

Diving Lice: The Exception to the Rule That There Are No Insects in the (Deep) Ocean [†]

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Abstract: Insects are present in virtually all possible habitats on the mainland but virtually absent in the ocean which constitutes 90% of the biosphere. Only a few species are present in the sea, but remaining at the surface, salt marshes, estuaries, or shallow waters. Remarkably, a group of species manages to endure long immersion periods in the open sea, as well as deep dives, i.e. seal lice. We discuss here some of the adaptations that allow seal lice to cope with the amphibious habits of their hosts and how they can help understanding why are insect so rare in the ocean.

Keywords: Adaptation to extreme environments; Anoplura; Echinophthiriidae; marine insects

1. Insects and the sea

Insects are the most ecologically and evolutionary successful organisms on Earth in terms of biomass and biodiversity [1]. They have virtually conquered any possible environment on our planet with a notable exception: the oceans [2]. Usually, in the literature, only a few species of *Halobates* (Heteroptera: Gerridae) are mentioned as truly marine insects living in open ocean [3]. However, these sea-skaters remain on the water surface and, therefore, are not actually exposed to high salinity, low temperature, the absence of atmospheric oxygen, and high hydrostatic pressure underwater. This absence of insects in the ocean (*i.e.*, 90% of the biosphere) and their infrequent presence in marine habitats contrast with their profuse occurrence on the mainland, giving origin to varied scientific hypotheses and speculation [4]. In this sense, Maddrell [5] argued that the absence of insects can be explained because they would be poor competitors against crustaceans since they could not survive beyond the first few meters of the water column because their tracheal system would not be able to support the increase in the hydrostatic pressure [5]. Yet, there exists a particular group of insects that manages to survive underwater at great depths and during extended immersion periods, e.g. seal lice.

2. The lice of the pinnipeds, living an amphibious life

Lice (Order Phthiraptera) are the only insects that have become obligate and permanent parasites throughout their entire life, living as ectoparasites in the feathers, fur, or hairs of their hosts [6, 7]. Sucking lice (suborder Anoplura) are a group of hematophagous insects from mammals, being present in all the mammalian genus, except the Monotremata, Cetacea, Sirenia, Pholidota, Edentata, and Proboscidea. Among the great diversity of Anopluran lice, the family Echinophthiriidae is unique in that they infest

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amphibious hosts, such as pinnipeds (walruses, seals, and sea lions) and the Northern river otter [8, 9].

Pinnipeds are diving mammals, and most sea lions and fur seals usually dive to feed [10]. The most extraordinary diver is the southern elephant seal which can reach 2000 m deep [11]. During the periods of feeding, pinnipeds can spend several months of the year on the open sea [12]. Therefore, during the evolutionary time, echinophthiriids managed to adapt to the amphibian biology of their hosts [13]. The survival of an originally terrestrial louse in the deep of the ocean implies necessarily that this insect managed to tolerate the particular conditions of this environment, as the high hydrostatic pressure, the low temperature, and the high salt concentration.

The adaptation of echinophthiriids to live in association with diving hosts started to be investigated only recently. This mini-review provides a reflexive glance on the state of knowledge about the adaptations of echinophthiriids, along with biological hypotheses and research ways deserving to be explored.

3. Tolerance to immersion

Undoubtedly, one of the greatest limitations for echinophthiriids is the fact that eggs do not survive underwater [14, 15]. Accordingly, lice reproduction could only occur during the periods that the hosts remain on land enough time to guarantee egg development, i.e. during host reproduction or molting seasons. For the life history of echinophthiriids, this implies that the number of lice generations per year should be constrained by the haul-out behavior of their hosts. For instance, for *Antarctophthirus microchir* from South American sea lions, the reproductive season is the only moment of the life cycle when the host spends enough time ashore and only newborn pups remain outside the water Figure 1 [15, 16]. While for *A. lobodontis* from the crabeater seal, the reproduction and transmission would be only possible on juveniles [17]. Therefore, the phenology of seal lice is adapted to the biology and ecology of their hosts [18].

To evaluate the tolerance of the nymphal and imaginal stages, we performed a series of experiments depicted in Figure 1, i.e. testing lice survival under different protocols of submersion and temperature [15]. We found that the first nymphs (N1) are unable to survive submerged but the following instars and adults tolerate it for several days [15]. Previous contributions by Murray and Nicholls [21], reported the death of eggs, but the survival of advanced nymphs and adults; however, N1 were not included in the experiment. Our results demonstrated that N1 survived submersion only for a couple of days. The reduced tolerance to immersions of N1 as compared to more advanced instars has been also alleged by Aznar et al. [15], based on the reduction of N1 in the South American sea lion pups population when they started to swim. Murray and co-workers arrived at a similar conclusion [14, 21], as well as by Kim [22] from the absence of N1 in old pups and adult pinnipeds on northern fur seals. The incapacity of N1 to survive underwater was suggested to be associated with the absence of abdominal scales [16, 22, 23], which are present over the body of the other instars.

The presence of specialized and modified spines, known as scales, is a diagnostic feature of echinophthiriids [24]. Scales are absent in the first nymphal stage [22, 23] and increase in density and size during their development [20, 23, 25, 26]. Several authors have suggested that scales are related to underwater survival [16, 18, 22]. The specific role of scales has been discussed by some authors, suggesting that scales could have two main functions. Whereas Murray [20] postulated that scales protect the cuticle from mechanical damage and against desiccation, Hinton [27] proposed that scales could potentially act as a plastron retaining air and allowing respiration underwater. Unfortunately, no critical observational or experimental evidence has been yet obtained, supporting or opposing either hypothesis.

When seal lice became in contact with seawater, they confront a decrease in oxygen concentration and temperature and an increase in the hydrostatic pressure. We observed that as soon as *Antarctophthirus microchir* makes contact with the seawater adopted a state

of quiescence, while for *Lepidophthirus macrorhini* this takes several minutes Video S1 [15, 19]. It seems that the tolerance to immersion depends on a reflex reduction in metabolism and activity triggered by contact with seawater. This behavior could decrease the need for nutrients and oxygen, allowing survival for several days underwater. However, their differential survival when submerged in normoxic or in hypoxic water strongly suggests that echinophthiriids would be able to exchange gases with the surrounding water [15], a capacity never observed previously in the group. Further anatomical and physiological research should shed light on the adaptations and mechanisms of aquatic respiration.

4. Tolerance to hydrostatic pressure

In another series of experiments depicted in Figure 1, we also found that lice from elephant seals can tolerate hydrostatic pressures equivalent to 2000 m depth [19], which represents a depth equivalent to seven times the Eiffel Tower under the sea. Moreover, before the experiment, a louse was accidentally exposed to 450 kg cm⁻² for a couple of minutes, and it survived. This represents 30% more hydrostatic pressure than the supported by the deepest marine mammal, *i.e.* the Cuvier's beaked whale [28] for which a maximum diving depth of 3000 m was reported. These experiments showed that seal lice exhibit an extraordinary tolerance to hydrostatic pressure (*i.e.*, piezotolerance or barotolerance), including rapid dives and climbs to the surface of their hosts [19]. Another important feature is that seal lice can tolerate the hydrostatic pressure by themselves, in the sense that they do not need to be associated with the host to do so. Therefore, we can assume this ability is an intrinsic feature of echinophthiriids [19] and that insects are intrinsically capable of tolerating these conditions.

Furthermore, taking up the idea of Maddrell that postulated that there is a structural limitation of the tracheal system to tolerate the pressure [5], we can assume that only air-filled parts of the body are affected by high pressures. In this sense, it is expected that only the tracheal and the digestive systems collapse during diving. Therefore, we can expect that the louse expels all the air from the tracheal system to tolerate this collapse. If, as we mentioned before, lice survive the long trips at sea maintaining a basal metabolism, the unresolved question is how they can survive without atmospheric oxygen. In this sense, some adaptations present in many other insects could be associated, one is the ability to obtain oxygen from the water (through tegumentary diffusion or a plastron) and another is the storage of oxygen associated to respiratory pigments. Even though infrequent in insects, these pigments have been found in species living in environments where oxygen is scarce or its availability erratic [29, 30].

5. Conclusions and future research

Beyond any doubt, seal lice are quite unique insects. Their long evolutionary history in association with amphibious hosts, combined with obligatory ectoparasitic nature along with their whole hemimetabolous life, have exposed them to selective pressures that no other insect experiences. The understanding of the specific morphological, physiological, and behavioral adaptations making it possible to tolerate the extreme conditions that they endure during their ectoparasitic life has just begun. A major piece of information recently acquired is particularly revealing: they do not die during the long excursions in the open sea of their deep-diving hosts. As trivial as this assertion could appear, it puts aside the conservative idea that lice would die in the sea and those remaining in the mainland would somehow survive and wait for the return hosts ashore the next reproductive season. Their capacity to survive in extreme environments being adequately confirmed, we can now focus on the next scientific challenge, *i.e.*, explaining how. The previous sections present some hypotheses to be tested and research leads to follow, which should help to complete the puzzle.

Beyond their own biology, seal lice push us to abandon the vision that "*insects are not made to survive in the ocean*", based on arguments related to their body plan, as their

respiratory system or non-transparency. Our present knowledge does not reveal unique or extraordinary structural or physiological adaptations in seal lice explaining their extraordinary endurance. On the contrary, simply the adequate combination of characteristics present in many other insects could justify their performances, at least hypothetically.

So, if insects are able to live in the oceans, a legitimate question is why are there virtually absent? The study of seal lice has begun to shed some light on this major question in entomology and we hope that they will continue to do it in the close future, despite the constraints imposed on scientists by their particular biology.

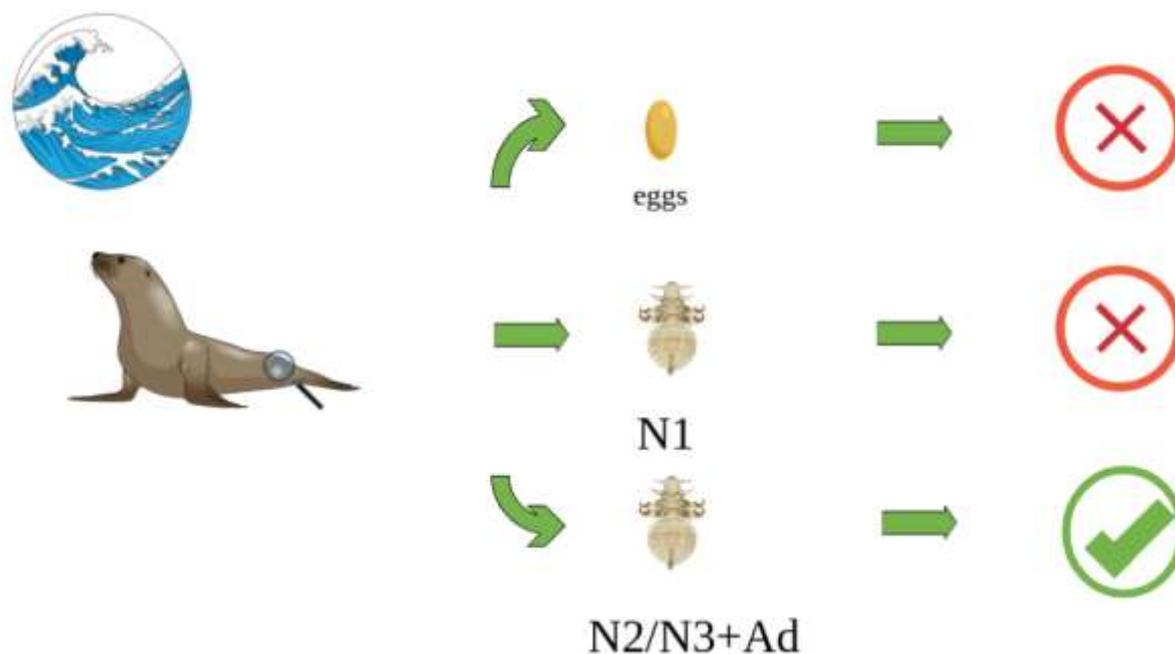


Figure 1. Differential tolerance to immersion in seawater of seal lice. Only advanced nymphs and adults survive, but not eggs or early nymphs.

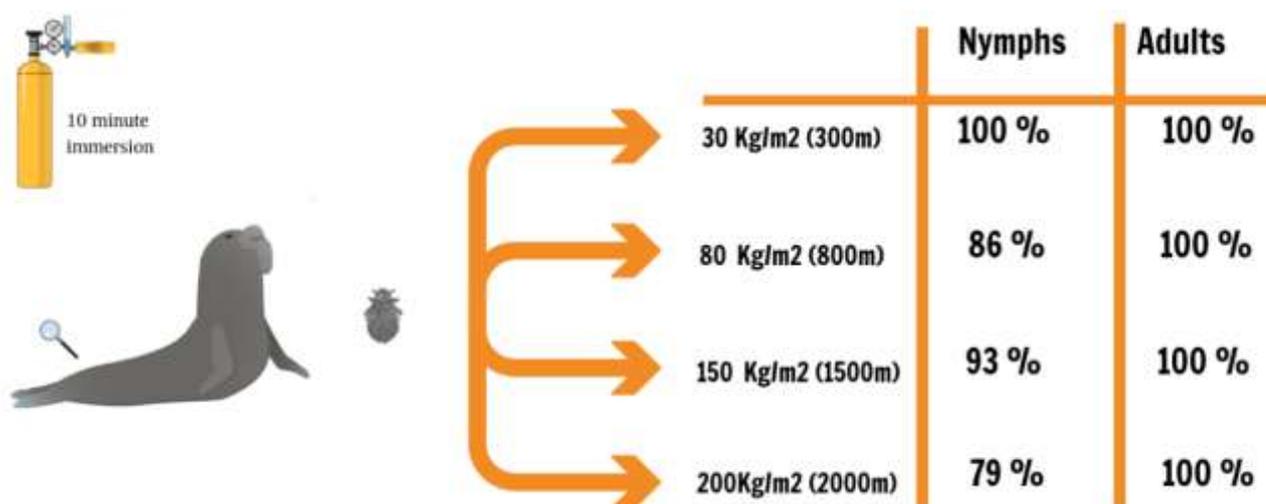


Figure 2. Tolerance to high hydrostatic pressure in seal lice, tested in a hyperbaric chamber, simulating different diving depths.

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