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Effect of Parasitism by *Philonema agubernaculum* (Nematoda: Philometridae) on the Ability of Dolly Varden to Capture Prey in Fresh and Salt Water

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Abstract: Dolly Varden *Salvelinus malma* parasitized by a single nematode *Philonema agubernaculum* had significantly reduced ability to capture pink salmon fry *Oncorhynchus gorbuscha* in laboratory tests. Predator-prey trials, in which half the Dolly Varden were parasitized, were conducted in fresh water and salt water. Unparasitized Dolly Varden in fresh water captured a mean of 64% of the pink salmon during the test period and unparasitized Dolly Varden in salt water captured 61% of their available prey in the time allotted. In contrast, parasitized Dolly Varden in fresh water captured 32% of their prey as opposed to 29% in salt water. Nematode parasitism has the potential to reduce the foraging ability of Dolly Varden in the laboratory under conditions of abundant food, but the broader ecological consequences remain unclear.

INTRODUCTION

The Dolly Varden *Salvelinus malma* is one of the most common fish predators in coastal freshwater lakes and estuaries of the Pacific Northwest and Alaska. After an initial freshwater residence of 3 to 5 years, Dolly Varden in most coastal lakes migrate each spring into marine waters for feeding and return in the fall to overwinter in the lakes. During the freshwater residence, the fish can become infested with a wide range of parasites, notably nematodes. *Philonema agubernaculum* (Simon and Simon 1936) is a parasitic dracunculoid nematode occurring in the coelomic cavity of salmonid fishes in the northern parts of North America (Hoffman 1999). Adult nematodes are present, often in great numbers, in the coelomic cavities of adult salmon. As a gravid adult, the female *P. agubernaculum* can reach a length of 23 cm (Smedley 1934).

Little is known about the possible effects of this common nematode on fish performance regarding competition, growth, or whether infection is even stressful. Some of the best measures of performance are predator–prey studies that integrate various physiological stressors into a single behavioral response. Parasitism can increase the probability of being eaten by a predator when parasitism forces fish to replenish energy reserves lost through parasitism rather than avoiding predators (Milinski 1985, Curio 1988). The parasite thus facilitates passage to the next host by increasing the odds that the current host will be eaten. Some parasites alter the behavior of their hosts to facilitate capture by predators (Krause and Godin 1994), such as increasing the oxygen demand so that fish swim closer to the surface where avian predators can harvest the fish (Curio 1988).

In contrast, there is little or no information about the effect of parasites on the performance or survival of predatory fish such as Dolly Varden. Examining the effects of the parasite on an ecologically important variable, such as the ability to obtain prey in the laboratory, may provide some insight on the role the parasite might play in survival and performance in the wild. Recently, we noted that adult *P. agubernaculum* (from 8 to 12 cm) were present in more than half the necropsies performed on Dolly Varden juveniles migrating from Auke Lake in southeast Alaska. This observation provided an opportunity to examine the effects of *P. agubernaculum* parasitism on the ability of Dolly Varden to capture the smaller salmon that constitute a portion of their prey (Lagler and Wright 1962). Necropsies performed on 100 fish migrating from Auke Lake indicated that 55% were parasitized, most by a single worm in the body cavity.

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METHODS

Predation trials were conducted during June 2000 in nine 800 L circular fiberglass tanks (122 cm diameter, 70 cm depth). A cobble substrate was added and three lengths of polyvinyl chloride pipe (5 cm diameter, 35 cm length) were suspended horizontally at the water's surface to provide cover for the fry. The tanks were located outdoors under a translucent fiberglass cover that permitted passage of ambient light. Water flow through each tank was 4 L/min through a central standpipe.

Dolly Varden (average fork length=13 cm, average weight=19 g), both unparasitized and parasitized by *P. agubernaculum*, were used as predators. These fish were collected from fresh water at a counting weir located on Auke Creek near Juneau, Alaska. About 6,000 wild Dolly Varden, ranging in size from 7 to 50 cm, leave Auke Lake each April and May. One hundred of the smallest outmigrants were selected and presumed to represent fish that had never spent a summer at sea and had not yet adapted to salt water. Size rather than age governs outmigration and has proven to be the most reliable method for obtaining Dolly Varden smolts of similar age rather than scale analysis (Armstrong and Morrow 1980). Fish were fed pink salmon fry for 2 d to acclimate the predators to the prey item, then uniformly starved for 10 d prior to testing.

The pink salmon used as prey were collected in fresh water from Auke Creek during their normal volitional migration to the estuary. Pink salmon fry typically outmigrate within days of emergence from the stream gravel. The fry collected for this study still had a small amount of yolk material and were of similar sizes (32 mm, 300 mg) with a variation less than 5% (range/mean). The pink salmon were randomly divided into two groups; one group was held in fresh water and the other was gradually acclimated to salt water by increasing salinity 10‰ per d over 3 d to simulate normal estuarine transition. This was followed by 7 d of full strength salinity (30‰) before predation tests were performed. Fry were fed Oregon Moist Pellet[1] starter mash to satiation using a continuous belt feeder.

Each of the nine tanks contained a single Dolly Varden that had been starved and allowed to acclimate to the tank for 1 d before the tests. Dolly Varden used in the saltwater tests were moved directly from freshwater holding tanks to the test tanks with no period of salinity acclimation. Parasitism by *P. agubernaculum* imparted a slight abdominal distention, making it possible to ensure that about half the tanks contained parasitized Dolly Varden. Twenty pink salmon fry, randomly chosen from the corresponding holding tank, were acclimated for 30 min in a perforated box (23 cm on a side) suspended in the center of each freshwater or saltwater test tank. The bottom of the perforated box was then removed, allowing the fry to swim unrestricted. Observations were made at 1 h intervals until 90 of the 180 pink salmon (20 fish per tank x 9 tanks) had been eaten, typically by 7 h. The Dolly Varden were killed and measured for fork length and weighed following removal of stomach contents and parasites. Condition factor (weight/length^3) was calculated for each fish as a measure of nutritional state. Fish parasitized by more than a single nematode or by other visible parasites were removed from the analysis (a total of 5 fish). The digestive tract was removed and weighed separately. Gut index was calculated for each fish as the ratio of digestive tract weight to total fish weight. This index measures changes in mesenteric fat stores relative to fish body weight and is a good predictor of energy reserves in char and trout (Jensen 1980). No predator or prey fish was used more than once, preserving independence of observations. The test series was repeated 9 more times for a total of 85 trials (5 trials were unsuccessful).

Differences in the number of pink salmon captured after 7 h were compared between treatment groups by two-way analysis of variance. Salinity (fresh water or salt water) and parasitism (parasitized or unparasitized) were the two sources of variation tested. Differences in length and weight between the predation groups were tested using a rank sum test because these data were not normally distributed. Differences in condition factor, gut index, and viscera weight between the predation groups were tested using a Student's t-test.

RESULTS

There was a definite effect of parasitism on prey capture ability. Dolly Varden parasitized with *P. agubernaculum* captured approximately half the number of pink salmon fry that unparasitized Dolly Varden were able to capture during the test interval. Parasitized Dolly Varden captured a mean of 6 fry or 29 to 32% of the pink salmon during the test period, whereas unparasitized Dolly Varden captured a mean of 13 fry or 61 to 64% of their available prey in the time allotted (Table 1). The effect of parasitism on capture rates was highly significant ($P<0.001$).

In contrast, the salinity of the test water made little difference. Whether the test was conducted in fresh or salt water did not alter the capture rates for parasit-

[1]Use of brand names does not imply endorsement by the National Marine Fisheries Service.

Table 1. Mean length, weight, condition factor, and gut index (±se) of Dolly Varden test fish and mean percent of prey captured.

	n	Length (cm)	Weight (g)	Condition Factor	Gut Index	Percent Capture
Parasitized						
Fresh Water	24	13.5±0.3	18.8±1.3	0.75±0.02	0.12±0.01	32.0%±0.8%
Salt Water	20	13.2±0.9	19.8±1.1	0.66±0.04	0.09±0.01	29.0%±0.7%
Unparasitized						
Fresh Water	21	13.4±0.4	18.7±1.7	0.74±0.01	0.12±0.01	64.0%±1 %
Salt Water	20	12.5±0.9	17.6±1.8	0.69±0.05	0.11±0.01	61.0%±0.8%

ized or unparasitized Dolly Varden. In salt water, the results were nearly identical with the freshwater tests for fish with the same number of parasites (0 or 1). In fresh water, unparasitized Dolly Varden captured 64% of their prey and in salt water captured 61% in the time allotted. The difference in the mean number of pink salmon consumed was not affected by the salinity ($P=0.94$). When capture rates were combined for parasitized and unparasitized fish, Dolly Varden in fresh water captured a mean of 9.4 fish compared to a mean of 10.6 fish in saltwater. This difference was not great enough to exclude the possibility that the difference was due to sampling variability, after allowing for the effects of the nematodes. There was not a significant interaction between the salinity and the presence of nematodes ($P=0.47$).

Size, condition factor, and gut index differences between the Dolly Varden groups was not a factor in the tests (Table 1). Mean lengths ($P=0.80$) and weights ($P=0.99$) were not significantly different among the four test groups (parasitized/unparasitized, fresh water/salt water). The smallest group by wet weight was the unparasitized Dolly Varden in salt water, which captured 61% of their prey. The largest group was the parasitized Dolly Varden in salt water, which captured 29% of their prey. The mean condition factors ($P=0.40$) of the fish and the gut indices ($P=0.63$) also did not differ significantly.

DISCUSSION

Generally, behavior modifications of intermediate hosts caused by parasites improve the chances for parasitizing a final host or completing the parasite life cycle (Zimmer 2000). The ability of a predator to obtain prey is reduced through altering one or more of three interactions in the sequence of encounter, attack, and capture. Reduced foraging among the parasitized Dolly Varden was probably caused by either reduced appetite (encounter), a reduction in energy reserves used in swimming (attack), or physical impairment (capture).

Large parasites, such as the body cavity nematodes in this study, are reported to affect all three of these interactions. If the predator does not perceive hunger or is easily satiated, forage rates may be lower than if hunger remains an active component of the behavior. For example, threespine sticklebacks *Gasterosteus aculeatus* parasitized with the cestode *Schistocephalus solidus*, despite higher energy requirements due to parasitism, fed on prey of lower nutritional value and tended to have stomachs that were less full than in uninfected fish (Tierney 1994). The amount of food eaten could also be reduced if a large parasite displaced stomach volume.

Nematode parasitism may deplete sufficient energy from the hosts to cause lower swimming rates. A link has been found between large metazoan parasitism and reduced stamina of fishes that results in lower capture rates of prey even for definitive hosts when there appears to be no advantage for the parasite to enhance predation of the host. As an example, sockeye salmon *O. nerka* heavily parasitized with the cestode *Eubothrium salvelini* had a lower critical swimming speed (Boyce 1979) and earlier fatigue (Smith 1973) than unparasitized fish. Burst-swimming performance, particularly important in predation, was reduced in coho salmon *O. kisutch* and steelhead trout *O. mykiss* infested with the trematode *Nanophyetus salmincola* (Butler and Millemann 1971). Tort et al. (1987) demonstrated reduced cardiac output, and by implication reduced swimming performance, in rainbow trout *O. mykiss* infested with digenetic trematodes. However, not all large helminths reduce swimming ability in fish. The body cavity nematode *Truttaedacnitis truttae*, having a direct life cycle similar to *P. agubernaculum,* had no effect on growth or swimming performance of rainbow trout (Russell 1980). Speculation to explain these observations was that *T. truttae* doesn't compete with the host for oxygen or encyst in muscle tissue.

The most plausible explanation for the alteration of prey capture may be that the *P. agubernaculum* in this study reduced the body flexibility of the host, causing more difficulty in capturing prey. Despite the lowered foraging ability, the similar condition and gut

indices for all predators used in the study suggested that energy reserves were not measurably depleted by parasitism. A reduction in physical ability of parasitized fish is further supported by the large size of the nematodes that were all more than 9 cm long, often exceeding the body length of the host. Infestation by *P. agubernaculum* often results in adhesions of the viscera in trout and salmon caused by host reaction to the irritating movement of the nematodes within the body cavity (Nagasawa 1985). In severe cases, the adhesions bind the entire visceral mass, interfering with normal function (first noted by Meyer 1960). Such adhesions were observed in the fish used in this study and could have reduced host flexibility.

During saltwater adaptation, salmonids typically show a decrease in food consumption coupled with higher metabolic demands as a result of biochemical and hormonal changes associated with ion transport (reviewed in Høgåsen 1998). Similar changes occur in readapting to fresh water, although far less research has been conducted on the associated metabolic costs. This decrease in feeding and the higher metabolic costs suggest that Dolly Varden should have reduced predatory capabilities during the initial adaptation to salt water. In this study there was no difference in feeding rates between Dolly Varden in saltwater and freshwater predation trials. This suggests that Dolly Varden, once physiologically prepared, can move readily from fresh water to estuarine habitats and this is consistent with their summer behavior of entering and leaving fresh water at will.

Although parasitism by *P. agubernaculum* did affect the number of salmon the Dolly Varden could consume during a set time interval, the biological consequences of such infection may be minimal under conditions of abundant food. The population of Dolly Varden in Auke Lake produces a stable outmigration of more than 6,000 fish per year, despite a current parasitism rate of 55%. Furthermore, the condition factors and gut indices, both indicators of fish health, were the same for parasitized and unparasitized Dolly Varden. During lake residency and early outmigration, forage capability did not appear to be limiting fish survival when equal numbers of parasitized and unparasitized fish emigrate from the lake. However, under conditions of limited food the ability of unparasitized Dolly Varden to capture more prey with less energy expended could result in a competitive advantage.

These results also indicate that nematode infection may be a factor in predator–prey interactions of Dolly Varden and their salmon prey, suggesting some ecological significance to nematode infections beyond simple host mortality. Parasitism by *P. agubernaculum* is sufficiently stressful to alter predator–prey relationships. The remaining challenge is to determine the implications of stress from nematode parasitism on the health of the community and structure of fish populations.

LITERATURE CITED

Armstrong, R. H. and J. E. Morrow. 1980. The Dolly Varden charr, *Salvelinus malma*. Pages 99–140 *in* E. K. Balon, editor. Charrs: Salmonid Fishes of the Genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, The Netherlands.

Boyce, N. P. 1979. Effects of *Eubothrium salvelini* (Cestoda: Pseudophyllidae) on the growth and vitality of sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Zoology 57:597–602.

Butler, J. A, and R. E. Millemann. 1971. Effect of the "salmon poisoning" trematode, *Nanophyetus salminicola*, on the swimming ability of juvenile salmonid fishes. Journal of Parasitology 57:860–865.

Curio, E. 1988. Behavior and parasitism. Pages 149–160 *in* H. Mehlhorn, editor. Parasitology in Focus: Facts and Trends. Springer-Verlag, New York.

Hoffman, G. L. 1999. Parasites of North American freshwater fishes, second edition. Comstock Publishing Associates, Ithaca, New York.

Høgåsen, H. R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences 127.

Jensen, A. J. 1980. The 'gut index,' a new parameter to measure the gross nutritional state of arctic char, *Salvelinus alpinus* (L.) and brown trout, *Salmo trutta* L. Journal of Fish Biology 17:741–747.

Krause, J., and J. G. J. Godin. 1994. Influence of parasitism on the shoaling behavior of banded killifish, *Fundulus diaphanus*. Canadian Journal of Zoology 72:1775–1779.

Lagler, K. F., and A. T. Wright. 1962. Predation of the Dolly Varden, *Salvelinus malma*, on young salmons, *Oncorhynchus* spp., in an estuary of Southeastern Alaska. Transactions of the American Fisheries Society 91:90–93.

Meyer, M. C. 1960. Notes on *Philonema agubernaculum* and other related dracunculid nematode infecting salmonids. Libro Homenaje al Dr. Eduardo Caballero Jubileo 1930–1960: 487–492.

Milinski, M. 1985. Risk of predation of parasitized sticklebacks (*Gasterosteus aculeatus* L.) under competition for food. Behavior 93:203–216.

Nagasawa, K. 1985. Prevalence of visceral adhesions in sockeye salmon, *Oncorhynchus nerka*, in the central north Pacific Ocean. Fish Pathology 20:313–322.

Russell, L. R. 1980. Effects of *Truttaedacnitis truttae* (Nematoda: Cucullanidae) on growth and swimming of rainbow trout, *Salmo gairdneri*. Canadian Journal of Zoology 58: 1220–1226.

Smedley, E. 1934. Some parasitic nematodes from Canadian fishes. Journal of Helminthology 12:205–220.

Smith, H. D. 1973. Observations on the cestode *Eubothrium salvelini* in juvenile sockeye salmon (*Oncorhynchus nerka*) at Babine Lake, British Columbia. Journal of the Fisheries Research Board of Canada 30:947–964.

Tierney, J. F. 1994. Effects of *Schistocephalus solidus* (Cestoda) on the food intake and diet of three-spined stickleback, *Gasterosteus aculeatus*. Journal of Fish Biology 44:731–735.

Tort, L., J. J. Watson, and I. G. Priede. 1987. Changes in in vitro heart performance in rainbow trout, *Salmo gairdneri* Richardson, infected with *Apatemon gracilis* (Digenea). Journal of Fish Biology 30: 341–347.

Zimmer, C. 2000. Parasites make scaredy-rats foolhardy. Science 289:525–527.