

RESEARCH ARTICLE

Under pressure: the extraordinary survival of seal lice in the deep sea

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ABSTRACT

Lice from pinnipeds – sea lions, seals and walruses – are the only insects capable of surviving marine dives. Throughout their evolutionary history, they have adapted to tolerate hypoxia, high salinity, low temperature and, in particular, to tolerate conditions of high hydrostatic pressure. To understand the limits of the capacity of lice to survive during host deep dives, we conducted a series of controlled experiments in the laboratory. We collected lice from elephant seals and submitted the different life stages to high pressure conditions. Lice were first exposed to one of four hydrostatic pressures: 30, 80, 150 or 200 kg cm⁻². They were then exposed a second time to higher or lower hydrostatic pressure conditions to test for the impact of the first experience, which could either be deleterious or trigger physiological adaptation, allowing them a better tolerance to high pressure. We found that lice from elephant seals can tolerate hydrostatic pressures higher than 200 kg cm⁻² (close to 200 atm), which is equivalent to 2000 m depth. Adults exhibited lower recovery times than nymphs after immersion at high hydrostatic pressure. Our findings show that lice have developed unique adaptations to endure extreme marine conditions. We discuss these extreme performances in relation to the morphological characteristics and physiological responses to diving in these insects.

KEY WORDS: Marine insects, Diving adaptations, Extreme environments

INTRODUCTION

Despite their impressive success in colonizing land, insects are almost absent in the marine environment (see Cheng, 1976). Only five species of *Holobates* (Heteroptera: Gerridae) are considered truly marine insects (Spence and Andersen, 1994). However, these species remain on the water surface and, therefore, are not truly exposed to marine conditions, i.e. high salinity, low temperature, no gaseous oxygen and high hydrostatic pressure. The only insects known to be capable of surviving under these conditions are lice of pinnipeds, which spend a long time in the open sea performing deep dives with their hosts.

The family Echinophthiriidae (Phthiraptera: Anoplura) includes those unique species infesting amphibious hosts, such as pinnipeds (walruses, seals, and sea lions) and river otters (Durden and Musser, 1994; Leonardi and Palma, 2013). Pinnipeds are diving mammals, and most sea lions and fur seals usually dive to ~100 m, whereas true seals have maximum dive depths beyond 1000 m (Stewart, 2009; McIntyre et al., 2010) and can have much of their bodies submerged for several months of the year (Teilmann et al., 1999). The most extraordinary diving seal is the southern elephant seal *Mirounga leonina*, which dives as deep as 2000 m (McIntyre et al., 2010).

The adaptation of echinophthiriids to live in association with diving hosts started to be investigated only recently. In a study under controlled laboratory conditions, it has been shown that lice recover after several days drowned in seawater; their survival being dependent on the amount of dissolved oxygen, suggesting the existence of a mechanism to recover or to spare oxygen (Leonardi and Lazzari, 2014). However, many open questions remain as to how lice cope with the challenges of the marine realm.

One of the main unresolved questions is whether or not lice actually survive during the diving excursions of their hosts. The only evidence available suggesting that they do, comes from the finding in Antarctica of lice-infested adult seals. Given that infestation usually takes place as pups, lice on those adult seals have probably been living on their hosts for several months or years (Leonardi et al., 2018). Although suggestive, this is not definitive evidence that lice were already present when seals came ashore. At present, there is no clear evidence that echinophthiriid lice could survive under high hydrostatic pressure, like those experienced during host dives. In addition, available knowledge does not allow us to completely exclude the possibility that lice could die in the sea with seals getting re-infested from other individuals upon their return to shore. The objective of this study was to shed light on the capacity of echinophthiriid lice to survive under high hydrostatic pressures. Additionally, we evaluated whether adults and nymphs perform similarly when exposed to increasing hydrostatic pressure.

MATERIALS AND METHODS

Lice samples

Lepidophthirus macrorhini Enderlein 1904 (Fig. 1A) associated with southern elephant seals *M. leonina* (Fig. 1B) were used for this study, since it is the echinophthiriid species that should be theoretically exposed to the highest hydrostatic pressure. The samples were taken in the Natural Reserve of Península Valdés (42° 45'S, 63°38'W), Chubut Province, Argentina, during the seal reproductive season of 2019. We collected lice from 15 weaned southern elephant seal pups (prevalence 94%) which were captured and handled manually. Lice were collected from the hind flippers with tweezers and taken from the field to the laboratory immersed in seawater where they were maintained in aquaria at 13±1°C with

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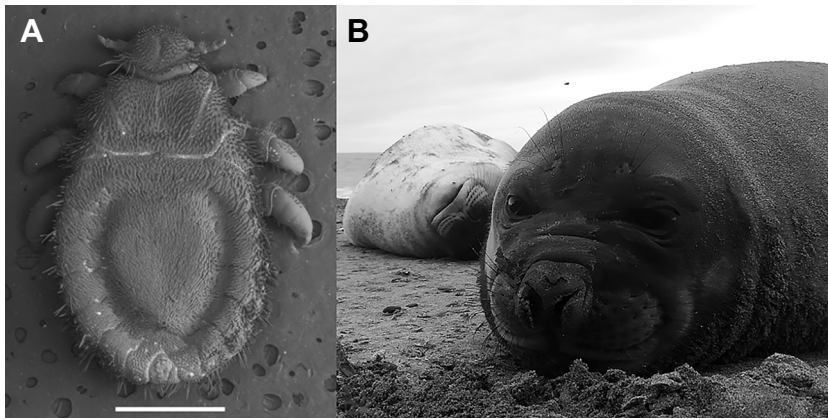


Fig. 1. *Lepidophthirus macrorhini* lice infest elephant seals. (A) Scanning microscope image of an adult female *L. macrorhini*. Scale bar: 1 mm. (B) This louse is a parasite of the elephant seal *Mirounga leonina*.

UV-sterilized and aerated seawater, until used in the experiments. The only way to keep these insects alive when removed from hosts is underwater, otherwise, they desiccate and die quickly. Apparently, they can cope with hypoxia by reducing their metabolism (Leonardi and Lazzari, 2014), but they cannot handle water loss through the cuticle when exposed to air.

All necessary permits for the described field studies were obtained from Subsecretaría de Turismo y Áreas Protegidas and Dirección de Fauna y Flora Silvestre (Chubut Province, Argentina). Seal pups were manually restrained in order to avoid the use of anaesthesia.

High pressure experiment

To determine the ability of *L. macrorhini* to tolerate high hydrostatic pressure in seawater, we set up the experimental device depicted in Fig. 2. The bronze chamber was filled with seawater and lice (Table 1) placed inside, and the chamber was then connected to a scuba diving system.

Immersion and recovery

In order to verify the viability of lice, they were exposed to air at room temperature ($\sim 25^{\circ}\text{C}$) until they presented some movement. Individuals that showed leg and/or antennae movement were used in the experiments.

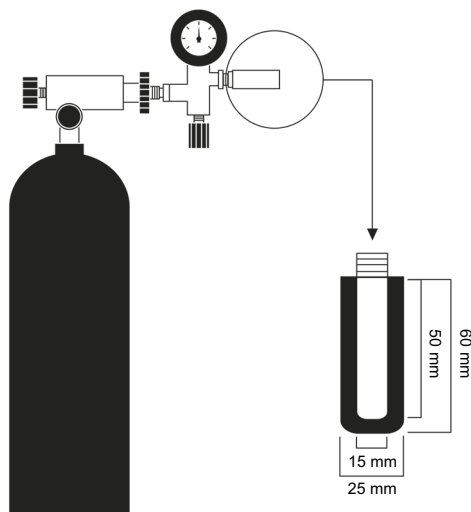


Fig. 2. Hydrostatic pressure apparatus. Lice were placed in a bronze pressure chamber, connected to a diver tank with its corresponding manometer.

To test if lice were capable of surviving and to study the recovery time to increasing diving pressures, adults and nymphs were first exposed to one of four hydrostatic pressures: (a) 30, (b) 80, (c) 150 and (d) 200 kg cm^{-2} ; it took around 2 min to reach each pressure and the same amount of time to depressurize. Every hydrostatic pressure was selected following McIntyre et al. (2010) and represent diving depths related to host diving behaviour to depths of 300, 800, 1500 and 2000 m under sea surface, respectively. The units used for indicating hydrostatic pressures, i.e. kg cm^{-2} , are the most frequently used and its equivalence to depth quite intuitive, given that pressure increases with depth at a rate of 1 kg cm^{-2} every 10 m. It is worth mentioning that kg cm^{-2} and atmospheres (atm) are not identical, but very close to each other when referring to saltwater.

Lice were exposed for 10 min to a particular hydrostatic pressure inside the chamber. After that, they were exposed to air at room temperature on a filter paper and motility assessed under a stereomicroscope at different times, i.e. 1, 5, 10, 15, 30, 45, 60, 90 and 120 min after exposure. Lice were categorized as mobile (and hence alive) if they walked and/or moved the antennae or immobile if no movement was observed. If a louse showed no sign of recovery after 120 min, it was considered dead.

Following the first exposure to hydrostatic pressure and 40 min recovery, individuals were re-exposed to different hydrostatic pressure conditions in order to test if their tolerance had changed. The rationale behind this second test was that the first experience could have had a physiological impact, inducing either an adaptive response to increase survival or, on the contrary, an injury that reduced the ability to tolerate a second exposition. In either of these cases, the recovery time and survival probability would change.

Lice were grouped as exposed during the first test either to the lower pressures (treatments a or b) or to higher pressures (treatments c or d). Half of the lice in each group were then re-exposed to the lowest pressure and the other half to the highest pressure. So, four new groups were established (Table 1), which were exposed to the

Table 1. Proportion of *Lepidophthirus macrorhini* surviving different hydrostatic pressures, equivalent to 300–2000 m depth

Pressure	Stage	N	Survival
30 kg cm^{-2}	Adult	5	100%
	Nymph	11	100%
80 kg cm^{-2}	Adult	5	100%
	Nymph	14	86%
150 kg cm^{-2}	Adult	6	100%
	Nymph	14	93%
200 kg cm^{-2}	Adult	6	100%
	Nymph	14	79%

Table 2. Results of the log-link model for recovery times for *L. macrorhini* adults and nymphs exposed to increasing hydrostatic pressures

	d.f.	Deviance	Residual d.f.	Residual deviance	P
Pressure	3	63.12	83	147.55	<0.001
Stage	1	10.04	82	137.51	0.0075
Pressure×stage	3	30.52	79	106.99	<0.001

following pressures: (a+b; 5 adults + 10 nymphs) at 30 kg cm⁻² (Low–Low); (a+b; 5 adults + 7 nymphs) at 200 kg cm⁻² (Low–High); (c+d; 6 adults + 11 nymphs) at 30 kg cm⁻² (High–Low); and (c+d; 6 adults + 11 nymphs) at 200 kg cm⁻² (High–High). It was ensured that both nymphs and adults were represented in all pressure combinations. In re-exposure experiments, survival and recovery time were evaluated after 10 min of immersion.

Data analysis

We analyzed survival of lice over an 8-sample test for equality of proportions without continuity correction given the small number of insects that were available (75 for the 8 treatments, Table 1). Recovery times were analysed through generalized linear models. To analyse recovery time after exposure to increasing hydrostatic pressures, we generated a model with a Gamma distribution and an identity link function. For this model, the hydrostatic pressure (factor with the four pressure levels), life stage (factor with two levels: nymph or adult) and their interactions were included as predictors.

For analysing the recovery time after re-exposure to different combinations of hydrostatic pressures, we generated a model with a Gamma distribution and a log-link function. For this model, the initial hydrostatic pressure (factor with four levels), the final hydrostatic pressure (factor with two levels: 30 kg cm⁻² or 200 kg cm⁻²), life stage (factor with two levels: nymph or adult) and their interactions were included as predictors.

Whenever interaction was found, Tukey *a posteriori* contrasts were performed with the R software package emmeans (<https://CRAN.R-project.org/package=emmeans>). In order to compare treatments, we calculated confidence intervals for the mean

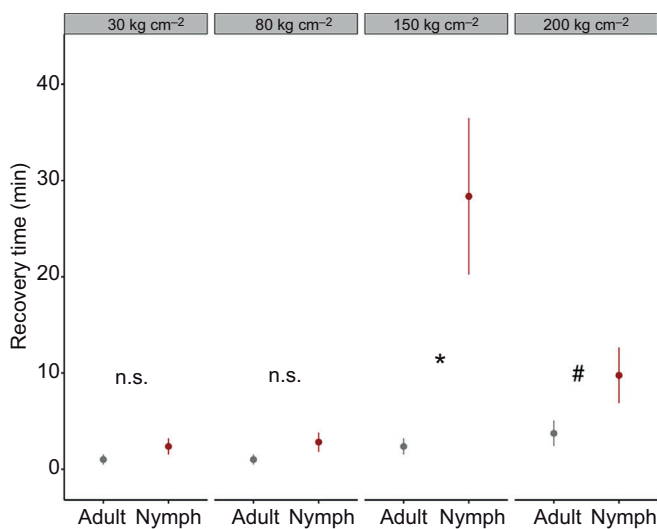


Fig. 3. Recovery times for *L. macrorhini* adults and nymphs after exposure to different hydrostatic pressures for 10 min. Data are means ± s.e.m. of $N=5, 11, 5, 14, 6, 14, 6, 14$, respectively. n.s., non-significant difference; * $P<0.05$ and # $0.05<P<0.1$, two-tail probability.

Table 3. Tukey contrasts for recovery times between *L. macrorhini* adults versus nymphs

Pressure	Estimate	s.e.	Lower CI	Upper CI	P
30 kg cm ⁻²	-1.36	0.996	-3.316	0.589	0.17
80 kg cm ⁻²	-1.82	1.137	-4.047	0.410	0.11
150 kg cm ⁻²	-25.99	8.186	-42.034	-9.944	<0.005
200 kg cm ⁻²	-6.02	3.178	-12.252	0.207	<0.06

differences between treatments. For the model with a log-link function whenever 1 is included in the range of confidence intervals, no significant difference occurs. For the model with an identity link function if 0 is included in the range of confidence intervals, no significant difference occurs.

All the statistical analyses were performed using R v.3.6.1 (<https://www.r-project.org/>) and the MASS packages for the analyses (Venables and Ripley, 2002). Graphs were made using the software package ggplot2 (Wickham, 2009).

For recovery times after a second exposition, our null hypothesis (H_0) predicted no difference from first immersion, whereas the alternative hypothesis (H_a) anticipated change, but without stipulating about shorter or longer recovery times. As a consequence, statistical significance was considered in a parsimonious way, as two-tail probabilities.

RESULTS

We found that most lice, 69 out of 75, survived exposure to pressures reaching up to 200 kg cm⁻², equivalent to 2000 m depth. No difference was found in the proportion of lice, nymphs or adults, surviving the different hydrostatic pressures ($\chi^2=7.07$, d.f.=7, $P=0.42$, Table 1). We found differences between adults and nymphs in the recovery time after exposure to increasing hydrostatic pressures (Fig. 3 and Table 2). For the lowest pressures (i.e. 30 kg cm⁻² and 80 kg cm⁻²), recovery times were similar between adults and nymphs (Table 3). For the higher

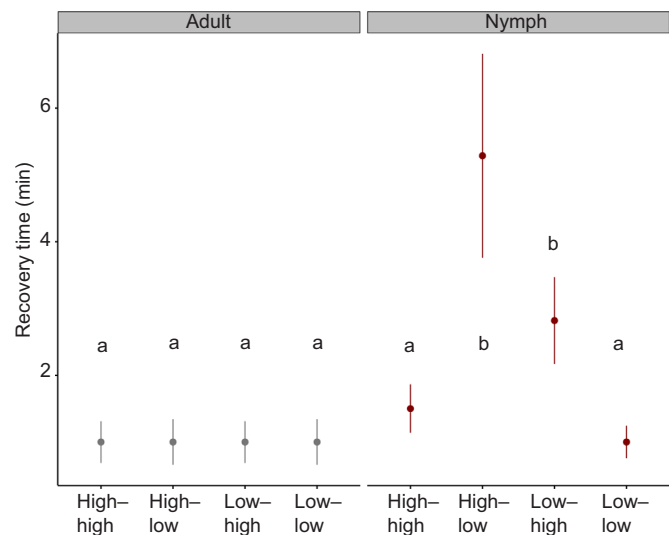


Fig. 4. Recovery time after re-exposure to different hydrostatic pressures for *L. macrorhini* adults and nymphs. Exposure pressures are indicated on the abscissa as first exposure–final exposure (e.g. the group High–Low indicates a first exposure to high pressure and a final exposure to low pressure). Data are means ± s.e.m. of $N=5, 10, 5, 7, 6, 11, 6, 10$, respectively. Same letter indicates no significant statistical difference. The comparison between recovery times of nymphs submitted to a High–High and Low–Low treatment are not significant, but a noticeable difference was observed; two tail $0.05<P<0.1$.

Table 4. Results of the log-link model for recovery times for adults and nymphs of *L. macrorhini* re-exposed to different hydrostatic pressures

	d.f.	Deviance	Residual d.f.	Residual deviance	P
Initial pressure	1	0.501	58	45.727	0.35
Final pressure	1	1.148	57	44.579	0.16
Stage	1	9.675	56	34.904	<0.01
Initial pressure× final pressure	1	7.554	55	27.351	<0.01
Initial pressure× stage	1	0.003	54	27.348	0.95
Final pressure× stage	1	0.516	53	26.832	0.35
Initial pressure× final pressure× stage	1	4.461	52	22.371	<0.01

pressures, we found that nymphs had higher recovery times than adults (Fig. 3 and Table 3).

Finally, when we analyzed the recovery times after re-exposure to different hydrostatic pressures, again we found differences between adults and nymphs (Fig. 4 and Table 4). In the case of adults, recovery times were always short and similar regardless of the treatment (Fig. 3, Table 5). Conversely, we found that if nymphs were exposed or re-exposed to high pressures, recovery times increased compared with those of the low-pressure group (Table 5).

DISCUSSION

The present study revealed that an air-breathing insect survives to immersion at hydrostatic pressures of at least 200 kg cm⁻², a depth equivalent to seven times the Eiffel Tower under the sea surface. Accidentally, during the calibration of the equipment, an adult louse was submitted to 450 kg cm⁻² for several minutes, and surprisingly enough it survived, suggesting that they might tolerate much higher pressures. The equivalent sea depth to this pressure exceeds by 1500 m the deepest record for a marine mammal, the Cuvier's beaked whale (Schorr et al., 2014). Additionally, our experiments showed that adults tolerate increments in hydrostatic pressure better than nymphs. Given the rapid pressure changes in our experiments, we can also conclude that, not only do seal lice exhibit an extraordinary piezotolerance (also called barotolerance), but in addition they tolerate rapid changes in hydrostatic pressure, corresponding to a rapid descent to depths and return to the surface of a diving host (Sala et al., 2011). Apparently, no gradual physiological adaptation is required to endure rapid pressure increases and decreases.

However, our experiments showed that seal lice tolerate the hydrostatic pressure by themselves, meaning that they do not need to be associated with the host to do so. It is worth mentioning that Murray and Nicholls (1965) described that *L. macrorhini* burrows in the first epidermal layer to feed. Consequently, lice remain protected under the skin of the host during periods ashore. As was postulated by those authors, this behaviour would be related to survival during moulting, but it does not seem to be relevant for pressure tolerance. Because lice were placed in the experimental chamber without any other element, we can assume that the ability to tolerate the hydrostatic pressure is an intrinsic feature of these insects.

Some previous studies showed that echinophthiriid lice can survive underwater for several days (Murray and Nicholls, 1965; Murray et al., 1965; Leonardi and Lazzari, 2014). These authors also reported a differential survival between life stages, adults being more tolerant than nymphs. Although these works were conducted at sea level, i.e. at atmospheric pressure, we found a similar pattern when adults and nymphs were exposed to different hydrostatic pressures. In our experiments, we found a differential response between adults and nymphs. When exposed to low hydrostatic pressure, the recovery time was similar between stages. However, when the pressure increased, nymphs required more time to recover

their movement. One of the main differences between imaginal and nymphal stages in echinophthiriid lice is the presence and abundance of scales (Leonardi et al., 2012), which can be appreciated in the female depicted in Fig. 1A. The presence of scales covering the thorax and abdomen is one of the main characteristics of echinophthiriid lice. Scales, which are modified spines, are absent in the first nymphal stage and start to develop in nymph 2 (Kim, 1975; Leonardi et al., 2012). It has been previously suggested that the presence and development of scales could be involved in underwater survival (Kim, 1975; Aznar et al., 2009; Leonardi et al., 2013).

Murray (1976) proposed that scales could provide mechanical protection. In this sense, Mehlhorn et al. (2002) showed that the dorsal cuticle of *Antarctophthirus carlinii*, lice parasitizing Weddell seals, is thicker than on the ventral side. These authors suggested that this feature is an adaptation to survive in extremely cold temperatures. However, the thicker cuticle covered by scales could reinforce the mechanical protection at high hydrostatic pressure. Therefore, if scales are involved in mechanical protection, a reduced number of them would be reflected in a higher susceptibility to hydrostatic pressure, as we have seen for *L. macrorhini* nymphs.

Mechanical protection provided by scales could explain in part, the differential response we have found in our experiments between nymphs and adults. However, there are other hypotheses meriting exploration. Indeed, given that internal tissues are mostly composed of water and are incompressible, it could be that only air-filled parts of the louse body are affected by high pressures. In this sense, one may expect that the digestive tract and the tracheal system would collapse during diving, but the rest of the organs should remain unaffected. Previous experiments by Leonardi and Lazzari (2014) revealed that when seal lice contacted water, they enter a state of akinesis (i.e. reflex immobility) and, in this condition, insects tolerated immersions lasting for several days. In the species studied here, lice kept moving underwater for a couple of minutes, but eventually, they became immobile. We can speculate that this response would be associated with a rapid reduction in metabolism

Table 5. Recovery times following re-exposure to different hydrostatic pressures between *L. macrorhini* adults and nymphs

Stage	Initial pressure	Final pressure	Mean recovery time (min)	s.e.	Lower CI	Upper CI
Adult	High	High	1.00	0.31	0.54	1.84
	High	Low	1.00	0.31	0.54	1.84
	Low	High	1.00	0.34	0.51	1.96
	Low	Low	1.00	0.34	0.51	1.96
Nymph	High	High	1.50	0.36	0.93	2.41
	High	Low	5.29	1.53	3.00	9.32
	Low	High	2.82	0.65	1.79	4.43
	Low	Low	1.00	0.24	0.62	1.61

and this may help lice to survive high pressures. If the most important effect of diving is hypoxia and the collapse of the tracheal system, reducing metabolism to a minimum could allow the insects to survive until the next opportunity to breathe air and feed. If, in addition, they are able to recover oxygen from the water, as seems to be suggested by their differential response to submersion in normoxic versus hypoxic water (Leonardi and Lazzari, 2014), lice would turn into true underwater breathers and high pressure would not compromise survival during the long dives of their hosts. Hinton (1976) emphasized the possibility that scales could form a pressure-resistant respiratory plastron, recognising at the same time the difficulty in unravelling its existence. These two hypotheses, i.e. metabolic arrest and underwater breathing, can be tested experimentally, by means of metabolic measures on lice breathing air and immersed. At present, highly sensitive optic oxygen sensors are commercially available; however, collecting enough lice for experiments requires a considerable effort.

In conclusion, the study of seal lice could help to answer a major outstanding question in insect biology – why have insects been able to conquer virtually any environment, except the deep oceanic realm. Several authors have provided their point of view, speculating about different morphological and physiological characteristics of insects (Maddrell, 1998; Harrison et al., 2012); yet, we now know an exception: seal lice. Understanding how lice survive in the depth of the sea is a fascinating challenge, but it could provide key information to shed light on the reasons of this limited success of insects in marine habitats.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.S.L., J.E.C., C.R.L.; Methodology: M.S.L., J.E.C., F.A.S., R.B.V., J.C.R.; Formal analysis: J.E.C., C.R.L.; Investigation: M.S.L., F.A.S., R.B.V., J.C.R.; Data curation: J.E.C.; Writing - original draft: M.S.L., J.E.C., C.R.L.; Writing - review & editing: M.S.L., J.E.C., C.R.L.; Supervision: M.S.L., C.R.L.; Funding acquisition: M.S.L.

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Data availability

The rough data and the R script are available from Mendeley: <http://dx.doi.org/10.17632/zm4c4y4z5.1>

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