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Estimating Winter Mortality in Juvenile Marble River Chinook Salmon

by

Marc Trudel[1,2], Katherine R. Middleton[2], Strahan Tucker[1], Mary E. Thiess[1], John F.T. Morris[1], John R. Candy[1], Asit Mazumder[2], and Terry D. Beacham[1]

[1]Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC, Canada
V9T 6N7

[2]Department of Biology
University of Victoria
Victoria, British BC, Canada
V8W 3N5

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ABSTRACT

Winter is generally considered a critical period for juvenile salmon due to low temperatures and food availability. However, mortality rates have not been quantified for juvenile salmon during the winter months. Here, we use changes in the catch-per-unit effort (CPUE) for five brood years (2004-2008) of juvenile Marble River Chinook salmon between fall and winter to estimate stock-specific overwinter mortality rates in juvenile salmon. This stock is ideal for estimating overwinter mortality, as the catch distribution suggest that they remain in Quatsino Sound, British Columbia, for a year before migrating to the open ocean. CPUE of juvenile Marble River Chinook salmon in the Quatsino Sound system were 7- to 169-fold lower in the winter relative to the fall. CPUE varied significantly among brood years and seasons, but the interaction term between brood years and seasons was not significant. Overall, 80% of these fish died over winter, and mortality rates averaged 0.014-0.017 d^{-1}. The variance in fish size did not decrease during winter. Taken together, these results indicates that overwinter mortality can be substantial and variable in juvenile salmon, but that it is size-independent, at least, for this population.

INTRODUCTION

Pacific salmon experience heavy and highly variable losses in the ocean, with natural mortality rates generally exceeding 90-95% during their marine life (Bradford 1995). Most of this mortality is thought to occur during two critical periods: an early predation-based or physiological-based mortality that occurs within the first few weeks to months following ocean entry and a starvation-based mortality that occurs following their first winter at sea (Beamish and Mankhen 2001). Early studies indicated that 55-95% of the smolts died within the first 1-3 months following sea entry (Parker 1964, 1968; Karpenko 1998; Wertheimer and Thrower 2007; Beamish et al. 2011), supporting the hypothesis that the early marine residence is a critical period for juvenile salmon. In contrast, mortality rates of juvenile salmon have rarely been quantified during their first winter at sea. For instance, Beamish and Mankhen (2001) estimated that approximately 90% of the juvenile coho salmon caught in the Strait of Georgia in September died over a period of 12-14 months, though it is unclear when this mortality actually occurred. Middleton (2011) estimated that overwinter mortality was 80-90% in juvenile Chinook salmon.

The objectives of this study were to expand on the work of Middleton (2011) and estimate the magnitude of the mortality that occurs during winter in juvenile Pacific salmon. Using trawl surveys conducted in Quatsino Sound in the fall and winter, we use changes in the catch-per-unit effort (CPUE) between these seasons to estimate stock-specific overwinter mortality rates in juvenile Chinook salmon for five distinct brood years.

METHODS

Study area

This study focused on juvenile Marble River Chinook salmon in the Quatsino Sound system located on the northwest coast of Vancouver Island, British Columbia (Figure 1). DNA analyses have been performed on over 9000 juvenile Chinook salmon caught from the west coast of Vancouver Island to Southeast Alaska between 1998 and 2011 (Tucker et al. 2011, 2012; Trudel et al. 2012). Of these, 1337 were identified as Marble River Chinook salmon. Overall, 99.2% of the juvenile Marble River Chinook were caught within the Quatsino Sound system during their first year at sea despite substantial sampling effort north and south of this area (S. Tucker, unpublished data). Hence, for this study, we assumed that this stock remained in this geographic area within their first year at sea and use fall and spring catch-per-unit effort data to estimate overwinter mortality.

The Quatsino Sound system is composed of three interconnected inlets and one sound, which opens onto the continental shelf of west coast Vancouver Island (Figure 1). At the eastern end of the system, Rupert Inlet and Holberg Inlet are separated from Neurotsos Inlet and Quatsino Sound by the Quatsino Narrows. The Marble River flows into the south western part of Rupert Inlet (127º32.6’ W and 50º33.4’ N). Combined, the length of the system measures approximately 133 km. Juvenile Marble River Chinook salmon migrate to sea as subyearlings a few months after emerging from the gravel. They initially disperse throughout Rupert Inlet and Holberg Inlet, and then to Neurotsos Inlet and Quatsino Sound where they remain for a year before venturing into continental shelf waters (Figure 2; S. Tucker, unpublished data).

Sampling

Trawl surveys were conducted in Quatsino Sound in October-November 2005-2009 and February-March 2006-2010 (Table 1; Figure 2). A rope trawl originally manufactured by Cantrawl Nets Ltd., Richmond, British Columbia, and later modified to a model 240 trawl by the fishing crew, was towed at the surface for 30 minutes (Trudel et al. 2012). The trawl has a heavy-duty front end of hexagonal web made from 3/8 in. (9.5 mm) and 5/16 in. (7.9 mm) Tenex rope, and a tapered body made-up of 64 in. (163 cm), 32 in. (81.3 cm), 16 in. (40.6 cm), 8 in. (20.3 cm) and 4 in. (10.2 cm) polypropylene sections, an intermediate section of 3 in. (7.6 cm) polypropylene, and a codend of 1.5 in. (3.8 cm) knotted nylon lined with 0.25 in. mesh (64 mm). The trawl has three 40 m bridles of 5/8 in. (1.6 cm) wire rope per side that are attached with a single hook-up to 5 m Jet doors. Typically, 100-150 m of 1.25 in. (3.2 cm) warp was paid out to tow the trawl at the surface. The trawl is towed at the surface at 5 knots (2.6 m s^{-1}) in good sea conditions, and this typically achieved a mouth opening that was approximately 28 m wide by 16 m deep as measured acoustically by a Scanmar trawl eye mounted on the headrope.

Fish samples obtained from the trawl were sorted by species, enumerated, and measured onboard the ship to characterize the nekton community in epipelagic waters of British Columbia and Southeast Alaska (Brodeur et al. 2006; Orsi et al. 2007). All the juvenile Chinook salmon were systematically scanned for coded-wire tags, even if the adipose fin had been clipped or not, as not all CWT-tagged fish are clipped (Morris et al. 2004). We used a combination of coded-wire tag recoveries of known-age fish and DNA analyses to establish size-classes in order to separate juveniles from adults, and to differentiate life history types (Fisher et al. 2007; Trudel et al. 2007a, 2007b), as there is considerable overlap among size modes that represent the multiple age groups. Up to 30 juvenile Chinook salmon were randomly selected from each tow and measured to the nearest gram. For these fish, we also took a skin sample from the operculum using a hole-punch and preserved in 95% ethanol to determine their stock of origin using microsatellite DNA (Beacham et al. 2006; Tucker et al. 2011, 2012) and removed calcified-structures (i.e. scales and otoliths) for age determination. These fish were then preserved by freezing individually at minus 20ºC for later chemical and calorimetric analyses such as stable isotopes, and stomach contents analyses.

Overwinter mortality

Overwinter mortality was determined by dividing the mean winter catch-per-unit effort ($CPUE_{winter}$) by the mean fall catch-per-unit effort ($CPUE_{fall}$) for each brood year as follow:

$$OWM = \left[1 - \left(\frac{CPUE_{winter}}{CPUE_{fall}}\right)\right] * 100 \quad (1)$$

where *OWM* is the overwinter mortality (in percent). Overwinter mortality was calculated separately for each brood years. CPUE was estimated by dividing the total number of juvenile Marble River Chinook salmon caught in a tow by the product of the distance towed.

In this study, we assumed that the catchability was the same for both seasons. We also initially assumed that the catches obtained in the top 15 m reflected the abundance of juvenile Chinook salmon in the water column. However, this assumption is unlikely to be accurate, as juvenile Chinook salmon tend to occur in deeper waters as they get larger and in the winter (Orsi and Wertheimer 1995). As such, the CPUE values determined for the top 15 m may not accurately represent the CPUE for the entire water column (or 0-30m in the case of this analysis). We tested this assumption in the winter of 2009 and 2010 by sampling juvenile Chinook salmon in Quatsino Sound at 0-15 m and at 15-30 m. DNA analyses indicated that the CPUE of juvenile Marble River Chinook salmon is approximately two-fold higher in the 15-30 m stratum compared to the top 15 m in the winter (S. Tucker, unpublished data). Similar analyses have not been performed in the fall yet. However, sampling conducted in the fall of 2011 indicated that, in general, the CPUE of juvenile Chinook salmon in the top 15 m was two-fold higher than for the 15-30 m stratum during this season (M. Trudel, unpublished data), but the stock ID of these fish has not yet been determined. Hence, to more accurately estimate the CPUE of juvenile Marble River Chinook salmon in the top 30 m, we adjusted the CPUE obtained for the top 15 m as follows:

- In winter, we multiplied the CPUE estimate for the top 15 m by 1.5, which represents the average CPUE for the 0-15 m and 15-30 m depth strata combined ($CPUE_{Winter}$ x 1.5).

- To account for the uncertainty in vertical distribution during fall, we repeated the analysis with 2 different scenarios to adjust the CPUE estimates for the top 15 m: 1) no juvenile Marble River Chinook salmon were below the top 15 m ($CPUE_{Fall}$ x 0.5), or 2) juvenile Marble River Chinook salmon were twice as abundant in the top 15 m compared to the 15-30 m stratum ($CPUE_{Fall}$ x 0.75).

Statistical Analyses

Fork length and CPUE were compared among brood years and seasons using a permutation-based two-way analysis of variance (Legendre and Anderson 1999). This approach was necessary, as the design was unbalanced, the data were not normally distributed and the variance was not equal among groups. This analysis was performed in R (R Development Core Team. 2012) using the *anova.2way.unbalanced* function written by P. Legendre (Université de Montréal, Montréal, Canada) and available on the web (http://numericalecology.com/). The number of permutations was set to 10,000. We excluded the 2006 brood year for the fork length comparison, as only three juvenile Marble River Chinook salmon were caught during winter for that brood year.

RESULTS AND DISCUSSION

Ten surveys were conducted in Quatsino Sound in the fall and winter between 2005 and 2010 (Table 1). Individual surveys covered 20-50% of the length of Quatsino

Sound. Except for small catches in the fall of 2006, no juvenile Marble River Chinook salmon were caught near the mouth of Quatsino Sound during fall (Figure 2). Small catches of juvenile Marble River Chinook salmon were observed near the mouth of Quatsino Sound during winter. However, surveys conducted during the 2006-2010 winters from the south end of Vancouver Island to Southeast Alaska caught only a single juvenile Marble River Chinook salmon out of the 865 juvenile Chinook salmon that have been genotyped as Marble River Chinook during these winters (Tucker et al. 2011, 2012; S. Tucker, unpublished). These results suggest that Marble River Chinook salmon are restricted to the Quatsino Sound system during their first year at sea. However, given the limited sampling performed in deeper strata on the continental shelf by Fisheries and Oceans Canada, it is possible that earlier emigration of juvenile Marble River Chinook salmon out of the Quatsino Sound system may have been missed or that they have moved closer to shore and inaccessible to the trawl net. Future sampling design will include towing at multiple depth strata during fall and winter to evaluate the validity of the assumption used in this study. Alternatively, acoustic tagging of fish collected in the fall could help resolve this key uncertainty (Welch et al. 2011), provided the fish are large enough to carry an acoustic tag.

CPUE of juvenile Marble River Chinook salmon in the Quatsino Sound system were 7- to 169-fold lower in the winter relative to the fall (Figure 3). CPUE varied significantly among brood years ($F=5.6$, $p < 0.0005$) and seasons ($F=52.3$, $p < 0.0001$), but the interaction term between brood years and seasons was not significant ($F=0.7$, $p > 0.5$). The estimation of overwinter mortality varied depending on the assumed vertical distribution of juvenile Marble River Chinook salmon in the Quatsino Sound system (Table 2). We estimated that 61-98% of the juvenile Marble River Chinook salmon died during winter when they were assumed to remain in the top 15 m during fall (Table 2). Corresponding mortality rates ranged from 0.008 d^{-1} to 0.027 d^{-1} for these five brood years, and averaged 0.014 d^{-1} (Table 2). When they were assumed to be twice as abundant in the top 15 m compared to the 15-30 m stratum during fall, we estimated that 74-99% of the juvenile Marble River Chinook salmon died over winter (Table 2). Corresponding mortality rates ranged from 0.011 d^{-1} to 0.030 d^{-1} for these five brood years, and averaged 0.017 d^{-1} (Table 2). Mortality estimates for the 2006 brood year are unrealistically high, as these values imply that there was a complete brood year failure for that brood year. Yet, approximately 3,000-4,000 Chinook salmon returned to the Marble River every year from 2007 to 2011 (CTC 2012), indicating that the 2006 brood year did not collapse, and that this estimate of winter mortality is unrealistic. This suggests either that juvenile Marble River Chinook salmon had left the Quatsino Sound area earlier or were inaccessible to the trawl net during winter (e.g. deeper or closer to shore) for that brood year.

Previous studies have showed that 55-95% of the juvenile pink salmon died within their first 40 days at sea, with mortality rates ranging between 0.019 d^{-1} and 0.072 d^{-1} (Parker 1964, 1968; Karpenko 1998). For chum salmon in southeast Alaska, 72-97% of the smolts died within the first 20-90 days with mortality rates ranging between 0.016 d^{-1} and 0.085 d^{-1} (Wertheimer and Thrower 2007). Beamish et al. (2012) estimated that 68-92% of the juvenile Cowichan Chinook salmon died from May to September of their first year at sea, with mortality rates ranging approximately between 0.009 d^{-1} and 0.021 d^{-1}. These studies indicate that early marine mortality can be substantial for juvenile salmon. The higher mortality rates observed for juvenile pink salmon and chum salmon smolts compared to juvenile Chinook salmon are not surprising given that they are much smaller than the fish collected in this study (<1 g vs 26-110 g; Table 3). Nevertheless, the overwinter mortality rates observed in this study were substantial with approximately only 20% of the juvenile Marble River Chinook salmon surviving through their first winter. These results support the hypothesis that winter is a critical period for juvenile salmon.

It is generally believed that winter mortality is size-selective, with smaller fish suffering greater mortality (Beamish and Manhken 2001). This hypothesis predicts that 1) the mean size of a cohort would increase between fall and winter, whereas 2) the variance of size would decrease over the same period. In this study, the length and mass of juvenile Marble River Chinook salmon increased by 40-59 mm and 34-63 g between fall and winter, respectively (Table 3). Fork length varied significantly among brood years ($F=804.4$, $p < 0.0001$) and seasons ($F=61.3$, $p < 0.0001$). The interaction between brood years and seasons was also significant ($F=5.3$, $p < 0.005$), indicating that the changes in fork length between fall and winter was not constant among brood years. However, the variance in fork length did not decrease between fall and winter (Table 3). These results suggest that overwinter mortality is not size-selective, at least for this population, and that fish are simply growing during winter. The cause(s) of this mortality is currently unknown, but may involve disease or mammalian predation (Middleton 2011)

Two critical periods have been recognized for juvenile salmon in the marine environment: an early period following smolt entry and the first winter at sea (Beamish and Manhken 2001). The strong correlation observed between smolt-to-adult returns and ocean conditions measured during the first few months of coastal ocean residence in several stocks and species of Pacific salmon (e.g. Mackas et al. 2007; Kline et al. 2008; LaCroix et al. 2009; Borstad et al. 2011; Duffy and Beauchamp 2011; Tanasichuk et al. 2011; Tomaro et al. 2012; Wells et al. 2012) supports the hypothesis that recruitment variability in Pacific salmon is primarily driven by changes in early marine survival. The results obtained in this study suggest that overwinter mortality of Pacific salmon also varies from year to year and could be yet another contributing factor to the recruitment variability of Pacific salmon.

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Table 1. Juvenile salmon surveys conducted by Fisheries and Oceans Canada in Quatsino Sound (QS), British Columbia, during fall and winter (2005-2010). Marble River Chinook migrate to sea as subyearlings (i.e. ocean type) , hence the ocean entry year is simply the brood year plus one for this stock. For instance, smolts of the 2004 brood year migrated to sea in 2005.

Sampling date	Season	Distance Towed (km)	Percent of QS Covered	Number of Sets
		2004 Brood Year		
November 1-3, 2005	Fall	65.5	49.2	17
March 7-8, 2006	Winter	64.5	48.5	14
		2005 Brood Year		
November 17-18, 2006	Fall	41.6	31.3	10
March 5-6, 2007	Winter	54.3	40.8	11
		2006 Brood Year		
October 18-19, 2007	Fall	44.8	33.7	12
March 16-17, 2008	Winter	57.2	43.0	13
		2007 Brood Year		
November 11-12, 2008	Fall	37.0	27.8	8
March 8-9, 2009	Winter	27.4	20.6	6
		2008 Brood Year		
October 20-21, 2009	Fall	41.7	31.3	9
February 25-26, 2010	Winter	31.0	23.3	7

Table 2. Overwinter mortality rates of juvenile Marble River Chinook salmon in Quatsino Sound, British Columbia (2005-2010). Method A assumes that no juvenile Marble River Chinook salmon were below the top 15 m, whereas Method B assumes that juvenile Marble River Chinook salmon were twice as abundant in the top 15 m compared to the 15-30 m stratum (see Methods for details). BY: Brood year; OEY: Ocean entry year.

BY/OEY	Period	Mortality (%)		Mortality rate (d^{-1})	
		Method A	Method B	Method A	Method B
2004/05	Nov 2005 – Mar 2006	72.9	81.9	0.010	0.014
2005/06	Nov 2006 – Mar 2007	61.1	74.1	0.009	0.012
2006/07	Oct 2007 – Mar 2008	98.3	98.8	0.027	0.030
2007/08	Nov 2008 – Mar 2009	86.7	91.1	0.017	0.021
2008/09	Oct 2009 – Feb 2010	63.0	75.3	0.008	0.011
Average		76.4	84.3	0.014	0.017

Table 3. Mean fork length (mm) and mass (g) of juvenile Marble Chinook salmon caught in Quatsino Sound, British Columbia, during fall and winter (2005-2010). *n*: sample size. Standard deviations are in parentheses.

Sampling date	Fork length	Mass	*n*
	2004 Brood Year		
November 1-3, 2005	163.0 (11.6)	47.9 (10.9)	289
March 7-8, 2006	212.1 (15.1)	109.8 (26.9)	34
	2005 Brood Year		
November 17-18, 2006	165.9 (22.4)	54.9 (28.5)	258
March 5-6, 2007	205.7 (23.2)	101.0 (41.6)	142
	2006 Brood Year		
October 18-19, 2007	140.1 (12.0)	29.5 (8.1)	163
March 16-17, 2008	199.0 (25.5)	92.3 (36.1)	3
	2007 Brood Year		
November 11-12, 2008	154.7 (11.7)	40.7 (9.7)	127
March 8-9, 2009	207.0 (23.0)	103.2 (28.6)	13
	2008 Brood Year		
October 20-21, 2009	135.7 (9.1)	26.4 (5.9)	45
February 25-26, 2010	178.6 (12.4)	60.8 (12.5)	20

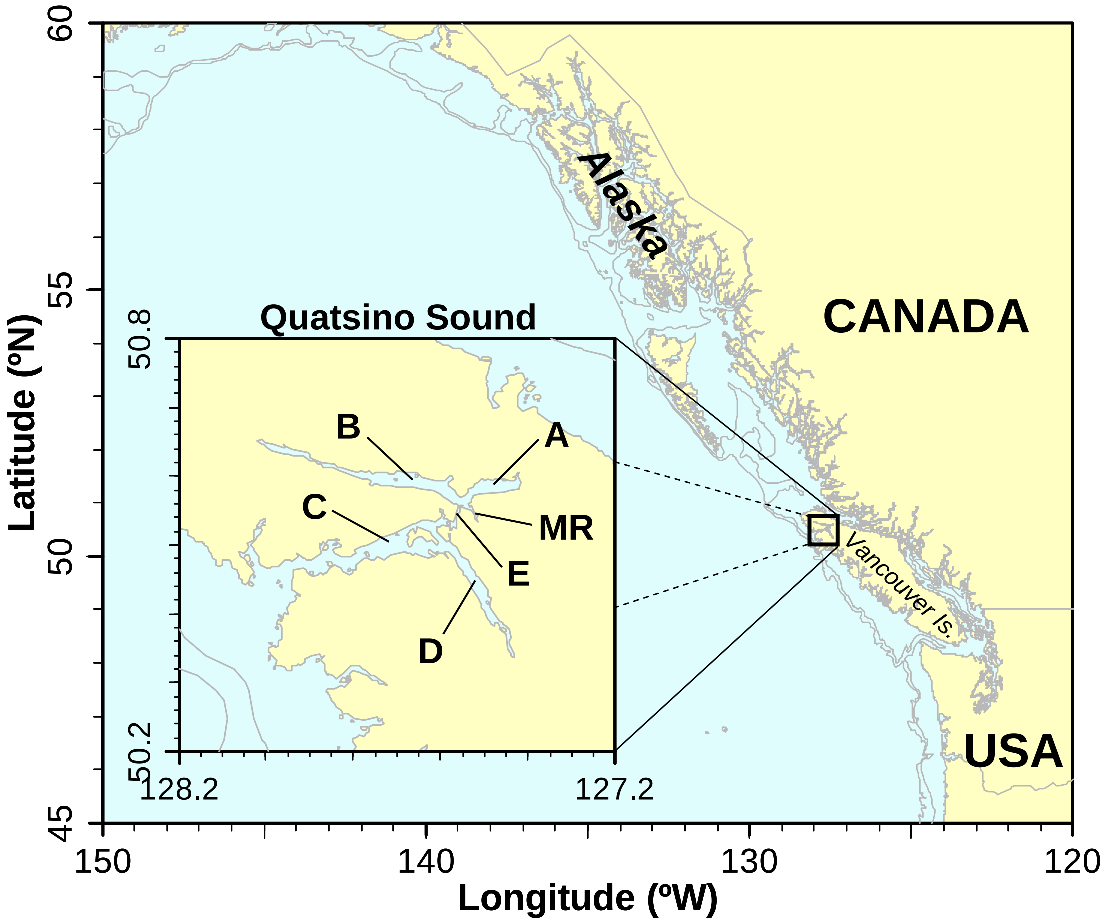
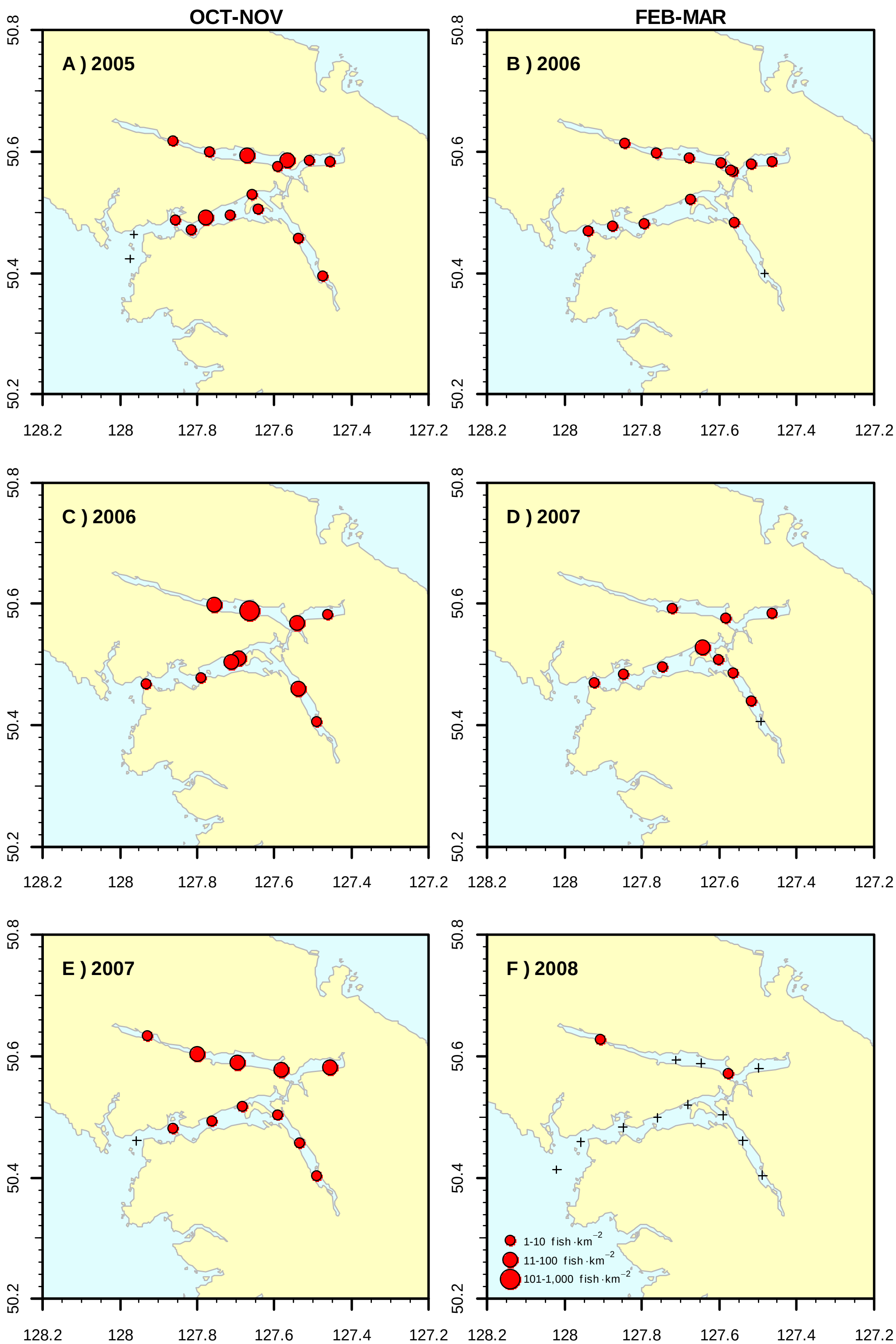


Figure 1. Location of the Quatsino Sound System and Marble River (MR) in British Columbia, Canada. A: Rupert Inlet; B: Holberg Inlet; C: Quatsino Sound; D: Neurotsos Inlet; E: Quatsino Narrows.



OCT-NOV
FEB-MAR
A) 2005
B) 2006
C) 2006
D) 2007
E) 2007
F) 2008
50.8
50.6
50.4
50.2
128.2
128
127.8
127.6
127.4
127.2
1-10 fish·km⁻²
11-100 fish·km⁻²
101-1,000 fish·km⁻²

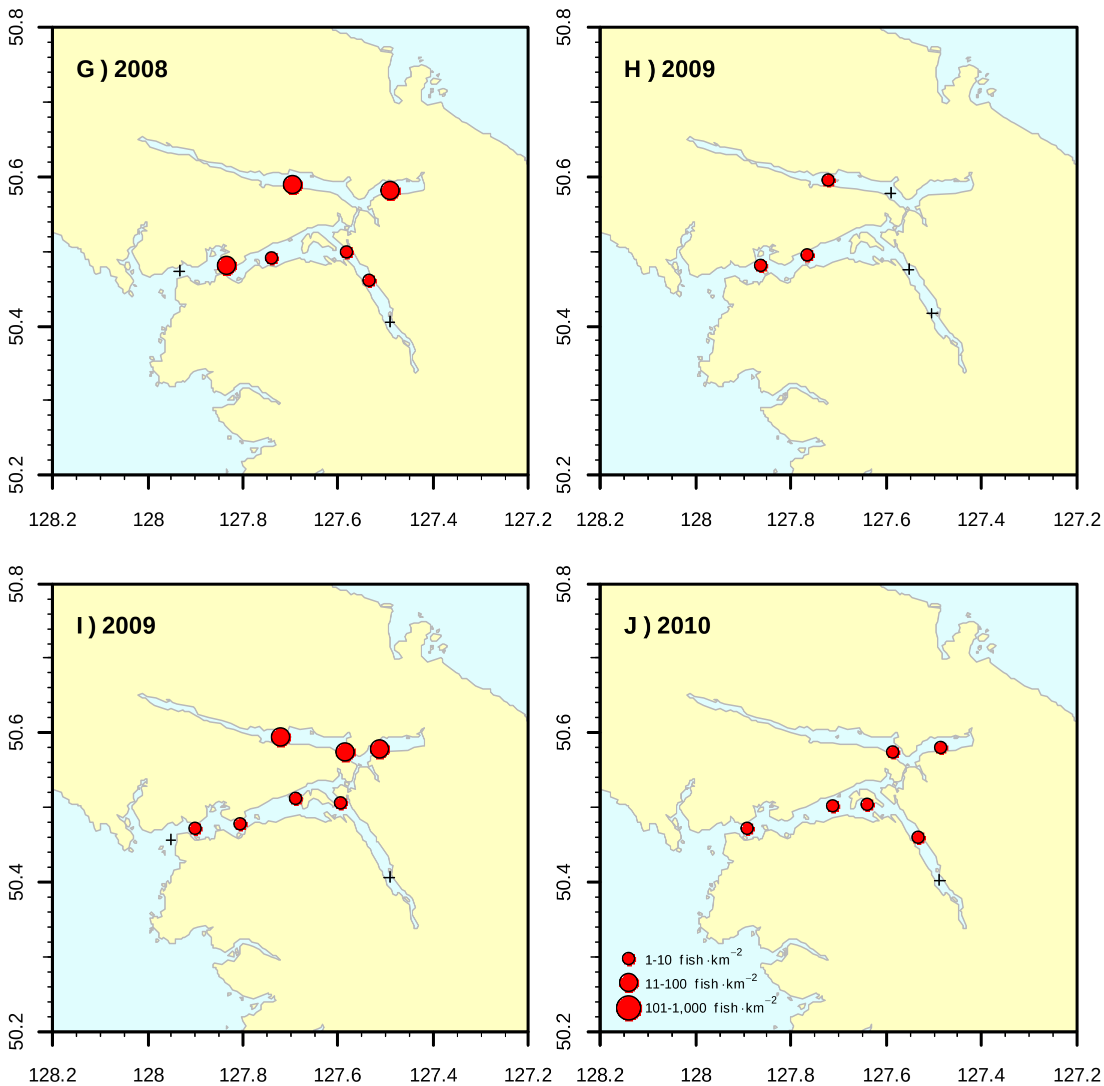


Figure 2. Catch-per-unit-effort (number of fish caught per km) of juvenile Marble River Chinook salmon in Quatsino Sound, British Columbia, during fall and winter (2005-2010).

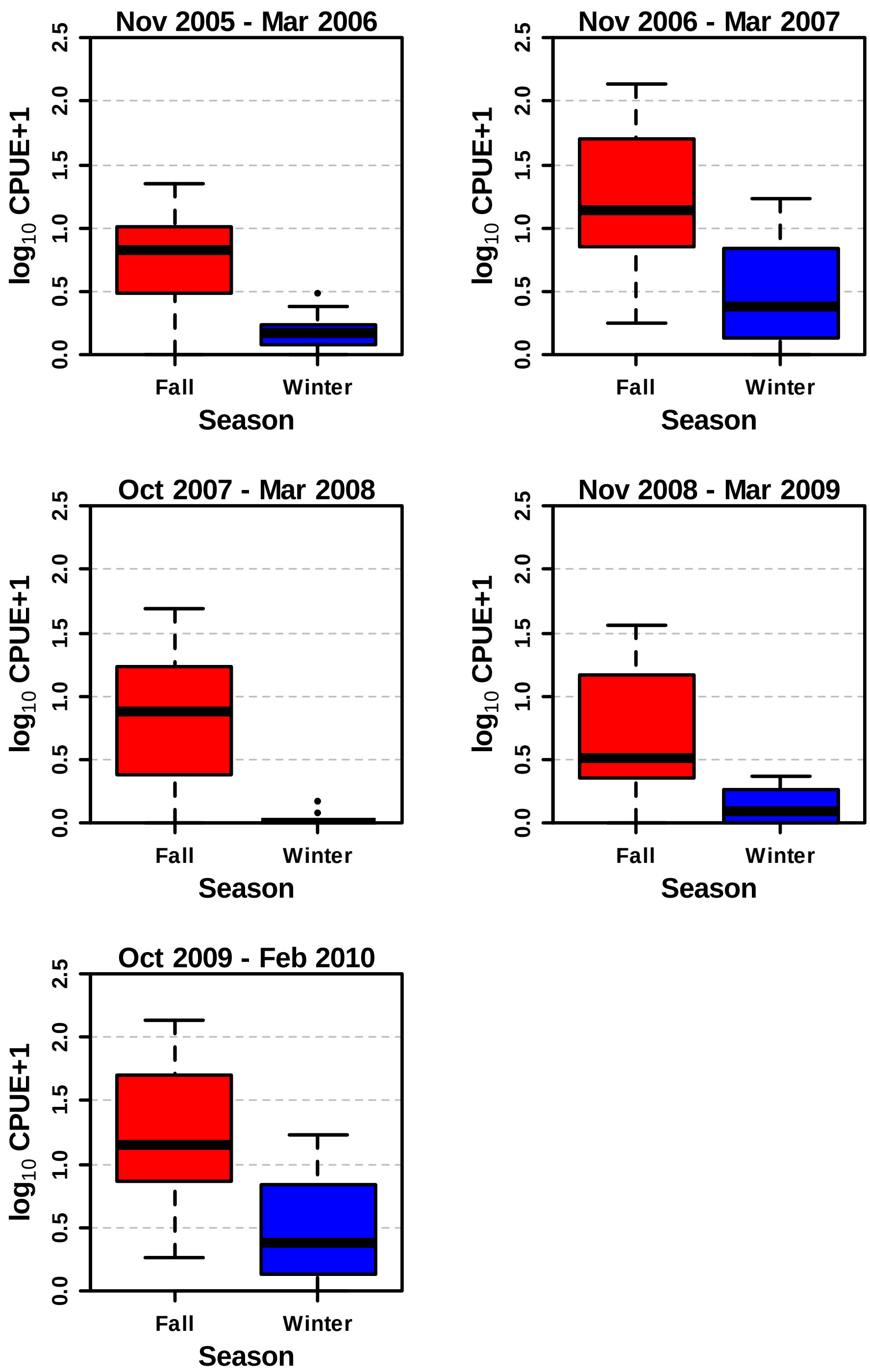


Figure 3. Boxplot of the catch-per-unit-effort (CPUE, number of fish caught per km towed) of juvenile Marble River Chinook salmon in Quatsino Sound, British Columbia, during fall and winter (2005-2010). Note that the y-axis is in logarithmic units to facilitate the comparison of the CPUE data and to homogenize the variance.