CONSEQUENCES OF A SOCKEYE SALMON SHORTAGE FOR THE BROWN BEAR IN THE BASIN OF LAKE KURILSKOE, SOUTHERN KAMCHATKA

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We studied the behavioural ecology of *Ursus arctos* (hereinafter – brown bear or bear) in the basin of Lake Kurilskoe (Kamchatka Peninsula) in the summer and autumn of 2017–2018. The aim of this study was a comparative assessment of the behaviour of brown bears with respect to the heterogeneity of trophic conditions. In 2018, considering an extremely high commercial catch of *Oncorhynchus nerka* (hereinafter – sockeye salmon or salmon) and high flood in the first half of the summer, the decline in the abundance and availability of salmon led to significant changes in the behaviour and distribution of bears. The success of fishing behaviour of bears in 2018 was found to be lower than in 2017. During the periods of salmon abundance in 2017, solitary bears formed temporary friendly associations that we did not observe in 2018. Due to the increased incidence of intraspecific predation in 2018, bears began to show aggression towards humans. Deterioration of the physical condition of some females and behavioural changes in food-procuring strategies were accompanied by the appearance of abandoned cubs. The peak of negative changes in the bear populations was noted in the first half of September when the energy requirements of bears increased. A modern approach to the development of the resources of sockeye salmon in the Basin of Lake Kurilskoe and River Ozernaya requires a serious revision of the fishing load in accordance with the characteristics of the population structure of sockeye salmon and its exclusive role in the local ecosystem. It is necessary to reconsider the «optimal» number of sockeye salmon allowed into the Lake Kurilskoe and its tributaries. The current practice of cancelling the passing days during which salmon can migrate unobstructed into and up the River Ozernaya towards Lake Kurilskoe is unacceptable.

Key words: abandoned bear cubs, cannibalism, commercial overfishing, *Oncorhynchus nerka*, South Kamchatka Sanctuary, *Ursus arctos*

Introduction

In the ecosystem of the basin of Lake Kurilskoe and River Ozernaya (Kamchatka Peninsula), *Oncorhynchus nerka* Walbaum, 1792 (hereinafter – sockeye salmon or salmon) is a keystone species, forming the basis of trophic relationships for many of its inhabitants. The spawning grounds of these schools, the largest in Asia, are under protection due to the special status of the territory, the South Kamchatka Sanctuary, classified as a UNESCO World Natural Heritage Site. The abundance and availability of sockeye salmon in the Lake Kurilskoe from mid-summer to the beginning of winter determine the well-being of *Ursus arctos* Linnaeus, 1758 (hereinafter – brown bear or bear) population and contribute to the maintenance of one of the highest population densities of this species in the world (Revenko, 1993; Gordienko et al., 2006).

In the basin of Lake Kurilskoe, the dynamics of the bear spatial distribution is tightly related to the salmon spawning run in the summer-autumn period (Zavadskaya et al., 2019). The sockeye salmon run of the basin of Lake Kurilskoe and River Ozernaya has a complex structure. It includes several genetically heterogeneous subpopulations (Varnavskaya, 1988; Pilganchuk, 2014), which spawn in spatially separated areas at various times (Selifonova, 1978). The River Ozernaya is the only water body flowing out of Lake Kurilskoe. From the Sea of Okhotsk, salmon enter the river and swim upstream until they reach the Lake Kurilskoe spawning grounds, which includes the littoral and several of the lake's tributaries. An intense surge of fish is observed from mid-July to early September. The majority of salmon arrive between late July to mid-August (Bugaev et al., 2009). Bears congregate at river mouths and along their channels, as well as at the outlet of Lake Kurilskoe, i.e. the River Ozernaya. It is much easier for bears to catch salmon in

shallow areas of rivers than in the littoral zone of the lake (Zavadskaya et al., 2019). River spawning grounds account for only 29% of the total spawning area of the basin of Lake Kurilskoe and River Ozernaya (Ostroumov, 1970), which places some limitations on the exploitation of salmon resources by bears.

Adverse changes in food resources across the landscape can lead to an increase in stress (Bryan et al., 2013), changes in the spatial distribution of brown bears (Barnes, 1990; Reinhart, 1990; Deacy et al., 2016, 2019), changes in foraging behaviour (Luque & Stokes, 1976), to an increase in the level of intraspecific competition (Olson, 1993; Ustinov, 1993; Zavatsky, 1993; Chestin et al., 2006), and aggression (Egbert & Stokes, 1976). Decreases in salmon runs can have significant demographic impacts. For example, a survey of the northern and northwestern parts of the coast during the winter of 1974, the catastrophically low run of sockeye salmon into the Lake Kurilskoe in the previous summer (260 000 individuals), resulted in dozens of frozen corpses of bears that were found (Pogodaev et al., 2004). In North America, the salmon proportion in the diet of brown bears has been found to be positively correlated with the body size, body weight of females, litter size, and population density (Hilderbrand et al., 1999a; Mangipane et al., 2020).

To date, commercial fishing is the main factor affecting the timing and abundance of sockeye salmon escapement into the basin of Lake Kurilskoe. The commercial catch affects the number of fish entering the system, and, consequently, the food supply for predators and scavengers and the reproduction rates of the salmon population. Sockeye salmon fishing areas are situated outside the South Kamchatka Sanctuary, namely the Sea of Okhotsk and the River Ozernaya within 10 km of the mouth. According to Bugaev et al. (2009), the current fishing and production facilities make it possible to almost completely intercept all fish attempting to enter the river. The forecast of broodstock entry and catch quotas are calculated based on the size of the parent stock taking into account the success of reproduction (assessment of smolt migration from lake to ocean). At the same time, the catch volumes do not have fixed quotas. So, the catch volume increases after the estimated optimal number of salmon (escapement) have passed into the Lake Kurilskoe. The calculation of the escapement into the lake is carried out at the Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO) fish weir on the River Ozernaya just below Lake Kurilskoe. Among ichthyologists, there is no consensus on the optimum escapement level (Egorova et al., 1961; Semko, 1961; Ostroumov, 1970; Selifonov, 1988; Bugaev & Dubynin, 2002; Dubynin, 2012), but the various estimates do not take into account the trophic needs of the ecosystem. In the last decade the escapement was maintained at the level of 1 500 000–1 800 000 fish under the recommendation of Dubynin (2012), wherein escapement into tributaries of the lake is not quantified. To ensure the unobstructed passage of a sufficient salmon number to the system of Lake Kurilskoe, the Commission for the regulation of the catch of anadromous fish species in the Kamchatsky Krai establishes a schedule of passing days, when commercial fishing is stopped in the River Ozernaya. This schedule may be changed by the decision of this Comission during the season. When this Commission decides that enough fish have entered the system to the date, it may happen that passing days are canceled entirely and commercial fishing continues daily.

In 2018, the sockeye salmon population of the River Ozernaya returns were at a near-record high. The fishing quotas were constantly increased and as a result, the commercial catch had reached an almost historical maximum. During periods of commercial fishing in 2018, an average of 90% of salmon was removed from River Ozernaya, which excluded the unobstructed passage of a sufficient number of salmon to the spawning grounds. The main migration of salmon occurred during the unobstructed passing days (Bugaev & Dubynin, 2019). However, in mid-August, the formally agreed-upon escapement level was reached, and therefore the days of unobstructed migration were completely cancelled. This likely led to the removal of some subpopulations of sockeye salmon by the commercial fishing fleet and the absence of fish in much of the Lake Kurilskoe spawning grounds available to bears.

This study aimed to assess the changes in the brown bear behaviour due to the decreased escapement into the Basin of Lake Kurilskoe in the summer-autumn period of 2018. Several hypotheses have been proposed:

1) The lack of salmon affects the success and tactics of the fishing behaviour of the brown bear and the patterns of the space use by animals.

2) Reducing the salmon availability leads to an increase in antagonistic relations among bears, which may be accompanied by cannibalism and an aggressive behaviour towards humans.

In accordance with this, the following tasks were set: (1) to compare the success of the fishing behaviour of bears at reprentative sites, namely the mouths of the River Severnaya and River Khakytsin; (2) to identify the influence of decreased salmon availability on the foraging strategies of bears; (3) to compare the seasonal dynamics of the relative abundance of bears on the mouths of some of the main spawning rivers flowing into Lake Kurilskoe; (4) to assess the bear abundance in relation to the salmon abundance along the River Khakytsin; (5) to identify possible changes in the social behaviour of bears caused by food shortages.

Material and Methods

Study area

Lake Kurilskoe is a crater lake inside a large caldera, located in the southern part of the Kamchatka Peninsula (51.457222° N, 157.098611° E). The surface area of the lake is 77 km^2 (12 × 10 km). The catchment basin area is 392 km^2. Several rivers and streams flow into the lake. Of them, the largest ones are the River Severnaya, River Vychenkia, River Gavrushka, River Kirushutk, River Khakytsin, and River Etamynk. The River Ozernaya (48 km long) flows out of the Lake Kurilskoe into the Sea of Okhotsk (Fig. 1).

The material for this paper was the result of field studies of the behavioural ecology of brown bears carried out in the Basin of Lake Kurilskoe in July – September 2017 and June – October 2018 (83 and 97 days of observation, respectively). They were obtained using various field methods.

Assessment of the success of the fishing behaviour of brown bears

For a comparative assessment of the success of the fishing behaviour of bears, we used the results of observations of focal individuals, i.e. bears that were recognised individually and were under continuous observation during long periods of daylight hours. Observations were carried out on the mouth of the River Severnaya from 14.07.2017 to 13.08.2017 and from 10.07.2018 to 12.08.2018, as well as on the mouth of the River Khakytsin from 08.07.2017 to 17.09.2017 and from 07.07.2018 to 11.09.2018. On other rivers, observations were scarce and sporadic.

We analysed the observations that lasted at least one hour. For each individual, the number of fish caught was recorded, as well as we calculated the average number of fish caught per hour. The sample size, representing the average values of catching success per hour for different individuals, was 63 observations and 30 observations in 2017 and 2018 respectively for River Severnaya, as well as 115 observations and 180 observations in 2017 and 2018 respectively for River Khakytsin. Comparison of two years of observations was carried out using the Wilcoxon test. Statistical analysis was performed using R version 3.6.2 (R Core Team, 2019).

Assessment of the seasonal dynamics of the presence of brown bears on the mouths of spawning rivers

On the shores of Lake Kurilskoe, concentrations of bears occur on the mouths of spawning rivers. To assess the seasonal dynamics of the bear presence on the mouths of the four main rivers, six Seelock S308 camera traps were used (Fig. 1, Fig. 2). One camera was installed on a tree on the mouth of each spawning river (River Severnaya, River Kirushutk, and River Gavrushka), except for the largest tributary (River Khakytsin), where three cameras worked simultaneously, attached to the observation tower. The camera traps were fixed at a height of about 3–5 m, so that a vast area of a sandy spit and the littoral shore of the lake near the mouth of the river was monitored, where bears are concentrated during salmon fishing. Camera traps were programmed to take images at a 30-min interval during daylight hours. In 2017 and 2018, 480 trap-days and 498 trap-days were recorded, respectively. In each photograph, the number of bears was counted. Then the average number of bears in photographs was calculated for each day. The obtained data did not reflect the absolute number of bears because the angle of view of the camera trap lens did not cover the entire area used by bears. However, the area recorded by the camera traps for the same rivers remained constant for two years of observations.

Fig. 1. Map of the study area within the basin of Lake Kurilskoe in the South Kamchatka Sanctuary (Kamchatka Peninsula). On the incut map, the red line shows the borders of the South Kamchatka Sanctuary. The red dots on the river mouths show the locations of the remote camera traps.

Fig. 2. The mouth of River Severnaya (A), River Gavrushka (B), River Kirushutk (C) and River Khakytsin (D, one of three camera traps).

Assessment of the number of brown bears on the River Khakytsin and the shoreline of Lake Kurilskoe

We conducted systematic foot surveys along the River Khakytsin in order to assess the seasonal dynamics of the number of bears on the river's spawning grounds. Along its channel, we carried out a regular visual survey of animals along a 4.5 km long hiking route leading upriver from the river mouth to the Sypuchiy Kamen tract, namely extensive outcrop of volcanic and sedimentary rocks on the right bank of the river (Fig. 3). Khakytsin is the largest watercourse in the basin of Lake Kurilskoe, providing up to 73% of the river flow (Ukolova, 2008). It includes the most extensive areas of river spawning grounds in the basin of the lake (Selifonova, 1978), which is used by bears during the entire spawning run of sockeye

salmon. We conducted 15 counts during August – September and 18 counts during July – September along the River Khakytsin survey route in 2017 and 2018, respectively. During each survey, the salmon presence in the river was noted using the 4-point visual scale: 0 – no salmon, 1 – patchy amounts, 2 – moderate quantities, 3 – peak run and/or large quantities of spawned sockeye salmon carcasses.

In addition, we carried out systematic surveys of bear occupancy along the shoreline of Lake Kurilskoe from a rubber motorboat during September and October 2018 (five route surveys with a total length of 225 km). September and October form an important period when bears exploit beach spawning sockeye salmon.

For both surveys, we recorded the adult bear's gender, age, behaviour (foraging, social, resting and moving), as well as estimated age and the number of cubs of the year or one-year-old cubs or two-year-old cubs accompanying females. We also recorded bear associations, including temporary friendly groups of 2–3 independent individuals that feed, played or travelled together.

Salmon escapement and commercial catch volumes of sockeye salmon of the basin of Lake Kurilskoe and River Ozernaya

To assess the dynamics of the sockeye salmon entry into Lake Kurilskoe, we used data collected at the Ozernovsky fish counting weir (KamchatNIRO), located at the source of the River Ozernaya. Data on the regulation of the fishery and the catch of sockeye salmon in the Kamchatka-Kuril subarea in 2017 and 2018 were taken from open sources. These are protocols of the Commission for the regulation of the catch of anadromous fish species in the Kamchatsky Krai and information from the North-Eastern Territorial Administration of the Federal Agency for Fisheries (https://www.kamgov.ru/minfish/2017, http://xn--b1a3aee.xn--p1ai/).

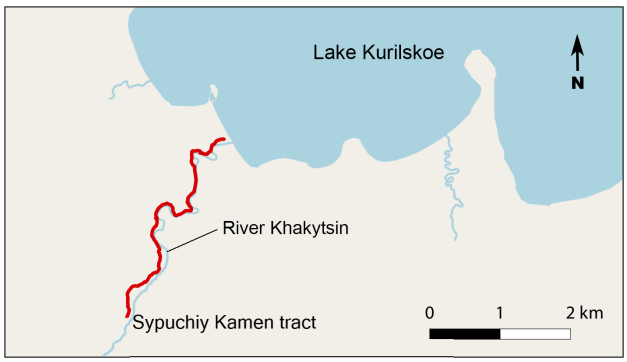

Fig. 3. The scheme of the foot route for a visual survey of brown bears along the River Khakytsin.

Results

Foraging success of brown bears

In 2017, the conditions were favourable for foraging bears. So, along with a drop in the water level in July and the exposure of sand spits in the feeding areas, the escapement was 2 300 000 salmons, providing abundant foraging opportunities. In 2018, flooding and high water caused by a snowy spring and a cold and rainy summer resulted in submerged sandbanks and spawning grounds, which persisted on various rivers until early – mid-August. High water levels adversely influenced the success of the fishing behaviour of bears on the River Severnaya, where spawning entries usually end in the first half of August. In addition to a high water level adverseley impacting foraging opportunities the first half of the spawning cycle, the total number of salmon in the river's spawning grounds was relatively low for the entire spawning run, with a total escapement of 1 500 000 salmon. In 2017, bear's fish catch rates were higher than in 2018 both on the River Severnaya (Wilcoxon test, $W = 1202.5$, $p = 0.03$) and on the River Khakytsin ($W = 12012$, $p = 0.02$) (Table, Fig. 4). Catching success was also lower in 2018 on the River Khakytsin. Individual bears succeeded in catching sockeye salmon on the River Khakytsin in 2018 only during short periods when strong pulses of fish were entering the river.

Seasonal dynamics of the number and distribution of brown bears

The different conditions in 2017 and 2018 caused significant differences in the distribution of animals, mainly affecting the seasonal dynamics of the bear numbers on various river mouths (data from camera traps) (Fig. 5). In 2018, camera traps registered the lowest number of bears (0–2 animals) for the shortest durations on the mouths of the River Severnaya and River Kirushutk, which probably indicates extremely weak runs in those two rivers. Also in 2017 and in 2018, the actual absence of bears from the mouth of the River Severnaya between the second half of August to the end of the observation period, corresponds with the natural occurrence of bears here. So, by mid-August, the spawning of sockeye salmon subpopulations is completed in this river. A higher relative number of bears was obtained in the River Khakytsin. So, the highest number of bears was concentrated on the vast sandbanks at the mouth of this river.

Table. Median foraging success of brown bears in 2017 and 2018 in River Khakytsin and River Severnaya

Year	River	n	Median catching success per hour	SE
2017	Severnaya	63	0.67	0.15
2018	Severnaya	30	0.22	0.19
2017	Khakytsin	115	0.40	0.06
2018	Khakytsin	180	**0.00**	0.11

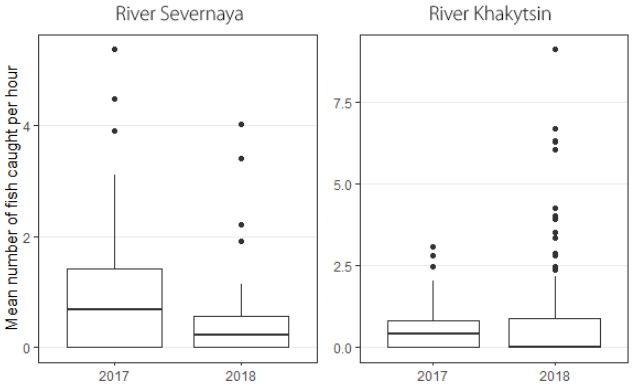

Fig. 4. Box plots of the mean values of the number of fish captures by brown bears on the mouths of the River Severnaya and River Khakytsin in 2017 and 2018. In the boxplots, the black midline is the median; the upper and lower limits of the box are the 3rd and 1st quartile (75th and 25th percentile), respectively. Outliers show the exceptional success of some individuals.

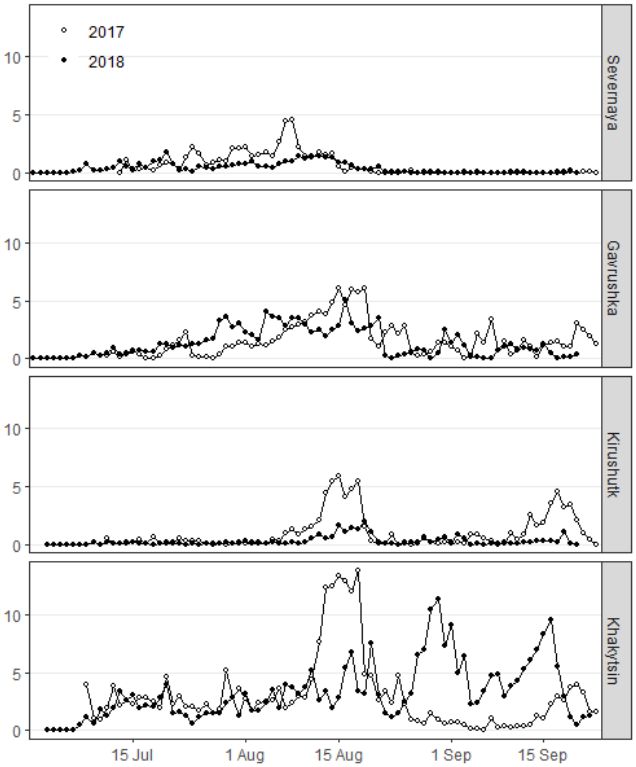

Fig. 5. Seasonal dynamics of the relative number of brown bears at the mouth areas of various rivers in 2017 and 2018 (daily average values are shown).

Comparative observations carried out on the River Khakytsin deserve special attention. The River Khakytsin is one of the most important rivers for the sockeye salmon reproduction in the basin of Lake Kurilskoe. In 2017, the peak movement of sockeye salmon from the lake into the river was recorded on 18 August. This was concurrent with the peak number of bears at the mouth (up to 45 individuals at the same time), after which the number of bears decreased sharply (Fig. 5). Then, bears shifted their salmon foraging activity to the spawning grounds within the river itself (Fig. 6).

In 2018, bears temporarily left the mouth of the River Khakytsin (Fig. 5) in late August and early September when there were pulses of salmon entering the river to shift their salmon foraging activities to the River Khakytsin itself. The salmon spawning season of 2017 was characterised by a consistently high abundance of sockeye salmon. The number of bears encountered along the survey route decreased the very next day after the peak entry of salmon into the river, remaining low for the next two weeks. With an excess of fish protein, many animals temporarily switched to feeding on the fruits of *Sorbus sambucifolia* (Cham. & Schltdl.) M. Roem., and, locally, berries of *Lonicera caerulea* L., *Vaccinium uliginosum* L. and *Empetrum nigrum* L., alternating between various food types, which was confirmed through both visual observations and examining feces. During times when salmon are abundant, bears are quickly satiated. As a result, some animals will rest longer and more often and could therefore not always be counted. From the end of the first half of September, on the route, the number of bears began to increase again. This was probably due to the fruit availability, a decrease in berry crops, average daily temperatures, and an increase in the energy requirements of bears, indicative of the beginning of the second peak of salmon consumption by bears (Fig. 6).

The year 2018 was notable for a low salmon abundance. So, sockeye salmon entered the river in separate small pulses. There was no peak movement. Remains of dead fish were not found along the river banks. On the route, the maximum number of bears did not reach the peak values of 2017. Starting in the middle of the first half of September, the number of bears sharply decreased, remaining steadily low until the end of the whole observation period (Fig. 6). Only the fruits of *Sorbus sambucifolia* were available for the bears as an alternative food source. Other potential food sources such as various species of berries and *Pinus pumila* (Pall.) Regel nuts were available in limited areas within the basin.

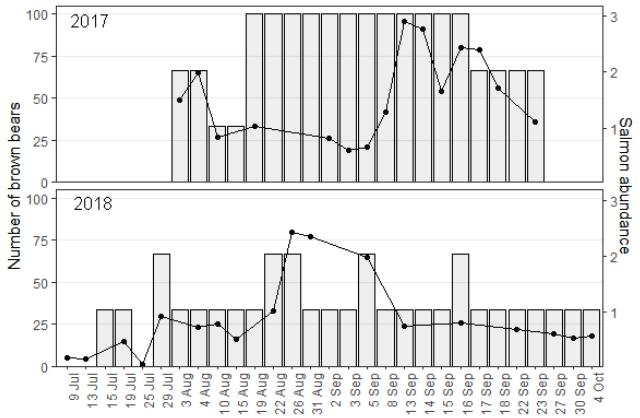

Fig. 6. The number of brown bears (points) in relation to the abundance of salmon (columns) on the stationary route along the River Khakytsin in 2017 and 2018. Designations: 0 – no salmon, 1 – patchy amounts, 2 – moderate quantities, 3 – peak run and/or large quantities of spawned sockeye salmon corpses.

Temporary associations of brown bears

Several behavioural characteristics of bears were also associated with low salmon number. In 2017, during conditions of a high salmon abundance, bears were often seen in groups and engaging in non-aggressive behaviour with each other, contrary to their normally solitary lifestyle. These individuals were observed playing with each other, moving together and feeding in close proximity (Fig. 7, Fig. 8). Among other bears, such associations included large adult males, which exhibit the least social tolerance under normal conditions. On the survey route along the River Khakytsin, bear associations were recorded on 1–23 September 2017. In 2018, no such bear associations were noted.

Changes in foraging strategies and the emergence of orphaned bear cubs

With a shortage of sockeye salmon in the rivers in 2018, the bears were searching for salmon in the littoral areas along the spawning grounds, venturing far out into the lake. In 2018, a regular survey of bears along the lake perimeter showed that they were actively swimming in search of spawned out salmon from 10.09.2018 to 01.10.2018, including five encounters (9.6%, n = 52) on 10 September, two encounters (5.7%, n = 35) on 17 September, 12 encounters (46%, n = 26) on 20 September, 14 encounters (22.6%, n = 62) on 28 September, 17 encounters (25.4%, n = 67) on 01 October. In such situations, the forced separation of members of family groups took place. So, females abandoned their cubs on the shore, swam away in search of food, losing contact with cubs. When females are undernourished, lactation can be prematurely interrupted, which can weaken the intrafamily bond between the mother and the cub. From late July to early October, 17 encounters of abandoned cubs of the year and yearlings were recorded (in total, 22 individuals). The largest number of encounters of abandoned cubs occurred in the first half of September (Fig. 9). In 2017, no abandoned cubs were observed in the basin of Lake Kurilskoe.

Fig. 7. Friendly associations between adult males (A, B) and females (C, D) of brown bears. The valley of the River Khakytsin, September 2017.

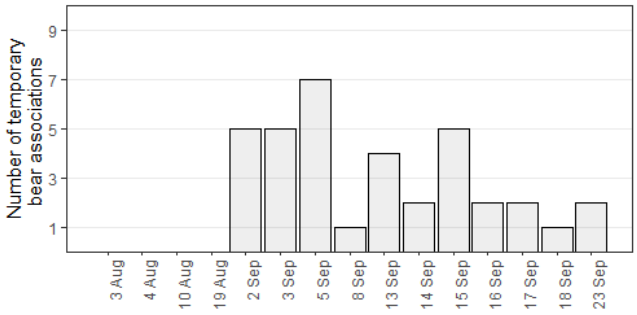

Fig. 8. Registrations of encounters of temporary brown bear associations on a stationary route along the River Khakytsin in 2017.

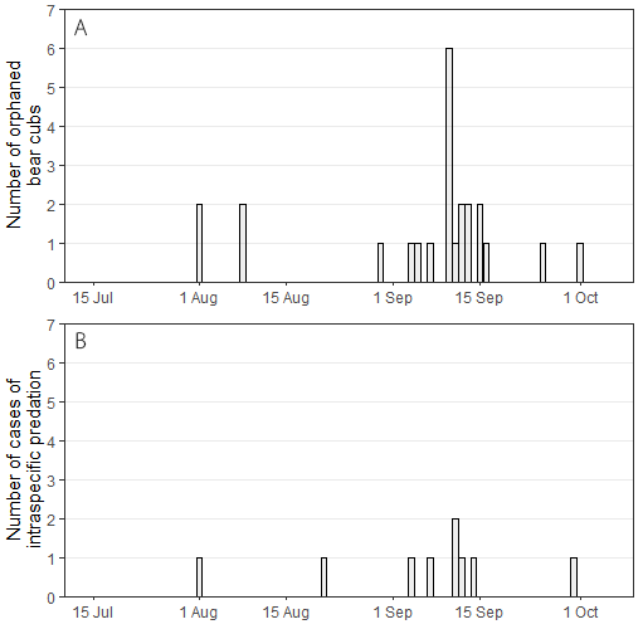

Fig. 9. Registration of sightings of orphaned bear cubs (A) and cases of intraspecific predation (B) in 2018.

Cannibalism and brown bear attacks on humans

In 2018, during the same period (from mid-July to late September), nine cases of intraspecific predation were recorded where bears killed and ate conspecifics (Fig. 9). Of those nine cases, five episodes were observed visually. There were three cases cub infanticide; two cases adult females being killed; three cases of subadult individuals being killed; and one case of an adult bear of unknown sex being killed and eaten. During the same period of 2017, only one case was recorded when an adult male killed a subadult female, leaving her carcass untouched.

With the increased incidence of cannibalism among bears of Lake Kurilskoe, an extremely dangerous situation has also been created for humans. The bears feeding on the corpses of their conspecifics were distinguished by increased aggressiveness and twice attacked humans in attempts to protect their prey. One of the episodes ended in a tragedy.

On 18.08.2018, on the right bank of the River Ozernaya, 250 m below the fish counting fence of the KamchatNIRO observation post, a bear killed a ranger of the Kronotsky State Nature Biosphere Reserve who accidentally approached him, while the bear was eating the corpse of an adult female. The bear moved the human body 160 m (a gun and part of the clothes torn off by the bear were found at the place of death) and, while the search for the deceased was carried out, it was almost completely eaten by several bears. Two adult males were shot at the site of the discovery of the human remains. The tragedy that occurred was the first officially confirmed case of a bear killing a person in the Basin of Lake Kurilskoe in the last 22 years (since August 1996).

On August 30th, 2018, on the banks of the River Khakytsin, 4.5 km above its mouth, a large adult male bear was sitting near the corpse of an adult female he had killed. To protect his food source, the male charged from a distance of 20 m when unwittingly approached by three employees of the Kronotsky State Nature Biosphere Reserve. The bear was stopped by a shot at his feet and with the help of a flare.

Discussion

In the basin of Lake Kurilskoe, the exceptionally favourable conditions for the bear habitation have always determined their naturally high abundance (Derzhavin, 1916; Revenko, 1993; Gordienko et al., 2006). In the last decade, after the successful protection of the South Kamchatka Sanctuary, poaching of bears and sockeye salmon had ceased. This significant development has fostered favourable conditions for the conservation and continued ecological integrity of the South Kamchatka Sanctuary.

In the basin of Lake Kurilskoe, the brown bear is one of the few inhabitant of the ecosystem actively hunting sockeye salmon. The ability of these mobile animals to move widely throughout the season and to find salmon in their spawning grounds is well known (Deacy et al., 2016, 2019). The seasonal numbers of bears within the spawning grounds of the basin of Lake Kurilskoe in the years of our study differed significantly due to the heterogeneity of the salmon spawning run. The most significant differences were shown for the River Severnaya, River Kirushutk and River Khakytsin as a result of the low abundance and availability of sockeye salmon for bears in 2018 (Fig. 5, Fig. 6).

According to KamchatNIRO specialists (Shevlyakov, 2016), the brown bears of the River Ozernaya and Lake Kurilskoe system catch as many as 180 000 pre-spawning sockeye salmon. Shevlyakov (2016) stated that the average daily consumption of an adult bear is 30 kg of fish. Two periods were identified during which bears feed on unspawned salmon of an early and a late form of sockeye, for two weeks each in July and in October, respectively (Shevlyakov, 2016). However, the period of active feeding of bears on sockeye salmon lasts much longer (from July to November). For example, on the spawning grounds of the River Khakytsin, with an abundance of salmon in 2017, we identified three peaks in sockeye consumption by bears, namely in early August, mid-August, and mid-September (Fig. 5, Fig. 6). The needs of the brown bear for this abundant resource are significant. However, along with salmon abundance in the lake basin (escapement), it is important that this amount is evenly distributed throughout the season among the river spawning grounds available to bears. This can be achieved only if each sockeye salmon subpopulation is able to enter Lake Kurilskoe. This not only spreads salmon availability across a broad spatial area, but also provides a longer foraging period due to the the staggering of these subpopulation runs.

During years of favourable escapement levels and timing, the bears of the Lake Kurilskoe exhibit an exceptionally high intraspecific tolerance, including amicable social interactions, a behaviour not common among unrelated individuals (Bledsoe, 1975; Egbert & Stokes, 1976; Smith et al., 2005) (Fig. 7, Fig. 8). During periods of salmon deficiency, the frequency of aggressive interactions, injuries and deaths of bears become more common (Egbert & Stokes, 1976; Luque & Stokes, 1976; McLellan, 1994; Mattson & Reinhart, 1995). Cannibalism has been widely documented for brown bears, perhaps as a food-procuring strategy in response to the deterioration of salmon runs (Hessing & Aumiller, 1994; Chestin et al., 2006) (Fig. 9). The number of cases of human-brown bear conflict and brown bear attacks on humans also increases in years of food shortages (Krechmar, 1993; Gordienko & Gordienko, 2006). Bears can be especially defensive when protecting protein-rich carcasses of large animals, they have killed or found (Herrero, 1985).

The high incidence of abandoned bear cubs may also be largely due to abnormally low salmon runs (Fig. 9). Family groups are one of the most vulnerable social classes of bears. In the face of intense competition, females with cubs are often forced to occupy habitats with poorer forage conditions (Schoen et al., 1986; Hilderbrand et al., 1996; Ben-David et al., 2004; Gende & Quinn, 2004). This makes it even more difficult for the female to provide energy for herself and her offspring. This is evidenced by the changes in the bear behaviour observed in 2018 in the basin of Lake Kurilskoe.

The low salmon availability for bears in 2018 was associated with both natural and anthropogenic reasons. High floods, persisting on some rivers until mid-August, coincided with a significantly lower salmon number entered the lake when compared to 2017 (Fig. 10). According to the KamchatNIRO survey data, the movement of sockeye salmon into the lake was late and low. So, the arrival of the fish was delayed by 10–14 days compared to their usual arrival time (Bugaev & Dubynin, 2019). The sockeye salmon arrival usually coincides with the period of low water levels and rise in temperature (Bugaev et al., 2009). By mid-August 2018, the water level had dropped, and more favourable conditions for bears to catch fish appeared. At that time, the commercial fishery was completely opened, resulting in few fish making it into Lake Kurilskoe (Protocol of the Commission for the regulation of the production (catch) of anadromous fish species in the Kamchatsky Krai of 15.08.2018 №23) (Fig. 10). The increase in commercial fishing during that time limited the number of migrating sockeye salmon to critically low values.

In 2018, with the significantly lower salmon escapement compared to 2017 (a decrease of 55.5%), the commercial quota for sockeye salmon increased, exceeding that in 2017 by 28% (Fig. 11, according to the Protocol of the meeting Commission). The commercial catch volumes of the sockeye salmon in the basin of Lake Kurilskoe and River Ozernaya in 2018 approached historical maximum levels (2013, 2015, and 2016). Despite near-record salmon oceanic populations (catch of 26 500 tons in 2018), the escapement into Lake Kurilskoe was depressed and many of its tributaries had either extremely low runs or complete absence of sockeye salmon. It appears that some sockeye salmon subpopulations did not make it up into the River Ozernaya/ Lake Kurilskoe system at all.

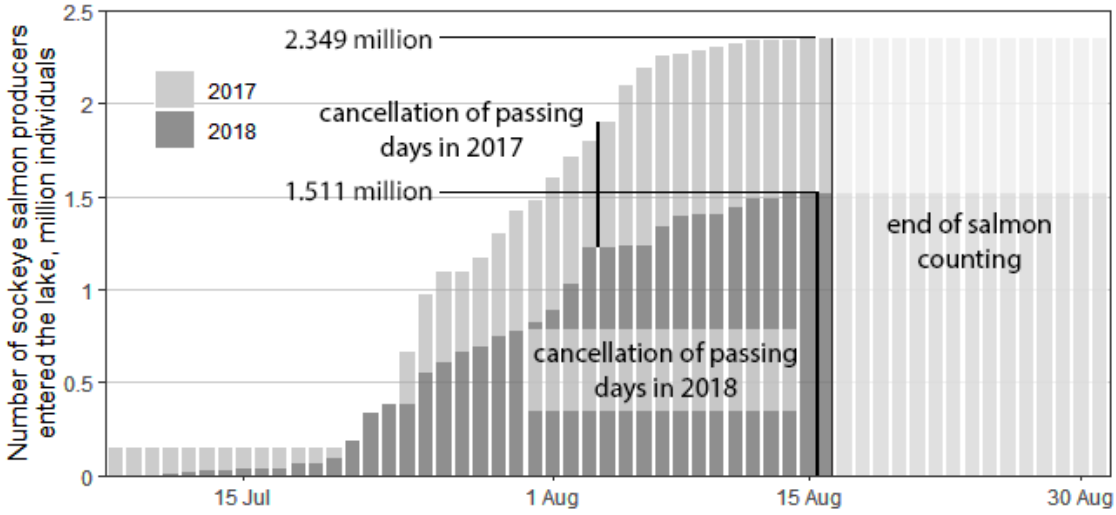

Fig. 10. Dynamics of the sockeye salmon entry into Lake Kurilskoe in July – August of 2017 and 2018 (data from the Ozernovsky observation point of KamchatNIRO).

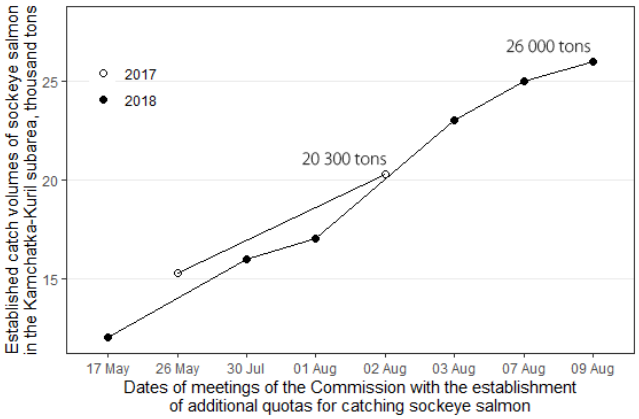

Fig. 11. Dynamics of the established catch volumes of sockeye salmon in the Kamchatka-Kuril subarea in 2017 and 2018. The proportion of sockeye salmon in Lake Kurilskoe and the River Ozernaya in the total catch exceeds 95%.

In recent years, the seasonal gathering of bears at Lake Kurilskoe and the opportunity to observe their natural behaviour have attracted thousands of tourists from all over the world. The ecotourism development, including observing and photographing bears from close distances, has so far been possible due to the tolerant attitude of these bears towards humans. The main factor supporting this bear behaviour was the salmon abundance. The steady increase in recreational tourism at Lake Kurilskoe (Zavadskaya et al., 2019) is pressuring bears and this fragile ecosystem as a whole. At the same time, an increase in the commercial fishing industry have the same effect on its key species, namely sockeye salmon. If the current processes persist, interruptions of ecological balance in the ecosystem are inevitable, which in the long term can lead to its degradation, and a significant issue when it comes to the human-bear relationship. Since in the basin of Lake Kurilskoe no comprehensive studies of the bear behaviour have been carried out to date, the results of this study are the first step to draw attention to this issue. Disruption of this brown bear-salmon dynamic could also have consequences for other coastal temperate ecosystems (Hilderbrand et al., 1999b, 2004; Levi et al., 2020).

Conclusions

In the basin of Lake Kurilskoe, the state of the brown bear population reflects the well-being of the entire local ecosystem. Changes in the social and foraging behaviour, the appearance of abandoned bear cubs, a decrease in the success of fishing behaviour, an increase in the cannibalism incidence, and dynamics of the bear numbers in the spawning rivers noted in 2018 in Lake Kurilskoe are directly related to the decrease in the abundance, timing and availability of their main food source, sockeye salmon. This change was caused primarily by the allowable commercial catch of salmon and the resulting removal of these fish from the Lake Kurilskoe ecosystem. The dramatic and sudden changes that took place, indicate that for the future stability of the precious Lake Kurilskoe ecosystem, a new and more modern approach to fisheries and wildlife management is required.

It is necessary to reconsider the «optimal» escapement of sockeye salmon allowed into Lake Kurilskoe and its tributaries. This number must reflect the trophic needs of not only bears but all animals depending on the yearly return of this crucial protein source. The current practice of cancelling the days during which salmon can migrate unobstructedly into and up the River Ozernaya towards Lake Kurilskoe is unacceptable.

Management also needs to allow sufficient numbers of each salmon subpopulation to enter the lake. Otherwise, we run the risk of adversely impacting

these subpopulations and/or causing them to go extinct. This has happened within other systems and has had adverse impacts at numerous trophic levels. Through systematic genetic analyses it would be possible to determine when each of the subpopulations pass the fish weir. Therefore, this information could be used in decisions regarding the opening and closing of commercial fishing.

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ПОСЛЕДСТВИЯ НЕДОСТАТКА НЕРКИ ДЛЯ БУРОГО МЕДВЕДЯ В БАССЕЙНЕ КУРИЛЬСКОГО ОЗЕРА (ЮЖНАЯ КАМЧАТКА)

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Мы изучали поведенческую экологию *Ursus arctos* (далее – бурый медведь или медведь) в бассейне Курильского озера (полуостров Камчатка) в летне-осенний периоды 2017–2018 гг. Целью настоящего исследования стала сравнительная оценка поведения животных относительно неоднородности трофических условий двух лет. В 2018 г. на фоне высокого коммерческого вылова *Oncorhynchus nerka* (далее – нерка) и паводка в первой половине лета, снижение обилия и доступности лосося вызвали значительные изменения в поведении и распределении медведей. Успешность рыбодобывающего поведения животных в 2018 г. оказалась ниже, чем в 2017 г. В период обилия лосося в 2017 г. одиночные медведи формировали временные дружеские ассоциации, которые не наблюдались в 2018 г. Из-за увеличения случаев внутривидового хищничества в 2018 г. медведи начали проявлять агрессию по отношению к человеку. Ухудшение физического состояния некоторых самок и изменение ими стратегий пищедобывательного поведения сопровождались появлением медвежат-сирот. Пик негативных изменений в группировке медведей наблюдался в первой половине сентября 2018 г., когда потребность животных в усиленном питании возросла. Современный подход к освоению ресурсов нерки бассейна Курильского озера и р. Озерная требует серьезного пересмотра и распределения промысловой нагрузки в соответствии с особенностями популяционной структуры этого лосося и его исключительной роли в местной экосистеме. Необходим пересмотр «оптимального» количества производителей нерки, пропускаемых в Курильское озеро и его притоки. Текущая практика отмены проходных дней, во время которых лосось может беспрепятственно подниматься по р. Озерная в Курильское озеро, недопустима.

Ключевые слова: *Oncorhynchus nerka*, *Ursus arctos*, каннибализм, медвежата-сироты, перевылов рыбы, Южно-Камчатский заказник