



Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion

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ABSTRACT: Following their first detection in Newfoundland in 2007, populations of invasive European green crabs *Carcinus maenas* (Linnaeus, 1758) have increased and spread throughout eelgrass *Zostera marina* meadows. Green crabs can reduce eelgrass biomass by damaging rhizomes and plant shoots when burrowing for shelter and digging for prey. Empirically demonstrating large spatial-scale impacts of green crabs on eelgrass and subsequent cascading effects on the ecosystem has proven difficult because of the general absence of effective baseline studies prior to an invasion of green crabs. We conducted surveys in Placentia and Bonavista bays, Newfoundland (20 sites) to compare eelgrass and associated fish communities before and after an invasion of green crabs. We analyzed eelgrass surveys from 1998 and 1999 (before green crab) and again in 2012 (after green crab) using a Before-After-Control-Impact (BACI) study design in order to isolate effects of crab-induced eelgrass loss from effects independent of green crabs. Underwater video sampling evaluated eelgrass change over time and indicated a 50% decline in eelgrass percent cover since 1998 at sites with green crabs, and eelgrass declines up to 100% at sites with highest abundances and longest established presence of green crabs. Beach seining showed a sharp decline in abundance and biomass of fish (~10-fold between sites with and without green crabs) and indicated changes in fish community structure after green crab arrival at a site. Our results suggest cascading effects on fish communities and substantial potential impacts in coastal ecosystems occur following green crab invasion.

KEY WORDS: Invasive species · Green crab · Eelgrass · Fish community · Before-After-Control-Impact · BACI

INTRODUCTION

Invasive species can change evolutionary pathways of indigenous species, modify biological community structure, and alter habitat complexity (Ruiz et al. 1997, Carlton & Cohen 2003, Molnar et al. 2008). A well-developed literature documents such potential

impacts through direct and sometimes complex indirect trophic relationships between indigenous and non-indigenous organisms (e.g. Trussell et al. 2004, Matheson & Gagnon 2012a,b). Globalization has accelerated the spread and subsequent establishment of new populations of non-indigenous species (Ruiz et al. 1997, Cohen & Carlton 1998). The European

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green crab *Carcinus maenas* Linnaeus, 1758, one of the best studied marine invasive species, is renowned for its omnivorous diet, aggressive behaviour, and tolerance to wide-ranging environmental conditions (Cohen et al. 1995, Matheson & Gagnon 2012a,b). The green crab was first detected on the New England coast in the early 1800s (Say 1817) and its range expanded into Atlantic Canada by the early 1950s (Carlton & Cohen 2003). Genetic analyses suggest that separate introductions from disparate European origins expedited the spread of green crabs throughout Atlantic Canada (Roman 2006, Blakeslee et al. 2010), creating population-level behavioural and physiological differences among regions (Rosson et al. 2012). Following the initial discovery of green crabs in 2007, surveys revealed high abundances of crabs restricted to the most northern regions of Placentia Bay (in southern Newfoundland, Canada) that suggested introduction in this region likely occurred several years before these surveys (ca. 2002), and that populations in 2007 were already established (Blakeslee et al. 2010). However, its range expanded rapidly southward in subsequent years and now occupies most nearshore habitats throughout Placentia Bay (DFO 2011; C. H. McKenzie unpubl. data).

Eelgrass *Zostera marina* Linnaeus, 1753, a perennial flowering seagrass, is restricted to shallow and relatively protected coastal marine ecosystems and can form large monospecific meadows from expansive underground rhizome networks (Olesen & Sand-Jensen 1994a, Green & Short 2003). Such structurally complex meadows support substantial biodiversity and biomass and provide key ecological functions and services (e.g. provision of food and nutrients, sequestering and exporting nutrients, stabilizing shorelines, and creating habitat), which rank seagrasses as one of the most productive and important ecosystems globally (Costanza et al. 1997, Hemminga & Duarte 2000). Eelgrass can colonise new areas, form enduring meadows when undisturbed, and recover rapidly in the absence of anthropogenic influence (Olesen & Sand-Jensen 1994b, DFO 2009, Cote et al. 2013, Kilminster et al. 2015). Anthropogenic disturbances (e.g. sediment and nutrient loading, invasive species, mechanical damage, salinity changes, changes in current or wave exposure) can adversely affect seagrasses, along with associated ecosystem services and biotic communities (Fonseca & Bell 1998, Duarte 2002, Orth et al. 2006, Williams 2007).

As the predominant seagrass species in coastal regions of North America (Green & Short 2003), eelgrass provides important nursery habitat and refuge

from predation for fish and other organisms, including commercially important species such as Atlantic cod *Gadus morhua* Linnaeus, 1758 (Gotceitas et al. 1997, Laurel et al. 2003a, Robichaud & Rose 2006). Canada lists eelgrass as an 'ecologically significant species' because no other species can replace comparable trophic dynamics and ecological services in the event that eelgrass is irrevocably damaged or lost from a region (DFO 2009). Substantial declines in local fish abundance and biomass (including Atlantic cod and Greenland cod *G. ogac* Richardson, 1836 and white hake *Urophycis tenuis* Mitchell, 1814; Laurel et al. 2003a) occurred after experimental removal of eelgrass. In contrast, fish populations and communities increase with eelgrass recovery (Warren et al. 2010, Cote et al. 2013). Long-term monitoring (since 1995) of eelgrass in areas of Newfoundland (Newman Sound, Bonavista Bay) with little localized anthropogenic influence demonstrated natural expansion of enduring eelgrass meadows since 2001 (Warren et al. 2010), in contrast with global trends of seagrass decline (Orth et al. 2006). Eelgrass meadows occur historically in Newfoundland because of the widespread presence of optimal habitat characteristics, including protection from prevailing winds, shallow subtidal zone, a coastal zone influenced primarily by oceanic waters, and limited anthropogenic influences.

The first discoveries and largest abundances of green crabs in Newfoundland were in shallow coastal areas, including eelgrass meadows and non-vegetated soft sediment substrates (DFO 2011), directly overlapping the shallow coastal regions with low wave and current energy, ideal for formation of large, persistent eelgrass meadows (Orth et al. 2006, DFO 2011, Kilminster et al. 2015). Favoured prey for green crabs (e.g. soft-shelled clams *Mya arenaria* Linnaeus, 1758) requires digging within the sediment (Cohen et al. 1995). Small-scale laboratory and field experiments demonstrate that such feeding activities, along with burrowing in surficial sediments and grazing by juvenile green crabs, damage eelgrass roots and rhizomes and reduce eelgrass biomass (Malyshev & Quijón 2011, Garbary et al. 2014, Neckles 2015). Garbary et al. (2014) linked these destructive green crab behaviours with increased eelgrass wrack comprised almost entirely of whole shoots (with rhizomes) instead of individual blades and the decline of eelgrass at their Nova Scotia study site. Previous studies linked green crabs to declines in local eelgrass meadows (Locke & Hanson 2004, Garbary et al. 2014), but impacts at large spatial scales remain unclear.

A paucity of baseline data and lack of (uninvaded) control sites often limits conclusions regarding environmental impacts (Underwood 1992), such as the source and degree of eelgrass decline (Garbary & Munro 2004). During early stages of an invasion, population growth rates and range expansion by invasive species may vary markedly and unpredictably (Crooks & Soulé 1999). The rapid range expansion of the green crab throughout Placentia Bay (i.e. >200 km within 10 yr) established that manipulative control on the level of impact across locations could not be standardized or predetermined. This inherent unpredictability of species invasions, coupled with the time frame necessary to plan and undertake field research programs, makes studies of biotic effects of such invasions difficult to plan and undertake.

Our study benefited from the serendipitous existence of 2 standardized surveys of eelgrass habitat and fish communities in Placentia and Bonavista bays in Newfoundland, established prior to the invasion of green crabs in Placentia Bay, which used identical sampling methodologies and protocols (see Robichaud & Rose 2006, Laurel et al. 2003a, Warren et al. 2010). These surveys provided a rare opportunity to implement a Before-After-Control-Impact (BACI) survey design to compare eelgrass habitat and associated fish communities before and after the green crab invasion at numerous control and impact locations across an invasion front spanning a relatively large geographic range (>200 km) and test the hypothesis that green crab reduces eelgrass cover with cascading effects on fish communities. We hypothesized that eelgrass would decline in sites where green crabs have invaded relative to uninvaded control locations with cascading effects on eelgrass fish communities.

MATERIALS AND METHODS

Environmental and site characteristics

Our study surveyed fish communities and eelgrass meadows at 20 sheltered coastal sites in Placentia Bay (17 sites) and Bonavista Bay (3 sites), New-

Table 1. Fish community and eelgrass survey details of 17 study sites in Placentia Bay and 3 sites in Bonavista Bay (Newman Sound). Though not part of the Before-After-Control-Impact experiment design, the 2007 survey details are included as additional information

Site (north to south)	Impact or Control	Eelgrass surveys		Fish community surveys			
		1998	2012	1998	1999	2007	2012
Placentia Bay							
North Harbour	I	x	x	x	x	x	x
Swift Current	I	x	x	x	x	x	x
Woody Island	I	x	x	x	x	x	x
Bar Haven Gravel	I	x	x	x	x	x	x
Southern Harbour	I	x	x	x	x		x
Bar Haven North	I	x	x	x	x	x	x
Little Sandy Harbour	I	x	x	x	x		x
Great Brule	I	x	x	x	x	x	x
Kingwell	I	x	x	x	x		x
Baine Harbour	I	x	x	x	x	x	x
Ship Harbour	I	x	x	x	x	x	x
Fox Harbour	I	x	x	x	x	x	x
Placentia Sound	I	x	x		x		x
NE Placentia	I	x	x	x	x	x	x
SE Placentia	I	x	x	x	x	x	x
Spanish Room	C	x	x	x	x	x	x
Little Bay	C	x	x	x	x	x	x
Bonavista Bay (Newman Sound)							
Big Brook	C			x	x	x	x
Mistaken Cove	C			x	x	x	x
Minchin Cove	C			x	x	x	x
Total sites	20	17	17	19	20	16	20

foundland 10 years (in 1998 and 1999) before the initial discovery of green crabs in Placentia Bay in 2007 and again 5 years (in 2012) after green crabs became well established in much of the coastal areas of the bay (Table 1, Fig. 1). In 1998, undisturbed eelgrass meadows characterized 16 of the 17 sites in Placentia Bay and all 3 sites in Bonavista Bay; the remaining site in Placentia Bay (Bar Haven Gravel) was barren of eelgrass. By 2012, of the 17 Placentia Bay sites, only 2 sites (used as controls) had no green crabs, whereas Bonavista Bay sites retained persistent eelgrass communities and green crabs were not yet detected. Our 'before-invasion' data were collected as part of an earlier research project in Placentia Bay (Robichaud & Rose 2006) and for research in Bonavista Bay (Newman Sound) ongoing since 1995 (Gregory et al. 1997, Cote et al. 2013). Both research projects followed a standardized protocol used throughout Newfoundland for sampling nearshore fish communities, which we repeated in 2012 in combination with our eelgrass surveys (Fig. 1). We sampled all sites in as short a period as possible near the end of September during each year to avoid seasonal variability. We sampled during late-September because fish communities in

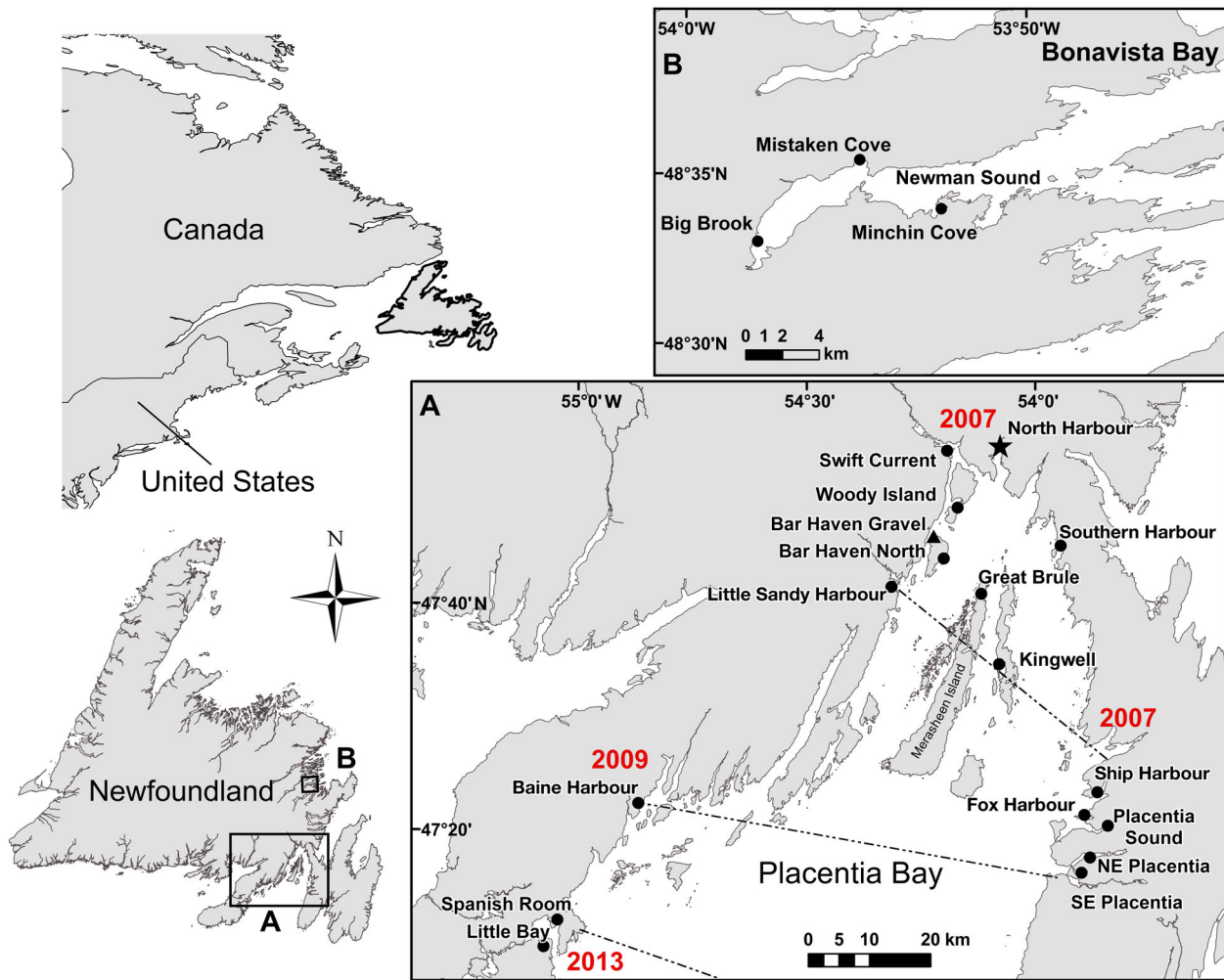


Fig. 1. (A) Placentia Bay, Newfoundland showing the 20 survey sites, including 16 sites designated as eelgrass (circles and star) and 1 site (Bar Haven Gravel) designated as non-eelgrass (triangle). (B) 3 control sites in Newman Sound. In (A), red year labels and dot-dashed lines detail year and location of detection in North Harbour (star) and subsequent spread of green crab through Placentia Bay

coastal Newfoundland exhibit the least interannual variability at this time of year (Gregory et al. 2006). A subset of sites (16) was surveyed in mid-October 2007 (during initial stages of the invasion). These data were not analyzed as part of the BACI design because 'during invasion' does not meet assumptions of such a design. We report them here as they qualitatively bear on the 'Discussion'.

We selected sites that were at least 5 km apart to ensure that samples between sites were independent, but similar in depth, salinity, exposure, and substrate. Our study design consisted of 17 study sites in Placentia Bay (2 control [no green crab] sites; and 15 impact [green crab] sites) and 3 sites in Bonavista Bay (all 3 of which were control [green crab] sites) to control for potential location-specific differences at control sites (Underwood 1992). Furthermore, because of the non-linear and inconsistent range expansion and population increases of green crabs

among Placentia Bay coves, likely driven by irregular coastal geography, larval movements, and anthropogenic transfers, we consider the likelihood of spatial autocorrelation of our results to be minimal.

Temperature and salinity values at study sites were 11.2–15.2°C and 23.1–30.6‰, respectively, based on opportunistic measurements taken at the date of sampling. Continuous monitoring data on these variables was not available. Sediment ranged from mud-sand to varying combinations of mud, small-gravel, and cobble. The maximum depth at each site was generally <6 m, with the exception of 2 sites which were >9 m (Kingwell 9.1 m, Little Bay 9.7 m). All study sites were protected from high fetch (<1 km), given prevailing wind directions (225°, SW). Most sites were located far from urban areas (>500 inhabitants), agricultural activities, or other point-source anthropogenic influences, with the exception of the town of Placentia (population ~3500).

Eelgrass and fish community surveys

At each site ($n = 17$) within Placentia Bay, we used scuba and underwater video to quantify eelgrass along 2 transects (57 m in length) that ran perpendicular to shore, beginning at the mid-tide mark. Transects at each site were spaced between 30 and 100 m (dependent on site geography). After marking transects every 0.5 m, we used fixed-distance lasers mounted to the underwater video camera to divide each transect into 57 contiguous 1 m² quadrats. We measured eelgrass presence and percent coverage by determining the number of 1 m² quadrats containing eelgrass and percentage of each quadrat covered with eelgrass in each transect, respectively. During underwater surveys, divers also conducted rapid visual assessments of benthos to determine whether each transect characterised surrounding benthic environments. Eelgrass meadows at our Bonavista sites were assessed annually by visual inspection of percent bottom cover to 55 m from shore, and have had consistently >60% bottom cover since 2001 (Cote et al. 2013, R. S. Gregory unpubl. data).

In 2012, we determined presence or absence and abundance of green crabs at each site in Placentia Bay using 3 Fukui traps (60 × 45 × 20 cm, 12 mm mesh, with 45 cm expandable slit at either end; baited with herring) in shallow (≤3 m) subtidal habitats for approximately 2 h. Captured green crabs were counted, sexed, and measured (carapace width, notch–notch; in mm). We used scuba surveys to confirm the absence of green crabs at each site in Placentia Bay. No traps were set during earlier surveys (1998–1999) as green crabs had not been observed anywhere in the bay, or captured in beach seines at that time. Similarly, green crabs have not been observed at any of our Bonavista Bay sites during extensive beach seine sampling over the 20 yr period 1995–2015 (e.g. Cote et al. 2013), numerous scuba surveys 1998–2000 (e.g. Laurel et al. 2003a, Sargent et al. 2006), and annual scuba surveys since 2009 (R. S. Gregory unpubl. data).

We conducted 2 beach seine hauls at each site (one at each transect) in Placentia Bay (see Robichaud & Rose 2006) and 1 seine haul at each site in Bonavista Bay (see Warren et al. 2010). For all surveys, a 25 m seine (constructed of 19 mm stretched knotless nylon mesh, in the wings and belly, and 12.7 mm in the codend) was deployed 55 m from shore using a small boat and pulled toward the coast by 2 individuals standing on shore 16 m apart. The seine sampled 2 m of water above the benthos and a total standardized area of 880 m² (Schneider et al. 1997). Beach seines

were conducted 30 min after transect surveys. We conducted dive transect surveys first to avoid disturbance of sediment by seines, which would otherwise reduce visibility of substrate in video. Fish species were identified, counted, measured (± 1 mm SL), and returned alive to the site of capture. We estimated fish biomass using species-specific length-weight regressions calculated from previous coastal fish community research in Newfoundland (D. Methven unpubl. data, University of New Brunswick, Saint John, NB).

Data analyses

Eelgrass habitat and impact of green crabs

To investigate the effects of Year (1998 and 2012), Impact (Green crab and No green crab), and their interaction on eelgrass presence and percent cover relative to the green crab invasion, we fitted generalized linear models (GLMs) to our fish abundance and biomass data. Furthermore, we used GLMs to identify the effect of Year (1998 and 2012), Site (each of the 17 sites in Placentia Bay), and their interaction on changes in eelgrass presence and percent cover relative to the green crab invasion. We used a Poisson error structure with a log-link for eelgrass presence data and a binomial error structure with a logit-link for percent coverage data, as recommended by (Crawley 2007) and a Pearson chi-squared estimate in instances of overdispersion.

To assess further relationships between green crab population parameters and percent change in eelgrass presence and percent cover before and after invasion of green crabs, we fitted 2 GLMs with Gaussian error structure and an identity link. We added metrics of the green crab population as initial explanatory variables in the models, including abundance (crabs trap⁻¹ h⁻¹), mean carapace width (mm), and sex ratio (percent male). Stepwise forward and backward procedures optimized model selection by considering all explanatory factors and subsequently removing redundant factors based on the Akaike information criterion (AIC, Crawley 2007). Previous studies recommend measuring percentage change as $\log(\text{final}/\text{initial})$ and analysis with normal errors (Crawley 2007). We used least-square means multiple comparison tests (Tukey-Kramer; Sokal & Rohlf 1995) with a significance threshold of $\alpha = 0.05$ for all statistical tests in SPSS and R (Version 2.15.2, R Core Team 2012) to detect differences among levels within factors.

Fish community abundance and biomass

We analyzed changes in total fish abundance and biomass following a BACI (Before-After-Control-Impact) model design using resampling techniques based on principles of Randomized Intervention Analyses (RIA; Carpenter et al. 1989) to compare the differences in both fish abundance and biomass between sites with and without green crabs (i.e. Impact vs. Non-impact) before (1998 and 1999) and after (2012) the green crab invasion (19 sites surveyed across all years; Table 1). Data were log-transformed [$y = \log_{10}(x + 1)$] prior to analyses to control for natural inter-annual and inter-site variation; however, non-normality of data does not influence results of RIA (Carpenter et al. 1989). Differences in both fish abundance and biomass among all combinations of Impact and Non-impact sites were determined for each year of the study and the absolute mean difference was compared before and after invasion of green crabs (for all year combinations) to 10000 random permutations of the calculated differences to calculate a p-value. RIA analyses and emphasis on the differences between Impact and Non-impact sites, rather than comparing means, further reduced influence from expected spatial and temporal variation in fish dynamics between sites. We calculated relative differences (RD) in both fish abundance and biomass between Impact and Non-impact sites using log-transformed data. For example, an RD of 1.0 indicated an order of magnitude (i.e. 10×) greater fish abundance or biomass at Impact than Non-impact sites, whereas an RD of zero indicates no effect of green crabs.

We used the Bray-Curtis Index (Bray & Curtis 1957) to analyze similarities and dissimilarities in multivariate fish assemblages (abundance and biomass) and we applied a fourth-root transformation to our census data to reduce the relative importance of numerically dominant species and account for the presence of rarer species (Clarke & Warwick 2001). Differences in fish assemblage structure (abundance and biomass) were determined using two 3-way nested permutational multivariate analyses of variances (PERMANOVA; 9999 permutations) with factors Year (1998, 1999, and 2012), Impact (Green crab and No green crab), and Site (nested within Impact). We excluded the Year × Site(Impact) interaction because we were most interested in variation between treatments rather than among Sites. We deliberately accepted the former variance as part of our measurement error structure *a priori*, knowing there is high variance among sites. We used permutational tests of

multivariate dispersion (PERMDISP) on a Bray-Curtis matrix calculated on the basis of distance from centroids to explore homogeneity of multivariate dispersions. Non-metric multi-dimensional scaling ordinations (nMDS; using distances among centroids derived from Principal Coordinates Analysis) were used to visualise multivariate dissimilarities in community structure. We used centroids, multivariate representations of data centres in resemblance measures, to aggregate data for visual representation. We used SIMPER to identify percent contribution of each fish taxon to Bray-Curtis similarity within, and dissimilarity among, factors (Clarke & Warwick 2001). All fish community analyses were conducted using PRIMER 7 and PERMANOVA+ 1.0.5.

RESULTS

Changes in eelgrass and abundance of green crabs

In 1998, eelgrass was present in $70 \pm 4\%$ (\pm SE) of 1 m² quadrats (of 57 quadrats per transect) at sites within Placentia Bay, with $72 \pm 5\%$ eelgrass coverage within those quadrats. Eelgrass presence declined 27% in 2012 from 1998 levels, but these changes varied spatially (GLM; Factor = Year × Site; Wald chi-squared = 139.5, df = 13, N = 2 for each combination of Year × Site, $p < 0.01$; Fig. 2A). In particular, eelgrass presence decreased >80% at 4 sites in northern Placentia Bay where abundance of green crabs was high (16 ± 3 crabs trap⁻¹ h⁻¹; LS means, $p < 0.01$), and increased at 1 site, approximately threefold, where green crabs were rarely captured (0.8 ± 0 crabs trap⁻¹ h⁻¹; LS means, $p < 0.01$). Further analyses of eelgrass percent coverage revealed a significant interaction between Year and Site (GLM; Factor = Year × Site; Wald chi-squared = 43.0, df = 15, N = 2 for each combination of Year × Site, $p < 0.01$; Fig. 2B). Across all sites, eelgrass coverage averaged only $34 \pm 8\%$ in 2012, approximately half the coverage observed in 1998. Eelgrass coverage decreased to a relatively barren state (from 83 ± 4 to $2 \pm 2\%$) at 5 sites with high abundance of green crabs (LS means, $p < 0.01$; Fig. 2B), but did not increase at any site. The interaction between Year and Impact (i.e. Green crab vs. No green crab) was only significant for eelgrass percent coverage (GLM; Factor = Year × Impact; Wald chi-squared = 4.1, df = 1, N = 2 for each combination of Year × Impact; $p = 0.044$; Fig. 2B). Eelgrass coverage was significantly lower at Impact sites in 2012 than in 1998 (LS means, $p < 0.01$), and eelgrass coverage was consistent between Impact and Non-impact sites be-

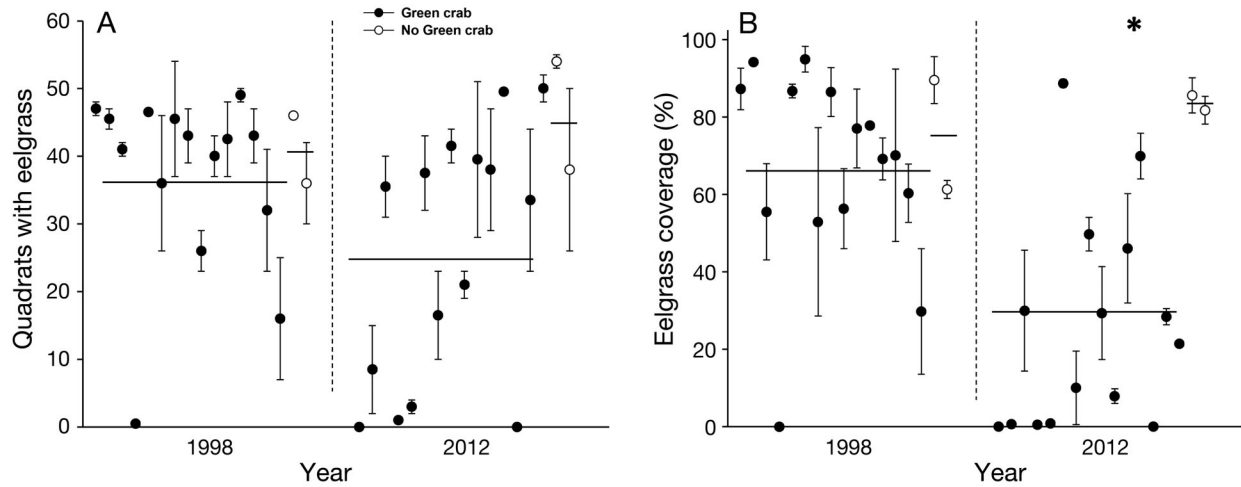


Fig. 2. (A) Mean (\pm SE) number of quadrats with eelgrass and (B) eelgrass percent coverage per transect in 1998 and 2012 at Impact (green crab, black circles) and Non-impact (no green crab, white circles) sites from the head (i.e. northern site with first detection of green crabs) to mouth (i.e. south; left to right) of Placentia Bay, Newfoundland. Horizontal solid lines represent overall average of Impact and Non-Impact sites during each sampling year ($n = 2$ for each combination of Site \times Year). *Significant difference ($p < 0.05$) between Impact and Non-Impact sites within each year

fore the green crab invasion and between years at Non-impact sites (LS means, $p > 0.51$). The one non-eelgrass site (Bar Haven Gravel) remained without eelgrass or other vegetation between 1998 and 2012.

Our 2012 surveys confirmed rapid range expansion of green crabs throughout Placentia Bay and the absence of green crabs in Bonavista Bay. Only 2 sites within Placentia Bay (Spanish Room and Little Bay) remained without green crabs (i.e. Non-impact) in 2012, both of which are in the southwestern region of the bay. In fact, we observed small numbers of green crabs at both of these sites one year later in 2013. We generally captured the highest number of crabs in northern Placentia Bay, where the green crab was first detected and we have previously observed high numbers. At sites with green crabs in Placentia Bay, crab abundances ranged from 1 ± 0 (SE Placentia) to 24 ± 14 crabs $\text{trap}^{-1} \text{h}^{-1}$ (North Harbour), which included a non-eelgrass site (Bar Haven Gravel) with a catch rate of 20 ± 7 crabs $\text{trap}^{-1} \text{h}^{-1}$. Average carapace width (notch–notch) ranged from 35.2 ± 0.9 (Great Brule) to 59.1 ± 1.3 (NE Placentia) and the percentage of male crabs varied from 41.2 (Bar Haven Gravel) to 98.1% (Placentia Sound).

Our most parsimonious GLMs assessing the relationships between green crab population metrics and percent change in eelgrass presence

and percent coverage included crab abundance and percent males as important factors, explaining 60 and 64% of deviances in percent change in eelgrass presence and coverage data, respectively (Table 2). We removed the non-significant interaction terms. Crab abundance and percent males were both negatively related to percent change in eelgrass presence and coverage, although the parameter crab abundance was marginally non-significant (Table 2). Percent male accounted for a greater reduction of deviance (19.8 and 22.8%) than crab abundance (16.5 and 13.9%), in predicting eelgrass presence and percent coverage, respectively.

Table 2. Analysis of deviance and parameter estimates for generalized linear models for percent change in eelgrass presence and percent coverage. Explanatory variables shown were selected based on the Akaike information criterion. Initial variables in the models included crab abundance, percent male, and crab size

GLM deviance				GLM summaries		
Source of variation	df	Deviance	p	Parameter	Estimate \pm SE	p
Coverage (% change):						
Family = Gaussian (identity-link), Explained Deviance = 64.03%						
Error	12	36.75		Intercept	5.16 ± 1.60	0.01
Crab abundance	1	8.90	0.027	Crab abundance	-0.09 ± 0.04	0.059
Percent male	1	14.63	<0.01	Percent male	-6.97 ± 2.09	0.01
Presence (% change):						
Family = Gaussian (identity-link), Explained Deviance = 60.2%						
Error	12	36.34		Intercept	5.16 ± 1.67	0.01
Crab abundance	1	9.95	0.025	Crab abundance	-0.10 ± 0.05	0.051
Percent male	1	11.93	0.017	Percent male	-6.29 ± 2.19	0.02

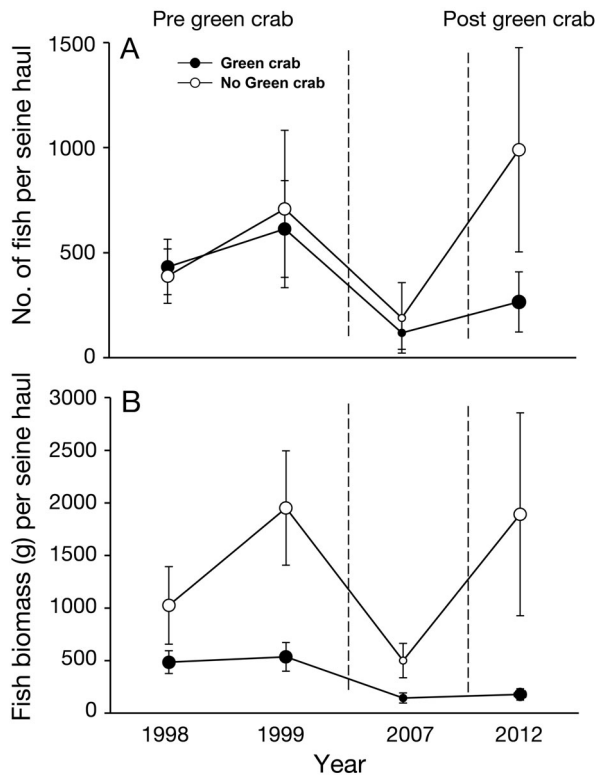


Fig. 3. Interannual mean (\pm SE) (A) fish abundance and (B) fish biomass at Impact (green crab, black circles) and Non-impact sites (no green crab, white circles) for survey years pre- (1998 and 1999) and post-established and widespread invasion of green crabs (2012). Data from 2007 surveys is also included (smaller symbols, surrounded by dashed lines) for visual comparison of data only. For Impact and Non-impact sites, $n = 14$ and 5 , respectively (1998, 1999, 2012).

Changes in fish community abundance and biomass

Fish abundance and biomass varied greatly among sites (from 0 to 2542 fish haul⁻¹ and 0 to 5573 g fish haul⁻¹, respectively; Fig. 3). Generally, fish abundance and biomass was greater at Impact than Non-impact sites in all years and although total numbers varied annually, RIA indicated that absolute RD values between Impact and Non-impact sites increased significantly following invasion of green crabs (i.e. 2012 vs. 1998 and 1999; $p < 0.01$; Fig. 4). Although RD values for fish abundance were significantly different across all year combinations before and after green crabs were detected (i.e. 1998, 1999, and 2012), fish abundance differed most between Impact and Non-impact sites when comparing surveys before and after green crab ($p < 0.032$, Fig. 4). In fact, average differences between Impact and Non-impact sites in 2012 (RD = -1.19) were almost a full order of magnitude greater than in 1998 (RD = -0.24) and over half

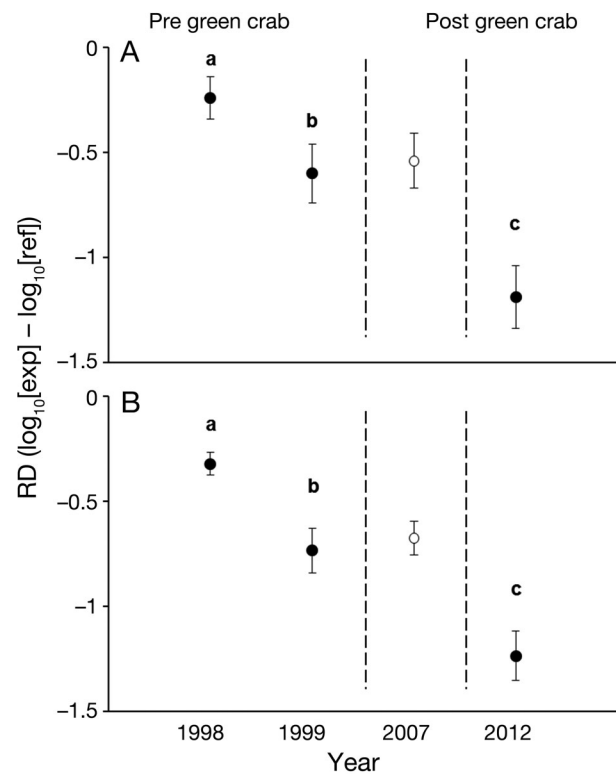


Fig. 4. Relative differences (RD; \pm SE) in (A) fish abundance and (B) fish biomass between Impact and Non-impact sites for survey years pre (1998 and 1999) and post (2012) established and widespread invasion of green crabs (black circles). The subset data from 2007 (during invasion in Placentia Bay) is represented to maintain inclusivity of data (white circles, surrounded by dashed lines) and was not part of data analyses. Different letters denote significant differences among the relative difference values before and after green crab as determined using principles of Randomized Intervention Analyses ($\alpha = 0.05$; for Impact and Non-impact sites, $n = 14$ and 5 , respectively)

an order of magnitude greater than in 1999 (RD = -0.60) (Fig. 4). These results paralleled RD calculations of biomass between Impact and Non-impact sites. Differences across sites in 2012 (RD = -1.24) were almost an order of magnitude greater than in 1998 (RD = -0.32) and half an order of magnitude greater than in 1999 (RD = -0.73). In 1999 and 2012 in particular, we captured a large number of larger-bodied winter flounder at one Non-impact site and although such unusual values strongly influence raw values (Fig. 3), RIA analyses controls for such potential outliers.

The composition of fish abundance and biomass assemblages did not vary significantly among Impact and Non-impact sites across survey years, despite a marginally non-significant interaction term between Year and Impact (PERMANOVA [Abun-

Table 3. Summary of 3-way nested PERMANOVA parameters (applied to Bray-Curtis dissimilarities using 4th-root transformed data) evaluating the differences in fish communities between Year (1998, 1999, and 2012) and Impact (Green crab and No green crab) in Placentia and Bonavista bays, Newfoundland

Source of variation	df	MS	Pseudo- F	p	Components of variation
Abundance					
Year	2	1429.7	1.4	0.18	4.4
Impact	1	7085.3	2.1	0.071	11.2
Site (Impact)	17	4001.2	4.0	<0.01	23.6
Year \times Impact	2	1813	1.8	0.068	8.6
Residuals	79	1092.8			31.6
Total	101				
Biomass					
Year	2	1799.6	1.5	0.15	5.1
Impact	1	9359.2	2.9	0.017	14.2
Site (Impact)	17	3895.7	3.1	<0.01	22.3
Year \times Impact	2	2173.9	1.8	0.06	9.2
Residuals	79	1231.3			35.1
Total	101				

dance], $F_{2,101} = 1.8$, $df = 2$, $p = 0.068$; PERMANOVA [Biomass], $F_{2,101} = 1.8$, $df = 2$, $p = 0.060$; Table 3, Fig. 5). Both PERMANOVA models suggest that Site (Impact) primarily drove variation (Table 3) and was significant in each model (PERMANOVA [Abundance], $F_{17,101} = 4.01$, $df = 17$, $p < 0.01$; PERMANOVA [Biomass], $F_{17,101} = 3.2$, $df = 17$, $p < 0.01$). Our examination of nMDS plots revealed that assemblages of fish abundance at Impact sites in 2012 differed more from Impact sites before green crab than assemblages at Non-impact sites across all years, although these differences were not significant (Fig. 5). The same pattern was less clear for assemblages of fish biomass, particularly because of the large number of large winter flounder captured at one Non-impact site in 2012 (Fig. 5). Furthermore, analyses of multivariate dispersion among assemblages of fish abundance and biomass showed no significant differences between Impact sites in 2012 and other years, or between Non-impact sites across years.

SIMPER analyses identified 9 species that consistently influenced dissimilarities in fish assemblages between Impact and Non-impact sites in each year (Table 4). Three-spined sticklebacks contributed most to dissimilarities in fish abundance (27.8 to 39.0%). Greenland cod contributed most to dissimilarities in biomass (18.6%) between Impact and Non-impact sites among years before the green crab invasion (i.e. 1998 and 1999), but three-spined sticklebacks drove dissimilarities after green crab populations were established (25.1%). Overall, larger-bodied

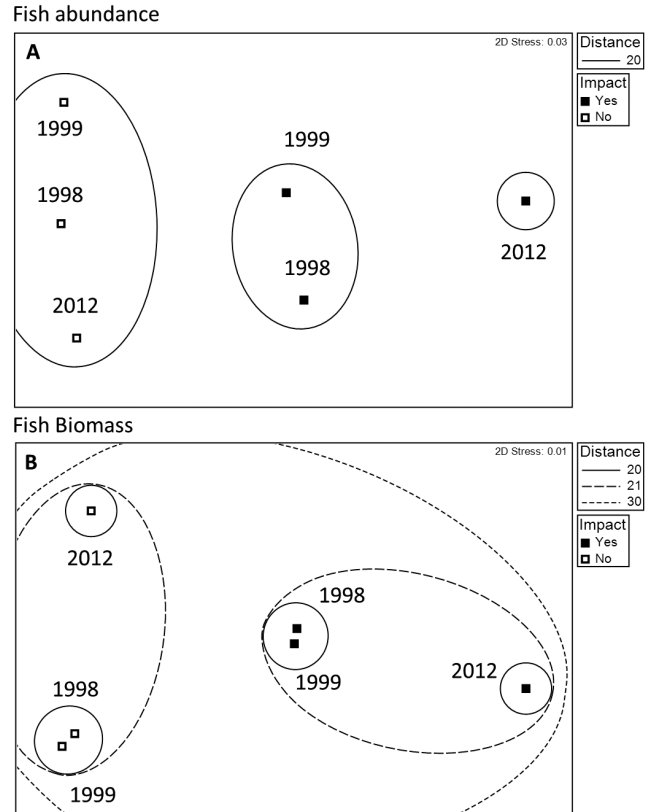


Fig. 5. Differences in fish assemblage patterns in (A) abundance and (B) biomass of fish between Impact and Non-impact sites before (1998 and 1999) and after widespread invasion and establishment of green crabs (2012) depicted by multi-dimensional scaling ordination plots. Data points represent centroids (from Principal Coordinate Analysis) of fish community abundance and biomass data aggregated within Years \times Impact. Resemblance groupings are shown with superimposed clusters using distances among centroids as defined by the Bray-Curtis measure with a 4th-root transformation

ied fish, such as Greenland cod, sculpin (*Myoxocephalus* spp.), white hake, and winter flounder (*Pseudopleuronectes americanus* Walbaum, 1792) contributed proportionately more to biomass dissimilarities in fish assemblages than smaller-bodied fishes that dominated abundance patterns (Table 4).

DISCUSSION

Our study took advantage of extensive data on eelgrass meadows and associated fish communities collected as part of standardized surveys prior to the discovery of green crabs in Newfoundland. We replicated surveys subsequent to the green crab invasion and our results link green crabs to dramatic declines in eelgrass habitat and associated fish abundance and biomass across scales of 100s of km. We docu-

Table 4. Summary of SIMPER tests of dissimilarity in fish community abundance and biomass between factors Year and Impact (Green crab and No green crab). Species contributing over 90% of dissimilarity and total dissimilarity between groups (bold) are shown. Dissimilarity values before the green crab invasion were averaged across Year (1998 and 1999) to show patterns more clearly. Though not part of the Before-After-Control-Impact experiment design, the 2007 survey details are included as additional information

Fish species	Average abundance Impact	Non-impact	% Contribution (Average Diss.)	Fish species	Average biomass Impact	Non-impact	% Contribution (Average Diss.)
Pre-green crab (1998–1999) (48.6)				Pre-green crab (1998–1999) (53.78)			
<i>G. aculeatus</i>	504.91	555.07	27.78	<i>G. ogac</i>	108.73	516.49	18.59
<i>G. ogac</i>	5.73	29.57	13.93	<i>P. americanus</i>	38.32	262.19	14.86
<i>G. morhua</i>	0.47	47.79	11.4	<i>Myoxocephalus</i> spp.	57.9	162.31	14.64
<i>T. adspersus</i>	2.26	5.86	9.17	<i>G. aculeatus</i>	386.96	157.08	13.92
<i>Myoxocephalus</i> spp.	2.56	4.42	8.81	<i>T. adspersus</i>	27.0	102.95	10.09
<i>P. americanus</i>	0.74	3.21	8.63	<i>U. tenuis</i>	57.74	43.90	9.81
<i>U. tenuis</i>	4.49	3.29	7.77	<i>G. morhua</i>	4.6	56.48	8.73
<i>P. gunnellus</i>	0.25	1.07	6.04	<i>P. gunnellus</i>	1.59	9.70	4.61
Green crab (early invasion) 2007 (64.12)				Green crab (early invasion) 2007 (67.71)			
<i>G. aculeatus</i>	105.5	232.14	30.38	<i>G. ogac</i>	58.83	133.10	18.09
<i>G. morhua</i>	17.1	6.57	13.55	<i>P. americanus</i>	8.94	61.35	15.78
<i>G. ogac</i>	1.0	4.14	10.64	<i>Myoxocephalus</i> spp.	27.58	119.98	15.19
<i>C. lumpus</i>	0	0.86	10.2	<i>G. aculeatus</i>	40.96	11.63	11.58
<i>Myoxocephalus</i> spp.	1.6	1.43	9.3	<i>U. tenuis</i>	11.36	26.88	10.51
<i>U. tenuis</i>	0.7	3.14	8.55	<i>G. morhua</i>	10.71	16.56	10.42
<i>P. americanus</i>	0.35	0.43	6.97	<i>T. adspersus</i>	3.07	53.37	7.05
<i>T. adspersus</i>	0.25	2.71	6.11	<i>C. lumpus</i>	0	0.92	6.82
Green crab (established invasion) 2012 (59.8)				Green crab (established invasion) 2012 (60.31)			
<i>G. aculeatus</i>	207.74	1234.43	39.02	<i>G. aculeatus</i>	107.0	647.71	25.1
<i>G. ogac</i>	2.59	36.71	11.8	<i>U. tenuis</i>	7.8	326.71	14.66
<i>T. adspersus</i>	6.44	14.71	11.0	<i>G. ogac</i>	41.35	154.19	12.84
<i>U. tenuis</i>	1.37	17.71	9.94	<i>Myoxocephalus</i> spp.	16.36	122.32	12.75
<i>G. morhua</i>	0.07	6.71	7.48	<i>P. americanus</i>	8.23	460.05	10.83
<i>Myoxocephalus</i> spp.	1.44	2.86	6.55	<i>T. adspersus</i>	10.33	131.09	10.31
<i>P. americanus</i>	0.48	2.57	6.34	<i>G. morhua</i>	1.82	18.79	6.3

mented significant changes in eelgrass meadows between surveys within Placentia Bay, which varied in degree across study sites, but declines in eelgrass presence and percent coverage correlated strongly with the presence of green crabs. Eelgrass disappeared completely from 4 sites and eelgrass coverage declined 90% at a fifth site following the discovery of green crabs. In contrast, we did not observe declines in eelgrass at sites where green crabs were absent, although our study could only formally compare eelgrass at 2 control sites in Placentia Bay. Differences in survey techniques precluded a direct comparison of eelgrass meadows between Placentia Bay and Bonavista Bay (no green crabs), but a combination of aerial photography and visual surveys from small boats and scuba indicated no declines in persistent meadows in Bonavista Bay during the 1998–2012 study period (Cote et al. 2013, R. S. Gregory unpubl. data). Indeed, eelgrass has expanded into formerly barren areas in some areas near our Bonavista Bay study sites (Cote et al. 2013). Unfortunately,

techniques to monitor changes in eelgrass (i.e. quadrats and transects) often lack strong statistical power and only detect large losses (i.e. >80% in our study) indicative of substantially damaged meadows (Duarte 2002). In Placentia Bay, we observed a 25% or greater decline in eelgrass coverage at 12 of 16 eelgrass sites and eelgrass presence at 5 of 16 eelgrass sites, suggesting a dramatic decline in eelgrass cover and clear evidence of localized disappearance of eelgrass at sites now occupied by green crabs.

Recent laboratory and cage experiments demonstrate that green crabs can reduce eelgrass biomass by burrowing for shelter, digging for prey, and directly cutting basal meristems (Malyshev & Quijón 2011, Garbary et al. 2014, Neckles 2015). Further mesocosm experiments also correlate eelgrass losses with crab density (Davis et al. 1998). Without conducting *in situ* caging or complementary laboratory experiments during our field study, we rely on results from such experiments to imply causality from our observed negative relationship between green crabs

and eelgrass coverage. As reported in other field studies (e.g. Garbary et al. 2014), we observed pits in mud in areas with high abundances of green crabs, indicative of digging and foraging behaviours that can damage eelgrass rhizome and root systems. Such bioturbation activities can also re-suspend fine sediments that coat eelgrass shoots, likely adding further stress to eelgrass from green crab activities (Garbary et al. 2014). Although not quantified, we noted accumulation of fine sediments on eelgrass at several sites where eelgrass appeared to be declining (i.e. experienced eelgrass decline, but not total loss). In particular, dive surveys at one of these sites (NE Placentia) documented almost complete loss of remaining eelgrass 1 yr later (October 2013; Carman et al. 2016). Our study encompassed sites across various stages of a rapidly expanding invasion front in Placentia Bay (C. H. McKenzie unpubl. data), which may explain the weak signal at some sites. The frequency and magnitude of disturbances are key indicators of the dynamic equilibria that support a continuous seagrass meadow, patchy landscape, or substrate barren of seagrass (Hemminga & Duarte 2002). The general absence of eelgrass at study sites in northern regions of Placentia Bay, where green crabs are most abundant and have been established the longest (i.e. ≥ 5 yr), further demonstrates this pattern. Large numbers of adult green crabs have been captured in more southerly locations within Placentia Bay (i.e. closer to the invasion front), but we anticipate less impact after a shorter disturbance duration (i.e. ≤ 5 yr since invasion). Although our research takes advantage of a unique opportunity to study a system in which a recently introduced invasive species has not yet spread across all locations, we were limited in our ability to evaluate temporal gradients of change across an invasion front.

Eelgrass at locations with no green crabs remained consistent or showed signs of expansion across our pre- and post-impact years (Warren et al. 2010). Although green crabs appear to cause eelgrass decline in Placentia Bay, previous studies were unable to attribute widespread eelgrass declines definitively to green crab invasions in Atlantic Canada. Confounding spatial trends (Locke & Hanson 2004), insufficient baseline data prior to arrival of green crabs (Garbary & Munro 2004), or lack of control locations (Underwood 1992) have all constrained conclusions about causality. Garbary et al. (2014) used quantitative experimental and observational data through a whole-ecosystem approach to effectively link green crabs to eelgrass declines in Nova Scotia (Canada). While highly suggestive, their study lacked control loca-

tions, limiting broader inference. More widespread anecdotal evidence links large-scale eelgrass decline to increasing green crab populations throughout Nova Scotia (Garbary et al. 2004), but cannot address potential interactions with other stressors on eelgrass or cascading impacts of such losses. Our research supports and expands on findings of Garbary et al. (2004, 2014) by providing the first large-scale research which encompasses locations with and without green crabs, both before and after a green crab invasion that documents a clear negative relationship between green crab and eelgrass.

Sites with green crabs exhibit varying levels of impact, likely because green crab population dynamics and parameters (e.g. crab abundance or time since introduction) have differed among Placentia Bay embayments (C. H. McKenzie et al. unpubl. data), which may mitigate impacts to eelgrass habitat. Compact sediments or hard substrate might also reduce the ability of crabs to bury or forage for prey in sediments (Rebach 1974, Sponaugle & Lawton 1990), and subsequently reduce their capacity to disrupt eelgrass. For example, eelgrass persisted at >1 green crab site (e.g. Fox Harbour and Great Brule), which contained more cobble and small rocks than soft, fine sediments (i.e. mud and sand) that characterized many other sites where eelgrass declined dramatically (e.g. Placentia Sound). Furthermore, green crabs dig in order to obtain infaunal prey, such as the preferred soft-shell clam (Ropes 1968). Variation among infaunal communities across sites will likely further shape crab behaviours and subsequent relationships between green crabs and eelgrass. Location-specific variables, such as substrate and associated infaunal communities, may contribute to the susceptibility of eelgrass habitat to damage by green crabs.

Previous studies document generally higher abundance and biomass of juvenile fish in eelgrass than nearby barren sediment (Hughes et al. 2002, Laurel et al. 2003a) and cascading trophic effects in coastal benthic ecosystems with changes in crab abundance (Quijón & Snelgrove 2005). Experimental eelgrass removals led to declines of up to 80% in fish abundance and biomass (Laurel et al. 2003a), a pattern strongly supported by our results. We observed declines of up to 95% in fish abundance and biomass, but only at locations where the green crab invasion preceded complete eelgrass loss. Overall, changes in fish abundance and biomass without complete eelgrass loss (i.e. $\geq 10\%$ eelgrass coverage) also suggest a compromised functional role of eelgrass as fish habitat prior to complete elimination of eelgrass (Hughes et al. 2002, Laurel et al. 2003a).

The complex interplay of marine seascapes with biological and physical oceanography contributes to natural variability in coastal fish communities. Predictability and resilience to environmental stressors decrease and fish community variability increases with reduced habitat complexity (Cote et al. 2013), resulting in disruption of trophic organization, altered ecological dominance, and replacement of formerly stable food-webs with opportunistic species (Livingston 1984). Our study links changes in structure of fish communities to substantial decline of eelgrass after a green crab invasion. Most strikingly, we observed sharp declines in abundances of three-spined sticklebacks. Sticklebacks spawn in eelgrass meadows (Schein et al. 2012) and represent significant prey for many commercially important piscivorous fish (Reimchen 1994). We also observed declines in biomass and, to a lesser extent, abundance of white hake and Greenland cod linked to declines in eelgrass following the invasion of green crabs. Although similar patterns in Atlantic cod were not obvious in this research, our study encompassed a period of generally poor recruitment for this species. Moreover, the fact that our study encompassed sites across various stages of an invasion of green crabs (C. H. McKenzie unpubl. data) with varying eelgrass loss, may explain weaker signals in some taxa. Previous studies clearly demonstrate similar demersal habitat use and behaviours between juvenile Greenland and Atlantic cod and the importance of eelgrass nearshore habitat for early life-history stages (Gotceitas et al. 1997, Laurel et al. 2003a, Robichaud & Rose 2006). The complex structure of eelgrass offers protection for juvenile cod given that predation by piscivorous fishes increases over less structurally complex or fragmented habitats (Laurel et al. 2003b, Thistle et al. 2010). Disappearance of eelgrass may further influence settlement behaviours in juvenile fish, noting that Atlantic cod delay settlement until they encounter preferred habitat (i.e. eelgrass; Laurel et al. 2003a). As evident in our study, strong natural variation may occur in coastal fish assemblages, which suggests that increased temporal sampling replication may have further clarified patterns. However, research has shown little interannual variation in fish communities in persistent eelgrass meadows of coastal Newfoundland, relative to unvegetated habitats (Cote et al. 2013). Our findings reinforce fundamental connections between eelgrass and fish communities and imply a high-level of cascading ecological impacts with disappearance of eelgrass following invasion of green crabs.

In general, undisturbed large patches and continuous eelgrass meadows resist disturbances more than small fragmented patches, because greater root development anchors eelgrass shoots more firmly to the substrate matrix (Olesen & Sand-Jensen 1994b). This physical stability can support more consistent and resilient fish communities better able to buffer effects of external environmental forces than unvegetated nearby habitats (e.g. Cote et al. 2013). In 2007, additional data from a subset of our sites were available. Although not appropriate for our BACI analysis ('during invasion' does not meet qualifications of our BACI design), these additional data provided unique insight into the early phase of the green crab invasion in Placentia Bay and suggested that the invasion was in its earliest stages. Although eelgrass coverage was not quantified explicitly in 2007, it was present at all sites in which the plant was observed in 1998. Observations of abundance and biomass, and assemblages of fish communities in 2007, further indicated that green crabs, although present in several sites at the time, had not yet begun to show strong impact on these sites. Furthermore, small crabs impact eelgrass less than large adult green crabs (Malyshev & Quijón 2011), and although not a significant metric in our study, average crab size may indicate the maturity of a newly introduced population, which may determine impacts on eelgrass ecosystems. We suspect that sites with primarily small green crabs are indicative of early stages of invasion and will become increasingly susceptible to declines in eelgrass and changes to local fish communities as larger crabs appear.

Eelgrass can recover when physically disrupted if rhizomes remain intact, when a large seed bank persists, or when other eelgrass meadows occur in close proximity (Greve et al. 2005, Warren et al. 2010). However, areas devoid of eelgrass for long time periods and without adjacent eelgrass meadows may require more than a decade to recover (Frederiksen et al. 2004). In fact, Garbary et al. (2014) recently reported improvement in eelgrass to about 60% of earlier cover within ~5 yr following declines in green crabs, but eelgrass declines persisted in subsequent years likely because of ongoing impact by green crabs. Field-based studies suggest that densities of Atlantic and Greenland cod associated with eelgrass can increase rapidly with simulated enhancement or natural expansion of eelgrass habitat (Laurel et al. 2003a, Warren et al. 2010, Cote et al. 2013). We predict declines and losses in eelgrass in nearshore regions will become more prevalent and widespread with continued spread and population growth of

green crabs. Sustained natural or anthropogenic loss of large areas of critical fish habitat (e.g. eelgrass) can reduce opportunities for rapid habitat recovery and introduce long-term cascading consequences for fish species or communities that delay ecosystem recovery following physical damage (Laurel et al. 2003a, Warren et al. 2010, Cote et al. 2013).

Increases in coastal human populations and related development activities have been recognized as primary stressors and causes of declines of seagrass and associated ecosystem functions (Orth et al. 2006). We acknowledge the many documented reasons for seagrass decline globally, but did not observe any of the other typical causes anywhere in our study region. (1) Our sites were relatively protected from high wave energy and situated away from major human development, including any agriculture in the catchments, which are likely to cause increases in disturbance, sedimentation, or eutrophication (Fonseca & Bell 1998, Duarte 2002, Newfoundland and Labrador Statistics Agency 2013). (2) Eelgrass can tolerate a broad range of salinity and temperature conditions and optimal growth occurs between 10–35‰ and 10–20°C, respectively (Nejrup & Pedersen 2008), well within the range of our study environment. Coastal temperatures monitored continuously at locations within both Placentia Bay since 2007 and Bonavista Bay since 2002 rarely exceed 20°C (C. H. McKenzie unpubl. data, R. S. Gregory unpubl. data). (3) Eelgrass within our study and elsewhere in Newfoundland show little evidence of shoots with blackened areas indicative of infection with *Labyrinthula zosterae* D. Porter & Muehlst., in Muehlstein & Short, 1991 (Burdick et al. 1993). Lastly, no records exist of increased herbivory or introductions of other species in Newfoundland that may lead to loss of eelgrass from persistent meadows. Interestingly, long-term eelgrass and fish community monitoring (since 1995) of pristine environments in Bonavista Bay demonstrated consistency of enduring eelgrass meadows and natural expansion since 2001 with relatively steady fish communities (Warren et al. 2010, Cote et al. 2013). Therefore, we can infer from these observations that direct human disturbance or environmental change 1999–2012 (e.g. temperature or salinity) at study sites did not cause eelgrass loss and associated impacts on fish communities in our study.

Invasive species represent an increasingly prevalent threat to aquatic ecosystems. Our study examined the response of eelgrass and associated fishes to green crabs across many impact and control locations before and after the green crab invasion, and demonstrated (1) a strong negative link between presence

of green crabs and subsequent declines in eelgrass presence and percent coverage compared to pre-invasion conditions; (2) that certain green crab population parameters, such as the percent of male crabs, may negatively influence eelgrass; and (3) that a green crab invasion can influence fish abundance, biomass, and likely assemblages in nearshore ecosystems, probably via impacts on eelgrass. Ecosystem engineers—i.e. species that modify environments through habitat creation or destruction (Jones et al. 1994)—change the physical state of abiotic and biotic variables, which can lead to trophic cascades influencing accessibility of resources among organisms in a habitat (Crooks 2002). Past studies that clearly link fish community dynamics to complex eelgrass habitat (e.g. Laurel et al. 2003a,b), considered in tandem with the potential vulnerability of eelgrass to unabated invasion of green crabs in Newfoundland coastal regions, suggest the potential for a disproportionate decrease in abundance, biomass, and productivity of associated fish communities in the coastal zone (Morris et al. 2011).

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LITERATURE CITED

- Blakeslee AMH, McKenzie CH, Darling JA, Byers JE, Pringle JM, Roman J (2010) A hitchhiker's guide to the Maritimes: anthropogenic transport facilitates long distance dispersal of an invasive marine crab to Newfoundland. *Divers Distrib* 16:879–891
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27: 325–349
- Burdick DM, Short FT, Wolf J (1993) An index to assess and monitor the progression of wasting disease in eelgrass *Zostera marina*. *Mar Ecol Prog Ser* 94:83–90
- Carlton JT, Cohen AH (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. *J Biogeogr* 30:1809–1820
- Carman MR, Colarusso PD, Nelson EP, Grunden DW and others (2016) Distribution and diversity of tunicates uti-

- lizing eelgrass as substrate in the western North Atlantic between 29° and 47° North latitude (New Jersey to Newfoundland). *Manag Biol Invasions* 7:51–57
- Carpenter SR, Frost TM, Heisey D, Kratz TK (1989) Randomized intervention analysis and the interpretation of whole-ecosystem experiments. *Ecology* 70:1142–1152
- Clarke KR, Warwick RM (2001) Changes in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558
- Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Mar Biol* 122:225–237
- Costanza R, d'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Cote D, Gregory RS, Morris CJ, Newton BH, Schneider DC (2013) Elevated habitat quality reduces variance in fish community composition. *J Exp Mar Biol Ecol* 440:22–28
- Crawley MJ (2007) *The R book*. John Wiley & Sons, Chichester
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166
- Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: causes and implications. In: Sandlund OD, Schei PJ, Viken A (eds) *Invasive species and biodiversity management*. Kluwer Academic, Dordrecht, p 103–125
- Davis RC, Short FT, Burdick DM (1998) Quantifying the effects of green crab damage to eelgrass transplants. *Restor Ecol* 6:297–302
- DFO (Fisheries and Oceans Canada) (2009) Does eelgrass (*Zostera marina*) meet the criteria as an ecologically significant species? DFO Can Sci Advis Sec Sci Advis Rep 2009/018
- DFO (2011) Ecological assessment of the invasive European green crab (*Carcinus maenas*) in Newfoundland 2007–2009. DFO Can Sci Advis Sec Sci Advis Rep 2010/033
- Duarte CM (2002) The future of seagrass meadows. *Environ Conserv* 29:192–206
- Fonseca MS, Bell SS (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar Ecol Prog Ser* 171:109–121
- Frederiksen M, Krause-Jensen D, Holmer M, Laursen JS (2004) Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. *Aquat Bot* 78:167–181
- Garbary D, Munro J (2004) Eelgrass decline: reality and causation. In: Hanson AR (eds) *Status and conservation of eelgrass (Zostera marina) in Eastern Canada*. Technical Report Series No. 412. Canadian Wildlife Service, Atlantic Region, Sackville, NB, p 23–26
- Garbary DG, Miller AG, Sermour NS (2004) Destruction of eelgrass beds in Nova Scotia by the invasive green crab. In: Hanson AR (eds) *Status and conservation of eelgrass (Zostera marina) in Eastern Canada*. Technical Report Series No. 412. Canadian Wildlife Service, Atlantic Region, Sackville, NB, p 13–14
- Garbary DJ, Miller AG, Williams J, Seymour NR (2014) Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). *Mar Biol* 161:3–15
- Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54:1306–1319
- Green EP, Short FT (2003) *World atlas of seagrasses*. UIMEP World Conservation Monitoring Centre, University of California Press, Berkeley, CA
- Gregory RS, Gotceitas V, Fraser S, Lundrigan P, Brown JA (1997) Temporal and spatial survey of the fish community and its distribution among nearshore habitat types in the marine environment in the vicinity of Terra Nova National Park. Final Report to Canadian Heritage-Parks Canada. Memorial University of Newfoundland, St. John's, NL
- Gregory RS, Morris C, Sheppard GL, Thistle ME, Linehan JE, Schneider DC (2006) Relative strength of the 2003 and 2004 year classes, from nearshore surveys of demersal age 0 & 1 Atlantic cod in Newman Sound, Bonavista Bay. DFO Can Sci Advis Sec Res Doc 2006/038
- Greve TM, Krause-Jensen D, Rasmussen MB, Christensen PB (2005) Means of rapid eelgrass (*Zostera marina* L.) recolonization in former dieback areas. *Aquat Bot* 82:143–156
- Hemminga MA, Duarte CM (2000) *Seagrass ecology*. Cambridge University Press, Cambridge
- Hughes JE, Deegan LA, Wyda JC, Weaver MJ, Wright A (2002) The effects of eelgrass habitat loss on estuarine fish communities of southern New England. *Estuaries* 25:235–249
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Kilminster K, McMahon K, Waycott M, Kendrick GA and others (2015) Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Sci Total Environ* 534:97–109
- Laurel BJ, Gregory RS, Brown JA (2003a) Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. *Mar Ecol Prog Ser* 262:241–252
- Laurel BJ, Gregory RS, Brown JA (2003b) Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Mar Ecol Prog Ser* 251:245–254
- Livingston RJ (1984) Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* 65:1258–1275
- Locke A, Hanson JM (2004) Changes in eelgrass in southern Gulf of St. Lawrence estuaries. In: Hanson AR (eds) *Status and conservation of eelgrass (Zostera marina) in Eastern Canada*. Technical Report Series No. 412. Canadian Wildlife Service, Atlantic Region, Sackville, NB, p 10–12
- Malyshev A, Quijón PA (2011) Disruption of essential habitat by a coastal invader: new evidence of the effects of green crabs on eelgrass beds. *ICES J Mar Sci* 68:1852–1856
- Matheson K, Gagnon P (2012a) Temperature mediates non-competitive foraging in indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs from Newfoundland and Labrador. *J Exp Mar Biol Ecol* 414–415:6–18
- Matheson K, Gagnon P (2012b) Effects of temperature, body size, and chela loss on competition for a limited food resource between indigenous rock crab (*Cancer irroratus* Say) and recently introduced green crab (*Carcinus maenas* L.). *J Exp Mar Biol Ecol* 428:49–56
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008)

- Assessing the global threat of invasive species to marine biodiversity. *Front Ecol Environ* 6:485–492
- Morris CJ, Gregory RS, Laurel BJ, Methven DA, Warren MA (2011) Potential effect of eelgrass (*Zostera marina*) loss on nearshore Newfoundland fish communities, due to invasive green crab (*Carcinus maenas*). *DFO Can Sci Advis Sec Res Doc* 2010/140
- Neckles HA (2015) Loss of eelgrass in Casco Bay, Maine, linked to green crab disturbance. *Northeast Nat* 22: 478–500
- Nejrup LB, Pedersen MF (2008) Effects of salinity and water temperature on the ecological performance of *Zostera marina*. *Aquat Bot* 88:239–246
- Newfoundland and Labrador Statistics Agency (2013) Statistical information for Newfoundland & Labrador. www.stats.gov.nl.ca/Statistics/ (Accessed 5 March 2013)
- Olesen B, Sand-Jensen K (1994a) Demography of shallow eelgrass (*Zostera marina*) populations—shoot dynamics and biomass development. *J Ecol* 82:379–390
- Olesen B, Sand-Jensen K (1994b) Patch dynamics of eelgrass *Zostera marina*. *Mar Ecol Prog Ser* 106:147–156
- Orth R, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. *Bioscience* 56:987–996
- Quijón PA, Snelgrove PVR (2005) Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-Arctic fjord. *Oecologia* 144:125–136
- R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org/
- Rebach S (1974) Burying behavior in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*. *Ecology* 55:195–198
- Reimchen TE (1994) Predators and morphological evolution in threespine stickleback. In: Bell AB, Foster SA (eds) *The evolutionary biology of the threespine stickleback*. Oxford University Press, New York, NY, p 240–276
- Robichaud D, Rose GA (2006) Density-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland. *ICES J Mar Sci* 63: 766–774
- Roman J (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proc R Soc B* 273: 2453–2459
- Ropes JW (1968) The feeding habits of the green crab *Carcinus maenas*. *Fish Bull* 67:183–203
- Rossong MA, Quijón PA, Snelgrove PVR, Barrett TJ, McKenzie CH, Locke A (2012) Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada. *Biol Invasions* 14:659–669
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- Sargent PS, Gregory RS, Schneider DC (2006) Density responses of subarctic coastal marine fish and crabs to artificial reefs. *Trans Am Fish Soc* 135:348–360
- Say T (1817) An account of the Crustacea of the United States. *J Acad Nat Sci Phila* 1:57–64
- Schein A, Courtenay SC, Crane CS, Teather KL, van den Heuvel MR (2012) The role of submerged aquatic vegetation in structuring the nearshore fish community within an estuary of the southern Gulf of St. Lawrence. *Estuar Coast* 35:799–810.
- Schneider DC, Methven DA, Dalley EL (1997) Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. *Can J Fish Aquat Sci* 54(Suppl. 1):187–199
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biology research*. WH Freeman, New York, NY
- Sponaugle S, Lawton P (1990) Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Mar Ecol Prog Ser* 67:43–53
- Thistle ME, Schneider DC, Gregory RS, Wells NJ (2010) Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity. *Mar Ecol Prog Ser* 405:39–56
- Trussell GC, Ewanchuk PJ, Bertness MD, Silliman BR (2004) Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects. *Oecologia* 139:427–432
- Underwood AJ (1992) Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J Exp Mar Biol Ecol* 161:145–178
- Warren MA, Gregory RS, Laurel BJ, Snelgrove PVR (2010) Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. *J Exp Mar Biol Ecol* 394:154–160
- Williams SL (2007) Introduced species in seagrass ecosystems: status and concerns. *J Exp Mar Biol Ecol* 350: 89–110

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