atlantic Ocean, predation, species interactions, temperature

Introduction

In community ecology, there has been a long-standing discussion about the relative importance of bottom-up (climate and resources) and top-down (predation and herbivory) regulation of ecosystems (Oksanen *et al.* 1981; Hunter & Price 1992; Frank *et al.* 2006). For exploited species, this conceptual model is complicated by the direct effects of harvesting on the target species, as well as potential indirect effects via predator or prey release (Worm & Myers 2003; Frank *et al.* 2011). Furthermore, these ecological controls may vary or interact along different parts of a species' range. For example, top-down control of prey species is thought to be particularly strong in colder waters, attenuating at increasing temperatures (Worm & Myers 2003) or switching to bottom-up control (Frank *et al.* 2006; Frank, Petrie & Shackell 2007). Here, we present a comprehensive analysis of these interactions for a heavily exploited crustacean, the American lobster (*Homarus americanus*), throughout its entire range in the northwest (NW) Atlantic Ocean.

Crustaceans are an interesting case study because they are targeted by major commercial fisheries world-wide and are the only major invertebrate group that continues to rise in global catches (Anderson *et al.* 2011). It is unclear how much of this increase is forced simply by increasing fishing effort or by widespread shifts in community and ecosystem structure. For example, in the NW Atlantic continental shelf ecosystem there has been a well-documented shift from large-bodied groundfish to invertebrates, including crustaceans (Worm & Myers 2003; Frank *et al.* 2005). Several lines of evidence suggest that the decline of large-bodied groundfish in some regions has released large decapods, namely American lobster and snow crab (*Chionoectes opilio*), from predation (Boudreau & Worm 2010; Boudreau, Anderson & Worm 2011; Ste-neck & Wahle 2013). Commercial landings and abundance of American lobster have steadily increased since the 1980s and continue to generate large catches, particularly in the centre of their range; however, these abundance trends have since reversed in the more southern regions (ASMFC 2009). With the exception of a disease event in the late 1990s (Mullen *et al.* 2004), which impacted the southern New England (SNE) stock (Wahle,

*Correspondence author. E-mail: s.boudreau@dal.ca

Gibson & Fogarty 2009), it is unclear which factors are driving the waxing and waning of these populations. Given sharp biogeographical gradients (Wahle, Brown & Hovel 2013), it is possible that the forces acting upon lobster populations differ along the species' range (e.g. Holt & Barfield 2009).

We examined four competing hypotheses to explain variation in lobster abundance. Lobster abundance may be regulated by top-down control from (i) groundfish, resulting in negative relationships between lobster and various groundfish species abundances, or (ii) fishing effort, with increased effort reducing lobster abundance. Alternatively, lobster abundance may be regulated primarily by bottom-up forces such as (iii) changes in bottom temperature or (iv) regional climate forcing, represented here by the North Atlantic Oscillation (NAO) index. As ecological controls may act differently on various life stages and in different temperature regimes (Frank *et al.* 2006), we tested these hypotheses across biologically relevant time-lags and in relation to the strong gradients in temperature along the lobster's range.

Materials and methods

DATA

To explore statistical relationships between lobster, groundfish, fishing, temperature and climate, we compiled available lobster abundance indices and paired them with groundfish, temperature, NAO index and fishing effort time series for all major lobster fishing regions in the NW Atlantic, including both the United States (US) Eastern seaboard and Eastern Canada (Fig. 1; Table S1 in Supporting Information). These areas encompassed the entirety of the species' known range and a strong thermal gradient, from approximately 4–16 °C mean annual bottom temperature. Where possible, we used fishery-independent scientific survey and assessment data. The US Eastern seaboard included three larger regions for which trawl surveys and assessments are conducted: the Gulf of Maine (GOM), Georges Bank (GB) and SNE (Fig. 1). In addition, several states have conducted long-term nearshore trawl surveys; we included time series from Massachusetts (MA), Rhode Island (RI) and Connecticut (CT).

In contrast, there are presently no long-term survey indices available in Atlantic Canada. Hence, we tested the additional hypothesis that lobster landings can be used to approximate population trends in this species; this may be justified since high fishing pressure tends to remove a large and relatively constant fraction of new recruits each year (Fogarty 1995). The Canadian regions included Nova Scotia (NS), specifically the Scotian Shelf and Bay of Fundy [lobster fishing areas (LFA) 27–36, 38], southeast Newfoundland (NL) (LFAs 10 and 11) and the southern Gulf of St. Lawrence (SGSL) (LFAs 23–26A and 26B). We first regressed lobster landings against existing abundance and biomass indices (Table S2 in Supporting Information) from trawl surveys in a linear model on a log–log scale to test the hypothesis that abundance can be predicted from landings data for these fisheries. We included available fishery-independent data (1999–2010) from NS, as well as longer-term data from National Marine Fisheries Service (NMFS) research-survey abundance for SNE, GOM and GB. For state-run surveys in

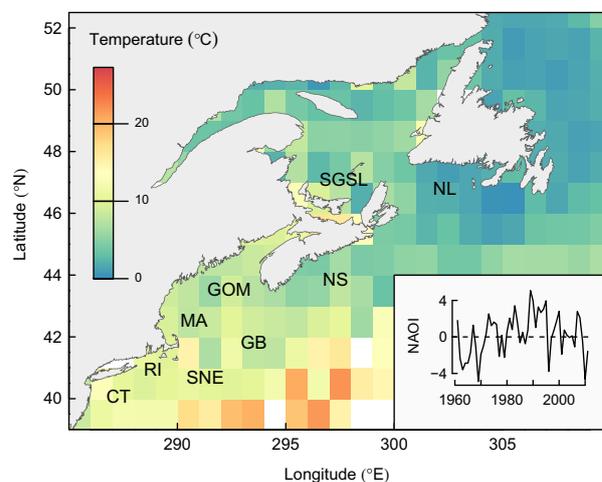


Fig. 1. Study regions. To illustrate gradients in ambient temperature, we overlaid the median temperature across all recorded temperature samples from a depth of 0–100 m at $1^\circ \times 1^\circ$ resolution between 1 January 2005 and 1 January 2012. SGSL, southern Gulf of St. Lawrence; NL, Newfoundland; NS, Nova Scotia/Bay of Fundy; GOM, Gulf of Maine; GB, Georges Bank; SNE, southern New England; MA, Massachusetts; RI, Rhode Island; and CT, Connecticut. Insert shows the leading climate index for the region, the North Atlantic Oscillation (NAO) Index (December–March). Temperature data were accessed from the Fisheries and Oceans Canada Ocean and Ecosystem Science's Hydrographic Climate Database on May 5 2014 (<http://www.bio.gc.ca/science/data-donnees/base/data-donnees/climate-climat-eng.php>).

MA, RI and CT, the standardized survey abundance index was similarly correlated with landings recorded by these states.

We spatially and temporally matched lobster abundance indices (USA) and landings (Canada) with estimates of an ecosystem index represented by groundfish abundance from research surveys conducted by the NMFS and the Canadian Department of Fisheries and Oceans (DFO) as closely as the available data sources allowed. Specifically, in USA regions, we matched lobster abundance with predator research-survey abundance (# tow⁻¹). For Canadian regions, we matched lobster landings with groundfish research-survey biomass (kg tow⁻¹). In MA, RI and CT, a survey-based index of abundance is available from the Atlantic States Marine Fisheries Commission (ASMFC) (mean catch per tow summed for 53–228 mm carapace length). For SNE, GOM and GB, a fisheries assessment is conducted, which provides an estimate of total abundance. Here, we used output from the University of Maine model (abundance, millions), which assimilates both trawl survey and landings data (Chen, Kanaiwa & Wilson 2005; ASMFC 2009).

We selected groundfish species based on existing stomach content data bases (i.e. the top 10 predators of lobster documented in Hanson & Lanteigne 2000; Comeau *et al.* 2008; Boudreau & Worm 2010), with some additional species selected because they were identified as potential predators on lobster by regional experts (Table S3 in Supporting Information). Cod was included in all regions except SGSL due to lack of evidence of predation on lobster (Hanson & Chouinard 2002) and in CT due to scarcity of records (State of Connecticut Department of Energy & Environmental Protection (CTDEEP) 2012). The abundance indices of the selected species were summed for each region to produce a

synthetic predator abundance ecosystem index. The suite of species included teleost groundfish, small demersal sharks and skates, collectively referred to as 'groundfish'. The groundfish indices for the SNE, GOM and GB were provided by the Northeast Fisheries Science Centre (NEFSC), with the SNE lobster indices being paired with the Mid-Atlantic Bight. In Canada, the research surveys were obtained from the Department of Fisheries and Oceans' ecosystem trawl survey, and indices for each State (CT, MA, RI) were obtained from state-run surveys (Table S1 in Supporting Information). We also explored individual species correlations with lobster abundance at lags 0–8 years.

We extracted bottom temperature data from trawl surveys (RI, CT) and the DFO hydrographic climate data base (all other regions; Gregory 2004). We extracted temperature at depth ranges of 0–50 m for GOM, SNE, NS and SGSL (DFO 2006, 2007; ASMFC 2009). To reflect the distribution of lobsters in NL and GB (ASMFC 2009; DFO 2009), we used depths of 0–40 and 100–300 m, respectively. Since MA is divided into GOM and SNE stock groups, we used the average temperature of these two regions for MA. We assumed that broad-scale climate conditions were reflected in the NAO index (December–March), which represents the difference of normalized sea-level pressure between Portugal and Iceland (Hurrell 1995). The NAO index reflects the dominant weather pattern in the North Atlantic region and captures decadal trends in climate and physical oceanography (Hurrell 1995). Support of the NAO's influence on ecological processes has been building in recent decades (Visbeck *et al.* 2001; Drinkwater *et al.* 2003; Fogarty & Gendron 2004). We obtained the index from 1950 to 2013 from the National Center for Atmospheric Research (Hurrell 2013). To assess the effects of fishing effort, we used the number of reported traps (ASMFC 2009) in the USA, with the exception of RI which was excluded due to a short time series ($N = 8$). In Canada, we used the total number of licenced traps for the SGSL, NS and NL. Since the fishing power of traps and hauling patterns of individual harvesters may have changed through time in the Canadian regions (Fisheries Resource Conservation Council 2007), we also considered an alternative analysis where we excluded the Canadian regions from the effort analysis.

DATA TRANSFORMATION AND STANDARDIZATION

We log-transformed the lobster, predator, effort and temperature data to fit our models on a multiplicative scale. While it is difficult to correctly age lobsters, there is a consensus that recruitment into the fishery occurs at around age 7 and that it is therefore necessary to incorporate time-lags of 6–9 years into predictive models that relate larval or settlement processes to catches or changes in adult abundance (Flowers & Saila 1972; Drinkwater *et al.* 1996; Acheson & Steneck 1997; Wahle, Incze & Fogarty 2004; Wahle, Gibson & Fogarty 2009). We therefore lagged the lobster time series by 0–8 years, so that lobster abundance followed the predator, temperature or climate series, to reflect probable effects on early life stages of lobster that would be detected later in the catch or trawl survey time series. We correlated the lagged lobster abundance time series with predation, temperature and climate time series for each region. We corrected correlation confidence intervals for temporal autocorrelation using the modified Chelton method (Pyper & Peterman 1998) and transformed the correlation coefficients with the variance stabilizing Fischer z transformation prior to fitting meta-analytic models. We correlated traps and lobster abundance at positive (traps

leading lobster) and negative (lobster leading traps) lags of 3 years, because it was not clear *a priori*, whether fishing effort would lead or follow changes in lobster abundance.

STATISTICAL ANALYSES

We used a meta-regression of correlation coefficients to consider the evidence for multiple hypothesized drivers of lobster abundance. Since the strength of top-down and bottom-up control can vary with temperature and latitude (Worm & Myers 2003; Frank *et al.* 2006; Frank, Petrie & Shackell 2007), we plotted the correlation coefficients between lobster abundance and predation, temperature, and climate against latitude and mean temperature. Both revealed systematic curved trends in the correlation coefficients. To formally test the effect of temperature on the correlations, we fit meta-regressions with region-level mean temperature as a quadratic modifier using the *METAFOR* package (Viechtbauer 2010) for the statistical software *R* (R Core Development Team 2012). This approach can be thought of as a sliding meta-analysis in which the intercept (the meta-analytic mean correlation) is allowed to vary with some modifying variable (mean region temperature).

We can express the quadratic meta-regression model for each potential correlate (predation, temperature, climate or effort) and at each lag as

$$r_i = \beta_0 + \beta_1 T_i + \beta_2 T_i^2 + \epsilon_i, \epsilon_i \sim N(\theta_i, v_i) \quad \text{eqn 1}$$

where r_i represents the log- and Fischer z-transformed correlation coefficient for region i , β_0 represents the intercept, β_1 the slope, β_2 the quadratic coefficient and T_i the mean annual bottom temperature in region i . The sampling error ϵ_i is assumed to be normally distributed with mean zero ($\theta_i = 0$) and within-region variance v_i . We also considered a random-effect version of the model where θ_i was modelled as a random variable drawn from a normal distribution, but results were similar and not systematically biased; we present the fixed-effect version for simplicity.

We are using relative abundance estimates and this could be problematic when combining different predators from trawl survey data, as these species might differ in their catchability. Hence, our composite predator index may not accurately reflect the actual abundance of different predators in the ecosystem. For this reason, we also explored correlations between lobster and each predator species by region over the same time-lags.

Results

The available lobster abundance time series spanned *c.* 25 years in the USA and 25–50 years in Canada (Fig. 2). Over much of the observed period, lobster populations in the NW Atlantic increased in abundance, despite intensive fisheries. Some regions (particularly from GB southwards) have also shown recent declines, while abundance trends and landings appeared mostly stable or increasing from the GOM northwards (Fig. 2). Predator time series spanned between *c.* 20 and 40 years. The total abundance or biomass of lobster predators declined in most regions, with some recent increases, for example in GB dogfish (*Squalus acanthias*) and haddock (*Melanogrammus aeglefinus*) populations (Murawski *et al.* 2000).

Temperature has fluctuated widely, but tended to increase in many regions over time (Fig. 2). Fishing effort, measured as the number of traps, approximately tracked lobster abundance trends in most regions (Fig. 2). The NAO index (Fig. 1 inset) was predominantly in a ‘high’ (above average) phase from 1980 until the early 1990s and has since decreased.

Most of the lobster abundance indices examined were correlated with landings (Fig. S1, Supporting Information). In NS, landings were not statistically significantly related to survey abundance ($R^2 = 0.07$, $P = 0.24$, note low sample size of $N = 10$ years), but were positively correlated to survey biomass ($R^2 = 0.43$, $P = 0.03$). For the larger regions of GOM, SNE and GB, landings correlated well with the University of Maine stock assessment model

estimates, maybe in part because landings are included in the model inputs (likely violating assumptions of independence). However, similarly strong relationships were seen between landings and raw survey abundance indices of lobster in the individual regions of MA, RI and CT (Fig. S1, Supporting Information).

We found significant meta-analytic correlations between predator and lobster abundance at lags of 2–5 years at the extremes of the lobsters’ thermal range (Fig. 3). The quadratic coefficient was significant ($P = 0.01–0.06$) at lags of 3–5 years (Table S4 in Supporting Information). The relationship between lobsters and the NAO index was most consistently positive across regions at long time-lags of 4–7 years and in warmer regions (Fig. 3). Overall, bottom temperature alone did not appear to have a

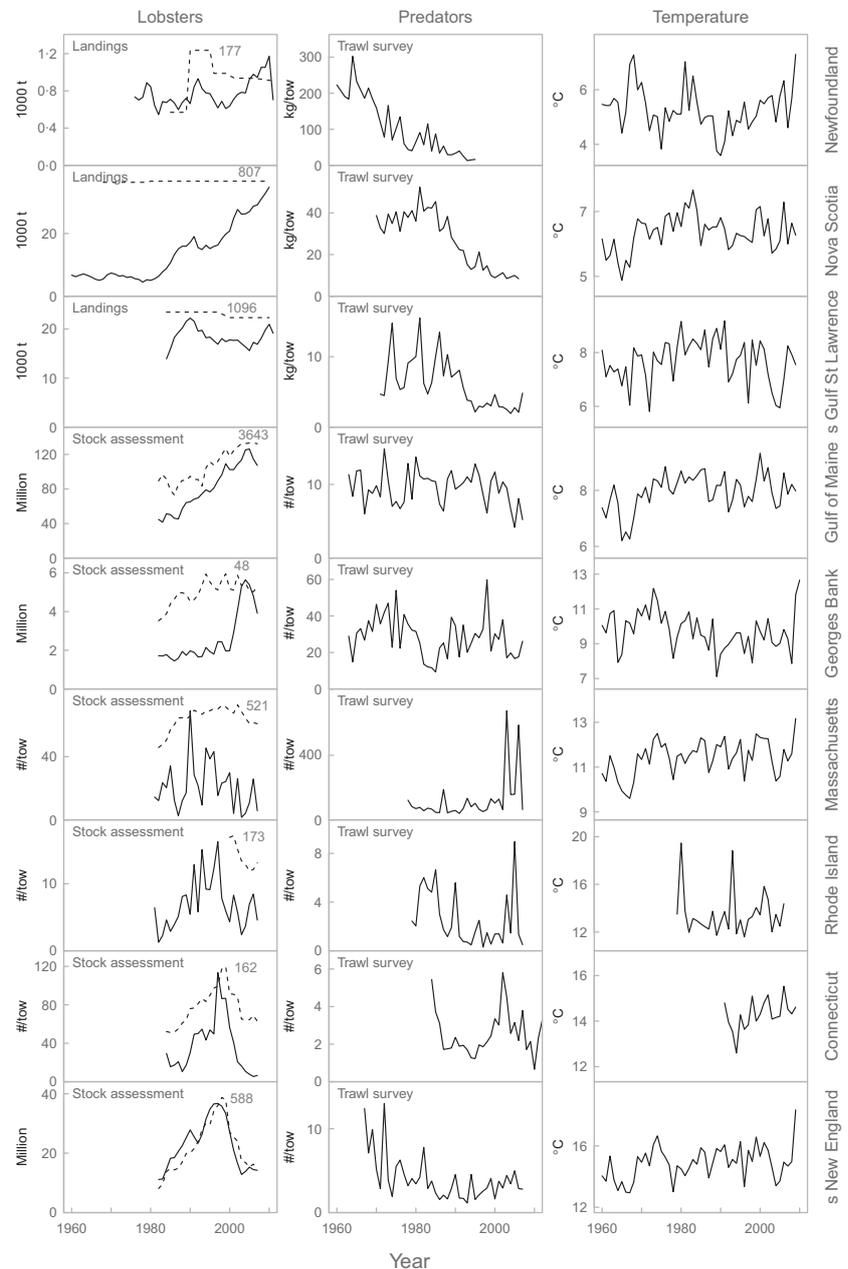


Fig. 2. Time-series data. Shown are untransformed abundance indices for lobsters (solid line) as well as fishing effort (dashed line), groundfish predator abundance or biomass (see Table S3 in Supporting Information, for species) and temperature (°C). Regions are arranged from coldest (Newfoundland) to warmest (southern New England). The y-axes for lobster predators are anchored at 0, and the value printed on the lobster abundance panels indicates the maximum number of traps (in 1000 s, dashed line).

strong or consistent effect on lobster abundance (Fig. 3). Across predators, the NAO index and temperature, we failed to find strong effects in the middle of the lobsters' thermal range at any lag. We found little evidence that the model residuals were spatially correlated after accounting for mean temperature in each region (Fig. S2, Supporting Information). Effort was most positively correlated with lobster at lags of 0 to -3, particularly in warmer regions, meaning effort closely followed abundance trends (Fig. 4). These conclusions remained unchanged when we removed Canadian regions from the meta-analysis (Fig. S3, Supporting Information).

Individual predators (Table S3 in Supporting Information; Fig. 5) correlated to varying degrees with lobster abundance indices across regions. At the cold end of the range, Atlantic cod, wolffish, thorny skate and cusk were negatively correlated with lobster in the GOM and NS. Cod, halibut and wolffish were also negatively correlated with lobster in NL. At the warm end of the range (SNE, CT), smooth dogfish was negatively correlated with lobster, as well as striped bass in CT and shorthorn sculpin in the SGS. In summary, it appeared that predator effects in the north were most commonly related to changes in cod abundance, while in the south they are mostly related to changes in smooth dogfish. Again, weak or no correlations were observed along the centre of the species range (i.e. in MA and RI, Fig. 5).

Discussion

The super abundance of lobsters in the face of heavy fishing has presented an enigma to natural resource managers and has been part of a wider trend of increasing reliance on invertebrate fisheries in the region (Anderson, Lotze & Shackell 2008; Steneck *et al.* 2011; Steneck & Wahle 2013) and around the globe (Anderson *et al.* 2011). Our analysis provides evidence that changes in groundfish abundance as well as climate may both play a role in regulating recent changes on lobster abundance, but that these effects vary systematically with life stage (as evidenced by different time-lags) and across the species' range. We detected negative correlations between groundfish and lobsters – particularly at the extremes of the lobsters' thermal range at lags of 2–5 years – but not in regions of intermediate temperature. Climate variation, as captured by the NAO index, was positively correlated with lobster abundance, mostly at long lags, and again at the warm end of the lobsters range. Further, as the effect of fishing effort on lobster was positive at leading lags, it does not appear that fishing is driving lobster abundance, but rather that fishing effort follows changes in abundance over time. Thus, a combination of release from predation pressure by groundfish and favourable climatic conditions may explain the super abundance of lobsters across part of their range (Steneck & Wahle 2013). Importantly, our results suggest that thermal range boundaries may interact to increase the roles of predation and climate

forcing in regulating these populations and possibly others. As many species tend to be surveyed at the core of their distribution, rather than at the edge (Sagarin & Gaines 2002), the relative impact of top-down and bottom-up forces on such populations may be systematically underestimated.

TOP-DOWN CONTROL AND THERMAL RANGE LIMITS

Our findings of stronger top-down control at the thermal range limits of American lobster may be partly explained by the 'abundant-centre hypothesis'. The hypothesis holds that a species' abundance is often greatest at the centre of its range and lower towards the edges of the range (Sagarin & Gaines 2002). Following from this phenomenon are expectations that edge populations are more variable and extinction more likely at range edges. These types of dynamics can also explain increased effects of predation pressure at range edges for metapopulations (Holt & Keitt 2000). Although the abundant-centre distribution is a widely held paradigm in biogeography, empirical evidence is tentative as many populations are undersampled along their range edges (Sagarin & Gaines 2002). Lobster populations, however, are well sampled across their range; thus, our results may provide empirical evidence of stronger groundfish control at thermal range limits. This might result, in part, from the pattern of overlap in the thermal ranges of predators and prey (Fig. 6). Cold-adapted Atlantic cod are found in regions between 2 and 11 mean annual water temperature (Brander 1995). This species appeared to dominate predation effects in the cool regions in our study (Fig. 5); smooth dogfish, in contrast, is a warm-tolerant, subtropical species (Compagno 1984) that dominated the warm regions; it is also evident how these effects diminish towards the regions at the centre of the lobsters' range (Fig. 5). At the range edge, based on the abundant-centre hypothesis, populations will also tend to be smaller, growth rates slower and more susceptible to changes in survival (Sagarin & Gaines 2002). Thus, these predator-prey range dynamics might be expected to interact resulting in stronger top-down control at the range limits of the prey (Fig. 6). At the southern edge of the American lobster population, where the water is often warm, the growth rates deviate from this hypothesis as individuals grow faster (e.g. SNE), except when environmental extremes (such as hot summers) challenge their physiological limits (ASMFC 2009). Lobsters may, however, be more susceptible to changes in survival since shell disease, a source of natural mortality, may be thermally mediated (Glenn & Pugh 2006).

At first glance, our results appear at odds with previous work in the North Atlantic that has examined the effect of temperature on top-down and bottom-up control (Worm & Myers 2003; Frank *et al.* 2006; Frank, Petrie & Shackell 2007). These studies found that negative predator-prey correlations were strongest in northern regions and weaker (or positive) in warmer regions. Species

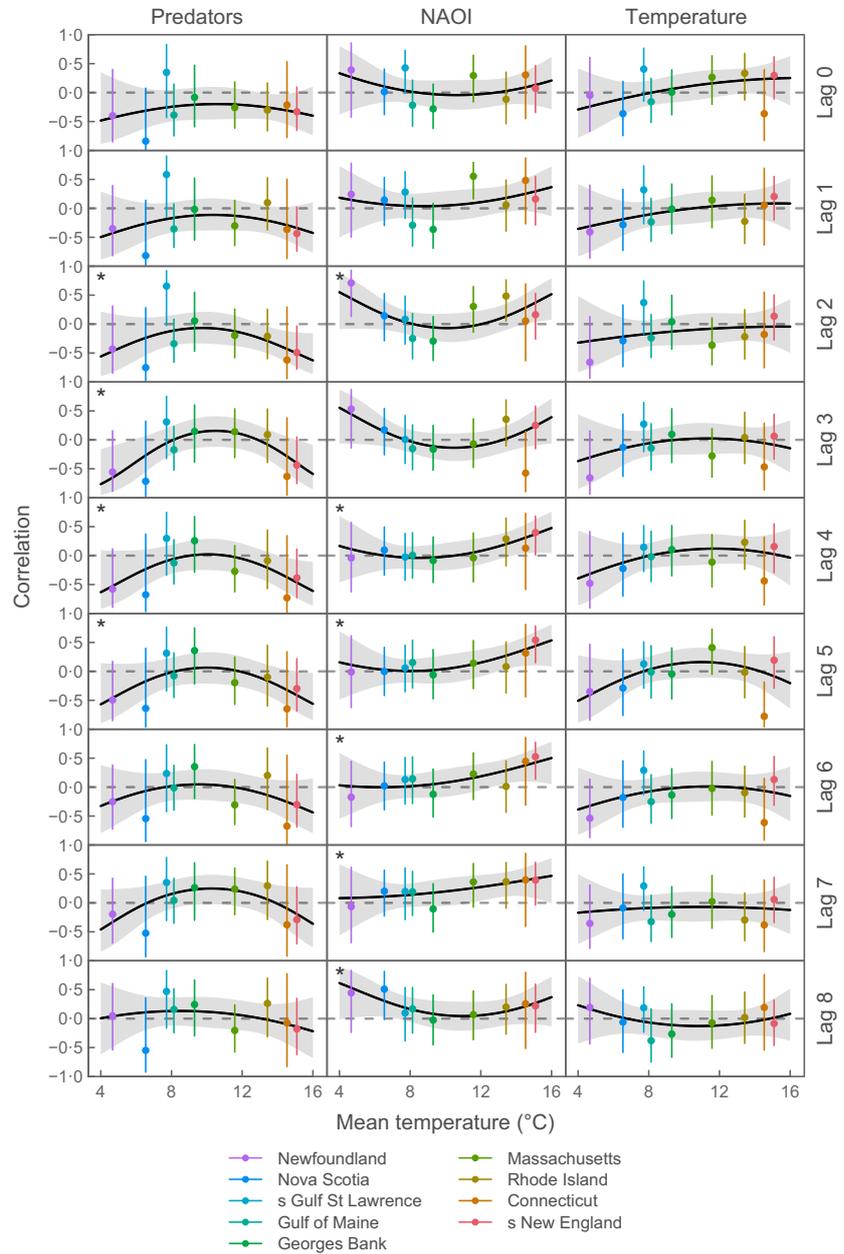


Fig. 3. Explaining variation in lobster abundance. Meta-regression curves are shown across mean temperature by region. Individual coloured points and line segments represent region-level correlation coefficients and 95% confidence intervals. Trend line is the meta-analytic mean, and shaded region is the 95% confidence interval. Panels with significant meta-analytic means within the range of mean temperatures observed are indicated with an asterisk. Panels are arranged from top to bottom by lag (in years) of predators, the North Atlantic Oscillation index and temperature leading lobster abundance.

richness, differences in primary production and temperature itself were proposed as mechanisms underlying these patterns (Frank *et al.* 2006; Frank, Petrie & Shackell 2007). The key difference between our study and previous results, however, is that we extended our analysis to the range limits of our prey species – whereas Worm & Myers (2003) and Frank *et al.* (2006) examined correlations at mean temperatures from 0 to about 8 °C, we extended the analysis to a mean temperature of about 16 °C. Our results show the same decline in correlation strength in moderately warm regions, but stronger negative correlations at the thermal extremes of the prey’s range (Fig. 3). Thus, our results extend patterns of top-down and bottom-up control to the entirety of a species’ range. While the previously proposed mechanisms likely continue to act, we suggest that the dynamics of predators and prey

at the prey thermal range boundary might increase the strength of top-down control there.

Our results are consistent with those of Boudreau & Worm (2010) who documented negative effects of a more limited suite of predatory groundfish (Atlantic cod, cusk, longhorn sculpin, monkfish and wolffish) on lobsters in the GOM. Other predators or pathogens may play additional roles; we note that one factor not accounted for in our study was the disease contributing to the sudden decline in SNE lobster abundance in the late 1990s (Wahle, Gibson & Fogarty 2009). Similarly, we did not quantify the effects of changes in predator size composition. There is some recent evidence to suggest that examining predator abundance may only capture some part of top-down effects and that changes in groundfish body size may be of similar importance (Shackell *et al.* 2010;

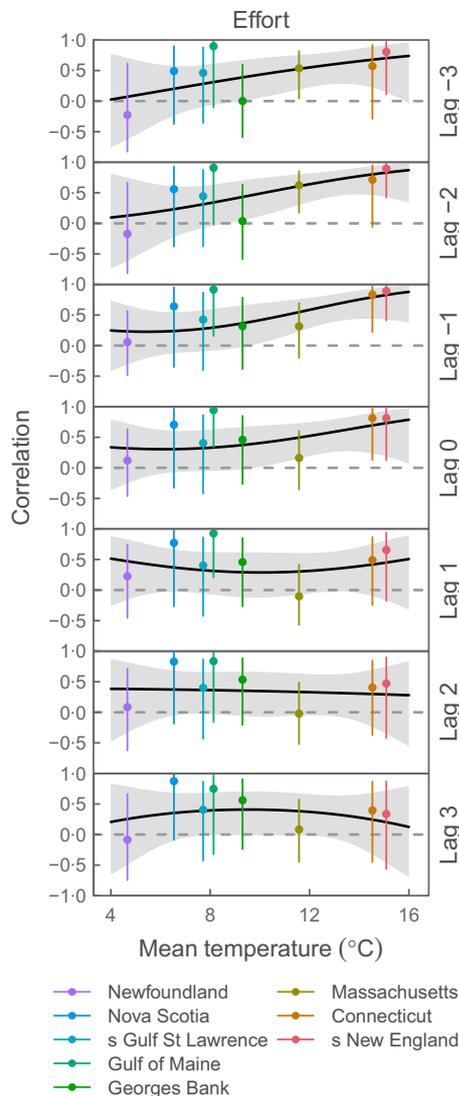


Fig. 4. Effects of fishing effort on lobster abundance. Correlations between the number of traps and lobster abundance are shown across mean temperature by region. Trend line is the meta-analytic mean, and shaded region is the 95% confidence interval. Panels are arranged from top to bottom by lag (in years) effort leading lobster abundance. Therefore, a negative lag refers to lobster abundance leading effort.

Wahle, Brown & Hovel 2013). The argument is that the removal of larger fish from an assemblage can effectively diminish their function as predators, even if collective groundfish biomass remains stable or even increases in some areas.

We used lags in our analysis to account for the possible effects of predators on different lobster life stages. Lobsters, like most decapods, undergo ontogenic habitat shifts, and early benthic life stages are largely dependent on sheltering habitats to minimize predation risk (Wahle 1992; Wahle & Steneck 1992). At later stages, the species might be outgrowing many of their predators and becoming less dependent on shelter (Wahle 1992; Wahle & Steneck 1992). Negative correlations between individual groundfish predators and lobster occurred predominantly

in the colder regions (Fig. 5; Fig. S4 Supporting Information); however, the strength of these interactions did not change substantially over a range of plausible time-lags (0–8 years). Thus, according to our meta-analysis (Fig. 3) groundfish may be having an impact on a number of sub-adult life stages preceding the recruitment of lobsters to the fishery. This result was consistent in an alternative analysis with cod abundance included in the SGSL's groundfish index (Fig. S5 Supporting Information). We note, however, that the lobster indices are integrated annually whereas generally the groundfish surveys are seasonal and of shorter duration, hence not necessarily capturing full seasonal variation in groundfish abundances.

Fishing, in contrast to predation, did not appear to be driving lobster population dynamics at the regional scale. Instead, effort appeared to be following lobster abundance, with positive correlations at negative lags (Fig. 4), indicating that landings may be an appropriate proxy for lobster abundance in this instance. Although trap and licence limits have been in effect in Atlantic Canada since 1968 (Pezzack *et al.* 2006), the number of traps has generally increased along with landings in the US (ASMFC 2009). Changes in trap design over time and associated changes in catchability could also have an influence on effort, yet this is difficult to quantify (Miller 1990). Undersized lobsters are largely protected from the fishery, as instantaneous fishing mortality (time-lag 0) acts on lobsters of minimum legal size, whereas climate and groundfish play a role across all life stages. Overall, the fishery appeared to be following increases in lobster abundance with up to a 3-year lag, implying delayed increases in effort as abundance increased (Fig. 4). These large increases in effort have brought about a precarious reliance on lobster fishing, particularly in the GOM (Steneck *et al.* 2011).

Increased fishing effort also leads to large quantities of bait being used to lure lobsters into traps; this is believed to help fuel the increase in lobster abundance in the GOM, where effort is extremely high (millions of traps deployed year round), and large bait inputs may help to 'farm' lobsters (Grabowski *et al.* 2009). This explanation is not believed to explain abundance increases in other regions, such as southwest NS (Boudreau & Worm 2010), which features much lower, and more constant trap densities (Myers *et al.* 2007; Grabowski *et al.* 2009). More generally, our results indicate that effort is following abundance with several years lag, that is, fishermen are adjusting their effort as abundance changes, not driving abundance either via fishing mortality or bait inputs.

BOTTOM-UP EFFECTS

When exploring the roles of climate variation and temperature, we found that the NAO was an important variable explaining changes in lobster abundance at intermediate to long time-lags, roughly corresponding to the age of lobsters at recruitment – lobster take 6–8 years to recruit

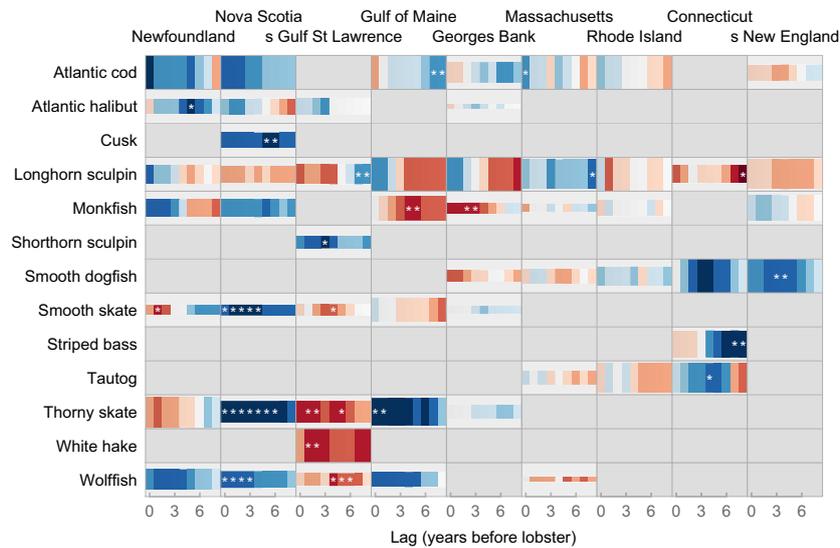


Fig. 5. Predator effects by species. Correlations between individual groundfish predator species abundance or biomass and lobster abundance indices are shown across year lags. The correlation colour scheme runs from -1 (blue) to 0 (white) to 1 (red). Height of the coloured bars indicates relative proportion of the species in total predator abundance or biomass within a region. To make the difference between smaller proportions visible, we transformed the proportions by a power of $\frac{1}{4}$. This transformation approximates a log transformation but is continuous through zero. Significant correlations after accounting for serial autocorrelation (Pyper & Peterman 1998) are indicated with an asterisk. Regions are arranged from cold to warm from left to right. Species included are: Atlantic cod (*Gadus morhua*); Atlantic halibut (*Hippoglossus hippoglossus*); Cusk (*Brosme brosme*); Longhorn sculpin (*Myoxocephalus octodecemspinus*); Monkfish (*Lophius americanus*); Shorthorn sculpin (*Myoxocephalus scorpius*); Smooth dogfish (*Mustelus canis*); Smooth skate (*Malacoraja senta*); Striped bass (*Morone saxatilis*); Tautog (*Tautoga onitis*); Thorny skate (*Amblyraja radiata*); White hake (*Urophycis tenuis*); Wolffish (*Anarhichas lupus*).

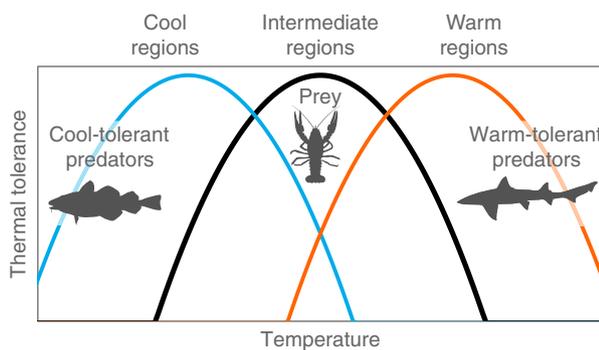


Fig. 6. Illustration of a thermal range hypothesis consistent with our results. Blue, black and orange curves represent thermal tolerance for cold-tolerant predators (such as Atlantic cod), prey (lobster) and warm-tolerant predators (such as smooth dogfish) across the range of regions and temperatures in our study. We hypothesize that these range dynamics result in stronger top-down regulation at species range edges by warm- and cold-tolerant predators.

to the fishery on average. These findings are consistent with previously documented region-wide influences of NAO climate forcing (Hurrell 1995), but did not appear to be easily explained by temperature variation within each region (Fig. 3). Temperature is known to play an important role on different life stages of American lobster, including hatching, settlement and growth. For example, in Maine, 54% of the variance in lobster landings from 1946 to 1986 could be explained by a positive

relationship with sea surface temperature (SST) at the time of larval settlement (Acheson & Steneck 1997). In NS (1929–1970), 68% of the variance in landings was explained by SST in addition to the previous year’s catch (Flowers & Sails 1972). In accordance with our findings, Drinkwater *et al.* (1996) were not able to link SST with the increase in lobster landings throughout the American lobster’s range in the 1980s and early 1990s, although they acknowledged a potential role of SST in the past. In 2012, the GOM experienced anomalously high SST, on average about 2 °C higher than the 1982–2011 mean (Mills *et al.* 2013). Sea surface temperatures in the GOM have increased by an average of 0.026 °C year⁻¹ since 1982, accelerating after 2004 to 0.26 °C year⁻¹ (Mills *et al.* 2013). The 2012 temperatures influenced lobsters by triggering their movement inshore 3 weeks earlier than in past years and increasing their moulting rate, and thereby boosted the number of legal-sized lobsters available to the fishery (Mills *et al.* 2013).

In the present study, we typically used yearly temperature averages, in order to match the temporal scale at which lobster and groundfish survey data were aggregated; however, we note that the summer season tends to be the most important time for lobster growth, movement, feeding and possibly predation (ASMFC 2009). Future studies could focus on changes in finer-scale temperature patterns (e.g. seasonal means, variability, extremes) and may uncover subtle temperature effects that were obscured in our analysis.

Other effects of the NAO on prevailing winds, near-shore currents and larval advection may be more influential in driving lobster abundance at the scale of our study. Since larval lobsters are planktonic (Harding, Drinkwater & Vass 1983), their feeding success and survival could depend on climatically driven changes in on plankton communities. For example, in the GOM, *Calanus finmarchicus* abundance (1961–1991) showed a positive relationship with the NAO index (Conversi, Piontkovski & Hameed 2001). In Narragansett Bay and RI Sound, a shift (1980–2005) from benthic to pelagic fish and invertebrate species strongly correlated with an increase in the winter NAO index and a reduction in chlorophyll a concentration (Collie, Wood & Jeffries 2008). These changes could be expected to influence lobsters at the larval stage and result in correlations with lobster abundance at longer lags.

Alternatively, the NAO could impact lobster abundance by affecting the supply and settlement of postlarva. Postlarval supply and settlement are believed to be major drivers of adult lobster population size and favourable environmental conditions have been inferred as a mechanism for observed increases in lobster abundance and recruitment (ASMFC 2009). There are many factors which play a role in settlement success, including the transport of the larvae, the distribution of the brooding females (and larval release), temperature, advection and turbulence (Incze, Wahle & Palma 2000; Chassé & Miller 2010; Incze *et al.* 2010); hence, the effect of the NAO on lobster abundance patterns could be complex. We note that wind direction, wind curl, temperature and geopotential height (the altitude of 700 mb pressure surface) have all been correlated to American lobster settlement in New England (Pershing *et al.* 2012).

Conclusions

As global fisheries are expanding increasingly towards forage fish and invertebrates (Pauly *et al.* 1998; Branch *et al.* 2010; Anderson *et al.* 2011), it is important to expand the ecological knowledge base for these low trophic level fisheries (Anderson, Lotze & Shackell 2008). In this study, we found evidence for both top-down (predator release) and bottom-up (large-scale climate) regulation of lobster abundance in the NW Atlantic. Evidence for these mechanisms was strongest at the edges of the lobster's thermal range, with top-down effects dominating at the cold and warm extremes (influencing subadults), and bottom-up effects in the warmer regions (influencing recruitment). Thus, our results suggest that the relative influence of top-down and bottom-up forcing in regulating these marine populations may intensify at thermal range boundaries and weaken at its core. Given that species tend to be sampled near the core of their range (Sagarin & Gaines 2002), we may therefore tend to underestimate the role of top-down and bottom-up control in marine communities. The central role of species' thermal range limits in our results

emphasizes the importance of considering community regulation across large spatial scales and suggests that climate change may alter current patterns of community regulation as species' thermal ranges are shifting in sync with regional temperature change (Pinsky *et al.* 2013).

Acknowledgements

We thank H. Lotze, J. Tremblay, R. Wahle, S. Walde and anonymous reviewers for helpful comments and discussions, and to W. Coffey, M. Fogarty, P. Howell, J. King, T. Lynch, D. Pezzack, D. Ricard, for data. Funding was provided by the National Sciences and Engineering Research Council, Fulbright Canada, Dalhousie University and Simon Fraser University.

Data accessibility

The data for this study have been archived on figshare: <http://dx.doi.org/10.6084/m9.figshare.1226921> (Boudreau, Anderson, & Worm 2014).

References

- Acheson, J. & Steneck, R.S. (1997) Bust and then boom in the Maine lobster industry: perspectives of fishers and biologists. *North American Journal of Fisheries Management*, **17**, 826–847.
- Anderson, S.C., Lotze, H.K. & Shackell, N.L. (2008) Evaluating the knowledge base for expanding low-trophic-level fisheries in Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Science*, **65**, 2553–2571.
- Anderson, S.C., Flemming, J.M., Watson, R. & Lotze, H.K. (2011) Rapid global expansion of invertebrate fisheries: trends, drivers, and ecosystem effects. *PLoS ONE*, **6**, e14735.
- ASMFC. (2009) *American Lobster Assessment for Peer Review*. Stock assessment report, Atlantic States Marine Fisheries Commission.
- Boudreau, S.A., Anderson, S.C. & Worm, B. (2011) Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean. *Marine Ecology Progress Series*, **429**, 169–183.
- Boudreau, S.A. & Worm, B. (2010) Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. *Marine Ecology Progress Series*, **403**, 181–191.
- Boudreau, S.A., Anderson, S.C. & Worm, B. (2014) Time series to accompany, "Top-down and bottom-up forces interact at thermal range extremes on American lobster". *Figshare*. doi: 10.6084/m9.figshare.1226921
- Branch, T.A., Watson, R., Fulton, E.A., Jennings, S., McGilliard, C.R., Publico, G.T. *et al.* (2010) The trophic fingerprint of marine fisheries. *Nature*, **468**, 431–435.
- Brander, K.M. (1995) The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, **52**, 1–10.
- Chassé, J. & Miller, R.J. (2010) Lobster larval transport in the southern Gulf of St. Lawrence. *Fisheries Oceanography*, **19**, 319–338.
- Chen, Y., Kanaiwa, M. & Wilson, C. (2005) Developing and evaluating a size-structured stock assessment model for the American lobster *Homarus americanus* fishery. *New Zealand Journal of Marine and Freshwater Research*, **39**, 645–660.
- Collie, J.S., Wood, A.D. & Jeffries, H.P. (2008) Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Science*, **65**, 1352–1365.
- Comeau, M., Hanson, J.M., Rondeau, A., Mallet, M. & Chassé, J. (2008) *Framework and Assessment for American Lobster, Homarus americanus Fisheries in the Southern Gulf of St. Lawrence: LFA 23, 24, 25, 26A and 26B*. Canadian Science Advisory Secretariat Science Advisory Report, Fisheries and Oceans Canada.
- Compagno, L.J.V. (1984) *Sharks of the World. An Annotated and Illustrated Catalogue of the Shark Species Known to Date. Part 2*. FAO, Rome.
- Conversi, A., Piontkovski, S. & Hameed, S. (2001) Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Research II*, **48**, 519–539.
- DFO (2006) Framework assessment for lobster (*Homarus americanus*) in Lobster Fishing Area (LFA) 34. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. **2006/024**.

- DFO (2007) Framework and assessment for lobster (*Homarus americanus*) in the Southern Gulf of St. Lawrence Lobster Fishing Areas 23, 24, 25, 26A and 26B. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* **2007/035**.
- DFO (2009) Assessment of American lobster in Newfoundland. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* **2009/026**.
- Drinkwater, K.F., Harding, G.C., Mann, K.H. & Tanner, N. (1996) Temperature as a possible factor in the increased abundance of American lobster, *Homarus americanus*, during the 1980s and early 1990s. *Fisheries Oceanography*, **5**, 176–193.
- Drinkwater, K.F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C.H. *et al.* (2003) The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *The North Atlantic Oscillation: Climatic Significance and Environmental Impact* (eds Y. Hurrell, K. Kushnir, G. Ottersen & M. Visbeck), pp. 211–234. American Geophysical Union, Washington, DC.
- Fisheries Resource Conservation Council (2007) *Sustainability Framework for Atlantic Lobster 2007: Report to the Minister of Fisheries and Oceans*. FRCC, Ottawa, ON, Canada.
- Flowers, J.M. & Saila, S.B. (1972) An analysis of temperature effects on the inshore lobster fishery. *Journal of the Fisheries Research Board of Canada*, **29**, 1121–1125.
- Fogarty, M.J. (1995) Populations, fisheries, and management. *Biology of the Lobster Homarus americanus* (ed. J.R. Factor), pp. 111–138. Academic Press Inc, San Diego, CA.
- Fogarty, M.J. & Gendron, L. (2004) Biological reference points for American lobster (*Homarus americanus*) populations: limits to exploitation and the precautionary approach. *Canadian Journal of Fisheries and Aquatic Science*, **61**, 1392–1403.
- Frank, K.T., Petrie, B. & Shackell, N.L. (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution*, **22**, 236–242.
- Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science*, **308**, 1621–1623.
- Frank, K.T., Petrie, B., Shackell, N.L. & Choi, J.S. (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters*, **9**, 1096–1105.
- Frank, K.T., Petrie, B., Fisher, J.A.D. & Leggett, W.C. (2011) Transient dynamics of an altered large marine ecosystem. *Nature*, **477**, 86–89.
- Glenn, R.P. & Pugh, T.L. (2006) Epizootic shell disease in American lobster (*Homarus americanus*) in Massachusetts coastal waters: interactions of temperature, maturity, and intermolt duration. *Journal of Crustacean Biology*, **26**, 639–645.
- Grabowski, J.H., Gaudette, J., Clesceri, E.J. & Yund, P.O. (2009) The role of food limitation in lobster population dynamics in coastal Maine, United States, and New Brunswick, Canada. *New Zealand Journal of Marine and Freshwater Research*, **43**, 185–193.
- Gregory, D.N. 2004 *Climate: A Database of Temperature and Salinity Observations for the Northwest Atlantic*. DFO Can. Sci. Advis. Sec. Res. Doc. 2004/075 http://www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2004/2004_075-eng.htm
- Hanson, J.M. & Chouinard, G.A. (2002) Diet of Atlantic cod in the southern Gulf of St. Lawrence as an index of ecosystem change, 1959–2000. *Journal of Fish Biology*, **60**, 902–922.
- Hanson, J.M. & Lanteigne, M. (2000) Evaluation of Atlantic cod predation on American lobster in the southern Gulf of St. Lawrence, with comments on other potential fish predators. *Transactions of the American Fisheries Society*, **0**, 13–29.
- Harding, G.C., Drinkwater, K.F. & Vass, W.P. (1983) Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. *Canadian Journal of Fisheries and Aquatic Science*, **40**, 168–184.
- Holt, R.D. & Barfield, M. (2009) Trophic interactions and range limits: the diverse roles of predation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **276**, 1435–1442.
- Holt, R.D. & Keitt, T.H. (2000) Alternative causes for range limits: a metapopulation perspective. *Ecology Letters*, **3**, 41–47.
- Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 723–732.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.
- Hurrell, J.W. (2013) NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA. URL <http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based>
- Incze, L.S., Wahle, R.A. & Palma, A.T. (2000) Advection and settlement rates in a benthic invertebrate: recruitment to first benthic stage in *Homarus americanus*. *ICES Journal of Marine Science*, **57**, 430–437.
- Incze, L.S., Xue, H., Wolff, N., Xu, D., Wilson, C., Steneck, R.S. *et al.* (2010) Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. *Fisheries Oceanography*, **19**, 1–20.
- Miller, R.J. (1990) Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Science*, **47**, 1228–1251.
- Mills, K., Pershing, A., Brown, C., Chen, Y., Chiang, F.-S., Holland, D. *et al.* (2013) Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography*, **26**, 191–195.
- Mullen, T.E., Russell, S., Tucker, M.T., Maratea, J.L., Koerting, C., Hinckley, L. *et al.* (2004) Paramoebiasis associated with mass mortality of American lobster *Homarus americanus* in Long Island Sound, USA. *Journal of Aquatic Animal Health*, **16**, 29–38.
- Murawski, S.A., Brown, R., H-L, L., Rago, P.J. & Hendrickson, L. (2000) Large-scale closed areas as a fisheries management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science*, **66**, 775–798.
- Myers, R.A., Boudreau, S.A., Kenney, R.D., Moore, M.J., Rosenberg, A.A., Sherrill-Mix, S.A. *et al.* (2007) Saving endangered whales at no cost. *Current Biology*, **17**, 10–11.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, **118**, 240–261.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998) Fishing down marine food webs. *Science*, **279**, 860–863.
- Pershing, A.J., Wahle, R.A., Meyers, P.C. & Lawton, P. (2012) Large-scale coherence in New England lobster (*Homarus americanus*), settlement and associations with regional atmospheric conditions. *Fisheries Oceanography*, **21**, 348–362.
- Pezzack, D.S., Tremblay, J., Claytor, R., Frail, C.M. & Smith, S. (2006) *Stock Status and Indicators for the Lobster Fishery in Lobster Fishing Area 34*. Canadian Science Advisory Secretariat Research Document, Fisheries and Oceans Canada, Ottawa, Ontario.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. & Levin, S.A. (2013) Marine taxa track local climate velocities. *Science*, **341**, 1239–1242.
- Pyper, B.J. & Peterman, R.M. (1998) Comparison of methods to account for autocorrelation in correlation analysis of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2127–2140.
- R Core Development Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org> (Accessed October 12, 2012).
- Sagarin, R.D. & Gaines, S.D. (2002) The “abundant centre” distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Shackell, N.L., Frank, K.T., Fisher, J.A., Petrie, B. & Leggett, W.C. (2010) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **277**, 1353–1360.
- State of Connecticut Department of Energy and Environmental Protection (CTDEEP) (2012) *Project Title: A Study of Marine Recreational Fisheries in Connecticut. Long Island Sound Trawl Survey (LISTS)*. Federal Aid in Sport Fish Restoration F-54-R-32 Annual Performance Report March 1, 2012–February 28, 2013.
- Steneck, R.S. & Wahle, R.A. (2013) American lobster dynamics in a brave new ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 1612–1624.
- Steneck, R.S., Hughes, T.P., Cinner, J.E., Adger, W.N., Arnold, S.N., Berkes, F. *et al.* (2011) Creation of a gilded trap by the high economic value of the Maine lobster fishery. *Conservation Biology*, **25**, 904–912.
- Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, **36**, 1–48.
- Visbeck, M.H., Hurrell, J.W., Polvani, L. & Cullen, H.M. (2001) North Atlantic Oscillation: past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 12876–12877.
- Wahle, R.A. (1992) Body-size dependent anti-predator mechanisms of the American lobster. *Oikos*, **65**, 52–60.
- Wahle, R.A., Brown, C. & Hovel, K. (2013) The geography and body-size dependence of top-down forcing in New England’s lobster-groundfish interaction. *Bulletin of Marine Science*, **89**, 189–212.
- Wahle, R.A., Gibson, M. & Fogarty, M.J. (2009) Distinguishing disease impacts from larval supply effects in a lobster fishery collapse. *Marine Ecology Progress Series*, **376**, 185–192.

Wahle, R.A., Incze, L.S. & Fogarty, M.J. (2004) First projections of American lobster *Homarus americanus* recruitment from a settlement index. *Bulletin of Marine Science*, **74**, 101–114.

Wahle, R.A. & Steneck, R.S. (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology*, **157**, 91–114.

Worm, B. & Myers, R.A. (2003) Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, **84**, 162–173.

Received 16 June 2014; accepted 14 November 2014

Handling Editor: William Gurney

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Data sources for lobster and groundfish-predator abundance analyses.

Table S2. Data sources for lobster biomass/abundance and landings for log-log regression (see Fig. S1).

Table S3. Included groundfish predators of lobster for each study region.

Table S4. Quadratic meta-regression coefficients.

Fig. S1. Lobster landings in relation to abundance estimates.

Fig. S2. Residuals from the meta-regression model in Fig. 3.

Fig. S3. Effects of fishing effort on lobster abundance without Canadian regions.

Fig. S4. Abundance or biomass time series for individual predator species.

Fig. S5. Same as Fig. 3 but with Atlantic cod included in the southern Gulf of St. Lawrence region.