



# The effects of physical disturbance and sediment refuge on the growth of young native freshwater mussels *Elliptio complanata* (Eastern Elliptio)

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**Abstract** Native freshwater mussels form a critical component of benthic foodwebs, but are endangered worldwide, making their study an important conservation issue. Many unionids live in shallow environments where they are potentially vulnerable to natural disturbances, but the impact of physical forces on their growth and the role of sediments as a refuge is poorly understood. Here, we validate the use of two types of shell internal lines (nacreous, prismatic) as indicators of physical disturbance and shell coloration as an indicator of sedimentary habitat. We use these indicators to test (1) whether the sediments provide an effective refuge for juvenile and young adult mussels from natural disturbances and (2) whether disturbance events affect their growth. *Elliptio complanata* (Eastern Elliptio) emerge from the sediments when they are 20–50 mm in size and 2.5–7 years old. Juvenile and young adults lay down more disturbance lines at more exposed nearshore sites, but also in small lake basins with dense mussel populations.

Disturbance lines are produced during both endo- and epibenthic growth periods, but in contrast to adults, they are not associated with growth anomalies. Sediments accumulating in shallow nearshore areas of lakes provide an imperfect but effective refuge for native mussels that warrant protection.

**Keywords** Wave disturbance · Disturbance line · Refuge · Unionid mussel · Juvenile · *Elliptio complanata* · Eastern Elliptio

## Introduction

Native freshwater mussels provide a wide range of ecosystem services worldwide (Strayer, 2014; Vaughn & Hoellein, 2018). Their filter feeding is a key process in many benthic foodwebs that transfers organic matter from the water column to the sediments through the production of feces and pseudo-feces (material filtered from the water column but not ingested) (Vaughn & Spooner, 2006; McCasker & Humphries, 2021). At high density, mussels can play an important role in sediment dynamics and biogeochemical cycling, including nutrients (Strayer, 2014; Vaughn & Hoellein, 2018). However, populations of many native freshwater mussels are threatened due to pressures from habitat alteration and fragmentation, climate change, invasive predators and competitors, and pollution (Lopes-Lima et al., 2017; Ferreira-Rodr iguez et al., 2019). At least 37 of the Unionid

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species present in the 1800s in North America have since gone extinct and more than 100 of the remaining ~300 species are endangered (Williams et al., 2017; Vaughn & Hoellein, 2018). Given freshwater mussels' ecological significance and the myriad threats they face, understanding the factors that influence their growth and development is important for conservation (Ferreira-Rodríguez et al., 2019).

Native freshwater mussels live in soft sediments and are vulnerable to physical forces that can dislodge and transport both the sediments and benthic organisms (Strayer, 1999; Allen & Vaughn, 2010). Several studies have shown that various measures of hydrodynamic forces can help us predict the local distribution of mussels in rivers and nearshore lake areas (Daraio et al., 2010; Cyr et al., 2012, 2017b; Lopez & Vaughn, 2021). For example, landscape variables (e.g., stream size) and fine-scale hydrological variables (e.g., bed shear stress, Reynolds number) are useful predictors of the spatial distribution and community composition of unionids in rivers (Daraio et al., 2012; French & Ackerman, 2014; Lopez & Vaughn, 2021). In lakes, unionids are most abundant in shallow sedimentary areas (Cyr et al., 2012) and at greater depths in large lakes with deep wave-mixed layers and along steep slopes (Cyr, 2008; Cyr et al., 2017b). Hydrodynamic forces can thus play a major role in delimiting unionid distributions.

Mussel growth is also influenced by hydrodynamics. Water flow is required to supply food (Vanden Byllaardt & Ackerman, 2014; Mistry & Ackerman, 2018) and remove wastes, and higher flows are related to higher bivalve growth rates (Grizzle & Morin, 1989; Menge et al., 1997; Dycus et al., 2015). In shallow nearshore areas of lakes, mussel growth declines with increasing exposure to wind-driven physical forces (Cyr, 2020a, 2020b), but the presence of sediments provides a refuge for unattached freshwater mussels (Balfour & Smock, 1995; Schwab & Pusch, 2007; Cyr, 2009). The role of physical forces and disturbances in freshwater ecosystems is understudied compared to marine ecosystems (but see Cyr et al., 2017b and Cyr, 2020b for lakes; Lopez & Vaughn, 2021 for rivers).

Mussel shells record disturbances (Haag & Commens-Carson, 2008; Cyr, 2020b). The manipulation of unionid mussels has long been known to result in the production of disturbance lines in their shells (Coker et al., 1921; Negus, 1966; Haag &

Commens-Carson, 2008). Disturbance lines also appear in wild mussels collected from the field (e.g., Veinott & Cornett, 1996; Cyr, 2020b), suggesting that mussel shells record natural physical disturbances as well. The intensity and characteristics of natural disturbances that result in the production of disturbance lines are not known, although wind-driven waves and thermocline seiche are two probable candidates (Cyr, 2020b). A disturbance line is thought to be produced when a disturbed mussel retracts its mantle, detaching it temporarily from the edge of the shell (Haag & Commens-Carson, 2008). When growth resumes, a dark line is laid down that comes up through the nacreous (interior) layer (e.g., DL in Fig. 2). These “nacreous” disturbance lines have been associated with decreased growth (Haag & Commens-Carson, 2008), although Cyr (2020b) reported increased growth in adult lake mussels exposed to natural physical disturbances.

Another type of internal line which may indicate disturbance are the prismatic lines (intra-shell periostracal layer) described by Checa (2000). The formation of prismatic lines occurs when the mussel reinitiates shell growth following a period of inactivity, and full prismatic lines are a normal part of annual growth lines (Checa, 2000). However, we commonly observe orphan prismatic lines that extend down from the periostracum and partially or fully through the prismatic layer, but contrary to growth lines, do not extend through the nacreous layer (e.g., PL in Fig. 2). It is unknown whether these orphan prismatic lines indicate disturbances.

This research tests how natural physical disturbance affects ecologically important native freshwater mussels, whether the sediments provide an effective refuge for them and what kind of impact natural disturbance has on the early development and growth of young mussels. More specifically, we test whether nacreous and prismatic disturbance lines in *Elliptio complanata* (Lightfoot, 1786) (Eastern *Elliptio*) are (1) more common at wind and wave-exposed compared to sheltered nearshore sites in lakes, (2) limited to growth periods after young adults emerge from the sediments, and (3) associated with anomalous shell growth rates in juveniles and young adults, as reported for adults (Haag & Commens-Carson, 2008; Cyr, 2020b). Mussels have indeterminate growth so factors affecting their early growth can have long-term effects on their populations (Haag, 2012).

We worked with *E. complanata*, a unionid mussel that inhabits a wide variety of substrates in shallow nearshore areas of lakes (Cyr, 2008). This species is locally abundant and widely distributed in lakes and rivers of the Atlantic Slope drainage of North America (Graf & Cummings, 2007). As a result, we can study their growth without having an impact on their population, something that cannot be done with threatened or endangered species.

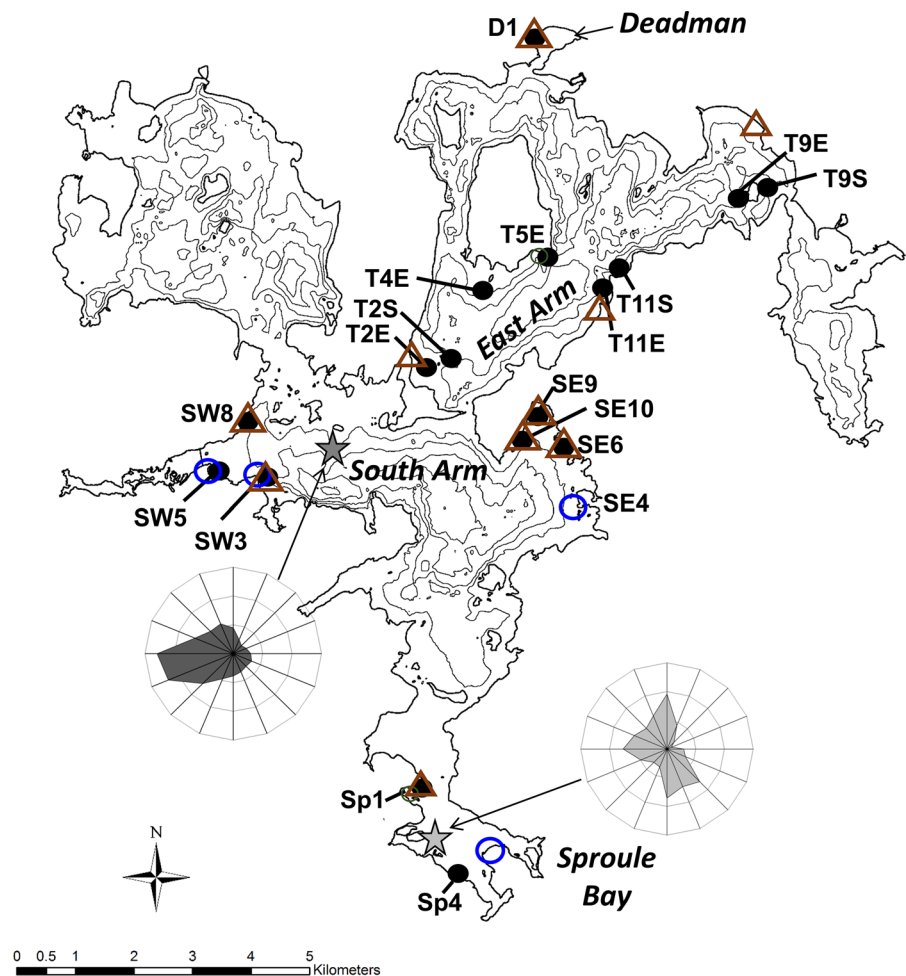
## Methods

### Study site

Lake Opeongo is a multi-basin oligo-mesotrophic lake located in Algonquin Provincial Park on the Canadian Precambrian Shield, Ontario, Canada

(45°42'N, 78°22'W) (Cyr, 2020b). This lake has been protected from human development since the park was established in 1893 (St. Jacques et al., 2005). We sampled nearshore areas in South Arm and East Arm, two large stratified basins of similar size (surface area: 22.1 and 18.1 km<sup>2</sup>, mean depth: 14.6 and 16.3 m, maximum depth: 50 and 44 m, respectively), and in Sproule Bay and Deadman, two small shallow polymictic basins (surface area: 2.1 and 0.3 km<sup>2</sup> respectively, maximum depth: 7 m for both; Fig. 1). Both large basins have an elongated shape with their main axis aligned with the predominant W-SW winds. This allowed us to select nearshore sampling sites exposed to a wide range of wind-generated physical forces (waves, currents) within and across basins. The sediments at our sampling sites ranged with site exposure, from deep fine and organic sediments at sheltered

**Fig. 1** Location of sampling sites in Lake Opeongo, where small mussels (17 sites; black circles), snails (4 sites; open blue circles), and sediments (10 sites; brown open triangles) were collected. Wind rosettes show the proportion of wind blowing from each direction at the South Arm and Sproule Bay weather stations (stars). Depth contours at 10-m intervals



**Table 1** Characteristics of sampling sites and of the mussels collected at each site

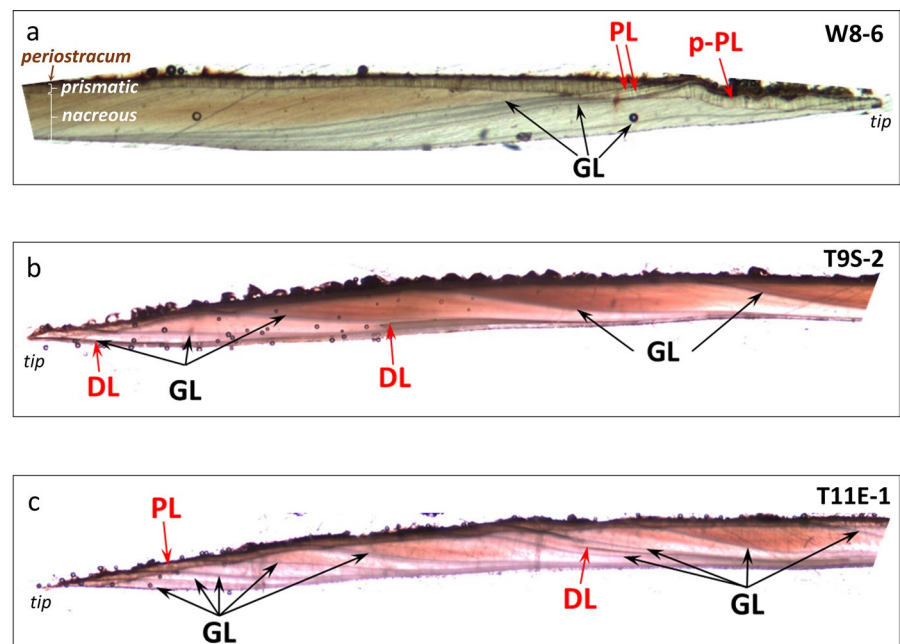
Site	Effective fetch (m)	Sediment depth (cm)	n <sub>mussels</sub>	Mussel TL range (mm)	n <sub>shells</sub>	Range of est. age (years)
<i>East arm</i>						
T2E	487	3	9	46–68 <sup>a</sup>	8	5–14
T2S	392	2	6	48–68 <sup>a</sup>	6	4–8
T4E	1170	3	10	41–63	9	6–11
T5E	913	15	10	23–59	8	3–6
T9E	1441	0	9	50–66 <sup>a</sup>	6	7–36
T9S	94	38	10	27–64	9	4–9
T11E	1500	10	10	33–66	10	2–5, 14
T11S	577	45	10	33–63	9	3–6
<i>South arm</i>						
SW3	428	25	10	27–61	10	4–10
SW5	179	11	10	28–55	10	3–7
SW8	501	10	10	28–56	9	4–9
SE6	1178	22	10	36–60	10	5–6, 37
SE9	600	16	10	32–62	9	3–6, 26
SE10	632	18	10	28–58	8	3–7
<i>Small basins (Sproule Bay, Deadman)</i>						
Sp1	398	18	10	20–60	10	3–12, 26
Sp4	334	55	10	18–63	8	5–9, 16
D1	68	31 <sup>b</sup>	10	24–64	9	5–13
			164	18–68	148	2–37

<sup>a</sup>Could not find smaller mussels despite extensive search

<sup>b</sup>Estimated from sediment organic content (see Methods)

n<sub>mussels</sub> is the number of mussels collected from the sediment surface at each site, TL is total shell length of these mussels, n<sub>shells</sub> is the number of thin shell cross sections analyzed at each site and the estimated (est.) age of these mussels. Sampling sites are ordered by basin and are shown in Fig. 1

**Fig. 2** Thin shell cross sections of young mussels from three different sites: **a** W8-6 (TL = 39.7 mm), **b** T9S-2 (TL = 60.9 mm), **c** T11E-1 (TL = 65.9 mm) showing shell coloration, transition to clear nacre toward the tip, growth lines (GL), nacreous disturbance lines (DL), and prismatic disturbance lines (PL, p-PL is a partial PL at the top of the prismatic layer). The three layers of mussel shells mentioned in the text are identified in (a) periostracum, prismatic layer, and nacreous layer. Full series of annual growth rates for these three mussels are shown in Fig. 3. Location of sampling sites shown in Fig. 1



sites to small pockets of sediments between boulders at very exposed sites (Table 1) (Cyr, 2009; Cyr et al., 2012). Much of the shoreline, including all sampling sites, have sparse or no aquatic vegetation. *Elliptio complanata* is abundant and is the only unionid species in this lake.

### Sampling

Mussels were sampled from 17 shallow nearshore sites (eight sites in East Arm, six in South Arm, two in Sproule Bay and one in Deadman; Table 1, Fig. 1). Mussels were collected between 6 and 10 July 2010, during the peak of *E. complanata* emergence (Matteson, 1948; Cyr, 2009). At each site, a snorkeler swam slowly along the bottom, parallel to shore at 2 m depth to collect all mussels found at the sediment surface. Most mussels were clearly visible, but some mussels were fully buried with only their open siphon visible at the sediment surface. These mussels were brought back to the boat, where their total shell length (TL; longest axis from anterior to posterior end) was measured with calipers. Where possible, we selected 10 small mussels per site (ideally TL < 60 mm) covering as wide a range of (small) sizes as possible. Fewer mussels (6–9) were collected at three rocky sites (T9E, T2E, T2S), where mussels were sparse and where we could only find adult-size mussels despite extensive searches (Table 1).

Sediment depth was measured to quantify the availability of a refuge. These data were originally collected for two different studies (Cyr, 2009; Cyr et al., 2012), using slightly different, but comparable, sampling designs. A diver inserted a 0.8-cm-diameter plastic-coated metal rod as deep as possible into the sediments at 5-m interval along a 30-m transect in East Arm ( $n=7$ ), and at 2-m interval along a 10-m transect in South Arm and Sproule Bay ( $n=5$ ). Where resistance was not felt, sediment depth was recorded as the length of the rod (60 cm; i.e., sediment depth was underestimated). Two divers compared their sediment depth measurements at two sites and were usually within 5–10 cm of each other (median difference = 6.5 cm, range = 0–26 cm). Large differences in measurements could be due to differences in the force applied to the sampling rod by different divers, but also to small-scale variability in sediment structure, including the presence of buried rocks and branches. We calculated geometric mean

sediment depth ( $Z_{seds}$ ) for each site. Deeper sediments are found in sediment accumulation areas and tend to have finer particles and higher organic content than shallow erosional areas (Cyr et al., 2012). Sediment depth was not measured at site D1, so we used our measurements of sediment organic content at that site to predict sediment depth with a model developed in Lake Opeongo that includes sediment data from six sites in Sproule Bay and 20 sites in South Arm (linear regression,  $R^2=0.58$ ,  $P<0.00001$ ).

Site exposure was quantified using effective fetch measurements, which account for the effect of predominant winds (Håkanson & Jansson, 1983). We measured the distance of open water in front of each site (fetch,  $F$ , in m) along eight cardinal directions ( $d$ ). Effective fetch ( $F_{eff}$ ) is then calculated by weighing the distance of open water by the average wind speed (in  $m\ s^{-1}$ ) blowing from each cardinal direction ( $w_d$ ):

$$F_{eff} = \frac{\sum_d (F_d \times w_d)}{\sum_d w_d}$$

Winds were measured at weather stations maintained by the Ontario Ministry of Natural Resources and Fisheries (OMNRF; stars in Fig. 1). We used wind data collected on South Arm from May–October 2001–2009 (10 min intervals) to calculate fetch in South Arm, East Arm, and Deadman. Winds measured in Sproule Bay over two summers (May–October 2003, 2005) were used for that basin.

### Processing of mussel shells

Thin shell sections were prepared as explained in Cyr (2020a). Internal growth lines were identified as those extending from the periostracum to the base of the nacreous layer (GL in Fig. 2). These are considered annual growth lines based on  $\delta^{18}O$  profiles in Lake Opeongo mussels (Cyr, 2020a). Annual growth was measured as the curved distance along the shell surface between successive growth lines measured at 20X magnification with an image analysis software (Infinity Analyze 6.5, Teledyne Lumenera, Ottawa, Canada).

We also identified two types of disturbance lines: nacreous disturbance lines (DL) and prismatic lines (PL). DL are dark lines coming up through the nacre that often do not reach the top of the nacreous layer

(Veinott & Cornett, 1996; Haag & Commens-Carson, 2008) (Fig. 2b–c). Dark lines closely associated and merging with a (light) growth line were also considered nacreous disturbance lines (e.g., DL close to the tip in Fig. 2b; Cyr 2020a, b). PL are short and usually light lines coming down from the periostracum that run partially or fully through the prismatic layer and occasionally extend into the top of the nacreous layer, as described by Checa (2000; Fig. 2a, c). We identified and counted both types of disturbance lines in thin shell sections over as many growth periods as possible.

### Emergence of young mussels from the sediments

We used two indicators to estimate when young mussels emerged from the sediments. First, we measured the  $\delta^{15}\text{N}$  signature of all mussels to test whether their  $\delta^{15}\text{N}$  signature shifts with increasing body size. Cyr (2020a) showed that endobenthic mussels (in one of the basins studied here) have a more depleted  $\delta^{15}\text{N}$  signature than (larger) mussels collected on the sediment surface. Sediment  $\delta^{15}\text{N}$  becomes more depleted with increasing sediment depth (Kohzu et al., 2011) and provides an interesting tracer of endobenthic life. All (small) mussels in the present study were collected from the sediment surface, but it takes time for the isotopic signature of an organism to shift depending on the turnover rate of their tissues (Vander Zanden et al., 2015). Therefore, we expect recent emergence to be reflected in a mussel's isotopic signature.

The second indicator of emergence is the internal shell coloration observed in the earliest years of mussel growth that disappears in later years as their growth drops to low adult growth rates (Fig. 2). We noticed a more or less sudden shift in shell coloration in the hundreds of shell cross sections analyzed in previous studies. In this study, we determined visually the last year of shell coloration in as many mussel cross sections as possible. We did not attempt to quantify the intensity of coloration since it varies with thickness and quality of the shell cross sections.

### Isotopic signatures

The mantle tissues from each mussel were dissected, dried, and prepared for stable isotope analysis ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) (Cyr, 2020a). We also used tissue samples from previous studies for comparison: whole body mussel samples collected on 28–29 September 2004 at four sites in South Arm (Griffiths & Cyr, 2006) and mantle tissue samples collected on 6 June and 26–27 September 2006 at sites Sp1 and Sp4 in Sproule Bay (Cyr, 2020a).

Baseline isotopic signatures were measured from plankton, benthic primary consumers (snails), and sediments (Cyr et al., 2017a). Offshore plankton were collected with four to five vertical tows of a 100  $\mu\text{m}$  Wisconsin net through the epilimnion and metalimnion of South Arm, East Arm, and Sproule Bay on two dates (16–17 June, 22–23 July 2009). We have no plankton baseline data from Deadman. For comparison, we also used plankton samples collected at two South Arm offshore sites on 29 September 2004 (Griffiths & Cyr, 2006) and on 5 July and 26 September 2006 in Sproule Bay and South Arm (Cyr, 2020a).

Herbivorous snails were collected from nearshore sites (~2 m depth) in Sproule Bay in early July 2006 (*Physella*, *Gyraulus*) and in South Arm on 21 July 2009 (*Helisoma*; open blue circles in Fig. 1). We have no benthic baseline data from East Arm or Deadman. The snails were left at least 30 min in lake water to clear their gut, dried at 60 °C, and the soft body of three individuals per site was analyzed separately after removing their shell and operculum.

Sediments were collected at five of our sampling sites in South Arm (SW3, SW8, SE6, SE9, SE10) and at site Sp1 in Sproule Bay during summer 2006, and at three sites in East Arm and at site D1 in Deadman during summer 2009 (open triangles in Fig. 1). Sediment samples were collected with handheld Lexan corers (5.6 cm internal diameter) and the surface 1 cm was extruded with a piston. In East Arm, samples of the top 5 cm of sediments were also collected at two sites for comparison. The sediments were wet-sieved and the isotope signature of the finest (most organic) size fraction analyzed (<63  $\mu\text{m}$  in South Arm, Sproule Bay and Deadman; <110  $\mu\text{m}$  in East Arm).

All samples for isotopic analysis were dried at 60 °C for at least 24 h, ground to powder with

mortar and pestle, and analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. Average precision (median standard error) of replicates is 0.09‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $n = 41$ ).

### Statistical analyses

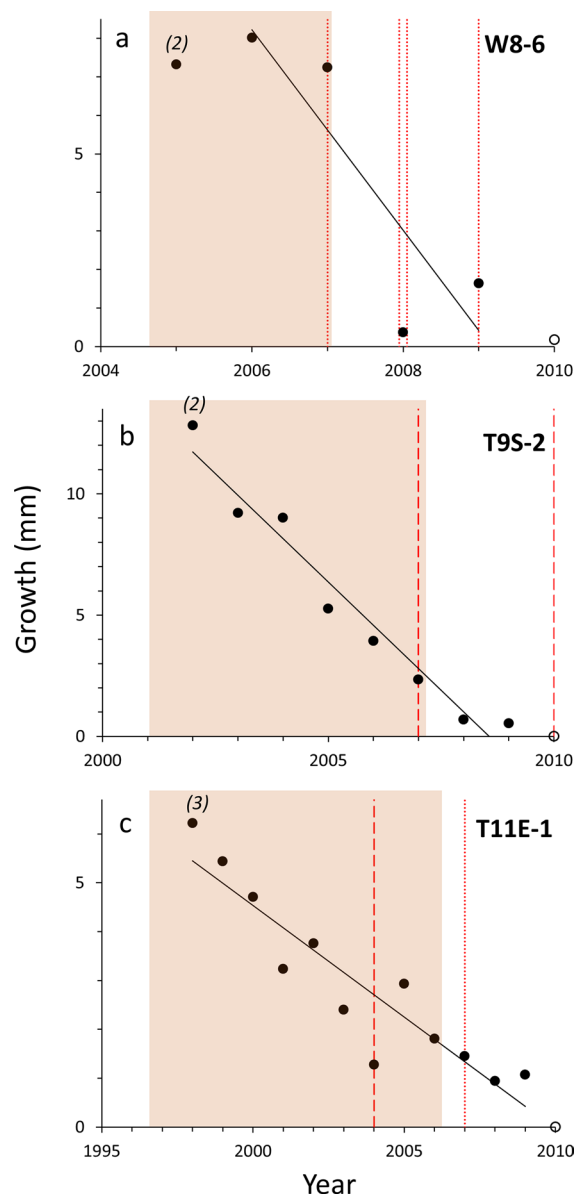
We used simple linear regression analysis to test for relationships between  $\delta^{15}\text{N}$  and shell size (TL) at each of our 17 sampling sites.  $P$  values were corrected for multiple comparisons using False Discovery Rate (FDR; Benjamini & Hochberg, 1995).

We tested whether disturbance lines (DL, PL) occurred equally in colored and clear growth periods using ANOVA. This analysis was restricted to mussel shells that contained disturbance lines. We used linear mixed-effect models (Zuur et al., 2009) in the *nlme* package in R (Pinheiro et al., 2019) to compare the proportion of growth periods in individual mussels that had disturbance lines in colored vs clear growth periods (fixed factor). Heteroscedasticity in the data was accounted for where appropriate by adding a random effect term in the model (Zuur et al., 2009).

Our first main objective was to determine whether nacreous/prismatic disturbance lines were more common at more exposed study sites. To address this question, we calculated disturbance line density in each mussel by dividing the number of disturbance lines counted by the number of annual growth periods visible, and averaged across all mussels from a given sampling site. We then used Generalized Additive modeling (GAM, Zuur et al. 2009) to test for a relationship between mean disturbance line density ( $D_{DL/PL}$ ) and site exposure (2 measures:  $Z_{seds}$  is sediment depth in cm,  $F_{eff}$  effective fetch in km) in different basins (3 categories: small basins, South Arm, East Arm) with the following model:

$$D_{DL/PL} = s(Z_{seds}) + aF_{eff} + b\text{Basin} + c[F_{eff} \times \text{Basin}] \quad (1)$$

In this model, we test for a non-linear relationship with  $Z_{seds}$  without imposing a particular shape to this relationship (fitted with a thin plate regression spline,  $s$ ).  $a$ - $c$  are fitted parametric coefficients for the other variables and their interaction. We fitted the model with maximum likelihood and removed variables sequentially using the highest Akaike's Information Criterion (AIC; Burnham & Anderson, 2002).



**Fig. 3** Time series of annual growth rates for the three young mussels shown in Fig. 2: **a** W8-6 (TL=39.7 mm), **b** T9S-2 (TL=60.9 mm), **c** T11E-1 (TL=65.9 mm). Solid black lines are modeled trends in growth used to calculate growth anomalies. Note that these trends span from the earliest maximum growth and do not include data from the partial 2010 growth period (open circles). Red vertical lines are nacreous disturbance lines (DL, dashed) and prismatic disturbance lines (PL, dotted) observed during these growth periods. Shading indicates growth periods with shell coloration. In panel (a), the double red lines in 2008 means there were two PL during that growth period (see Fig. 2a). Numbers in parentheses are estimated ages during the first measurable growth period in each shell. Figure 2 shows the most recent portions of thin shell cross sections (i.e., from the tip) for these mussels

We then used restricted maximum likelihood estimate to calculate all fitted coefficients in the final (optimal) model (Zuur et al., 2009). The analysis was done using the *mgcv* Package (Wood, 2022) in R.

Our second main objective was to determine whether the presence of disturbance lines (DL, PL) in a growth period was associated with growth anomalies. Growth anomalies were calculated by fitting a linear or exponential model (best fit) through the time series of growth measured in each mussel, from the earliest growth period with maximum growth to the most recent full growth period (i.e., excluding 2010; Fig. 3). In old mussels (age = 14–37,  $n = 5$ ), we excluded all growth periods after the mussel reached low adult growth rates (< 1 mm). Trends were only fitted in mussels with at least three growth periods matching these restrictions. Growth anomalies were calculated as the difference between the observed growth in each growth period and the trend line. We then used a nested analysis of variance (ANOVA) to compare growth anomalies in periods with and without disturbance lines. This was done using Generalized Linear Mixed modeling (GLMM) and was restricted to mussels with at least one disturbance line. As a result, some sites were excluded entirely from the analysis (sites SE9, SE10, SW5, T11S excluded from DL analysis). The GLMM was fitted with the *nlme* package in R, with growth anomaly in each growth period (described above) as the independent variable, the presence/absence of disturbance lines as a fixed factor, and sampling site (13 sites for DL, 17 sites for PL) and basin (3 levels: small basins, South Arm, East Arm) as random factors to account for the hierarchical structure of the data. Heteroscedasticity in the data was accounted for by adding random effects in the model (Zuur et al., 2009).

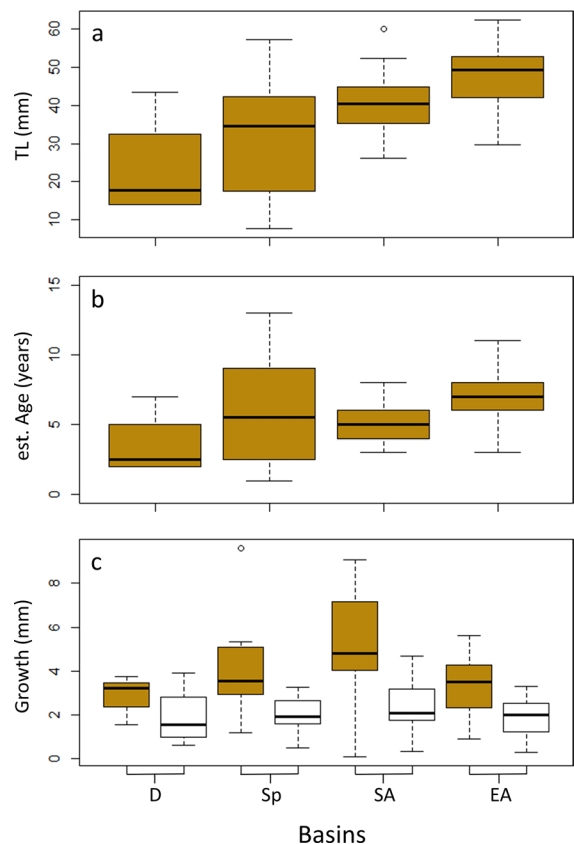
## Results

We collected as wide a range of juvenile and young adult-size mussels (< 60 mm TL) at each site, except for three rocky sites in East Arm (T9E, T2E, T2S) where we could not find mussels smaller than 45–50 mm (Table 1). Internal growth lines confirmed that most mussels were young (Table 1) and

were still growing faster than adults in this lake (Cyr, 2020b; ~ 70% of mussels with > 2 mm growth in the last growth period before sampling). Eggs were found in the gills of four (out of 164) mussels, all of whom were larger than 50 mm (TL).

### Internal shell coloration in early growth periods

All shell cross sections that could be analyzed, except one, showed some internal coloration, and more than half showed coloration throughout the shell up until they were sampled in 2010 (80 of 148 mussels; TL = 24–68 mm, est. age = 2–13 years). In the other mussels, we typically observed translucent



**Fig. 4** Boxplots showing shell size (TL, total shell length) during the last colored growth period, estimated age during the last colored growth period and growth during the last colored growth period (brown shading) and the first clear growth period (white) in mussels from each basin. Boxplots show median (thick line), 25<sup>th</sup>–75<sup>th</sup> percentiles (box), minimum and maximum without outliers (whiskers) and outliers (open circles, > 1.5 × interquartile range). D: Deadman, Sp: Sproule Bay, SA: South Arm, EA: East Arm



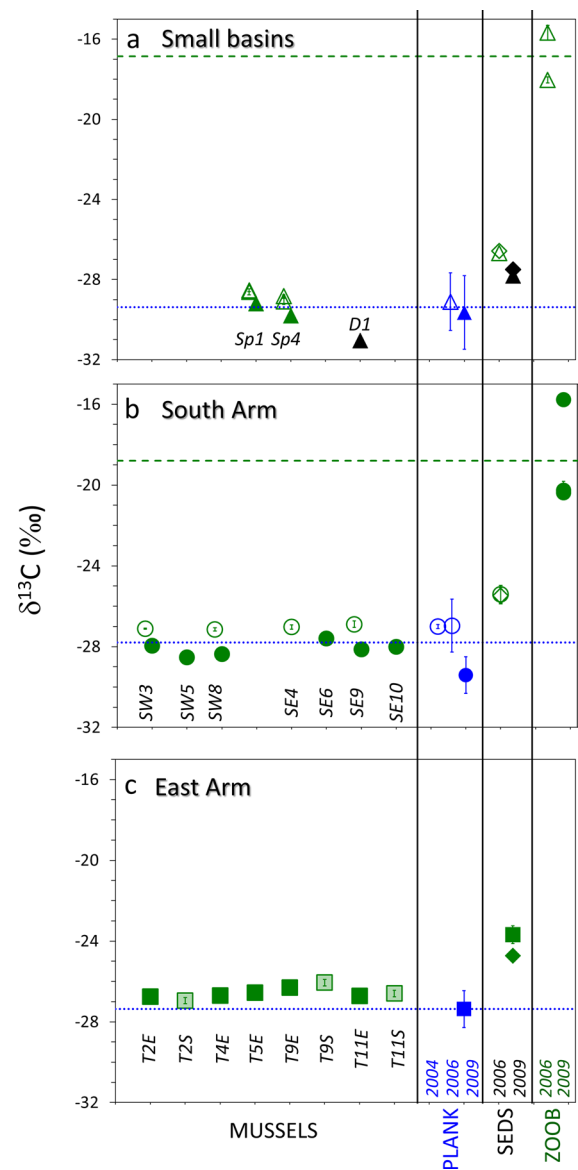
brown shell coloration during early growth periods with a more or less sharp transition to clear shell cross sections in more recent growth periods (Fig. 2). This transition occurred as growth declined from high juvenile to low adult growth rates (Figs. 3, 4c), in mussels with median shell length 20–50 mm (Fig. 4a) that were on average 2–7 years old (Fig. 4b).

Shell coloration also varied within individual growth periods, usually starting with clear nacre secreted in the lower nacreous layer below the previous year's growth, followed by fully colored nacre later in the growth period (e.g., Fig. 2b). A few mussels showed more complex banding patterns in some growth periods but these were all recorded as “colored.”

### Isotopic signatures

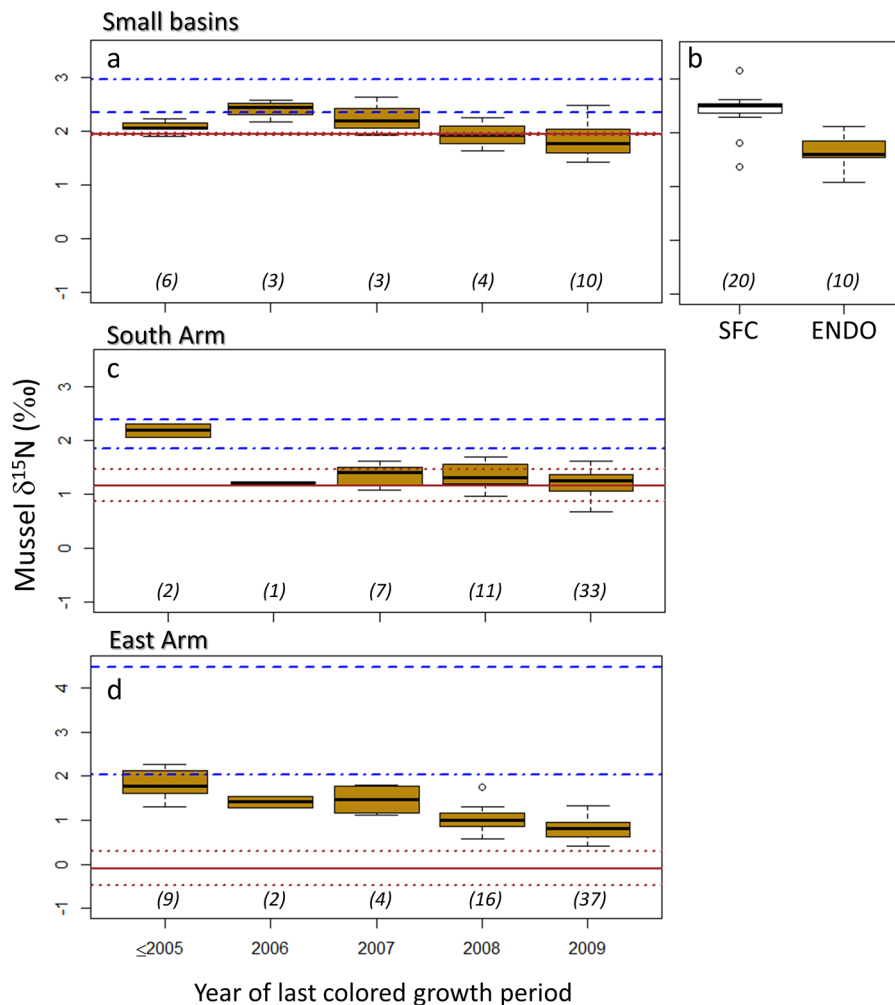
The mussels within each lake basin had very similar  $\delta^{13}\text{C}$  signatures, both between individuals at a given site (small error bars) and between sites (Fig. 5). The  $\delta^{13}\text{C}$  signatures of mussels were most similar to those of plankton, slightly more depleted than sediments and much more depleted than benthic primary consumers (snails; Fig. 5). Mean mussel  $\delta^{13}\text{C}$  signature was more enriched in the two large basins ( $-26.6\text{‰} \pm 0.1$  in East Arm, Fig. 5c;  $-28.1\text{‰} \pm 0.1$  in South Arm, Fig. 5b) compared to the two small basins ( $-29.5\text{‰} \pm 0.3$  in Sproule Bay,  $-31.0\text{‰}$  in Deadman; Fig. 5a), as observed in zooplankton across lakes of different sizes (Post, 2002).

Mussel  $\delta^{15}\text{N}$  signatures were not related to their shell length (regressions by site, all FDR-corrected  $P > 0.4$ ), but varied with internal shell coloration (Fig. 6). Mussels with their most recent full growth period (2009) showing internal coloration had the most depleted  $\delta^{15}\text{N}$  signature, most similar to  $\delta^{15}\text{N}$  in the sediments (Fig. 6a, c–d). Mussel  $\delta^{15}\text{N}$  signatures increased with increasing time since their last colored growth period, and mussels with more than three to four recent clear growth periods reached the  $\delta^{15}\text{N}$  signature of plankton. These changes are consistent with the difference in  $\delta^{15}\text{N}$  measured between endobenthic and epibenthic mussels collected in Sproule Bay in 2006 (Fig. 6b).



**Fig. 5** Comparison of the  $\delta^{13}\text{C}$  signature of mussels at each sampling site with plankton (PLANK), sediments (SEDS), and benthic primary consumers (snails; ZOOB) in **a** small basins (Sproule Bay in green, Deadman in black; PLANK and ZOOB data for Sproule Bay only), **b** South Arm and **c** East Arm (no ZOOB data). Shaded symbols are 2010 (mussels) and 2009 (PLANK, ZOOB) samples; open symbols are as follows: **a** 2006 samples, **b** 2004 (mussels), and 2006 (PLANK, SEDS) samples. Sieved surface sediments (top 1 cm; **a–b**  $< 63\ \mu\text{m}$ , **c**  $< 110\ \mu\text{m}$ ) are shown on the left, other fractions on the right (**a–b** coarser  $63\text{--}125\ \mu\text{m}$  fraction; **c** top 5 cm,  $< 110\ \mu\text{m}$ ). Error bars are  $\pm$  standard errors, most smaller than the symbols. Horizontal reference lines for PLANK (blue dotted) and ZOOB (green dashed) signatures. Location of sampling sites is shown in Fig. 1

**Fig. 6** Boxplots comparing the  $\delta^{15}\text{N}$  signature of mussels with their last colored growth period observed in different years prior to sampling in: **a** small basins (Sproule Bay, Deadman), **c** South Arm and **d** East Arm. Panel **b** shows 2006 data from surface (SFC) and endobenthic (ENDO) mussels collected at Sp1 and Sp4. Horizontal reference lines for plankton (blue dash for June, dash-dot for July) and sediments (brown; solid line for mean  $\pm$  dotted lines for standard error). Boxplots as in Fig. 4. Number of samples shown in parentheses

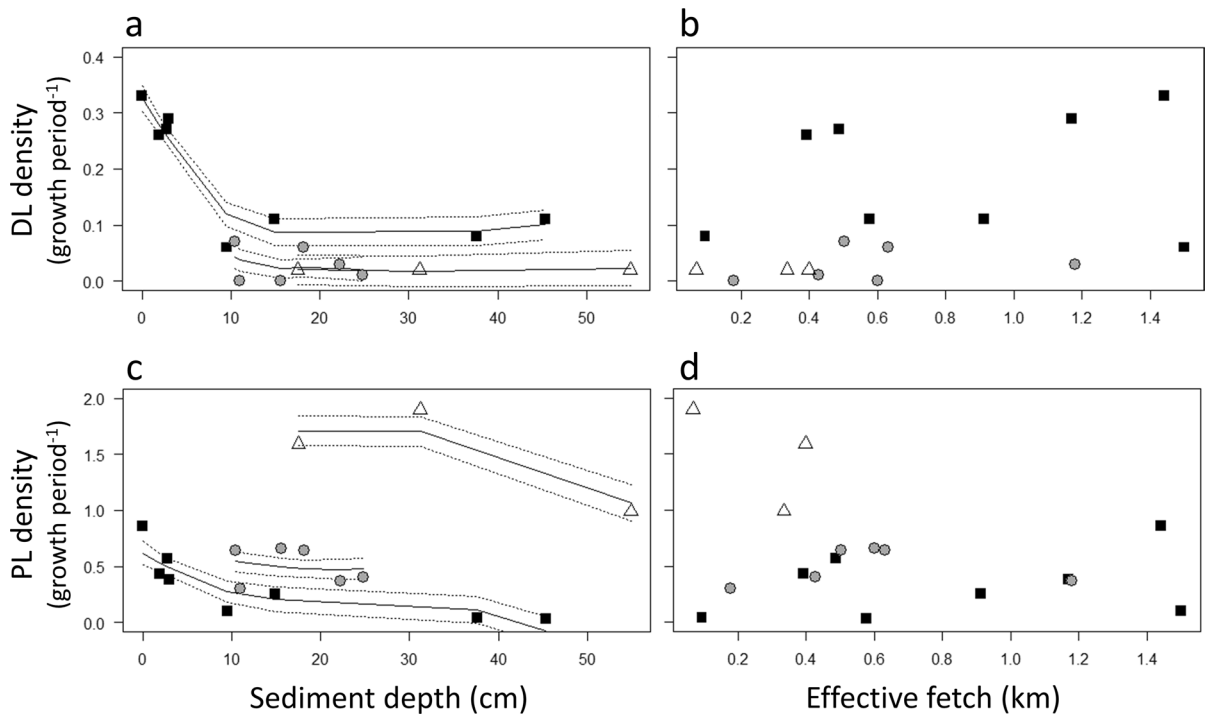


### Disturbance lines

Both types of disturbance lines (DL, PL) were equally common in the colored and clear portion of small mussel shells. Nacreous disturbance lines (DL) were present in 25% of the (early) colored growth periods and in 27% of the (late) clear growth periods per mussel, on average (ANOVA,  $P > 0.1$ ;  $n = 43$  and 28 mussels with colored and light growth periods, respectively), and there was rarely more than one DL per growth period. Prismatic disturbance lines (PL) were found in 50% of the colored growth periods and in 62% of the clear growth periods per mussel, on average (ANOVA,  $P > 0.09$ ;  $n = 84$  and 44 mussels, respectively) and there were often multiple PL per growth period. This suggests that disturbance lines are produced during early growth periods when the

mussels were presumably spending most of their time in the sediments.

Mussels at different sites had an average (mean) of 0 to 0.3 DL per growth period (Fig. 7a, b). DL density declined non-linearly with sediment depth (Fig. 7a), but was not significantly related to effective fetch (GAM model,  $P > 0.6$ ; Fig. 7b, Table 2). The non-linear relationship with sediment depth could be interpreted as a threshold, where mussels at sites with very little fine sediments ( $\leq 3$  cm) have three times as many disturbance lines as mussels with access to deep sediments ( $> 10$  cm; Fig. 7a). Interestingly, the four sites with  $\leq 3$  cm of fine sediments are the only ones located on small islands and DL density at these four sites appears to increase with increasing effective fetch (high points in Fig. 7b).



**Fig. 7** Relationships between mean number of disturbance lines per growth period and two measures of nearshore site exposure: sediment depth (left panels) and effective fetch (right panels). Top panels for nacreous disturbance lines (DL), bottom panels for prismatic disturbance lines (PL). Each point is mean number of disturbance lines per growth period in mus-

sels from one site ( $n_{\text{shells}}$  listed in Table 1) and different symbols identify the basin (filled squares: East Arm, shaded circles: South Arm, open triangles: small basins). Panels **a**, **c** solid lines ( $\pm$  standard error) are fitted GAM models (Table 2). Panels **b**, **d** no significant relationship with effective fetch

Prismatic disturbance lines (PL) were much more common than DL, and were also related non-linearly to sediment depth (Fig. 7c), but not to effective fetch (Fig. 7d, Table 2). Interestingly, PL density was much higher in the two small lake basins (open triangles in Fig. 7) compared to the large basins.

Contrary to expectations, the presence of disturbance lines (DL, PL) did not affect growth in a systematic way. Growth anomalies during periods with disturbance lines showed no significant difference compared to growth periods without disturbance lines (hierarchical ANOVA,  $p \geq 0.5$  for DL and PL; Fig. 8). We found no evidence that the presence of disturbance lines in juvenile and young adult mussels is related to stunted or enhanced shell growth.

## Discussion

### Sediments as habitat

Our data clearly show that juveniles spend many years in the sediments and that there is variability in the size and age at which they emerge from the sediments (Fig. 4). Juvenile mussels in Lake Opeongo lay down colored nacreous material during early growth periods, which likely reflect high organic content in surrounding sediment porewater. We confirmed that shell coloration is consistent with changes in the  $\delta^{15}\text{N}$  signature of their soft bodies. Juveniles with fully colored shells had  $\delta^{15}\text{N}$  signatures similar to the sediments and to endobenthic mussels, whereas young mussels who laid down clear shell material over the last three to four growth periods had  $\delta^{15}\text{N}$  signatures progressively approaching that of plankton (Fig. 6). Given the rapid growth of juveniles, we expect the nitrogen in mantle tissues to turn over rapidly (Dubois

**Table 2** Best General Additive Mixed models describing the relationships between disturbance line density ( $D_{DL}$  for nacreous,  $D_{PL}$  for prismatic), site exposure (effective fetch,  $F_{eff}$  in m), and sediment depth ( $Z_{seds}$ , in cm) in different basins (East Arm as baseline, South Arm: SA, small basins: small; model 1 in text)

	Coefficients	Variables	Partial $P$ -value	Adj. $R^2$	$n$
$D_{DL}$	$0.14 \pm 0.02$	intercept	0.00001	0.91	17
	$-0.06 \pm 0.03$	BASIN (SA)	0.04		
	$-0.07 \pm 0.03$	BASIN (small)	0.07		
	–	$s(Z_{seds})$	0.0001		
$D_{PL}$	$0.23 \pm 0.08$	intercept	0.01	0.88	17
	$0.3 \pm 0.1$	BASIN (SA)	0.047		
	$1.5 \pm 0.2$	BASIN (small)	<0.00001		
	–	$s(Z_{seds})$	0.006		

Smoothing functions for sediment depth,  $s(Z_{seds})$ , are fitted splines without parametric coefficients (–) and with approximate partial  $P$  values (Zuur et al., 2009); their non-linear shapes are plotted in Fig. 7. Effective fetch was not significant (partial  $P > 0.6$ ; Fig. 7b, d) and was dropped from the final models

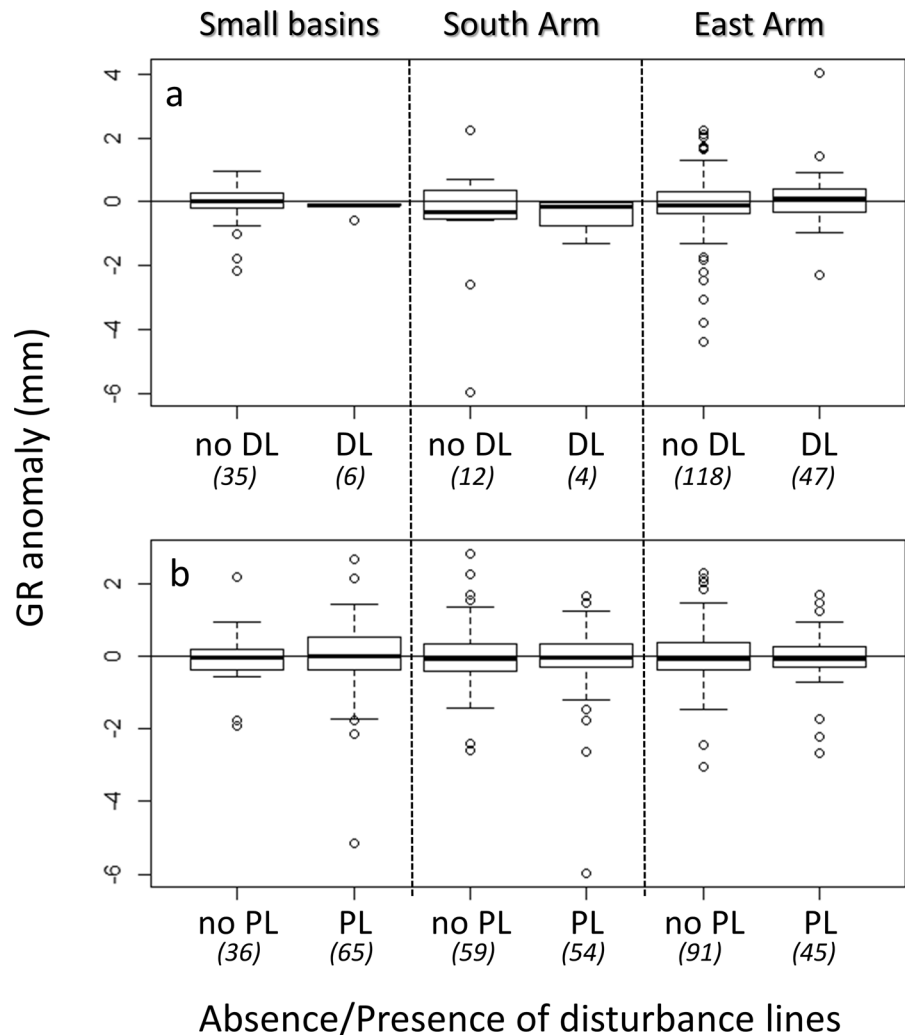
et al., 2007; Kasai et al., 2016). Therefore, the slow (multi-year) change in juvenile  $\delta^{15}N$  signature we observed after they emerge from the sediments (i.e., time since last colored growth period) is likely due to a slow change from deposit feeding in the sediments to full suspension feeding on plankton (Araujo et al., 2018; Lavictoire et al., 2018). Using shell coloration as an indicator of habitat, we determine that juvenile *E. complanata* emerge from the sediments when they are on average (median) about 20–50 mm (TL) in size and approximately 2.5–7 years old. These results are consistent with independent estimates of shell size when mussels first emerge from the sediments (30–50 mm; Cyr, 2020a) and when they mature (45–50 mm; Downing et al., 1993; H. Cyr pers. obs.). Matteson (1948) also reported maturation “at least as early as the end of the third growing season.”

The isotopic data show that while in the sediments, juvenile and young adult mussels feed on material of planktonic origin, either directly from the water column or by selective feeding in the sediments. The  $\delta^{13}C$  signature of small mussels was most similar to plankton  $\delta^{13}C$ , with very little variability across a range of body sizes and between sampling sites in each basin (Fig. 5). Small mussel  $\delta^{13}C$

signatures were also more depleted than the  $\delta^{13}C$  signature of the sediments where they feed. Juvenile mussels have the capacity to feed selectively (Beck & Neves, 2003; Fung & Ackerman, 2020) allowing them to use higher quality material (e.g., algae) needed for growth (Gatenby et al., 1997). Cyr (2020a) also reported that small endobenthic mussels feed on material of planktonic origin and our results here extend this finding from one shallow lake basin (Sproule Bay) to nearshore areas across lake basins of different sizes. This result is also consistent with findings of higher concentrations of planktonic algae in river sediments compared to the overlying water column, particularly in depositional areas (e.g., behind boulders), which resulted in efficient feeding by endobenthic juvenile mussels (Fung & Ackerman, 2020).

Our data also suggest changes in shell coloration over the growing season. The growth periods we labeled as “colored” were rarely uniform in color. The most common pattern of coloration was clear nacre laid down early in the growth period in the lower portion of the nacreous layer, which darkened through the growth period (Fig. 2b). Other banding patterns were observed (e.g., clear-dark-clear, dark-clear), but were relatively rare. Assuming that shell coloration is due to colored dissolved organic matter (CDOM) in surrounding sediment porewater, there are several possible explanations for this seasonal change in shell coloration. One possibility is seasonal changes in CDOM concentration in the sediment porewater, due to seasonal changes in organic matter inputs and degradation (microbial, photochemical; Clark et al., 2014) or to water exchange between sediment porewater and the overlying water column. Water exchange is most likely in coarse permeable sediments (Rocha, 2000; Janssen et al., 2005) but was not detected in the shallow nearshore sediments of Lake Opeongo (Cyr, 2012). We did not measure CDOM, but we expect seasonal changes in porewater CDOM concentration to produce similar shell coloration patterns in all buried mussels, whereas in any given year, we observed mussels with different coloration patterns, casting doubt on this explanation. A second possible explanation is that endobenthic mussels move to different depths in the sediments at different times of the year. Juveniles are usually found in the upper few mm-cm of sediments, but they are quite motile and can quickly position themselves vertically

**Fig. 8** Comparison of Growth Rate (GR) anomalies between growth periods with or without **a** nacreous (DL) and **b** prismatic (PL) disturbance lines in different basins. There are no significant differences for either type of disturbance lines (hierarchical ANOVA,  $P \geq 0.5$ ). Number of growth periods included in each category is shown in parentheses. Box plots as in Fig. 4



in the sediments in response to oxygen and surface disturbances (Sparks & Strayer, 1998; Bílý et al., 2021; Hyvärinen et al., 2021). Seasonal patterns of vertical migration are known in adults (Amyot & Downing, 1997; Cyr, 2009), but not in juveniles (Bílý et al., 2021). A third possible explanation is seasonality in juvenile growth rate, with “dilution” of CDOM during periods of rapid growth resulting in lighter shell color. Interestingly, Negishi & Kayaba (2010) reported earlier initiation of growth in young mussels compared to adults, with high growth rates early in the growing season followed by lower growth. It is unclear whether the changes in shell coloration we observed indicate seasonal shifts in environmental conditions within the sediments or in juvenile growth.

#### Sediment refuge and disturbance lines

We found that nacreous (DL) and prismatic (PL) lines both become more abundant at exposed nearshore sites with little or no sediment refuge ( $Z_{\text{seds}} < 2\text{--}3$  cm). Mussels in sediments deeper than  $\sim 9$  cm had low DL density, and given that the mussels we sampled were less than 7 cm in length, this allowed them to entirely bury themselves in the substrate. This supports the hypothesis that DL and PL are both indicators of natural physical disturbances and that nearshore sediments provide a refuge against physical disturbances. Interestingly, we observed both types of disturbance lines in growth periods with a colored nacreous layer, when juveniles presumably spend most of their time

buried in the sediments. Moreover, the density of DL we measured in juveniles and young adults was similar to that observed in adults (0.1–0.4 DL per growth period, Cyr 2020b), who spend a lot more time above the sediment surface. Juvenile and adult mussels have both been observed to bury quickly (within minutes) when exposed to stressful conditions (Schwalb & Pusch, 2007; Cyr, 2009; Kemble et al., 2020), so sediments provide a refuge for mussels throughout their life. The existence of disturbance lines in young juveniles suggests that the sediments are an effective but imperfect refuge from natural disturbances.

Prismatic (PL) disturbance lines are much more abundant than nacreous (DL) disturbance lines, but were related in a similar non-linear fashion to sediment depth (Fig. 7a, c), suggesting PL are formed under more benign conditions than DL. However, PL were much more abundant in the small relatively sheltered basins than in the large basins, so natural physical disturbances cannot be the only cause for their formation. Several authors have suggested that direct interactions could be stressful at high mussel densities (e.g., competition for food, interference competition; Peterson, 1982; Allen & Vaughn, 2009). In lakes, mussel density varies in a unimodal fashion with depth of the water column and mussels reach maximum density at greater depths in larger lake basins (Cyr, 2008; Cyr et al., 2017b). At our 2-m sampling depth, mussel density in the two small basins (Sproule Bay and Deadman; mean density = 73 mussels  $m^{-2}$ , range = 59–82) was more than an order of magnitude higher than in South Arm (mean = 3.6 mussels  $m^{-2}$ , range = 0.4–6.1), and more than two orders of magnitude higher than in East Arm (mean = 0.5 mussels  $m^{-2}$ , range = 0.07–1.1; early July data from Cyr, 2009; Cyr et al., 2012 and unpublished). We hypothesize that benign physical disturbances in small lake basins and direct interactions between mussels at high densities are not as disruptive as natural physical disturbance at exposed sites in large basins that cause nacreous disturbance lines (DL). Mussels in small basins would experience frequent partial mantle retractions producing prismatic lines (PL), but few full mantle retractions producing nacreous disturbance lines (DL).

## Disturbance and mussel growth

The distribution and growth of juvenile and of adult *E. complanata* in shallow nearshore areas of lakes are related to wind exposure (fetch) and to sediment characteristics (Cyr et al., 2012; Cyr, 2020a, b). Mussels are more abundant and grow faster at more sheltered shallow nearshore sites, but also at wind-exposed sites with fine sediments. So mussel growth in nearshore areas of lakes is limited by wind-driven physical forces, but it is unclear whether this is a direct effect of physical disturbances or is indirectly related to other factors.

The presence of disturbance lines is usually thought to indicate lower shell growth. Disturbance lines are produced after a mussel is exposed to stressful conditions that cause the mantle to retract and detach from the edge of the shell and results in temporary cessation of growth. If growth stops for long enough and cannot be compensated over the remaining growth period, these disturbances will result in lower annual growth. This was confirmed by Haag & Commens-Carson (2008) who found slightly lower growth in mussels that were handled and marked with small notches carved into the shell, and who produced disturbance lines. In contrast, Cyr (2020b) found that the presence of disturbance lines (DL) in adults exposed to natural physical disturbances was related to higher, not lower, growth. Mussels quickly respond to stressful conditions by burying into the sediments but also resume their activities soon after these events (Neves & Moyer, 1988, H. Cyr pers. obs.), so under natural conditions we would expect them to easily compensate for short periods of inactivity. However, adults living at exposed nearshore sites have shorter periods of activity over the growing season than those at sheltered sites (Cyr, 2009), and mussels who remain active longer at these exposed sites would acquire more food and grow better but also increase the risk of being exposed to stressful events. In the present study, we find that juveniles and young adults produce disturbance lines but these have no detectable effect on annual growth, suggesting that small mussels compensate for temporary cessation of growth. Juveniles may also be more plastic than adults in their tolerance to stress (Gleason et al., 2018).

We found no evidence that natural disturbances have a negative impact on the growth of juvenile

and small adult mussels in shallow nearshore areas of small to intermediate-size lakes. It is unclear how these results extend to mussels living in more dynamic benthic environments, such as streams and rivers. In highly dynamic marine intertidal areas, mussels and clams grow better at wave-exposed than at sheltered sites, in large part due to higher food influx (Grizzle & Morin, 1989; Menge et al., 1997). Native freshwater mussels are usually unattached to their substrate, meaning that accumulated sediments in shallow nearshore areas of lakes, and possibly in flow refuges of streams and rivers (Strayer, 1999), provide an important, but imperfect refuge from natural physical disturbances. Given that previous studies have also found nearshore fine sediments can host high juvenile mussel densities and growth even in areas highly exposed to natural physical disturbance (Cyr et al., 2012; Cyr, 2020a), it is clear that these zones of sediment accumulation warrant protection. The expansion of land development prohibitions, which has already been proposed in the EU to preserve the habitat of endangered riparian freshwater mussels (Dobler et al., 2019), is one option worthy of further investigation. Action to preserve these zones is all the more necessary given that these important areas for benthic organisms are directly exposed to nearshore industrial and recreational development, and are impacted by large-scale anthropogenic and climate-related hydrological changes (Pip, 2006; Strayer & Dudgeon, 2010; O'Neill & Thorp, 2011).

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**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors have no financial or proprietary interests in any material discussed in this article.

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