



ELSEVIER

Contents lists available at ScienceDirect

## Marine Pollution Bulletin

journal homepage: [www.elsevier.com/locate/marpolbul](http://www.elsevier.com/locate/marpolbul)

## Interactions between finfish aquaculture and lobster catches in a sheltered bay

Ronald H. Loucks<sup>a,\*</sup>, Ruth E. Smith<sup>a</sup>, E. Brian Fisher<sup>b</sup>

<sup>a</sup> RH Loucks Oceanology Ltd., 24 Clayton Park Drive, Halifax, Nova Scotia B3M 1L3, Canada

<sup>b</sup> Port Mouton, Nova Scotia BOT 1T0, Canada

### ARTICLE INFO

Article history:  
Available online xxx

Keywords:  
Lobster  
Aquaculture  
Displacement  
Open-net  
Finfish  
Olfactory

### ABSTRACT

Interactions between open-net pen finfish aquaculture and lobster catches in a sheltered bay in Nova Scotia, Canada, were investigated using fishermen's participatory research in annual lobster trap surveys over seven years.

Fishermen recorded lobster catches during the last two weeks of May from 2007 to 2013. Catches for each trap haul were recorded separately for ovigerous and market-sized lobsters. Catch trends within the bay were compared to regional trends. Results of correlation analyses indicated that ovigerous catch trends were strongly affected by the fish farm's feeding/fallow periods. There was no significant correlation between trends for bay and LFA lobster landings.

Patterns of lobster catch per unit effort extending over considerable distance in Port Mouton Bay appear to be influenced by proximity to the fish farm regardless of year-to-year variation in water temperatures and weather conditions. Odours and habitat changes surrounding open-net pen finfish operations are potential factors affecting lobster displacement.

© 2014 Elsevier Ltd. All rights reserved.

### 1. Introduction

American lobster (*Homarus americanus*) currently supports the most valuable fishery in Atlantic Canada. Increases in lobster landings in recent years have been linked to reduced predation related to the decline of the groundfish stocks (Boudreau and Worm, 2010), resulting in almost complete reliance for coastal communities on this high-value fishery (Steneck et al., 2011).

Management areas for the lobster fishery are large geographic units called Lobster Fishing Areas (LFAs). As part of the Canadian government's fisheries management regime, lobster fishermen are required to report landings and trap hauls to the Department of Fisheries and Oceans (DFO) (Coffen-Smout et al., 2013).

Concurrent with the increase in lobster landings has been the rise of open net pen finfish aquaculture. These operations are largely, but not exclusively, located in sheltered areas of the coastal zone which provide protection from heavy seas, suitable year-round temperatures and, depending on location, some tidal flushing (Milewski, 2001). The number of fish stocked per farm site can range from 200,000 to 700,000 depending on the farm production plan. In Atlantic Canada, the province of New Brunswick is the largest producer of farmed fish (30,359 mt in 2012) followed by Nova Scotia (6087 mt) (DFO, 2012).

Where traditional fisheries and aquaculture operate in the same area, conflicts have arisen (Wiber et al., 2012; Harvey and Milewski, 2007; Walters, 2007). Fishermen have reported that two years after a fish farm has been established within their area ovigerous or egg-bearing lobsters and herring avoid the area, (Wiber et al., 2012). Lobster, as well as crab and shrimp, mortalities have also been reported due to legal and illegal pesticides used to treat sea lice infestation on salmon farms (Wiber et al., 2012; Harvey and Milewski, 2007). Some aquaculture operators point to the record high lobster landings as proof that fish farms and aquaculture can co-exist and claim that net pens attract lobsters and increase local landings (Milewski, 2014).

Fishermen of Port Mouton Bay, Nova Scotia, are part of LFA 33 management area (Fig. 1). In recent years, they report abandoning historical lobster fishing 'territories' within the bay because of very low catches. This trend developed after 1995 when an open net pen Atlantic salmon (*Salmo salar*) farm began operating in the bay (Fig. 1). Fishermen believe these territories had been lobster spawning and moulting areas (Fishermen, pers comm.) Historical lobster trap surveys conducted by the federal Department of Fisheries and Oceans (Miller et al., 1989, unpublished records in DFO files 1946-7) support local ecological knowledge that Port Mouton Bay had been a destination for lobster migration.

Fishermen have detailed knowledge of their resource and fishing practices. This information can be quantified and applied to

\* Corresponding author.

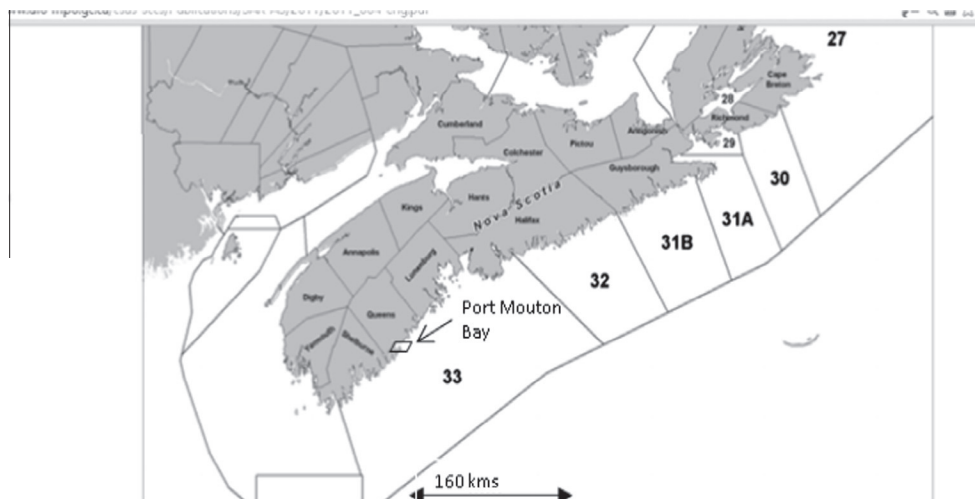


Fig. 1. Location of Port Mouton Bay, Nova Scotia (Canada), within Lobster Fishing Area (LFA) 33.

discern trends within fisheries (Berkes, 1999; Neis et al., 1999; Hutchings and Ferguson, 2000; Johannes et al., 2000; Hutchings et al., 2002; Maunder et al., 2006; Garcia and Charles, 2007; Miller et al., 2010; Wiber et al., 2011, 2012). Information on lobster catch-per-trap-haul or catch per unit effort (CPUE) reveals important trends and patterns (Tremblay et al., 2011).

This study combines fishermen's local knowledge, participatory research and established scientific methods to examine lobster catch data in the vicinity of an established finfish farm over a seven year period.

## 2. Methods

Fishermen recorded lobster catches within Port Mouton Bay during the last two weeks of May for seven years (2007–2013). This period represents a time when higher numbers of lobsters historically migrate into the bay. Catches for each trap haul were recorded separately for ovigerous and market lobsters. Market lobsters are defined as having a carapace length of at least 82.5 mm. Catch-per-unit effort (CPUE) was calculated as a function of kilograms caught per trap haul for market lobsters and numbers caught per 1000 trap hauls for ovigerous lobsters. Data for market lobsters, not collected in 2008, was resumed in 2009.

Catch statistics were compiled for each of five contiguous regions of Port Mouton Bay (Fig. 2). Regions were delineated geographically based on historic fishing territories, areas where the same fishermen occupy the same territories year after year. Region 2 includes the Atlantic salmon farm site which was fallowed from late July 2009 until June, 2012, and then re-stocked with Rainbow trout (*Oncorhynchus mykiss*) (Fig. 2). Fallowing refers to a temporary cessation in production at the farm site.

Data for lobsters landings in LFA 33 for 2007–2010 were taken from Tremblay et al. (2011); those for 2011–2013, were derived from landed value and average price per pound in the Department of Fisheries and Oceans, Maritimes Region Economic Update (DFO, 2013). DFO Statistical Lobster Fishing Area LFA 33 includes and is spatially much larger than Port Mouton Bay.

Pearson's correlation analysis was carried out between the CPUE for ovigerous and market lobster in each fishing region and the fish farm's feeding/fallow period and lobster landings for LFA 33. A one-sided t-test was used in significance testing.

Bottom temperature data for Port Mouton Bay was provided by a temperature recorder placed in a trap in Region 4. The recorder was operated by the Fishermen and Scientist Research Society, a

partnership between fishermen and scientists whose goal is to promote the sustainability of the marine fishing industry in Atlantic Canada.<sup>1</sup>

## 3. Results

Overall, the number of trap hauls was lowest in all fishing regions in the bay during the periods of fish farm operation (2007, 2008, 2009 and 2013) compared to years of fallow (2010, 2011 and 2012) (Table 1). Each trap haul represents costs in time, fuel and bait – fishermen optimize their catch per unit effort, otherwise costs may exceed revenue. The average number of fishing days lost to poor weather during the two-week survey period was slightly less in 2013 (2.4 days/boat) than in 2011 (2.6 days/boat).

The farm was operating at an estimated 50% capacity in July, 2009, documented by an aerial photograph (Loucks et al., 2012).

During operation of the fish farm in 2007, 2008 and 2009, CPUE for ovigerous lobsters was low in all regions (Fig. 3). During the fallow period (2010, 2011 and 2012), CPUE for ovigerous lobsters increased markedly everywhere except in Region 2. In 2013, with the fish farm restocked, all regions again showed low CPUE, although Region 5, the outermost region, showed a pattern of some resemblance to LFA 33 landings.

Market lobster CPUE in 2007, 2009–2013 ranged from 0.15 to 0.3 kg/trap haul in Region 2 (Fig. 4). Lobsters were caught in peripheral areas of Region 2, but not near the fish farm. In the other regions, market lobster CPUE ranged from 0.1 up to 0.6 kg/trap haul. During the fallow period Regions 1, 3 and 4 adjacent to the fish farm generally showed increased CPUE. In 2013, with the farm re-stocked, market lobster CPUE were again at low levels – from 0.1 to 0.4 kg/trap haul (Fig. 4).

The feeding/fallowing period sequence at the fish farm and the LFA 33 pattern of landings were each tested for correlation with the five regional patterns for ovigerous lobsters (Table 2). A corresponding set of 10 correlations was prepared for market lobsters (Table 3).

The feeding/fallowing period at the fish farm had an effect on CPUE for ovigerous lobsters in Regions 1, 3, 4 and 5 at the 95% confidence level (Table 2). Region 2 was unresponsive. Feeding/fallowing explained 57–72% of the variability in CPUE for ovigerous lobster in Regions 1, 3, 4, and 5. In Region 2, CPUE for ovigerous lobster

<sup>1</sup> [www.fsr.ca](http://www.fsr.ca).

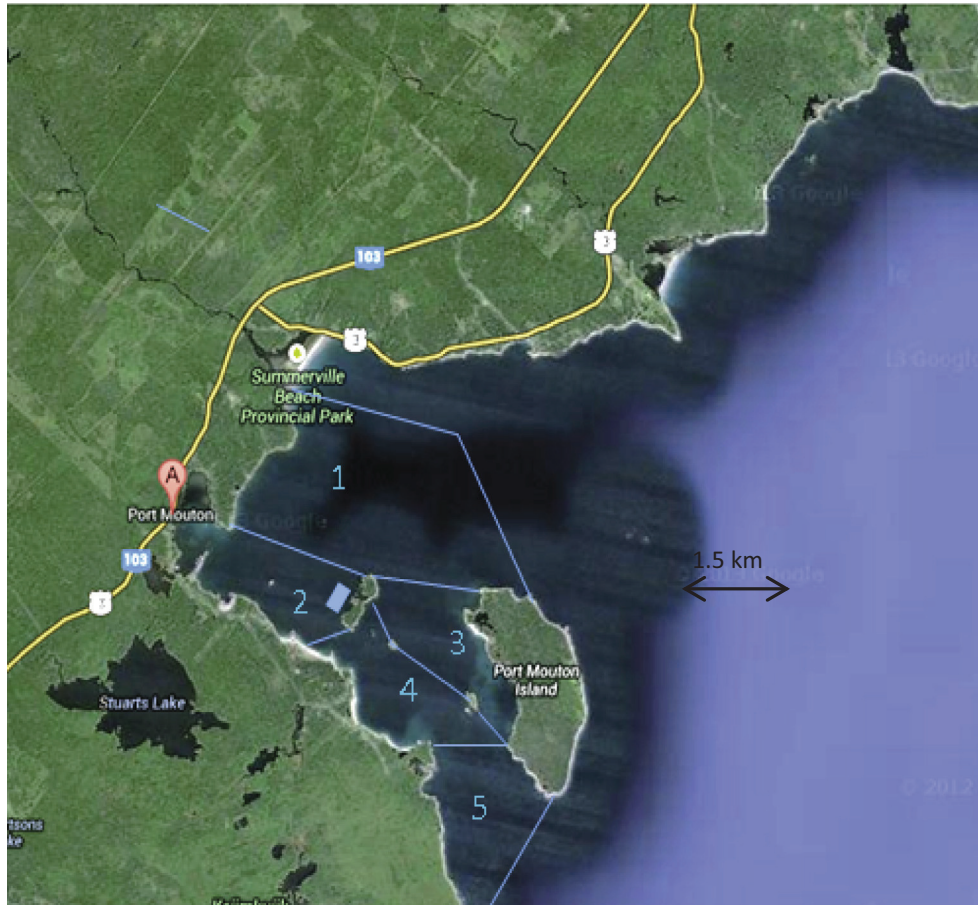


Fig. 2. Assigned lobster catch regions within Port Mouton Bay. The Spectacle Island finfish aquaculture site is the blue rectangle in Region 2.

**Table 1**  
Number of boats and number of trap hauls for each year of survey.

Year	# Boats	# Hauls
2007	7	5779
2008	12	5238
2009	15	10,230
2010	14	13,045
2011	12	11,597
2012	13	11,717
2013	11	8558

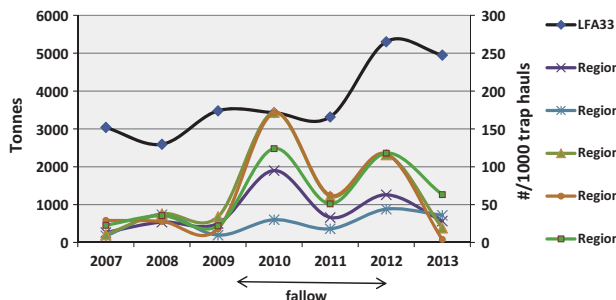


Fig. 3. CPUE (number per 1000 trap hauls) for ovigerous lobsters for five regions in Port Mouton Bay compared with market lobster landings in tonnes for LFA 33.

was low, and remained low throughout the seven year period of the study regardless of the feeding/fallow activity at the fish farm. There was no significant correlation between CPUE for ovigerous lobster and landings in LFA 33.

The relationships between market lobster CPUE and the feeding/fallow period were significant at the 95% confidence level for

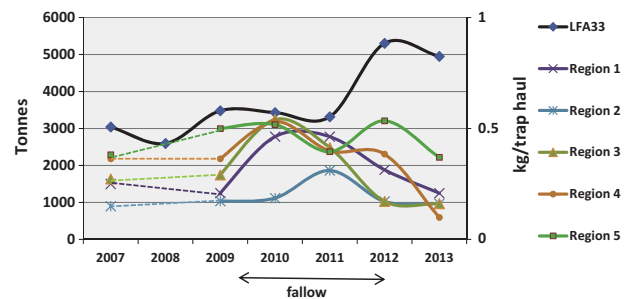


Fig. 4. Market lobster CPUE (kg/trap haul) for five regions in Port Mouton Bay compared to landings (tonnes) for Lobster Fishing Area (LFA) 33.

Region 1, at the 90% confidence level for Regions 3 and 4 and not significant for Region 2 or 5. Market lobsters CPUE showed no relationship with landings in LFA 33 (Table 3).

Bottom temperature data in Port Mouton Bay showed higher temperatures for the May 17–31 survey period in 2010 than in 2008 or 2009 and more variable temperatures in 2012. The temperature recorder failed in 2011 but unofficial reports indicate lower temperatures for May in that year. Temperatures in 2013 were comparable to those in 2010 until temperatures dropped in days 11–14 of the survey (Fig. 5).

#### 4. Discussion

Region 2 lobster catch rates in Port Mouton Bay hardly responded to changes in fish farm production located within its

**Table 2**

Pearson's correlation coefficients and proportion of variation explained between candidate drivers and responsive CPUE for ovigerous lobsters for five fishing regions in Port Mouton Bay.

Potential drivers	Ovigerous lobsters response, fishing region	Correlation coefficient	Percent of variation 'explained'
Feeding/fallow period	1	0.76**	57
	2	0.28	8
	3	0.82**	67
	4	0.85**	72
	5	0.77**	60
LFA 33 landings	1	0.27	7
	2	0.56	31
	3	0.19	3
	4	0.15	2
	5	0.56	32

\*\* Correlation significant at  $p < 0.05$ .

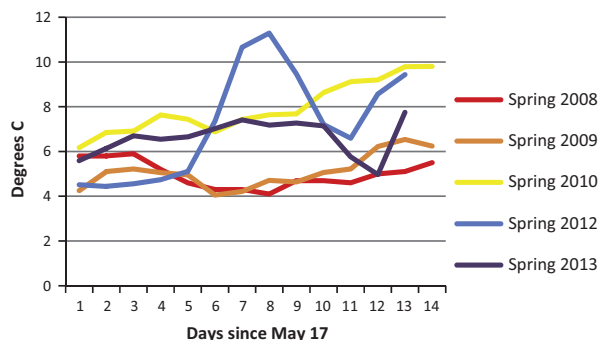
**Table 3**

Pearson's correlation coefficients and proportion of variation explained between variables and CPUE for market lobsters for five fishing regions in Port Mouton Bay.

Potential drivers	Market lobsters response, fishing region	Correlation coefficient	Percent of variation 'explained'
Feeding/fallow period	1	0.78**	61
	2	0.46	21
	3	0.62*	38
	4	0.72*	52
	5	0.33	11
LFA 33 landings	1	-0.28	8
	2	-0.51	26
	3	-0.57	32
	4	-0.57	32
	5	0.02	0

\* Correlation significance at  $p < 0.1$ .

\*\* Correlation significance at  $p < 0.05$ .



**Fig. 5.** Sea bottom temperatures record in Region 4 during the survey period.

region. Catch rates remained low in all years for both ovigerous and market lobsters, unlike the catch rates in other regions of the Bay which were responsive even in the far-field. For example, partial recovery was recorded for fishing regions (other than Region 2) where catch rates increased in 2010 – the first of three years of fallow – while LFA33 landings were approximately constant. Increase in Port Mouton Bay lobster CPUE for all regions except Region 2 generally continued through 2012 except for a decrease in 2011 associated with poor weather conditions. In 2013 when the fish farm resumed feeding operations, Port Mouton Bay lobster catch rates in all regions except Region 2 dropped significantly while LFA33 landings continued at a high level. Overall,

lobster CPUE patterns in Port Mouton Bay did not match the upward trend with time shown for LFA 33 and were different from the LFA 33 pattern.

Correlation results also showed that for both ovigerous and market lobsters there was little or no correlation to the landing trends in LFA 33 but that the responses to the fish farm's feeding/fallow periods were strongly suggestive especially for ovigerous lobsters.

A possible explanation for the persistently lower catch rates in Region 2 is degraded water quality and habitat. Lobsters are olfactory predators and possess olfactory neurons that constantly discharge small bursts of electrical pulses, much like radar. It is speculated that these “bursting” neurons might cue the crustaceans to an odor's location—especially important when they are searching for food or trying to avoid danger (Park et al., 2014). It has been proposed that the highly sensitive nature of the olfactory receptors in crustaceans such as lobsters and corresponding behavioural reactions to pollutants could be used in ecological and toxicological investigations (Blinova and Cherkashin, 2012).

Open net finfish aquaculture operations can produce odours and change benthic habitat and water quality which may affect lobster behaviour and movement. These changes could include the production of hydrogen sulphide and anoxic conditions from decomposing fecal particles, (Kalantzi and Karakassis, 2006) and macro- and microalgal blooms caused by excess nutrient loading (Islam, 2005; Worm and Lotze, 2006; Strain and Hargrave, 2005; Robinson et al., 2005; Hargrave, 2010). Spatial impacts will depend on a range of factors including the number of farm sites per area, the duration of their operation, feeding practices, water depth and strength of tidal or bottom currents.

Fishermen in this study reported lobster traps covered with odorous, nuisance ‘slime’ algae at distances of several kilometers when the fish farm was in operation and restricted to a zone nearer the fish farm site during the period of fallow (Fig. 6). Fishermen in New Brunswick have described the sea bottom around fish farms as “mildewed or mouldy” (Wiber et al., 2012).

Factors other than the presence of the fish farm wastes could conceivably explain the lower catch rates in Region 2. For example lobster catch rates are known to be influenced by water temperature. In general, warm waters lead to higher catch rates (Jury and Watson, 2013; Drinkwater et al., 2006). If temperature was a factor in this study, catch rates should be high across all regions of the bay in 2010 when bottom temperatures were highest over the seven-year period. Catch rates did increase in 2010 in all regions except Region 2. Lower temperatures, therefore, are an unlikely explanation for the low catch rates in the vicinity of the fish farm.

Statistically, lobster catch rates can be biased if the spatial distribution or the extent of fishing changes through time (Walters,



**Fig. 6.** A lobster trap hauled up 24 h after being set approximately one kilometre from farm site (May 19, 2013) is coated with epiphytic algae.

2003; Maunder et al., 2006). The information from this lobster survey is stratified spatially, although not randomized – there is a bias toward elevated CPUE because the fishermen follow the lobsters to optimize their catch – a consistent feature of the fishing practice, but not a driver of the trends. The results are conservative because CPUE is larger than for a random survey, yet the low CPUE numbers are striking. While not a stratified random survey, it approaches one.

The Port Mouton Bay survey results are supported by observations reported by lobster fisherman in the adjacent province of New Brunswick. They reported that within two years of a finfish aquaculture operation being established ovigerous lobsters abandon the area, overall lobster abundance decreases, and female lobsters return when fish farming is discontinued in an area (Wiber et al., 2011, 2012).

To our knowledge, this study provides the only relatively long-term, published data series for examining the potential impact of an open net pen finfish farm on lobster catches. Other than the wastes released from the fish farm, it is unclear what factors could explain the displacement of lobsters from the surveyed portions of Port Mouton Bay and their partial return and recovery with following.

### Acknowledgements

We value the expert advice of Robert Miller, Anthony Charles, Boris Worm, Jeffrey Hutchings, Inka Milewski and the diligent recording of catch data by Port Mouton Bay fishermen.

### References

- Berkes, F., 1999. Sacred Ecology. Taylor and Francis, Philadelphia, PA.
- Blinova, N.K., Cherkashin, S.A., 2012. The olfactory system of crustaceans as a model for ecologo-toxicological studies. *J. Evol. Biochem. Physiol.* 4 (20), 155–165.
- Boudreau, S.A., Worm, B., 2010. Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. *Mar. Ecol. Prog. Ser.* 403, 181–191.
- Coffen-Smout, S., Shervill, D., Sam, D., Denton, C., Tremblay, J., 2013. Mapping inshore lobster landings and fishing effort on a maritimes region modified grid system. *Can. Tech. Rep. Fish. Aquat. Sci.* 3024, 33.
- DFO, 2012. <<http://www.dfo-mpo.gc.ca/stats/aqua/aqua12-eng.htm>>.
- DFO, 2013. 2007–2011 LFA 33 Landings, Maritimes Region Economic Update – Presentation to the Regional Advisory Lobster Committee Oct. 11, 2013. <[http://gallery.mailchimp.com/9cc0597231/files/Economic\\_Update\\_Maritimes\\_Region\\_RLAC\\_Oct11\\_2013\\_PE.pdf](http://gallery.mailchimp.com/9cc0597231/files/Economic_Update_Maritimes_Region_RLAC_Oct11_2013_PE.pdf)>.
- Drinkwater, K.F., Tremblay, M.J., Comeau, M., 2006. The influence of wind and temperature on the catch rate of the American lobster (*Homarus americanus*) during spring fisheries off eastern Canada. *Fish. Oceanogr.* 15 (2), 150–165.
- Garcia, S.M., Charles, A., 2007. Fishery systems and linkages: from clockwork to soft watches. *ICES J. Mar. Sci.* 64, 580–587.
- Hargrave, B.T., 2010. Empirical relationships describing benthic impacts of salmon aquaculture. *Aquacult. Environ. Interact.* 1 (1), 33–46.
- Harvey, J., Milewski, I., 2007. Salmon Aquaculture in the Bay of Fundy: An Unsustainable Industry. Conservation Council of New Brunswick, Fredericton, New Brunswick, Canada.
- Hutchings, J.A., Ferguson, M., 2000. Links between fishers' knowledge, fisheries science, and management: Newfoundland's inshore fishery for northern Atlantic cod, *Gadus morhua*. In: *Finding Our Sea Legs: Linking Fishery People and their Knowledge with Science and Management*. ISER Books, St. John's, NF, pp. 82–110.
- Hutchings, J.A., Neis, B., Ripley, P., 2002. The nature of cod: perceptions of stock structure and cod behaviour by fishermen, 'experts' and scientists from the nineteenth century to present. In: Ommer, R. (Ed.), *The Resilient Outport: Ecology, Economy and Society in Rural Newfoundland*. ISER Books, St. John's, NF, pp. 140–185.
- Islam, M.S., 2005. Nitrogen and phosphorus budget in coastal and marine cage aquaculture and impacts of effluent loading on ecosystem: review and analysis towards model development. *Mar. Pollut. Bull.* 50 (1), 48–61.
- Johannes, R.E., Freeman, M.M.R., Hamilton, R.J., 2000. Ignore fishers' knowledge and miss the boat. *Fish Fisheries* 1 (3), 257–271.
- Jury, S.H., Watson, W.H., 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Can. J. Fish Aquat. Sci.* 70, 1650–1657.
- Kalantzi, I., Karakassis, I., 2006. Benthic impacts of fish farming: meta-analysis of community and geochemical data. *Mar. Pollut. Bull.* 52 (5), 484–493.
- Loucks, R.H., Smith, R.E., Fisher, C.V., Brian Fisher, E., 2012. Copper in the sediment and sea surface microlayer near a fallowed, open-net fish farm. *Mar. Pollut. Bull.* 64, 1970–1973.
- Maunder, M.N., Siebert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J. Mar. Sci.* 63, 1373–1385.
- Milewski, I., 2001. Impacts of salmon aquaculture on the coastal environment: a review. In: Tlustý, M.F., Bengston, D.A., Halvorson, H.O., Oktay, S.D., Pearce, J.B., Rheault, R.B., Jr. (Eds.), *Marine Aquaculture and the Environment: A Meeting for Stakeholders in the Northeast*. Cape Cod Press, Falmouth, Massachusetts, pp. 166–197.
- Milewski, I., 2014. Ocean planning: thinking globally, acting regionally. *Fishermen's Voice* 9 (3), 1–2.
- Miller, R.J., Duggan, R.E., Robinson, D.G., Zheng, Z., 1989. Growth and Movement of *Homarus americanus* on the outer coast of Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1716.
- Miller, K., Charles, A., Barange, M., Brander, K., Gallucci, V.F., Gasalla, M.A., Khan, A., Munro, G., Murtugudde, R., Ommer, R.E., Perry, R.I., 2010. Climate change, uncertainty and resilient fisheries: institutional responses through integrative science. *Prog. Oceanogr.* 87, 338–346.
- Neis, B., Schneider, D.C., Felt, L., Haedrich, R.L., Fischer, J., Hutchings, J.A., 1999. Fisheries assessment: what can be learned from interviewing resource users? *Can. J. Fish. Aquat. Sci.* 56, 1949–1963.
- Park, I.M., Bobkov, Y.V., Ache, B.W., Principe, J.C., 2014. Intermittency coding in the primary olfactory system: a neural substrate for olfactory scene analysis. *J. Neurosci.* 34 (3), 941–952.
- Robinson, S.M.C., Auffrey, L.M., Barbeau, M.A., 2005. Far-field impacts of eutrophication on the intertidal zone in the bay of fundy, Canada with emphasis on the soft-shell clam, *Mya arenaria*. In: Hargrave, B.T. (Ed.), *Handbook of Environmental Chemistry*, vol. 5, Part M. Springer, Berlin, Germany, pp. 253–274.
- Steneck, R.S., Hughes, T.P., Cinner, J.E., Adger, W.N., Arnold, S.N., Berkes, F., Boudreau, S.A., Brown, K., Folke, C., Gunderson, L., Olsson, P., Scheffer, M., Stephenson, E., Walker, B., Wilson, J., Worm, B., 2011. Creation of a gilded trap by the high economic value of the Maine lobster fishery. *Conserv. Biol.* 25, 904–912.
- Strain, P.M., Hargrave, B.T., 2005. Salmon aquaculture, nutrient fluxes and ecosystem processes in southwestern New Brunswick. In: Hargrave, B.T. (Ed.), *Handbook of Environmental Chemistry*, vol. 5, Part M. Springer, Berlin, Germany, pp. 29–57.
- Tremblay, J., Pezzack, D., Denton, C., Reeves, A., Smith, S., Silva, A., Allard, J., 2011. Framework for Assessing Lobster off the Coast of Eastern Cape Breton and the Eastern and South Shores of Nova Scotia (LFAs 27–33), Research Document – 2011/058, Canada Department of Fisheries and Oceans. <[http://www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2011/2011\\_058-eng.html](http://www.dfo-mpo.gc.ca/csas-sccs/Publications/ResDocs-DocRech/2011/2011_058-eng.html)>.
- Walters, C.J., 2003. Folly and fantasy in the analysis of spatial catch rate data. *Can. J. Fish. Aquat. Sci.* 60 (12), 1433–1436.
- Walters, B.B., 2007. Competing use of marine space in a modernizing fishery: salmon farming meets lobster fishing on the bay of fundy. *Can. Geographer* 51 (2), 139–159.
- Wiber, M., Young, S., Wilson, L., 2011. Aquaculture – Traditional Fishery Interactions in South West New Brunswick: Implications for Further Research, vol. 1. OCN – Canada Policy Briefs.
- Wiber, M., Wilson, L., Young, S., 2012. Impact of aquaculture on commercial fisheries: fishermen's local ecological knowledge. *Human Ecol.* 40 (1), 29–40.
- Worm, B., Lotze, H., 2006. Effects of eutrophication, grazing and algal blooms on rocky shores. *Limnol. Oceanogr.* 51 (1, Part 2), 569–579.