Natural Transfer of Helminths of Marine Origin to Freshwater Fishes, with Observations on the Development of *Diphyllobothrium alascence*

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NATURAL TRANSFER OF HELMINTHS OF MARINE ORIGIN TO FRESHWATER FISHES, WITH OBSERVATIONS ON THE DEVELOPMENT OF *DIPHYLLOBOTHRIUM ALASCENSE*

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ABSTRACT: Infective stages of helminths of 5 species that occur as adults in marine mammals were found in burbot, *Lota lota* (L.) (Gadidae), from the lower Kuskokwim River (southwestern Alaska): *Diphyllobothrium alascense* Rausch et Williamson, 1958; *Pyramicocephalus phocarum* (Fabricius, 1780); *Corynosoma strumosum* (Rudolphi, 1801); *Corynosoma semerme* (Forsell, 1904); and *Pseudoterranova decipiens* (Krabbe, 1878). Some larval stages were obtained also from smelt, *Osmerus mordax dentex* Steindachner, an anadromous fish important as prey of burbot. Burbot, which are freshwater fish, could become paratenic hosts of those helminths by means of at least 3 interactions: by consuming marine fishes in brackish waters at river mouths, by feeding on marine fishes that enter lower reaches of rivers, or by preying on anadromous fishes as they migrate up rivers. Consumption of burbot by people may result in infection by helminths of marine origin; of those recorded, only *P. decipiens* may be significantly pathogenic. Attempts to rear *P. phocarum* in dogs were unsuccessful. Plerocercoids of *D. alascense,* of very small size and found only in the gastric lumen of burbot, readily infected dogs. For study of their development, strobilae were obtained at intervals of 48 hr to 32 days postinfection. In heavy infections, some strobilae developed slowly, while others underwent rapid development.

In the North Pacific region, helminths for which marine mammals serve as final host have been reported frequently from people who consume marine and anadromous fishes containing infective larvae. Other terrestrial mammals as well may acquire such helminths; dogs are especially receptive if they are maintained on raw fish, as in coastal settlements in western Alaska. In marine fishes, plerocercoids of cestodes (Diphyllobothriidae) and larvae of nematodes (Anisakidae) evidently are often ingested by terrestrial hosts. Juvenile acanthocephalans (*Corynosoma* spp.) also have been reported from them, although the frequency of their occurrence in people is difficult to discern. We have found that freshwater fishes also may serve as paratenic hosts for helminths of marine origin and may provide a source of infection for terrestrial mammals.

Anadromous fishes such as salmon, *Oncorhynchus* spp., become infected by helminths of numerous species during both the freshwater and marine phases of their cycles (Margolis, 1963), and the diversity of the helminths acquired depends mainly on duration of periods spent in the respective waters (Dogiel, 1963). Of the Pacific salmon, the sockeye, *Oncorhynchus nerka* (Walbaum), stays for the longest time in freshwater when juvenile and has the largest variety of helminths of freshwater origin (Burgner, 1991). Some populations of sockeye have a high prevalence of plerocercoids of *Diphyllobothrium ursi* Rausch, 1954 when they migrate to the sea after 1–3 yr in freshwater lakes (Rausch and Hilliard, 1970). The plerocercoids persist in that fish in the marine environment and develop to the strobilar stage, most notably in brown bears, *Ursus arctos* L., that feed on the salmon returning to spawning streams after 1–4 yr in the sea.

In the marine habitat, salmon acquire plerocercoids of diphyllobothriids for which marine mammals appear to be the final host (Gofman-Kadoshnikov et al., 1970; Muratov, 1982, 1985; Ruttenber et al., 1984; Yamane et al., 1986). Such cestodes have been recorded commonly from indigenous peoples in the North Pacific region, but the distribution of salmon commercially may lead to the infection of people at localities widely separated geographically (Ruttenber et al., 1984).

The first record of plerocercoids in salmon in the North Pacific region appears to be that of Zschokke and Heitz (1914), who found specimens in *O. nerka* in Kamchatka. Investigations during recent years have demonstrated that 3 additional species of *Oncorhynchus* are important second intermediate hosts of diphyllobothriids. Plerocercoids of *Diphyllobothrium nihonkaiense* Yamane et al., 1986 occur in the pink salmon, *Oncorhynchus gorbuscha* (Walbaum), and in the masu salmon, *Oncorhynchus masou* (Brevoort), in Hokkaido, Japan. Those of *Diphyllobothrium klebanovskii* Muratov et Posokhov, 1988 are known from the pink salmon and the chum salmon, *Oncorhynchus keta* (Walbaum), in the lower Amur River region, Russian Far East; there, rates of infection in salmon have been reported by Muratov (1985). Both of those diphyllobothriids occur in people. The presence of plerocercoids in other anadromous fishes has not been investigated.

Whereas marine and anadromous fishes have been well documented as hosts of helminths of marine origin transmissible to people, that freshwater fishes can acquire infective stages of such helminths would seem improbable. During the period 1949–1975, our investigations in Alaska included surveys of fishes for the collection of plerocercoids in order to obtain identifiable strobilae in experimental animals. At that time, Yup'ik people of villages in the lowland tundra of western Alaska subsisted mainly on fishes abundant in the rivers and innumerable ponds and lakes of the region. Because certain fishes or organs thereof often were eaten raw (Heller and Scott, 1967), they were the source of infection by diphyllobothriids that attained rates of 30% or more in residents of some villages (Rausch et al., 1967). Of the large series of those cestodes obtained from the people, most consisted of species whose cycles involved freshwater hosts (Rausch and Hilliard, 1970).

Burbot, *Lota lota leptura* Hubbs et Schultz, were obtained during 4 yr from the lower Kuskokwim River. They were found to serve as paratenic hosts for helminths of at least 5 species of marine origin. The occurrence of larval helminths in boreal smelt, *Osmerus mordax dentex* Steindachner, an anadromous fish that is an important prey of burbot, also was investigated. Some preliminary observations concerning plerocercoids in
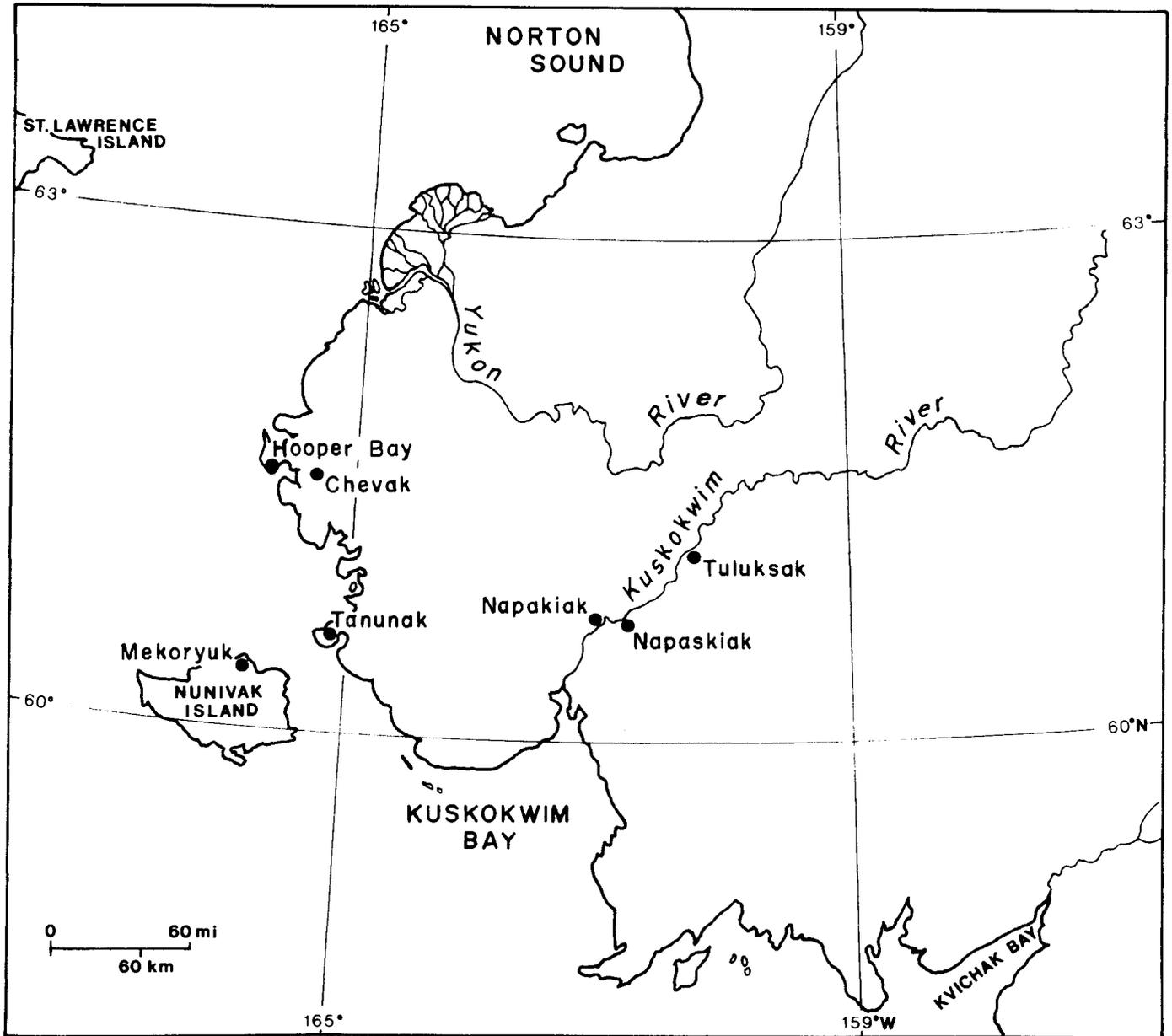
FIGURE 1.   Map of the region of the Yukon–Kuskokwim Delta showing localities from which specimens were collected.

burbot were reported by Rausch and Hilliard (1970). Herein, we present detailed information concerning diphyllobothriids and report observations on the other helminths found. Development of the strobilar stage of *Diphyllobothrium alascense* in dogs is described.

MATERIALS AND METHODS

The burbot were trapped in the Kuskokwim River at the village of Tuluksak, ca. 120 km north of the mouth of the river (map, Fig. 1), as follows: 15 in March 1969, 17 in December 1969, 18 in January 1970, 11 in April 1970, and 4 in February 1971. Of 175 boreal smelt, collected during their migration upriver to spawn, 26 were obtained in June 1955, at Napakiak; and 49 in June 1955 and 100 in May 1956, at Napaskiak. The burbot were refrigerated and examined within 48 hr after capture; smelt were examined in the field. Of the 65 burbot, 28 were males, 35 were females, and sex was not recorded for 2; those

trapped in December were spawning. For males, standard lengths ranged from 440 to 650 mm; for females, 410 to 670 mm (not including 4 smaller specimens collected in 1971). Assuming that the rate of growth of burbot in the Kuskokwim River is similar to that of those in the Tanana and Yukon Rivers, 61 of the burbot ranged from about 6 to 13 yr in age (Chen, 1969). Each fish was dissected and examined for larval stages of helminths in internal organs and musculature. Stomach contents of the burbot were collected for identification.

Laboratory-reared beagles (inbred strain) usually received larval stages of helminths at or soon after weaning. One adult sled-dog was also infected. All animals were necropsied immediately after death. The intestine of each was removed and opened lengthwise in water, after which all helminths present were collected. Plerocercoids from smelt were reared also in helminth-free glaucous-winged gulls, *Larus glaucescens* Naumann, hatched in an incubator. All experimental animals were maintained on commercially prepared diets.

Cestodes were relaxed in water and fixed in hot 10% formalin, stained in acetic carmine, processed by standard methods, and mounted

permanently. Transverse and medial sagittal sections were routinely made with use of a razor blade. The tegument and underlying layers of muscle were removed from portions of selected strobilae, usually from the ventral surface. Diphyllobothriids of other species (from naturally infected marine mammals) with which comparisons were made were processed by the same methods. Acanthocephalans also were stained and mounted permanently. Nematodes were cleared in lactophenol.

Observations on development of the strobilar stage of *D. alascense* were based on 262 specimens from 12 experimentally infected dogs examined at intervals from 48 hr to 32 days postinfection (PI). Those were compared with 65 strobilae from dogs necropsied at the villages of Chevak and Hooper Bay.

Means ($\bar{x}$) and standard deviations (SD) were calculated using functions provided by Microsoft® Excel 97. Regression curves were applied to data using the CA-Cricket Graph program by Computer Associates®.

RESULTS

Larval stages of helminths of 5 species were obtained from the burbot: *D. alascense* Rausch et Williamson, 1958; *Pyramicocephalus phocarum* (Fabricius, 1780); *Corynosoma strumosum* (Rudolphi, 1801); *Corynosoma semerme* (Forsell, 1904); and *Pseudoterranova decipiens* (Krabbe, 1878). Larval helminths were recorded also from smelts.

Diphyllobothrium alascense

Diphyllobothrium alascense typically coexisted with other diphyllobothriids in dogs in the region of the Yukon–Kuskokwim Delta, *Diphyllobothrium dendriticum* (Nitzsch, 1824) and *Diphyllobothrium dalliae* Rausch, 1956 being the most numerous. A survey of helminths in dogs in Alaska during 1949–1959, involving animals from 6 ecologically distinct districts, indicated that diphyllobothriids were abundant in western Alaska, including the delta (R. L. Rausch, unpubl. obs.). Of the 414 dogs necropsied, 97 originated in the western district. *Diphyllobothrium alascense* occurred in 11 (13%); diphyllobothriids of other species in 73 (75%). By contrast, diphyllobothriids (not including *D. alascense*) were obtained from only 4 of the 316 dogs (ca. 1%) from the remaining districts. In a series of 10 dogs having mixed infections, for example, numbers of *D. alascense* ranged from 1 to 126 ($\bar{x} = 31$), whereas diphyllobothriids of other species ranged from 1 to 638 ($\bar{x} = 271$). The greatest diversity of helminths (>20 spp.) was recorded in dogs also in the western district.

Most plerocercoids of *D. alascense* used in experimental infections were obtained from 35 burbot in December 1969 and January 1970; all were found only in the stomachs, within the mucus covering the gastric mucosa. Plerocercoids were numerous, but total numbers were not determined, as those mingled with the gastric contents were not counted. Overall, the prevalence in burbot was in excess of 50%. As compared with plerocercoids of most species of *Diphyllobothrium,* those of *D. alascense* were very small, ranging from 730 μm to 1.5 mm ($\bar{x} = 1.218$ mm, SD = 0.263) in length (Fig. 2). The entire organism was clavate. The scolex, not distinctly set off from the body, made up from about ⅓ to ½ of the total length of the organism and ranged in maximal width from about 250 to 360 μm ($\bar{x} = 305$ μm, SD = 33.381) (Fig. 2). Voucher specimen: a slide containing plerocercoids of *D. alascense* has been deposited in the U.S. National Parasite Collection, No. 89095.

Identifiable remains of fishes were present in the stomachs of 16 (ca. 46%), as follows: boreal smelt in 4 (11%); pond smelt, *Hypomesus olidus* (Pallas), in 1 (ca. 3%); northern pike,
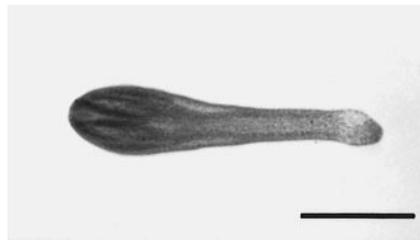

FIGURE 2. Plerocercoid of *Diphyllobothrium alascense* from the gastric lumen of a burbot, *Lota lota.* Scale = 500 μm.

Esox lucius L., in 4 (11%); blackfish in 1 (ca. 3%); burbot in 3 (8%); and unidentifiable remains of fishes in 3. Additional records were obtained from the stomachs of 3 burbot collected at Napaskiak in June 1955: 2 lampreys, *Lampetra japonica* (Martens), and 12 young smelt; remains of adult smelt; and 4 blackfish, respectively.

Two dogs that received plerocercoids on the day weaned first had eggs of *D. alascense* in the feces on day 19 PI. When necropsied at 21 days PI, 9 and 77 cestodes at different degrees of development were present, attached in the jejunum. The 9 cestodes in the first animal were found within 39% of the length of the small intestine, whereas 77 in the second dog were distributed over 51% of the intestinal length. Their localizations suggested that the linear distribution of the cestodes increased in proportion to their numbers.

In general, length of strobila increased with time but with a lag-phase during the first week. Growth of strobilae could be described by a linear equation, $y = 0.23813 + 1.0130x$; $r^2 = 0.95254$ (Fig. 3). By day 32 PI, strobilae attained an average length of 29.5 mm (SD = 21.339), a mean increase in length of 0.88 mm/day. Considerable variation in growth of individual strobilae was evident. Some developed rapidly, while others grew little, retaining the appearance of plerocercoids. For example, by day 10, 16 of 35 strobilae (46%) were still shorter than the maximal length (6 mm) that had been attained by some cestodes by day 5. By day 21 PI, 38% of the cestodes recovered from 3 dogs still had not attained a length of 6 mm. At that time, length ranged from 840 μm to 122 mm ($\bar{x} = 24.5$ mm, SD = 28.164). From 1 dog, only 3 tapeworms were collected, all of which were similar in size (91–110 mm). Twelve strobilae from the second dog were 11–111 mm long ($\bar{x} = 46$ mm, SD = 30.048). The 83 cestodes from dog 3 varied considerably in length (840 μm to 122 mm; $\bar{x} = 20$ mm, SD = 25.157). The longest cestode had increased by 5.8 mm/day, much more than the mean rate of 1.1 mm/day for the others of that series. Strobilae in naturally infected dogs attained observed maximal lengths of 730 mm or more.

Throughout the period of observation, scolex lengths increased, including those of strobilae that developed little beyond the plerocercoid stage. No initial lag-phase was discerned. The average rate of growth of scoleces up to day 14 PI was linear ($y = 478.21344 + 56.99138x$; $r^2 = 0.94912$), with the rate of increase in length slowing with time. Overall, the mean rate of growth of the scoleces can be described by the polynomial equation $y = 410.63591 + 99.31129x - 3.76886x^2 + 0.04208x^3$; $r^2 = 0.95185$ (Fig. 4). The mean rate of increase in scolex length was 61.4 μm/day by day 14 PI, as compared with 22 μm/day by day 32. The maximal observed length of a scolex
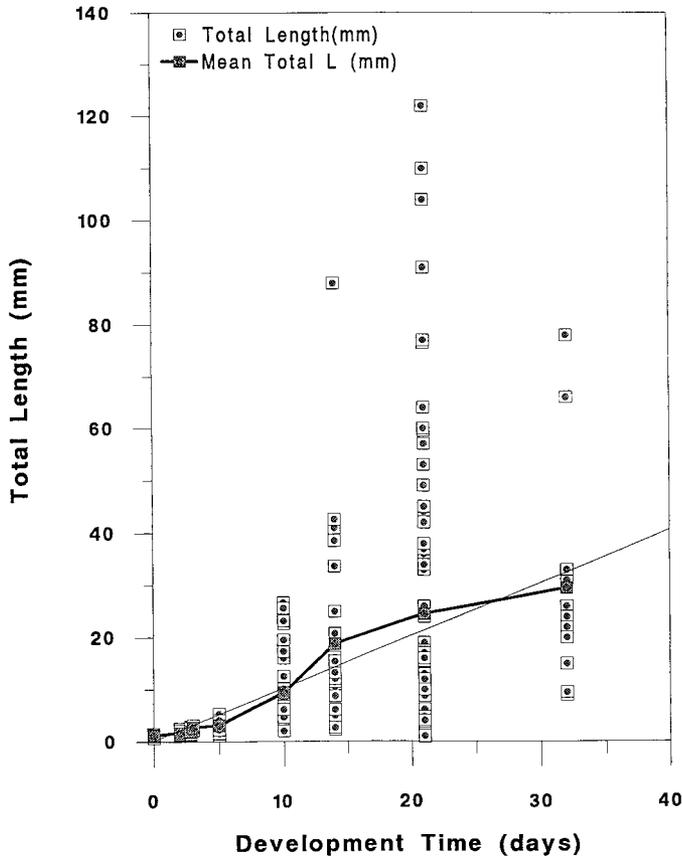
FIGURE 3. Graph of total lengths of strobilae versus time of development. Growth of strobilae described by the linear equation $y = 0.23813 + 1.0130x$; $r^2 = 0.95254$ (thin line).
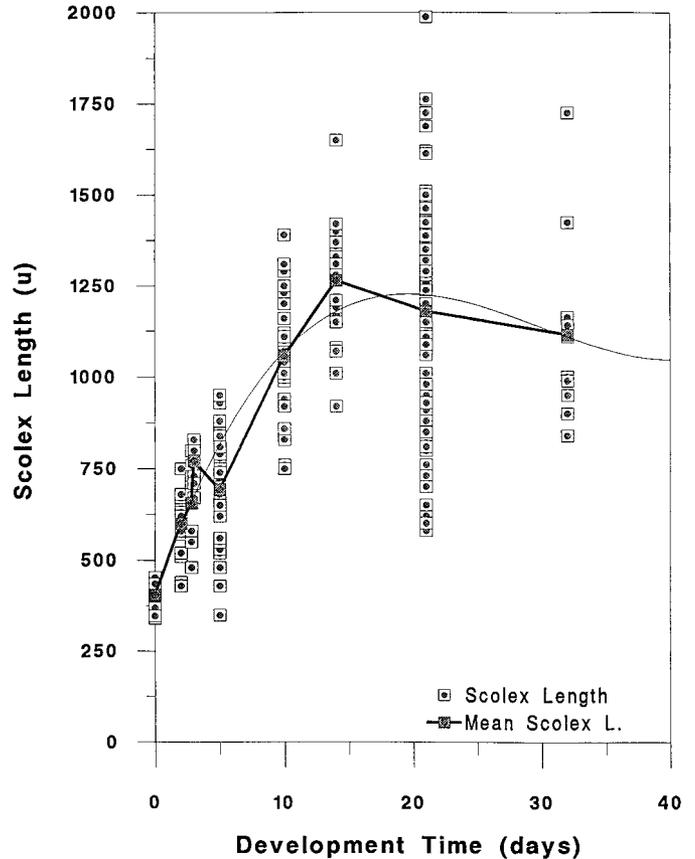

FIGURE 4. Graph of scolex length (μm) versus time of development. Growth of strobilae described by the polynomial equation $y = 410.63591 + 99.31129x - 3.7688x^2 + 0.04208x^3$; $r^2 = 0.95185$ (thin line).

was 1,988 μm. In cestodes from natural infections, length of scoleces ranged from 1,100 μm to 2,925 μm. The ratio strobila length : scolex length increased linearly with time ($y = 1.63118 + 0.75796x$; $r^2 = 0.98746$).

Segmentation first appeared on day 5 PI, when 22 of 38 (58%) cestodes had 4–38 ($\bar{x} = 17.83$, SD $= 9.283$) proglottids. Segmentation was rapid in some strobilae, with formation of as many as 12 segments/day. Through 21 days of development, unsegmented strobilae were still present. The range for that period was 0–250 ($\bar{x} = 67$, SD $= 66.711$) proglottids, although the extent of development was greater among those strobilae from the less heavily infected hosts. The 3 cestodes from 1 dog averaged almost 200 proglottids each. The 12 from the second dog had 37–190 ($\bar{x} = 93$, SD $= 45.792$). Those from the most heavily infected dog ranged from 0 to 250 ($\bar{x} = 60$, SD $= 65.562$). In another animal, at 32 days PI, only 30–96 ($\bar{x} = 58$, SD $= 18.628$) proglottids had been produced. That apparent difference in rates of development may be attributable to difference in sample size (98 strobilae versus 12). In 47 cestodes from a naturally infected dog, numbers of segments ranged from 1 to 381.

Genital primordia appeared as early as day 10 PI but in some strobilae not until day 32. The genital primordia were visible in the 7th segment posterior to the scolex at 21 days, or as far as the 89th on day 14. Their formation evidently progressed anteriad with time. That observation compared well with find-

ings in naturally infected dogs, in which the primordia first appeared in the 11th to the 75th proglottids. Genital and uterine pores were discernible by day 14 PI in some strobilae. By day 21, 14% of 98 cestodes were gravid. Maturation could be rapid, as indicated by the presence of eggs in the 48th segment in a strobila on day 32 PI.

Pyramicocephalus phocarum

The plerocercoids of *P. phocarum* attain a large size in marine fishes, suggesting that growth may be continuous in the second intermediate host. Ten unselected, permanently mounted specimens from cod, *Eleginus gracilis* Tilesius, and sculpins, *Myoxocephalus quadricornis* (L.) and *Megalocottus platycephalus laticeps* (Gilbert), collected in the region of the Yukon–Kuskokwim Delta (at Mekoryuk, on Nunivak Island; at Tanunak on Nelson Island; and at Hooper Bay), ranged in length from 50 to 81 mm ($\bar{x} = 64$ mm). A slide containing a plerocercoid of *P. phocarum* has been deposited in the U.S. National Parasite Collection, no. 89096. The body of the plerocercoid was more or less cylindrical, muscular, about 2–2.5 mm in maximal diameter, and attenuated caudally. The scolex was large and lanceolate (Fig. 5), ranging from about 4 to 5 mm in length by 1.2 to 2.2 mm in maximal width. The margins of the bothria were somewhat crenulate.

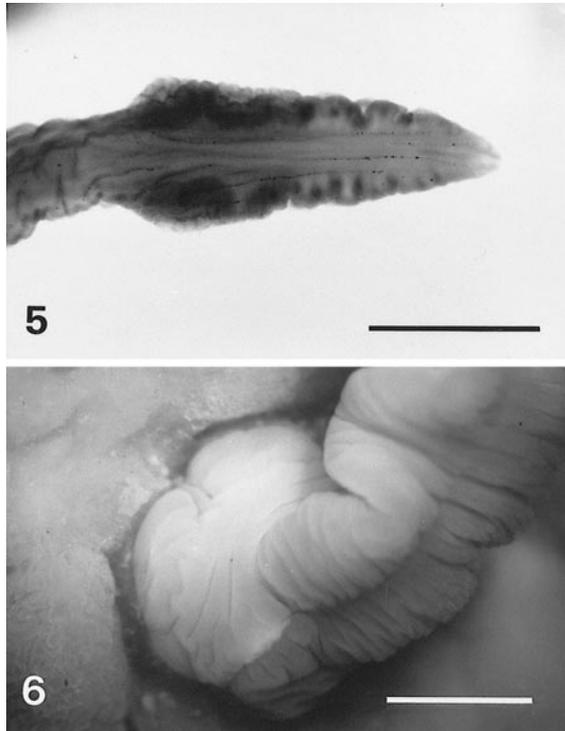Plerocercoids of *P. phocarum* occurred commonly in burbot

FIGURE 5.   Scolex of a plerocercoid of *Pyramicocephalus phocarum* from a cod, *Eleginus gracilis,* Mekoryuk, Nunivak Island. Scale = 2 mm.

FIGURE 6.   Scolex of *Pyramicocephalus phocarum* attached to the gastric mucosa of an adult bearded seal, *Erignathus barbatus,* St. Lawrence Island, Bering Sea. Scale = 2 mm.

of 3 of the 4 series of older fishes. None was found in those collected in April 1970. Nine (60%) were infected of 15 burbot collected in March 1969 (range 1–10 plerocercoids, $\bar{x} = 5$); 11 (65%) were infected of 17 collected in December 1969 (range 1–14, $\bar{x} = 4$); and 7 (39%) were infected of 18 collected in January 1970 (range 1–11, $\bar{x} = 4$). The overall prevalence in the 61 burbot was 44%. In all, 129 plerocercoids were found; their distribution by organ was as follows: 83 (64%) in the wall of the stomach; 36 (29%) encysted superficially on the ceca; 2 (1.5%) in the intestinal wall; and 1 each in the liver, mesentery, and muscle. Four plerocercoids were free in the stomach, indicating that they had escaped from tissues of fishes recently ingested. One larva, in the stomach wall, was dead and undergoing degeneration. Plerocercoids removed from the burbot were mostly smaller than those obtained from marine fishes. Those used for experimental infections were not measured; but of 9 preserved in formalin, total lengths ranged from 9 to 44 mm, with scolex length of 2.5–4 mm.

The stomach contents of burbot did not provide definite indications of a source of the plerocercoids of *P. phocarum.* None was found in any of the smelt from the Kuskokwim River. In the smelt, however, plerocercoids of *Diphyllobothrium* sp. were common, usually encysted on the external surface of the stomach (see Adams and Rausch, 1997: fig. 154-2), occurring in 45 of the 75 (60%) smelt examined in June 1955 and in 60 of the 100 (60%) dissected in May 1956. In all, 320 plerocercoids were found, all apparently representing a single species. Numbers ranged from 1 to 11 ($\bar{x} = 2.9$; mode 1) in the first series;

in the second series, numbers ranged also from 1 to 11, excepting 1 fish that had 25. Excluding the latter, the mean was 3.1, with a mode of 1 or 2 (1 plerocercoid in 19 fishes, and 2 in 18). The plerocercoid in smelt was perhaps that described as *D. osmeri* (von Linstow, 1878), now usually considered to be synonymous with *Diphyllobothrium ditremum* (Creplin, 1825) (Bylund, 1973; Deliamure et al., 1985). None had transferred to the burbot examined.

Attempts to rear the strobilar stage of *P. phocarum* in dogs were unsuccessful. Sixteen animals received 2–6 plerocercoids each and were examined at intervals from 48 hr to 28 days postexposure, with negative results. A domestic cat received a single plerocercoid and was negative at 10 days postexposure. Two human volunteers (adult males) ingested 4 and 5 plerocercoids from the burbot. Both were treated with quinacrine after a month, also with negative results.

Corynosoma strumosum

Corynosoma strumosum occurs commonly in pinnipeds and has been recorded, usually as juveniles, from birds and mammals of various species in the Holarctic (cf. Deliamure et al., 1976; Rausch et al., 1990). Two encysted juveniles were found in a burbot collected at Tuluksak in April 1970, and we infected a dog with a larval stage from a smelt. Artificial digestion of the fishes would have been necessary to determine the prevalence of *Corynosoma* spp. In the lower Yukon–Kuskokwim region, we recorded *C. strumosum* from a sled-dog at Tanunak, from a glaucous-winged gull at Napaskiak, and twice from people at Chevak, following treatment with quinacrine (cf. Schmidt, 1971).

Corynosoma semerme

Juvenile specimens of *C. semerme* were found in a burbot collected at Tuluksak in April 1970. Neiland (1962) reported a cysticanth of that species from a smelt collected in the Kvichak River that empties into Bristol Bay via Kvichak Bay to the southeast of the mouth of the Kuskokwim River.

Pseudoterranova decipiens

Larvae of *P. decipiens* were recorded from 3 of the 4 series of burbot examined, 46 fish in all, collected in December 1969 and January and April 1970, of which 26 (56%) were infected. Numbers in individual burbot ranged from 1 to 5, 1 to 7, and 2 to 6 in fishes of the 3 groups. The overall range was 1–7 ($\bar{x} = 2.5$). The nematodes localized predominantly in the dorsal musculature; 4 were encysted on the stomach; and 1 on the small intestine. They were much less common in smelt, occurring in only 29 of the 175 (17%) specimens (range 1–3, $\bar{x} < 2$). Again, the larval nematodes localized typically in the dorsal musculature. Only 1 was found elsewhere (attached to the stomach).

DISCUSSION

Diphyllobothrium alascense

Diphyllobothrium alascense was described from 19 well developed strobilae from among 142 specimens found in December 1955 in 10 sled-dogs at the village of Chevak, on the Yu-

kon–Kuskokwim Delta. At the time, the local people were subsisting largely on freshwater fishes that could be trapped in large quantity in winter, including the nine-spined stickleback, *Pungitius pungitius* (L.), and blackfish, *Dallia pectoralis* Bean. The diet of the dogs also consisted mainly of such fishes. The cestode was found as well in 3 of 7 dogs at Chevak in late January 1958 and in 2 of 5 at Hooper Bay in mid-March 1958.

The diet of the dogs and the presence of many undeveloped strobilae led to the conclusion that *D. alascense* had a freshwater cycle (Rausch and Williamson, 1958). Evidence is accumulating to support the concept that the cycle involves marine organisms (see below). The natural final host has not been identified, and no further records of *D. alascense* have been obtained (Deliamure et al., 1985).

Morphologically, *D. alascense* most closely resembles *Diphyllobothrium cordatum* (Leuckart, 1863), a cestode of pinnipeds, especially common in the bearded seal, *Erignathus barbatus* (Erxleben), in northern seas. Leuckart's description of *D. cordatum* was a composite, based on a single cestode of human origin and about 20 specimens from 5 dogs, all collected at Godhavn, in northern Greenland. Those from dogs were considered by Leuckart to be merely ''Jugendformen'' of the cestode from the person, which was about 115 cm in length, with maximal width of 7–9 mm. According to Leuckart (1863: 438, fig. 136), the strobila was ribbon-like, with parallel lateral margins, and not attenuated posteriorly, but the terminal segment, apolysis having occurred, was quadrate. The cestodes from dogs were much smaller, with a maximal length of about 26 cm and a width of 6 mm. None had undergone apolysis. Specimens from pinnipeds identified by us as *D. cordatum* were identical in form with those from dogs illustrated by Leuckart (1863: fig. 142). All were attenuated posteriorly, and, as with Leuckart's strobilae, apolysis had not occurred. We judge those differences sufficient to indicate that Leuckart was dealing with not 1 but 2 species of *Diphyllobothrium* (see below).

A cestode from a walrus, *Odobenus rosmarus* (L.), was identified as *D. cordatum* by Deliamure (1955: 140 and figs. 74–77), but it also represented a species differing from that obtained from dogs by Leuckart. The strobila was 91 cm in length, with a maximal width of 14 mm. The scolex was also cordate in form, and a neck was absent. In contrast to the arrangement in *D. cordatum,* in which testes occur in 2–3 layers, testes in the cestode from the walrus formed a single layer. Large papillae were present in the area of the genital pore, and the uterine loops were more numerous and differently arranged as compared with those in *D. cordatum.* The description and figures were repeated by Deliamure et al. (1985).

Diphyllobothrium cordatum was characterized more adequately by Markowski (1952), who studied specimens from pinnipeds of 3 species, including material from a walrus collected at the type locality. Closely resembling those obtained by Leuckart in dogs, Markowski's specimens ranged up to about 20 cm in length, with a maximal width of about 5 mm, and as described by Leuckart, the scolex was more or less cordate and sessile, its posterior margins overlapping the first segments dorsally and ventrally; a neck was lacking.

Leuckart's collections stored in Leipzig were destroyed during World War II. We propose that the illustrations of the cestodes obtained from dogs at Godhavn (Leuckart, 1863: 446, fig. 142) be designated the lectotype of *D. cordatum* (Leuckart, 1863), in accordance with Article 24, International Code of Zoological Nomenclature.

Diphyllobothrium alascense is a relatively large cestode as compared with *D. cordatum,* having a maximal length of at least 73 cm and width to 6.5 mm. Immature specimens are attenuated posteriorly, but apolysis had occurred in all of our fully developed strobilae. The scolex is broadly lanceolate, and a well developed neck is present. The testes are arranged in 2–3 layers, like those of *D. cordatum.* The dog is evidently an atypical host of *D. alascense,* but we consider that the differential characteristics of that cestode are not host induced. Other species of *Diphyllobothrium,* including *D. dendriticum* and *D. dalliae,* when reared in dogs and other carnivores, and in gulls, did not exhibit host-induced morphological variation. In Alaska, we identified *D. cordatum* in 2 dogs at Kotzebue.

The source of plerocercoids of *D. alascense* found in stomachs of burbot is unknown. The strobilar stage of that cestode has not been recognized in the course of extensive surveys of helminths of marine mammals conducted in the North Pacific region and in the arctic basin. Further comparisons have shown that the report by Rausch and Hilliard (1970) of *D. alascense* from a harbor seal, *Phoca vitulina* L., was incorrect, and the domestic dog remains the only known final host. That *D. alascense* has a marine cycle is supported also by Hilliard's (1960) determination that its egg has a thick, pitted shell, and that the coracidium is adapted to existence in seawater.

The high prevalence and abundance of plerocercoids of *D. alascense* in burbot seem to indicate that the second intermediate host of that cestode is regularly and often infected. Because of their small size, the plerocercoids could be easily overlooked if they localize in the musculature of the second intermediate host. Plerocercoids of similar small size (designated Type A) have been reported only by Hasegawa et al. (1980), who found them in the stomach wall of Alaskan haddock, *Theragra chalcogramma* (Pallas), from the Sea of Japan. Those differed, however, in the form of the relatively large scolex (cordate) and, on the basis of strobilae reared by Hasegawa et al. (1980) in golden hamsters, were found to represent another, undescribed species of *Diphyllobothrium.*

In comparison with some other species of *Diphyllobothrium,* the daily increment in length of strobila of *D. alascense* in experimentally infected dogs was relatively small, and little growth evidently took place during the first week. Growth of *Diphyllobothrium latum* (L.) has been rather intensively studied experimentally. In the human host, the length of strobila attains maxima of 20–25 m in Finland and Russian Karelia (von Bonsdorff, 1977). The greatest length recorded in Alaska was 11.4 m (Rausch and Hilliard, 1970). In experimental studies, a person who swallowed 3 plerocercoids expelled 3 cestodes when treated 124 days PI (Pavlovskii and Gnezdilov, 1939, cited in Pavlovskii and Gnezdilov, 1953). Lengths of strobilae were 1.5 m, 3 m, and 12 m, with corresponding mean daily increments of 12, 24, and 96 mm. Nonuniform results were obtained by Petruschewsky and Tarassow [Petrushevskii and Tarasov] (1933), who reported that 1 subject who ingested 4 plerocercoids from ersh, *Acerina cernua* (L.) (Percidae), found eggs in the feces after 2 wk. Four cestodes with lengths of 6.4 m, 1.5 m, 1.2 m, and 0.2 m were expelled by treatment 96 days PI. For the longest strobila, the mean daily increment was 63 mm. The small size of the remaining specimens was attributed to

spontaneous expulsion of portions of strobilae prior to treatment. A second person, who ingested 7 plerocercoids from pike, was treated after only 36 days PI, expelling 7 cestodes from 2 to 8 m in length ($\bar{x} = 5.5$ m). Calculated in proportion to strobilar lengths, average daily increments ranged from 15 to 222 mm ($\bar{x} = 153$ mm).

Petruschewsky and Tarassow (1933) necropsied a dog 36 days after it was fed 5 plerocercoids of *D. latum,* and 6 days after a second exposure of 6, all from pike. Of 10 strobilae found, those judged to be 6 days old were 11–53 mm in length ($\bar{x} = 27$ mm); mean daily increments in length were 2–9 mm ($\bar{x} = 4.5$ mm). Those believed to be 36 days old were 1,300–1,700 mm in length ($\bar{x} = 1,540$ mm), for which mean daily increments ranged from 36 to 47 mm ($\bar{x} = 42.5$ mm). Pavlovskii and Gnezdilov (1949) reared *D. latum* from plerocercoids from ersh in dogs 1.5–2.5 mo old. Eggs appeared in the feces 13–15 days PI, and the animals were necropsied 20–25 days PI. The relationships of strobilae reared from numbers of plerocercoids given were: 12:13, 91:100, 177:200, and 460:500. Ranges in lengths of strobilae from the 4 dogs were 15–140 cm ($\bar{x} = 70$ cm); 2–150 cm ($\bar{x} = 38.1$ cm); 1–65 cm ($\bar{x} = 17$ cm); and 0.5–49.0 cm ($\bar{x} = 13.4$ cm). In a second trial, 718 cestodes obtained from a dog that received 1,000 plerocercoids ranged from 0.5 to 40 cm ($\bar{x} = 5.7$ cm) in length. Pavlovskii and Gnezdilov (1949) considered that cestodes attached more anteriorly in the intestine increased in length more rapidly than those in the middle and posterior areas. In 16 dogs infected with plerocercoids of *D. latum* by Pavlovskii and Gnezdilov (1953), numbers of cestodes found in each ranged from 3 to 2,057; the findings indicated that mean length of strobila was inversely proportional to the number of cestodes. They also concluded that maturation of the reproductive organs was accelerated in the more massive infections.

Only a few observations have been reported on the rate of growth of other species of *Diphyllobothrium.* Wardle and Green (1941) used plerocercoids from fish (species and geographic origin not given) to infect dogs. The cestode was designated *D. latum,* and the plerocercoids presumably were obtained in Manitoba. The identification of the species, however, was evidently incorrect. In cestodes they obtained in the dogs, length of strobila increased at a mean rate of 48 mm/day for the period 6–15 days PI, and 61.5 mm/day for the period 15–30 days. *Diphyllobothrium ursi* is another cestode of large size, its strobila attaining a maximal observed length of 11.7 m in the brown bear (Rausch, 1954). In a black bear, *Ursus americanus* (Pallas), infected experimentally with plerocercoids from sockeye salmon obtained at Karluk Lake, Kodiak Island, a strobila at 10 days PI exhibited a mean daily increment of 96 mm (length of strobila 960 mm, with 620 proglottids). One cestode obtained from a second black bear at 61 days PI had a total length of 3.16 m, with 932 proglottids. Apolysis had occurred and the minimal mean daily increment in length was 51.6 mm (R. L. Rausch, unpubl. obs.).

The strobila of another species, *D. dendriticum,* attaining a maximal length of around 1 m, also develops rapidly as compared to that of *D. alascense.* Kuhlow (1953) reported an average daily increment in length of strobila to be 70–100 mm (58–75 proglottids) in gulls, *Larus ridibundus* L., over a 6-day period. Our findings for *D. dendriticum* in experimentally infected gulls and canids (to be reported elsewhere) were similar.

Possibly, the slower development of the strobila of *D. alascense* is species specific, but this remains to be determined. The development of *Diphyllobothrium* spp. may lack uniformity when many strobilae are present in a host. In the case of *D. alascense,* some specimens in heavy infections developed rapidly and produced eggs, while others were greatly retarded. Such delay in development evidently is not a result of the crowding effect noted in Cyclophyllidean cestodes, in which strobila length tends to be reduced uniformly. We consider developmental delays exhibited by *D. alascense* to be engendered by the tapeworms rather than by the host.

Pyramicocephalus phocarum

Pyramicocephalus Monticelli, 1890 was placed in synonymy with *Diphyllobothrium* Cobbold, 1858 by Bray et al. (1994), on the grounds that the strobilar stage had not been adequately described. However, that cestode exhibits certain unusual morphological features, including a complex form of the scolex in the strobilar stage (Fig. 6), which we judge to be sufficient to justify its retention in a monotypic genus (see also Deliamure et al. [1985: 158]). If *P. phocarum* were to be transferred to the genus *Diphyllobothrium,* it would become a homonym of *D. phocarum* Deliamure et al., 1964, described from the Caspian seal, *Phoca caspica* Gmelin.

Pyramicocephalus phocarum is a symbiont of the bearded seal and a characteristic component of the helminth fauna of that phocid throughout its holarctic range. Bearded seals collected in the Chukchi, Bering, and Okhotsk Seas had prevalences of 91%, 53%, and 78%, respectively (Deliamure et al., 1976). Intensities of infection ranged from 1 to 250 specimens. In the bearded seal, the scolex of *P. phocarum* attains its full development. The scolex attaches firmly to the gastric mucosa (Fig. 6), and when detached typically leaves a deep crater about 5 mm in diameter. The strobila passes posteriad through the pylorus, with most of its length lying within the duodenum.

This cestode has been reported from pinnipeds of other genera, as well as from other marine mammals, but records usually have not specified the state of development of the specimens. Plerocercoids were found free in the stomachs of 2 ringed seals, *Phoca hispida* Schreber, as well as in the stomach of a porpoise, *Phocoena phocoena* L., examined by one of us (R.L.R.) at Hooper Bay in June 1957. Adams (1988) reported a mean prevalence of 14% for the plerocercoid in the alimentary canal of 299 ringed seals collected at 10 localities in the North Pacific and in the Arctic Ocean during the period 1976–1986. A record from a sea otter, *Enhydra lutris* L., was based on a single, poorly developed strobila only 58 mm in length from an animal examined on Amchitka Island (Aleutian Islands) (Rausch, 1953). It was obviously a Kümmerform in an atypical host. We have never observed attached specimens in any marine mammal other than the bearded seal. Evidently, plerocercoids released from fishes by the digestive process may persist for a time in the alimentary canal of various marine mammals, but they probably are expelled without further development. The negative results obtained by us in attempting to infect dogs and people support the concept that *P. phocarum* exhibits a high degree of host specificity, in contrast to many species of *Diphyllobothrium.*

The plerocercoids of *P. phocarum* appear to have been ac-

quired by burbot from marine fishes, such as cod and sculpins, inhabiting shallow, coastal waters near the delta of the Yukon and Kuskokwim Rivers, and that would be available to burbot entering such brackish waters, as is characteristic of them (Walters, 1955). The sculpin *M. quadricornis* reportedly prefers brackish waters and often ascends rivers for considerable distances (Walters, 1955; McPhail and Lindsey, 1970).

The plerocercoids of *P. phocarum* found free in the stomach of burbot were judged to have been ingested recently and had not yet begun penetration into the wall of that organ. As we have observed when nonmigratory steelhead trout, *Oncorhynchus mykiss* (Walbaum), serve as paratenic hosts of the plerocercoids of *D. dendriticum,* most of the larval cestodes localize in the wall of the stomach. Little information is available on the rate of invasion of tissues of the paratenic host. Gnezdilov and Talyzin (1936) stained plerocercoids of *D. latum* using neutral red and traced their migration in experimentally infected burbot and pike. Some remained free in the stomach for as long as 15–24 hr before penetrating the wall of that organ. Halvorsen and Wissler (1973) administered plerocercoids of *D. latum, D. ditremum,* and *D. dendriticum* to burbot and steelhead trout. They found that the respective species differed in their ability to establish themselves in paratenic hosts. As noted above, plerocercoids occurring in smelt have been considered to be those of *D. ditremum.* Halvorsen and Wissler (l973) found that the plerocercoids of *D. ditremum* rarely transferred to paratenic hosts. Similarly, we found that the plerocercoids commonly present in smelt in the Kuskokwim River did not transfer to burbot.

Plerocercoids in smelt

On ecological grounds, we are uncertain that grebes and loons are responsible for the high prevalence of plerocercoids in smelt in the Kuskokwim River. Those birds in the Kuskokwim Delta region nest and feed in ponds and lakes, and they seem rarely to frequent large rivers, except perhaps during migration. In 65 loons of 4 species and 52 grebes of the genus *Podiceps* examined for helminths in Alaska, cestodes were common (83% and 94%, respectively), but *Diphyllobothrium* spp. were poorly represented (Rausch, 1983). The boreal smelt reportedly spawns in rivers, but perhaps the young fish enter habitat more favorable for the birds. Gulls are common along the Kuskokwim River, but *D. dendriticum* is the diphyllobothriid occurring typically in them.

Acanthocephalans

Cysticanths of the 2 acanthocephalan species recorded occur in a considerable variety of fishes. Burbot could become paratenic hosts through consumption of smelt and nonanadromous marine fishes. Acanthocephalans of both species have been recorded as juveniles in various piscivorous birds and mammals, but they only rarely mature in other than marine mammals.

Pseudoterranova decipiens

Burbot in the Kuskokwim River might accumulate third-stage larvae of *P. decipiens* through the consumption of smelt, which make up a significant component of their diet. Boreal smelt migrate up the Kuskokwim River in great numbers in early June, but our identification of stomach contents of the burbot confirms that some are present during much of the year. Marine fishes also commonly harbor the larvae of that nematode.

Pseudoterranova decipiens occurs typically in pinnipeds in the North Pacific region and has been reported infrequently from other marine mammals. It was found to be a cause of significant mortality among sea otters on Amchitka Island (Rausch, 1953) and may produce gastric lesions in people. Margolis (1977) listed 46 human cases of infection, the majority in Japan. Third-stage larvae have been reported from marine fishes of numerous species (Margolis and Arthur, 1979).

Freshwater fishes that become paratenic hosts of helminths of marine origin evidently can acquire larval stages in any of 3 ways—by entering brackish water near river mouths, where they consume marine fishes; by preying on marine fishes that come into the lower reaches of rivers; or by feeding on anadromous fishes migrating upstream for spawning. With respect to burbot in the Kuskokwim River, all of those interactions may be involved in the transfer of helminths of marine origin.

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