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Predation risk management of sea stars (*Asterias amurensis* and *Distolasterias nipon*) by adjusting the density and size of seeded scallops (*Mizuhopecten yessoensis*): an improvement to local mariculture

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Abstract

Optimizing the release density and size of juvenile commercial species for local ecosystems is a critical issue that should be considered when countering predation impacts. To ascertain whether mariculture production of the Japanese scallop (*Mizuhopecten yessoensis*) could be enhanced by modifying releasing practices, we experimentally investigated the effects of density and size of scallop seeds on their survival in the presence of two sea star species, *Asterias amurensis* and *Distolasterias nipon*, with different predation capacities. Under current mariculture practices, the juveniles are briefly exposed to air just before release; therefore, we also examined how air exposure stress increased the predation risk. Scallop survival in the presence of both sea stars increased by $>20\%$ by increasing scallop size from 30 to 50 mm. Increasing scallop density (range: 5 to 30 scallops m^{-2}) increased each individual's survival in the presence of *A. amurensis* but had no significant effect on predation by *D. nipon*. Therefore, the release of smaller quantities of large-sized scallops rather than larger quantities of small scallops is recommended to reduce *D. nipon* predation. In the presence of sea stars, especially by *D. nipon*, the predation impact on small scallops increased after just a few hours of air exposure, indicating that air exposure of juvenile scallops should be minimized. Our results will mitigate the economic cost of mariculture by facilitating the determination of optimal release conditions for juvenile scallops.

Keywords Air exposure · Mariculture · Predator–prey relationship · Prey density · Prey size

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Introduction

While bivalve mariculture, commercial cultivation of high-value mollusks (e.g., oysters, clams, mussels, and scallops) in the open ocean, is increasing globally (FAO 2021; National Research Council 2010), losses through predation are one of the major threats to this industry. Sea stars and crabs are general predators of various mariculture bivalve species (Schweitzer and Feldmann 2010; Byrne et al. 2013; Brand 2016). Local predators are often removed before the release of juvenile mariculture species because this is thought to effectively decrease the mortality rate of these juveniles (Bax et al. 2006; Barkhouse et al. 2007); however, sea stars can be keystone species in the local ecosystems (Byrne et al. 2013). Therefore, excessive removal of predators can directly or indirectly affect the interactions of various species in communities and should be avoided (Dulvy et al. 2004; Heithaus et al. 2008).

Scallops, pectinid bivalves, are important species for both aquaculture and mariculture around the world. The Japanese scallop (*Mizuhopecten yessoensis*) is currently the most harvested scallop in the world (Kosaka 2016). They can swim short distances and have a high-escape ability (Brand 2016). In contrast, two sea stars, *Asterias amurensis* and *Distolasterias nipon*, are reported as major predators of Japanese scallops in mariculture fields (Volkov et al. 1983; Silina 2008) and their predation abilities differ from each other (Miyoshi et al. 2019; Nishimura et al. 2019). Currently, to minimize predation mortality, there is exhaustive removal of sea stars from the scallop fishing grounds before releasing juvenile stocks; however, Miyoshi (2018) reports that those sea stars have a relatively high mobility (e.g., 45.9 m h^{-1} maximum in *A. amurensis*) and they can quickly invade fishing grounds from outside areas. Thus, scallops are exposed to predation threats immediately after release, and alternative ways to prevent predation, that do not depend on sea star removal, are needed. To enhance the survival of mariculture species, optimizing the density and size of mariculture juveniles is thought to be a viable alternative to excessive removal of predators. For Japanese scallop, the effects of scallop size and water temperature on the predation behavior of sea stars have been examined (Miyoshi et al. 2019; Nishimura et al. 2019). These studies reported that the size of the scallop is most relevant to the predation success of sea stars and that the predation success drastically decreased with increasing scallop size. However, the studies only tested a single size of scallops ranging from 30 to 120 mm in each trial; the predation vulnerability of various mixed scallops with sizes ranging from 30 to 60 mm and their interaction with scallop density has not been investigated.

Furthermore, when juvenile Japanese scallops are released, they are often exposed to the air for several hours due to handling. Tamura et al. (1956) reported that the mortality of juvenile Japanese scallops increased after air exposure. Moreover, Miyazono et al. (2008) report that triglyceride content, representing energy reserves in the adductor muscle, decreased after air exposure and handling stress. In other scallops, an effective escape response (e.g., jumping and swimming) against predators requires a vigorous adductor muscle, whose activity might be weakened by exposure to air and handling stress (Minchin et al. 2000; Pérez et al. 2008). Although the predation risk of Japanese scallop is also expected to increase after air exposure and handling stresses, how those stressors can be mitigated by changing density or size of the releasing seeds is yet unknown.

In the present study, we carried out two laboratory experiments to investigate: (1) the effect of different densities and release size classes of juvenile Japanese scallops on survival rate and number of consumed individuals by sea stars *A. amurensis* and *D. nipon* and (2) the effect of air exposure on predation risk by sea stars in juvenile scallops.

Through these examinations, we attempted to optimize the release density and size of scallops against sea star predation and to propose a basis for the releasing process that can be applied to mariculture.

Materials and methods

Collection and acclimation of scallops and sea stars

Experiments were conducted between May and July 2016 to 2018 to ensure that both water and air temperatures were similar to those during the actual scallop release season along the Sea of Okhotsk coast of Hokkaido in northern Japan, where over 50% of Japanese scallop production occurs. The light/dark regime in all experiments was approximately 16/8 h.

Before the start of the experiments, sea stars were collected by towing fishing dredges (at approximately 35–50-m depths) across the scallop fishing ground near Abashiri, in the Sea of Okhotsk, to obtain sea stars similar in size to those observed in mariculture fields (*A. amurensis*, $n=53$, 133.1 ± 24.9 mm in ray length, 395.5 ± 48.6 g in wet body mass; *D. nipon*, $n=53$, 139.2 ± 22.1 mm in ray length, 322.9 ± 38.2 g in wet body mass). Scallops were acquired from natural spat that was cultured in a cage for 1 year to obtain juvenile scallops of the size used in mariculture operations (shell height, measured as the distance between the umbo and the tip of the valves: 20.1–59.8 mm). Sea stars and scallops were acclimated separately in tanks (length × width × height: 1.8 m × 0.9 m × 0.7 m) in the Abashiri Fisheries Science Centre for 2–3 weeks. The density of the acclimated animals was 6–10 individuals m^{-2} in each tank. Natural seawater flowed into each tank at a rate of approximately 0.9 $L{\cdot}h^{-1}$, and no food was supplied to the sea stars or scallops. Sea stars and scallops were not reused in subsequent experiments.

Effects of density and size on predation of scallops

To examine how predation risk from sea stars changed in relation to the density and size of juvenile scallops, we conducted an experiment in round tanks (base area: 1.1 m^2, height: 0.8 m) with natural seawater flowing at a rate of approximately 0.9 $L{\cdot}h^{-1}$ and with a temperature range of 10.6–14.9 °C. We randomly selected scallops from the acclimation tank and placed 5, 10, 20, and 30 scallops (21.5–59.4 mm in shell height) in round tanks of different sizes kept a constant density, that is, five scallops per m^{-2}. Subsequently, one individual of either *A. amurensis* or *D. nipon* was added to each tank. Thus, a predator had a choice of prey sizes. Six to nine replicate experimental trials were conducted for each combination of sea star species and scallop density category, and each trial lasted 5 days. The experiments were conducted in eight tanks from May to June 2016 and from May to July 2017. Experimental tanks were monitored once a day during each trial (10:00–12:00).

Dead scallops without any soft tissues were considered preyed-upon individuals, and those with remaining soft tissues were considered to have died naturally. The natural death of the scallops was not observed in any experiment; therefore, it was assumed that natural death did not affect the results of the analysis. Dead scallops were replaced with live scallops of a similar size once a day to maintain prey availability. At the end of each trial, the shell height of all scallops, living and dead, was measured (± 0.1 mm).

Effect of air exposure on predation of scallops

In Japanese scallop mariculture, juvenile scallops are temporarily exposed to air when they are removed from aquaculture cages before their release (Nishihama 1994; Kosaka 2016). To estimate predation risk due to air exposure, either *A. amurensis* or *D. nipon* (1 individual per m^{-2}) and 10 juvenile scallops (shell height: 22.1–59.4 m) were placed in a tank (tanks were of the same size as above, 10 scallops per m^{-2} density). Since juvenile scallops may be exposed to air for approximately several tens of minutes in actual release operations, the exposure time was set at 60 min in this study. One group of scallops was exposed to air for 60 min, whereas the other group was not exposed before being transferred to a tank. Ten replicate trials were conducted for each combination of sea star species and each condition. The experiments were conducted in six or eight tanks at a time from May to June 2017 and from May to July 2018. Experimental tanks were monitored once a day during each trial (10:00–12:00). The air and water temperatures during the experiment were 14.6–18.2 °C and 13.6–16.9 °C, respectively.

Statistical analyses

All data processing and statistical analyses were performed in R version 3.6.1. (R Core Team 2019) using "lme4" (https://cran.r-project.org/web/packages/lme4/lme4.pdf) and "MuMIn" (https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf) packages. For the first experiment, the effects of scallop density and scallop shell height on the survival rate (defined as the proportion of scallops alive at the end of the experiment) of scallops in the presence of each sea star species (*A. amurensis* or *D. nipon*) were analyzed using generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function. The response variable was the binary data describing whether the scallops were preyed upon by sea stars during the experiment (i.e., preyed = 0, survived = 1). The explanatory variables were density (numeric class) and scallop shell height (numeric class). The occurrence of predation by *A. amurensis* and *D. nipon* on scallops was opportunistic (Miyoshi et al. 2019; Nishimura et al. 2019), whereas other *Asterias* spp. selected a prey of a particular size (Barbeau and Scheibling 1994a). In the present analysis, therefore, we considered the effect of prey size preference with randomly located tanks as the random factor with Gaussian distribution. For model selection, the interaction of explanatory variables was also evaluated. The multicollinearity between explanatory variables was evaluated using variance inflation factors (VIF). The log-likelihood was also assessed by maximum likelihood estimation for the adoption of explanatory variables. The optimal GLMMs were selected using the Akaike information criterion (AIC; Burnham and Anderson 2004). Residual deviance and degrees of freedom (df) are the number of parameters included in a model determined using the maximum likelihood procedure; those factors were used to evaluate the overdispersion for each model. Finally, the range of shell height at which the scallop survival rate was 50% (M_{50}) was calculated for each combination of sea star species and scallop density category.

For the first experiment, we also analyzed the number of consumed scallops per day as a response variable to assess the change in predation amount by each sea star species in relation to scallop density. We used GLMMs with Poisson error distribution and log link function, scallop density (numeric class) as an explanatory variable, and the replication tanks as a random factor. In this analysis, the scallop size was not considered (i.e., scallop size was pooled) because sea stars could select from among scallops of various sizes that were simultaneously available to them. The multicollinearity between explanatory variables was also evaluated using VIF. The log-likelihood was assessed by maximum likelihood estimation for the adoption of explanatory variables, and the optimal GLMMs were selected using the AIC. Residual deviance, df, and Pearson's chi-squared tests were used to evaluate the overdispersion for each model.

For the second experiment, the effects of scallop size and air exposure condition on the survival rate of scallops (binary data: preyed = 0, survived = 1, similar to above) in the presence of each sea star species were analyzed using a GLMM with a binomial error distribution and logit link function. The explanatory variables shell height (numeric class), air exposure condition (unexposed or air-exposed, factorial class), and replication tanks were random factors. For the model selection, the interaction of explanatory variables was also evaluated. The multicollinearity between explanatory variables was evaluated using the VIF. The log-likelihood was assessed by maximum likelihood estimation for the adoption of explanatory variables, and the optimal GLMMs were selected using AIC. Residual deviance and df were used to evaluate the overdispersion for each model. Finally, the range of shell heights at M_{50} for scallops was calculated for each sea star species.

Results

Effects of density and size on predation of scallops

In the presence of *A. amurensis*, the density and shell height of Japanese scallops were selected as the explanatory variables in the model for determining the survival rate of scallops using the maximum likelihood procedure (Table 1A: model ID #4, log-likelihood: – 184.7, AIC: 377.4, in *A. amurensis*). Scallop survival rate increased with increasing shell height (Table 2A; Fig. 1A). Scallop density affected the relationship between shell height and survival rate, whereby the survival rate of scallops with the same shell height decreased at lower densities. Shell height at M_{50} decreased with increasing scallop density; M_{50} at 5, 10, 20, and 30 individuals m^{-2} was 31.3 mm, 24.1 mm, 9.8 mm, and – 4.5 mm, respectively. In contrast, in the presence of *D. nipon*, only shell height was selected as the explanatory variable in the model for the survival rate of scallops (Table 1A: model ID #3, log-likelihood: – 109.0, AIC: 224.0, in *D. nipon*); shell height at M_{50} was estimated at 39.4 mm. Although the difference between models #3 and #4 was quite small, the result of this model selection implied that the effect of density on predation was smaller for *D. nipon* than *A. amurensis*. In the presence of *D. nipon*, the survival rate of Japanese scallop changed more abruptly at around M_{50}-shell height than it did with *A. amurensis* (Table 2A; Fig. 1B).

Density was selected as the explanatory variable in the model for the number of consumed scallops under predation by both sea stars (Table 1B). Log-likelihoods and AICs of best models were – 100.9 and 207.8 in *A. amurensis* (model ID #2) and – 181.6 and 369.2 in *D. nipon* (model ID #2), respectively. The number of consumed scallops increased with increasing scallop density. When density of Japanese scallop was constant, *D. nipon* predated more scallops than *A. amurensis* (Table 2B; Fig. 2).

Table 1 Results of generalized linear mixed models (selected using AIC) for (A) the survival rate of scallops (*Mizuhopecten yessoensis*) and (B) number of consumed scallops per day under different scallop densities and (C) the survival rate of scallops under different air exposure conditions when preyed upon by sea stars (*Asterias amurensis and Distolasterias nipon*) in laboratory experiments

Response variable	Sea star species	Model ID	Explanatory variable	Log-likelihood	AIC	Residual deviance	Degree of free-dom
(A) Survival rate of scallops	*A. amurensis*	4	DS + SH	−184.7	377.4	369.4	507
		3	SH	−191.4	388.8	382.8	508
		2	DS	−197.1	400.3	394.3	508
	D. nipon	3	SH	−109.0	224.0	218.0	566
		4	DS + SH	−108.5	225.1	217.1	565
		1	-	−354.5	713.1	709.1	567
(B) The number of consumed scallops	*A. amurensis*	2	DS	−100.9	207.8	201.8	92
		1	-	−107.1	218.1	214.1	93
	D. nipon	2	DS	−181.6	369.2	363.2	110
		1	-	−203.5	410.9	406.9	111
(C) Survival rate of air exposed scallops	*A. amurensis*	2	SH	−78.9	163.8	157.8	143
		5	SH + CD	−78.9	165.8	157.8	142
		1	-	−100.5	205.1	201.1	144
	D. nipon	4	SH + CD	−90.5	189.1	181.1	248
		3	SH	−112.8	231.7	225.7	249
		2	CD	−133.6	273.2	267.2	249

AIC Akaike information criterion, *DS* density of scallops, *SH* shell length of scallops, *CD* condition of scallops (exposed to air or not). (A), (B) and (C) were evaluations for 8, 2, and 8 models, respectively, in the presence of different sea stars *A. amurensis* and *D. nipon*. The model numbers indicate the ID in models evaluated for (A), (B), and (C), respectively. Residual deviance and degrees of freedom (df) are the number of parameters included in a model, determined using the maximum likelihood procedure, and those factors were used to evaluate the overdispersion for each model. Log-likelihood and AIC were used to evaluate the goodness of fit for each model

Table 2 Details of the best models produced for (A) the survival rate of scallops (*Mizuhopecten yessoensis*) under different scallop densities and offered to two predatory sea star species (*Asterias amurensis and Distolasterias nipon*), with a binomial error distribution and logit link function, (B) the number of consumed scallops per day under different scallop densities with a Poisson error distribution and log link function, and (C) the survival rate of scallops under different air exposure conditions when preyed upon by sea stars in laboratory experiments with a binomial error distribution and logit link function

Response variable	Sea star species	Explanatory variable	Estimate	SE	*Z*-value	Random effect parameter (SE)
(A) Survival rate of scallops	*A. amurensis*	Intercept	−2.98	0.70	−4.21	0.46 (0.21)
		SH	0.06	0.01	4.66	
		DS	0.09	0.01	4.78	
	D. nipon	Intercept	−14.85	1.29	−11.49	< 0.001 (< 0.001)
		SH	0.37	0.03	11.87	
(B) Number of consumed scallops	*A. amurensis*	Intercept	−1.14	0.28	−3.97	0.06 (0.02)
		DS	0.04	0.01	3.50	
	D. nipon	Intercept	−0.46	0.17	−2.66	< 0.001 (< 0.001)
		DS	0.05	0.01	7.83	
(C) Survival rate of air exposed scallops	*A. amurensis*	Intercept	−6.56	1.27	−3.72	< 0.001 (< 0.001)
		SH	0.19	0.03	3.63	
	D. nipon	Intercept	−13.35	2.00	−6.67	0.66 (0.33)
		CD	3.60	0.82	4.38	
		SH	0.26	0.04	6.49	

SE standard error, *DS* density of scallops, *SH* shell length of scallops, *CD* condition of scallops (exposed to air or not). *Z*-value is calculated by dividing the estimate by the SE. Random effect parameters indicate variation in the replication tanks in each experiment

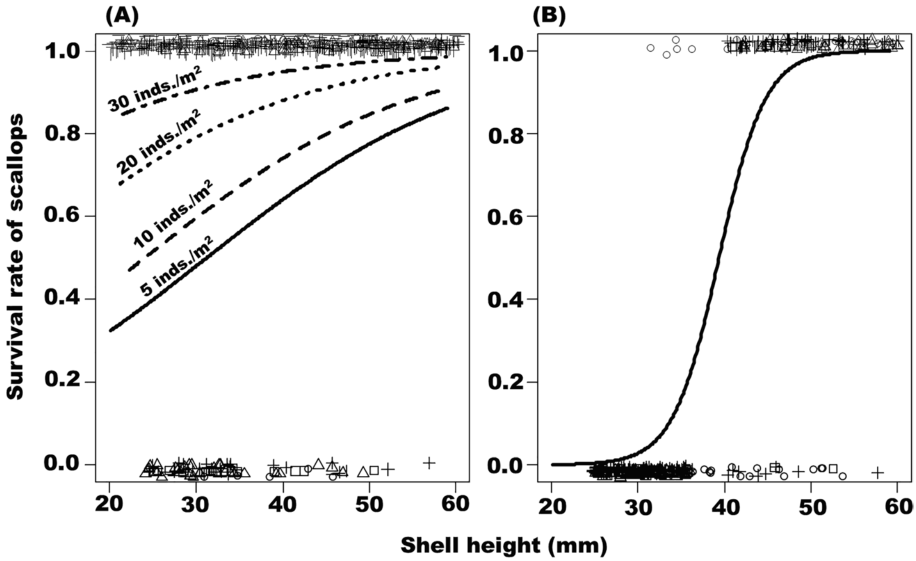
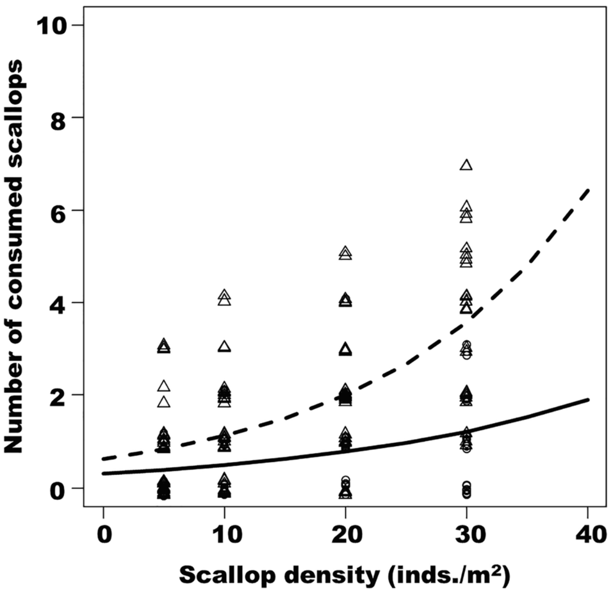


Fig. 1 Relationship between the survival rate of *Mizuhopecten yessoensis* scallops and their shell height under different scallop densities preyed upon by sea stars *Asterias amurensis* (**A**) and *Distolasterias nipon* (**B**). Open circles (solid line), squares (dashed line), triangles (dotted line), and crosses (chain line) represent values obtained at scallop densities of 5, 10, 20, and 30 individuals m^{-2}, respectively. The four logistic curves represent scallop survival probability estimated using a generalized linear mixed model

Fig. 2 Relationship between the number of consumed *Mizuhopecten yessoensis* scallops (shell height: 20.1–59.8 mm) and scallop density for predatory sea star species *Asterias amurensis* and *Distolasterias nipon*. Open circles (solid line) and triangles (dashed line) represent values for *A. amurensis* and *D. nipon*, respectively. The two curves represent consumption rate estimated using a generalized linear mixed model



Effect of air exposure on predation of scallops

In this experiment, shell height was selected as the explanatory variable in the model for the survival rate of scallops under predation by both sea star species (Table 1C); however, the treatment of air exposure was selected as the explanatory variable only in the presence of *D. nipon*, whereby shell height at M_{50} of air-exposed scallops was larger (45.3 mm) than that of unexposed scallops (34.3 mm) and that of under *A. amurensis* treatment (34.2 mm). The survival rate around M_{50} of air-exposed scallops changed more abruptly than for the unexposed scallops in the presence of *D. nipon* (Table 2C; Fig. 3). Log-likelihoods and AICs of best models were − 78.9 and 163.8 in *A. amurensis* (model ID #2) and − 90.5 and 181.1 in *D. nipon* (model ID #4), respectively.

Discussion

Effect of density and size on predation of scallops

The survival rate of Japanese scallops increased with increasing shell height in the presence of both sea star species (Fig. 1). Miyoshi et al. (2019) and Nishimura et al. (2019) gave the different size ranges of scallops separately to the sea star species and reported that the predation success of sea stars on Japanese scallop drastically decreased with increasing scallop size compared to other predation factors. The present study gave multiple size classes of juvenile scallops to sea stars at one time, and the results were consistent with

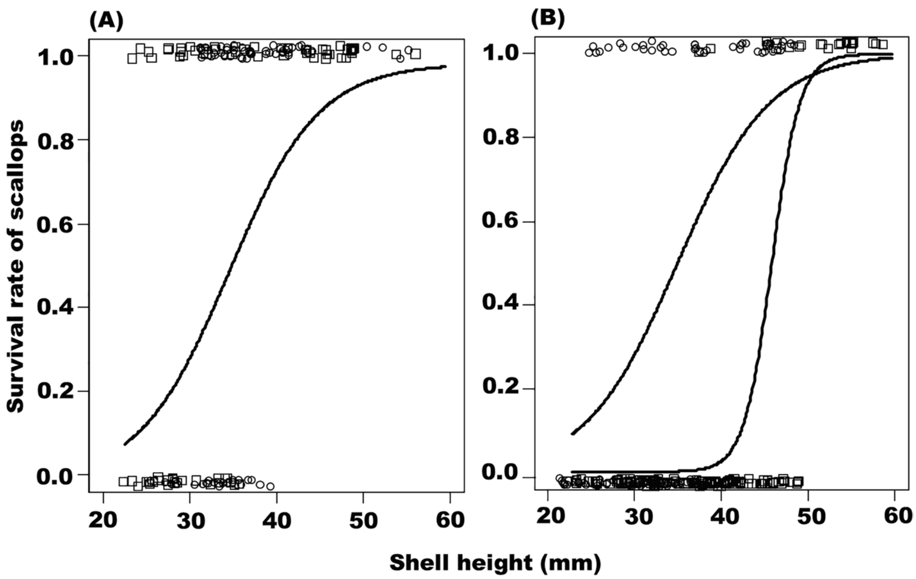


Fig. 3 Relationship between the survival rate of *Mizuhopecten yessoensis* scallops and their shell height under different air-exposure conditions (no exposure and 60-min exposure) preyed upon by sea stars *Asterias amurensis* (**A**) and *Distolasterias nipon* (**B**). Open circles (solid line) and squares (dashed line) represent values obtained for unexposed and air-exposed scallops, respectively. The two logistic curves represent scallop survival probability estimated using a generalized linear mixed model

these previous studies (Miyoshi et al. 2019; Nishimura et al. 2019). Those studies and our results indicate that increasing the size of released scallops is probably most effective for improving their survival rate in the presence of both sea star species, regardless of the density of scallops. The survival rate of scallop *Placopecten magellanicus* increases with increasing scallop size because their escape ability develops with size until approximately 70 mm (Dadswell and Weihs 1990; Manuel and Dadswell 1993). Our results were similar to those findings, and therefore, the positive relationship between shell height and scallop survival is a common feature of Pectinidae.

The effect of scallop density on the relationship between shell height and juvenile scallop survival differed among sea star species. In the presence of *A. amurensis*, the survival rate at same-shell height was higher at more dense conditions, and survival rate of smaller scallops was greatly improved with increased density. Additionally, the increase of scallop consumption by *A. amurensis* as scallop density increases is slight and suggests a limited consumption level by this sea star species, regardless of available scallop numbers (Fig. 2). From these results, we suggest that *A. amurensis* could not consume large quantities of scallops even when their density was high. *A. amurensis* caught only one scallop during one predation cycle (Miyoshi et al. 2019). Our findings are supported by previous studies that reported restricted scallop consumption by *Asterias* species due to their long prey-handling time and slow movement (Barbeau and Scheibling 1994a, c; Barbeau et al. 1998). Therefore, assuming the abundance of *A. amurensis* is constant, increasing the number of juvenile scallops possibly improves the ratio of survived scallops to released scallops.

In contrast, with *D. nipon*, the density of Japanese scallop had no obvious effect on the relationship between the survival rate of scallops and the shell height (Fig. 1). Also, *D. nipon* significantly increased the number of consumed juvenile scallops with increasing scallop density (Fig. 2). *D. nipon* has a shorter searching time for scallops and attacks multiple scallops simultaneously possibly due to the wider moving range of their rays (Miyoshi et al. 2019). We propose that their morphology and higher mobility allow *D. nipon* to prey on many scallops and suggest that the predation by *D. nipon* is a major threat to released scallops.

Effect of air exposure on predation of scallops

The effect of air exposure on the survival of Japanese scallops differed among sea star species. In the presence of *D. nipon*, the survival rate of air-exposed scallops was noticeably lower than that of unexposed scallops. An effective escape response in scallops (e.g., jumping and swimming) against predators requires a vigorous adductor muscle. However, air exposure and other handling stressors are reported to reduce arginine phosphate and ATP in the adductor muscle of scallops (Chih and Ellington 1983; Guderley and Pörtner 2010); consequently, those stressors possibly weaken the escape ability of scallops (Minchin et al. 2000; Fleury et al. 2005; Guderley and Pörtner 2010; Pérez et al. 2008). From our results and previous studies, it is possible that air exposure inhibited the escape behavior of young Japanese scallops and that *D. nipon* could consume many scallops. Previous studies examined the vulnerability of scallops after long-term air exposure and handling stress (> 12 h; e.g., Minchin et al. 2000). Our study demonstrates that the predation risk by sea stars on juvenile Japanese scallops increased even after a relatively short period of air exposure (60 min).

In the presence of *A. amurensis*, air exposure was not selected as an explanatory variable, and shell height of scallops was only selected as explanatory variable in the model for the survival rate of scallops. This indicates that air exposure had little effect on the level of predation by *A. amurensis*, and the size of scallops was a more critical factor. As mentioned above, *A. amurensis* moves slowly and has a long prey-handling time. Thus, the consumption rate by *A. amurensis* could not increase even if scallops were weakened by the air exposure. This indicates that air exposure had little effect on the predation by *A. amurensis*, and the size of scallops was probably most critical for scallop survival. In contrast, *A. vulgaris* and *A. rubens* selectively preyed upon scallops that were less active, regardless of their size (Barbeau and Scheibling 1994b). Although the survival of scallops was not affected by the air exposure by *A. amurensis*, air exposure should be avoided because weakened scallops may not be able to escape from them even though *A. amurensis* has a low predation ability.

Implications for scallop mariculture

The survival of scallops can be improved by approximately 10–20% by increasing the release size of scallops from 30 to 40 mm and 50 mm in the presence of both sea stars (1 individual m^{-2}). Scallop size ranges at M_{50} survival were 31.2–38.4 mm in the presence of *A. amurensis* and 40.3 mm in the presence of *D. nipon*, with 5–10 scallop individuals m^{-2}, which is the typical release density in the Japanese scallop mariculture (Goshima and Fujiwara 1994). Although juvenile scallops of around 40 mm in shell height are generally released in the current Japanese mariculture, the releasing size depends on the year and location and seems to range from 30 to 50 mm without any scientific reason (Miyoshi personal communication). The present study emphasizes the importance of being conscious about the juvenile size during release because the predation risk is greatly decreased by releasing larger scallops. The size of the juveniles can be increased by postponing the nursing period in the cage. However, this method may not be favorable, at least in our study site, because it takes about 1 month for a juvenile scallop of 30 mm to grow over 40 mm and air temperature rapidly increases during this postponing period (from May to June). The increased temperature would lead to another risk of mortality of the juveniles at the time of release. Therefore, we suggest growth enhancement of the juveniles by decreasing density in the nursing cage.

Our rearing experiment showed that the release of high-density scallops might improve their survival in the presence of only *A. amurensis*. However, the release of high-density scallops may incur a disadvantage for the survival and growth of scallops in the mariculture field. Silina (2008) reported that the growth rate of scallops decreased at high scallop density (up to 6 individuals m^{-2}) and that high densities of scallops attracted *A. amurensis* and *D. nipon*. Moreover, *D. nipon* tend to aggregate in response to the presence of young scallops immediately after their release (Volkov et al. 1983; Silina 2008). The release of low-density scallops could prevent aggregations of sea stars, and consequently, the excessive removal of sea stars from mariculture fields may not be needed.

The present study showed that relatively short-term exposure to air might increase vulnerability to sea star predation. In the mariculture fields, air exposure cannot be completely prevented, whereas a low air temperature reduced the effect of air exposure and handling stress for scallops when compared to higher temperatures (Minchin et al. 2000), and the recovery of scallops after transportation has been recommended to be carried out in water temperatures lower than 10 °C (Christophersen et al. 2008). Thus, the impact of air exposure can be reduced by releasing scallops during low-temperature seasons in the mariculture fields. Pérez et al. (2008) reported that air-exposed scallops *P. magellanicus* recovered from the stress 3 h after being released into seawater. Thus, predation mortality may also be higher for Japanese scallops during first 3 h after release. *Asterias amurensis* can move at a maximum speed of 45.9 m h^{-1} (Miyoshi et al. 2018). Therefore, the impact of air exposure can be reduced, and the unnecessary removal of sea stars from scallop fishing grounds can also be avoided by removing sea stars within a radius of about 150 m.

Our study proposed improvements to the release density and size of scallop juveniles in scallop mariculture. In the present mariculture process, there is a problem with releasing high-density and small scallops (Miyoshi 2018). Juvenile scallops are continuously released from the boat while sailing in the mariculture fields. Therefore, released scallops often form high-density clusters in a belt-like distribution immediately after the release (Yamamoto et al. 1999). Our results indicated that scallop survival rates significantly decreased with high densities in the presence of *D. nipon* and that the release process itself should be improved. Nishimura et al. (2019) demonstrated that the maximum allowable size of scallop prey for *A. amurensis* and *D. nipon* was 71% and 74% of their rays, respectively. Therefore, < 50 mm sea stars are almost not able to prey on > 40 mm scallops. Therefore, size selective removal of sea stars is required.

In conclusion, we recommend that low density (e.g., $5-8$ individuals m^{-2}) and increased scallop size (e.g., > 40 mm) might be more advantageous than the present common procedure (high density and small size). Additionally, mariculture operations with unavoidable air exposure should be done in the low-temperature seasons because air exposure at higher temperatures had a significant impact on the predation of scallops by *D. nipon*. Applying the results of our study to mariculture operations requires further investigations. The interactions between prey density, prey size, and multiple predators (e.g., Barbeau and Caswell 1999) will need to be clarified. Although our study demonstrated the predation impact on scallops by sea stars, the effect of sea star density on the relationship between scallop density and size and the mortality rate should be clarified. Furthermore, the preference of sea stars as prey species and the predation impact on scallops by sea star species should be also clarified in the presence of multiple prey species. Applying the results of our study to mariculture operations requires further investigations. In particular, we need to carefully consider the difference in the predator–prey interaction between the laboratory and wild environments. Moreover, we might have overestimated scallop survival in the experimental tanks if escape responses of scallops were hindered by the tank wall (Barbeau and Scheibling 1994b; Nishimura et al. 2019). However, there is also the possibility that released scallops encounter greater densities of sea stars in mariculture fields than expected in this study because sea stars *A. amurensis* and *D. nipon* occur at higher densities (> 1.5 individuals m^{-2}) in the fields (Miyoshi et al. 2018). Furthermore, we also need to compare sea stars' preference for prey to quantify the exact predation impact on scallops because *Asterias* spp. and *D. nipon* were only fed scallops in our experiment while they could also consume various animals (Wong et al. 2005). However, we also speculate that released juvenile scallops become the main prey of sea stars that invade from outside the fishing grounds because fishermen remove most of the benthic animals, including sea stars and other mollusks, prior to scallop release (Miyoshi 2018). Although our findings may be modified by accumulating knowledge regarding predator–prey interaction in the future, we conclude that the present study provides an overlooked point for improving scallop mariculture technique.

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Availability of data and material Results from the experiments performed by the authors are available from the authors on reasonable request.

Code availability The R codes used in this study are based on the publicly available packages presented in the Materials and Methods.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Declarations

Consent to participate Not applicable.

Consent for publication Not applicable.

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