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Burying beetle *Nicrophorus investigator* reproduction on Pacific salmon carcasses

M. D. HOCKING, R. A. RING and T. E. REIMCHEN Department of Biology, University of Victoria, Victoria, British Columbia, Canada

Abstract. 1. In many undisturbed watersheds along the Pacific Rim, anadromous salmon (*Oncorhynchus* spp.) provide a predictable source of carrion to the riparian zone, largely due to horizontal transfer of salmon carcasses by bears (*Ursus* spp.) and other vertebrates.

2. Burying beetles are important members of the north-temperate carrion fauna, and may utilise salmon carcasses and remnants for breeding. In this study, isotopic and observational data are reported that demonstrate previously unrecognised *Nicrophorus investigator* (Zetterstedt) reproduction on large salmon carcasses from five watersheds in coastal British Columbia.

3. Stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) of adult beetles collected in autumn indicate a diet of salmon origin in all but one individual from all watersheds, suggesting that this beetle–salmon association is widespread. Comparison of autumn isotope signatures to individuals collected randomly in summer suggests that isotope signatures represent the larval carrion source from the previous autumn rather than immediate adult diet.

4. In a survey of *N. investigator* use of salmon carcasses from two watersheds, 35 broods were observed on chum and pink salmon carcasses, including 16 natural brood complexes containing over 100 larvae, and five ranging from 250 to 750 larvae.

5. Overall, north-coastal populations of *N. investigator* breed on the rich and reliable salmon resource and may exhibit a system of communal breeding on these carcasses. This is most relevant when the dramatic reduction in salmon spawning biomass over the last century is considered.

Key words. Burying beetles, communal breeding, diet, marine-derived nutrients, *Nicrophorus investigator*, salmon carcasses, stable isotopes.

Introduction

Every autumn, anadromous Pacific salmon (*Oncorhynchus* spp.) provide a pulse of marine-derived nutrients to terrestrial habitats throughout the Pacific Rim (Gende *et al.*, 2002; Stockner, 2003). Primarily as a consequence of vertebrate foraging, salmon carcasses and remnants are distributed up to 150 m into the forest adjacent to salmon spawning streams (Reimchen, 2000). These carcasses are a predictable source of large carrion to many coastal watersheds and attract an array of invertebrate consumers. Salmon nutrient transfer has indirect implications for litter invertebrate food webs (Hocking & Reimchen, 2002), although a detailed assessment of the invertebrate community directly associated with the carcasses is lacking. To date, studies have emphasised the dominant role of blowflies (Calliphoridae) and other Diptera in salmon carrion decomposition (Reimchen *et al.*, 2003; Meehan *et al.*, 2005), but have ignored the potential role of the Coleoptera. Burying beetles (Silphidae: *Nicrophorus* spp.) are important members of the north-temperate carrion fauna, although their association with salmon carcasses has yet to be investigated. Herein, isotopic and observational evidence is presented that demonstrates *Nicrophorus*

Correspondence: M. D. Hocking, Department of Biology, University of Victoria, PO Box 3020, Stn CSC, Victoria, British Columbia, Canada V8W 3N5. E-mail: mhock@uvic.ca

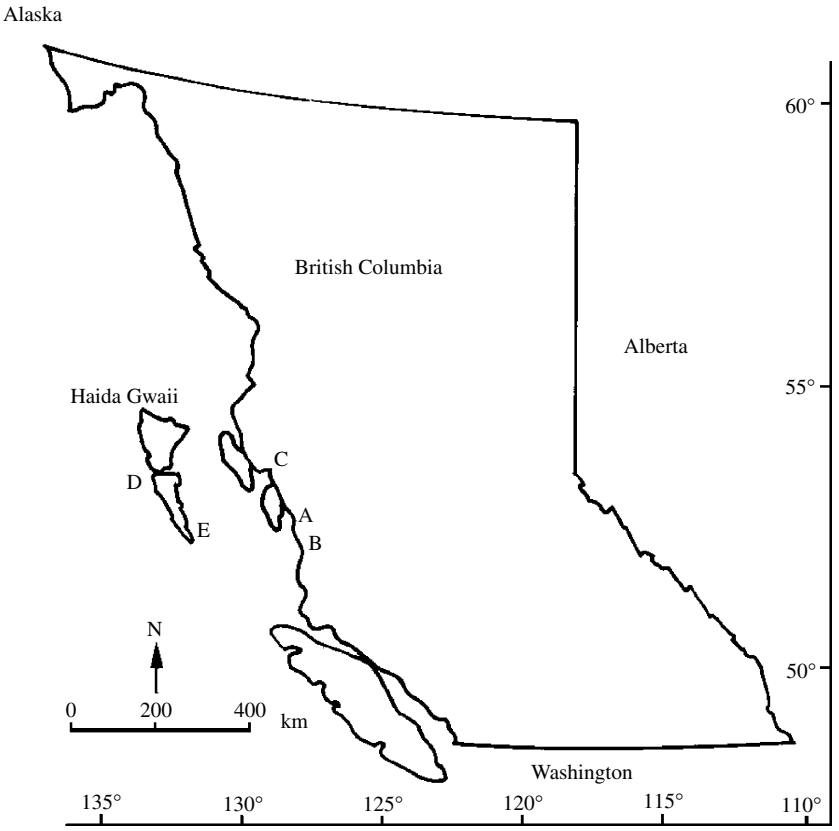

Fig. 1. Study sites where *Nicrophorus investigator* burying beetles were collected from Pacific salmon carcasses on the central coast of British Columbia, Canada. A, Neekas River; B, Clatse River; C, Evelyn Creek; D, Government Creek; E, Bag Harbour Creek.

investigator (Zetterstedt) reproduction on wildlife-transferred chum (*Oncorhynchus keta*) and pink (*Oncorhynchus gorbuscha*) salmon carcasses from five watersheds in coastal British Columbia.

The stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) provide dietary information, including trophic level of feeding (Minigawa & Wada, 1984) and sources of primary productivity (Tieszen & Boutton, 1988), and, in this case, evidence for direct feeding on salmon (examples: Hilderbrand *et al*., 1999; Hocking & Reimchen, 2002). Stable isotope signatures were examined in adult beetles collected in the summer and autumn from five watersheds to (1) determine the importance of salmon to *N. investigator* diet over a large geographic area and; (2) determine whether observed isotope signatures were derived from the larval diet and/or adult diet on carrion.

Salmon carrion ranges in mass from small remnants to whole carcasses weighing up to 10 kg (Reimchen, 2000), and it is unknown how carcass size may affect the breeding structure of invertebrates that utilise salmon carcasses. *Nicrophorus* beetles typically bury and prepare small vertebrate carcasses < 50 g in size, although there have been some reports of breeding on larger carcasses (Milne & Milne, 1944; Anderson, 1982; Trumbo, 1992). In some cases, *Nicrophorus* spp. can develop a strategy of communal breeding on large carcasses due to increased competition with flies, and increased difficulty in burying and defending the carcass (Trumbo & Fiore, 1994; Scott, 1994, 1998; Trumbo, 1995). On two watersheds, adult aggregations and larval brood sizes were surveyed to examine the breeding structure of *N. investigator* on salmon carcasses.

Materials and methods

Study sites

This study was primarily conducted on two salmon-bearing watersheds, the Clatse and Neekas rivers, on the central coast of British Columbia, Canada (Fig. 1; further site description in Hocking & Reimchen, 2002). Additional study sites included Government Creek and Bag Harbour Creek on the Queen Charlotte Islands, and Evelyn Creek on Hawkesbury Island near the community of Hartley Bay. Chum and pink salmon spawn from late August to early November in all five watersheds, with populations of black bears acting as the principal vectors of salmon carcasses into the forest (Manzon & Marshall, 1981; Reimchen, 2000).

Contribution of salmon to diet

The importance of salmon to the diet of *N. investigator* was investigated with simple observations as well as stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ on multiple adults from a broad geographic area. *Nicrophorus investigator* analysed

for $\delta^{15}N$ and $\delta^{13}C$ included adults collected in the autumn from salmon carcasses from the Clatse ($n = 5$), Neekas ($n = 8$), Government ($n = 5$), Evelyn ($n = 3$), and Bag Harbour ($n = 2$) watersheds, as well as adults collected in baited traps on the Clatse River in mid-August of 2000 and late July of 2003 prior to salmon arrival ($n = 80$).

Nicrophorus investigator adults were stored in 70% ethanol. Whole specimens were dried at 60 °C for at least 48 h and were ground into a fine homogeneous powder using a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Illinois). *Nicrophorus investigator* sub-samples ($\approx$ 1 mg) were assayed for total N, $\delta^{15}N$, total C and $\delta^{13}C$, at the University of Saskatchewan Stable Isotope Facility, by continuous-flow isotope ratio mass spectrometry (CF-IRMS). Stable isotope ratios of $^{15}N/^{14}N$ ($\delta^{15}N$) and $^{13}C/^{12}C$ ($\delta^{13}C$) are given in parts per mil (‰) deviations from isotopic standards [N_2 in air for nitrogen isotope analyses and Pee-Dee Belemnite (PDB) limestone for carbon isotope analysis]. Measurement precision is approximately $\pm$ 0.16‰ and $\pm$ 0.10‰ for ^{15}N and ^{13}C respectively (95% CI).

Isotope signatures were examined relative to possible dietary sources, which include salmon and a variety of terrestrial carrion. The isotopic signatures of pink and chum salmon muscle range from approximately 11‰ to 14‰ for $\delta^{15}N$ and -22‰ to -18‰ for $\delta^{13}C$ (Welch & Parsons, 1993; Kaeriyama *et al*., 2004), while terrestrial carrion such as songbirds and small mammals range from 0‰ to 10‰ for $\delta^{15}N$ and -27‰ to -21‰ for $\delta^{13}C$ (Ben-David *et al*., 1998; M. D Hocking, unpubl. data). Diet-tissue fractionation in animals is typically around +3‰ for $\delta^{15}N$ (Minigawa & Wada, 1984) and $\approx$ 0‰ for $\delta^{13}C$, although diets high in lipid content can result in $\delta^{13}C$ isotopic depletion from diet to tissue (Tieszen & Boutton, 1988). In the case of *N. investigator* feeding on a 100% salmon diet, $\delta^{15}N$ signatures are expected to be $\approx$ 3‰ higher than salmon while $\delta^{13}C$ equal to or slightly lower than salmon.

To investigate possible seasonal differences in isotopic signatures, the distribution of isotope signatures of adult beetles collected in summer prior to salmon arrival were compared with those collected in the autumn directly off salmon carcasses. Because *N. investigator* are univoltine (Smith *et al*., 2000), this tested whether observed autumn signatures likely reflected recent feeding or a legacy of the larval diet from the previous year (ANCOVA with $\delta^{15}N$ as dependent variable, $\delta^{13}C$ as a covariate and season as a fixed factor). All analysis was conducted using SPSS version 11.0 (SPSS Inc., Chicago, Illinois).

Field survey

In early October 2003, *N. investigator* use of naturally transferred pink and chum salmon carcasses was surveyed on the Clatse and Neekas rivers. This period corresponds to the peak period of salmon carcass density in each watershed (Manzon & Marshall, 1981). A detailed search was conducted for adults and larvae under all carcasses and remnants within 50 m of the stream edge on both watersheds. On Clatse this encompassed nearly the entire spawning length ($\approx$ 1 km), while on Neekas this covered roughly half of the 2 km of spawning. When adults or larvae were discovered on a carcass, the carcass was flagged and monitored until the majority of the larvae reached full size. At this time, larvae on the carcass were hand-counted by carefully removing them one by one and placing them into a temporary holding container. Throughout all phases of carcass decay all adults in the vicinity of each carcass were captured, counted, sexed, and then released. However, due to variation in brood development upon initial discovery of the carcass, the number of initial adults associated with each brood was not determined in all cases.

Results

Contribution of salmon to diet

Nicrophorus investigator adults were observed breeding on chum and pink salmon carcasses deposited on the forest floor by vertebrate scavengers from all five watersheds across a large geographic region in coastal British Columbia (Figs 1 and 2). Aggregations of 1–18 adults were observed on salmon carcasses in early phases of decomposition, including five aggregations of at least 12 individuals in three of the five watersheds (Clatse, Neekas, and Government).

With the exception of one beetle from the Clatse River, $\delta^{15}N$ and $\delta^{13}C$ isotope signatures in adult *N. investigator* collected in autumn from all five watersheds indicated a diet of salmon origin (Fig. 3a). *Nicrophorus investigator* $\delta^{15}N$ and $\delta^{13}C$ signatures were similar to or higher than the isotope signatures of salmon and did not differ among watersheds (ANOVA, $\delta^{15}N$: $F_{4,18} = 1.99$, $P = 0.14$; $\delta^{13}C$: $F_{4,18} = 2.55$, $P = 0.08$; Tukey's post hoc: all $P > 0.14$). The only exception was one individual from Clatse, which had an isotope value ($\delta^{15}N = 8.55$; $\delta^{13}C = -25.46$) within the range defined by terrestrial carrion.

Since autumn $\delta^{15}N$ and $\delta^{13}C$ signatures were similar across watersheds, all individuals were pooled ($n = 23$). Beetles collected directly from salmon carcasses in the autumn were compared with adult beetles collected randomly in summer 2–4 weeks prior to salmon arrival along the Clatse spawning channel ($n = 80$) (Fig. 3b). $\delta^{13}C$ values were highly positively correlated to $\delta^{15}N$ values across both seasons ($F_{1,99} = 70.25$, $P < 0.001$) while no differences were observed by season ($F_{1,99} = 0.21$, $P = 0.65$) or for the interaction term between season and $\delta^{13}C$ ($F_{1,99} = 0.16$, $P = 0.69$) (ANCOVA of $\delta^{15}N$ by season with $\delta^{13}C$). The isotopic variance and the high frequency of a salmon diet was also similar between seasons ($\delta^{15}N$: Levene's $F_{22,79} = 0.128$, $P = 0.721$; $\delta^{13}C$: Levene's $F_{22,79} = 0.918$, $P = 0.340$; autumn frequency of salmon diet = 95.7%; summer frequency of salmon diet = 88.7–95%; Fig. 3b).

Fig. 2. (a) A male chum salmon carcass (*Oncorhynchus keta*) transferred into the riparian zone of the Neekas River, British Columbia by a black bear attracts adult burying beetles (*Nicrophorus investigator*), and (b) a *N. investigator* brood complex developing under the same carcass 9 days later. Photographs taken by M. Hocking, October 2003.

Field survey

A total of 35 broods were observed on wildlife-transferred salmon carcasses from the Clatse ($n = 15$) and Neekas ($n = 20$) rivers (Fig. 4a). This included 16 broods (or brood complexes) with greater than 100 larvae and five ranging from 250 to 750 larvae. With the exception of three broods that developed under pink salmon on the Clatse, all remaining broods developed under chum salmon carcasses. The number of adults was counted for both sexes present on each carcass early in brood development (Fig. 4b,c). Because some broods had larvae that were almost completely developed upon discovery, counts of initial adults include a subset of total number of broods (total adults $n = 19$ carcasses; females $n = 15$ carcasses). Initial number of adults ranged from 0 to 16 individuals (mean = 3.8), while initial number of females ranged from 0 to 11 (mean = 2.7). The number of females found initially on a carcass was found to be correlated to brood size (linear regression: $F_{1,8} = 48.5$, $P < 0.001$, $R^2 = 0.86$; Fig. 4d).

Overall, no carcasses were buried. All broods developed underneath the carcass, often in multiple brood centres. The largest brood observed (738 larvae) was from a large male chum carcass, and although it was not weighed, probably measured 4–5 kg in mass. Several females were breeding in each of the multiple brood centres (in gills and mouth, under belly, and in dorsal muscle region). Nine days after counting 11 adult females and five males on the carcass, larvae of multiple instars were observed scattered throughout the carcass, while four adult females and two males remained.

Discussion

Pacific salmon carcasses transferred into the forest by bears, wolves, and other vertebrates are a predictable

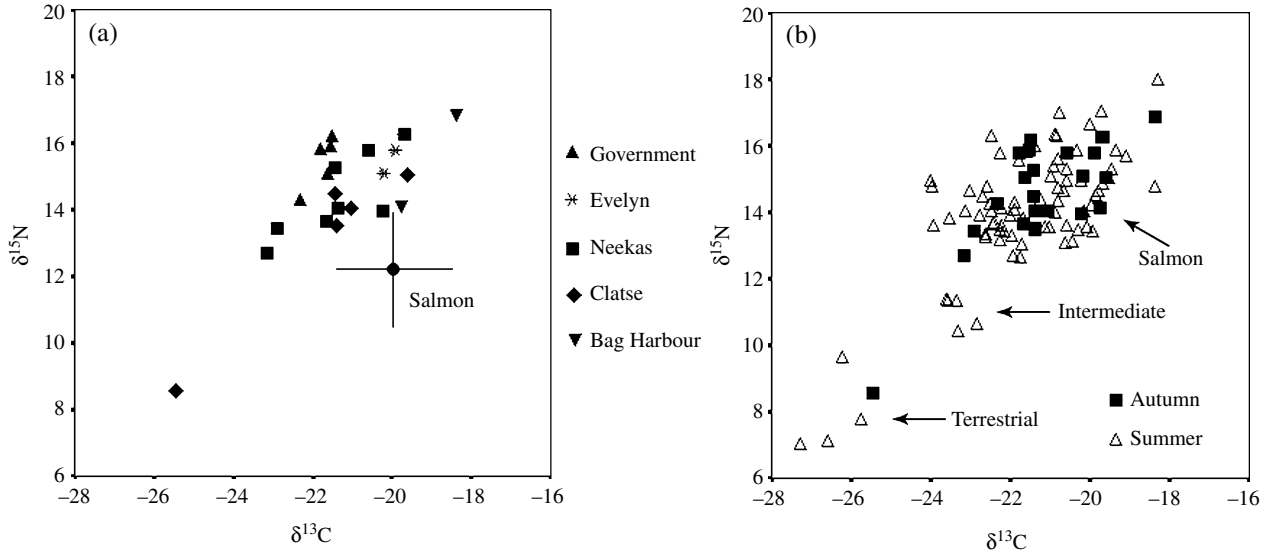

Fig. 3. δ^{15}N and δ^{13}C stable isotope signatures in individual adult *Nicrophorus investigator* beetles collected in (a) the autumn from salmon carcasses at five watersheds in coastal British Columbia compared with (b) individuals collected at random in summer 2–4 weeks prior to the return of the salmon on the Clatse River, British Columbia. Autumn data are shown in both (a) and (b). For comparison, the approximate isotope signature of salmon is included. In summer, isotope signatures were derived from salmon (88.7%), terrestrial carrion (5%), or an unknown intermediate (6.3%) (see Methods and Discussion).

source of carrion to the riparian zone in many coastal watersheds (Reimchen, 2000), and attract an array of invertebrate scavengers (Jauquet *et al*., 2003; Meehan *et al*., 2005). Here, isotopic and observational evidence is presented for burying beetle *N. investigator* reproduction on salmon carcasses from the central coast of British Columbia, Canada.

Stable isotope analysis of δ^{15}N and δ^{13}C in animal tissues provides information on individual diet integrated over long time periods (Minigawa & Wada, 1984; Tieszen & Boutton, 1988), and, in this case, evidence for a widespread diet of salmon carrion in *N. investigator*. *Nicrophorus investigator* is univoltine with reproduction in late summer and autumn, with individuals typically surviving for just one breeding season (Smith *et al*., 2000). Except for one individual at the Clatse River, all isotope signatures in adult *N. investigator* collected in the autumn indicated a diet of salmon origin, with no detectable differences among watersheds. Furthermore, no seasonal differences were observed between adult beetles collected directly off of salmon carcasses in the autumn to those collected randomly in summer prior to salmon arrival. This includes the variance of adult isotope signatures and the slope of the relationship between δ^{15}N and δ^{13}C. The observed frequency of a salmon diet in autumn (95.7%) was also similar to that in the summer (88.7–95.0%) with five individuals in summer with intermediate isotope signatures that could not be clearly placed in either category. These intermediate signatures could represent a larval diet from terrestrial carrion that is itself enriched in salmon nutrients (for example, a shrew: Ben-David *et al*., 1998). Alternatively, they could represent individuals that were raised on salmon as larvae but have fed as adults on terrestrial carrion, and thus have intermediate signatures (see Tallamy & Pesek, 1996). It seems likely, however, that observed isotope signatures in adults representing a salmon diet collected in both summer and autumn represent a legacy of the larval diet of salmon from the previous autumn.

Salmon carcasses range in size from several gram remnants to whole chum carcasses up to 10 kg in weight (Reimchen, 2000; M. D. Hocking, unpubl. data). They are often much larger (up to two orders of magnitude) than those known to be accepted by *N. investigator* in several previous studies, which have demonstrated beetle preference for small mammal carcasses 50 g or less in size (Smith & Heese, 1995; Smith *et al*., 2000; Smith & Merrick, 2001). Overall, *Nicrophorus* spp. display a wide range of behaviours from bi-parental care to communal breeding (Trumbo, 1992; Scott, 1998), although only a handful of studies have investigated *Nicrophorus* use of large carcasses (Milne & Milne, 1944; Peck, 1986; Kozol *et al*., 1988; Trumbo, 1992). On the Clatse and Neekas rivers a total of 35 brood complexes were observed on salmon carcasses within a 2-week period, with 17 containing over 100 larvae, and five between 250 and 750 larvae. This demonstrates a system of possible communal breeding on salmon carcasses. The large chum carcasses most often chosen by *N. investigator* were not buried, but rather mounded at the side with litter to give a sunken appearance. Broods then developed underneath the carcass, often in multiple brood centres, although multiple females (two or three) were often observed sharing these separate brood centres.

Communal breeding in *Nicrophorus* on larger carcasses is thought to have evolved as a consequence of high brood

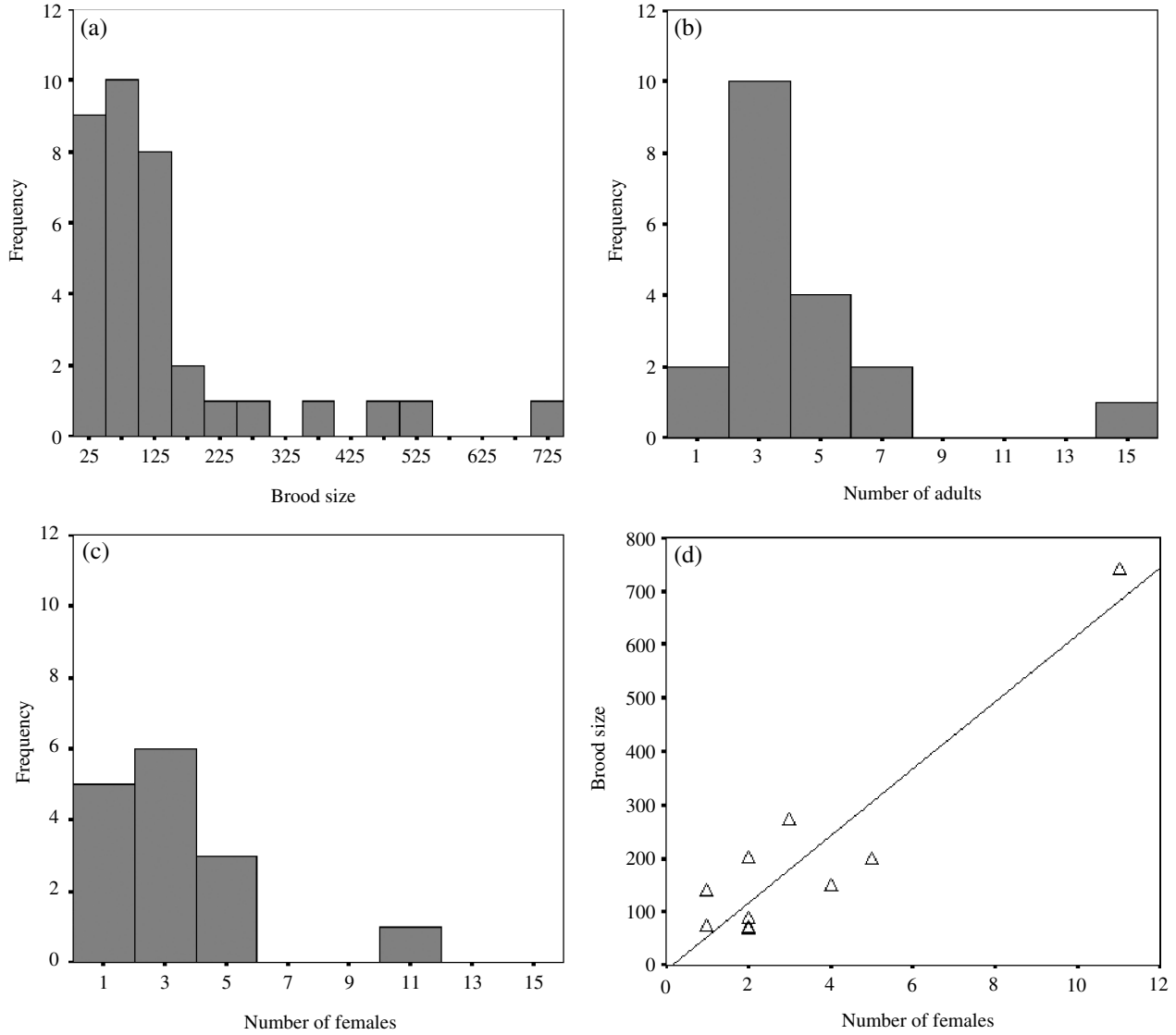

Fig. 4. Frequency distribution of (a) brood size, (b) number of initial adults, (c) number of initial females, and (d) the relationship between brood size and number of initial females, from a survey of *Nicrophorus investigator* breeding structure on salmon carcasses from both the Clatse and Neekas rivers, British Columbia, October 2003.

failure due to increased competition with flies, and increased difficulty in burying and preparing the carcass (Scott, 1994; Trumbo & Fiore, 1994; Trumbo, 1995; Scott, 1998). Necrophagous flies are excellent competitors for large carrion, and can rapidly detect carcasses and gain priority (Williams & Richardson, 1984; Kouki & Hanski, 1995). Flies (Calliphoridae, Dryomyzidae, Heleomyzidae, Muscidae, and Sphaeroceridae) are highly competitive for salmon carcasses and have been observed as dominant salmon-carcass consumers in various studies, including this one (Reimchen *et al.*, 2003; Meehan *et al.*, 2005). *N. investigator* is likely competitively excluded from many carcasses, which may favour aggregation and cooperation on a small proportion of available carcasses.

Anadromous salmon spawn in thousands of watersheds throughout the Pacific Rim and are a temporally and spatially predictable source of carrion to the terrestrial ecosystem (Gende *et al.*, 2002; Reimchen *et al.*, 2003). This contrasts with many alternate sources of carrion that are typically much less predictable in time and space (Hanski, 1990). Pacific coastal populations of *N. investigator* are known to extend from northern California to Alaska, including Russian Kamchatka and Japan (Katakura & Fukuda, 1975; Anderson & Peck, 1985; Nishikawa, 2000), and reproductive associations with large salmon carcasses, including possible communal breeding, may also occur in these regions where intact salmon runs and their predators remain.

In conclusion, isotopic and observational data suggest a strong association between coastal populations of the burying beetle *N. investigator* and salmon carcasses. Stable isotope analysis indicated that 89–96% of *N. investigator* individuals collected in summer and autumn from five watersheds were likely raised on salmon carrion as larvae the previous autumn, with 4–11% originating from terrestrial carrion sources. Observations of breeding structure in *N. investigator* revealed large aggregations and brood sizes from multiple watersheds, suggesting possible communal breeding on these large and predictable carcasses. Overall, the beetle–salmon interaction highlights the dynamic evolutionary interdependence between marine and terrestrial ecosystems in the North Pacific, and the need for ecosystem-level conservation that includes salmon, their riparian habitats, and their vertebrate and invertebrate scavengers. This is most relevant when one considers the dramatic reduction in spawning salmon biomass over the last century (Gresh *et al.*, 2000).

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