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EVALUATING COMPOSITIONAL FIDELITY AND SOURCES OF MORTALITY OF SHORELINE FISH CARCASSES IN A FRESHWATER LAKE COMMUNITY IN WESTERN CANADA

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ABSTRACT: Taxonomic comparisons of death assemblages with extant communities continue to provide insight for ecological studies but whether demographic aspects such as age structure, sex ratio, and causes of mortality are accurately captured by the former remains little studied. At a 110 ha dystrophic lake in western Canada, seasonal shoreline accumulations of fish carcasses were collected annually for 12 years (N=4499) during 95 full lake-circuits and analyzed for taxa, body size frequencies, sex ratio relative to live-captures and sources of mortality. Rank order of the four fish species (*Gasterosteus aculeatus*, *Oncorhynchus clarki*, *O. keta*, *Salvelinus malma*) was similar for live-captures and carcasses. Of the dominant species (*G. aculeatus*), modal adult body length (~80 mm SL) was the same for carcasses and live-captures and shifted by about 10% over 30 years with parallel trends between the groups for both sexes. Age-specific body size was about 5% larger ($P < 0.001$) in carcasses than live-captures. Carcasses were significantly female-biased (2:1) each year relative to a population sex ratio of 1:1 in the lake. There was a complete absence of juvenile fish (<30 mm) among carcasses but these constituted 70% of the live population. Estimated relative contributions to mortality for the carcasses include starvation (<1%), parasitism (3%), senescence (4%) and lethal injuries from predator attack (70–80%). If these carcasses are representative of a fossil series in freshwater lake sediments, then several demographic parameters including age-specific body size, age-class frequencies and sex ratio depart substantially from the live population. As well, the virtual absence of avian piscivores in the carcass assemblage, the major source of predation on the fish population, warrants additional attention in paleoecological studies.

INTRODUCTION

Taphonomic studies that compare the seasonal accumulation of carcasses with the live population establish a framework for inferring community composition in paleocommunities from a fossil series. Ideally, for time-averaged data, the accumulation of carcasses will reflect the actual composition of the living community. There is strong support for this assumption in mollusks (Kidwell and Flessa 1995; Kidwell and Rothfus 2010; Kidwell 2013, 2015; Meadows et al. 2019), but in fishes, differences in body size and skeletal integrity can alter rates at which carcasses are deposited and progressively distort the resemblance to the original community (Lyman 1984; Elder and Smith 1988; Davidson et al. 2003; Lockwood and Chastant 2006; Zohar et al. 2008; Kidwell 2013; Heness et al. 2017). Overall, analyses of live-dead assemblages have focused on taxonomic fidelity and size as these are the dominant metrics that persist in fossils (Elder and Smith 1988; Albert et al. 2009; Kidwell 2013; Terry 2010). However, more targeted demographic features such as age classes and sex identification have received very little attention in analyses of death assemblages, yet these metrics could be essential in interpreting morphometrics and paleoecological structure (Wilson 1984, 1988). For example, in fishes, sexes can differ in morphology and in habitat (Selander 1966) and consequently, spatial or temporal shifts in sex ratio could produce inaccurate interpretations of a death assemblage if the sexes were not distinguished. As well, causes of mortality are frequently unknown in death assemblages or fossil series although these are occasionally evident when skeletal parts occur in coprolites (Wilson 1987) or when distinctive predator-induced injuries occur on shell or skeletal parts (Reimchen 1982; Kowalewski 2002; review in Vermeij 1987). Such information is also relevant for conservation biologists as to the extent to which death

assemblages produced in this manner accurately reflect the structure of the living population (review in Dietl et al. 2015).

During studies of predator-prey interactions among fish and avian piscivores at a remote freshwater lake in coastal British Columbia (Reimchen and Douglas 1984; Reimchen 1988, 1994), I noticed that fish carcasses were being swept by onshore winds and incorporated into the shore sediments. Such processes over time hypothetically provide the skeletal elements in a fossil series and it was apparent that these carcasses, collected over multiple years, could be used to evaluate the extent to which these natural 'death assemblages' reflected actual community and population structure. This 110 ha dystrophic lake has four species of fish as well as multiple species of avian piscivores and in those respects is probably fairly representative of temperate freshwater lakes of similar size in the northern hemisphere (Reimchen 1994). Over 12 years, I made multiple shoreline circuits of the lake each year and collected all intact carcasses, most of which were threespine stickleback (*Gasterosteus aculeatus*). I also took samples of live fish for direct comparison. In this paper, I examine (1) species composition; (2) size and age frequencies; (3) sex ratio; and (4) causes of mortality in shoreline carcasses and compare these parameters with the living community. These detailed demographic data are novel among taphonomic studies and potentially can inform paleoecological interpretations in fossil sequences.

STUDY AREA AND METHODS

Drizzle Lake is located on the north-eastern region of the Haida Gwaii archipelago, 100 km off the west coast of Canada (53.933861°N, 132.072865°W). The oval-shaped lake occurs on a broad expanse of

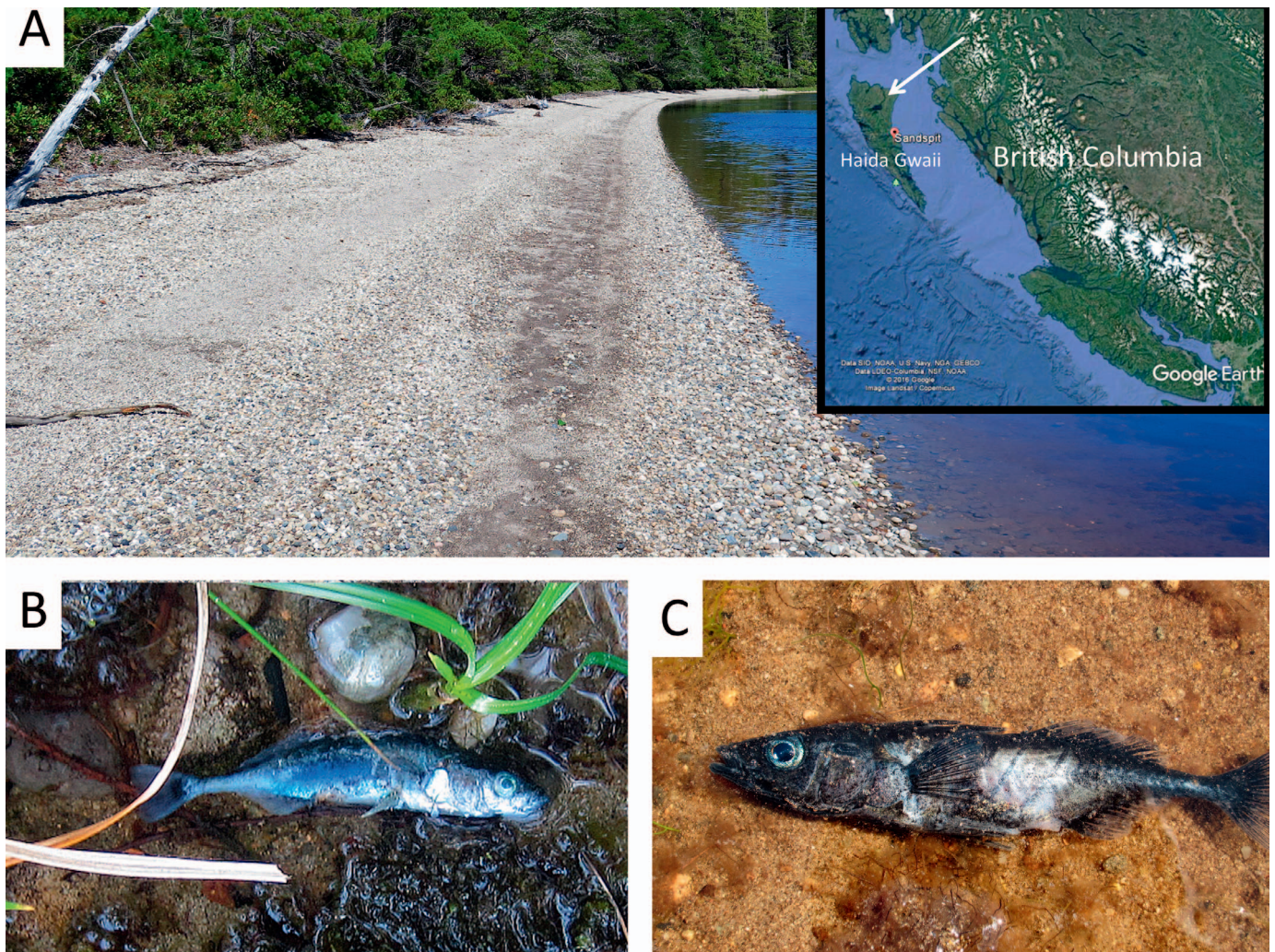


FIG. 1.—Study area. **A)** Shoreline on northwest region of Drizzle Lake (inset shows Google Earth image. Arrow shows position of Drizzle Lake). **B)** *In situ* 80 mm SL stickleback carcass at waterline in emergent vegetation. **C)** *In situ* stickleback carcass showing avian-induced integumentary injury (see Reimchen 1988 for details).

Sphagnum-dominated bog and patchy coniferous forests. It has a gentle sloping shore ($<5^\circ$) throughout much of its 5 km perimeter and reaches a maximum depth of ~ 20 m. The substrate is a combination of hardpan, gravel and sand throughout most of the lake apart from soft sediment near the plume of the single, slow-moving inlet stream. As with most watersheds in these *Sphagnum* landscapes, the lake is acidic (pH = 4.8) and dystrophic, with limited development of littoral macrophytes. Surface (10 cm depth) temperatures generally range from 5°C , occasionally freezing in severe winters, to 17°C during summer (Reimchen 1990). Winds throughout the year result in most shoreline deposition of carcasses on the northwest and the southeast shorelines, both substrates largely characterized by coarse sand and gravel deposits (Fig. 1A). Lake water levels fluctuate approximately 0.2 m vertically over the year but vary weekly and are seasonally dependent on rainfall, lowest levels occurring in summer.

The four resident fish species are threespine stickleback, cutthroat trout (*Oncorhynchus clarki*), Dolly Varden (*Salvelinus malma*), and coho salmon parr (*O. kisutch*). Up to 36 species of aquatic birds including 16 species of piscivores (equating to 8,300 bird days per year, i.e., the number of birds for each species per day for the number of days present in the year) occur on the lake, primarily during summer and autumn (Reimchen and Douglas 1984). Sampling techniques and mark-release-recapture estimates

for live fish are provided elsewhere (Reimchen 1988, 1990, 1994); in summary, standard body lengths (SL) and population estimates (N) of the fish species are (1) stickleback: juveniles (<30 mm SL; $N > 1$ million); 1st and 2nd y sub-adults (30–70 mm SL; $N \sim 500,000$); adult (70–95 mm SL; $N \sim 75,000$); (2) trout: 130–400 mm SL, $N \sim 220$; (3) Dolly Varden: 100–400 mm SL, $N \sim 100$; and (4) coho salmon parr: 40–130 mm SL, $N \sim 4000$). This yields approximate abundance ratios of 16,000:40:2:1 for stickleback, salmon, trout, and Dolly Varden, respectively.

From 1987 to 1990 and from 2011 to 2018, 95 full lake-shore circuits were completed and all vertebrate carcasses on the shoreline were collected. The majority of carcasses were intact and within 2 m of the waterline, independent of the distance to the treeline (Fig. 1B, 1C). Occasional carcasses that occurred at greater distances from the waterline (from reduction in lake levels) were decomposed and disarticulated and were not collected. Each lake circuit was undertaken on foot (~ 3 hours per circuit) and most were done either by myself or with occasional field assistants (listed in the Acknowledgments). During days with strong winds, wave action resulted in increased shoreline accumulation of carcasses yet these were usually visually obscured by the shoreline foam and as such, I would make an additional circuit the following day when the foam had disappeared. There were very few carcasses in autumn, winter or early spring but during the peak summer periods of carcass accumulation, I

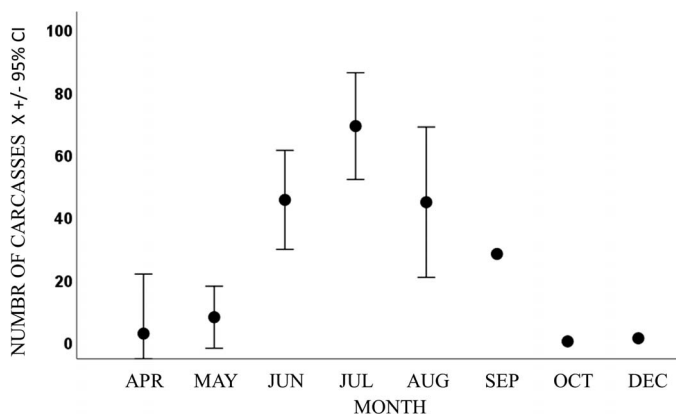


FIG. 2.—Average monthly shoreline carcass counts at Drizzle Lake, Haida Gwaii. Data based on 95 full lake circuits (1987–2018).

made one or two full lake circuits each week. The dominant scavengers on the carcasses at the waterline were larval caddisflies (Trichoptera) while carcasses farther from the waterline (from dropping lake levels) usually exhibited fungal decomposition and disarticulation. All intact carcasses were collected and preserved in 95% ethanol. To provide comparisons with the carcass data, I examined samples of live-captured stickleback taken from all regions of the lake between 1980 and 1986, prior to carcass collections (Reimchen 1988) and then in eight additional years overlapping with shoreline carcass surveys (Permit Authorization to the author, 105566, Government of British Columbia, Canada).

All carcasses were identified for species and measured for standard length (SL \pm 2 mm). For stickleback, I opened the body cavity and identified sex from the gonads when possible, recorded if the female was gravid (with well-developed eggs) and counted macroparasites (nematodes). I scored damage to carcasses. Stickleback have robust armor that provides defense during handling by vertebrate predators (Reimchen 1983). The Common Loon (*Gavia immer*), the major avian piscivore on the lake, attempts to break the dorsal and pelvic spines prior to swallowing, yet some stickleback escape following capture and these may have fractures to the armor and scarring to the integument (Reimchen 1988). Some of these injuries are lethal and the fish succumb from osmotic shock and tissue damage (Reimchen 1992a). I scored injuries including fractures to the skull, lateral plates, pelvic girdle, and spines. Spines are robust at the base and tapered towards the tip and I measured position of the fracture along the spine as a major break: 0–30% from base of spine; mid-break: 30–80% along length of spine; minor-break: >80% along length of spine. Length of any spine regrowth at the position of the fracture was measured as this allowed old versus fresh fractures to be distinguished (Reimchen 1988). Integumentary lacerations were scored and comprise three major categories: 1 = major curvilinear scratches and punctures from tooth lacerations by predatory salmonids (Reimchen 1992a) as well as avian piscivores; 2 = parallel, bilateral scars (aviscars) from direct manipulation and compression by the bill of avian piscivores (Reimchen 1988); and 3 = minor scratches and abrasions that could not be assigned to an explicit source and could range from intraspecific agonistic encounters, substrate contact, and predator manipulation. All of the integumentary scratches, scars, and abrasions are identifiable as disruptions in the epidermal pigmentation and would occur only when the fish was alive. Carcasses that were dehydrated, decomposed, or covered in fungus could not be reliably scored for integumentary lacerations.

Stickleback body growth in this lake is asymptotic, approaching reproductive size (70–85 mm SL) in their third year (Reimchen 1992b). I used annual growth rings in spines to directly estimate age in years. The right pelvic spine was removed on the majority of fish, decalcified,

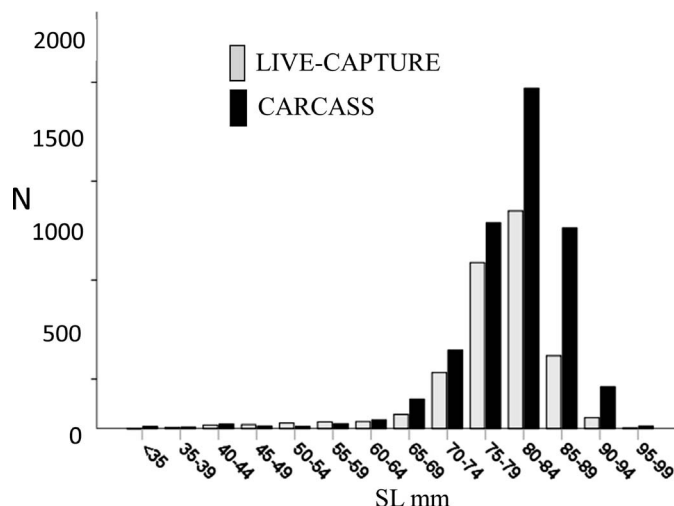


FIG. 3.—Standard length (SL) frequency distributions of stickleback carcasses and live-captures from Drizzle Lake.

embedded with resin, sectioned, and scored, with ages confirmed with mark-release-recapture methods (Reimchen 1992b). Multiple closely spaced rings on older fish (>6 y) progressively reduce reliability of individual ages.

Data were analyzed with a combination of Pearson's Chi-Square, Loglinear models and ANOVA (SPSS v.24, IBM, USA).

RESULTS

Number of carcasses collected per lake circuit ranged from 0 to 284 (\bar{x} = 55) with the highest counts during July (Fig. 2). In total, of the 4499 carcasses, most were stickleback (N = 4489), with occasional trout (N = 7), Dolly Varden (N = 2) and coho salmon (N = 1). Among the aquatic birds on the lake, no carcasses were found during the major shoreline accumulations of fish carcasses but a single carcass (Long-tailed Duck *Clangula hyemalis*) was found during a winter transect when fish carcasses were rare.

Body sizes (SL) of the carcasses (stickleback: 30–99 mm; trout: 150–250 mm; Dolly Varden: 100–140; salmon: 110 mm) were largely representative of those found in the lake (see Methods). Binning SL categories for stickleback (Fig. 3) indicates the same mode for carcasses and live-captures (80–84 mm) but with disproportionate over-representation of carcasses in the progressively larger body size classes. Binned and raw SL data have a strong left skew (-2.2 , Kolmogorov-Smirnov test of normality = 0.12, DF = 7534, P < 0.001) that is not removed with either log or square-root transformations ($K-S$, P < 0.001). Therefore, excluding all fish within the left skew (<60 mm SL) improves normality and among these, there is a modest but highly significant increased SL on carcasses relative to live-captures (carcass \bar{x} = 81.8 mm, SD = 5.7, N = 4585; live: \bar{x} = 80.5 mm, SD = 5.3, N = 2754). Young of the year fish (<30 mm SL) are smaller than the mesh size of the collecting methods used for the live-captures but using recruitment from nest clutches, this age class represents 70% of the stickleback population (see Reimchen 1990). However, these sticklebacks were not found in any shoreline surveys for carcasses.

I examined age-structure, predicting that if senescence was a major cause of mortality for the carcasses, the oldest fish (7–10 years of age) would be the most common. However, only 4% of the carcasses were this age. Age frequency distributions in carcasses show 3 y and 4 y to be the most prevalent ages relative to 5 y for live-captures (Fig. 4), inconsistent with senescence being a major source of mortality.

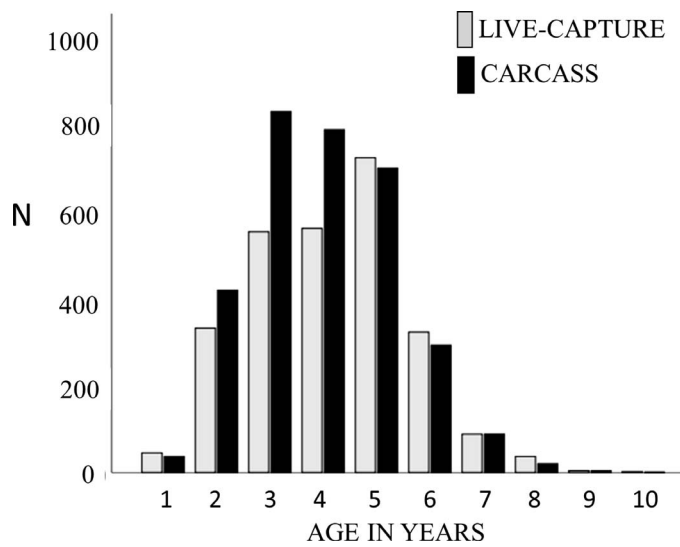


FIG. 4.—Age frequency distributions of stickleback carcasses and live-captures from Drizzle Lake.

Because the carcass collections were replicated in multiple years, I was able to test for temporal consistency in adult body sizes. The data were partitioned for sex, as body size is slightly larger in females than in males. In both carcasses and live-captures, there was an approximate 10% fluctuation in adult body size among years both for males (Fig. 5A; Year: $F_{17,1903} = 53.4, P < 0.001$) and females (Fig. 5B; Year: $F_{17,4095} = 128.9, P < 0.001$).

Sex ratios in live-captures were close to equality (females = 49.7%, $N = 8641$). I predicted that if the sex ratio of carcasses departed from 1:1, there

might be a male-bias, not only due to their shoreline proximity in both spring and summer reproductive season as well as in autumn (Reimchen and Nelson 1987) but also due to the elevated mortality rates associated with male-dominated parental care in this taxon (Wootton 1976). Yet, contrary to prediction, among all carcasses, females were twice as common as males (66.5% vs. 33.5% respectively, $N = 4068; \chi^2_1 = 314.2, P < 0.001$), a female bias occurring in 11 of the 12 years of sampling (Binomial test, $P < 0.003$).

One source of mortality for the carcasses could be poor body condition, possibly resulting from inferior competitive ability relative to live-captures. If so, I predicted that age-specific body size of carcasses would be smaller than for live-captures. While there was marginal support for this prediction for Year1, in the majority of comparisons (10 of 14), carcasses were significantly larger than live-captures of the same ages (unpaired t-test, $P < 0.05$ in all cases), this occurring in males (Fig. 6A) and females (Fig. 6B). I infer that apart from Y1, reduced competitive ability is not identifiable as a cause of mortality in the carcasses.

Parasites can compromise the condition of fish. In the Drizzle Lake population, the stickleback acquire the first life stage of the nematode *Eustrongylides* sp. from consumption of an infected oligochaete following which the nematode uses stickleback as the intermediate host where it encysts in the musculature. I predicted that if parasitism was a cause of mortality, it would be higher in the carcasses relative to live-captures. This was supported, as among 4779 carcasses, 3.6% had nematode parasites compared with 1.0% of the live-captures ($N = 3060$) ($\chi^2_1 = 49.1, P < 0.001$). Such a difference could be a simple correlate of host body size because the incidence of nematode infection increases with age of stickleback (Reimchen 1997). Separating the data for age classes shows that elevated infection rates in the carcasses relative to live-captures occurred across all years (Fig. 7; interaction between nematode and live-dead comparison [nematode*live-Dead, Log Linear partial $\chi^2_1 = 45.4,$

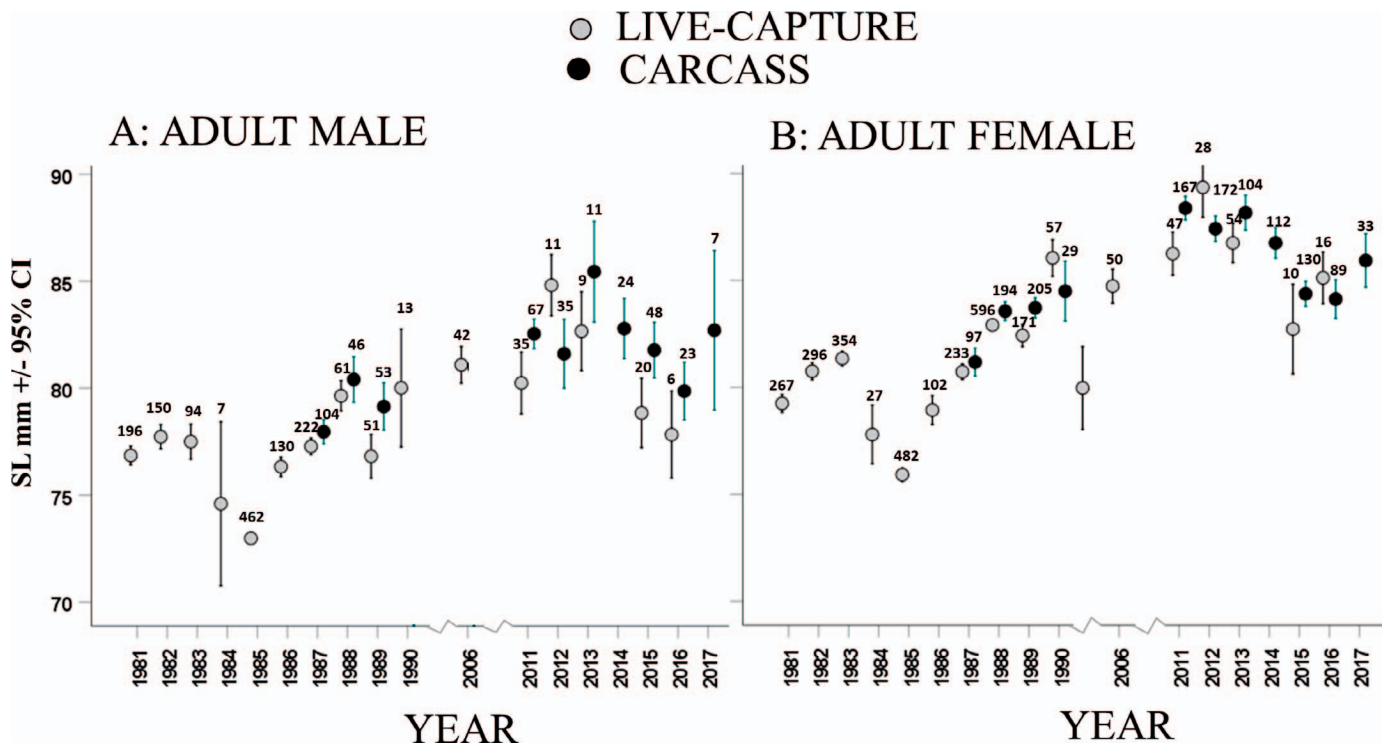


FIG. 5.—Mean adult SL (+/- 95% CI) of stickleback carcasses and live-captures from Drizzle Lake separated for sex and year. To remove influences of younger adults confounding differences in adult body size among years, only fish equal or greater than 4 years of age are included. Samples sizes shown adjacent to symbols.

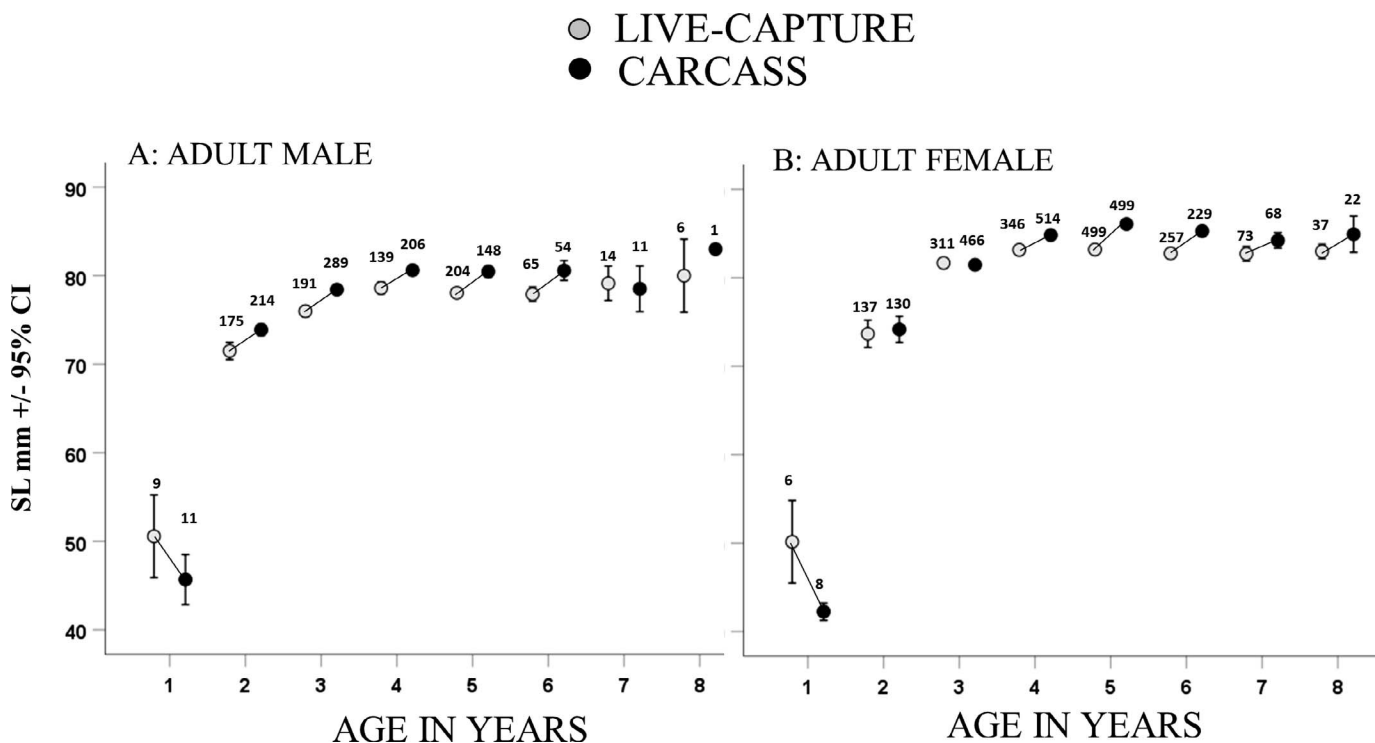


FIG. 6.—Mean adult SL (+/- 95% CI) of stickleback carcasses and live-captures from Drizzle Lake separated for sex and year. All fish restricted to age 4 y. Samples sizes shown adjacent to symbols.

P<0.001). Therefore, nematode-induced mortality would account for about 3% of the carcasses.

I also examined to what extent integumentary and skeletal injuries contributed towards mortality in the carcasses. Among 4070 carcasses and 8718 live-captures, scarring from attacks by avian piscivores (aviscars) were the most common, occurring on 69.3% of the carcasses and 4.5% of the live-captures ($\chi^2_1 = 6199, P<0.001$), a trend that occurred in all years where live-dead comparisons were possible (Fig. 8). While this could be inflated due to the positive correlation between lacerations and body size (Reimchen 1988), when I partitioned for age, the same trend was present in all classes (Fig. 9). On carcasses, aviscars often were associated with damage to the base of the dorsal and anal fins that would presumably

compromise swimming ability. I did not observe this damage on live-captures. Bone fractures (spines, plates, and skull) occurred in 41% of the carcasses in contrast to 11% in live-captures ($\chi^2_1 = 1520, P<0.001$), and were often (71%) associated with scarring. The proportionally higher occurrence of fractures in carcasses occurred in all years (Fig. 10) and was present in each age class of stickleback (Fig. 11). I was also able to identify

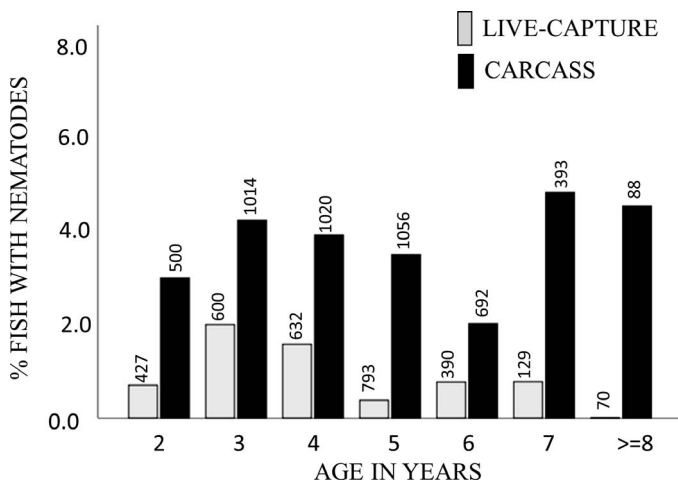


FIG. 7.—Percent of fish with nematodes against age in years for Drizzle Lake carcasses and live-captures. Samples sizes shown above bars.

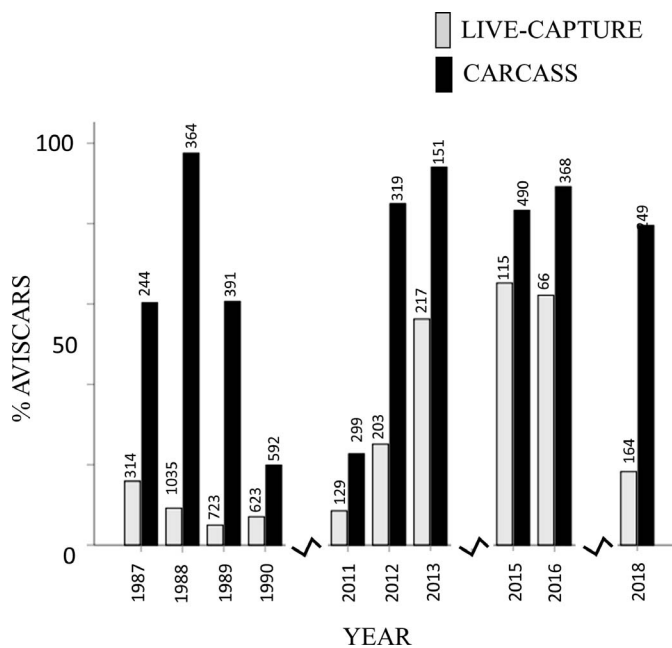


FIG. 8.—Percent of fish with aviscars (bird-induced injuries) for Drizzle Lake carcasses and live-captures separated for year. Samples sizes shown above bars.

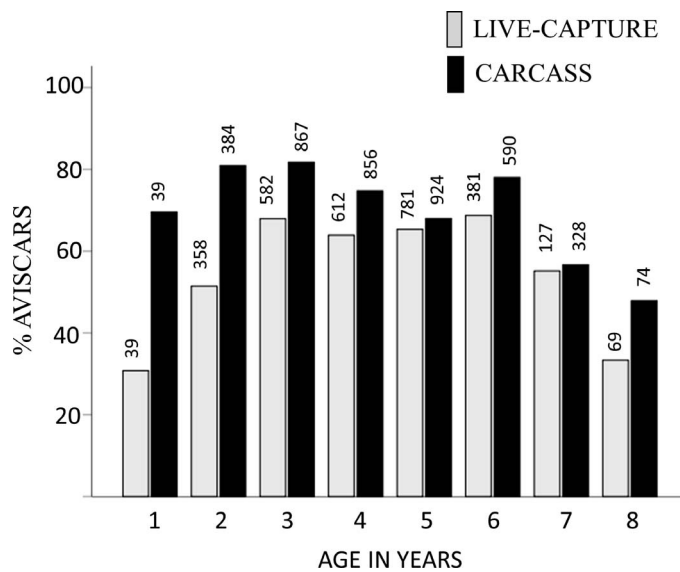


FIG. 9.—Percent of fish with aviscars (bird-induced injuries) for Drizzle Lake carcasses and live-captures separated for age class. Samples sizes shown above bars.

whether the carcass injuries were recent based on the presence or absence of spine regrowth and fusion of skeletal fractures. Among all carcasses with fractures, 60% had fresh injuries compared with 34% among live-captures ($\chi^2_1 = 192.5$, $P < 0.001$). The elevated frequency of scarring on carcasses, in addition to fresh fractures on carcasses with or without scarring, suggests that predator-induced injuries accounts for 70 to 80% of mortality in the carcasses.

DISCUSSION

In the current study, I collected over multiple years intact fish carcasses ($N = 4499$) that accumulated on a lake shore. Whether these yearly accumulations would form a fossil assemblage is unknown. However, I observed that higher on the shoreline decomposed and disarticulated carcasses were incorporated into the sands and gravels and into the encroaching terrestrial bryophytes that characterize successional processes

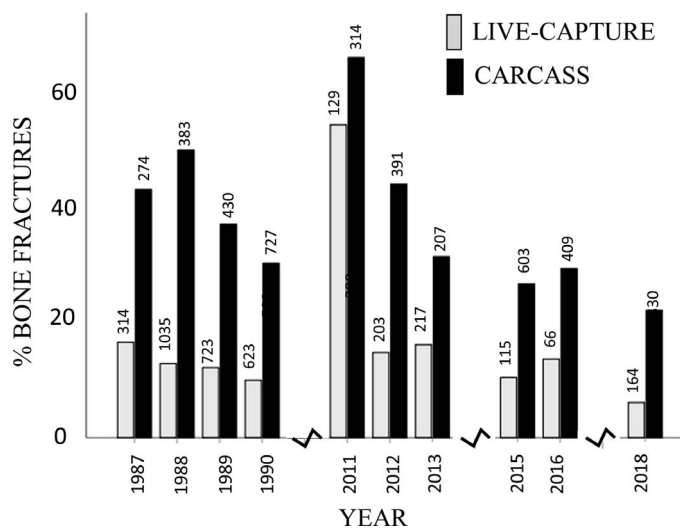


FIG. 10.—Percent of fish with skeletal fractures (spines, skull, and lateral plates) for Drizzle Lake carcasses and live-captures separated for year. Samples sizes shown above bars.

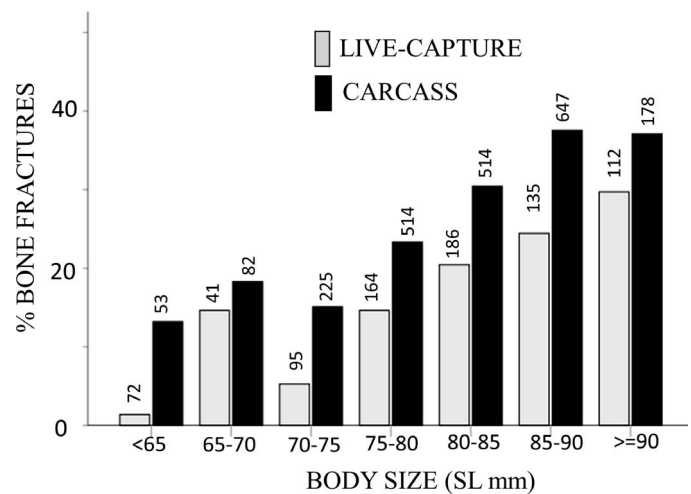


FIG. 11.—Percent of fish with skeletal fractures (spines, skull, and lateral plates) for Drizzle Lake carcasses and live-captures separated for body size classes.

occurring in many bog lakes (Smith and Smith 2015). The purpose of this study was to assess the extent to which the carcass assemblage reflected the composition of the live community. In addition to the basic taxonomic analysis, this study is useful as it examines demographic parameters, including age class frequencies, sex ratios, and sources of mortality across multiple years. Of the four fish species in the lake, each was represented in the shoreline carcasses with an abundance largely resembling their relative abundance in the lake. However, among the 36 species of aquatic birds on the lake, including Common Loon, which is the major avian predator on adult and subadult stickleback in the lake (Reimchen and Douglas 1984; Reimchen 1994), only a single carcass of an uncommon species (Long-tailed Duck) was found in the 95 lake circuits.

A basic metric in live-dead comparisons and in fossil series is body or trait size (Hallam 1967; review in Kidwell and Holland 2002). Most extant fish populations exhibit a Type III survivorship curve and as a result, an ideal death assemblage would track such a frequency distribution. This was not observed in the current study as juvenile fish (<30 mm SL) comprised more than 70% of the live population (Reimchen 1990) yet were absent among the carcasses in all years. Such deficiencies can result from one or more taphonomic processes that can distort the fidelity of body size frequencies, including increased rates of decomposition (weak ossification), disarticulation and differential transport from the source area (Jepsen 1964; Elder and Smith 1988; Paul 2009). However, in this study, the major deficiency of juvenile fish in the carcass assemblages was largely due to their capture and consumption by avian and salmonid piscivores in the lake (Reimchen and Douglas 1984; Reimchen 1990, 1994). Apart from the deficiency of juveniles, to what extent do body size frequencies of the fish carcasses reflect those in the live population? I found that modal SL class (80–84 mm) of stickleback was the same for carcasses and for live-captures, yet mean sizes of carcasses were larger relative to live-captures, the difference being accentuated among the largest body size classes. Body-size biases are well-recognized in fossil series, which can complicate morphological comparison with extant populations (e.g., Behrensmeier et al. 1979; Cooper et al. 2006). I was able to identify five factors relevant to adult body size variation between live-captures and carcasses: temporal shifts in adult size, sex ratio, condition factor, senescence, and sources of mortality.

Unexpectedly, there were substantial changes (10–13%) in asymptotic adult SL among years. Because body growth in a poikilotherm such as stickleback is correlated with temperature and resource availability (Allen and Wootton 1982), parsimony suggests that the yearly changes in

asymptotic body size, changes that were concordant between sexes, reflect temporal variation in these basic ecological processes but also indicate strong temporal fidelity between live-captures and carcasses for this metric. Yet if such differences of a 10% asymptotic body size were observed in a fossil series with high-temporal-resolution, they are potentially interpreted as an evolutionary response (e.g., Barton and Wilson 1999, 2005; Bell 2009). Using published studies, Hendry and Kinnison (1999) computed rates of evolutionary change for a diversity of extant taxa that were transplanted to new geographical areas or were subject to substantive climatic fluctuations. These rate estimates were sensitive to temporal scale (Darwins) and to number of generations (Haldanes), consistent with previous recognition of the importance of scale (Gingerich 1983). How do the differences in adult size observed in the carcass assemblage of this study compare with those in other microevolutionary studies? Based on the \log_{10} relationship between evolutionary rate and time interval (Hendry and Kinnison 1999), the predicted average rates for 27 years and nine generations (the temporal duration of these data) would be approximately 3500 Darwins (range among other studies: 100 to 10,000) and approximately 0.05 Haldanes (range: 0.01 to 0.1). I computed rates for the differences between the lowest and highest adult SL (all ages) separated for carcasses and live-captures and for sex. These data (Table 1) indicate average rates of 3400 Darwins and 0.002 Haldanes, with carcasses showing about one-half the rates of the corresponding live-captures and males with marginally lower rates than females in each comparison. Combining adults of all ages into a single category could lead to spurious estimates if samples varied in the proportion of age classes that differed in average SL. Consequently, I computed rates for a single and most common adult age class (4 y) yet these showed largely equivalent rates to the grouped data. Therefore, these evolutionary rates for adult body size over the 27 years are either average (using Darwins) or low (Haldanes) relative to other microevolutionary rate estimates. That the carcasses exhibited half the evolutionary rates than did live-captures could result from differential predation (see below). Such estimates are informative with respect to the continued interest in integrating micro- and macroevolutionary changes in body size (Uyeda et al. 2011).

Fishes are often sexually monomorphic and as such, the sexes are rarely differentiated in death assemblages, least of all in fossil series where differentiation might not be possible (Elder and Smith 1988; Kidwell 2013). Among extant fishes, sex ratio is generally close to unity (Helfman et al. 1997) and it is reasonable to expect that death assemblages as well as fossil fish series would on average reflect such equality of sex ratios. Departures from this in shoreline carcasses might be expected in some species such as stickleback, in that males are more common in littoral zones than are females (Reimchen and Nelson 1987; Reimchen and Nosil 2004; Reimchen et al. 2016) and might be over-represented relative to females. As well, stickleback males have a shorter life span than females (Wootton 1976; Dufresne et al. 1990) which would further facilitate a male bias as short-lived species are often over-represented in death assemblages (Kidwell and Rothus 2010; Cronin et al. 2018). As such it was unexpected that the carcasses in this study were substantially female-biased, a trend that persisted over multiple years. The cause for this is not known but several interpretations are possible. Stickleback vary in their bone density and buoyancy (Myhre and Klepaker 2009) so if females had higher buoyancy then did males, increased flotation and surface transport would increase their representation on the shoreline. There are no current data to evaluate this possibility. An alternative mechanism for the sex ratio bias could be associated with post-capture escape from predators. Most vertebrates that swallow their prey whole are gape-limited; this provides an advantage to prey that approach or exceed the gape of the predator (Vermeij 1982). In stickleback, females tend to be larger than males (Reimchen et al. 2016), including those in the present population, and would have a greater chance of escape from gape-limited predators. Assuming that a proportion of post-capture escapes succumb to their

TABLE 1.—Evolutionary rates for adult body size (SL) of stickleback at Drizzle Lake, Haida Gwaii, western Canada. Darwins are calculated as $(\ln(X_{t_2}) - \ln(X_{t_1})) / \Delta t$ where t is the time in millions of years. Haldanes are computed from $((\ln(X_{t_2}/S_x) - \ln(X_{t_1}/S_x)) / (t_2 - t_1)) / S_x$ where S_x is the pooled standard deviation of $\ln X_2$ and $\ln X_1$ and $t_2 - t_1$ is the difference in time converted to generations (Gingerich 1983). 'Age' ≥ 4 includes all adult age classes (4–10) or only Y4. 'N' are the sample sizes of fish for the low and high years differing in mean SL. 'Years' represents the duration between the lowest and highest average SL values. Generation time is 3 years (Reimchen 1992b).

	Source	Age	N L-C	Years	Gen	Darwins	Haldanes
Male	Carcass	≥ 4	104/48	28	9.3	1714	0.001
	Live	≥ 4	462/35	26	8.7	3462	0.003
Female	Carcass	≥ 4	97/167	24	8	3542	0.002
	Live	≥ 4	482/28	27	9	6037	0.004
Male	Carcass	4	22/43	28	9.3	1857	0.002
	Live	4	334/23	26	8.7	3385	0.003
Female	Carcass	4	19/60	27	9	2556	0.002
	Live	4	332/30	28	9.3	4821	0.003

injury, this would result in over-representation of females in shoreline carcasses. Stickleback are also sexually dimorphic in other traits including spine morphology, pelvic girdle, lateral plates, and vertebral number (Reimchen et al. 2016). If the sexes were not differentiated, then temporal differences in the sex ratio would strongly affect the compositional fidelity of the death assemblage. Multiple oscillations in morphometric traits in high-resolution assemblages of Eocene stickleback (Bell et al. 1985; Bell 2009) could possibly reflect sex ratio effects rather than random walks over evolutionary time (Bookstein 2013).

Identifying causes of mortality in death assemblages remains a challenge in many taphonomic and paleontological studies (Elder and Smith 1988; McAllister 2003) but it is essential for inferring ecological interactions and selective pressures in fossil communities. I observed no evidence for anoxia-induced mass mortality, which has been well-documented in fishes and provides high confidence in the taxonomic fidelity of the fish community (Bell et al. 1989; Helfman et al. 1997; Hurst 2007). An alternate cause of mortality could be a poor-condition factor, occasionally inferred in analyses of death assemblages (Elder and Smith 1988). I predicted that if poor-condition was a source of mortality for the carcasses, these individuals would have smaller age-specific body size than live-captures but contrary to prediction, I found that carcasses had a significantly larger body size than live-captures of the same age class, suggesting that they had high growth rate. In other fish taxa, there are costs associated with higher growth rates (Rollo 2002; Fischer et al. 2005); these include reduced longevity due to resource allocations directed towards growth rather than to internal homeostasis (Cichon 1997) or to increased susceptibility to predator attacks because higher growth rates require greater foraging activity and exposure to predators (Arendt 1997; Metcalfe and Monaghan 2003). That the carcasses had substantially greater frequency of predator-induced injuries relative to live-captures would support increased risk. Although this is a reasonable inference, the same trend would occur if attack rates by predators were the same on different size classes but the post-capture escape rate (and subsequent mortality) was greater on larger fish.

Another potential source of mortality in death assemblages is parasitism. I observed that relative to live-captures, carcasses had up to ten times the level of nematode infection. Parasites can impose substantial costs on their fish hosts, including increased metabolic demands and weakened body condition (Barber and Huntingford. 1995). Stickleback are one of many fish species that act as an intermediate host for the nematode parasite

Eustrongylides (Margolis and Arthur 1979) and this infection can result in significant inflammation and pathology to the host (Paperna 1974). Experimental evidence with nematode-infected mosquitofish (*Gambusia holbrooki*) shows increased susceptibility to capture by predators (Coyner et al. 2001). Also, even without reduced physiological condition, parasites can manipulate behavior of intermediate hosts to facilitate transfer to the definitive hosts (Thomas et al. 2010). As avian piscivores are the definitive host for this parasitic nematode (Paperna 1974), the elevated occurrence of infected stickleback carcasses could reflect higher predation attempts by these piscivores. High frequency of aviscars in the carcasses is consistent with such a possibility. Based on total infection, the nematode parasite accounts for 4% of the mortality of all the carcasses.

Another source of mortality leading to death assemblages in fishes is post-reproductive senescence (Helfman et al. 1997) and for an iteroparous and long-lived population such as the stickleback in the current study (Reimchen 1992b), senescent fish will be older than live-captures that are still reproductively active. Adult carcasses accumulated on shore during summer reproductive season and it initially appeared that senescence could be a significant source of mortality in adult fish. However, quantification of fish age indicated that the majority of carcasses were not senescent but rather younger than the age distribution of live-captures. I estimate that less than 5% of the carcasses can be attributed to senescent mortality and therefore this cannot explain the larger age-specific body size of the carcasses.

Skeletal abrasions and fractures on carcasses and skeletal material can offer insight to sources of mortality as well as body size distributions. These injuries may originate from transport, deposition and scavengers, but occasionally there are distinctive signatures that define predator attack. For example, gastropod shells often exhibit fresh or repaired fractures that extend from decapod crab attacks, the frequencies of which vary among species both at microspatial scales (Vermeij 1971; Reimchen 1982) and over geological time (review in Vermeij 1987). In the current study, approximately 10% of the live-captured stickleback had non-lethal injuries, including spine fractures and scarring from attacks by predatory birds and salmonids, the frequencies of injuries increasing with body size (Reimchen 1988, 1992a). In contrast, over 70% of the shoreline carcasses had predator-induced injuries. Furthermore, carcasses accumulated on the shoreline in the summer months when large numbers of foraging Common Loons (*Gavia immer*) occurred, the major avian piscivore on fish in this lake (Reimchen and Douglas 1980; Reimchen 1994). Shoreline accumulations during summer are possibly also facilitated by the warmer temperatures that encourage bacterial decay and flotation of submerged carcasses (Elder and Smith 1988). That the death assemblage in this lake is predominantly due to predator attacks may inform interpretations of fossil assemblages if these empirical data are representative of aquatic communities. Unsuccessful predation is taxonomically widespread and has been considered an important driver of evolutionary change (Vermeij 1982).

In summary, what taphonomic insight emerges from this comparison of lacustrine shoreline carcasses with the actual community? Despite the short-duration of the study (12 years between 1987 to 2018), there is good concordance for the taxonomic composition of the fish taxa as well as for their approximate abundance ranking, trends that are consistent with meta-analyses of death assemblages (Kidwell 2013). For demographic attributes of the carcasses, there are consistent departures relative to the live-captures, including a female-skewed sex-ratio, an elevated age-specific growth rate, an elevated mortality of fish with higher growth rate and a major deficiency of younger age classes, each of which would potentially distort ecological inferences in the fossil assemblages that would be derived from this. Based on characteristic predator-induced injuries on live-captured fish, I conclude that integumentary injuries by avian piscivores are the dominant cause of mortality of shoreline carcasses in this locality. These would not be identifiable on intact or disarticulated skeletal elements in a fossil series.

When combined with the exceptionally rare occurrence of avian remains in the death assemblages, it suggests that the major role of avian piscivory on the structure of this freshwater fish community would not have been identified or would have been greatly underestimated. Because avian piscivores are global in distribution and would probably have been prevalent on freshwater lakes throughout the Cenozoic (e.g., Wilson 1987; Bell 1994; Bajdek et al. 2017), it is likely that their influence on aquatic communities and on evolutionary adaptations in fish was potentially substantive.

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