Effect of salinity on survival and emigration behaviour during the sea-to-land transition of three terrestrial hermit crab species (Decapoda: Anomura: Coenobitidae) under laboratory conditions

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Abstract.— Salinity is an important abiotic factor affecting the survival and development of decapod crustacean larvae and juveniles. We investigated the effect of salinity on survival and emigration behaviour during the sea-to-land transition of three terrestrial hermit crab species in the family Coenobitidae (genera *Birgus* and *Coenobita*): *B. latro*, *C. brevimanus* and *C. purpureus*. We cultured laboratory-born individuals from megalopae for 63 days in vessels containing both a hard substrate and seawater controlled at four different salinity levels (25, 30, 35 and 40 ppt). The overall, survival, shell-carrying and landing activities of the animals were enhanced at lower salinity conditions. Interspecific variability in survival and emigration behaviour was evident: *C. brevimanus* and *C. purpureus* showed relatively high performance even at higher salinity levels when compared with *B. latro*, indicating the differences in hypo-osmoregulatory ability among coenobitids. The microhabitats occupied by megalopae and early juveniles of coenobitids could be attributed to the interspecific variability in the osmoregulatory capacity of these animals.

Key words: Coconut crab, land hermit crab, early life history, environmental adaptation

■ Introduction

Terrestrial hermit crabs in the family Coenobitidae Dana, 1851 comprise land hermit crabs of the genus *Coenobita* Latreille, 1829 with approximately 17 species as well as the coconut crab *Birgus latro* (Linnaeus, 1767), the only species in the genus *Birgus* Leach, 1816 (Hartnoll, 1988; Poupin, 1996; McLaughlin *et al.*, 2010; Rahayu *et al.*, 2016). These crabs are mainly found in subtropical and tropical coastal regions (Hartnoll, 1988). Coenobitid crabs carry gastropod shells, while the shell-carrying behaviour of *B. latro* is an ancestral habit that appears only during the juvenile stage (Kadiri-Jan & Chauvet, 1998; Greenaway, 2003; Hamasaki *et al.*, 2014a).

Birgus latro is the largest terrestrial arthropod, and it serves as an important local re-

source for human consumption (Brown & Fielder, 1991). However, coconut crab populations have been severely depleted on most inhabited islands because of overharvesting and habitat loss (Amesbury, 1980; Brown & Fielder, 1991; Drew *et al.*, 2010). Land hermit crabs are also the subject of conservation concerns owing to their exploitation as ornamental animals (Nakasone, 2001; Pavia, 2006).

The larvae of coenobitid crabs hatch on the shore and develop in the sea through several zoeal stages before their metamorphosis into the megalopal stage (Hartnoll, 1988; Nakasone, 2001; Hamasaki *et al.*, 2015a, 2020). After settlement, megalopae acquire empty gastropod shells, migrate onto land and moult to the first crab stage (Reese, 1968; Harvey, 1992; Brodie, 1999; Hamasaki *et al.*, 2014b, 2015b). Therefore, knowledge of the biotic and abiotic

factors that affect the survival and emigration behaviour of these animals during sea-to-land transition is essential to better understand the recruitment mechanism of coenobitids as well as to develop the artificial propagation technologies of these animals for use by humans.

Salinity is one of the most important abiotic factors known to affect the survival and development of decapod crustacean larvae and juveniles (Anger, 2001, 2003). When animals are exposed to the unfavourable salinity conditions, delayed development, reduced survival, feeding and growth rates, and altered behaviour occur due to enhanced metabolic energy demands for osmoregulation and maintenance (Anger, 2003). Salinity fluctuates temporally and spatially in natural environments where coenobitids may recruit (Tottori *et al.*, 2004; Kawachi & Ishikawa, 2008; Kawachi *et al.*, 2009; Hamasaki *et al.*, 2018). However, the influence of salinity on survival and emigration behaviour during the sea-to-land transition of coenobitid species remains largely unknown. To date, survival, development, and behaviour such as landing and shell wearing activities have been reported for laboratory-raised megalopae and early juveniles of two coenobitid species: *Coenobita rugosus* H. Milne-Edwards, 1837 and *C. violascens* Heller, 1862, under two different salinity levels (24 and 34 ppt) (Fujikawa *et al.*, 2018).

The present study aimed to investigate the effect of salinity on survival and emigration behaviour during the sea-to-land transition of three terrestrial hermit crab species—*B. latro*, *C. brevimanus* Dana, 1852, and *C. purpureus* Stimpson, 1858—that occur in Japan.

Materials and Methods

Test animals

Culture experiments were conducted in a laboratory at the Tokyo University of Marine Science and Technology, Tokyo, from 2014 to 2016. Ovigerous females of three coenobitid

species, *B. latro*, *C. brevimanus* and *C. purpureus*, were captured by hand during late June to early July on Hatomajima Island (24°28'N, 123°49'E) or Ishigakijima Island (24°23–31'N, 124°07–18'E) of the Ryukyu Archipelago, Japan. They were transported to the laboratory where the air temperature was controlled at ~27–28°C, which is equivalent to the summer temperature during the reproductive season of coenobitid crabs in natural habitats.

The crabs were maintained in tanks equipped with simulated land and sea areas (artificial seawater, 34 ppt salinity; Sealife, Marineteck Co. Ltd., Tokyo, Japan) according to the methods of Hamasaki *et al.* (2009) and Hamasaki (2011). Larval hatching occurred during mid to late July, and newly hatched zoeae from a single female of each species were cultured until metamorphosis to the megalopal stage, according to the methods of Hamasaki *et al.* (2013).

The larvae metamorphosed into megalopae during the period from late July to early August. The 0-day-old megalopae of each species were housed individually for three days in the wells of 6 six-well cell culture plates, which contained 10 ml artificial seawater (34 ppt salinity, ~28°C) in each well. They were transferred daily into clean culture wells with fresh seawater using a large-mouthed pipette and fed frozen mysid shrimps (Seahorse Ways Co. Ltd., Minamikyushu, Kagoshima, Japan).

All species of the genus *Coenobita* in Japan are collectively recognised as a Natural Monument Animal to promote their conservation. *Coenobita* spp., therefore, were collected and cultured under permission (license certificate no. 4-2058) from the Agency for Cultural Affairs, Ministry of Education, Culture, Sports, Science and Technology of Japan. In addition, *B. latro* is listed as 'vulnerable' in the Red Data Book of the Ministry of the Environment of Japan. Therefore, the wild crabs used in the present study were returned to their natural habitats after the experiments were completed.

Test salinity conditions

The survival and behaviour of the test animals were examined under the four different salinity levels (25, 30, 35, and 40 ppt). The salinity levels of 25, 30 and 35 ppt were adopted for the following reasons. The salinity was recorded at approximately 34–35 ppt in the open ocean around the Ryukyu Archipelago (Hydrographic and Oceanographic Department, 2021), and the salinity fluctuated between approximately 0 and 34 psu in accordance with a tidal cycle in the river mouth of the Nagura Amparu lagoon, Ishigakijima Island (Kawachi & Ishikawa, 2008; Kawachi *et al.*, 2009). A few mortalities were observed after 24 h in the coenobitid megalopae when they were abruptly transferred from 34 to 20 ppt salinity, but no mortalities occurred at 24 ppt (Hamasaki *et al.*, unpublished data). Additionally, the highest salinity level of 40 ppt was assumed to occur in intertidal pools under the low tidal condition. Seawater with different salinities was prepared using dechlorinated tap water and artificial seawater salts.

Culture experiments

The 3-day-old megalopae of each species were housed individually and cultured in transparent plastic containers (8 cm wide $\times$ 20 cm long $\times$ 6.5 cm high) equipped with an inclined simulated land surface (350 g of coral sand; grain diameter = 0.5 mm) and designated test seawater (80 ml), as illustrated by Hamasaki *et al.* (2011). Three sizes of cleaned gastropod shells of *Littorina brevicula* (Philippi, 1844)

(shell length: small, 4.00–4.29 mm; medium, 4.30–4.69 mm, and large, 4.70–4.99 mm) were placed at the bottom of the sea area in each container because juvenile terrestrial hermit crabs prefer larger shells as they increase in size (Hamasaki *et al.*, 2015b). A total of 15 animals of each species were used for each salinity level. The containers were covered with 0.9 mm mesh-sized plankton netting to prevent the animals from escaping. The test containers were placed in 2-cm-deep water baths (38 cm $\times$ 60 cm $\times$ 7.5 cm) to maintain similar temperature and humidity among the culture containers. The photoperiod (13 h light : 11 h dark) and temperature ($\sim 28^{\circ}\text{C}$) in the culture room approximated the summer environment.

According to the methods of Hamasaki *et al.* (2011, 2015b), the cultured animals were observed once daily until 63 days after metamorphosis into the megalopal stage for survival, shell use (carrying or not), wearing-shell type (small, medium or large) and location (seawater or land). After the daily data collection, the seawater in each test container was renewed with seawaters with designated salinity levels. Frozen mysid shrimps and freeze-dried polychaete (Kyorin Co. Ltd., Himeji, Hyogo, Japan) were given to the cultured animals as food in the seawater and on land, respectively. Feeding of freeze-dried polychaete was initiated after the first landing event occurred for each cultured animal.

The air temperature, relative humidity and seawater temperature were recorded every 10 min with data loggers (Hygrochron and

Table 1. Culture conditions (mean $\pm$ standard deviation) of three terrestrial hermit crab species in the genus *Birgus* and *Coenobita* during sea-to-land transition. The air temperature (AT), relative humidity (RH), and seawater temperature (SWT) were recorded every 10 min with data loggers in the containers, and the salinity of the seawater was measured from the containers of each salinity level after the daily data collection.

Species	AT ($^{\circ}\text{C}$)	RH (%)	SWT ($^{\circ}\text{C}$)	Salinity level (ppt)			
				25	30	35	40
<i>B. latro</i>	27.9 $\pm$ 0.8	81.8 $\pm$ 4.3	27.4 $\pm$ 0.8	26.1 $\pm$ 1.1	31.0 $\pm$ 1.0	35.9 $\pm$ 1.2	41.3 $\pm$ 1.3
<i>C. brevimanus</i>	28.4 $\pm$ 0.8	82.9 $\pm$ 5.0	27.8 $\pm$ 0.8	25.9 $\pm$ 1.1	31.1 $\pm$ 1.2	35.4 $\pm$ 3.2	40.8 $\pm$ 1.0
<i>C. purpureus</i>	27.9 $\pm$ 0.4	89.4 $\pm$ 1.7	28.0 $\pm$ 0.4	25.8 $\pm$ 1.5	30.6 $\pm$ 0.9	35.8 $\pm$ 1.1	41.1 $\pm$ 2.5

Thermochron SL, KN Laboratories Co. Ltd., Osaka, Japan) in the containers during the culture period. These records (mean $\pm$ standard deviation values) are summarised for each species in Table 1. The seawater salinity measured from the containers of each salinity level after the daily data collection is also summarised for each species in Table 1.

Data analysis

The daily survival rate of animals was calculated for each salinity level for each species as (number of animals surviving)/(initial number of animals) $\times$ 100. Additionally, we considered the following data as behavioural aspects of animals: the daily proportions of (1) animals carrying shells, (2) observed on land, and (3) carrying small, medium or large shells. The proportion of animals was calculated as follows: (number of animals engaged in designated behaviour) / (number of animals surviving for (1) and (2) or number of animals carrying shells for (3)) $\times$ 100. Three animals of *B. latro* cultured at 35 ppt, one *C. purpureus* cultured at 35 ppt and one *C. purpureus* cultured at 40 ppt escaped from the culture containers during the experiments; these animals were excluded from the data analyses.

Statistical analyses were performed using R statistical software (R4.1.1; R Core Team, 2021) at a 5% significance level. We employed a generalised linear model (GLM) with a binomial family using the *glm* function (logit link) to evaluate the effect of salinity on animal survival, taking into account the interspecific comparison. In the GLM analyses, the final survival rate was the response variable, and the salinity level and species were categorical explanatory variables. A generalised linear mixed-effects model (GLMM) with a binomial family was also performed using the *glmer* function (logit link) implemented in the lme4 package (Bates *et al.*, 2015) to evaluate the daily behavioural aspects because these data were collected repeatedly in each animal group

under the designated salinity level (Zuur *et al.*, 2009). In the GLMM analyses, the daily proportions of animals carrying shells and landing during the experiments were response variables. The salinity level and species were categorical explanatory variables, and the identity of salinity groups was included as a random intercept effect. The GLMM analysis was also employed to evaluate the daily proportion of animals carrying large shells because wearing a gastropod shell is energetically costly for land hermit crabs (Osorno *et al.*, 2005) and thus shell-size preference by test animals may differ among salinity levels.

The statistical significance of the response variables was evaluated with the likelihood ratio test (type II) and Wald chi-square test (type II) for the GLM and GLMM analyses, respectively, using the *Anova* function implemented in the car package (Fox & Weisberg, 2011). Additionally, differences in the survival and behavioural traits between the species were tested with Tukey's method using the *glht* function in the multcomp package (Hothorn *et al.*, 2008).

Results

The analysis deviance table based on the GLM and GLMM evaluating the effects of salinity and species on survival and behavioural aspects of the animals is summarised in Table 2. The daily proportions of animals surviving, carrying shells and landing as well as those carrying small, medium or large shells are shown for each salinity level for each species in Figs. 1–3 and 4–6, respectively. The predicted values, with 95% confidence intervals, of the proportions of animals that survived at the end of the experiments and those engaged in designated behaviours were derived from the GLM and GLMM analyses for each salinity level for each species; they are shown in Fig. 7.

The GLM and GLMM analyses detected the significant influences of salinity and species on animal survival and behaviour (Table 2).

Table 2. Analysis of deviance table by the likelihood ratio test for survival (generalised linear model) and the Wald chi-square test for behaviour (generalised linear mixed-effects model) to evaluate the effects of salinity and species on the proportions of animals that survived at the end of the culture experiments as well as daily proportions of animals carrying shells and landing among surviving animals and those carrying large shells among shell-wearing animals during the culture experiments with three terrestrial hermit crab species.

Response variable	<i>N</i>	Explanatory variable	χ^2 value	<i>df</i>	<i>P</i> value
Survival	12	Salinity	22.34	3	<0.0001
		Species	137.72	2	<0.0001
Carrying shells	681	Salinity	11.77	3	0.0082
		Species	33.78	2	<0.0001
Carrying large shells	681	Salinity	39.89	3	<0.0001
		Species	26.23	2	<0.0001
Landing	681	Salinity	71.61	3	<0.0001
		Species	65.81	2	<0.0001

N, number of data analysed; *df*, degree of freedom.

Survival

B. latro showed the lowest survival rates (Figs. 1A–3A), and all animals died at 35 ppt and 40 ppt (Fig. 1A). For the *C. brevimanus*, mortality occurred only at 40 ppt (Fig. 2A). For the *C. purpureus*, survival rates were high (>90%) at >35 ppt but lower (~70%) at 40 ppt (Fig. 3A). The final survival rate decreased with increasing salinity level in all species, and it was significantly lower in *B. latro* than in the other species (Fig. 7A).

Shell-carrying behaviour

The daily proportions of animals carrying shells increased linearly and reached >80% at the age of 10 days in all species at all salinity levels except for *C. purpureus* at 40 ppt, in which the proportion carrying shells reached >80% at the age of 24 days (Figs. 1B–3B). Thereafter, a large number of animals wore shells, but, for *B. latro*, the proportions carrying shells fluctuated greatly at 35 ppt during the later experimental period (Fig. 1B). The overall proportions of animals carrying shells decreased with increasing salinity level in all species, and they were significantly different between the species (Fig. 7B).

The animals in the experiment occasionally changed shells. In general, animals of early

Fig. 1. Changes in the proportions of animals surviving (A), carrying shells (B) and landing (C) during the sea-to-land transition of *Birgus latro* under four different salinity levels (25, 30, 35 and 40 ppt). The culture experiments started with 3-day-old animals.

Fig. 2. Changes in the proportions of animals surviving (A), carrying shells (B) and landing (C) during the sea-to-land transition of *Coenobita brevimanus* under four different salinity levels (25, 30, 35 and 40 ppt). The culture experiments started with 3-day-old animals.

ages tended to wear medium or large shells in all species (Figs. 4–6), but the proportions of animals carrying these shells decreased during the first landing phase and then re-increased according to age. The overall proportions of animals carrying large shells decreased with increasing salinity level in all species, and they were significantly larger in *C. purpureus* than in the other species (Fig. 7C).

Landing behaviour

After migrating onto land, all species often moved between land and seawater. For the *B. latro*, the daily proportions of animals landing

Fig. 3. Changes in the proportions of animals surviving (A), carrying shells (B) and landing (C) during the sea-to-land transition of *Coenobita purpureus* under four different salinity levels (25, 30, 35 and 40 ppt). The culture experiments started with 3-day-old animals.

increased at the age of 10 days (Fig. 1C); afterwards, they fluctuated between approximately 40% and 100% at 25–35 ppt. However, they fluctuated greatly at 35 ppt during the later experimental period and decreased to 0% after 28 days at 40 ppt. The proportions of *C. brevimanus* and *C. purpureus* landing increased linearly until the ages of 15–20 days (Figs. 2C and 3C), after which they fluctuated between approximately 60% and 100%, while showing higher values at lower salinity levels. The overall proportions of animals landing decreased with increasing salinity level in all species, and they were significantly lower in

Fig. 4. Changes in the proportions of animals carrying small, medium, and large shells during the sea-to-land transition of *Birgus latro* under four different salinity levels: 25 (A), 30 (B), 35 (C) and 40 ppt (D). The culture experiments started with 3-day-old animals.

B. latro than in the other species (Fig. 7D).

Discussion

Our experiments demonstrated that salinity significantly affected the survival and emigra-

Fig. 5. Changes in the proportions of animals carrying small, medium, and large shells during the sea-to-land transition of *Coenobita brevimanus* under four different salinity levels: 25 (A), 30 (B), 35 (C) and 40 ppt (D). The culture experiments started with 3-day-old animals.

tion behaviour during the sea-to-land transition of three terrestrial hermit crab species. Overall, survival rates and the proportions of animals engaged in designated behaviour decreased linearly with increasing salinity in coenobitid species (Fig. 7). These results suggest that the en-

Fig. 6. Changes in the proportions of animals carrying small, medium, and large shells during the sea-to-land transition of *Coenobita purpureus* under four different salinity levels: 25 (A), 30 (B), 35 (C) and 40 ppt (D). The culture experiments started with 3-day-old animals.

ergetic requirements of these coenobitids may increase for hypo-osmoregulation at higher salinities (Anger, 2001, 2003; Greenaway, 2003), resulting in low survival rates. Wearing a gastropod shell is vital but energetically costly for hermit crabs (Osorno *et al.*, 2005). Terrestrial

Fig. 7. The predicted values, with 95% confidence intervals, of the proportions of animals that survived at the end of the experiment (A) and those carrying shells (B), carrying large shells (C) and landing (D) that were derived from the generalised linear model and generalised linear mixed-effects model analyses for each salinity level for each species. Differences in the survival and behavioural traits between the species ($P < 0.05$) are indicated by different lowercase letters in the tables following the species names.

hermit crab megalopae are expected to expend a high energetic cost to carry shells at sea and to emigrate with them onto land. Therefore, delayed or insufficient shell-carrying and landing behaviours and lower proportions wearing large shells may occur in animals cultured at higher salinity levels (Figs. 1–7).

Hamasaki *et al.* (2014b, 2015b) examined the survival, moulting and emigration behaviour during the sea-to-land transition of six terrestrial hermit crab species—*B. latro*, *C. brevimanus*, *C. cavipes*, *C. purpureus*, *C. rugosus* and *C. violascens*—using similar culture containers as employed in the present study (salinity 34 ppt, temperature 27–28°C, and relative humidity 80–90%) for 60 days after metamorphosis to the megalopal stage. Fujikawa *et al.* (2018) also examined these traits of *C. rugosus* and *C. violascens* under two different salinity conditions (24 and 34 ppt) (temperature 28°C and relative humidity 86%) for 44 days. They reported that the animals moulted to the second or third crab stages. In the present study, we did not monitor the moulting of animals, but our observations should evaluate the survival and behaviour from megalopae to early juveniles, according to these previous studies. Fujikawa *et al.* (2018) also documented the similar behavioural responses to salinity by megalopae and early juveniles of *C. rugosus* and *C. violascens* as in the present study. In that study, reduced salinity (24 ppt) stimulated shell-wearing activity and/or landing activity and enhanced the moulting and survival of the animals.

Our experiments also demonstrated the distinct interspecific variability in the salinity adaptation of megalopae and early juvenile coenobitid crabs (Fig. 7), indicating that osmoregulatory capacity differs among coenobitids. *C. brevimanus* and *C. purpureus* showed relatively high survival rates even at higher salinity levels compared with *B. latro*. Thus, the hypo-osmoregulatory ability may be stronger in *C. brevimanus* and *C. purpureus* than in

B. latro.

Early juveniles of *C. purpureus* inhabit sandy beach conditions (Hamasaki *et al.*, 2018; Sanda *et al.*, 2018a, 2018b; Inutsuka *et al.*, 2020) with high ground temperatures (Hamasaki *et al.*, 2018) that may induce overheating and desiccation, thereby leading to hypersaline environments. Megalopae and early juveniles of *C. purpureus* might have evolved the strong hypo-osmoregulatory ability to adapt to the high-temperature niche. On the other hand, *C. brevimanus* is a primarily coastal forest dweller; however, the main habitats of early juveniles of this species remain largely unknown because few early juveniles have been collected in the wild (Hamasaki *et al.*, 2018). Our results suggest that the early juveniles of *C. brevimanus* may adapt to a niche similar to that of *C. purpureus*. Future field studies are required to elucidate the habitats of early juveniles of *C. brevimanus*.

B. latro inhabits the limestone shore and inland area (Fujikawa *et al.*, 2017; Hamasaki *et al.*, 2018; Tsuru *et al.*, 2018), while megalopae and early juveniles of *B. latro* carrying shells prefer environments with high humidity. Laboratory-raised megalopae of *B. latro* show a strong preference for coral fragments for settlement (Hamasaki *et al.*, 2015c), and they gather under shelters, such as coral rubble, after migrating onto land (Hamasaki *et al.*, 2011). The cryptic habits of *B. latro* megalopae and early juveniles with shells make it difficult to locate them in natural habitats, and we never found them in our field surveys (Hamasaki *et al.*, 2018). On a few occasions, these cryptic animals were found under piles of coconuts or in coral rubble (Kadiri-Jan & Chauvet, 1998; Fujita & Ito, 2008; Drew *et al.*, 2010). Megalopae and early juveniles of *B. latro* may adapt to the high humidity environment under the debris, thereby reducing their hypo-osmoregulatory ability.

Early megalopae tended to acquire medium or large shells in all coenobitid species (Figs.

4–6). Hamasaki *et al.* (2014a) analysed the relationship between body size and shell size occupied by the laboratory-raised juveniles of *B. latro* and suggested that smaller juveniles may use relatively larger shells because the shells that best fit the animal body sizes may limit the growth of smaller juveniles with shorter moulting intervals, i.e. higher moulting frequency. The proportions of animals carrying medium or large shells once decreased during the first landing phase in all species probably because they expended a high energetic cost to emigrate with them onto land. Animals then changed their preference for shells from the small to large size according to age (i.e. growth) (Figs. 4–6) as previously demonstrated for megalopae and early juveniles of coenobitid crabs (Hamasaki *et al.*, 2014a, 2015b).

Furthermore, interspecific variability was evident in shell size preference, and *C. purpureus* preferred large shells compared with the other species (Fig. 7D). This can be explained by the body size differences among coenobitid megalopae. Hamasaki *et al.* (2015b) detected a significant negative correlation between megalopal body size and the number of days when megalopae wore a small-sized shell during the sea-to-land transition of six coenobitids under laboratory experiments, and megalopae of *C. purpureus* were larger than those of *C. brevimanus* and *B. latro*.

Our laboratory experiments highlight the interspecific variability in performance of megalopae and early juveniles during the sea-to-land transition of three terrestrial hermit crab species under different salinity conditions. Our results suggest that 25 ppt salinity is an appropriate condition for culturing megalopae and early juveniles of these coenobitids. To further elucidate the salinity adaptation of megalopae and early juveniles of coenobitid crabs, survival and emigration behaviour as well as osmoregulatory capacity should be investigated under a broader range of salinity levels in future studies.

■ Acknowledgements

We would like to acknowledge the Okinawa Prefectural Board of Education and the Agency for Culture Affairs, Ministry of Education, Culture, Sports, Science and Technology of Japan, for permission to collect the land hermit crabs. We are grateful to the anonymous reviewers and the editor for their valuable comments and suggestions, which have improved the manuscript. This study was supported by JSPS KAKENHI grant number JP24310171 to KH.

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