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WINTERKILL OF ALASKA BLACKFISH (*DALLIA PECTORALIS*) IN METHANE DISCHARGING LAKES OF DENALI NATIONAL PARK'S MINCHUMINA LAKE BASIN

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Alaska Blackfish (Esociformes: Esocidae: *Dallia pectoralis*) are small pikes similar in morphology to mudminnows belonging to the esociform genera *Umbra* and *Novumbra* (Nelson 2006; Campbell and others 2013). The species rarely exceeds 20 cm in length (Morrow 1980), and has a relatively small distribution when compared to species from similar latitudes (Campbell 2011). Its small size, lack of anadromy or large scale migration, short life span, and high degree of genetic structuring (Blackett 1962; Aspinwall 1965; Campbell and others 2014; Campbell and López 2014) combined with its relictual distribution (Campbell 2011) suggest a poor dispersal ability.

Alaska Blackfish can tolerate hypoxic conditions in both summer (ice-free) and winter conditions (Ostdiek and Roland 1959; Ultsch 1989), and have been observed in water of 2.3 ppm oxygen at a temperature of 7.8°C (Ostdiek and Roland 1959). They compensate for low oxygen concentrations by using a

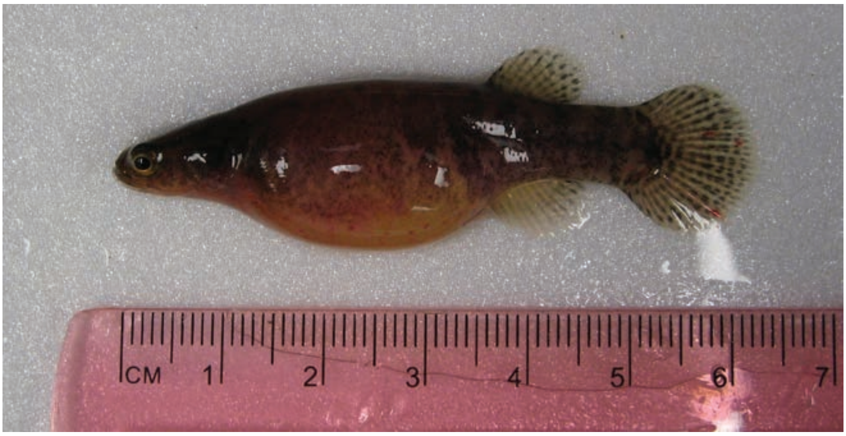

FIGURE 1. An Alaska Blackfish (*Dallia pectoralis*) caught at the surface through a hole in the ice in January 2011 at Ballaine Pond, Fairbanks, Fairbanks North Star Borough, Alaska. The fish exhibited edema.

modified esophagus to obtain atmospheric oxygen (Crawford 1974). Within the biogeographic region including the former Bering land bridge and adjacent areas in Alaska and northeastern Siberia known as Beringia (Pielou 1991) they are the only air-breathing fish. During ice-free months, individuals have ready access to the surface, while during winter holes created by Muskrats (*Ondatra zibethicus*) may be used to access the surface (Campbell 2011). In some cases, Alaska Blackfish survive under ice but show signs of physiological stress through edema (Fig. 1), an accumulation of liquid in interstitial spaces (Doyle 1977). Edema and other observations suggest the species may have other undocumented mechanisms to tolerate hypoxia (Ultsch 1989). Fish captured with edema appear to recover quickly when exposed to moderate dissolved oxygen concentrations (9–12 mg/l O_2 and 1–3°C water temperature) (Doyle 1977). Typically, characteristics of Alaska Blackfish such as a low dispersal rate, small range, and small body size are associated with higher extinction and extirpation rates (Gaston 1994; Olden and others 2008; Giam and others 2011); however, their ability to supplement respiration through air breathing and their remarkable winter survivability have undoubtedly played a large role in their survival in multiple Beringian refugia during Pleistocene glaciations (Campbell and López 2014). Despite their survival abilities, overwintering fish kills were recently observed in Alaska, as reported here.

In the winter of 2010–2011, a die-off of Alaska Blackfish was observed in the vicinity of Lake Minchumina, Alaska (UTM: Zone 5, E537377, N7084931, NAD83), in 3 separate bodies of water (Table 1). On 23 May 2011 at 12:15, hundreds of dead fish were observed along the margin of Caribou Lake approximately 40 km south of Lake Minchumina. The fish were bloated and covered with a thin film of fungi, indicating they had died some days earlier, likely when the lake was still ice-covered. On a 50-m transect, 34 carcasses were counted, and a comparable density of dead fish was observed along 800 m of shoreline where they were concentrated by wind action. Using the transect count, 544 dead fish (34 fish/50 m × 800 m = 544 fish) were estimated to have died in this 75-ha lake (7.25 dead fish/ha). On 31 May 2011 at 14:00, dead Alaska Blackfish were also observed on a 2nd small shallow lake (lake 663) approximately 20 km east of Lake Minchumina. Five fish were dead and others were bloated and weakly swimming upside down near the lake surface.

Both Caribou Lake and lake 663 are located in a lake-rich region typified by shallow lakes that are heavily vegetated with submersed aquatic macrophytes, including *Potamogeton robinsii*, *P. richardsonii*, and *P. perfoliatus*. These lakes are connected to adjacent lakes via small waterways through muskeg and are primarily surrounded by Black Spruce (*Picea mariana*) muskeg. Degraded permafrost is present along the shores of both lakes, which is known to produce high

TABLE 1. General characteristics of die-offs of Alaska Blackfish (*Dallia pectoralis*) and lakes in which die-offs were observed. Additional fish were observed to be distressed in lake 663.

Lake name	Date of observation	Number of dead fish observed	Fish with edema	Degrading permafrost	Lake size (ha)	Lake depth (m)	Lake location (UTM Zone 5 NAD 83)
Caribou Lake	23 May 2011	544	Perhaps	Present	75	1.3–1.5 (average)	E527784, N7047108
lake 663	31 May 2011	5	Yes	Present	18	1.3–1.5 (average)	E558195, N7088412
Holek Lake	15 April 2011	>13	No	Unknown	89	4 (maximum)	E540747, N7081901

levels of methane discharge (Bubier and others 1995).

On 15 April 2011, another fish kill was observed on Holek Lake, approximately 4 km south of Lake Minchumina. Approximately 13 dead fish were observed in an open hole in the ice, where JC and MC were collecting water samples for methane ebullition studies. One distressed individual contained a swim bladder full of gas (Fig. 2), and all dead fish were gas-filled. Several other openings in the ice were maintained by methane bubbles that rise from the sediment transporting warm water to the surface, and all contained additional dead fish. A small stream drains the lake and is periodically flooded with turbid water from the adjacent Foraker River, a large glacial river originating in the Alaska Range.

In the 3 observations of fish kills, fish appeared to have died under different circumstances as the presence of edema and environmental characteristics were not uniform across observations. While Alaska Blackfish are able to survive extreme conditions, it is clear that they often live at the edge of their physiological abilities and consequently may experience die-offs. The mudminnows (*Umbra* spp.) are capable of air breathing using the swim bladder (Graham 1997; Magnuson and others 1983). Central Mudminnows (*U. limi*) can survive winterkill conditions by breathing air bubbles trapped below ice (Klinger and others 1982; Magnuson and others 1983, 1985) and can breathe bubbles containing mixtures of methane (up to 80%) and oxygen (Magnuson and others 1983). In general, Central Mudminnows visited gas bubbles in a random fashion under the ice but took fewer breaths at bubbles with higher oxygen content, yet the fish were not able to discriminate between gas concentrations without breathing from the bubble (Magnuson and others 1983). If the same pattern is inferred for Alaska Blackfish, methane ebullition may have a significant role in winter mortality. Methane discharge trapped under ice would reduce the concentration of oxygen in trapped bubbles, diminishing the value of air breathing to the fish. Thus, Alaska Blackfish may continue air breathing from bubbles but not recover sufficient oxygen from air-breathing or through the gills to survive.

The Alaska Blackfish we observed likely died as a result of hypoxia. In some lakes dead fish

FIGURE 2. Living Alaska Blackfish (*Dallia pectoralis*) taken on 15 April 2011 at Holek Lake, Minchumina Lake basin, Alaska. The fish was bloated with a gas-filled swim bladder (indicated by white arrow) but lacked signs of edema.

had edema, and all lakes were shallow and had been ice covered for many months. Combined with ice cover in shallow lakes, methane discharge may contribute to the death of fish. Methane discharge is typical of thermokarst lakes, where Alaska Blackfish are frequently found on the Chukchi Peninsula (Gudkov 1998) and in Interior Alaska (Blackett 1962). Thermokarst lakes, also known as thaw lakes, often undergo expansion as ice-rich permafrost melts. The lake expands vertically and horizontally, and as the ground thaws microbial activity increases producing methane. Methane ebullition can be extremely rapid and serves to maintain open leads in the ice that may be frequented by Alaska Blackfish. Methane ebullition from Siberian thermokarst lakes and the 2.2 m deep Goldstream Lake in the Goldstream Valley near the study area of Blackett (1962) averaged 73 to 78% methane by volume and 27,450 mg methane m^{-2} d^{-1} (Walter Anthony and others 2010). Discharge from a hotspot, an area in a lake where ebullition keeps the water open throughout winter, is composed of 88.7 ± 1.4% methane (average ± standard deviation) (Walter and others 2008) and remains consistent in methane discharge through the year (Walter Anthony and others 2010). Winter discharge in the lakes in the Minchumina Basin may have a methane ebullition rate comparable to those studied elsewhere in Alaska and Russia. A large proportion (30 to 99%) of methane produced in lakes can be oxidized (Bastviken and others 2008), and aerobic oxidation of methane under ice will decrease oxygen concentrations while producing carbon dioxide.

Although Alaska Blackfish are air-breathing and hypoxia tolerant, access to sufficient oxygen for respiration may not be enough for survival during winter under ice. When available oxygen under the ice drops in lake environments, anaerobic oxidation of methane can produce hydrogen sulfide (H_2S) (Bridgham and others 2012), an extremely toxic compound to fishes (Magnuson and others 1985; Reiffenstein and others 1992). Generally, H_2S is not deleterious to fish because they will die from hypoxia under ice before concentrations of H_2S rise to toxic levels (Scidmore 1957; Magnuson and others 1985). With air-breathing and hypoxia tolerance exhibited by Alaska Blackfish, the concentration of H_2S may become high enough to cause fish mortality.

Alternatively, methane input through ebullition may contribute to the long-term survival of Alaska Blackfish by inhibiting ice formation and producing open holes in ice (Walter Anthony and others 2010). Alaska Blackfish have been observed by MC when fishing in midwinter; fish were attracted to a newly opened hole in the ice for air-breathing. Subsistence fishermen frequently take advantage of this behavior (Andersen and others 2004). Commonly, areas of high methane discharge are known as ''blackfish holes'' by local residents (K Walter Anthony, University of Alaska Fairbanks, pers. comm.).

The mass die-offs observed indicate that Alaska Blackfish may not permanently occupy all available habitat, and certain ponds and lakes may be population sinks due to winterkill. A particular pond or lake may not provide suitable overwintering habitat at all, or only for some years. Alaska Blackfish are known to undergo seasonal migration and are actively moving and dispersing in the spring (Blackett 1962). Fish entering ponds and lakes during spring freshets or through temporary connections may die in winter if they do not leave these water bodies in fall. The life history and physiology of this species remains poorly described, and how overwintering conditions, lake chemistry, and population dynamics interact is unknown. We are, therefore, unsure if the die-offs are typical or unusual. However, increased permafrost degradation and methane emissions as a result of climate change may pose a threat to the viability of this species in regions with extensive permafrost.

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