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Original Article

Phenological diversity of a prey species supports life-stage specific foraging opportunity for a mobile consumer

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Dynamic prey resources influence foraging opportunities for consumers. In coastal food webs, forage fish abundance and seasonal reproduction mediate foraging opportunities for mobile consumers. Recent declines in Chinook salmon productivity have prompted efforts to determine whether poor marine survival is caused by limited feeding opportunities. To establish the importance of phenological diversity in Pacific herring for Chinook salmon, we used genetic stock identification to assign individual herring collected from the guts of juvenile and adult Chinook salmon to populations with distinct spawning phenologies. The majority of herring in the guts of adult Chinook salmon across seasons and geographic areas were dominated by the March–April herring spawn group, but juvenile Chinook salmon diets varied seasonally, with a higher proportion of January–February spawners in summer than in spring. Our results suggest that (1) population diversity of Pacific herring is used by juvenile Chinook salmon and thus contributes to their growth, and (2) stock-specific distribution of Pacific herring extends well beyond documented spawning grounds. Herring population diversity may therefore support foraging opportunities for Chinook salmon during a critical period and highlights the need for future research to quantify seasonal distribution and abundance of phenologically distinct groups of Pacific herring within Salish Sea.

Keywords: consumption, Chinook salmon, Pacific herring, phenology, population genetics.

Introduction

Trophic resources often exhibit variation in their abundance, quality, and accessibility to consumers. Spatial and temporal overlap between consumers and their prey (Cushing, 1969; Cushing, 1990) as well as developmental changes in prey or predator size (Polis *et al.*, 1989) may regulate resource availability and influence recruitment to consumer populations. As a result of these phenomena, consumers are faced with variable foraging opportunities that influence their growth and survival. Phenological and spatial diversity in food resources can prolong foraging opportunities for mobile consumers (Armstrong *et al.*, 2016). For example, herbivore populations follow shifting plant resources as a function of plant growth in response to precipitation across landscapes (Aikens *et al.*, 2017). In aquatic systems, predators such as bears and gulls track asynchronous spawning assemblages of sockeye salmon across a watershed in order to maximize foraging opportunities (Schindler *et al.*, 2013). However, there are few examples (e.g., Lok *et al.*, 2012) demonstrating the importance of phenologically diverse prey populations in marine systems, in part because of difficulties in reliably distinguishing populations in many marine species.

Forage fish are particularly important to marine food webs (Pikitch *et al.*, 2014) and often represent a considerable proportion of the pelagic community, thus providing a reliable source of energy for consumers. Along the Pacific Coast of North America, forage fish species account for > 75% of total nekton biomass (Brodeur *et al.*, 2005) and are consumed by many predators such as seabirds (Cury *et al.*, 2011), marine mammals (Alder *et al.*, 2008), and migratory fishes (Litz *et al.*, 2017). Although generally abundant, schooling forage fishes tend to have patchy spatial and temporal distributions driven by oceanographic and environmental conditions as well as life history strategies and behaviors (Emmett *et al.*, 2005; Brodeur *et al.*, 2006; Duguid *et al.*, 2019). The degree to which forage fish vary in their distribution and abundance likely influences their accessibility to populations of predators.

Pacific herring (*Clupea pallasii*) constitute a large proportion of the forage fish assemblage and an important component of the food web (Brodeur *et al.*, 2005; Willson and Womble, 2006) in the Northeast Pacific Ocean. Although herring are common throughout their range, differences in the seasonal distribution, abundance, and spawn timing of herring populations may influence their interactions with predators (Womble and Sigler, 2006; Murphy *et al.*, 2014). While the location of herring spawning can determine spatial overlap between herring and potential predators, the timing of herring spawning may influence temporal overlap as well as the relative size of individual herring compared to potential predators. Most herring in the northeastern Pacific spawn from January to April (Beacham *et al.*, 2008) but several populations spawn later in the year in May and June (Small *et al.*, 2005; Beacham *et al.*, 2008). This variability in reproductive timing forms a resource wave that gives mobile consumers the opportunity to access herring in the nearshore environment over an extended time (Willson and Womble, 2006; Lok *et al.*, 2012) and at a variety of developmental stages and sizes. Herring with different spawn times are relatively isolated from each other (Petrou *et al.* 2021), and can be assigned to specific spawning groups with genetic markers. This genetic and life history diversity in Pacific herring may be important to the diets of marine predators by regulating prey abundance and size availability.

One such predator of herring is Chinook salmon (*Oncorhynchus tshawytscha*), a culturally and economically important anadromous fish with distinct population segments federally recognized as "threatened" or "endangered" under the Endangered Species Act of the United States and as "threatened," "endangered," or of "special concern" by the Committee on the Status of Endangered Wildlife in Canada. Chinook salmon inhabit riverine and coastal environments along the west coast of North America. During their residence in coastal marine waters, adult Chinook salmon are almost exclusively piscivorous and prey heavily on Pacific herring to maintain growth (Daly *et al.*, 2009). Juvenile Chinook salmon also incorporate Pacific herring into their diets, especially when herring of the appropriate size are present and abundant (Chamberlin *et al.*, 2017; Davis *et al.* 2020). It has been hypothesized that variability in the growth of juvenile Chinook salmon is driven by differences in the availability and abundance of Pacific herring (Chamberlin *et al.*, 2017). In particular, young-of-year juveniles of May-spawning herring are thought to be an important prey resource for gape-limited juvenile salmon during early marine residence (Chamberlin *et al.*, 2017). Given the complex migrations and multiple life stages of Chinook salmon present in coastal environments, it is plausible that the underlying population structure of Pacific herring influences the spatial, temporal, and demographic overlap between herring and Chinook salmon and dictates resource availability for individuals at sea.

Recent declines in the abundance of Chinook salmon populations have prompted research efforts to identify the factors contributing to reduced survival and productivity. Growth during early life history stages has been linked to survival in Chinook salmon (Duffy and Beauchamp, 2011; Tomaro *et al.*, 2012; Howard *et al.*, 2016), therefore research has been focused on quantifying the relationships between salmon and their prey. While the importance of herring as prey for Chinook salmon is well documented (Chamberlin *et al.*, 2017), the extent to which different populations of herring support piscivory and influence the growth of juvenile and adult Chinook salmon is currently unknown.

In this study, we quantify the relative contributions of phenologically distinct populations of herring to Chinook salmon diets by analyzing herring DNA collected from the gut contents of juvenile and adult salmon. The overarching goal of our study is to assess the effects of life history diversity of a prey population on the feeding strategy of a threatened species. Specifically, we ask the following questions: (i) Which populations of herring do Chinook salmon prey upon? (ii) Does the proportion of different herring populations in salmon diets vary as a function of season, geography, or salmon life stage? We also address the hypotheses from Chamberlin *et al.* (2017) that May-spawning herring will be disproportionately represented in juvenile salmon diets because these populations likely produce appropriately sized prey for juvenile salmon during their early marine rearing period. Our work will build upon research linking the ecology of Pacific herring with the growth and survival of Chinook salmon (Chamberlin *et al.*, 2017; Davis *et al.*, 2020; Duguid *et al.*, 2021).

Methods

Study site

We quantified the population-specific consumption of Pacific herring by Chinook salmon in the Salish Sea, a large inland sea spanning the border between northern Washington State and southern British Columbia. The Salish Sea comprises the Strait of Georgia (SoG) to the north and Puget Sound (PS) to the south, both of which are connected to the Pacific Ocean via the Strait of Juan de Fuca (Figure 1). Oceanographic conditions throughout the Salish Sea are dominated by large river flows, and each sub-basin differs slightly with respect to stratification, tidal mixing and thermal regimes. The Strait of Georgia is strongly influenced by the Fraser River, the largest source of freshwater input into the sea, which maintains a highly stratified and productive environment in the northern Salish Sea (Griffin and LeBlond, 1990; MacCready *et al.*, 2021). Puget Sound is characterized by a number of freshwater inputs as well as a series of sills and fjordal complexes that encourage tidal mixing and create a mosaic of thermal conditions (Babson *et al.*, 2006; MacCready *et al.*, 2021). The Strait of Juan de Fuca is primarily influenced by conditions along the coast and temperatures remain relatively cooler than other parts of the Salish Sea throughout the year (Chandler, 2020).

Chinook salmon collection

We used targeted sampling efforts, archived collections (Gamble *et al.*, 2018), and opportunistic collections by recreational anglers (Quindazzi *et al.*, 2020) to obtain salmon gut contents. Individual

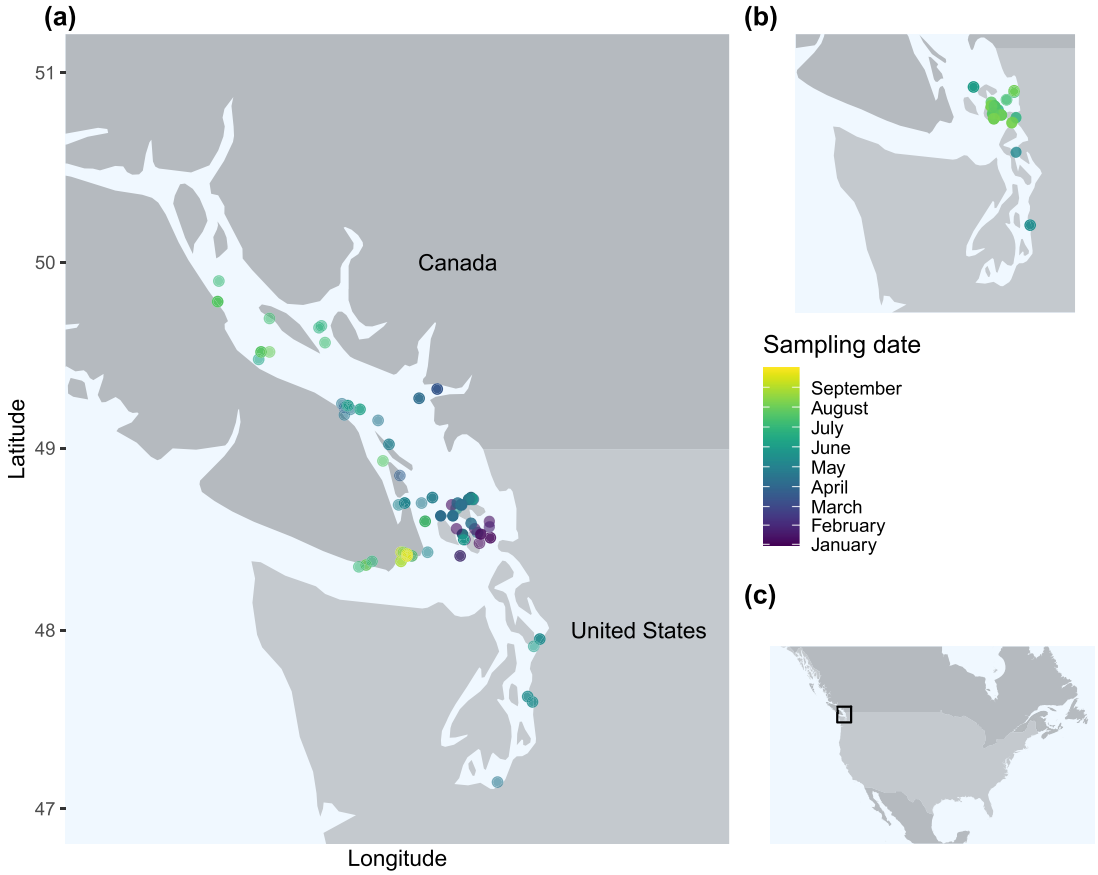

Figure 1. Sampling locations of adult (a) and juvenile (b) salmon collected from the Salish Sea. Salmon were classified as juveniles if they were less than 25 cm fork length. The black rectangle (c) shows the relative geographic location of the Salish Sea.

Chinook salmon were classified in subsequent analyses as either juvenile ($\leq$ 25 cm) or adult ($>$ 25 cm) based on their length. Juvenile Chinook salmon were collected from May to August (2014–2018) using beach seines and purse seines (see Gamble *et al.*, 2018 for detailed description of methods) under the appropriate federal permits for Canada and the United States. Adult Chinook salmon were collected entirely by hook and line from January to September (2014–2019), and were generally captured from small boats by trolling at depths of 10–90 m and using a variety of lures and bait. In addition to targeted sampling efforts, we supplemented our adult Chinook salmon collections via opportunistic sampling by recreational anglers and during fishing derbies. Adult salmon collected opportunistically were obtained under recreational fishing licenses and thus subject to size restrictions (Washington State: $>$ 56 cm; British Columbia $>$ 45 or $>$ 62 cm depending on region) and season/area closures. These restrictions resulted in unequal sample distributions through space and time and a bias toward larger (i.e. legal size) Chinook salmon. To offset the potential size bias in adult samples collected by recreational anglers, we also supplemented our collections with sub-legal size adult Chinook salmon (between 25 and 56 cm) captured throughout the year under a US federal permit. However, the supplemental adult sampling under this permit was restricted geographically to the Puget Sound and thus no herring were collected from sub-legal size Chinook salmon in Canadian waters. As such all samples that were classified as "juvenile" were also limited geographically to US waters.

For each individual salmon, we recorded the following data: capture location, date, length, and weight. The majority of gut contents were obtained through lethal retention of individual Chinook salmon. When whole guts were extracted, samples were quickly frozen or placed on ice for transport to the lab for processing. A subset of gut content samples was collected using gastric lavage following methods in Gamble *et al.* (2018). Gut contents sampled via lavage were placed into individually labeled bags with seawater and frozen prior to transport.

Gut content processing

Prey items were identified based on their external morphology. Fish prey were first separated from other contents and identified to species. Partially digested prey items were identified based on diagnostic hard parts or similarity to positively identified fish within the same stomach using reference collections. Length and weight of each intact herring were measured directly. For heavily digested herring, individual lengths were estimated using a log-linear regression of otolith width to standard length in intact fish such that:

$$\mathrm{Log}\left(\mathrm{standardlength}\right) \sim \mathrm{Log}\left(\mathrm{otolithwidth}\right) * 1.2635 + 4.4027;\ \mathrm{adj}R^2 = 0.937,\ \mathrm{p} < 0.001$$

A total of $N = 72$ herring lengths were estimated using this regression method (Supplementary Table S1). When necessary, Pacific herring measured to standard length were converted to

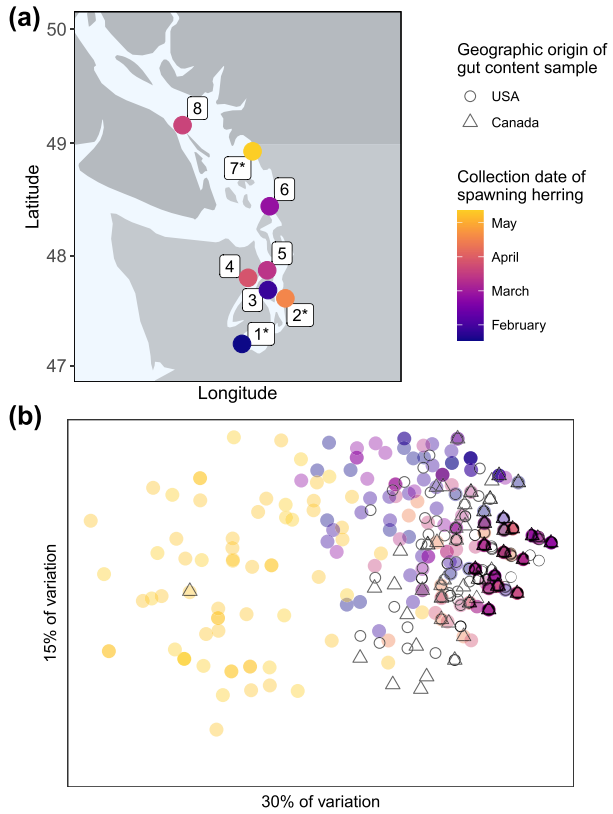

Figure 2. (a) Locations of Herring collections on spawning grounds. Numeric labels match the map codes in Supplementary Table S1. Locations with an asterisk after the numeric label indicate that additional samples were collected at those sites to assess the accuracy of mixed stock analysis. The colour of each point represents the date of spawning and sample collection. For additional information on the classification of spawning populations into reporting groups, please see Supplementary Table S1 and Supplementary Figure S1. (b) PCA of herring samples collected from spawning grounds (colorful points) and salmon gut contents (open shapes).

fork length to enable combination of datasets for analysis using species-specific values as reported in Karpov and Kwiecien (1988). Where herring were heavily digested and no otoliths were obtained ($N = 71$) we were unable to measure lengths accurately. These samples were removed from any analysis using fork length but retained for genetic analysis. Finally, a clean scalpel was used to remove a small piece (0.5 cm^2) of tissue or bone from herring samples and stored in 100% ethanol for molecular analysis.

Development of SNP assays from spawning herring

Herring populations spawning at different times of year are genetically distinct from each other (Petrou *et al.*, 2021). We used restriction-site associated DNA (RAD) sequencing data reported in Petrou *et al.* (2021) to identify reporting groups and select highly divergent loci for genetic stock identification. In brief, these RAD data consist of 347 herring collected from eight distinct spawning aggregations in the Salish Sea (Figure 2a and Supplementary Table S1) and genotyped at 6718 polymorphic RAD loci. Reporting groups for mixed stock analysis were designed to represent three major biological groups of herring that reproduce in the Salish Sea: January-February spawners, March–April spawners, and May-spawners (Supplementary Figure S1 and Supplementary Table S2). We identified seven SNPs showing high differentiation between these groups (Supplementary Table S2) and developed custom TaqMan™ assays (Thermo Fisher Scientific, Waltham, MA) to genotype SNPs at these highly divergent loci. Detailed information on locus selection and assay development is included in the Supplemental Material.

We evaluated whether the seven highly divergent loci could be used to estimate the proportion of populations in a mixed-stock fishery using the Bayesian method of Moran and Anderson (2018) that is implemented in the R package *rubias*. In brief, this approach uses Markov chain Monte Carlo (MCMC) to estimate the proportion of individuals in a mixture that originate from different reference populations (or aggregates of reference populations known as reporting groups), given genotypic data in those reference populations. We assessed the predicted accuracy of mixed stock analysis by simulating multiple mixtures of known mixture proportions using herring samples collected from spawning herring (simulated mixture size = 48 individuals; number of repetitions of mixture simulation and MCMC = 50) and comparing estimated with simulated mixture proportions. Individual genotypes in the simulated mixtures were generated by sampling from the allele frequency distribution of a reference population, following the "leave one out" method (Moran and Anderson, 2018). We also conducted "100% simulations," where all simulated individuals in the mixture were generated from the allele frequency distribution of a single reference population. We analyzed the simulated data using three reporting groups (January–February spawners vs. March–April spawners vs. May spawners).

To avoid upward bias in the predicted accuracy of mixed stock analysis, we followed the recommendations of Anderson (2010) and empirically tested the accuracy of these seven loci for mixed stock analysis. This was accomplished by genotyping additional herring samples that were not part of the genetic baseline used to select the set of seven loci (double cross-validation *sensu* Anderson, 2010). These additional samples of spawning herring ($N = 119$) were collected from three different locations belonging to the three different reporting groups in the Salish Sea: Squaxin Pass (January–February spawners), Elliot Bay (March–April spawners), and Cherry Point (May spawners, Supplementary Table S3).

DNA extraction and SNP genotyping of gut content samples

Before DNA extraction, each herring sample collected from salmon gut contents was treated with bleach to remove exogenous DNA contamination (Petrou *et al.*, 2019). DNA was subsequently extracted from each sample using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA).

In order to increase the amount of template DNA available for TaqMan genotyping reactions, we first conducted a preamplification PCR with all primers following the protocol of Smith *et al.* (2011). Preamplification reactions were conducted in 10 µl volumes containing Qiagen Multiplex PCR Master Mix, 0.2 µM of each forward and reverse SNP primer, ultra-pure water, and 4 µl of template DNA. Thermal cycling was performed on a Bio-Rad C1000 Touch (Hercules, CA), using these conditions: initial denaturation at 95°C

for 15 min, followed by 14 cycles of 94°C for 30 s, 57°C for 90 s, 72°C for 60 s, and a final extension of 72°C for 10 min.

We diluted these preamplification PCR products at a 1:3 ratio for use in subsequent TaqMan genotyping reactions. All genotyping reactions took place in 12 µl volumes containing 1X TaqMan Universal PCR Master Mix, 1X TaqMan assay, nuclease-free water, and 2 µl of template DNA. Thermal cycling was performed on an Applied Biosystems 7900HT Fast Real-Time PCR system (Foster City, CA) as follows: initial denaturation at 95°C for 10 min, followed by 60 cycles of 95°C for 15 s and 60°C for 60 s.

Genetic stock identification of gut content samples

Patterns of genetic differentiation in the herring samples were visualized using a PCA conducted with the R package *adegenet* (Jombart and Ahmed 2011). To estimate the proportions of genetically distinct herring populations in salmon diets, we conducted a mixed stock analysis using the Bayesian method described in Moran and Anderson (2018) and implemented in the R package *rubias*. Herring collected from spawning grounds (Figure 2a) were designated as reference populations, while gut content samples were analyzed as mixed fisheries. Gut content samples were sorted into sets based on predator fork length (< 25 cm = juvenile; >25 cm adult) and season of capture (winter: December–March, spring: April–June, and summer: July–September) and each set was analyzed separately. We conducted mixed stock analyses (number of MCMC iterations = 10 000 and burn-in steps = 1000) on these sets of samples using three reporting groups for herring (January–February spawners vs. March–April spawners vs. May-spawners). We identified the most likely reporting group of origin for individual herring using the individual posterior probabilities of assignment estimated by *rubias*. To compare proportions of herring reporting groups between juvenile and adult Chinook guts within a season and separately, but between seasons, we used Fishers exact test for small sample sizes. For the analyses of prey/predator length relationships, individual herring were assigned to a specific reporting group using the sum of posterior probabilities across collections in a reporting group. We subsequently used linear mixed models, with individual salmon as a random effect, to evaluate the relationship between predator and prey length by for adult and juvenile salmon separately in R.

RESULTS

Gut content collections

From 2014 to 2019, we sampled gut contents from a total of 256 Chinook salmon (SI Data 1). Sampling occurred from January to September, and the number of salmon captured in each month varied from $N = 11$ in February to $N = 142$ in April. Adult salmon were captured in most months, while juvenile salmon were only collected in spring and summer (Figure 1). Juvenile salmon fork lengths ranged from 7.8 to 21.5 cm, while adult fork lengths ranged from 27.1 to 96.0 cm (Figure 3).

A total of 544 Pacific herring were identified in the stomachs of these salmon (SI Data 1). Most herring samples ($N = 419$) were collected from the guts of adult salmon, and a smaller number of herring ($N = 116$) were collected from juvenile salmon or salmon whose fork lengths were not recorded ($N = 9$). Herring standard length ranged from 2.2 to 23.0 cm, with the smallest herring sampled during spring and summer collections (Figure 3). Herring lengths were positively correlated with salmon lengths for adult Chinook salmon captured during spring (coef = 1.113, $p = 0.001$; Supplementary Figure S3). There was no statistically significant relationship ($p > 0.05$) between predator and prey size for the remaining collections of juvenile and adult Chinook salmon (Supplementary Figure S3).

Evaluation of loci for mixed stock analysis

We identified seven loci that were highly differentiated between herring populations spawning at different times of year (additional details in Supplemental Material). A total of five of these loci were located within genes (*THSb, CADPS, SYNE2, NFATC2*, and *GRB2*) and two were in intergenic regions. We evaluated whether these seven loci could be used to estimate the proportion of distinct populations in a mixed fishery using simulated data. With three reporting groups (January–February spawners vs. March–April spawners vs. May-spawners), the correlation between simulated and estimated stock proportions was $r^2 = 0.69$ for January–February spawners, $r^2 = 0.62$ for March–April spawners, and $r^2 = 0.88$ for May spawners (Figure 4a). Simulated mixtures originating from a single reporting group (also known as 100% simulations) resulted in mean estimates of mixture proportions of ranging from 82 to 98% (Figure 4b). Empirical herring samples that were not used in locus selection (Supplementary Table S3) yielded high estimates of the proportions of the correct reporting group (97–99%, Figure 4c).

Genetic analysis of herring from salmon gut contents

We were able to successfully genotype 90% of herring ($N = 489$) collected from salmon gut contents at six or more SNP loci, and negative controls did not amplify in any genotyping reaction. PCA showed that almost all samples collected from salmon gut contents clustered with herring populations that spawn in winter (January–February) and early spring (March–April; Figure 2b). Only one herring collected from gut contents was assigned to the May-spawning population: this herring was captured in June from the Canadian Gulf Islands and had a standard length of 13.4 cm.

Between 96% (Credible Interval (CI): 91–100%) and 99% (CI: 97–100%) of herring eaten by adult salmon across all sampling seasons originated from populations spawning in March and April (Figure 5). However, juvenile salmon exhibited some seasonal variation in their diets. In spring, 96% (CI: 88–100%) of herring consumed by juvenile salmon were March–April spawners while in summer 81% (CI: 63–96%) of herring were March–April spawners and 18% (CI: 4–36%) were January–February spawners (Figure 5).

Using the individual posterior probabilities of assignment, we evaluated differences in the proportions of herring spawn groups among and between juvenile and adult Chinook salmon and across seasons. Juvenile Chinook salmon consumed a significantly greater proportion of January–February spawners than adult Chinook salmon during the summer (Fisher exact test; $p = 0.003$). Juvenile Chinook salmon also consumed more January–February spawners during summer than they did in the spring ($p = 0.045$). Proportions of herring reporting groups were not different for juvenile and adult Chinook salmon during spring and did not vary at all seasonally for adult Chinook salmon.

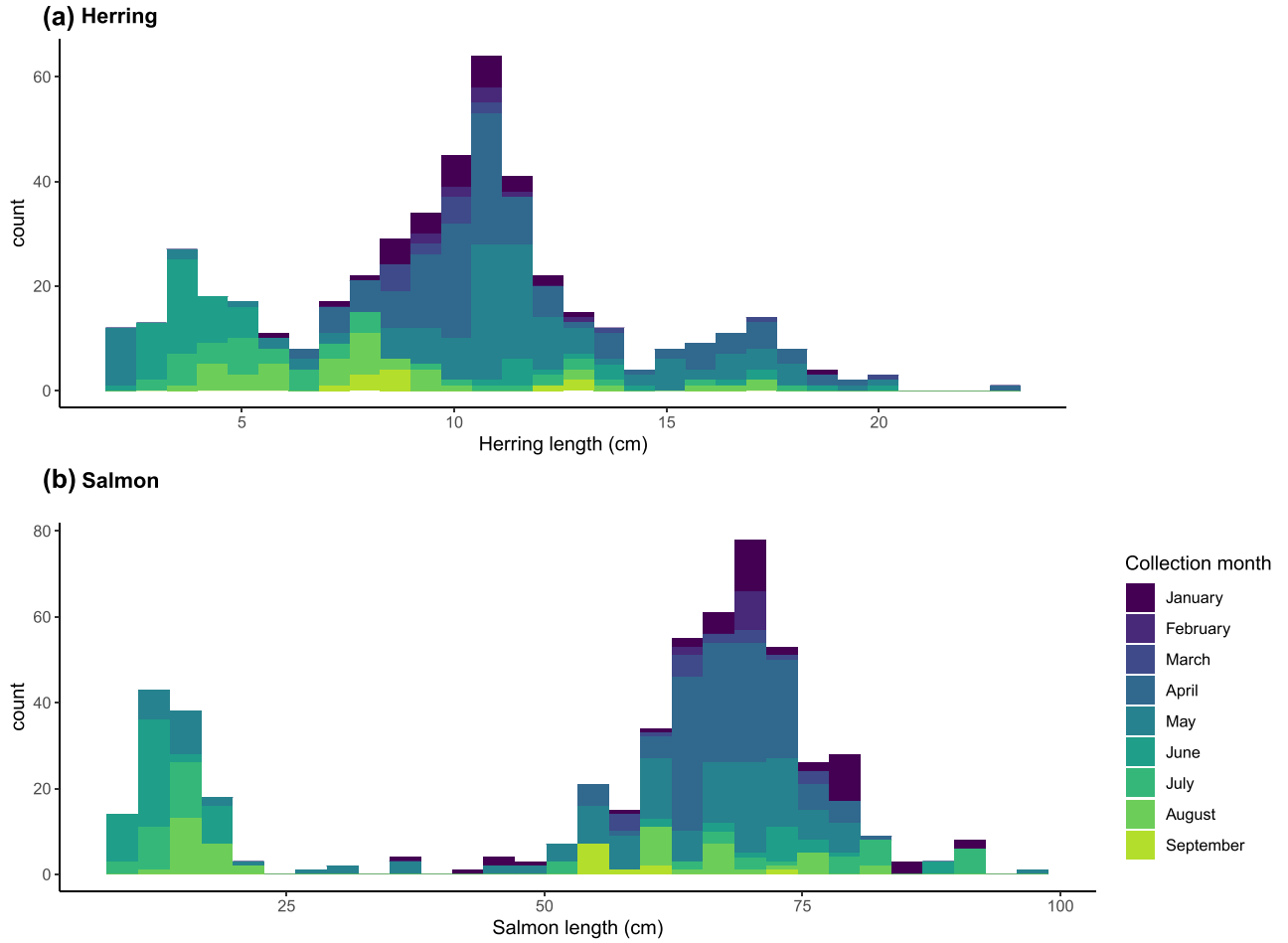

Figure 3. Fork length distributions for (a) herring and (b) salmon analyzed in this study; bars are colored by the month in which sampling occurred. See Supplementary Figures S3 and S4 for the relationship between predator length, prey length, and genetic assignments.

DISCUSSION

By analyzing the gut contents of juvenile and adult Chinook salmon using genetic stock identification, we were able to identify herring populations that are important prey resources for Chinook salmon and highlight how population diversity of a prey species supports consumption for an important predator species. Adult Chinook salmon overwhelmingly consumed herring that spawned in early spring (March–April spawners) and this pattern was consistent across all sampling seasons and geographic locations. In contrast, juvenile salmon ate seasonally variable mixtures of herring. In spring, juvenile salmon predominantly consumed March–April spawners, while in summer juvenile salmon diversified their diets and also preyed upon greater proportions of January–February spawners (Figure 5).

Overall, the contribution of Pacific herring spawning groups to Chinook salmon diets were similar to the relative proportions from estimated spawning biomass of herring in the Salish Sea (Haegele and Schweigert, 1985; Sandell *et al.*, 2019; Figure 6). This may be expected given the overwhelming contribution of the "primary spawners" in the Strait of Georgia and the recent record production of Quilcene Bay in Puget Sound to the overall herring biomass in the region (both stocks spawn in March and April). However, the increased proportion of January–February spawners in juvenile Chinook salmon summer diets appears to be greater than expected based on spawning biomass. Much more information is needed to determine if these changes significantly differ from the relative proportions of the different spawning groups in the environment. Spawning biomass estimates represent only a spatial and temporal snapshot of estimated biomass, as these surveys are limited to spawning grounds during the spawning season. While data on the seasonal abundance and distribution of juvenile herring are available (Beamer and Fresh, 2012; Chamberlin *et al.*, 2017; Boldt *et al.*, 2019), these data do not differentiate between the genetically distinct spawning groups. In the discussion below, we describe several potential processes or mechanisms that may influence the contribution of specific herring spawning groups to juvenile and adult Chinook salmon diets.

Processes contributing to predator-prey interactions between salmon and herring

Spatial and temporal overlap between consumers and their prey can influence foraging opportunities (Albon and Langvatn, 1992; Armstrong *et al.*, 2016). However, the seasonal movements and distribution of Pacific herring in the Salish Sea outside of their spawning season are still poorly understood. Early research on herring distributions in British Columbia (and specifically the Strait of Georgia) suggested that populations may be either "resident" (i.e.

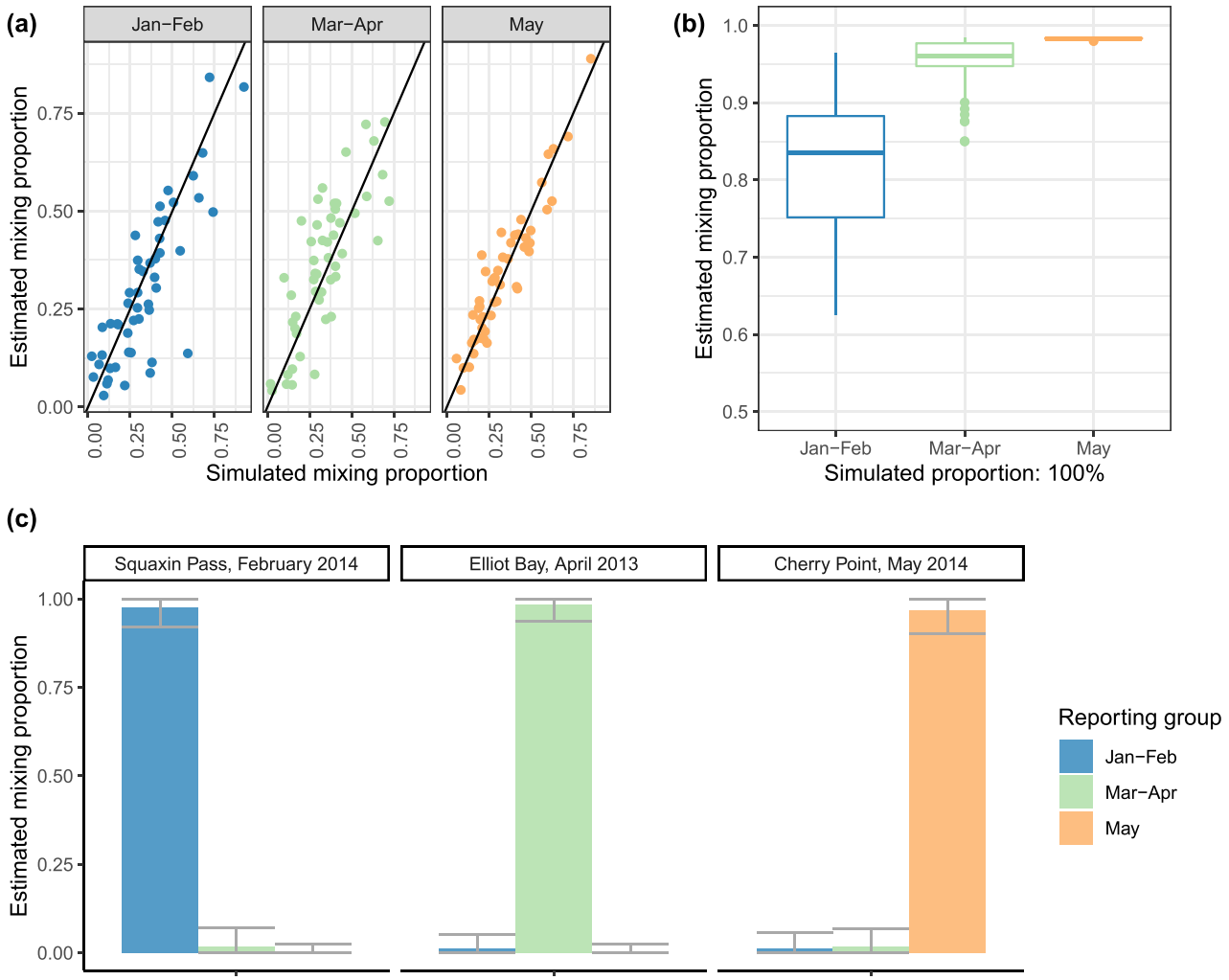

Figure 4. Predicted accuracy of mixed stock analysis using seven loci and three reporting groups (indicated by color). (a) Correlation between the estimated and true mixture proportions using simulated data; the diagonal line indicates expectations for perfect assignment. (b) Results of 100% simulations using simulated data. (c) Evaluation of mixed stock analysis using additional samples (not used for locus discovery) collected from Squaxin Pass, Elliot Bay, and Cherry Point. Error bars indicate the 5th–95th credible intervals around the mean estimated proportion of individuals assigned to a particular reporting group.

remain within the Salish Sea) or "migrant" (i.e. move offshore to feed; Stevenson, 1962; Taylor, 1964). Contaminants (West *et al.*, 2008) and isotopic signatures (Gao *et al.*, 2001) of Puget Sound and Strait of Georgia herring indicated that herring spawning in the Strait of Georgia (including the May-spawning Cherry Point stock) are migratory while herring spawning in the Puget Sound are resident. However, the distinction between resident and migratory groups is not absolute nor well-understood, as individuals within a population or spawning group, and/or at different life stages, may exhibit both strategies (Gao *et al.*, 2001; Beacham *et al.*, 2008). Thus, while distinctions in migratory behavior may generally explain overlap between certain herring populations and Chinook salmon predators, future research should quantify the distribution of genetically distinct herring populations outside of their spawning season. Data on these stock-specific movements and abundances would be useful for exploring potential interactions between Pacific herring and Chinook salmon.

Ontogenetic habitat shifts from spawning grounds to nursery areas are documented in many marine fishes (Gillanders *et al.*, 2003; Adams *et al.*, 2006;, Polte *et al.*, 2017), and these distributional changes can also influence interactions with predators (Dahlgren and Eggleston, 2000). The contribution of January–February spawners to juvenile salmon diets increased from 3% in spring to 18% in summer, suggesting that January–February spawners are important trophic resources for salmon during early life history stages. However, there is no contemporary evidence of herring spawning activity from January to February in the in the San Juan archipelago (Sandell *et al.*, 2019). Thus, the gut content data could indicate movement of the January–February spawning group into the archipelago where they were preyed upon by juvenile Chinook salmon.

Young-of-the-year (YOY) herring have been observed in high abundances in northern Puget Sound and southern Strait of Georgia during summer months (Beamer and Fresh, 2012; Chamberlin *et al.*, 2017) and a multidecadal time-series (Greene *et al.*, 2015)

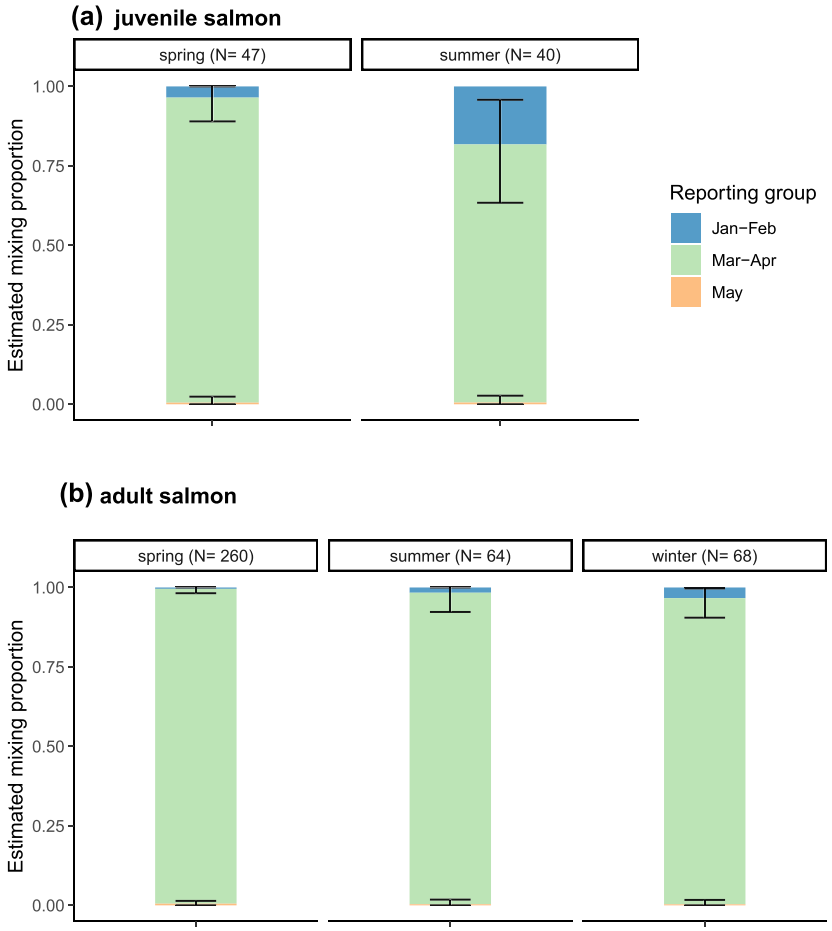

Figure 5. Results of mixed stock analysis for herring collected from the gut contents of juvenile (a) and adult (b) Chinook salmon. Estimated mixture proportions are displayed on *y*-axis and error bars indicate the 95% credible intervals. Different panels show salmon captured in different seasons.

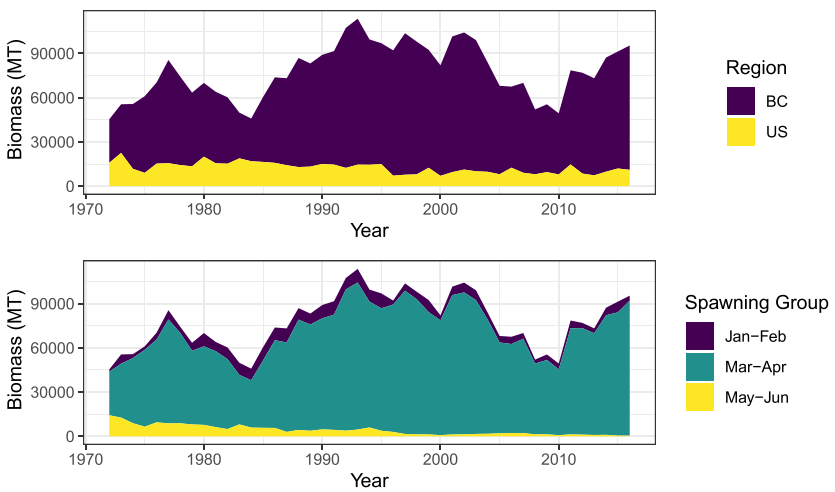

Figure 6. Total estimated Pacific herring biomass in the Salish Sea by region (United States or Canada) and year (top) and spawning group and year (bottom). Estimated biomass acquired from Sandell *et al.* (2019) and DFO (2020).

identified these areas as "relative hotspots for forage fish production." Perhaps as a result of this spatially localized abundance, the highest contributions of YOY herring to juvenile salmon diets are observed in this geographic region (Davis *et al.,* 2020). Boldt *et al.* (2019) found that the abundance of YOY herring was correlated with the abundance of juvenile salmon in the Strait of Georgia suggesting that conditions (e.g. prey abundance) favorable for YOY herring may also support juvenile salmon and thus encourage overlap among the species in space and time. High densities of juvenile herring and increased feeding opportunities for juvenile salmon suggest that the islands of the Southern Strait of Georgia (i.e. Gulf and San Juan Islands) may be a nursery habitat for both species but further research is needed to directly test this hypothesis. Nonetheless, our results underscore the importance of protecting habitats that support population diversity, as these coastal ecosystem mosaics (Sheaves, 2009) mediate food web interactions and support important life history stages. Future research to characterize and describe seasonal distributions and ontogenetic movements of specific spawning groups of YOY herring will undoubtedly be useful for management Pacific herring and recovery of Chinook salmon in the Salish Sea.

Size-selective processes may also play a role in determining relative contributions of herring spawn groups to Chinook salmon diets. Size-dependent interactions between predators and prey are common in aquatic food webs (Juanes and Conover, 1994), and morphological constraints such as gape limitations are believed to drive many of the dynamics between size-structured populations (Nilsson and Brönmark, 2000; Mihalitsis and Bellwood, 2017). Variability in herring spawn timing may influence the size ratio between herring and Chinook salmon during periods of overlap in coastal waters. Given the gape limitations for juvenile Chinook salmon, distinct differences in individual size between herring spawning groups could influence their observed proportions in diets. For example, Chamberlin *et al.* (2017) hypothesized that small May spawning herring would be an important prey for juvenile Chinook salmon, and drive the increased occurrence of herring in diets during summer in Puget Sound. While we were unable to test this hypothesis due to lack of May spawners in diets, it is possible to explore the relevance of seasonal changes in January–February spawners found in juvenile Chinook salmon diets. If size-selective processes were indeed responsible for driving the observed variability, we would expect to see size differences among the spawn groups that made the early spawners more susceptible to predation when accounting for the size of the predator. However, our qualitative comparisons of herring lengths from gut contents did not reveal any differences among January–February and March–April spawners, as size ranges for each spawn group (Supplementary Figures S3 and S4) and the average size range of the juvenile salmon was relatively similar (136 mm and 152 mm, respectively). Thus, the observed increase of January–February spawners in juvenile Chinook salmon guts was not likely driven by size-selective processes.

Lastly, we should note that our analyses and conclusions rely on correctly accounting for and precisely describing the genetic variation of Pacific herring in the Salish Sea. We were only able to sample a single spawning population from Canadian waters of the Salish Sea (Gabriola Island), and thus may have failed to sample the full extent of herring genetic diversity in that geographic region. However, most herring in Canadian waters spawn in March and April (Haegele and Schweigert, 1985) and genetic differentiation between populations spawning at the same time is subtle and follows an isolation by distance pattern (Petrou *et al.,* 2021). As our panel of SNP assays was designed to distinguish the much larger genetic differences between temporally isolated spawners in the Salish Sea, it does not have the statistical power to distinguish between geographically distinct populations whose spawn timing overlaps. Future studies using whole genome sequencing might discover loci that can be used to identify individuals which spawn at similar times of year but are geographically isolated.

Herring population diversity and implications for Chinook salmon survival

Quantifying interactions between Chinook salmon and the Salish Sea food web is important given recent observations of declining salmon survival (Zimmerman *et al.*, 2015; Ruff *et al.*, 2017). Several studies have pointed to the ontogenetic shift from planktivory to piscivory as a crucial transition linked to marine survival (Daly *et al.*, 2009; Litz *et al.,* 2017) because piscivory results in faster growth (Davis *et al.,* 2020). Coinciding with declining trends in Chinook salmon survival over the last half century, the population diversity of Pacific herring within the Salish Sea has also declined considerably (Siple and Francis, 2016). While total herring biomass (over all populations) has declined only slightly over this period, changes in the relative proportions of phenologically diverse populations have been more dramatic including the drastic reduction in May spawner biomass (Figure 6). These reductions in population diversity and fluctuations in localized abundance may result in resource patchiness and have important ecological consequences for predators.

The benefits of protracted resource availability for mobile consumers have been documented in aquatic and marine systems (Schindler *et al.*, 2013; Armstrong *et al.*, 2016). When herring spawn timing diversity is intact, it results in an extended period during which spawning adults are present in the nearshore environment and juvenile herring recruit to the pelagic food web. The extended presence and broad spatial distribution of pre-spawning and spawning adult herring also extends foraging opportunities for resident Chinook salmon in the Salish Sea. Additionally, spawn timing diversity likely benefits gape-limited juvenile Chinook salmon. Juvenile herring develop rather rapidly after hatching and growth is temperature dependent (McGurk, 1984), but herring generally recruit to the pelagic food web 2–3 months after hatching (Therriault *et al.*, 2009). Thus, with a protracted spawning period we would expect juvenile herring to recruit to the pelagic food web from March through July, a time when juvenile salmon are abundant in marine waters and experience critical growth that contributes to their marine survival (Duffy and Beauchamp, 2011; Rice *et al.,* 2011). The substantial decline of early spawning (January–February) and late spawning (May) herring populations throughout the Salish Sea (Therriault *et al.,* 2009; Sandell *et al.*, 2019) has likely truncated the period during which salmon and herring overlap, thus reducing foraging opportunities for Chinook salmon during critical life history stages. Recovery efforts aimed at building, or maintaining, population diversity in Salish Sea herring may therefore aid the recovery of threatened Chinook salmon.

In conclusion, we provide evidence phenological diversity of important prey species is reflected in the diets of a threatened predator species. Further research is warranted to determine if a declines in Pacific herring diversity have had negative effects on Chinook salmon or throughout the food web. Such effects are not only mediated via decreased demographic stability of a less diverse prey

population (Moore *et al.*, 2010), but also via decreased foraging opportunities to their predators (Schindler *et al.,* 2013; Armstrong *et al.,* 2016). Even though population extinctions are less conspicuous than species extinctions, they are ubiquitous even in common species (Ceballos *et al.*, 2017) such as herring, and may affect entire ecosystems and the services that they provide. Given the ecological, cultural and economic importance of many marine species, the effects of declining marine biodiversity may be more widespread than the small number of reported species extinctions suggests (Webb and Mindel, 2015).

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Data Availability

Genotyping data generated in this project have been submitted to DRYAD and are accessible through doi: 10.5061/dryad.7sqv9s4ss. Scripts are accessible through https://github.com/EleniLPetrou/gut_contents_manuscript.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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