Fitness decline in hatchery-enhanced salmon populations is manifested by global warming

Running head: Hatchery-climate interaction and fitness

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Despite historical maximum hatchery releases and biomass of chum salmon in the North Pacific, chum salmon returning to Japan, where the world largest chum salmon hatchery programme runs, have declined substantially for two decades. However, the causal mechanisms are unknown. We analysed catch/release data of chum salmon and SST in Japanese coastal waters, and synthesized LDH (lactate dehydrogenase) and PEPB (tripeptide aminopeptidase) gene frequencies of 21,911 adult chum salmon collected from 166 rivers and areas in the North Pacific Rim. We also evaluated athletic performance of Japanese chum salmon in comparison with foreign salmon populations on social network videos. We found significant negative correlation between the average SST for spring and summer and total catch of Japanese chum salmon (r=-0.77), and 59% of the variation in the decreasing catch was explained by the increasing SST. Frequencies of the thermal adaptation genes LDH-A1 and LDH-B2 were altered disregarding with directions of natural selection which eventually lead hatchery fish to adapt to colder environments, while those of the digestive gene PEPB-1 were positively correlated with latitude. Because LDH-A and LDH-B are found in skeletal and cardiac muscles, this change may have lowered the survival rates particularly for juveniles and growth of Japanese chum salmon. We argue that the long-term hatchery releases have reduced the athletic ability of hatchery fish, resulting in a continuous decline in fitness of whole populations. A genetic mechanism of fitness decline in hatchery-enhanced salmon populations is first manifested by global warming at the southern margin of the species.

Keywords: allozyme gene frequencies, hatchery, LDH, PEPB, Pacific salmon

1 | INTRODUCTION

Release of hatchery-reared animals is one of the popular tools for fishery management (Laikre, Schwartz, Waples, & Ryman, 2010) and more than 26 billion juveniles of 180 marine species are released into the wild annually (Kitada, 2018). Evidence for reduced fitness of hatchery-reared fish in the wild and altered age and size at maturation is a serious reason for caution in hatchery stocking (Araki, Cooper, & Blouin, 2007, 2009; Bolstad et al., 2017; Fleming et al., 2000; McGinnity et al., 2003; Reisenbichler & McIntyre, 1977; Reisenbichler & Rubin, 1999). However, there has been no empirical evidence for reduced fitness in wild populations caused by hatchery releases (Kitada, 2018). Decreased time duration of spawning in natal freshwater habitat (Cline, Ohlberger, & Schindler, 2019) and advanced spawning dates by 1–3 weeks (Tillotson, Barnett, Bhuthimethee, Koehler, & Quinn, 2019) were found for sockeye salmon. The results suggested that artificial selection in hatcheries might drive maladaptation to climate change and act to opposite directions of natural selection (Tillotson, Barnett, Bhuthimethee, Koehler, & Quinn, 2019). However, mechanisms for hatchery-climate interactions on fitness largely remain unknown. Understanding thermal adaptation is a challenging theme and active studies are currently performed (Chen, Farrell, Matala, & Narum, 2018). Here, we focus on declining hatchery-enhanced Japanese chum salmon (*Oncorhynchus keta*, Salmonidae) populations at the southern margin of the species range to elucidate the mechanisms for fitness decline in warming environment.

Chum salmon hatchery stocking represents one of the world's major marine stock enhancement and sea-ranching programmes (Kitada, 2018). Around 60% of chum salmon in the North Pacific are of hatchery origin (Ruggerone & Irvine, 2018). Japanese chum salmon stocking, initiated in the late 1880s, is the world's largest hatchery release

programme (Amoroso, Tillotson, & Hilborn, 2017; Kitada, 2018; Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013). Releases of chum salmon juveniles from ~260 salmon hatcheries in Japan has increased remarkably since the 1970s to ~1.5 billion in 2018 (Figures S1, S2). The numbers of chum salmon returning to Japan sharply increased after the 1970s, but steeply decreased since 1996 when the catch recorded the historical maximum of 81 million fish, despite the continuous efforts of hatchery releases.

In Japanese chum salmon hatcheries, eggs and sperm are taken artificially from parent fish collected in the enhanced rivers (Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013). Fertilized eggs are kept undisturbed in hatcheries, avoiding vibration, until hatching (http://salmon.fra.affrc.go.jp/zousyoku/sakemasu.html). Rearing water temperature is kept stable ~8°C on average, which mimics temperature of spring water near redds, while the mean water temperature is much lower in the natural stream for this period; it ranged 1.1–2.8°C in the tributary of Ishikari River, Hokkaido (Ando et al., 2014). Hatching begins when the accumulated temperature reaches 480 degrees (~two months after fertilisation). Hatched larvae (BL ~19mm, BW ~0.05g) emerge (BL ~38mm, BW ~0.28g) 40 days after and grow to fry (BL ~43mm, BW ~0.69g) two months after hatching (Kaeriyama, 1986). They are fed to the size at release (BL ~50mm, BW ~1g) in rearing ponds during January and May until sea water temperature exceeds 5 °C (https://www.hro.or.jp/list/fisheries/marine/o7u1kr000000dc2m.html). Rearing duration primarily depends on rearing temperature, but juveniles are reared for more than six months in hatcheries. Survival rates are very high, usually >90%.

Since the early 1980s, efforts to increase the early-run population have caused changes in run timing distribution and the late-run populations have almost disappeared in

Hokkaido (Miyakoshi, Nagata, Kitada, & Kaeriyama, 2013), the major production area producing more than 80% of Japanese chum salmon. The past transplantation history of Japanese chum salmon populations has altered population structures with some populations nested within management units (Beacham, Sato, Urawa, Lei, & Wetklo, 2008; Kitada, 2014). Unintended and intended artificial selection in hatcheries can relax natural selection and reduce fitness of hatchery-reared salmonids in the wild (Araki, Cooper, & Blouin, 2007, 2009; Fleming et al., 2000; McGinnity et al., 2003; Reisenbichler & McIntyre, 1977; Reisenbichler & Rubin, 1999). Genetic adaptation to hatchery environments may occur within a single generation or early generations of hatchery fish (Christie, Marine, French, & Blouin, 2012; Christie, Marine, Fox, French, & Blouin, 2016; Le Luyer et al., 2017). Moreover, hatchery environments favour certain genotypes; when hatchery broodstock is introgressed by farmed escapees, farmed genotypes associated with domestication are amplified in the stocked population (Hagen et al., 2019). Because all chum salmon returning to Japan could be hatchery-released fish or wild-born hatchery descendants after long-term hatchery operations (Kitada, 2018), historical releases may have selected genes adapted to hatchery environment.

Allozyme markers were used to study the population genetics of chum salmon during the 1970s and the 1990s. Here, we focus on LDH (lactate dehydrogenase) as candidate gene markers by which underlying physiological adaptations were pinpointed (Chen, Farrell, Matala, & Narum, 2018). White skeletal muscle, whose metabolism is predominantly anaerobic expresses the Ldh-A locus, while red muscle, which possesses significant aerobic metabolism, expresses almost exclusively Ldh-B (Somero, 2004). The A_4-LDH gene works principally in the conversion of pyruvate to lactate (i.e., anaerobic glycolysis), while B_4-LDH principally converts lactate to pyruvate (i.e.,

gluconeogenesis and aerobic metabolism) (Somero, 2004, 2010; Powers, Lauerman, Crawford, & DiMichele, 1991). We also analyse PEPB (tripeptide aminopeptidase) because the aminopeptidase PEPB is a digestive enzyme of fish (Govoni, Boehlert, & Watanabe, 1986), which may relate to selection in hatcheries.

2 | DECLINING JAPANESE CHUM SALMON POPULATIONS

Catch and release data were retrieved from the statistics of North Pacific Anadromous Fish Commission (NPAFC, 2019). Simple return rates (number of returned fish after four years /number of released juveniles) in Hokkaido and Honshu were cited from FRA (http://salmon.fra.affrc.go.jp, accessed August, 2019). Major components of returned fish were age 3-age 6 fish and age 4 was the largest in proportions. The simple return rate therefore is an expectation of the true return rate throughout their lives. Spring, summer, autumn and winter sea surface temperature (SST) data for Kushiro-oki (Hokkaido Pacific coast), Hokkaido Sea of Japan coasts, Sanriku-oki (Honshu Pacific coast) and Honshu Sea of Japan coasts were retrieved from Japan Meteorological Agency (http://www.data.jma.go.jp/kaiyou/shindan/index_gw.html, accessed August, 2019). We averaged SST over the four areas for each season and for spring and summer. Exponential curves were fitted to the simple return rates for Hokkaido and Honshu during 1996 and 2018, respectively. The linear regression analyses between the numbers of chum salmon returning to Japan and the SST anomaly were performed using the lm function. We also fitted an exponential curve to the salmonid relative reproductive success (RRS) data (Araki, Cooper, & Blouin, 2007) and estimated the coefficients using the nls function. We calculated mean body weights of chum salmon returning to Japan for each year between 1975 and 2018 by dividing the catch weight by the number of returned fish, based on the catch statistics of NPAFC. All analyses were

performed and figures were created using R statistical software (https://www.r-project.org/). All data used for the analyses were included in Supplementary Data excluding easy-accessible NPAFC salmon statistics.

The catch of chum salmon in Japan steeply decreased, while the total catch remained high in the North Pacific (Figure 1a). A significant exponential decline in return rates was found for Hokkaido and Honshu (Figure 1b, $t = -5.52, p = 0.0082;\ t = 3.69, p = 0.0014$, respectively). The exponential rate of decline in Honshu was about twice that in Hokkaido, suggesting that the warming effect was stronger in southern Japan (Table 1), but there was no significant difference between them, with a combined average of 3.1 ± 0.9% per year ($z = 0.983$, $p = 0.1627$). The exponential decay rates of chum salmon were much lower than that of the red sea bream (Kitada et al, 2019), and of RRS of captive-reared salmonids (Araki, Cooper, & Blouin, 2007) (Table 1). Regression analysis combining Hokkaido and Honshu indicated that the average sea surface temperature (SST) anomaly over northern Japan was negatively correlated with the overall decrease in the Japanese catch of chum salmon (1996–2018) ($r = -0.67$) (Table 2). Interestingly, the average SST in spring (April–June) and summer (July–September) was highly correlated with the catch, while in autumn and winter there was no significant correlation. The correlation between the average SST for spring and summer and total catch was much higher ($r = -0.77, \mathrm{t} = -5.52, \mathrm{df} = 21, \mathrm{p} = 1.76 \times 10^{-5}$), and 59% of the variation in decreasing chum salmon catch was explained by the increasing spring and summer SST anomaly (Figure 1c).

The number of chum salmon returned and caught was the largest in the Sea of Okhotsk and the Pacific coast of northern Japan that was affected by the cold Oyashio current

particularly in Iwate Prefecture in 1996 when the catch in Japan recorded the historical maximum of 81 million (Figure 2), showing that chum salmon abundance was rich in the cold waters. In contrast, they were very small on the Sea of Japan coast that is affected by the Tsushima warm current and the southern Pacific coast. In 2006, populations in the Pacific coast of Honshu were rapidly decreased. In contrast, decreases in the Pacific coast of Hokkaido were not substantial and even high in the Sea of Okhotsk. However, substantial declines occurred in all areas in 2014, which further shrunk in 2017. On the other hand, numbers of chum salmon released were stable for the two decades in whole Japan (Figure 3). The mean body weights of chum salmon returning to Japan have continued to decrease since 2004 (Figure S3).

3 | THERMAL ADAPTATION AND DIGESTIVE GENE FREQUENCIES

We screened scientific literature, using the Google Scholar online database search system to collect publications using keyword searches of "salmon", "allozyme", "LDH" and "PEPB". Studies known to us were also manually screened. We found studies including gene frequencies of LDH-A1, LDH-B2 and PEPB-1 in the Pacific Rim including whole Japan (Kijima, & Fujio, 1979; Okazaki, 1982), Russia, Alaska, British Columbia and Washington (Seeb, Crane, & Gates, 1995; Winans, Aebersold, Urawa, & Varnavskaya, 1994). We organized frequencies of LDH-A1, LDH-B2 and PEPB-1 genes and recorded approximate longitudes and latitudes of the sampling sites based on the names of rivers and/or areas and maps of the original studies using Google Maps. Maps were drawn using the sf package and sampling points were located on the maps. The allele frequency for *i*th sampling point (x_i) was visualized by colour gradients in the data range based on: $\mathrm{rgb}(1 - y_{0,i}, 0, y_{0,i})$, where $y_{0,i} = (x_{0,i} - a)/(b - a)$ and $x_{0,i} = pmin(pmax(x_i, a), b)$. We set a=0.7 and b=1.0 for LDH-A1, and a=0.6 and

b=1.0 for LDH-B2 and PEPB-1, considering the ranges of the gene frequencies. This conversion visualizes the magnitude of the gene frequencies at the sampling point in colours between blue and red on the map.

The gene frequencies of 21,911 adult chum salmon from 21 Russian rivers and 81 Japanese rivers (including the same rivers analysed in different studies) were organized, and 64 rivers and areas in America (Figure 4). The Japanese samples were caught at weirs in enhanced rivers and hatcheries (Kijima & Fujio, 1979; Okazaki, 1982) and were, therefore, hatchery-reared fish and/or hatchery descendants, while the Russian samples were collected by stream surveys and were expected to be wild fish because the majority of Russian chum salmon are maintained by wild fish (Winans, Aebersold, Urawa, & Varnavskaya, 1994). Samples collected from hatcheries were excluded in samples from Alaska, Alaskan Peninsula, British Columbia and Washington (Seeb, Crane, & Gates, 1995). The American samples were collected during 1986 and 1994, when the numbers of released chum salmon were low and similar the levels in Russia (Figure S1a). It is possible that some hatchery fish were included in the American samples, but the numbers would have been low.

In the Russian and American samples, we found a clear geographical cline from south to north in the LDH-A1 gene frequencies, and a negative correlation with latitude ($r = -0.44, \mathrm{t} = -4.07, \mathrm{df} = 71, \mathrm{p} = 0.000$) (Figure 5a, b). In the southern samples from Washington and British Columbia, LDH-A1 gene frequencies were close to or exactly 1.0, while those from the Alaskan Peninsula were generally <0.95, and <0.8 in Alaska. The outlier (0.63) in American samples was from the almost closed Peterson Lagoon, Alaska (#148 in Fig. 3b). Alaska and Kamchatka had a similar range of gene

frequencies of around 0.7–0.9 (Figure 5a). Japanese samples exhibited similar variation to the Russian and Alaska ones at higher latitudes. The gene frequency varied largely among the Japanese samples but had a weak and positive correlation with latitude ($r = 0.27, \mathrm{t} = 2.63, \mathrm{df} = 89, \mathrm{p} = 0.001$). Its range corresponded to the range of the gene frequencies in Russia, Alaska and Canada (Figure 5a, b). The four outliers (#57, 97, 99, 101) were collected from the most southern coastal areas of the Sea of Japan (Figure 4d). In contrast, LDH-B2 gene frequencies were 1.0 or close to 1.0 for all samples (Figure 5c, d), except for those from eastern Queen Charlotte Islands, Canada (#157 in Figures. 4a, 5c) that are affected by the warm Alaska Current, and had the lowest gene frequency (0.95). Almost all Russian samples from Kamchatka had slightly lower gene frequencies than the others. Japanese samples had similar LDH-B2 gene frequencies to those of the northern populations. In contrast, PEPB-1 gene frequencies were positively correlated with latitude (Figure 5e, f).

4 | ATHLETIC PERFORMANCE OF JAPANESE CHUM SALMON: A VISUAL EVALUATION

We searched videos on the internet which could show athletic performance of Japanese chum salmon and other salmonid species from a social network “youtube”. We analysed nine videos, of which four were on chum salmon from Hokkaido and fives were from the Pacific Northwest, Alaska and England. In Okushibetsu River, Shiretoko, Hokkaido, is an enhanced river, where thousands of chum salmon return every year (The Hokkaido Shimbun Press, 2017). Almost fish were caught at the weir located ~500 m from the sea and many were used for artificial fertilization in the hatchery. There are ~1,500 rivers in Hokkaido and 238 rivers have lengths longer than 8 km. Hatchery releases of chum salmon are operated in 140 major rivers and no hatchery is operated in small rivers

(Miyakoshi et al., 2013). Japanese chum salmon moved slowly. In contrast, sockeye salmon moved vividly and went up the Hansen Creek to spawn (Taylor, 2014). Jumping trials of returned Japanese chum salmon at a small fall, Hokkaido, Esashi Town facing the Sea of Okhotsk (Sapporo TV House Stock Footage, 2015), resulted in no success for 64 jumps excluding two jumps which were difficult to judge. When we counted the two jumps as succeeded ones, the rate of success was 3.0% (=2/66). At another small fall in northern Hokkaido (Kawamura, 2008), the success was one out of 47 jumps (success rate=2.1%). At a small weir in Hamamasu River, Hokkaido (Onishi, 2009), only one chum salmon succeeded for 219 jumps (success rate=0.5%). These small rivers had no hatchery, therefore they were strayed hatchery fish or natural-born fish in the rivers. Chum salmon are very powerful swimmers even swimming across roads during floods on the coast and along Puget Sound (Allison, 2016). The success rate of jumping was 15% (=10/66) for sockeye salmoln (*O. nerka*, Salmonidae) in Katmai National Park, Alaska (WallnerPhotos, 2014), 33% (=2/6) for coho salmon (*O. kisutch*, Salmonidae) in Lagunitas, California (Turtle Island Restoration Network, 2015) and 50% (=13/26) for Atlantic salmon (*Salmo salar*, Salmonidae) in England (JettyBox Stock Video, 2015), respectively. All species had much higher athletic performance for jumping and upstreaming than Japanese chum salmon even in the stronger streams.

5 | DISCUSSION

A previous study found that ~30% of variation in the decreasing catches of Japanese chum salmon was attributed to the increasing annual average SST anomaly (1996–2016), and that 62% of the variation in Russian catches was explained by the SST (Kitada, 2018). However, earlier tagging studies revealed that there were clear differences in the run timing and migration routes between Russian (June–August) and

Japanese (September–November) chum salmon populations (Kondo, Hirano, Nakayama, & Miyake, 1965; Morita, 2016). The fishing season for chum salmon begins in late August in Hokkaido with a high fishing season in September to October. In Honshu, the high season runs from October to November. The apparent differences in run timing and migration routes between Japanese and Russian chum salmon suggest that the majority of Japanese chum salmon are caught in Japanese coasts and rivers. Therefore, the negative correlation between Japanese and Russian catches reported in a previous study should be spurious. We found that warming SST in spring and summer negatively correlated with declining Japan chum salmon populations. Juvenile chum salmon (almost hatchery fish) migrate down to the sea in late winter to early summer and remain in coastal waters until early August (Ueno & Ishida, 1996). Reduced chum salmon returns could be caused by lower survival rates of juvenile stages in coastal waters from spring to summer with warming SST. Ages at return of Japanese chum vary between two and eight (http://salmon.fra.affrc.go.jp/zousyoku/sakemasu.html), therefore the average SST value over two to eight years before the year of return could affect the survival of juveniles. Indeed, the correlation between the eight year moving average SST for spring and summer and total catch was significant ($r = -0.55, \mathrm{t} = -3.03, \mathrm{df} = 21, \mathrm{p} = 0.006$), suggesting that the chum salmon decline was caused by reduced survival rates of juvenile stages in coastal waters from spring to summer with warming SST. Natural selection on released fish that are used for broodstock may be responsible for the lower exponential decay rate of chum salmon than that of the red sea bream (Kitada et al., 2019) and RRS of captive-reared salmonids (Araki et al., 2007) (Table 1). In contrast, a model-based prediction indicated that global warming decreased suitable areas of habitat in the North Pacific Ocean and loss of migration route to the Sea of Okhotsk, but positively affected growth and survival of Hokkaido

295 chum salmon populations (Kaeriyama, Seo, & Qin, 2014).

296

297 LDH-A-mediated reactions have the lowest energy requirement in most cold-adapted
298 species, and highest in most warm-adapted species (Somero, 2004), which agrees with
299 higher LDH-A gene frequencies of chum salmon in the lower latitudes. Because Japan
300 is located south of the other surveyed locations in Russia, Canada, and USA, a high
301 gene frequency close to 1.0, the value for British Columbia and Washington, is
302 predicted in this country. The values far below 1.0 may suggest substantial artificial
303 selection on the LDH-A1 gene. Population divergence for LDH measured by Q_{ST}
304 (=0.58) was greater than divergence measured by pairwise F_{ST} for microsatellite
305 markers (0-0.077) in brook trout populations (Dufresne, Barroux, DitleCadet, & Blier,
306 2015). The result indicated that that LDH has diversified more than neutral population
307 structure and significant plasticity of LDH for artificial selection (Whitlock, 2008). A
308 single amino acid substitution is sufficient to modify function and stability of
309 temperature adaptation of the LDH-A gene (Somero, 2004). An amino acid substitution
310 in the LDH-A gene, common in vertebrate skeletal (white) muscle, may occur, leading
311 to adaptation of hatchery-reared salmon to colder environments.

312

313 Furthermore, artificial selection in hatcheries slows movement of hatchery fish and
314 reduces agility for feeding in the wild. Indeed, mean body weights of chum salmon
315 returning to Japan have continued to decrease since 2004 (Figure S3). Intra-and
316 interspecific competition for food was very strong for chum salmon including other
317 salmonid species in the North Pacific (Kitada, 2018), supporting this speculation.
318 Rearing experiments (5°C and 9°C) for embryos and alevin of brook trout (*Salvelinus*
319 *fontinalis*, Salmonidae), cold adapted species, found that mass differences and routine

320 metabolic rate among fry were strongly influenced by population origins and rearing
321 temperatures (Cook, Wilson, & Burness, 2018). The water temperature (~8°C) for egg
322 hatching standardly used in Japan chum salmon hatcheries was much higher than that in
323 the natural stream. The artificial rearing condition with constant water temperature and
324 reduced vibration might alter the routine metabolic rate that needs low energy
325 requirement for LDH-A-mediated reactions as in most cold-adapted species.
326
327 The LDH-B2 gene frequencies in southern Hokkaido and Honshu were exactly 1.0
328 (Figures. 4d, 5c). The LDH-B2 gene frequencies of killifish (*Fundulus heteroclitus*,
329 Fundulidae) were correlated with the direction of change in mean water temperature.
330 They were well fitted to a sigmoid curve with values near 1.0 at latitude 44°N and 0.2–
331 0.8 at latitudes 36–42°N (Powers et al., 1991). LDH-B plays a key role in re-oxidizing
332 NADH to NAD^+ in low O_2 environment in redband trout (O. *mykiss gairdneri*,
333 Salmonidae) (Chen, Farrell, Matala, & Narum, 2018). Oxygen consumption in heart
334 ventricles was significantly greater in northern killifish populations than that in southern
335 populations, and the cardiac metabolism was significantly higher in populations from
336 cold climates than those from warm climates (Podrabsky, Javillonar, Hand, &
337 Crawford, 2000). These results consistently showed that LDH-B2 gene frequencies
338 were lower in southern populations and higher in northern populations. The LDH-B2
339 gene frequencies in Japan populations were 1.0, contrary to that expected in adaptation
340 to a warm-water environment, which might be caused by reduced heart (red muscle)
341 activity and athletic performance in hatchery fish. The videos were cited from
342 "youtube" with including only nine samples and not our observations. However, the
343 results agreed with our analyses, demonstrating weaker athletic performance of
344 Japanese chum salmon. In contrast, gene frequencies of PEPB-1 were positively

correlated with latitude. This agreed the population structure in the North Pacific based on microsatellite markers (Beacham et al., 2009), suggesting that hatchery operations did not compromise digestive ability.

Repeated hatchery operations substantially altered gene frequencies of thermally adapted LDH-A1 and LDH-B2 in Japanese chum salmon populations, which could be reflected in the reduced performance of skeletal and cardiac muscles. This may be a causal mechanism for fitness decline in Japan chum salmon populations. Altered distributions of the gene frequencies of LDH-A1 and LDH-B2 are likely to result from adaptation to hatchery environments, which eventually should lead hatchery fish to adapt to colder environments. Our results suggest that artificial and natural selection act in opposite directions on LDH-A1 and LDH-B2 but exert no selective pressure on the digestive enzyme PEPB-1. However, selection on LDH-A1 and LDH-B2 genes reduced survival rates in the wild in a warming environment, particularly for juveniles. Reduced agility for feeding could also reduce the growth of chum salmon. Reduced activity of cardiac muscle could affect their long-distance migrations. An overwhelming proportion of hatchery fish and hatchery descendants (Kitada, 2018) should reduce the fitness of whole populations. The hatchery operation has continued for ~25 generations, assuming 5 years per generation. After 40 years of domestication (30–35 generations) of wild foxes, 70%–80% became human-friendly, and all domesticated foxes that escaped for days returned to the farm (Trut, 1999). Apparently, ‘domesticated’ Japan chum salmon are now human-friendly and return to hatcheries each year (Figure S4). Fitness reduction in a hatchery-reared population is cohort-specific and constant over time within the cohort (Kitada et al., 2019), but it will continue as long as the current hatchery operations continue with a variation reflecting the environmental effects.

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AUTHOR CONTRIBUTIONS

S.K. and H.K conceived of the study, analysed the data and wrote the manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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SUPPORTING INFORMATION

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

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TABLE 1 Exponential decay rates of fitness in the wild for captive-bred fish.

Species	Estimate	SE	*t*	*p*	Source
Chum salmon (Hokkaido) †	0.022	0.007	2.93	0.0082**	This study
Chum salmon (Honshu) †	0.040	0.011	3.69	0.0014**	This study
Red sea bream†	0.156	0.017	9.02	0.0000***	Kitada et al., 2019
Salmonids RRS‡	0.365	0.058	6.27	0.0008**	Araki et al., 2007

† Return rate per year. ‡ Relative reproductive success per generation in captivity.

TABLE 2 Linear regression of chum salmon catches on SST anomaly.

Season†	Coefficient	Estimate	*SE*	*t*-value	*p*	R^2
Average	Intercept	59.9	3.24	18.5	0.000***	0.45
	SST	-28.1	6.72	-4.2	0.000***	
Winter	Intercept	51.8	3.25	15.9	0.000***	0.07
	SST	-8.2	6.74	-1.2	0.237	
Spring	Intercept	54.4	2.93	18.6	0.000***	0.32
	SST	-15.4	4.93	-3.1	0.005*	
Summer	Intercept	56.2	3.25	17.3	0.000***	0.30
	SST	-1.0	3.32	-3.0	0.007**	
Autumn	Intercept	54.0	4.50	12.0	0.000***	0.04
	SST	-6.8	6.97	-1.0	0.339	

† Winter; Jan.-Mar., Spring; Apr.-June, Summer; July-Sept., Autumn; Oct.- Dec.

Figure Legends

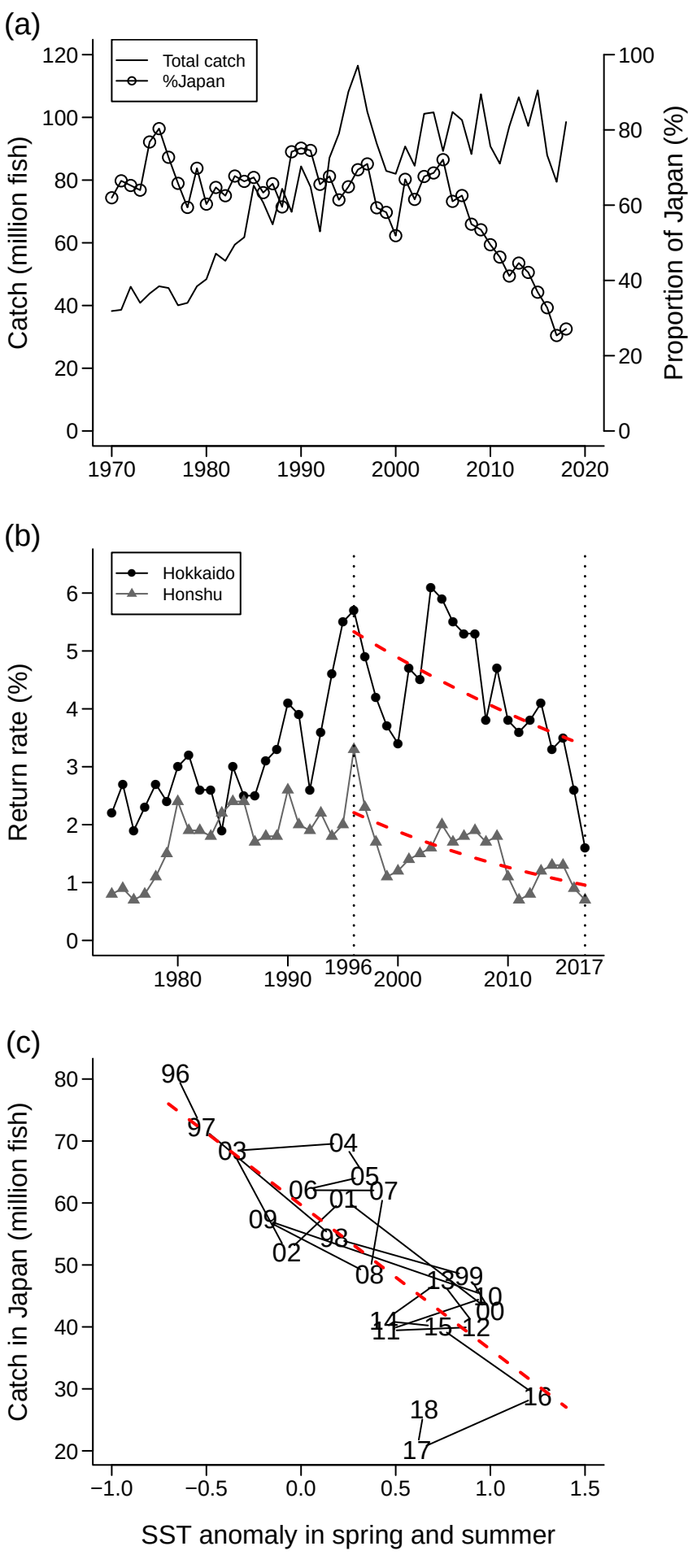
FIGURE 1 Chum salmon in the North Pacific. (a) Changes in the total catch of chum salmon in the North Pacific and the proportion of Japan. Data from North Pacific Anadromous Fish Commission, www.npafc.org accessed August 2019. (b) Return rates in Hokkaido and Honshu. Dotted lines show exponential curves fitted to return rates (1996-2017). (c) Mean SST anomaly for spring and summer in Hokkaido and the northern Honshu vs. number of adult fish returning to Japan, with estimated regression lines. Numbers on the graph indicate years. [The colour figure can be viewed at wileyonlinelibrary.com]

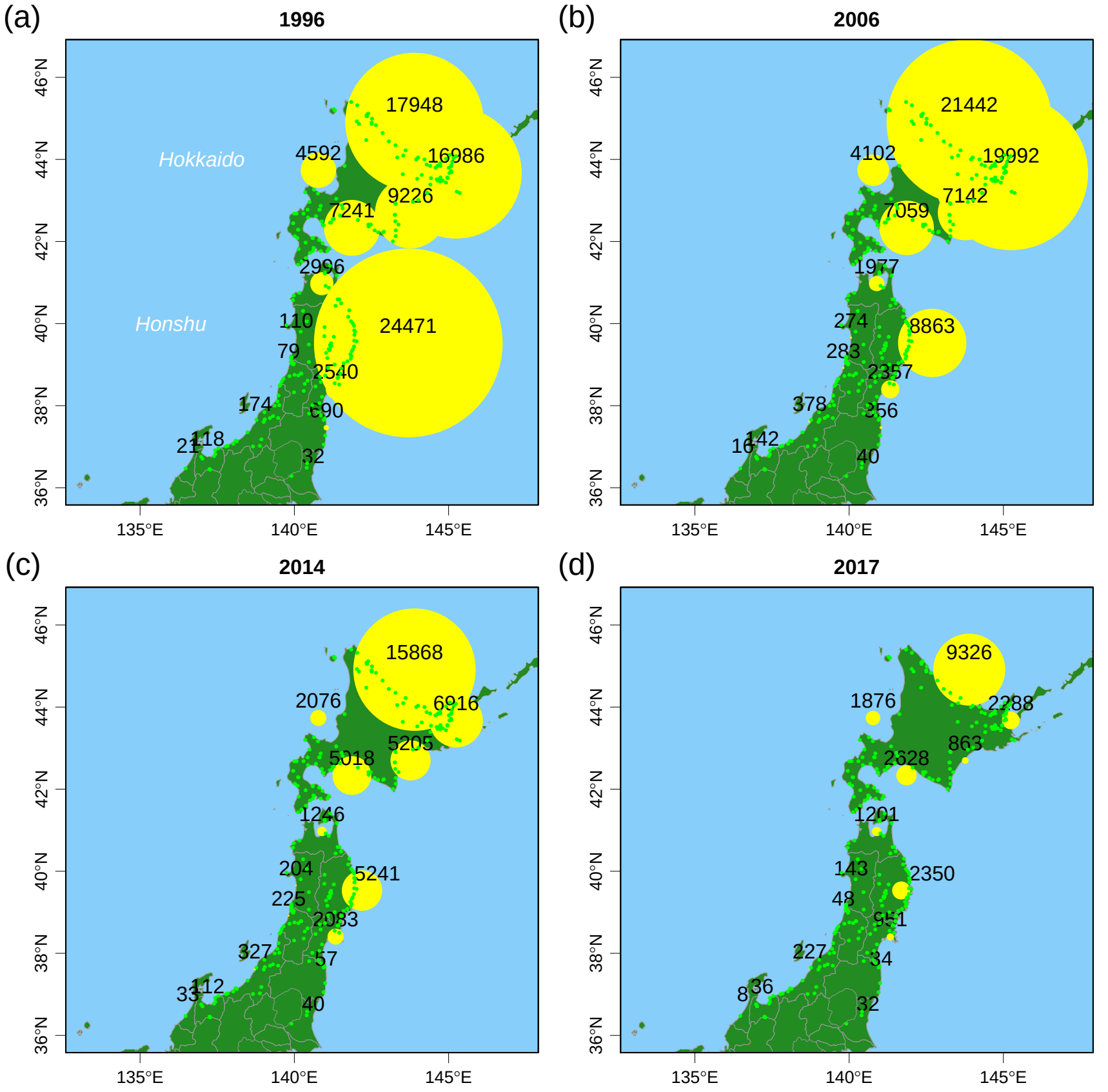
FIGURE 2 Changes in number of chum salmon returned to Japan in recent two decades. (a) 1996 with the historical maximum catch. (b) 2006. (c) 2014. (d) 2017 (latest statistics). The numbers show chum salmon returned in thousand. The sizes of the circle are proportional to the numbers. Green dots show hatcheries (Figure S2).

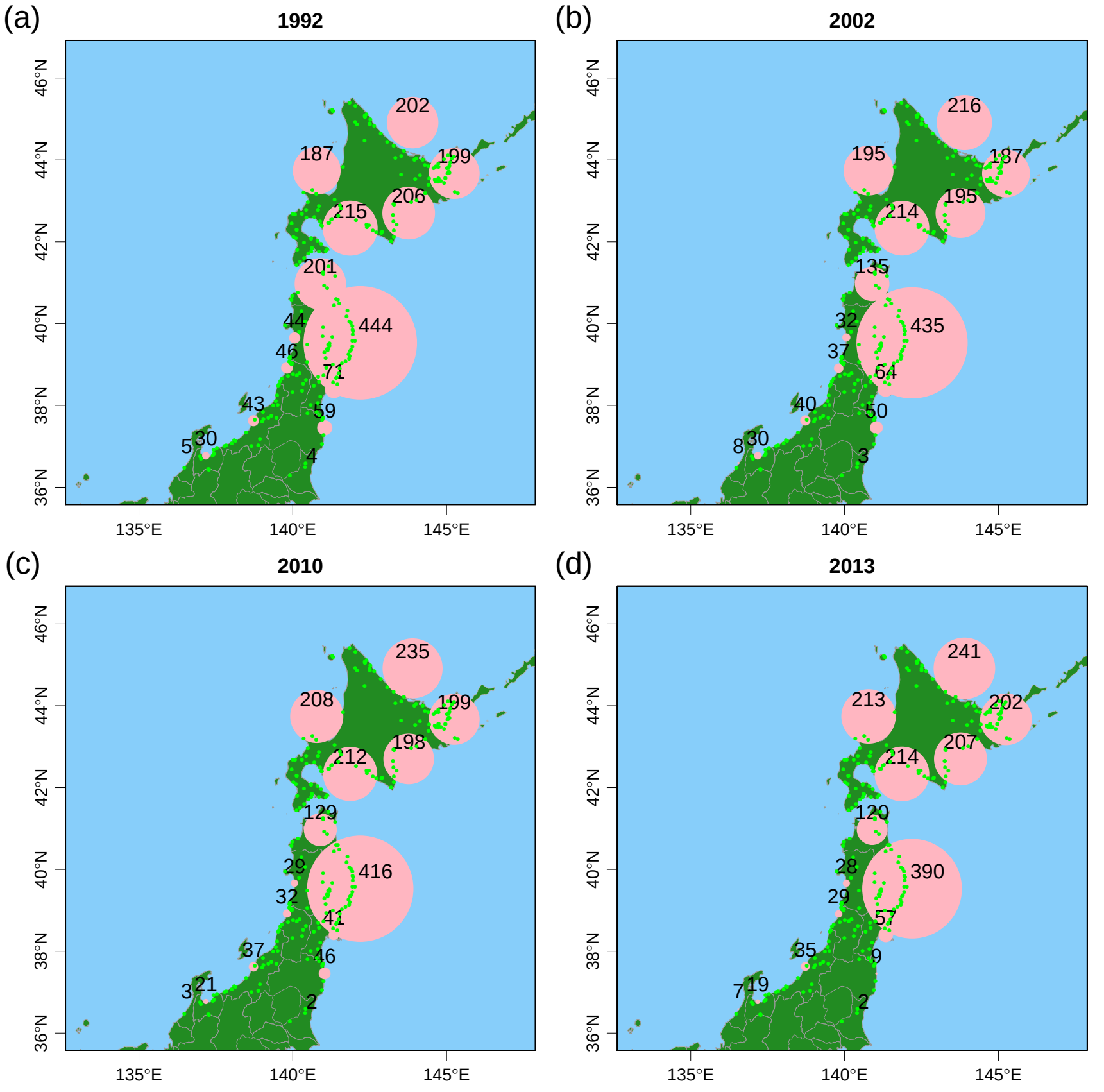
FIGURE 3 Changes in number of chum salmon released in Japan in recent two decades. (a) 1992. (b) 2002. (c) 2010. (d) 2013. The number show chum salmon released in million. The sizes of the circles are proportional to the numbers. The years were four years before ones for catches in Figure 2. Green dots show hatcheries (Figure S2).

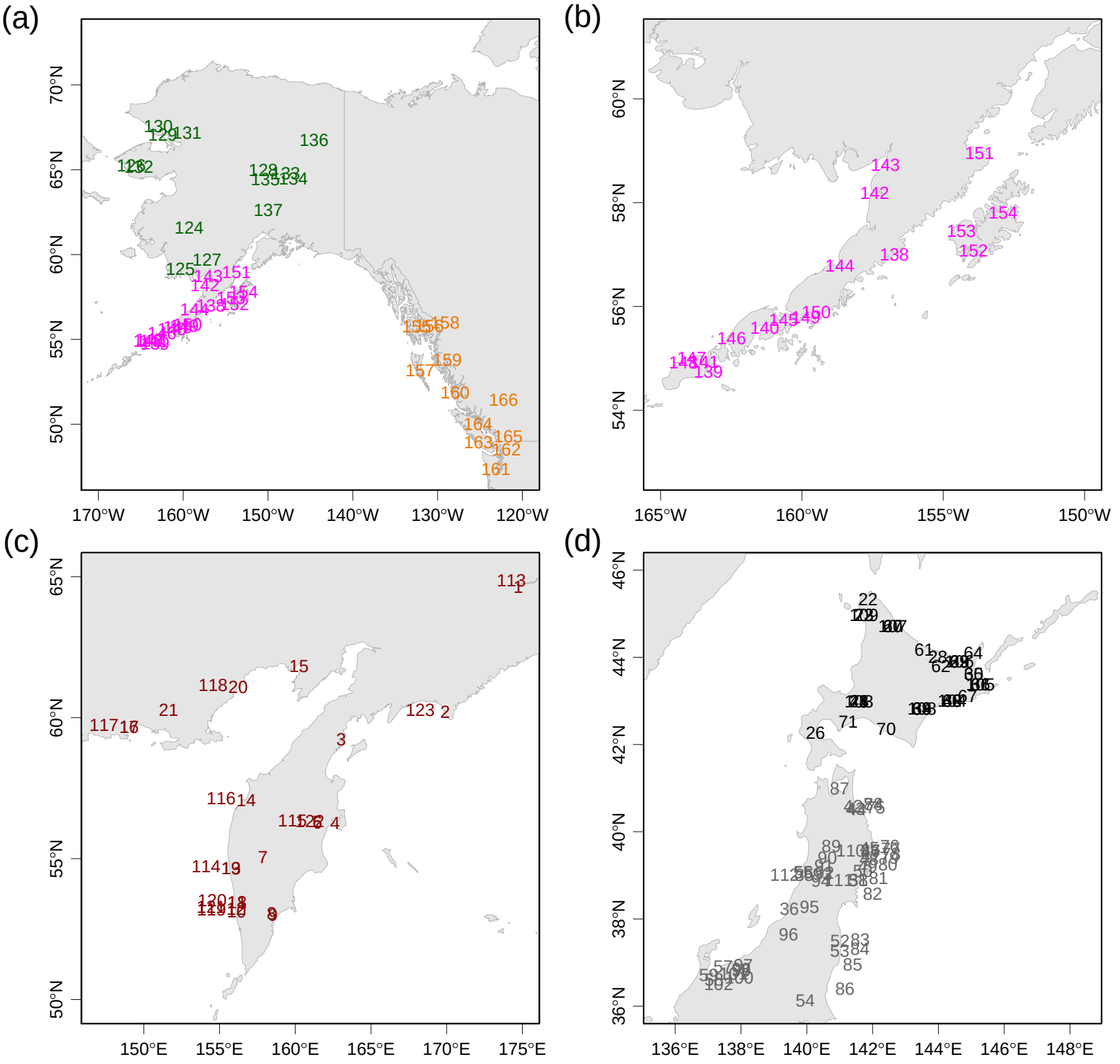
FIGURE 4 Locations for chum salmon allozyme gene frequencies across the Pacific Rim (*n*=166). (a) Alaska, British Columbia and Washington. (b) Alaska Peninsula. (c) Russia. (d) Japan. Numbers and names of the locations and gene frequencies were given in Supplementary Data. Data from the original study (Kijima, & Fujio, 1979; Okazaki, 1982; Winans, Aebersold, Urawa, & Varnavskaya,1994; Seeb, Crane, & Gates, 1995).

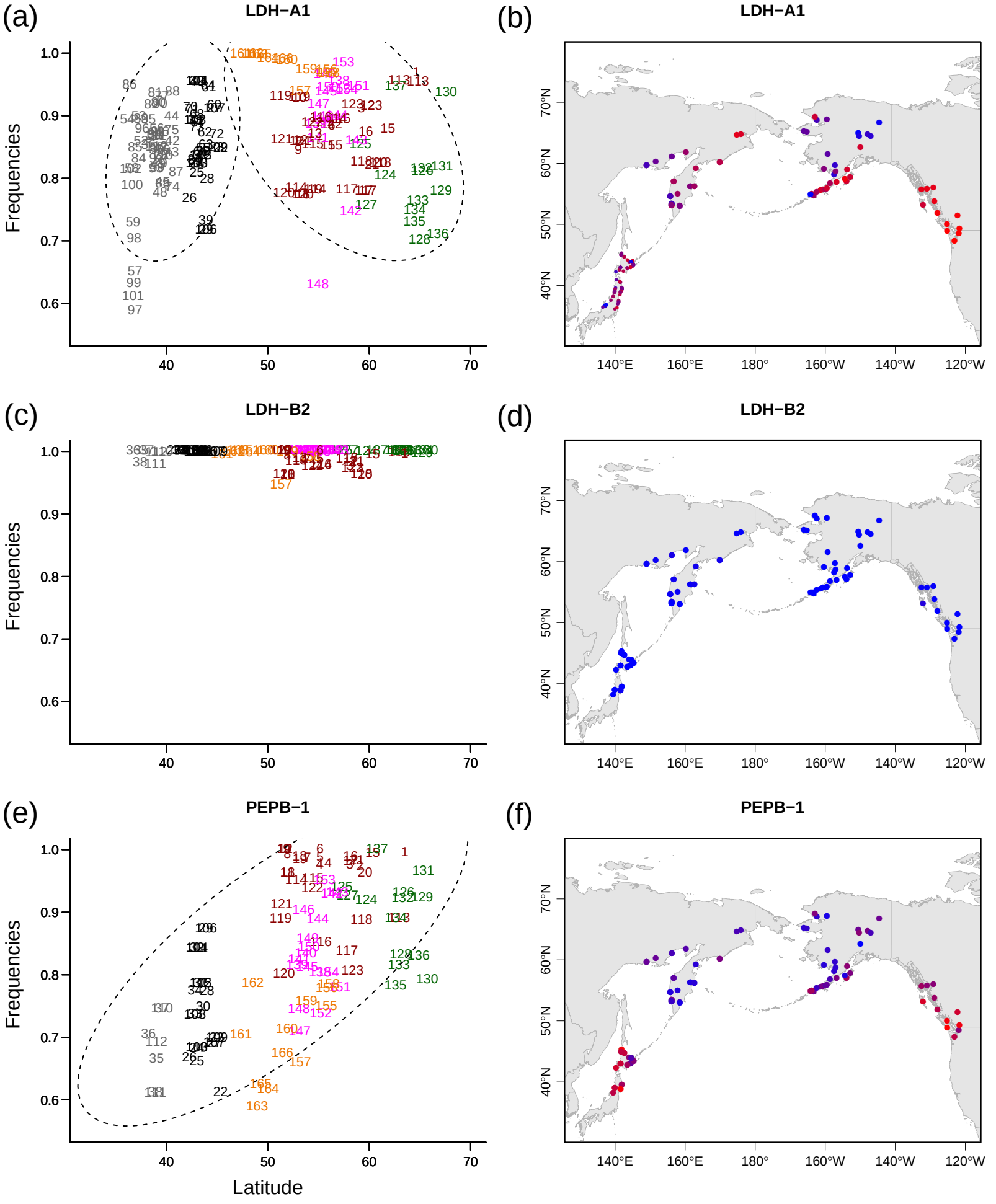
FIGURE 5 Geographical distribution of chum salmon allozyme gene frequencies in the North Pacific. (a), (b) LDH-A1. (c), (d) LDH-B2. (e), (f) PEPB-1. Colours and numbers in panels (a), (c) and (e) refer to sampling locations in Figure 3. Colours for sampling locations in panels (b), (d) and (f) visualize the magnitude of gene frequencies. The dotted circles show 95% confidence ellipses.


(a)
Total catch
%Japan
Catch (million fish)
Proportion of Japan (%)
0
20
40
60
80
100
120
1970
1980
1990
2000
2010
2020
(b)
Hokkaido
Honshu
Return rate (%)
0
1
2
3
4
5
6
1980
1990
1996
2000
2010
2017
(c)
Catch in Japan (million fish)
SST anomaly in spring and summer
20
30
40
50
60
70
80
−1.0
−0.5
0.0
0.5
1.0
1.5
96
97
03
04
05
06
07
01
09
98
02
08
13
99
10
00
14
11
15
12
16
18
17


(a)
1996
Hokkaido
Honshu
17948
4592
16986
9226
7241
2996
24471
110
79
2540
174
690
21
118
32
(b)
2006
21442
4102
19992
7142
7059
1977
274
8863
283
2357
378
356
16
142
40
(c)
2014
15868
2076
6916
5205
5018
1246
204
5241
225
2983
327
57
33
112
40
(d)
2017
9326
1876
2288
863
2628
1201
143
2350
48
951
227
34
8
36
32
46°N
44°N
42°N
40°N
38°N
36°N
135°E
140°E
145°E


(a)
1992
202
187
199
206
215
201
44
444
46
71
43
59
5
30
4
(b)
2002
216
195
187
195
214
135
32
435
37
64
40
50
8
30
3
(c)
2010
235
208
199
198
212
129
29
416
32
41
37
46
3
21
2
(d)
2013
241
213
202
207
214
120
28
390
29
57
35
9
7
19
2
46°N
44°N
42°N
40°N
38°N
36°N
135°E
140°E
145°E


(a)
70°N
65°N
60°N
55°N
50°N
170°W
160°W
150°W
140°W
130°W
120°W
(b)
60°N
58°N
56°N
54°N
165°W
160°W
155°W
150°W
(c)
65°N
60°N
55°N
50°N
150°E
155°E
160°E
165°E
170°E
175°E
(d)
46°N
44°N
42°N
40°N
38°N
36°N
136°E
138°E
140°E
142°E
144°E
146°E
148°E


(a)
LDH−A1
(b)
LDH−A1
(c)
LDH−B2
(d)
LDH−B2
(e)
PEPB−1
(f)
PEPB−1
Frequencies
Latitude
1.0
0.9
0.8
0.7
0.6
40
50
60
70
70°N
60°N
50°N
40°N
140°E
160°E
180°
160°W
140°W
120°W