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Niche variation in burying beetles (*Nicrophorus* spp.) associated with marine and terrestrial carrion

M.D. Hocking, C.T. Darimont, K.S. Christie, and T.E. Reimchen

Abstract: Ecological opportunity can influence niche variation within and among species. Forensic reconstruction of diet has been made possible with the now widespread use of stable isotope analysis, although it has not to date been applied to communities based on carrion resources. Within a salmon-bearing watershed in coastal British Columbia, we reconstructed the dietary niches of two burying beetle species (Silphidae: *Nicrophorus investigator* Zetterstedt, 1824 and *Nicrophorus defodiens* Mannerheim, 1846) using stable isotopes (δ^{15}N, δ^{13}C). We separated available carrion sources for beetles of chum salmon (*Oncorhynchus keta* (Walbaum, 1792)) and pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)), the shrew *Sorex monticolus* Merriam, 1890, songbirds (*Troglodytes troglodytes* (L., 1758), *Catharus ustulatus* (Nuttall, 1840), *Catharus guttatus* (Pallas, 1811)), and black-tailed deer (*Odocoileus hemionus hemionus* (Rafinesque, 1817)) into three isotopically homogeneous subsets: (1) salmon, (2) shrews and songbirds, and (3) deer. The majority (86.5%) of *N. investigator* individuals were raised on a diet of salmon carrion, while 100% of *N. defodiens* individuals had a larval diet consistent with carrion from shrews and songbirds. Larger isotopic variance predicts wider dietary niches, which may be useful for testing functional ecological variation within and among species.

Résumé : En écologie, les occasions peuvent influencer la variation de niches entre les espèces ou chez une même espèce. La reconstitution forensique du régime alimentaire est maintenant possible à l'aide des méthodes courantes d'analyse des isotopes stables, bien que celles-ci n'aient pas encore été appliquées à des communautés utilisant des charognes comme ressource alimentaire. Dans un bassin versant contenant des saumons de la région côtière de la Colombie-Britannique, nous avons reconstitué les niches alimentaires de deux espèces de nécrophores (Silphidae : *Nicrophorus investigator* Zetterstedt, 1824 et *Nicrophorus defodiens* Mannerheim, 1846) à l'aide d'isotopes stables (δ^{15}N, δ^{13}C). Nous avons séparé les sources de charognes disponibles aux coléoptères, soit les saumons kéta (*Oncorhynchus keta* (Walbaum, 1792)) et roses (*Oncorhynchus gorbuscha* (Walbaum, 1792)), les musaraignes *Sorex monticolus* Merriam, 1890, les passereaux chanteurs (*Troglodytes troglodytes* (L., 1758), *Catharus ustulatus* (Nuttall, 1840), *Catharus guttatus* (Pallas, 1811)) et le cerf à queue noire (*Odocoileus hemionus hemionus* (Rafinesque, 1817)) en trois sous-ensembles homogènes d'après leur isotopes : (1) les saumons, (2) les musaraignes et les passereaux et (3) les cerfs. La majorité (86,5 %) des individus de *N. investigator* se développent à partir d'un régime de charognes de saumons, alors que la totalité (100 %) des individus de *N. defodiens* ont un régime alimentaire larvaire compatible avec la charogne de passereaux et de musaraignes. Une variance isotopique élargie laisse croire à une niche alimentaire plus vaste et cela peut être utile pour tester la variation écologique fonctionnelle chez les espèces individuelles et entre les espèces.

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Introduction

Niche variation within and among species has been conventionally studied using dietary analyses, habitat choice, and phenotypic variation in trophic structures and body size (Grant 1968; Roughgarden 1974; Schoener 1986). In carrion communities, niche distribution can occur along dimensions of season, habitat, and carcass size or succession, with species partitioning typically determined using standard field collections or laboratory experiments (Anderson 1982; Kneidel 1984; Hanski 1987). In communities of burying beetles (Silphidae: genus *Nicrophorus* Fabricius, 1775), carcass size can be an important determinant of species partitioning and breeding success (Trumbo 1992; Smith and Heese 1995; Scott 1998).

As an alternative to traditional approaches of niche characterization, stable isotope analysis of animal tissues can provide a forensic a posteriori measure of dietary niche, par-

M.D. Hocking.[1] Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.
C.T. Darimont, K.S. Christie, and T.E. Reimchen. Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC V8W 3N5, Canada.

[1]Corresponding author (e-mail: mhocking@sfu.ca).

ticularly if the isotopic signatures of food sources are known (Bearhop et al. 2004). Nitrogen and carbon isotopes have been used to measure dietary variation, trophic structure, and sources of nutrients and energy within populations and communities (Vander Zanden et al. 2000; Kelly et al. 2004; Podlesak et al. 2005), although to date isotopes have not been applied within carrion communities. Populations with larger isotopic variance are expected to have wider niches, provided that the range of available diet items is the same (Bolnick et al. 2003; Matthews and Mazumder 2004).

Here, we reconstruct the larval carrion diet in two species of burying beetles (*Nicrophorus investigator* Zetterstedt, 1824 and *Nicrophorus defodiens* Mannerheim, 1846) from a salmon-bearing watershed in coastal British Columbia using stable isotope analysis. These two species are the only *Nicrophorus* documented from this region (Anderson and Peck 1985). Burying beetles typically bury and prepare small vertebrate carcasses to raise their young, and can successfully breed on small-mammal carrion such as shrews (Smith et al. 2000), as well as the carcasses of terrestrial and marine birds (Holloway and Schnell 1997; Wilhelm et al. 2001). *Nicrophorus investigator* has also been recently observed breeding on large Pacific salmon (genus *Oncorhynchus* Suckley, 1861) carcasses from multiple coastal watersheds (Hocking et al. 2006). Salmon carcasses provide a nutritionally valuable and predictable marine resource throughout the west coast of North America and influence the life histories of potentially hundreds of species (Reimchen 2000; Gende et al. 2002; Stockner 2003). We hypothesized that black-tailed deer (*Odocoileus hemionus hemionus* (Rafinesque, 1817)), a common large mammal in the region, may also be a feeding resource for *Nicrophorus* species, as gray wolves (*Canis lupus* L., 1758) commonly leave deer remains for scavengers (Darimont et al. 2007). Although *N. defodiens* has not been previously observed from salmon carrion, the basic problem is that the larval carrion source is not known when adult beetles are collected. Accordingly, we collected tissue samples from the shrew *Sorex monticolus* Merriam, 1890), songbirds (*Troglodytes troglodytes* (L., 1758), *Catharus ustulatus* (Nuttall, 1840), *Catharus guttatus* (Pallas, 1811)), deer, and chum (*Oncorhynchus keta* (Walbaum, 1792)) and pink (*Oncorhynchus gorbusha* (Walbaum, 1792)) salmon. We classified both *Nicrophorus* species based on a larval diet that we inferred from stable isotope analysis to differentiate among individuals which used potential terrestrial carrion or salmon remains.

An important consideration here relates to tissue turnover and the seasonality of sampling. Isotope signatures in insects can be affected by season of collection, particularly when diets vary over time or between larval and adult life stages (Tallamy and Pesek 1996; Fischer et al. 2004). We previously observed no seasonal variation (summer to fall) in isotope signatures in *N. investigator* (Hocking et al. 2006) and conclude that adult whole body isotope signatures predominantly reflect their larval diet. As a further test, we examine potential spring to summer seasonal variation in *N. defodiens*. Burying beetles typically feed on carcass resources for several weeks prior to sexual maturity (Trumbo 1997), although adult diet may be largely allocated to adult activity and tissues used in reproduction (Fischer et al. 2004).

Materials and methods

This study was conducted from 2000 to 2003 on the Clatse River (52°20.6′N, 127°50.3′W), a relatively undisturbed watershed near Bella Bella, on the central coast of British Columbia, Canada (Hocking and Reimchen 2002, 2006; Hocking et al. 2006). Chum and pink salmon spawn from late August to late October, with populations of black bears (*Ursus americanus* Pallas, 1780) and gray wolves acting as the principal vectors of salmon carcasses into the forest.

From late July to mid-August of 2000 and 2003, at least 2 weeks before salmon enter the watershed, we collected both *N. investigator* ($n = 80$) and *N. defodiens* ($n = 50$) individuals in ground-level baited pitfall traps (2000) or hanging baited traps (2003) from sites within 20 m of the river. All captured adults were stored in 70% ethanol. To provide a seasonal comparison, additional *N. defodiens* ($n = 8$) were collected in spring 2001 (mid-June). Overall, no spring to summer isotopic variation was observed (δ^{15}N: $t_{[56]} = 0.87$, $p = 0.417$; δ^{13}C: $t_{[56]} = 1.29$, $p = 0.201$).

We collected tissue samples from a range of potential carrion sources in the Clatse watershed, including marine (salmon) and terrestrial carrion. In autumn of 2001, dorsal muscle samples of chum and pink salmon ($n = 6$ for each species) were collected from recently senesced carcasses. Shrews ($n = 19$) were collected in pitfall traps in August of 2000 and June and September of 2001 (Hocking and Reimchen 2002), reflecting the seasonality and location of *Nicrophorus* sampling. In the fall of 2003, songbirds were captured using mist nets (banding permit No. 10429AL, scientific permit No. 59-03-0396) from sites that coincided with *Nicrophorus* collections. Multiple generations of feathers were sampled from hatch-year *T. troglodytes* ($n = 4$), *C. ustulatus* ($n = 2$), and *C. guttatus* ($n = 6$) undergoing their first prebasic moult. From each individual, we collected summer-grown tail feathers, grown while in the nest after hatching, and autumn-grown body feathers, identified as new owing to the presence of a sheath partially enclosing the feather. We used the mean signatures across seasons to best represent potential resources sampled by *Nicrophorus* species. Hair from black-tailed deer ($n = 9$) was sampled from day beds in late May and early June along random 1 km upslope transects starting at sea level or low-elevation roads and often terminating in the subalpine (Darimont et al. 2007). Sampled winter pelage of deer grows from mid-July to the end of October and is carried through the winter.

Whole *Nicrophorus* specimens and salmon muscle tissue were rinsed with distilled water and then dried at 60 °C. Samples were ground into a homogeneous powder using a Wig-L-Bug® grinder (Crescent Dental Co., Chicago, Illinois). Songbird feathers and mammal hair samples were rinsed with distilled water, soaked in a 2:1 chloroform: methanol solution for 24 h, and then dried at 60 °C. Feathers and hair were then chopped into small fragments and loaded into tin capsules. All samples (approximately 1 mg) were assayed for total N, δ^{15}N, total C, and δ^{13}C, at the University of Saskatchewan Stable Isotope Facility, by continuous flow – isotope ratio mass spectrometry (CF–IRMS). Measurement precision is approximately ±0.35‰ for ^{15}N and ±0.10‰ for ^{13}C.

Nicrophorus specimens and salmon muscle tissue δ^{13}C

Table 1. Tissue standardization procedures (muscle, hair, feathers, whole beetles) and resulting isotopic modifications of sampled consumers in burying beetles (*Nicrophorus* species) and their potential carrion prey (salmon (*Oncorhynchus keta* and *Oncorhynchus gorbusha*), the shrew *Sorex monticolus*, songbirds (*Troglodytes troglodytes*, *Catharus ustulatus*, *Catharus guttatus*), and black-tailed deer (*Odocoileus hemionus hemionus*)).

Tissue or organism	Standardization	Isotopic modification (‰)		References
		δ^{15}N	δ^{13}C	
Salmon muscle	Lipid standardization of δ^{13}C	—	–0.76±0.06	McConnaughey and McRoy 1979
Shrew hair	Diet–hair$_{\text{FRACTIONATION}}$ > diet–muscle$_{\text{FRACTIONATION}}$	—	–1.5	Roth and Hobson 2000
Songbird feathers	Diet–feather$_{\text{FRACTIONATION}}$ > diet–muscle$_{\text{FRACTIONATION}}$	–2	—	Vanderklift and Ponsard 2003
Deer hair	Diet–hair$_{\text{FRACTIONATION}}$ > diet–muscle$_{\text{FRACTIONATION}}$	—	–1	Sponheimer et al. 2003
Nicrophorus beetles	Lipid standardization of δ^{13}C	—	1.17±0.04	McConnaughey and McRoy 1979
	Tissue–diet$_{\text{FRACTIONATION}}$ from whole beetle to muscle diet	–2	0	Scrimgeour et al. 1995; Ostrom et al. 1997

values were lipid-normalized based on equations derived from McConnaughey and McRoy (1979) (also Satterfield and Finney 2002):

$$[1] \qquad L = \frac{93}{[1 + (0.246CN - 0.775)^{-1}]}$$

$$[2] \qquad \delta^{13}C' = \delta^{13}C + D\left[-0.207 + \frac{3.90}{(1 + 287/L)}\right]$$

where L is percent lipid, $\delta^{13}C'$ is the lipid-normalized δ^{13}C value for each individual, CN is the carbon to nitrogen ratio, and D is the depletion of ^{12}C (‰) relative to protein and assigned a value of 6‰. In the absence of standard lipid extraction procedures, lipid normalization has been used to standardize δ^{13}C values to a constant low-lipid content more indicative of a protein rather than a lipid metabolism pathway (for new model developments see Kiljunen et al. 2006).

We used Pearson's correlation to test whether lipid transformation had an effect on the relationship between δ^{13}C and C/N ratios. High C/N ratios can indicate high lipid content with depleted δ^{13}C (Kiljunen et al. 2006). Unstandardized δ^{13}C values were negatively correlated to tissue C/N ratios in both *Nicrophorus* species (*N. defodiens*: $R = -0.407$, $p = 0.002$; *N. investigator*: $R = -0.397$, $p < 0.001$), and lipid transformation changed the slopes so that they were not different from zero (*N. defodiens*: $R = -0.030$, $p = 0.825$; *N. investigator*: $R = -0.138$, $p = 0.211$).

Hair and feather samples were not lipid-normalized, although several modifications were needed to most accurately reflect the stable isotope signatures of potential resources of sampled consumers (i.e., muscle tissue) (Table 1). Hair δ^{13}C values in shrews were reduced by 1.5‰ to approximate muscle tissue, since diet–fur fractionation is higher than diet–muscle fractionation by ~1.5‰ in mammalian carnivores (Roth and Hobson 2000). We similarly reduced δ^{13}C values in deer hair by 1‰ to approximate muscle tissue (mammalian herbivores: Sponheimer et al. 2003). For birds, diet-to-tissue fractionation of δ^{15}N is higher (~2‰) in feathers than in muscle tissue (Vanderklift and Ponsard 2003). Accordingly, we applied a 2‰ correction factor.

Diet source for *Nicrophorus* species was determined using a hierarchical cluster analysis that included both burying beetle species and their potential carrion sources. Cluster classification was based on Euclidean distance from cluster centers using the within-group linkage method. We used the number of homogeneous subsets of potential carrion prey (Tukey's post hoc) as the most parsimonious choice for the total number of clusters of beetles and their carrion prey.

To match adult burying beetle signatures to their potential carrion prey in the cluster analysis, we needed to apply a correction based on estimated diet–tissue fractionation. There have been only a few studies that have investigated dietary fractionation in adult Coleoptera. We use values reported in predaceous lady bird beetles (1.2‰–1.7‰ for δ^{15}N (Scrimgeour et al. 1995); 2.9‰ ± 0.3‰ for δ^{15}N, –0.2‰ ± 0.1‰ for δ^{13}C (Ostrom et al. 1997)) as our best available comparison. From these values, we assume that diet–tissue fractionation in *Nicrophorus* is approximately 2‰ for δ^{15}N and 0‰ for δ^{13}C (Table 1). All analyses were conducted using SPSS® version 11.0 (SPSS Inc. 2001).

Results

Potential carrion sources for *Nicrophorus* species differed in both δ^{15}N and δ^{13}C isotopic signatures. Salmon had the highest values, and deer the lowest (ANOVA for both isotopes: $F_{[3,48]} > 56.60$, $p < 0.001$; $R^2 > 0.78$; Fig. 1*a*). Shrews and songbirds overlapped in both δ^{15}N and δ^{13}C and were classified as a homogeneous subset (Tukey's multiple comparison tests). Three isotopically divergent carrion subsets were identified: (1) salmon, (2) shrews and songbirds, and (3) deer.

Nicrophorus investigator and *N. defodiens* had different isotopic niches. δ^{15}N and δ^{13}C isotope signatures were higher in *N. investigator* (*t* tests for both isotopes: $t_{[128]} > 11.95$, $p < 0.001$). *Nicrophorus investigator* also exhibited a broader range in isotope signatures than did *N. defodiens* (δ^{15}N: 10.96‰ vs. 5.35‰; δ^{13}C: 8.46‰ vs. 5.09‰) (Fig. 1*b*).

There was further niche differentiation within species. Eighty-seven percent of *N. investigator* individuals were classified within cluster 1, consistent with a diet of salmon carrion. In contrast, 100% of the *N. defodiens* individuals were

Fig. 1. $\delta^{15}N$ and $\delta^{13}C$ stable isotope signatures in (*a*) a range of carrion sources including salmon (*Oncorhynchus keta* and *Oncorhynchus gorbusha*), the shrew *Sorex monticolus*, songbirds (*Troglodytes troglodytes*, *Catharus ustulatus*, *Catharus guttatus*), and black-tailed deer (*Odocoileus hemionus hemionus*) and in (*b*) adult *Nicrophorus investigator* and *Nicrophorus defodiens* (Coleoptera: Silphidae) captured in summer from the Clatse River, British Columbia.
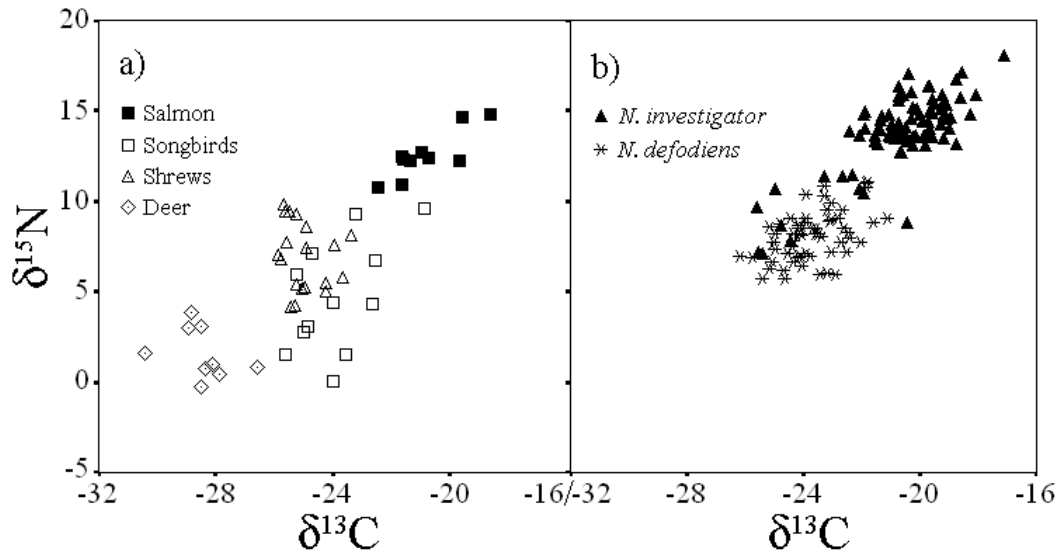

Fig. 2. Hierarchical cluster classification of $\delta^{15}N$ and $\delta^{13}C$ stable isotope signatures from *N. investigator* and *N. defodiens* and their potential carrion prey, including salmon, shrews, songbirds, and black-tailed deer. All samples were collected from the Clatse River, British Columbia. Cluster 1: salmon (100%), songbirds (8.3%), and *N. investigator* (86.5%); cluster 2: shrews (100%), songbirds (91.7%), and *N. defodiens* and *N. investigator* (100%); cluster 3: deer (100%).
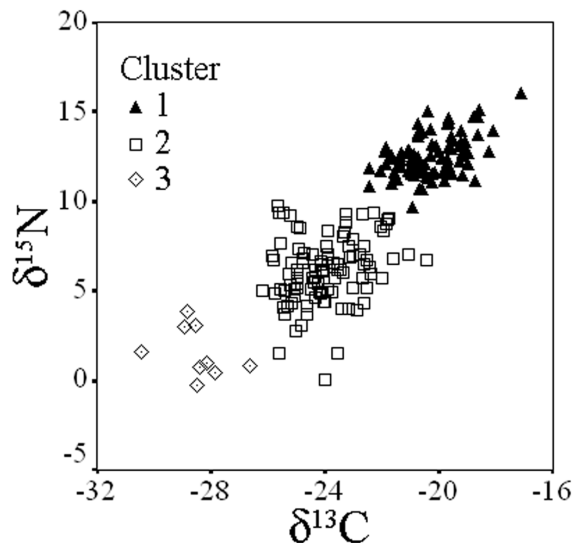
classified within cluster 2, which contained all of the shrews (100%) and all but one songbird sample (92%). The remaining *N. investigator* individuals (13%) were also classified into cluster 2. No burying beetles of either species had isotope signatures consistent with a diet of deer (cluster 3; Fig. 2).

Discussion

Niche partitioning among burying beetle species has been investigated previously using standard techniques in multiple habitats and time periods (Anderson 1982; Ohkawara et al. 1998; Kočárek 2001). Vertebrate carcasses are unpredictably distributed in time and space, and there is often intense competition for these resources. To reduce interspecific competition, *Nicrophorus* beetles partition themselves by time of emergence and seasonal activity, diurnal vs. nocturnal activity, carcass size, and by habitat (Scott 1998). In Newfoundland, for example, *N. investigator and N. defodiens* co-occur on seabird colonies and may be partitioned by habitat rather than by seabird carrion type (Wilhelm et al. 2001).

In contrast, we provide stable isotope evidence for dietary differences between the two species related to carrion source within the same habitat. Specifically, *N. defodiens* individuals were associated with small omnivorous vertebrates, while *N. investigator* individuals were mainly associated with Pacific salmon carcasses. Neither species were found to be associated with carcasses of large herbivores such as the black-tailed deer.

The use of stable isotopes to characterize within and among population variation in dietary niche has been applied to populations and communities of fish (Vander Zanden et al. 2000), birds (Podlesak et al. 2005), mammals (Darimont et al. 2007), and invertebrates (Kelly et al. 2004). Isotopic dietary reconstructions are powerful tools for documenting community organization and trophic structure, fluxes of nutrients and energy in ecosystems, and dietary shifts including population and individual specialization (Bolnick et al. 2003).

To our knowledge, however, isotopic dietary reconstruction has not been applied to carrion communities. Communities of insects on carrion represent an interesting case because the predominant source of larval nutrition is determined by a choice by one or both parents to reproduce on a single carcass resource. Therefore, a forensic a posteriori reconstruction of larval diet can be made when candidate carrion sources are known and are isotopically differentiated. In this study, salmon, deer, and small omnivorous vertebrates

(shrews and songbirds) were observed to have distinct isotope signatures.

The reasons for observed niche differences between the two burying beetle species are unclear but may relate to carcass size, seasonal activity, and timing of reproduction. *Nicrophorus investigator* and *N. defodiens* are sympatric in forested habitats along Clatse River for at least 2 months in the summer. Whereas *N. investigator* adults have been observed breeding on salmon carrion until mid-October (Hocking et al. 2006), we failed to detect *N. defodiens* later in the fall than early September, a period that coincides with the start of the salmon run. In other communities of burying beetles, carcass size has been noted as an important determinant of breeding success and species partitioning (Scott 1998). Larger individuals often win competitive bouts for carcasses and may be particularly favoured on large carcasses such as salmon (Trumbo 1992; Smith and Heese 1995; Hocking et al. 2006). Perhaps *N. investigator* can actively exclude *N. defodiens* from breeding on salmon remains owing to its larger body size. Alternatively, niche differences may simply relate to differences in seasonal activity and overwintering strategy. *Nicrophorus investigator* is univoltine and is able to breed in late summer or fall because it overwinters as prepupae (Smith et al. 2000; Smith and Merrick 2001). In contrast, *N. defodiens* overwinters as an adult and must breed early enough so that the young can complete metamorphosis (Anderson and Peck 1985).

Overall, stable isotope analysis is a powerful tool to detect within and among population variation in dietary niche, and can be applied to communities based on carrion resources. As summarized by Bearhop et al. (2004), the observed isotopic variance within a population is often of more ecological interest and relevance than the mean, and may provide a proxy for population niche breadth. In our study, *N. investigator* had approximately twice the isotopic range for both $\delta^{15}N$ and $\delta^{13}C$ than *N. defodiens*, reflecting the contribution of both salmon and terrestrial carrion to larval diet. A component of Van Valen's (1965) niche variation hypothesis suggests that broader ecological niches are associated with higher morphological variation. Coupling of stable isotope techniques with life history and morphological data may yield opportunity for testing this hypothesis. For example, one would predict such a functional response in this study system given the history, magnitude, predictability, and nutritional value of salmon (Reimchen 2000; Gende et al. 2002; Stockner 2003).

Acknowledgements

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