Parasites with fishes as hosts have been extensively studied, revealing ways the parasite can deplete the host’s energy (Schultz et al., 2006), affect host behaviour (Seppälä et al., 2008) and increase host mortality (Granath & Esch, 1983; Bourque et al., 2006; Jacobson et al., 2008; Ferguson et al., 2011; Markle et al., 2014; Michálková & Ondráčková, 2014). Cestodes of the genus *Schistocephalus* have received particular attention (Barber, 2013) due to their ability to alter the behaviour (Giles, 1983; Barber & Huntington, 1995) and population dynamics of their hosts through effects on reproduction (Heins, 2012) and survival (Heins & Baker, 2011), the complexity of their lifecycle (Hammerschmidt et al., 2009) and their host specificity (Braten, 1966; Henrich et al., 2013). The cestode *Schistocephalus solidus* infects three-spined sticklebacks *Gasterosteus aculeatus* L. 1758, a fish species that has been extensively investigated by behavioural and evolutionary ecologists (Bell & Foster, 1994). Cestode larvae infect copepods which, when consumed by *G. aculeatus*, grow inside the fish’s body cavity before eventually altering the host’s swimming behaviour, reducing predator avoidance (Giles, 1983; LoBue & Bell, 1993; Quinn et al., 2012). To complete the parasite’s life cycle, the fish must be consumed by a bird, within which it reaches sexual maturity, and produces eggs that are excreted back into fresh water to be consumed by copepods (Barber & Scharsack, 2010).
Preliminary observations revealed the presence of a parasite superficially similar to S. solidus in coastrange sculpin Cottus aleuticus Gilbert 1896 and slimy sculpin Cottus cognatus Richardson 1836 in Iliamna Lake, Alaska, U.S.A. but segment count distributions from the sculpin cestodes differed from those of cestodes in sympatric G. aculeatus (B. S. Harmon, unpubl. data). A new species of cestode, Schistocephalus cotti, was described from Finland in Cottus gobio L. 1758 by Chubb et al. (2006), and the segment counts of these cestodes were similar to those of the Iliamna Lake cestodes. More recently, French & Muzzall (2008) reported Schistocephalus in C. cognatus from Lake Michigan. Thus, cottids can become hosts to these cestodes but the taxonomy and ecology of these parasites in sculpins have not been extensively investigated. Cottids often constitute a large fraction or even the majority of fishes in lakes and streams of north-western North America in numbers and biomass (Eggers et al., 1978; Roni, 2002). Considering their abundance, sculpins have received little scientific attention but can affect other freshwater fishes as predators (Patten, 1975; Foote & Brown, 1998; Tabor et al., 2007), competitors (Zimmerman & Vondracek, 2006) and prey (Beauchamp, 1990; Hudson et al., 1995). Consequently, if the parasites are prevalent and exert strong effects on sculpins, there could be consequences for other parts of the aquatic community. Given the results of research on the cestode in G. aculeatus (Barber, 2013), the parasites might be expected to affect food consumption, growth, population age structure and survival in sculpins. Accordingly, the purposes of this study were to quantify the proportions of infected C. cognatus and C. aleuticus in a habitat where both are abundant, quantify possible effects of the cestodes on feeding and growth and estimate annual rates of infection and survival of infected and uninfected fish of each species.

Sculpins were collected using hand-nets in water of 0–2 m deep at a rocky beach used annually by spawning sockeye salmon Oncorhynchus nerka (Walbaum 1792) on Northwest Woody Island in Iliamna Lake, in south-west Alaska (Adkison et al., 2014). Sculpins are very common at this site but the lake is large and physically diverse, and both Cottus species are widely distributed in streams and beaches (P.B. Roger, unpubl. data), so the sampling was not designed to assess the variation in parasite prevalence in the lake. Snorkellers attempted to capture each fish that was seen to minimize collection biases with respect to size and species. Smaller individuals, however, were difficult to detect among the rocks and so were probably under-sampled relative to their true abundance, and subsequent age determination indicated that no young-of-the-year were collected. Fishes were euthanized using a lethal dose of buffered MS-222 and transported to the laboratory. All sampling was conducted under permits from the Alaska Department of Fish and Game, and the University of Washington’s Institutional Animal Care and Use Committee. The two species were differentiated by the number of pores on the anterior of the chin (C. aleuticus: one pore and C. cognatus: two pores; Scott & Crossman, 1973).

Fishes were weighed and measured for total body length ($L_T$) from the anterior point of the mouth to the posterior portion of the caudal fin and the body cavity was opened and visually inspected for the presence of Schistocephalus (Cestoda) using a dissecting microscope. Any cestodes detected were removed from the fish, counted, weighed and measured for length. Possible effects of cestodes on fish body condition were assessed by analysis of covariance (ANCOVA). The effect of the presence or absence of cestodes on the ln of fish mass (minus parasite mass) was assessed using ln $L_T$ as a covariate. This analysis was conducted separately for each species. The stomach contents of the
fish were then examined. Diets of sampled fishes consisted entirely of *O. nerka* eggs in 2012, and primarily eggs in 2013. The eggs were readily identifiable and some were intact but in others the egg membrane was broken. So, they were counted rather than weighed to assess foraging by fish of each species as a function of cestode infection and *L. T.* Foote & Brown (1998) reported that sculpin consumption of eggs was limited by the fish's gape (55 mm for *C. aleuticus* and 50 mm for *C. cognatus*), so analysis of fish diets only considered fish greater than these lengths.

Both sagittal otoliths were removed from the fish and examined for age determination under a microscope. Dark rings were assumed to be annuli and the counts on the two otoliths were compared for 136 *C. aleuticus* and 89 *C. cognatus*. Paired otoliths were read blind with respect to one another and in cases when the ages were inconsistent (13 of 225 pairs = 5.8%), another separate reading was used for final determination. In addition, 26 pairs (10% of the otoliths) were re-examined (blind with respect to the first reading) on a different day and 24 of the 26 pairs matched their original reading. One fish was judged to be a year older, and one a year younger than the previous reading; in these cases, the second reading was used.

A simple age-structured population dynamics model was constructed to estimate the proportion of fish becoming infected each year, and the survival rates of uninfected and infected fish of each species, using the number of fish that were uninfected of age *a*, species *s Xs*, and the number that were infected *Ysa*. Aggregating data across the 2 years implicitly assumes that the age distribution did not change between years but this cannot be determined from the samples in this large, open population. No infected 1 year-old fish were found so it was assumed that infection first occurred between ages 1 and 2 years. The dynamics of the uninfected population is

\[ X_{sa+1} = X_{sa} p_s (1 - g_s) \]

where *p_s* is the fraction of uninfected fish of species *s* that survive from 1 year to the next and *g_s* is the fraction of uninfected fish of species *s* that become infected each year and *p_s* and *g_s* were assumed to be independent of age. The dynamics of the infected population is

\[ Y_{sa+1} = Y_{sa} q_s + p_s g_s X_{sa} \]

where *q_s* is the fraction of infected fish of species *s* that survive from 1 year to the next. The number of individuals of each type and age are predicted assuming that the probability of capture *c_s*, which is a function of age and species, follows the standard logistic form (Quinn & Deriso, 1999):

\[ c_s = \left\{ 1 + e^{[-d_s(a - e_s)]} \right\}^{-1} \]

where *a* is the age at which the fish have a 50% probability of capture and the parameter *d_s* determines the slope of the selectivity curve through the point *x = e_s c_s = 0.5*. Thus, the predicted number observed for each species and age is

\[ X^*_{sa} = c_s X_{sa} \]

and

\[ Y^*_{sa} = c_s Y_{sa} \]

The number of observed uninfected (*X^* sa) and observed infected (*Y^* sa) were collected in the field (Table I).

To compare alternative model specifications, it was assumed that the data were normally distributed (with s.d. *σ*) around the expected value (*X^* sa, *Y^* sa) so the likelihood is:

\[ L = \prod \left( \frac{1}{\sqrt{2\pi} \sigma_s} \right)^{-1} e^{-\left( \frac{X^* - X^*}{2\sigma^2_s} \right)} \prod \left( \frac{1}{\sqrt{2\pi} \sigma_s} \right)^{-1} e^{-\left( \frac{Y^* - Y^*}{2\sigma^2_s} \right)} \]

With this formulation, the parameters of the model were estimated and Akaike information criterion (AIC) was used to determine whether the survival and infection rates differed between species (Hilborn & Mangel, 1997). The parameters to be estimated were therefore *p_s, q_s, g_s, e_s, d_s, σ_s* and *Xs, Ys*. It is certainly possible that there are age-specific differences in survival of infected and uninfected individuals as well as age-specific infection rates. A model with age-specific rates, however, would be very much over-parameterized, given the amount of data available.

Table I. Counts of sculpins *Cottus aleuticus* and *Cottus cognatus* in each age group, categorized as uninfected and infected with *Schistocephalus* based on examination under a dissecting microscope.

<table>
<thead>
<tr>
<th>Age (years)</th>
<th><em>C. aleuticus</em></th>
<th></th>
<th></th>
<th><em>C. cognatus</em></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Uninfected</td>
<td>Infected</td>
<td></td>
<td>Uninfected</td>
<td>Infected</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>0</td>
<td></td>
<td>10</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>13</td>
<td>17</td>
<td></td>
<td>16</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>28</td>
<td></td>
<td>24</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>14</td>
<td></td>
<td>14</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>13</td>
<td>11</td>
<td></td>
<td>4</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>0</td>
<td></td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>0</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>NA</td>
<td>1</td>
<td>2</td>
<td></td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>67</td>
<td>72</td>
<td></td>
<td>71</td>
<td>23</td>
<td></td>
</tr>
</tbody>
</table>

NA, fishes whose ages could not be determined.

Cestodes accounted for up to 28% of the mass of infected fishes, were up to 129% of the fish’s $L_T$ and were more prevalent in *C. aleuticus* (52% of 139 fish had at least one cestode) compared with *C. cognatus* (23% of 94 fish, $\chi^2 = 18.79$; d.f. = 1, $P < 0.001$). Sculpins contained up to 10 cestodes, and infected *C. aleuticus* had more cestodes on average (2.08, maximum = 10) than did *C. cognatus* [average = 1.32, maximum = 3; unpaired t-test, $t = 3.12$, d.f. = 92, $P$ (two-tailed) = 0.002; Fig. 1].

In 2012, diets of sculpins on Woody Island consisted entirely of *O. nerka* eggs during the period sampled. In 2013, eggs were the most important but not the sole item, with the remainder being aquatic macroinvertebrates. Combining the 2 years, *C. aleuticus* with cestodes consumed fewer eggs (mean ± s.d. = 0.97 ± 1.41 eggs per fish) than those without cestodes [mean ± s.d. = 1.60 ± 1.85 eggs per fish; $t = 1.68$, d.f. = 82, $P$ (one-tailed) < 0.05]. *Cottus cognatus* with cestodes did not consume significantly fewer eggs than those without cestodes (mean ± s.d. = 1.39 ± 2.06 eggs per fish) [unpaired t-test, $t = 1.68$, d.f. = 82, $P$ (one-tailed) = 0.051].

Fig. 1. Proportions of *Cottus aleuticus* (■, n = 139) and *Cottus cognatus* (□, n = 94) sampled in Iliamna Lake with different numbers of *Schistocephalus* cestodes.
fewer eggs (mean ± s.d. = 1.09 ± 3.96 eggs per fish) than those without cestodes [mean ± s.d. = 1.40 ± 4.10 eggs per fish; \( t = 0.09 \), d.f. =76, \( P \) (one-tailed) > 0.05].

ANCOVA indicated that uninfected \( C. \) aleuticus were lighter for their \( L_T \) than infected fish (\( F_{1,129} = 4.335, P < 0.05 \)) but uninfected \( C. \) cognatus did not differ from infected fish (\( F_{1,83} = 0.028, P > 0.05 \)). \( L_T \) and mass plots (Fig. 2) also revealed that the fish with parasites tended to represent a narrower range of \( L_T \) than those without parasites. The variances in \( L_T \) were greater for fish without cestodes compared with fish with cestodes for both sculpin species (\( C. \) aleuticus: \( F = 2.02, P < 0.01 \); \( C. \) cognatus: \( F = 2.79, P < 0.05 \)). The presence of cestode, however, was not associated with a significant reduction in \( L_T \) at age in \( C. \) aleuticus (\( F_{1,131} = 1.18, P > 0.056 \)) or in \( C. \) cognatus (\( F_{1,85} = 0.68, P = 0.41 \)).

The two sculpin species differed in age distribution (\( \chi^2 = 20.6, P = 0.01 \); Table I); \( C. \) aleuticus tended to be older than \( C. \) cognatus. Using the data on age composition and proportions of fish at each age with cestodes allowed a comparison of models in which each species had separate parameters against models in which the annual survival and infection rates were the same for both species. There was no significant difference between species in the survival rates of infected fish (0.3% for \( C. \) aleuticus and 8.3% for \( C. \) cognatus), but the estimated annual infection rates (54.0% for \( C. \) aleuticus and 20.7% for \( C. \) cognatus) and survival rates of uninfected fish (100% for \( C. \) aleuticus and
23.1% for *C. cognatus*) differed significantly between species (ΔAIC: 7 for survival rate of uninfected fish and 17 for infection rate). Given the relatively small amount of data and the fact that the differences between infection rates and survival rates may be affected by differences in age structure between the two species, the important result is the very clear difference in survival between uninfected and infected individuals seen in both species.

Taken together, these results indicated that infection by the cestode was common at the study site, and it affected several aspects of the ecology of the sculpin hosts. *Cottus aleuticus* were more frequently infected, had more cestodes when infected, higher estimated annual infection rates and a larger effect on egg consumption than *C. cognatus*, despite the fact that the two species were collected at the same place and time, are difficult to distinguish without the aid of a microscope and share many ecological attributes in Iliamna Lake (P. B. Roger, unpubl. data). Egg consumption tended to be lower in parasitized sculpins of both species but was significantly so only in *C. aleuticus*. It is unclear whether the cause of reduced egg consumption was behavioural or physiological. In *G. aculeatus* (Cunningham *et al.*, 1994; Barber & Huntingford, 1995), *S. solidus* restricts room for the stomach to expand at heavy infections, thereby limiting consumption, and to the extent that this is the case for sculpins the parasites might limit consumption of large items such as salmonid eggs. The effect on feeding depends on infection severity, however, and feeding may be initially stimulated by infection (Wright *et al.*, 2006), so the patterns can be complicated. The data indicated that *C. aleuticus* (but not *C. cognatus*) with cestodes were heavier for their $L_T$ (after removal of the cestodes themselves from the fish) than conspecifics without cestodes, although $L_T$ at age did not differ in either species. This effect in condition factor was unexpected but consistent with the weak and very mixed effects of a microsporidian parasite on growth and condition in a different sculpin species (Homola *et al.*, 2014).

The sampling was conducted during the brief period of the year when energy-rich *O. nerka* eggs are most available at the beach where samples were taken and others nearby (Foote & Brown, 1998; Adkison *et al.*, 2014; P. B. Roger, unpubl. data). Analysis of stable isotopes of carbon and nitrogen (Kline *et al.*, 1993) indicated that eggs and other *O. nerka* tissue were a comparatively small part of the overall food intake by *C. aleuticus* (no data were reported for *C. cognatus*). The stable-isotope analysis further indicated that sculpins <60 mm consumed primarily food resources derived from the littoral zone but they relied more heavily on limnetic prey (e.g. zooplankton such as copepods) as they became larger. Assuming a life cycle similar to that known for the *Schistocephalus* species infecting *G. aculeatus* (Barber & Scharsack, 2010), the cestodes probably infect sculpins via consumption of copepods, so the ontogenetic shift in prey may be an important part of the infection pattern in sculpins. Extensive diet analysis by P. B. Roger (unpubl. data), however, indicated consumption of only littoral prey (other than *O. nerka* eggs and fry); both sculpin species consumed primarily snails and larval chironomids and no instances of zooplankton in the diets were reported, so it is unclear when and how infection occurs.

Heins & Baker (2011) found that high mortality rates in infected *G. aculeatus* affected the age composition of the population, and few older (age 6 or 7 years) sculpins had cestodes, although these ages were poorly represented in the samples. This was taken as evidence of parasite-related mortality, and the model estimated very high mortality rates in infected fish of both species but especially *C. aleuticus*. The 100% estimated annual survival rate in *C. aleuticus* without cestodes is certainly
inaccurate but the higher estimate compared with *C. cognatus* and the higher estimated infection rate (54% for *C. aleuticus* v. 21% in *C. cognatus*) were indicated from both years of sampling. Thus, the cestode is a prominent feature of the ecology of both sculpin species but especially *C. aleuticus*, at the habitat sampled, in terms of the proportion of fish infected and the consequences for them. The excess annual mortality of cottids with *Schistocephalus* probably reflects the parasite’s need to infect an avian host to reproduce and complete its life cycle. In Iliamna Lake, the common loon *Gavia immer* is the most frequently observed diving bird in the littoral area where sculpins would be vulnerable. The sculpins congregate on rocky beaches of many flat islands in Iliamna Lake (P. B. Roger, unpubl. data) where *O. nerka* spawn in water of 1–3 m deep near shore during a brief period in mid-late August (Adkison et al., 2014). In these habitats, sculpins are very dense, and probably accessible to predation by birds. If *Schistocephalus* alters sculpin behaviour, sculpins probably are more available to avian, and perhaps aquatic, predators. Loss of large sculpins may affect recruitment, as they typically produce more eggs than younger, smaller fishes (Patten, 1971). Conversely, the loss of older fishes may allow more young sculpins to feed in the nearshore areas. Thus, *Schistocephalus* may have broad effects on the population biology of the hosts.

It is unclear whether the cestodes in Iliamna Lake are a separate species from the *S. cotti* in Finland (Chubb et al., 2006), a range extension of that species, or a variant of the *S. solidus* infecting sympatric *G. aculeatus*. Due to the complex, host-specific life history of *Schistocephalus* (Braten, 1966), and differences in segment counts between cestodes taken from *G. aculeatus* and sculpins in Iliamna Lake (B. S. Harmon, unpubl. data), it appears likely that *G. aculeatus* and sculpins are infected by different cestode species in Iliamna Lake. Regardless of the taxonomic status of the parasites, the cestode–sculpin relationship is a fruitful area for further research and comparisons to the well-studied cestode–*G. aculeatus* relationship (Barber & Scharsack, 2010; Barber, 2013).

The University of Washington’s Alaska Salmon Program is thanked for logistical, field and financial support, the National Science Foundation and the School of Aquatic and Fishery Sciences for additional funding, and many staff members and students for helping with the collection of the specimens. M. Bond and D. Heins provided essential advice and assistance contributing to this research, and anonymous reviewers provided helpful comments.

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