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ARTICLE

Using Survival Models to Estimate Invertebrate Prey Identification Times in a Generalist Stream Fish

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Abstract

Estimates of predator feeding rates are important for understanding trophic dynamics. One common method for quantifying feeding rates in fishes combines mass-based diet data with gastric evacuation times to estimate prey mass consumed per predator. An alternative approach is to estimate the rates of prey individuals consumed using prey identification time—the time period over which prey remain identifiable in a predator’s stomach. One challenge with the analysis of prey identification times, however, is that the response variable is likely to be censored because the “true” prey identification time cannot be observed directly. Here, we applied survival analysis that can incorporate censored data to estimate the effects of predator body size, water temperature, and prey characteristics (type, count, and body size) on identification times in Reticulate Sculpin *Cottus perplexus*. We focused on seven types of prey that are common in this generalist predator’s diet: mayflies (Ephemeroptera), caddisflies (Trichoptera), stoneflies (Plecoptera), true flies (Diptera), beetles (Coleoptera), worms (Annelida), and sculpin eggs. An information-theoretic model comparison approach indicated that an accelerated failure time Weibull model with all five covariates provided the best relative fit to the full data set. Prey type had a strong effect on prey identification time, with annelid worms having the shortest times (<1 h) and caddisflies having the longest times (>15 h). Water temperature decreased prey identification time (7.5% per 1°C increase), whereas prey count (i.e., meal size) increased prey identification time (15.5% per additional prey item). Predator body size had a weak negative effect on prey identification time (0.04% per 1-mm increase). Body sizes of some prey taxa, including mayflies, caddisflies, and stoneflies, increased prey identification times, leading to an interaction between prey type and prey size. Our study highlights the utility of survival analysis for quantifying variation in prey identification times in the diets of generalist predators.

Estimates of predator feeding rates are key to understanding how trophic interactions affect community dynamics and ecosystem functioning (de Ruiter et al. 1995; Link 2002). Bioenergetics models present one approach that can be used to estimate fish consumption rates, particularly when direct estimates of feeding rates are impractical (Chips and Wahl 2008). Alternatively, feeding rates can be estimated from predator diet data in the field. One method for estimating fish feeding rates combines mass-based representations of stomach content data obtained from field surveys with gastric evacuation rates of prey mass (e.g., Benkwitt et al. 2009; Facendola and Scharf 2012; Hughes et al. 2014; Haskell et al. 2017). The latter are obtained by regression using laboratory experiments in which the mass of prey in the stomachs of a sample of

individuals fed at known times is measured after varying lengths of elapsed time (Jobling 1986). The approach capitalizes on the fact that, on average, the rate at which prey mass is digested or passes out of the stomach must equal the rate at which prey mass is entering the stomach by consumption (Bajkov 1935; Eggers 1979; Bromley 1994). Gastric evacuation is often assumed to exhibit a linear, exponential, or square-root functional form, with models frequently incorporating effects of explanatory covariates, such as prey size, predator size, or temperature (Jobling 1986; Persson 1986; Richter et al. 2004).

Although gastric evacuation studies are commonly used to estimate mass-based feeding rates for fishes, their application may be challenging for certain study systems or research

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questions (Bromley 1994; Beaudreau and Essington 2009). For instance, because it is often difficult to distinguish prey material by species when viewed through the lens of prey mass, studies of gastric evacuation in fishes generally (1) involve feeding individuals a single prey item per trial and (2) consider a relatively low diversity of prey types (Bromley 1994). As a result, feeding trials involving a single prey item have the potential to bias feeding rate estimates if the digestion of one prey item is affected by the presence of other prey (Andersen and Beyer 2005). For some fish, such as generalist insectivores, this single-prey approach would be inconsistent with natural feeding patterns, and alternative approaches may be better. Additionally, predator individuals in an experiment that are sampled after complete digestion has already occurred present a challenge to the estimation of gastric evacuation rates by regression because their “true” evacuation times are unknown. Hence, prior studies either have discarded individuals with empty stomachs from analyses or have treated the sampling times as being representative of the true time to complete prey evacuation (Bromley 1994). Both approaches bias inferences, either because the fastest evacuation rates are selectively removed from the study or because evacuation times are overestimated as the gastric evacuation function approaches the x -axis (Olson and Mullen 1986; Bromley 1988, 1994).

An alternative to mass-based measures of feeding rate is the number of individual prey items consumed per predator per unit of time. The method for quantifying the rate at which prey items are consumed per predator relies on prey identification times rather than on gastric evacuation rates (Woodward et al. 2005; Novak and Wootton 2008; Novak et al. 2017). For instance, following Woodward et al. (2005) and Novak et al. (2017), feeding rates may be estimated as

$$\hat{f}_i = \frac{n_i}{p} \frac{1}{d_i}, \quad (1)$$

where \hat{f}_i is the population-level mean feeding rate, n_i is the number of prey items of species i that are found in a sample of p predator stomachs, and d_i is prey i 's estimated identification time (i.e., our focus in this paper). Prey identification time is defined as the period over which a prey item remains present and identifiable within the stomach of a predator. The equation permits the field-based estimation of predator feeding rates by using simple counts of identifiable prey items observed in a random sample of predator stomachs. Stomach content samples can be obtained from nonlethal gastric lavage during “snapshot” diet surveys of a predator population or from harvested individuals that are dissected in the laboratory. Samples of stomach contents could be further subdivided by covariates (e.g., predator size or sex) to examine variation within a population (e.g., Wolf et al. 2017). The estimation of prey identification times will typically require laboratory- or field-based feeding trials (see Methods below). Prey

identification times may be represented as means for a prey species or may be described by functions incorporating additional covariates (e.g., predator size, prey size, water temperature, etc.), as we do here. Feeding rates calculated by using this approach can then be used to quantify species interaction strengths in food webs or to inform bioenergetics models (when prey counts can be converted to biomass or energy).

Prey identification times are more conducive to calculating prey-specific feeding rates for generalist predators than methods based on gastric evacuation rates, particularly when unidentifiable prey are abundant and when the rate of prey individuals consumed—rather than total prey mass—is the metric of interest. This situation is common in studies of fishes that feed on a large diversity of small prey with potentially variable evacuation and identification times, such as benthic macroinvertebrates or plankton (e.g., Allan 1981). Applications of gastric evacuation models have frequently ignored this prey-specific variation, instead focusing on a predator's total feeding rate summed over all prey types (e.g., Benkwitt et al. 2009; Facendola and Scharf 2012; Haskell et al. 2017). In contrast, the presence of unidentifiable prey in a predator's stomach is irrelevant to the approach based on prey identification times (Woodward et al. 2005; Baker et al. 2014; Novak et al. 2017). Identification times will be shorter than or equal to mass-based gastric evacuation times because prey items can become unidentifiable prior to complete evacuation.

A key challenge to determining prey identification times is that it is impossible to directly observe when prey items become unidentifiable. Instead, it is feasible to observe only the identification status (identifiable or unidentifiable) of prey items that are recovered from a predator's stomach. With this response variable, the data are binary rather than continuous as in gastric evacuation studies. The true prey identification times are unknown, occurring either before or after the sampling time point (i.e., the data are right-censored or left-censored, respectively). Survival analysis offers a solution for estimating prey identification times with censored data (Klein and Moeschberger 2005; Kleinbaum and Klein 2006). Survival analysis involves the fitting of a survival function, usually by using methods of maximum likelihood. The survival function describes the probability that a given prey item will remain identifiable beyond a given time. The survival function has a corresponding hazard function describing the probability that a given prey item will become unidentifiable in the next time instant given that it is still identifiable (which in turn is based on a probability density function describing the probability of prey becoming unidentifiable at a given time). A prey item's identification times reflect the expectation (i.e., mean) of its probability density function conditioned on explanatory covariates.

We used survival analysis to estimate prey identification times for seven types of prey that were fed to a generalist predator, the Reticulate Sculpin *Cottus perplexus*. The prey

included nymphs of mayflies (Ephemeroptera) and stoneflies (Plecoptera); larvae of caddisflies (Trichoptera), true flies (Diptera), and beetles (Coleoptera); worms (Annelida); and Reticulate Sculpin eggs (hereafter, sculpin eggs). For most feeding trials, individual fish were fed multiple taxa (orders) of prey, paralleling natural feeding patterns. In addition to characterizing the variation in prey identification times among prey types, we also examined the effects of prey size, prey count, predator size, and temperature on identification times. We predicted that prey size and count would increase the prey identification time, whereas predator size and temperature would decrease the prey identification time (Bromley 1994).

METHODS

Study system.—The Reticulate Sculpin inhabits small streams west of the Cascade Range in Oregon, Washington, and northern California (Bond 1973). Various aspects of its ecology have been studied, including its life history (Bond 1963), habitat associations (Roni 2002), trophic ecology (Phillips and Claire 1966; Pasch and Lyford 1972), interactions with co-occurring species (Brocksen et al. 1968; Finger 1982), and reproductive biology (Bateman and Li 2001). We collected extensive data on Reticulate Sculpin diets in three streams near Corvallis, Oregon, over three seasons and found that they consumed at least 60 different taxa of aquatic invertebrates (our unpublished data). These data informed the prey items on which we focused our laboratory feeding trials (see Table 1 for prey details).

Field collections.—We collected Reticulate Sculpin and prey from Berry, Oak, and Soap creeks in Oregon State University's McDonald-Dunn Research Forest northwest of

Corvallis (44.638°N, 123.292°W). All three streams are small (~2-m width) and well oxygenated, and they flow through mixed coniferous forests into larger tributaries of the Willamette River. To collect Reticulate Sculpin, we utilized a backpack electroshocker (Smith-Root LR20B), a block net (1.0 × 1.0 m), and dip nets (0.30 × 0.25 m) that were positioned downstream of the electroshocker in fast-moving water. Fish were collected in batches of approximately 30 individuals during September, October, and November 2015 and in April 2016 (14 total collections). The size range of collected fish represented the size range observed in the streams except that we excluded individuals less than approximately 25 mm, as performing gastric lavage to obtain gut contents from individuals of this size is difficult. Captured fish were rejuvenated in oxygenated stream water and then transported to the laboratory. Prey were collected at the same times and locations as Reticulate Sculpin by using kick sampling with dip nets and block nets. All prey types except annelid worms *Lumbriculus variegatus* were collected in the field. Annelid worms were purchased from a supplier (California Blackworm Co., Fresno).

Feeding trials.—Reticulate Sculpin were acclimated to dechlorinated water in the laboratory for up to 5 h before being transferred into aquaria holding 4.0 L of water (30 cm long × 20 cm high × 15 cm wide). Each aquarium was fitted with an air stone and was covered on the sides with paper to prevent the fish from seeing one another. Aquaria were kept within a temperature-controlled environmental chamber on a 12-h light : 12-h dark cycle. Feeding trials were conducted in batches of approximately 30 individually housed fish, across which temperatures of the aquaria were varied from 10.4°C to 20.2°C (mean = 14.2°C) by using a combination of heated water baths and variation in the air temperature of the chamber. This temperature range reflects the observed range of water temperatures over the course of the year in the local streams where Reticulate Sculpin and their prey were collected (our unpublished data). Aquarium water temperatures were recorded using electronic loggers ($n = 8$) that were placed in a subset of aquaria during each set of trials (TidBit loggers; Onset Computer Corp., Bourne, Massachusetts). The mean values from the temperature loggers and the number of feeding trials at each temperature were as follows: 10.4°C ($n = 79$), 10.5°C ($n = 57$), 12.5°C ($n = 58$), 12.6°C ($n = 68$), 13.3°C ($n = 4$), 13.6°C ($n = 84$), 14.4°C ($n = 79$), 16.0°C ($n = 74$), 16.1°C ($n = 63$), 17.3°C ($n = 23$), 17.6°C ($n = 80$), 17.9°C ($n = 4$), and 20.2°C ($n = 32$).

We began each feeding trial after the fish had been acclimated without food for 3 d to ensure empty stomachs. Food was administered between 0730 and 2300 hours. The type and body length of each prey item were recorded immediately before the time of feeding (Table 1). Body lengths of mayflies and stoneflies excluded the cerci. We repeatedly placed live prey items individually in front of each fish by using a plastic pipette, recording the time at which each prey item was ingested. The number of prey items fed per fish (i.e., the prey count) ranged from 1 to 7, and each prey item fed to an

TABLE 1. Summary of the prey types, sample sizes, body sizes, and families of prey that were fed to Reticulate Sculpin in laboratory feeding trials. Multiple families were included within some orders as follows: mayflies (Ameletidae, Baetidae, Heptageniidae, and Leptophlebiidae), caddisflies (Calamoceratidae, Glossosomatidae, Hydropsychidae, and Rhyacophilidae), stoneflies (Perlidae, Perlodidae, Nemouridae, and Chloroperlidae), true flies (Chironomidae, Simuliidae, Athericidae, Ceratopogonidae, and Tipulidae), annelid worms (Lumbricidae), and beetles (Elmidae).

Prey identity	Sample size	Minimum length (mm)	Maximum length (mm)	Mean (SD) length (mm)
Mayflies	141	0.5	9.0	5.35 (1.59)
Caddisflies	116	2.0	15.0	5.75 (2.46)
Stoneflies	106	2.0	22.0	8.2 (3.20)
True flies	148	2.0	26.0	6.06 (4.07)
Annelid worms	74	4.0	52.0	25.4 (8.27)
Beetles	51	1.5	4.0	2.87 (0.66)
Eggs	57	3.0	3.0	3

individual fish belonged to a different order. For caddisflies, we removed the larvae from their cases because the fish typically refused to eat them when they were inside cases, and stomach contents from Reticulate Sculpin collected in the field suggested that they rarely consumed the cases. The size of the prey item, the size of the predator, and the water temperature of the feeding trial were varied in a randomized manner for each batch of feeding trials, reflecting the treatment of all predictors as continuous variables in our analysis. After subsequent time periods varying in length from 10 min to 31 h postfeeding, we used gastric lavage to recover the remaining prey items. This involved the use of Aquí-S (Bowker et al. 2017) as an anesthetizing agent and the use of a 60-cm³ syringe fitted with a blunt, 18-gauge needle. Water was syringed into the stomach of each fish, and prey items were collected into a tray, filtered through a coffee filter (Melitta brand), and preserved in ethanol for inspection under a dissecting microscope. The time of lavage, wet mass, and total body length of each fish were recorded.

A co-author who had extensive experience identifying each of these prey types in sculpin diets but who had no knowledge of the specific prey type(s) fed to each fish then examined the stomach contents under a dissecting microscope (8–35× magnification), considering an invertebrate prey item to be “identifiable” based on whether the head, thorax, and/or abdomen remained and whether features of these body parts allowing identification to the order level persisted (see Supplementary Figure S.1 available in the online version of this article for examples of identifiable and unidentifiable prey). For arthropod prey, the head typically persisted in the stomach longer than other body parts, making it the focal point of most designations. We generally did not base the designations for arthropods on other “minor” body features alone (in absence of head, thorax, and abdomen), such as legs, wing pads, mouthparts, antennae, or cerci. For sculpin eggs, the prey item was considered identifiable if it maintained its color and spherical shape, which were distinct from those of other possible prey items. Annelid worms were considered identifiable if there were clear signs of segmentation, if chaetae were present, or both. We note that the key to using equation (1) to estimate feeding rates is that any prey items in a predator’s stomach from the field are identified and counted in a manner that is consistent with their designation during the estimation of identification times in the laboratory. The efficacy of lavage was assessed on a subset of 10 fish that were euthanized and dissected. We did not find prey items in the stomachs of any of these fish.

Analyses.—Our primary aims in the analysis were to determine which of four candidate survival models provided the most parsimonious description of our data and to quantify the importance of prey type, prey count, prey size, predator size, and water temperature in driving the variation in prey identification time. To accomplish the first

aim, we first assessed the general appropriateness of parametric survival models by graphically comparing a nonparametric Kaplan–Meier model to four candidate parametric models, which are described below (Klein and Moeschberger 2005). After this initial comparison, we focused on parametric survival models because they can accommodate both right- and left-censored observations within a regression framework, and they allow for the incorporation of random effect terms (often referred to as a “frailty” terms in survival analysis) to account for the nonindependence of multiple prey items per individual fish. Although nonparametric models are more flexible in the shape of their survivorship function, they are unable to accommodate both right- and left-censored data in a regression framework and cannot incorporate random effects (Klein and Moeschberger 2005; Kleinbaum and Klein 2006). The preliminary graphical model comparison that included the nonparametric models therefore omitted covariates and random effect terms.

We compared the relative performance of the four parametric models more formally using Akaike’s information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2010), thereby placing emphasis on both parsimony and the predictive capacity of the considered models (Aho et al. 2014). The four parametric models that we compared entailed lognormal, log-logistic, Weibull, and exponential survival functions. Survival functions, written as $S(t) = P(T > t)$, describe the probability of an event that takes place at time T occurring after time point t . In our context, the survival function describes the probability that a prey item remains identifiable beyond the sampling time t . For the lognormal distribution, the survival function is

$$S(t) = 1 - \Phi \left[\frac{\log_e(t) - \mu}{\sigma} \right], \quad (2)$$

where $\Phi(\cdot)$ is the cumulative density function of the standard normal, μ is the mean of $\log_e(t)$, and σ is the variance of $\log_e(t)$. Hence, this model assumes that the time it takes prey items to transition from identifiable to unidentifiable (i.e., $\log_e[t]$) follows a lognormal distribution. The corresponding hazard function—describing the probability that a given prey item will become unidentifiable in the next time instant given that it is still identifiable—is hump-shaped, starting at zero, increasing to a maximum, and then again approaching zero as the prey item continues to be digested.

The survival function of the log-logistic distribution is

$$S(t) = \frac{1}{1 + \lambda t^\alpha}, \quad (3)$$

where λ is the scale parameter, specifying the “characteristic life” of a prey item’s identifiability; and α denotes the shape parameter. When $\alpha < 1$, the hazard function decreases monotonically

with time; when $\alpha > 1$, the hazard function is hump-shaped. The log-logistic model assumes that $\log_e(t)$ follows a logistic distribution.

The survival function of the Weibull model is

$$S(t) = \exp(1 - \lambda t^\alpha), \quad (4)$$

where λ denotes the scale parameter and α represents the shape parameter. The hazard rate increases with time when α is greater than 1 and decreases with time when α is less than 1. The Weibull model reduces to the exponential model when α equals 1, reflecting decay at a constant hazard rate equaling λ , as is commonly assumed in many gastric evacuation studies (Persson 1986).

Note that the above parameterizations of the parametric survival models follow Klein and Moeschberger (2005); alternative formulations are common. For instance, in R, both the “rweibull” function (in the “stats” package) and the “Survival” package (Therneau 2015) use different parameterizations of the Weibull’s survival and hazard functions.

We next describe how covariates were considered in our analyses, and we use the accelerated failure time version of the Weibull model to illustrate. The accelerated failure time extension of the Weibull model allows the scale parameter λ to vary in response to covariates that can either “accelerate” or “decelerate” the survival function by specifying

$$\lambda = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p), \quad (5)$$

where the β terms are regression coefficients associated with each of p different X covariates. Interpretation of the regression coefficients is eased by conveying them as “acceleration factors,” expressed as $\exp(\beta)$. These reflect the proportional change in an event time due to a unit increase in the covariate relative to a baseline survival rate (Kleinbaum and Klein 2006).

We compared the aforementioned parametric models in the full data set with all prey types together as well as in seven prey-specific models that included each prey type separately. After our initial graphical comparison of parametric versus nonparametric models, we included covariates for predator size, prey size, prey count, and water temperature in all subsequent models. In the model with all prey together, we included a random effect term for individual fish identity and a categorical covariate for prey type (mayfly, caddisfly, stonefly, true fly, annelid worm, beetle, or sculpin egg). This random effect term was not included in the prey-specific models because multiple prey items of the same type were not fed to the same predator. We predicted that the effect of prey size would be dependent on the type of prey, so we also included a prey type \times prey size interaction in the full data set model. We then compared the relative importance of all five covariates in the full data set model using AIC_c . We compared the

performance of eight total models: a full model with all five covariates and the prey type \times prey size interaction, a model with all five covariates but lacking the interaction term, an intercept-only null model, and five models in which one of the five covariates was dropped. We assessed potential collinearity in predictor variables using graphical analyses and Pearson’s product-moment correlation coefficients (Figures S.2, S.3).

The analysis of the full data set allowed us to test for differences in identification times between prey types and to compare the importance of prey type relative to the other covariates. The taxon-specific models were then included with the aim of using these models for future prediction of prey identification times when calculating prey-specific feeding rates from field data. Analyses were conducted in the R computing environment (R Core Team 2014) by utilizing the “Survival” package (Therneau 2015).

RESULTS

In total, we quantified prey identification status for 705 individual prey items that were fed to 237 Reticulate Sculpin (Table 1). The number of prey fed per fish ranged from 1 to 7 (mean = 2.9 prey; SD = 1.4). Reticulate Sculpin varied in body length from 32 to 104 mm (mean = 54.7 mm; SD = 8.6). The overall number of prey fed to predators was 141 mayflies, 106 stoneflies, 116 caddisflies, 148 true flies, 51 beetles, 74 annelid worms, and 57 sculpin eggs. Prey varied in body length from 0.5 to 55 mm (mean = 7.8 mm, SD = 7.3; Table 1).

Support for the Weibull model was expressed by its estimated survival curves aligning closely with those inferred using the nonparametric Kaplan–Meier estimates (Figure S.4) and by the relationship between the log negative-log of survival time (i.e., $\log_e\{-\log_e[S(t)]\}$) and \log_e (event time) being roughly linear (Figure S.5). The Weibull distribution performed better than the other parametric models when considering all prey types in one model, exhibiting an AIC_c difference (ΔAIC_c) value of 17.23 relative to the next-best model and hence an AIC_c weight (w_i) of 0.99 (reflecting the conditional probability that it was the best-performing model; Supplementary Table S.1). When applied to each prey type separately, the Weibull was the top-performing model for five prey types (mayflies, stoneflies, true flies, beetles, and sculpin eggs) and performed similarly well to the top-performing model for the other two prey types ($\Delta AIC_c \leq 1.65$ for all models; Table S.1).

The full accelerated failure time Weibull model with all five covariates (prey type, prey count, prey size, predator size, and water temperature) and the prey type \times prey size interaction was the top-performing model relative to models that dropped any of the covariates ($w_i = 0.93$; Table 2). Excluding the prey type covariate had the largest effect on relative model fit, with a ΔAIC_c value of 279.7 relative to the full model. Prey size ($\Delta AIC_c = 115.7$ relative to the full model) and water

TABLE 2. Comparisons of accelerated failure time models predicting identification probabilities for all prey items collectively that were fed to Reticulate Sculpin (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c value between the given model and the best-performing model; w_i = Akaike weight). The full model included predator body size (mm), water temperature ($^{\circ}C$), prey body size (mm), prey count (number of prey per individual predator), prey type, and the prey size \times prey type interaction. The null model did not include any of those covariates. Each model included a random effect term for predator identity.

Model	AIC_c	ΔAIC_c	Log likelihood	w_i
Full model	423.4	0.0	-95.8	0.93
Full model without fish size	428.9	5.5	-96.5	0.06
Full model without prey count	432.7	9.3	-96.4	0.00
Full model without temperature	443.3	19.9	-98.1	0.00
Full model without interactions	499.5	76.1	-131.6	0.00
Full model without prey size	539.1	115.7	-177.4	0.00
Full model without prey type	703.1	279.7	-344.6	0.00
Null model (intercept only)	732.3	308.9	-363.7	0.00

temperature ($\Delta AIC_c = 19.9$) were the next most important covariates, followed by prey count ($\Delta AIC_c = 9.3$) and Reticulate Sculpin body size ($\Delta AIC_c = 5.5$). Dropping the interaction term decreased the model fit substantially ($\Delta AIC_c = 76.1$), indicating that the effect of prey size was dependent on the type of prey. Other than the full model, the only other model with a nonzero w_i was the model that excluded the predator body size covariate ($w_i = 0.06$). The worst-performing model included only an intercept term, with a ΔAIC_c of 308.9 relative to the top model.

When interpreted as acceleration factors, the estimated coefficients of the full model indicated that a one-unit increase in prey count increased the prey identification time by 15.5% (95% confidence interval [CI] = 7.8–23.8%). In contrast, a unit increase in temperature ($^{\circ}C$) decreased the prey identification time by 7.5% (95% CI = -10.7% to -4.1%). Over the range of Reticulate Sculpin sizes investigated, an increase in predator size by 1 mm weakly decreased the prey identification time by 0.04% (95% CI = -1.4% to 0.006%).

The covariate effects in the prey-specific models were relatively consistent with the covariate effects inferred from the full data set (Table 3). In general, covariate effects on mayflies, caddisflies, and stoneflies were more consistent than the covariate effects on true flies, worms, beetle larvae, and sculpin eggs. The former three taxa showed the largest effects of prey size, leading to a prey type \times prey body size interaction effect on identification time. Point estimates for the Weibull model's shape parameter varied from 0.80 to 5.42 across prey types, while point estimates for the scale parameter varied from 2.8×10^{-6} to 1.28 (Table 3). Mean prey identification time for each prey type correspondingly ranged from less than 1 h to over 15 h (Table 3; Figures 1, 2). The shortest prey identification times were those estimated for annelid worms (mean of the probability density function = 0.8 h; Figures 1E, 2E), followed by mayflies (mean = 5.8 h; Figures 1A, 2A), sculpin eggs (mean = 9.8 h; Figures 1G, 2G), true flies (mean = 10.0 h; Figures 1D, 2D), beetles (mean = 11.0 h; Figures 1F, 2F), and stoneflies (mean = 11.3 h; Figures 1B, 2B). The longest prey identification times were those estimated for caddisflies (mean = 15.7 h; Figures 1C, 2C). The overall mean for all prey was 9.2 h (Figures 1H, 2H).

DISCUSSION

Our study demonstrates the utility of survival analysis for estimating prey identification times when data with covariates are censored. Such data present a challenge for the traditional

TABLE 3. Accelerated failure time Weibull model parameters for each prey type fed to Reticulate Sculpin. Each model included water temperature ($^{\circ}C$), prey size (mm), prey count, and predator size (mm) as covariates. The scale parameter (λ) and shape parameter (α) of the Weibull models; the mean of the probability density function (i.e., mean prey identification time); and the acceleration factors (95% confidence interval [CI] in parentheses) for each covariate are shown. Sculpin egg size did not exhibit sufficient variation to be retained in the model.

Prey type	λ	α	Time (h)	Acceleration factor (95% CI)			
				Temperature	Prey size	Prey count	Predator size
Mayflies	4.9×10^{-4}	4.12	5.76	0.97 (0.92–1.02)	1.22 (1.11–1.34)	1.12 (1.01–1.23)	0.98 (0.97–1.00)
Caddisflies	3.5×10^{-4}	2.77	15.73	0.89 (0.84–0.95)	1.16 (1.08–1.26)	1.03 (0.91–1.16)	0.99 (0.97–1.02)
Stoneflies	8.1×10^{-5}	3.73	11.27	0.90 (0.85–0.95)	1.21 (1.13–1.28)	1.07 (0.95–1.21)	0.97 (0.95–0.99)
True flies	1.1×10^{-2}	1.86	10.04	0.95 (0.91–1.00)	1.02 (0.97–1.08)	1.21 (1.07–1.37)	0.99 (0.98–1.01)
Annelid worms	1.28	0.80	0.83	1.09 (0.84–1.43)	1.07 (0.98–1.17)	1.28 (0.85–1.92)	0.98 (0.90–1.06)
Beetles	8.4×10^{-3}	1.89	10.99	0.97 (0.89–1.06)	1.03 (0.68–1.56)	1.14 (0.86–1.50)	1.02 (0.99–1.05)
Eggs	2.8×10^{-6}	5.42	9.77	0.91 (0.86–0.96)	NA	0.93 (0.72–1.20)	0.99 (0.98–1.02)

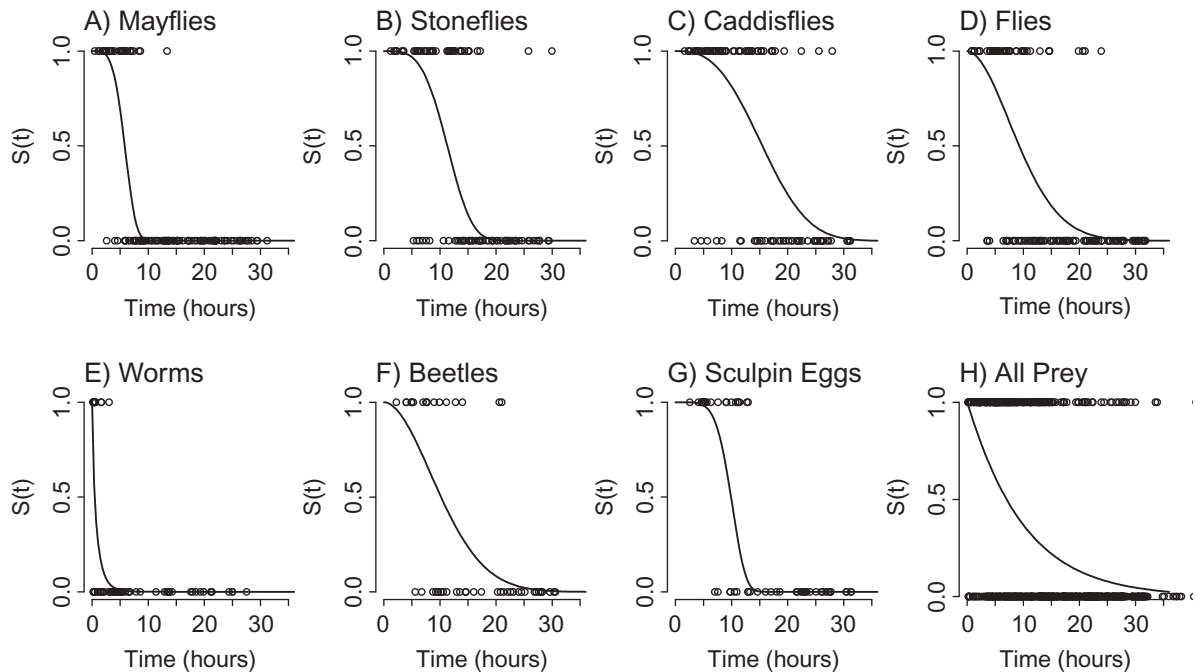


FIGURE 1. Survival functions for seven prey types fed to Reticulate Sculpin in the laboratory, including (A) mayflies (Ephemeroptera), (B) stoneflies (Plecoptera), (C) caddisflies (Trichoptera), (D) true flies (Diptera), (E) worms (Annelida), (F) beetles (Coleoptera), (G) sculpin eggs, and (H) all prey collectively. The y -axis indicates the probability ($S(t)$) that a prey item will remain identifiable beyond the corresponding time point. The observed data are shown on each plot, with the fitted model curve corresponding to the best-fitting accelerated failure time survival function assuming a Weibull distribution. Each function is shown for the mean covariate values within each prey type. In panel H, the function that is shown omits the categorical prey type covariate.

regression approaches used in gastric evacuation studies. Specifically, by including all of the censored data in an accelerated failure time Weibull model, we were able to estimate the effects of covariates and avoid biases associated with truncating the data set or omitting unidentifiable prey. Focusing on prey identification times rather than on changes in prey mass also facilitated the use of multiple prey types per predator, increasing the consistency of our experiments with the feeding patterns that predator individuals exhibit in nature.

The use of parametric accelerated failure time models has several advantages over using alternative approaches for estimating prey identification times. Unlike nonparametric or semiparametric models (e.g., Cox proportional hazards), parametric models can handle left-, right-, and interval-censored data (Kleinbaum and Klein 2006). They can also permit the inclusion of random effects, which are useful when multiple prey items are fed to a single fish—a factor that is often ignored in gastric evacuation studies (e.g., Andersen 1999). Another useful feature is that model-derived estimates of acceleration factors allow for interpretation of covariate effects in an intuitive way. Acceleration factors less than 1 indicate that a given covariate has a negative relationship with prey identification time; acceleration factors greater than 1 indicate that the covariate has a positive relationship with prey identification time. Extrapolations of covariate effects are also simplified. For

instance, while an acceleration factor of 0.96 for temperature indicates that a 1°C increase relative to a baseline temperature would result in a new prey identification time that is 4% shorter, a 3°C increase in temperature would shift the baseline prey identification time by $0.96^3 = 0.89$ (i.e., an 11% decrease). Acceleration factors can also be easily used to compare prey identification times between categorical prey types relative to either a mean prey identification time for all prey items or a baseline prey type. Acceleration factors therefore provide a simple way to apply the effects of covariates from laboratory trials to the estimation of feeding rates with covariates using data from field surveys.

Nevertheless, accelerated failure time survival models also require making several assumptions, the validity of which must be evaluated. Among the primary disadvantages associated with such models is that assuming an inappropriate parametric distribution can lead to inaccurate inference. Additionally, models use covariate information to adjust the scale parameter but not the shape parameter of (for example) the Weibull model. This can be problematic when the shape parameter differs across covariate values or categorical groups. For the Weibull model, the validity of this assumption may be assessed by plotting $\log_e\{-\log_e[S(t)]\}$ against \log_e (time) because the slope of this relationship corresponds to the shape parameter (Figure S.5; Kleinbaum and Klein 2006). Importantly, taxonomic variation in the shape parameter was

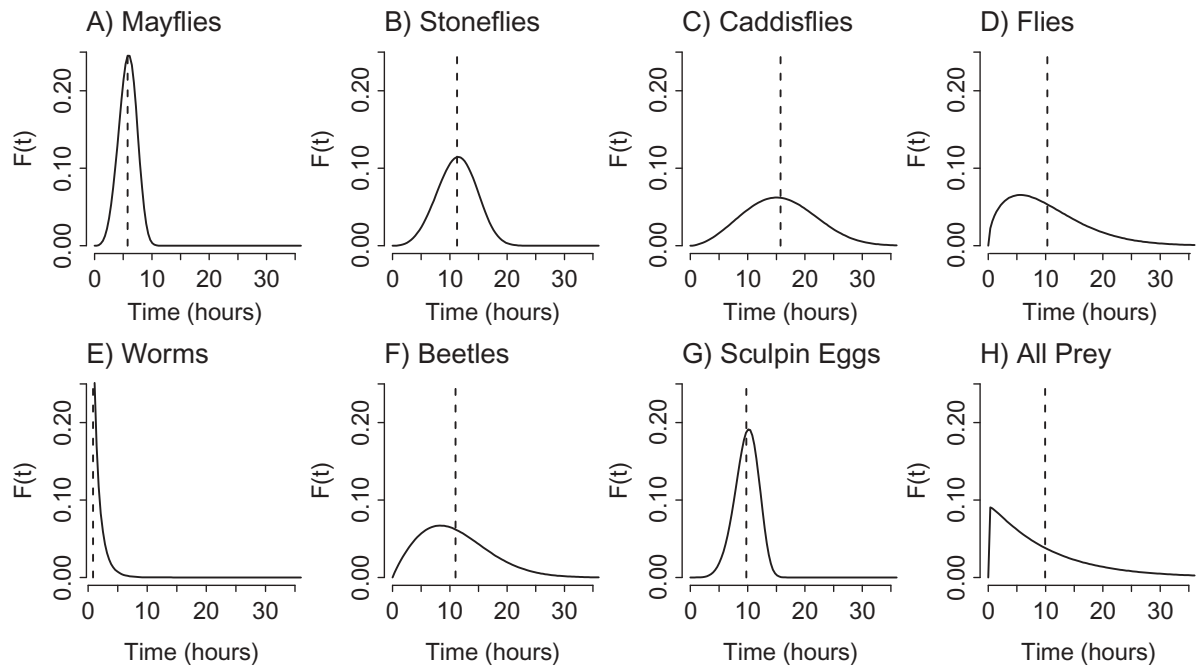


FIGURE 2. Probability density functions for seven prey types fed to Reticulate Sculpin in the laboratory, including (A) mayflies (Ephemeroptera), (B) stoneflies (Plecoptera), (C) caddisflies (Trichoptera), (D) true flies (Diptera), (E) worms (Annelida), (F) beetles (Coleoptera), (G) sculpin eggs, and (H) all prey collectively. The y-axis indicates the probability ($F(t)$) of a prey item becoming unidentifiable at the corresponding time point. The dashed vertical lines correspond to the expectation (i.e., mean) of the probability density function.

masked in our full model that included all prey types together, highlighting the use of prey-specific models for prediction of prey identification times within our data set.

In our study, the Weibull model performed better than three alternative parametric models in characterizing prey identification probabilities. The Weibull's shape parameter was estimated to be greater than 1 for all prey types except annelid worms (Table 3), indicating that the hazard rates associated with becoming unidentifiable increased the longer a prey item was in a predator's stomach. This inference is consistent with the process of prey digestion removing identifiable features at an increasing rate over time. By contrast, the lognormal and log-logistic models implied that the probability of prey becoming unidentifiable first increased then decreased at the later stages of digestion (i.e., the hazard functions were unimodal). The exponential model, reflecting a constant, time-independent probability of becoming unidentifiable rather than a constant rate of digestion per se, could not accommodate the high prey identification probabilities in the earliest hours of digestion, when prey remained identifiable for some time after consumption. The Weibull model accommodates this early persistence of identifiability. We note that gastric evacuation studies have occasionally found a similar type of lag in the mass change of prey items (Hopkins and Larson 1990; Rogers and Burley 1991; Beaudreau and Essington 2009).

The effects of temperature, prey size, and predator size estimated in our study are relatively consistent with past

work on gastric evacuation rates in fishes (Bromley 1994). The negative effect of temperature has been demonstrated in many other studies and is often modeled by assuming an exponential relationship with evacuation rate (e.g., Elliott 1972; Persson 1981; Amundsen and Klemetsen 1988; Miyasaka et al. 2005). We found a positive effect of prey size in the full data set. This was driven primarily by three prey types: mayflies, caddisflies, and stoneflies. These groups had a relatively large range of prey sizes compared to some other groups that did not show strong effects of prey size on identification time (i.e., larval beetles). Although the prey sizes were relatively consistent with the prey size distributions that we have observed in Reticulate Sculpin diet samples from the field, a wider range of prey sizes for some taxa may have increased the effect of this variable on identification time. However, the Reticulate Sculpin in our study were often uninterested (or unsuccessful) in consuming the largest prey items, thereby placing an upper limit on the size of some prey. Our results for the effect of prey size contrast with one prior study involving macroinvertebrate prey: Elliott (1972) reported that there was no discernable effect of prey size on evacuation rates for amphipods (*Gammarus* spp.), mayflies (*Baetis* spp.), or midges (Chironomidae) that were fed to Brown Trout *Salmo trutta*, although this may have been due partly to the limited size range within a given prey taxon.

The covariate with the weakest effect in our study was predator body size. We note that the size range of Reticulate

Sculpin (32–104 mm) did not include very small young-of-the-year individuals, as it was not possible to perform non-lethal gastric lavage on those fish; their inclusion could have driven a stronger effect of predator size on prey identification times. If more statistically powerful comparisons were made across different fish taxa or within species having more widely ranging sizes, it is likely that predator size would have a stronger effect. Past studies have often found either no effect or a negative effect of predator size on evacuation rates, but the strength of the relationship appears to vary greatly across predator taxa (Jones 1974; Santos and Jobling 1991; Andersen 1999). In our study, some prey types (i.e., annelid worms and sculpin eggs) had relatively low variability in their identification times and did not exhibit strong effects of any covariates. These prey types were also among the most rapidly digested, with the least potential variation in prey characteristics, such as body size and the proportion of hard versus soft parts.

We found a relatively strong effect of prey count (i.e., meal size in terms of the number of individual prey items) on prey identification time, with increasing meal size associated with longer times. The effects of multiple meals and multiple prey taxa on prey identification times remain relatively little studied, with some evidence suggesting that the presence of multiple meals accelerates gastric evacuation times (Jones 1974) or that the net effect depends on characteristics of the prey (e.g., size, energy content, and resistance to digestion; Andersen and Beyer 2005). Other work has also found that early meals are evacuated more rapidly when subsequent meals are provided, but the overall evacuation time of the entire food mass is unchanged (Elliott 1991). We note that the number of prey fed per fish in our trials (mean of ~3) provided greater realism than feeding only a single prey item but was still lower than the typical number of prey items per Reticulate Sculpin in our field data set (mean of ~10; our unpublished data). Future studies that include a greater range of prey per predator and higher prey diversity would be useful to test for nonlinearities in the digestion process driven by these factors.

Differences in identification time between prey types were likely the result of differences in hard body parts that affect digestion rates. The shortest identification times (<1 h) were observed for soft-bodied annelid worms. Prey with hard head capsules (e.g., true flies and caddisflies) or extensive exoskeletons (e.g., stoneflies) were identifiable for longer periods of time, typically exceeding 10 h. Head capsules of chironomid midge larvae fed to Slimy Sculpin *Cottus cognatus* were found to pass through the digestive tract intact and appear in the fish's feces (Hershey and McDonald 1985). When fly larvae and caddisflies were identifiable at later stages of digestion in our study, their bodies were usually completely digested, but the head capsules remained (see Figure S.1 for examples). We did not examine the feces of Reticulate Sculpin for the presence of head capsules, but it is likely that some of the head capsules passed through intact. Differences in digestion rates

between soft-bodied and hard-bodied invertebrates are largely consistent with past work on other types of prey as well. For instance, digestion trials using in vitro stomach acid solutions demonstrated that soft-bodied marine invertebrates (i.e., jellyfish) are digested much more rapidly than prey items with hard parts (i.e., crustaceans and fish; Jackson et al. 1987). Similarly, studies of gastric evacuation in marine fishes have shown that worms and small fish are evacuated two to five times faster than crustaceans with hard exoskeletons (Jones 1974; Singh-Renton and Bromley 1996; Andersen 1999). The chitinous exoskeletons of isopods have also been found to persist longer than their soft body parts within the gut of Rainbow Trout *Oncorhynchus mykiss* (Kionka and Windell 1972).

Prior studies on digestion in other sculpin species (Family Cottidae) provide information for comparison with our results. For instance, Andersson et al. (1986) reported that approximately half of the amphipods *Gammarus pulex* fed to European Bullheads *Cottus gobio* were identifiable after 6 h at 15°C. This prey identification time is comparable to those observed for some of the invertebrates in our study, such as mayflies. Another study (as mentioned above) found that the head capsules of chironomid larvae passed through the stomach and intestines and into the feces of Slimy Sculpin after approximately 24 h at 16°C (Hershey and McDonald 1985). This is longer than the prey identification time we estimated for true flies (10 h) but is consistent in that the time to passage in feces must be longer than the identification time in the stomach (i.e., due to time spent in the intestines). Other studies at lower temperatures than those used in our experiments have detected much longer prey persistence times in sculpin (Miyasaka et al. 2005; Mychek-Londer and Bunnell 2013). For example, Mychek-Londer and Bunnell (2013) found that *Mysis* shrimp and trout eggs persisted in the gut of Slimy Sculpin and Deepwater Sculpin *Myoxocephalus thompsonii* for as long 5–10 d at approximately 3°C. Lastly, Western (1971) found that *Tubifex* worms were no longer recognizable at 13 h postingestion in European Bullheads at 10°C, although it appears that the stomachs were not examined prior to this time point. Collectively, these studies suggest that digestion rates in different sculpin taxa are comparable and that differences due to temperature, prey taxon, and the methodology of experiments may be responsible for much of the variation observed to date. This emphasizes the point that (1) detection time experiments performed in the laboratory should reflect the typical conditions experienced by a focal predator species when field-based diet surveys are performed or (2) the relationships between detection time and other putative covariates should be characterized over a range of covariate values reflecting the range in the field.

Several factors likely contributed to unexplained variation in prey identification times that was not captured by our models and covariates. For a given prey type (e.g., stoneflies), we included multiple different taxa of prey from within the same taxonomic order, but often they were from different

families. This diversity is likely to be associated with variation in prey characteristics that can affect digestion and hence identification time. For instance, several prey types exhibit considerable variation in the amount of hard, sclerotized parts across families and species (e.g., baetid mayflies versus heptageniid mayflies). There were also differences in surface-to-volume ratios (e.g., tipulid fly larvae versus chironomid fly larvae) and perhaps in energy content, which are both thought to affect digestion rates (Jobling 1987; Salvanes et al. 1995; Andersen and Beyer 2005). Specific tissue composition (e.g., lipids versus proteins) also has potential to drive variation in identification time (Jobling 1987). Lastly, it is possible that seasonality, photoperiod, or both could drive physiological or behavioral mechanisms that indirectly influence digestion processes. In our study, we combined data from fish that were collected at different times of the year (fall and spring).

The use of prey identification times for the estimation of feeding rates requires a consistent definition of “identifiable” that could vary with logistical constraints, among personnel, and with the ecological question of interest. For example, fine-scale taxonomic resolution of prey will often require the use of taxonomic features that are rapidly lost during digestion. Hence, a reliance on fine-scale anatomical features for identification will ultimately result in shorter prey identification times. Shorter identification times in turn will result in smaller numbers of identifiable prey in field diet samples, necessitating a greater sample size of predator individuals to achieve a representative picture of the predator population’s feeding habits. It is therefore important to consider the balance between feasible taxonomic resolution for prey identification, sample sizes of prey items in the field, and data requirements for answering a given question of interest. For example, in our field data set, we observed over 60 prey taxa, most of which could be identified to the family level (our unpublished data). However, the streams where we collected Reticulate Sculpin are known to support more than 325 species of aquatic invertebrates (Anderson and Hansen 1987), many of which require significant technical expertise to identify to the species level (e.g., chironomid midges). This challenge makes it unlikely that species-level identifications will be practical for our diet data and obviates the need for species-level prey identification times. However, in other study systems, it may be feasible and advantageous to develop species-specific prey identification models. Generally, the lower the taxonomic resolution of the estimated identification times, the more likely it is to mask true taxonomic variation in feeding rates because prey with widely differing identification times will be lumped together.

Our study highlights the large variation in identification times that can exist among prey taxa consumed by a generalist predator and demonstrates the utility of survival analysis for estimating identification times. Future work should aim to incorporate additional mechanistic models for prey identification times that can incorporate censored data in a survival analysis framework. For instance, models including

surface area dependence and the dynamics related to the concurrent digestion of multiple prey items should serve to further improve identification time and feeding rate inferences (Andersen and Beyer 2005). Furthermore, estimates of prey identification time would benefit from increased consistency between the field conditions where inferences of feeding rates are to be made and the laboratory conditions under which digestion and identification times are studied. The effects of stress levels, reproductive cycle, and environmental variables in addition to temperature (e.g., light, water movement, availability of cover, etc.) have the potential to influence digestion processes and may be inconsistent between the field and laboratory. Conducting prey identification time studies or gastric evacuation rate studies in the field or under more field-like conditions (e.g., mesocosms) could assist in overcoming such challenges. Lastly, assessing the generality of the mechanisms affecting digestion and differences in underlying rates across fish species should be a priority. Although many mechanisms are likely consistent (e.g., temperature dependence), the degree to which prey identification times and digestion rates can be extrapolated across fish taxa deserves further attention.

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