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Spawning habitat characteristics and egg mortality in relation to river geomorphology and run-times of chum salmon (*Oncorhynchus keta*) in a metropolitan river system, northern Japan

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ABSTRACT

We investigated the geomorphology and environmental variables in which early- and late-run chum salmon groups spawn in an urban section of the Toyohira River, northern Japan, in relation to egg mortality, where a braided riverbed had been developing before river improvement occurred. Geomorphic units in the river channel having the highest proportions were riffles > the upwelling zone of gravel bars > pools > secondary channels. Most redds (> 60%) in the early-run group were built in the upwelling zone of gravel bars in the primary stream, indicating that salmon chose this geomorphic unit for spawning. A greater proportion of spawning redds in the late-run group occurred in secondary channels (i.e. smaller subsidiary channels that branch from the main, active channel). The buried-egg experiment showed that egg mortality was lower in the early-run group and higher in spawning redds that were shallower and had a higher maximum water temperature in winter. Late-run salmon need to select habitat with relatively higher water temperatures for spawning to compromise between egg mortality risk and the later timing of offspring hatching. Annual variation in the number of out-migrating fry was most associated with the number of spawning redds of the early-run group. A metropolitan river system may be highly regulated by humans and represents a monotonous river morphology, which nonetheless provides favorable spawning habitat for certain run-time populations because wild salmon may facultatively utilize limited diverse environments for natural reproduction.

KEYWORDS: chum salmon, metropolitan watershed, river geomorphology, run time, spawning habitat, upwelling zone of gravel bar

INTRODUCTION

Human activities are causing biodiversity declines at an alarming rate, including genetic, species, and ecosystem diversity globally (Cardinale et al. 2012). The coexistence of humans and wildlife in urban areas has received much attention in recent years (Gehrt et al. 2009; Jokimaki et al. 2011; Thatcher et al. 2020; Wookey 2022). In particular, there is a need to understand how cities affect biodiversity and how urban biodiversity affects humans (Zari 2018).

Pacific salmon (*Oncorhynchus* spp.) are less vulnerable to anthropogenic impacts during their growth period in the open ocean but are more susceptible during their juvenile downstream migration to the sea and upstream migration to fresh water, as human land use affects spawning and offspring habitats. Adult migration and juvenile out-migration of Pacific salmon through urban waterways are particularly vulnerable to human activities. For example, high pre-spawning mortality rates have been reported in heavily populated cities having Pacific salmon runs, such as San Francisco and Seattle in the United States, and Vancouver, Canada, because of the influx of pollutants into rivers (Feist et al. 2011; Scholz et al. 2011; Spromberg et al. 2016). In northern Japan, the Toyohira River flows through the city of Sapporo which has a population of over 1.9 million. The chum salmon (*Oncorhynchus keta*) run there had once almost disappeared, but since the 1980s the run has recovered following water-quality rehabilitation and hatchery releases of fry. The majority of chum salmon that now migrate to the Toyohira River are wild salmon originating from natural spawning (Aruga et al. 2014).

The spawning habitat of Pacific salmon is known to be closely related to river geomorphology (Montgomery et al. 1999; Hanrahan 2007; Mouw et al. 2014). Various environmental components can determine the location of spawning redds, such as sites

of downwelling into the riverbed, upwelling of subsurface water at gravel bars, and the influence of groundwater on spring channels. Diverse spawning environment lead to variation in the choice of spawning habitat utilization and in the run-times of Pacific salmon species (Geist et al. 2002). It is now widely recognized that genetic differentiation based on different breeding times in the same river (isolation by time) is as important as allopatric differentiation (isolation by distance), which has long been considered the most common type of genetic differentiation (Hendry and Day 2005; Braga-Silva and Galetti 2015). Habitat diversity leads to different optimal spawning times, resulting in a population with varied run-timing. Two races of chum salmon, summer-run and fall-run, are well known in the Yukon River in Alaska and in the Amur River in Russia. The summer-run salmon enter the river in summer and spawn in downwelling areas of the river, while the fall-run salmon enter in fall and spawn in river areas with groundwater upwelling (Olsen et al. 2008). Populations with diverse reproductive timing improves abundance stability (portfolio effect) and enhances resilience (Schindler et al. 2010).

River engineering works for flood control and urban water utilization alter river geomorphology and hyporheic flows, thereby affecting the spawning habitat of salmon. Previous studies on salmon spawning habitats have been conducted in natural rivers in large watersheds, such as in Alaska and the Kamchatka Peninsula (Leman 1993; Mouw et al. 2014), but scarce research has examined the spawning habitats with respect to river morphology in metropolitan areas. Moreover, salmon in large urban rivers often die before they complete spawning (Feist et al. 2011; Scholz et al. 2011; Spromberg et al. 2016). Rivers that have been straightened by channelization projects present a more homogeneous environment than natural rivers which have meandering and braided

channels, and thus the portfolio effect whereby diverse population structures contribute to ecosystem stability is unlikely to function. Urban rivers with artificially altered environments may not provide favorable spawning habitat for certain run-time populations. To clarify those hypotheses, it is necessary to examine not only adult spawning habitats but also egg mortality and egg-to-fry survival, which have seldom been elucidated for an urban river. Such investigations are needed to formulate conservation plans for wild salmon in urban rivers, which in turn would contribute to strategies to reconcile wildlife–human conflicts in urban areas. Ecosystem services provided by nature in urban areas also support the physical and mental health of urban residents (Coutts and Hahn 2015; Banerjee et al. 2021).

Significant improvements in the water quality of Japanese rivers, including the Toyohira River, since the 1980s (Morita et al. 2006), allowed us to direct our attention to river geomorphology, which has been degraded by river regulation. This study aimed to reveal the geomorphology and environment in which early-run and late-run groups of chum salmon spawn in the Toyohira River, where it flows through Sapporo City, in relation to egg mortality. Thus, we investigated the geomorphic characteristics of spawning sites, egg mortality, and egg-to-fry survival, using data from three different field studies. We examined specific geomorphic units, defined based on riverbed morphology and hyporheic flow, where salmon tend to spawn in different seasons. Environmental variables at spawning redds were also studied to understand their relationship to egg survival, and the numbers of out-migrating fry were estimated by trap surveys. Channels of the Toyohira River flowing through the city have been narrowed and straightened. The number of secondary channels has been substantially reduced by river regulation. Secondary channels have higher water temperatures than

the main channel during the winter (Swale et al. 1986). In addition, the groundwater level has dropped significantly because of urbanization (e.g., reduction of rain seepage due to paving material, overuse of groundwater, and development of subways). Therefore, we hypothesize that late-run chum salmon, which depend on the warm groundwater seepage (Mouw et al. 2014) in secondary channels, are more impacted in this metropolitan area. Based on the results, we discuss factors that help to maintain the natural reproduction of wild salmon in an urban river and share perspectives for future conservation measures.

MATERIALS AND METHODS

Study area and salmon monitoring

The Toyohira River is a 72.5-km long tributary of the Ishikari River and has a watershed of ~902.4 km^2; the confluence is ~17.5 km upstream of the river mouth (Fig. 1). Old maps indicate that prior to development the Toyohira River was wide and consisted of braided river channels. At the fan ends, springs originating from groundwater appeared and created ponds and numerous small streams. The river runs through Sapporo city, which has a population of more than 1.9 million. The riverbed gradient in the urban residential area is 1/150–1/300, which is relatively steep for a river flowing through a metropolitan area. Since the late 19th century, artificial levees and revetments have been constructed to manage frequent flooding (Kudo et al. 2012). Though the river once exhibited a braided channel pattern extending as much as 700 m in width, it has been narrowed to 130–280 m for the last hundred years (Ishida 2002). Where the floodplain is now used for a baseball park and cycling road, the low-flow channel has been especially narrowed by revetments (Fig. 2). The flow rates and

discharge volumes of the Toyohira River did not change significantly from 2003 to 2020 (Fig. S1). Chum salmon spawn in the river at a distance of ~10–21 km upstream of the confluence of the Ishikari River (Fig. 1). The riverbed in this segment consists of sandy gravel originating from alluvial sediment which has accumulated to ~50 m thick. Groundwater upwelling can be observed at an elevation of approximately 6 m above sea level where the railroad bridge crosses the Toyohira River (Sakata et al. 2011).

The Sapporo Salmon Museum has monitored chum salmon spawning redds in the Toyohira River since 1990. We used data from spawning redd surveys conducted approximately every 14 days between late September and early January, from 2015 to 2020, along the approximately full spawning area (~11 km in length). The spawning redds were located using a handheld global positioning system (Garmin GPS MAP62SJ). Observation error of surveyors when counting spawning redds includes missing, mispositioning, or double-counting redds. Since the same investigators, including the first author, conducted the surveys each time, we believe that the precision was sufficiently high. Chum salmon in the Toyohira River Basin may have formerly spawned in a more diverse landscape than they do today, when small spring-origin streams once remained. Currently, salmon in Japan are managed based on their run timing, with separate early-run and late-run groups (Kitada 2014; Abe et al. 2019). However, this management approach does not necessarily correspond to genetically separable populations; previous studies in North America have analyzed run timing for convenience, even in cases where bimodality was not present (Beacham 1984). The adult chum salmon in the Toyohira River have an approximately 4-month run from September to January, which we divided into early-run (spawned before 15 November) and late-run (spawned after 15 November) groups. During the spawning redd surveys,

post-spawn salmon carcasses were also collected and measured for fork length and their scales were analyzed to infer age.

Spawning redd distribution with respect to geomorphic units of the riverbed

The study reach of the Toyohira River is 11.45–14.95 km upstream of the confluence (elevation 5.4–27 m), where ~80% of all chum salmon spawning redds are distributed. We inspected the river geomorphology where the salmon constructed their spawning redds. The redds used in the analysis were located through eight field observations, conducted approximately every 14 days, from 29 September 2020 to 6 January 2021.

The geomorphic units of the river were defined primarily by pool–riffle sequences in the channels (Leopold et al. 1964; Montgomery and Buffington 1997; Hanrahan 2007). In consideration of the effect on spawning by chum salmon, classification of the units was also based on hyporheic water flows (Brunke and Gonser 1997; Tonia and Buffington 2011) and the presence of subsidiary channels branching from the main channel (Mouw et al. 2014). Consequently, the riverbed was classified into seven geomorphic units: gravel bar, riffle, pool, secondary channel, downwelling zone of gravel bar, upwelling zone of gravel bar, and artificial structure, using aerial photographs and field surveys (Fig. 2). Gravel bar refers to either bare or vegetated land that is above the water level during the salmon spawning season. A riffle included rapids and runs, with fast water velocities and shallow depths. A pool denoted areas of slow water velocities and deeper depth, typically situated between two riffle areas. A secondary channel was smaller subsidiary channels that branch from the main, active channel and tend to flow parallel or subparallel to the main channel before rejoining it downstream (Moir and Pasternack 2008; Wohl et al. 2016). The secondary channels are

191 influenced by groundwater seepage because the area is located at the foot of an alluvial
192 fan where the surrounding groundwater level is higher than the river water (Aruga et al.
193 2014). Hyporheic upwellings and river downwellings can generally be observed at the
194 edges of gravel bars (Brunke and Gonser 1997; Tonia and Buffington 2011; Zhou and
195 Endreny 2013). Therefore, we classified the upstream and downstream areas of gravel
196 bars into downwelling and upwelling zones. Finally, artificial structures signify
197 groundsill structures or riverbed protection works.
198 QGIS software (version 3.20.3) was used to overlay the geomorphic units with the
199 locations of spawning redds. A 10- × 10-m mesh was created based on the planar
200 rectangular coordinates, and the number of spawning redds relative to the geomorphic
201 units were counted for each mesh. We found that 41.4% of the riverbed was occupied by
202 gravel beds with a height above the water level; but, because the terrestrial area was not
203 available for salmon to spawn, we used only the submerged area for the analysis.
204 Chi-square tests with a Bonferroni correction were used to determine differences
205 between geomorphic units available for spawning and units actually used for spawning,
206 in relation to the two run-times. There were two null hypotheses: 1) spawning redds
207 occur randomly in available areas, regardless of geomorphic units; 2) there is no
208 difference in the geomorphic units available for the early-run and late-run groups to
209 spawn. Furthermore, multinomial logistic regression analysis was used to assess
210 whether the composition of geomorphic units supporting spawning redds varied with
211 time across the surveys.
212 ***Buried-egg experiment: egg mortality in relation to run-times and environmental***
213 ***variables***

To examine egg mortality during incubation in relation to environmental variables and adult run-times, we set up an experiment in which artificially fertilized eggs were buried in the spawning ground. The sites used for the buried-egg experiments are shown in Fig. 1. The data shown here are a re-analysis of that of Aruga and Suzuki (2009). Eggs obtained from the Toyohira River chum salmon hatchery program were used in this experiment. Eggs artificially fertilized from two females and two males on 8 October 2003 were used for the early-run group, and eggs artificially fertilized from four females and two males on 10 December 2003 were used for the late-run group. The fertilized eggs were incubated in a hatching tank until the eyed-egg stage, when they were then planted in river redds.

Eyed eggs were placed in Whitlock–Vibert boxes (200 eggs per box) and buried to a depth where naturally spawned eggs were found. The Whitlock–Vibert box system comprises a top tray filled with eyed eggs, which are allowed to develop and hatch until slipping through to the bottom nursery chamber as sac fry, until they start to swim and are able to eventually leave the box. Eyed eggs of the early-run group were buried on 5 November 2003 into spawning redds where early-run salmon had spawned; those of the late-run group were buried on 5–7 January 2004 into spawning redds where late-run salmon had spawned. Five redds were selected in each the early-run and late-run groups, with six Whitlock–Vibert boxes buried in each redd. In total, 10 redds × 6 boxes × 200 eggs were planted. Of the 6 boxes buried in a single redd, 3 boxes were recovered at the time of hatching and the number of dead eggs was then counted. The remaining 3 boxes were covered with nets that were water permeable and allowed space (and therefore would not affect fry survival) to prevent fry from escaping, and kept buried until the time of fry emergence, when the number of dead individuals (eggs and fry)

were then counted. Hence, the egg-to-emergence process included hatching. During the period between hatching and emergence, one spawning redd in the early-run group became frozen in the river, and in the late-run group the Whitlock–Vibert boxes at one spawning redd were washed away, so those data were not available.

The number of dead individuals in each box was counted at the time of hatching and again at emergence (with the boxes covered with nets), and data-loggers were used to monitor the water temperature at the redds. The times until hatching and fry emergence differed between the early-run and late-run groups. In the early-run group, dead eggs were counted at the time of hatching 52 days after burial of the eyed eggs, and at the time of emergence 144 days after egg burial. In the late-run group, dead eggs were likewise counted after 81–83 days, and after 158–160 days. These differences in the time (number of days) until hatching and emergence between the two run-time groups are attributable to differences in the water temperatures at the redds, which influenced the required cumulative temperature for each event (400–600 degree-days to hatching and 700–1,000 degree-days to emergence: Salo [1991]). The mortality rate was expressed as the number of dead eggs or fry divided by 200 (total buried eggs).

The environmental variables characterized at the spawning sites where the Whitlock–Vibert boxes were buried were water depth, flow velocity, particle size composition, and water temperature. Depth (cm) was measured as the height from a raised spawning redd (mount) to the water surface. The flow velocity (cm/s) was measured 10 times just above each spawning redd, using a propeller-type meter, and the average value was used for the analysis. A sediment sample from the spawning redd (25-cm length and width, 20-cm depth) was collected with a shovel and sieved through 0.25-mm mesh. The Fredle index, an indicator of the water permeability and therefore

suitability of the spawning gravel, was calculated from the particle size distribution (Lotspeich and Everest 1981; Rubin and Glimsäter 1996; Dumas and Marty 2006; Iida et al. 2017). An underwater data logger (StowAway TBI32-20+50, Onset) was placed in each of the 10 experimental redds where eyed eggs were buried, at a depth of ~30 cm, to measure water temperature at 1-h intervals; the analysis used the highest water temperature recorded between 1 and 20 January in 2004 as the maximum riverbed temperature during winter. Winter was defined as the period from 26 December 2003 to 25 March 2004, the season when the average river water temperature is below 3°C.

Differences in environmental variables at the spawning redds of the early-run and late-run groups were tested using general linear models (GLMs) with a Gaussian distribution. The environmental parameters were aggregated by principal component analysis. The numbers of dead eggs between the two run-time groups were tested using generalized linear mixed models (GLMMs). The GLMM with negative binomial distribution, and with spawning redds as random effects for the buried-egg experiments, was described as:

Number of dead eggs ~ Run time + Stage

where the run time (early-run or late-run) and stage (hatched or emerged) are categorical variables. Or, alternately, the run-time effect was replaced by environmental variables, as follows:

Number of dead eggs ~ PC1 + PC2 + Stage

where PC1 and PC2 are the principal component scores (continuous variables) of the environmental variables.

Estimation of the number of out-migrating fry and egg-to-fry survival

285 Trap surveys were conducted to estimate the numbers of out-migrating fry. Note that
286 fry born from adult salmon with different run-times had the same out-migrating timing,
287 so fry could not be distinguished by the parents' run-time. Out-migrating fry traps were
288 periodically set at the downstream end of spawning redds, each day for on average 7.3
289 days (1–14 days) during the period 9 March to 10 May, in 2016–2020. The trapping was
290 carried out from 30 minutes after sunset until a maximum of 3.5 h after sunset, as this is
291 reported to be the time when salmon fry primarily out-migrate (Kobayashi 1953; Hoar
292 1958; Ali et al. 1959; Hasegawa and Takahashi 2013). In 2016 and 2017, 900-cm^2 area
293 nets (length 30 cm, width 30 cm, and mesh size 3 mm) were used to trap the out-
294 migrating fry; the number of trapping attempts ranged from 14 to 24, with 1 min of
295 capture followed by an interval of several minutes, for a total of at least 70 min of
296 trapping time. From 2018 to 2020, the out-migration traps used were made of 5-mm
297 plastic mesh and had an area of 2,150–2,500 cm^2 (length 50 cm, width 43–50 cm) and
298 were affixed to the riverbank structure. One trapping time varied depending on the
299 amount of debris coming in, but ranged from 3 to 37 min per trap. The trapping was
300 done at least three times per night for a total of at least 30 min.
301 Based on the water velocity and discharge volume at the time of the trap survey, the
302 filtration rate was determined and the number of out-migrating fry per unit time was
303 estimated. River discharge data were obtained from the Water Information System of
304 the Ministry of Land, Infrastructure, Transport and Tourism (http://www1.river.go.jp).
305 The survey was conducted during the primary out-migration diel period of chum salmon
306 fry (for 3.5 h, sometime after sunset); 24-h continuous monitoring showed that the
307 hourly counts of out-migrating fry during the primary out-migrating time constituted

22.8%–32.3% of the total daily counts of out-migrating fry (Table S1). The daily number of out-migrating fry was estimated using the formula:

Estimated number of out-migrating fry per day = observed number of fry per hour / [(out-migrating fry per hour corresponding to the observed time in the 24-h monitoring period) / (total number of out-migrating fry in the 24-h monitoring period)]

In addition, fry out-migration abundance for the entire season was estimated by integrating the out-migration abundance for the entire study period by calculating the area under the curve (Hilborn et al. 1999). Although the area under the curve method is prone to errors, we assumed a linear trend across the survey dates and estimated the number of fry that out-migrated during the surveyed year.

Only wild salmon fry born from natural spawning were used in the analysis. Some hatchery-reared fry had been released upstream and were also captured, but most were easily identified by their larger size (>50 mm) due to artificial feeding before release; however, some smaller sized individuals were identifiable from the otolith thermal marks applied to hatchery fish. Therefore, from 2016 to 2019, some fry were sacrificed and checked for otolith thermal marks (68–159 fish/year). Although we found that hatchery and wild fish were mostly distinguishable by body size in 2020, the individuals sacrificed (n = 16, 10.2%) still ranged in size, so we again checked for thermal marks.

The total numbers of eggs produced in the brood years 2015–2019 was estimated by multiplying the number of spawning redds by the average number of eggs per redd (Table S2). The average number of eggs per redd was estimated based on the mean fork length of spawned females in each year, following the method of Okamoto (2001). Because salmon eggs can be lost after spawning (e.g., washed away, predated, dug up,

or unfertilized), we did not assume that all eggs deposited by females remained in the spawning redds.

Egg-to-fry survival was determined from the estimated total number of eggs and the estimated number of out-migrating fry in the same brood year. The total number of eggs was calculated by multiplying the average number of eggs per redd by the number of redds counted (Table S2). Next, we examined the relationship between the total number of eggs produced and the subsequent number of out-migrating fry (i.e., the stock-recruitment relationship). In addition to the relationship between the total number of spawning redds and the total number of out-migrating fry, the relationship was also analyzed for the number of spawning redds between the early-run and late-run groups using Pearson's correlation analysis.

RESULTS

Geomorphic composition of riverbed in the Toyohira River used by chum salmon for spawning redds

The geomorphic units of the riverbed where adult salmon constructed redds differed significantly from the geomorphic units available to them ($\chi^2 = 492.86$, df = 5, $p < 0.01$; Fig. 3). The geomorphic units used for spawning redds also differed significantly between the early-run and late-run groups ($\chi^2 = 38.59$, df = 5, $p < 0.005$). In the surveyed reaches, the most common geomorphic units were riffle (31%), upwelling zone of gravel bar (22%), pool (19%), secondary channel (13%), and downwelling zone of gravel bar (11%). However, more than 60% of the spawning redds of the early-run group were constructed in the upwelling zone of gravel bars, even though that represented only 22% of the whole geomorphology. The second major geomorphic unit

used for spawning redds was secondary channels, which was selectively used for spawning habitat by the late-run group. The spawning habitat utilized also changed depending on the run-timing (polynomial logistic regression model, $\chi^2 = 52.18$, df = 5, $p < 0.001$; Fig. 4). Early-run salmon spawned mainly in the upwelling zone of gravel bars, whereas late-run salmon spawned equally as often in secondary channels as in the upwelling zone of gravel bars. Therefore, secondary channels were significantly selected by the late-run group as compared with the early-run group.

Egg mortality during incubation in relation to environmental variables and adult run-times

The number of dead eggs differed significantly between the redds of the early-run and late-run groups irrespective of the stages ($\chi^2 = 67.93$, df = 1, $p < 0.001$; Table 1). In addition, the maximum riverbed temperature during winter was significantly higher for the spawning redds of late-run salmon compared with that of early-run salmon ($F_{1,8} = 8.541$, $p = 0.019$; Table 1). The principal components PC1 and PC2 had eigenvalues greater than 1.0, with explained variances of 56.0% and 27.5%, respectively. PC1 was negatively correlated with maximum riverbed temperature during winter and positively correlated with water depth and flow velocity; PC2 was positively correlated with the Fredle index, an index of gravel permeability based on particle size composition (Table 1). The number of dead eggs was significantly less in association with PC1 ($\chi^2 = 6.60$, df = 1, $p = 0.010$; Fig 5), but no relationship was found with PC2 ($\chi^2 = 0.44$, df = 1, $p = 0.507$) (Table 1).

Egg-to-fry survival and stock-recruitment relationship

An average of 634 spawning redds (range 497–824) were counted annually in the surveys from 2015 to 2019, yielding an average of 1.8 million eggs produced annually

379 in the Toyohira River (Table S2). The fry trap surveys showed an estimated 112,000–
380 457,000 out-migrating fry were produced by natural spawning in a given year, with egg-
381 to-fry survival rates of 6.1%–23.9% during the survey period (Table S2). There was no
382 correlation between the total number of spawning redds and the number of out-
383 migrating fry for the survey years ($r = 0.438$, $p = 0.461$; Fig. 6). However, when data for
384 the early-run and late-run redds were analyzed separately, significant positive
385 correlation was found between the number of out-migrating fry and the number of
386 spawning redds for the early-run group, whereas there was no correlation for the late-
387 run group (early-run redds: $r = 0.994$, $p < 0.001$; late-run redds: $r = -0.015$, $p = 0.982$;
388 Fig. 6), indicating that early-run spawners contribute significantly to the chum salmon
389 fry production in the Toyohira River.
390
391 **DISCUSSION**
392 We investigated spawning habitat characteristics and egg mortality in relation to
393 river geomorphology and the adult run-times of chum salmon in a metropolitan river in
394 northern Japan. Areas of the Toyohira River where salmon spawned were concentrated
395 in certain geomorphic units, indicating that the salmon chose specific habitats for
396 spawning. The geomorphic units where spawning redds were built differed between the
397 early-run and late-run groups, revealing that the former preferred the upwelling zone of
398 gravel bars, whereas the latter preferred sites with groundwater seepage. The buried-egg
399 experiment revealed higher egg mortality in the spawning redds of late-run salmon, in
400 which maximum riverbed temperature during winter was high. We surmise that early-
401 run spawners currently contribute most to fry production in the Toyohira River.
402 Importantly, wild salmon in this metropolitan waterway, which is highly regulated by

403 humans and represents a monotonous river morphology, are able to facultatively utilize
404 spatiotemporally changing environments for natural reproduction.
405 In this study we assessed the geomorphology of the active channel that was a
406 spawning ground for chum salmon and found that >40% of the area constituted gravel
407 bars that extended above the water level during the spawning season, and therefore
408 could not be used as spawning habitat. This morphology is due to channel incisions
409 associated with immobilization of the low-flow channel with revetment (Aruga et al.
410 2021). Previous studies have likewise found that early-run spawning sites were more
411 often influenced by subsurface water discharge into the river, and late-run spawning
412 sites by groundwater seepage (Leman 1993; Mouw et al. 2014). However, in the
413 Toyohira River, ~60% of the total spawning redds were built at sites influenced by
414 subsurface water, whereas in the Kamchatka River of the Russian Far East ~60% of
415 where chum salmon spawned was influenced by groundwater seepage (Leman 1993).
416 This difference may be attributable to differences in groundwater temperatures, which
417 were as low as 4–5 °C year-round in the Kamchatka River, as well as to higher
418 dissolved oxygen content. Thus, redds built at groundwater seepage sites would enable
419 the best timing for summer salmon embryos to hatch and so ensure higher egg survival.
420 Most rivers studied as spawning habitat for chum salmon have been large rivers
421 with widths of several kilometers, large meanders, and numerous flood plains and
422 spring channels formed by abundant groundwater (Leman 1993; Mouw et al. 2014). In
423 contrast, the Toyohira River is an alluvial fan river with a fairly steep gradient, but
424 because it flows through a large city the watercourse and floodplain have been heavily
425 regulated and altered, resulting in a low-flow channel constrained by revetments. Areas
426 with upwelling and downwelling around gravel bars offer strong hyporheic fluxes with

427 short residence times, which maintains the oxygen concentration (Tonia and Buffington
428 2011). Subsurface water flowing through gravel bars can acquire a higher temperature
429 than river water—conditions that would promote the growth of salmon eggs during
430 winter (Geist et al. 2002). Furthermore, subsurface water at the upwelling zone of gravel
431 bars may contain high dissolved oxygen. In the Toyohira River, the minimum water
432 temperature at the upwelling zone of gravel bars during the winter was higher than the
433 river temperatures. Together, these findings suggest that the upwelling zone of gravel
434 bars in this river remains a suitable environment for chum salmon to spawn.
435 The second-largest number of spawning redds was found in secondary channels, and
436 late-run salmon tended to choose secondary channels for building redds. The spawning
437 redds of both early-run and late-run chum salmon in the Toyohira River are mainly
438 located in the reach at the foot of the alluvial fan, where the groundwater level is higher
439 than the riverbed elevation, and where seepage of groundwater past low-water
440 revetments can be observed (Aruga et al. 2021). For instance, on 24 February 2005 the
441 groundwater temperature was 10.2°C and the river water was 0.8°C (unpublished data).
442 In rivers with high groundwater levels, the winter water temperatures in secondary
443 channels can be higher than in the main channel because of upwelling (Mouw et al.
444 2014). The chum salmon spawning period in the Toyohira River is about 4 months,
445 from late September to early January; for juveniles to survive on the coast, the fry must
446 out-migrate during a limited period (~1 month) in spring (March to May) (Morita and
447 Nakashima 2015; Iida et al. 2018). Eggs spawned in areas with higher water
448 temperatures during the winter showed faster growth than eggs spawned in other
449 habitats (Leman 1993; Webb and McLay 1996; Lisi et al. 2013). In the Toyohira River
450 this situation would allow fry from late-run salmon to out-migrate simultaneously with

451 fry from early-run salmon. This suggests that geomorphology and hydrology interact to
452 produce a heterogeneous thermal template to influence salmon spawning times (Lisi et
453 al. 2013). There is heritability in the time of spawning (Morita 2018), but there might
454 also be heritability in the location of spawning as aligned with different spawning
455 periods. Even if the area of secondary channels is not large, the presence of a
456 geomorphic unit with different water temperatures in winter may sustain the natural
457 reproduction of different run-time groups of salmon in an urban river.
458 The buried-egg experiment revealed that shallower water depths, lower flow
459 velocity, and higher water temperatures in winter were associated with increased egg
460 mortality. Pacific salmon eggs are buried ~20 cm deep from the top of the redd (Burner
461 1951; Smith 1973; Aruga and Suzuki 2009), and therefore eggs spawned in shallower
462 water are more likely to eventually emerge above the water level, resulting in
463 mortalities. Moreover, as the flow velocity increases, the deeper areas within redds
464 become more oxygenated (Cardenas et al. 2016). Because egg survival is highly
465 dependent upon the dissolved oxygen concentrations of hyporheic water (Rubin and
466 Glimsäter 1996; Malcolm et al. 2003), the high flow velocities probably reduced the
467 rate of egg mortality. In contrast, the dissolved oxygen content of groundwater tends to
468 be low (Fraser and Williams 1998; Winter et al. 1998), and this condition may
469 contribute to egg mortalities. Oxygen consumption by salmonid embryos varies with the
470 stage of development, water temperature, and dissolved oxygen concentration (Greig et
471 al. 2007). In particular, low dissolved oxygen increases the risk of mortality because of
472 the increased oxygen requirement from the time of hatching to fry emergence (Peterson
473 and Quinn 1996). The low oxygen concentration of groundwater seepage in the
474 secondary channels may have contributed to egg mortality. The relationship between

PC1 and egg mortality was significant, yet egg mortality was comparatively higher in the late-run group at the same PC1 values. Groundwater seeping into the Toyohira River, as compared with that in other rivers, has reportedly low dissolved oxygen content as well as high electrical conductivity, which could indicate water pollution (Negishi, unpublished data). These groundwater qualities may collectively increase egg mortality. The late-run group spawned in secondary channels with higher water temperatures despite the risk to egg mortality, which could be explained by a trade-off between egg mortality and post-hatching fry mortality. Because the timing of outmigration affects fry survival (Morita and Nakashima 2015), females in late-run groups would need to spawn at sites with warmer water temperatures to accelerate the time to hatching. If the fry hatch later in the season (if they even survive to the fry stage), they are less likely to survive after entry into the ocean. Therefore, the spawning sites where the late-run group is currently spawning would provide the highest fitness for late-run spawners. In other words, there may be a trade-off between choosing a spawning site with warmer water temperatures during winter (which would allow for faster embryo development) although the site has lower dissolved oxygen (causing a risk of egg mortality) (Mouw et al. 2014) in addition to the disadvantage being influenced by the potentially polluted groundwater entering the river. Therefore, the environmental variables examined in this study will not explain all factors contributing to egg mortality.

In this study, there was no significant relationship between PC2, which represents the Fredle index, and the numbers of dead eggs. The mortality of salmonids eggs and alevins abruptly increases when the Fredle index, an indicator of the water permeability of the gravel bed, is <4.8 (Suzuki 2008). Because chum salmon construct spawning

redds in the river section examined, and because sufficient permeability of the spawning gravel was maintained at the study sites (average Fredle index of ≥4.8), we believe this was not a factor contributing to egg mortality.

More precise daily counts of out-migrating fry would require multiple 24-h continuous monitoring surveys over multiple years and in different seasons, but this was not logistically feasible in the present study. However, several previous studies have shown that emerging fry begin their migration to the ocean several hours after sunset (Kobayashi 1953; Hoar 1958; Ali et al. 1959; Hasegawa and Takahashi 2013). Thus, our estimate derived from one 24-h continuous monitoring period conducted in just one year may not have caused a large source of error in the overall results. Although the estimated number of out-migrating fry in this study might include substantial uncertainty, it is valuable for estimating the efficiency of wild fry reproduction in an urban river.

The average egg-to-fry survival rate for chum salmon in the Toyohira River was estimated at 12.7% (though the precision may not be high). This rate is lower than for salmon in the Chitose River (~20%), another tributary of the Ishikari River, though less altered by urbanization (Morita et al. 2013). Egg-to-fry survival might be expected to be low in an urban river, as represented by the Toyohira River. We speculate that the major contributor to low egg-to-fry survival is large numbers of dead eggs among late-run spawners, as proven by our buried-egg experiment, and because the annual variation in the number of out-migrating fry was correlated only with the spawning redds of the early-run group.

Most previous investigations of salmon spawning in relation to river morphology, such as in Alaska or the Kamchatka Peninsula, were conducted in meandering gravel-

bed rivers. In these river systems, flood channels and spring channels are formed that connect with the main channel, with different magnitudes of inundation, and late-spawning groups predominantly selected channels influenced by groundwater seepage (Leman 1993; Mouw et al. 2014). The Toyohira River was once an extensively braided channel with many spring channels originating from groundwater (Fig. 1); salmon bones and fishing gear for catching salmon have been found at ruins along the river (Amano 2009), suggesting an environment that could once support abundant reproduction by late-spawning salmon. By the 1920s, however, with the urbanization of Sapporo city, streams originating from groundwater vanished (Ishida 2002), artificial embankments were largely completed, and low-water revetments started to be constructed (Kudo et al. 2012). In the 1920s, most of the salmon run occurred in early October to mid-November (Hokkaido Salmon Hatchery 1929), suggesting that the Toyohira River salmon population consisted mainly of early-run salmon, and that late-run salmon could spawn only under limited conditions where groundwater seeped into secondary channels. Currently, the natural reproduction of wild chum salmon populations in the Toyohira River depends on the early-run group, and the upwelling zone of gravel bars is an especially important geomorphic unit for their spawning. The population of wild salmon forming the late-run group in the river has deteriorated following urbanization, and yet it should be recovered for sustaining a diversity of life-history traits and to enhance portfolio effects (Schindler et al. 2010).

We conclude that the natural reproduction of chum salmon in the Toyohira River is most sustained by the early-run salmon which build redds mainly in the upwelling zone of gravel bars, where higher water velocity, deeper water, and a lower maximum riverbed temperature during winter result in less egg mortality. This habitat has been

preserved even in the regulated urban river and is especially important for the early-run group. Secondary channels have relatively warm water temperatures in the winter and thereby provide essential habitat for the late-run group, even though the egg mortality rate may be higher, which contributes to the life-history diversity of this salmon population. We suggest that these geomorphic features of a river in a metropolitan watershed are key for maintaining the diversity of a wild salmon population.

CONSERVATION IMPLICATIONS

Gravel bars are an important geomorphic unit for maintaining the wild chum salmon population in the Toyohira River; this morphological feature is typically maintained dynamically by hydrologic forces in natural rivers. However, the current situation in many Japanese rivers, including the Toyohira River, is problematic as salmon habitat, because controlled flows by reservoir dams and reduced sediment supplies owing to erosion-control dams and gravel extraction promote immobilized gravel bars and vegetation expansion over natural gravel bars and floodplains (Takahashi and Nakamura 2011; Nakamura et al. 2017; Aruga et al. 2021). To solve these problems, we believe that restoration of the natural flow regime and sediment regime (Nakamura et al. 2017) and a redesign of the river channel morphology are necessary. In addition, in regard to late-run salmon, the impact of the current quality of the groundwater seepage on salmon egg survival should be examined and remedial measures taken if necessary. Although the proportion of the late-run group is not large, these salmon perform several ecosystem functions, such as providing an important food resource for overwintering animals such as eagles (Ueta et al. 1999; Kamauchi et al. 2012). Moreover, the late-run

group is necessary to maintain the genetic diversity of the wild chum salmon population in the Toyohira River.

There is also a need to boost the interest of river managers and citizens in wild salmon. The Sapporo Wild Salmon Project, launched in 2014, is an NGO devoted to conserving wild salmon, and its conservation efforts in the Toyohira River have gradually received greater support from the general public and river managers. For example, with the cooperation of a construction company who offered to participate in the conservation of wild salmon, we were able to improve spawning habitat by restoring a secondary stream channel. Although this restoration was a localized improvement, many late-run chum salmon have since spawned in this secondary channel, thereby contributing to the natural reproduction efficiency of the salmon (Aruga et al. 2019). Because urban rivers are greatly affected by human activities, we believe that improving the awareness of city residents and communities is a key component of wild salmon conservation.

DECLARATIONS

Not applicable.

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CONFICTS OF INTEREST

Not applicable.

AVAILABILITY OF DATA AND MATERIAL

Raw data are available by request from the corresponding author.

CODE AVAILABILITY

All codes are available by request from the corresponding author.

AUTHORS CONTRIBUTION

NA and KM conceived the research idea. NA, KM, MA, KU, KF, KO and KW designed the methods and performed the collections. NA and KM analyzed the data. NA, KM and FN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ETHICS APPROVAL

The survey was conducted with the permission of the Governor of Hokkaido, Japan. The buried salmon eggs were handled appropriately.

CONSENT TO PARTICIATE

Not applicable.

CONSENT FOR PUBLICATION

The authors consent to publication of the manuscript.

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REFERENCES

Abe TK, Kitagawa T, Makiguchi Y (2019) Chum salmon migrating upriver adjust to environmental temperatures through metabolic compensation. J Exp Biol 222:jeb186189. https://doi.org/10.1242/jeb.186189

Ali MA, Hoar WS (1959) Retinal responses of pink salmon associated with its downstream migration. Nature 184:106-107. http://dx.doi.org/10.1038/184106a0

Amano T (2009) Life on the Sakshukotni Riverbank. Introduction of Salmonology, Hokkaido University Press Sapporo, 185-193 (in Japanese).

Aruga N, Morita K, Suzuki T, Sato N, Okamoto M, Ohkuma K (2014) Evaluation of population viability of wild chum salmon *Oncorhynchus keta* in the Toyohira River, Sapporo metropolitan watershed, Japan. Nippon Suisan Gakk 80:946-955 (in Japanese with English abstract). https://doi.org/10.2331/suisan.80.946

Aruga N, Morita K, Kataoka T, Ueda K, Mukai T, Fujii K, Nunokawa M, Aruga M, Maruyama M, Watanabe K, Sato N, Nakamura S, Nishitani K, Okamoto M, Ohkuma K (2019) Example of restoration work to improve salmon spawning habitat in the Toyohira River. Research Report of the Sapporo Salmon Museum 1-22 (in Japanese).

Aruga N, Morita K, Aruga M, Ueda K, Watanabe K, Nakamura F (2021) Decadal changes in river geomorphology, and its effect on chum salmon spawning habitat, Toyohira River, Japan. Ecology and Civil Engineering 23:295-307 (in Japanese with English abstract). http://dx.doi.org/10.3825/ece.20-00025

Aruga N, Suzuki T (2009) Environmental conditions and buried-egg mortality experiments on chum salmon spawning redds in the Toyohira River. FRA Salmonid Research Report 3:3-5 (in Japanese).

Banerjee S, Banerjee A, Palit D (2021) Ecosystem services and impact of industrial

642 pollution on urban health: evidence from Durgapur, West Bengal, India. Environ
643 Monit Assess 193:744. http://dx.doi.org/10.1007/s10661-021-09526-9
644 Beacham TD (1984) Age and morphology of chum salmon in southern British Columbia.
645 T Am Fish Soc 113:727-736. https://doi.org/10.1577/1548-
646 8659(1984)113<727:AAMOCS>2.0.CO;2
647 Braga-Silva A, Galetti PM Jr (2015) Evidence of isolation by time in freshwater migratory
648 fish *Prochilodus costatus* (Characiformes, Prochilodontidae). Hydrobiologia
649 765:159–167. http://dx.doi.org/10.1007/s10750-015-2409-8
650 Brunke M, Gonser T (1997) The ecological significance of exchange processes between
651 rivers and groundwater. Freshwater Biol 37:1-33. https://doi.org/10.1046/j.1365-
652 2427.1997.00143.x
653 Burner CJ (1951) Characteristics of spawning nests of Columbia River salmon. U.S. Fish
654 and Wildlife Service Fishery Bulletin 61:97-110
655 Cardenas MB, Ford AE, Kaufman MH, Kessler AJ, Cook LM (2016) Hyporheic flow and
656 dissolved oxygen distribution in fish nests: The effects of open channel velocity,
657 permeability patterns, and groundwater upwelling. J Geophy Res–Biogeo 121:3113-
658 3130. https://doi.org/10.1002/2016JG003381
659 Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace
660 G, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace J, Larigauderie A,
661 Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature
662 486:59-67. http://dx.doi.org/10.1038/nature11148
663 Church M (1992) Channel morphology and typology, in Carlow P, Petts GE, eds., The
664 rivers handbook: Oxford, United Kingdom, Blackwell Scientific Publications, pp
665 126–143.

666 Coutts C, Hahn M (2015) Green infrastructure, ecosystem services, and human health.
667 Int J Env Res Pub He 12:9768-9798. http://dx.doi.org/10.3390/ijerph120809768
668 Dumas J, Marty S (2006) A new method to evaluate egg-to-fry survival in salmonids,
669 trials with Atlantic salmon. J Fish Biol 68:284-304. http://dx.doi.org/10.1111/j.0022-
670 1112.2006.00907.x
671 Feist EB, Buhle ER, Arnold P, Davis JW, Scholz NL (2011) Landscape ecotoxicology of
672 Coho Salmon spawner mortality in urban streams. PLoS ONE 6:e23424.
673 https://doi.org/10.1371/journal.pone.0023424
674 Fraser BG, Williams DD (1998) Seasonal boundary dynamics of a groundwater/surface-
675 water ecotone. Ecology 79:2019–2031. https://doi.org/10.1890/0012-
676 9658(1998)079[2019:SBDOAG]2.0.CO;2
677 Gehrt SD, Anchor C, White LA (2009) Home range and landscape use of coyotes in a
678 metropolitan landscape: conflict or coexistence? J Mammal 90:1045-1057.
679 https://doi.org/10.1644/08-MAMM-A-277.1
680 Geist DR, Dauble DD (1998) Redd site selection and spawning habitat use by fall
681 Chinook Salmon: the importance of geomorphic features in large rivers. Environ
682 Manage 22:655-669. http://dx.doi.org/10.1007/s002679900137
683 Geist DR, Hanrahan TP, Arntzen EV, McMichael GA, Murray CJ, Chien YJ (2002)
684 Physicochemical characteristics of the hyporheic zone affect redd site selection by
685 Chum Salmon and fall Chinook Salmon in the Columbia River. N Am J Fish Manage
686 22:1077-1085. https://doi.org/10.1577/1548-
687 8675(2002)022<1077:PCOTHZ>2.0.CO;2
688 Greig SM, Sear DA, Carling PA (2007) A review of factors influencing the availability of
689 dissolved oxygen to incubating salmonid embryos. Hydrol Process 21:323-334.

690 https://doi.org/10.1002/hyp.6188
691 Hanrahan TP (2007) Bedform morphology of salmon spawning areas in a large gravel-
692 bed river. Geomorphology 86:529–536.
693 https://doi.org/10.1016/j.geomorph.2006.09.017
694 Hasegawa K, Takahashi S (2013) Microscale environment along the seaward route of
695 stocked chum salmon fry. T Am Fish Soc 142:1232-1237.
696 https://doi.org/10.1080/00028487.2013.804006
697 Hendry AP, Day T (2005) Population structure attributable to reproductive time: isolation
698 by time and adaptation by time. Mol Ecol 14:901-916.
699 http://dx.doi.org/10.1111/j.1365-294X.2005.02480.x
700 Hilborn R, Bue BG, Sharr S (1999) Estimating spawning escapements from periodic
701 counts: a comparison of methods. Can J Fish Aquat Sci 56:888–896.
702 https://doi.org/10.1139/f99-013
703 Hoar WS (1958) The evolution of migratory behaviour among juvenile salmon of the
704 genus *Oncorhynchus*. Journal of the Fisheries Board of Canada 15:391-428.
705 https://doi.org/10.1139/f58-020
706 Hokkaido Salmon Hatchery (1929) Annual report. Hokkaido Salmon Hatchery, Sapporo
707 (in Japanese)
708 Iida M, Imai S, Katayama S (2017) Effect of riverbed conditions on survival of planted
709 eyed eggs in chum salmon *Oncorhynchus keta*. Fisheries Sci 83:291-300.
710 http://doi.org/10.1007/s12562-016-1052-2
711 Iida M, Ban M, Noguvchi D, Miyauchi Y, Kitayama S (2018) Comparison of return rates
712 of chum salmon *Oncorhynchus keta* released at various times into the Gakko River,
713 Yamagata Prefecture, Japan. Aquaculture Science 66:137-140 (in Japanese with

714 English summary). https://doi.org/10.11233/aquaculturesci.66.137
715 Ishida K (2002) How dams are built: Houheikyou Dam. HokkaiMonthly report of Civil
716 Engineering Research Institute 588:3-6 (in Japanese)
717 Japan Map Center (1995) Sapporo in Maps 1, circa 1896. Midorikawa Map Printing Co.
718 Jokimaki J, Jokimaki MLK, Suhonen J, Clergeau P, Pautasso M, Fernandez-Jiricic E
719 (2011) Merging wildlife community ecology with animal behavioral ecology for a
720 better urban landscape planning. Landscape Urban Plan 100:383-385.
721 https://doi.org/10.1016/j.landurbplan.2011.02.001
722 Kamauchi H, Sato S, Hayashi D, Okabe Y, Katsuyama T, Fukushima K, Yoshioka A, Sato
723 T, Tokuchi N, Nakaoka M (2012) Consumer of salmon carcasses in early winter of
724 Eastern Hokkaido. For. Res. Kyoto 78:81-87 (in Japanese with English summary)
725 Kitada S (2014) Japanese chum salmon stock enhancement: current perspective and
726 future challenges. Fisheries Sci 80:237–249. http://doi.org/10.1007/s12562-013-
727 0692-8
728 Kobayashi T (1953) An ecological study on the salmon fry, *Oncorhynchus keta* (3)
729 Observation on the out-migration of salmon fry, 1. Scientific reports of the Hokkaido
730 Salmon Hatchery 8:81-85 (in Japanese with English summary).
731 Kudo T, Konishi H, Kanaya M (2012) River channel changes in the Toyohira River and
732 its condition after the 2011 flood. Hokkaido Development Technology Research and
733 Presentation Meeting 2011 (in Japanese).
734 Leman VN (1993) Spawning site of Chum Salmon, *Oncorhynchus keta*:
735 microhydrological regime and viability of progeny in redds (Kamchatka River
736 Basin). Journal of Ichthyology 33:104-117
737 Leopold LB, Wolman MG, Miller JP (1964) Fluvial Processes in Geomorphology.

738 Freeman, San Francisco, CA 522 pp
739 Lisi PJ, Schindler DE, Bentley KT, Pess GR (2013) Association between geomorphic
740 attributes of watersheds, water temperature, and salmon spawn timing in Alaskan
741 streams. Geomorphology 185:78-86.
742 https://doi.org/10.1016/j.geomorph.2012.12.013
743 Lotspeich FB, Everest FH (1981) A new method for reporting and interpreting textural
744 composition of spawning gravel. U.S. Forest Service Research Note PNW-369
745 Malcolm IA, Youngson AF, Soulsby C (2003) Survival of salmonid eggs in a degraded
746 gravel-bed stream: effects of groundwater-surface water interactions. River Res
747 Appl 19:303-316. https://doi.org/10.1002/rra.706
748 Moir HJ and Pasternack GB (2008) Relationships between mesoscale morphological
749 units, stream hydraulics and Chinook salmon (*Oncorhynchus tshawytscha)*
750 spawning habitat on the Lower Yuba River, California. Geomorphology 100:527-
751 548. https://doi.org/10.1016/j.geomorph.2008.02.001
752 Montgomery DR, Buffington JM (1997) Channel-reach morphology in mountain
753 drainage basins. Geol Soc Am Bull, 109:596–611. https://doi.org/10.1130/0016-
754 7606(1997)109<0596:CRMIMD>2.3.CO;2
755 Morita K (2018) Earlier migration timing of salmonids: an adaptation to climate change
756 or maladaptation to the fishery? Can J Fish Aquat Sci 76:475-479.
757 https://doi.org/10.1139/cjfas-2018-0078
758 Morita K, Nagashima A (2015) Temperature seasonality during fry out-migration
759 influences the survival of hatchery-reared chum salmon *Oncorhynchus keta*. J Fish
760 Biol 87:1111-1117. https://doi.org/10.1111/jfb.12767
761 Morita K, Saito T, Miyakoshi Y, Fukuwaka M A, Nagasawa T, Kaeriyama M (2006) A
762 review of Pacific salmon hatchery programmes on Hokkaido Island, Japan. ICES J

763 Mar Sci 63:1353-1363. https://doi.org/10.1016/j.icesjms.2006.03.024
764 Morita K, Hirama Y, Miyauchi Y, Takahashi S, Ohnuki T, Ohkuma K (2013) Efficiency
765 of natural reproduction of chum salmon in the Chitose River, Hokkaido, Japan.
766 Nippon Suisan Gakk 79:718-720 (in Japanese).
767 https://doi.org/10.2331/suisan.79.657
768 Mouw JEB, Tappenbeck TH, Stanford JA (2014) Spawning tactics of summer chum
769 salmon *Oncorhynchus keta* in relation to channel complexity and hyporheic
770 exchange. Environ Biol Fish 97:1095–1107. http://doi.org/10.1007/s10641-013-
771 0200-0
772 Nakamura F, Seo J, Akasaka T, Swanson FJ (2017) Large wood, sediment, and flow
773 regimes: Their interactions and temporal changes caused by human impacts in Japan.
774 Geomorphology 279:176-187. https://doi.org/10.1016/j.geomorph.2016.09.001
775 Olsen JB, Flannery BG, Beacham TD, Bromaghin JF, Crane PA, Lean CF, Dunmall KM,
776 Wenburg JK (2008) The influence of hydrographic structure and seasonal run timing
777 on genetic diversity and isolation-by-distance in chum salmon (*Oncorhynchus keta*).
778 Canadian Journal of Fisheries and Aquatic Sciences 65:2026–2042.
779 https://doi.org/10.1139/F08-108
780 Peterson NP, Quinn TP (1996) Spatial and temporal variation in dissolved oxygen in
781 natural egg pockets of chum salmon, in Kennedy Creek, Washington. J Fish Biol
782 48:131-143. https://doi.org/10.1111/j.1095-8649.1996.tb01424.x
783 Rubin JF, Glimsäter C (1996) Egg-to-fry survival of the sea trout in some streams of
784 Gotland. J Fish Biol 48:585–606. https://doi.org/10.1111/j.1095-
785 8649.1996.tb01454.x
786 Sakata Y, Ito K, Ikeda R (2011) A distribution model of permeability derived from
787 undisturbed gravelly samples in alluvial fan. Japanese Geotechnical Journal 6:109-

788 119 (in Japanese with English summary). http://doi.org/10.3208/jgs.6.109
789 Salo EO (1991) Life history of chum salmon (*Oncorhynchus keta*). Pacific salmon life
790 histories. UBC Press, 233-309
791 Sapporo City History Editorial Board (1953) Sapporo Fan Area Old River Map, History
792 of Sapporo City Politics and Administration. Sapporo City, Japan.
793 Schindler DE, Hilborn R, Chasco B, Boartright CP, Quinn TP, Rogers LA, Webster MS
794 (2010) Population diversity and the portfolio effect in an exploited species. Nature
795 465:609-612. http://doi.org/10.1038/nature09060
796 Scholz NL, Myers MS, McCarthy SG, Labenia JS, McIntyre JK, Ylitalo MG, Rhodes DL,
797 Laetz AC, Stehr MC, French LB (2011) Recurrent die-offs of adult coho salmon
798 returning to spawn in Puget Sound lowland urban streams. PLoS ONE 6:e28013.
799 https://doi.org/10.1371/journal.pone.0028013
800 Smith AK (1973) Development and application of spawning velocity and depth criteria
801 for Oregon salmonids. T Am Fish Soc 102:312-316. https://doi.org/10.1577/1548-
802 8659(1973)102<312:DAAOSV>2.0.CO;2
803 Spromberg JA, Baldwin DH, Damm SE, McIntyre JK, Huff M, Sloan CA, Anulacion BF,
804 Davis JW, Scholz NL (2016) Coho salmon spawner mortality in western US urban
805 watersheds: bioinfiltration prevents lethal storm water impacts. J Appl Ecol 53:398-
806 407. https://doi.org/10.1111/1365-2664.12534
807 Suzuki T (2008) Grappling with conservation of chum salmon resource considering
808 natural reproduction. FRA Salmonid Research Report 2:3-5 (in Japanese)
809 Swales S, Lauzier RB, Levings CD (1986) Winter habitat preferences of juvenile
810 salmonids in two interior rivers in British Columbia. Can J Zool 64: 1506-1514.
811 https://doi.org/10.1139/z86-225

812 Takahashi M, Nakamura F (2011) Impacts of dam-regulated flows on channel
813 morphology and riparian vegetation: a longitudinal analysis of Satsunai River, Japan.
814 Lands Ecol Eng 7:65-77. http://doi.org/10.1007/s11355-010-0114-3
815 Thatcher HR, Downs CT, Koyama NF (2020) Understanding foraging flexibility in urban
816 vervet monkeys, *Chlorocebus pygerythrus*, for the benefit of human-wildlife
817 coexistence. Urban Ecosyst 23:1349-1357. http://doi.org/10.1007/s11252-020-
818 01014-1
819 The Geospatial Information Authority of Japan (1918) Topographic map at 1/25,000 scale.
820 The Geospatial Information Authority of Japan (2021) Flood Control Topographic
821 Classification Map.
822 Tonia D (2005) Interaction between river morphology and intra-gravel flow paths within
823 the hyporheic zone, PhD dissertation, 129 pp, Univ. of Idaho, Boise
824 Tonia D, Buffington JM (2011) Effects of stream discharge, alluvial depth and bar
825 amplitude on hyporheic flow in pool-riffle channels. Water Resour Res 47:1-13.
826 https://doi.org/10.1029/2010WR009140
827 Ueta M, Koita M, Fukui K (1999) The relationship between the autumn distributions of
828 salmon and of Steller's and White-tailed Sea Eagles in Hokkaido, Japan. Strix 17:
829 25-29 (in Japanese with English summary)
830 Webb HJ, McLay HA (1996) Variation in the time of spawning of Atlantic salmon (*Salmo*
831 *salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. Can J
832 Fish Aquat Sci 53:2739-2744. https://doi.org/10.1139/f96-240
833 Winter TC, Harvey JW, Franke OL, Alley WM (1998) Groundwater and surface water, a
834 single resource. US Geological Survey Circular 1139
835 Wohl E, Allen AO, Mersel MK, Kichefski SL, Fritz KM, Lichvar RW, Vanderbilt FB

(2016) Synthesizing the scientific foundation for ordinary high water mark delineation in fluvial systems. US Army Engineer Research and Development Center (ERDC) Hanover United States.

Wookey OA (2022) Human-wildlife coexistence in the urban domain: promoting welfare through effective management, responsibility and the recognition of mutual interest. Human/Animal Relationships in Transformation 317-338. http://dx.doi.org/10.1007/978-3-030-85277-1_15

Zari MP (2018) The importance of urban biodiversity – an ecosystem services approach. Biodiversity International Journal 2:357-360. http://dx.doi.org/10.15406/bij.2018.02.00087

Zhou T, Endreny AT (2013) Reshaping of the hyporheic zone beneath river restoration structures: flume and hydrodynamic experiments. Water Resour Res 49:1-12. https://doi.org/10.1002/wrcr.20384

Table 1 Inter-spawning group comparison of environmental variables (mean ± SD) and numbers of dead eggs by run-times of chum salmon in the Toyohira River, Japan (The original data is presented in Table S3). The number of dead eggs reported from the buried-egg experiment is the number of dead eggs per 200 eggs initially buried, with the corresponding mortality rate (%) in parentheses. The loadings of each environmental factor on PC1 and PC2 (with eigenvalues of >1.0), the proportion of each PC's account variability (%), and the results of each GLMM model are shown.

856

Variable	Early-run	Late-run			Factor loading	
					PC1 (56.0%)	PC2 (27.5%)
Environmental variables			*F*	*p*-value		
Flow velocity (cm/s)	31.0 ±11.5	22.0 ± 19.7	0.776	0.404	0.756	−0.339
Water depth (cm)	32.9 ± 5.6	23.2 ± 12.8	2.382	0.161	0.965	0.054
Fredle index	11.3 ± 8.6	9.4 ± 2.2	0.233	0.642	−0.046	0.947
Maximum riverbed temperature during winter (°C)	2.7 ± 0.8	5.5 ± 1.9	8.541	0.019	−0.857	−0.289
Number of dead eggs						
Egg to hatching stage	11.1 ± 3.3 (5.6%)	25.0 ± 7.9 (12.5%)				
Egg to emergence stage	4.8 ± 6.4 (2.4%)	58.7 ± 31.1 (29.4%)				
Model			χ^2	*p*-value		
RunTime model: Dead eggs ~ RunTime + Stage						
RunTime			67.93	<0.001		
Stage			0.66	0.418		
PC model: Dead eggs ~ PCs + Stage						
PC1			6.60	0.010		
PC2			0.44	0.507		
Stage			0.25	0.616		

857

858 **FIGURE LEGENDS**

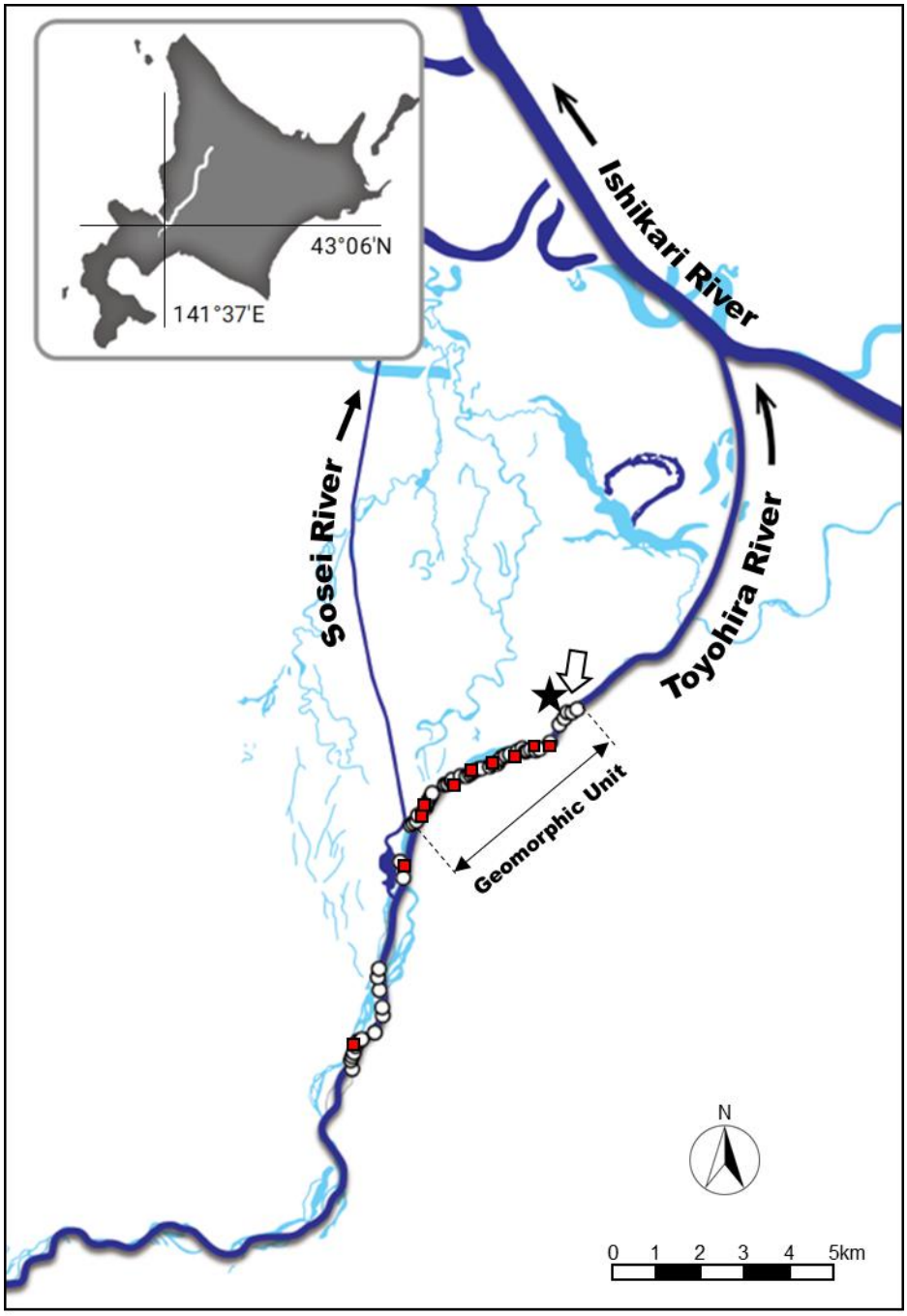
859 **Fig. 1** Map showing the current, straightened channel of the Toyohira River (dark blue),
860 Hokkaido, Japan, and the likely configuration of the river's meandering or braided
861 channels circa 1900 (light blue) (sources: Geospatial Information Authority of Japan
862 [1918, 2021]; Sapporo City History Editorial Board [1953]; and The Japan Map
863 Center [1995]). Dashed lines mark the study area of the geomorphic units; red
864 squares denote locations in the buried-egg experiment; open arrows show the
865 locations of fry out-migration traps; and open circles signify the spawning redds of
866 chum salmon in 2020. The thinner dark blue line labeled the Sosei River is an
867 artificially excavated waterway created in the 1870s. The discharge volumes on Fig.
868 S1 is recorded at the Kariki point indicated by a star symbol.

869 **Fig. 2** Schematic diagram of the Toyohira River riverbed and floodplain geomorphology
870 in the metropolitan area (Sapporo city), depicting hyporheic and groundwater flows
871 (modified from Geist and Dauble [1998]; Tonia [2005]). The riverbed is demarcated
872 into two distinct zones: the floodplain, which is utilized for human activity, and the
873 low-flow channel, where river water flows between revetments during normal water
874 levels. The channel was divided into riffles (thin blue arrows) and pools (thick blue
875 arrows); there is a downwelling zone upstream of gravel bars (open arrows), with
876 hyporheic flows through the gravel bar (dashed blue lines), and an upwelling zone
877 downstream or to the side of gravel bars (gray arrows). Because the groundwater
878 level was higher than the lowest riverbed elevation, groundwater would seep into
879 the secondary channels (dashed red arrows). A series of groundsills (parallel black
880 lines) have been constructed across the riverbed.

881 **Fig. 3** Proportion of the geomorphic units available for spawning chum salmon (hatched

882 bars, n = 1,665 total units) and the units where salmon built redds (early-run group:
883 filled bars, n = 518 redds; late-run group: open bars, n = 132 redds).
884 **Fig. 4** The proportion (**a**) and numbers (**b**) of chum salmon spawning redds by
885 geomorphic unit, as recorded in each survey that was conducted over one spawning
886 season, from September 2020 to January 2021. The geomorphic units suitable for
887 chum salmon to spawn were categorized as: upwelling zone of gravel bars (dark
888 gray), riffles (light gray), secondary channels (unfilled), or other morphology
889 (vertical stripes). Fitted logistic regressions show the accumulated probability for
890 the habitats: upwelling zone of gravel bars (solid black line), riffles (solid grey line),
891 and secondary channels (dashed black line).
892 **Fig. 5** Relationship between the principal component score (PC1) and the numbers of
893 dead eggs in the buried-egg experiment (per 200 eggs) at the end of the egg-to-hatch
894 stage (solid line, filled circles: early-run group; filled squares: late-run group), and
895 at the end of the egg-to-emergence stage (dashed line, open circles: early-run group;
896 open squares: late-run group). Regression lines are from the GLMM in Table 1.
897 **Fig. 6** Relationships between the total number of chum salmon spawning redds (gray
898 circles), the number of spawning redds of the early-run group (filled circles), the
899 number of spawning redds of the late-run group (open circles), and the estimated
900 total number of out-migrating fry. A liner regression line is shown for a significant
901 relationship. r is the Pearson's correlation coefficients for the early-run, the late-run,
902 and the total spawning redds. Asterisk denotes significance at $p < 0.001$.
903

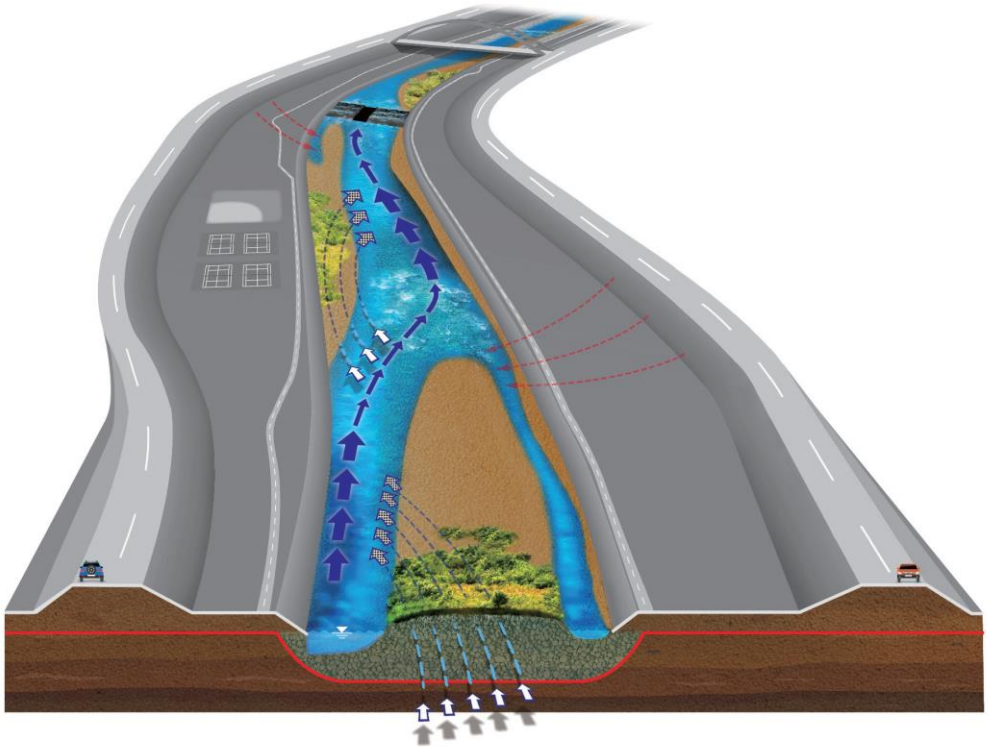
904 **Fig. 1**



905

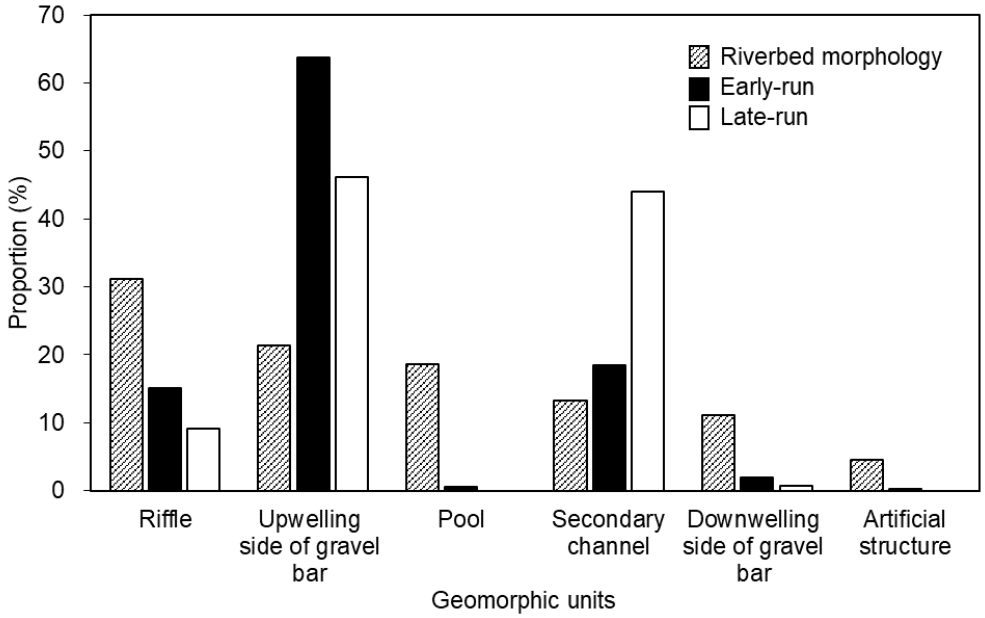
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907 **Fig. 2**



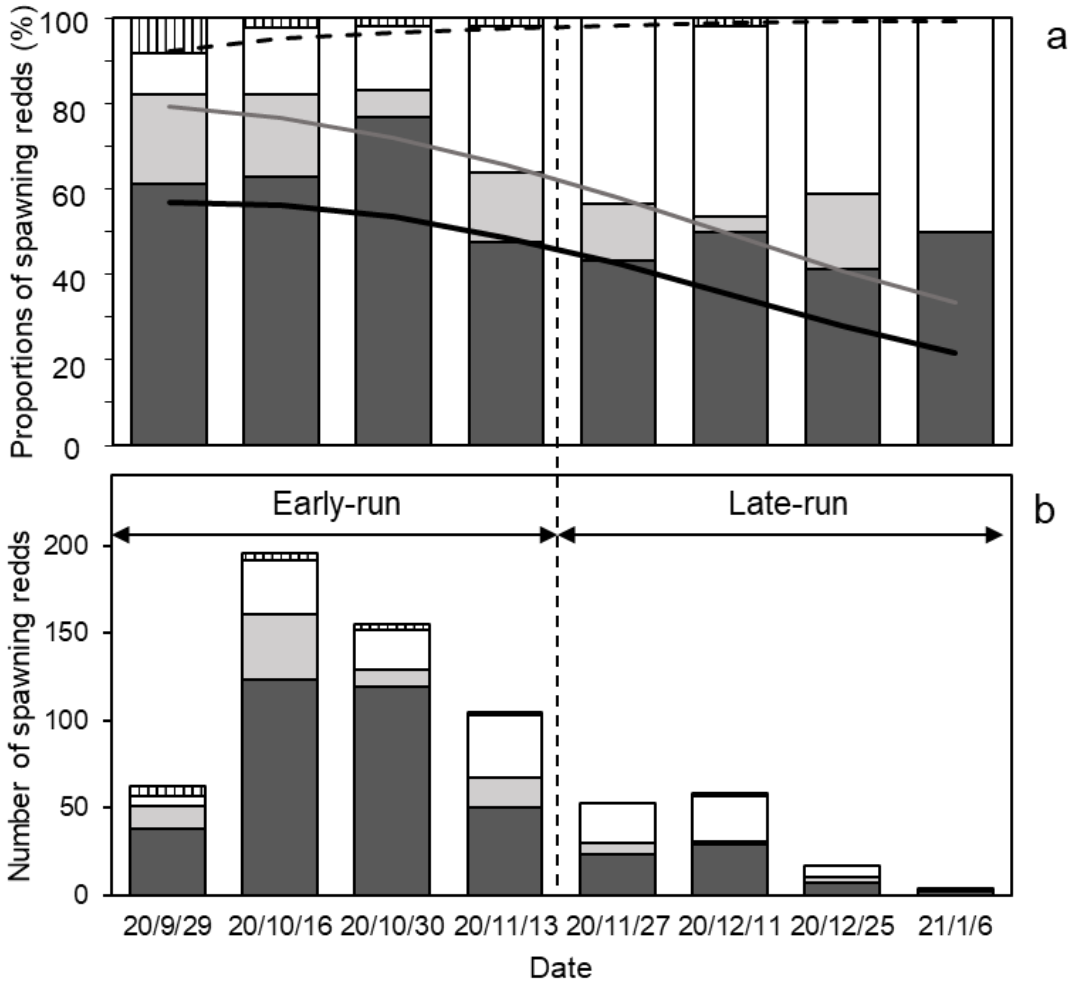
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Fig. 3


70
60
50
40
30
20
10
0
Proportion (%)
Riverbed morphology
Early-run
Late-run
Riffle
Upwelling side of gravel bar
Pool
Secondary channel
Downwelling side of gravel bar
Artificial structure
Geomorphic units

913 **Fig. 4**

914



915

916

Fig. 5

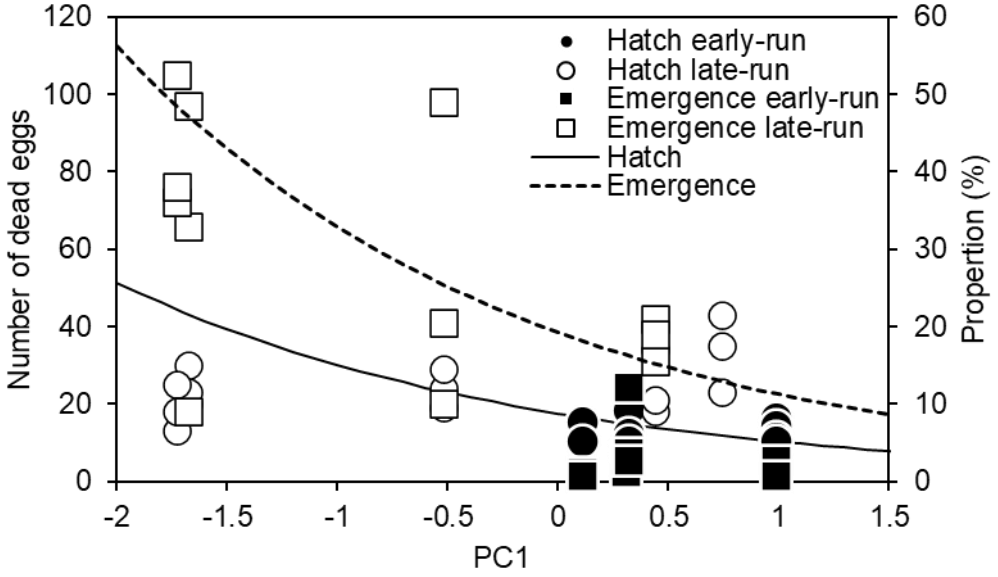
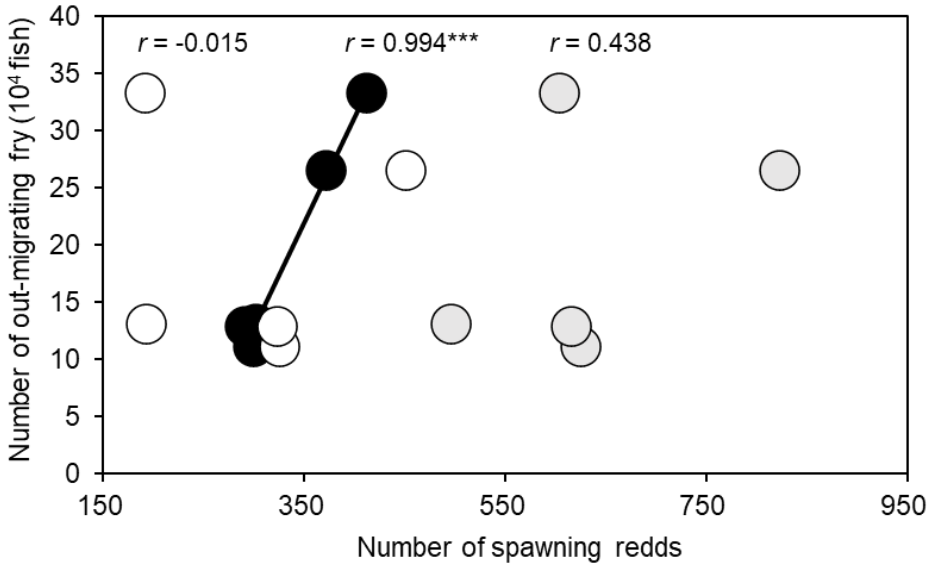

Hatch early-run
Hatch late-run
Emergence early-run
Emergence late-run
Hatch
Emergence
Number of dead eggs
Propertion (%)
PC1
120
100
80
60
40
20
0
60
50
40
30
20
10
0
-2
-1.5
-1
-0.5
0
0.5
1
1.5

Fig. 6


r = -0.015
r = 0.994***
r = 0.438
Number of out-migrating fry (10⁴ fish)
Number of spawning redds
0
5
10
15
20
25
30
35
40
150
350
550
750
950