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Evolution of introduced Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Huron: emergence of population genetic structure in less than 10 generations

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Abstract – Population genetic structure was detected in Chinook salmon *Oncorhynchus tshawytscha* in their non-native range of Lake Huron using microsatellite DNA. All Chinook salmon in this system descend from Green River, Washington cohorts, originally transplanted to Michigan hatcheries in the late 1960s. We tested for population genetic differentiation of age 0 fish collected from 13 rivers and two hatcheries in 2007. The amount of genetic differentiation among collection sites was low but statistically significant, with F_{ST} values ranging from 0.036 to 0.133 and R_{ST} values ranging from 0.008 to 0.157 for specific loci. Based on pairwise F_{ST} and R_{ST} values and Bayesian cluster analysis, the Maitland River population in the Main Basin of Lake Huron was genetically distinct from the remaining collection sites. Based on analysis of bycatch data from commercial gill net fisheries, Chinook salmon likely colonised the Main Basin by 1975 (10 generations ago) and the North Channel and southern Georgian Bay regions by 1980 (eight generations ago). Thus, population genetic structure has emerged in Lake Huron Chinook salmon in <10 generations.

Key words: introduced species; Salmonidae; population genetics; evolutionary divergence; rapid evolution

Introduction

Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) in Lake Huron provide an exceptional opportunity to explore the dynamics of contemporary evolution at an early postcolonisation phase, in a large number of populations, and at a large spatial scale. In the 1960s, the lower four Laurentian Great Lakes were suffering the consequences of the extirpation of almost all populations of lake trout (*Salvelinus namaycush* Walbaum) from overharvesting and predation by sea lamprey (*Petromyzon marinus* Linnaeus) (Coble et al. 1990; Eshenroder et al. 1992). In response, fisheries managers initiated a Pacific salmonid stocking programme to control burgeoning alewife (*Alosa pseudoharengus* Wilson) populations and provide recreational fishing opportunities to coastal communities (Hansen 1999; Crawford 2001). This programme has involved artificial breeding and the release of hatchery-reared juveniles (age 0) into tributaries and along lakeshores. Since the initiation of the stocking programme, Chinook salmon have established feral populations[1] in Lake Michigan, Lake Superior, Lake Huron, and, to a lesser extent, Lake Ontario (e.g., Peck et al. 1999; Weeder et al. 2005; Smith et al. 2006; Johnson et al. 2010). Indeed, large-scale mark–recapture studies show that wild Chinook salmon can comprise the majority of the recreational catch in some regions (Peck et al. 1999; Johnson et al. 2010). In Lake Huron, Chinook salmon are known to

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[1]Defined as a group of individuals using a particular river for breeding and, due to natal homing, unlikely to interbreed with other such groups.

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least 17 tributaries, with most of these
the Niagara Escarpment regions of
he upper peninsula of Michigan
al. 2011). Little is yet known about
netic differentiation among these feral
Chinook salmon and whether they are
ted to be undergoing local adaptation.
programme for Chinook salmon in
and Huron began in 1966–1968 with
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fish for release into Lake Huron: three state-operated facilities in Michigan obtain gametes from adults returning to the Swan River, and four community-ru facilities in Ontario obtain gametes from ad returnin ocal tributaries of Lake Huron (pri the S am River, Saugeen River, Beav and n Manitoulin Island; Fig. 1).
st evidence of successful natu ook salmon in Lake Huron w ge 0 fish were captured i y Pottawatomi Rivers ( ). s record was followe the scovery of age 0 out- urveys n these and four addi southern Georgian Bay regi Sauble, and Saugeen Rivers addition to evidence of e spawning observed i Lake Huron (Powell that hatch not c ul 1984, the is s (i.e., 'str ed fish fro of Lake

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Typically, adults from wild populations show philopatry to natal spawning areas because of imprinting before and during the parr-smolt transformation (Dittman & Quinn 1996; Hendry et al. 2004). The release of hatchery-reared fish at non-natal sites disrupts imprinting and subsequent homing ability (e.g., Quinn 1993; Candy & Beacham 2000) and may have promoted colonisation of Ontario tributaries of Lake Huron.

Our objective was to test for population genetic structure of Chinook salmon in Lake Huron using microsatellite loci. Previously, Weeder et al. (2005) observed a lack of genetic differentiation among feral populations of Chinook salmon in Lake Michigan based on data from allozyme loci. This was attributed to the combined effects of recent colonisation and straying by hatchery-reared fish. However, microsatellites may be better loci for discriminating population structure because of their relatively high mutation rate. To complement the genetic results, we used commercial fisheries monitoring data to establish when Chinook salmon colonised different regions of Lake Huron and how many generations had passed since colonisation. We hypothesised that some feral populations of Chinook salmon would be genetically distinct because of founder effects, postcolonisation genetic drift and/or natural selection.

Methods

Collection of age 0 Chinook salmon

Age 0 Chinook salmon of wild and hatchery origin were collected from 15 collection sites within the Lake Huron watershed during April–June 2007 (Fig. 1). Wild fish, identified by their small size and lack of any fin clips, were collected from 13 feral populations, whereas hatchery-origin fish were collected from two hatcheries. Our fish samples comprised a subset of those used in a study of otolith microchemistry from 17 known feral populations and seven hatcheries in Lake Huron (Marklevitz et al. 2011). Because our objective was to assess genetic differentiation among extant populations in Lake Huron, not divergence from the source population, we did not collect archived samples from the Green River. Previous research already indicates a significant founder effect because of the transfer of gametes from the Green River to Michigan (Weeder et al. 2005). Wild fish were sampled in rivers by electrofishing suitable juvenile habitats (e.g., side channels of main rivers) near areas where spawning had been observed by local biologists. In these systems, finding juveniles was challenging and took a lot of effort. Hatchery fish were sampled from raceways using dip nets. Fish were euthanised with clove oil or MS222. From each individual fish (n = 20–24 per collection site), a tail fin clip was preserved in 95% ethanol.

The feral populations in our study have variable stocking histories, with no recorded hatchery releases in the Root River, Spanish River, Manitou River, Beaver River and Bighead River, <200,000 hatchery releases in the Nottawasaga River (n = 60,000 in 1988), Maitland River (n = 100,000 in 1985 and 1987) and Carp River (n = 125,114 from 1980 to 1985), 0.5–1 million hatchery releases in the Sauble River (n = 712,776 from 1986 to 2002) and Saugeen River (n = 860,798 from 1985 to 1998), and over 1 million hatchery releases in the St Marys River (n = 1,730,866 from 1977 to 2003), Sydenham River (n = 3,612,675 from 1985 to 2002) and Nunn's Creek (n = 5,984,490 from 1988 to 2010) (GLFC Fish Stocking Database). The two hatcheries in our study collect gametes from adults returning to local tributaries, with the Lake Huron Fishing Club (LHFC) usually collecting from the Saugeen River and Sydenham River and the Sydenham Sportsmen's Association (SSA) usually collecting from the Sydenham River. The Beaver River also is a gamete collection site in some years. The LHFC releases fish at a variety of sites in local tributaries and along lakeshores, whereas the SSA releases the majority of its fish in the Sydenham River (GLFC Fish Stocking Database).

Microsatellite DNA genotyping

We used nine previously published microsatellite loci for genotyping: *Oneμ3*, *Oneμ8*, *Oneμ14* (Scribner et al. 1996), *Ssa85* (O'Reilly et al. 1998), *Omy207*, *Omy325* (O'Connell et al. 1997), *OtsG311*, *OtsG432* and *OtsG474* (Williamson et al. 2002). All forward primers were fluorescently labelled (Sigma-Genosys, The Woodlands, TX, USA). Genomic DNA was extracted from the tail fin of each fish by the Wizard Genomic DNA purification kit (Promega, Madison, WI, USA), following the manufacturer's protocol. We used a T1 Thermocycler (Biometra, Göttingen, Germany) to amplify the microsatellites with the following programme: 94 °C for 10 min, 35 cycles of 30 s denaturating at 94 °C, 30 s at 58 °C (*Oneμ3*, *Oneμ8*, *Oneμ14*, *Omy207*, *Omy325* and *OtsG474*) or 61 °C (*Ssa85*, *OtsG311* and *OtsG432*) for annealing the primers, and 30 s at 72 °C for nucleotide extension and final elongation at 72 °C for 10 min. Each 10-ml PCR contained 75 ng of total DNA, 3 mM $MgCl_2$, 10× PCR buffer (Invitrogen Life Technologies, Carlsbad, CA, USA), 0.25 mM of each deoxynucleotide (Sigma-Aldrich, St Louis, MO, USA), 0.25 units *Taq* DNA polymerase (Invitrogen Life Technologies) and 0.25 mM of each forward and reverse primer (Invitrogen Life Technologies). PCR products were

size-fragmented following the standard protocol for the CEQ 8000 Genetic Analysis System (Beckman Coulter, Mississauga, ON, Canada).

Genetic data analysis

Genetic diversity was quantified by the number of alleles per locus, observed heterozygosity H_O, and expected heterozygosity H_E (Nei 1987) using ARLEQUIN 3.1 (Schneider et al. 1997). Deviations from Hardy–Weinberg equilibrium (HWE) were tested for each locus–population combination using the GENEPOP 3.1d package (Raymond & Rousset 1995) with the exact test based on a Markov chain method (Guo & Thompson 1992). For tests over all loci, the significance of departures from expected HWE genotype frequencies was assessed (see F_{IS} in Table 1). MICROCHECKER (van Oosterhout et al. 2006) was used to detect possible technical artefacts, such as null alleles, large allele dropout and accidental scoring of stutter bands. ML-RELATE (Kalinowski et al. 2006) was applied to test whether there was a family effect in our sampling and analyses.

We used approaches to the extent of genetic differentiation and structuring among collection sites. The statistics make different assumptions about the mode of mutation at microsatellites and are derivedfrom either the infinite allele model (IAM) or the stepwise mutation model (SMM). Although statistics based on the SMM typically suffer high sampling variances, those based on the IAM can underestimate differentiation among highly structured populations in which mutation rates are greater than migration rates (Balloux & Lugon-Moulin 2002). As a conservative approach, both families of statistics were used in the present study. We estimated pairwise F_{ST} (Weir & Cockerham 1984) and pairwise R_{ST} (Michalakis & Excoffier 1996) values using GENEPOP. M2547dimensional scaling analysis (MSA), based on pairwise F_{ST} values, was used to visualise the genetic relationships among collection sites using VISTA 5.6.3 (Young 1996). Differentiation by distance was analysed by calculating the correlation coefficient of $F_{ST}{\cdot}(1 - F_{ST})^{-1}$

Sampling of commercial fisheries

Commercial fisheries monitoring data (1975–2008) were used to estimate the generation time of Chinook salmon in Lake Huron and to determine when the three main regions (Main Basin, Georgian Bay and North Channel; Fig. 1) were colonised. In combination with the genetic data, these data provide information on the time course for genetic differentiation. In Lake Huron, on-vessel catch samplers collect

Table 1. Summary of the nine microsatellite loci used to study the genetic differentiation of Chinook salmon among collection sites in Lake Huron.

Loci	Size range (bp)	*A*	H_O	H_E	F_{IS}	F_{ST}	R_{ST}
Omy325	81–103	13	0.870	0.844	−0.095	0.066*	0.044*
One3	161–169	4	0.603	0.469	−0.343	0.044*	0.044*
OtsG474	150–206	13	0.773	0.726	−0.088	0.036*	0.013*
Ssa85	118–168	17	0.866	0.851	−0.052	0.043*	0.038*
OtsG311	230–362	32	0.928	0.951	−0.028	0.053*	0.035*
Omy207	77–81	4	0.092	0.081	−0.181	0.133*	0.157*
OtsG432	105–184	14	0.875	0.860	−0.067	0.051*	0.008*
One8	139–195	12	0.773	0.734	−0.093	0.055*	0.017*
One14	188–244	15	0.638	0.848	0.157*	0.102*	0.034*

Data include allele size range in base pairs (bp), total number of alleles (*A*), mean observed (H_O) and expected heterozygosity (H_E), F_{IS}, F_{ST} and R_{ST}. *$P < 0.05$.

standard data on fisheries catch and bycatch (e.g., Gile & Milne 2006). Fishing effort is targeted primarily towards lake whitefish (*Coregonus clupeaformis* Mitchell) using trap nets or gill nets of variable mesh size. Chinook salmon caught as bycatch are enumerated, measured and in some cases aged using scales. We estimated mean generation time based on data from fish assigned as mature (will spawn in the current year), excluding those ($n = 4$) with assigned ages of 0. Annual bycatch of Chinook salmon was estimated for the gill net fishery as catch rate (number captured·km gill net^{-1}·24 h^{-1}). In an effort to account for the potential effect of mesh size on catch rates, only sets using large mesh (>90 mm stretched mesh) were used in the determination of catch rates. Median annual catch rates were calculated for each 5-year period in each fisheries assessment area (Fig. 1).

Results

Observed heterozygosity (H_O) was high (average H_O's > 0.6) for all loci except for *Omy*207 with a $H_O = 0.09$ (Table 1). The number of alleles per locus ranged from 4 to 32. Based on its high F_{IS} value, only *One*μ14 had genotype frequencies that departed significantly from HWE within populations. MICRO-CHECKER revealed that *One*μ14 had a significant probability of null alleles in five populations (Table 2). There was no significant departure from HWE at the population level (Table 2). Mean F_{ST} values for specific loci ranged from 0.04 to 0.13, whereas mean R_{ST} values ranged from 0.01 to 0.16. Genetic differentiation among populations was evident based on significant values of F_{ST} and R_{ST} for all loci (Table 1). Mean F_{ST} across all loci was 0.065, indicating that $n = 20$–44 per population warranted further statistical analyses (Kalinowski 2005). Exact tests for genetic linkage disequilibrium did not reveal any significant effects, suggesting the absence of physical linkage of the loci (data not shown). Maximum likelihood estimation of relatedness and relationship by ML-RELATE did not reveal any family effect in our sampling and genetic analysis; more than 90% of the possible individual pairs were unrelated in all collection sites (95% confidence set with 10,000 randomisations).

Based on pairwise F_{ST} values averaged across loci, differentiation was strongest in the Maitland River population ($F_{ST} = 0.09$–0.21, 14 significant F_{ST} values), followed by the Root River population ($F_{ST} = 0.03$–0.14, 12 significant F_{ST} values), Sauble River population ($F_{ST} = 0.01$–0.11, 8 significant F_{ST} values), Nunn's Creek population ($F_{ST} = 0.05$–0.21, 5 significant F_{ST} values) and the LHFC Hatchery ($F_{ST} = 0.02$–0.16, $F_{ST} = 5$ significant F_{ST} values; Table 3). Based on pairwise R_{ST} values averaged across loci, differentiation was most apparent for the Maitland River population (14 significant R_{ST} values; Table 3). The distinct nature of the Maitland River population was also evident from the multidimensional scaling plot of pairwise F_{ST} values (Fig. 2). The Mantel test failed to find any correlation between genetic differentiation and geographic distance (pairwise F_{ST} values: $r = 0.164$, $P = 0.98$; pairwise R_{ST} values: $r = 0.021$, $P = 0.54$).

In the Bayesian analysis of population structure, log-likelihood ratios reached a plateau at $K = 6$, indicating that most of the genetic variation was captured in six genetic clusters (Table 4). In 12 collection sites, most individuals (43–100%) were assigned to cluster 3. In contrast, the majority of individuals from Nunn's Creek (75%), Maitland River (71%) and Saugeen River (50%) were assigned to

Table 2. Summary of genetic characteristics of Chinook salmon from 15 collection sites in Lake Huron.

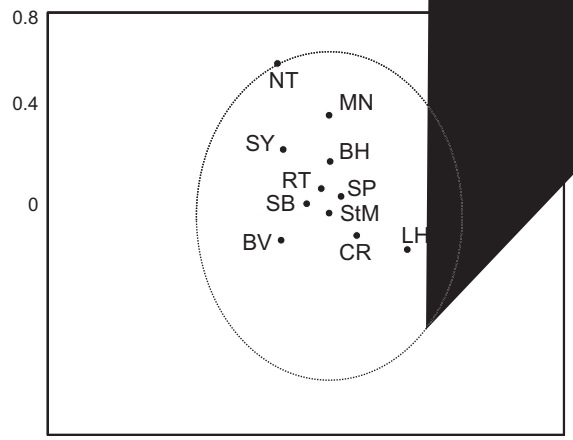
Collection site	Code	*n*	AR	H_E	H_O	F_{IS}	Loci departing from HWE
Sydenham River	SY	44	5.610	0.658	0.675	–0.025	*One*μ*14*
Nunn's Creek	NN	20	4.392	0.569	0.667	–0.101	
Sauble River	SB	20	5.940	0.750	0.753	–0.004	*One*μ*14*
Saugeen River	SG	20	4.923	0.660	0.703	–0.064	
St Marys River	StM	20	5.741	0.707	0.722	–0.022	*One*μ*14*
Spanish River	SP	25	6.061	0.703	0.730	–0.040	
Nottawasaga River	NT	25	5.142	0.665	0.699	–0.052	
Manitou River	MN	22	5.850	0.705	0.756	–0.075	*One*μ*14*
Beaver River	BV	20	5.633	0.713	0.682	0.045	
SSA Hatchery	SSA	20	5.439	0.673	0.708	–0.053	
Root River	RT	20	5.244	0.710	0.792	–0.119	
LHFC Hatchery	LHFC	20	5.050	0.605	0.689	–0.144	
Carp River	CR	20	5.888	0.683	0.751	–0.104	
Maitland River	MT	21	3.997	0.562	0.644	–0.151	
Bighead River	BH	21	5.664	0.691	0.724	–0.049	*One*μ*14*

Shown are the collection site, collection site code, sample size (*n*), allelic richness (AR), mean expected (H_E) and observed heterozygosity (H_O), F_{IS}, and any loci departing from Hardy–Weinberg equilibrium.
SSA, Sydenham Sportsmen's Association; LHFC, Lake Huron Fishing Club.

Table 3. Genetic differentiation parameters (F_{ST} and R_{ST})

Site	SY	NN	SB	SG	StM	SP						
SY		0.042	0.029	0.070	0.007	0						−0.002
NN	0.082		0.045	0.199	0.017	0						−0.003
SB	0.047*	0.086		0.065	−0.002	0					39*	0.017
SG	0.045	0.124	0.045*		0.076*	0					.180*	0.091
StM	0.031	0.048	0.014	0.051		−0					0.006*	−0.020*
SP	0.017	0.033	0.028	0.048	0.003						−0.004*	−0.013
NT	0.026	0.100	0.037*	0.067	0.037	0				012	0.128*	0.053
MN	0.033	0.074	0.029*	0.055	0.020	0				0.028	0.112*	0.046
BV	0.030	0.101*	0.018	0.047	0.026	0				−0.010	0.087*	0.033
SSA	0.034	0.090	0.042	0.070	0.026	0			0	0.040	0.018*	0.007
RT	0.065*	0.076*	0.054*	0.074*	0.028*	0			.025	0.002	0.035*	0.004
LHFC	0.052	0.067*	0.067*	0.102	0.048	0				0.003	0.021*	−0.009
CR	0.051	0.087	0.034	0.067	0.038	0		0.058*			0.113*	−0.009
MT	0.093*	0.205*	0.111*	0.116*	0.125*	0	37*	0.162*	0.153*			0.049*
BH	0.034	0.067	0.039*	0.054	0.023	0	0.035	0.054	0.053	0.106*		

Estimates of F_{ST} appear below the diagonal, and estimates … eviations defined in Table 2). *$P < 0.05$.



different clusters (2, 4 and 6, respectively). Saugeen River also had a large fraction of individuals (40%) assigned to cluster 3. Based on the clustering pattern, we considered Nunn's Creek, Maitland River and the set of the remaining 13 collection sites as three separate groups in the AMOVA. Under the IAM, there was small but significant genetic variance among groups (1.9% of total variance, $P < 0.0001$) and among collection sites within groups (5.2%, $P < 0.0001$). Most of the genetic variance was found in the residual component (92.9%, $P = 0.065$). The same conclusions were obtained under the SMM. There was small but significant genetic variance among groups (1.3%, $P = 0.001$) and among collection sites with groups (2.7%, $P = 0.003$), and most of the genetic variance was found in the residual component (96.0%, $P = 0.2$).

Maturity and age information was available for 716 of the 19,073 Chinook salmon caught as bycatch in Ontario waters of Lake Huron from 1975 to 2008. The mean age of the 216 mature individuals was 2.2 years for a mean generation time of 3.2 years. In 1975–1979, the majority of Chinook salmon in the large mesh gill net fishery was captured in the Main Basin (in particular, areas 5, 8 and 9; Fig. 3). By 1980–1984, Chinook salmon started to be caught in southern Georgian Bay (areas 19–20) and the North Channel (areas 21–24). Throughout the 1980s, catch rates were highest in areas 5 and 9 of the Main Basin. By 1990–1994, catch rates in area 20 of southern Georgian Bay peaked and exceeded those elsewhere. During 1995–2004, catch rates in the North Channel (in particular, areas 21–23) peaked and exceeded those elsewhere. By 1995, Chinook salmon were being caught in the majority of assessment areas in Lake Huron.

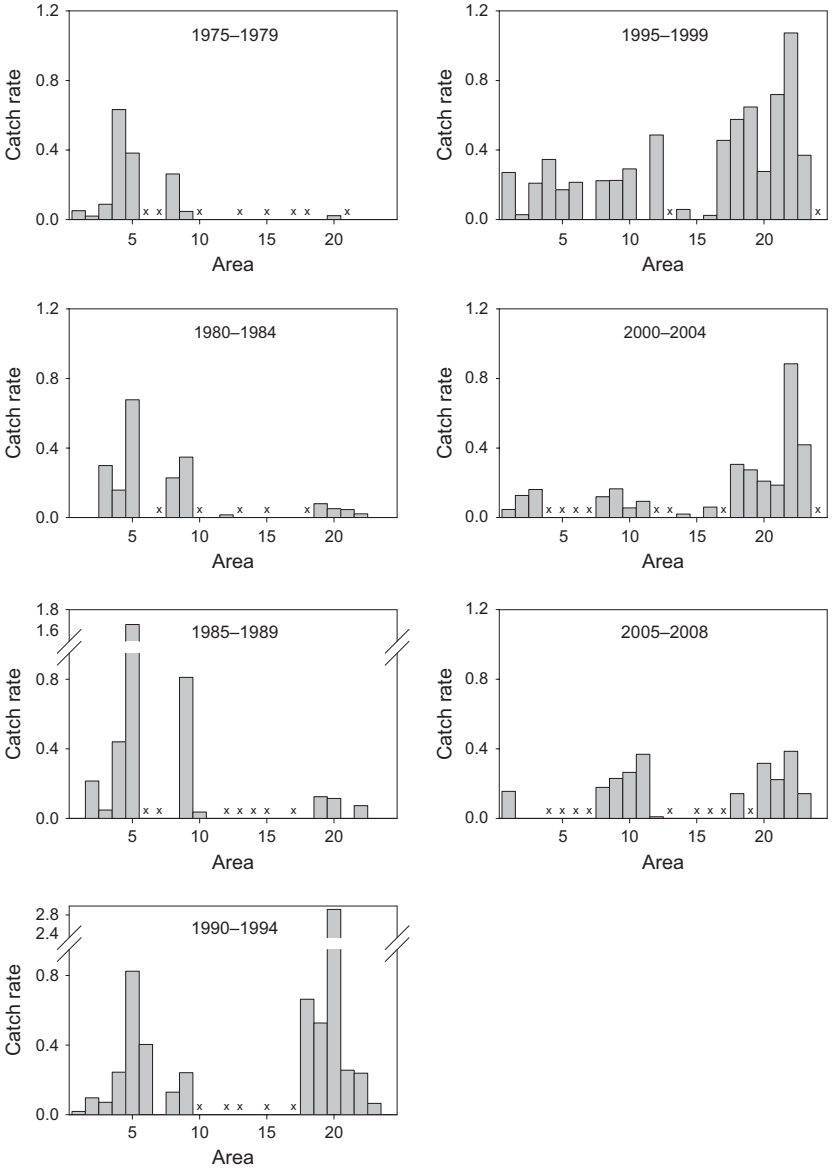


Fig. 3. Median catch rates (number captured·km^{-1}·24 h^{-1}) of Chinook salmon in large mesh, commercial gill net fisheries by assessment area within 5-year periods from 1975 to 2008. The xs indicate assessment areas without data, either because of no commercial fishing of large mesh gill nets or lack of catch samplers.

Discussion

Since their introduction in the 1960s, Chinook salmon have become widespread in Lake Huron at every life history stage (Johnson et al. 2010; Marklevitz et al. 2011) and have played a vital role in the lake's food web dynamics (Dobiesz et al. 2005). They also support a multi-million dollar recreational fishing industry in Ontario and Michigan, with most of the angled fish originating from wild populations, not hatcheries (Johnson et al. 2010). Feral populations of Chinook salmon likely vary in their degree of wildness, with some populations heavily influenced by hatchery supplementation and others not. We were able to estimate timeframes for colonisation of tributaries in different regions of Lake Huron using commercial fisheries bycatch data and have provided new information about the level of genetic divergence among feral populations.

Pinpointing the exact year Chinook salmon colonised tributaries of Lake Huron is challenging because of the lack of any long term, standardised, stream monitoring programme. Moreover, genetic divergence among populations was too low to reconstruct colonisation history with precision. Commercial bycatch data, however, provided useful information because the presence of fish in an area at least suggests the potential for access to tributaries. The spatial distribution of the catch shifted over time, suggesting different colonisation patterns among regions. High catch rates of Chinook salmon in the Main Basin in 1975–1979

suggest the potential for colonisation of Main Basin tributaries, including the Maitland River, Carp River, and Nunn's Creek, as early as 1975. In the southern Georgian Bay region, commercial catch data in combination with stream assessments suggest a slightly later colonisation date of 1980. Age 0 fish were found in the Sydenham and Pottawatomi Rivers in 1983 (Kerr & Perron 1986), and Chinook salmon bycatch was observed in nearby fisheries in the early 1980s. The commercial bycatch data also suggest the potential for colonisation of North Channel tributaries in the early 1980s. Chinook salmon are effective colonisers, and by 1995–1999, they had expanded their range into all areas of Lake Huron. With a mean generation time of 3.2 years, populations likely have been reproducing for a maximum of 10 generations in Main Basin tributaries and eight generations in southern Georgian Bay and North Channel tributaries.

We detected emerging population structure of Chinook salmon in Lake Huron. Based on multiple lines of evidence, the Maitland River population showed the greatest degree of genetic distinctness from the remaining populations. In this population, all pairwise F_{ST} and R_{ST} values were significant, and individuals were assigned to a separate genetic cluster in the Bayesian analysis. Thus, significant genetic differentiation has occurred in fewer than 10 generations in Lake Huron Chinook salmon. The Root River also showed evidence of genetic differentiation based on a large number of significant pairwise F_{ST} and R_{ST} values. Finally, the Nunn's Creek population had evidence of genetic differentiation based on five significant pairwise F_{ST} and R_{ST} values and on their assignment to a separate cluster. Because Nunn's Creek is heavily supplemented by the State of Michigan using gametes from returns to the Swan River (where no natural reproduction occurs), its differentiation most likely reflects divergence of the Swan River stock from feral populations elsewhere in Lake Huron.

Founder effects likely account for some of the genetic differentiation we observed among feral populations. In addition, because F_{ST} is approximately equal to $1/(4Nm + 1)$ (Wright 1969), significant genetic structuring could arise because of low effective population sizes (N) or low migration rates between populations (m). With the exception of the few populations receiving hatchery-reared fish from non-natal sources, we expect m in our study system to be similar to published values. Pacific salmon imprint to cues from natal or release sites, resulting in low rates of straying ($m = 0.01$–0.04) (Quinn 2005). Assuming $m = 0.01$–0.04, our largest observed value of F_{ST} (0.13) would be expected for $N = 42$–167. Thus for reasonable values of m, small effective populations can lead to significant genetic differentiation because of genetic drift. Moreover, compared to larger populations, smaller populations allow F_{ST} to increase from zero to $1/(4Nm + 1)$ in fewer generations (Allendorf & Phelps 1981). Unfortunately, data on effective population sizes are not available for our study system for comparison with these estimated values of N. We know the Nottawasaga River likely has the largest feral Chinook salmon population in Lake Huron, but little else. To summarise, founder effects followed by genetic drift in small populations likely explains the differentiation of the Maitland River and Root River populations.

The amount of genetic differentiation among the remaining collection sites in Lake Huron was low. Weeder et al. (2005) concluded that hatchery practices, in addition to recent colonisation, contributed to a lack of genetic differentiation in allozyme loci among feral Chinook salmon populations in Michigan, and the same argument could be made in our study. For example, the Sydenham River population, which is a significant source of gametes to hatcheries that release hatchery-reared juveniles into non-natal water bodies, was not genetically distinct from other populations. Not only does the Sydenham River contribute gametes to the LHFC hatchery, it contributes gametes to a hatchery in Sarnia, Ontario (south-eastern Main Basin), which releases age 0 juveniles at several sites in local streams and along the lakeshore. Adults returning to these release locations would not find spawning sites (there are no known significant spawning sites south of the Maitland River) and would likely stray elsewhere. Recent colonisation and continued hatchery supplementation may also explain the absence of any signal of genetic isolation by distance in our study.

In situations involving the colonisation of new habitats by invasive or transplanted populations, trait evolution can happen very rapidly (Stockwell et al. 2003). Studies of *Oncorhynchus* spp. have provided fundamental insights into the dynamics of contemporary adaptation. Following colonisation, divergent habitat-mediated selection can be sufficiently strong to detect trait evolution and local adaptation in as few as 13–26 generations (Hendry et al. 2000; Kinnison et al. 2001; Quinn et al. 2001). Adaptation is likely in Great Lakes populations because imprinting naturally favours a higher degree of reproductive isolation and environmental selection pressures likely would be different from those experienced by the ancestral, Green River population. In particular, selection should be responsive to altered seasonal patterns of stream temperature and flow (Jonsson & Jonsson 2009). To test for local adaptation in Lake Huron, further study could focus on the characterisation of functional, non-neutral genetic markers such as MHC (major histocompatibility complex). Further study of local

adaptation could also focus on phenotype-habitat correlations, reciprocal transplant experiments or formal analyses of selection (Endler 1986; Reznick & Travis 1996; Schluter 2000). Adaptation might happen first in large populations, such as the Nottawasaga River, that may be less subject to genetic drift. Adaptation might also happen quickly at range limits where environmental selection pressures would be most divergent within the Great Lakes.

Until recently, Chinook salmon fisheries in the Great Lakes were believed to be sustained by hatchery supplementation programmes. It is now apparent that wild reproduction is rampant, and many feral populations may be self-sustaining (Johnson et al. 2010). In our study, we detected emerging population genetic structure among feral populations in Lake Huron. Local adaptation of reproductively isolated populations should favour the persistence of Chinook salmon in Lake Huron, and even more so if stocking programmes cease. While the recreational fishery may benefit by the continued availability of a desirable species, there is also the potential for negative ecological effects on native species such as brook trout (*Salvelinus fontinalis* Mitchill) (Janetski et al. 2011) and lake trout (Negus 1995; Kitchell et al. 2000) and unknown effects on aquatic species at risk such as lake sturgeon (*Acipenser fulvescens* Rafinesque), northern brook lamprey (*Ichthyomyzon fosser* Reighard and Cummins) and redside dace (*Clinostomus elongates* Kirkland).

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