

## SPECIAL FEATURE (ORIGINAL ARTICLE)

Marine ecosystem services: Ecological, socioeconomic and cultural sustainability

# Estimating the maximum sustainable yield of snow crab (*Chionoecetes opilio*) off Tohoku, Japan via a state-space stock assessment model with time-varying natural mortality

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**Abstract**

A maximum sustainable yield (MSY) obtained by maintaining or restoring fish stock levels is a tangible benefit of ecosystem services. Snow crab (*Chionoecetes opilio*) off Tohoku, Japan has been managed by a total allowable catch since 1996, although the abundance has not increased. Surprisingly, there was no increase after 2011, when fishing pressure was greatly reduced because of the Great East Japan earthquake. This implies that some of the crab's biological characteristics, such as recruits, natural mortality coefficient ( $M$ ) and terminal molting probabilities ( $p$ ), might have changed. We developed “just another state-space stock assessment model” to estimate the MSY of the snow crab off Tohoku considering interannual variations in  $M$  and  $p$ . The multimodel inference revealed that  $M$  increased from 0.2 in 1997 to 0.59 in 2018, although it did not vary according to instars, sex or terminal molt. The parameter  $p$  also increased by 1.34–2.46 times depending on the instar growth stages from 1997 to 2018. We estimated the MSYs in three scenarios, which changed drastically if  $M$  and  $p$  were set as they were in the past or at the current values estimated from this study. This result indicated that the MSY of snow crab would also vary with time based on their time-varying biological characteristics.

**KEYWORDS**

probability of terminal molt, random walk, stock assessment, the Great East Japan earthquake, time-varying ecosystem services

**1 | INTRODUCTION**

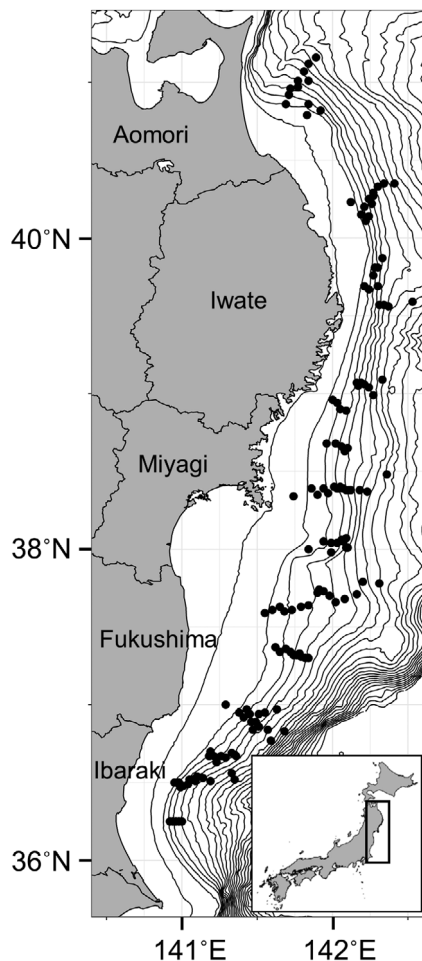
Ecosystem services are the benefits that nature can provide to households, communities and economies (Boyd & Banzhaf, 2006), and fish production (yield) is a

tangible benefit of ecosystem services (Tomscha & Gergel, 2016). The sustainable development goals (SDGs) comprise 17 goals and 169 targets, and maintaining or restoring fish stock levels to achieve maximum sustainable yield (MSY), as determined by their biological

characteristics, is one of the primary targets of the SDGs (UN General Assembly, 2015).

The Fisheries Law in Japan was amended in 2018, and it has been deemed necessary to set a target for fish abundance that maintains the MSY of a (spawning stock) biomass calculated under natural conditions in the present and reasonably foreseeable future (Fisheries Agency; <https://www.jfa.maff.go.jp/j/kikaku/kaikaku/attach/pdf/suisankaikaku-20.pdf> last accessed July 14, 2020). Some fish stocks that are legally managed by regulated total allowable catch (TAC) have begun to be managed under this amended Fisheries Law.

Snow crab (*Chionoecetes opilio*) off the Tohoku region (Figure 1) has been managed by a TAC since 1996 and is one of the most valuable exploited species in Japan. Although total landings in the Tohoku area were around 100 gross ton before 2011, total landings and fishing efforts (the number of tows by bottom trawl vessels that caught at least one snow crab) rapidly decreased in 2012

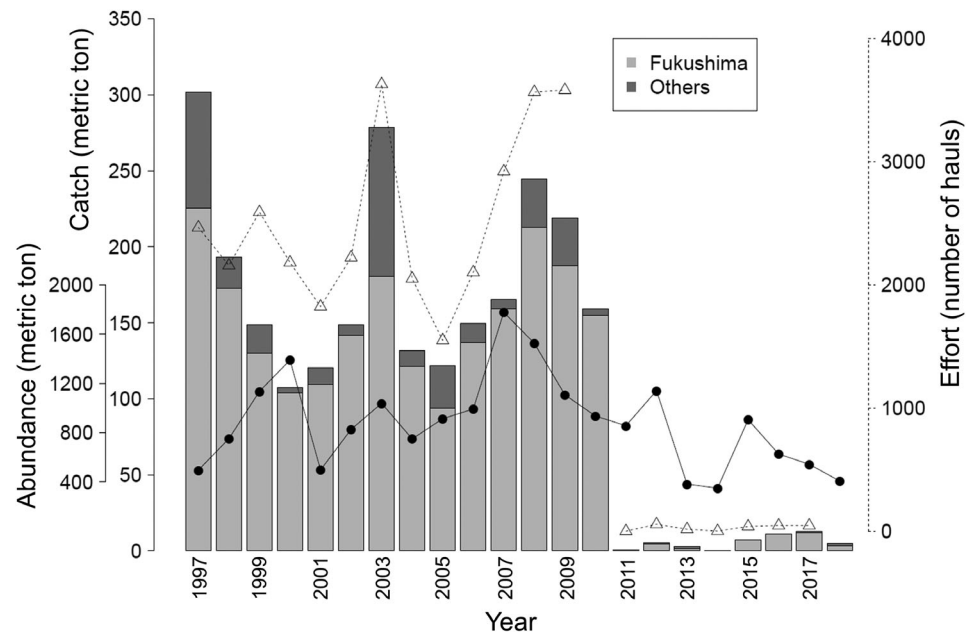


**FIGURE 1** Stations surveyed by the R/V *Wakataka-maru* since 1997 (black circles, 150 stations). The survey area covered off Aomori, Iwate, Miyagi, Fukushima and Ibaraki prefectures from 150 to 900 m depth. Contours drawn by 100 m depth

(Figure 2) because of the Great East Japan earthquake and tsunami in March 2011, which destroyed much of the fisheries-related infrastructure, such as vessels, ports and marine-product processing factories. The tsunami also hit the Fukushima-Daiichi Nuclear Power Plant in Fukushima Prefecture and caused leakage of radiocesium (Buesseler, Aoyama, & Fukasawa, 2011; Kaeriyama, 2015). Although only one specimen of marine produce has been found above the Japanese standard limit for foodstuffs (100 Bq/kg-wet) after April 2015 as of June 2020 (Fisheries Agency; <https://www.jfa.maff.go.jp/j/housyanou/kekka.html> last accessed in July 14, 2020), fishing efforts for snow crab after the earthquake have been less than 2% of those before 2011 (Shibata et al., 2019). Regarding bottom trawl fishing off Fukushima, only trial fishing has been carried out since 2011 (Shibata et al., 2017). The stock status of snow crab has been assessed by scientists from the Japanese Fisheries Research and Education Agency (FRA), based on their estimated abundance (fishable biomass, males: only for carapace width [ $cw$ ]  $\geq 80$  mm, females: only for matured) by a swept area method from the survey results of a research vessel (R/V) every year. Here, the word “fishable” means “no problem to fish and retain snow crab legally.” Regardless of the quite low fishing efforts, the observed abundance has continued to decrease rather than increase, contrary to expectations (Figure 2). Because fishing pressures have been low since March 2011, other factors have caused this continued decrease. In fact, the 2-year projected abundances that were needed to calculate the allowable biological catch (ABC) had probably been overestimated since 2012 by a previously developed model (Ueda, Ito, Hattori, Narimatsu, & Kitagawa, 2009), with the fishing mortality coefficient ( $F$ ) set at almost zero (Shibata et al., 2019).

One possible reason for this overestimation is that the biological characteristics, such as recruits, natural mortality coefficient ( $M$ ) and terminal molting probability ( $p$ ), could have changed in recent years. Recruits and  $M$  directly affect abundance and  $p$  also has an effect because terminal molting stops body growth as it matures (Conan & Comeau, 1986; Yoshida, 1941). In other words, the body weight of a matured individual will never heavier than that of an immature individual of the same age. This is related to a decrease in abundance because the mean body weight in the population decreased. In fact, the R/V data showed maturity ratio for each instar for males increased over a survey period (Supporting Information 1). Although the previous model assumed that  $M$  and  $p$  were fixed term, it is also necessary to consider whether they are time-varying and maintained high values in recent years. Usually, for  $M$  and  $p$ , especially  $M$ , the parameters have been impossible to estimate from

**FIGURE 2** Total catch (metric ton, bar graph), estimated abundance (metric ton) by a swept area method from survey data of the R/V *Wakataka-maru* (black circles) and effort of bottom trawl vessels (number of hauls, white triangles). Total catch was distinguished between that of Fukushima (gray) and other prefectures (dark gray). Effort value in 2018 was under calculation



fishery data in many cases. On the other hand, the scientific bottom trawl survey data have been available to estimate yearly abundance, and this is independent of fishery data. It might be possible to estimate and verify whether the parameters varied with time in this study.

Since we are interested in the time variation of the parameters, it is necessary to estimate these parameters using an appropriate statistical model. We assumed that the biological parameters followed a constant or a first- or second-order differential random walk (RW) to express whether the parameters were stable or time-varying with some smoothness during survey periods, although these parameters had often been treated as a constant or random effects (Murphy, Rugolo, & Turnock, 2018; Szuwalski & Turnock, 2016; Yamasaki, 1988). A state-space stock assessment model (SAM) has been reported (Nielsen & Berg, 2014), in which some parameters vary by an RW process. Although an age-structured model, such as statistical catch at age, usually assumes that a selectivity pattern is constant over time (Butterworth & Rademeyer, 2008), SAM can estimate a time-varying selectivity following an RW with a multivariate normal (MVN) distribution (Nielsen & Berg, 2014). As opposed to the penalized likelihood approach, SAM enables the use of information criteria, such as Akaike's information criterion (AIC) (Akaike, 1974), for model selection (Nielsen & Berg, 2014). Since the model developed in this study has some structures in common with SAM, it will be called JASAM (just another SAM). In JASAM,  $M$  and  $p$  can be stably estimated because the number at instar and maturity ratio have been obtained based on the scientific bottom trawl survey.

The purpose of this study is to develop a state-space model that considers variations and predicts the future abundance based on the stock-recruitment (SR) relationship

defined in this study, thereby estimating the MSY of snow crab off the Tohoku region, Japan, taking into account inter-annual variations in biological characteristic parameters, such as recruits,  $M$  and  $p$ .

## 2 | MATERIALS AND METHODS

### 2.1 | Scientific bottom trawl surveys

To estimate the abundance of snow crab, scientific surveys by the R/V *Wakataka-maru* using a bottom trawl net were carried out between 1997 and 2018 off the northern part of Honshu Island, Japan (Tohoku region; Figure 1). A total of 150 survey stations were set for towing at depths from 150 to 900 m from September to November, where the spatial distribution of snow crab was at depths ranging from 150 to 700 m, and the main distribution range of fishable crabs (males with  $cw \geq 80$  mm and mature females) is approximately 400–550 m (Kitagawa, 2000). The total length and mouth width of the trawl net were 44.1 and 5.4 m, respectively. The mesh size of the net was 50 mm, and a cover net with an 8 mm mesh was set at the cod-end. All tows were carried out during the daytime at a mean ship speed of 3.0 knots for 30 min. The tow area (i.e., survey effort) of each station was calculated by recording the arrival and departure point on the bottom and horizontal open width of the net using the Net Recorder system (Furuno Electric Co., Hyogo, Japan or Marport, Reykjavik, Iceland).

The catch was divided into male and female crabs, and the number of individuals was counted. For males, the  $cw$  and right (if not available, left) cheliped height was measured to the nearest 0.01 mm using a digital caliper

(CD67-A20PM, Mitsutoyo, Kanagawa, Japan) to identify their maturity (Fujita, Takeshita, & Matuura, 1988; Watson, 1970). For females, the *cw* was also measured and recorded, and the abdominal pleon was observed to determine maturity; adult females are characterized by a broad abdominal pleon after terminal molt (Yoshida, 1941). Instars of snow crabs off Tohoku were distinguished by their *cw* intervals (Table 1) (Ueda et al., 2007). In snow crab, the number of molts after instar VI is once a year; this can be used as an age trait (Kuwahara, Shinoda, Yamasaki, & Endo, 1995). The minimal instar of the snow crab obtained by this scientific bottom trawl was instar VIII, where the interval of *cw* is 24–42 mm (Table 1).

We then calculated the density at the station and estimated the total number at instar (*na*) with coefficients of variation (CVs) for the whole Tohoku region by multiplying by the area based on a swept area method (Shibata et al., 2019). Taylor's power law was used to correct the CVs (Supporting Information 2). The estimated catch efficiency (Hattori, Ito, Shibata, Yano, & Narimatsu, 2014) of the trawl net and the variance–covariance matrix were used to estimate an unbiased abundance (see below Equation (36)).

## 2.2 | Catch data

Snow crabs have only been caught off the coast of the Tohoku region by offshore bottom trawl fisheries (>17

gross ton), and their annual catches of snow crab were used as a total catch. The catch statistics were distinguished for males (only for *cw* ≥ 80 mm) and females (only for matured). Crabs were sampled, and their *cw* measured to reflect a whole composition of *cw* in the total catch by the Fukushima Fisheries Experimental Station. (On June 1, 2018, the experimental station was renamed as Fukushima Prefectural Research Institute of Fisheries Resources.) Additionally, their right or left cheliped height (only for male) and maturity (only for female) were measured. Then, catch at instar (*c<sub>a</sub>*) was calculated based on the instar and maturity composition in the sample data. The representativeness of the samples was guaranteed because Fukushima Prefecture represented 78% (on average) of the total catch in 1997–2018 (Figure 2). The instar and maturity composition in 1999 and an average composition from 2002 and 2004 were used to represent data from 1997 to 1998 and 2003, respectively, because the sample sizes were small. Sample data from 2008 to 2010 were also not available because a hard disk containing those data was lost to the massive tsunami in March 2011. A composition of 2007 data was used to obtain *c<sub>a</sub>* values for those 3 years. Compositions from 2011 to 2017 were substituted by those of the scientific bottom trawl survey because there were few catches, and measurements were not carried out in the period. In 2018, *c<sub>a</sub>* was available because measurements were carried out by scientists belonged to

**TABLE 1** Relationships among CW, instar, TM and sex that decide if the crab is fishable or not

| Sex    | Instar categories in population model | CW intervals | Terminally molted | Fishable |
|--------|---------------------------------------|--------------|-------------------|----------|
| Male   | VIII                                  | 24–42        | No                | No       |
|        | IX                                    | 42–56        | No                | No       |
|        | X with not TM                         | 56–74        | No                | No       |
|        | X with TM                             | 56–74        | Yes               | No       |
|        | XI with not TM and not fishable       | 74–80        | No                | No       |
|        | XI with TM and not fishable           | 74–80        | Yes               | No       |
|        | XI with not TM and fishable           | 80–86        | No                | Yes      |
|        | XI with TM and fishable               | 80–86        | Yes               | Yes      |
|        | XII with not TM                       | 86–98        | No                | Yes      |
|        | XII with TM                           | 86–98        | Yes               | Yes      |
|        | XIII with not TM                      | 98≤          | No                | Yes      |
|        | XIII with TM                          | 98–110       | Yes               | Yes      |
|        | XIV with TM                           | 110≤         | Yes               | Yes      |
| Female | VIII                                  | 24–42        | No                | No       |
|        | IX                                    | 42–56        | No                | No       |
|        | X with not TM                         | 56–74        | No                | No       |
|        | XI with TM and fishable               | —            | Yes               | Yes      |

Abbreviations: CW, carapace width; TM, terminal molting.

FRA and Fukushima Prefectural Research Institute of Fisheries Resources.

### 2.3 | Statistical modeling

We developed an SAM coupled with an RW process, such as a fishing mortality coefficient ( $F$ ) used in the SAM (Nielsen & Berg, 2014) and names as JASAM. In JASAM,  $M$  and  $p$  can be stably estimated because the number at instar and maturity have been obtained based on the scientific bottom trawl survey. JASAM has two model structures, state and observation models, for the modeling of latent population dynamics and the catch (observation) process. Unlike the situation with SAM, not only  $F$  but also  $M$  and  $p$  (i.e., biological parameters), can have RW schemes in this model (see below).

## 3 | MODELING OF NATURAL MORTALITY COEFFICIENT

### 3.1 | Definition of $M$ at group

We are interested in an instar-specific natural mortality rate  $M_a$ , where  $a$  ( $a = 8, \dots, 13$ ) shows the instar. On the other hand, the adjacent instars may take the same  $M$  because individuals of adjacent instars have similar body sizes, habitats, and are exposed to similar environments. In this study, instar group  $g$  ( $g = 0, \dots, 5$ ) was used to select  $M$  at group ( $M_g$ ), and instars were categorized for all groups (Supporting Information 3). The group consisted of successive instar groups. For example, if instar VIII and X are in the same group, instar IX is also in the same group.

### 3.2 | Time-varying $M$

As we explained in the introduction, it is suspected that  $M$  and/or  $p$  maintained a high value in recent years. Considering the possibility that  $M$  varies with time, variations in  $M$  were assumed to follow one of three patterns: a constant, an RW of first-order difference or that of second-order difference. In the constant style,  $M_{g,t+1} = M_g$ ,  $t = M_g$ , where  $t$  shows year ( $t = 1997, \dots, 2018$ ). In the first-order RW style:

$$\ln(M_{g,t+1}) \sim \text{Normal}\left(\ln(M_{g,t}), \sigma_{M,g}^2\right), \quad (1)$$

where  $\sigma_M$  is the SD of the normal distribution used for RW. In the second-order RW style, this is shown as:

$$\ln(M_{g,t+1}) \sim \text{Normal}\left(2\ln(M_{g,t}) - \ln(M_{g,t-1}), \sigma_{M,g}^2\right). \quad (2)$$

These three patterns of  $M_{g,t}$  were selected by model selection (see below).

### 3.3 | $M$ after the terminal molting

We categorize the number of years elapsed after the terminal molting,  $j$  ( $j = 0, 1, 2$ ), into immature ( $j = 0$ ), terminally molted within 1 year ( $j = 1$ ) and terminally molted after more than 1 year ( $j = 2$ ) (Shibata et al., 2019). The crabs mature functionally at the same time that they undergo the terminal molt and cease to grow. Then, since the individuals never experience a soft-shell period after molting,  $M$  can be lower than in an immature crab (Yamasaki, Sinoda, & Kuwahara, 1992). To express the change in  $M$  after the terminal molt,  $M$  of an individual 1 year after the terminal molt was multiplied by a multiplier  $\varphi$  ( $0 < \varphi < 1$ ) because it has been assumed that  $M$  decreases for individuals 1 year after terminal molting ( $j = 2$ ) in the stock assessment of snow crab:

$$M'_{g,t} = M_{g,t}\varphi, \quad (3)$$

$$\varphi = \begin{cases} 1 & (j = 0, 1), \\ \frac{1}{1 + \exp(-T_\varphi)} & (j = 2), \end{cases} \quad (4)$$

where  $M_{g,t}'$  is the natural mortality rate corresponding to the number of years elapsed after the terminal molting, and  $T_\varphi$  is a parameter that should be estimated.

### 3.4 | Modeling of fishing mortality coefficient

Because the spatial distribution of snow crab off Tohoku is basically divided between mature and immature individuals by sex rather than instar (Kitagawa, 2000),  $F$  at instar has not been estimated in the stock assessment in Japan (Shibata et al., 2019). We also use fishing mortality  $F$ , specified by maturity status and sex. The time-varying  $F$  is shown in the following:

$$\ln(F_{k,t+1}) = \ln(F_{k,t}) + \varepsilon_{k,t}, \quad (5)$$

where  $k = 1$  (immature male),  $k = 2$  (mature male) and  $k = 3$  (mature female). Note that  $t$  did not take 2010 from Equations (5) to (9) because the rapid decrease of fishing



#### 4.1 | From instar VIII to IX ( $\alpha = 8$ )

The number at instar from instar VIII to IX can be shown as:

$$\ln(N_{a+1,j=0,t+1}) = \ln(N_{a,j=0,t}) - M'_{g,t}. \quad (12)$$

#### 4.2 | From instar IX to X ( $\alpha = 9$ , immature)

From instar IX to X, some individuals mature (undergo terminal molting). The population dynamics model can be expressed as:

$$\ln(N_{a+1,j=0,t+1}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(1 - p_{a,t}), \quad (13)$$

where  $1 - p_{a,t}$  is the probability that an individual is not terminally molted.

#### 4.3 | From instar IX to X ( $\alpha = 9$ , mature)

Terminal molting at instar X results in maturing with a  $cw$  of less than 80 mm, and the individual ends its life without recruiting to a stock. The dynamics from immature to mature are shown as:

$$\ln(N_{a+1,j=1,t+1}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(p_{a,t}). \quad (14)$$

A plus group of instar X is shown in the following:

$$\ln(N_{a+1,j=2,t+1}) = \ln \left[ \sum_{j=1}^2 N_{a+1,j,t} \exp(-M'_{g,t}) \right]. \quad (15)$$

#### 4.4 | From instar X to XI ( $\alpha = 10$ , immature)

Since male snow crabs with a  $cw$  larger than 80 mm are fishable, the number of crabs at instar XI (74–86 mm) multiplied by  $r$  ( $0 < r < 1$ ) are fishable. In other words, the number of crabs at instar XI were separated into ranges (74–80 mm as not fishable [ $c = 0$ ], and 80–86 mm as fishable [ $c = 1$ ]). Although it had been assumed that  $r$  was 0.5 in a previous study (Shibata et al., 2019), we estimated  $r$  in this report. No fishable snow crab such as  $cw < 80$  for male and immature female are also fished because a bottom trawl is an indiscriminate type of fishing. Although no fishable snow crab is thrown back into the sea from on deck, bycatch mortality is unknown and

ignored in this study. Individuals of instar XI with a  $cw$  of 74–80 mm without terminal molting can be modeled as:

$$\ln(N_{a+1,j=0,t+1,c=0}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(1 - p_{a,t}) + \ln(1 - r). \quad (16)$$

The individuals of instar XI with a  $cw$  of 80–86 mm without terminal molting are then modeled as:

$$\ln(N_{a+1,j=0,t+1,c=1}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(1 - p_{a,t}) + \ln(r), \quad (17)$$

where  $r = 1/(1 + \exp(-T_r))$  and  $N_{a+1,j=0,t+1} = \sum_{c=0}^1 N_{a+1,j=0,t+1,c}$ .

#### 4.5 | From instar X to XI ( $\alpha = 10$ , mature)

Individuals of instar XI with a  $cw$  of 74–80 mm with terminal molting are modeled as

$$\ln(N_{a+1,j=1,t+1,c=0}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(p_{a,t}) + \ln(1 - r), \quad (18)$$

$$\ln(N_{a+1,j=2,t+1,c=0}) = \ln \left[ \sum_{j=1}^2 N_{a+1,j,t,c=0} \exp(-M'_{g,t}) \right]. \quad (19)$$

Individuals of instar XI with a  $cw$  of 80–86 mm with terminal molting are modeled as

$$\ln(N_{a+1,j=1,t+1,c=1}) = \ln(N_{a,j=0,t}) - M'_{g,t} + \ln(p_{a,t}) + \ln(r), \quad (20)$$

$$\ln(N_{a+1,j=2,t+1,c=1}) = \ln \left[ \sum_{j=1}^2 N_{a+1,j,t,c=1} \exp(-M'_{g,t} - F_{k=2,t}) \right], \quad (21)$$

where individuals that had experienced terminal molting were caught with a fishing mortality coefficient of  $F$ .

#### 4.6 | From instar XI to XII ( $\alpha = 11$ , immature)

Of the 74–80 mm and 80–86 mm individuals at instar XI, only the latter were subject to catch and were expressed as follows:

$$\begin{aligned} \ln(N_{a+1,j=0,t+1}) &= \ln[N_{a,j=0,t,c=0} \exp(-M'_{g,t}) \\ &+ N_{a,j=0,t,c=1} \exp(-M'_{g,t} - F_{k=1,t}) (1 - p_{a,t})]. \end{aligned} \quad (22)$$

#### 4.7 | From instar XI to XII ( $\alpha = 11$ , mature)

Because the 80–86 mm individuals are terminally molted and included into a plus group of instars as:

$$\begin{aligned} \ln(N_{a+1,j=1,t+1}) &= \ln[N_{a,j=0,t,c=0} \exp(-M'_{g,t}) \\ &+ N_{a,j=0,t,c=1} \exp(-M'_{g,t} - F_{k=1,t}) p_{a,t}], \end{aligned} \quad (23)$$

$$\ln(N_{a+1,j=2,t+1}) = \ln \left[ \sum_{j=1}^2 N_{a+1,j,t} \exp(-M'_{g,t} - F_{k=2,t}) \right]. \quad (24)$$

#### 4.8 | From instar XII to XIII ( $\alpha = 12$ , immature)

The number at instar from instar XII to XIII not terminally molted can be shown as:

$$\ln(N_{a+1,j=0,t+1}) = \ln(N_{a,j=0,t}) - M'_{g,t} - F_{k=1,t} + \ln(1 - p_{a,t}). \quad (25)$$

#### 4.9 | From instar XII to XIII ( $\alpha = 12$ , mature)

The number at instar from instar XII to XIII terminally molted can be shown as:

$$\ln(N_{a+1,j=1,t+1}) = \ln \left[ N_{a,j=0,t} \exp(-M'_{g,t} - F_{k=1,t}) p_{a,t} \right], \quad (26)$$

$$\ln(N_{a+1,j=2,t+1}) = \ln \left[ \sum_{j=1}^2 N_{a+1,j,t} \exp(-M'_{g,t} - F_{k=2,t}) \right]. \quad (27)$$

#### 4.10 | From instar XIII to XIV ( $\alpha = 13$ )

Because all individuals at this instar stage mature at probability one, the equation is as follows:

$$\begin{aligned} \ln(N_{a+1,t+1}) &= \ln[N_{a,j=0,t} \exp(-M'_{g,t} - F_{k=1,t}) \\ &+ \sum_{j=1}^2 N_{a+1,j,t} \exp(-M'_{g,t} - F_{k=2,t})]. \end{aligned} \quad (28)$$

## 5 | STATE MODEL OF FEMALE

### 5.1 | From instar VIII to IX and IX to X ( $\alpha = 8$ and 9, immature)

Because females do not mature at instar X, the population transition is described as:

$$\ln(N_{a+1,j=0,t+1}) = \ln(N_{a,j,t}) - M'_{g,t} \exp(T_{Mg}), \quad (29)$$

where  $T_{Mg}$  is the female-specific term, although  $T_{Mg}$  is tested for whether the term is zero or not.

### 5.2 | From instar X to XI ( $\alpha = 10$ , immature)

In females, because only instar XI is fishable, the transition is shown as:

$$\begin{aligned} \ln(N_{a+1,t+1}) &= \ln[N_{a,j=0,t} \exp(-M'_{g,t} \exp(T_{Mg})) \\ &+ \sum_{j=1}^2 N_{a+1,j,t} \exp(-M'_{g,t} \exp(T_{Mg}) - F_{k=2,t})]. \end{aligned} \quad (30)$$

### 5.3 | Estimation of the number of individuals at instar VIII

Because our survey can observe snow crabs older than instar VIII, we treated the number of individuals at instar VIII as recruits. As Tohoku region is at the southern limit of distribution of the species, snow crab distributed off Tohoku could take less time to become recruits compared to those in other areas because molting duration is shorter when the water temperature is increased under laboratory conditions (Kobayashi, 1989; Yamamoto et al., 2015). In fact, the SR relationship has not been estimated for this population (Shibata et al., 2019) because the life cycle of snow crab off Tohoku is unknown. In this paper, we assumed a RW scheme to estimate recruits as follows:

$$\ln(N_{a=8,j=0,t+1}) \sim \text{Normal}(\ln(N_{a=8,j=0,t}), \sigma_{rec}^2), \quad (31)$$

where the numbers of males and females were assumed to be the same (i.e., the sex ratio of recruits was assumed as 0.5). On the other hand, we considered three types of SR relationships just for estimation of MSY (see Section 7.2), although this contradiction should be solved in future research.

## 6 | OBSERVATION MODEL

### 6.1 | Scientific bottom trawl survey

The estimated number of individuals in the trawl survey  $n$  is obtained by multiplying the catch efficiency  $q$  by the true number of individuals  $N$ . The elapsed years after the terminal molting are not revealed by the trawl survey; only the identification before or after the terminal molting ( $u = 0$  where  $j = 0$ ,  $u = 1$  where  $j = 1$  and 2) can be determined. An observation model for the trawl survey is shown in the following:

$$\ln(n_{a,u,t}) \sim \text{Normal}(\ln(q_{a,t}N_{a,u,t}), V_{a,u,t}^2 + W_{a,u,t}^2), \quad (32)$$

$$V_{a,u,t}^2 = \ln(1 + CV_{a,u,t}^2), \quad (33)$$

$$W_{a,u,t}^2 = \ln(1 + \omega_{a,u,t}^2), \quad (34)$$

$$\ln(\omega_{a,u,t}) \sim \text{Normal}(\mu_\omega, \sigma_\omega^2). \quad (35)$$

Here, we assumed that observed survey data followed a normal distribution, where the mean was  $\ln(qN)$  and the variance was  $V^2 + W^2$ . The CV of the number of individuals estimated by the swept area method is used in Equation (33). Although we assumed additional variances as  $W^2$ , we adopted a random effect term in Equation (35) to reduce the number of parameters (or we had to estimate the  $a \times u \times t$  number of parameters as fixed effects). It was considered that the variation of omega showed a degree to which the scientific survey covered a spatial distribution of snow crabs. We calculated the likelihood as both  $n_{a,u,t,c} = 0$  and  $n_{a,u,t,c} = 1$  for males, although the suffix was omitted in Equation (32). The catch efficiency  $q$  is a function of mean  $cw$  each instar and shown as follows:

$$q_{a,t} = \gamma_0 / (1 + \exp(-(\gamma_2 + \gamma_3 cw_{a,t}))), \quad (36)$$

$$\gamma_0 = 1 / (1 + \exp(-\gamma_1)), \quad (37)$$

where  $cw_{a,t}$  is the average  $cw$  of each instar obtained from the annual trawl survey. The catch efficiency  $q_{a,t}$  was treated as a random effect term and the average  $\gamma_1$ – $\gamma_3$  and their variance–covariance matrix was plugged in from the previous analysis (Hattori et al., 2014).

$$\gamma_h \sim \text{MVN}(\hat{\gamma}_h, \sum_\gamma), \quad (38)$$

$$\sum_\gamma = \begin{pmatrix} 0.214 & & \\ -0.003 & 8.758 \times 10^{-5} & \\ 0.002 & -0.001 & 0.074 \end{pmatrix}. \quad (39)$$

Here, upper triangular components were omitted and  $\hat{\gamma}_1 = 0.683$ ,  $\hat{\gamma}_2 = -4.276$  and  $\hat{\gamma}_3 = 0.0792$ .

### 6.2 | Catch at instar

Here,  $c_a$  is the observed number of catch at instar and  $C_a$  is the estimated number of catch at instar; these are shown in the following:

$$\ln(c_{a,u,t}) \sim \text{Normal}(\ln(C_{a,u,t}), \tau_{a,u}^2), \quad (40)$$

$$C_{a,u=0,t} = N_{a,u=0,j=1,t} \exp(-M'_{g,t}/6) (1 - F_{k=1,t}) w_{a,u=0,t}, \quad (41)$$

$$C_{a,u=1,t} = \sum_{j=1}^2 N_{a,u=1,j,t} \exp(-M'_{g,t}/6) (1 - F_{k,t}) w_{a,u=1,t}, \quad (42)$$

where the catch of male snow crab was applied using both Equations (41) and (42) ( $k = 2$ ), although that of females was applied using Equation (42) ( $k = 3$ ) alone, because only mature females were caught. The fishing season of snow crab continues for approximately 4 months (i.e., from December 10 to March 31) and, for simplicity of the model, we assumed that pulse fishing is carried out on February 1. We also assumed the estimated abundance from the survey was at December 1 because the survey of main fishing ground has been finished the end of November (Shibata et al., 2019). We multiplied one-sixth for  $M$  in this calculation because fishing is assumed to occur 2 months after the survey.

## 7 | MODEL SELECTION

### 7.1 | State and observation models

Seven factors needed to be selected for the model: (a) the variables/types of difference in  $M_g$  to be selected were 32 combinations for  $M_g$  (Supporting Information 3), (b) three types of difference for  $M_{g,t}$ , (c) either  $\varphi$  and  $T_{Mg}$  is set as 1 or estimated, (d) either  $T_\rho$  is set as 0 or estimated, (e) five combinations for  $T_{\rho k}$  and (f) either  $\beta_0$  was time-varying or not (Table 2). Consequently, the number

of tested models is 7,680 ( $=32 \times 3 \times 2 \times 2 \times 2 \times 5 \times 2$ ). The number of parameters for  $M_{g,t}$  depended on whether a constant ( $M_g$ ), a first-order difference ( $\sigma_{M_g}^2$ ) or a second-order difference ( $\sigma_{M_g}^2$ ) model was selected because the number of parameters equaled the number of groups. The first-order difference may be selected more easily than the other two because it is considered to be the most flexible for fitting. Therefore, we performed model selection for each of three types for  $M_{g,t}$ , and selected the best one by both AIC (Akaike, 1974) and Bayes' information criterion (BIC) (Schwarz, 1978). Although AIC has been widely used, a more complex model tends to be selected compared with BIC when the sample size is large (Maunder & Punt, 2004; Schwarz, 1978). It is expected that BIC selects the optimum model asymptotically even when the sample size becomes large (Burnham & Anderson, 2002; Schwarz, 1978), but it has been reported that AIC sometimes achieves better performance even when the sample size is 100,000 (Burnham & Anderson, 2002). In this study, not only AIC but also BIC was used for model selection. Six models will ultimately be chosen as candidates for the best model through this procedure.

The estimated abundance  $A_{T-i}$  ( $A = \sum_a N_a w_a$ ,  $T = 2018$ ,  $i = 1, \dots, 5$ ) of both males and females was calculated using all the data from 1997 to 2018. The estimated abundance using the data period from 1997 to  $T-i$  ( $i = 1, \dots, 5$ ) was denoted as  $A_{T-i,R_i}$  ( $R_i = R_1, \dots, R_5$ ), where  $R_i$  is a suffix indicating how many years of data are excluded. As an index representing retrospective bias, Mohn's rho ( $\rho_{\text{past}}$ ) (Mohn, 1999) was calculated by the following equation:

$$\rho_{\text{past}} = \frac{1}{5} \sum_{i=1}^5 \left( \frac{A_{T-i,R_i} - A_{T-i}}{A_{T-i}} \right) \times 100. \quad (43)$$

**TABLE 2** Combination of all variables/types of difference for model selection

| Variables/types of difference | Number of combinations | Equation number          |
|-------------------------------|------------------------|--------------------------|
| $M_g$                         | 32                     | Supporting Information 3 |
| Types of $M_{g,t}$            | 3                      | (1) and (2)              |
| $T_{Mg}$                      | 2                      | (29) and (30)            |
| $\varphi$                     | 2                      | (3) and (4)              |
| $T_p$                         | 2                      | (8)                      |
| $T_{pk}$                      | 5                      | (8)                      |
| $\beta_0$                     | 2                      | (10) and (11)            |
| Total                         | 7,680                  |                          |

In addition, a retrospective forecasting (Brooks & Legault, 2015) approach was used to estimate an error in future projections for 2 years ahead because the ABC of snow crab had been calculated based on data from 2 years previously (Shibata et al., 2019). First, the abundance was estimated using the data from 1997 to  $T-j$ , excluding the data for  $j$  years ( $j = 3, \dots, 7$ ). Then,  $\tilde{A}_{T-h,R_h}$  ( $h = j - 2$ ) was projected for the abundance 2 years ahead; for example, when  $j = 3$  then  $h = 1$ . The abundance and the parameter estimations were performed using the data up to 2015, and the abundance in 2017 was predicted. This procedure was repeated to calculate  $\rho_{\text{future}}$  using the following formula:

$$\rho_{\text{future}} = \frac{1}{5} \sum_{h=1}^5 \left( \frac{\tilde{A}_{T-h,R_h} - A_{T-h}}{A_{T-h}} \right) \times 100. \quad (44)$$

All parameter values were given their average over the last 3 years to calculate  $\rho_{\text{future}}$ . The biases in the estimation and prediction of the abundance for the six best models were evaluated using  $\rho_{\text{past}}$  and  $\rho_{\text{future}}$ , and the best model was selected. As a sensitivity test, the CVs of the observed number of instars were multiplied by 1.5 using the best model. We then calculated  $\rho_{\text{past}}$ ,  $\rho_{\text{future}}$  and time-varying  $M_{g,t}$ .

## 7.2 | Stock–recruitment relationship

We fitted three types of SR relationship between the estimated spawning stock biomass (SSB) and recruitment (instar VIII) that were obtained from the best model from the above model selection phase for future predictions. We used three types of SR relationships as hockey stick (HS) (Clark, Charles, Beddington, & Mangel, 1985), Beverton–Holt (Beverton & Holt, 1957) (BH) and Ricker (RI) (Ricker, 1954) models for Equations (45)–(47), respectively, as follows:

$$\hat{R}_{t+5} = \begin{cases} \alpha_0 \text{SSB}_t & \text{SSB}_t < \alpha_1 \\ \alpha_0 \alpha_1 & \text{SSB}_t \geq \alpha_1 \end{cases}, \quad (45)$$

$$\hat{R}_{t+5} = \frac{\alpha_0 \text{SSB}_t}{1 + \alpha_1^{-1} \text{SSB}_t}, \quad (46)$$

$$\hat{R}_{t+5} = \alpha_0 \text{SSB}_t \exp(-\alpha_1^{-1} \text{SSB}_t), \quad (47)$$

where  $t$  is year ( $t = 1997, \dots, 2013$ ). In snow crab, although there is no information on the length of each instar duration in the Tohoku region, it has been assumed that 5 years are needed to reach instar VIII in the Sea of Japan

(Ueda et al., 2007), and we assumed this to be true in these equations. SSB is the spawning stock biomass after a fishing season and is calculated as follows:

$$SSB_t = \left( N_{a,u=1,t} \exp(-M_{g,t}) - c_{a,u=1,t} \exp\left(-\frac{5}{6}M_{g,t}\right) \right) w_{a,u=1,t}, \quad (48)$$

where  $N$ ,  $c$  and  $w$  are the estimated number, observed catch number and mean weight of mature female, respectively. We multiplied  $5/6$  for  $M$  here because fishing is assumed to occur 2 months after the survey. Parameters  $\alpha_0$  and  $\alpha_1$  are estimated by maximizing the log likelihood ( $LL$ ) function for each model, as follows:

$$\eta_t = \ln(R_{t+5}) - \ln(\hat{R}_{t+5}), \quad (49)$$

$$\sigma_{SR} = \sqrt{\frac{1}{n} \sum_{t=2002}^{2018} \eta_t^2}, \quad (50)$$

$$LL = \ln \left[ \prod_{t=1997}^{2013} \frac{1}{\sqrt{2\pi\sigma_{SR}^2}} \exp\left(-\frac{\eta_t^2}{2\sigma_{SR}^2}\right) \right]. \quad (51)$$

Szuwalski and Punt (2013) state that snow crab may have both a warm and cold regime for their recruitment in the eastern Bering Sea. Although such a phenomenon has not been reported around Japan, we considered the possibility that an autocorrelation existed in residuals ( $\eta$ ) to express the regime of recruitment, as shown in the following:

$$\eta_t = \rho_{SR} \eta_{t-1} + \xi_t, \quad (52)$$

$$\xi_t \sim \text{Normal}(0, (1 - \rho_{SR}^2) \sigma_{SR}^2), \quad (53)$$

$$\sigma = \sqrt{\frac{1}{n} \left\{ \eta_{t=2002}^2 + \frac{1}{1 - \rho_{SR}^2} \sum_{t=2003}^{2018} (\eta_t - \rho_{SR} \eta_{t-1})^2 \right\}}. \quad (54)$$

Here, we did not estimate  $\alpha_0$ ,  $\alpha_1$  and  $\rho_{SR}$  simultaneously because it had been reported that estimates would be unstable, and bias could arise (Johnson et al., 2016). In summary, we carried out a model selection using AICc (Hurvich & Tsai, 1989) from the three SR relationships. We then estimated  $\rho_{SR}$  and tested whether the autocorrelation in the residuals estimated for  $\rho_{SR}$  was zero or not (i.e.,  $\alpha_0$  and  $\alpha_1$  were fixed).

## 8 | ESTIMATION OF MSY

Because  $M$  and  $p$  were time-varying, we defined their values used to estimate the MSY. We prepared three scenarios in  $M$  and  $p$  as: (a) the mean values for 2016–2018, (b) the mean values for 1997–1999 and (c) mean values for all the years. For future prediction, the best model of the SR relationship was used. To estimate the MSY, we used the equations below for  $F$ :

$$F_{k,\text{latest}} = \frac{1}{3} \sum_{t=2007}^{2009} F_{k,t}, \quad (55)$$

$$F_{k,\text{candi}} = F_{k,\text{latest}} \times X, \quad (56)$$

$$X = \frac{10}{1 + \exp(-x)}. \quad (57)$$

We changed  $x$  from  $-10$  to  $10$  by  $0.01$  (i.e., 2,001 steps) to get an appropriate initial value of  $x$  before estimating  $x$  directly. The maximum age of snow crab in Newfoundland was reported to be 13 and 19 years old for females and males, respectively (Comeau et al., 1998). Although snow crab longevity has not been studied in detail in Japan, the maximum age of snow crab is often assumed to be more than 10 years old (e.g., Shibata et al., 2019). We assumed the life span of snow crab to be 15 years and simulated the future prediction as 20 times the life span to obtain initial values for the population. In other words, we carried out the prediction for 400 years, and the mean catches between 301 and 400 years were recorded, where the first 300 years were not used to delete the effects of the initial values. We repeated this procedure 1,000 times and calculated a median catch each  $x$  (i.e., a mean catch between 301 and 400 years was obtained 1,000 times each  $x$ , and 2,001 medians from the mean catches were obtained). Then, we selected  $x$  that maximized the medians of catch and used as an initial value of  $x$  to estimate  $F_{msy}$ , MSY and  $SSB_{msy}$ . The calculation was carried out using freely available statistical analysis software R (R Core Team, 2019) and the Template Model Builder (Kristensen, Nielsen, Berg, Skaug, & Bell, 2015).

## 9 | RESULTS

### 9.1 | The best models of state and observation models

Models that had minimal AIC and BIC values are shown in Table 3. The result also showed the combination of  $g$ ,

**TABLE 3** Results of the model selection and retrospective analysis. The column  $M$  showed three types of  $M_{g,t}$  (constant, first-order or second-order difference).  $M_g$  was same if the numbers expressed in columns from VIII to XIII were the same. If the cell showed “In,” that indicated that the variable was selected in the model by information criteria, and “-” showed that it was not selected.  $\beta$  was selected as  $p$  was time-varying (indicated as “ $t$ ”) in all cases. AIC and BIC indicate AIC and BIC, respectively

| $M$      | Criterion | VIII | IX | X | XI | XII | XIII | $T_\varphi$ | $T_{Mg}$ | $T_p$ | $\beta$ | AIC/BIC | $\rho_{past}$ | $\rho_{future}$ |
|----------|-----------|------|----|---|----|-----|------|-------------|----------|-------|---------|---------|---------------|-----------------|
| Constant | AIC       | 0    | 0  | 1 | 1  | 1   | 2    | -           | -        | -     | $t$     | 1,191.3 | 33.8          | 88.3            |
|          | BIC       |      |    |   |    |     |      |             |          |       |         | 1,372.0 |               |                 |
| First    | AIC       | 0    | 0  | 1 | 1  | 2   | 2    | In          | In       | -     | $t$     | 1,070.0 | -2.1          | 116.8           |
|          | BIC       | 0    | 0  | 1 | 1  | 2   | 2    | -           | -        | -     | $t$     | 1,269.9 | -1.5          | 64.3            |
| Second   | AIC       | 0    | 0  | 0 | 0  | 1   | 1    | -           | -        | -     | $t$     | 1,201.0 | 4.7           | 61.5            |
|          | BIC       | 0    | 0  | 0 | 0  | 0   | 0    | -           | -        | -     | $t$     | 1,292.2 | 1.5           | 3.9             |

Abbreviations: AIC, Akaike's information criterion; BIC, Bayes' information criterion.

the variables included in a model, and values of retrospective analysis for each model (see also Supporting Information 5). The models with constant  $M_g$  through time were the same regardless of the information criteria. The model showed that instars VIII and IX, and instars X, XI and XII were the same groups. The models with a first-order difference of  $M_g$  were the same whether the criterion was AIC or BIC, where instars VIII and IX, instars X and XI and instars from XII to XIII were grouped, respectively. The parameters  $T_\varphi$  and  $T_{Mg}$  were selected in the model. The model had the minimum AIC (1,070.0) and BIC (1,269.9) among the three formulations of  $M_{g,t}$ . In the case of the model with a second-order difference of  $M_g$ , the model based on AIC showed instars from VIII to XI and from XII to XIII were the same group, respectively, although the best model based on BIC had the smallest values when all the age groups were combined. The parameter of terminal molting probability  $\beta$  was selected as time-varying, and  $T_{\rho k = 1}$  was not different from  $T_{\rho k = 2}$  in all cases.

The values of  $\rho_{past}$  did not greatly change among models and were relatively small, except in the constant model (Table 3). In contrast,  $\rho_{future}$  showed poor performance except in the BIC best model with a second-order difference of  $M_{g,t}$ . Although the model with the first-order difference of  $M_{g,t}$  had the smallest AIC and BIC among the three formulations of  $M_{g,t}$ , we decided that the minimal BIC model with a second-order difference of  $M_{g,t}$  was the best model from the synthetic evaluation of model performance, including retrospective bias and retrospective forecasting. All the estimated parameter values of the best model are shown in Table 4, and the results indicated that the estimated values were well fitted to the observed values and the residuals were normally distributed (Supporting Information 6).

Estimated time-varying  $M_{g,t}$  and terminal molting probabilities from the best model are shown in Figures 4 and 5, respectively. Although the time-varying  $M_{g,t}$  was

not so high in 1997 ( $M_{g,t} = 0.20$ ), values increased from around 2005 to 2012. The  $M_{g,t}$  kept a high value of more than 0.59 after 2012. This result indicated that the abundance of snow crab could not increase if the total catch was kept at quite low values after the earthquake because the natural mortality also kept a high value. Terminal molting probability kept increasing from around 2005 in all instars with terminal molts (Figure 5). Although the values were 0.09, 0.19, 0.38 and 0.61 in 1997 for each instar (IX, X, XI and XII), they increased to 0.21, 0.41, 0.64 and 0.82 in 2017. This result indicated that the terminal molting probabilities increased 2.46-, 2.10-, 1.67- and 1.34-fold, respectively, from 1997 to 2018. It also showed that the decreasing abundance was caused by both the high natural mortality and terminal molt probability. The estimated abundance and SSB were shown in Figures 6 and 7, respectively. Both results showed that estimated values decreased after 2008 but before the earthquake when estimated fishing mortalities were kept quite low ( $F = 0.04$  for immature males in 2016 was the maximum) after 2011 (Figure 8).

## 9.2 | Sensitivity analysis of CV

The result showed that the  $M_{g,t}$  did not change substantially even if the CV was multiplied by 1.5 (Figure 9). This multiplication changed  $\rho_{past}$  and  $\rho_{future}$  from 1.5 to -1.4% and 3.9 to -5.8%, respectively (see Table 3). This result showed that the estimates and predicted values were robust against the CVs of the number of snow crabs observed by the scientific bottom trawl survey.

## 9.3 | Estimated MSY

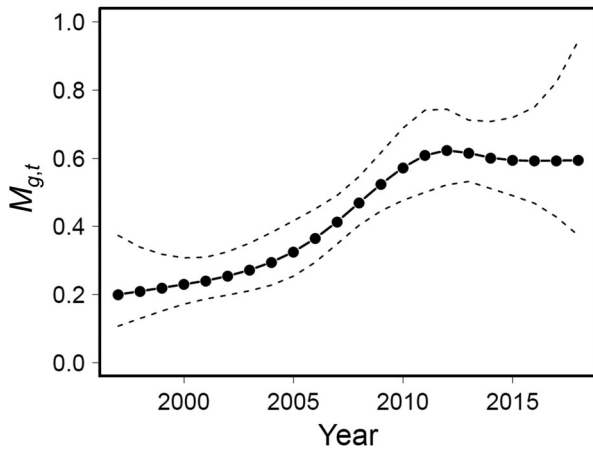
The HS model had minimal AICc because the calculated AICc values were 29.9, 32.2 and 32.0 for the HS, BH and

**TABLE 4** Estimated parameter values and their *SEs* by the best second-order difference model

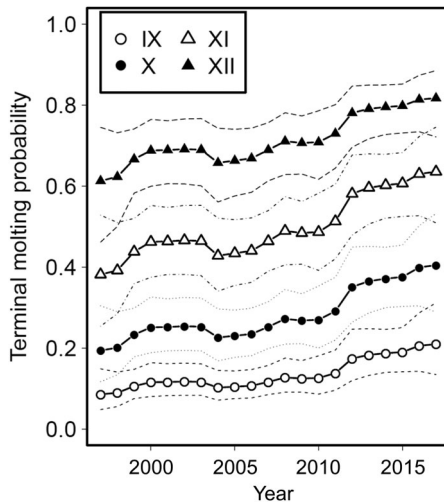
| Parameters                       | Estimates | SE    | Either male or female |
|----------------------------------|-----------|-------|-----------------------|
| $\ln((\sigma_{k=1}^F)^2)$        | -0.116    | 0.244 | Male                  |
| $\ln((\sigma_{k=2}^F)^2)$        | -1.289    | 0.371 | Male                  |
| $\ln((\sigma_{k=3}^F)^2)$        | -1.436    | 0.746 | Female                |
| $T_{\sigma_{k=1}}^F$             | 0.594     | 0.370 | Male                  |
| $T_{\sigma_{k=2}}^F$             | 1.748     | 0.482 | Male                  |
| $T_{\sigma_{k=3}}^F$             | 2.022     | 0.770 | Female                |
| $\ln(\sigma_{M,g}^2)$            | -2.995    | 0.775 | Both                  |
| $\ln(\tau_{a=11,u=0}^2)$         | -0.982    | 0.468 | Male                  |
| $\ln(\tau_{a=11,u=1}^2)$         | -0.921    | 0.220 | Male                  |
| $\ln(\tau_{a=12,u=0}^2)$         | -0.796    | 0.340 | Male                  |
| $\ln(\tau_{a=12,u=1}^2)$         | -1.079    | 0.211 | Male                  |
| $\ln(\tau_{a=13,u=0}^2)$         | -0.219    | 0.210 | Male                  |
| $\ln(\tau_{a=13,u=1}^2)$         | -1.107    | 0.234 | Male                  |
| $\ln(\tau_{a=14,u=1}^2)$         | -0.329    | 0.166 | Male                  |
| $\ln(\tau_{a=11,u=1}^2)$         | -1.270    | 0.391 | Female                |
| $\ln(N_{a=9,u=0,t=1997})$        | 6.971     | 0.243 | Male                  |
| $\ln(N_{a=10,u=0,t=1997})$       | 6.338     | 0.243 | Male                  |
| $\ln(N_{a=10,u=1,t=1997})$       | 4.915     | 0.562 | Male                  |
| $\ln(N_{a=11,u=0,t=1997,74-80})$ | 5.357     | 0.351 | Male                  |
| $\ln(N_{a=11,u=1,t=1997,74-80})$ | 4.448     | 0.466 | Male                  |
| $\ln(N_{a=11,u=0,t=1997,80-86})$ | 5.020     | 0.352 | Male                  |
| $\ln(N_{a=11,u=1,t=1997,80-86})$ | 5.408     | 0.281 | Male                  |
| $\ln(N_{a=12,u=0,t=1997})$       | 4.714     | 0.342 | Male                  |
| $\ln(N_{a=12,u=1,t=1997})$       | 5.316     | 0.275 | Male                  |
| $\ln(N_{a=13,u=0,t=1997})$       | 3.306     | 0.587 | Male                  |
| $\ln(N_{a=13,u=1,t=1997})$       | 5.527     | 0.245 | Male                  |
| $\ln(N_{a=14,u=1,t=1997})$       | 4.938     | 0.300 | Male                  |
| $\ln(N_{a=9,u=0,t=1997})$        | 6.788     | 0.460 | Female                |
| $\ln(N_{a=10,u=0,t=1997})$       | 7.615     | 0.499 | Female                |
| $\ln(N_{a=11,u=0,t=1997})$       | 8.300     | 0.352 | Female                |
| $\ln(\beta_1)$                   | -0.060    | 0.060 | Both                  |
| $\ln(\sigma_{\rho 0})$           | -1.610    | 0.666 | Both                  |
| $T_{\rho,k=1}$                   | 2.953     | 0.685 | Both                  |
| $T_{\rho,k=3}$                   | -1.157    | 0.335 | Both                  |
| $T_r$                            | -0.149    | 0.105 | Both                  |
| $\ln(\sigma_{rec}^2)$            | -1.084    | 0.203 | Both                  |
| $\mu_{\omega}$                   | -0.803    | 0.089 | Both                  |
| $\ln(\sigma_{\omega}^2)$         | -1.138    | 0.299 | Both                  |

RI SR models, respectively. The SR relationship estimated by the HS model and estimated  $\rho_{SR}$  are shown in Figure 10a,b, respectively. Although the number of instar VIII crabs as recruits decreased since 2015 (Figure 10a), the timing of the decrease was different from that of the

abundance (Figure 2). Because the estimated coefficient of autocorrelation was significantly different from zero if the lag was 1 year (Figure 10b), we used the HS model with autocorrelation in the residuals for future predictions to estimate MSYs based on the three scenarios.

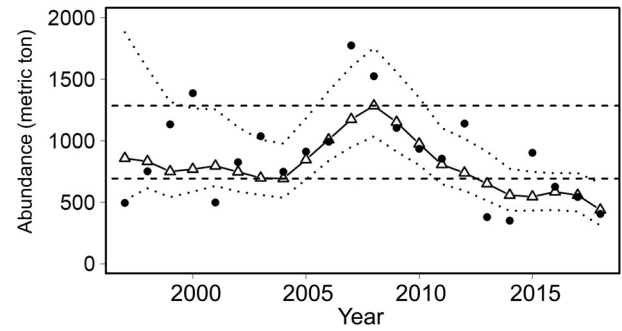


**FIGURE 4** Estimated time-varying natural mortality coefficient ( $M_{g,t}$ ) of the best model with a 95% confidential interval (break lines)

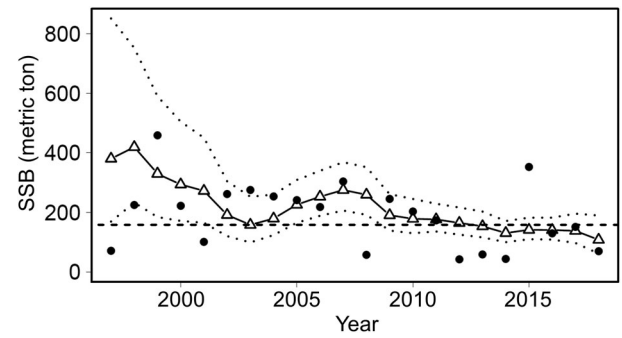


**FIGURE 5** Estimated time-varying terminal molting probability ( $p_{a,t}$ ) of the best model with their 95% confidential intervals (break lines). The symbols indicate those of instars IX (white circles), X (black circles), XI (white triangles) and XII (black triangles)

Here, the estimated  $MSY$ ,  $SSB_{MSY}$  and  $F_{msy}$  of females are shown in Table 5. Although Scenario 1 showed that the  $MSY$  and  $SSB_{MSY}$  were quite high values that had not been experienced in the historical catch (Figure 2) and estimated  $SSB$  (Figure 7), both  $MSY$  and  $SSB_{MSY}$  in Scenario 2 were almost zero because the abundance was also almost zero. In Scenario 3, the  $MSY$  was low compared to the observed historical catch, although the estimated  $SSB_{msy}$  was near the median value from 1997 to 2018 (185.8 gross ton).



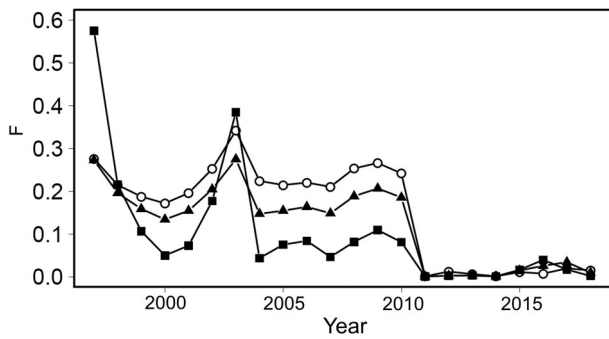
**FIGURE 6** Estimated abundance (white triangles) of the best model with 95% confidential interval (dotted lines). The two horizontal dashed lines show the minimum and maximum estimates before 2011. Black circles show estimated abundance using a swept area method



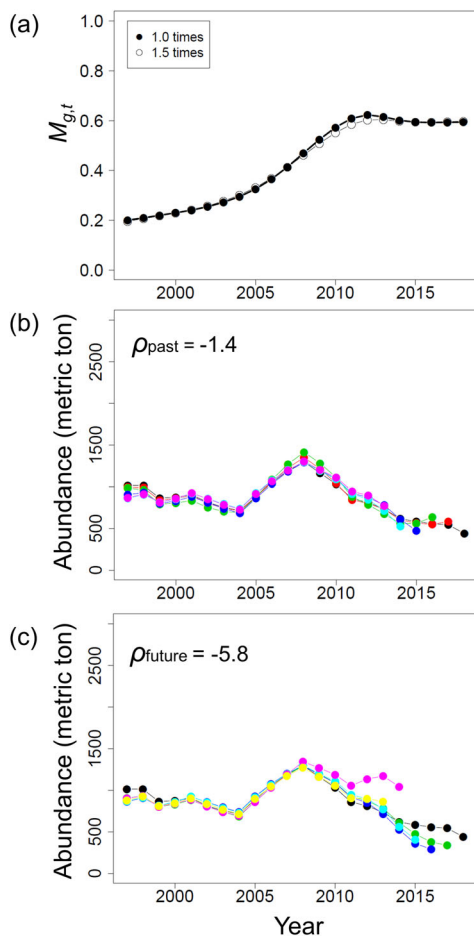
**FIGURE 7** Estimated spawning stock biomass (SSB, white circles) after a fishing season of the best model with a 95% confidential interval (dotted lines). The horizontal dashed line shows the minimum estimates before 2011. Black circles show estimated SSB using a swept area method and Equation (48)

## 10 | DISCUSSION

In this study, we showed that the natural mortality coefficient  $M$  and the terminal molting probability  $p$  of snow crab in the Tohoku region have increased since 1997. In stock assessments, it was assumed that  $M = 0.35$  for individuals that have not experienced a terminal molt, and for those that have experienced a terminal molt within 1 year, and  $M = 0.2$  for those that have undergone a terminal molt two or more years ago (Shibata et al., 2019). In contrast, regardless of the time elapsed since the terminal molt, this study found that  $M$  was around 0.59 in 2018. This finding means that previous stock assessments overestimated future survival. Indeed, it had been expected that abundance would increase since 2011 because of the rapid decline in the total catch (Shibata et al., 2019), although the abundance has maintained a



**FIGURE 8** Estimated fishing mortalities of the best model by immature male (black squares), mature male (black triangles) and mature female (white circles)



**FIGURE 9** Estimated natural mortality coefficient ( $M_{g,t}$ ) (a) after coefficients of variation (CV) in Equation (33) was multiplied by 1.0 (black circles) and 1.5 (white circles). Estimated (b) and predicted (c) abundance to calculate indices representing retrospective bias ( $\rho_{\text{past}}$  and  $\rho_{\text{future}}$ ) where different color lines show different data periods to estimate and predict abundance [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

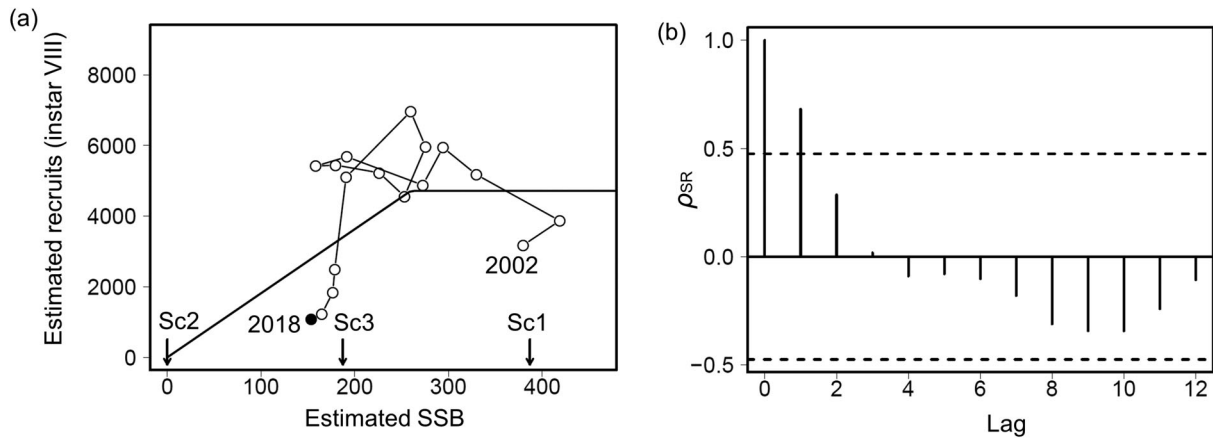
declining trend (Figure 6) despite  $F$  being nearly zero (Figure 8). Since  $F$  has been nearly zero and the scientific bottom trawl survey covered the whole habitat of snow

crab off Tohoku, the result of this estimation is naturally that  $M$  and  $p$  have increased.

One potential cause for the increase of  $M$  could be an increased bottom water temperature (BWT). The BWT data were not used in this model since the periods of the surveys were different from those of BWT, and we were interested in time-varying parameters through the bottom trawl survey period. In contrast, it was suggested that the mean BWT in the Tohoku region was on an upward trend (Figure 11), and a method to draw Figure 11 is shown in Supporting Information 7. An aquarium study indicated that the energy consumed inside the crab exceeds the energy absorbed from outside at a water temperature of  $7^{\circ}\text{C}$ ; therefore, it would be energetically impossible for the crab to live continuously in this water temperature range (Foyle, O'dor, & ELNER, 1989). In other words, the increased BWT off Tohoku could be one reason for the increase in  $M$ . Although the main fishing ground for snow crab has been concentrated in the area from the Miyagi to Ibaraki prefectures (Nemoto, 2007), the area of unsuitable environment in the major distribution area of snow crab could have expanded (Figure 11). In contrast, since the trends of BWT and  $M$  do not completely match, it seems that factors other than the BWT are affecting  $M$ .

Another possible reason for the increase in  $M$  is predation pressure. It has been shown that predation pressure by Atlantic cod (*Gadus morhua*) affects the abundance of snow crab (Chabot, Sainte-Marie, Briand, & Hanson, 2008). In the Tohoku region, the abundance of Pacific cod (*Gadus macrocephalus*) increased rapidly since fishing pressure was reduced by the earthquake (Narimatsu, Shibata, Hattori, Yano, & Nagao, 2017), and snow crabs have been found in their stomachs. This may have affected the abundance of snow crabs (Ito, Hattori, Narimatsu, & Shibata, 2014). In contrast, the estimated natural mortality coefficient  $M$  was the same for all age groups in this study. If the predation pressure by Pacific cod affects the rise in  $M$ , then  $M$  should differ between small and large snow crabs. In fact, it has been reported that snow crabs larger than 65.1 mm rarely appear in the stomach of Atlantic cod (Chabot et al., 2008). The abundance of Pacific cod peaked in 2015 and started to decrease (Narimatsu et al., 2019); however, that of instar VIII snow crab has not shown an increase, but, instead, has decreased (Figure 10a). These trends indicate that predation pressure from Pacific cod is not the main reason for the increase in  $M$  of all instars.

Not only the natural mortality  $M$  but also the terminal molting probability  $p$  have increased. It has been reported that the terminal molting probability of snow crab off Miyagi and Fukushima prefectures was higher than that off Ibaraki Prefecture, and this might be



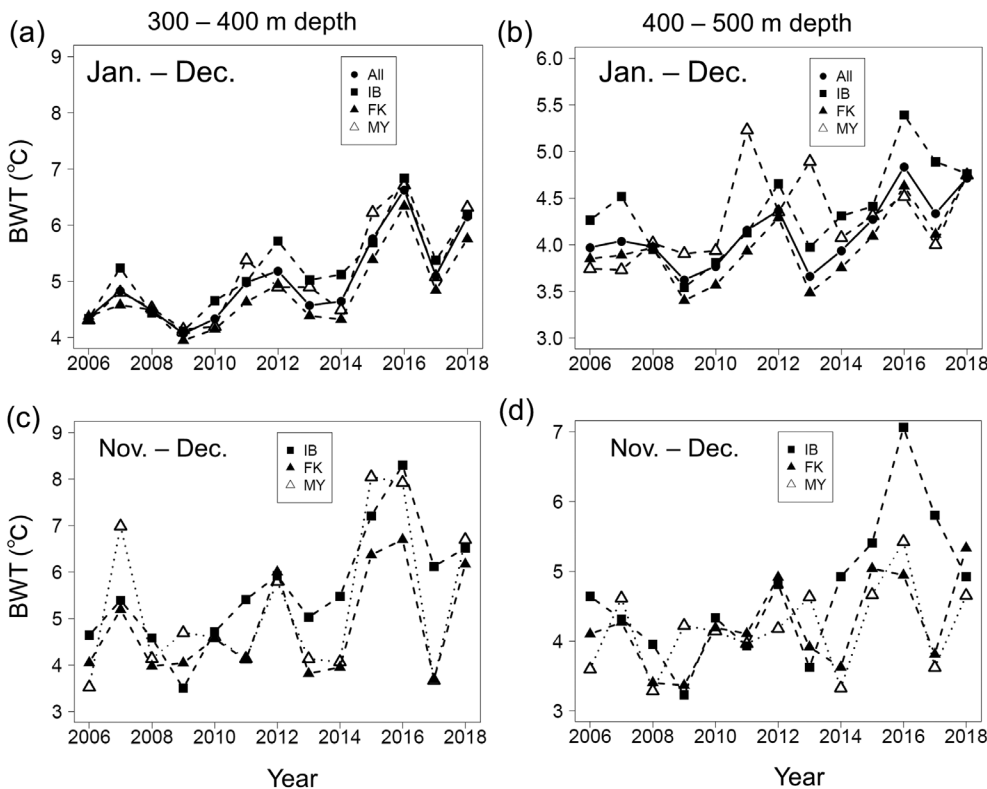
**FIGURE 10** Relationship between estimated spawning stock biomass (SSB) and recruits (white circles) with estimated hockey stick relationship as the best model (black line) where arrows show calculated SSB to obtain maximum sustainable yield (SSB<sub>msy</sub>) in each scenario (a). Coefficient of autocorrelation ( $\rho_{SR}$ ) with 95% confidence intervals (break lines) (b)

**TABLE 5** Estimated MSY, SSB to obtain MSY (SSB<sub>MSY</sub>) and fishing mortality coefficient to obtain MSY (F<sub>msy</sub>) of female for each scenario with their *M* values

| Scenario | MSY               | SSB <sub>msy</sub> | <i>M</i> | F <sub>msy</sub> |
|----------|-------------------|--------------------|----------|------------------|
| 1        | 604               | 386                | 0.21     | 0.41             |
| 2        | <10 <sup>-8</sup> | <10 <sup>-8</sup>  | 0.59     | 0.01             |
| 3        | 28                | 187                | 0.43     | 0.05             |

Abbreviations: MSY, maximum sustainable yield; SSB, spawning stock biomass.

because large individuals were selectively caught under high fishing pressure, resulting in genetically smaller maturity size (Takasaki & Tomiyama, 2017). In contrast, this study shows that *p* has been on an upward trend since 2011 when *F* decreased rapidly because of the earthquake. This pattern suggests that fishing mortality was not solely responsible for the terminal molting probability. One hypothesis is that recent increases in BWT may affect *p*. Although several studies have reported a



**FIGURE 11** Estimated mean bottom water temperatures (BWT, °C) from January to December (i.e., 12 months) at depths 300–400 m (a) and 400–500 m (b). Mean from November to December (i.e., 2 months) was also calculated for each depth range (c,d) because the period was the warmest off Ibaraki prefecture (the southern limit of snow crab distribution in the Tohoku region)

positive correlation between water temperature and size-at-terminal molt (Burmeister & Sainte-Marie, 2010; Dawe, Mullaney, Moriyasu, & Wade, 2012; Orensanz, Ernst, & Armstrong, 2007; Somerton, 1981; Zheng, Kruse, & Ackley, 2001); however, the Tohoku region has higher water temperatures than any previous studies (Figure 11). It will be necessary to examine the size-at-terminal molt in relatively high-water temperatures through an aquarium experiment.

Our study revealed that the value of MSY changed when the values of  $M$  and the terminal molting probability changed in three scenarios (Table 5). Similar results also obtained in the previous study (Legault & Palmer, 2015). The result suggests that the MSY of snow crab as an ecosystem service varies greatly with time and that fishing pressure needs to be reduced to almost zero when  $M$  and  $p$  are high. It has been reported that snow crab could have a warm and cold regime for recruitment in the eastern Bering Sea and show drastic stock fluctuation (Szuwalski & Punt, 2012, 2013). This study revealed, even in the Tohoku region, the possibility of dynamic stock fluctuations regardless of changes in fishing pressure, because  $M$  and  $p$  varied with time. Although recruits decreased since 2015 (Figure 10a), this was not the main reason for decreased abundance (Figure 2) because instar VIII as recruits needed at least three more years to be fishable (i.e., instar XI). In other words, the lower abundance since 2012 was not caused by the reduced numbers of recruits since 2015, but by  $M$  and  $p$ . Although the catch of snow crab has been limited because bottom trawlers in Fukushima prefecture voluntarily reduced fishing effort, the effort should not increase if  $M$  and  $p$  maintain high values.

Because the study design allowed for the estimation of  $M$  and  $p$ , we could show that ecosystem services can vary with time. Changes in productivity due to global warming have been observed worldwide (Free et al., 2019), and it could affect biological parameters, such as  $M$  and  $p$ . There could be many species other than snow crab whose biological parameters vary with the environment in the seas around Japan, but there are few examples where the biological parameters have been estimated. Japan is currently moving to a new stock management system targeting MSY, but it is commonly assumed that the value of  $M$  has mainly been based on empirically derived equations and does not change over time (Tanaka, 1960). For species that are likely to be greatly affected by the environment, scientific surveys designed to estimate abundance should be prepared to elucidate the parameters and capture the temporal changes.

We showed that  $M$ ,  $p$  and recruits as biological parameters did not change drastically in 2011, although catch amount and  $F$  decreased rapidly. These results indicated that the effects of the earthquake and subsequent

tsunami in 2011 on the biological parameters were little rather than big. This is not the special case. For example, the abundance of Japanese flounder (*Paralichthys olivaceus*) had increased rapidly after 2011 because the decreased fishing effort caused the number of juveniles to increase (Kidokoro, Togashi, Narimatsu, & Shibata, 2019) where their growth rate (mm/day) did not change before and after 2011 (Kurita et al., 2017). In addition, their abundance after 2011 was predicted where observed fishing effort was given and the predicted values well matched to observed values obtained from other surveys, although biological parameters such as  $M$  and migration parameters were the same through simulation periods (Shibata et al., 2017). Although the tsunami effected on some biological parameters of other species such as Pacific cod (*G. macrocephalus*) (Narimatsu et al., 2015), the event could not affect on all species.

One of the features of JASAM is that it estimates parameters for population dynamics using the annual abundance observed independently of fisheries. It is conceivable that the parameters will have other specifications, such as an RW with an MVN distribution, as in the case of  $F$ , and a step function. It is also possible to change the state model for snow crab to another age-structured model so it can be applied to species other than snow crab. However, if the estimated abundance does not reflect the entire distribution area of the target species,  $M$  can be confounded with migration rates to adjacent sea areas. In this case, it may be necessary to assume the rates of migration to the off-site area separately, or to design a survey (e.g., estimation of abundance in the adjacent sea areas) that can estimate the migration rates.

Some of the estimated number at instars (especially instar X of males before terminal molt) was not well fitted for observation (Supporting Information 6). Although the cause was not clear regardless of the implementation of numerous model selections, an assumption that molt occurs once a year may be violated. Aquarium experiments have shown that the duration was shorter if the water temperature increased for instars I to VII (Yamamoto et al., 2015) and for instars I to XI (Kobayashi, 1989). These results indicated an instar could jump up more than two numbers once a year (e.g., from instar VIII to X in a year) if the relationship was inherent in snow crab in the Tohoku region, and this violates the model assumption. To update the model in the future, the relationships in the seas off Tohoku should be studied through aquarium experiments.

We assumed that the relationship between age and instar (Table 1) was deterministic. On the other hand, the relationship could be probabilistic by some degree (Ueda et al., 2007), and several studies have shown the effects of aging error on estimates (Mills & Beamish, 1980;

Richards, Schnute, Kronlund, & Beamish, 1992; Yule et al., 2008). For example, a CW of 70 mm crabs may belong not only to instar XI but also to instar XII under a certain probability, and this may reduce the precision of estimates. Although it was difficult to estimate the probability and evaluate the effect on estimates because observed data was too vague to fit a mix normal distribution especially after the earthquake (e.g., Shibata et al., 2019) unlike the previous study (Ueda et al., 2007), this evaluation by simulation study would be useful.

Although a potential for skip-molting has been reported in the Sea of Japan (Yamamoto et al., 2018), the probability of skip-molting was higher in low water temperatures (Dawe et al., 2012). Also, molting duration was shortened when water temperature increased under laboratory conditions (Kobayashi, 1989; Yamamoto et al., 2015). On the other hand, intervals of BWT in the main habitat area of snow crab in the Tohoku region are approximately 3–8°C (Figure 11), and the approximate intervals are higher than other regions such as Wakasa bay in the Sea of Japan (1–3°C) (Kon & Adachi, 2005), Bonne Bay on the west coast of Newfoundland (–1 to 1°C) (Comeau et al., 1998), a shelf on the east coast of Newfoundland (–1.5 to 4.0°C) (Dawe & Colbourne, 2002), the Gulf of St. Lawrence (–1 to 6.3°C) (Moriyasu & Lanteigne, 1998) and the eastern Bering sea (–2 to 5°C) (Murphy, 2020). These results indicate that the molting duration can be shortened in the Tohoku region, although we had assumed the duration was once a year in the model we developed. Aquarium experiments should clarify this point and the resulting data should be used to update the model in the future.

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## REFERENCES

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Beverton, R. J. H., & Holt, S. J. (1957). *On the dynamics of exploited fish populations*, London: Her Majesty's Stationery Office.
- Boyd, J., & Banzhaf, S. (2006). What are ecosystem services? The need for standardized environmental accounting units. *Ecological Economics*, 63, 616–626. <https://doi.org/10.1016/j.ecolecon.2007.01.002>
- Brooks, E. N., & Legault, C. M. (2015). Retrospective forecasting—Evaluating performance of stock projections for New England groundfish stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(6), 935–950. <https://doi.org/10.1139/cjfas-2015-0163>
- Buesseler, K., Aoyama, M., & Fukasawa, M. (2011). Impacts of the Fukushima nuclear power plants on marine radioactivity. *Environmental Science and Technology*, 45(23), 9931–9935. <https://doi.org/10.1021/es202816c>
- Burmeister, A., & Sainte-Marie, B. (2010). Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland. *Polar Biology*, 33(6), 775–788. <https://doi.org/10.1007/s00300-009-0755-6>
- Burnham, D., & Anderson, K. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. New York, NY: Springer.
- Butterworth, D. S., & Rademeyer, R. A. (2008). Statistical catch-at-age analysis vs. ADAPT-VPA: The case of Gulf of Maine cod. *ICES Journal of Marine Science*, 65(9), 1717–1732. <https://doi.org/10.1093/icesjms/fsn178>
- Chabot, D., Sainte-Marie, B., Briand, K., & Hanson, J. M. (2008). Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. *Marine Ecology Progress Series*, 363, 227–240. <https://doi.org/10.3354/meps07384>
- Clark, C. W., Charles, A. T., Beddington, J. R., & Mangel, M. (1985). Optimal capacity decisions in a developing fishery. *Marine Resource Economics*, 2(1), 25–53. <https://doi.org/10.1086/mre.2.1.42628875>
- Comeau, M., Conan, G. Y., Maynou, F., Robichaud, G., Therriault, J.-C., & Starr, M. (1998). Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(1), 262–279. <https://doi.org/10.1139/f97-255>
- Conan, G. Y., & Comeau, M. (1986). Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. *Canadian Journal of Fisheries and Aquatic Sciences*, 43(9), 1710–1719. <https://doi.org/10.1139/f86-214>
- Dawe, E. G., & Colbourne, E. B. (2002). Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador shelf. In A. J. Paul, E. G. Dawe, R. Elner, G. S. Jamieson, G. H. Kuse, R. S. Otto, B. Sainte-Marie, T. C. Shirley, & D. Woodby, (Eds.), *Crabs in cold water regions: Biology, management, and economics* (pp. 577–594). Fairbanks, AK: Alaska Sea Grant. <https://doi.org/10.4027/ccwr/bme.2002.42>
- Dawe, E. G., Mullowney, D. R., Moriyasu, M., & Wade, E. (2012). Effects of temperature on size-at-terminal molt and molting frequency in snow crab *Chionoecetes opilio* from two Canadian Atlantic ecosystems. *Marine Ecology Progress Series*, 469, 279–296. <https://doi.org/10.3354/meps09793>
- Foyle, T. P., O'dor, R. K., & ELNER, R. W. (1989). Energetically defining the thermal limits of the snow crab. *Journal of Experimental Biology*, 145(1), 371–393.

- Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363(6430), 979–983. <https://doi.org/10.1126/science.aau1758>
- Fujita, H., Takeshita, K., & Matuura, S. (1988). Relative growth of chela and size at maturity in Tanner crabs, *Chionoecetes oppilio* and *C. bairdi*. *Researches on Crustacea*, 17, 7–13. [https://doi.org/10.18353/rcrustacea.17.0\\_7](https://doi.org/10.18353/rcrustacea.17.0_7)
- Hattori, T., Ito, M., Shibata, Y., Yano, T., & Narimatsu, Y. (2014). Net efficiency of a bottom trawl survey for snow crab *Chionoecetes opilio* off the Pacific coast of northern Honshu, Japan. *Nippon Suisan Gakkaishi*, 80(2), 178–184. <https://doi.org/10.2331/suisan.80.178>
- Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, 76(2), 297–307. <https://doi.org/10.1093/biomet/76.2.297>
- Ito, M., Hattori, T., Narimatsu, Y., & Shibata, Y. (2014). Predation of snow crab *Chionoecetes opilio* by Pacific cod *Gadus macrocephalus* off northeastern Honshu, Japan. *Tohoku Sokou Kenkyu*, 34, 123–132.
- Johnson, K. F., Councill, E., Thorson, J. T., Brooks, E., Methot, R. D., & Punt, A. E. (2016). Can autocorrelated recruitment be estimated using integrated assessment models and how does it affect population forecasts? *Fisheries Research*, 183, 222–232. <https://doi.org/10.1016/j.fishres.2016.06.004>
- Kaeriyama, H. (2015). Impacts of the Fukushima nuclear accident on fish and fishing grounds. In K. Nakata & H. Sugisaki (Eds.), *134Cs and 137Cs in the seawater around Japan and in the North Pacific. Impacts of the Fukushima Nuclear accident on Fish and Fishing Grounds*, Japan: Springer. <https://doi.org/10.1007/978-4-431-55537-7>
- Kidokoro, H., Togashi, H., Narimatsu, Y., & Shibata, Y. (2019). Stock assessment and evaluation for the Japanese flounder of northern Pacific stock (fiscal year 2018). In *Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2018/2019)*, Japan: Fisheries Agency and Fisheries Research and Education Agency of Japan.
- Kitagawa, D. (2000). Distribution and some biological characters of the snow crab *Chionoecetes opilio* in the Pacific region of northeastern Honshu. *Bulletin of the Tohoku National Fisheries Research Institute*, 63, 109–118.
- Kobayashi, K. (1989). Temperature influence on growth of the Zuwai crab *Chionoecetes opilio*. *Suisan Zoshoku*, 37(1), 35–41. <https://doi.org/10.11233/aquaculturesci1953.37.35>
- Kon, T., & Adachi, T. (2005). Duration of the embryonic development for snow crab, *Chionoecetes opilio*, off Wakasa Bay, the sea of Japan. *Suisan Zoshoku*, 53(2), 199–204. <https://doi.org/10.11233/aquaculturesci1953.53.199>
- Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. (2015). TMB: Automatic differentiation and Laplace approximation. *Journal of Statistical Software*, 70(1), 1–21. <https://doi.org/10.18637/jss.v070.i05>
- Kurita, Y., Uehara, S., Okazaki, Y., Sakami, T., Nambu, R., & Tomiyama, T. (2017). Impact of the great tsunami in 2011 on the quality of nursery grounds for juvenile Japanese flounder *Paralichthys olivaceus* in Sendai Bay, Japan. *Fisheries Oceanography*, 26(2), 165–180.
- Kuwahara, A., Shinoda, M., Yamasaki, A., & Endo, S. (1995). Managements of the snow crab resource in the western Japan Sea. In *Suisan Kenkyu Sousho* (Vol. 44, pp. 2–51). Tokyo, Japan: Japan Fisheries Resource Conservation Association.
- Legault, C. M., & Palmer, M. C. (2015). In what direction should the fishing mortality target change when natural mortality increases within an assessment? *Canadian Journal of Fisheries and Aquatic Sciences*, 73(3), 349–357. <https://doi.org/10.1139/cjfas-2015-0232>
- Maunder, M. N., & Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. *Fisheries Research*, 70(2–3), 141–159. <https://doi.org/10.1016/j.fishres.2004.08.002>
- Mills, K. H., & Beamish, R. J. (1980). Comparison of fin-ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(3), 534–544. <https://doi.org/10.1139/f80-068>
- Mohn, R. (1999). The retrospective problem in sequential population analysis: An investigation using cod fishery and simulated data. *ICES Journal of Marine Science*, 56(4), 473–488. <https://doi.org/10.1006/jmsc.1999.0481>
- Moriyasu, M., & Lanteigne, C. (1998). Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. *Canadian Journal of Zoology*, 76(11), 2040–2048. <https://doi.org/10.1139/z98-147>
- Murphy, J. T. (2020). Climate change, interspecific competition, and poleward vs. depth distribution shifts: Spatial analyses of the eastern Bering Sea snow and Tanner crab (*Chionoecetes opilio* and *C. bairdi*). *Fisheries Research*, 223, 105417.
- Murphy, J. T., Rugolo, L. J., & Turnock, B. J. (2018). Estimation of annual, time-varying natural mortality and survival for Eastern Bering Sea snow crab (*Chionoecetes opilio*) with state-space population models. *Fisheries Research*, 205, 122–131. <https://doi.org/10.1016/j.fishres.2018.04.001>
- Narimatsu, Y., Takehi, S., Ito, S., Okazaki, Y., Inagawa, R., & Yano, T. (2015). Impact of the Great East Japan earthquake tsunami on growth and survival of Pacific cod (*Gadus macrocephalus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 72(11), 1629–1638.
- Narimatsu, Y., Shibata, Y., Hattori, T., Yano, T., & Nagao, J. (2017). Effects of a marine-protected area occurred incidentally after the Great East Japan earthquake on the Pacific cod (*Gadus macrocephalus*) population off northeastern Honshu, Japan. *Fisheries Oceanography*, 26(2), 181–192. <https://doi.org/10.1111/fog.12201>
- Narimatsu, Y., Shibata, Y., Suzuki, Y., Morikawa, E., Tokioka, S., & Nagao, J. (2019). *Stock assessment and evaluation for the Pacific cod stock of north Pacific off Honshu, Japan (fiscal year 2018)*, Japan: Fisheries Agency and Fisheries Research and Education Agency of Japan.
- Nemoto, Y. (2007). Stock condition of snow crab *Chionoecetes opilio* from catch informations. *Tohoku Sokou Kenkyu*, 27, 54–60.
- Nielsen, A., & Berg, C. W. (2014). Estimation of time-varying selectivity in stock assessments using state-space models. *Fisheries Research*, 158, 96–101. <https://doi.org/10.1016/j.fishres.2014.01.014>
- Orensanz, J. M., Ernst, B., & Armstrong, D. A. (2007). Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. *Journal of Crustacean Biology*, 27(4), 576–591. <https://doi.org/10.1651/S-2790.1>
- R Core Team. (2019). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing Retrieved from <https://www.r-project.org/>

- Richards, L. J., Schnute, J. T., Kronlund, A. R., & Beamish, R. J. (1992). Statistical models for the analysis of ageing error. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(9), 1801–1815. <https://doi.org/10.1139/f92-200>
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11(5), 559–623. <https://doi.org/10.1139/f54-039>
- Schwarz, G. (1978). Estimating the dimension of a model. *The Annals of Statistics*, 6(2), 461–464.
- Shibata, Y., Narimatsu, Y., Suzuki, Y., Morikawa, E., Tokioka, S., & Nagao, J. (2019). Stock assessment and evaluation for the snow crab of northern Pacific stock (fiscal year 2018). In *Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2018/2019)*, Japan: Fisheries Agency and Fisheries Research and Education Agency of Japan.
- Shibata, Y., Sakuma, T., Wada, T., Kurita, Y., Tomiyama, T., Yamada, M., ... Yamanobe, A. (2017). Effect of decreased fishing effort off Fukushima on abundance of Japanese flounder (*Paralichthys olivaceus*) using an age-structured population model incorporating seasonal coastal-offshore migrations. *Fisheries Oceanography*, 26(2), 193–207. <https://doi.org/10.1111/fog.12179>
- Somerton, D. A. (1981). Regional variation in the size of maturity of two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. *Canadian Journal of Fisheries and Aquatic Sciences*, 38(2), 163–174. <https://doi.org/10.1139/f81-022>
- Szuwalski, C., & Punt, A. E. (2012). Fisheries management for regime-based ecosystems: A management strategy evaluation for the snow crab fishery in the eastern Bering Sea. *ICES Journal of Marine Science*, 70(5), 955–967. <https://doi.org/10.1093/icesjms/fss182>
- Szuwalski, C., & Punt, A. E. (2013). Regime shifts and recruitment dynamics of snow crab, *Chionoecetes opilio*, in the eastern Bering Sea. *Fisheries Oceanography*, 22(5), 345–354. <https://doi.org/10.1111/fog.12026>
- Szuwalski, C., & Turnock, J. (2016). A stock assessment for eastern Bering Sea snow crab. Stock Assessment and Fishery Evaluation Report for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands Regions. Retrieved from [https://www.npfmc.org/wp-content/PDFdocuments/resources/SAFE/CrabSAFE/2018/1-EBSsnow\\_SAFE\\_2018.pdf](https://www.npfmc.org/wp-content/PDFdocuments/resources/SAFE/CrabSAFE/2018/1-EBSsnow_SAFE_2018.pdf)
- Takasaki, K., & Tomiyama, T. (2017). Geographic variation in the size-related terminal-molt proportion and carapace width of the male snow crab *Chionoecetes opilio* off the Pacific coast of southern Tohoku, Japan. *Nippon Suisan Gakkaishi*, 83(2), 156–162. <https://doi.org/10.2331/suisan.16-00059>
- Tanaka, S. (1960). Studies on the dynamics and the management of fish populations. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 28, 1–200.
- Tomscha, S. A., & Gergel, S. E. (2016). Ecosystem service trade-offs and synergies misunderstood without landscape history. *Ecology and Society*, 21(1), 43. <https://doi.org/10.5751/ES-08345-210143>
- Ueda, Y., Ito, M., Hattori, T., Narimatsu, Y., Fujiwara, K., Yoshida, T., & Kitagawa, D. (2007). Growth of the snow crab *Chionoecetes opilio* estimated by carapace width frequency analysis in the water off the Pacific coast of northern Honshu, Japan. *Nippon Suisan Gakkaishi*, 73(3), 487–494. <https://doi.org/10.2331/suisan.73.487>
- Ueda, Y., Ito, M., Hattori, T., Narimatsu, Y., & Kitagawa, D. (2009). Estimation of terminal molting probability of snow crab *Chionoecetes opilio* using instar- and state-structured model in the waters off the Pacific coast of northern Japan. *Fisheries Science*, 75(1), 47–54. <https://doi.org/10.1007/s12562-008-0016-6>
- UN General Assembly. (2015). Transforming Our World: The 2030 Agenda for Sustainable Development. A/RES/70/1. Retrieved from <http://www.igbp.net/download/18.62dc35801456272b46d51/1399290813740/NL82-SDGs.pdf>
- Watson, J. (1970). Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. *Journal of the Fisheries Board of Canada*, 27(9), 1607–1616. <https://doi.org/10.1139/f70-181>
- Yamamoto, T., Yamada, T., Kinoshita, T., Ueda, Y., Fujimoto, H., Yamasaki, A., & Hamasaki, K. (2015). Effects of temperature on growth of juvenile snow crabs, *Chionoecetes opilio*, in the laboratory. *Journal of Crustacean Biology*, 35(2), 140–148. <https://doi.org/10.1163/1937240X-00002309>
- Yamamoto, T., Yamada, T., Kinoshita, T., Ueda, Y., Yamasaki, A., & Hamasaki, K. (2018). Moulting and growth in earlier and later moulters of adolescent male snow crabs (*Chionoecetes opilio*) (Brachyura: Majoidea) under laboratory conditions. *Invertebrate Reproduction & Development*, 62(1), 49–55.
- Yamasaki, A. (1988). Ecological studies on Zuwai crab, *Chionoecetes opilio*, in the Sea off Kyoto Prefecture-IV. *Bulletin of the Kyoto Institute of Oceanic and Fishery Science*, 11, 35–42.
- Yamasaki, A., Sinoda, M., & Kuwahara, A. (1992). Estimation of survival rate after terminal molting of male snow crab *Chionoecetes opilio*. *Nippon Suisan Gakkaishi*, 58(2), 181–186. <https://doi.org/10.2331/suisan.58.181>
- Yoshida, H. (1941). On the reproduction of useful crabs in North Korea. *Suisan Kenkyushi*, 36(7), 116–123.
- Yule, D. L., Stockwell, J. D., Black, J. A., Cullis, K. I., Cholwek, G. A., & Myers, J. T. (2008). How systematic age underestimation can impede understanding of fish population dynamics: Lessons learned from a Lake Superior cisco stock. *Transactions of the American Fisheries Society*, 137(2), 481–495. <https://doi.org/10.1577/T07-068.1>
- Zheng, J., Kruse, G. H., & Ackley, D. R. (2001). Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. In G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, & D. Witherell, (Eds.), *Spatial processes and management of marine populations* (pp. 233–255). Fairbanks: Alaska Sea Grant. <https://doi.org/10.1016/j.pcean.2006.02.002>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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