

## The role of food limitation in lobster population dynamics in coastal Maine, United States, and New Brunswick, Canada

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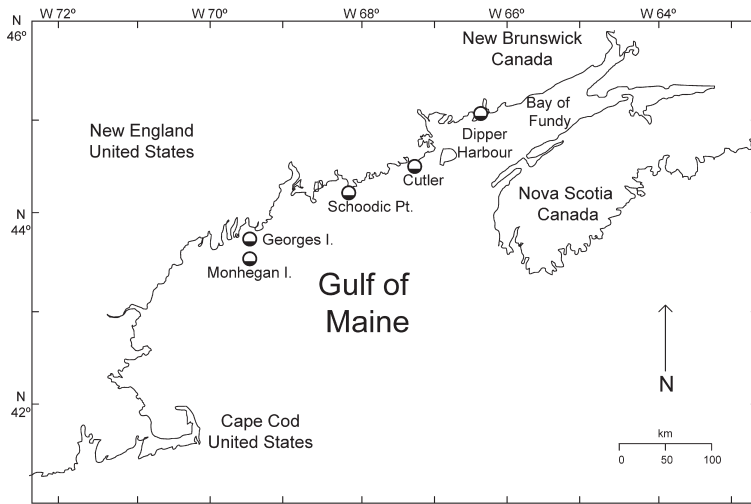
**Abstract** Lobster (*Homarus americanus*) landings in Maine, United States have increased steadily over the past two decades to levels that are consistently more than triple the 40-year (1950 to 1990) annual average of c. 9000 MT. Meanwhile, the use of herring (*Clupea harengus*) as bait has increased fourfold since the 1970s, and is currently subsidising lobster productivity in mid-coast Maine by augmenting the diet and growth of large juvenile and young adult lobsters before they recruit to the fishery. We investigated whether herring bait in the eastern portions of the Gulf of Maine is also subsidising these lobster populations. In 2004, we compared stomach contents, tissue production via stable isotope ratios,

and growth rates of lobsters from seasonally open (Cutler, Maine, United States) and closed (Dipper Harbour, New Brunswick, Canada) fishing areas in the spring, summer, and autumn. Contrary to previous results in mid-coast Maine, lobsters from seasonally closed sites at Dipper Harbour outgrew those from fished sites around Cutler. Yet examination of the diet of lobsters revealed several differences between open and closed sites that did not exist at sites in mid-coast Maine. For instance, lobsters at Dipper Harbour consumed markedly more bivalves than those at Cutler. Furthermore, quantification of trap densities and the number of licensed fishers in mid-coast versus eastern Maine determined that fishing effort was greatly reduced in eastern Maine. Thus, our results indicate that herring bait subsidies are not important in eastern portions of the Gulf of Maine, but the availability of natural prey seemingly limits the growth of lobsters in eastern Maine. Moreover, our study suggests that bottom-up forcing (i.e., food limitation) can have important consequences for lobster population dynamics and the productivity of lobster fisheries.

**Keywords** American lobster; *Homarus americanus*; herring bait; *Clupea harengus*; ecosystem management; fisheries ecology

### INTRODUCTION

Commercial fishery landings of the American lobster (*Homarus americanus*, H. Milne Edwards 1837) in the Gulf of Maine, United States have continued to rise over the past two decades despite intense fishing pressure, whereas most other regional fisheries have collapsed or failed to recover to historic levels (Witman & Sebens 1992; Jackson et al. 2001; Steneck & Wilson 2001; Saila et al. 2002). Landings in Maine for 1999 were estimated at 24 265 metric tons of lobster with a direct value of over US\$184 million to Maine's coastal communities from Eastport to York (National Marine Fisheries Service 2006). Landings currently are more than triple the annual



**Fig. 1** Sites near Cutler, Maine and Dipper Harbour, New Brunswick in the eastern portions of the Gulf of Maine.

average from 1950 to 1990, and fishery-independent surveys also suggest that lobster populations have increased over the past decade (Steneck & Wilson 2001). The lobster fishery currently accounts for a disproportionately large percentage of the total fishery value in the Gulf of Maine. Moreover, lobster landings continue to thrive despite intensive fishing effort, which is of interest to lobster scientists, fishery managers, and fishers.

Scientists have posited that the increase in lobster populations and landings is a result of declines in lobster predators such as Atlantic cod (*Gadus morhua*) from overfishing over the past century (Jackson et al. 2001). Cod and other demersal fish species in the northwest Atlantic historically were important predators of lobsters until overfishing substantially reduced predation pressure, especially in nearshore waters of the Gulf of Maine (Witman & Sebens 1992; Steneck 1997). However, the cod fishery collapse occurred well before the more recent increase in lobster populations (Steneck & Wilson 2001). Furthermore, the spatial extent of surges in lobster abundance greatly exceeds that of the collapse of cod populations (Steneck & Wilson 2001).

Another possible explanation is that lobster management practices have promoted the expansion of lobster populations throughout the northwest Atlantic. The American lobster fishery has benefited from relatively low bycatch of sublegal (i.e., <83 mm carapace length, CL) lobsters, and several regions in the United States and Canada have put into practice management regulations that may reduce the risk of overfishing. For instance, Maine, United States adopted policies over the past 150 years such

as restricting the harvest of large (>127 mm CL) lobsters and egg-bearing females, and Canada has capped fishing effort over the past three decades and has implemented seasonal closures (Myers et al. 2007). Although these practices collectively guard against the collapse of the lobster fishery, lobster management practices vary widely among states in United States and lobster fishing areas in Canada. Therefore, the degree to which recent increases in lobster populations are a direct response to lobster management initiatives is unclear.

A third hypothesis is that oceanographic conditions in the northwest Atlantic are responsible for increases in lobster abundance (Incze et al. 2000). Changes in physical factors such as water temperature are poorly correlated with recent changes in lobster populations in southern New England, Maine, and the Maritime Provinces of Canada (Drinkwater et al. 1996; Saila et al. 2002). However, lobster scientists have demonstrated that lobster recruitment has increased over the past two decades, and that this increase corresponds with greater juvenile abundance and commercial landings (Steneck & Wilson 2001; Incze et al. 2003).

Whether or not lobster growth rates and productivity are limited by resources remains unclear. The use of herring (*Clupea harengus*) as bait to catch lobsters in coastal Maine has been suggested as a contributing factor to recent surges in lobster landings (Saila et al. 2002; J. H. Grabowski unpubl. data). Approximately 50 000 metric tons of herring are landed in Maine each year (111 415 metric tons in 1999 worth US\$7.71 million), and c. 70% of the herring landings are used in coastal waters as lobster

bait, constituting c. 95% of the lobster bait used by lobster fishers (Saila et al. 2002). Juvenile lobsters enter traps to consume bait and either escape (as much as 90% escape; Jury et al. 2001) or are released and eat discarded bait on the sea floor. Sublegal lobsters (66–82 mm CL) in fished areas in mid-coast Maine grow c. 15% more per moult than lobsters from seasonally closed areas in this region (J. H. Grabowski unpubl. data), suggesting that herring bait is augmenting the productivity of the lobster fishery in this region.

Nitrogen stable isotope ratios act as a chemical tracer that can be used to examine trophic interactions and diet composition (Peterson & Howarth 1987; Anderson & Polis 1998). Lobsters from fished areas in mid-coast Maine also had  $\delta^{15}\text{N}$  values that were 1.5‰ higher than tissue values of lobsters from unfished sites in October 2002, indicating that herring bait accounts for a substantial portion of the diet of lobsters (J. H. Grabowski unpubl. data). These results suggest that herring is important for lobster population dynamics and could augment landings by as much as US\$40 million annually in Maine. However, whether herring bait subsidises lobster populations throughout coastal Maine remains unclear.

In 2004, we evaluated how much herring bait contributes to the production of lobster biomass by quantifying the diet of lobsters in areas with and without bait in eastern portions of the Gulf of Maine. The objective of this study was to determine if herring bait augmentation of the diet and growth of lobsters that occurs in mid-coast Maine is also prevalent in eastern portions of the Gulf of Maine. We hypothesised that food is limiting lobster populations in the eastern Gulf of Maine, and that herring bait is an important subsidy in their diet. We also conducted a mark-recapture experiment in fished versus closed areas in eastern portions of the Gulf of Maine to quantify whether fishing activity influences lobster growth rates. We predicted that herring bait subsidies from fishing activity also augment lobster growth rates in eastern portions of the Gulf of Maine.

## MATERIALS AND METHODS

### Study site

To determine if herring bait subsidises lobster populations in the Gulf of Maine, we compared the growth and diet of lobsters at sites near Cutler, Maine, United States (N44°15'00"; W67°24'00") and Dipper Harbour, New Brunswick, Canada

(N45°15'00"; W66°25'00"), which is located inside the Bay of Fundy (Fig. 1). The Canadian fishery closes seasonally from the end of June until late November, when water temperatures are warm and lobsters are actively growing (Campbell 1983). Thus, this site pair provided an opportunity to examine whether herring subsidies are important to lobster populations in eastern portions of the Gulf of Maine. Although Dipper Harbour was located further from Cutler than other potential control sites (e.g., Grand Manan Island, New Brunswick), it was isolated from the confounding effects of herring weir and salmon aquaculture activities, which are common at the mouth of the Bay of Fundy (P. Lawton pers. comm.).

### Lobster growth

To determine the effects of fishing activity on lobster growth rates, we conducted a mark-recapture experiment at Cutler and Dipper Harbour in 2004. Sublegal lobsters were captured via commercial lobster traps at each site in early summer before the seasonal peak in moulting activity. Intermoult stage lobsters were targeted to reduce mortality rates (Moriyasu et al. 1995). Lobsters were sexed, moult stage determined, measured (CL;  $\pm 0.5$  mm), tagged with Floy Co. streamer tags that are retained through multiple moult cycles (Aiken 1977; J. H. Grabowski unpubl. data), and released at the site where they were captured. Streamer tags could have influenced lobster growth negatively, so that we may have underestimated lobster growth in this study; however, it is unlikely that this potential confounding effect of tagging on growth rates varied with our treatments (i.e., Cutler versus Dipper Harbour). 1996 tagged lobsters were released at Cutler, and 1862 were released at Dipper Harbour. Recapture of lobsters was initiated upon the opening of the fisheries in the winter and spring of 2004/05 at Dipper Harbour. Fishers were offered a US\$10 reward for recovered lobsters. Recaptured lobsters were measured (CL) to compare the proportion of recovered lobsters that moulted at fished versus seasonally closed sites and to quantify growth increment (% gain in CL) of those that moulted. Comeau & Savoie (2001) found no relationship between growth increment and CL; therefore, growth increment comparisons were considered to be robust against small differences in initial lobster size.

### Lobster diet

Stomach content analysis of sublegal lobsters was conducted seasonally in 2004 at Cutler and Dipper Harbour to determine the impact of fishing

activity on the relative proportion of herring bait and natural prey in the lobster diet. Sixty lobsters (20 per sampling period) ranging from 45 to 82 mm CL were collected via SCUBA at each site: 20/sampling period during three sampling periods (May, July/August, and October of 2004) and measured (CL;  $\pm 0.5$  mm). Stomachs of all lobsters were removed, preserved in 70% ethanol, and taken to the laboratory. Stomach fullness was quantified and standardised by size of the lobster, and individual dietary items were identified to functional groups (e.g., fish bones, molluscs, decapods) and weighed (wet weight, 0.0001 g). Fish bones (largely herring) can easily be identified in the stomach (J.H. Grabowski unpubl. data), along with non-digestible material of natural prey (i.e., crab carapace material, mollusc shells, polychaete jaws). Stomachs that presented gastroliths ( $n = 11$  at Dipper Harbour,  $n = 12$  at Cutler) were excluded from analysis because the onset of gastrolith development on the outer lining of the stomach indicates that the lobster is no longer actively feeding because it is preparing to moult (Waddy et al. 1995).

Nitrogen isotope ratios offer a potential advantage over analysis of stomach contents because they measure the integrated assimilated diet (Wainwright et al. 1993), which is a function of both average diet throughout the lifespan and actual assimilation. Because lobsters are a trophic level above their prey, the absolute value of  $\delta^{15}\text{N}$  for lobster is higher than the prey  $\delta^{15}\text{N}$ . The relative difference in lobster  $\delta^{15}\text{N}$  between fished and seasonally closed sites would be detectable if herring constitutes a main portion of the lobster diet because the  $\delta^{15}\text{N}$  value of herring is c. 2–6‰ higher than the values of the most common natural prey of lobsters (i.e., crabs, urchins, and molluscs) (Lawton & Lavalli 1995) at our study sites (J.H. Grabowski unpubl. data). Thus trophic fractionation ( $\delta^{15}\text{N}$  difference between consumer and food) values suggest that herring are c. 1 to 1½ trophic levels above typical lobster prey (Minagawa & Wada 1984). Adult herring consume zooplanktivorous copepods, whereas typical lobster prey feed lower in the food web, primarily on herbivores (sea urchins and mussels) and secondary consumers (crabs). Differences in  $\delta^{15}\text{N}$  should be attributable to herring unless lobsters at seasonally closed sites consume more crabs than lobsters in baited sites, but this assumption can be directly tested with stomach content information.

Lobster tissue samples were dissected from all captured lobsters in the field and stored on ice (c. 5°C) in glass scintillation vials until frozen in the

laboratory. Samples were freeze dried before stable isotope analysis via an elemental analyser (Carlo Erba NA 1500) coupled to an isotope ratio mass spectrometer (Finnigan MAT 252) via a continuous flow interface. Precision was  $>0.2\%$  for  $\delta^{15}\text{N}$ , and  $\delta^{15}\text{N}$ -isotope compositions were expressed in standard notation in parts per thousand (‰) relative to atmospheric  $\text{N}_2$  for N ( $^{15}\text{N}/^{14}\text{N}_{\text{standard}} = 0.03676$ , international standard). The following formula was used to calculate  $\delta^{15}\text{N}$  stable isotope ratios:

$$\delta^{15}\text{N}_{\text{sample}} = [(^{15}\text{N}/^{14}\text{N}_{\text{sample}})/(^{15}\text{N}/^{14}\text{N}_{\text{standard}}) - 1] \times 1000$$

Because nitrogen stable isotope ratios of herring ( $\delta^{15}\text{N}$  11.8‰) are markedly higher than those for the natural prey of lobsters ( $\delta^{15}\text{N}$  6.3–9.5‰; J. H. Grabowski unpubl. data), determining the nitrogen-stable isotope ratios of lobster tissues before and after the fishery closes and herring bait is available can be used to indicate the relative contribution of herring to the lobster diet.

### Fishing intensity

Fishing intensity was quantified in summer and autumn 2004 at fished sites in mid-coast Maine around Georges Islands and in eastern Maine near Cutler to determine whether fishing intensity differed between mid-coast and eastern Maine. During each sampling period (May/June, August, and October), the number of buoys within a 500 m radius was recorded at two subsites. Fishers from each region were consulted to determine the average number of traps that were fished per buoy line (Cutler: J. Cates pers. comm.; Georges Islands: P. Poland pers. comm.). The number of fishers and traps licensed in eastern versus mid-coast Maine were also compared (<http://www.maine.gov/dmr/rm/lobster/licensesandtags.htm>).

### Data analysis

The effect of fishing activity (fished versus seasonally closed sites) on average percentage growth of moulted lobsters was analysed using an unpaired *t* test (Sokal & Rolfe 1995). Average size (CL) of lobsters that were used in stomach content analyses was analysed using a two-way ANOVA with fishing activity (fished versus seasonally closed sites) and season (spring, summer, and autumn) as independent variables to ensure that lobsters analysed were similar in size (Underwood 1981). The effects of fishing activity and season on the amount of total lobster prey, fish, molluscs, and decapods that were consumed were analysed first using a MANOVA and then

using separate two-way ANOVAs for each response variable (Underwood 1981). The effects of fishing activity and season on the  $\delta^{15}\text{N}$  stable isotope values of lobsters were analysed using two-way ANOVA (Underwood 1981). The effects of season (summer versus autumn) and region (mid-coast versus eastern Maine) on trap density were analysed using two-way ANOVA (Underwood 1981). Significant interaction terms and main effects were examined with Tukey's post hoc test (Day & Quinn 1989). Each data set was tested for violations of the assumption of homoscedasticity and transformed using square root transformations when heterogeneous variances were diagnosed (Underwood 1981).

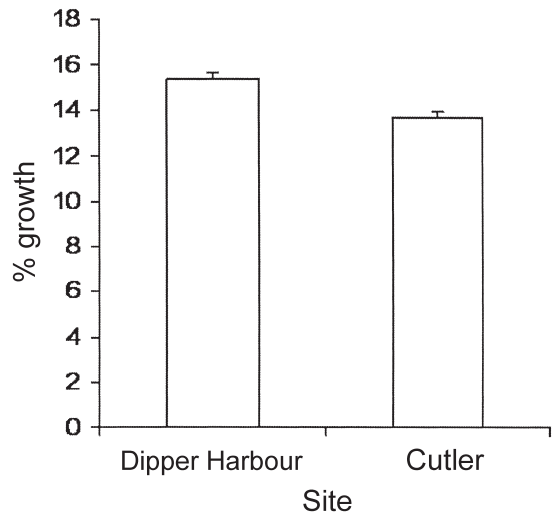
## RESULTS

### Lobster growth

Lobsters tagged at Dipper Harbour sites outgrew those from Cutler, Maine by 13.5% (Fig. 2;  $t_{245} = -4.6$ ,  $P < 0.0001$ ). Of the 1862 lobsters that were tagged at Dipper Harbour sites, 124 were recaptured in November 2004 that had moulted since being tagged. These lobsters grew  $15.4 \pm 0.3\%$  (mean  $\pm 1$  SE). Meanwhile, lobsters that were tagged at Cutler were recaptured between November 2004 and February 2005. The 123 recaptured lobsters (out of 1996 tagged) that had moulted since being tagged at Cutler sites grew  $13.6 \pm 0.3\%$ . Less than 9% of recaptured lobsters from both sites did not moult; these lobsters were used to verify that measurements of lobsters were consistent across sampling dates and sites. Specifically, the length of only 1 of 23 recaptured lobsters differed detectably (1 mm) from its measurement when it was tagged, which was likely attributable to human error.

### Lobster diet

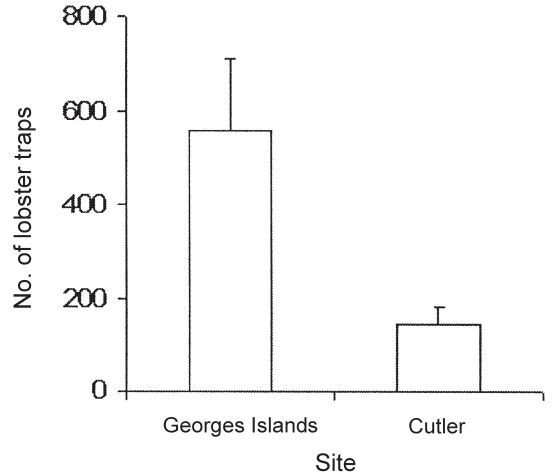
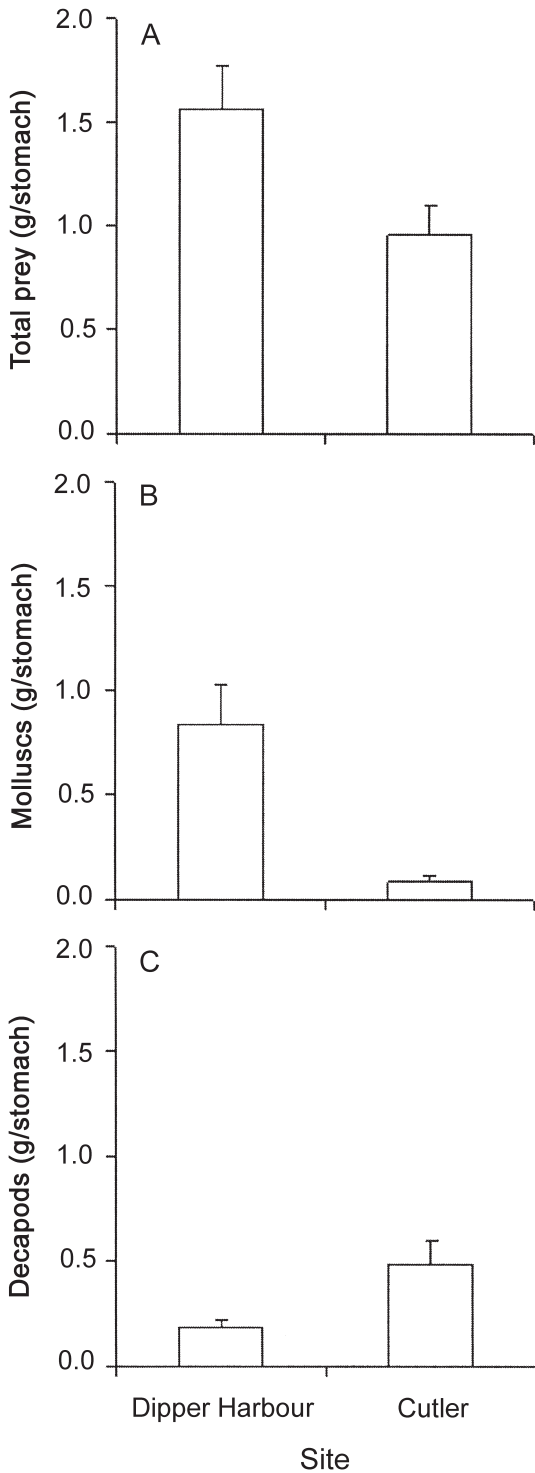
The CL of lobsters that were dissected to analyse stomach contents did not differ between fished and seasonally closed sites in eastern portions of the Gulf of Maine ( $F_{1,91} = 0.03$ ,  $P > 0.1$ ), nor did they differ by season ( $F_{2,91} = 0.2$ ,  $P > 0.1$ ). The mean size of lobsters that were sampled for stomach contents from Cutler was 64.0 mm CL and from Dipper Harbour 64.3 mm CL. MANOVA determined that both fishing activity (site) and season influenced the diet of lobsters (site: Wilks'  $\Lambda_{4,88} = 7.8$ ,  $P < 0.0001$ ; season: Wilks'  $\Lambda_{8,172} = 4.6$ ;  $P < 0.0001$ ), and separate ANOVAs were conducted for each response variable (total lobster prey, fish, mollusc, and decapod biomass). Both fishing activity



**Fig. 2** Lobster growth rates (mean  $\pm 1$  SE) at Dipper Harbour, New Brunswick, Canada (seasonally closed;  $n = 124$ ) and Cutler, Maine, United States (open;  $n = 123$ ) sites in 2004.

and season influenced total lobster prey consumption, but these factors did not interact (fishing activity  $\times$  season:  $F_{2,91} = 0.5$ ,  $P > 0.1$ ). Lobsters from Dipper Harbour (seasonally closed) consumed 64% more total prey biomass than those from Cutler (Fig. 3A,  $F_{1,91} = 5.0$ ;  $P < 0.05$ ). Lobsters at both sites consumed fourfold more total prey biomass in the summer and autumn than in the spring ( $F_{2,91} = 14.4$ ;  $P < 0.0001$ ; mean  $\pm 1$  SE: spring:  $0.415 \pm 0.099$  g/stomach; summer:  $1.723 \pm 0.313$  g/stomach; and autumn:  $1.777 \pm 0.225$  g/stomach). Lobsters from Cutler consumed marginally (but non-significantly) more fish biomass than those from Dipper Harbour ( $F_{1,91} = 3.2$ ;  $P > 0.05$ ; Cutler:  $0.042 \pm 0.022$  g/stomach and Dipper Harbour:  $0.001 \pm 0.001$  g/stomach), but bait consumption was negligible ( $< 0.002$  g/stomach) at either site in summer when warmer water temperatures promote lobster growth. Neither season nor the interaction between fishing activity and season were significant ( $P > 0.43$  for both effects; spring:  $0.001 \pm 0.001$  g/stomach; summer:  $0.041 \pm 0.023$  g/stomach; and autumn:  $0.022 \pm 0.018$  g/stomach). Fish bones or tissue were present in 50% of the stomachs of lobsters from Cutler, whereas 14% of those from lobsters from Dipper Harbour contained fish.

Mollusc biomass (predominately mussels *Mytilus* spp.) was significantly more prevalent in



**Fig. 4** Fishing effort (mean +1 SE, no. of traps/500 m) around Georges Islands and Cutler, Maine, United States.

**Fig. 3** (left) Results from stomach content analysis of lobsters from Dipper Harbour, New Brunswick, Canada and Cutler, Maine, United States: mean +1 SE. **A**, Total prey; **B**, mollusc; and **C**, decapod biomass (Dipper Harbour,  $n = 49$ ; Cutler,  $n = 48$ ).

the stomachs of lobsters from Dipper Harbour than from Cutler (Fig. 3B,  $F_{1,91} = 14.9$ ;  $P < 0.001$ ). There was also a (non-significant) trend of higher mollusc biomass in summer and autumn than in spring ( $F_{2,91} = 2.8$ ;  $P > 0.05$ ; spring:  $0.155 \pm 0.062$  g/stomach; summer:  $0.612 \pm 0.334$  g/stomach; and autumn:  $0.665 \pm 0.155$  g/stomach). Decapod biomass (mostly exoskeleton fragments from cancer crabs (*Cancer* spp.)) was over twice as high in lobsters from Cutler than in those from Dipper Harbour (Fig. 3C,  $F_{1,91} = 10.1$ ;  $P < 0.01$ ), and it also was elevated in summer and autumn in comparison with spring ( $F_{2,91} = 8.0$ ;  $P < 0.001$ ; spring:  $0.073 \pm 0.025$  g/stomach; summer:  $0.537 \pm 0.114$  g/stomach; and autumn:  $0.449 \pm 0.121$  g/stomach). There was a non-significant trend for the interaction between fishing activity and season, because there was no difference between sites in spring, but lobsters in summer and autumn consumed slightly more decapods at Cutler ( $F_{2,91} = 2.7$ ;  $P > 0.05$ ). Although the remaining prey items were less important by weight and occurred less frequently than decapods and molluscs, there was a trend of more echinoderm (Dipper Harbour:  $0.045 \pm 0.022$  g/stomach; Cutler:  $0.013 \pm 0.008$  g/stomach), cirriped (Dipper Harbour:  $0.006 \pm 0.004$  g/stomach;

Cutler:  $0.0001 \pm 0.0001$  g/stomach), algal (Dipper Harbour:  $0.004 \pm 0.004$  g/stomach; Cutler:  $0.0005 \pm 0.0004$  g/stomach), unidentified shell fragment (Dipper Harbour:  $0.16 \pm 0.44$  g/stomach; Cutler:  $0.124 \pm 0.024$  g/stomach), and unidentified tissue biomass (Dipper Harbour:  $0.285 \pm 0.059$  g/stomach; Cutler:  $0.191 \pm 0.045$  g/stomach) in the stomachs of lobsters from Dipper Harbour.

Similar to stomach content results, fishing activity and season both influenced nitrogen stable isotope ratios of lobsters, but the interaction between fishing activity and season, which indicates whether herring bait is prevalent in the diet of lobsters, was not significant ( $F_{2,114} = 1.5$ ;  $P > 0.1$ ). Nitrogen stable isotope ratios were substantially higher in lobsters from Cutler ( $\delta^{15}\text{N} = 11.7 \pm 0.1\text{‰}$ ) than from Dipper Harbour ( $\delta^{15}\text{N} = 10.2 \pm 0.1\text{‰}$ ) regardless of season ( $F_{1,114} = 189.5$ ;  $P < 0.0001$ ). Stable isotope ratios were also higher in spring ( $\delta^{15}\text{N} = 11.1 \pm 0.2\text{‰}$ ) and summer ( $\delta^{15}\text{N} = 11.1 \pm 0.2\text{‰}$ ) than in autumn ( $\delta^{15}\text{N} = 10.6 \pm 0.2\text{‰}$ ;  $F_{2,114} = 7.7$ ;  $P < 0.001$ ).

### Fishing intensity

Trap counts conducted during the summer and autumn sampling periods revealed that local fishing intensity was c. 4 times greater at fished sites in mid-coast Maine (Georges Islands) than at those sampled in eastern Maine (Fig. 4;  $F_{1,4} = 22.0$ ;  $P < 0.01$ ). Fishing intensity was also higher in summer than in autumn in both regions by a factor of c. 2 ( $F_{1,4} = 11.0$ ;  $P < 0.05$ ). The interaction between season and region was not significant ( $F_{1,4} = 3.8$ ;  $P > 0.1$ ), indicating that fishing intensity was consistently higher in the mid-coast region regardless of the season.

Overall fishing effort in mid-coast Maine was approximately twice that in eastern Maine. In 2004, 1522 licenses and 626 043 trap tags were issued by the Maine department of Marine Resources for fishers for eastern Maine (i.e., between Schoodic Point and the United States-Canada border). Meanwhile, 2711 licenses and 1 257 082 trap tags were issued for an equivalent amount of coastline in mid-coast Maine (<http://www.maine.gov/dmr/rm/lobster/licensesandtags.htm>).

## DISCUSSION

It has been suggested that herring as bait has the potential to substantially augment lobster populations in coastal Maine by augmenting growth rates and consequently increasing landings (Saila et al. 2002). However, in this study there was little evidence that

herring bait is augmenting lobster populations in the coastal waters of eastern Maine. For instance, lobsters from the seasonally closed sites at Dipper Harbour in the Bay of Fundy outgrew those from the fished sites at Cutler, Maine by 13.5%. This result was in marked contrast to previous research conducted in mid-coast Maine, where lobsters from fished areas outgrew those from seasonally closed sites by c. 15% (J. H. Grabowski unpubl. data).

Dietary analyses also suggested that herring bait subsidies were less prevalent in eastern portions of the Gulf of Maine. Although there was marginally more herring bait biomass in the stomachs of lobsters from fished sites, it was present in less than half of the lobsters captured in spring and summer 2004, suggesting that these lobsters were consuming relatively little bait. In contrast, nitrogen stable isotope ratios of lobsters from around Monhegan Island declined precipitously after the fishing season closed at the end of May (J.H. Grabowski unpubl. data). This decline, which occurred only at the seasonally closed sites after the fishery closed, indicated a shift in the diet of lobsters around Monhegan Island from a mixture of herring bait and natural prey to a diet consisting of predominately natural prey. In eastern portions of the Gulf of Maine, nitrogen stable isotope ratios did not indicate a shift in the diet of lobsters at seasonally closed sites after the fishery closed. Specifically, nitrogen stable isotope ratios of lobsters were consistently lower at Dipper Harbour regardless of closure status. Although bait subsidies have been shown to be important in the central portions of the Gulf of Maine where fishing activity is intense (J.H. Grabowski unpubl. data), the results from this study suggest that interactions between the lobster and herring fisheries are less pronounced further east in the Gulf of Maine and Bay of Fundy.

Comparison of the field sites in the eastern Gulf of Maine with those from previous investigations in mid-coast Maine (J.H. Grabowski unpubl. data) could explain why herring bait is seemingly having little effect on lobsters in eastern Maine. In mid-coast Maine, field sites were located in close proximity to each other (i.e., c. 10 km), whereas in the present study, sites were located much further apart owing to constraints in finding a bait-free control site more proximal to Cutler, Maine. Given that Dipper Harbour is located in the Bay of Fundy, it is possible that differences in oceanographic and biological conditions between Gulf of Maine and Bay of Fundy confounded our ability to determine whether herring bait is augmenting lobsters in eastern Maine. Both assessments of fishing pressure also indicated that

trap effort is two to four times greater in mid-coast Maine. These results suggest that herring bait effects on lobsters are non-linear, and that growth augmentation from bait may occur only in high density fishing areas where bait thresholds are achieved.

Unlike mid-coast Maine, where the primary difference in the diet of lobsters from fished versus closed sites was the increased prevalence of herring bait at the fished sites, several differences were detected between the diets of lobsters at fished versus seasonally closed sites in the eastern portions of Gulf of Maine. Stomach fullness of lobsters from Dipper Harbour was almost double that of lobsters from Cutler, whereas in mid-coast Maine, stomach fullness of lobsters did not differ between fished and closed sites. Dipper Harbour lobsters consumed markedly more mollusc biomass (i.e., mussels). Except for bait and decapods (i.e., cancer crabs), most prey (molluscs, urchins, cirripeds, unidentified tissue) were more prevalent in the diet of lobsters from Dipper Harbour, suggesting that high abundance of prey could be augmenting the growth of these lobsters. Lobsters from Dipper Harbour also had lower nitrogen stable isotope ratios, suggesting a larger fraction of their diet consisted of prey such as molluscs positioned lower in the food web.

Although herring bait subsidies are purportedly less important in the eastern portions of the Gulf of Maine, our results suggest that food resources more generally are limiting lobster growth throughout this region. In particular, the availability of lobster prey resources, whether from anthropogenic (mid-coast Maine) or natural (eastern Gulf of Maine) sources, can influence lobster metabolic and growth rates and impact the productivity of these lobster fisheries. Although the potential for bait to augment lobster populations in the Gulf of Maine is becoming more widely recognised (Saila et al. 2002; J.H. Grabowski unpubl. data), variability in lobster growth rates at large spatial scales has largely been attributed to the physiological effect of water temperature on lobster metabolic and growth rates. Bottom-up forcing has been shown to be important in a diversity of ecosystems (Power 1992; Strong 1992). Parslow-Williams et al. (2001) found that the Norway lobster *Nephrops norvegicus* is resource limited when its density is high, such as in the Clyde Sea area, Scotland, United Kingdom. The degree to which bait or natural prey is limiting the productivity of other crustacean fisheries globally deserves further attention given the ecological importance and economic value of these fisheries worldwide.

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