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ECOLOGY AND MORPHOLOGICAL ADAPTATION OF THE SUCKING LICE (ANOPLURA, ECHINOPHTHIRIIDAE) ON THE NORTHERN FUR SEAL[1]

K. C. Kim

The Frost Entomological Museum, Department of Entomology, Pennsylvania State University, University Park, Pennsylvania, 16802, USA

INTRODUCTION

The sucking lice of the Echinophthiriidae (Anoplura) are permanent, obligate parasites exclusive to the aquatic carnivora, mainly Pinnipedia. Survival of the obligate ectoparasites of marine carnivores depends solely upon the host animals and the microenvironment that the host provides. The sucking lice of the Pinnipedia, being ectoparasitic and essentially terrestrial, are uniquely adapted to microhabitats that are directly influenced by two contrasting environments, land and sea. The pinnipeds must have provided acceptable ecological settings for survival and the lice successfully survived and propagated on the northern fur seal in the past, despite unusually severe selection pressure as the host animal ventured into the marine environment. The life cycle and transmission of sucking lice is to a large extent determined by the biology and social behavior of the host animal. Thus, sucking lice in the northern fur seal must have adapted for survival to the combination of marine and terrestrial environments.

Two distinct species of sucking lice, *Antarctophthirus callorhini* (Osborn) and *Proechinophthirus fluctus* (Ferris) are found together on the northern fur seal, *Callorhinus ursinus* Linneaeus. Kim (1971) described and illustrated the adult and immature stages of *A. callorhini* and *P. fluctus,* and subsequently Kim (1972) reported on infestation, density and structures of populations, distribution, and transmission of these lice on the northern fur seal.

The present study was initiated in 1969, and the major portion was carried out on St. Paul Island, Pribilof Islands, Alaska in the summers of 1969, 1970 and 1972. The Pribilof Islands form the major breeding ground of the northern fur seal and provide easy access to a large population. The facilities of the U. S. National Marine Fisheries Service Marine Mammal Biological Laboratory on St. Paul Island form an excellent field base for ecological study of the seal and its ectoparasities.

The paper deals with density and population structure, dispersion and transmission, distribution and microhabitat, and the morphological adaptations of the sucking lice, *A. callorhini* and *P. fluctus,* on the northern fur seal.

MATERIALS AND METHODS

The major portion of the materials studied was collected on St. Paul Island, and the pelagic collections made in the Pacific Ocean off the coast of the State of Washington provided additional information on the lice of pelagic seals. Laboratory extraction of sucking lice from the host skins was made by a modified Cook's technique (Kim, 1972).

For life history and transmission studies, two major techniques were used in addition to field observation. Pregnant cows were captured at a rookery and caged on a sand dune away from the other animals. Pups were born within two days of capture and were examined every day for development of the lice. A feeding technique was developed for the sucking lice. A live pup was restrained on the table, and its belly shaved. Lice of known age and sex were fed on the shaved area of the pup abdomen for about 60 minutes. The fed lice were kept in culture dishes at room temperature until the next feeding.

Several behavioral experiments were conducted on the shaved area of the live pup abdomen. Large numbers of sucking lice were collected from pups at the rookery, and they were starved overnight before experiments.

A few ecological parameters were studied. Temperatures of the dermis layer and several points above the skin were measured with thermistor probes which were affixed and encased in plexiglass tubing: a hypodermic probe (YSI Cat. No. 524) for the dermal layer and 4 implementation type probes (YSI Cat. No. 511) for the other points. Temperatures were read directly from a telethermometer (YSI Model No. 44) and corrected by using a calibration chart provided by Yellow Spring Instrument Co., Inc. Oxygen content of the underfur layer was analyzed by a Beckman's Physiological Gas Analyzer unit with Modular Cuvette (Model No. 160). Oxygen samples were obtained by a hand syringe connected to polyethylene tube (No. PX018; I.D. 0·018 × O.D. 0·038). A needle (B-D25) which was connected to the polyethyl tube was penetrated through, pushed under the skin, and came out to the surface. This needle was placed and surgically sewn on the skin, so that the end of this needle was placed right above the surface of the skin.

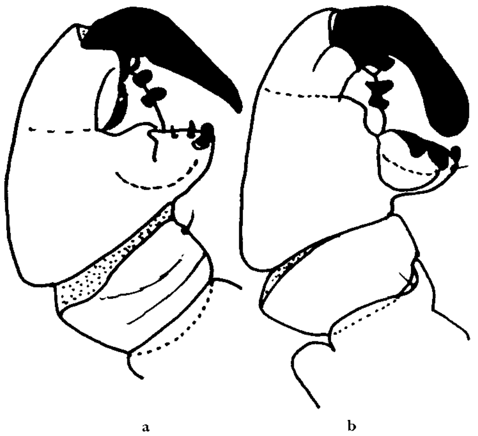

Figure 342. Tibiatarsus II: a. *A. callorhini*, b. *P. fluctus*.

RESULTS

Biology of the Northern Fur Seal

Northern fur seals are seen on and around the Pribilof Islands during every month of the year, but the greatest number comes ashore during the months of June to October (Peterson, 1968). Most fur seals migrate to the southwest and southeast over vast areas of the Pacific Ocean. They rarely land from the time they leave their rookery islands in the fall until they return the following spring.

Territorial bulls begin to arrive in the middle of May about a month earlier than breeding cows. The mean arrival date of nursing cows is calculated as 30 June and the mean departure date is 9 November, when most cows wean their pups (Peterson, 1968). After the initial departure of breeding cows, the bulls soon leave. Juvenile and nonbreeding seals usually land and congregate on separate beaches of the islands, generally known as "hauling grounds".

The territorial or breeding bulls established territories within the first four to eight days after landing on the rookeries. The sizes of the territories vary considerably. Each territory may hold from one or two to a hundred cows, but the mean size of groups of females in some rookeries observed ranged from 3·6 to 17·5 (Peterson, 1968).

Parturition occurs on average 0·9 days after the pregnant cow's arrival, and is followed in 5·3 days by copulation and then departure from the land for feeding after another 1·3 days. The newly conceived embryo will usually be implanted in the alternate horn of the bicornuate uterus. The gestation period is just short of a year. After the first departure, breeding cows return to the land periodically and suckle their pups; they come ashore approximately 10 times in four months. The mean date of weaning is 2 November (Peterson, 1968). Pups are gregarious and form "pods" when not suckling. They usually complete their first molt during the 13th week after birth, about 7 October (Bauer, Peterson, and Scheffer, 1964). The pups depart from land following the breeding cows.

There is no indication of a stable social organization in fur seals while at sea. They appear to spend their time alone or in small groups migrating (Fiscus and Kajimura, 1966).

Taxonomy and morphology of the sucking lice

The Echinophthiriidae includes 5 genera and 12 known species. Their distribution has not yet been confirmed for 11 living species of Pinnipedia which remain to be examined for these parasites.

Pinnipedia are considered to be descendants of an-

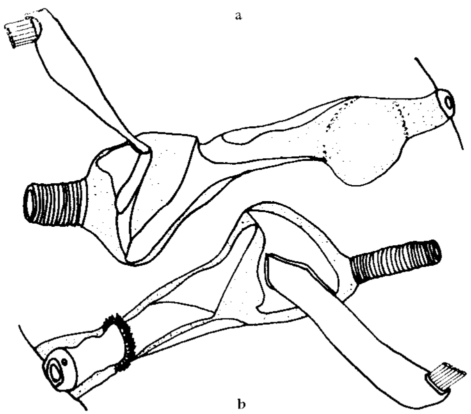

Figure 343. Spiracle and atrium with triangular plate and apodeme: a. *A. callorhini* b. *P. fluctus*.

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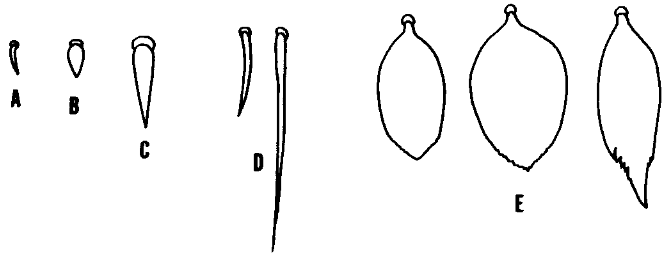

Figure 344. Setae. a. microsetae, b. peg, c. spiniform setae, d. normal setae and e. scales.

cestral carnivores with possibly a diphyletic origin (Mitchell, 1967). The Anoplura are considered to be evolved from ancestral psocopteroids in Permian time. Evidence shows that sucking lice appeared in the Miocene (Rodendorf, 1962). The morphological and biological traits of the echinophthiriids strongly suggest that the ancestral pinnipeds must have harbored sucking lice before they ventured into the marine environment. Moreover the study of nymphal stages suggests that the Echinophthiriidae may be diphyletic, as are the Pinnipedia.

Several unique morphological traits are found in the spiracles, setae, and abdomen of the echinophthiriids that are not found in other groups of Anoplura (Kim, 1971): the spiracles are highly modified and the spiracular atrium is elongated, with an unusual closing apparatus; setae are modified into spines, scales, and pegs; and the abdomen is completely membranous, and usually covered with dense scales and modified setae.

Six species of *Antarctophthirus* are known from a wide range of pinniped hosts: *Eumetopias jubata, Neophoca cinerea, Phocarctos hookeri, Otaria byronia, Zalophus californianus,* and *Callorhinus ursinus* (Fam. Otariidae); *Odobenus rosmarus* (Odobenidae); *Hydrurga leptonyx, Leptonychotes weddelli, Lobodon carcinophagus,* and *Ommatophoca rossi* (Monachinae; Phocidae). The type host of *A. callorhini* is the northern fur seal. Two known species of *Proechinophthirus* are confined to fur seals *Arctocephalus pusillus* and *Callorhinus ursinus* (Arctocephalinae, Otariidae). The type host of *P. fluctus* is the Steller sea lion *Eumetopias jubata,* but the primary host for both louse species is the northern fur seal. By living close to or on northern fur seal rookeries, Steller sea lions and Pribilof foxes (*Alopex pribilofensis*) are occasionally infested with *A. callorhini* and *P. fluctus.*

Antarctophthirus and *Proechinophthirus* have considerable morphological similarity. In both taxa the forelegs are small, weak, with acuminate claws, while the middle and hindlegs are enlarged and specialized for holding. Both taxa have well-developed thoracic phragmata, a distinct notal pit, and specialized spiracles.

In *Antarctophthirus* the antennae of the adults are 5-segmented, but those of nymphs are 4-segmented with a compound terminal segment. The antennae of *Proechinaphthirus* are 4-segmented in the nymphal and adult stages. Adults and nymphs of *A. callorhini* have scales on the abdomen as in other species of *Antarctophthirus* and *Lepidophthirus* (Fig. 344), but the 1st stage nymph lacks distinct scales. *Proechinophthirus* has setae of various sizes and shapes but no scales on the abdomen (Figs 344 a, d) and is similar to the polytypic species *Echinophthirius horridus.* Nymphs of *P. fluctus* have large, heavily sclerotized spines and pegs on the head, the basal antennal segment, and each of the thoracic segments (Fig. 344 b). The spiracular atrium of *A. callorhini* consists of a large triangular plate, a large chitinous apodeme, and a peculiar sclerotized collar which marks the beginning of a tubular part (Fig. 343 a). On the other hand, *P. fluctus* has the spiracular atrium which consists of a smaller triangular plate, a smaller chitinous apodeme and simple tube which is subapically bulbous (Fig. 343 b) and rather similar to that of other sucking lice (Kim, 1971). In *A. callorhini* claws of the middle and hind tarsi are pointed and relatively short (Fig. 342 a), but in *P. fluctus* they are blunt long, suitable for grasping hairs (Fig. 342 f).

Proechinophthirus and *Antarctophthirus* have two ovaries, one on each side of the abdomen. In *P. fluctus* each ovary usually consists of four ovarioles, while in *A. callorhini* each ovary consists of five ovarioles.

Life cycles

Sucking lice go through 3 nymphal stages (Kim, 1971) before becoming adults, and all instars require blood meals.

Development of sucking lice was studied on 5 caged pups by daily examination. Five pregnant cows were caught and caged on dunes away from the rookery. Pups were born to these cows within 2 days after capture. The pups were examined daily for louse infestation and a sample of visible lice was taken for closer examination of the population structure.

The new-born pups were infested with lice of both species within 12 hours post-partum. In the first 4 days post-partum, *A. callorhini* was represented by nymphs of stage 2 and occasionally stage 3, but only adults of *P. fluctus* were found on the pup. By the fifth day post-partum numerous stage 3 nymphs of *A. callorhini* appeared, and on the sixth day adults began to appear. By the ninth day post-partum the majority of *A. callorhini* had molted and become adults. On the other hand, within 48 hours after birth numerous eggs of *P. fluctus* were found on new-born pups.

P. fluctus females possess two ovaries, each consisting of 4 ovarioles, but *A. callorhini* females have 5 ovarioles in each ovary. In a high maturation period *P. fluctus* usually oviposits about 8 eggs per day, and *A. callorhini* about 8–10 eggs. From cage experiments the incubation period of the *P. fluctus* egg is estimated to be about 7 days at average ambient temperature of 10°C on land during the summer.

The length of lifecycle for sucking lice has been estimated by observations made in the cage and feeding experiments. In ambient temperatures of 11–15° C the stage 1 nymph af *A. callorhini* takes 2–3 days before the first molt, nymph 2 takes 4 days before the third molt, and nymph 3 takes another 4 days before the last molt prior to becoming adult. In other words, *A. callorhini* takes approximately 17 days to complete its life cycle on the pup, the skin temperature of which is about 31°. No equivalent data are yet available for *P. fluctus,* but it may be assumed that *P. fluctus* requires about the same length of time for completion of the life cycle.

The life cycle of *Lepidophthirus macrorhini* Enderlein can be completed within 3 weeks on a flipper of the elephant seal, the skin temperature of which is 25–35°C (Murray and Nicholls, 1965). *Antarctophthirus ogmorhini* Enderlein requires a longer period of 3–4 weeks for completion of its life cycle on the outer dorsal surface of the hind flipper. About 15 days are required for incubation of the eggs of *A. ogmorhini* at a skin temperature of 6–10° C (Murray, Smith and Soucek, 1965).

The optimal temperature of development for *A. callorhini, P. fluctus* and *L. macrorhini* on the skin surface is 21–35°C. A skin temperature of about 10°C seems to be optimal for *A. ogmorhini.*

Infestation rate and population density

A considerable difference exists between estimates of infestation rate and population density made by visual examination and by a modified Cook's technique (Kim, 1972). Only the "absolute" estimate made by Cook's technique will be discussed in this paper.

Table 126. Infestation rate of the northern fur seal with *P. fluctus* (P.f.) and *A. callorhini* (A.c.). Black pups = 1–3 months old; adults = 1–11 years old

Seals examined			No. Infest.	% Infest.	% Infest. W/Both Spp.	% Infest. W/*P.f.*	% Infest. W/*A.c.*
Age	Sex	No.					
Black pups	Male	6	6	100·0	83·3	83·3	100·0
	Female	2	2	100·0	100·0	100·0	100·0
	Total	8	8	100·0	85·0	85·0	100·0
Adults	Male	3	2	66·6	33·3	66·6	33·3
	Female	13	12	92·3	92·3	100·0	100·0
	Total	16	14	87·5	81·2	83·3	81·2

Infestation rates of *Proechinophthirus fluctus* and *Antarctophthirus callorhini* are presented in Table 126. Of 24 fur seals examined 22 were infested with lice, representing approximately 92 % infestation with either *A. callorhini* and *P. fluctus* or both. About 83 % of the seals examined harbored both species simultaneously. The rate of infestation is always lower in the adult seals than in the pups. Approximately 87·5 % of the adult seals examined harbored the lice, and 81·2 % were infested simultaneously with both species. All the pups examined harbored the lice and about 85 % were infested with both species simultaneously or with *P. fluctus.* All the pups harbored *A. callorhini.* A sexual difference is shown between infestation rates of the adult seals, but it may be attributed to the small sample size of the males. There is no significant sexual difference in the rate of infestation for black pups.

The population density of sucking lice is expressed here as the mean population size per seal; this was 107·6 lice per infested host based on 18 seals. The population density was at its peak on the black pups, and decreased as the host animals became older. The mean louse population size was 163·3 for black pups, 97·3 for silver pups, and 48·3 for adults. The mean population size was 88·5 for *P. fluctus* and 74·8 for *A. callorhini* on black pups, and 20·3 for *P. fluctus* and 28 for *A. callorhini* on adults. The female seals generally harbored more lice than did the males for all age-groups (Kim, 1972).

Table 127 gives the levels of infestation and the population structures of sucking lice on 16 adult seals. The seals collected in the Pacific Ocean off the coast of Washington during March, April and May harbored larger numbers of lice than seals captured on St. Paul Island, Alaska in July and August. The mean population size was 250·2 lice per pelagic seal and 2·1 lice per seal on St. Paul Island. There were no adult lice found in pelagic samples collected in the spring. This aspect of the population density requires further study.

On St. Paul Island the density of lice on black pups is more than 3 times larger than on adult seals. Reproduction and development of the lice is therefore much more vigorous on black pups than on any other age-group. Dubini (1955) reported that *A. callorhini* multiplied rapidly around the penial and umbilical orifices until the pups were about 6–8 weeks old. At this time, multiplication ceased and the louse population persisted at this level. He considered this to be due to the development of host resistance and termed this phenomenon "Parasithophoria". The population density of black and silver pups seems to support Dubini's observation. The factors influencing acceleration of reproduction and development of sucking lice on black pups remain to be studied.

Structure of louse populations

Of all lice collected about 45 % were *Proechinophthirus fluctus* and 55 % *Antarcthophthirus callorhini*. The first arrivals on newborn pups were adults of *P. fluctus* and mostly stage 2 nymphs of *A. callorhini*. Silver pups collected on St. Paul Island in October were infested with 69·2 % adults and 19·2 % stage 3 nymphs of *P. fluctus* and 50·4 % stage 1 nymphs and 36·5 % adults of *A. callorhini* (Kim, 1972). As shown in Tables 127 and 128, *P. fluctus* was represented by 51·6 % stage 1 nymphs and 47·6 % adults on black pups and by 57·1 % adults on adult seals on St. Pauls Island. On the other hand, *A. callorhini* was represented by 39·8 % adults, 27·4 % stage 2 nymphs and 24·2 % stage 1 nymphs on black pups, and 33·3 % adults, 33·3 % stage 2 nymphs and 33·3 % stage 1 nymphs on adult seals.

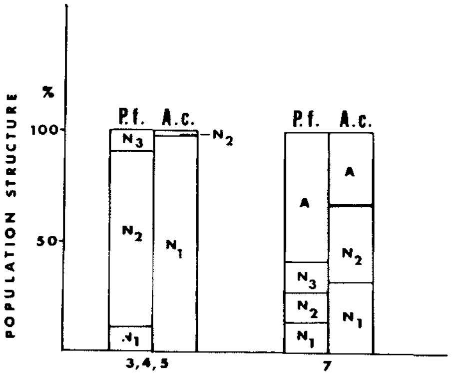

Figure 345. Population structures $(^{\circ}/_{00})$ of *P. fluctus* (P.f.) and *A. callorhini* (A.c.) on the northern fur seal in spring and summer. A = adult, N_1 = nymph 1, N_2 = nymph 2, N_3 = nymph 3.

Figure 345 gives population structures of sucking lice on adult seals collected in different months. *P. fluctus* was represented mostly by stage 2 nymphs in March, April and May; 66·8 %, 71·7 % and 100 % respectively. No adult lice were found on 11 pelagic adult seals examined. The population of *P. fluctus* consisted of 57·1 % adults and 14·3 % each of the three nymphal stages in July. On the other hand, *A. callorhini* was represented by exclusively stage 1 nymphs in pelagic samples, and by mixture of adults, stage 1 and stage 2 nymphs on the adult seal captured on St. Paul Island in July.

The data from the cage experiments and population analysis suggest that adult seals harbor stage 1 and 2 nymphs of *A. callorhini* and adults of *P. fluctus* when they land in June and July. When seals leave the breeding island *P. fluctus* found on the host are mainly adults and stage 3 nymphs, and those on *A. callorhini* are stage 1 nymphs and adults. In other words, *A. callorhini* may have already started a new pelagic generation, but *P. fluctus* is in the process of completing a land generation when the host leaves the breeding island.

Table 127. Levels of infestation and population structures of *P. fluctus* and *A. callorhini* on northern fur seal adults. Land collections were made on St. Paul Island, Alaska, and ocean collections made off the coast of Seattle, Washington. A-adult, N3-nymph 3, N2-nymph 2, N1-nymph 1, F-female, M-male, B-both sexes

Seals				*P. fluctus*					*A. callorhini*					Total No. Lice	Mean Population Size
Habitat	Sex	No. Exam.	No. Infest.	A	N3	N2	N1	Total	A	N3	N2	N1	Total		
Ocean	M	1	1	0	67	99	96	262	0	0	0	13	13	275	275·0
	F	9	9	0	116	908	146	1 170	0	0	2	1 055	1 057	2 227	247·4
	B	10	10	0	183	1 007	242	1 432	0	0	2	1 068	1 070	2 502	250·2
Land	M	4	3	2	0	1	1	4	1	0	1	1	3	7	1·7
	F	2	1	5	1	0	0	6	0	0	0	0	0	6	3·0
	B	6	4	7	1	1	1	10	1	0	1	1	3	13	2·1
Total	B	16	14	7	184	1 008	243	1 442	1	0	3	1 069	1 073	2 515	157·1

Table 128. Population structure $(^0/_0)$ of *P. fluctus* and *A. callorhini*, found on northern fur seals on St. Paul Island. A-adults, N3-nymph 3, N2-nymph 2, N1-nymph 1; Black pups, 1–3 months old, silver pups, about 4 months old

Seal examined			*Proechinophthirus fluctus*					*Antarctophthirus callorhini*				
Age	Month	No.	A	N3	N2	N1	Total	A	N3	N2	N1	Total
Black pups	July	8	47·6	0·7	0	51·6	54·2	39·8	8·5	27·4	24·2	45·8
Silver pups	Oct.	3	69·2	19·2	3·8	7·7	9·0	36·5	6·0	7·1	50·4	91·0
Adults	July	3	57·1	14·3	14·3	14·3	70·0	33·3	0	33·3	33·4	30·0
All seals		14	–	–	–	–	44·4	–	–	–	–	55·6

Dispersion and transmission

Transmission of sucking lice is almost impossible while seals are at sea and most likely occurs on land. Kim (1972) suggested several possible paths in louse trasmission. In the rookery, transmission may take place from nursing cows to pups, from breeding bull to cows, from pups to pups, and from breeding cows to other cows. On a beach separated from the rookery, transmission may be possible from young bulls to bulls and to occasional young cows.

As shown in Table 127 the population density of sucking lice on adult seals is very small, 2·1 lice per animal; therefore louse transmission between adult seals is unlikely to occur. Because of the pups' gregarious behavior, louse transmission may occur among pups in "pods". On the rookery, lice from dead pups may be attracted to the warm bodies of live pups.

New-born pups were infested with lice soon after birth and louse transmission from cow to pup continued throughout nursing (Kim, 1972). The cage experiments and field observations strongly suggest that the major transmission of sucking lice takes place between the nursing cow and pup.

Sucking lice usually stay with their host when it dies. However, the lice may migrate to neighboring seals in the rookery, as soon as their host's body has cooled to the ambient temperature (Kim, 1972).

Distribution and microhabitat

Different species of Echinophthiriidae occupy definite areas of the host body. *Antarctophthirus ogmorhini* has been found on the tail, ankle, hip, and hind flippers of the Weddell seal (Murray, Smith and Soucek, 1965), while *Lepidophthirus macrorhini* has been found on the digits, webs between digits and frequently along the posterior margin of the hind flippers of the elephant seal (Murray and Nicholls, 1965). On the hind flipper, ankle, hip, tail, and to a lesser extent on the fore flippers, the skin temperature fluctuates with thermoregulatory requirements of the seal. The skin temperature of these areas can rise from 0 to 30°C while that of rest of the body remains at 0 to 5°C.

Distribution: Proechinophthirus fluctus was found on the pelage proper, particularly of the neck, belly and hip, while *Antarctophthirus callorhini* was consistently found on the naked parts of the body surface, namely nostrils, auditory canals, eyelids, penial orifice of the male, and umbilical area on black pups. *A. callorhini* was also occasionally found around the anus, at the base of the tail and flippers or other parts of the body, and clustered in the inner corner of the eyes and in the nostrils (Kim, 1971; 1972).

This definite pattern of louse distribution found on black pups does not occur on silver pups and adults. On silver pups the most *P. fluctus* were found on the head and hip. Table 129 gives the topographic distrubution of lice on the fur seal adults which seems to change at different times of the year. *P. fluctus* occupies the belly of the host animal in March and April at sea, but is scattered on the abdomen and back in July on land. On the other hand, *A. callorhini* mostly occupies an apical area of the abdomen and dorsally the base of the tail (anal area) of the host in March and April at sea, but is found on the belly in July on land.

In the cage experiments the movements and distribution of lice were closely studied by daily examination of caged pups. In the first 2–3 days post-partum both *A. callorhini* and *P. fluctus* were scattered around the

Table 129. Topographic distribution (%) of *P. fluctus* and *A. callorhini* on northern fur seal adults. Seal skins for March and April were collected in the Pacific Ocean off the coast of Seattle, Washington, and those for July collected on St. Paul Island, Alaska

Species	Month	No. seals examined	Total no. lice	Head	Belly	Back	Anal area
Proechinophthirus fluctus	March, April	9	1374	14·9	66·3	17·1	1·7
	July	3	7	0·0	42·8	42·8	14·4
Antarctophthirus callorhini	March, April	9	970	5·0	6·7	1·4	86·8
	July	3	3	0·0	100·0	0·0	0·0

penial orifice and general area of the abdomen. No lice were found on other parts of the body. On the 4th and 5th day *A. callorhini* was densely aggregated in and around the penial orifice and on the anal area, and *P. fluctus* was commonly found on the abdomen and chest. The auditory canal was infested with *A. callorhini* stage 2 nymphs as early as the 2nd postparturition day and at the latest by the 6th day. Dense infestation of *A. callorhini* were found in the nostrils and on the eyelids by the 7th and 8th day. Within 10 days after birth, pups were heavily infested with *A. callorhini* on the penial orifice, eyelids, nostrils, and auditory canal, and with *P. fluctus* on pelage of the chest, abdomen, and occasionally of the back.

Microhabitat: The microhabitats of the sucking lice are the pelage and skin of the northern fur seal. *Proechinophthirus fluctus* inhabits the pelage, and *Antarctophthirus callorhini* prefers the naked or thinly haired parts of the skin. The pelage of the northern fur seal covers all the body except for the nose, lips, rim of the eye (eyelid), inside of the ear pinna, penial orifice, vestibular opening, teats, anus, and flippers.

Many factors may influence the microhabitat; namely, substratum (skin), pelage, temperature, relative humidity, oxygen, light and the metabolism of the seal. The skin provides the base for attachments, food, and shelter. The structures of the skin, such as sweat glands and panniculus adiposus, may influence the relative humidity and temperature of the microclimate in the underfur layer. The quality, size, and density of the pelage will determine the characteristics of the microhabitat on the skin for the lice. Thermoregulation and other physiological activities may also affect the temperature gradient in the underfur layer while the seal is at sea.

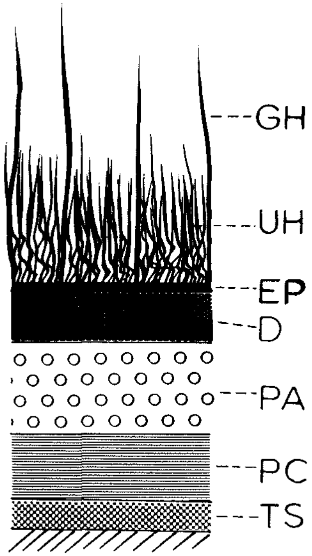

Figure 346. Cross section of the northern fur seal skin. GH = guard hairs, UH = underfur hairs, EP = epidermis, D = dermis, PA = paniculus adiposus, PC = paniculus carnosus, TS = tela subcutana.

1. Skin and pelage of the seal

In the northern fur seal the epidermis is usually less than 60 μ thick and the dermis is 3 to 4 mm thick (Fig. 346). The dermis is thicker in adult seals than in young, and in males than in females. The panniculus adiposus or blubber is about 15 to 20 times thicker in adult seals than in new-born pups; blubber thickness for mature bulls is about 60 mm, for breeding cows about 50 mm, and for new-born pups 3 mm (Scheffer, 1962).

The pelage consists of hair bundles which emerge from the skin surface through a common pilosebaceous funnel and opening. Each hair originates in its own follicle. A guard hair is placed at the anterior side, and the underfur bundle is at the posterior part of each follicular bundle. The paired sebaceous glands lie along the sides of the follicular bundle (Scheffer, 1962).

The pelage of the adult seal is composed of clearly defined bundles, each with a coarse guard hair and 35 to 40 fine underfur hairs; there are more than 300 000 fibers to the square inch. Guard hairs are about 33 mm long on the male and 20 mm on the female, and underfur hairs about 14 mm long on the male and 13 mm on the female. On the other hand, the pelage of the pup is composed of small, scattered bundles, each containing 1 to 3 fibers, some of the fibers being underhairs and some guard hairs; this pelage resembles that of certain land carnivores (Scheffer, 1962). Guard hairs of the pup are about 15 to 20 mm in length, and the underhairs are 6 to 15 mm long. The first molt from black birthcoat to silvery, adult coat, occurs about the 13th week after birth in mid-September and October. The pelage of the silver pup consists of 97·5 % underfur fibers, 2·25 % small guard hairs, and 0·25 % large guard hairs.

In the northern fur seal the hair fibers of the belly are much shorter than those of the other parts of the body surface. In black pups the underhairs of the coat are so thinly distributed that the pups may become soaked to the skin in rain, but the underfur of the adult coat is dense and water repellent.

The behavior and microhabitat preference of the sucking lice was studied on the skin and pelage of fur seal pups. Each live pup was restrained on the table, and the major part of the belly was shaved with a No. 10 scalpel blade except for two areas of 100 mm² in the center. The anterior area of 100 mm² was sheared with a No. 40 blade to remove guard hairs and the top 2 to 3 mm of the underhairs (Type II area). Only the long guard hairs were sheared for the posterior area, leaving short guard hairs and underhairs (Type III area). The area of about 100 mm² between Type II and III areas was completely shaved with No. 10 blade (Type I area). Ten females of *P. fluctus* and 10 females *A. callorhini* which had not been fed for 24 hours were simultaneously placed on different types of microhabitat. The lice found on any particular area were counted and recorded 10 minutes after the initial placement. At the end of each experiment the lice were removed from the skin and counted. This experiment was repeated five times. The result is presented in Table 130. *P. fluctus* moved away from the area of initial placement and into the surrounding pelage, but *A. callorhini* usually stayed on the area of initial placement, penetrated into the thick underhairs, and immediately fed on the surface of the skin with their heads down. *A. callorhini* engorged within 10 minutes. *P. fluctus* showed difficulty walking on the shaved skin without grasping the hairs, but *A. callorhini* walked easily on the skin.

Table 130. Mean number of sucking lice recovered from different microhabitats on fur seal pups. I = area completely shaved with No. 10 blade; II = area with only short underhairs, guard hairs and top 2–3 mm underhairs, sheared with No. 40 blade; III = area with underhairs and short guard hairs, only long guard hairs sheared, IV = pelage proper

Species	Area of initial placement	Area of recovery			
		I	II	III	IV
Proechinophthirus fluctus	I	1·34	0	0	8·66
	II	1·50	1·00	0	7·50
	III	1·50	0	1·50	7·00
Antarctophthirus callorhini	I	5·67	1·00	0	3·33
	II	1·00	7·00	0	2·00
	III	0	0	10·00	0

2. Temperature

The climate of St. Paul Island is typically maritime, resulting in considerable cloudiness, heavy fog, high humidity and rather restricted daily temperature ranges. The mean air temperature for the period 1933–1966 was 8° C and the mean relative humidity for 1966 was 89 % during the months of July, August and September (USCOMMES-ASHEVILLE-500, Local Climatological Data, 1966).

Temperature measurements of the northern fur seal were taken at 5 altitudinal points on 9 topographic areas of the body surface: (1) 5 mm below the skin surface in the dermis layer; (2) right on the skin surface; (3) 5 mm above the skin surface; (4) 10 mm above the skin surface; and (5) 20 mm above the skin surface. At the same time, measurements of rectal and ambient temperature were also taken.

In each microhabitat a definite temperature gradient was observed at the 5 altitudinal points (Fig. 347). The mean temperature of the dermis layer was 34·2° C which was 5 to 6 degrees lower than the rectal temperature (39·7° C); the skin surface was 0·5 to 1·0 degrees cooler than the dermis layer, and the pelage surface temperature was about 2 to 4 degrees higher than the air temperature of 20° C. The temperature of the skin surface was generally 6 to 8 degrees lower than the rectal temperature.

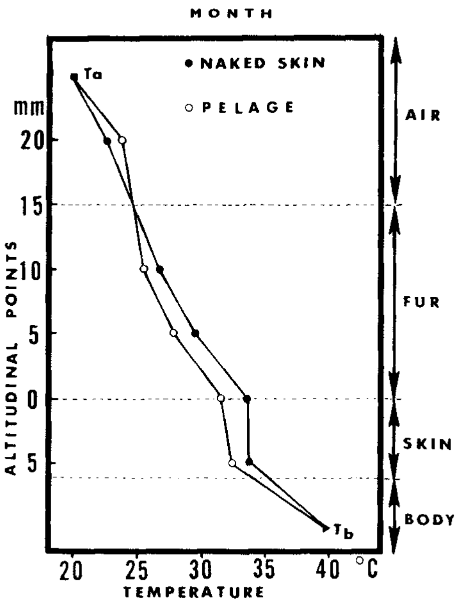

Figure 347. Mean temperature of the naked skin and the fur layer of fur seal pups at 5 altitudinal points on or above the body surface. Ta = air temperature, Tb = rectal temperature.

On the black pup the skin temperature of the naked parts was generally higher than that of the pelage at the air temperature of 20° C (Fig. 347). The mean temperature of the skin surface of the naked parts was 33·6° C and of the pelage was 31·6° C with the rectal temperature of 39·7° C. However, temperatures of the naked parts, such as nose and eyelids, fluctuated considerably as the air and rectal temperatures dropped. The skin surface temperature of the eyelid was 33·4° C at the air temperature and 20° C and rectal temperature of 39·7° C, and 31·4° C at an air temperature of 8·3° C and rectal temperature of 37·7° C. Differences in the temperature of the eyelid increased gradually at the higher altitudinal points; 3 degrees at 5 mm above the skin and 4 degrees at 10 mm and 20 mm above the skin. On the other hand, temperatures in the pelage generally remained constant despite lower air and rectal temperatures.

The skin surface temperature of the adult seal was 33·4° C in air, at an ambient temperature of 22° C in water at a temperature of 11° C (rectal temperature 39·7° C). The temperature of the underfur layer at 10 mm above the skin was 27·7° C in air and 18·3° C in water.

As Scheffer (1958) recorded, the body temperature was 37·7° C for adult and 38·2° C for young fur seals at rest with a range of about 4 degrees. At an air temperature of 13° C the skin surface temperature of the belly was 34·4° C for the new-born pup and 28·4° C for the nursing cow, and the temperature at 10 mm above the skin was 27·1° C for the pup and 23·5° C for the nursing cow. A difference of about 3 degrees existed in the skin surface temperature between the black pup and nursing cow (Fig. 348).

An exploratory experiment was made to study the effect of temperature on survival of the lice. Five males and 5 females of *A. callorhini* were placed in a vial with sufficient moisture. One vial was placed in an oven at 21° C and the other at 37° C. This experiment was repeated twice. The same procedure was also repeated for *P. fluctus*. After 24 hours each vial was examined and the dead lice were counted. *A. callorhini* was unable to survive for 24 hours at 37° C but attained 100 % survival at 21° C. On the other hand, *P. fluctus* had 65 % mortality at 37° C and 35 % at 21° C. The optimum temperature for the sucking lice may lie between these temperatures.

3. Other microclimatic factors

The effects of light, relative humidity and oxygen content of the underfur layer on the behavior and survival of the sucking lice were three others factors that were explored.

Half of a petri dish was covered with vinyl plastic electric tape on both sides. A circular filter paper was placed on the bottom. Ten adults of *P. fluctus* and 10 adults of *A. callorhini* were placed on the center of the dish, and the dish was illuminated for 30 minutes. In another experiment lice were placed on various areas of the petri dish. Each experiment was repeated 4 times. No direct response of the sucking lice to light was observed in these experiments. In a further experiment a petri dish was completely covered with black electric tape except for one side. Ten lice were placed in the center of the dish, and the dish was illuminated from the open side for 30 minutes. This experiment was performed for both *P. fluctus* and *A. callorhini*. No response of the lice to light was observed. In these experiments the sucking lice were wandering around the point of initial placement, and no obvious movement away or toward light was observed.

There was no accurate means of measuring the relative humidity in the fur layer of the seal in the field laboratory. Thus, simple experiments were made to explore the possible effect of moisture on survival of the lice. Ten lice of each species were placed in several

6-dram vials. One set of 2 vials was saturated with 100 % moisture and the other set was kept in a relative humidity of 50 % at room temperature. Two replications were made for each species of lice. The number of dead lice was counted daily. After 3 days 75 % of *P. fluctus* survived in 50 % relative humidity and 43 % survived in 100 % moisture, and 62 % of *A. callorhini* survived in 50 % relative humidity and 75 % survived in 100 % moisture. Thus *A. callorhini* seems to be tolerant to various levels of moisture, but the survival of *P. fluctus* is poor at 100 % humidity.

Oxygen content was measured in the fur layer of an adult seal submerged in a tank of sea water. Four measurements were taken on a 3-year old bull (body weight 23 kg, rectal temperature 39·7° C) in 10° C water for a period of 30 minutes. The level of oxygen (PO_2) in the fur layer was relatively constant at 148 mm Hg (152 mm Hg in air).

DISCUSSION AND SUMMARY

Approximately 92 % of northern fur seals are infested with either *A. callorhini* or *P. fluctus* or both. About 83 % of the seal examined harbored both species simultaneously. All seal pups were infested with sucking lice, but only about 88 % of adult seals. The mean population size was 88·5 for *P. fluctus* and 74·8 for *A. callorhini* on black pups and 20·3 *P. fluctus* and 28 *A. callorhini* on adult seals. The mean population size was 250·2 lice per pelagic adult seal and 2·1 lice per seal on St. Paul Island. No adult lice were found in pelagic samples collected in the spring.

Approximately 45 % of the sucking lice per host were *P. fluctus* and 55 % *A. callorhini*. *P. fluctus* was represented mostly by stage 2 nymphs and no adults in March, April, and May, and *A. callorhini* had only stage 1 nymphs in pelagic samples. The *P. fluctus* population consisted of 57·1 % adults and 14·3 % per each of 3 nymphal stages, and *A. callorhini* had a mixture of adults and stage 1 and 2 nymphs in July samples.

The major transmission of lice takes place between the nursing cow and the newborn pup. *P. fluctus* inhabits the pelage proper of the belly, hip, and neck. *A. callorhini* usually inhabits the naked parts of the body surface such as nostrils, auditory canal, eyelids, penial opening of the male, umbilical area of the black pup, head and hip of the silver pup and belly of the adults.

Life cycle and population structures

The life cycle of sucking lice includes egg, 3 nymphal stages and adult. *Proechinophthirus fluctus* usually oviposits about 8 eggs per day, and *Antarctophthirus callorhini* produces 8–10 eggs daily. The incubation period of the *P. fluctus* egg is about 7 days at average ambient temperature af 10° C on land during the summer. Each nymphal stage of *A. callorhini* takes 3–4 days before molting. The length of the life cycle for *A. callorhini* was estimated to be 18–20 days, from time of oviposition to the last molt, at the skin temperature of about 31·0° C on the pups on St. Paul Island. No equivalent data were available for *P. fluctus*, but it may require about the same length of time for completion of its life cycle.

The northern fur seal harbors stage 1 and 2 nymphs of *A. callorhini* and adults of *P. fluctus* when they land on St. Paul Island in June and July. The newborn pups are heavily infested with stage 2 nymphs of *A. callorhini* and adults of *P. fluctus* within 6 hours after parturition. If the life cycle is continuous, the lice should have 4 full generations on land based on an estimate of 18 days per life cycle. Assuming the same rate of development for both species of lice, *A. callorhini* is expected to have adults and 1st stage nymphs, and *P. fluctus* adults and stage 3 nymphs in October. The present data confirm this expectation. On the silver pup collected in October, *P. fluctus* was represented mainly by adults and stage 3 nymphs, and *A. callorhini* consisted of stage 1 nymphs and adults. In other words, *P. fluctus* on seals leaving the breeding island was still in the process of completing the last land generation and *A. callorhini* had already started a new pelagic generation in late October and early November.

P. fluctus was represented mostly by stage 2 nymphs in March, April, and May, and *A. callorhini* consisted exclusively of stage 1 nymphs in pelagic samples taken in the spring. No adult lice were found on 11 pelagic adult seals examined. As shown in land generation samples usually contain 2 or 3 instars of the sucking lice. Thus pelagic samples should include different nymphal instars and adults, if their life cycle is continuous on the host while at sea. The present pelagic data strongly suggest that *P. fluctus* and *A. callorhini* go through a single generation on the northern fur seal at sea. In *P. fluctus* the egg and stage 1 nymphs may require a longer period of time for development, and the stage 2 nymphs become the dominant form on the host in March, April, and May. On the other hand, development of stage 1 nymphs of *A. callorhini* may be delayed until the next spring when seals are returning to the breeding island.

At the present time it is not certain which factors influence the delayed or slow development of the sucking lice on fur seals at sea. Some possibilities which might be examined experimentally are circadian rhythm and changes in the hormonal and physiological activities of the seal.

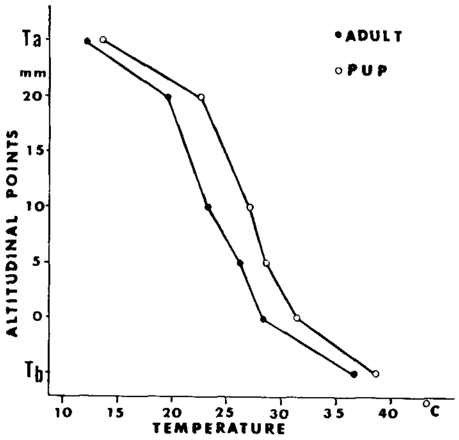

Figure 348. Mean temperature of the pelage at 4 altitudinal points on and above the body surface of the northern fur seal. Ta = air temperature, Tb = rectal temperature.

Transmission of the sucking lice

The terrestrial phase of the fur seal's life history provides an ideal ecological setting for sucking lice. The major path of transmission of lice is from the nursing cow to the new-born pup on the rookery. In the cage experiments new-born pups were heavily infested with sucking lice within 6 hours. Effort was made to determine the factors influencing the mass movement of lice to the new-born pups from nursing cows.

Differences in temperatures and pelage structure between pup and adult are the most striking of many possible factors influencing the movement of lice. The mean temperature of the skin surface on the belly was 34·3° C for the newborn pup and 28·4° C for the nursing cow. Furthermore, on the newborn pup the underhairs of the coat are thinly distributed, but the underfur of the adult coat is dense and water repellent.

The human louse *Pediculus humanus* prefers a temperature of 29–30° between the clothes and the skin, and shows acute response to a temperature difference of 2–3 degrees (Wigglesworth, 1941). The louse moves in a more or less straight line at 30° C, but turns at random to right and left if it comes to a place with a slightly higher or lower temperature. Upon entering a zone of adverse stimulation an increase in random turning movements results in an immediate return to the favorable zone if the response is strong and immediate. Wigglesworth (1941) found no evidence that the human body louse was "attracted" by a favorable stimulus.

The rapid infestation of the newborn pup by sucking lice is considered as a mass movement in response to a "favorable" factor. Although the human body louse is not attracted by a stimulus, the mechanism of orientation in *P. fluctus* and *A. callorhini* would have to be initiated by a strong and immediate stimulus or stimuli in order to result in a mass movement from the cow to the pup. The topographic distribution of sucking lice on adult seals may make a rapid movement from the cow to the newborn pup possible in response to the higher body temperature and thin pelage at the time of parturition.

Microhabitat and morphological adaption

Species of *Antarctophthirus* are usually found on the naked skin of the host, such as hind flippers, tails, eyelids, and hip. *A. ogmorhini* is found on the hind flippers, and *A. callorhini* inhabits the naked parts of the body surface on the pup and the thinly haired parts of the skin on the northern fur seal adult. It is well documented that on the hind flippers, ankles, hip and tail, the skin temperature fluctuates with thermoregulatory requirements of the seal. On the fur seal pup the skin temperature on the naked areas also fluctuates with changes in ambient temperature and thermoregulatory activity. On the other hand, *Proechinophthirus fluctus* is found on the pelage proper of the northern fur seal. On the basis of the available data *Proechinophthirus* is endemic to fur seals (Arctocephalinae) with thick underfur layer.

The mean temperature of the skin surface on the naked parts of black pup was 33·6° C, and of the pelage was 31·6° C at an air temperature of 20°C and a rectal temperature of 39·7° C. The skin surface temperature of the adult seal was 33·4° C in air 22° C, and 25·6° C in water at 11° C. Temperatures of naked parts such as nose and eyelids, fluctuate considerably as the air and rectal temperatures drop, but the skin surface temperature under the pelage generally remains constant in similar conditions.

A definite morphological correlation has been found for the microhabitats of *A. callorhini* and *P. fluctus*. *A. callorhini* have dense scales on the abdomen in addition to normal setae (Fig. 344). The spiracular atrium of *A. callorhini* consists of a large triangular plate, a large chitinous apodeme, and a tubular part which has a peculiar sclerotized collar (Fig. 343 a). Furthermore, in *A. callorhini* claws of the middle and hind tarsi are pointed and relatively short (Fig. 342 a). Abdominal scales and a specialized spiracular atrium seem to be correlated with the microhabitat of *Antarchtophtirus*. Acuminate claws of the thoracic legs support the behavior and movement of *A. callorhini* on the naked skin. *A. callorhini* digs in and holds on the naked skin with pointed claws.

Proechinophthirus has long, thin setae on the abdomen, lacking scales completely (Fig. 344 a, c, d). The spiracular atrium of *P. fluctus* consists of a smaller triangular plate, a small chitinous apodeme, and a simple, subapically bulbous tube (Fig. 343 b). Nymphs of *P. fluctus* lack the abdominal scales and have few rows of short setae on the abdomen. They also bear large, heavily sclerotized spines and pegs on the head, the basal antennae segment and each of the thoracic segments (Fig. 344 b, c). Furthermore, *P. fluctus* has blunt and long claws on the middle and hind legs which are suited for grasping hairs (Fig. 342 b). *P. fluctus* finds difficulty in walking on the naked skin with the blunt claws of the middle and hind legs, but moves very rapidly in the fur once more hairs are grasped with the tarsal claws. Once attached to the hairs *P. fluctus* is quite difficult to remove. The lack of the abdominal scales in *P. fluctus* is directly correlated with its microhabitat requirement, as the abdominal scales of *Antarctophthirus* are related to marine habitat.

Various morphological traits found in the Echinophthiriidae are unique to the pinniped-infesting lice. The comparative morphology suggests that the sucking lice on pinnipeds must have developed these morphological traits in response to the marine habitat of the host animal. Furthermore, the echinophthiriids appear to have evolved with pinnipeds since primitive pinnipeds ventured into marine life.

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