

Helminth Parasites of Sea Otters (*Enhydra lutris*) from Prince William Sound, Alaska: Comparisons with Other Populations of Sea Otters and Comments on the Origin of Their Parasites

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ABSTRACT: The helminths found in the gastrointestinal tracts and gallbladders of 68 sea otters (*Enhydra lutris*) from Prince William Sound, Alaska, and their prevalences were: *Corynosoma enhydri* (Acanthocephala), intestine, 51.5%; *Orthosplanchnus fraterculus* (Trematoda), gallbladder, 50%; *Diplogonoporus tetraapterus* (Cestoda), intestine, 12%; and *Pseudoterranova decipiens* (Nematoda), stomach, 1.5%. One pup examined was free of helminth parasites. Throughout its range from the Kuril and Komandorski islands in Russia, across the Aleutian Islands, Alaska, and south to California, the sea otter harbors a total of 17 or 18 species of helminths, of which 5 or 6 are incidental infections with larval (2 species of *Anisakis*) or juvenile worms (3 or 4 species of *Polymorphus*). The adult worms of sea otters (12 species) are derived primarily (9 species) from pinnipeds. One species, *Microphallus pirum* (Trematoda), found widely in sea otters from the Komandorski Islands to California, may be primarily a parasite of various shorebirds. Only one species, *C. enhydri*, is uniquely a parasite of sea otters, occurring throughout its range at prevalences greater than 50%. California populations of sea otters harbor only *M. pirum*, *C. enhydri*, and *Polymorphus* species, lacking any species known to be transmitted by fish; the diet of these sea otters consists almost entirely of invertebrates. Northern sea otter populations from Russia and Alaska have a more varied diet and are hosts for at least 5 fish-transmitted parasites. Among the commonly occurring parasites, the most striking difference between Russian and Alaskan populations of sea otters is the absence of *O. fraterculus* from Russian populations and its frequent occurrence in Alaskan populations.

KEY WORDS: parasites, helminths, *Orthosplanchnus fraterculus*, *Diplogonoporus tetraapterus*, *Pseudoterranova decipiens*, *Corynosoma enhydri*, sea otters, *Enhydra lutris*, Alaska, North Pacific Ocean, zoogeography.

In spring 1989, a major oil spill in Prince William Sound, Alaska, caused by the grounding of the T/V *Exxon Valdez*, resulted in substantial mortalities among the sea otter (*Enhydra lutris*) population. More than 1,000 dead sea otters were recovered during rescue operations in Prince William Sound and neighboring coastal areas (Bayha and Kormendy, 1990). We report on the helminth parasites collected from some of the necropsied animals and compare the findings with previous reports on helminth parasites of sea otters from North American and Asian populations. We conclude with a discussion of the origin of the sea otter parasite fauna.

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Materials and Methods

Data on helminth parasites were recorded from 69 sea otters (37 ♀: 27 adults, 7 juveniles, 3 undetermined maturity; 26 ♂: 12 adults, 8 juveniles, 6 undetermined maturity; 1 pup; 6 undetermined sex: 3 adults, 3 undetermined maturity). Fifty-nine of these animals were collected live and necropsied either immediately following death or euthanasia (usually within 1 to 6 days, rarely up to 10 days), or they were refrigerated and examined within several (maximum 6 to 8) hours after death. The remaining 10 otters were dead upon collection, but appeared sufficiently fresh to yield valid parasite prevalence data. Stomach, intestine, and gallbladder were examined macroscopically for all but 1 ♀ and 1 ♂, for which only the gallbladder was examined. Field circumstances did not permit microscopic examination or the use of such techniques as sieving, decanting, or centrifugation of gastrointestinal or gallbladder contents to detect very small helminths. Because the number of worms of each species encountered in each animal was not counted, we report only data on parasite prevalence.

Representative samples of helminths were fixed and preserved in 10% formalin. For microscopic study, nematodes were cleared in lactophenol; trematodes and cestodes were stained in Semichon's acetic carmine,

Table 1. Prevalence of helminth parasites in adult and juvenile sea otters (*Enhydra lutris*) from Prince William Sound, Alaska.

	Site	No. examined	No. infected	Prevalence (%)
Trematoda				
<i>Orthosplanchnus fraterculus</i>	Gallbladder	68	34	50.0
Cestoda				
<i>Diplogonoporus tetraapterus</i>	Intestine	66	8	12.1
Nematoda				
<i>Pseudoterranova decipiens</i>	Stomach	66	1	1.5
Acanthocephala				
<i>Corynosoma enhydri</i>	Intestine	66	34	51.5

dehydrated in a series of ethanols, cleared in xylene, and mounted in Canada balsam; and acanthocephalans were studied unstained. For cestodes, transverse and longitudinal sections of mature and gravid proglottids were prepared, stained in hematoxylin, and mounted in permount after dehydration in ethanol and clearing in xylene. Representative voucher specimens have been deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland: *Orthosplanchnus fraterculus* (USNPC 86771), *Diplogonoporus tetraapterus* (USNPC 86772), *Pseudoterranova decipiens* (USNPC 86773), and *Corynosoma enhydri* (USNPC 86774). The terms *prevalence* and *intensity* are used in accordance with the definitions provided by Margolis et al. (1982). Parasite prevalences among male, female, adult, and juvenile sea otters were compared statistically using Fisher's exact probability test (Sokal and Rohlf, 1981).

Results

Four species of helminth parasites were found in the sea otters, one each of Cestoda, Trematoda, Nematoda, and Acanthocephala (Table 1). Except for a statistically significant ($P < 0.05$) difference between adult male and female hosts in prevalence of *Diplogonoporus tetraapterus* (von Siebold, 1848) (4 of 12 males and 1 of 27 females infected), no significant differences in parasite prevalence were detected between male and female hosts or between adult and juvenile hosts. We therefore have summarized prevalence data for all sea otters combined (Table 1).

The most frequently encountered parasites were the acanthocephalan *Corynosoma enhydri* Morozov, 1940, in the intestine and the digenean trematode *Orthosplanchnus fraterculus* Odhner, 1905, in the gallbladder. Both were found in half of the animals examined. The cestode *D. tetraapterus* occurred in the intestine of 12% of the otters, and the nematode *Pseudoterranova decipiens* (Krabbe, 1878) (3 specimens) was recov-

ered from the stomach of only 1 adult female otter. The 1 pup examined was free of helminths.

Discussion

The sea otter is an exclusively marine species of the mammalian family Mustelidae. It inhabits coastal areas on the North American and Asian sides of the North Pacific Ocean (Riedman and Estes, 1987) and was the object of intensive human exploitation for its valuable pelt in the 18th and 19th centuries, which resulted in elimination of the species from vast areas of its original range. With complete protection from harvesting, population numbers have been increasing in recent decades, and parts of the former sea otter range have been reoccupied by natural invasion or by deliberate reintroduction of the species. At present, populations exist in a disjunct distribution between about 35°N and 60°N on the North American coast and between about 45°N and 55°N on the Asian coast (Fig. 1).

Within this distributional range, reports on parasites of the sea otter have been published for populations from the Komandorski (Commander) and Kuril islands on the Asian side of the Pacific, and from the Aleutian Islands, Prince William Sound, and California on the North American side (Table 2). Isolated records of parasites of sea otters from islands north and south of the western end of the Alaska Peninsula and from southeast Alaska also have been documented (Van Cleave, 1953; Adams and Rausch, 1989), as well as a record of *C. enhydri* from an unspecified locality in Alaska (Kikuchi and Nakajima, 1993).

Of the 4 parasite species recovered in the present study, *C. enhydri* is the only one specific

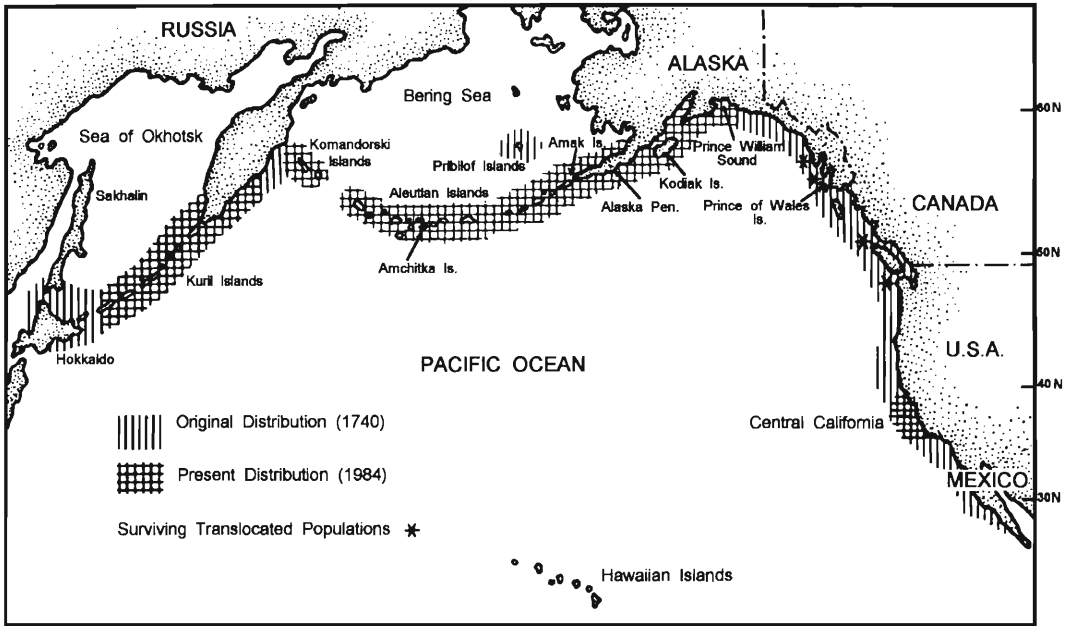


Figure 1. North Pacific region showing original and present sea otter distribution. (Modified from Riedman and Estes [1987].)

to the sea otter. No other definitive hosts are known. Although not reported by Rausch and Locker (1951) or Rausch (1953) from the 31 sea otters they examined from Amchitka Island (Aleutian Islands), it appears to be widely distributed around the North Pacific rim from the Kuril Islands in Asia to California in North America (Table 2). It is probably the most prevalent, although not necessarily the most numerous, parasite of sea otters. In the 3 studies in which more than 60 animals were necropsied (Kuril Islands, Kovalenko, 1975; California, Hennessy and Morejohn, 1977; Hennessy et al., 1979; Prince William Sound, present study), prevalences ranged from 52% (Prince William Sound) to >90% (California) for adult and juvenile (excluding pups) hosts combined.

Orthosplanchnus fraterculus, the second most frequently encountered parasite in our study, also was commonly found by Rausch and Locker (1951) and Rausch (1953) in sea otters from Amchitka Island (prevalence, 90%), but was not found in the Asian populations of sea otters and is probably also absent from the California population. This parasite was found also in southeast Alaska (Adams and Rausch, 1989). It appears, therefore, to be a core parasite of only Alaskan sea otter populations.

The tapeworm *Diplogonoporus tetrapterus* apparently has a low prevalence in northern populations of sea otters from both Asia and North America and is absent from California sea otters. The highest reported prevalence (12%) is for the Prince William Sound population examined in the present study. The difference in *D. tetrapterus* prevalence between adult male and female hosts in our study suggests a more frequent occurrence of fish, the probable second intermediate host of this cestode, in the diet of adult males.

Like *D. tetrapterus*, *P. decipiens* has been found in the northern populations of sea otters in Asia and North America but has not been reported from California sea otters. Prevalences of *P. decipiens* are difficult to interpret from the information provided in most of the Asian and Aleutian Islands studies, but in all cases, they appear to be substantially greater (up to 35–40% or even higher in some small samples) than the 1.5% prevalence reported by us for Prince William Sound sea otters. Intensity of infection also reached much higher levels in Asian and Aleutian Island host samples, with up to 200 worms in some otters (Afanasev, 1941; Kovalenko, 1975).

Among sea otter parasites not reported in our

Table 2. Comparison of helminth parasite occurrence in sea otters (*Enhydra lutris*) from Asian and North American populations.*

	Amchitka, Aleutian Islands	Prince William Sound, Alaska	California	Komandorski Islands	Kuril Islands
Trematoda (Digenea)					
<i>Microphallus pirum</i> (syn. <i>M. enhydrae</i>)†	+	+	+	+	-
<i>Nanophyetus</i> sp.	-	-	-	+	-
<i>Orthosplanchnus fraterculus</i>	+	+ #	??*	-	-
<i>Phocitrema fusiforme</i>	+	-	-	-	-
<i>Pricitrema zalophi</i>	+	-	-	-	-
Cestoda					
<i>Diplogonoporus tetraapterus</i>	+	+	-	?	+
<i>Diplogonoporus</i> sp.‡	-	-	-	+	-
<i>Pyramicocephalus phocarum</i> §	+	-	-	-	-
Nematoda					
<i>Anisakis</i> sp. larva I	-	-	-	-	+
<i>Anisakis</i> sp. larva II	-	-	-	-	+
<i>Pseudoterranova azarasi</i>	-	-	-	-	+
<i>Pseudoterranova decipiens</i>	+	+	-	+ ††	+
Acanthocephala					
<i>Corynosoma enhydri</i> syn. <i>C. macrosomum</i>	-	+	+	+	+
<i>Corynosoma strumosum</i>	+	+	-	-	-
<i>Corynosoma villosum</i> syn. <i>C.</i> sp. of Rausch and Locker, 1951 and of Rausch, 1953	+	+	-	-	+
<i>Polymorphus altmani</i>	-	-	+	-	-
<i>Polymorphus kenti</i>	-	-	+	-	-
<i>Polymorphus major</i>	-	-	+	-	-

* Data compiled from Rausch and Locker (1951), Rausch (1953, 1964), Van Cleave (1953), and Kenyon (1969) for the Aleutian Islands; from Golvan (1959), Neiland (1962), Rausch (1964), Kenyon (1969), and the present paper for Prince William Sound; from Hennessy and Morejohn (1977) and Hennessy et al. (1979) for California; from Barabash-Nikiforov (1935, 1947), Morozov (1940, 1957), Afanasev (1941), and Kontrimavichus (1969) for the Komandorski Islands; and from Kovalenko (1975) for the Kuril Islands. All, except *O. fraterculus* (a parasite of the gallbladder), are parasites of the gastrointestinal tract.

† Deblock and Pearson (1969) and Deblock (1971) regarded *M. enhydrae* and *M. pirum* as distinct species, but we treat them here as a single species. Lauckner (1985) believed that the sea otter "is host for 2 species of the genus *Microphallus*," but accepted the use of the name *M. pirum* for Rausch's (1953) material from Amchitka Island.

‡ Probably *D. tetraapterus* (see Rausch, 1964), but reported as *Diplogonoporus grandis* by Barabash-Nikiforov (1947) and Barabash-Nikiforov et al. (1968).

§ Unidentified cestodes reported from a Komandorski Islands sea otter by Barabash-Nikiforov (1935) were considered by Lauckner (1985) to be "possibly attributable to *Pyramicocephalus phocarum*." As the parasites were not described, there is no evidence to support this suggestion.

|| Although *C. enhydri* was not reported from Amchitka Island by Rausch and Locker (1951) or Rausch (1953), it has been found in sea otters from islands to the north and south of the western end of the Alaska Peninsula, adjacent to the eastern Aleutian Islands (Van Cleave, 1953, as *Corynosoma* sp.; Margolis, unpubl., based on specimens collected by Dr. Karl Kenyon at Amak Island, north side of the Alaska Peninsula). Kenyon (1969) reported from 1 to 98 *Corynosoma* sp. (total, 271 specimens) from 8 Amchitka Island sea otters. It is possible that this collection contained some *C. enhydri*.

Also reported from Prince of Wales Island, southeast Alaska, by Adams and Rausch (1989).

** The gall bladder, the site of *O. fraterculus* infection, was not examined in the California sample of sea otters. However, it appears to be a holarctic pinniped parasite not found in California waters.

†† Without providing any justification for their decision, Barabash-Nikiforov et al. (1968) referred to nematodes previously identified (Afanasev, 1941; Barabash-Nikiforov, 1935, 1947) from Komandorski Islands sea otters as *P. decipiens* to *P. azarasi*.

study, the trematode *Microphallus pirum* (Afanasev, 1941) and the 3 acanthocephalan species of the genus *Polymorphus* deserve special mention. *Microphallus pirum* was originally described from the Komandorski Islands (Afanasev,

1941), and was commonly found in the intestine of Amchitka Island sea otters by Rausch and Locker (1951) and Rausch (1953) and in California sea otters by Hennessy et al. (1979). It also was reported previously from a Prince

William Sound sea otter (Kenyon, 1969). Thus, it is widely distributed in sea otters. In our study, this species may have been overlooked because of its small size (<1 mm in length). The three species of *Polymorphus* uniquely reported from California sea otters, with individual species prevalences up to 5% (Hennessy and Morejohn, 1977), are primarily parasites of aquatic birds. Hennessy et al. (1979) referred to 4 (unnamed) species of *Polymorphus*, with combined prevalence of 10%, among California sea otters. The parasites did not reach sexual maturity in sea otters (Hennessy, 1972; Hennessy et al., 1979).

Differences between the parasite fauna of the southern (California) and northern populations of sea otters are largely the consequence of differences in their diets. California sea otters feed almost entirely on a variety of macroinvertebrates, whereas Alaskan and Russian populations of sea otters include fish as well as invertebrates as important elements in their diet (Riedman and Estes, 1990). The fish-transmitted parasites include *D. tetraapterus*, *P. decipiens*, *P. azarasi* (Yamaguti and Arima, 1942), *C. strumosum* (Rudolphi, 1802), and *C. villosum* (Van Cleave, 1953) (see Schiller [1954] and Shults and Frost [1988]), all of which were absent from California sea otters. In contrast to *C. strumosum* and *C. villosum*, *C. enhydri*, as already noted, is found commonly in both the California and northern populations of sea otters and is therefore probably transmitted by 1 or more invertebrates. Afanasev (1941) claimed to have found juvenile *C. enhydri* in the cottid fish *Myoxocephalus stelleri* from the Komandorski Islands. However, the few morphometric data he provided (length 4.6 mm; swollen proboscis with 24 longitudinal rows of hooks) suggest that he may actually have been dealing with *C. villosum*, a species not known at the time. Only 1 other parasite, *M. pirum*, has been found in both northern and California sea otters. Transmission to sea otters is via shore crabs, in which the metacercariae develop. Schiller (1954, 1959) found metacercariae in *Pagurus hirsutiusculus* and *Telmessus* sp. in Alaska, Tsimbalyuk et al. (1968) reported metacercariae in *P. hirsutiusculus* and *Pagurus middendorffii* in the littoral zone of the Komandorski Islands, and Kulikov et al. (1970) discovered metacercariae in *P. middendorffii* and *Pagurus pubescens* in the northern Kuril Islands area. Although the metacercariae of *M. pirum* have not been reported from California, it can

be assumed that they occur in crabs, a frequent item in the diet of California sea otters (Riedman and Estes, 1990).

A total of 17 (or possibly 18) parasitic helminth species have been reported from sea otters throughout their distributional range. Five (or 6) species are represented by juvenile forms that occur infrequently and have been found in 1 locality only. In addition to the species of *Polymorphus* from California already mentioned, individual encounters of 2 species of *Anisakis* larvae from Kuril Islands sea otters have been documented by Kovalenko (1975). Species of these genera apparently do not mature in sea otters, which are dead ends in their life cycles. The normal definitive hosts are primarily anseriform birds for the *Polymorphus* species and cetaceans for the *Anisakis* species.

Among the 12 species that use sea otters as definitive hosts, 3 (*C. enhydri*, *M. pirum*, and *O. fraterculus*) may be considered core species, at least in some sea otter populations, because of their high prevalence and intensity of occurrence. Of these 3 species, 2 use the sea otter as the only (*C. enhydri*) or a frequent (*M. pirum*) definitive host. *Orthosplanchnus fraterculus* is a common parasite of some pinnipeds, as are 8 of the remaining 9 species of helminths found in sea otters (Rausch, 1953; Delyamure, 1955; Dailey and Brownell, 1972; Margolis and Dailey, 1972; Shults, 1986; Shults and Frost, 1988; Margolis and Arai, 1989). The only exception is *Nanophyetus* sp., presumably *N. salmincola* (Chapin, 1926), a parasite of various piscivorous birds and mammals, whose metacercarial stage occurs primarily in freshwater and anadromous salmonids (Millemann and Knapp, 1970). Infection has been reported from only 1 Komandorski Islands sea otter (Afanasev, 1941), which must be considered an accidental or occasional host of this parasite acquired by ingestion of an anadromous salmonid.

The helminth fauna of sea otters is thus made up principally of species acquired indirectly from pinnipeds through intermediate hosts in the food chain, plus 2 core species, also acquired through the food chain, that have not been reported from pinnipeds. None of the parasites of sea otters reflect the terrestrial ancestry of this mammal or its relationship with its extant terrestrial-freshwater feeding relatives (Kontrimavichus, 1969). With respect to this dominance of pinniped parasites among the parasites found in

the sea otter, we note that the sea otter evolved in the North Pacific Ocean some 1 to 3 million years ago (Riedman and Estes, 1990) when otariid pinnipeds, and presumably their parasites, were already well established there. These parasites were thus available for colonizing a new mammalian host when the sea otter arrived on the scene. Phocid pinnipeds invaded the North Pacific basin about 2.5 to 3 million years ago (see Hoberg and Adams [1992]) and thus their parasites also became available for colonizing the sea otter early during the latter's appearance in the North Pacific.

The origins of the nonpinniped parasites *C. enhydri* and *M. pirum* remain speculative, although evidence has been accumulating to suggest that the latter species may be primarily a parasite of shorebirds. *Corynosoma* and *Microphallus* each comprise more than 40 species (Deblock, 1971; Amin, 1985). The definitive hosts of members of the genus *Corynosoma* are marine mammals and aquatic birds, with the largest number of species occurring in pinnipeds, which are the likely original hosts for species of this genus. *Corynosoma enhydri*, therefore, presumably arose from an ancestral species parasitic in pinnipeds. Because there are no *Corynosoma* species specific for terrestrial mammals one can rule out the possibility that *C. enhydri* parasitized the sea otter's ancestors before they inhabited the oceans.

Microphallus pirum has been found in large numbers in the arctic fox (*Alopex lagopus*), as well as in the sea otter, on the Komandorski Islands (Afanasev, 1941). Schiller (1959) demonstrated that the glaucous-winged gull (*Larus glaucescens*) could be readily infected experimentally. The worms reared in gulls were larger than those reared in hamsters or recovered from natural infections in sea otters (Schiller, 1959) or arctic foxes (Afanasev, 1941). Although sea otters did not inhabit the Kodiak Island area at the time of Schiller's studies, and the other known mammalian definitive host, the arctic fox, also is absent from Kodiak Island, *M. pirum* metacercariae were nevertheless commonly found there in hermit crabs (*Pagurus hirsutiusculus*). Clearly, some other definitive host was responsible for maintaining infections at Kodiak Island. It is well known that microphallid trematodes lack host specificity in the adult stage (Stunkard, 1953).

The above facts led Schiller (1959) to spec-

ulate that lariform birds may prove to be important natural definitive hosts of *M. pirum*. This would not be surprising, because the majority of the 40+ species of *Microphallus* use aquatic birds as definitive hosts (Deblock, 1971). However, Schiller (1954) did not find *M. pirum* in any of 59 shorebirds of 18 species, including 2 specimens of glaucous-winged gulls, examined from Amchitka Island, where sea otters were commonly found by Rausch (1953) to be infected with this trematode. Contrary to Schiller's (1954) findings, Ching (1965) reported *M. pirum* in the white-winged scoter *Melanitta deglandi* from an unspecified locality on the Pacific coast of North America, Tsimbalyuk and Tsimbalyuk (1967) reported 3 species of sandpipers (*Calidris alpina*, *Calidris maritima*, and *Tringa incana*) and the glaucos-winged gull as definitive hosts on the Komandorski Islands, Hoberg (1979) reported *M. pirum* from the glaucos-winged gull at Ugaiushuk Island (located on the south side of the Alaska Peninsula) and Kodiak Island, and Alekseev and Smetanina (1970) and Smetanina (1981) found the parasite common in *Larus crassirostris* from Peter the Great Bay (the Japan Sea coast of Russia), thus reinforcing the likelihood of seabirds being important and perhaps the original definitive hosts of *M. pirum*. In this context, it is significant that Peter the Great Bay lies outside the historical range of the sea otter.

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