Restricted recovery of *Eisenia bicyclis* kelp forest following sea urchin removal on the Pacific coast of Tohoku, Japan

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ABSTRACT: Little information is available on the destruction of *Eisenia bicyclis* kelp forests (Phaeophyceae: Laminariales) due to overgrazing by sea urchins. In Shizugawa Bay, on the northeastern Pacific coast of Japan, overgrazing by the sea urchin *Mesocentrotus nudus* caused the destruction of *E. bicyclis* forests between 2014 and 2015. This study investigated the recovery of an adult kelp forest in relation to sea urchin densities through the continuous removal of sea urchins at 3 permanent experimental transects spanning 100 m^2 for 3.8 yr from September 2015 to June 2019. The relationship between the densities of sea urchins and kelp juveniles was also analyzed. Estimates of the threshold density and biomass of sea urchins required to trigger the phase shift from an *E. bicyclis* forest to a barren were 15.5 ind. m^{-2} and 712.0 g m^{-2}, respectively. The removal of sea urchins expanded the offshore kelp growth area. However, an increase in adult kelp following the return of juveniles was restricted to the nearshore half of the transects. The successful recruitment of kelp juveniles, followed by the recovery of adult kelp forest, requires reduction of the density of *M. nudus* of 40—50 mm diameter to 0 or 1 ind. m^{-2}. Reducing sea urchin densities in autumn, when many move from barrens to invade kelp forests, is crucial to ensure the survival of kelp juveniles. This study highlights the presence of an intensified positive feedback mechanism of the barren state due to high grazing intensity and a weakened Oyashio Current.

KEY WORDS: *Eisenia bicyclis* · Recruitment · Phase shift · Barren · *Mesocentrotus nudus* · Oyashio Current

1. INTRODUCTION

Kelp forests are one of the most productive ecosystems on Earth (Mann 1973). Their high productivity provides abundant food for species that graze directly on the anchored kelps, filter-feed on suspended kelp-associated particulate organic material, or prey on kelp-associated organisms (Norderhaug et al. 2005, Christie et al. 2009, O'Brien & Scheibling 2016). Large amounts of detached drifting kelp are also transported to adjacent or distant habitats, where they become a primary food source. Their decomposition by microorganisms establishes diverse detritivores and consumers, which significantly increases secondary production (Bustamante et al. 1995, Krumhansl & Scheibling 2012). Kelp forests provide complex biogenic habitats (Christie et al. 2009, Thomsen et al. 2010, Teagle et al. 2017), which

impact the physical conditions of their environment (Eckman et al. 1989, Wernberg et al. 2005, Krause-Jensen et al. 2016). They provide ecosystem goods and services that are of increasing importance to human society (Vásquez et al. 2014, Bennett et al. 2016). Kelp forests have also emerged as a promising solution to combat ocean warming through blue carbon strategies. Several studies have demonstrated their potential (including those of Krause-Jensen & Duarte 2016, Duarte et al. 2017, Krause-Jensen et al. 2018, Froehlich et al. 2019, Filbee-Dexter & Wernberg 2020). However, a recent global analysis found that 38% of the world's kelp forests have declined over the past 5 decades (Krumhansl et al. 2016). Along temperate and subarctic coastlines, phase shifts from kelp forests to barrens have resulted from sea urchin overgrazing (North & Pearse 1970, Chapman 1981, Andrew & Underwood 1993, Johnson et al. 2005, 2011, Ling 2008). Physiological stress caused by the increase of water temperature and/or nutrient-poor conditions resulting from large-scale oceanographic changes, ocean warming, and marine heatwaves has also led to phase shifts in warm temperate coastlines (Harrold & Reed 1985, Steneck et al. 2002, Pehlke & Bartsch 2008, Díez et al. 2012, Filbee-Dexter & Scheibling 2014, Ling et al. 2015, Wernberg et al. 2016, Rogers-Bennett & Catton 2019). Intensive herbivory of native or new-arrival fishes has been identified as a contributing factor to these shifts (Vergés et al. 2014a,b, 2016).

In Japan, *Eisenia bicyclis* is found in the Pacific Ocean from northern to central Honshu and eastern Shikoku to the Seto Inland Sea as well as in the Sea of Japan in southern Honshu. This species creates forests on rocky reefs between the intertidal fringe and the upper subtidal zone (Kamiya 2012). These forests are prolific primary producers, exhibiting high productivity at a rate of 20 kg m^{-2} yr^{-1} (Yoshida 1970). Feeding on *E. bicyclis* enhances the somatic and/or gonadal growth of the sea urchin *Mesocentrotus nudus* (Sano et al. 2001, Agatsuma et al. 2005) and growth of the abalone *Haliotis discus hannai* (Uki et al. 1986) in the subtidal reefs of the Pacific off Miyagi and Fukushima Prefectures of Tohoku (northeastern Honshu). These enhancements result in an increase in the fishery production of these animals.

The genus *Eisenia* and the closely related genus *Ecklonia* (Rothman et al. 2015, Kawai et al. 2020) consist of 7 and 9 species, respectively (Guiry & Guiry 2023). Among them, *Ecklonia radiata* is distributed around the southern half of Australia, from southern Queensland to Western Australia (Wernberg et al. 2019). It has recently experienced a significant de-

cline due to a marine heatwave (Smale & Wernberg 2013, Wernberg et al. 2016) and the invasion of tropical herbivorous fishes (Vergés et al. 2016, Zarco-Perello et al. 2017). The disappearance of *Ecklonia cava*, *E. kurome*, *E. radicosa*, and *Eisenia bicyclis* in southern and western Japan has been attributed to ocean warming and/or an increase in the size of the herbivorous fish population and their grazing effects (Serisawa et al. 2004, Tanaka et al. 2012, Kiyomoto et al. 2013, 2021, Terada et al. 2016, 2021, Kumagai et al. 2018). However, little is currently known about the destruction of *Eisenia* and *Ecklonia* kelps caused by overgrazing from sea urchins, except for *E. radiata* (Ling 2008, Ling et al. 2009, Marzloff et al. 2013, Kriegisch et al. 2016).

The population dynamics of *E. bicyclis* have been studied extensively over 4 decades off Tomarihama (38° 21' N, 141° 32' E) along the Oshika Peninsula in Miyagi Prefecture. The abundance of juvenile kelp varies annually, increasing from February to July when water temperatures are low (Taniguchi et al. 1986, 1987, Taniguchi & Kito 1988). This coincides with the first intrusion of the Oyashio Current, which brings low water temperatures and high nutrient concentrations into the coastal onshore waters (Mizuno 1984, Okuda 1986). Nutrient-rich conditions improve the growth of the gametophytes of Laminariales and thereby enhance successful reproduction (Hoffmann et al. 1984, Ladah & Zertuche-González 2007, Carney & Edwards 2010). Furthermore, the expansion of adult forests the following year is linked to juveniles becoming established on deeper sea floors across the lower fringe (Taniguchi et al. 1987). At present, the surface water temperatures have increased (Japan Metrological Agency 2023a), and the Oyashio Current has weakened in the Pacific Ocean off Tohoku (Mensah & Ohshima 2021, Miyama et al. 2021). The effects of these physical oceanographic changes on the recruitment of kelp and the abundance of kelp juveniles and adults are unknown.

In a study of an *E. bicyclis* forest growing along 2 prominent hidden reefs facing the southern shore of Nojima Island (38° 40' N, 141° 30' E) in Shizugawa Bay, Miyagi Prefecture, widespread damage to this forest due to overgrazing by the sea urchin *M. nudus* has been recorded since 2011 due to high juvenile recruitment and subsequent population explosion (Agatsuma et al. 2018). Consequently, kelp holdfasts remained only until May 2015, leading to a phase shift from a kelp forest to a barren area (Agatsuma et al. 2018, 2019, Y. Agatsuma pers. obs.).

Concerning such shifts between alternative stable states (Connell & Sousa 1983, Knowlton 1992), one of

the most frequently observed phase shifts in shallow subtidal temperate reefs is the transition from kelp forests to barrens dominated by crustose coralline algae (CCA; Rhodophyta: Corallinophycidae). This shift is a result of sea urchin overgrazing (Steneck et al. 2002). To restore kelp forests, sea urchin populations must be reduced to levels significantly below the threshold at which overgrazing occurs. This is due to the hysteresis effect (Ling et al. 2009, 2015, Filbee-Dexter & Scheibling 2014, Steneck & Johnson 2014) and a discontinuous phase shift (Scheffer et al. 2001, Scheffer & Carpenter 2003). However, the exact threshold density and biomass of *M. nudus* required to trigger the destruction of an *E. bicyclis* forest is currently unknown. Muraoka (2008) reported that intensive grazing by dense populations of *M. nudus* near the lower fringe of *E. bicyclis* forest hindered the growth of juvenile sporophytes off Tomarihama. However, the density of sea urchins required to enable the successful recruitment of kelp juveniles has yet to be determined. Several studies have demonstrated that kelp forests can be restored by removing sea urchins (Chapman 1981, Johnson & Mann 1988, Williams et al. 2021). On the Japan Sea coast of southwestern Hokkaido, where barren areas have persisted for ~40 yr, the removal of dense populations of *M. nudus* resulted in the growth of a *Sargassum confusum* forest on a previously barren site (Agatsuma et al. 1997). Off the coast of Rishiri Island in the Sea of Japan, the removal of sea urchins *M. nudus* and *Strongylocentrotus intermedius* resulted in a climax community of *Saccharina japonica* var. *ochotensis* forest (Agatsuma 1999). However, the possible effects on reforestation of *E. bicyclis* by removing *M. nudus* are untested.

The present study aims to (1) estimate the threshold density and biomass of *M. nudus* required to trigger the phase shift from *E. bicyclis* forest to a barren, (2) clarify the recovery process to adult kelp forest in relation to sea urchin abundance by continuously removing the sea urchins, and (3) estimate the sea urchin abundance required for successful recruitment of kelp juveniles and indicate the key season for successful reversion to *E. bicyclis* forest.

2. MATERIALS AND METHODS

2.1. Study area and experimental design

Along the southern shore of Nojima Island in Shizugawa Bay, Miyagi Prefecture, 3 permanent experimental transects were selected: an area with boulders on a flat reef (E1; 20 m long and 2 m wide) and 2 promi-

nent hidden reefs (E2 and E3; 15 m long and 2 m wide) covered with CCA (Fig. 1). Transects E2 and E3 are in the same area where the process of degradation of an *Eisenia bicyclis* forest due to grazing by *Mesocentrotus nudus* had been observed (Agatsuma et al. 2019).

The 3 experimental transects E1, E2, and E3 were marked using a 50 m fiberglass line with a scale (Quick Winder YSL3-50, TJM DESIGN) placed in the center of the transects on 30 July, 25 June, and 30 July, respectively, in 2015. U-shaped stainless-steel markers were embedded and anchored to the seafloor using an epoxy adhesive at 5 m intervals along the line, where water depth was measured using a dive computer (IQ1204 DC Solar LINK, TUSA). These water depths were calculated at the level of the shallowest water according to the tide table at Ofunato, Iwate Prefecture (39° 01' N, 141° 45' E) near Shizugawa Bay (Japan Meteorological Agency 2023b). Three
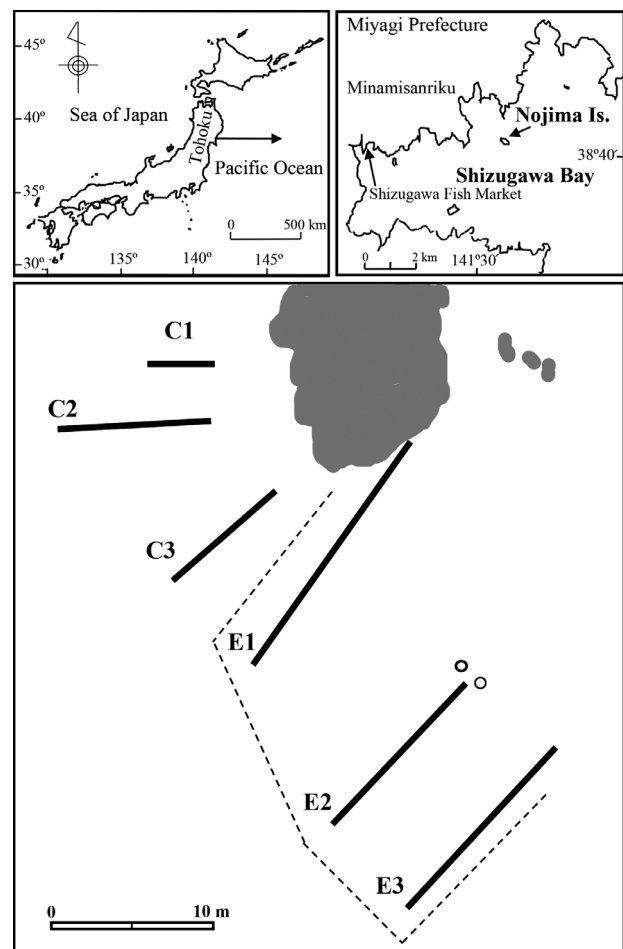

Fig. 1. Shizugawa Bay, showing experimental (E1, E2, and E3) and control (C1, C2, and C3) transects. Dashed line: area where sea urchins were removed. Open circles: locations of the 2 data loggers

control transects (C1, 5 m long and 2 m wide; C2 and C3, 10 m long and 2 m wide) were deployed on flat reefs with CCA-covered boulders adjacent to the experimental transects, oriented in a northwesterly direction (Fig. 1). Water depths were measured on 4 September 2015, using the same methods as for the experimental transects. The transect installations and water depth measurements were performed by SCUBA diving.

The water depths of E1, E2, and E3 were 0.8–3.1, 1.7–3.2, and 0.5–2.2 m, respectively; and those of C1, C2, and C3 were 0.5–2.9, 0.4–3.1, and 1.3–3.5 m, respectively, indicating slightly steeper slopes compared to the experimental transects (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p017_supp.pdf).

2.2. Sea urchin and kelp abundance before sea urchin removal

Concurrently with measuring water depths of the experimental transects, the density of individuals (ind. m^{-2}) of *M. nudus* and *E. bicyclis* was surveyed using a 1 × 1 m quadrat. The survey of sea urchin density extended from 15–30 m in E2 and 15–20 m in E3. This was because density was observed to increase at deeper sites. To confirm the density of kelp according to holdfast only, the kelp surveys at E2 and E3 were extended to 20 and 30 m, respectively. The quadrat was positioned to the right and left of the line set along the U-shaped markers from the start and rolled in consecutive steps down the transect. The number of individuals of *M. nudus* and *E. bicyclis* was counted per quadrat.

According to Yoshida (1970), *E. bicyclis* sporophytes undergo distinct developmental stages. After recruitment, they have only one central blade in the first-stage juvenile (FSJ), followed by the formation of several lateral blades in the second-stage juvenile (SSJ). Agatsuma et al. (2019) classified thallus herbivore damage to adult kelps into 4 different types, with or without sea urchin grazing marks: entire (undamaged) thallus; thallus without fronds (branches, stipe, and holdfast intact); thallus without fronds and branches (stipe and holdfast intact); and holdfast only without fronds, branches, and stipe. The number of individuals per quadrat were recorded on aqua-notes. A total of 140 quadrats was surveyed for data on both sea urchin density and kelp density, in addition to the 0–20 m range surveyed in E1. A total of 207 sea urchins were collected from the quadrats positioned to the right of the center of each transect at 5 m intervals from 0–

20 m on E1 and E3, and up to 30 m on E2 (n = 17 quadrats). The test diameters (TD) of the sea urchins were measured by using a vernier caliper (0.1 mm accuracy) aboard a research fishing vessel.

The threshold density of sea urchins required to trigger the phase shift from *E. bicyclis* forest to barren was calculated by averaging the density of sea urchins in the 101 quadrats positioned below the lower fringe of the forest of kelp, except for stipes and branches only, and holdfasts only. The threshold biomass of sea urchins was calculated using an equation developed by Fuji (1967) which correlates their biomass and TD with body weight (BW). Fuji (1967) found no statistically significant differences in this relationship throughout the year and suggested that seasonal changes in gonad size were being compensated by coelomic fluid content. The equation used is BW = aTD^b, which was logarithmically transformed to log(BW) = log(a) + b(logTD). The coefficients a and b were calculated by substituting the measured TD and BW using a vernier caliper (0.1 mm accuracy) and an electronic balance (0.1 g accuracy), respectively. These measurements were taken from a sample of 111 individuals randomly selected from the experimental area on 4 September 2015 and demarcated by a broken line in Fig. 1. The diameters of 207 individuals collected in 17 quadrats were then converted to BW using the equation provided. The mean biomass (g m^{-2}) was then determined and threshold biomass was estimated. These estimates were assessed by comparison with previously published papers.

2.3. Sea urchin and kelp densities during sea urchin removal

On 4 September 2015, removal of *M. nudus* from the experimental area began (Fig. 1). Over the course of 3.8 yr until 20 June 2019, sea urchins were removed from the experimental area 22 times with the participation of 1–5 divers each time. The duration of each removal varied from 25–728 min (Table 1). The removed sea urchins were transported to Shizugawa Fish Market (Fig. 1) via a research fishing vessel. The biomass was measured using a digital weight scale (100 g accuracy). The biomass of the sea urchins removed was 2299 kg in total, and it exceeded 100 kg in September 2015, December 2015, November 2016, May 2018, November 2018, and March 2019 (Table 1).

Surveys of sea urchin and kelp densities were conducted along the experimental transects (E1: 0–20 m; E2 and E3: 0–15 m) and the control transects,

Table 1. Biomass of *Mesocentrotus nudus* removed from the experimental area by SCUBA diving. Sea urchins were removed after completion of the sea urchin and kelp density survey, except on 23 March 2016. Asterisks indicate dates when sea urchin removal was conducted without the survey

Date	Biomass (kg)	Number of divers	Total dive duration (min)
4 Sep 2015*	467.75	5	728
30 Sep 2015	170.70	2	220
21 Oct 2015	39.30	1	70
2 Dec 2015	137.10	3	210
12 Jan 2016	63.80	5	175
4 Feb 2016	51.60	5	154
23 Mar 2016	0	0	0
19 May 2016	27.30	2	72
5 Aug 2016	52.55	3	105
28 Sep 2016	96.80	5	247
27 Oct 2016	29.60	1	60
2 Nov 2016*	259.20	3	335
28 Nov 2016	76.20	4	185
5 Jan 2017	49.00	3	115
24 Mar 2017	5.30	2	25
5 Jun 2017	41.50	3	135
29 Aug 2017	79.30	4	260
26 Oct 2017*	84.00	2	170
29 Nov 2017	42.20	4	150
14 May 2018	112.40	4	225
20 Aug 2018	47.10	3	122
13 Nov 2018*	197.20	4	516
15 Mar 2019*	119.30	5	252
20 Jun 2019	50.10	3	100
Total	2299.3		

using the same method as before sea urchin removal, starting on 30 September 2015. Sea urchin densities at the 15–20 m plot (PL) of E1 were not surveyed in October 2015. Only juvenile kelp was surveyed on 30 September 2015 as well as in December 2015, and in January, February, April, and May 2016. The survey was conducted 8 times from 30 September 2015 to June 2019 at the control transects (C1: 0–5 m; C2 and C3: 0–10 m), excluding C1 and C2 in October 2015. The densities of *M. nudus* and *E. bicyclis* juveniles (FSJ and SSJ) and adults were calculated by PL at 5 m intervals (n = 10 quadrats) in both the experimental and control transects before and after the removal of sea urchins. Sea urchins were collected simultaneously with their density survey at both the experimental and control transects. The TD of all sea urchins collected from the experimental transects, as well as randomly collected sea urchins from the control transects, was measured aboard a research fishing vessel using a vernier caliper with an accuracy of 0.1 mm.

To demonstrate the relationship between the densities of kelp juveniles and sea urchins, the densities of FSJ and SSJ at different sea urchin densities in the experimental transects during the research survey were analyzed among 4 seasons: winter (January–March), spring (April–June), summer (July–September), and autumn (October–December).

2.4. Water temperature

Water temperature was measured every 15 min using 2 data loggers (HOBO UA-002-64, Onset) attached to each of 2 small concrete blocks resting on the sea floor at a depth of 1.5 m near the 0 m point of E2 from 29 July 2015 to 12 May 2018 (Fig. 1). The mean daily water temperature was calculated from a data logger retrieved on alternate days and was calculated as the mean of 96 measurements each day. The maximum temperatures were 24.2°C in August 2015, 24.1°C in September 2016, and 22.7 °C in August 2017. The minimum temperatures were 8.2°C in March 2016, 7.6°C in February 2017, and 8.2°C in February 2018 (Fig. 2A).

Daily sea surface temperature (SST) at Enoshima fishing port (38° 24' N, 141° 36' E), located near Shizugawa Bay in Onagawa, Miyagi Prefecture, was calculated from hourly measurements taken from 1 January to 30 June in 2016–2019. Additionally, the mean SST from 1989–2018 was also calculated (Japan Fisheries Research and Education Agency 2023). During March–April 2016, 2017, and 2018, SST was higher than the mean, with a peak of >3°C in 2018 (10.6°C at Enoshima fishing port; Fig. 2B), coincident with the value at Nojima (Fig. 2A). SST decreased from 7.7°C in late March to 5.3°C in early April 2019 (Fig. 2C), which was >2°C lower than the mean temperature over the past 30 yr (Fig. 2B).

2.5. Statistical analysis

Pearson's correlation coefficient was used to statistically analyze the correlation between log-transformed sea urchin TD and BW. Factors affecting the densities of *M. nudus* and FSJ, SSJ, and adults of *E. bicyclis* were analyzed using a generalized linear mixed model (GLMM). In the analyses, date and treatment were set as fixed effects and transect and PL were set as random effects. The densities of FSJ and SSJ at different sea urchin densities among 4 seasons in the experimental transects were analyzed using 2-way ANOVA with aligned rank transform (ART) because the normality of these density data was not detected by the Shapiro-Wilk *W*-test (Wobbrock et al. 2011). Subsequently, the
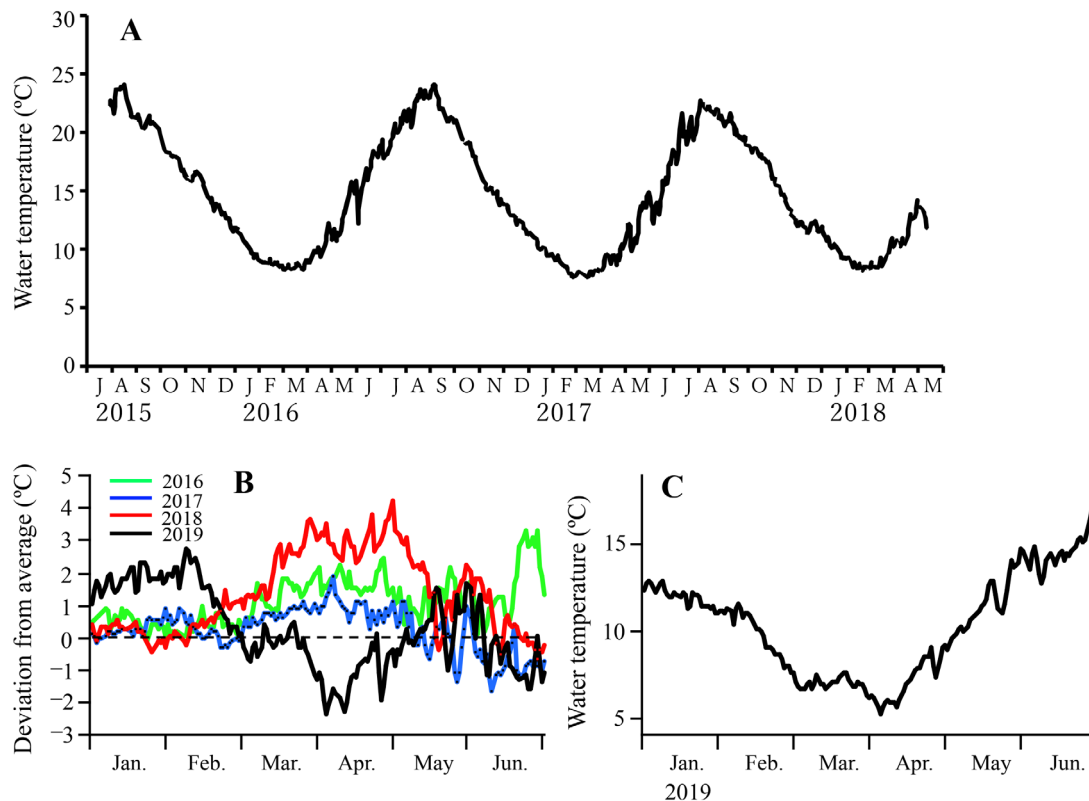
Fig. 2. (A) Daily water temperature at the experimental site during the research survey. (B) Deviations from the 30 yr mean between 1989 and 2018 (dashed line) from January to June in 2016, 2017, 2018, and 2019 at Enoshima fishing port, Onagawa, Miyagi Prefecture. (C) Daily sea surface temperature in 2019 at Enoshima

significances of the data without ART were analyzed by the Steel-Dwass multiple comparison test. All research survey density data used were pooled for the analyses. All statistical analyses were performed with R v.4.4.0 (R Core Team 2023) using the packages 'lme4', 'lmerTest', and 'ARTool'.

3. RESULTS

3.1. Threshold of sea urchin density and biomass

The mean (±SE) density of sea urchins in the 101 quadrats located below the lower fringe of the kelp forest was 15.5 ± 0.9 ind. m^{-2}. This density indicates the threshold density of *Mesocentrotus nudus* required to trigger the phase shift from *Eisenia bicyclis* forest to barren. There was a statistically significant positive correlation between TD and BW ($r^2 = 0.8941$, $p < 0.0001$). The equation to calculate BW was:

$$BW = 0.0011 \times TD^{2.8101} \quad (1)$$

Using this equation, the threshold biomass was estimated to be 712.0 ± 59.6 g m^{-2}.

3.2. Sea urchin and kelp densities before and during sea urchin removal

Fig. 3 shows the mean densities of sea urchins and kelp with different types of damage due to sea urchin grazing by PL at 5 m intervals along the experimental transects before sea urchin removal. Sea urchin grazing marks were found on all *E. bicyclis*. The mean sea urchin densities at the 0−5 m PL of E1 and E2 and the 0−10 m PL of E3 were <10 ind. m^{-2}. Notably, the densities exceeded 20 at the 15−20 m PL of E2. No juvenile kelp were found along any of the transects. At E1 and E3, entire adult *E. bicyclis* plants grew from the 0−10 m PL. At E2, these were limited to the 0−5 m PL, with damage forms of 'thallus without fronds', 'stipe and holdfast only', and 'holdfast only'. The latter was also found at the 15−20 m PL of E2 and at the 25−30 m PL of E3, indicating adult kelp growth prior to sea urchin grazing. No 'holdfast only' damage was found in the 10−20 m PL of E1.

The results of the GLMM analysis of factors affecting the densities of *M. nudus* are shown in Table 2. Generally, positive effects on sea urchin densities and their significant increase were found in autumn
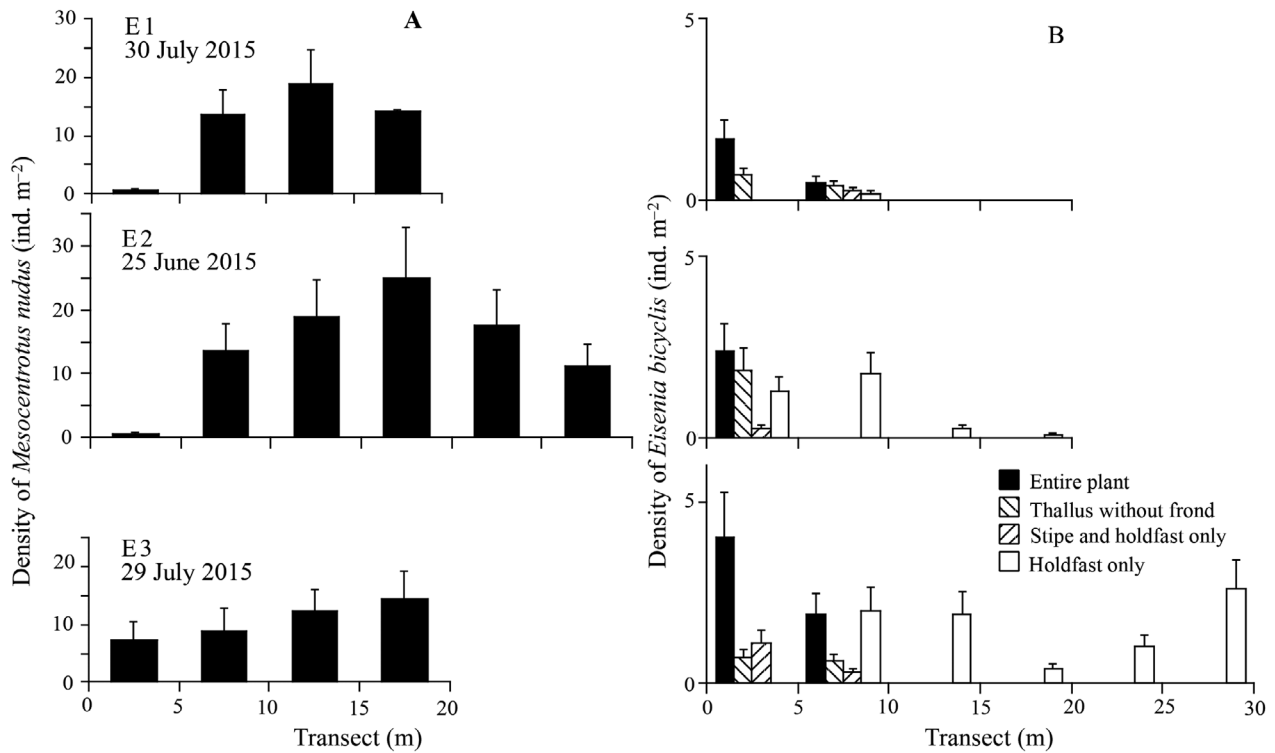
Fig. 3. Mean (+SE) densities of (A) *Mesocentrotus nudus* and (B) *Eisenia bicyclis* with different types of damage due to sea urchin grazing along the experimental transects (E1, E2, and E3) before sea urchin removal. Densities are expressed by plot at 5 m intervals using a 1 × 1 m quadrat (n = 10 quadrats). E2 and E3 are extended over 15 m

in 2015 and 2016, particularly in October 2016, but also in spring and summer in 2017, 2018, and 2019. Sea urchin densities differed significantly between treatments of the experimental and control transects (p < 0.01).

Changes in sea urchin densities during sea urchin removal along the experimental and control transects are shown in Fig. S2 and Table S1. At the 0−5 m PLs of E1, E2, and E3, the densities were generally low (<0.8 ind. m^{-2}). At the PLs of 5−10, 10−15, and 15−20 m of E1, the densities sharply increased to >20 ind. m^{-2} in September and October 2016 and then remained high. At the 5−10 m PLs of E2 and E3, the densities were low (<1.7 ind. m^{-2}). In October 2016, the densities at the 10−15 m PLs of E2 and E3 increased to >12.0 ind. m^{-2}. In C2 and C3, the densities at the 5−10 m PLs were higher than those at the 0−5 m PL. Occasionally, the densities exceeded 30 ind. m^{-2} at the 5−10 m PL of C2 and C3.

The results of GLMM analysis of factors affecting the densities of FSJ, SSJ, and adult *E. bicyclis* are shown in Table 3. Generally, there were positive effects on FSJ densities and negative effects on SSJ and adult densities. The adult densities significantly decreased in most months. The densities of FSJ and SSJ significantly increased and decreased, respectively, except for 1−3 months in autumn and winter. Significant differences in the densities between treatments were found in FSJ (p < 0.01) and adult *E. bicyclis* (p < 0.05), but not in SSJ (p > 0.05).

Changes in densities of FSJ, SSJ, and adult *E. bicyclis* along the experimental and control transects are shown in Figs. S3 and Table S2. During the research survey, no adults grew at the 10−15 and 15−20 m PLs of E1, where FSJ densities were low. No SSJ grew at the 15−20 m PL. At the 0−5 and 5−10 m PLs, FSJ frequently occurred, but the densities of SSJ were low. Notably, the density of adults in May 2018 (3.1 ind. m^{-2}) was high at the 0−5 m PL. In E2, FSJ and SSJ grew at the 0−5 and 5−10 m PLs until October 2016. After that, the density of SSJ increased until December 2016 or January 2017. Adult densities at the 5−10 m PL were high from October 2016 to June 2019 but did not exceed 4.0 ind. m^{-2}. In E3, adult densities at the 0−5 m PL were high and greatly variable. The FSJ densities were highest (>4.0 ind. m^{-2}) in September and October 2016, followed by the high occurrence of SSJ in November 2016 and January 2017 (~5 ind. m^{-2}). Adult density increased (>6.0 ind. m^{-2}) in January 2017. High den-

Table 2. Generalized linear mixed model (GLMM) analysis of factors affecting the density of *Mesocentrotus nudus*. Significant p-values (p < 0.05) in **bold**

Fixed effects	Estimate	SE	t	p
Intercept	20.51	2.61	7.86	**<0.001**
30 Sep 2015	1.35	0.83	1.63	0.102
21 Oct 2015	2.01	0.88	2.28	**0.023**
2 Dec 2015	0.62	0.83	0.75	0.455
4 Feb 2016	−1.02	0.89	−1.14	0.254
23 Mar 2016	−0.76	0.90	−0.84	0.400
20 Apr 2016	0.17	0.83	0.21	0.834
19 May 2016	0.28	0.90	0.32	0.752
5 Aug 2016	0.82	0.90	0.91	0.363
28 Sep 2016	3.57	0.90	3.98	**<0.001**
27 Oct 2016	6.83	0.83	8.19	**<0.001**
28 Nov 2016	0.69	0.90	0.76	0.447
5 Jan 2017	2.12	0.90	2.34	**0.023**
24 Mar 2017	1.19	0.92	1.29	0.196
5 Jun 2017	3.23	0.83	3.89	**<0.001**
29 Aug 2017	2.45	0.90	2.73	**0.003**
29 Nov 2017	2.11	0.90	2.34	**0.023**
14 May 2018	3.33	0.90	3.71	**<0.001**
20 Aug 2018	2.46	0.90	2.74	**0.003**
20 Jun 2019	3.21	0.83	3.86	**<0.001**
Treatment	−19.09	2.87	−6.65	**0.003**
Random effects	Variance	SD		
Transect	12.05	3.47		
Plot	8.60	2.93		

sities of FSJ and SSJ recurred until November 2017, resulting in high adult density in May 2018. Similarly, adult density at the 5–10 m PL of E3 was high in May 2018. At the 10–15 m PLs of E2 and E3, the densities of FSJ and SSJ as well as subsequent adult densities were low. In June 2019, the densities of FSJ were highest at the 0–5 and 5–10 m PLs of E1 (>9.0 ind. m^{-2}) and E3 (> 5.0 ind. m^{-2}), which showed a significant large effect during the research survey (Table 3).

FSJ, SSJ, and adult kelp occurred at the 0–5 m PL of C1 and C2 but disappeared from December 2015 and/or April 2016. At the 0–5 m PL of C3, FSJ and SSJ disappeared after April 2016. From April 2016 to June 2019, adult densities decreased. No FSJ, SSJ, or adults grew at the 5–10 m PL of C2 and C3.

3.3. Densities of juvenile kelp and sea urchins

The densities of FSJ and SSJ at different sea urchin densities in each of the 4 seasons in the experimental transects, and the significances among sea urchin densities and seasons, are shown in Fig. 4 and Table 4. A significant difference in FSJ densities was found among seasons ($F_{3,1937}$ = 3.240, p < 0.01) but not

Table 3. Generalized linear mixed model analysis of factors affecting the density of first- and second-stage juveniles (FSJ and SSJ, respectively) and adults of *Eisenia bicyclis*. Significant p-values (p < 0.05) in **bold**

| Fixed effects	FSJ Estimate	SE	t	p	SSJ Estimate	SE	t	p	Adult Estimate	SE	t	p
Intercept	−1.51	0.53	−2.88	**0.021**	0.49	0.32	1.54	0.151	0.23	0.66	0.34	0.740
30 Sep 2015	1.61	0.30	5.34	**<0.001**	−1.01	0.18	−5.79	**<0.001**	−0.28	0.33	−0.86	0.393
21 Oct 2015	1.45	0.32	4.54	**<0.001**	−1.06	0.19	−5.71	**<0.001**	−1.82	0.24	−7.69	**<0.001**
2 Dec 2015	0.80	0.30	2.65	**0.003**	−0.65	0.18	−3.69	**<0.001**				
4 Feb 2016	0.02	0.32	0.07	0.944	−0.09	0.19	−0.48	0.632				
23 Mar 2016	0.09	0.33	0.28	0.778	−0.20	0.19	−1.07	0.283	−1.98	0.28	−7.11	**<0.001**
20 Apr 2016	0.65	0.30	2.15	**0.022**	−0.60	0.18	−3.43	**<0.001**	−0.74	0.33	−2.24	**0.025**
19 May 2016	1.56	0.33	4.80	**<0.001**	−0.85	0.19	−4.44	**<0.001**				
5 Aug 2016	1.97	0.33	6.03	**<0.001**	−0.71	0.19	−3.69	**<0.001**	−1.20	0.24	−4.95	**<0.001**
28 Sep 2016	1.07	0.33	3.30	**<0.001**	−0.55	0.19	−2.90	**0.003**	−1.42	0.24	−5.94	**<0.001**
27 Oct 2016	0.79	0.30	2.62	**0.003**	−0.42	0.18	−2.39	**0.017**	−1.39	0.23	−6.17	**<0.001**
28 Nov 2016	0.14	0.33	0.44	0.660	0.35	0.19	1.83	0.068	−1.45	0.24	−6.02	**<0.001**
5 Jan 2017	−0.07	0.33	−0.22	0.826	0.29	0.19	1.50	0.133	−0.62	0.24	−2.6	**0.010**
24 Mar 2017	0.09	0.33	0.28	0.778	−0.34	0.19	−1.77	0.076	−1.12	0.24	−4.67	**<0.001**
5 Jun 2017	0.63	0.30	2.11	**0.021**	−0.89	0.18	−5.08	**<0.001**	−0.82	0.23	−3.63	**<0.001**
29 Aug 2017	1.02	0.33	3.14	**0.003**	−0.99	0.19	−5.21	**<0.001**	−0.57	0.24	−2.38	**0.018**
29 Nov 2017	0.38	0.33	1.16	0.245	−0.26	0.19	−1.34	0.179	−0.72	0.24	−3.01	**0.003**
14 May 2018	0.06	0.33	0.19	0.851	−0.87	0.19	−4.57	**<0.001**				
20 Aug 2018	0.01	0.33	0.03	0.975	−0.91	0.19	−4.78	**<0.001**	−0.18	0.24	−0.76	0.445
20 Jun 2019	2.13	0.30	7.09	**<0.001**	−0.97	0.18	−5.51	**<0.001**	−0.49	0.23	−2.19	**0.029**
Treatment	1.45	0.30	4.77	**0.005**	0.6	0.25	2.41	0.062	1.99	0.53	3.74	**0.015**
Random effects	Variance	SD			Variance	SD			Variance	SD		
Transect	0.10	0.31			0.08	0.28			0.38	0.62		
Plot	0.64	0.80			0.18	0.42			0.99	0.99		
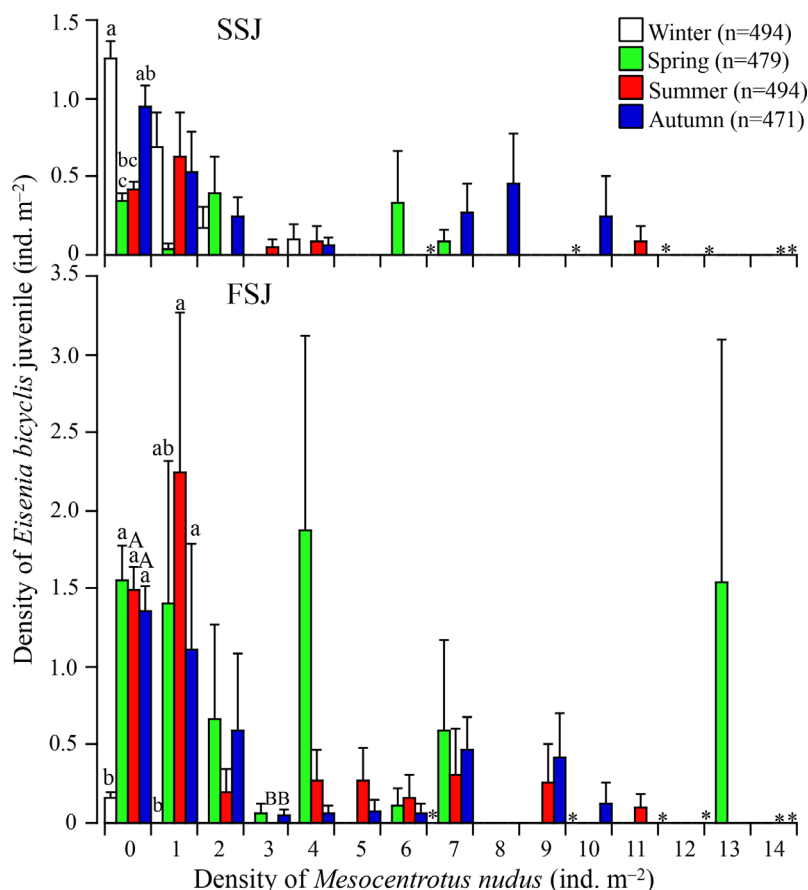
Fig. 4. Mean (+SE) densities of juvenile *Eisenia bicyclis* at different densities of *Mesocentrotus nudus* in each of 4 seasons in the experimental transects during sea urchin removal. Kelp juveniles were divided into first and second stages (FSJ and SSJ, respectively). 'n' indicates the number of 1 × 1 m quadrats. Uppercase and lowercase letters indicate significant differences in the densities of FSJ and SSJ among sea urchin densities and among the 4 seasons, respectively (p < 0.05). Sea urchin densities are adopted with >4 quadrats. Data obtained from 1−4 quadrats are indicated as asterisks, excluded from n, and are not illustrated

Table 4. Two-way ANOVA with aligned rank transform of the densities of first- and second-stage juveniles (FSJ and SSJ, respectively) of *Eisenia bicyclis* at different sea urchin densities among 4 seasons in the experimental transects. Significant p-values (p < 0.05) in **bold**

		df	F	p
FSJ	Sea urchin density	18	1.341	0.152
	Season	3	3.240	**0.021**
	Sea urchin density × season	36	1.828	**0.002**
SSJ	Sea urchin density	18	8.914	**<0.001**
	Season	3	20.408	**<0.001**
	Sea urchin density × season	36	2.059	**<0.001**

among sea urchin densities ($F_{18,1937}$ = 1.341, p > 0.05). In SSJ, significant differences were found among sea urchin densities ($F_{(8,1937}$ = 8.914, p < 0.001) and

seasons ($F_{3,1937}$ = 20.408, p < 0.001). There were significant interactions between sea urchin densities and seasons for FSJ ($F_{36,1937}$ = 1.828, p < 0.01) and SSJ ($F_{36,1937}$ = 2.059, p < 0.001). From a post hoc test, when sea urchins were absent, the density of FSJ during winter (January−March) was significantly lower than in other seasons (p < 0.01). When sea urchin density was 0 or 1 ind. m^{-2} during spring, summer, and autumn (October−December), FSJ density was consistently >1.0 ind. m^{-2}. The densities of FSJ during summer and autumn decreased significantly with an increase in sea urchin densities from 0−3 ind. m^{-2} (p < 0.05). In contrast, the densities during spring were occasionally elevated (>1.5 ind. m^{-2}) when sea urchin densities exceeded 3 ind. m^{-2}, which resembled those observed at the 0−10 m PL of E1 in June 2019. In contrast to FSJ, the density of SSJ during winter was significantly higher than during spring (April−June) and summer (July−September) (p < 0.01). When sea urchins were absent, the density of SSJ during autumn was significantly higher than that in spring (p < 0.05).

3.4. Sea urchin body size

The frequency distributions of TD for *M. nudus* in the experimental transects before and during sea urchin removal as well as in the control transects are shown in Figs. S4 & S5. In the experimental transects, except for February−April 2016 when the number sampled was small, sea urchins with a TD of 40−50 mm were the most abundant (41.6−64.9%), while those of 35−40 and 50−55 mm varied. Small individuals with a TD of 10−20 mm were observed in June and August 2017 and in June 2019. In the control transects, except for October 2015 when the sample number was small, sea urchins with a TD of 40−50 mm were abundant (31.8−54.3%), but in June 2019, their predominance shifted to 50−60 mm (54.3%), as relatively few sea urchins with a TD of <40 mm were recorded. At both the experimental and control sites, there were only a few individuals with a TD of >60 mm.

4. DISCUSSION

4.1. Threshold density and biomass of *Mesocentrotus nudus* for kelp forest destruction

This investigation determined the threshold density (15.5 ind. m^{-2}) and biomass of *Mesocentrotus nudus* (712.0 g m^{-2}) required to trigger the phase shift from an *Eisenia bicyclis* forest to a barren state. Filbee-Dexter & Scheibling (2014) evaluated the threshold densities and biomass of sea urchins required to trigger the phase shift from kelp to a barren state (forward shift) and vice versa (reverse shift) in 6 regions: Alaska and California, USA; Chile; Nova Scotia, Canada; Norway; and Tasmania, Australia. In these regions, the threshold density of sea urchins required to trigger the forward shift was 72 ind. m^{-2} for *Strongylocentrotus polyacanthus* herbivory on *Laminaria dentigena*, *L. yezoensis*, and other kelp species in Alaska (Konar & Estes 2003). The threshold densities for *S. droebachiensis* amongst *L. longicruris* and *L. digitata* in Nova Scotia were 31–65 and 45–75 ind. m^{-2}, respectively (Breen & Mann 1976, Chapman 1981, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007) and 45–75 on *L. hyperborea* in Norway (Hagen 1995, Leinaas & Christie 1996, Sjøtun et al. 1998). The densities of *Centrostephanu rodgersii* and *Heliocidaris erythrogramma* in an *E. radiata* kelp forest were 4–10 ind. m^{-2} in Tasmania (Ling 2008, Ling et al. 2009, Marzloff et al. 2013) and 8 ind. m^{-2} in Victoria, Australia (Kriegisch et al. 2016). Threshold densities of sea urchins in Alaska, Nova Scotia, and Norway were significantly higher than those of *M. nudus* in a kelp forest of *E. bicyclis.*

The present study was conducted immediately following kelp destruction by aggregated sea urchins at the grazing front, which had led to overgrazing. However, at the control transects where sea urchin densities exceeded 20 ind. m^{-2}, there was an early disappearance or marked decrease in FSJ, SSJ, and adults of *E. bicyclis* at the 0–5 m PLs of C1, C2, and C3. During the present study, there was a significant increase in sea urchin densities of >20 ind. m^{-2} at the 5–20 m PL of E1; a high grazing intensity with the potential to destroy the adult *E. bicyclis* forest. Thus, the density and biomass of sea urchins immediately following kelp destruction is estimated to be the threshold level.

According to Filbee-Dexter & Scheibling (2014), threshold densities are associated with body sizes among dominant sea urchin species. They summarized the biomass thresholds in 6 regions and found them to be relatively consistent, displaying order-of-magnitude differences between forward shifts to barren areas (*A*: 1–3 kg m^{-2}) and reverse shifts to kelp forests (*B*: 0.1–0.6 kg m^{-2}). These variations indicate a 77–91% decrease (($A - B$) × 100 / *A*) in biomass resulting in the forward shift. In Victoria, the biomass threshold for the forward shift in *H. erythrogramma* (0.427 kg m^{-2}; Kriegisch et al. 2016) was lower than that for *M. nudus* in the present study.

Adult kelps increased at the 0–10 m PL of E2 and E3 in the present study. This was attributed to the continuous removal of sea urchins, resulting in low densities. The sea urchin biomass range was 0–92.2 g m^{-2}, as converted from the mean TD (47.8 mm, n = 107; calculated from individuals at the 0–10 m PL of E2 and E3 during sea urchin removal), and the density range was 0–1.6 ind. m^{-2} (Fig. S2). These values for the reverse shift were lower than those observed in other regions, indicating an 87.1–100% decrease in biomass resulting in the forward shift, suggesting a significant hysteresis effect.

4.2. Recovery process of adult kelp forest

Low sea urchin densities observed at the 0–5 m PL of all the experimental transects before sea urchin removal reflect their location just beneath the turbulent wave base (Witman 1987, Siddon & Witman 2003, Lauzon-Guay & Scheibling 2007). At the 0–10 m PL of E3 on a hidden prominent reef, occasional changes in the density of adult kelp is a manifestation of the impact of high wave action, which also curbs sea urchin grazing and the movement of *M. nudus* (Kawamata 1998, 2012). Additionally, the kelp thalli might be detached due to the shallower depths in comparison with E1 and E2. There was an increase in adult kelp at the 0–5 m PL of E1 and the 0–10 m PLs of E2 and E3 since spring, following the occurrence of FSJ in summer and subsequent SSJ in autumn in the previous year. These seasonal occurrence patterns generally coincided with those at the depths of 0.5, 0.8, and 2.5 m surveyed at Kitsunezaki (38° 21' N, 141° 25' E) along the Oshika Peninsula from 2011–2013 (Suzuki et al. 2021). These kelp forest increases were due to the near-perfect regulation of sea urchin densities at <1.0 ind. m^{-2} for 3.8 yr.

In E1, the temporal increase was found only at the 0–5 m PL. At the 5–20 m PL, the substrate consists of boulders on a flat reef without kelp growth. Before the removal of sea urchins, at 10 m offshore, many sea urchins immediately invaded, occasionally exceeding the threshold density of the northwest and offshore barrens. The adult kelp forest failed to recover. Sea urchin densities of >4.0 ind. m^{-2} at the 10–15 m PLs of E2 and E3 after October 2016, resulting from

invasion from deep and/or northeast barrens, impeded any increase in adult kelp density.

Adult kelp recovery was limited to the nearshore half of the experimental transects. Sea urchins with a diameter of 40−50 mm were predominant at both experimental and control transects. The relative variation of individuals of diameter 35−40 and 50−55 mm may be affected by juvenile recruitment and somatic growth, respectively. The rarity of individuals with a diameter of >60 mm may be attributed to stagnation in somatic growth due to aging and limited food availability (Agatsuma 2014).

4.3. Sea urchin densities required for successful recruitment of juvenile kelp

There were significant interactions in the densities of FSJ and SSJ between sea urchin densities and season. ANOVA results indicated a low density of FSJ during winter; high densities of FSJ during spring, summer, and autumn; and high densities of SSJ during winter and autumn at sea urchin densities of 0 or 1 ind. m^{-2}. These density patterns reflect the phenology of *E. bicyclis*, where FSJ grow to SSJ from autumn to winter. However, GLMM analysis indicated that the densities of SSJ were not significantly affected in November, January, February, and March. As the density of FSJ during summer and autumn decreased significantly with an increase in sea urchin density from 0−3 (Fig. 4), an increase in the number of sea urchins would decrease SSJ density in winter. Indeed, although sea urchins were removed monthly from August−November 2016, their density remained extremely high at the 10−20 m PL of E1 in October and November 2016. This mirrors the seasonally active foraging migration of many *M. nudus* away from barren areas, with their large population, to find and consume available food, thereby ensuring their reproduction in autumn (Agatsuma & Kawai 1997, Sano et al. 1998). The results of data analyses indicate that reducing sea urchin densities to 0 or 1 ind. m^{-2} during autumn is crucial to ensure the survival of SSJ in winter and to enable the growth of adult kelp forests in summer. In spring, a high density of FSJ (>1.5 ind. m^{-2}) was observed even at sea urchin densities exceeding 3 due to a large FSJ recruitment in June 2019. In early April 2019, SST at Enoshimma fishing port dropped to around 5°C due to the first intrusion of the Oyashio into onshore waters starting in late March 2019 (Miyagi Prefecture Fisheries Technology Institute 2019). A large recruitment of FSJ is probably associated with the decreased food intake

and foraging activity of *M. nudus* at low water temperatures (Agatsuma et al. 2000) in addition to the presence of high nutrient levels. Following such a large recruitment of FSJ, maintenance of strict regulation of sea urchin densities at 0 or 1 ind. m^{-2} would promote the recovery of the kelp forest.

The *E. bicyclis* forest reaches its seasonal maximum biomass in July and August (Yoshida 1970). In July 1982 and 1983, Taniguchi et al. (1987) observed the lower fringe depth of the kelp forest off Tomarihama to be 8 m. The density of adult kelp in the forest was ~5 ind. m^{-2}. The mean density in areas of dense growth at depths of 3−6 m in 1982 and 2−5 m in 1983 ranged from 10−18 ind. m^{-2}. The depth of the lower fringes of the kelp forest off Tomarihama was 5−6 m in July 1995 and September 1996 (Sano et al. 1998). By June 2008, it had decreased to a depth of 2.4 m (Muraoka et al. 2017). The adult densities recorded in the kelp forest were 1.08 ind. m^{-2} in 2000 (Muraoka 2008) and an estimated 0.3 ind. m^{-2} in 2008 (Fig. 5 of Muraoka et al. 2017). These studies over the past quarter century have shown a dramatic decrease in the density of this kelp forest.

In the present study, the maximum density of adult kelp was lower than 4.0 ind. m^{-2}, except for 6.5 ind. m^{-2} at the 0−5 m PL and 4.0 ind. m^{-2} at the 5−10 m PL of E3. The densities are lower than those recorded off Tomarihama in 1982 and 1983 (Taniguchi et al. 1987). According to the Japan Meteorological Agency (2023a), SST off the Pacific coasts of Miyagi, Iwate, and Aomori Prefectures have increased significantly during winter (January−March) (p < 0.01), spring (April−June) (p < 0.05), and autumn (October−December) (p < 0.01) over the past 100 yr (1911−2021). The rates of increase were 1.25°, 0.81°, and 0.97°C, respectively. Miyama et al. (2021) demonstrated that a marine heat wave occurred in the Oyashio Current region off the Pacific coast of Hokkaido and Tohoku during summers between 2010 and 2016. This was attributed to weakening of the southward intrusion of the Oyashio Current near the coast in the summer from 2010, accompanied by an increase in anticyclonic eddies from the Kuroshio Extension.

M. nudus spawns from September−October (Agatsuma 2020). Increased autumn temperatures (~20°C) enhance juvenile abundance, possibly due to a shortening of their larval duration, ultimately improving larval survival rates (Agatsuma et al. 1998). Furthermore, the increase in winter and spring temperatures in 2016, 2017, and 2018 suggests a decrease in nutrient levels without the impact of the first intrusion of the Oyashio Current into onshore waters. Consequently, the recruitment of kelp juveniles decreases (Hoffmann

et al. 1984, Ladah & Zertuche-González 2007, Carney & Edwards 2010). Additionally, the intensified grazing of *M. nudus* at elevated temperatures (Machiguchi et al. 1994) would accelerate the consumption and depletion of kelp recruits. The high sea urchin grazing intensity and unfavorable oceanographic conditions suggest that a significant decrease in *M. nudus* densities is required for the reverse shift to an *E. bicyclis* forest that can act as an intensified positive feedback mechanism with significant hysteresis, resulting in the restricted recovery of kelp density and growth area.

Mensah & Ohshima (2021) reported that warming and tidal cycles strongly impact the Oyashio Intermediate Water, which is responsible for high production in the western subarctic Pacific. Warming of the Oyashio Intermediate Water suppresses vertical mixing, resulting in the reduction of nutrients supplied from deep layers. It is expected that this warming will increase at a faster pace from the mid-2020s until the mid-2030s, which suggests that kelp recruitment will be further suppressed even if sea urchins are completely removed.

5. CONCLUSIONS

In the present study, we first estimated the threshold density and biomass of *Mesocentrotus nudus* required to trigger the phase shift from an *Eisenia bicyclis* forest to a barren off Nojima Island in Shizugawa Bay, along the Pacific coast of Tohoku, northeastern Japan. As a result of continuous sea urchin removal for 3.8 yr, the kelp growth area has expanded offshore. However, increases in adult kelp following the occurrence of juveniles were restricted to the nearshore half of the experimental transects. The successful recruitment of kelp juveniles and the subsequent recovery of adult kelp forest requires *M. nudus* of 40–50 mm TD to be restricted to a density of 0–1 ind. m^{-2}. Reducing sea urchin density in autumn, when many invade from barrens, is crucial to ensure the survival of kelp juveniles. This study highlights the intensified positive feedback mechanism of the barren state due to high grazing intensity and the weakened Oyashio Current on the eastern Tohoku Pacific coast.

The subtidal rocky reef ecosystem along the Pacific coast of Tohoku has evolved under the influence of the Oyashio Current and its variability, which has a significant impact on the expansion or reduction of *E. bicyclis* forests through the interaction of bottom-up (nutrient) and top-down (sea urchin grazing) effects. Future climate change is expected to have further adverse effects on this ecosystem's foundation species.

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