

Research Paper

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Habitat selection and populations of *Corynosoma* (Acanthocephala) in the intestines of sea otters (*Enhydra lutris*) and seals

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Abstract

Acanthocephalans are common intestinal parasites of marine mammals, the most widespread of which is the genus *Corynosoma*. In this study, parasite infrapopulations of two closely related species of *Corynosoma* were examined: *Corynosoma enhydryi* from sea otters (*Enhydra lutris*) in Alaska ($n=12$) and California ($n=19$), and *Corynosoma strumosum* from seals in Germany ($n=22$). Prevalence of *C. enhydryi* was 100% in Californian otters, with a mean abundance of 30, and 83% in Alaskan otters, with a mean abundance of 232. In seals, *C. strumosum* had a prevalence of 65%, with a mean abundance of 33. Female *C. enhydryi* dominated both Californian (82%) and Alaskan (79%) infections, while, in seals, female *C. strumosum* made up 68% of the parasite population. Reproduction rates for *C. enhydryi*, with 16% (California) and 18% (Alaska) of females mated, were low compared to *C. strumosum* in seals, of which 40% of females were mated. Habitat selection also differed significantly between the two species. *Corynosoma enhydryi* was found most frequently in the second and third fifths of the small intestine, while *C. strumosum* was found most frequently in the fourth. The differences in habitat selection and prevalence analysed in this study may be related to a trade-off between growth and reproduction between the two species.

Introduction

Corynosoma enhydryi (Acanthocephala) is the most common parasite of sea otters (*Enhydra lutris*) and the only one known to use them as their main definitive host (Hennessey & Morejohn, 1977; Margolis *et al.*, 1997; Mayer *et al.*, 2003). Members of the genus *Corynosoma* are obligate marine parasites, infecting the intestines of marine mammals and birds worldwide, most commonly in pinnipeds (Aznar *et al.*, 2006). Knowledge about the ecological relevance and sub-lethal effects of these parasites for marine mammals is limited (Shanebeck & Lagrue, 2019). *Corynosoma enhydryi* infections in otters are reported to not cause peritonitis and to induce limited localized tissue reactions (Rausch, 1953; Kreuder *et al.*, 2003; Mayer *et al.*, 2003). In seals, *C. strumosum* infections can cause enteritis, damage to the villi and blockage of the lumen (Lehnert *et al.*, 2007; Amin *et al.*, 2011; Lakemeyer *et al.*, 2020). It is unclear how large-scale infections may affect hosts, and how immune suppression or metabolic disruption may influence health impacts; though infections with *Corynosoma semerme* have been associated with colonic ulcers in Baltic grey seals (Lakemeyer *et al.*, 2020).

The genus is a wide-reaching group; *C. strumosum* and *C. enhydryi* are the closest related members of *Corynosoma* and share a recent common ancestor, likely first evolving in seals as they predate otter evolution in the ocean (García-Varela *et al.*, 2005; Rybczynski *et al.*, 2009). In Europe, another member of the genus, *C. semerme*, also commonly infects seals (Nickol *et al.*, 2002). Although closely related, *C. enhydryi*, *C. strumosum* and *C. semerme* vary significantly in size, body shape and proboscis morphology (Hennessey & Morejohn, 1977; Nickol *et al.*, 2002). *Corynosoma enhydryi* is the largest, with a maximum size of around 29 mm (Hennessey & Morejohn, 1977), while *C. strumosum* peaks at 9 mm and *C. semerme* at 2 mm (Nickol *et al.*, 2002), and infect different portions of the intestine (Nickol *et al.*, 2002; [fig. 1](#)). Prevalence of infection with *C. enhydryi* in southern sea otters has been seen at 90% (Hennessey & Morejohn, 1977) and 94.4% (Mayer *et al.*, 2003), while northern sea otters were observed to have a prevalence of 51% (Margolis *et al.*, 1977). Prevalence of *Corynosoma* infections in seals showed strong variability in geographic location and, over time, measured 56% in the Baltic ($n=26$) (Nickol *et al.*, 2002), 23% in the Wadden Sea ($n=23$) (Lehnert *et al.*, 2007), 87.5% in Japan ($n=40$) (Kaimoto *et al.*, 2018), 100% in Ireland ($n=26$) (O'Neill & Whelan, 2002) and 29.5% in Alaska ($n=105$) (Kuzmina *et al.*, 2012). This difference may be due to host species location, diet and availability of fish intermediate hosts (Nickol *et al.*, 2002).

Clustering of *Corynosoma* species within microhabitats of the intestine has been reported (Helle & Valtonen, 1981; Valtonen & Helle, 1988; Nickol *et al.*, 2002; Kaimoto *et al.*, 2018).

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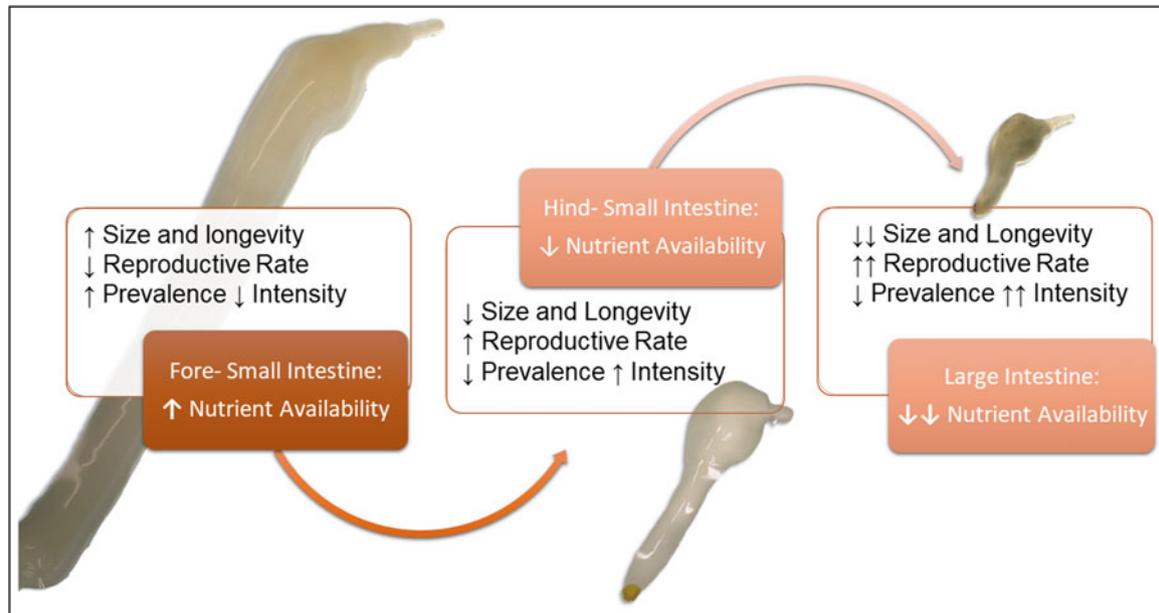


Fig. 1. Visual hypothesis of *Corynosoma* spp. site selection in the gastrointestinal tract. We hypothesize the differentiation in size and site selection seen previously in *Corynosoma strumosum* and *Corynosoma semerme* may be related to a life-history trade-off between longevity and reproduction (MacArthur & Wilson, 1967). Since simple carbohydrate availability decreases along the intestine, parasite longevity (in terms of size and lifespan) will be reduced. Conversely, reproductive rates should increase, as parasites in nutrient-poorer habitats emphasize reproductive output at the cost of adult growth. If this is the case, parasites in low-nutrient environments should show increased intensity associated with seasonality (MacArthur & Wilson, 1967), which has been reported for *C. semerme* (Helle & Valtonen, 1981). Parasites in the beginning of the small intestine, where nutrients are richer, will show increased size, longevity and stable populations (MacArthur & Wilson, 1967), which should be related to higher prevalence but lower intensities in the host population.

The gastrointestinal (GI) tract offers a range of physiochemical gradients, microbiota, immune factors and intraspecific parasite competition for niche differentiation (Berrilli *et al.*, 2012). Microclimates can be created due to availability of nutrients at different stages of digestion, the metabolic processes of gut microbes and their resulting waste products, or even localized immune responses to bacteria or helminth infection (Hooper *et al.*, 1998; Berrilli *et al.*, 2012). As helminths tend to clump in smaller assemblages due to low numbers in the host, and the intestine is not homologous, site selection may be a significant behaviour for *Corynosoma* spp. (Holmes, 1990).

Corynosoma strumosum in seals tend to congregate just past the midgut, and *C. semerme* has adapted to life in the nutrient-poor colon of seals (Helle & Valtonen, 1981; Nickol *et al.*, 2002; Kaimoto *et al.*, 2018). These two species differ in size and proportion, with *C. semerme* being smaller and stouter, with a shorter trunk than *C. strumosum* (Valtonen & Helle, 1988). *Corynosoma strumosum* is also reported to have increased longevity in comparison to *C. semerme* (Valtonen & Helle, 1988), which may be related to this size differential and location higher in the intestinal tract. Previous research has not conclusively explained observed differences in site selection (Valtonen & Helle, 1988; Nickol *et al.*, 2002; Kaimoto *et al.*, 2018); however, due to the differences in size, it is possible that site specificity may be related to available nutrients. Acanthocephalans are absorptive feeders, with carbohydrates as their main source of energy (Kennedy, 2006). Easily accessible monosaccharides are predominantly absorbed in the upper GI tract of mammals; complex polysaccharides are fermented by commensal bacteria and absorbed downstream, often in the large intestine (Hill, 1986). Pinnipeds and sea otters have very short large intestines – in seals, less than 1% of the entire intestinal length on average (Horstmann, 2018). Both groups secrete digestive enzymes to break down macromolecules

like carbohydrates in the duodenum, but have remarkably fast digestive transit times (from ingestion to excretion) – three hours for sea otters (Costa & Kooyman, 1984) and 5–12 hours for pinnipeds (Horstmann, 2018). This may limit opportunity for the breakdown of complex carbohydrates by commensal bacteria.

This study aims to compare infections of *C. enhydri* in otters from Alaska and California (isolated otter host populations), with *C. strumosum* infections of seals from Germany. Distribution in the intestinal tract and sexual success were investigated to better understand the ecology and life-history trade-offs for the genus. Due to previous observations of differences in site selection, size and longevity between *C. strumosum* and *C. semerme* (Nickol *et al.*, 2002), we suspect differences in site selection by this parasite may be related to a life-history strategy of optimization between size (k-selection, longevity) and reproduction (r-selection, transmission) (MacArthur & Wilson, 1967; fig. 1). We hypothesize that *C. enhydri*, as the largest of the *Corynosoma* spp., would prefer anterior sections of the intestinal tract where simple carbohydrates are more abundant; this trade-off from proximity to the colon for ease of transmission versus nutrients and growth would then also be related to a reduction in reproductive rates.

Materials and methods

Parasite removal and identification

The GI tracts of 19 stranded otters in good condition (dead between zero and four days, with intact intestines) were dissected at the Marine Wildlife Veterinary Care and Research Center in Santa Cruz, California, part of the California Department of Fish and Wildlife (CDFW). Otters were collected through a

collaborative stranding network and were part of CDFW's ongoing monitoring of sea otter health, from three different counties (Shanebeck *et al.*, 2020). In Alaska, 12 otters in good condition were collected by a volunteer stranding network through the US Fish and Wildlife Service, Alaska Region, from the Nelson Lagoon (Alaskan Peninsula) and Homer, in the Kachemak Bay (Kenai Peninsula). Alaskan and Californian sea otters were necropsied by staff biologists or veterinarians, the entire intestines removed and frozen for later analysis, except in four cases in California where intestines were investigated directly at necropsy. The collaborating institutions recorded health, estimated age (determined by physical characteristics and dental analysis) (Kreuder *et al.*, 2003), sex and location of stranding, except for one animal in Alaska.

To compare the differences between *C. enhydri* in otters and *C. strumosum* in seals, the intestines of 22 seals were analysed in Schleswig-Holstein, Germany, from the Baltic (8) and North Seas (14). These included 15 harbour seals (*Phoca vitulina*) and seven grey seals (*Halichoerus grypus*). They were necropsied at the Institute for Terrestrial and Aquatic Wildlife Research, BÜsum, University of Veterinary Medicine Hannover, Foundation, either freshly or frozen, and age, sex and health were determined (Siebert *et al.*, 2007).

GI tracts were thawed overnight if frozen, then cleaned of the mesentery and omentum by careful removal with a scalpel. The intestine was laid out in full; the small intestine was measured for total length, and cut into five equal sections, the large intestine left intact as the sixth (Nickol *et al.*, 2002; Sinisalo *et al.*, 2003; Aznar *et al.*, 2004; Kaimoto *et al.*, 2018). Each section was then opened, and parasites were removed with soft forceps. Individuals were stored in tap water for one to two hours to secure the protuberance of the proboscis, then in 70% ethanol for preservation. Parasites were not always attached to the intestinal wall but found floating in the lumen. This is a possible source of error in our calculations of distribution and conclusion about the preferred niche. However, due to the broad sectioning of the intestine and viscous nature of the intestinal chyme, post-mortem movement between sections would be limited.

Acanthocephalan parasites were identified according to the morphological information outlined by Neiland (1962), Hennessy (1972) and Nickol *et al.* (2002). Prevalence (percent of total otters infected), intensity (total parasites per infected otter) and abundance (average intensity of parasites in infected otters) of acanthocephalan infection were recorded (Bush *et al.*, 1997). Demographic information for the sea otters can be found in Shanebeck *et al.* (2020). Total counts of *C. enhydri* and *C. strumosum* were recorded, including sex and number of mated females, identified by the presence of a copulatory plug (Violante-Gonzalez *et al.*, 2017), or if the female was gravid (with fully formed embryonated eggs). Total numbers were recorded for each intestinal section. The average proportion of females to the whole *Corynosoma* infrapopulation within one otter, as well as mated females to total females, were calculated, excluding cases where there were less than five parasites, or no males were present.

Statistical analysis

Distribution and site selection were analysed statistically using RStudio version 3.5 (Rstudio Team, 2016), with the packages 'gepack' (Hojsgaard *et al.*, 2006) for use of the generalized estimating equation generalized linear model (GEEGLM), 'ggplot2'

(Wickham, 2009) and 'sciplot' (Morales, 2017) for graphical representation. Distribution was based on the total number of parasites per section of intestine, weighed as a dependent variable against the effect of intestinal section, the host's geographic location, intensity of the infrapopulation and the presence/absence of co-infecting parasites per section for otters; and intestinal section, seal species and presence/absence of co-infecting parasites per section for seals. A Poisson distribution with a loglink function was used, and an 'AR-1' autoregressive correlation structure which accounts for the correlation of adjacent sites, which we used due to the continuous nature of the intestine (AR-1 assumes the correlation between section 1 and 2 will be α , between section 1 and 3 α^2 , between section 1 and 4 α^3 , and so on), individual otter ID defining the clustering and corrected for zero-inflation (Zuur *et al.*, 2009).

All models at first included all factors and interactions as covariates, then were reduced to the minimum adequate model via stepwise deletion of those that were insignificant. ANOVA and the resulting Wald Statistic table confirmed significance of the regression analyses. GEEGLM was chosen to account for the longitudinal nature of an intestine when determining significance of distribution, and also because this model includes an estimated general mean for the population, helping to avoid bad standard error (SE) estimation because of the limited sample size (Ballinger, 2004; Zuur *et al.*, 2009); it was also chosen instead of a generalized linear mixed model due to its better performance in analyses with many individuals (parasites sometimes in the hundreds) but low observations (limited otter sample size) (Zuur *et al.*, 2009).

Results

Corynosoma enhydri in sea otters

Prevalence of infection in California was 100% of otters infected, and in Alaska 83% of animals were infected. Females had an average abundance of 23, while males had an average abundance of five. Proportionally, females made up 80.7% (± 12.5) of southern sea otter intestinal parasite infrapopulations, with 16.9% (± 6.7) of females mated (table 1). Northern sea otters showed higher intensities of infection, females making up the majority again, with an average abundance of 244, while males had an average abundance of 33. Proportionally, females made up an average of 84.1% (± 9.3) of infrapopulations, with 18.4% (± 17.1) mated (table 1). Coinfection with another acanthocephalan species (*Proflicollis* sp.) occurred in nine of the southern and two of the northern sea otters.

Corynosoma strumosum in seals

Prevalence of *Corynosoma* infections in grey seals ($n=7$) was 71%, intensities ranged from two to 78 parasites, with a mean abundance of 19. Prevalence of *Corynosoma* infections in harbour seals ($n=15$) was 67%, intensity ranging from nine to 130 parasites, with an average abundance of 65. Females made up 74.0% (± 6.8) of *C. strumosum* infrapopulations, with 31.8% (± 24.9) females mated in grey seals. In harbour seals, females made up 64.4% (± 17.6) of parasite infrapopulations, with 43.1% (± 17.5) mated (table 2). Two cases of co-infection with *C. semerme* were observed. Prevalence of *C. semerme* infections in the Baltic grey seals was 80% ($n=5$). A single individual of *Corynosoma magdaleni* was found in the colon of one adult male grey seal

Table 1. Average female composition and mating success of *Corynosoma enhydri*. Mean percent composition of adult female parasites per infected sea otter including standard deviation (SD) and geographic location (Alaska and California) of the host otters, including the mean percent of mated females by total females, and excluding cases where there were less than five parasites or males were not present.

Location	<i>n</i>	Sex	Mean %	SD
California	15	Total females	80.7	12.5
		Mated	16.9	6.7
Alaska	7	Total females	84.1	8.7
		Mated	18.4	22.7
Combined	22	Total females	81.9	11.4
		Mated	17.4	10.9

from the Baltic Sea, along with *C. semerme*. Another *C. strumosum* infected a sub-adult Baltic male grey seal, which was found with co-infection of *C. semerme* in its colon. Two grey seals not infected with *C. strumosum* were infected with *C. semerme* in their colons. Co-infections with tapeworm (*Diphyllobothrium* spp.) were seen in three harbour seals from the North Sea and one grey seal from the Baltic Sea. In all four tapeworm co-infected animals, tapeworms were not found in the fourth or fifth section of the intestine. Tapeworms were also recovered from another harbour seal that was not infected with *C. strumosum* and, in this individual, they were found throughout the small intestine.

Distribution of *Corynosoma*

In sea otter intestines, the number of parasites discovered by section of intestine was analysed in order to determine the preferred habitat of *C. enhydri*. The interaction of intestinal section and total number of parasites was significant in determining the number of parasites present per section ($df = 5$, $X^2 = 39$, $P < 0.001$), the second and third sections were observed to have the largest averages (fig. 2), the third section having the strongest correlation (estimate = 1.75, SE = 0.768, $z = 2.28$). The interaction effect of geographic location with total parasite number was also significant in determining the number of parasites per section ($df = 1$, $X^2 = 173$, $P < 0.001$); southern sea otters had less parasites overall compared to northern sea otters. The interaction effect between intestinal section and geographic location was also significant ($df = 5$, $X^2 = 12$, $P = 0.041$), as seen in the differences in averages per section between sea otters from California and Alaska (fig. 2). Co-infection with *Profilicollis* sp. was not significant in the model. There was no significant difference in distribution between virgin females, mated females and males in the intestine, though it should be noted in otters from Alaska that males were more often found in the third and fourth sections.

Corynosoma strumosum retrieved from seals was found most frequently in the fourth section of the intestine (fig. 3). The interaction effect of intestinal section and total number of parasites per host was significant in determining the number of parasites removed per section ($df = 5$, $X^2 = 63.1$, $P < 0.001$). Though on its own, the total number of parasites was not strongly correlated with the number of parasites per section (estimate = 0.005, SE = 0.006, $z = 0.82$). The fourth section had the largest average number of *C. strumosum* (fig. 3), though both the third (estimate = 2.14, SE = 0.464, $z = 4.61$) and fourth sections (estimate = 2.83,

Table 2. Average female composition and mating success of *Corynosoma strumosum*. Mean percent composition of female adult parasites by total parasites including standard deviation (SD), as well as the mean percent of mated females by total females. Measured in infected seals in Germany, including harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*); excluding one grey seal, which had only two parasites (one male, one female).

Seal species	<i>n</i>	Sex	Mean %	SD
<i>Phoca vitulina</i>	10	Total females	64.4	17.4
		Mated	43.1	17.5
<i>Halichoerus grypus</i>	4	Total females	74.0	6.8
		Mated	31.8	24.9
Combined	14	Total females	67.1	15.6
		Mated	40.0	20.0

SE = 0.398, $z = 7.10$) were positively correlated with parasites per section. Distribution between the sexes of *C. strumosum* was not significantly different. Co-infections with other parasites and seal species were not significant in the model.

Discussion

Corynosoma populations and reproduction

Knowledge about *C. enhydri* ecology, infection patterns and pathogenicity is limited, and only a few publications are available (Rausch, 1953; Hennessey, 1972; Hennessey & Morejohn, 1977; Margolis et al., 1997; Mayer et al., 2003; Shanebeck & Lagrue, 2019; Shanebeck et al., 2020). Previous prevalence (90%, Hennessey & Morejohn, 1977; 94.4%, Mayer et al., 2003), compared with the 100% observed in this study, shows consistent infections in southern sea otters that suggest a stable *Corynosoma* population. Mean abundance of 30, however, was markedly lower in this study when compared to the previous study by Hennessey & Morejohn (1977), which observed a mean abundance of 375. While Mayer et al. (2003) did not provide an overall abundance, they provided averages across all age classes; from that, the overall abundance would be approximately 400 (approximation is based upon graphical representation of abundance ('mean density') for *C. enhydri* across all age classes) (Mayer et al., 2003). The difference between our observed mean abundance and previous work may be due to our lower host sample size, and the tendency of parasites to aggregate (Kennedy, 2006; Perrot-Minnot et al., 2020), our survey perhaps missing the severe infections that may occur. Sample availability was low in Alaska due to logistical constraints, and it remains unclear if the observed difference in prevalence – 83.3% in this study versus 51% in a previous study (Margolis et al., 1997) – is due to increased infection, or low sample size.

This is the first study reporting on sexual dynamics and site selection for *C. enhydri* in sea otters. In both Alaska and California, females of *C. enhydri* made up the majority of the population. This is supported by previous research suggesting this dynamic exists because of increased male mortality rates due to higher activity and male–male competition (Poulin & Morand, 2000; Sasal et al., 2000). Interestingly, there was a limited number of females observed to be mated in both California (15.88%) and Alaska (18.29%) (table 1). The slight depression in mating success for Californian *C. enhydri* may be due to the low intensities of infection in the investigated otters. If infection

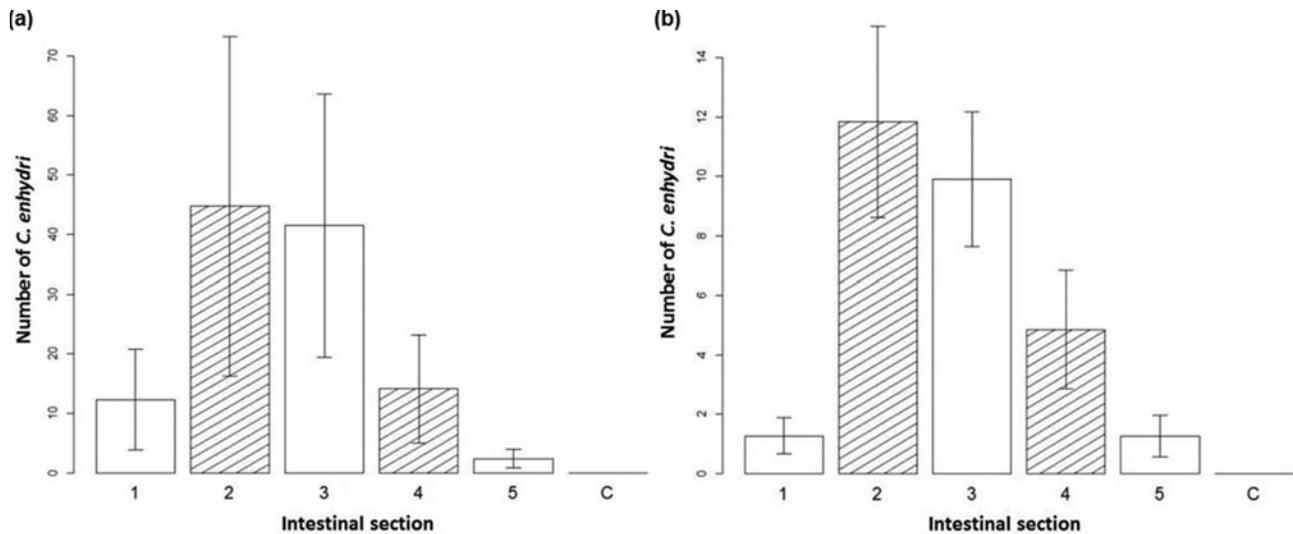


Fig. 2. Distribution of *Corynosoma enhydri* in sea otters. Bar graph of the average number of *C. enhydri* counted per section of removal on the y-axis, with the intestinal section they were removed from (equal small intestine sections 1–5; C, colon) on the x-axis for (a) northern sea otters, Alaska, and (b) southern sea otters, California, with standard error given.

intensities were higher, mating rates would increase as well. In Alaska, most infections were at similar intensities as southern sea otter cases, with two exceptions (872 and 1680 respectively).

This may explain the slight increase in mating success overall in Alaska, but with a larger variance (table 1). The proportion of mated females was low compared to the findings from *C. strumosum* in seals, in which females made up 68% of the population and 40% were mated (table 2). Prevalence was also lower in seals than otters, with 65% of seals infected. This is similar to previous observation of harbour and grey seals in the Baltic Sea, with a prevalence of 56% (1986–1987, $n = 26$; Nickol *et al.*, 2002) and 70% in harbour seals along the Dutch coast (1988, $n = 94$; Borgsteede *et al.*, 1991), though others have seen prevalence as low as 23% (1997–2000, $n = 107$; Lehnert *et al.*, 2007) and as high as 95% (1988–1989, $n = 110$; Strauss *et al.*, 1991) in the German Wadden Sea, the high prevalence occurring concurrently with an epidemic of phocine distemper virus. Other studies of *C. strumosum* among various species of seals have confirmed that prevalence can be highly variable: 87.5% in Japan (Kaimoto *et al.*, 2018), 100% in Ireland (O’Neil & Whelan, 2002) and as low as 8.75% in Alaska (Kuzmina *et al.*, 2012). These variations are likely tied to fish distribution and abundance, as well as prey availability between localities, as *C. strumosum* relies on several different fish species as its transport host (Nickol *et al.*, 2002). In the Baltic Sea, a previous study showed a strong correlation between infection rates and the availability of important transport fish hosts and environmental conditions (Valtonen *et al.*, 2004).

The observed differences in prevalence and sexual success between *C. strumosum* and *C. enhydri* may be due to a variety of reasons. The higher prevalence of females in the population of *C. enhydri* may limit male access to females or heighten male–male competition (Poulin and Morand, 2000; Sasal *et al.*, 2000). Or it is possible that size differentiation between these closely related species of *Corynosoma* (*C. enhydri*, *C. strumosum* and *C. semerme*) could be related to a life strategy trade-off between delegation of resources for growth and longevity or reproduction (Valtonen & Helle, 1988; Nickol *et al.*, 2002). Reproductive success may also be tied to intensity of infection and the clumping of parasites within the host, similar to the

Allee effect (Greene, 2008). However, due to the low sample size available, the correlation between intensity of infection and reproductive success was not analysed; future projects should investigate intrapopulation differences in reproductive success and intensity of infection. Otters compared to seals have a high consumption/metabolic rate, healthy adults taking in 23–33% of their body weight daily (Yeates *et al.*, 2007). Since *C. enhydri* are much larger than *C. strumosum* (Henessey, 1972; Nickol *et al.*, 2002), this may be a result of a richer environment. As sea otters have a high daily caloric intake, perhaps *C. enhydri* can afford to put more energy into growth before reproduction, and this may explain why *C. enhydri* have such lower proportions of mated females.

Corynosoma distribution

An important aspect of this study was to discover the ultimate realized intestinal niche of *C. enhydri* in sea otters and compare it between localities, and to its closest relative *C. strumosum* in seals. Analysis of distribution revealed a significant clumping by *C. enhydri*, found most frequently in the second and third section of the small intestine, and *C. strumosum* found most frequently in the fourth section of the small intestine. These closely related acanthocephalan species are not only differentiated in morphology, but also in site selection. Distribution of *C. strumosum* was not significantly different between grey and harbour seals, which agrees with previous analyses (Valtonen & Helle, 1988; Nickol *et al.*, 2002; Kaimoto *et al.*, 2018). There was no significant difference in the distribution between virgin females, mated females and males, even though in Alaskan otters, male *C. enhydri* were found more often in the third and fourth section; however, perhaps due to the lower sample size in Alaska, this was not significant. Future research should focus on the possible interaction between the number of males and intestinal location on the proportion of mated females.

Since co-infections with *Proflicollis* spp. were not significant in determining the distribution of *C. enhydri* in the intestine, interspecific competition is not likely a determining factor of their ultimate realized niche. In seals, co-infections with

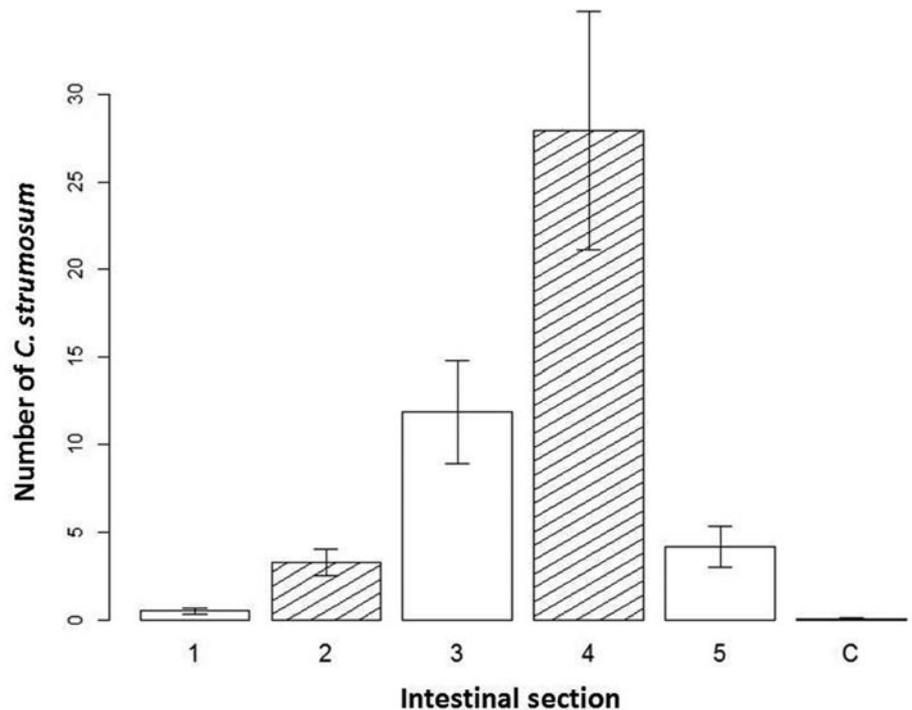


Fig. 3. Distribution of individuals of *Corynosoma strumosum* in seals. Bar graph of the average number of *C. strumosum* counted per section of removal on the y-axis, with the intestinal section they were removed from (equal small intestine sections 1–5; C, colon) on the x-axis, with standard error given.

tapeworm and *C. semerme* had no significant effect on *C. strumosum* distribution. Our results and previous research reveal an interesting size-related pattern among *Corynosoma*. The largest, *C. enhydri*, was found in the second and third sections of the intestine; the much smaller *C. strumosum* was found in the fourth section; and *C. semerme*, the smallest, was found only in the nutrient-poor colon and caecum (Valtonen & Helle, 1988; Nickol *et al.*, 2002). This very specific localization within the intestine in relation to size, starting with the largest in the foregut and smallest in the colon, is a fascinating example of closely related species specializing in habitat (Valtonen & Helle, 1988; Nickol *et al.*, 2002; García-Varela *et al.*, 2005).

This may be related to physiochemical gradients within the intestine, as acanthocephalans are absorptive feeders and carbohydrates are their main source of nutrition (Hill, 1986; Kennedy, 2006). The hindgut is also dominated by the highest concentration and diversity of bacteria in the intestinal tract, which may be a source of competition (Rerat, 1978). Seals and sea otters also have fast digestive transit times, and short large intestines, which may further limit access to carbohydrates downstream (Costa & Kooyman, 1984; Horstmann, 2018). This could explain the size gradient observed between these three closely related *Corynosoma* species (Hennessey & Morejohn, 1977; Nickol *et al.*, 2002; García-Varela *et al.*, 2005). This distribution may also be related to a life-history strategy between longevity and reproduction. Previous studies comparing *Corynosoma* in seals noted that *C. semerme* experience more seasonality in their prevalence, with periods of high abundance (Valtonen & Helle, 1988). *Corynosoma strumosum* tends to have higher prevalence but lower abundance, suggesting longer longevity (Valtonen & Helle, 1988). This trend continues in our observations of *C. enhydri*, which had an even higher prevalence than *C. strumosum*, with relatively low abundance and, most significantly, a lower mating rate. Previous reports of *C. enhydri* saw no significant changes in abundance by season, and prevalence was consistently over 90% (Mayer *et al.*, 2003). This suggests

our broader hypothesis concerning the relationship between site selection and life-history strategies may be true (fig. 1).

It should be noted that, in addition to differences in site selection, there have also been observed differences in physical damage to the intestine between these species. *Corynosoma semerme*, the smallest *Corynosoma*, are more likely associated with colitis and lesions in the colons of grey seals (Lakemeyer *et al.*, 2020), while *C. enhydri* have not been observed to be associated with serious physical damage in sea otters (Mayer *et al.*, 2003). It is possible that site selection and changes in the physiochemical gradient may be related to these observed differences. Alterations in nutrient availability can affect intestinal microbiota and influence prevalence and severity of enteritis (Tsukikawa *et al.*, 2001; Mohr *et al.*, 2008; Tsiouris *et al.*, 2014). Lowered resource availability and increased competition between parasites and microbes in the large intestine could be the cause of increased pathogenicity by *C. semerme*. We suggest further investigation into the possible relationship between physiochemical gradients and parasite-induced ulceration and inflammation.

Corynosoma enhydri tends to have a weaker penetrative attachment to the intestinal wall (Mayer *et al.*, 2003), and some were found floating in the lumen, which should be noted as a possible source of error in our analysis of habitat selection. However, given the size of the intestines, the limited handling after they were laid out in full and the broad sectioning, artificial movement between sections would be small and limited to the parasites already close to the next section, and should not change our general conclusions about the preferred niche. However, the majority of parasites were found attached to the intestinal wall.

Conclusion

While there were limitations to this study, both in time (samples were collected only in one year) and sample size (collecting from naturally stranded marine mammals greatly limits sample availability), this project gave an invaluable look into an

underrepresented species. It was hypothesized that *C. enhydri* would be found predominantly in the upper intestinal tract due to their large size in relation to other species of *Corynosoma*, which may be related to a life-history trade-off between growth and reproduction. We observed both a significant clustering in the upper intestine as predicted, as well as lower mating rates than those observed in *C. enhydri*'s smaller relative, *C. strumosum*, in seals. This discovery offers a fascinating exploration of the little-understood site selection of GI parasites in marine mammals, and suggests further research is needed to properly understand the mechanisms instructing habitat differentiation by parasites and microfauna in the digestive system.

Though still sporadically done, the integration of parasites into the study of ecology is essential for our understanding of marine ecosystems (Lafferty *et al.*, 2008). Like many parasites, *Corynosoma* spp. rely on marine food webs to transmit to their final host, and as soft-bodied absorptive feeders, can be particularly helpful in the monitoring of abiotic changes in marine ecosystems (Kennedy, 2006). Yet, though sea otters are such charismatic and vulnerable species, little knowledge exists about the only parasite that uses sea otters as its preferred definitive host (Mayer *et al.*, 2003; Shanebeck & Lagrue, 2019). This study investigated the demographics of *C. enhydri* in sea otters and established a baseline of their population structure, to better understand their ecology and microhabitat preferences. Acanthocephalans are ubiquitous wildlife parasites and may be useful bioindicators for health and ecosystem-wide effects in vulnerable mammals (Kennedy, 2006; Shanebeck & Lagrue, 2019).

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Ethical standards. None.

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