# Conservation implications of demographic changes in the horse mussel *Modiolus modiolus* population of the inner Bay of Fundy

**Jessica A. Sameoto[1],*, Kelly Hall[1,2], Susan E. Gass[2], David Keith[1], Stephane Kirchhoff[3], Craig J. Brown[4]**

[1]Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada
[2]Department of Earth and Environmental Sciences, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada
[3]Nova Scotia Community College, Ivany Campus, Dartmouth, Nova Scotia B2Y 0A5, Canada
[4]Department of Oceanography, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada

ABSTRACT: Horse mussels *Modiolus modiolus* can occur in dense aggregations and form areas of ecological and biological significance. In the Bay of Fundy, Canada, aggregations of horse mussels are associated with flow parallel bedforms, and this area is under consideration for designation as a sensitive benthic area which would provide protective measures. Basic demographic information is required to inform the development of effective conservation and management strategies and although general life-history characteristics of *M. modiolus* are known, detailed quantitative demographic information on this population is limited. The objective of this study was to characterize the population structure of horse mussels in the Bay of Fundy and assess change in key demographic characteristics since the last study in this area in 1997/1998. There have been significant changes in the population since 1998: the 2017 population contains larger, older, mature individuals, with significantly more females; 35% of the current population is over 20 yr of age. Direct evidence that this population has been impacted by bottom-contact fishing gear was also observed. Consistent with *M. modiolus* populations worldwide, this population demonstrates life-history traits (e.g. slow growth rates, late age of maturity, long lifespan) that make it sensitive and susceptible to disturbance. Coupled with the knowledge that this population overlaps with significant fishing activity, this study supports the assumption that this population is vulnerable to bottom-contact fishing and that recovery from adverse impacts would be slow and uncertain.

KEY WORDS: Horse mussel · *Modiolus modiolus* · Demographics · Population structure · Vulnerable marine ecosystem

## 1. INTRODUCTION

Horse mussels *Modiolus modiolus* can occur in dense aggregations and form structurally complex biogenic habitat, often referred to as bioherms, reefs, or beds (Holt et al. 1998, Wildish et al. 2009, Shaw et al. 2014). Dense aggregations of *M. modiolus* are unique marine habitats that support increased biodiversity (Rees et al. 2008), help stabilize seabed substrate (OSPAR Commission 2009), and provide important secondary production pathways (Wildish & Peer 1983) and nutrient cycling (Strong et al. 2016, Kent et al. 2017). Horse mussels occur on a variety of substrates from muddy gravels and sands, to cobble and bedrock from the intertidal zone to depths greater than 200 m (OSPAR Commission 2009, Wildish et al. 2009); however, dense aggregations that form biogenic habitat have a more limited distribu-

tion (Rowell 1967, Wildish et al. 1998a,b, Guijarro Gar-cia et al. 2006, OSPAR Commission 2009, Solyanko et al. 2011, Cook et al. 2013, Gormley et al. 2015).

Although fisheries have targeted *M. modiolus* as bait or for human consumption (Jeffreys 1863, Wiborg 1946, Holt et al. 1998), the greatest threats to horse mussel aggregations are incidental impacts from mobile bottom-contact fishing gear, such as trawls and dredges (Kenchington et al. 2006, 2007, Cook et al. 2013, Fariñas-Franco et al. 2018). Significant re-ductions in epifauna of 90 and 59% have been ob-served for a single pass of a trawl and a scallop dredge, respectively, on horse mussel reefs off the Isle of Man and Wales, with further reductions in as-sociated community diversity and *M. modiolus* abun-dance also observed (Cook et al. 2013). Given that *M. modiolus* is a slow-growing and long-lived species, its resilience to physical disturbance, such as trawl-ing or dredging, is expected to be low. Regeneration times have been estimated between 10 and 20 yr (Wiborg 1946, Kenchington et al. 2006) and in Strang-ford Lough, there was no evidence of recovery of horse mussel beds after 7 yr of fishery restrictions (Roberts et al. 2011, Fariñas-Franco et al. 2018). In the Northeast Atlantic, these biogenic habitats are a priority marine habitat of high conservation value and are currently listed as endangered or threatened (OSPAR Commission 2009, 2011).

In the Northwest Atlantic, *M. modiolus* aggrega-tions in the inner Bay of Fundy, Canada, currently have no protected status but are under consideration as a Sensitive Benthic Area (SBA; Buzeta 2014, DFO 2015). SBAs are ecologically and biologically signifi-cant areas that are vulnerable to proposed or ongo-ing fishing activity (DFO 2015). If designated as SBA, management options are guided based on ecological risk, and in cases of high risk, fishery closures may be considered (DFO 2006). Consideration as an SBA is based on criteria for the identification of vulnerable marine ecosystems (FAO 2009) and includes (1) uni-queness, (2) functional significance of the habitat, (3) fragility, (4) structural complexity, and (5) life-history traits of component species that make recovery diffi-cult (e.g. slow growth rates, late age of maturity, low or unpredictable recruitment, and a long lifespan) (FAO 2009, DFO 2015). Although *M. modiolus* is present throughout the Bay of Fundy region (Rowell 1967, Wildish et al. 1998a,b, Beazley et al. 2017), horse mussel aggregations associated with flow parallel bedforms have only been identified in local-ized areas in the inner Bay of Fundy (Wildish et al. 1998a,b, Shaw et al. 2014, Todd et al. 2014, 2020, Wilson 2020). These areas are characterized as linear

ridges of up to 3 m high and 16 km long aligned with the tidal current direction and are formed by the accumulation of horse mussel shell and sand, with associated live horse mussels and other attached epi-fauna (e.g. bryozoans, sponges; Shaw et al. 2014, Todd et al. 2014).

Although these flow parallel bedforms have been spatially delineated (Wildish et al. 2009, Shaw et al. 2014, Todd et al. 2014, 2020), information on the gen-eral population characteristics of the main structure-forming species, *M. modiolus*, in and around this area is limited. Physical sampling and population characterization of the inner Bay of Fundy horse mussel was last conducted in 1997 and 1998, but a full demographic characterization was not conducted at that time (Wildish et al. 1998b). The Bay of Fundy is also a highly fished area with significant activity by fisheries that use bottom-contact gear, mainly groundfish and scallop (Butler & Coffen-Smout 2017, Koen-Alonso et al. 2018). Given the potential risk to this *M. modiolus* population, current baseline infor-mation on the status of the species is critical to inform future conservation and management strategies. The objective of the present study was to characterize the current population structure of horse mussels in the inner Bay of Fundy and to conduct a comparative analysis with the results of Wildish et al. (1998b) to assess if there have been any shifts in demographic characteristics over 2 decades between horse mus-sels sampled in 1997 and 1998 and those in 2017. This study provides the first full quantitative demo-graphic characterization of the *M. modiolus* popula-tion of the inner Bay of Fundy, which has important implications for future conservation planning in this area.

## 2.  MATERIALS AND METHODS

### 2.1.  Study site

The Bay of Fundy is a shallow macrotidal body of water situated between New Brunswick and Nova Scotia in the Northwest Atlantic Ocean (Shaw et al. 2014). It is a tidally dominated funnel-shaped bay, dividing into branches in the northeast, while deep-ening to over 200 m towards the southwest (Shaw et al. 2014, Li et al. 2015). The study area was approx-imately 80 × 25 km within the inner Bay of Fundy (Fig. 1), where depths range from 50 to 90 m (Shaw et al. 2014). This area is well mixed due to tidal action and experiences some of the world's highest tides (O'Reilly et al. 2005), with tidal current speeds gener-
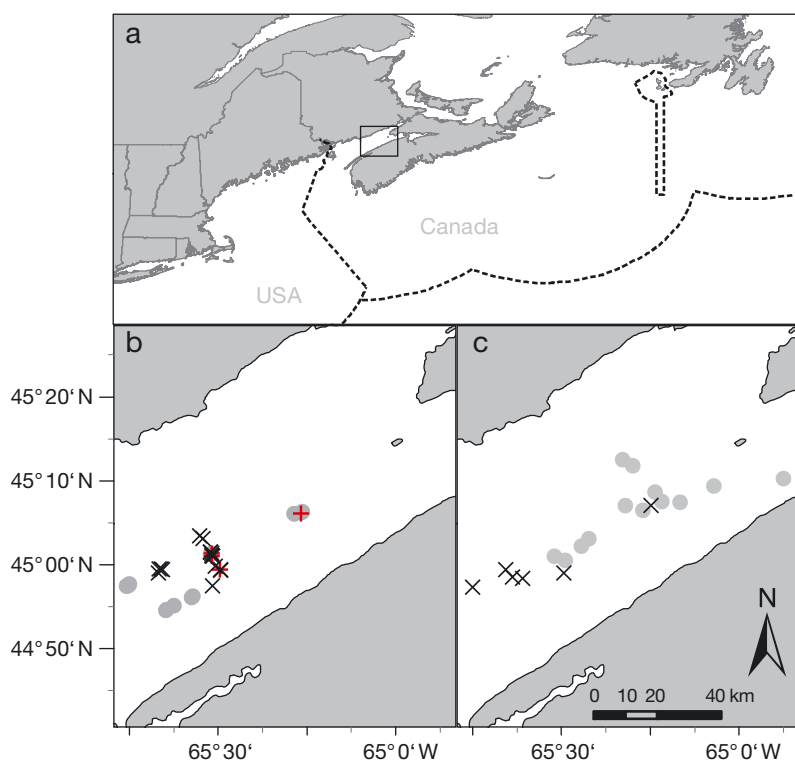
Fig. 1. Study site showing (a) the exclusive economic zone (dashed line) and sampling stations in the inner Bay of Fundy area in (b) 1998 and (c) 2017. (×) Stations with zero live horse mussel; (+) stations sampled in 1998 that had ≤6 live horse mussels and subsequently were not included for analysis by Wildish et al. (1998b); (●) stations with live horse mussels that were included in the analysis for 1998 and 2017

ally >50 cm s⁻¹ (Li et al. 2015). Environmental conditions within the study area were expected to be relatively similar (Greenlaw et al. 2010, Shaw et al. 2014, Li et al. 2015). Locations of potential aggregations of horse mussels *Modiolus modiolus* associated with flow parallel bedforms were first identified in 1995 using seismic reflection and sidescan sonograms (Wildish et al. 1998a) and, more recently, were further spatially delineated using multibeam echo sounders (Shaw et al. 2014). However, it has recently been demonstrated that aggregations of horse mussels occur both on and near these bedforms but not all bedforms are horse mussel habitat (Wilson 2020, Wilson et al. 2021).

## 2.2. Sampling

Sampling of horse mussels present in and around the identified flow parallel bedforms has been limited, with sampling first conducted in June 1997 and May 1998 using a 0.5 m² hydraulic grab and a 0.5 m² Van Veen grab, respectively (Wildish et al. 1998b). Targeted sampling in 1997 and 1998 consisted of 37

grab samples taken in and around the area coincident with the bedforms; this sampling was informed based on previous seismic reflection and sidescan sonogram work in the area (Wildish et al. 1998a). Only successful grabs (grab fully closed) were analyzed, and of the 37 stations, 21 had horse mussels present; however, detailed analyses were only conducted when there were more than 6 individuals per grab (Wildish et al. 1998b). Therefore, the analysis for this study represents horse mussels obtained from 17 stations in 1997 and 1998 (12 and 5 stations, respectively). Data collected in 1997 and 1998 on live horse mussels (n = 628) from the 17 stations were transcribed from Wildish et al. (1998b) and consists of viscera wet weight (g), valve length (mm), and sex/maturity (male, female, hermaphrodite, undetermined, juvenile). In 1997, horse mussels were opened with a knife and sexed, and the viscera were removed with a scalpel and frozen (−20°C) to be processed later in the laboratory. In 1998, approximately half of the mussels were processed as in 1997, and the other half were frozen whole at sea until further processing in the laboratory.

In 2017, sampling locations for horse mussels were chosen based on the spatial delineation of the bedforms (Kostylev 2009, Shaw et al. 2014), multibeam echo sounder backscatter maps, station information on horse mussel presence from Wildish et al. (1998b), imagery survey data from prior geological missions (Todd et al. 2010, 2012), and bycatch data from DFO stock assessment surveys (unpubl.). These data sources were used to identify areas of potential horse mussel habitat for targeted sampling. Nineteen stations were surveyed over 3 days; (n = 1 on July 18, 2017, n = 9 on September 30, 2017, n = 9 on October 1, 2017). Sampling in 2017 was initially attempted with a Van Veen grab; however, these sampling attempts were unsuccessful due to substantial volumes of shell debris that obstructed the closure of the jaws, causing the grabs to fail. Sampling was therefore conducted using a modified scallop dredge comprised of a single gang of scallop miracle gear with a steel frame and a bag made of rings that were 82 mm in diameter and lined with a 27 mm polypropylene

mesh (maximum diagonal dimension of 38 mm). Similar gear with the same liner was used by Kenchington et al. (2007) in a comparable area of the Bay of Fundy and shown to retain species above approximately 50 mm in size. Dredge dimensions were 0.61 × 0.61 × 0.30 m (width × length × depth) with 5 teeth that were 5.1 cm long and 6.4 cm wide. At each station, the modified scallop dredge was towed for approximately 1 km on bottom. Positional information was recorded using the navigation software QINSy (Version 8.17.1). Tow contents were sorted and processed for horse mussels that were either live or dead (where dead is defined as empty paired hinged shells). Live and dead horse mussels were bagged, labeled, and frozen until further processing in the laboratory (n = 458).

In 1997 and 1998, thawed viscera were patted dry and weighed to the nearest 0.001 g (Wildish et al. 1998b). Valves were scrubbed to remove epifauna, and the length of the left valve was measured from anterior to posterior with electronic calipers to the nearest 0.1 mm (Wildish et al. 1998b). In 2017, mussels were thawed, scrubbed clean of their epifauna, and classified as live or dead. For live mussels, the viscera was removed with a scalpel and weighed to the nearest 0.001 g with a calibrated Mettler AE240-S analytical balance. The length of the left valve was measured from anterior to posterior to 0.01 mm with Mitutoyo digital IP67 calipers. In both studies, if the left valve was broken, the right valve was used. All shells were evaluated for evidence of shell repair to distinguish between repaired damage and shell distortions due to other causes (Dinesen & Morton 2014). For samples in all years, sex was determined by the gonad color: bright orange for female and creamy yellow for male (Rowell 1967). If the gonad displayed both orange and creamy yellow, the sample was classified as a hermaphrodite. When not possible to determine sex based on color, the mussel was classified as undetermined. Mussels were classified as juvenile if there was no gonad present (Rowell 1967).

Horse mussels have 2 types of growth lines found on the valves (thin white winter lines and wide dark summer lines), which are indicative of age in years (Wiborg 1946, Rowell 1967, Wildish et al. 1998b). Although aging was conducted for samples collected in 1997 and 1998, the data were unreliable (Wildish et al. 1998b) and therefore not included in the present study. In 2017, the periostracum was removed by soaking the left valve in bleach; if the left valve was broken the right valve was used. With the aid of a backlight, the winter lines were identified, and only mussels with distinguishable winter lines were used (n = 292).

Due to significant differences in depth due to tidal fluctuations in the Bay of Fundy, depth information for each station for all years was determined by spatial analysis (ArcGIS v. 10.5) with a bathymetry layer standardized to mean sea level (Todd et al. 2014).

## 2.3. Statistical analysis

Analyses were conducted to determine population characteristics of horse mussels, and the effect of the year of the study (1997/1998 versus 2017) was evaluated; for ease of reporting, the years are hereafter reported as 1998 (representing 1997 and 1998 combined) and 2017, respectively. Depth differences between 1998 and 2017 were evaluated using $t$-tests; tests were conducted using depth by station and depth by sample. A Kruskal-Wallis test was used to test for differences in mean shell length between years (Kruskal & Wallis 1952).

To test if the proportion of mature to immature individuals and sex ratios within the population had significantly changed between 1998 and 2017, maturity and sex were analyzed. For the maturity analysis individuals identified as either male or female were classified as mature, and individuals identified as juveniles were classified as immature. The sex ratio analysis used only mature individuals classified as male or female, and an additional analysis was performed to test whether the sex ratios within years differed from 1:1. Maturity and sex ratio are binary and were modelled with generalized linear models with a binomial family and logit link:

$$m_i \sim \text{Bernoulli}(\pi_i); \ \text{E}(m_i) = \pi_i \\ \text{logit}(\pi_i) = \text{year}_i \quad (1)$$

where $m_i$ is the maturity status or sex ratio of an individual $i$, and year is a fixed covariate (categorical; 1998 or 2017).

To evaluate if length at maturity had changed significantly between 1998 and 2017, maturity was modelled using a binomial generalized linear model with logistic link function:

$$y_i \sim \text{Bernoulli}(\pi_i); \ \text{E}(y_i) = \pi_i \\ \text{logit}(\pi_i) = \text{year}_i + \text{vlength}_i + \text{year}_i \times \text{vlength}_i \quad (2)$$

where $y_i$ is the maturity of individual $i$, which follows a Bernoulli distribution (a special case of the binomial when the number of trials = 1) with a mean of $\pi$. The fixed covariates in this model are the year (categorical) and valve length (vlength; continuous), and the model also includes the interaction between year and vlength.

Since horse mussels were collected at different times of year between 1998 and 2017, the length-to-weight relationship of *M. modiolus* was modelled independently for each year; however, the 2017 samples were limited to those collected in fall, since that was when the majority of stations were sampled (18 of 19 stations). To assess the length-to-weight relationship of *M. modiolus*, valve length and viscera weight were modelled using a generalized linear model with Gamma family and log link for each year:

$$w_i \sim \text{Gamma}(\mu_i, \phi); E(w_i) = \mu_i; \text{var}(w_i) = \frac{\mu^2}{\phi}$$
$$\log(\mu_i) = \text{vlength}_i \qquad (3)$$

where $w_i$ is the viscera weight of individual $i$, which follows a Gamma distribution with a mean of μ and a shape parameter of φ. The fixed covariate was valve length (vlength; continuous).

Growth, as defined by the valve length-to-age relationship, was modelled using the von Bertalanffy growth function (commonly used to estimate growth rates in fish and marine invertebrate species; Pardo et al. 2013, Ogle & Isermann 2017) for data from 2017:

$$\text{vlength}_i \sim N(\mu_i, \sigma^2); E(\text{vlength}_i) = \mu_i$$
$$\mu_i = L_\infty(1 - e^{-K(\text{age}_i - t_0)}) \qquad (4)$$

where $\text{vlength}_i$ is the valve length of individual $i$ and is assumed to be normally distributed ($N$) with a mean of μ and a standard deviation of σ. The covariate in this model is the age of each individual (continuous). The 3 estimated model parameters are: (1) $L_\infty$, the asymptotic maximum shell length, (2) $K$, the curvature parameter that describes how rapidly the individual approaches $L_\infty$, and (3) $t_0$, the theoretical age where an individual has 0 length (Sparre & Venema 1998). Growth parameters were estimated by non-linear least squares, and 95% confidence intervals were estimated from 5000 bootstrap samples using the packages FSA (Ogle et al. 2019) and nlstools (Baty et al. 2015).

Model selection was performed using Akaike's Information Criterion (AIC), and analyses were conducted using the statistical software R v3.5.2 (R Core Team 2018). Mixed effect models using station as a random effect were also tested (see the Supplement at www.int-res.com/articles/suppl/m670p093_supp.pdf), but we only present results for the fixed effect models, because (1) the parameter estimates and conclusions did not differ from the mixed effects models, and (2) the fixed effects models utilized all the available data, whereas the low sample size of 3 stations in 2017 resulted in the exclusion of these data (Zuur et al. 2009).

# 3. RESULTS

Horse mussels *Modiolus modiolus* were found throughout the study area in both 1997/1998 (Wildish et al. 1998b) and in the present study (2017). From the 17 stations where Wildish et al. (1998b) found >6 horse mussels per grab, 628 live mussels (418 at 12 stations in 1997 and 210 at 5 stations in 1998) contributed to the present study's analyses; no details on the numbers of dead horse mussels were available (Wildish et al. 1998b). In 2017, a total of 450 live (98.3%) and 8 dead horse mussels (1.7%) were present at 13 of 19 sampled stations (Table 1). Recently dead horse mussels were found at 4 stations and ranged in valve length from 98 to 132 mm with a median of 113 mm. All live and dead horse mussels collected in 2017 were evaluated for signs of incidental damage to their shells, and of the total 458 mussels, eight individuals from 5 stations displayed distinctive shell deformations that were indicative of non-lethal damage caused by interactions with heavy fishing gear (Fig. 2). Mean depth at the 30 stations where horse mussels were found was 74 and 66 m in 1998 and 2017, respectively. The depth distributions by samples and stations were not significantly different between the 2 time periods ($t_{747} = -1.30$, p = 0.194 and $t_{17} = 2.09$, p = 0.052, for samples and stations, respectively).

Shell length frequencies were significantly different between the 2 time periods (Kruskal-Wallis, $\chi_1^2 = 567.8$, p < 0.001): the median valve length of live horse mus-

Table 1. Numbers of live horse mussels observed within the inner Bay of Fundy in 1998 and 2017

| Study | Females | Males | Herma-phrodites | Juveniles | Unde-termined | Total |
|-------|---------|-------|-----------------|-----------|---------------|-------|
| 1998  | 232     | 262   | 0               | 52        | 82            | 628   |
| 2017  | 287     | 128   | 1               | 5         | 29            | 450   |
| Total | 519     | 390   | 1               | 57        | 111           | 1078  |



Fig. 2. An example of a horse mussel shell with incidental damage sampled from the Bay of Fundy in 2017

sels was 62 mm in 1998 and 113 mm in 2017. Shell length frequencies ranged from 20.2 to 124.1 mm in 1998 and from 20.8 to 146.8 mm in 2017 (Fig. 3).

The majority of horse mussels observed were mature in both sampling periods. Of those individuals whose maturity was identifiable ($n_{1998}$ = 546, $n_{2017}$ = 420; Table 1), 90.5 and 98.8% were mature in 1998 and 2017, respectively (Table 1); this was a significant increase in the proportion of mature individuals within the population (GLM, $z_{964}$ = 4.58, p < 0.001).

Of adult mussels in 1998, 47% were female and 53% were male (Table 1); this is a 0.9:1 female to male ratio, which was not significantly different from 1:1 (0.53 [95% CI: 0.49, 0.57], p = 0.18). In 2017, there were 69% females and 31% males (287 and 128, respectively; Table 1), which was significantly different from 1:1 (0.31 [95% CI: 0.27, 0.35], p < 0.001). There was a significant increase in the percentage of females in the population from that observed in 1998 (GLM, $z_{907}$ = −6.67, p < 0.001). There was 1 individual observed in 2017 that phenotypically displayed both male and female gonads (valve length of 112 mm); no observations of hermaphrodites were recorded in 1998 (Wildish et al. 1998b).

Length-at-maturity did not change between years. Model selection based on AIC indicated there was no effect of year; therefore, data were pooled from both time periods. Length at 50% maturity was estimated at 39.8 mm (95% CI: 36.1, 42.7 mm; Fig. 4), and length at 90% maturity was estimated at 53.3 mm (95% CI: 51.0, 55.8 mm). The timing of the sampling during the 2 study periods precludes a direct comparison of the morphometric relationship between viscera weight and valve length given potential confounding effects of seasonal patterns in gametogenesis and spawning. The viscera weight at length was observed to be heavier in the fall in 2017 than in early summer in 1998 (14 and 17 g for 100 mm valve length in 1998 and 2017, respectively; Fig. 5).

Aging indicated the youngest horse mussels were between 2 and 3 yr old at approximately 20 mm in valve length, and the maximum age observed was 34 yr at a valve length of 133.1 mm in 2017. All model parameters of the von Bertalanffy growth

function ($L_\infty$, $K$ and $t_0$) were significant and therefore important in describing the length-at-age relationship (Fig. 6). The von Bertalanffy growth function indicates that horse mussels grow to approximately 125.9 mm valve length (95% CI: 122.5, 129.9 mm), the exponential rate of approach to this asymptote was 0.17 (95% CI: 0.14, 0.19) and the estimated value of $t_0$ was 1.64 (95% CI: 0.91, 2.27). Based on a length-to-age conversion, assuming growth rates were similar in 1998, the observed median length of horse mussels in 1998 (62 mm) corresponds to 6 yr old, whereas the observed median length in 2017 (113 mm) corresponds to an age of 15 to 16 yr (Fig. 6). The predicted age at 50% length-at-maturity in both years was 4 yr and 90% length-at-maturity corresponded to 5 yr.

## 4. DISCUSSION

The life-history characteristics of species within areas identified as ecologically or biologically significant will impact the areas' sensitivity and susceptibility to disturbance. Traits that make population recovery difficult include late age of maturity,
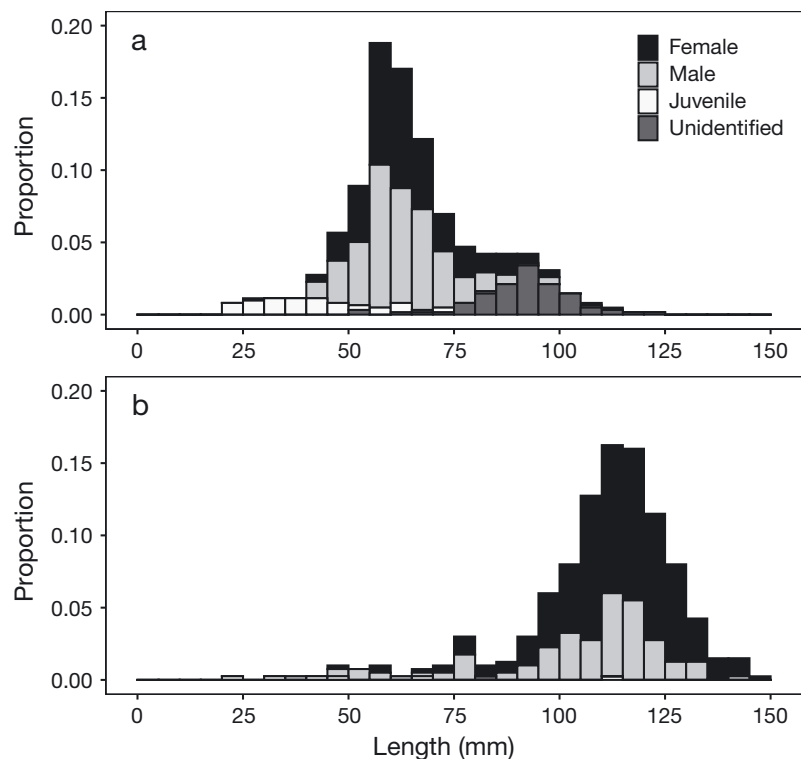


Fig. 3. Length frequency of valves, proportional to the population, of live horse mussels in the different sex/maturity categories sampled from the inner Bay of Fundy via (a) a grab in 1998 and (b) a modified dredge with 27 mm mesh liner in 2017. Bin width = 5 mm
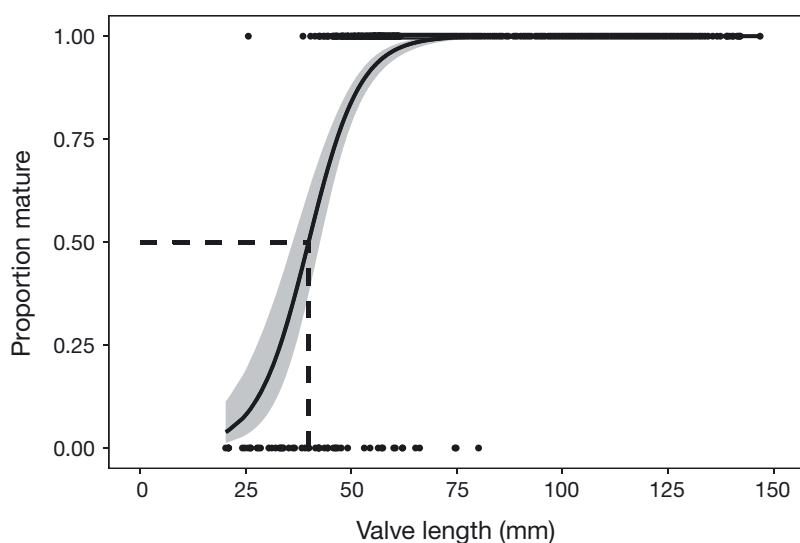
Fig. 4. Length-at-maturity of live horse mussels collected from the Bay of Fundy in 1998 and 2017. Black line: predicted values of the mature proportion of the population; gray shading: 95% CI; dashed lines: size at 50% maturity (39.8 mm)
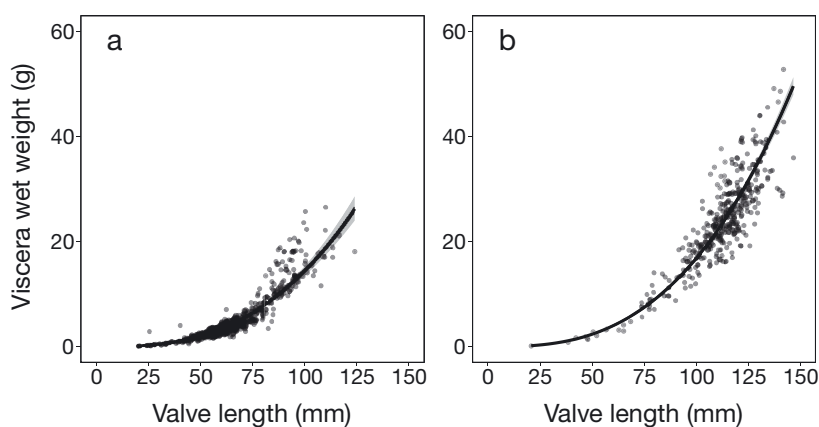


Fig. 5. Viscera weight (g) to valve length relationships for horse mussels in the Bay of Fundy sampled in (a) May and June in 1998 and (b) September and October 2017. Gray shading around line: 95% CI
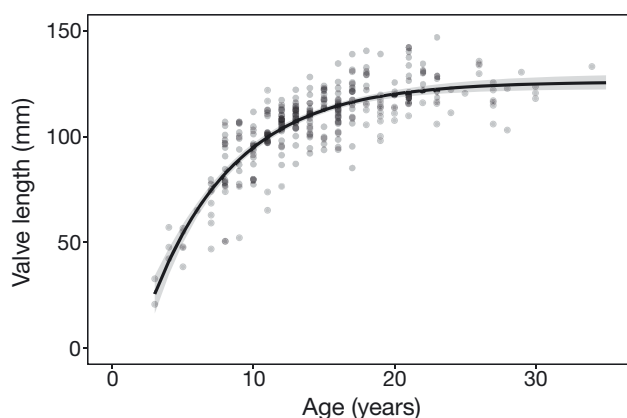


Fig. 6. von Bertalanffy growth model predicted for valve length-at-age for horse mussels in the Bay of Fundy in 2017. Gray shading around line: 95% CI

low or unpredictable recruitment, slow growth rates, and long lifespan (FAO 2009). Horse mussel aggregations associated with flow parallel bedforms are known only to occur within a localized area of the inner Bay of Fundy (Wildish et al. 1998a, 2009, Shaw et al. 2014, Todd et al. 2014, 2020, Wilson 2020, Wilson et al. 2021). Despite significant fishing activity in the Bay of Fundy (Butler & Coffen-Smout 2017, Koen-Alonso et al. 2018), live horse mussels were present in the area coincident with the multibeam delineated flow parallel bedforms (Shaw et al. 2014, Wilson 2020, Wilson et al. 2021). This represents a similar geographic area to that where high densities of *Modiolus modiolus* were found in 1998, although the length frequencies observed in 2017 were significantly different from those observed in 1998.

The methodologies of the surveys were not identical between 1998 and 2017, with samples from 1998 collected by grab, whereas a modified dredge with liner was used in 2017. Both gear types had mouth openings larger than the maximum valve lengths observed; therefore, the gear difference is not expected to have had an impact on the upper range of length frequencies. However, the difference in gear type may have had an impact on the relative frequency of smaller horse mussels. The maximum mesh opening of 38 mm in 2017 could have allowed horse mussels less than approximately 70 mm valve length to escape, given that valve length is much larger than valve height or width (Rowell 1967, Hall 2018). However, the catch composition associated with horse mussels in and around the bioherms suggests that it is unlikely that horse mussels with 50–70 mm valve length were present in frequencies greater than those observed. Kenchington et al. (2007) sampled a similar area within the Bay of Fundy using a similar dredge and the same liner as in our study; they reported that the clogging of the gear due to the leafy bryozoan *Flustra foliacea* led to the retention of organisms as small as approximately 50 mm in size, increasing the probability of retaining rare species and increasing the occurrence of small

individual sizes in their study. When sampling in 2017, in addition to horse mussels, the catch consisted of large volumes of *Flustra*, which is highly abundant in this area (Kenchington et al. 2007, Shaw et al. 2014, Wilson 2020, Wilson et al. 2021). Therefore, it is unlikely that horse mussels 50–70 mm in valve length were missed from our sampling in 2017 had they not already been present at low abundances. However, the differences in the gear used between the 2 sampling periods limit our ability to quantify changes in the relative abundance of horse mussels <50 mm.

Irrespective of the differences in sampling gear, the size distribution of the inner Bay of Fundy horse mussels indicates that the population in 2017 contained significantly larger, older individuals than in 1998. Populations of *M. modiolus* are frequently dominated by larger individuals of a range of ages with fewer smaller, younger age classes (Wiborg 1946, Rowell 1967, Anwar et al. 1990). However, Fariñas-Franco & Roberts (2018) and Brash et al. (2018) found distinct bimodal distributions across subpopulations of *M. modiolus* in Northern Ireland and Scotland, respectively, using diver sampling. In the Bay of Fundy population, few individuals less than 40 mm valve length were observed in 1998, when a grab sampler was used which is more similar to dive sampling than sampling via a dredge with liner (i.e. as used in 2017). Predation pressure is generally higher on small size classes and is expected to be high during the post-larval and juvenile stages (Seed & Brown 1978). Juveniles grow rapidly until they reach approximately 45 to 60 mm in length, at which point predation pressure is much reduced (Comely 1978, 1981, Seed & Brown 1978, Anwar et al. 1990).

Although our study cannot definitively conclude whether small horse mussels (<50 mm valve length) were present at low abundances in the inner Bay of Fundy in 2017, our results suggest that there were few individuals between 50 and 90 mm (5 to 9 yr old). Horse mussel populations may act as a source or sink for recruitment (Lipcius et al. 2008), and little is known about the connectivity of the inner Bay of Fundy *M. modiolus* population and whether the population is self-recruiting or reliant on recruits from outside the area. Although the Bay of Fundy is a high-energy and dynamic area, aggregations of shellfish alter the benthic boundary layer through changes to seabed roughness, increased drag, and modified flow (Green et al. 1998, Styles 2015, Kent et al. 2017). Variation in mussel density also influences recruitment success, as *M. modiolus* preferentially settle amongst conspecifics (Fariñas-Franco et al.

2013). Evidence suggests that adult populations provide refuge for new recruits from predation (Comely 1978, Brash et al. 2018, Fariñas-Franco & Roberts 2018) and that low habitat complexity can influence settlement success (spat recruitment; Fariñas-Franco et al. 2013). The different sampling approaches preclude a comparison of density or abundance between the 2 study periods; however, given the observation of few animals of <90 mm valve length, more research is needed to understand the spawning, recruitment, and connectivity of the inner Bay of Fundy horse mussels to inform future management strategies (Elsäßer et al. 2013, Gormley et al. 2015).

The variability in the timing of the sampling between the 2 time periods (summer in 1998 versus fall in 2017) precludes a direct comparison of horse mussel condition, since the timing of the reproductive cycle may have influenced the overall visceral mass observed. Spawning by horse mussels can be complex and irregular (Wiborg 1946, Seed & Brown 1977); however, Fariñas-Franco & Roberts (2018) found evidence of seasonality in spawning from populations in Northern Ireland. Horse mussels are broadcast spawners, with eggs and sperm released into the water column where fertilization occurs (Wiborg 1946, Seed & Brown 1977, Dinesen & Morton 2014). In the intertidal zone of the Bay of Fundy, Rowell (1967) failed to detect any significant spawning events over a 2 yr period, suggesting that horse mussels have a complex sexual cycle in which major spawning takes place at periods of 2 yr or more and a partial release of gametes may occur once or twice a year. The majority of horse mussels observed in 2017 were sexually mature, with the size at 50% maturity being 39.8 mm valve length (age 4), and 53.3 mm valve length at 90% maturity (age 5), consistent with findings from previous studies (Wiborg 1946, Rowell 1967, Seed & Brown 1977, Jasim 1986, Jasim & Brand 1989). However, further monitoring and study would be required to determine the timing and variability of the reproductive cycle of this population.

Sex ratios in natural populations tend towards a 1:1 ratio of males to females (Fisher 1999); however, reports on *M. modiolus* are mixed. Parity has been reported for populations in Scotland (Comely 1978) and the Isle of Man (Jasim & Brand 1989), whereas greater numbers of males than females have been reported in populations in Northern Ireland (Fariñas-Franco & Roberts 2018) and in the intertidal zone of the Bay of Fundy (Rowell 1967). Further, when restricted to smaller mussels (<60 mm), more males than females have been observed (Wiborg 1946, Rowell

1967). In contrast, more females than males have been reported in Norway, with ratios up to 1.7:1 (Wiborg 1946). The ratio of females to males we determined in the inner Bay of Fundy (2.2:1) is higher than those reported in previous studies, and the significant change in sex ratio observed between the 2 time periods is surprising. The implications of this significant deviation from parity are unknown. Interestingly, in free-spawning invertebrates, sperm limitation limits fertilization success, with sparseness of sperm linked to low and extremely variable fertilization rates (Levitan 1995, Levitan & Petersen 1995, Claereboudt 1999). With fertilization success as the first stage affecting subsequent larval dispersal and survival, success or failure at this stage may influence downstream dynamics of the adult population (Levitan & Petersen 1995, Claereboudt 1999). Further investigation of the population density, the degree of spatial aggregation, and size-related reproductive output of the inner Bay of Fundy horse mussel population would help assess if the observed sex ratio may be influencing fertilization success (Levitan 1995, Claereboudt 1999). Further, horse mussels are dioecious, and previous studies from Atlantic Canada indicate that these populations are gonochoristic with no evidence of hermaphroditism (Rowell 1967, Wildish et al. 1998b); however, a single hermaphroditic individual was found in the Bay of Fundy in 2017.

For bivalves, empty paired hinged shells are evidence of recent mortality (Merrill & Posgay 1964). Although no information on the proportion of dead horse mussels was reported by Wildish et al. (1998b), 1.7% of the samples in 2017 were empty paired hinged shells. The rate at which the hinge ligament decomposes is unknown for horse mussels; however, it has been estimated to range from 50 to 259 d for the sea scallop *Placopecten magellanicus* (Dickie 1955, Merrill & Posgay 1964). The agreement in length frequency distribution between dead and live horse mussels, coupled with the relatively dynamic nature of the Bay of Fundy and fishing activity within the region, suggests that the deaths of these horse mussels were relatively recent.

*M. modiolus* is known to be sensitive to mobile fishing gear. Collie et al. (2000) studied the impacts of bottom fishing on Georges Bank and found *M. modiolus* only present in undisturbed areas. Mobile fishing gear can reduce *M. modiolus* biomass (Kenchington et al. 2006), and several fish species either increased predation on, or switched to preying on, *M. modiolus* after trawling (Kenchington et al. 2005). The results from the present study support the assumption that the sampled population of horse mussels has been im-

pacted by fishing activity. Patterns of shell damage (consistent with blunt force trauma) and subsequent repair were observed in 1.7% of the population and at 5 of the 13 stations where horse mussels were sampled in 2017. Evidence of incidental damage is unsurprising, since the Bay of Fundy is a relatively heavily fished area, with scallop fishing by drag and groundfish trawling reported in the vicinity of the study area (Butler & Coffen-Smout 2017, Koen-Alonso et al. 2018). Further, incidental damage reflected in shell morphology has long been observed for sea scallops (e.g. shock marks; Caddy 1989, Harris & Stokesbury 2006). However, our results are not directly translatable into a quantifiable measure of this impact on the horse mussel population in the inner Bay of Fundy, since this damage is only manifested in those individuals that survive contact with heavy gear. Further study is required to quantify and evaluate the risk of bottom contact activity relative to this population.

The slow growth and longevity of *M. modiolus* are important considerations in relation to the species' ability to recover from disturbance. *M. modiolus* has been classified as partly fragile and slow to recover from bottom-contact fishing gear (MacDonald et al. 1996) and has been documented as commonly reaching ages of 22 to 23 yr (Wiborg 1946), with age estimates of 48 yr for an individual from the North Sea (Anwar et al. 1990) and over 50 yr for one off Northern Ireland (Fariñas-Franco & Roberts 2018). In the present study, we observed a maximum age of 34 yr, and the median age in 2017 was 15 to 16 yr. Based on the 2017 von Bertalanffy growth function, individuals with >120 mm valve length (35% of the current population) could be from the same cohort observed in 1998 and are therefore >20 yr of age. Results of the present study are comparable to estimates from other Atlantic Canadian populations (Rowell 1967) and are within the range of parameter values of various European populations (Anwar et al. 1990). Although total age-at-length was used to derive growth curves, alternate aging techniques such as shell growth increments (Wildish et al. 1998b) or acetate peels (Anwar et al. 1990) could be used for further study; however, Wildish et al. (1998b) found that growth lines were homogeneous and unreadable using the latter method.

Basic demographic information on populations of ecological and biological significance is required for baseline monitoring and to inform the development of effective conservation and management strategies. Here, we present the first quantitative population demographic characterization for the inner Bay

of Fundy horse mussel population. There have been significant changes in the population since 1998, with the current population containing larger, older, mature individuals and with significantly more females. Combined with knowledge of the complex and irregular spawning cycle of *M. modiolus* and the species' long life expectancy, the horse mussel population associated with the Bay of Fundy flow parallel bedforms demonstrates biological traits consistent with a vulnerable marine ecosystem (FAO 2009, DFO 2015). Although establishing if there has been an overall population decline was beyond the scope of this study, significant declines in horse mussel were observed between 1966–67 and 1997 in an area near the flow parallel bedforms (Kenchington et al. 2007); further, human activity has contributed to declines of *M. modiolus* in European populations (Jones et al. 2000, OSPAR Commission 2009, 2011). Coupled with the knowledge that this population overlaps with significant fishing activity (Butler & Coffen-Smout 2017, Koen-Alonso et al. 2018) and evidence of incidental damage by fishing gear, this study supports the assumption that this population is vulnerable to bottom-contact fishing and that its demographics and life-history traits would make its recovery from adverse impacts slow and uncertain.

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