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The American Lobster in a Changing Ecosystem: A US–Canada Science Symposium, 27–30 November 2012, Portland, Maine

Richard A. Wahle, Andrea Battison, Louis Bernatchez, Stephanie Boudreau, Kathy Castro, Jonathan H. Grabowski, Spencer J. Greenwood, Carla Guenther, Rémy Rochette, and Jim Wilson

To the American lobster (*Homarus americanus*) fishery in the Northeast US and Atlantic Canada, 2012 may have gone down as the year that drove climate change home. An ocean heat wave covered a large swath of the North Atlantic and broke ocean temperature records. It also triggered biological effects that upset the relatively harmonious economics of Canada's winter and New England's summer lobster fisheries. The early molt induced by the historical warm temperatures put a glut of US lobsters on the market well before the Canadian fishery closed for the season and, in turn, caused a price tumble that even caught the attention of *The Wall Street Journal*: "Lobster glut slams prices" (WSJ online, 16 July 2012).

The story of the American lobster, especially over the last two decades, is one of striking contrasts. Just as lobster abundance in Maine, Nova Scotia, and other parts of Maritime Canada has climbed to historic highs, the fishery in southern New England has collapsed, plagued by disease and mass mortality. In the wake of the widespread depletion of once diverse ground fish resources, coastal communities in Maine and Atlantic Canada are more economically dependent on the lobster fishery than ever before, and perilously so. Despite its 150-year history, the fishery in this region is seeing record abundance and harvests. Although the boom in lobster production has helped offset ever-rising fuel and bait costs, plummeting prices following the financial crash of 2008 and the ocean heat wave of 2012 precipitated an unforeseen crisis in the business of lobstering. In contrast, in southern New England, hot summers and disease have taken their toll. For the first time, lobster harvesters in Rhode Island have had to consider the prospect of a fishing moratorium. Waters in the southern Gulf of St. Lawrence are also seeing more frequent bouts of stressful summer temperatures that in some cases have triggered mass die-offs.

Such dramatic changes after decades of relative stability highlight the need for a greater understanding of the American lobster in the context of its changing environment. Acknowledging the merits of the mandate for "ecosystem-based" fishery science and management, fishery managers on both sides of the border are grappling with how to integrate new thinking into traditional single-species approaches.

Opportunities for lobster scientists from the US and Canada to gather and talk science are few, but necessary. In the past few years, major research initiatives on the American lobster have been generating ground-breaking results. For example, in the US there has been an infusion of National Oceanic and Atmospheric Administration (NOAA) dollars to examine shell disease in southern New England, and the National Science Foundation's Coupled Human–Natural Systems Program supports research on the ecology and socio-economics of lobster and groundfish fisheries in the Gulf of Maine. In Canada, the Natural Sciences and Engineering Research Council of Canada (NSERC) supports a lobster research "node" in one of its Strategic Network Capture Fisheries grants, and long-term studies are under way at the University of Prince Edward Island to establish baselines for health parameters and responses to disease and industry-supported fishery enhancement efforts in the Gulf of St. Lawrence.

The symposium grew out of a consensus among the scientific community that the response of lobsters to a changing environment is best viewed in an ecosystem context. Whether induced by man or nature, fundamental changes have occurred over the past few decades in the physical environment and food web interactions. The driving questions are as follows: What do we know now that we did not know even a decade ago? What are the common US–Canadian research priorities? How can researchers move forward with an agenda that makes the best use of dwindling funding?

The two-and-a-half-day symposium was divided into four themes:

- Anthropogenic and environmental stressors
- Foodweb dynamics
- Population connectivity and metapopulation dynamics
- Coupled human–natural systems and ecosystem-based management

Some 150 academic and government scientists, students, resource managers, and industry members attended the symposium. Themes were introduced with a plenary talk by a leader in the field, followed by 48 oral and 26 poster presentations. Under environmental stressors, Jeff Shields (Virginia Institute of Marine Science) reviewed the catalog of diseases plaguing lobsters and

Received 28 August 2013. Accepted 3 September 2013.

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called for a better understanding of the environmental factors in a changing climate that make lobsters and other marine organisms more vulnerable to disease. Bob Steneck (UMaine) used the Gulf of Maine as a case study of “trophic dysfunction” to question whether the maximum sustainable yield of traditional fishery management is an achievable goal in a system where the serial depletion of top consumers has destabilized food webs. Lew Incze (UMaine and National Science Foundation) recapped advances in our knowledge of population connectivity and pointed to the need to (i) reconcile interpretations of population structure that emerge from genetic studies and models of larval source–sink dynamics and (ii) apply these insights to optimize fishery spatial management. Finally, Mike Fogarty (National Marine Fisheries Service) repeated the mandate for ecosystem-based fishery management: “Although the American lobster supports quintessential single-species directed fisheries throughout its range, it is increasingly clear that management frameworks that ignore biological interactions, environmental/climate change, and the social and economic context cannot fully capture the relevant dimensions necessary for effective lobster management.”

Guided discussion sessions on the symposium themes engaged participants to identify research priorities and catalyze collaborations. Summaries of these discussions authored by the discussion leaders are provided in four Appendices following this introduction: **Appendix A.** Anthropogenic and environmental stressors, by Castro and Green; **Appendix B.** Food web dynamics, by Boudreau and Grabowski; **Appendix C.** Lobster metapopulation dynamics and connectivity, by Bernatchez and Rochette; and **Appendix D.** Human–natural systems and ecosystem-based management, by Guenther and Wilson. These sessions identified important research gaps and underscored the need for greater cross-border collaboration at all levels.

The nine papers included in these proceedings represent a partial cross-section of the presentations delivered at the symposium. Topics span the first three themes. Regrettably, two social-science-oriented manuscripts were not considered for these proceedings because they were beyond the current scope of this journal. Nonetheless, one outcome of the symposium is the recognition that balanced and enduring natural resource policy emerges from an understanding of coupled human–natural systems. On the theme of environmental stressors, Shields (2013) uses the infamous Long Island Sound lobster die-off as a case study to illustrate the syndromes and diseases associated with climate warming; Laufer et al. (2013) explains the prevalence and toxic effects of alkylphenols from plastic waste in the marine environment; and Kunkel (2013) examines the mechanism by which shell disease erodes the lobster shell. On foodweb dynamics, Steneck and Wahle (2013) trace a 4000-year history of human depletion of the Gulf of Maine coastal foodweb; and two new field studies illustrate how trophic interactions and lobster behavior change in an environment free of large predatory fish (McMahan et al. 2013 and Oppenheim and Wahle 2013). Thermal change affects movements as well as survival and, in turn, can alter population connectivity. Annis et al. (2013) find that only a degree or two of ocean warming can significantly increase areas suitable for larval settlement in the cooler parts of the species range; and Jury and Watson (2013) reveal that because female lobsters prefer cooler temperatures, they distribute differently than males along temperature gradients found in estuaries and with depth. Finally, Rycroft et al. (2013) describe a new morphometric image analysis approach to aid the geographic discrimination of lobster subpopulations.

The iconic American lobster has broad relevance, if not as the canary-in-the-coal-mine, then as a poster child for the sometimes contrasting impacts of environmental change on our living marine resources and, in turn, our coastal economies. The extensive international and local media coverage of the symposium goes to show that when climate change affects things people care about, they pay attention. Links to media highlights can be found at the

symposium web site: <http://www.seagrant.umaine.edu/lobster-symposium>. The 2012 ocean heat wave is only the most recent of a series of environmental changes — some episodic and dramatic in effect, some more gradual — that have occurred in Northwest Atlantic over our lifetime and have affected the American lobster and its ecosystem. This symposium therefore placed the lobster fishery in the broader context of both global and regional environmental and ecological changes — some more directly man-made than others — that have manifested themselves in Atlantic Canada and New England.

Finally, we express our gratitude to symposium co-chair Paul Anderson and the staff of Maine Sea Grant for spearheading fundraising and for the work with Great Gatherings to coordinate symposium venue, program, and volunteers. We also appreciate the help of The Lobster Institute, the Fishermen and Scientist Research Society, and the symposium steering committee for taking on specific tasks before, during, and after the meeting. We are grateful to the editorial staff of the Canadian Journal of Fisheries and Aquatic Sciences for undertaking the review of manuscripts submitted for these proceedings. Symposium financial support was provided by National Sea Grant College Program; National Oceanic and Atmospheric Administration; Fisheries and Oceans Canada; University of Maine; University of Rhode Island; University of New Brunswick; Maine Department of Marine Resources; Prince Edward Island Fisheries, Aquaculture and Rural Development; Nova Scotia Fisheries and Aquaculture; Newfoundland and Labrador Fisheries and Aquaculture; The Lobster Institute; Maine Coastal Program; Ocean Choice International; and Aquatic Science and Health Services.

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Appendix A. Discussion Summary: Anthropogenic and environmental stressors

Kathy Castro and Spencer J. Greenwood

Environmental stress is manifested in lobster by diseases and various pathologies. Crustacean pathologist, Jeffrey Shields (Virginia Institute of Marine Science) opened the session with the message that to understand the conditions promoting disease, one must study the interactions among the environment, host, pathogen, and human activities (figure 1 in Shields 2013). Some 26 oral and poster presentations covered a variety of topics in the areas of anthropogenic and environmental effects on the American lobster.

Much attention during the symposium focused on how climate change affects lobster health. Warmer than average summers have caused mass mortalities and disease at the southern edge of the American lobster's range, just as its numbers have expanded in historically cooler regions in the north. Highly publicized and contrasting cases in point include epizootic shell disease and the subsequent fishery collapse in southern New England, USA, and the lobster "glut" in the eastern Gulf of Maine. Discussion also turned to the degradation of lobster habitat through water pollution, the accumulation of human debris, including ghost traps, and direct disturbance by fishing activities, such as dredging and trawling.

Several key questions emerged:

- Are some lobsters more resistant to disease than others?
- How does fishing pressure affect the resilience of lobster populations to environmental change?
- How can fishers' observations be turned into a real-time data stream?
- Can lobster populations recover from mass mortality? At low numbers, is population reproductive performance compromised by sperm limitation?

Future directions and recommendations

Presenters highlighted the need for more longitudinal studies of environmental change. Retrospective and prospective studies on the influence of climate change on lobster health will allow us to define if anthropogenic or environmental changes make lobster stocks more vulnerable. A general epidemiological model for lobster diseases is needed to generate testable hypotheses and identify information gaps. This requires large-scale ecological- and laboratory-based approaches that permit integration of information over the entire species' range. It also requires better integration with fishery managers to mitigate disease effects. Correlative data on other marine species in these areas may further improve understanding of ecosystem health. This means coordinating centers of scientific expertise between the US and Canada. Discussion defined the type of studies needed to predict, prevent, or manage disease outbreaks as follows:

- standardized monitoring programs for all life stages, including health and disease indicators, and a method to rapidly incorporate fishers' observations and local knowledge
- rapid dissemination of survey data on trends or patterns of lobster abundance and disease prevalence
- a better understanding of lobster immunity and the development of disease resistance
- a lobster tissue bank to archive samples from different regions for retrospective studies of lobster health and gene expression
- physiological and functional genomics studies to evaluate host response to pathogens, contaminants, and environmental conditions

Reference

Shields, J. 2013. Complex etiologies of emerging diseases in lobsters (*Homarus americanus*) from Long Island Sound. *Can. J. Fish. Aquat. Sci.* 11: This issue. doi:10.1139/cjfas-2013-0050.

Appendix B. Discussion Summary: Food web dynamics

Jonathan H. Grabowski and Stephanie A. Boudreau

Four themes emerged from the plenary talk "Lobster dynamics in a brave new ocean" presented by Bob Steneck, six oral presentations, three posters, and the following round-table discussion. The presentations traced a 4000-year time line of human depletion of the top predators in the lobster ecosystem, with the decimation of the groundfish assemblage in our lifetime perhaps being only the most recent. Many attributed the dramatic expan-

sion of the lobster population in the Gulf of Maine and Atlantic Canada to the relaxation of predation pressure. These discussion themes are summarized below.

Theme 1: cod-lobster co-existence

Foodweb research has perhaps focused too much on Atlantic cod (*Gadus morhua*) alone as a keystone predator. Evidence is contradictory regarding the importance of cod dynamics as a top-down driver of the lobster surge (Hanson and Chouinard 2002; Link and Garrison 2002). The collective biomass of groundfish has remained largely constant in the Gulf of Maine and Scotian Shelf; however, individual groundfish have smaller body sizes on average, and the relative abundances of many species have changed (Shackell et al. 2009; Wahle et al. 2013). Although these changes would suggest lobsters now outgrow their groundfish predators at a smaller size, there is some question as to whether predators would consume more lobster today than in the past because smaller fish grow faster and have higher tissue turnover rates and greater mass-specific metabolic demands. Future studies need to consider the following: (i) how body size changes in cod and other predators influence interactions with lobsters; (ii) when and where lobster and cod overlap in habitat; (iii) whether other species in the groundfish assemblage are more important lobster predators than cod; and (iv) whether climate change will alter predator species ranges and, in turn, their interaction with lobsters.

Cod-lobster and predator-lobster interactions in general will likely be greatly influenced as a consequence of climate change. It is time to start focusing more on other potential predators, for example, those whose ranges are likely to shift northward into American lobster's geographic range, such as the smooth dogfish (*Mustelus canis*) and black seabass (*Centropristis striata*). Moreover, these other predators and their interactions with lobsters deserve greater research attention given the paucity of work that has been conducted on these relative to cod-lobster interactions (i.e., Boudreau and Worm 2010).

Theme 2: lobsters and food web diversity

Low diversity ecosystems like the coastal Northwest Atlantic may be more vulnerable to boom and bust dynamics because losses of a single consumer species can have greater proportional impacts on their prey. This is likely why the declines in the diversity and abundance of apex predators in the Northwest Atlantic have so dramatically altered the food web (Witman and Sebens 1992; Steneck 1997; Jackson et al. 2001; Baum et al. 2003; Steneck and Sala 2005). Not only were Atlantic cod and other groundfish larger and more abundant, but there is archaeological evidence that now-extinct mammalian predators such as sea mink and walrus may have been part of the lobster ecosystem. Future research efforts that partition the consequences of lower food web diversity on lobster and groundfish population dynamics will benefit efforts to understand and manage these food webs. Comparative trans-Atlantic studies of top-down mechanisms may also help us understand the consequences of food web diversity for the population dynamics of the ecologically similar *Homarus* sibling species on opposite coasts and could yield important insights needed to manage these food webs.

Theme 3: density dependence and lobster population dynamics

With lobster populations so high in parts of their range, do crowding effects and density-dependent feedbacks now occur? In an ecosystem free of apex predators, benthic mid-level consumers such as lobster and other crustacean populations may now be so high that they are consuming each other (i.e., intraguild predation). New evidence presented at the symposium suggests that surging lobster populations in the Gulf of Maine may result in lobsters consuming themselves (Oppenheim and Wahle 2013). We

note that these observations from tethering studies must be interpreted with caution owing to the tether altering the lobster's behavior. Stable isotope analysis is a promising technique (e.g., Grabowski et al. 2010) that, along with more conventional methods such as stomach content analysis and in situ predation experiments, may help discern the relative contribution of different sources of food.

Theme 4: What do we need to be monitoring?

Discussion participants felt that it was important to assess the predator-prey interaction correctly. For example, aggregating predatory species by functional groups or into more inclusive taxonomic categories could reveal correlations not evident in species-specific analyses. To date, the focus has been on apex predators, yet questions remain about other trophic interactions, such as the effects of increasing lobster populations on their prey. In a warming ocean, the Gulf of Maine is likely to gain more species than it loses and therefore may increase in diversity. We need to be monitoring these gains and how they impact species interactions.

Just as we consider top-down drivers, we equally need to assess bottom-up processes and the degree to which resources limit lobster numbers. Natural prey availability has been shown to be particularly important for lobster population dynamics (Grabowski et al. 2009), and lobsters consume herring bait, which may enhance lobster production in the Gulf of Maine (Saila et al. 2002; Grabowski et al. 2010). The importance of shelter habitat availability has also been demonstrated to mediate lobster population dynamics in the Gulf of Maine (Cobb 1971; Hovel and Wahle 2010). These factors deserve further attention, especially in the context of climate change.

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Appendix C. Discussion Summary: Lobster metapopulation dynamics and connectivity

Louis Bernatchez and Rémy Rochette

A metapopulation is defined as a group of local subpopulations connected by dispersal. Connectivity is the exchange of individuals among subpopulations. Tagging studies, biophysical dispersal modeling, and population genetics are tools used to understand connectivity. The plenary talk by Lew Incze (UMaine) and 18 contributed oral and poster presentations set the stage for discussion over seven questions during the round-table interactive sessions:

Question 1: Is knowledge of population genetic structure important to lobster management? Participants said yes, but there should be parallel ecological and genetic studies to cross-validate interpretations of connectivity. Recent advances in genomics now permit processing of thousands of genetic markers that could substantially improve resolution of population genetic structure. A mismatch between the spatial scale of genetic structure and management is likely, but the population response to fishing pressure may be more relevant to management.

Question 2: How is the concept of metapopulation dynamics applied in management? Literature suggests stock resilience to fishing pressure may be enhanced by an external subsidy of recruits from other areas. However, fishers may not support particular conservation measures if the benefit goes to neighboring areas more than their own. Redefining management boundaries might be prudent in such cases.

Question 3: What types of data are most important? Genetics, dispersal modeling, and tracking movements are all important and hard to prioritize. Pelagic larval transport has largely been understood through modeling, but adult movements have been studied by tagging. It is more important now to integrate approaches among areas of expertise.

Question 4: What spatial and temporal scales are most relevant? A hierarchy of integrated spatial scales is called for, but the smallest scales may not be relevant to fishery management. Growing evidence suggests lobsters may “self-recruit” at scales smaller than expected. That requires a better understanding of nearshore processes, cross-shore currents, and larval vertical migration and, in turn, the relevance to stock definition.

Question 5: Where are the knowledge gaps? Quantitative estimates of connectivity over the species range are still lacking. Incorporating postlarval behavior in dispersal models could improve connectivity estimates. These need to be validated against field data. A new class of genetic markers called single nucleotide polymorphisms could provide greater resolution to predict the location or persistence of population barriers. Finally, policy development could better align biological population boundaries with management boundaries, even at an international scale.

Question 6: Is it important to know what environmental factors shape population structure? Some subpopulations may be locally adapted to disease, heat, and pollutants. Population and functional genomics studies that evaluate gene expression in response to changes in the environment could be enlightening.

Question 7: Does fishing pressure affect our ability to apply these concepts to manage the fishery? Yes. Size- and sex-specific harvesting can be important selective forces shaping the genetic structure of lobster populations and need to be better understood.

Conclusions

The metapopulation concept is relevant to American lobster conservation. New population genomics methods coupled with larger-scale pelagic and benthic dispersal modeling, all verified by field and lab studies, will be important in developing a refined view of lobster population structure and local adaptation in a fast-changing environment.

Appendix D. Discussion Summary: Human–natural systems and ecosystem-based management

Carla Guenther and Jim Wilson

Mike Fogarty's (National Marine Fisheries Service) plenary talk underscored the need for ecosystem-based management (EBM): "management frameworks that ignore biological interactions, environmental/climate change, and the social and economic context cannot fully capture the relevant dimensions necessary for effective lobster management." Twelve contributed talks and five posters added fuel for discussion. Northern and southern segments of the lobster fishery may be walking divergent paths, but both face new economic challenges; the former because of a rapid increase in supply, the latter because of recruitment failure. Uncertainties over the future of the fishery stem in part from wariness about climate change impacts on lobster population dynamics and in part from the instability of the global and regional economies. Discussion included a broad scope of topics, from the value of ecosystem services in EBM, to property tax structures, to specific lobster management tools.

In the Gulf of Maine's new "lobster-dominated ecosystem," the old rules no longer seem to apply. The restraints that worked so well in a diverse fishery are not so clearly beneficial in a monoculture of super-abundant lobsters. Some fishers now question long-standing measures to protect egg-bearing females simply because there are "too many"; territoriality over ideal lobster habitat has lessened because lobster populations have expanded to occupy previously unsuitable expanses of shelterless mud habitat because predatory groundfish are now so depleted.

Different regional responses of lobsters to a warming climate and new studies showing self-recruitment at a finer scale than previously assumed both point to the possible need for management responses at less than a state-wide scale. What might be appropriate in one region may not be appropriate in another. The lobster zones used in Maine and Canadian lobster fishing areas may be well matched to the ecological scale at which harvesters are likely to reap the long-term rewards of area-specific management.

One big question is how fishers and managers might prepare for the surprise that everyone expects but cannot predict. The price collapses in 2008 and 2012 were caused by very different conditions: one rooted in global economics, the other a market surplus rooted in biology and ecology. In both cases the individual fisher had two choices: either stop fishing or fish harder. Consequently, in places where lobsters were abundant fishers worked harder; where they were not abundant, there was little choice but to stop fishing and switch to something more profitable. It is possible that a region-wide coordinated response to slow the supply may have helped the economics of the fishery by increasing the price, but the costs and way to accomplish that coordination are not known and will have to be explored. In contrast, the uncoordinated response in both 2008 and 2012 left individual fishers acting in their own best interests. The question remains: is there a smarter way to respond to the kinds of spatially differentiated external shocks the industry has experienced recently?

While there was strong support for long-standing conservation measures, the need was also expressed to think outside the box. EBM may offer a flexible and adaptive strategy to manage the response of the lobster fishery to shifts in lobster abundance and distribution and the vagaries of the economy. However, it remains unclear how EBM will monitor and incorporate the key ecological, social, and economic drivers of the fishery. EBM is a daunting, information-intensive undertaking — how to implement it remains one of the central challenges of the decade.