Aggregation of adult abalone *Haliotis discus hannai* during the spawning season, and its associations with seasonal and interannual changes in the macroalgal community

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ABSTRACT: Clarification of the biological and/or physical factors determining the location requirements for spawning aggregations is necessary for understanding the population dynamics of free-spawning marine animals. We monitored the density of adult abalone *Haliotis discus hannai* on 2 types of artificial reefs with different heights (tall and short blocks) and the surrounding seabed area in Otsuchi Bay, northeast Japan, from February 2016 to December 2019. In addition, the number of neighboring adults located within a 50 cm radius from each individual was counted from March 2017 to December 2019. Algal succession in the 3 types of location (tall and small blocks, seabed) was monitored and compared with temporal fluctuations in adult abalone density. Our results show that the fluctuations in density were different among the 3 locations, especially during the spawning season (August–October). On tall blocks, clear increases in adult abalone density and number of neighboring adults were confirmed during the spawning seasons in 2016 and 2019. In contrast, there was no clear increase in the adult density on small blocks and surrounding bottom areas. Aggregations on the tall blocks clearly differed among the 4 years, and the difference was considered to be influenced by differences in the macroalgal species and coverage during the spawning season. This is the first study to report that a difference in phenology among algal species is a key factor in the formation of spawning aggregations of a free-spawning marine animal.

KEY WORDS: Aggregation · Kelp bed · Haliotidae · Algal succession · Northeast Japan

1. INTRODUCTION

Mechanisms that ensure successful external fertilization are important for free-spawning animals. In shallow coastal waters, strong water flows caused by waves and tidal fluxes can rapidly disperse spawned gametes from both sexes (Denny & Shibata 1989, Metaxas et al. 2002). Thus, reproductive behaviors leading to high concentrations of gametes in the water column are necessary for marine invertebrates inhabiting shallow waters with highly hydrodynamic environments.

Known as the Allee effect (Allee 1931), lower densities of free-spawning marine invertebrates lead to larger distances between potential mates and thus lower probabilities of fertilization (Levitan & Petersen 1995, Lundquist & Botsford 2004). This inverse density dependence is an important factor for the population dynamics of various marine invertebrates, including sea urchins (Quinn et al. 1993), scallops

(Caddy 1989), giant clams (Munro 1993) and abalone (Babcock & Keesing 1999). Thus, sustaining the population densities of target species high enough to maintain a sufficient probability of fertilization is necessary for fisheries or conservation management.

Spawning in aggregations is an effective behavior that shortens the distance between potential mates and enables high concentrations of gametes at a small scale. In addition, closely aggregated individuals can share environmental cues for spawning, which ensures synchronous spawning. Thus, spawning aggregations can compensate in part for low overall densities, as reported for scallops (Bayer et al. 2018). Spawning aggregations of ripe adults have been detailed especially in echinoderms such as species of brittle stars (Selvakumaraswamy & Byrne 2000), sea stars (Clark 1968) and a cidaroid sea urchin (Young et al. 1992).

Abalone (Haliotidae, Mollusca) are dioecious, free-spawning marine invertebrates, and eggs require a high density of sperm within a short period of time after release to ensure a high fertilization rate (Babcock & Keesing 1999). Many abalone species are important fishery species, and thus have been exploited, and populations of some species are seriously depleted. *Haliotis discus hannai* is the only abalone species distributed along the Sanriku Coast, on the Pacific side of northeastern Honshu Island, Japan, and is economically important as a fishery resource. This species is a common and conspicuous grazer in the food web of the rocky shore ecosystem on the Sanriku Coast (Won et al. 2013). The population of *H. discus hannai* on the Sanriku Coast was strongly damaged by the tsunami and other events associated with the Great East Japan Earthquake in 2011, although the tsunami impacts on the abalone populations differed among areas and locations even inside bays (Kawamura et al. 2014, Hayakawa et al. 2017). In the recovery process of damaged populations, the extent to which the abalone aggregate during the spawning season is one of the critical factors for estimating potential population recovery.

Previous field studies elucidating the role of adult distributions during the spawning season have concluded that spawning aggregations can enhance successful fertilization for populations at low densities (*H. laevigata*, Shepherd 1986; *H. kamtschatkana*, Seamone & Boulding 2011; *H. corrugata*, Catton & Rogers-Bennett 2013). In addition, spawning of some haliotids is induced by the presence of neighboring individuals or gametes of the opposite sex (Morse et al. 1977, Counihan et al. 2001). Counihan

et al. (2001) inferred that gravid *H. asinina* delay releasing their gametes until more individuals surround them and found that males release sperm more frequently when more abalone are present. However, the effect of the presence or absence of spawning aggregations on gametic release and subsequent fertilization success has not been clarified for *H. discus hannai*.

Although the factors that directly synchronize gamete release in wild abalone populations remain largely unknown, previous studies on abalone spawning have identified water temperature (*H. cracheroidii*, Webber & Giese 1969; *H. discus discus*, *H. madaka* and *H. gigantea*, Tanaka et al. 1986), typhoon events (*H. diversicolor*, Onitsuka et al. 2007) and lunar cycle and/or tidal amplitude (*H. asinina*, Counihan et al. 2001) as environmental factors triggering spawning events. The spawning of *H. discus hannai* has been reported to be triggered by typhoons or minor storms during its spawning season (August–October) (Sasaki 1985, Sasaki & Shepherd 1995). As these environmental factors as spawning cues occur unpredictably, aggregations of abalone species need to be maintained until the cue for synchronized gamete release occurs. Thus, the locations where spawning aggregations are maintained are considered to provide favorable conditions for the survival of adults.

However, for marine benthic animals, including abalone species, little information is available about where spawning aggregations occur and what factors are important for the formation of aggregations. Moving to elevated positions on reefs during spawning events has been observed in *H. kamtschatkana* (Breen & Adkins 1980), ophiuroids and sea stars (Himmelman et al. 2008). Coleman et al. (2006) suggested that small-scale variations in abundance of food may influence patterns of aggregation of the limpet *Patella vulgata* in winter, thereby creating potential spawning aggregations. Although these previous studies offer information about biological and/or physical factors associated with the location of spawning aggregations, they are largely based on qualitative observations.

The abalone *H. discus hannai* shows clear ontogenetic habitat shifts among algal communities which offer suitable habitats for its different growth stages; the main habitat for adults is kelp beds (Takami & Kawamura 2018). All kelp species along the Sanriku Coast are annual species (except for *Eisenia bicyclis* in southern areas of the coast). The biomass of the kelp species is strongly affected by water temperature, especially during late winter and early spring,

which fluctuates from year to year, depending on the relative strengths of the 2 offshore current systems (the cold Oyashio Current and the warm Kuroshio Current) (Yatsuya et al. 2020). The perennial *Sargassum yezoense*, one of the dominant macroalgal species forming algal beds on the Sanriku Coast, shows a clear seasonal fluctuation in biomass resulting from defoliation of the thalli (Kodama et al. 2020). In addition, the perennial brown alga *Rugulopteryx okamurae*, which emits chemical cues to prevent grazing by herbivores, including abalone (Shiraishi et al. 1990, 1991), was reported to expand its turf-like distribution where kelp beds showed shrinkage on the Sanriku Coast (Taniguchi et al. 1987). Considering the relationships between the distribution of the abalone and the algal composition, temporal changes in macroalgal communities could affect the suitability of locations for abalone aggregations during the spawning season.

In our previous monitoring survey of abalone populations in Otsuchi Bay on the Sanriku Coast (Hayakawa et al. 2017), a large number of adult abalone were sometimes observed during the spawning season located on the crest areas of elevated reefs with kelp beds of *Saccharina japonica* var. *religiosa*. This phenomenon might have indicated the formation of spawning aggregations, but this could not be verified due to the lack of information on the distribution of abalone during the other seasons. In addition, which physical factor (elevated location) or biological factor (occurrence of kelp) was important remained unclear, even if these accumulations of closely spaced adults did represent spawning aggregations.

Here we conducted a monitoring survey of the density of adult abalone on artificial reefs of different heights and on the surrounding seabed area over a 4 yr period in Otsuchi Bay. In addition to measuring the density, we also counted the number of neighboring adults for each individual over 3 consecutive years. The algal composition on the artificial reefs was also monitored over a 4 yr period. Based on results from this long-term monitoring study, we evaluated (1) the presence or absence of aggregations formed by the abalone *H. discus hannai* during its spawning season, (2) which elevated places or the presence of specific algal species are important for forming an aggregation and (3) interannual changes in an aggregation during the spawning season and the reasons for the change.

2. MATERIALS AND METHODS

2.1. Study site

The survey was conducted at Nagane, at the entrance of Otsuchi Bay on the Sanriku Coast (Fig. 1). In the subtidal area at Nagane, algal zonation of kelp beds consisting of *Saccharina japonica* var. *religiosa* at 2–6 m depth and a crustose coralline algal (CCA) area at 7–12 m depth have been observed (Kawamura et al. 2014). Two types of concrete artificial reefs (n = 6 for each type) were set on the seabed at 8–9 m depth in 1980 (Fig. 2a,b). One type of artificial reef consisted of a concrete block of 2.6 m height shaped in a cross when viewed from above, and supported vertically by 4 legs (tall block). The other comprised a concrete block of 1.2 m height with a triangular shaped upper surface and supported by 3 hexagonally shaped vertical legs (small block). The tall and small blocks were located within a nearly flat area of seabed covering 30 m in a northeast–southwest direction × 15 m in a northwest–southeast direction (Fig. 2c). The seabed surrounding these artificial reefs consisted of stones and cobbles covered by CCA, accompanied by a conspicuously high density of the sea urchin *Mesocentrotus nudus*.

2.2. Field survey

The number of *Haliotis discus hannai* on each of the 6 replicate tall and small blocks was counted monthly from February 2016 to December 2019, except for January, February and March 2019. The undersides of the tall and small blocks were not observed because accurate observations were difficult. Preliminary observations showed that such shady areas were covered by various sessile animals and
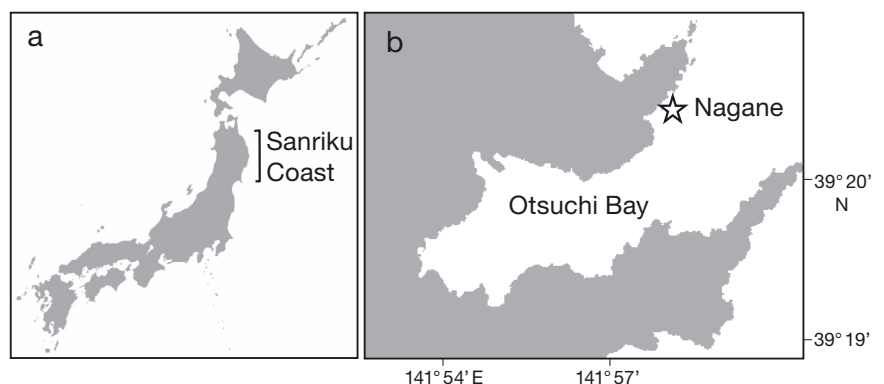

Fig. 1. (a) Study area along the Sanriku Coast, eastern Honshu, Japan. (b) Site where surveys were conducted at Nagane, at the entrance of Otsuchi Bay
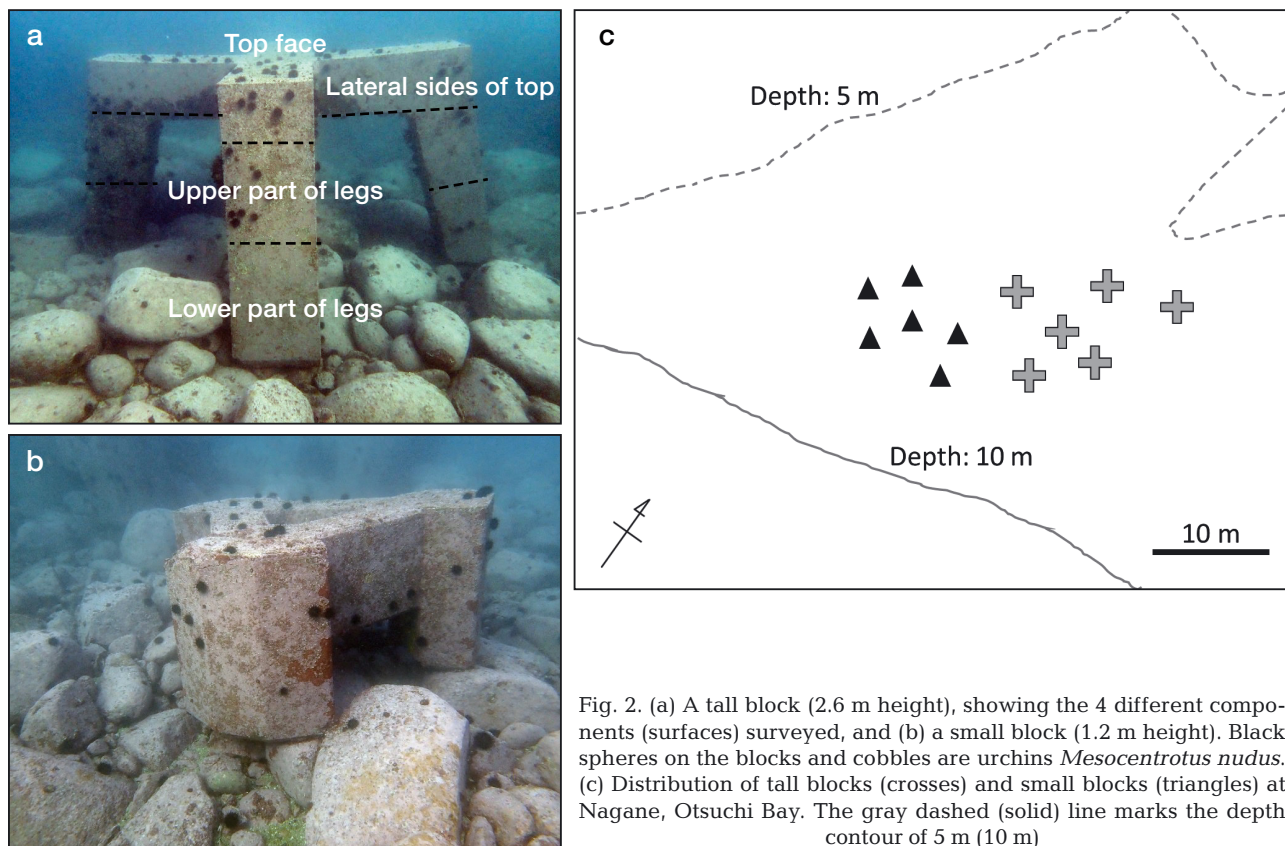
Fig. 2. (a) A tall block (2.6 m height), showing the 4 different components (surfaces) surveyed, and (b) a small block (1.2 m height). Black spheres on the blocks and cobbles are urchins *Mesocentrotus nudus*. (c) Distribution of tall blocks (crosses) and small blocks (triangles) at Nagane, Otsuchi Bay. The gray dashed (solid) line marks the depth contour of 5 m (10 m)

that abalone were scarce on the undersides of the blocks.

The shell length (SL), i.e. the maximum shell diameter, of each abalone was measured *in situ* with calipers to an accuracy of 0.1 mm. Individuals >50 mm SL were counted as adults (Won et al. 2010, Kawamura et al. 2014). The density of adults on each block was calculated as the number of adults divided by the horizontal top surface area of each block (5.43 m² for tall blocks and 2.35 m² for small blocks).

In terms of the tall blocks, the surface area was separated into 4 components (see Fig. 2a): top face (5.43 m²), lateral sides of the top (9.60 m²), upper part of legs (9.00 m²) and lower part of legs (9.00 m²). The density of the adults on each component was calculated as the number of adults divided by the surface area of each respective component.

In addition to the densities on the artificial reefs, the density of adult abalone on the seabed surrounding the blocks was surveyed monthly from April 2016 to December 2019, except for May 2016; July, September and November 2018; and January, February, March and April 2019. Six quadrats (2 × 2 m) were haphazardly placed on the seabed, and the number of abalone within each quadrat was counted. The SL

of each individual was measured in the same way as that for the abalone on the artificial reefs, and the densities of adults were calculated.

As CCA areas are habitats for juvenile abalone, whereas the main habitats for adult abalone are kelp beds (Takami & Kawamura 2018), we surveyed the abalone density on the seabed at 5–6 m depth, where algal beds of large brown algae (mainly *Saccharina japonica* var. *religiosa* and *Sargassum yezoense*) formed on bedrock and cobbles, as an additional index of the abalone abundance at Nagane, in October of every year during the survey. A 50 m long rope marked at intervals of 10 m was laid from the fixed start position in the same direction parallel with the shoreline, and 6 quadrats (2 × 2 m) were haphazardly placed on the seabed along the rope at intervals of 10 m. The number of abalone and SLs of the individuals inside the quadrats were recorded.

For all adult abalone on the tall and small blocks, the number of neighboring adults was surveyed at the same time as abalone were counted, from March 2017 to December 2019, except for January, February and March 2019. The number of adults located within a 50 cm radius from each individual on the same surface was counted. For 2 individuals on dif-

ferent sides (e.g. one on the top face and the other on a lateral side of the top) for which a direct distance could not be measured, the sum of the minimum lengths on the 2 faces between the 2 individuals was calculated. In this case, the individuals on a different surface within a 40 cm distance in sum were counted as neighboring adults, as well as individuals on the same side within a 50 cm radius. When no adult or only 1 adult was found on the tall blocks, the number of neighboring adults was counted as 0.

Concurrent with the counting of abalone, the coverage by algae, except for encrusting algae like CCA, on the top side of the tall and small blocks and on the seabed inside the quadrats was surveyed. The coverage of each algal species/group was estimated to the nearest 10%, based on visual observation by a diver. When coverage of an algal species/group was <10%, the degree of cover was recorded as either 5 or 1%, depending on its visually assessed abundance.

At each survey, water temperature immediately above the seabed adjacent to the artificial reefs was measured with a dive computer to the nearest 1°C. The data of water temperature in February and May 2019 were obtained separately by the same method.

2.3. Statistical analyses

Statistical analyses were conducted in order to determine whether abalone abundance differed between spawning (August to October) and non-spawning (May to July) seasons in each year. Because the horizontal top surface area differed between the tall and small blocks, the analyses were conducted separately. As abalone abundance is count data, generalized linear mixed models (GLMMs) with Poisson distributions and log link functions were used for data analysis. In the GLMMs, abalone abundance was set as the response variable, and spawning/non-spawning seasons and year were set as explanatory variables. Observation-level random effects were included to address overdispersion of residuals (Harrison 2014). In addition, random intercepts were included for each block to account for environmental differences.

For the small blocks, no abalone was observed during the non-spawning season in 2018. Therefore, the analyses were conducted by excluding the data from 2018. On the seabed, the number of adult abalone was very low throughout the 4 years, so that statistical analyses were not conducted.

To examine the effect of large brown algae and Dictyoteae species on the number of adult abalone in the

spawning and non-spawning seasons on the tall blocks, we conducted model selections in 2 ways. (1) Presence or absence of large brown algae (laminarian kelps, *Sargassum yezoense* and Dictyoteae species) were included as predictor variables in the global model, as were spawning season or non-spawning season. In this analysis, laminarian kelps and *S. yezoense* were assumed as facilitators for aggregations of abalone, whereas Dictyoteae species were assumed to be inhibitors of aggregations. The interactions between presence or absence of large brown algae and spawning/non-spawning season were included as predictor variables. (2) The coverage by large brown algae and by Dictyoteae species. were included as predictor variables in the global model, as well as spawning season or non-spawning season and the interaction between the coverage of large brown algae and spawning/non-spawning season. GLMMs with Poisson distributions of log link functions were used to analyze abalone abundance. Random intercepts were included for each year and each block to account for environmental and interannual differences. In addition, observation-level random effects were included and no overdispersion of residuals was found. Akaike's information criterion (AIC) was used to select the best fit models. All GLMMs were applied using the 'glmer' function in the R package 'lme4' in R version 4.0.2.

In order to determine if abalone abundance during the spawning season at Nagane differed among the 4 years, we used a 1-way ANOVA to examine if the density of the adults in the algal zone in October differed among the 4 years, as the data were homogeneous in variance (Levene test, $p < 0.05$). In addition, the density of the adults on the tall blocks in October was compared using a Kruskal-Wallis test with a Dunn-Bonferroni post hoc multiple comparison test among the 4 years, as the data were not homogeneous in variance (Levene test, $p > 0.05$). The density data were transformed ($\log n + 1$) in order to achieve homogeneity (Underwood 1981), before statistical analyses. One-way ANOVA and Kruskal-Wallis test with the Dunn-Bonferroni test were carried out with SPSS Statistics version 23.0 (IBM).

3. RESULTS

3.1. Size composition of *Haliotis discus hannai*

The total number of abalone found on the tall blocks, small blocks and surrounding seabed area during the survey was 1220, 169 and 72, respectively. The percentage of adults found in the 3 locations was

91.9, 91.1 and 70.8%, respectively. Thus, size composition was similar between the tall and small blocks, while the frequency of juveniles (<50 mm SL) was higher on the surrounding seabed than on the tall and small blocks (Fig. 3).

On tall blocks, the size composition of abalone on the top face and the lateral sides of the top were similar, and over 90% of the individuals on the 2 components were adults (Fig. 4). The number of abalone on the upper and lower parts of legs was lower, and the percentage of adults on the 2 components was lower than on the top face and the lateral sides of the top.
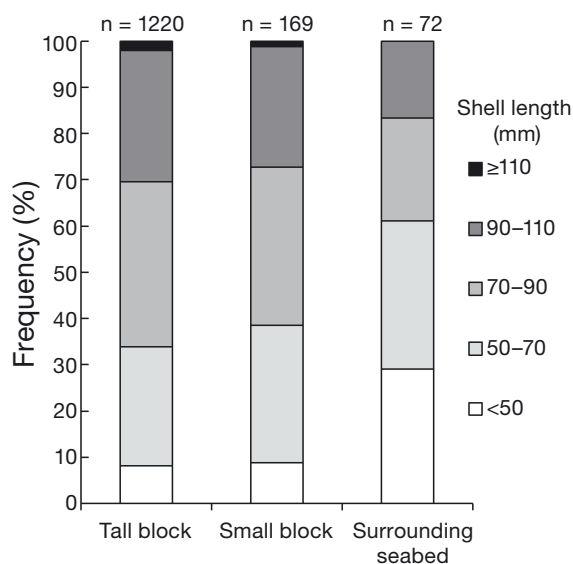

Fig. 3. Size compositions of *Haliotis discus hannai* on tall blocks, small blocks and the surrounding seabed. Sample sizes are shown above bars
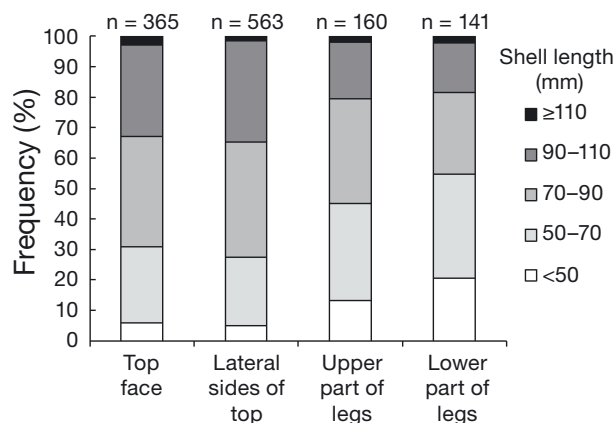

Fig. 4. Size compositions of *Haliotis discus hannai* on the 4 components of tall blocks (see Fig. 2a). Sample sizes are shown above bars

3.2. Adult density on artificial reefs

The average density of adult abalone on the tall blocks largely fluctuated during the survey period, ranging from 0.0 ind. m^{-2} (July and August 2018) to 3.4 ind. m^{-2} (October 2019) (Fig. 5). Significant increases in the average density on the tall blocks during the spawning season (from August to October) were confirmed in 2016 (p < 0.05, GLMM), and the coefficient of the interaction between spawning/non-spawning season and year 2019 was positive (Table 1). This means that the coefficient for spawning season was larger in 2019 than in 2016, suggesting a clearer increase in the average density during the spawning season in 2019 than in 2016. However, a significant negative effect was detected in the interaction between spawning/non-spawning season and year 2017 (p < 0.01, GLMM, Table 1). No clear increase in adult density during the non-spawning season was observed in the other 3 years.

The average density of adult abalone on the small blocks also fluctuated largely during the survey period, ranging from 0.0 to 1.3 ind. m^{-2} (February 2016), although the range of fluctuation was smaller than on the tall blocks (Fig. 5). For the small blocks, a significant increase in the adult density during the spawning season was confirmed in 2016 (p < 0.05, GLMM, Table 2), but a significant negative effect was confirmed in the interaction between spawning/ non-spawning season and the year 2019 (p < 0.01, GLMM, Table 2). The density of adult abalone on the seabed surrounding the blocks remained lower than 0.2 ind. m^{-2} during the survey, and no clear increase during the spawning season was found in all 4 years (Fig. 5).

On tall blocks, adult density on the top face and on the lateral sides of the top fluctuated largely during the survey, and the tendencies to increase and decrease were similar to those of the average density of adult abalone on the tall blocks (Fig. 6). In contrast, temporal fluctuation of the average densities of adults on the upper and lower parts of the legs were much smaller than those of the top face and the lateral sides of the top and remained lower than 0.2 ind. m^{-2}.

The average density in the algal zone in October (0.21–0.33 ind. m^{-2}) was not significantly different among the 4 years (ANOVA, $F_{3,20}$ = 0.314, p > 0.05). In contrast, the density on tall blocks in October was significantly different between 2018 and 2019, and between 2016 and 2018 (Kruskal-Wallis test with Dunn-Bonferroni test, p < 0.05).
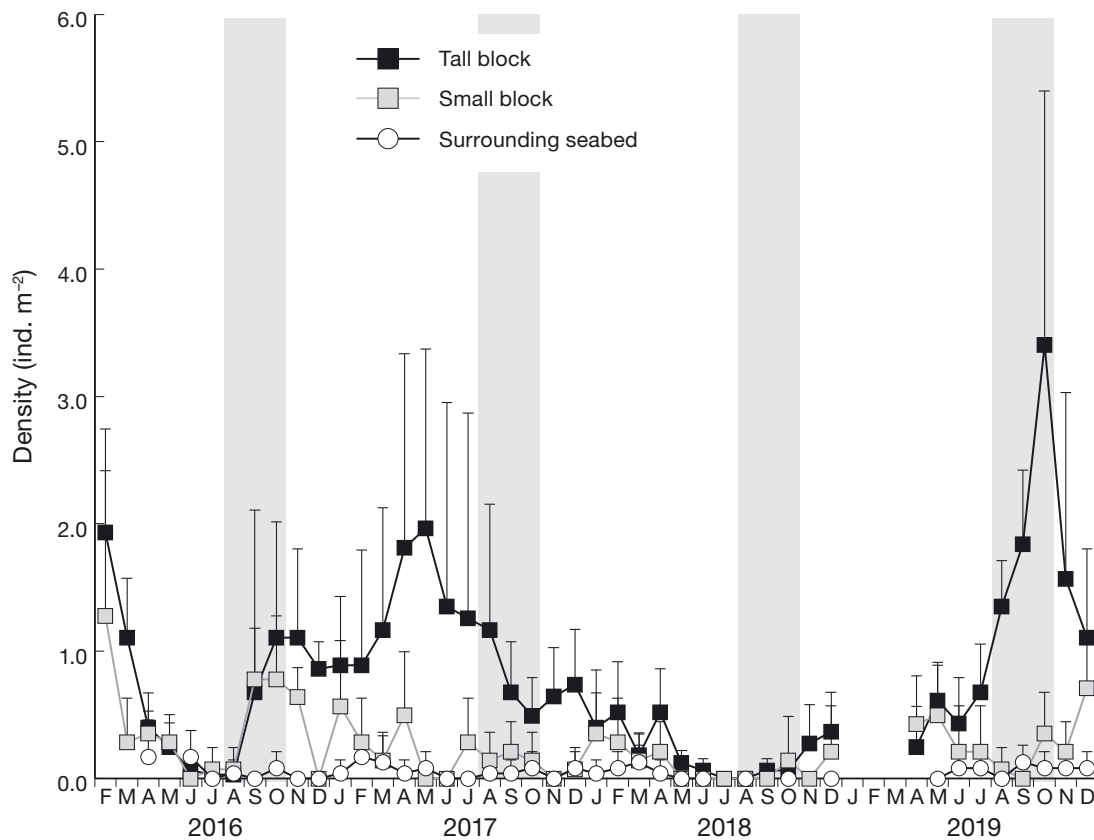
Fig. 5. Average density of adult *Haliotis discus hannai* on tall blocks, small blocks and the surrounding seabed in each month. Error bars: SD. Gray shading marks the spawning season of the abalone (August to October)

Table 1. Statistical results on whether abalone population densities on tall blocks vary with or without the spawning season (SS) among years. The spawning season spanned August to October, and the non-spawning season was from May to July. Significant p-values (p < 0.05) are in **bold**

Fixed-effect parameter	Coefficient	SE	z	p
Intercept	0.1169	0.2872	0.407	0.68
SS	0.7476	0.3297	2.267	**0.02**
2017	1.619	0.3118	5.192	**<0.001**
2018	−1.4372	0.5076	−2.832	**<0.01**
2019	0.8603	0.3255	2.643	**<0.01**
SS:2017	−1.2044	0.4216	−2.857	**<0.01**
SS:2018	−1.1526	0.7589	−1.519	0.13
SS:2019	0.5855	0.4199	1.395	0.16

Table 2. Statistical results on whether abalone population densities on small blocks vary with or without the spawning season (SS) among years. See Table 1 for the definition of spawning season and the non-spawning season. Significant p-values (p < 0.05) are in **bold**

Fixed-effect parameter	Coefficient	SE	z	p
Intercept	−1.5377	0.5079	−3.028	**<0.01**
SS	1.4445	0.5644	2.559	**0.01**
2017	−0.2282	0.7229	−0.316	0.75
2019	0.9525	0.5896	1.616	0.11
SS:2017	−0.8669	0.8863	−0.978	0.33
SS:2019	−2.2259	0.7959	−2.797	**<0.01**

3.3. Number of neighboring adults

The average number of neighboring adults fluctuated markedly, synchronized with the temporal change in the density of the adults (Fig. 7). The highest average number of neighboring adults was 4.5 (n = 111) in October 2019. On the tall blocks, the highest number of neighboring adults for an individual was 12.0 for 4 individuals in October 2019.

The average number of neighboring adults on the small blocks was 0 in all months except for January 2018 (1.3, n = 3), October 2018 (1.0, n = 2), May 2019 (0.3, n = 7) and October 2019 (0.3, n = 6). On the small blocks, the highest number of neighboring adults for an individual was 2.0 for 1 individual in January 2018.
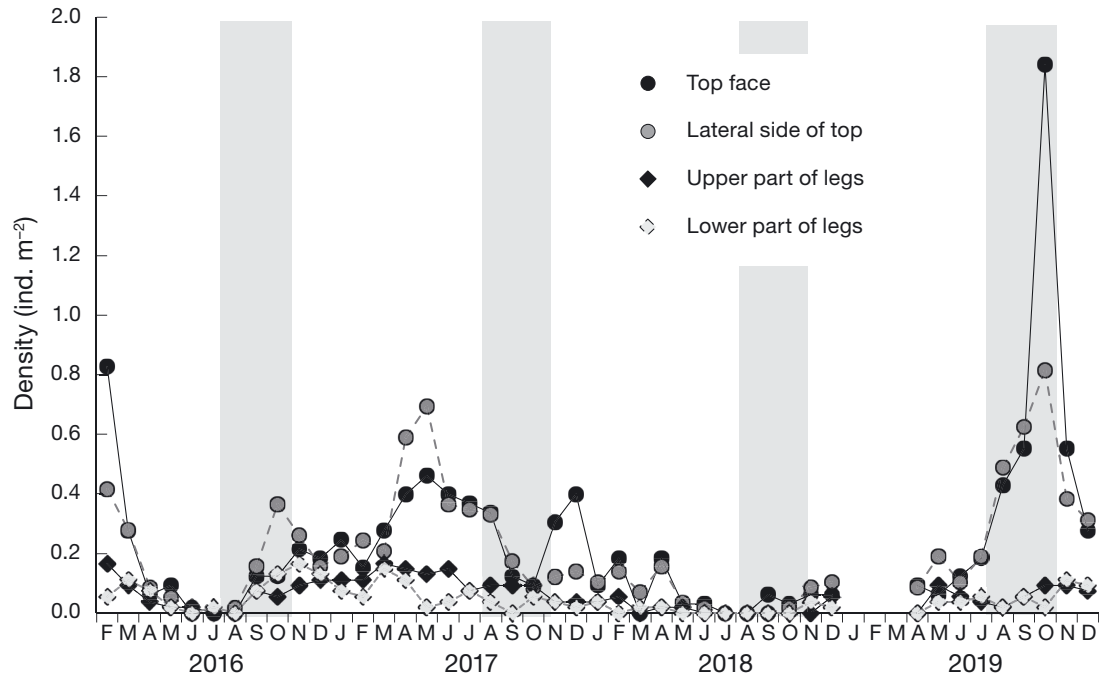
Fig. 6. Average density of adult *Haliotis discus hannai* on the 4 components of tall blocks (see Fig. 2a) in each month. Gray shading marks the spawning season of the abalone (August to October)
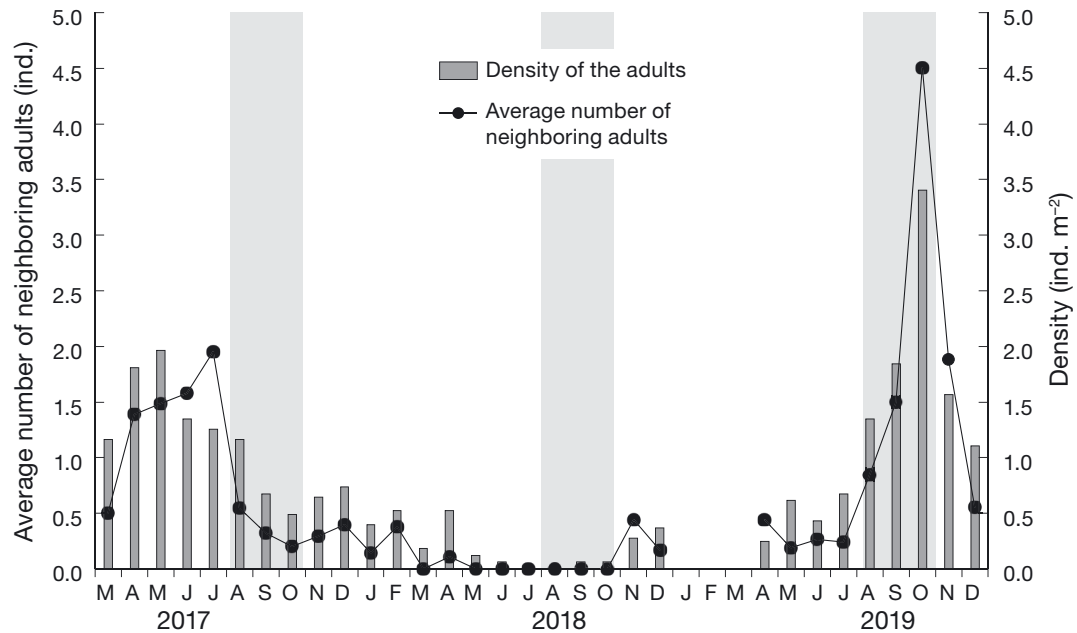

Fig. 7. Average number of neighboring adults and average density of adult *Haliotis discus hannai* on tall blocks in each month. Gray shading marks the spawning season of the abalone (August to October)

The average number of neighboring adults for individuals on the top face and on the lateral sides of the top fluctuated largely during the survey, although the fluctuations of individuals on the upper and the lower part of the legs were much smaller (Fig. 8). The highest average number of neighboring adults was 7.1 for the individuals on the top face (n = 58) in October 2019.
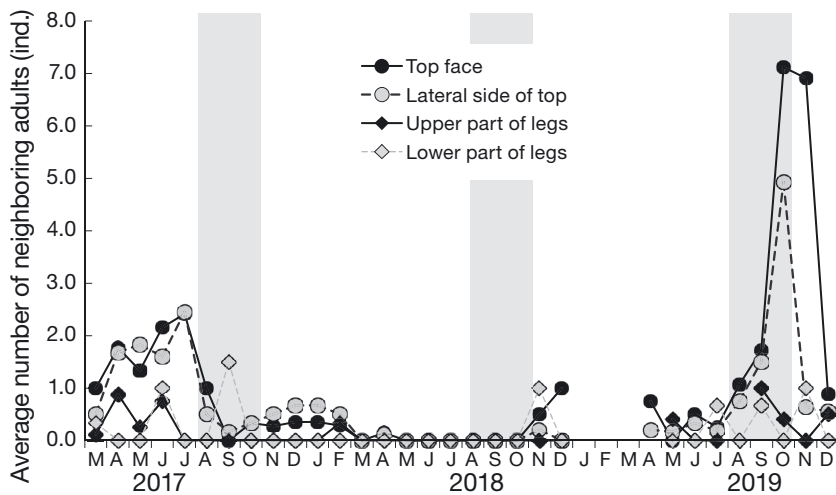
Fig. 8. Average number of neighboring adult *Haliotis discus hannai* on the 4 components of tall blocks (see Fig. 2a) in each month. Gray shading marks the spawning season of the abalone (August to October)

3.4. Algal succession

The average algal coverage was higher on the tall blocks than on the small blocks and the seabed area throughout the survey period (Fig. 9). In almost all months, the average algal cover on the small blocks and the seabed was <10%. The average algal coverage on the tall blocks fluctuated from 23.5% (August 2017) to 78.5% (April 2019), and the composition of algal species differed among the 4 years (Fig. 10). The combined average coverage of 1 *Sargassum* species (*S. yezoense*) plus 3 kelp species (*Saccharina japonica* var. *religiosa*, *Undaria pinnatifida* and *Costaria costata*) during the spawning sea-

son was 14.2 ± 2.2% (mean ± SD) in 2016, 10.3 ± 3.5% in 2017, 4.4 ± 1.0% in 2018 and 42.6 ± 17.5% in 2019.

As there were no data of algal coverage from January to March in 2019, data from April to December were used for comparisons among the 4 years. The average coverage of each algal species/group on the tall blocks from April to December in each year is shown in Fig. 11a. In 2016, *S. yezoense* and species belonging to the Dictyotaceae (mainly *Rugulopteryx okamurae*) dominated the tall blocks. Although the 2 types of algae were also the main components of the algal beds on the tall blocks in 2017 and 2018, the algal coverage of *S. yezoense* decreased in 2019. In 2017, *U. pinnatifida* was the most dominant on the tall blocks. *U. pinnatifida* was a major component of the algal beds on the tall blocks in 2019 as well; however, the algal beds in 2019 were strongly characterized by a high coverage of *S. japonica* var. *religiosa*.

As in the case of the tall blocks, the average algal coverage on the small blocks was highest in 2019, although the average coverage was much lower than that on the tall blocks during the survey period (Fig. 11b). The species composition of algae on the small blocks was clearly different from that on the tall blocks, and large brown algae such as *Sargassum* and kelp species did not occur on the small blocks except in 2019.
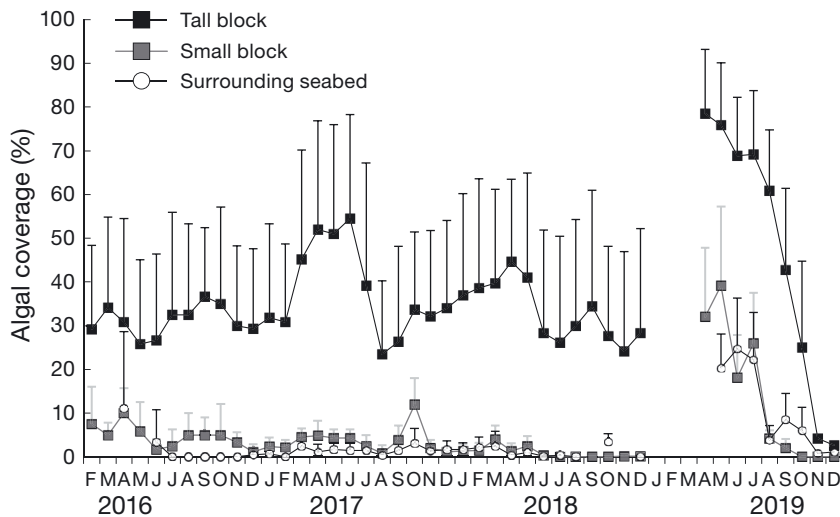
3.5. Factors affecting the number of adult abalone on tall blocks

The best fit models of the first model selection included all parameters, i.e. spawning or non-spawning season, presence or absence of Laminariales kelps and *S. yezoense* and the interaction between them (Table 3a). The interaction had a significant effect (p < 0.01; Table 4a). The best fit models of the second model selection also included all parameters, i.e. spawning or non-spawning season, coverage of Laminariales kelps and *S. yezoense* and the interaction between them (Table 3b). The interaction had a significant effect (p < 0.01; Table 4b).
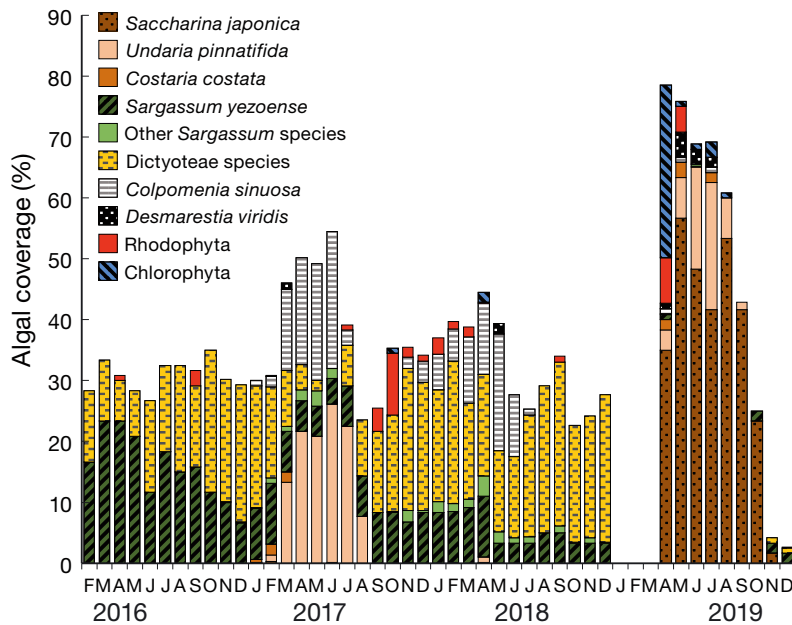

Fig. 9. Algal coverage on tall blocks, small blocks and surrounding seabed in each month. Error bars: SD. Blank areas: months with no data

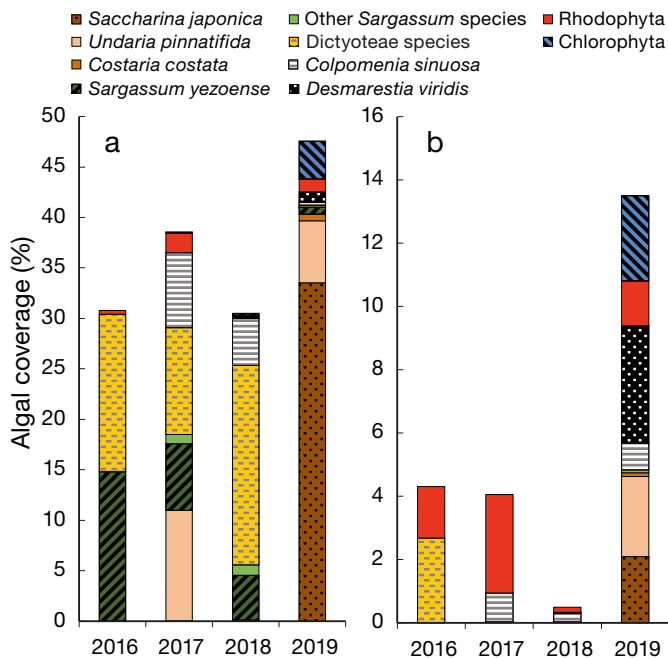Fig. 10. Species composition of macroalgae on tall blocks in each month

Fig. 11. Coverage of each algal species/group on (a) tall and (b) small blocks from April to December in each year

3.6. Water temperature

The water temperature on the seabed at Nagane fluctuated seasonally and was highest in September and lowest from February to April in every year (Fig. 12). The water temperature in February and

March 2019 was extremely low (2–3°C) due to an extension of the cold Oyashio Current into Otsuchi Bay.

4. DISCUSSION

4.1. Interannual differences in aggregations during the spawning season

The density of adult *Haliotis discus hannai* on the tall blocks fluctuated drastically during the 4 yr study. Aggregations of adult abalone occurred during the spawning seasons in 2016 and 2019. The dense concentrations of adults on the tall blocks resulted in an average of 7.1 neighboring adults per individual in 2019. The increases in adult density mainly occurred on the top face and on the lateral sides of the top of the tall blocks. On the other hand, no clear increases in adult density and the number of neighboring adults occurred during the spawning seasons of 2017 and 2018.

Coates et al. (2013) reported that *H. corrugata* shows homing behavior and that the homing behavior and small home ranges of this abalone may lead to spawning aggregations. In the present study, the adult density on the tall blocks fluctuated greatly, and occurrences of aggregations during the spawning season differed among the 4 years at the same location. Thus, aggregation during the spawning season was not caused by a consequence of fidelity to the same location for *H. discus hannai*.

In previous studies on the aggregation behavior of abalone species, interannual differences in aggregations were not discussed, as the distributions of adults were surveyed during single spawning seasons (Seamone & Boulding 2011, Coates et al. 2013) or clear interannual differences in aggregation size were not found (Catton & Rogers-Bennett 2013).

As the adult density on the surrounding seabed and that on the shallower algal beds in October remained at almost the same level during the survey period, the abundance of adult abalone in the survey area could not explain the interannual difference in the adult density on the tall and small blocks. Thus, factors other than the abundance of adults are considered to affect the interannual changes in aggregation during the spawning season, which is shown for the first time in this research.

Table 3. Akaike's information criterion (AIC) values of respective models for abalone abundance on tall blocks for models including (a) presence or absence of large brown algae (Laminariales kelps and *Sargassum yezoense*) and Dictyoteae species as predictor variables and (b) coverage of large brown algae and Dictyoteae species as predictor variables. BPA refers to the parameter whether large brown algae are present or absent. BC refers to coverage of Laminariales kelps and *S. yezoense*. DPA refers to the parameter whether Dictyoteae species are present or absent. DC refers to coverage of Dictyoteae species. SS refers to the parameter whether observed months are in the abalone spawning season (August–October) or non-spawning season (November–July). The model with the lowest AIC value is given in **bold**

(a) Presence or absence	
Model	AIC
Null	1283.1
BPA	1274.1
DPA	1285.0
SS	1285.0
BPA + SS	1276.1
DPA + SS	1287.0
DPA + BPA	1275.6
BPA + SS + BPA:SS	**1268.3**
DPA + BPA + SS	1277.5
BPA + SS + DPA + BPA:SS	1270.0
(b) Coverage	
Model	AIC
Null	1283.0
BC	1282.5
DC	1284.3
SS	1285.0
BC + SS	1284.4
DC + SS	1286.2
DC + BC	1284.5
BC + SS + BC:SS	**1277.8**
DC + BC + SS	1286.4
BC + SS + DC + BC:SS	1279.7

Table 4. Parameter estimates of the best fit models for abalone individuals on the tall blocks for models including (a) presence or absence of Laminariales kelps and *Sargassum yezoense* as a predictor variable and (b) coverage of Laminariales kelps and *S. yezoense* as a predictor variable. Abbreviations of parameters are the same as in Table 3. Parameter estimates with 95% confidence intervals that do not overlap 0 are in **bold**

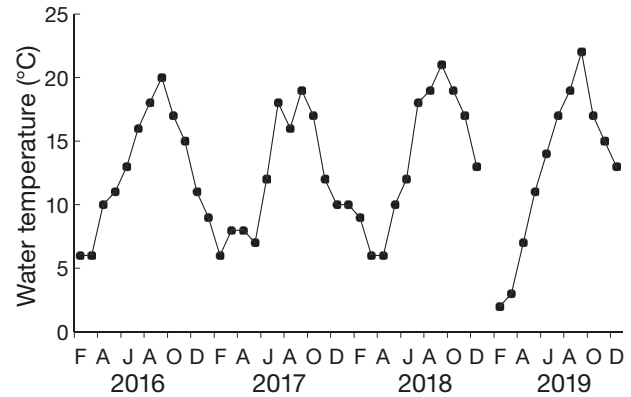| Fixed-effect parameter	Estimate	SE	z	p
(a) Presence or absence				
Intercept	0.7346	0.3221	2.281	**0.02**
BPA	0.3471	0.1827	1.900	0.06
SS	−0.5249	0.2269	−2.313	**0.02**
BPA:SS	0.9385	0.2929	3.204	**<0.01**
(b) Coverage				
Intercept	0.8549	0.3401	2.514	**0.01**
BC	0.0029	0.0039	0.736	0.46
SS	−0.3479	0.1923	−1.810	0.07
BC:SS	0.0172	0.0058	2.979	**<0.01**

Fig. 12. Water temperature immediately above the seabed at Nagane in each month. Blank area: months with no data

4.2. Relationships between aggregation of *H. discus hannai* and the macroalgal community

As kelp beds provide the main habitat for adult abalone (Takami & Kawamura 2018), the dynamics of the abundance of large brown algae such as *Sargassum* and kelp species may affect the distribution of *H. discus hannai*. In Otsuchi Bay, abundance of *Saccharina japonica* var. *religiosa* kelp was considered a major factor affecting the distribution of *H. discus hannai* (Hayakawa et al. 2017). On the tall blocks, the coverage of large brown algae largely fluctuated during the survey period. The density of adult abalone was not determined merely by the coverage and the presence or absence of the 3 kelp species and *Sargassum yezoense*, but seemed to be strongly affected by the interaction between spawning/non-spawning season and the 2 algal indexes (Tables 3 & 4). This means that the influence of temporal changes in the community of large brown algae on the aggregation of adult abalone is considered to differ between the spawning and non-spawning seasons.

In 2019, a distinct aggregation during the spawning season was observed, and the algal coverage of *Sargassum* and kelp species on the tall blocks during the spawning season was highest among the 4 years. In 2019, dense algal beds of annual kelp species were formed, and the kelp beds remained on the tall blocks during the spawning season. Dense groups of adult abalone were often formed around the rhizoidal part of the kelp inside the kelp beds on the top face of the tall blocks (Fig. 13a). Such dense groups of abalone inside kelp beds undergoing senescence with shortened blades were also often confirmed on natural substrata in autumn (Fig. 13b)

Aggregation of adults on the tall blocks during the spawning season in 2019 was thought to be caused
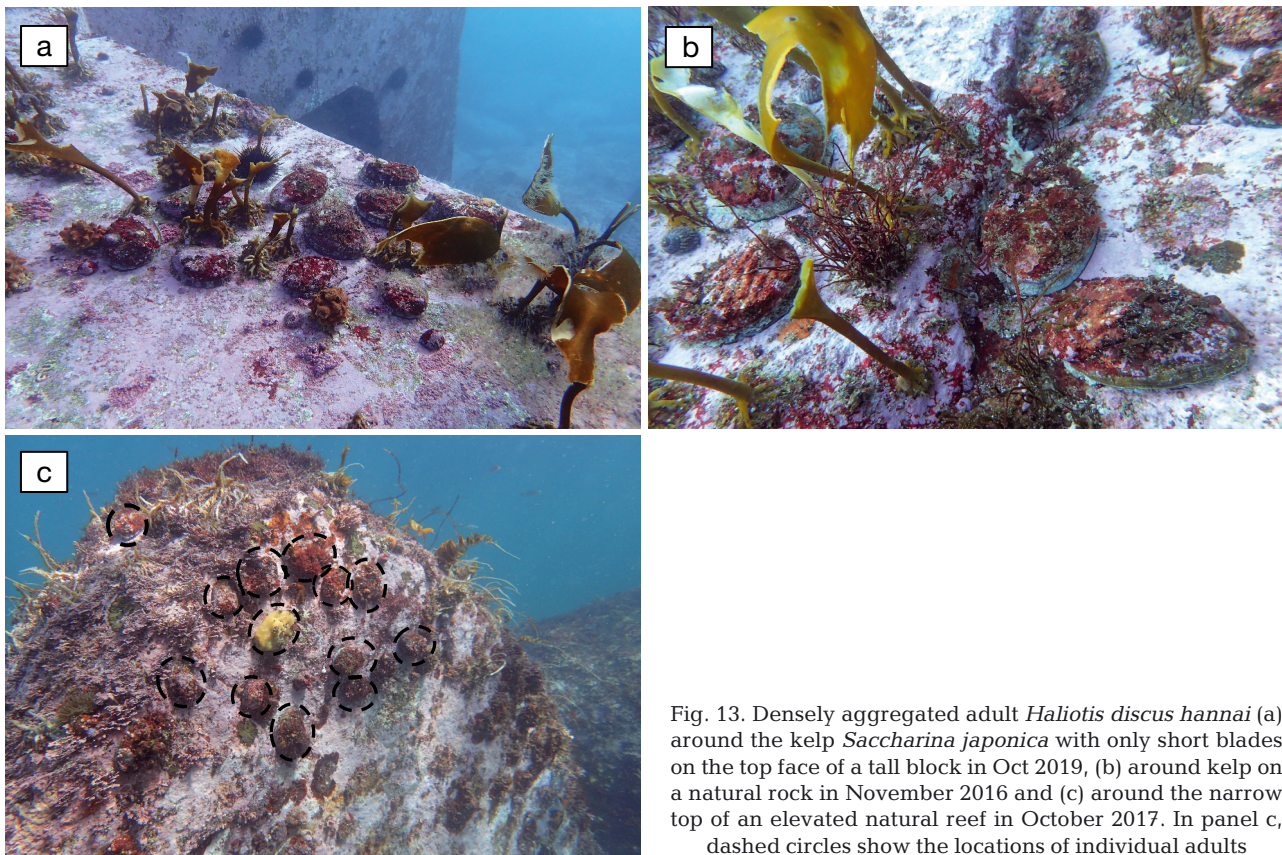
Fig. 13. Densely aggregated adult *Haliotis discus hannai* (a) around the kelp *Saccharina japonica* with only short blades on the top face of a tall block in Oct 2019, (b) around kelp on a natural rock in November 2016 and (c) around the narrow top of an elevated natural reef in October 2017. In panel c, dashed circles show the locations of individual adults

by active movement to kelp beds. However, the average density of adult abalone on the tall blocks before the spawning season was lower than that during the spawning season in 2019, although the coverage of the kelps before the spawning season was higher than that during the spawning season. The kelp bed cover on the tall blocks may have been too dense for the abalone to attach on the top face before the spawning season (Fig. 14a).

The kelp *S. japonica* var. *religiosa* is an annual macroalga whose standing crop decreases from summer to autumn (Funano 1983, Gao et al. 2015), and this senescence period of the kelp corresponds to the spawning season of the abalone (Fig. 14b). The seasonal shrinkage of kelp beds is considered to lead to increased space for the formation of the aggregation. The accordance between the senescence period of the kelp and the spawning season of the abalone is considered an important factor for the formation of spawning aggregations of this abalone species.

In 2016, aggregation during the spawning season was observed, and the algal coverage of large brown algae (*Sargassum* and kelp species) during the spawning season was second highest among the 4 years on the tall blocks. In 2016, algal beds of *S. yezoense* were formed and remained during the spawning season, although no kelp bed cover was formed on the tall blocks. The biomass of perennial *S. yezoense* decreases from July to September in Otsuchi Bay following a reduction in its length, and the shedding of the leaves (Kodama et al. 2020). Similar to kelp in 2019, the algal coverage of *S. yezoense* decreased during the spawning season of the abalone in 2016, and abalone adults were observed to locate around the edges of the *Sargassum* beds on the top face of the tall blocks. In 2016, along with *S. japonica* var. *religiosa*, the algal beds of *S. yezoense* are considered to have promoted the formation of the spawning groups during its senescence period. Dense mats of the rhizoidal part with short thalli of *S. yezoense* remain after the main part of the algal body is lost. Adult abalone cannot settle inside such dense algal mats, and the lack of sufficient space for an aggregation is considered as the reason why the density of the aggregated adults in 2016 was lower than in 2019 when *S. japonica* var. *religiosa*, which has a relatively small holdfast that leaves enough space to allow the aggregation in the understory, was dominant.
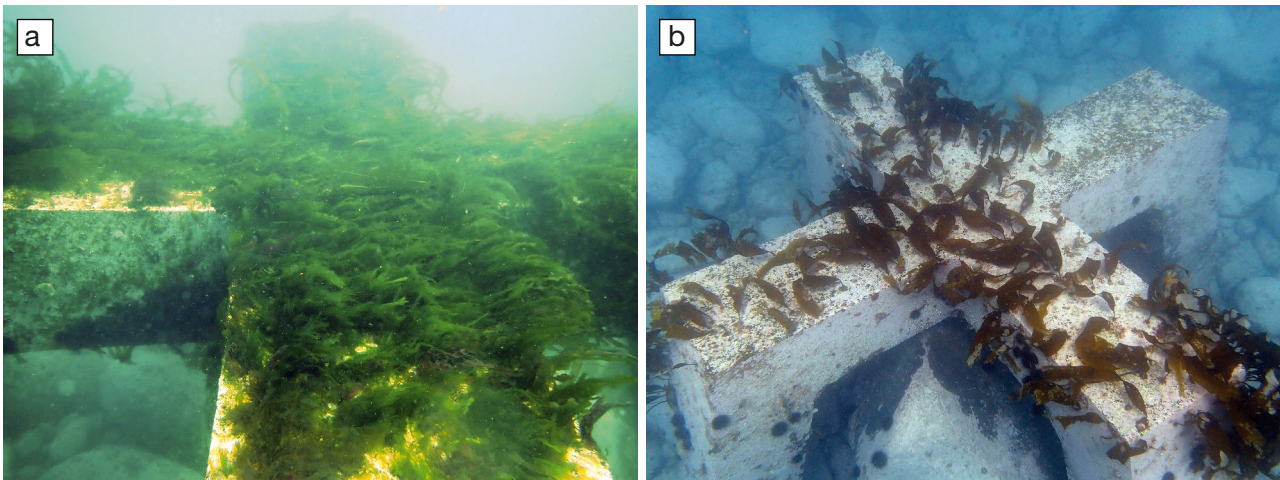
Fig. 14. Kelp *Saccharina japonica* (a) on the top face of a tall block in April 2019 and (b) on the top face of another tall block in September 2019

On the other hand, kelp beds of *Undaria pinnatifida* occurred on the tall blocks, and a high density of adult abalone was confirmed before the spawning season in 2017. The density of adults on the top face and lateral sides of the top increased from March to May, when the coverage of *U. pinnatifida* increased on the tall blocks. As the kelp is also a favorable food for the abalone (Uki 1981), abalone adults are considered to move up to the kelp beds of *U. pinnatifida* on the tall blocks. However, the algal coverage of *U. pinnatifida* decreased rapidly from July to August and disappeared in September. Concurrently with the decrease in *U. pinnatifida* cover, the density of adult abalone continued to decrease during the spawning season. In addition to the very low algal coverage of *S. japonica* var. *religiosa* and *S. yezoense*, the lack of correspondence between the senescence period of *U. pinnatifida* and the spawning season of the abalone is considered another reason why aggregation during the spawning season was not observed in 2017.

In 2018, small brown algae belonging to Dictyotaceae (mainly *Rugulopteryx okamurae*) were dominant on the tall blocks, and the algal coverage of the large brown algae (*Sargassum* and kelp species) during the spawning season was lowest among the 4 years. The density of adult abalone on the tall blocks remained low from summer to autumn, including during the spawning season. *R. okamurae* is reported to produce chemical cues to deter grazing by abalone (Shiraishi et al. 1990). In addition to the disappearance of the *Sargassum* and kelp species, the formation of algal turfs dominated by *R. okamurae* might well decrease the suitability of the top face of the tall

blocks as locations for abalone during the spawning season.

During the study period, differences in the dominant macroalgal species during the spawning season with different seasonal phenologies are considered to lead to the interannual differences in the aggregation of abalone during the spawning season. The phenology of the kelp and *Sargassum* species, including the timing of senescence and structure of the understory, may be important factors influencing the presence or absence and the degree of aggregation of adult abalone. This is the first study to suggest that differences in phenology among species of large brown algae strongly influence the formation of aggregations of a free-spawning marine animal during its spawning season.

4.3. Elevated locations may be important for spawning aggregations of *H. discus hannai*

Adult abalone density was higher on the tall blocks than on the small blocks and the surrounding seabed during each spawning season throughout this study. As the increase of adult abalone density on the tall blocks mainly occurred on the top face and the lateral sides of the top, and the number and percentage of adults was higher on these 2 components than on the upper and lower part of legs, aggregation during the spawning season appears to arise from the movement of the abalone to elevated positions. However, the formation of aggregations during the spawning season differed among the 4 years, yet the form and height of the blocks did not change during the study.

Algal coverage was higher on the tall blocks than on the small blocks during the survey period. Although a few *S. japonica* var. *religiosa* and *U. pinnatifida* appeared on the small blocks in spring of 2019, the 2 kelp species disappeared by September, and large brown algae such as *Sargassum* and kelp species were rarely found on the small blocks in the other 3 years. Sea urchins *Mesocentrotus nudus* were the most conspicuous grazers in the survey area, and these urchins were found on both types of artificial reef and surrounding seabed. *M. nudus* tend not to climb upright objects in the presence of moderate to strong water movements, and their feeding on algae is reduced by wave-induced oscillatory flows which are stronger in the shallow subtidal zone (Kawamata 1998, 2008). While *M. nudus* could climb the small blocks to exert strong grazing pressure on the macroalgae on the upper surfaces as well as the surrounding seabed area, the grazing pressure is likely to be more moderate on the tall blocks with higher legs and faster water velocity across the top surface. In addition, the 'whiplash' effect of the algal fronds (Konar 2000, Gagnon et al. 2006) may prevent urchins from climbing up onto the top face, once dense kelp bed cover is formed on the top face of the tall blocks. In our survey, the number of *M. nudus* on the tall blocks was relatively low in the summer of 2019 when dense kelp beds of *S. japonica* var. *religiosa* were formed, while a number of urchins were observed to climb upon the tall blocks especially in 2018, when the coverage of the large brown algae was quite low. Elevated locations with low urchin grazing pressure, such as the tall blocks, have physical environments enabling the growth of kelp beds, which subsequently promotes the aggregation of adult abalone, as observed in the 2019 spawning season.

Himmelman et al. (2008) reported that ophiuroids and sea stars moved to elevated surfaces before mass spawning events, and this behavior was speculated to increase the suspension and mixing of gametes. As the synchronous spawning of the abalone *H. discus hannai* is triggered by typhoons or minor storms (Sasaki 1985, Sasaki & Shepherd 1995), locating on areas of higher elevation with higher water flow velocity could negatively affect the success rate of fertilization of released gametes. However, climbing up to a narrow brow of elevated reefs could result in a high local density with a large number of neighboring mates, like the concentrations of adults on the top face of the tall blocks observed in this survey. Dense aggregations of adult abalone on the narrow brow of elevated reefs were confirmed during the spawning season (Fig. 13c). Moving up to elevated positions

could be considered important for successful fertilization of the abalone, although the elevated position itself is not the major factor for the formation of the spawning groups.

4.4. Implications for understanding the population dynamics of *H. discus hannai*

Seamone & Boulding (2011) reported that the abalone species *H. kamtschatkana* shows sufficiently dense spawning aggregations to enable successful fertilization, and spawning aggregations may compensate for low population densities that may otherwise reduce spawning efficiency. The population of *H. discus hannai* on the Sanriku Coast was seriously damaged by the massive tsunami caused by the Great East Japan Earthquake in 2011, and reductions in adult density following huge disturbances were reported in some areas (Takami et al. 2013, 2017, Kawamura et al. 2014, Hayakawa et al. 2017). Spawning aggregations are speculated to play an important role for the population recovery of abalone in disturbed areas. At the same time, it should be noted that spawning aggregations are not a stable phenomenon, as they are strongly influenced by algal succession.

The biomass of annual kelp species along the Sanriku Coast is strongly affected by the relative strengths of the 2 offshore current systems, the cold Oyashio Current and the warm Kuroshio Current (Yatsuya et al. 2020). In February and March 2019, water temperature within Otsuchi Bay was particularly low (2–3°C) due to an extension of the cold Oyashio Current. The occurrence of cold seawater from the Oyashio Current fatally affects the survival of young-of-the-year abalone (Takami et al. 2008). In contrast, the low seawater temperature in winter and early spring inhibits grazing pressure by herbivores, including the sea urchin *M. nudus* (Machiguchi 1993), and leads to an expansion of the kelp beds (Agatsuma 1994). In addition, occurrence of cold seawater from the Oyashio Current benefits growth of macroalgae, as the Oyashio Current is highly nutrient-rich (Sakurai 2007). The increased abundance of the kelp beds of *S. japonica* var. *religiosa* benefits adult abalone through a high availability of favorable food, which accelerates gonad maturation of adult abalone and potentially increases their reproductive output (Uki & Kikuchi 1982). In addition, the seasonally flourishing kelp appears to increase the number of suitable locations for spawning aggregations of adult abalone, as shown in this research. Enhanced

recruitment of juveniles in the following year is a positive and indirect effect of the Oyashio Current, and this could compensate for the decreased survival rate of young-of-the-year juveniles as a negative and direct effect of the current. In contrast, the density of juvenile abalone age 1+ after warm winters largely differed among years in Iwate Prefecture, and this fluctuation in recruitment after warm winters was reported to be strongly affected by the abundance of reproductive adults (Ohmura et al. 2015).

In our research, the algal composition on the artificial blocks differed among 2016, 2017 and 2018, when seawater from the Oyashio Current did not reach Otsuchi Bay, and the algal succession appears to have influenced the degree of the spawning aggregation in these 3 years. The temporal changes in algal vegetation — such as increases of *S. yezoense*, which is effective for the occurrence of spawning aggregations of the abalone (but less so compared to *S. japonica* var. *religiosa*) — could influence the recruitment after a warm winter through fluctuations in the amount of favorable locations for aggregations during the spawning season, in addition to the adult abundance. Temporal fluctuation in the physical ability to form spawning aggregations, which is influenced by algal succession in the habitats, may play an important role for the population dynamics of abalone.

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