

# Nonlinear relationships can lead to bias in biomass calculations and drift-foraging models when using summaries of invertebrate drift data

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**Abstract** Drift-foraging models offer a mechanistic description of how fish feed in flowing water and the application of drift-foraging bioenergetics models to answer both applied and theoretical questions in aquatic ecology is growing. These models typically include nonlinear descriptions of ecological processes and as a result may be sensitive to how model inputs are summarized because of a mathematical property of nonlinear equations known as Jensen's inequality. In particular, we show that the way in which continuous size distributions of invertebrate prey are represented within foraging models can lead to biases within the modeling process. We begin by illustrating how different equations common to drift-foraging models are sensitive to invertebrate inputs. We then use two case studies to show how different representations of invertebrate prey can influence predictions of energy intake and lifetime growth. Greater emphasis should be placed on accurate characterizations of invertebrate drift, acknowledging that inferences from drift-foraging models may be influenced by how invertebrate prey are represented.

**Keywords** Jensen's inequality · Bioenergetics · Net energy intake · Growth potential · Invertebrate size structure

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## Introduction

Drift-foraging bioenergetics models are an emerging tool for assessing impacts of multiple factors (flow, temperature, and drift densities) on growth potential, abundance and rates of energy intake of drift-foraging fish (Rosenfeld et al. 2014). Applications are increasing, providing valuable insights into conservation and management of drift-foraging fishes (e.g., Environ. Biol. Fishes vol. 97, issue 5). These models are process based, including mechanistic descriptions of the drift-foraging process to estimate energetic costs and benefits of drift feeding. They include functional relationships with prey size that are nonlinear, which potentially makes them sensitive to how prey-size distributions are summarized.

Many descriptions of ecological processes are nonlinear, such as functional feeding responses (Holling 1959) or size-biomass relationships (Benke et al. 1999). One important property of nonlinear functions is that for a set of  $x$  inputs with mean  $\bar{x}$ , and a nonlinear function,  $f$ , the value of the function based on the mean value of  $x$  usually is not equivalent to the mean of the function applied to each  $x$  (Jensen 1906). In other words, the mean of a curvilinear function is not the same as the function of the mean. Consider, for example, the function,  $f(x) = x^2$  and assume  $x$  takes values of 1, 2, and 3. Here the value of  $f$  based on the mean value of  $x$  ( $f(\bar{x})$ ) equals 4, while the mean value of  $f$  based on the individual  $x$ 's ( $\overline{f(x)}$ ) equals 4.5 ( $\frac{1^2+2^2+3^2}{3}$ ).

Jensen's inequality can thus introduce bias into calculations when researchers rely on statistical summaries of data, including binned data or means. The bias associated with Jensen's inequality has been recognized in several facets of ecology including predator-prey interactions (Okuyama 2008), terrestrial ecology (Duursma and Robinson 2003), and predicting how ecological systems may respond to environmental change (Ruel and Ayers 1999). However, the bias in aquatic ecosystems has received considerably less attention. Understanding where biases may arise as a result of Jensen's inequality is an important consideration, particularly for complex models such as drift-foraging bioenergetics approaches that include nonlinear relationships.

An informal review of the literature suggests that investigators employ a range of techniques to represent the size distribution of prey items used in drift-

foraging models. Commonly, the prey size distribution is summarized using average invertebrate length (Urabe et al. 2010, 2014). Discretizing the prey sizes into several length categories is another approach, with some investigators using size classes (< 2.5, 2.5–5.0, and >5.0 mm Rosenfeld and Taylor 2009) or 3-mm bins (Hayes et al. 2000) to smaller 1-mm bins used by Hughes et al. (2003) and Dodrill et al. (2016). The scale chosen for summarizing prey size depends on balancing the need to adequately characterize invertebrate drift and efficiently process drift samples in the lab. However, the way in which invertebrate drift is characterized potentially influences predictions of drift-foraging models. Common elements of drift-foraging bioenergetics models that may be affected include: consumption estimates, which are based on estimates of prey biomass from measured lengths (see Box 1), and estimates of foraging area, which is a function of prey length.

#### Box 1

The manner in which drift samples are collected and processed can lead to bias in estimates of prey biomass input data for drift-foraging models, as well as other applications. Often prey lengths are measured and biomass is estimated using a taxon specific length-mass relationship. Researchers may bin invertebrates into relatively fine (e.g., by 1 mm) or coarse size bins (e.g., by 3 mm), or summarize prey size as means. Consider, for example a hypothetical collection of invertebrates in which there exists three length classes (5 mm, 6 mm and 7 mm), but investigators do not consider how counts are distributed across the classes (i.e., they only record a total count instead of a count within finer 1 mm bins). When biomass is calculated based on 1-mm bins using the following equation:

$$\sum C_i * W_i = B_{1mm}$$

where the total biomass,  $B_{1mm}$ , is calculated as the sum of counts ( $C_i$ ) multiplied by weight ( $W_i$ ) for each size ( $i$ ), the total biomass will frequently differ from that estimated by multiplying the middle of the 3-mm bin (6 mm) by the sum of counts, i.e.,

$$W_6 * \sum C_i = B_{3mm}$$

Weight for each size bin is usually calculated using a length-mass regression of the form:

$$W_i = a * L_i^b$$

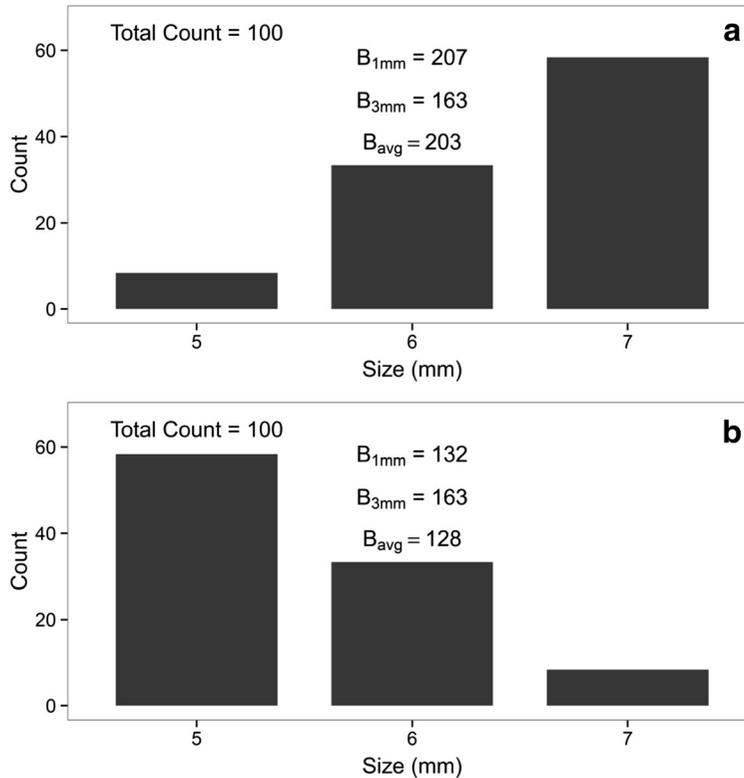
where  $L_i$  is the length of each size bin and  $a$  and  $b$  are species-specific parameters (for calculations in panels a and b below we used parameter estimates for *Gammarus* spp. (Benke et al. (1999):  $a = 0.012$ ,  $b = 2.74$ ).

Investigators may choose to use the average length ( $\bar{L}$ , based on counts of individuals, measured across finer 1-mm bins) to calculate average weight ( $\bar{W}$ ) with a length-mass regression, then calculate the total biomass  $B_{avg}$  as:

$$\bar{W} * \sum C_i = B_{avg}$$

We can calculate bias in biomass calculations as a function of the distribution of individuals among the finer bins. Consider a total count of 100 individuals, varying in frequency across size bins with panel a and panel b showing counts increasing and decreasing across size bins,

respectively ( $B_1$ ). For panel a, the estimate of  $B_{3mm}$  is lower than  $B_{1mm}$ , while  $B_{avg}$  is closer to  $B_{1mm}$ , yet still underestimated. For panel b, the estimate of  $B_{3mm}$  is higher than  $B_{1mm}$ , while  $B_{avg}$  is lower than the estimate of  $B_{3mm}$ . Note that while both panels a and b have the same estimates based on a 3-mm bin, the estimates based on a finer resolution are much lower or higher, depending on the distribution of counts. These examples illustrate how using the mean size of invertebrate prey vs. using fine or coarse size bins, may bias invertebrate prey biomass estimates passed as input data to fish drift-foraging models. While investigators may empirically estimate invertebrate prey biomass, thereby avoiding the potential bias discussed here, how this biomass is discretized into size bins can also potentially result in bias in drift-foraging models (see main text).



**B. 1** Hypothetical example demonstrating the effect of Jensen's inequality when calculating biomass of invertebrate prey distributed across several size classes.  $B_{1mm}$  is the estimated biomass using 1-mm size bins (representing the true biomass),  $B_{3mm}$  is the estimated biomass using 3-mm size bins, and  $B_{avg}$  is the estimated biomass using the mean size

In this paper we illustrate the potential bias in predicted fish growth resulting from summarizing invertebrate size structure at different scales using two salmonid drift-foraging bioenergetics models. We start by demonstrating how estimates of energy intake may be biased using a simplified example based on simulated data and then examine the bias using two case studies. In the first case study, a lifetime growth model developed by Hayes et al. (2000) and modified by Dodrill et al. (2016) is applied to rainbow trout (*Oncorhynchus mykiss*) in a large river. In the second, a drift-foraging bioenergetics model by Rosenfeld and Taylor (2009) is applied to estimate juvenile Chinook salmon (*Oncorhynchus tshawytsch*) growth potential (see Hafs et al. 2014).

## Methods

### Influence of alternative prey size distributions on energy intake

The foraging model proposed by Hughes and Dill (1990) serves as the basis for many drift-foraging applications. In this formulation, reactive distance has a linear relationship with prey size, and the foraging area is a nonlinear function of reactive distance, represented as the area of a half circle (Hughes and Dill 1990). We use the Hayes et al. (2000) foraging model, which is based on Hughes and Dill (1990) to demonstrate the influence of different representations of invertebrate prey on

predicted energy intake. The model is parameterized for brown trout (*Salmo trutta*) and estimates the energy intake of an average individual given attributes of the invertebrate prey (e.g., prey size, prey concentration and energy density) and water velocity estimates at a foraging location. We estimate water velocity at the focal point (holding position, near the bed) and invertebrate drift velocity following Hayes et al. (2000). For clarity, we focus on the foraging component of the model and predicted energy intake only in this first example. The estimated energy intake may exceed the predicted daily maximum consumption, yet this should not change the inferences from this exercise. Refer to Appendix A for an example using the same scenarios (described below) and the foraging model used by Rosenfeld and Taylor (2009).

We use a scenario approach to illustrate how different characterizations of invertebrate prey may lead to differences in predicted energy intake. For each set of scenarios, we consider three sizes of invertebrate prey (6, 7 and 8 mm) and distribute the prey concentrations or biomass between these sizes in four ways: (1) all in the middle size bin, (2) increasing proportions (1/12, 4/12, 7/12), (3) balanced proportions (1/4, 1/2, 1/4) and (4) decreasing proportions (7/12, 4/12, 1/12). In the first set of scenarios, we first estimate prey biomass given a constant prey concentration (1 individual per cubic meter) and the four different prey distributions (discussed above), then use these biomass estimates as input to the foraging model to estimate energy intake (kJ / day, S1, S2, S3, S4). To estimate prey biomass, we used the length-mass regression for Chironomids (Benke et al. 1999) and the prey sizes and distributions discussed above. For all scenarios an energy density of 22,694.02 joules per g dry mass is assumed (Cummins and Wuychek 1971). This set of scenarios shows how both the nonlinear length-mass relationship and the nonlinear equations within the foraging model can influence predicted energy intake.

In the second set of comparisons, we used a constant prey biomass estimate (from S2, above) and distributed the biomass in the four ways discussed above (S5, S6, S7, S8). The overall prey biomass is constant which illustrates the influence of only the nonlinear elements within the foraging model, replicating a situation in which the total or average prey biomass estimates are empirically measured by gathering many individuals and weighing them. By focusing on a constant biomass, these scenarios demonstrate the influence of the

nonlinear functions within the model singularly, in comparison to the first set of scenarios (S1, S2, S3, S4) where both the nonlinear length-mass regression and nonlinear functions within the model contribute to errors. For all of the scenarios, we estimate energy intake across a range of fish sizes from 5 to 300 g.

Case study 1: Influence of alternative prey size distributions on lifetime growth

### *Model overview*

We used the Hayes et al. (2000) drift-foraging model, originally developed for brown trout, parameterized for rainbow trout by Dodrill et al. (2016) to explore the effects of Jensen's inequality on predictions of life-time growth. Briefly, this model consists of a foraging model, a bioenergetics model, and an annual growth model. The foraging model estimates daily consumption based on drift concentrations, which is used by the bioenergetics model to estimate daily growth. The annual growth model tracks daily growth and applies reproductive costs after fish reach maturity. For additional model description, see Hayes et al. (2000) and Dodrill et al. (2016).

We apply this model to the Lees Ferry tailwater on the Colorado River downstream of Glen Canyon Dam, Arizona, U.S.A. This tailwater fishery provides both the physical and biological data necessary to explore how different summaries of invertebrate size structure influence predictions of life-time growth.

### *Invertebrate drift*

We used invertebrate drift data collected by a monitoring program which measured invertebrate drift at Lees Ferry (~25.5 km downstream of Glen Canyon Dam) approximately every month from 2009 to 2013 using the methods described in Kennedy et al. (2014). Samples were processed in the lab using nested sieves (1 mm and 250  $\mu$ m) and at 10X magnification all invertebrates retained in the coarse sieve were counted and measured (nearest 0.5 mm). For each sample, all invertebrates in the fine sieve (< 250  $\mu$ m) were counted and the first 30 were measured for length. This approach allowed us to summarize the invertebrate size distribution at a 1 mm resolution.

The foraging model estimates daily energy intake (consumption) using invertebrate drift concentrations (individuals · m<sup>-3</sup>), prey biomass (g dry weight), and energy density (calories · g<sup>-1</sup> dry weight). The biomass for each size bin was calculated using length-mass regressions taken from the literature (Benke et al. 1999) or developed for Lees Ferry for each taxon weighted by the taxon's proportion within each bin. We explore the bias associated with estimating prey biomass from measured lengths for a range of size binning strategies in Appendix B. The mean energy density was calculated using caloric equivalents for each taxa from the literature (Cummins and Wuychek 1971), weighted by each taxa's proportion within each bin.

### *Invertebrate drift scenarios*

We varied the invertebrate input while holding all other model input and parameters constant to compare two different strategies for summarizing the prey size distribution; 1-mm bins and 3-mm bins. Additionally, we ran the 1-mm bin model with the predicted prey biomass adjusted to match the 3-mm model and vice versa. This allowed us to compare predictions from both the 1- and 3-mm models at a common level of prey biomass, isolating the influence of nonlinear relationships within the model. For each model run, growth was simulated over a 6-year period, and initial fish weight was set to 1 g. For additional description of model settings and input, see Dodrill et al. (2016).

Case study 2: Influence of an alternative prey size distribution on juvenile growth potential

### *Model overview*

In order to explore the influence of prey size distribution on growth potential of juvenile fish, we adapted the model presented by Hafs et al. (2014) exploring the effects of woody debris on growth potential of juvenile Chinook salmon. Hafs et al. (2014) use predictions from a two-dimensional flow model across a range of woody debris loading to estimate growth potential over an 80-day simulation. The output from the flow model is used as input for a drift-foraging model developed and tested by Rosenfeld and Taylor (2009). We ported the original model provided as a Matlab script (see Hafs et al. 2014, supplement) to program R for all analyses (R Core Development Team 2014).

We used the original output from the Flow and Sediment Transport Morphological Evolution of Channels (FaSTMECH) model for the study reach presented in Hafs et al. (2014, data provided by the authors, personal communication, Andrew Hafs, Bemidji State University). Using the high wood loading scenario (12.3 m spacing, 10 m structure length, Hafs et al. 2014), we compared growth potential between the original invertebrate prey summaries used by Hafs et al. (2014) and a new prey scenario (see below).

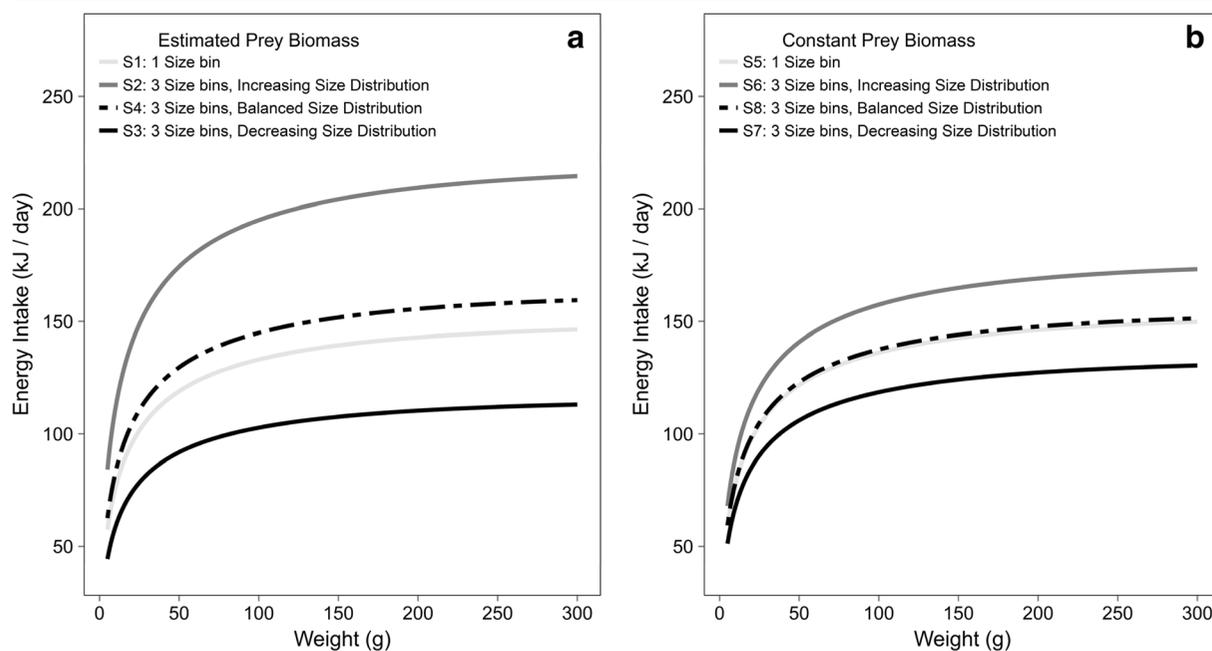
### *Prey scenario*

Hafs et al. (2014) use two aquatic insect taxa, *Baetis* and *Hydropsyche*, and calculated the mean drift concentrations for eight drift samples collected between April and June 2008, on the Merced River, California, USA. Juvenile salmon feed primarily on these two taxa within the study reach (Utz et al. 2012). Mean prey sizes of 3.7 and 8.3 mm were used for *Baetis* and *Hydropsyche*, respectively. We compare predicted growth potential estimated with the mean prey sizes with an alternative prey size distribution. For the alternative prey size distribution, invertebrate biomass was distributed between 5 size bins (1.7, 2.7, 3.7, 4.7, 5.7 mm for *Baetis* and 6.3, 7.3, 8.3, 9.3, 10.3 mm for *Hydropsyche*) with the proportions 0.1, 0.15, 0.2, 0.3, and 0.25 in each bin. These scenarios did not add any additional invertebrate biomass, but only distributed the biomass differently between size classes.

## **Results**

### Predicted energy intake and alternate prey distributions

Estimates of energy intake varied depending on how invertebrate prey were distributed between size bins, even when the starting concentration (Fig. 1, panel a) or the starting biomass were constant (Fig. 1, panel b). For the case where prey biomass was estimated from length (panel a), scenarios with three size bins resulted in 47 % higher, 9 % higher and 23 % lower estimates of energy intake relative to one size bin, for the increasing (S2), balanced (S3) and decreasing scenarios (S4), respectively. These differences were constant across a range of fish sizes. The scenarios where prey biomass was constant showed lower variation in predicted energy intake but a similar pattern to scenarios where



**Fig. 1** Energy intake (kJ/day) for a range of fish weight (g) predicted from the Hayes et al. (2000) foraging model. Comparisons are made between representations of invertebrate prey differing in the number of prey sizes and how prey are distributed between sizes. All scenarios in panel a have the same starting prey

concentration and prey biomass is estimated from the prey concentration and prey size using a length-mass relationship. All scenarios in panel b have the same starting prey biomass and differ in how this mass is distributed between prey sizes

biomass was estimated from length (Fig. 1, panel b). Absolute differences between scenarios were greatest at larger fish sizes (e.g., > 50 g), although the relative difference between scenarios was constant across fish size. The results from a similar foraging model used in Rosenfeld and Taylor (2009) show the same patterns (Appendix A, Fig. 4).

#### Case study 1: Influence of alternative prey size distributions on lifetime growth

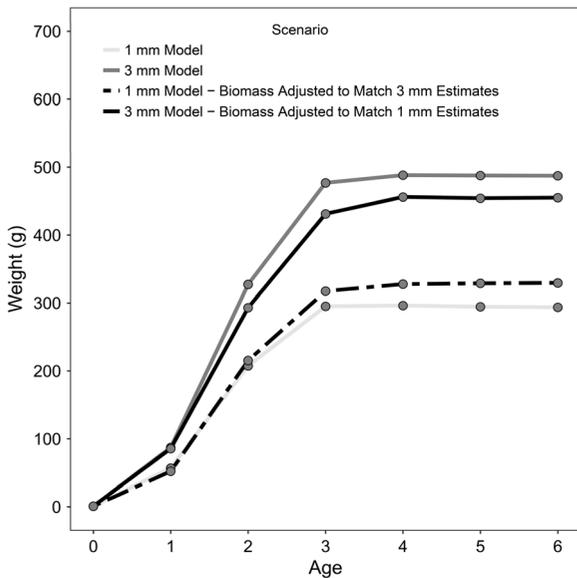
Predicted life-time growth of rainbow trout was higher when using 3-mm invertebrate size bins compared to 1-mm size bins (Fig. 2). When using 3-mm size bins, rainbow trout were predicted to reach a maximum size of 488 g, while using the 1-mm size bins rainbow trout were predicted to reach a maximum size of 296 g. Estimates of prey biomass using the 3-mm size bins are likely biased high compared to using the 1-mm size bins (Appendix B, Fig. 5). Differences in weight between scenarios increased as fish grew to maturity.

A scenario using 3-mm invertebrate size bins with the total prey biomass adjusted to match the predicted biomass under the 1-mm size bins resulted in lower

maximum size compared to the unadjusted 3-mm size bin model (a decrease of approximately 7%). The 1-mm model with prey biomass adjusted to match the predicted 3-mm prey biomass resulted in a larger maximum size compared to the unadjusted 1-mm model (an increase of approximately 12%). These differences were largely a function of the way in which prey biomass was calculated under the 1- and 3-mm scenarios. Differences between the 1- and 3-mm models at the same level of prey biomass were larger, resulting in 55% higher maximum weight under the 3-mm model with biomass adjusted to match the 1-mm model. Similarly, maximum weight was 45% less under the 1-mm model with biomass adjusted to match the 3-mm estimates.

#### Case study 2: Influence of an alternative prey size distribution on juvenile growth potential

Spatially explicit estimates of juvenile Chinook salmon growth potential over an 80-day simulation were similar between an alternative prey size distribution compared to using the mean prey sizes (Fig. 3, compare panel a with b). However, at a small number of locations, predicted growth potential was up to 98% higher when



**Fig. 2** Comparison of life-time predicted growth of rainbow trout using invertebrate prey discretized into either 1- or 3-mm prey size bins. Two curves are shown for the model based on 1- or 3-mm prey representations of prey. The remaining curves show the 1-mm model with prey biomass adjusted to match that predicted by the 3-mm model and vice versa

prey were distributed between five size bins compared to the baseline model using mean prey sizes (Fig. 3, lower plot). Most of the increases in growth potential with the model including five prey sizes came from cells where growth potential was low (generally <0.1 mm / day). Under these conditions, larger areas of habitat produced positive estimates of growth potential. Over the 80-day simulation, mean predicted growth potential was 1.7 mm greater with the five-size class distribution, compared to the growth potential based on mean prey size. In general, the differences in growth potential between the mean prey sizes and altered prey distribution were small for the small fish used in this case study.

**Discussion**

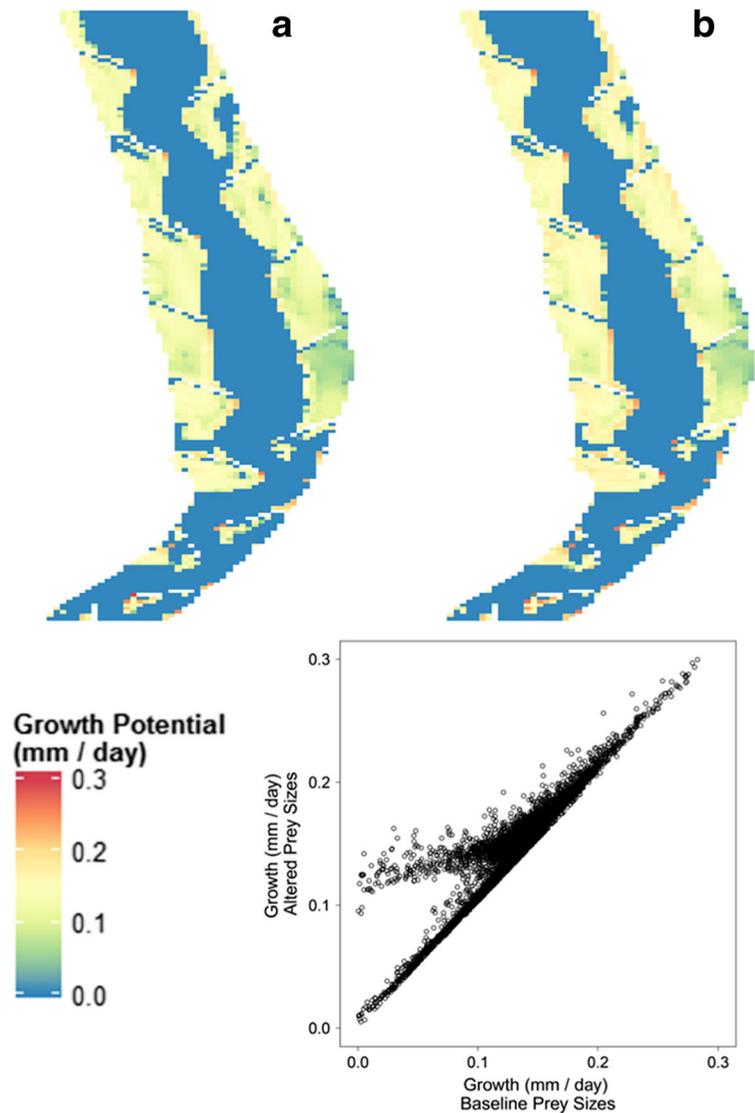
Biased estimates may arise in either the estimation of prey biomass (input to drift-foraging models) or within drift-foraging models as a result of the way that invertebrate prey is summarized. Estimation of prey biomass using the mean length versus finer length bins results in an under-estimation of prey biomass and the use of coarse length classes (i.e., 3-mm) can also result in biased estimates of prey biomass. The formulation of

foraging area, common to many drift-foraging models, can also introduce bias in the predicted energy intake of stream fish. For instance, when using a constant estimate of prey biomass as input to the foraging model used by Hayes et al. (2000), estimates of energy intake can vary from 110 kJ/day to 209 kJ/day for a 200 g fish, depending on how prey size is represented. In this example, an almost twofold difference in predicted energy intake results from alternative characterizations of the invertebrate size distribution, even with the same total biomass input to the foraging model. The bias in estimation of prey biomass using a nonlinear length-mass regression is additive to the bias observed in the foraging model. This result is demonstrated by the comparison between estimated energy intake for scenarios with constant and estimated prey biomass. Simulations of alternative ways to summarize invertebrate drift can be a powerful tool to identify potential bias in the application of drift-foraging bioenergetics models.

In our first case study, discretizing prey in either 3- or 1-mm size bins resulted in large differences in lifetime growth and predicted maximum size of trout. Under the 3-mm scenario, fish reached a maximum size of 488 g, 65 % higher than under the 1-mm scenario. Differences of this magnitude could potentially influence management recommendations based on drift-foraging models in applied settings. This highlights the importance of how invertebrate drift is summarized, an area of concern that has been raised elsewhere (Rosenfeld et al. 2014). While the estimation of prey biomass between the 1- or 3-mm size bins contributed to differences in lifetime growth, the nonlinear structure of the foraging model was also sensitive to the two representations of prey size structure. The larger effect was from how prey biomass was estimated, rather than from the foraging model. In our second case study, the growth potential of juvenile Chinook salmon was influenced by an alternative prey size distribution. Even with no increase in the prey biomass available to foraging fish, only distributing this biomass differently between sizes, some estimates of growth potential increased by up to 98 %. However, for the majority of locations, differences between the original estimates and an altered prey size scenario were small, partially due to the small sizes of juvenile fish considered.

Collecting and processing invertebrate drift samples to estimate biomass of invertebrate prey available to drift-foraging fish can be time consuming. When estimating biomass from measured lengths, a resolution of

**Fig. 3** Comparison of juvenile salmon growth potential calculated using mean prey sizes (panel a) and an alternative representation of invertebrate prey size for a woody debris loading scenario presented in Hafs et al. (2014). The prey were distributed between five size bins (centered on the mean) with proportions 0.1, 0.15, 0.2, 0.3, and 0.25 % (panel b). The plot below panel b shows a comparison between the alternative prey representation and the data shown in panel a



1 mm results in approximately unbiased estimates for a variety of prey size distributions (Appendix B). Whenever feasible, we suggest using 1-mm bins to summarize the size distribution of invertebrate drift. However, this resolution may not be practical in all instances and hybrid approaches where a portion of each sample is measured, characterizing the size distribution, while the whole sample is enumerated may offer a good compromise (Dodrill et al. 2016). In addition, we suggest the use of simulations to explore potential bias and guide field biologists in weighing different strategies for quantifying invertebrate drift.

Drift-foraging bioenergetics models can be widely applied to answer various questions and the importance of the bias introduced as a result of Jensen's inequality may depend on the application. For example, some applications use net energy intake (NEI) as an index of habitat quality (Urabe et al. 2010) or to assess habitat degradation (Urabe et al. 2014). In these applications, NEI is used in relative terms and if all estimates of NEI are biased in a similar manner, the overall effect of the bias on inferences may be trivial. In other applications, such as predicting abundance or reach-scale carrying

capacity (Hayes et al. 2007), the bias may lead to inaccurate predictions, contributing to the low correspondence of model predictions and observations shown in some studies (Wall et al. 2016). This is an important consideration in drift-foraging model validation studies, a research priority, particularly in novel locations (Rosenfeld et al. 2014).

Spatial variation in drift is a key factor influencing the distribution of stream fish which is being considered in more applications of drift-foraging models (Rosenfeld et al. 2014). Many applications assume that the spatial distribution of drift concentration is uniform (e.g. InSTREAM, Railsback et al. 2009), due to the added complexities and uncertainty of modeling spatial drift dynamics, including that caused by local depletion by feeding fish (Hayes et al. 2007). As more approaches consider spatial drift dynamics, an important consideration may be characterizing the variation in the invertebrate size distribution and the corresponding influences on modeling results. For example, the size distribution of drift may be more heavily weighted towards larger individuals near the bed, or head of pools, while locations higher in the water column may contain a larger proportion of smaller individuals. Such spatial asymmetries in drift size structure could result from prey size selection by drift feeding fish and invertebrate size-related swimming ability and settling velocities. We agree with Rosenfeld et al. (2014) that greater effort should be put towards characterizing invertebrate drift and highlight the characterization of invertebrate size distribution as an important consideration.

In the simulation example and both of the case studies that we consider, the drift-foraging models are based on the simple model presented by Hughes and Dill (1990). This foundational work on arctic grayling (*Thymallus arcticus*) has served as the basis for many subsequent drift-foraging models (see Piccolo et al. 2014). More recent work has focused on incorporating three-dimensional prey reaction volumes, the role of inedible debris, and incorporating prey detection functions thought to be important factors in development of more accurate drift-foraging models (Hughes et al. 2003; Piccolo et al. 2008; Neuswanger et al. 2014). While we have shown that variants of Hughes and Dill's model are sensitive to alternate representations of prey size, future drift-foraging models will be similarly sensitive. The importance of Jensen's inequality has been recognized

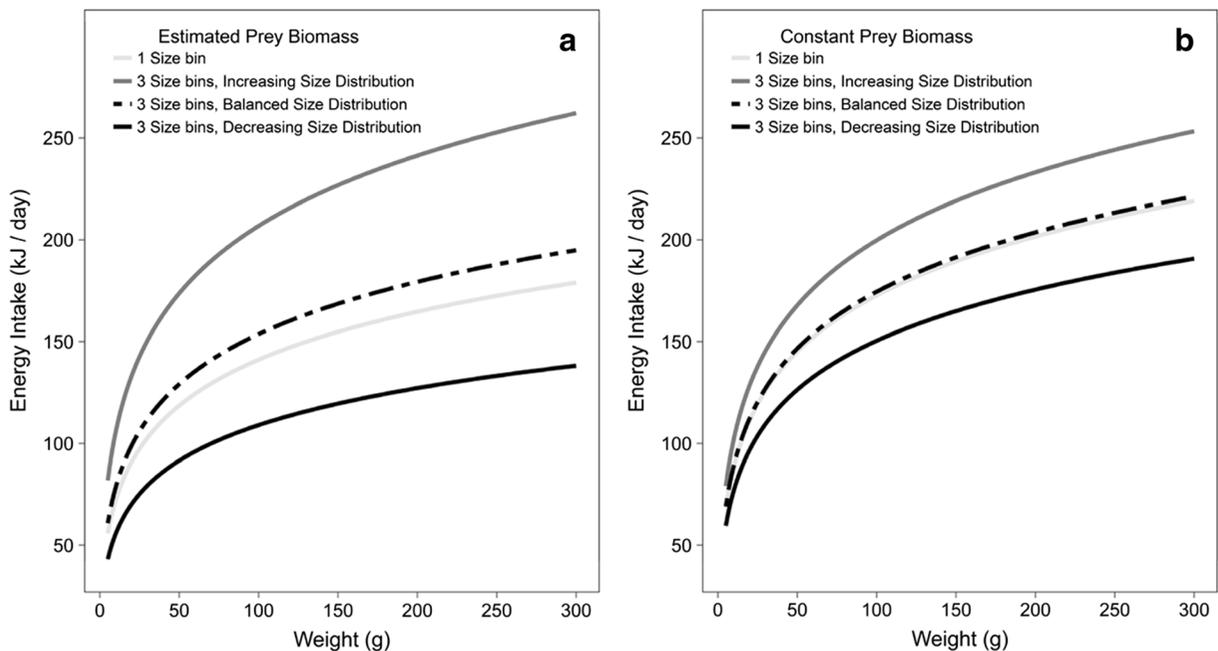
in many facets of terrestrial ecology. It deserves equal consideration in the application of drift foraging bioenergetics models, and aquatic ecology in general.

**Acknowledgments** We extend thanks to John Hayes, Andrew Hafs, Ted Kennedy, and Scott Vanderkooi whose insightful comments and suggestions considerably improved this paper. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Appendix A

We estimated fish energy intake for different summaries of invertebrate prey size using the foraging model developed by Rosenfeld and Taylor (2009) and applied by Hafs et al. (2014). The foraging model requires estimates of focal point velocities (position whereby fish hold, often near the bed) and velocity estimates of invertebrate drift in nearby faster velocity water. Hafs et al. (2014) used predicted velocities from a two-dimensional flow model to approximate velocities experienced by the fish. We used an equation based on Stewart (1980) to estimate focal point velocity, then a velocity differential based on Hayes and Jowett (1994) was applied to estimate the invertebrate drift velocity. The maximum swimming velocity was estimated using equations provided by Brett and Glass (1973). Rosenfeld and Taylor (2009) include a capture success function that adjusts the probability of intercepting prey to account for water velocity, fish size, and the distance of prey from the focal point. We did not use this capture success function and assumed that all prey items were captured (e.g. capture success = 1). Other parameters used in the foraging model were taken from Hafs et al. (2014). The same set of prey biomass distributions (see, methods) were used as input for the foraging model.

Under the Rosenfeld and Taylor (2009) foraging model, energy intake varied with how the prey biomass was calculated and with how prey was distributed between size bins (Fig. 4). The highest energy intake was under a scenario with the distribution of prey increasing between the three size bins and lowest estimates under a scenario with decreasing distribution (Fig. 4). The scenario with only one size bin resulted in intermediate energy intake and was similar to the scenario with three size bins and a balanced prey size distribution. These



**Fig. 4** Energy intake (kJ/day) for a range of fish weight (g) predicted from the foraging model used in Rosenfeld and Taylor (2009). Comparisons are made between representations of invertebrate prey differing in the number of prey sizes and how prey are distributed between sizes. All scenarios in panel a have the same

starting prey concentration and prey biomass is estimated from the prey concentration and prey size using a length-mass relationship. All scenarios in panel b have the same starting prey biomass and differ in how this mass is distributed between prey sizes

patterns were consistent regardless of whether prey biomass estimates were based on a constant concentration and varying prey sizes (Fig. 4, panel a) or prey biomass held constant but distributed differently between sizes (Fig. 4, panel b). However, in the former scenario, differences in energy intake between prey distributions were larger. Overall, the results were largely similar to those of the foraging model used by Hayes et al. (2000) and presented in the text (see Fig. 1).

### Appendix B

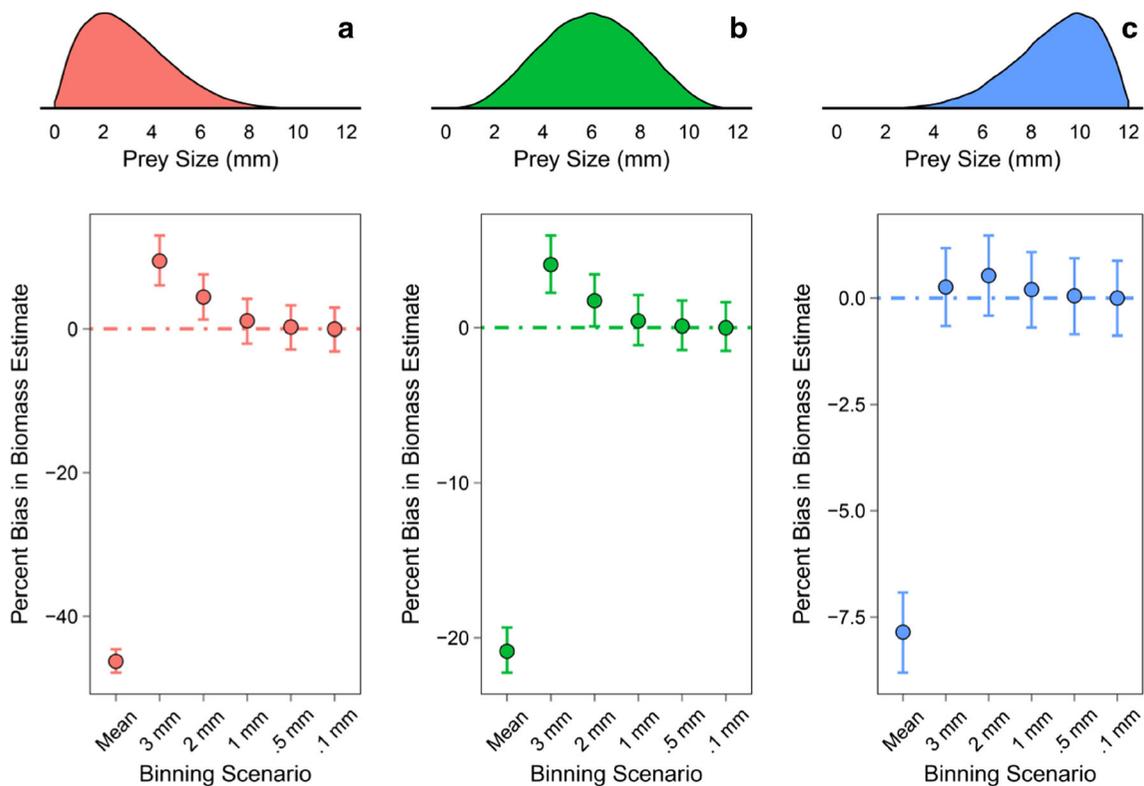
We use a simulation to explore the influence of alternative invertebrate prey size binning strategies on biomass estimates from measured lengths given a nonlinear length-mass regression. The common length-mass regression of the form:

$$W_i = a \cdot L_i^b$$

was used with parameters  $a = 0.012$  and  $b = 2.74$  for *Gammarus* spp. (Benke et al. 1999). We used the beta distribution to simulate the size distribution of invertebrates with a right skew (shape parameters 2, 6), centered (shape parameter 4, 4), and left skew (shape

parameters 6, 2). The beta distribution is bounded by 0 and 1, so we multiplied a constant (12) to simulate data over a range from 0 to 12 mm. We generated 10,000 random lengths and converted these lengths to mass, under each of the binning strategies and size distributions. This process was repeated 10,000 times and the mean and 95 % confidence intervals are presented for each scenario relative to the known true biomass estimate. This exercise was performed using the mean invertebrate size and five binning scenarios ranging from 0.1- to 3-mm size bins. The mid-points of the size bins were used when converting lengths to mass (e.g., size bin 0 to 3 mm, mid-point 1.5 mm).

Using the mean invertebrate size consistently underestimated the biomass across the three prey size distributions we considered (Fig. 5). The magnitude of the bias when using the mean invertebrate size is dependent on how the invertebrate sizes are distributed. The right skewed example underestimating the biomass by greater than 40 % (Fig. 5, Panel a). For the right skewed and centered examples, the 2- and 3-mm scenarios overestimate biomass, while for the left skewed example the 95 % confidence intervals overlap 0. Overall, the 1-mm size bins and smaller produced estimates that were



**Fig. 5** Percent bias in estimates of invertebrate biomass for alternative binning strategies (mean size down to 0.1-mm size bins) interacting with different invertebrate size distributions, right skewed (panel a), centered (panel b), and left skewed (panel c)

unbiased, regardless of how the sizes were distributed. Binning invertebrate drift collections at 1-mm intervals may be appropriate for many applications in order to balance precision in biomass estimates and efficiency of processing samples.

## References

- Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J N Am Benthol Soc* 18(3):308–343
- Brett JR, Glass NR (1973) Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J Fish Res Board Can* 30(3):379–387
- Cummins KW, Wuychek JC (1971) Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, no 18. E. Schweizerbart science publishers, Stuttgart, Germany, p 1–158
- Dodrill MJ, Yackulic CB, Kennedy TA, Hayes JW (2016) Prey size and availability limits the maximum size of rainbow trout in the Glen canyon dam tailwater: insights from a drift-foraging bioenergetics model. *Can J Fish Aquat Sci* 73(5):759–772
- Duursma RA, Robinson AP (2003) Bias in the tree model as a consequence of Jensen's inequality. *Forest Ecol Manag* 186(1–3):373–380
- Hafs AW, Harrison LR, Utz RM, Dunne T (2014) Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. *Ecol Model* 285:30–38
- Hayes JW, Hughes NF, Kelly LH (2007) Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecol Model* 207(2–4):171–188
- Hayes JW, Jowett IG (1994) Microhabitat models of large drift-feeding brown trout in three New Zealand rivers. *N Am J Fish Manag* 14(4):710–725
- Hayes JW, Stark JD, Shearer KA (2000) Development and test of a whole-lifetime foraging and bioenergetics model for drift feeding brown trout. *Trans Am Fish Soc* 129(2):315–332
- Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can Entomol* 91(5):293–320
- Hughes NF, Dill LM (1990) Position choice by drift-feeding salmonids—model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Can J Fish Aquat Sci* 47(10):2039–2048
- Hughes NF, Hayes JW, Shearer KA, Young RG (2003) Testing a model of drift-feeding using three-dimensional videography

- of wild brown trout, *Salmo trutta*, in a New Zealand river. *Can J Fish Aquat Sci* 60(12):1462–1476
- Jensen JLWV (1906) Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Mathematica* 30(1):175–193
- Kennedy TA, Yackulic CB, Cross WF, Grams PE, Yard MD, Copp AJ (2014) The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. *Freshw Biol* 59(3):557–572
- Neuswanger J, Wipfli MS, Rosenberger AE, Hughes NF (2014) Mechanisms of drift-feeding behavior in juvenile Chinook salmon and the role of inedible debris in a clear-water Alaskan stream. *Environ Biol Fish* 97(5):489–503
- Okuyama T (2008) Individual behavioral variation in predator-prey models. *Ecol Res* 23(4):665–671
- Piccolo JJ, Frank BM, Hayes JW (2014) Food and space revisited—the role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. *Environ Biol Fish* 97(5):475–488
- Piccolo JJ, Hughes NF, Bryant MD (2008) Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). *Can J Fish Aquat Sci* 65(2):266–275
- R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Railsback SF, Harvey BC, Jackson SK, Lamberson RH (2009) InSTREAM – The individual-based stream trout research and environmental assessment model. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif., p 254
- Rosenfeld JS, Bouwes N, Wall CE, Naman SM (2014) Successes, failures, and opportunities in the practical application of drift-foraging methods. *Environ Biol Fish* 97(5):551–574
- Rosenfeld JS, Taylor J (2009) Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. *Fish Manag Ecol* 16(3):202–218
- Ruel JJ, Ayers MP (1999) Jensen's inequality predicts effects of environmental variation. *Trends Ecol Evol* 14(9):361–366
- Stewart DJ (1980) Salmonid predators and their forage base in Lake Michigan – A bioenergetics-modeling synthesis. University of Wisconsin
- Urabe H, Nakajima M, Torao M, Aoyama T (2010) Evaluation of habitat quality for stream salmonids based on a bioenergetics model. *Trans Am Fish Soc* 139(6):1665–1676
- Urabe H, Nakajima M, Torao M, Aoyama T (2014) Application of a bioenergetics model to estimate the influence of habitat degradation by check dams and potential recovery of masu salmon populations. *Environ Biol Fish* 97(5):587–598
- Utz RM, Zeug SC, Cardinal BJ (2012) Juvenile Chinook salmon, *Oncorhynchus tshawytscha*, growth and diet in riverine habitat engineered to improve conditions for spawning. *Fish Manag Ecol* 19(5):375–388
- Wall CE, Bouwes N, Wheaton JM, Saunders WC, Bennett, SN. (2016) Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. *Can J Fish Aquat Sci* In Press