Consequences of hatchery stocking: Lessons from Japan

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Shuichi Kitada

[1]Tokyo University of Marine Science and Technology, Tokyo 108-8477, Japan.

E-mail: kitada@kaiyodai.ac.jp

Abstract

More than 26 billion juveniles of 180 marine species are released annually into the wild in over 20 countries, but the usefulness remains unclear. Here, I review the effects of stocking by Japanese marine and salmon stock-enhancement programmes, and evaluate the efficacy through a meta-analysis, with new cases added to those previously considered. The posterior mean recapture rates (±SD) was 8.2 ± 4.7%; mean economic efficiency was 2.7 ± 4.5, with many cases having values of 1–2, excluding consideration for personnel costs and negative impacts on wild populations. At the macro-scale, the proportion of released seeds to total catch was 76 ± 20% for Japanese scallop, 28 ± 10% for abalone, 20 ± 5% for swimming crab, 13 ± 5% for kuruma prawn, 11 ± 4% for Japanese flounder and 7 ± 2% for red sea bream. Stocking effects were generally small and population dynamics unaffected by releases but dependent on carrying capacity of the nursery habitat. Japanese scallop in Hokkaido was the most successful case with the highest economic efficiency (18 ± 5), and populations maintained by releases of wild-born spat. In contrast, captive breeding reduced the fitness of released red sea bream in the wild, while wild fish recovered due to increased seaweed community and reduced fishing efforts. All most chum salmon returning to Japan are hatchery fish and/or hatchery descendants, which may reduce the fitness of populations in the warming sea temperature. Nursery-habitat recovery and fishing-effort reduction outperform hatcheries in the long-run.

Keywords: Bayesian meta-analysis, genetic effects, nursery habitat, stocking effects

1 | Introduction

The history of stocking fish larvae dates back to the 1870s (Bell et al., 2005; Blaxter, 2000; Svåsand et al., 2000). Approximately 150 years later, seed production technology has progressed and releases of hatchery-reared animals into the wild have become a popular tool in fisheries, forestry, and wildlife management (Laikre, Schwartz, Waples, & Ryman, 2010). More than 26 billion juveniles of 180 marine species, including salmonids, are released into the wild every year (Kitada, 2018). Moreover, marine ranching is rapidly growing in China (Lee & Zhang, 2018; Wang, Yu, & Chen, 2018; Zhou, Zhao, Zhang, & Lin, 2019) and Korea (Lee & Rahman, 2018). Despite the huge number of seeds released every year, most studies have been conducted at the experimental stage, particularly for marine species, and empirical studies are still too few for determining the full effectiveness of hatchery-release efforts. The feasibility and risks of hatchery stocking cannot be tested by examining pilot-scale releases alone, but can be sufficiently tested only by considering full-scale releases (Hilborn, 2004). A global analysis of full-scale releases found that most cases were economically unprofitable as a consequence of the high costs of seed production when compared with the prevailing market prices, apart from a few successful cases or cases left unevaluated (Kitada, 2018). Further investigation is therefore needed to answer the fundamental question of whether hatchery stocking is useful or harmful (Araki & Schmid, 2010).

Japan releases the largest number of hatchery-reared species in the world and often on a large scale. Focused, in-depth analyses of full-scale releases can improve our understanding of the positive and negative effects of this practice, and would benefit future fisheries management and conservation practices. In a recent review, I summarised the status of the economic, ecological and genetic effects of marine stock enhancement and sea-ranching programmes (Kitada, 2018), but the focus was on a global scale. Several other reviews described Japanese

marine stock enhancement and sea-ranching programmes by focusing on the effects of stocking several fishes (Kitada, 1999; Kitada & Kishino, 2006; Masuda & Tsukamoto, 1998), kuruma prawn (Hamasaki & Kitada, 2006, 2013), abalone (Hamasaki & Kitada, 2008a), and decapod crustaceans (Hamasaki & Kitada, 2008b; Hamasaki, Obata, Dan, & Kitada, 2011). Attention has also been given to seed production (Fushimi, 2001; Le Vay et al., 2007; Takeuchi, 2001), seed quality and behaviour (Tsukamoto, Kuwada, Uchida, Masuda, Sakakura, 1999), broodstock management (Taniguchi, 2003, 2004) and the genetic effects on wild populations (Kitada et al., 2009). For salmonids, many reviews have covered large-scale hatchery releases (e.g., Kaeriyama, 1999; Kaeriyama, Seo, Kudo, & Nagata, 2012; Kitada, 2014; Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013; Morita, 2014; Morita et al., 2006; Nagata et al. 2012). However, as yet, there has been no integrated review that summarises results concerning both marine and salmon stock enhancement in Japan.

Here, I first outline the history and present status of Japanese salmon and marine hatchery programmes. Second, I evaluate the efficacy of major full-scale projects using a Bayesian meta-analysis, with new cases added since my previous study. Third, I predict changes in the contribution of hatchery releases to commercial catches for representative iconic species on a macro-scale. Fourth, I summarise consequences concerning the world's largest hatchery stocking programmes—namely those for red sea bream, Japanese scallop and chum salmon.

2 | Hatcheries, seed release, and stocking-effect surveys

Japan's marine stock-enhancement programme was initiated by the Fishery Agency in 1963. At that time, Japan aimed to become a fully developed country under its national industrialisation policy. Many Japanese coastlines to serve as nursery habitats for marine species were reclaimed (Figure 1), and separate coastal industrial zones were created; many

coastal fishers moved to cities to earn higher incomes and coastal fisheries were weak. The marine stock-enhancement programme was a mitigation policy to improve degraded habitats and thereby enhance the coastal fisheries. Salmon hatcheries in Japan have a much longer history, beginning in the 1880s to increase fishery production of returning chum salmon, and have endured for over 130 years. However, chum salmon stock enhancement did not succeed during the early 1960s as the level of spawning biomass remained as it was even before the dramatic increase of returned fish as explained below. Therefore, Japan's marine stock-enhancement programme was seemingly started with no successful case precedent. This situation implies that "many believe that the future of fisheries lies with artificial propagation to rebuild depleted fish stocks due to poor fisheries management or poor habitat management" (Hilborn, 1992).

First, I created maps of salmon and marine hatcheries; approximate locations of salmon hatcheries were plotted on a map of Japan using 15 regional maps of the locations of salmon hatcheries, obtained from the website of the Japan Fisheries Research and Education Agency (FRA, salmon.fra.affrc.go.jp). I identified 262 salmon hatcheries in 11 prefectures in northern Japan, of which 242 were private hatcheries, managed mainly by fishers and cooperatives (Figure 2a). The 7 prefectural and 13 national hatcheries are operated mainly for research work. The major target salmonid species are chum salmon (*Oncorhynchus keta*, Salmonidae) and pink salmon (*O. gorbuscha*, Salmonidae). According to statistics from the North Pacific Anadromous Fish Commission (NPAFC), the number of released chum salmon has remarkably increased since the 1970s, reaching a historical maximum of 2.1 billion per annum in 1991. But since then releases of chum salmon dropped to 1.5 billion in 2018 (NPAFC, 2019) (Figure S1). A similar increasing trend since the 1970s occurred with pink salmon; however, the number of released pink salmon was 113 million in 2018, about 7% that

of chum salmon. The number of masu salmon (*O. masou*, Salmonidae) released in 2018 amounted to 7 million. Sockeye salmon (*O. nerka*, Salmonidae) are also released, but at even smaller numbers (NPAFC, 2019).

The locations of "saibai-gyogyo" centres in Japan (hereafter, marine hatcheries) were also plotted, using a list of their addresses compiled by the National Association for Promotion of Productive Seas (NAPPS). Presently, 65 prefectural marine hatcheries are operated in 43 prefectures (Figure 2b). In addition, 12 FRA research stations undertake marine stock enhancement. These were once national marine hatcheries managed by the Japan Sea-Farming Association (JASFA), which merged with the FRA following administrative reform in 2003. The JASFA was disbanded after 40 years, and the promotion of hatchery releases was inherited by the NAPPS, established in 2003. Since the FRA aimed to reduce their involvement in hatchery releases, four national marine hatcheries were closed up to 2018.

By 2017, a total of 74 species were being released in Japan, which included 34 fishes, 10 crustaceans, 22 shellfishes and 8 other marine species (e.g., sea urchin, sea cucumber and octopus). I organized the numbers of released seeds for the 16 major species released, whose annual release exceeded million seeds, for the period 1983–2017, relying on the annual statistics of seed production and releases (Fishery Agency, FRA, & NAPPS, 1985–2019). These species are: abalone (*Haliotis* spp., Haliotidae), Japanese scallop (*Mizuhopecten yessoensis*, Pectinidae), Manila clam (*Venerupis philippinarum*, Veneridae), green tiger prawn (*Penaeus semisulcatus*, Penaeidae), kuruma prawn (*Marsupenaeus japonicus*, Penaeidae), offshore greasyback prawn (*Metapenaeus ensis*, Penaeidae), swimming crab (*Portunus trituberculatus*, Portunidae), black sea bream (*Acanthopagrus schlegeliir*, Sparidae), flatfish (e.g. *Limanda yokohamae*, Pseuronectidae), Japanese flounder (*Paralichthys olivaceus*,

Paralichthyidae), Pacific herring (*Clupea pallasii*, Clupeidae), red sea bream (*Pagrus major*, Sparidae), sailfin sandfish (*Arctoscopus japonicus*, Trichodontidae), tiger puffer (*Takifugu rubripes*), sea urchins (e.g. *Strongylocentrotus intermedius*, Strongylocentroidae; *Heliocidaris crassispina*, Echinometridae) and sea cucumber (*Apostichopus armata*, Stichopodidae). The number of releases has increased and/or been stable for 4 species: Japanese scallop, tiger puffer, Pacific herring and sea cucumber. Releases have been decreasing for the other 12 species, including iconic target species such as the kuruma prawn, swimming crab, abalone, red sea bream, Japanese flounder and sea urchin (Figures S2, S3; Supplementary Data).

In earlier surveys, counting external tags reported by fishers was the main method used to estimate recapture rates (Kitada, 1999). This type of survey was used to estimate migration, growth and life history, including comparisons of seed quality (Kitada, Hiramatsu, & Kishino, 1994; Kitada & Hirano, 1987; Okouchi, Kitada, Morioka, Imamura, 1994; Shiota, & Kitada, 1992; Takaba, Kitada, Nakano, Morioka, 1995). However, tag-reporting rates were often very small, and tag-shedding and tagging mortality caused biased estimates. Researchers became aware of bias in the results when they estimated stocking effectiveness. As an alternative approach, surveys of commercial landings at fish markets (SCFM) were applied to estimate landings of released seeds and the hatchery contribution in the landings. For the SCFM, researchers sampled landings by visiting fish markets to cover the range of the stocking effect. The SCFM approach was first applied to red sea bream in Kagoshima Bay, where almost all red sea bream landed at the Kagoshima Fish Market were checked for deformity of the internostril epidermis to identify released fish (Kitada et al., 2019; Shishidou, 2002; Shishidou & Kitada, 2007). In the case of Japanese flounder in Miyako Bay, all flounder at the Miyako fish market were examined (Okouchi, Kitada, Iwamoto, & Fukunaga, 2004; Okouchi, Kitada, Tsuzaki, Fukunaga, & Iwamoto, 1999). Such a census approach was generally difficult to

apply, therefore sample surveys were logically introduced throughout the country. The common procedure was that all fish landed and sold at a selected market on a selected day would be checked for released seeds versus wild individuals. This was regarded as a two-stage sampling procedure for the sake of formulating estimators and their variance (Kitada, Taga, & Kishino, 1992). Accordingly, this approach has been applied to abalone (Kojima, 1995), kuruma prawn (Yamaguchi, Ito, Hamasaki, & Kitada, 2006) and masu salmon (Miyakoshi, Nagata, Sugiwaka, & Kitada, 2001). When information on the total landing days was lacking, simple random sampling was assumed, and landings from releases were then estimated (Obata, Yamazaki, Iwamoto, Hamasaki, & Kitada, 2008). Some other studies using SCFM data chose to assume simple random sampling, but in most cases the precision was not evaluated. As another approach, genetic marking was applied to mud crab to estimate recapture rates using genetic stock identification (Obata, Imai, Kitakado, Hamasaki, & Kitada, 2006).

To enhance the effectiveness of hatchery releases, a marine-ranching project, led by the Fishery Agency, endeavoured to shape ‘natural’ farms with sound habitat, such as enhanced seaweed communities to promote nutrient-enrichment in deep-sea upwelling systems (AFFRC, 1989). Hatchery releases and artificial reef construction were the major technologies, and feeding systems with acoustic conditioning were the popular tool, applied for marine fishes that could be reared and released as seeds around artificial reefs (Kayano, Tanaka, & Hayashi, 1998; Kudo & Kimoto, 1994). However, I could not find scientific literature that evaluated the effectiveness of Japan’s marine-ranching projects, thus its usefulness remains largely unknown, and consequently the effects of marine ranching in Japan were excluded from my analyses.

3 | Meta-analysis of hatchery performance

3.1 | Methods

I used recapture rates, yield-per-release (YPR), and economic efficiency as indices of the performance of hatchery releases, following a preceding study. YPR is defined as weight of fish caught (g) per individual released (Hamasaki & Kitada, 2008b; Kitada & Kishino, 2006; Svåsand et al., 2000), as follows:

$$YPR = r \times w$$

where *r* is the recapture rate of released juveniles, and *w* (g) is mean body weight per recaptured individual. Economic efficiency (*E*) is calculated as the ratio of net income to the release costs:

$$E = YPR \times v/c$$

Here, *v* is fish price per gram, and *c* is the cost of each seed; therefore, *v*/*c* is the cost performance of a seed (Kitada, 2018).

The true mean for the recapture rate, YPR, and economic efficiency for each study (y_i) is not observed but estimated ($\hat{y}_i, i = 1, \ldots, n$), and $\hat{y}_i$ may follow a normal distribution by the central limit theorem. When samples (i.e., cases within a study) are taken by random sampling, then $\mathrm{E}(\hat{y}_i) = y_i$, and the variance within each study (σ_i^2) is also estimated from the data (s_i^2). However, the release variables, such as tags, sizes at release, release areas, and time periods of surveys, varied in each study; therefore, the summary statistics needed to take into account the variation among studies. Here, I assumed a superpopulation for the recapture studies, by applying a Bayesian approach similar as given in a previous study (Kitada, Kishino, & Hamasaki, 2011).

Studies are carried out in different areas and years, therefore each study can be regarded as

independent. The approximate likelihood of the sample mean $\hat{y}_i\ (i = 1, \dots, n)$ can be written as:

$$L(\hat{y}_i\ (i = 1, \dots, n) | y_i\ (i = 1, \dots, n)) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp\left(-\frac{1}{2\sigma_i^2}(\hat{y}_i - y_i)^2\right)$$

We assume a prior distribution for $y_i\ (i = 1, \dots, n)$. Here, y_i is assumed to be normally distributed around the mean μ with the variance σ^2. These are hyperparameters: namely, the mean and variance of the superpopulation. The prior distribution of $y_i\ (i = 1, \dots, n)$ can be written as:

$$\pi(y_1, \dots, y_n | \mu, \sigma^2) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{1}{2\sigma^2}(y_i - \mu)^2\right)$$

By integrating the product of the prior distribution and the likelihood function in terms of y_i, the marginal likelihood function is derived. In this case, it is explicitly obtained as:

$$\tilde{L}(\sigma^2, \mu\ | \hat{y}_i(1, \dots, n) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi(\sigma^2 + \sigma_i^2)}} \exp\left(-\frac{1}{2(\sigma^2 + \sigma_i^2)}(\hat{y}_i - \mu)^2\right)$$

This shows that the sample mean $\hat{y}_i$ is distributed around the mean μ, with variances calculated for between cases and within cases.

The log marginal likelihood function is:

$$\log\tilde{L}(\sigma^2, \mu\ | \hat{y}_i(1, \dots, n) = -\frac{n}{2}\log 2\pi - \frac{1}{2}\sum_{i=1}^{n} \log(\sigma^2 + \sigma_i^2) - \frac{1}{2}\sum_{i=1}^{n} \frac{1}{\sigma^2 + \sigma_i^2}(\hat{y}_i - \mu)^2$$

The first derivatives on μ and σ^2 are then:

$$\frac{\partial \log\tilde{L}}{\partial \mu} = \sum_{i=1}^{n} \frac{1}{\sigma^2 + \sigma_i^2}(\hat{y}_i - \mu)$$

$$\frac{\partial \log\tilde{L}}{\partial \sigma^2} = -\frac{1}{2}\sum_{i=1}^{n} \frac{1}{\sigma^2 + \sigma_i^2} + \frac{1}{2}\sum_{i=1}^{n} \frac{1}{(\sigma^2 + \sigma_i^2)^2}(\hat{y}_i - \mu)^2$$

From $\partial \log \tilde{L} / \partial \mu = 0$, we have the maximum likelihood estimator (MLE) of μ as a weighted average of $\hat{y}_i$ $(i = 1, \ldots, n)$:

$$\hat{\mu} = \sum_{i=1}^{n} \frac{\hat{y}_i}{\sigma^2 + \sigma_i^2} \Big/ \sum_{i=1}^{n} \frac{1}{\sigma^2 + \sigma_i^2} \qquad (1)$$

By substituting σ^2 with $\hat{\sigma}^2$ given in Eq. (2) and σ_i^2 with the sample variance s_i^2, we have the MLE of μ (posterior mean).

Assuming that σ_i^2 does not depend on a case for simplicity, $\sigma_i^2 = \sigma'^2$ for all i $(1, \ldots, n)$ and from $\partial \log \tilde{L} / \partial \sigma^2 = 0$, we have the MLE of σ^2 as:

$$\hat{\sigma}^2 = \frac{1}{n} \sum_{i=1}^{n} (\hat{y}_i - \mu)^2 - \sigma'^2$$

By estimating μ by the weighted average $\hat{\mu}$ given by Eq. (1) and σ'^2 by the mean of the sample variance s_i^2, we have the approximate variance estimator as:

$$\hat{\sigma}^2 = \frac{1}{n} \sum_{i=1}^{n} (\hat{y}_i - \hat{\mu})^2 - \frac{1}{n} \sum_{i=1}^{n} s_i^2 \qquad (2)$$

The MLE of μ has a different weight from the weighted mean (also the MLE) that was used in the previous study (Kitada, 2018), while $\hat{\sigma}^2$ is the same. Eq. (1) provided a more realistic estimate than use of the previous weighted average, particularly when very small $\hat{y}_i$ values ($\hat{y}_i < 1$) were included (i.e., when there was large variation in $\hat{y}_i$). The average and standard deviation (SD) with a 95% confidence interval (mean ± 2 SD) were visualised for each case using the 'forestplot' function in R. When the lower confidence limit took a negative value, it was replaced by 0.

3.2 | Recapture rate

247 I summarised 21 full-scale programmes (Table S1) that reported the recapture rate of hatchery
248 individuals, of which 18 programmes were revisited from the previous study (Kitada, 2018).
249 The mean recapture rate of chum salmon for the whole of Japan was re-calculated based on
250 the simple return rates (number of fish returned after four years/number released) taken from
251 the FRA website (salmon.fra.affrc.go.jp). The recapture rates of 17 of 21 studies were
252 estimated using the SCFM data and/or combining use of the SCFM approach and reported
253 recaptures. Recapture rates for red sea bream (Kitada & Kishino, 2006), kuruma prawn
254 (Hamasaki & Kitada, 2006, 2008b) and abalone (Hamasaki & Kitada, 2008a) were
255 summarised from previous reviews for the whole country, which included black rockfish
256 (*Sebastes schlegelii*, Sebastidae) (Nakagawa, Okouchi, & Adachi, 2004), Japanese flounder
257 (Atsuchi, & Masuda, 2004; Ishino, 1999; Kitada, Taga, & Kishino, 1992; Tominaga &
258 Watanabe, 1998; Tomiyama, Watanabe, & Fujita, 2008), Japanese scallop (Kitada, &
259 Fujishima, 1997), Japanese Spanish mackerel (*Scomberomorus niphonius*, Scombridae)
260 (Obata, Yamazaki, Iwamoto, Hamasaki, & Kitada, 2008), mud crab (*Scylla paramamosain*,
261 Portunidae) (Obata, Imai, Kitakado, Hamasaki, & Kitada, 2006), short-spined sea urchin
262 (*Strongylocent-rotus intermedius*, Strongylocentroidae) (Sakai, Tajima, & Agatsuma, 2004),
263 spotted halibut (*Verasper variegatus*, Pleuronectidae) (Wada, Kamiyama, Shimamura,
264 Mizuno, & Nemoto, 2012), swimming crab (Okamoto, 2004) and tiger puffer (Nakajima, Kai,
265 Koizumi, Tanaka, & Machida, 2008). I newly added four cases of three species: barfin
266 flounder (*Verasper moseri*, Pleuronectidae) in Hokkaido (Murakami, 2012; Koya, 2005;
267 NPJSEC, 2015), red spotted grouper (*Epinephelus akaara*, Serranidae) in Osaka Bay
268 (Tsujimura, 2007) and tiger puffer in the Ariake Sea (Matsumura, 2005, 2006), because the
269 stocking effect had been recently reported for the first two species, and because the number of
270 tiger puffer released has increased in recent years (Figure S3). Particularly for the barfin
271 flounder in Hokkaido, more than one million juveniles have been released annually along the

Pacific coast since 2006.

The results for recapture rates included 14 species, consisting of eight marine fishes, one salmonid, two crustaceans, two shellfishes, and one sea urchin (Table S1). Cases that reported only point estimates were excluded from the following analysis. The recapture rates of 20 marine species largely varied among species and cases, and ranged from 0.9% to 34.5% (Figure 3). The posterior mean recapture rates was 8.2 ± 4.7%, and the empirical distribution indicated that most cases had recapture rates between 6% and 12%. Japanese scallop had the highest recapture rate (34.5 ± 10.2%), followed by sea urchin (18.2 ± 17.5%), with relatively large variations. Most of the marine fishes, particularly barfin flounder, black rockfish, Japanese flounder, Japanese Spanish mackerel, spotted halibut and tiger puffer (to age 0+), had recapture rates in the range 11–15%. Abalone likewise had a relatively high recapture rate (12.2 ± 8.1%), also with high variation. Red sea bream had recapture rates of 7–8%, with small variation. In contrast, the return rate of chum salmon, on Hokkaido and Honshu islands combined, was much smaller, at 2.7 ± 0.8%, which was close to that of red spotted grouper, at 2.2 ± 1.0%. Crustaceans generally had values smaller than 5%; large variations in the recapture rates occurred for kuruma prawn (2.8 ± 4.5%) and mud crab (0.9 ± 0.7%).

3.3 | YPR and economic efficiency

I revisited cases otherwise reported on in the previous study (Kitada, 2018), of which the economic efficiency values of 10 cases were cited, and six cases were newly added: those of barfin flounder in Hokkaido, Japanese flounder at Fukushima, red spotted grouper in Osaka Bay, tiger puffer in the Ariake Sea, and swimming crab in Lake Hamana and in the Seto Inland Sea (see references in Table S2). YPR and economic efficiency values were calculated for kuruma prawan (Hamasaki & Kitada, 2006, 2008b), swimming crab (Hamasaki et al.,

2011) and abalone (Hamasaki & Kitada, 2008a), based on the previous reviews. For chum salmon, YPR was recalculated based on newly estimated mean body weights from catch statistics for 1974–2017 obtained from the NPAFC, and return rates for 1974–2017 from the FRA (http://salmon.fra.affrc.go.jp/zousyoku/sakemasu.html). The revised YPR for chum salmon was 86 ± 29 g. For Japanese scallop, mean body weights were recalculated based on the work of Kurata (1999), and the revised estimate was 177 ± 30 g. YPR values were reported for pink salmon in Hokkaido in terms of amount of money (1.5–2.2 yen/released individual), calculated based on the estimated proportion of Hokkaido-origin hatchery fish in the landings (Ohnuki, Morita, Tokuda, Okamoto, & Ohkuma, 2015). Thus, that case did not give the YPR in weight, the recapture rates, nor cost performance of a seed (v/c); therefore, I excluded the case of pink salmon in Hokkaido from the analysis.

Ultimately, YPR and economic efficiency were evaluated for 16 cases involving 12 species (Table S2). Meta-analysis was performed on 12 cases involving 9 species for YPR, and 13 cases of 10 species for economic efficiency, where the cases with only point estimates of YPR and/or those without information for calculating v and c were omitted from the analyses. The YPR values varied between species and cases. The empirical distribution of the summary statistics had a long tail to the right, with a posterior mean of 63 ± 71 g (Figure 4a). YPR was high for both barfin flounder (182 ± 9 g) and Japanese Spanish mackerel (170 ± 8 g), followed by that for chum salmon (86 ± 29 g) and Japanese scallop (61 ± 18 g). Red sea bream and Japanese flounder had YPR values of 30–59 g. Other YPR values were 34 ± 10 g for swimming crab, 26 ± 19 g for abalone, 4 ± 3 g for mud crab, and 0.9 ± 1.5 g for kuruma prawn.

The posterior mean of economic efficiency was 2.7 ± 4.5, while that of several cases was

about 1 (the break-even point) to 2, with the lower 95% confidence limit below 0 (Figure 4b). Economic efficiency was the highest for Japanese scallop (18 ± 5), followed by chum salmon in Hokkaido and Honshu combined (7 ± 2). Red sea bream in Kagoshima Bay also had a high value (5 ± 3). The consequences of the top three species were further explained in section 5. Similar economic performance was seen for abalone in all of coastal Japan (4 ± 2) and for barfin flounder on the Pacific coast of Hokkaido (3 ± 0.1). Japanese flounder had a much smaller economic efficiency, at 0.9–1.6. Crustaceans consistently exhibited economic efficiency values around 1, and kuruma prawn showed the lowest value, at 0.7 ± 0.9. Among these species, Japanese scallop, chum salmon and barfin flounder had a lower 95% confidence limit that was >1.0. Economic efficiency is a function of YPR (recapture rate × body weight) and cost performance of a seed (v/c). A scatter plot of YPR versus economic efficiency depicted the stocking-performance characteristic of each species (Figure 4c).

It is noted that the seed cost used in the analysis did not include personnel expenses, facilities, monitoring or administration costs. I did not analyse net present value (NPV) (Moksness & Støle, 1997; Moksness, Støle, & van der Meeren, 1998; Sproul &Tominaga, 1992; Svåsand et al., 2000) because various data, such as annual costs for harvest, management and interest rates, were not available for every case. If the NPV method were used, then the economic efficiency estimates obtained here would be less (Kitada, 2018), depending on the interest rate and the time duration, although recent interest rates in Japan are low (<0.1%). The seed cost also did not account for the cost of negative effects on natural populations and ecosystems (Amoroso, Tillotson, & Hilborn, 2017; Hilborn, 1998; Waples, 1991, 1999; Winton & Hilborn, 1994). Therefore, the estimates of economic efficiency obtained here are optimistic.

4 | Contribution of released seeds in the commercial landings

I estimated the contribution of hatchery releases in the commercial catch for eight species in the whole of Japan, based on national catch statistics (MAFF, 1964–2018). These are iconic species of Japan's marine stock enhancement and sea-ranching programmes and ones that are intensively released within range of Japanese waters. Among these eight species, catches increased after releases in the cases of Japanese scallop and Japanese Spanish mackerel (Figure 5), and catches were stable for Japanese flounder and red sea bream. In contrast, kuruma prawn and swimming crab have shown continuous decreases in catches since the mid-1980s. Continuous decline in abalone and sea urchin catches was also observed since the early 1970s. For cases with an increasing catch, management agencies and hatchery advocates often say that the practise of hatchery release should be successful. For cases displaying a stable catch, a poplar explanation is that hatchery release might support the resource. For instances of decreasing catch, one explanation is that this is because of decreased numbers of releases and that the catch could increase if more seeds were released. To answer this debate, estimates of the contribution of hatchery-released seeds in the catches could be helpful.

To evaluate the hatchery contribution for the major species in the whole of Japan, I computed the catch expected from released seeds by multiplying the average YPR (listed in Table S2) by the numbers of fish released for each year (Supplementary Data). Except for Japanese Spanish mackerel the contribution was calculated for the Seto Inland Sea alone because hatchery releases in Japan are only made at that location. This simple analysis assumed that YPR was constant over years and that released seeds created the catch in the same year, and thus it did not account for a time-lag. However, it allowed comparisons of the approximate contribution of hatchery releases between species in a macro-scale (Kitada & Kishino, 2006).

371 The proportion of released seeds, at 76 ± 20%, was largest for Japanese scallop, with released
372 spat contributing stably (Figure 5, vertical bars; Figure S4) and with a wild catch created by
373 natural reproduction among released scallops. The catch decreased substantially during 2015–
374 2017, following bottom disturbance off the Okhotsk coast caused by a low-pressure bomb in
375 winter of 2014, when the estimates showed that almost all of the catch comprised released
376 spat, indicating that scallop populations were heavily damaged by the bottom disturbance in
377 2014. Although the analysis was simple, the results indicated the approach could describe the
378 population dynamics of Japanese scallop.
379
380 The hatchery contribution to the increased catch of Japanese Spanish mackerel was small, at 2
381 ± 2%. The catch of this fish continued to recover after releases, however the number of
382 released juveniles was reduced 10 years after the release project started. The results clearly
383 indicated that the species' population dynamics were unaffected by the releases. A previous
384 study found 35% variation in the biomass of age-0 Japanese Spanish mackerel, which could
385 be explained by the biomass of a prey fish, Japanese anchovy (Nakajima et al., 2013). Genetic
386 stock identification following releases in 2001 and 2002 found that the mixing proportion of
387 hatchery-origin fish was high, at 8–15% (Nakajima et al., 2014). Interestingly, the genetic
388 admixture of hatchery fish was much higher than the estimated contribution rates in the Seto
389 Inland Sea, as found for red sea bream in Kagoshima Bay (Kitada et al., 2019), again
390 implying a trans-generation genetic effect. The hatchery contribution for Japanese flounder
391 was 11 ± 4%, and that for red sea bream was 7 ± 2%. Over two decades, the number of
392 released juveniles was decreased by ~50% for flounder and by ~63% for red sea bream, but
393 the catches of wild fish remained stable, indicating that the hatchery releases did not boost the
394 population size of either species on a macro-scale. Natural reproduction should have
395 supported the recruitment in the carrying capacity.

For crustaceans, the hatchery contribution was 13 ± 5% for kuruma prawn. The results agreed with the estimates of previous research (Hamasaki & Kitada, 2013), ~10% for kuruma prawn in all of Japan for the years 1977 to 2008, wherein it was concluded that the decline in kuruma prawn catches might be an outcome of warming ocean conditions, decreased fishing effort because of a fewer number of fishers, and reduced hatchery releases. A continuous decreasing trend in the catch implied a decline in natural recruitments, suggesting an environmental effect (Figure 5). Reduced fishing efforts would likely work to increase the population size given a sound nursery environment, as demonstrated in the case of red sea bream (Kitada et al., 2019); therefore, a reduction in fishing effort might be excluded as a cause of the decreasing catches of kuruma prawn. An environmental effect might be substantial for kuruma prawn, particularly extensive loss of tidal nursery habitat (Hamasaki & Kitada, 2006). For swimming crab, the hatchery contribution was 20 ± 5%; the catch continuously decreased, again revealing a decline in natural recruitment. Juvenile crabs are found on tidal flats after the C4 stage (~16 mm carapace width [CW]) and/or C5 stage (~22 mm CW) (Hamasaki, Obata, Dan, & Kitada, 2011); thus, extensive loss of tidal nursery habitat would be a logical cause of a decreasing catch. The catches of kuruma prawn and swimming crab were positively correlated ($r = 0.52,\ t = 4.49, \mathrm{df} = 53, p = 3.9 \times 10^{-5}$), suggesting losses of nursery habitat commonly affect these two crustaceans.

Abalone displayed a relatively high and stable hatchery contribution rate (28 ± 10%), yet the catch continued to decrease, indicating decreases in natural recruitment. A negative correlation was found between the Aleutian Low-Pressure Index, winter sea surface temperatures, and catches of Ezo abalone (*Haliotis discus hannai*, Haliotidae) in northern Japan (Hayakawa, Yamakawa, & Aoki, 2007; Nakamura, Kitada, Hamasaki, & Okouchi,

2005), plus cold winter seawater temperatures (<5 °C) affected the survival of young Ezo abalone (Takami et al., 2008). Seaweed community richness (carrying capacity) was the key factor for successful abalone stocking in Japan (Hamasaki, 2008). For sea urchin, I could not calculate the hatchery contribution rates because no published information available for calculating YPR values was found. However, the decreasing trend in the releases and catch of sea urchin was very similar to that of abalone ($r = 0.96, t = 24.63, \mathrm{df} = 53, p = 2.2 \times 10^{-16}$), indicating that sea urchin abundance likewise heavily depends on richness of the seaweed community.

5 | Consequences of the world's largest programmes

5.1 | Red sea bream in Kagoshima Bay

Red sea bream in Kagoshima Bay is one of the world's largest hatchery-release programmes for a marine fish, and it is the best-monitored one in Japan; it was started in 1974 and ~27 million hatchery-reared red sea bream (6–7 cm TL) have been released in the bay. During the period 1989–2015, 1.6 million red sea bream were examined at fish markets to identify hatchery fish caught in the bay. The catch of hatchery fish reached 126 tonnes by 1991, but thereafter consistently decreased, dropping to 3 tonnes by 2016. This was due to a decline in fitness of the hatchery-reared fish in the wild, caused by the repeated use of parent fish reared in captivity (captive breeding) since 1974 (~9 generations). In contrast, the catch of wild fish increased after 1991, and reached a maximum in 2016 following releases amounting to 168 tonnes. Increased seaweed communities and reduced fishing efforts were the primary factors in recovery of Japan's wild population of red sea bream (Kitada et al., 2019).

Importantly, the example of red sea bream in Kagoshima Bay shows that the hatchery releases substantially increased the fisheries production for the first 15 years—when this came to be

446 regarded as a representative, successful programme in Japan—but then the catch of hatchery
447 fish steadily decreased and remained very low. Ample evidence for salmonids shows that
448 captive breeding can reduce the fitness of hatchery salmon in the wild (Araki, Cooper, &
449 Blouin, 2007; Fleming et al., 2000; McGinnity et al., 2003; Reisenbichler & McIntyre, 1977;
450 Christie, Ford, & Blouin, 2014). The declining catch of red sea bream in Kagoshima Bay was
451 attributed to genetic effects through unintended domestication/selection by captive breeding
452 (Araki, Berejikian, Ford, & Blouin, 2008; Araki, Cooper, & Blouin, 2007; Ford, 2002).
453 Cumulative recapture rates until age 8+ decreased 15.6 ± 1.7% (standard error, SE) per year.
454 Since 1974, the broodstock of red sea bream intended for release in Kagoshima Bay have
455 been reared in a 100-m^3 concrete tank; about 130 non-local red seab ream broodstock have
456 been maintained in the concrete tank for natural spawning and were repeatedly used as
457 broodstock. In 1999 and 2014, a total of 395 wild, 33 farmed, and many 2-year-old hatchery
458 fish produced from the broodstock were added to the broodstock. The number of parent fish
459 used for seed production varies, between about 45 and 187, every year. The rate of fitness
460 reduction in hatchery-reared populations was cohort-specific and was constant over time
461 within the cohort, but it exponentially decreased with the duration in captivity (Kitada et al.,
462 2019). This suggests that, once a fitness decline arises in a hatchery population, the reduction
463 in fitness may continue until complete replacement of the broodstock.
464
465 Backcrossing to wild populations could work to diminish the genetic effects of captive
466 breeding if they were additive (Roberge, Normandeau, Einum, Guderley, & Bernatchez,
467 2008). The genetic effects of captive breeding could be gradually diluted if the proportion of
468 hatchery fish in the recipient population is not substantial. The proportion of hatchery fish in
469 the landings in the inner part, central part, and outside of Kagoshima Bay were highest in
470 1990, at 83.3%, 33.5% and 7.4%, respectively, but in 2015 the proportion was only ~1.0%

(even in the inner part). The genetic diversity indices recovered for fish in Kagoshima Bay suggested that the genetic effects were gradually diluted. Increasing wild fish showed no fitness decline in the recipient population due to small proportions of hatchery fish in the population.

We should be careful when speculating about cases with very high proportions of hatchery fish in the recipient population, particularly cases that use captive breeding. Captive-reared parents are repeatedly used for abalone, barfin flounder, black sea bream, Japanese flounder and tiger puffer (Table S1). In the case of barfin flounder, one million of juveniles (~8 cm TL) were released annually on the Pacific coast of Hokkaido. The catch remarkably increased from 0.01 tonnes in 1996 to over 100 tonnes in 2015, and almost all catches in the North Pacific, from Ibaraki Prefecture to Hokkaido (170 tonnes), consisted of hatchery fish (NPJSEC, 2015). In this case, ~500 parent fish have been used for seed production, for 1–3 generations in captivity, and the expected heterozygosity is very high, at 0.87 (Andoh, Misaka, & Ichikawa, 2013). We must wait for many more generations of barfin flounder before we can determine the consequences of this case.

5.2 | Japanese scallop

Japanese scallop account for ~27% of the landed amount of the Hokkaido fishery (www.pref.hokkaido.lg.jp) and all landings are created by releases of wild-born spat and naturally-reproduced spat from released individuals (Kitada & Fujishima; Nishihama, 2001; Nishihama, 2001; Uki, 2006). The scallop-ranching programmes in Hokkaido were initiated by fishers and are managed by cooperatives. Fishers pay most of the programme costs (Uki, 2006). The cooperatives use the following management system for the Japanese scallop fishery: (1) mass-releases of wild-born spat (wild-born larvae collected in the sea are reared in

net cages for one year, until release); (2) removal of predators, such as starfish, before release; (3) monitoring of the density of scallops in the fishing ground; and (4) rotation of the fishing grounds chosen for harvesting (Goshima & Fujiwara, 1994; Kitada & Fujishima; Nishihama, 2001; Uki, 2006). The fishing grounds are generally partitioned into four areas, and 1-year-old wild-born spat (~4.5 cm) that were reared in net cages are released into a given area after removing starfish, and the released scallops are harvested after three years, when they reach 4 years old. In the next year, the spats are released into another area. This fishing-ground rotation system enables complete prohibition of the fishery for three years after release.

Catches of Japanese scallop in the release areas have increased remarkably since the first releases in the 1970s, and reached the historical maximum of 359 000 tonnes in 2014 (Figure 6a, updated from Kitada, 2018). The catch substantially dropped to 232 000 tonnes (65%) in 2015 due to a bottom disturbance on the Okhotsk coast (accidentally caused by a low-pressure bomb on 16–17 December 2014, as reported in the previous study), but recovered to 305 000 tonnes in 2018, as expected; the catch recovery in 2018 would have been created by spat released in 2015. The long-term trends in the release and catch statistics demonstrate that sea ranching of scallop in Hokkaido is clearly successful with the highest economic efficiency (18 ± 5).

5.3 | Chum salmon

Chum salmon hatchery-stock enhancement in Japan is one of the world's largest salmon stocking programmes (Amoroso, Tillotson, & Hilborn, 2017). Hokkaido is Japan's major production area for chum salmon, with the returns accounting for 21% amount of Hokkaido's fishery (www.pref.hokkaido.lg.jp). Most of the landings are created by releases of hatchery-born fish, and fishers pay ~7% of the landings of chum salmon for hatcheries in Hokkaido

(Kitada, 2014). The long-term trends in releases and catches indicate that the carrying capacity in natural rivers is ~10 million fish maximum, and the great increase was created by hatchery stocks (Figure 6b, updated from Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013). Total production in Hokkaido reached a historical maximum of 61 million returns in 2004, then substantially decreased to 16 million in 2017. Chum salmon in Japan are at the southern margin of the species' range; the previous study found that 30% of the variation in decreasing catches was attributed to increasing sea surface temperature (SST) anomaly, and 62% was explained by SST and catches by Russian after 1996 (Kitada, 2018). However, there were clear differences between the run-timing of the chum salmon populations in Russia (Jun–Aug) and Japan (Sep–Nov) (Kondo, Hirano, Nakayama, Miyake, 1965; Morita, 2016). Migration routes were also different. These results suggested that the negative correlation between the Japanese and Russian catches, reported in the previous study, were spurious. The decline in Japan's catch might be caused by interactions between the long-term hatchery operations and a warming climate. This hatchery–climate interaction merits further study.

There is no reported evidence of fitness decline among hatchery-born and wild-born chum salmon in Japan. The observed genetic effect is an altered population structure, with some populations nested over the seven and/or eight regional groups (Beacham, Sato, Urawa, Le, & Wetklo, 2008; Kitada, 2014; Sato, Templin, Seeb, Seeb, & Urawa, 2014). This might be caused by past translocation history (Beacham, Sato, Urawa, Le, & Wetklo, 2008; Kaeriyama & Qin, 2014). The run-timing distribution of Hokkaido chum salmon was probably altered as a result of preferred enhancement of early-running fish (returning in September/October) while the late-running population almost disappeared (Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013). Lower reproductive success of the early spawners was observed in sockeye salmon in Washington State, USA, and early-emerging juveniles had relatively low

survival in recent years, suggesting fitness costs from early spawning, which could reduce population productivity during a warming climate (Tillotson, Barnett, Bhuthimethee, Koehler, & Quinn, 2019).

Almost all chum salmon returning to Japan were hatchery-reared fish (Kaeriyama, 1999). Hatchery fish are produced from returned adult fish every year, and the number of parent fish maintained has been large (i.e., 15 000–85 000) (Kitada, 2018). Even so, natural spawning of chum salmon was found in 31–37% of 238 non-enhanced rivers surveyed in Hokkaido (Miyakoshi et al., 2012), and in 94% of 47 enhanced rivers and 75% of 47 non-enhanced rivers on the northern coast of Honshu Island (Sea of Japan) (Iida, Yoshino, Katayama, 2018). In addition, a study using otolith thermal-marking estimated the proportions of naturally-spawned chum salmon to total production at 16–28%, among eight rivers surveyed in Hokkaido, with large variation within rivers (range 0–50%) (Morita, Takahashi, Ohkuma, & Nagasawa, 2013). Despite variations in the proportion of natural spawning in the rivers, gene flow facilitates the genetic admixture of hatchery-released fish, hatchery descendants and wild fish in the whole Japan populations.

To visualise the magnitude of gene flow between populations, I revisited the microsatellite data of 26 chum salmon populations in Japan (14 loci, n = 6 028; Beacham, Sato, Urawa, Lei, & Wetklo, 2008) and computed F_{ST} values between pairs of populations based on the bias-corrected G_{ST} (Nei & Chesser, 1983), using the GstNC function in the R package FinePop1.5.1. This G_{ST} estimator provides an unbiased estimate of F_{ST} when the number of loci becomes large (Kitada, Nakamichi, & Kishino, 2017). I tied population pairs when the pairwise F_{ST} value was <0.01 and superimposed this schematic with the locations of hatcheries (Figure 7). The mean of the pairwise F_{ST} was very small (0.007 ± 0.003). The

threshold $F_{ST} = 0.01$ was equivalent to $4N_e m = 99$, where N_e is the effective population size, and m is the migration rate. This means that 99 effective parents migrate between each pair of populations per generation (see Waples & Gaggiotti, 2006). Figure 7 depicts substantial gene flow between the chum salmon populations. The causal mechanisms of population structuring are migration and genetic drift, and differentiation depends on the number of migrants ($N_e m$) (Hauser & Calvalho, 2008; Waples & Gaggiotti, 2006). Even in a high-gene-flow species, the Atlantic cod (*Gadus morhua*, Gadidae), temporally stable but significantly differentiated structure was found in the populations (Hauser & Calvalho, 2008). Constant gene flow among populations can create a stable genetic mixture in a meta-population, as observed for Pacific herring populations in northern Japan (Kitada et al., 2017).

Hatchery practices might increase the likelihood of chum salmon to stray (Quinn, 1993). I summarised the results of the marking studies of chum salmon juveniles in Hokkaido, where 2 028 thousand hatchery-reared salmon juveniles (3.5–4 cm BL, 0.45–5 g) were fin-clipped and/or operculum-clipped and released without rearing between 1951 and 1955 (Sakano, 1960). The results revealed that 50 ± 22% of a total of 2 085 recoveries were recaptured in the river of their release, and 84 ± 12% were found including recoveries in nearby coasts (Supporting Data); hence, the spawning fidelity of hatchery-reared chum salmon was moderate. Estimates of straying can vary largely between specific hatchery releases and rivers, but the genetic integrity of a population can be altered by straying regardless of the strength of the native population's spawning fidelity (Quinn, 1993). Early theoretical work predicted that >99% (50%) of wild genes were replaced by hatchery genes in 12 (2) generations, in the case of equal fitness between hatchery and wild fish with additive effect, at a stocking rate of 0.5 (Matsuishi, Kishino, & Numachi, 1995; see also Kitada et al. 2019, Figure 5). From these results together, I speculate that all chum salmon returning to Japan are

hatchery-released fish or wild-born from hatchery descendants, resulting from the large-scale, long-term releases.

6| Conclusion

Many cases of hatchery releases were economically unprofitable if the costs of personnel and the negative impacts on wild populations are taken into account. Stocking effects were generally small and the population dynamics were unaffected by releases but instead essentially depended on the carrying capacity of the nursery habitat. Captive breeding reduces the fitness of hatchery-reared fish in the wild, and long-term, extensive hatchery releases can replace wild genes and may cause fitness decline in the recipient population. All chum salmon returning to Japan should be hatchery fish and/or hatchery descendants, which may reduce the fitness of populations in the warming environment. Recovery of nursery habitats and fishing effort reduction outperform hatcheries in the long run.

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Data Availability Statement

All source data used are in the public sector and links to their online sources are specified in the text or in Supplementary Data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Supporting Data.

Catch and release data for major species in Japanese marine stock enhancement and sea-ranching programmes, and the results of marking experiments with chum salmon conducted in Hokkaido in the 1950s.

Figure Legends

Figure 1 Changes in the areas of tidal flats and eel grass (*Zostera marina*, Zosteraceae) (1945–1996). From Ministry of Environment, www.env.go.jp and www.biodic.go.jp accessed July 2019

Figure 2 Maps plotting the locations of the marine and salmon hatcheries in Japan, operated by different sectors. From FRA (salmon.fra.affrc.go.jp accessed August 2019) and NAPPS (http://www.yutakanaumi.jp/, see text)

Figure 3 Forest plot of recapture rates for large-scale hatchery releases in Japan. Thin lines indicate 95% confidence intervals, and arrows indicate that the confidence intervals penetrate the scale; areas of the squares are proportional to the weight of the mean [The colour figure can be viewed at wileyonlinelibrary.com]

Figure 4 Performance of large-scale hatchery releases in Japan. Forest plots of **(a)** yield-per-release (YPR), **(b)** economic efficiency, and **(c)** YPR versus economic efficiency. Note: the seed cost used in the analysis did not include personnel expenses, facilities, monitoring, or administration costs. SIS = Seto Inland Sea [The colour figure can be viewed at wileyonlinelibrary.com]

Figure 5 Total catch and wild catches, with release statistics, for representative species in Japanese stocking programmes, for the whole of Japan. Vertical lines depict recovery (expected catch from releases), estimated by multiplying values of yield-per-release (YPR) (see Table 2) and the numbers released (Supplementary Data). For sea urchin, no YPR data were available

Figure 6 Long-term release and catch (return) statistics for **(a)** Japanese scallop (updated from Kitada, 2018) and **(b)** chum salmon in Hokkaido (updated from Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013)

Figure 7 Geneflow between Japanese populations of chum salmon. Populations were tied by lines for pairwise $F_{ST} < 0.01$, estimated from the microsatellite data of 26 populations (14 loci, $n = 6\,028$; Beacham, Sato, Urawa, Lei, & Wetklo, 2008).

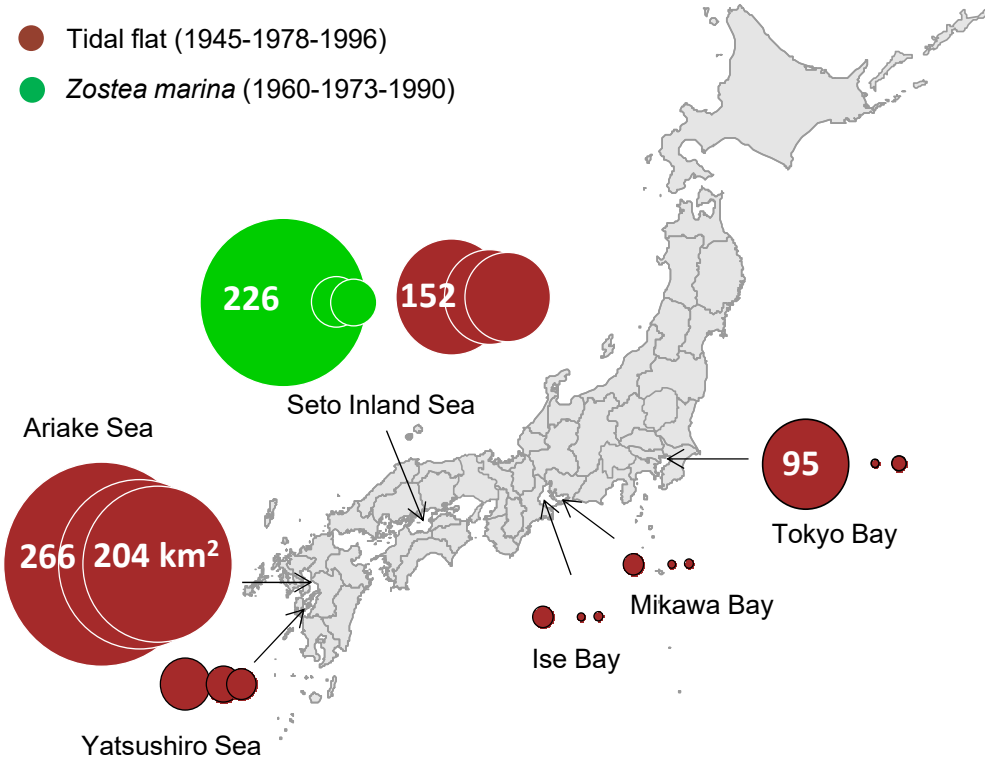
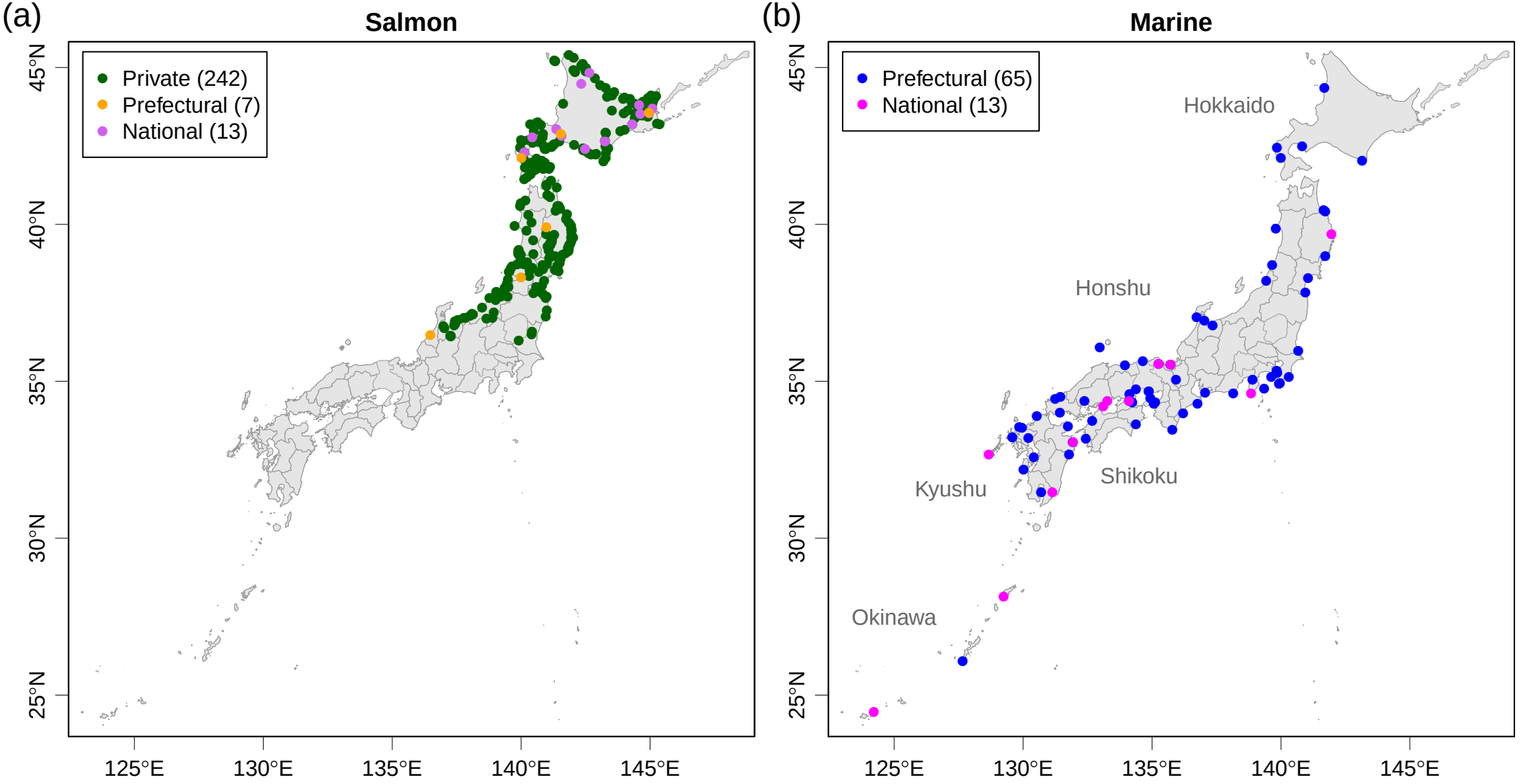
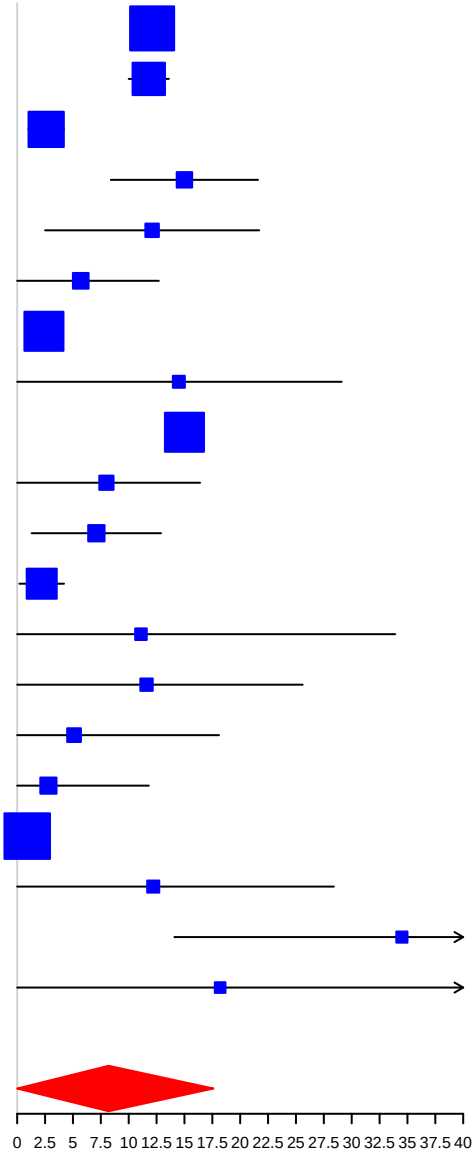

Tidal flat (1945-1978-1996)
Zostea marina (1960-1973-1990)
226
152
Seto Inland Sea
Ariake Sea
266
204 km²
95
Tokyo Bay
Mikawa Bay
Ise Bay
Yatsushiro Sea

Fig. 1

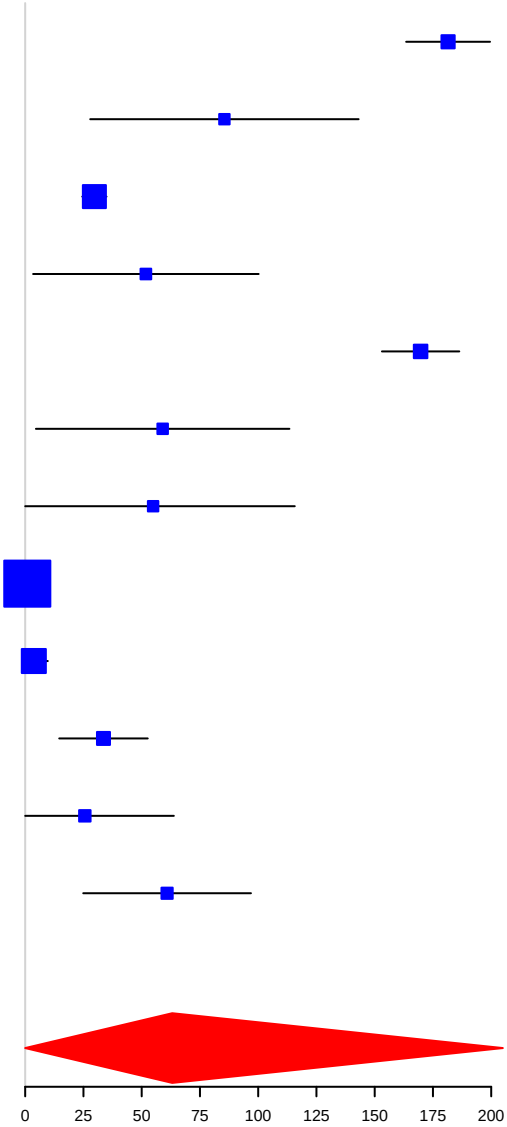

(a)
Salmon
Private (242)
Prefectural (7)
National (13)
45°N
40°N
35°N
30°N
25°N
125°E
130°E
135°E
140°E
145°E
(b)
Marine
Prefectural (65)
National (13)
Hokkaido
Honshu
Shikoku
Kyushu
Okinawa
45°N
40°N
35°N
30°N
25°N
125°E
130°E
135°E
140°E
145°E

Recapture rates (%)

Species	Mean (SD)
Barfin flounder (Hokkaido)	12.1 (0.6)
Black rockfish (Yamada Bay)	11.8 (0.9)
Chum salmon (Hokkaido, Honshu)	2.6 (0.8)
Japanese flounder (Fukushima87)	15.0 (3.3)
Japanese flounder (Fukushima94_02)	12.1 (4.8)
Japanese flounder (Ishikari Bay)	5.7 (3.5)
Japanese flounder (Kagoshima Bay)	2.4 (0.7)
Japanese flounder (Miyako Bay)	14.5 (7.3)
Japanese Spanish mackerel (SIS)	15.0 (0.7)
Red sea bream (Kagoshima Bay)	8.0 (4.2)
Red sea bream (Sagami Bay)	7.1 (2.9)
Red spotted grouper (Osaka Bay)	2.2 (1.0)
Spotted halibut (Fukushima)	11.1 (11.4)
Tiger puffer (Ariake Sea, Age0)	11.6 (7.0)
Tiger puffer (Mie)	5.1 (6.5)
Kuruma prawn (Western Japan)	2.8 (4.5)
Mud crab (Urado Bay)	0.9 (0.7)
Abalone (Japan coasts)	12.2 (8.1)
Japanese scallop (Okhotsk Sea)	34.5 (10.2)
Sea urchin (Hokkaido)	18.2 (17.5)
Posterior mean	**8.2 (4.7)**

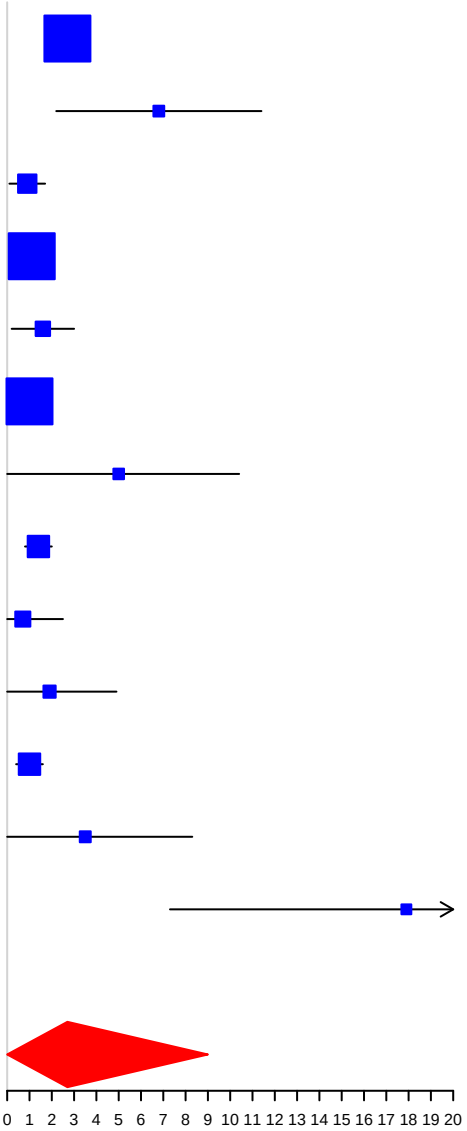


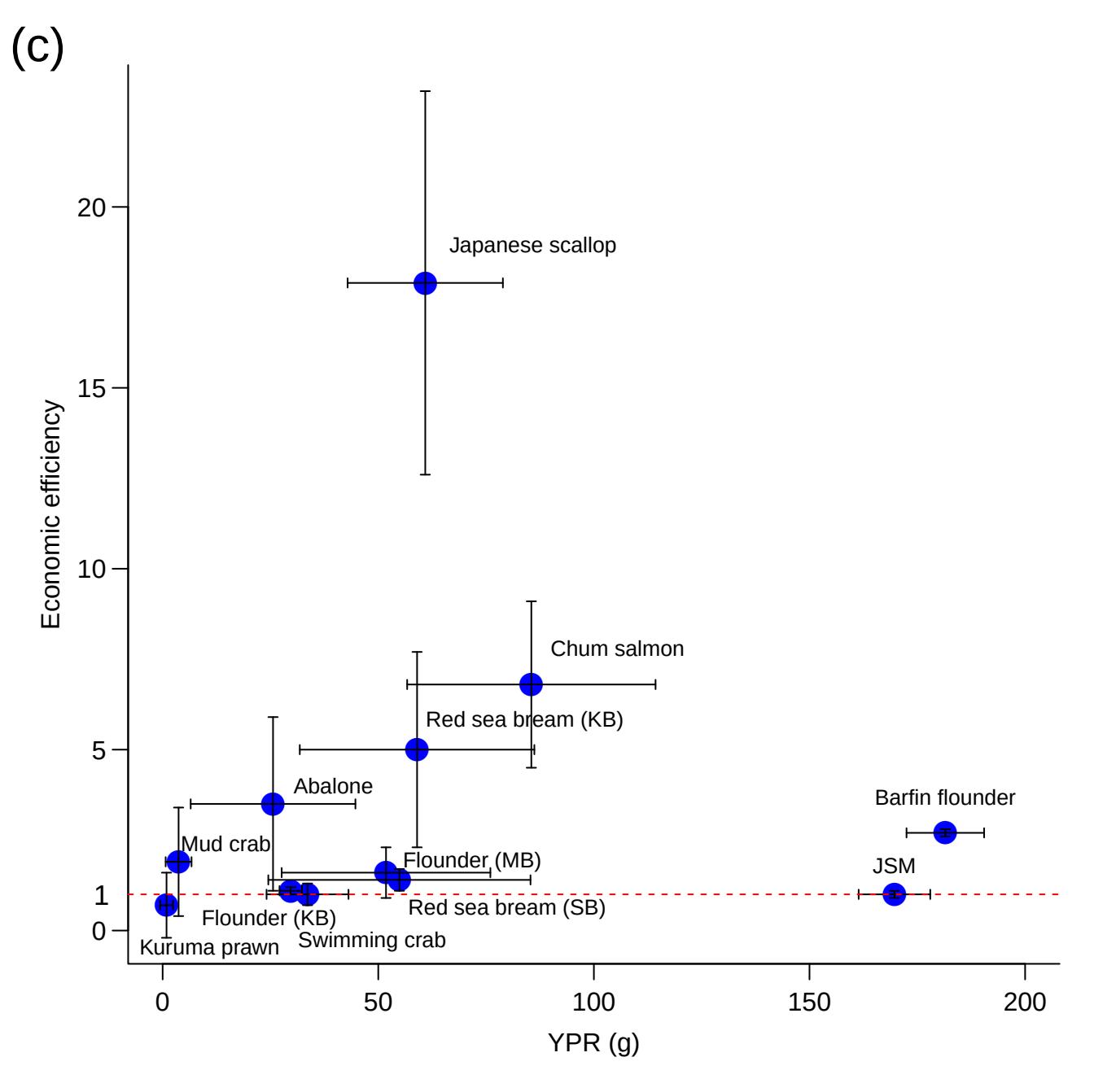
Species	YPR (g) Mean (SD)
Barfin flounder (Hokkaido)	181.5 (9.0)
Chum salmon (Hokkaido, Honshu)	85.5 (28.8)
Japanese flounder (Kagoshima Bay)	29.7 (2.6)
Japanese flounder (Miyako Bay)	51.8 (24.2)
Japanese Spanish mackerel (SIS)	169.7 (8.3)
Red sea bream (Kagoshima Bay)	59.0 (27.2)
Red sea bream (Sagami Bay)	54.9 (30.4)
Kuruma prawn (Western Japan)	0.9 (1.5)
Mud crab (Urado Bay)	3.7 (3.0)
Swimming crab (SIS)	33.6 (9.5)
Abalone (Japan coasts)	25.6 (19.1)
Japanese scallop (Okhotsk Sea)	60.9 (18)
Posterior mean	**63.1 (71.0)**

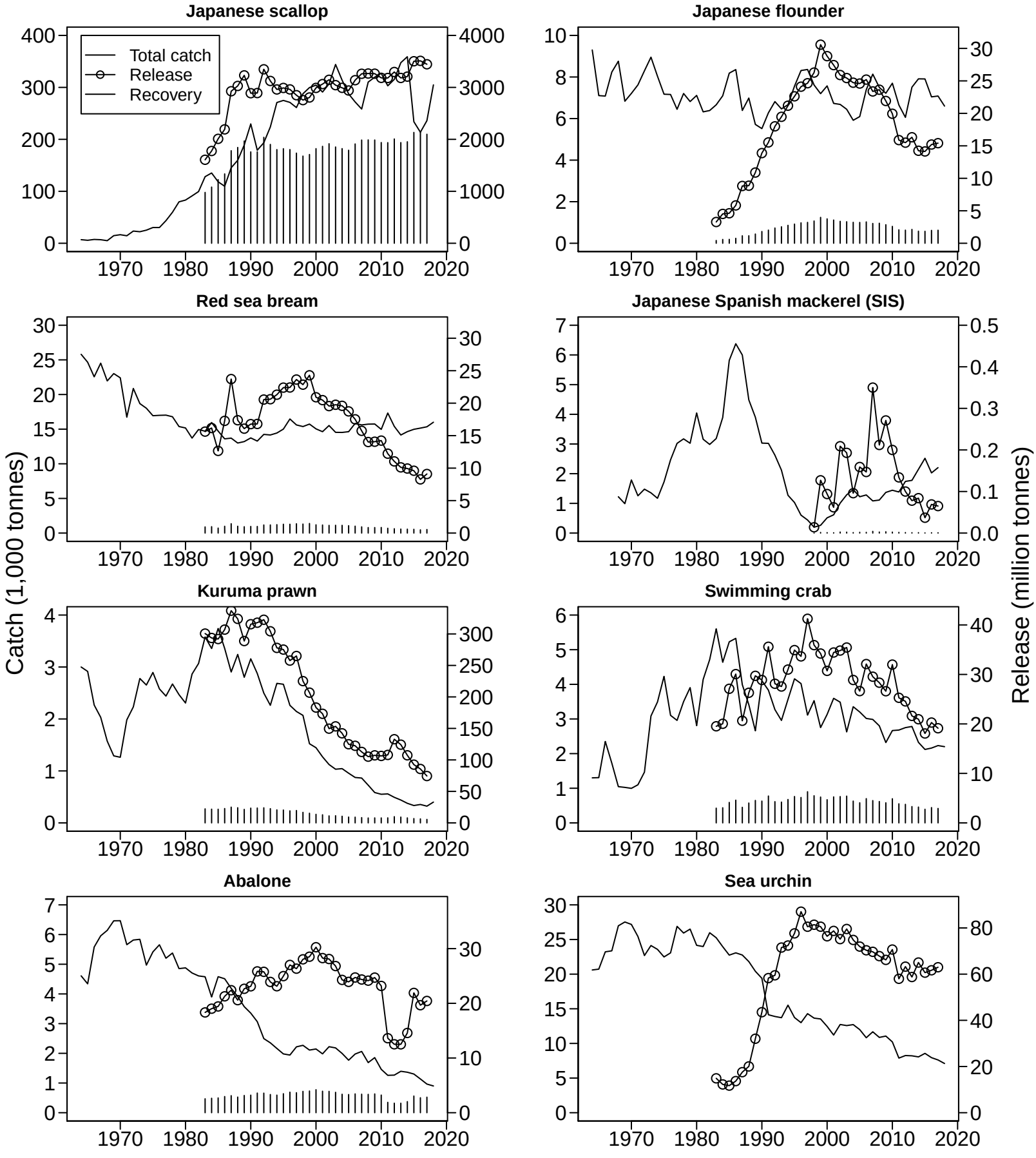


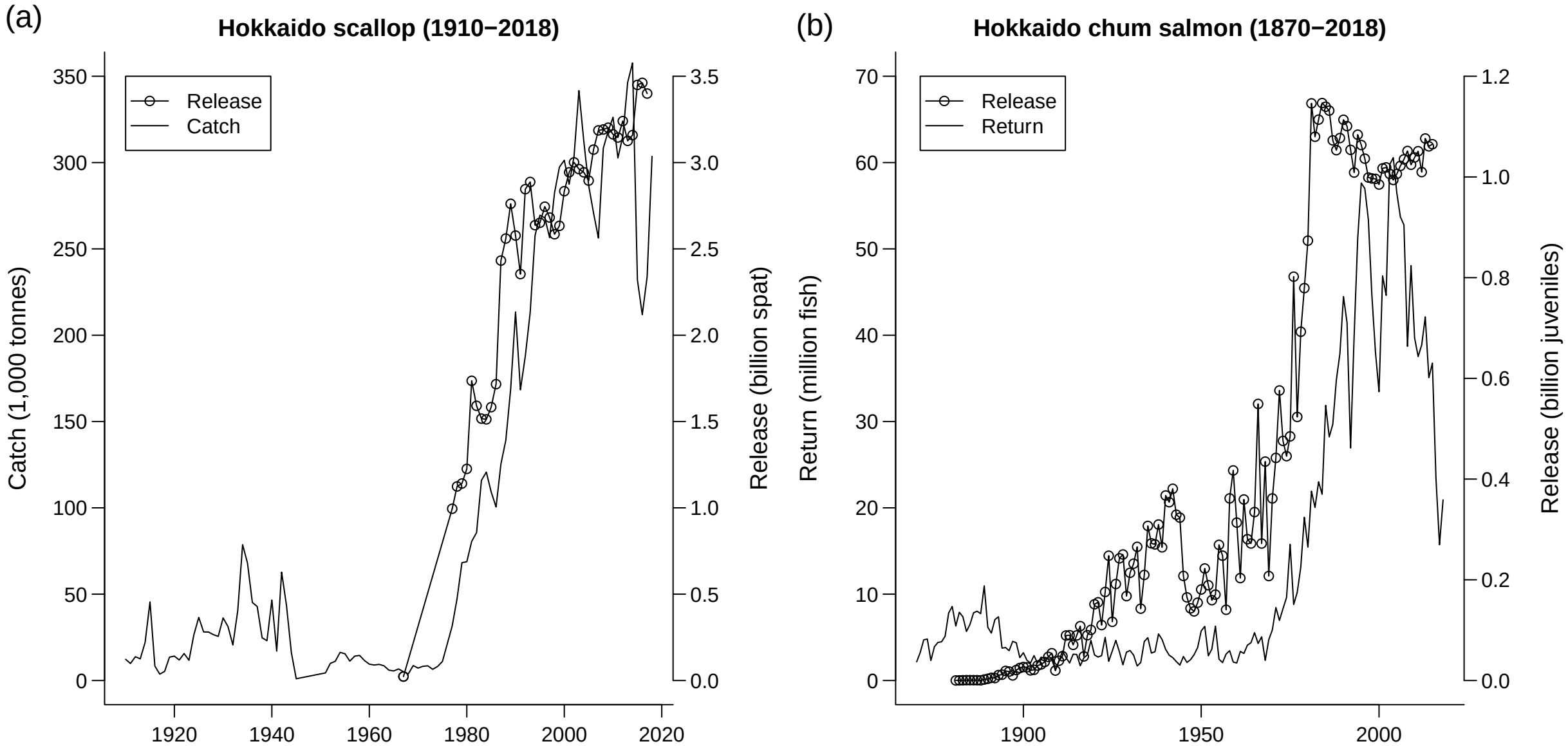
Economic efficiency

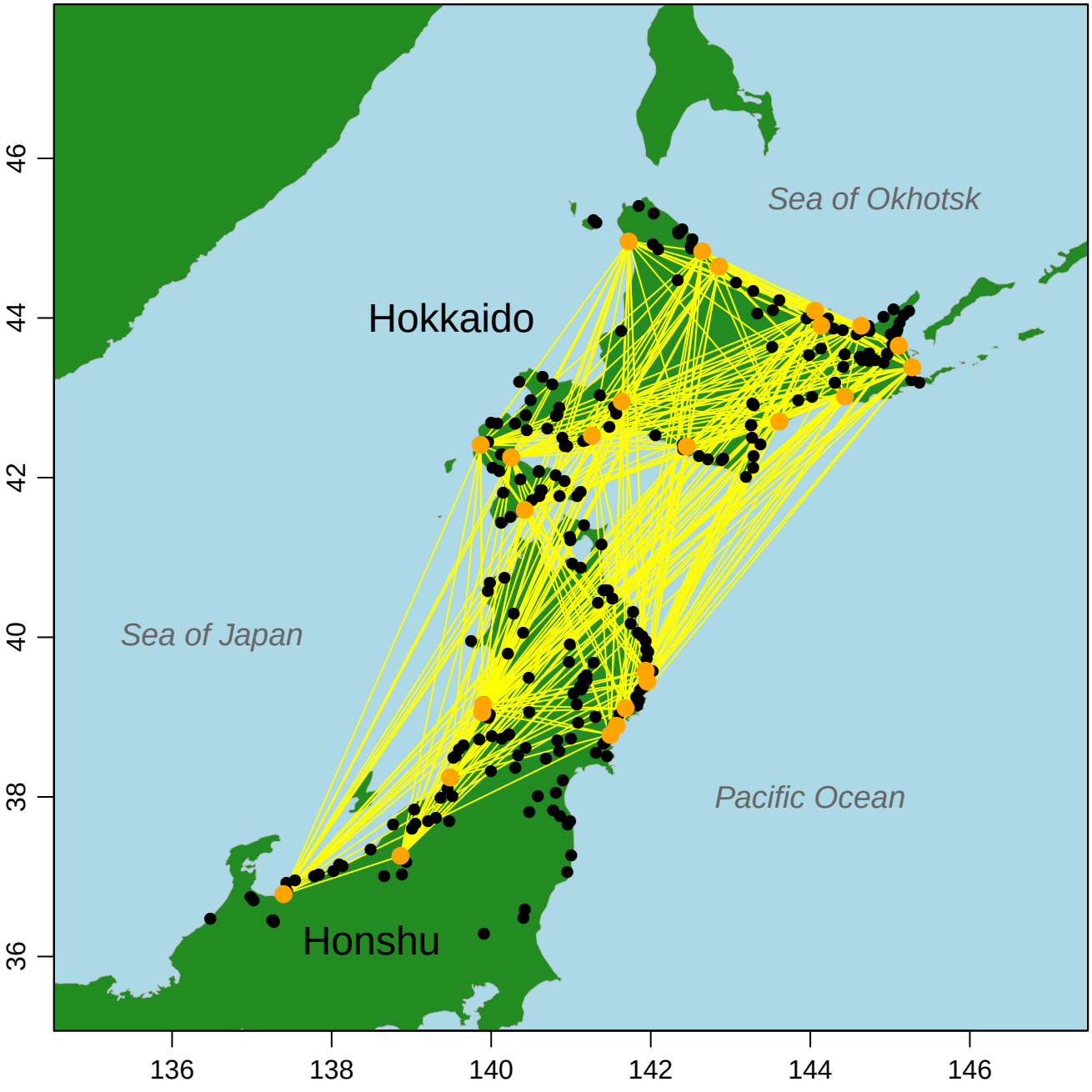
Species	Mean (SD)
Barfin flounder (Hokkaido)	2.7 (0.1)
Chum salmon (Hokkaido, Honshu)	6.8 (2.3)
Japanese flounder (Fukushima94_02)	0.9 (0.4)
Japanese flounder (Kagoshima Bay)	1.1 (0.1)
Japanese flounder (Miyako Bay)	1.6 (0.7)
Japanese Spanish mackerel (SIS)	1.0 (0.1)
Red sea bream (Kagoshima Bay)	5.0 (2.7)
Red sea bream (Sagami Bay)	1.4 (0.3)
Kuruma prawn (Western Japan)	0.7 (0.9)
Mud crab (Urado Bay)	1.9 (1.5)
Swimming crab (SIS)	1.0 (0.3)
Abalone (Japan coasts)	3.5 (2.4)
Japanese scallop (Okhotsk Sea)	17.9 (5.3)
Posterior mean	**2.7 (4.5)**




(c)
Economic efficiency
YPR (g)
0
1
5
10
15
20
0
50
100
150
200
Japanese scallop
Chum salmon
Red sea bream (KB)
Abalone
Barfin flounder
Mud crab
Flounder (MB)
JSM
Red sea bream (SB)
Flounder (KB)
Swimming crab
Kuruma prawn


Japanese scallop
Total catch
Release
Recovery
Japanese flounder
Red sea bream
Japanese Spanish mackerel (SIS)
Kuruma prawn
Swimming crab
Abalone
Sea urchin
Catch (1,000 tonnes)
Release (million tonnes)


(a)
Hokkaido scallop (1910−2018)
Release
Catch
Catch (1,000 tonnes)
Release (billion spat)
0
50
100
150
200
250
300
350
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
1920
1940
1960
1980
2000
2020
(b)
Hokkaido chum salmon (1870−2018)
Release
Return
Return (million fish)
Release (billion juveniles)
0
10
20
30
40
50
60
70
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1900
1950
2000


Sea of Okhotsk
Hokkaido
Sea of Japan
Pacific Ocean
Honshu
46
44
42
40
38
36
136
138
140
142
144
146