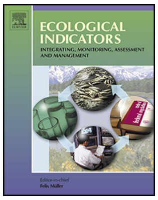
Ecological Indicators 60 (2016) 248–257

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



The influence of watershed land use cover on stream fish diversity and size-at-age of a generalist fish

R. Filgueira[a,*,1], J.M. Chapman[b,**,1], C.D. Suski[c], S.J. Cooke[b]

[a] Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB, Canada
[b] Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON, Canada
[c] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 S. Goodwin Ave., Urbana, IL, United States

ARTICLE INFO

Article history:
Received 25 January 2015
Received in revised form 4 June 2015
Accepted 6 June 2015

Keywords:
Size-at-age
Diversity
Land use
DEB
Umbra limi

ABSTRACT

Changes in land use have manifold effects on stream ecosystems. Consequently, the degradation of watersheds can cause extreme responses if the resilience of the stream is exceeded, triggering changes in fish communities and a reorganization of the ecosystem. Fish community surveys are frequently used to evaluate the impact of anthropogenic pressures on freshwater streams. Dynamic indices such as individual growth are also interesting because they integrate the effects of environmental conditions through time, providing an assessment in the long term. In this study we have investigated the ecological implications of watershed land use cover on fish diversity and growth of the generalist species *Umbra limi* (central mudminnow) in six streams in Southern Ontario (Canada). In detail, the growth of *U. limi* has been explored using a Dynamic Energy Budget (DEB) model, which pursues a mechanistic explanation of the bioenergetics of an individual under different environmental conditions. Given the mechanistic approach, the outcomes of the DEB model can provide a solid foundation for extrapolating the conclusions of this study to a broader spatial scale. The results of this study reveal that the proportion of modified land use of the watershed (agricultural and urban land) can reach a tipping point beyond which the functioning of the stream abruptly changes. Consequently, land use cover may be used as a precautionary indicator for watershed management. The results also demonstrate that *U. limi* could be used as a sentinel species to identify potential impacts on fish diversity and size-at-age as a cost-effective indicator for stream monitoring programs.

1. Introduction

Freshwater resource managers have long understood the intimate relationship between watercourses and the lands through which they flow (Hynes, 1975). Ongoing activities such as altered hydrological regimes (e.g. dams), source pollution from agriculture, industry and urban development, and habitat destruction also continue to alter ecological processes (Naiman et al., 1995). The development of watershed lands has been implicated in changes in fish abundance, distribution and community structure (Wang et al., 1997; Rahel, 2002; Allan, 2004), contributing to global declines in both abundance and diversity of freshwater fish (Ricciardi and Rasmussen, 1999; Jelks et al., 2008). Understanding the mechanisms driving relationships between organisms and ecological processes is a requisite for sustainable and responsible watershed development and management (Guégan et al., 1998; Cowx and Gerdeaux, 2004; Lapointe et al., 2014).

Fish community surveys are a frequently employed method used to perform environmental impact assessments (Karr, 1981; Cowx and Gerdeaux, 2004; Nicholson and Jennings, 2004). Fish assemblage composition or community metrics (e.g. biodiversity quality, Feest et al., 2010) in impacted watercourses can be extremely informative, providing insight through the presence or absence of species sensitive to certain environmental characteristics or contaminants (Karr, 1981; Guégan et al., 1998). Habitat characteristics and stream condition are strongly related to watershed land use (Allan, 2004). For example, Wang et al. (1997) found a positive correlation between fish community and forested land and negative correlation with urban and agricultural land in the riparian zone. They also suggested the existence of a threshold of proportional land use alteration beyond which the community

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[*] Corresponding author. Tel.: +1 613 404 9683.
[**] Corresponding author. Tel.: +1 613 520 4377.
E-mail addresses: ramonf@me.com (R. Filgueira), jacqchapman@gmail.com (J.M. Chapman).
[1] Both authors contributed equally to this work.

http://dx.doi.org/10.1016/j.ecolind.2015.06.006
1470-160X/

reorganizes and changes. Therefore, land use cover and community metrics such as structural and functional biodiversity can provide valuable information regarding ecosystem resilience, or lack thereof, in the face of anthropogenic disturbance (Reynolds, 2002).

The use of sentinel species to investigate environmental impacts enables the identification of physiological responses that may not be observable at the community level (Power and McCarty, 1997; Adams and Ham, 2011). The selection of sentinel species depends on hypothesis, site-specific variables and species' characteristics such as site fidelity and growth rate (Munkittrick, 1992). In addition, when the purpose of the study is to compare the status of different sites, the sentinel species must be present in all sites, which can be a challenging factor in heavily degraded streams due to the extirpation of the majority of species. Unlike more sensitive species, the central mudminnow (*Umbra limi* Kirkland 1840) is able to maintain populations in unaltered and heavily degraded systems (until a threshold is reached). *U. limi* has a broad native distribution and is capable of facultative air-breathing and able to withstand extreme variation in water temperatures, enabling the exploitation of diverse habitats compared to other species (Chilton et al., 1984; Martin-Bergmann and Gee, 1985; Currie et al., 2010). With respect to energy acquisition, mudminnows are able to utilize diverse foraging habitats across all seasons (Chilton et al., 1984; Paszkowski, 1984; Scott and Crossman, 1998). Consequently this species is a potential candidate to be used as sentinel species in watersheds with high proportions of disturbance (until a threshold is reached).

Biochemical and physiological indices of freshwater fish have also been used to assess stream condition (Adams and Ham, 2011; Blevins et al., 2013; Nagrodski et al., 2013). Dynamic indices, such as individual growth, are particularly interesting because they integrate the effect of environmental conditions over extended periods of time (Lucas and Beninger, 1985), providing an assessment in the long-term. Accordingly, fish growth rates have been used to empirically compare the condition of different streams (Van Weerd and Komen, 1998; Barton et al., 2002). Additionally, bioenergetic modeling can provide a way to explore the relationship between individual growth and environmental variables, ultimately providing a mechanistic explanation of fish performance (Beyers et al., 2002). A mechanistic explanation of fish growth is always desirable because the conclusions are not restricted to local and specific conditions, allowing extrapolation to other systems (Nisbet et al., 2012).

Dynamic Energy Budget (DEB) theory is a mechanistic theory for the uptake and use of substrates (food, nutrients and light) by an organism and their use for maintenance, growth, maturation and propagation (Kooijman, 2010). DEB theory focuses on an individual organism, with differential equations describing the rates at which energy is utilized throughout all stages of its life cycle in a dynamic environment (Nisbet et al., 2012). DEB builds on the premise that the mechanisms that are responsible for the organization of metabolism are not species-specific and consequently the 'standard' DEB model is assumed to be appropriate for most animals (Sousa et al., 2010). The use of general principles of biology, physics and chemistry and the possibility of estimating growth based on a mechanistic approach make the DEB framework an ideal tool for exploring *U. limi* growth in relation to environmental characteristics.

The effect of watershed land use on stream functioning would potentially exert a significant effect on fish community as well as on the growth of *U. limi*. Consequently, (1) the growth of *U. limi* as a function of watershed land use following a mechanistic approach, and (2) the potential links with fish community composition, together define a testable framework for using *U. limi* as a sentinel species of anthropogenic impact on stream watershed. Thus, the growth *of U. limi* has been explored following a DEB approach and related to watershed land use cover and fish diversity in six streams in Southern Ontario. This hypothesis has been organized into two main research questions:

- H_1: Watershed land use affects fish community composition, food availability and growth of *U. limi*.
- H_2: The simple metric size-at-age of the generalist *U. limi* captures the functioning of freshwater streams and consequently it can be used as a sentinel species in monitoring plans.

2. Materials and methods

2.1. *Study area,* Umbra limi *and community sampling*

This study took place in six tributaries of the St. Lawrence River in the eastern most portion of Ontario, Canada, near the city of Cornwall (Fig. 1) between spring 2012 and spring 2013. Land use data were obtained from the Southern Ontario Land Resource Information System (SOLRIS) and were combined with a GIS layer defining watershed boundaries developed by the local Raisin Region Conservation Authority using Quantum GIS Lisboa (1.8.0). The SOLRIS database includes 23 land cover types, 15 of which are found in the study area. Because watersheds varied in size, the proportion of different land use categories was determined using total hectares allocated to each land use divided by the total watershed area.

Central mudminnow were collected from six tributaries to the St. Lawrence River in the eastern-most portion of Ontario in Fall (Nov-2012) and Spring (Apr-2013). Logistical constraints limited our sampling efforts to 6 of the 9 streams within the study area. The three that were excluded were chosen because they had characteristics that made them difficult to sample (i.e. Fraser Creek, no access points/land owner permission), incomparable to other streams (i.e. Sutherland Creek, extensive restoration work), and had land-use that was extremely similar to other creeks (e.g. Westley's Creek, similar to Gunn and Wood). Fish were collected using backpack electrofishing in the downstream portions of watersheds, euthanized using dropwise addition of clove oil, and transported back to the laboratory for storage at the end of each field day. Each fish was removed from storage, weighed (total and gonads), and measured prior to otolith extraction. For this species, using otoliths to determine fish age is more effective than scales as a result of high scale regeneration, leading to consistent under-aging (Robinson et al., 2010). Large sagittal otoliths were removed from each fish, cleared of debris and stored dry in clearly labeled 1.5 ml vials until mounting.

Otolith preparation techniques followed methods described by Robinson et al. (2010) with slight variation. Single otoliths were mounted to glass slides, sulcus side up, using cyanoacrylate glue and allowed to cure for at least 24 h. Mounted otoliths were then polished to the focus with successively finer diamond lapping film (3 μ, 0.5 μ, 0.1 μ). In cases where the otolith was easily readable without polishing, otoliths were read untreated. Using stereomicroscopes and transmitted light to estimate ages, two different readers estimated age for each fish, and were unaware of fish measurements and the other reader's estimation. Age estimations that agreed were accepted, while a third reader was used in cases of discrepancy.

Fish community data included in this study was part of a larger, multi-year survey effort focusing on coastal wetlands, confluences and tributaries in the area (Suski et al., 2014). Tributary fish community was determined by seasonal sampling of tributaries using a backpack electrofisher (Haltech HT-2000, Guelph, ON, Canada). Two 150 m transects were sampled on the mainstem of each tributary, and site selection was based on land-owner permission and accessibility. This included a 'downstream' and 'upstream' site, 2 and 4 km from the confluence with the St. Lawrence River,

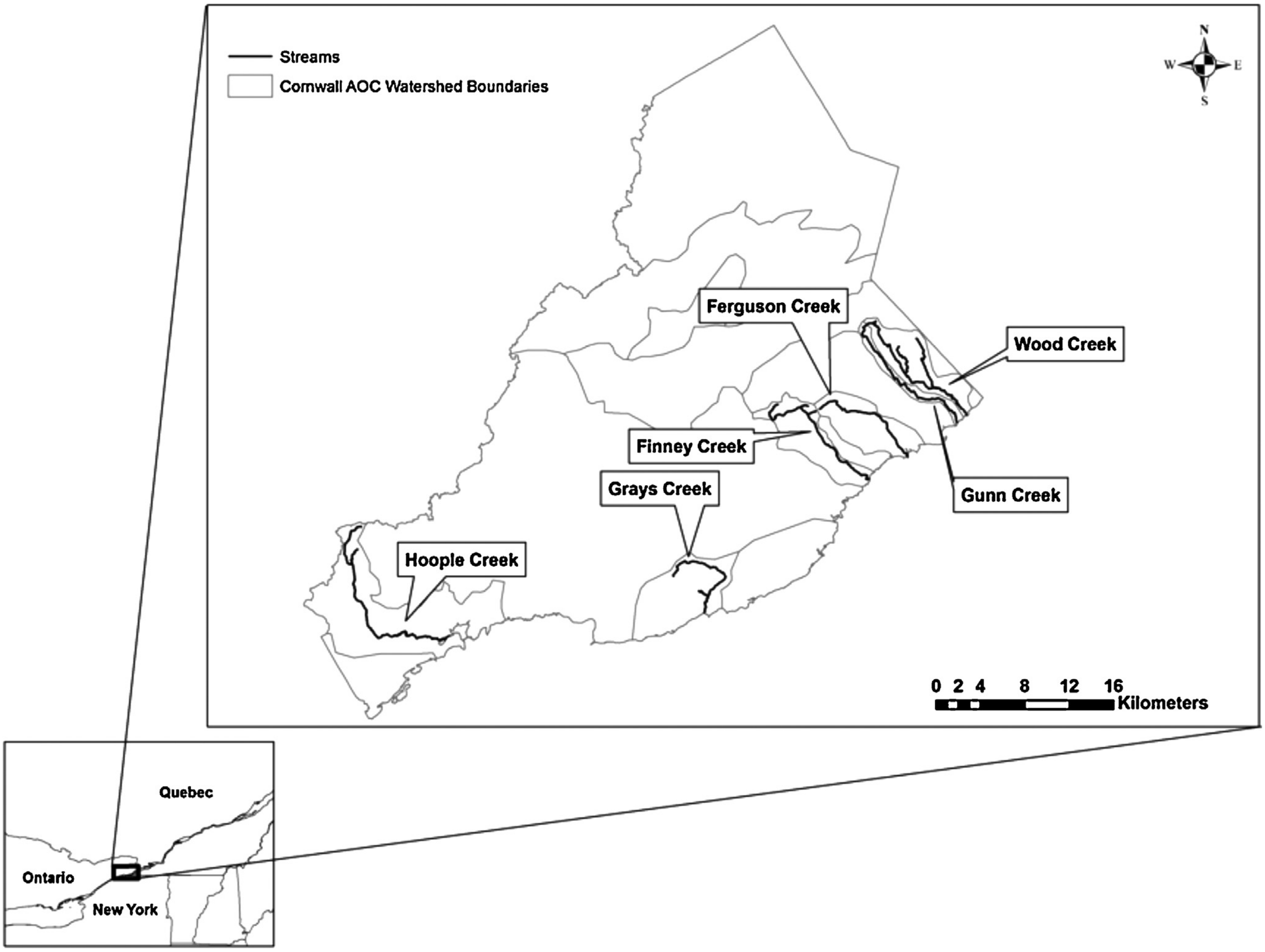

Fig. 1. Map of Cornwall watershed area with the six studied streams.

respectively. Both transects ensured that the samples included all the habitat types found with each system. During sampling, a single backpack operator and two netters conducted a single pass of each transect, netting all fish possible. This was followed by identification, enumeration and measurement of collected individuals. Surveys were conducted seasonally (spring, summer, fall, and winter) over a year. Further details regarding community sampling can be found in Suski et al. (2014). Shannon–Wiener index (H′) and effective number of species, exp(H′), were calculated following Jost (2006).

2.2. Dynamic Energy Budget model

The 'standard' DEB model (Fig. 2, Table 1) is based on Nisbet et al. (2012). The description of the model follows the original notation by Kooijman (2010), in which [] denote quantities expressed as per unit structural volume, {} denote quantities expressed as per unit surface-area of the structural volume and a dot over a symbol denotes a rate, or a dimension per time. DEB describes the individual in terms of three state variables: reserve(s), structure(s), and a maturity/reproduction buffer for juvenile and juvenile/adult, respectively. The energy assimilated from food is stored as reserves; a fixed fraction of this energy (κ) is directed toward maintenance and growth of the structural body, and the remainder ($1-\kappa$) is directed toward maturation, gamete production and maintenance of the reproductive system, depending on the life cycle stage of the organism. Although DEB allows for simulation of the complete life cycle (embryo, juvenile and adult), the model for *U. limi* has been initialized at the juvenile stage due to a lack of data available with which to parameterize the embryo stage. Two modifications have been incorporated into the Nisbet et al. (2012) model. First, maturity maintenance costs ($\dot{p}_J$) have been calculated based on Eq. (6) in Pouvreau et al. (2006). This simplification, based on the second

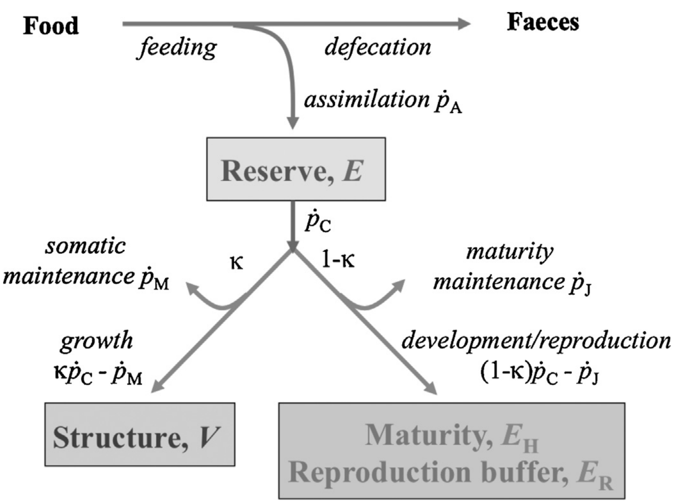

Fig. 2. Standard DEB model scheme for juvenile (development/maturity) and adult (reproduction/reproduction buffer) life stages. See Table 1 for differential equations.

Table 1
State and forcing variables, parameters for *Umbra limi* and equations of the standard Dynamic Energy Budget (DEB) model.

Symbol	Value	Units	Definition
State and forcing variables			
E		J	Reserve energy
V		cm^3	Structural volume
E_H		J	Cumulated energy invested in development
E_R		J	Reproduction buffer energy
T		K	Temperature
f			Scaled functional response
$c(T)$			Temperature correction factor
Parameters			
$[\dot{p}_M]$	30.0	$\text{J cm}^{-3}\,\text{d}^{-1}$	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	0	$\text{J cm}^{-2}\,\text{d}^{-1}$	Surface-specific somatic maintenance rate
$[E_G]$	5600	J cm^{-3}	Volume-specific cost for structure
$\dot{\nu}$	0.149	cm d^{-1}	Energy conductance
κ	0.761		Fraction of reserves to growth and maintenance
V_P	2.052	cm^3	Volume threshold at puberty
T_A	8057.5	K	Arrhenius temperature
T_1	283.15	K	Reference temperature
δ	0.212		Shape coefficient
l_m	14	cm	Maximum observed length
L_m	δl_m	cm	Maximum volumetric length
$\{\dot{p}_{Am}\}$	$L_m[\dot{p}_M]/\kappa$	$\text{J cm}^{-2}\,\text{d}^{-1}$	Maximum surface area-specific assimilation rate
g	$\dot{\nu}[E_G]/\kappa\{\dot{p}_{Am}\}$		Energy investment ratio
$[E_m]$	$\{\dot{p}_{Am}\}/\dot{\nu}$	J cm^{-3}	Maximum reserve density
Equations			
	$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$		
	$\frac{d}{dt}V = \frac{1}{[E_G]}\dot{p}_G = \frac{1}{[E_G]}(\kappa\dot{p}_C - \dot{p}_S)$		
	$\frac{d}{dt}E_H = (1-\kappa)\dot{p}_C - \dot{p}_J \quad \text{if}\, V < V_p, \quad \text{else}\, \frac{d}{dt}E_H = 0$		
	$\frac{d}{dt}E_R = 0 \quad \text{if} \;\; V < V_p, \quad \text{else}\, \frac{d}{dt}E_R = (1-\kappa)\dot{p}_C - \dot{p}_J$		
	with $\dot{p}_A = c(T)f\{\dot{p}_{Am}\}L^2$		
	$\dot{p}_C = c(T)\{\dot{p}_{Am}\}L^2\frac{ge}{g+e}\left(1 + \frac{L}{gL_m}\right)$		
	with $e = \frac{[E]}{[E_m]} = \frac{E}{V}\frac{\dot{\nu}}{\{\dot{p}_{Am}\}}$ and $L = V^{1/3}$		
	$\dot{p}_S = c(T)([\dot{p}_M]L^3 + \{\dot{p}_T\}L^2)$		
	$\dot{p}_J = c(T)\left(\frac{1-\kappa}{\kappa}\right)\min(V, V_p)[\dot{p}_M]$		
	$c(T) = \exp\left(\frac{T_A}{T_I} - \frac{T_A}{T}\right)$		

edition of the standard DEB model, avoids the parameterization of another primary parameter, the maturity maintenance rate coefficient (k_J), and the characterization of stage transition thresholds (birth and puberty in DEB jargon) in terms of energy. This simplification is based on the difficulty to parameterize k_J as well as the transition thresholds (Freitas et al., 2010). Accordingly, the maturity threshold at puberty has been parameterized based on size at first maturity, 5.1–6.4 cm (Scott and Crossman, 1998), which was converted to a volumetric threshold using the shape coefficient (Table 1). The second modification is related to the scaled functional response (f), which has been treated as a parameter rather than a function of food density and the half saturation coefficient. This approach is discussed below and is related to the difficulty in determining food density for a generalist species such as *U. limi*.

The shape coefficient (δ) determines how a specific length measurement relates to structural body mass and it is critical to convert structural volume into length. The estimation of δ was based on the allometric relationship wet weight (total minus gonad) vs length collected in the present study. The parameterization of maximum observed length for *U. limi* was based on personal observations and literature data (Martin-Bergmann, 1982; Schilling et al., 2006; Robinson et al., 2010). Volume-specific cost for structure ($[E_G]$) was assumed to be $5600\,\text{J cm}^{-3}$ based on Freitas et al. (2010) and van der Veer et al. (2009). All of the physiological rates in DEB are corrected using a function based on an Arrhenius function (Table 1). The Arrhenius temperature (T_A) has been calculated using respiration data from Currie et al. (2010). The scaled functional response (f) was assumed to be $f = 1$, which implies that feeding occurs ad libitum (Kearney, 2012). This assumption is based on the fact that *U. limi* is a generalist feeder, able to forage on a wide range of food sources (Martin-Bergmann and Gee, 1985), and consequently it is assumed that food is not a limiting factor. This assumption is commonly applied to marine species when food density data are not available and DEB is being used to explore functional responses of the organisms (e.g. Freitas et al., 2010). The remaining three parameters, volume-specific somatic maintenance rate ($[\dot{p}_M]$), energy conductance ($\dot{\nu}$) and the fraction of reserves to growth and maintenance (κ) were calibrated using PEST (Model-Independent Parameter Estimation, Watermark Numerical Computing, http://www.pesthomepage.org), an optimization utility that uses the Gauss–Marquardt–Levenberg algorithm to estimate the value of a parameter which minimizes the discrepancies between estimations and observations. In this case, the optimization procedure was applied to a historical dataset (Martin-Bergmann, 1982) to estimate the unknown parameters using length as the goal function. Martin-Bergmann (1982) provides data from four different streams, which were pooled together for this analysis.

The validation of the DEB model was carried out by applying the same set of parameters to an independent dataset of capture-recapture data (Bliss, 2014). The agreement between observed and modeled was evaluated using the reduced major axis regression method (RMA, Duarte et al., 2003), which takes into account sampling error for both the dependent and independent variables.

Once validated, the DEB model was run with the six datasets collected in this study. The model was run using PEST with the aim of optimizing the value of the scaled functional response (f) that minimizes the discrepancies between modeled and observed lengths at the end of the simulated period. The DEB parameter *f* is intrinsically related to food availability following a Michaelis–Menten term:

$$f = \frac{X}{X + X_K} \tag{1}$$

where X is the food density and X_K is the half saturation coefficient, which is a function of the time/energy that the individual spends searching for food. If food abundance is high and the individual does not need to spend time/energy searching, the scaled functional response (f) will tend to 1. On the contrary, f will tend to 0 if the available food is to some extent limited (e.g. dilution, competition). Therefore, f can be understood as a proxy for food availability (Saraiva et al., 2011).

2.3. Statistics

RMA and linear regression analysis were performed using IBM® SPSS® Statistics v20.0.0. The significance of the RMA regressions was tested using ANOVA and comparison of slopes and intercepts with 1 and 0, respectively, was carried out following Zar (1984). Dose response curves were calculated using GraphPad® Prism® v 5.0c.

3. Results and discussion

3.1. Dynamic Energy Budget (DEB) simulations

The auto-calibration of the DEB parameters volume-specific somatic maintenance rate ($[\dot{p}_M]$), energy conductance ($\dot{\nu}$) and the fraction of reserves to growth and maintenance (κ), using the Martin-Bergmann (1982) dataset showed a good agreement between modeled and observed values (Fig. 3). The values of the parameters reported by PEST were within the range of other fish species (see http://www.bio.vu.nl/thb/deb/). A sensitivity test was performed for each parameter by increasing and decreasing its value by 10% and quantifying the response of the individual length at the end of the simulation. This test highlighted that $[\dot{p}_M]$ was the most sensitive parameter causing an average change in final length of 4.6%. This outcome suggests that the most critical parameter to be validated using experimental data should be the volume-specific somatic maintenance rate. Further steps in data gathering are needed in order to improve the current DEB model, which could be ranked according to the scale of completeness described by Lika et al. (2011) between the levels 1 and 2. The validation of the model was carried out by applying the same set of parameters to an independent capture-recapture dataset (Bliss, 2014). The slope and intercept of the RMA regression between modeled and observed values (Fig. 4) are statistically similar to 1 and 0, respectively, suggesting that the model is able to simulate the length of *U. limi* over time.

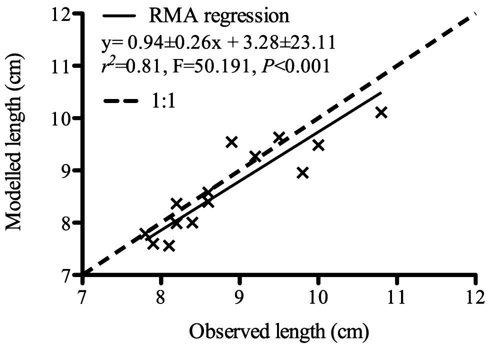

Fig. 4. Observed vs modeled *Umbra limi* length. Observed values were obtained from Bliss (2014) and modeled were generated with DEB. The continuous line represents the RMA regression for observed vs modeled and the dashed line the 1:1 relationship.

Once validated, the DEB model was used to simulate the average individual in each of the streams considered in this study. The average individual in each stream was characterized with the mean age and length after pooling together all the individuals collected in both sampling campaigns. The mean age ranged from 433 to 937 days for Ferguson and Finney, respectively (Fig. 5). These extreme differences in age, with Finney individuals doubling the age of Ferguson's, were not observed for length, which ranged from 6.80 to 8.14 cm for Hoople and Wood, respectively. The average individuals for the six streams differed considerably (Fig. 5), which matches one of the components of our main hypothesis (H_1), that is, food availability may be different among streams, which ultimately may cause differential growth in *U. limi*. This was theoretically tested using DEB by running the model for each stream and optimizing the value of the scaled functional response (f) that minimizes the discrepancies between modeled and observed lengths at the end of the simulated period. As stated above, f can be understood as a proxy for food availability in each stream. The optimized values of f ranged from 0.73 to 1.33 for Gray and Ferguson individuals, respectively (Fig. 5), suggesting that food availability in Ferguson is the greatest among the sampled streams. Although the maximum theoretical value of f according to Eq. (1) is 1, the optimal value for three of the streams, Wood, Gunn and Ferguson, was beyond that value. This suggests that the assumption that *U. limi* fed ad libitum, $f = 1$, in the calibration and validation datasets is not entirely correct. This assumption was made considering the difficulty in characterizing the food density that is available to a generalist species such as *U. limi*. Although this violation suggests that the DEB parameters proposed in this study should be considered with caution, there are no negative implications for the conclusions of the model regarding

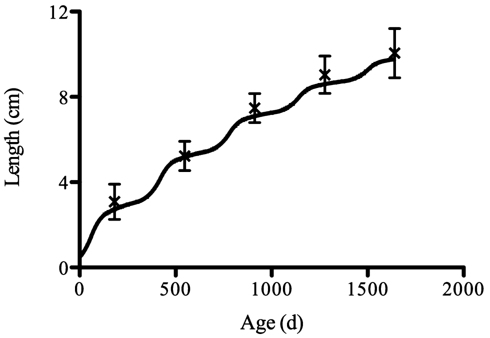

Fig. 3. Observed (×, mean ± std. dev.) and modeled (continuous line) *Umbra limi* length over a period of five years. Observed values were obtained from Martin-Bergmann (1982) and modeled values generated with DEB.

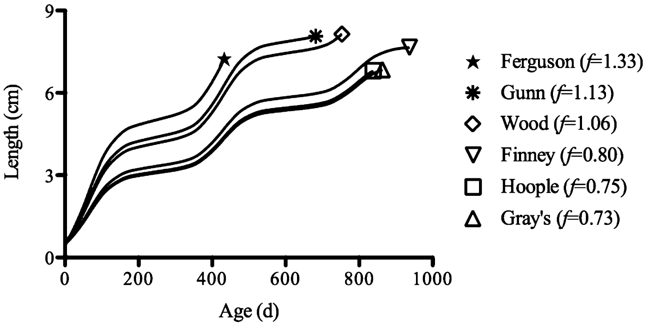

Fig. 5. Mean age vs mean length of *Umbra limi* in the different streams. Continuous lines represent the growth trajectories estimated with DEB for each stream using the optimal half saturation coefficient, *f*, which minimizes the discrepancy between observed and modeled values at the end of the simulation.

the comparisons among streams because *f* simply defines a relative scale of food availability using the calibration dataset as a reference. Given that *f* provides a relative rather than an absolute scale, the differences in optimal values of *f* among the streams can still be considered as differences related to food availability.

3.2. *Habitat, diversity and* Umbra limi *growth*

Watersheds of the six streams that were sampled in this study differed in SOLRIS land cover data (Table 2). Each land cover was classified into anthropogenic or natural land types as follows: agriculture, urban (built-up impervious and transportation), forest (all forest types, hedge rows, and tree cultivation lands), aquatic (bog, marsh, swamp, and open water) and recreation (built-up pervious lands e.g. parks). These uses were further sub-grouped into two categories to identify the impact of anthropogenic developments as a whole: modified (agriculture and urban) and natural (forest, aquatic and recreation). These two categories are selected with the intention of classifying land cover in the simplest way possible, which is critical for the implementation of land cover as an indicator of ecosystem function and its application to other watersheds in which the land cover classification is not necessarily the same as the streams considered in this study. Four of the streams presented a proportion of modified watershed above 0.80, mainly driven by the high contribution of agricultural land (Table 2). The least disturbed watersheds were Hoople and Gray's, with a proportion of natural land use of 0.41 and 0.31, respectively.

Fish community data were summarized (Table 3) in terms of: (1) Shannon–Wiener index (H′), which informs about the entropy of the dataset, that is, quantifies the uncertainty in the species identity of an individual that is randomly taken from the dataset (Jost, 2006); and (2) effective number of species, also called true diversity (Jost, 2006; Tuomisto, 2010), which refers to the equivalent number of equally abundant species that would be needed to give the same value of diversity index observed in the dataset (Gotelli and Chao, 2013), where all the species may not be equally abundant. The streams differed in terms of diversity, ranging from an effective number of species of 2.6–11.2 for Ferguson and Hoople, respectively (Table 3). Although watershed land use cover has previously been correlated to fish community (Wang et al., 1997; Rahel, 2002; Allan, 2004), these six streams did not show a significant correlation ($p = 0.064$) between land use cover, expressed as proportion of modified watershed, and diversity, expressed as effective number of species (Fig. 6). Nevertheless, the highest diversity (Table 3) was observed in the stream with the least modified watershed (Table 2), Hoople.

To test H_1, that watershed land use can affect food availability and ultimately *Umbra limi* growth, proportion of modified watershed was plotted vs the estimated food density and *U. limi* growth (Fig. 7a and c, respectively). The results suggest that the greater the modification of the habitat, the greater the food availability and consequently the better the growth of *U. limi* (Fig. 7c), which confirms H_1. Both food density and *U. limi* growth datasets were fitted using dose–response curves (Table 4). In each case, when fitting the six streams under the same curve, Ferguson was highlighted as a potential outlier. Accordingly, the dose–response curves were calculated with and without Ferguson. Excluding Ferguson from the curves increased the explained variance but the general pattern was similar (Fig. 7a, c and Table 4). The half maximal effective concentration (EC_{50}), which in this case corresponds to the proportion of modified watershed that induces a response halfway between the bottom and the top on the response variable, ranged between 0.83 and 0.86 (Table 4). The steep Hill Slope of the curves, especially when Ferguson is considered in the analysis (Table 4), suggests an abrupt response when the proportion of modified watershed reaches EC_{50}, that is 0.83–0.86. When the proportion of modified watershed reaches this threshold, DEB suggests a significant increase in food availability (Fig. 7a), with a concomitant increase in *U. limi* observed growth (Fig. 7c). This increment in food density that is available for *U. limi* could be a response to the degradation of the habitat, which could manifest in two different ways:

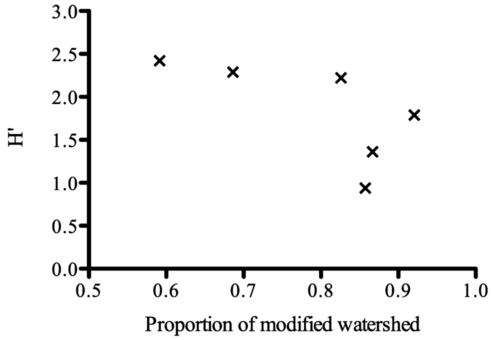

Fig. 6. Effective number of species vs proportion of modified watershed for the six studied streams.

- The high proportion of modified watershed, which is, in general, a consequence of the increase in agricultural land in the watershed (Table 2), is often associated with an increase of nutrients, manure, etc. This organic loading may increase the total amount of food that is available for a generalist species such as *U. limi* (H_3).
- The extensive degradation of the habitat can significantly alter the environmental conditions of the streams, modifying the ichthyofaunal community. These changes could effectively reduce inter-specific competition, benefiting *U. limi*, which is able to maintain populations in both unaltered and heavily degraded systems (H_4). Therefore, H_4 suggests that the total amount of food in degraded streams does not necessarily change but due to the lower number of competitors, food density for *U. limi* is relatively higher than in pristine streams.

H_3 is challenging to test due to the difficulty in characterizing food density available for a generalist species such as *U. limi* in each stream. However, H_4 can be tested by analyzing stream ichthyofaunal community. Accordingly, the effective number of species was plotted vs the estimated food density and *U. limi* growth (Fig. 7b

Table 2
Proportion of land use (Modified = agriculture + urban. Natural = forest + aquatic + recreation. Modified + Natural = 1) in watersheds sampled for fish community and *Umbra limi* growth.

Stream	Agriculture	Urban	Forest	Aquatic	Recreation	Modified	Natural
Hoople	0.53	0.05	0.14	0.26	0.01	0.59	0.41
Gray's	0.33	0.36	0.09	0.17	0.06	0.69	0.31
Finney	0.78	0.05	0.13	0.04	<0.01	0.83	0.17
Wood	0.84	0.03	0.11	0.02	<0.01	0.87	0.13
Gunn	0.87	0.05	0.05	0.03	0	0.92	0.08
Ferguson	0.82	0.04	0.12	0.03	0	0.86	0.14

Table 3
Shannon–Wiener index (first value) and effective number of species (second value) of fish communities collected from streams near Cornwall, Ontario in 2012.

Stream	Winter	Spring	Summer	Fall	Average
Hoople	2.00/7.4	2.13/8.4	2.24/9.4	2.44/11.5	2.42/11.2
Gray's	1.46/4.3	2.21/9.1	2.07/7.9	1.80/6.0	2.29/9.9
Finney	1.38/4.0	2.29/9.9	1.72/5.6	2.29/9.9	2.22/9.2
Wood	0.60/1.8	1.42/4.1	0.47/1.6	1.21/3.4	1.36/3.9
Gunn	N/A	1.63/5.1	1.43/4.2	1.77/5.9	1.79/6.0
Ferguson	0.00/1.0	1.08/2.9	0.79/2.2	0.63/1.9	0.94/2.6

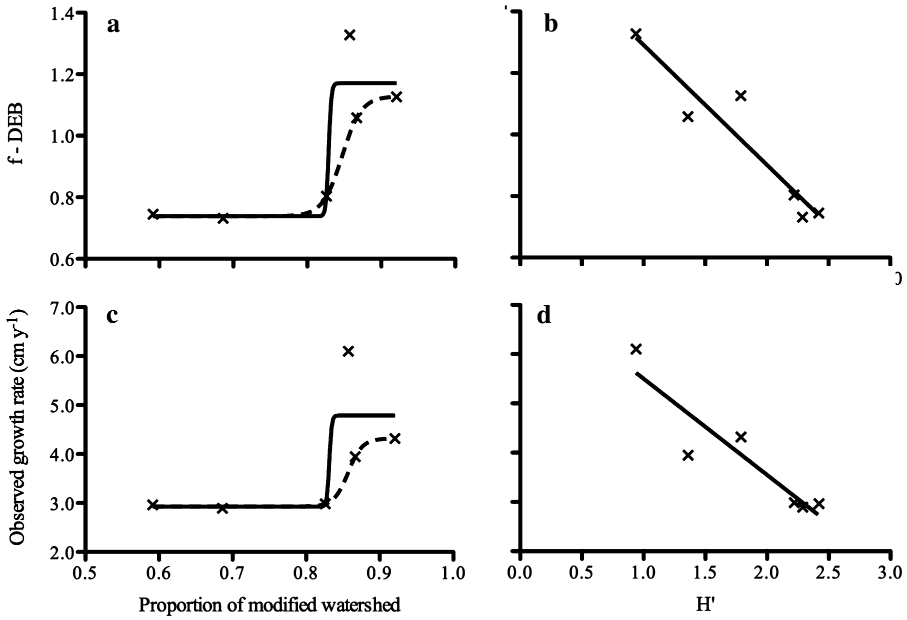

Fig. 7. Estimated food density (f-DEB) and *Umbra limi* growth vs proportion of modified watershed (a and c, respectively) and effective number of species (b and d, respectively). The statistics of the dose-response curves and linear regressions are presented in Table 4. In panels (a) and (b), continuous and dashed lines represent the dose–response curves with and without Ferguson, respectively.

and d, respectively). The statistically significant linear regressions suggest that fish diversity explains 89.3 and 77.3% of food density and *U. limi* growth, respectively (Table 4). This suggests that the degradation of stream habitat could lead to changes in diversity that eventually reduces inter-specific competition and enhances *U. limi* growth rate, confirming H_4. Nevertheless, H_3 cannot be rejected and an increase in total food availability in degraded streams could also act together with the reduction in inter-specific competition to increase growth rate in this species.

It thus appears that the effects of habitat degradation on stream functioning and diversity do not follow a linear pattern (Figs. 6 and 7). The steep change in *U. limi* performance when the proportion of modified watershed reaches 0.83–0.86 (Fig. 7c) suggests the existence of a threshold response. Fish diversity follows a similar pattern, as the linearity of its relationship with habitat seems to be sharply altered when the proportion of modified watershed reaches 0.83–0.86 (Fig. 6). This steep threshold could be considered a tipping point that triggers changes in trophic web structure and consequently ecosystem functioning (Groffman et al., 2006). This tipping point, or threshold at which a small perturbation can qualitatively alter the state or development of a system (Lenton et al., 2008), could suggest that at that level of habitat perturbation

Table 4
Statistics of regressions of Figs. 7 and 8.

Proportion of modified watershed (dose–response curves)

	Fig.	Bottom	Top	EC_{50}	Hill	*n*	r^2
With Ferguson							
f-DEB	7a	0.74 ± 0.099	1.17 ± 0.099	0.83	250	6	0.867
Growth rate	7c	2.93 ± 0.814	4.79 ± 0.816	0.83	273	6	0.657
Length at 2y	8a	6.92 ± 0.276	9.03 ± 0.277	0.83	250	6	0.946
Without Ferguson							
f-DEB	7a	0.74 ± 0.006	1.13 ± 0.006	0.85	33.2	5	0.999
Growth rate	7c	2.93 ± 0.035	4.32 ± 0.050	0.86	44.8	5	0.998

Effective number of species (linear regressions)

	Fig.	Intercept	Slope	*P*	*n*	r^2
f-DEB	7b	1.43 ± 0.088	−0.06 ± 0.011	<0.01	6	0.893
Growth rate	7d	6.10 ± 0.657	−0.31 ± 0.084	<0.05	6	0.776
Length at 2y	8b	10.1 ± 0.519	−0.27 ± 0.066	<0.05	6	0.811

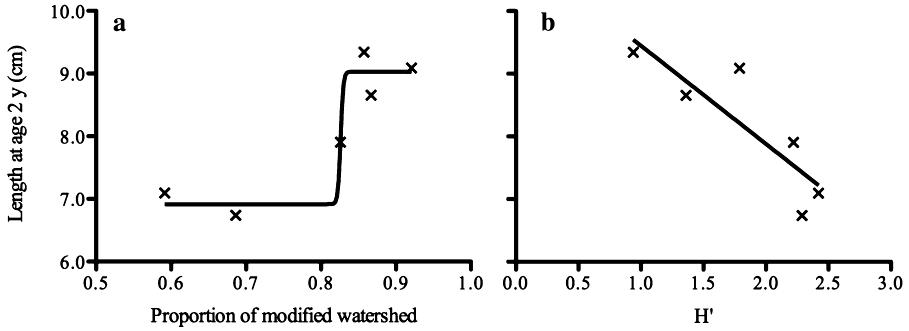

Fig. 8. Length of two-year-old individuals vs (a) proportion of modified watershed and (b) effective number of species. The statistics of the dose–response curves and linear regressions are presented in Table 4.

the resilience of the stream is exceeded and the fish community reorganizes in a manner that favors generalist feeders such as *U. limi*.

Observed patterns in diversity match Wang et al. (1997), who suggested the existence of a threshold proportion of watershed agriculture at which effects manifest in stream biotic integrity. Similar yet lower (10–15%) thresholds have been reported for impervious surfaces associated with urban development (Klein, 1979; Paul and Meyer, 2001). Further still, Jones et al. (1999) demonstrated threshold responses of species abundance to riparian deforestation, where thresholds were lowest for species requiring sediment-free flowing waters for spawning. However, extrinsic factor thresholds such as watershed land use may be too generalized for a single threshold to be applied to multiple systems, as complex environmental and biological factors may influence the susceptibility of systems to particular stressors (Allan, 2004). In this study area, the 0.83–0.86 threshold of overall disturbance appears to be important for effective number of species and *U. limi* growth, however this value may not be directly applicable to other watersheds.

3.3. Population structure and size-at-age

As mentioned above, the population structure of *U. limi* differed significantly among streams (Table 5). Year classes 1 and 2 y were the most abundant in most of the streams, but 0 y was the most abundant in Ferguson, which is the stream with the lowest diversity, the greatest apparent food availability (~*f*) and the highest *U. limi* growth rate. Nevertheless, the most striking difference between Ferguson and the other streams is the fact that no individuals of size class 3 or 4 were found in Ferguson (Table 5). These differences cannot be attributed to methodological aspects given that the same sampling techniques were applied to all streams, and at the same period of the year (all sampling occurred within a few days). Consequently, this study not only opens a new hypothesis related to the effects of land use on ichthyofaunal community but also on population structure. Several hypotheses can be formulated to explain the differences in population structure: (H_5) the lack of old individuals and the low diversity may suggest a catastrophic event in Ferguson, massive mortalities, and an ongoing recovery; (H_6) the lack of old individuals may suggest early mortality in this stream, which could be potentially related to a highly impacted habitat; (H_7) *U. limi* may be colonizing this stream for the first time; and/or (H_8) largest individuals are possibly being preyed upon. The presence of a top predator that feeds on the largest individuals of *U. limi* would explain the observation that the maximum observed length in all the streams is more or less the same independent of their age. These hypotheses (H_5–H_8) cannot be addressed with the data collected in the present study, which represent only a snapshot of the streams.

Table 5
Population structure of *Umbra limi* collected from streams near Cornwall, Ontario. Year class was determined by otolith analysis and includes fish sampled in Fall and Spring.

Stream	Year class					Total
	0	1	2	3	4	
Hoople	1	8	28	2		39
Gray's	6	13	8	15	2	44
Finney		10	24	9	2	45
Wood	3	19	23	2	1	48
Gunn	4	17	16	1		38
Ferguson	18	10	7			35
Total	32	77	106	29	5	249

Given the differences in age structure but the similarities in average length, size-at-age was chosen as a metric to compare the streams. Two-year-old individuals were the most abundant population group (Table 5) and accordingly size-at-age of these individuals was plotted versus the proportion of modified watershed (Fig. 8a) and effective number of species (Fig. 8b). The observed significant relationships (Table 4) followed a similar pattern than food density and growth rate (Fig. 7), establishing a solid foundation for using size-at-age of *U. limi* as a comparative metric among freshwater streams, confirming H_2. Size-at-age has been commonly studied in both marine and freshwater environments to assess stocks of exploited species such as Atlantic cod *Gadus morhua* (Sinclair et al., 2002) and walleye *Sander vitreus* (Henderson and Morgan, 2002). Size-at-age can be seen as a summary metric that incorporates multiple environmental variables, including quality of forage, predation pressure, temperature, and perhaps in this case, competition (Neuheimer and Taggart, 2007; Borcherding and Magnhagen, 2008; Billman et al., 2011). Intraspecific competition has been demonstrated to cause density-dependent growth in some species (e.g. Helser and Almeida, 1997). However to our knowledge, the relationships between size-at-age of generalist fishes, habitat quality, diversity and the potential effects of interspecific competition have not previously been demonstrated. Billman et al. (2011) demonstrated increased growth in high quality environments compared to low quality in leatherside chub *Lepidomeda aliciae* and how these relationships were influenced by the presence or absence of predators. However, no consideration was given to the relationship with the fish community as a whole. The use of size-at-age of sentinel species such as *U. limi* as would enable studies of this nature to occur in areas where sensitive species have been extirpated.

4. Conclusions

Ichthyofaunal community composition, diversity, and ecosystem functioning are influenced by the interactions of multiple environmental and ecological factors, including, for example hydrological regime, riparian vegetation, and habitat heterogeneity and connectivity (Palmer et al., 2010), all of which are strongly related to watershed land use (Wang et al., 1997; Townsend et al., 2003; Allan, 2004). The effect of land use on fish community becomes even more important when influential factors, including nutrient loading and sedimentation associated with intensive agriculture (Allan, 2004) are present in the watershed, as is the case for this study area. Results here support the notion that threshold responses in diversity and ecosystem functioning to watershed degradation exist, and that once these thresholds are surpassed, the community changes and the system reorganizes. Despite challenges associated with the incorporation of such intrinsic variability, the use of such biologically relevant thresholds may be an extremely effective goal for restoration and management (Groffman et al., 2006; Claireaux and Lefrançois, 2007; Trebitz et al., 2007). Through this, development planning could be allocated in such a way as to limit the proportion of specific land uses within watersheds that are approaching or have exceeded predetermined threshold levels, which could be understood as a precautionary approach to management.

The use of size-at-age and population structure analysis is common practice in stock assessment, however is rarely applied to ubiquitous generalists. Size-at-age fulfills all the characteristics of a ecological indicator given that it is easy to measure, integrates the effects of several environmental variables and consequently captures the complexities of the ecosystem into a single value (Dale and Beyeler, 2001). Accordingly, the outcomes of this study show the potentiality of size-at-age of generalist species such as *U. limi* as cost-effective indicators of ecosystem status (H_2). Fish aging has long been a routine component of many monitoring programs, though relating size-at-age to watershed-scale and ichthyofaunal community metrics is seemingly under represented in both research and monitoring programs. The inclusion of size-at-age may be an informative addition to monitoring regimes and give practitioners insight into trophic changes as a result of shifting food-web dynamics.

In summary, the results of this study highlight the potentiality of watershed land use cover as a precautionary indicator for watershed management and *U. limi* as a sentinel species through its response to change (H_1) to identify impacts on fish diversity. The novel mechanistic approach developed in this study, in which a Dynamic Energy Budget model is used as a core to integrate environmental data, avoids empiricism and consequently provides a solid foundation for extrapolating the conclusions of this study to a broader spatial scale. As for all biological indicators of ecosystem status, the specific values of *U. limi* size-at-age must be established according to stream characteristics for a detailed and quantitative assessment. Development of this indicator should be straightforward given that fish aging has long been a routine component of many monitoring programs. In addition, even in the total absence of data, the comparison of size-at-age of a generalist species in a set of freshwater streams could be used as a qualitative analysis of stream condition, and hence a powerful tool for early detection of environmental impacts. Therefore, although some effort is required in the short-term to perform the quantitative assessment, the possibility of then performing rapid qualitative detection of environmental impacts and the cost-effective benefits over the long-term, strengthen the potential use of size-at-age of generalist species in monitoring and management planning of freshwater streams.

Acknowledgements

Chapman and Cooke are supported by the Canadian Natural Science and Engineering Research Council. Funding for this study was provided in part by the US Fish and Wildlife Fish Enhancement, Mitigation and Research Fund. The authors are sincerely grateful to L. Pecquerie and J. van der Meer for providing insight on DEB modeling; T. Ward and G. King for field and laboratory assistance; S. Bliss for providing data on *U. limi* growth; M. Forbes for initiating collaboration between the authors; and two anonymous reviewers for the valuable feedback.

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