Applying the Krogh Principle to Find Shortcuts to Understanding Pacific Salmon Production

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Abstract: The Krogh Principle states that the selection of a particular animal can greatly facilitate understanding a particular mechanism. The principle could be applied to populations of Pacific salmon that are particularly productive within a region as a way of understanding more easily the mechanisms that regulate the productivity of all Pacific salmon. We show that an aggregate of Chinook salmon populations from the South Thompson River in the Fraser River drainage in British Columbia have anomalously high production, most likely related to their late ocean-entry life history. Similarly, sea-type Harrison River sockeye salmon from the same drainage also have a late ocean-entry life-history type and also have been exceptionally productive in recent years. These examples provide evidence that the exceptional production of late ocean-entry populations of Chinook and sockeye salmon may be caused by climate-related abundance increases in particular species of plankton in the early summer in the Strait of Georgia. The increased abundance of a preferred prey would allow the late ocean-entering juveniles to grow faster and be in better condition in the early marine period than the earlier ocean-entering juveniles. An understanding of the genetic, metabolic, and hormonal reasons for the improved productivity of these populations could help identify common mechanisms affecting productivity of other species of Pacific salmon.

Keywords: Krogh Principle, Pacific salmon production, Fraser River watershed, DNA analysis, migration

INTRODUCTION

Major changes in the abundances of the various species of Pacific salmon throughout the subarctic Pacific in recent years were largely unexpected. There are numerous examples that are familiar to most readers, but the decline in Chinook salmon abundances off the west coast of North America (Lindley et al. 2009; Schindler et al. 2013; Riddell et al. 2013) and the continuing record high catches of pink salmon by all countries producing Pacific salmon (Irvine and Fukuwaka 2011; Eggers 2009) are good examples. Historically, reasons for the declines were thought to have been associated with over-harvesting, poor escapement and freshwater habitat loss. More recently, it has been generally accepted that a fundamental cause of the major declines and increases appears to be climate-related changes in ocean habitats. Climate changes affecting Pacific salmon production occur for natural reasons (Beamish and Bouillon 1993; Beamish et al. 1999; Klyashtorin 2001; Mantua et al. 1997; Minobe 1999) and because of greenhouse gas accumulations, with global warming influences expected to be distinguishable by the mid-2000s (Overland and Wang 2007). As climate changes occur, it would benefit the management of all Pacific salmon producing countries if mechanisms regulating Pacific salmon production affected by ocean habitat changes were better understood, particularly for the optimization of hatchery production.

Understanding factors controlling ocean survival is a difficult problem. In comparative physiology, there is a principle named after the Danish scientist August Krogh that may help to simplify the problem. In a paper published in 1929, Krogh proposed that "for a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied" (Krogh 1929; Lindstedt 2014). According to the principle, the selection of a particular animal can greatly reduce the variability associated with a particular function. We propose that the Krogh Principle can apply to the need to improve the understanding of Pacific salmon production. Discoveries could be faster, if some research focuses on populations that are exceptionally productive in the current ocean and climate environment. In this paper, we focus on late ocean-entering Chinook and sockeye salmon in the Strait of Georgia, but we propose that the approach applies to other Pacific salmon species in other areas.
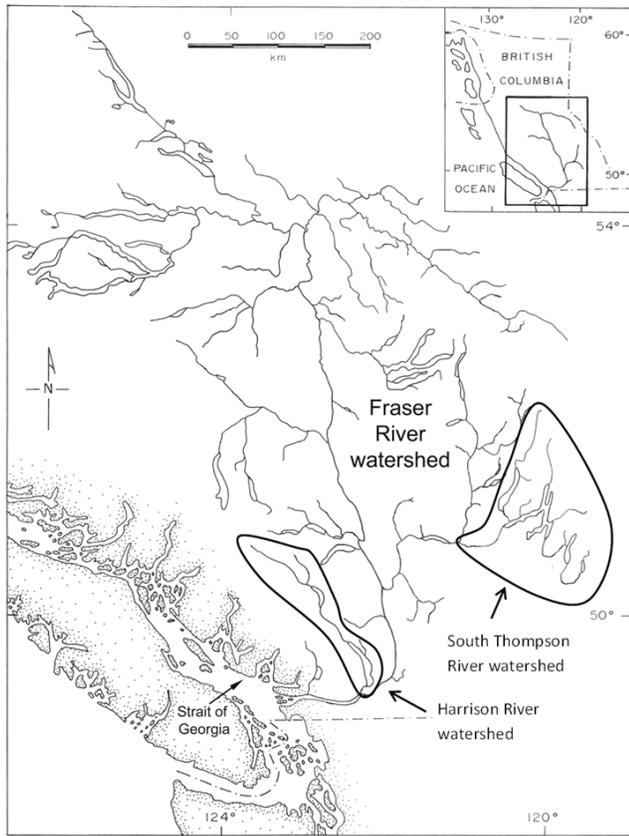
Fig. 1. Map of the Fraser River watershed and the Harrison River and South Thompson River watersheds that are part of it.

The Strait of Georgia, off the west coast of Canada is a semi-enclosed sea that is a major rearing area for juvenile Pacific salmon (Fig. 1, Beamish and McFarlane 2014). This is an ideal area for ocean research as the strait is readily accessible to researchers from a number of universities and government facilities.

Most of the populations of Chinook salmon that enter the Strait of Georgia originate in the Fraser River drainage. In the 1970s, there was a major commercial and recreational fishery for Chinook salmon in the Strait of Georgia (Argue et al. 1983). Catch data available from 1952 to 1969 indicated the average annual number of Chinook salmon caught by all fisheries was 284,000. Catches increased to 775,000 in 1976 and then declined to 175,000 in 1987. Catches continued to decline because of declining marine survival (Beamish et al. 1995) and the resulting restrictions on fishing. Today, the sport fishery catches an average of about 20,000 fish a year and the commercial fishery retains only a few thousand incidentally caught fish. The reasons for the declining survival were not determined, but it was shown that hatchery-produced juvenile Chinook salmon had poorer survival than wild Chinook salmon, indicating that they were more susceptible to the causes of mortality

(Beamish et al. 2012). There is an aggregate of Chinook salmon populations from the South Thompson River drainage in the Fraser River watershed (Fig. 1) that enter the Strait of Georgia and in recent years have exhibited anomalously good production. It is this aggregate of populations that we examined in this study.

Almost all sockeye salmon populations in the Fraser River drainage spend at least one year in a lake after emerging from the gravel (Foerster 1954). There also are
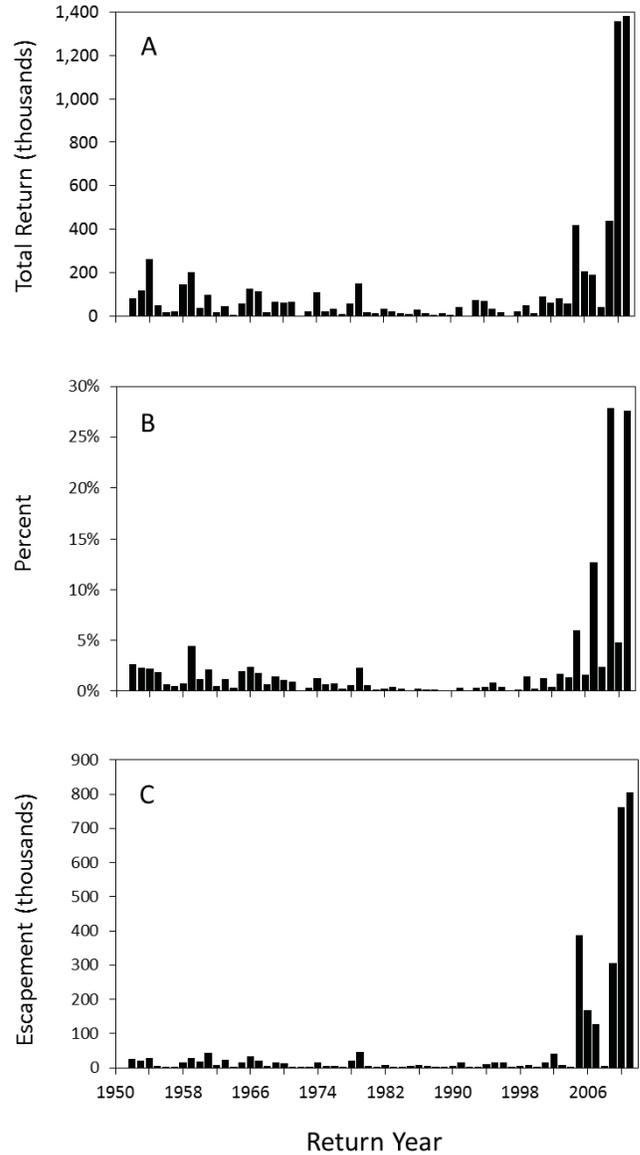

Fig. 2. Total return and escapement of sockeye salmon from the Harrison River (Fig. 1) for the years 1952–2011: (A) total return (thousands of fish) to the Harrison River; (B) percentage of Harrison River fish in the total return of all sockeye salmon to the Fraser River; and (C) escapement of adult Harrison River sockeye salmon (i.e., number of adults of all ages returning to the river in a single year).

sea-type sockeye salmon (Schaefer 1951; Gustafson et al. 1997) that enter the ocean in the same year that they emerge from the gravel. In the Fraser River drainage virtually all the sea-type sockeye salmon are from the Harrison River. Beginning in the early 1990s the productivity of Fraser River sockeye salmon declined steadily, reaching an historic low with the ocean-entry year 2007 (Beamish et al. 2012; Thomson et al. 2012; Peterman and Dorner 2012). The reason for the historic poor survival in 2007, as previously reported, was a result of highly anomalous ocean and climate conditions (Thomson et al. 2012; Beamish et al. 2012). As the lake-type sockeye salmon were declining in productivity in recent years, the sea-type, Harrison River sockeye salmon, were beginning to increase in productivity. From the early 1950s to present, Harrison River sockeye salmon represented about 2.2% of the production of all sockeye salmon populations in the Fraser River watershed (Fig. 2). From 2005 to 2011, they represented 11.9% of the total production.

We provide information on the biology and ecology of these sockeye salmon and the South Thompson River Chinook salmon and speculate why their survival is better than that of other populations of Chinook and sockeye salmon that enter the Strait of Georgia. We propose that our study provides an example of how the Krogh Principle could be applied to facilitate the understanding of the factors affecting the early marine survival of all Pacific salmon.

METHODS

Juvenile Chinook and sockeye salmon were caught in the Strait of Georgia using a modified mid-water trawl with a small-mesh cod-end (Beamish et al. 2000; Sweeting et al.

2003) that was fished along a standard track line. The net was fished with the head rope at depth intervals of 15 m from the surface. Most Chinook salmon were caught in the top 60 m, but deeper depths were fished. Most juvenile sockeye salmon were caught in the top 30 m. Sets were 30 minutes and the net was towed at 2.4 to 2.6 m/sec. The average net opening was approximately 15 m deep by 30 m wide. Surveys were conducted from late June to mid-July and in September. In this paper we refer to these as the July and September surveys. Surveys started in 1998 and continued until 2010 with some information available through to 2014. Juvenile Chinook and sockeye salmon were measured for fork length. Length frequencies were used to distinguish ocean age-0 Chinook salmon from older ocean ages. The lengths used to separate ages depended on a particular cruise, but ocean age-0 juveniles were consistently smaller than ocean age-1 and older individuals. Stomach contents were determined at sea from contents that were not preserved. All identifications were by the same expert. The volume of the contents and the percentage of prey were estimated. Catch per unit effort (CPUE) was standardized to one hour. Escapement estimates were from the Pacific Salmon Commission (CTC 2014).

In the lower Fraser River, a rotary screw trap was fished every fourth day in 2012 from April 20 to July 30 (Mahoney et al. 2013). The location of the trap was downstream of the spawning areas for Chinook salmon in the South Thompson River and all sockeye salmon populations except those from the Pitt River (49.2286°N, 122.7678°W). The stock origin of Chinook salmon collected in a rotary screw trap and over the sampling period was determined using DNA analysis conducted at the Molecular Genetics Laboratory at the Pacific Biological Station, Nanaimo, BC (Beacham et al. 2005).
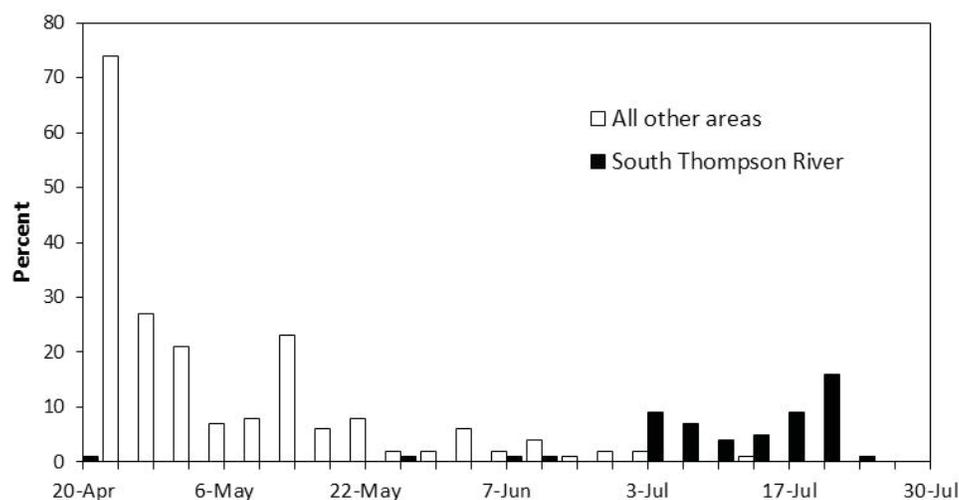

Fig. 3. Timing of the migration of 300 Chinook salmon smolts out of the Fraser River in 2012, showing the late migration of Chinook salmon from the South Thompson River drainage.
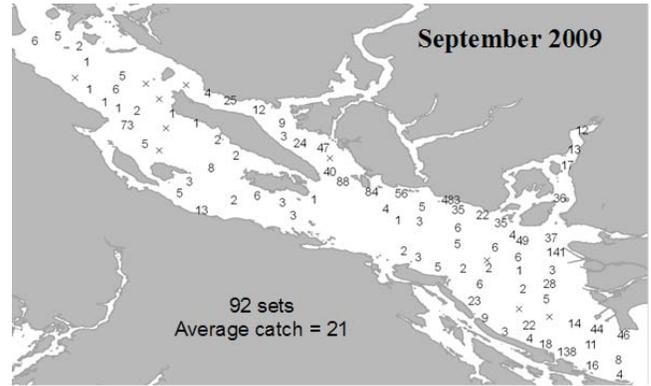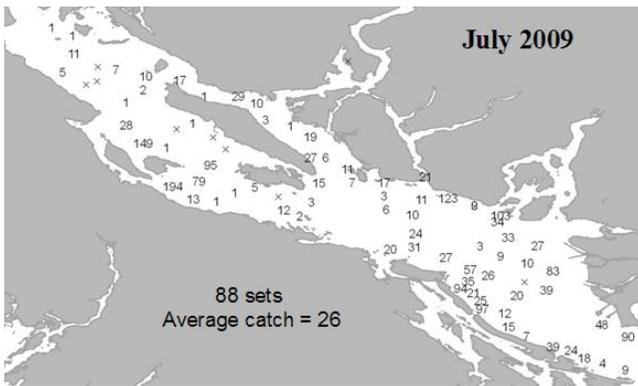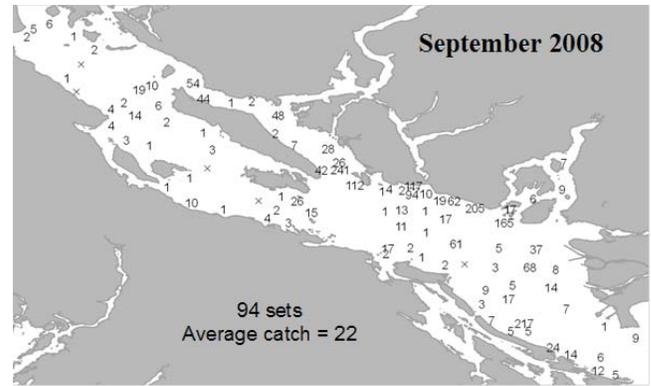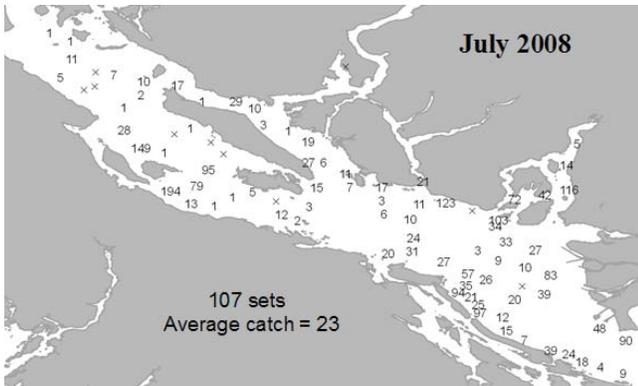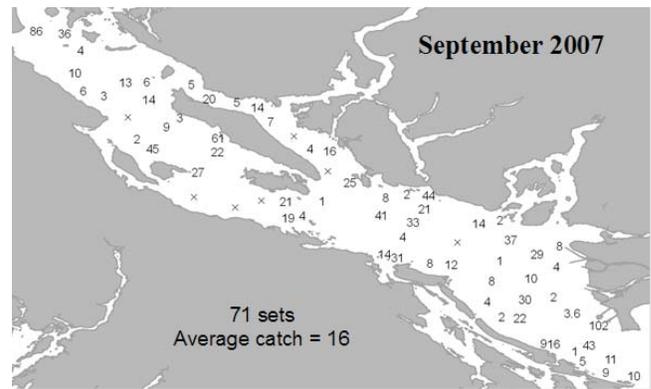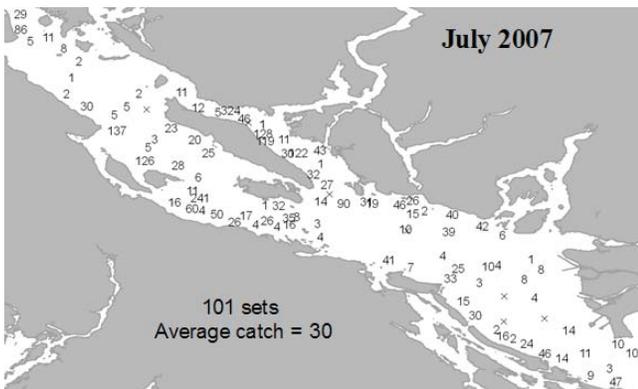
Fig. 4A. Examples of catches of juvenile Chinook salmon in the July surveys. Sets with 0 catch are identified by an X. Numbers represent catches in a 30-min set.

Fig. 4B. Examples of catches of juvenile Chinook salmon in the September surveys. Sets with 0 catch are identified by an X. Numbers represent catches in a 30-min set.

RESULTS

Chinook Salmon

Downstream Migration in 2012

There were 300 downstream migrating Chinook salmon smolts collected in the rotary screw trap and sampled for DNA. Of these, 18.7 % or 56 were South Thompson smolts (Fig. 3). Fifty-two of these 56 were captured between July 3 and 30. In contrast, only one of the other 244 was captured in July, indicating that virtually all of the smolts entering the Strait of Georgia later were from the South Thompson.

Trawl Surveys

Juvenile Chinook salmon were captured throughout the Strait of Georgia in the July and September surveys (Fig. 4A, B). An average of 10% of all sets did not catch at least one juvenile Chinook salmon (Table 1). There was very little trend in the average CPUE in July ($R^2 = 0.22$) or in September ($R^2 = 0.13$).

Length

The average length of juvenile Chinook salmon in their first ocean year captured in the July surveys (N = 25,200) ranged from 106 mm in 2007 to 144 mm in 2000 and in

Table 1. Results of trawl surveys for juvenile Chinook salmon in the Strait of Georgia, 1998 to 2014. CPUE is number of Chinook salmon caught per 1-hour trawl.

Year	Dates	Number of sets	Number of sets with 0 catch	Average CPUE	Average length, mm (SD)
1998	July	75	7	50.8	119.6 (36.8)
	September	84	2	39.8	169.2 (41.2)
1999	July	87	5	38.6	139.3 (28.9)
	September	80	2	32.0	174.0 (42.5)
2000	July	80	9	70.2	142.7 (37.2)
	September	87	3	25.1	184.7 (40.2)
2001	July	86	7	58.4	145.3 (29.8)
	September	91	8	24.1	188.3 (43.3)
2002	July	91	9	42.9	135.6 (24.1)
	September	76	3	37.7	151.7 (42.2)
2003	July		No survey		
	September	85	4	29.9	161.3 (31.7)
2004	July	101	10	77.4	119.6 (32.2)
	September	68	14	21.6	177.3 (42.1)
2005	July	76	9	18.1	134.5 (26.4)
	September	63	5	75.9	168.0 (23.8)
2006	July	72	7	87.0	127.2 (36.4)
	September	73	2	41.7	166.6 (58.4)
2007	July	70	5	60.2	106.5 (19.9)
	September	69	31	32.7	153.7 (17.9)
2008	July	87	5	40.6	128.4 (30.9)
	September	86	3	47.8	127.9 (26.4)
2009	July	79	8	49.7	132.8 (27.2)
	September	88	9	38.5	146.9 (31.4)
2010	July	83	4	37.5	132.6 (31.6)
	September	76	12	35.4	246.5 (34.8)
2011	July	76	9	34.3	142.6 (25.8)
	September	72	1	73.6	139.5 (7.1)
2012	July	79	17	33.1	146.3 (29.0)
	September	75	4	65.7	157.4 (47.2)
2013	July	67	5	26.0	134.7 (29.1)
	September	71	5	22.2	177.6 (41.8)
2014	July	88	8	18.9	126.3 (29.4)
	September	71	2	44.6	167.8 (46.2)

September (N = 31,000) from 128 mm in 2008 to 188 mm in 2001 (Fig. 5). There was a distinct bimodal distribution in September 2000, 2002, and 2006. In most other years the distribution had an extended tail to the right that identified the presence of larger fish.

DNA Analysis

DNA was analyzed from 2,022 fish that were captured in the 2007 to 2011 July surveys and 1,744 fish captured in the September surveys. South Thompson fish represented an average of 10.2 % of the samples in the July surveys and 68.8 % in the September surveys (Fig. 6). Juveniles from the South Thompson River drainage from Little River (31.1%) and Lower Thompson River (25.5%) dominated the catch in September. When the lengths of the fish sampled for DNA were separated into South Thompson populations and non-

South Thompson populations (Fig. 7), the South Thompson Chinook salmon were consistently the smaller fish in the distributions, although there were some small fish that were not from the South Thompson River area. In September 2010, South Thompson juveniles were caught throughout the water column with 76.4% caught from the surface to 44 m and the remaining below 45 m.

Diets

Juvenile Chinook salmon diets were analyzed from approximately 4,500 fish captured in July and approximately 9,000 fish in September (Fig. 8). Fish were the dominant prey item in all years for the July samples, except in 2007 when fish represented only 9.5% of the diet. Pacific herring (*Clupea pallasii*) was the major species of fish in the stomach, with an average of 63.5% of all fish remains
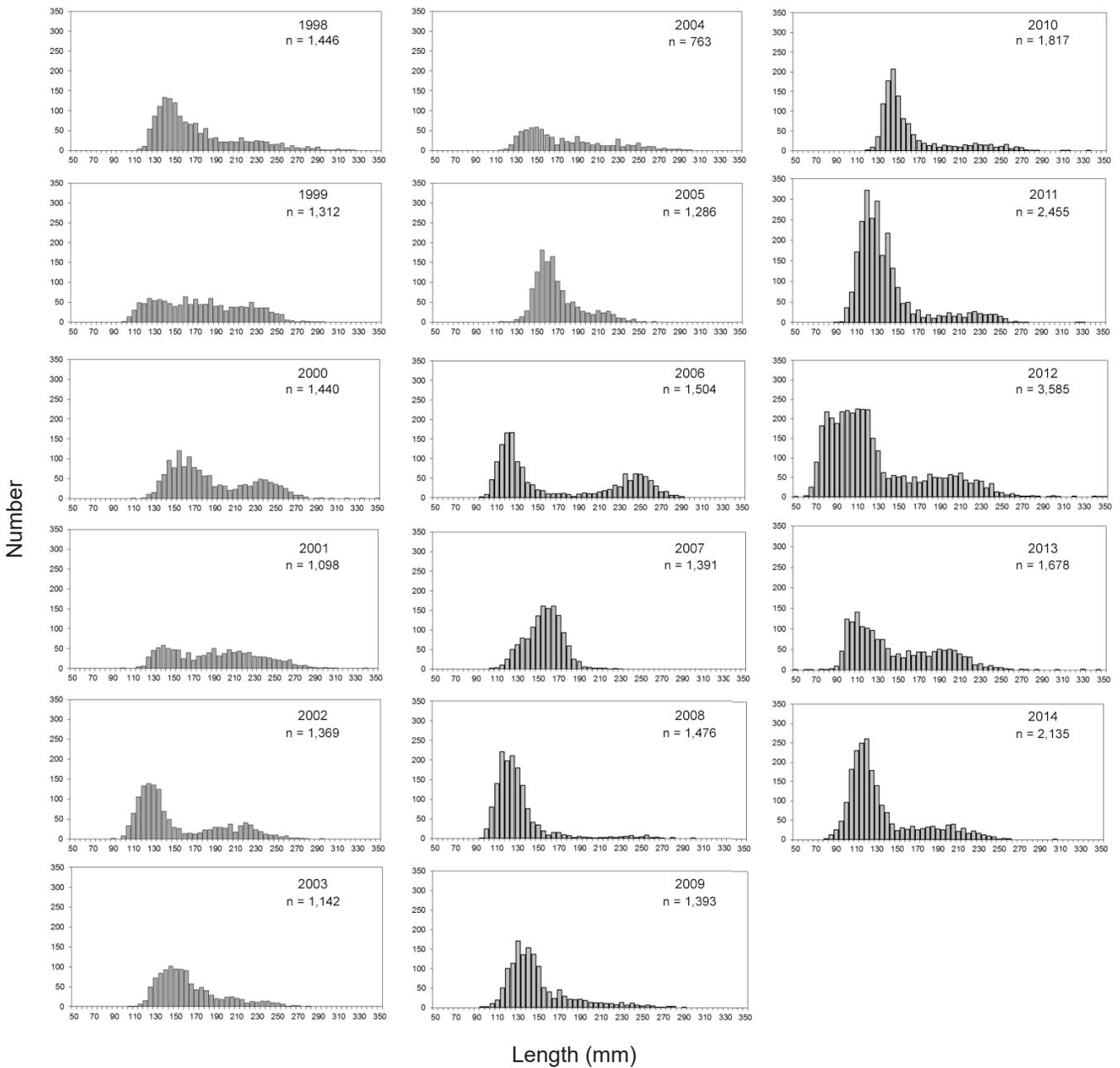
Fig. 5. Length-frequency of Chinook salmon measured in the September surveys, 1998–2014.

that could be identified. In 2007, no fish were identified as Pacific herring. (The exceptional change in diet in 2007 is not discussed in this paper, but was shown in Beamish et al. 2012 and Thomson et al. 2012 to be a result of extremely poor plankton production resulting from extreme climate and ocean conditions early in 2007). In the September samples, fish in the diet decreased to 42.3% and only 7% in 2007. Again, Pacific herring was the dominant prey item representing 52.9% of the identifiable remains. Amphipods comprised 11.5% of the diet in the July sam-

ples and 28% in the September samples. In both periods, hyperiid amphipods dominated with an average of 97.6% in July and 93.0% in September. The percentage of decapods decreased in September samples while the percentage of euphausiids increased (Fig. 8). In both periods, other species of fish included Pacific sand lance *(Ammodytes hexapterus)* and bay pipefish *(Syngnathus leptorhynchus)*. Major items in the "other" prey category included juvenile octopus, insects, small squid, calanoid copepods, and polychaetes.
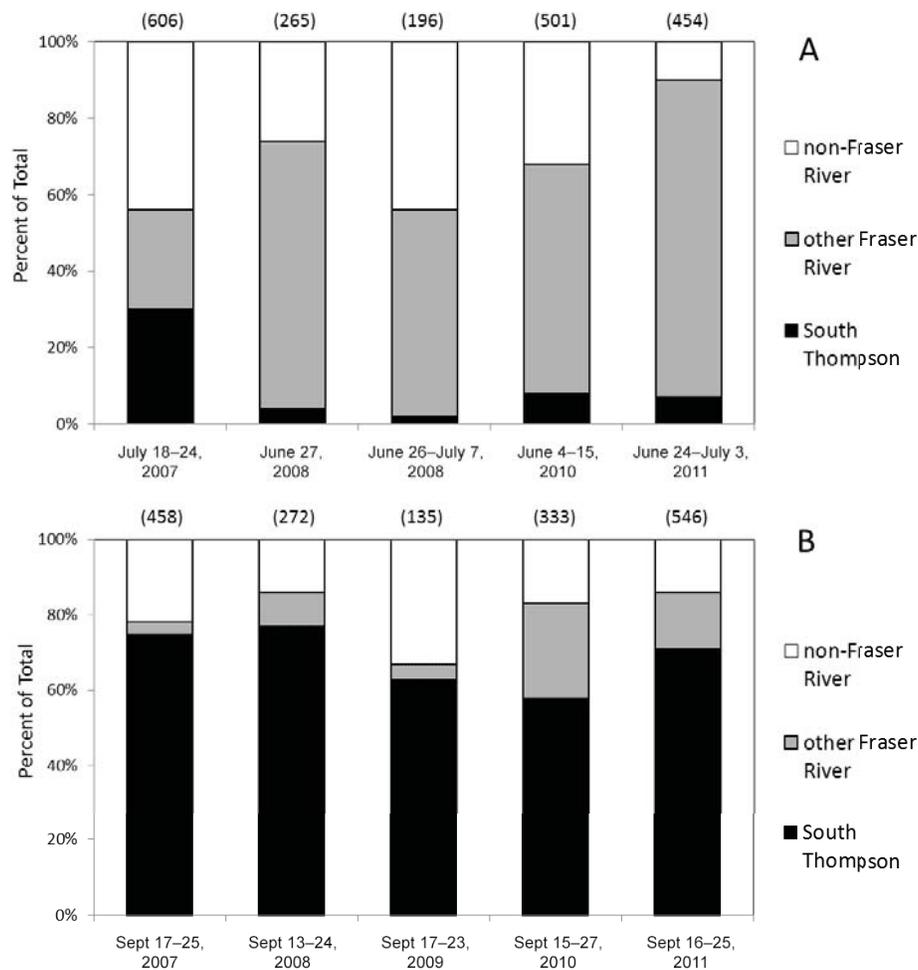
Fig. 6. Stock composition from DNA analysis of Chinook salmon captured in trawl surveys in the Strait of Georgia from 2007–2011: (A) in July; and (B) in September showing the large increase in the South Thompson River stocks in September. Sample size (n) is shown in parentheses.

November 2008 Trawl Survey

The sample of 55 juvenile Chinook salmon from the November 17–21, 2008, trawl survey consisted of 5% from the South Thompson area (Fig. 9) and the remainder were from other populations. The three fish identified as originating from the South Thompson were also the smallest in the sample (Fig. 9).

Escapements

The majority of adult Chinook salmon returning in the summer to the rivers in the South Thompson River drainage are considered four-year-olds (age-0.3). There was very little change in the escapements from 1975 to 1995 (Fig. 10), but beginning in 1996, escapements steadily increased with the average from 2006 to 2015 being 5.8 times the average from 1975 to 1995. The large return in 2010 was from the 2006 brood year that went to sea in 2007 and had a diet that was lowest in fish and highest in amphipods (Fig. 8).

There was a weak relationship ($R^2 = 0.026$) between the September survey CPUE and the adult return for a particular brood year (Fig. 11A). The relationship remained weak when CPUE was compared to the escapement in the previous year that produced the fish in the catch year ($R^2 = 0.197$, Fig. 11B). The relationship between escapement and the production from that escapement in four years (Fig. 11C) was weak ($R^2 = 0.166$) and similar to Fig. 11B.

Harrison River Sockeye Salmon

Ocean Entry Time

Beamish et al. (2016) showed that the Harrison River sockeye salmon enter the open ocean areas of the Strait of Georgia about eight weeks after the lake-type smolts and about the time that virtually all lake-type juveniles have left the Strait of Georgia. Beginning in 2008, DNA stock identification was used to show that in September 2008 and 2009, the percent of juvenile sockeye salmon from the Harrison
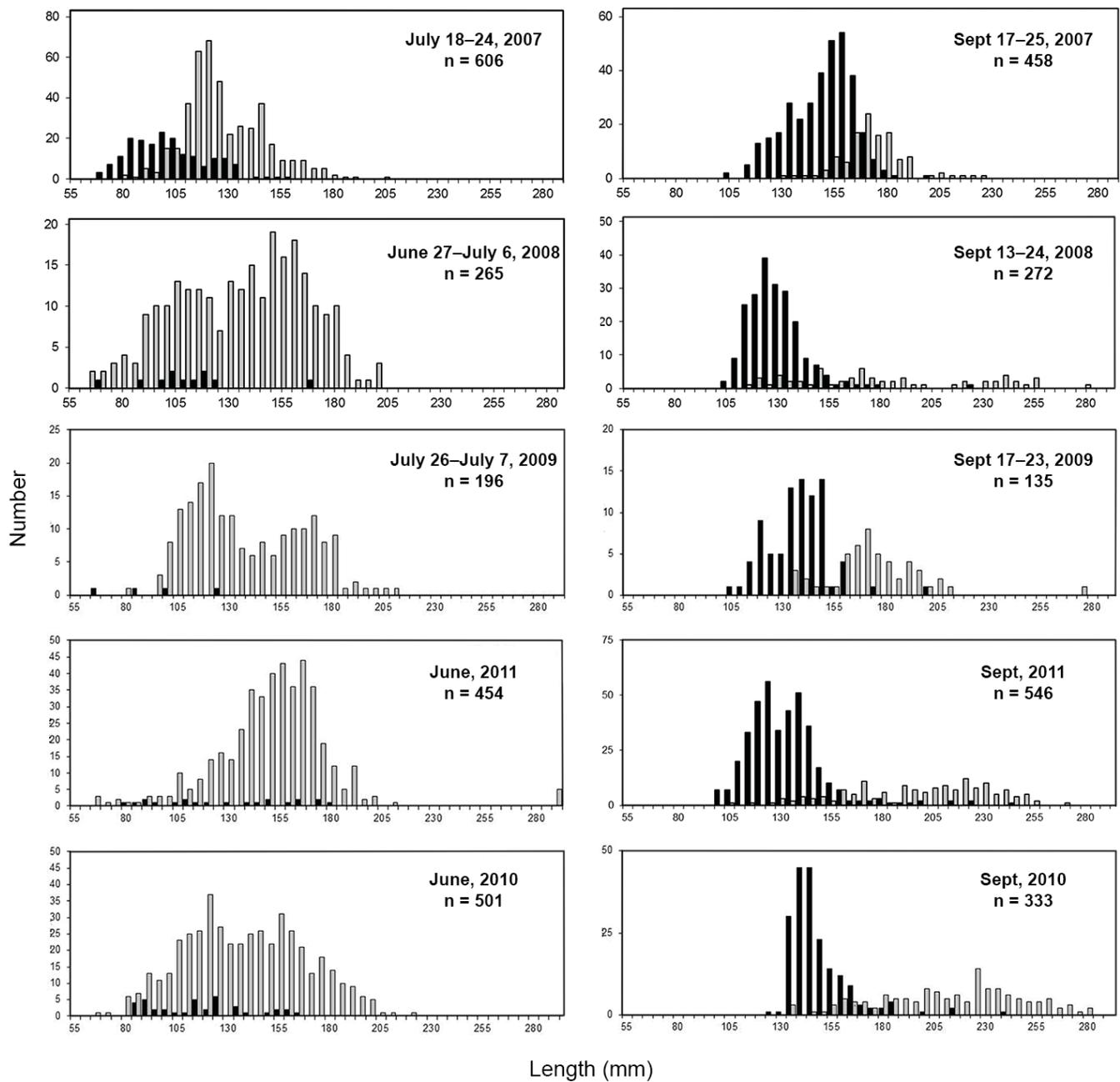
Fig. 7. Length-frequency distributions for Chinook salmon using DNA analysis to separate South Thompson River fish (black bars) from other populations (grey bars) captured in the Strait of Georgia in the July and September surveys 2007 to 2011.

River in the catches was 98% and 96%, respectively (Beamish et al. 2016). In 2010, the percent declined to 65%. Recent DNA analyses are available for only 2011 and 2014. In 2011, the percent of Harrison River juvenile sockeye salmon was 95.4% (n = 427) and in 2014 it was 92.4% (n = 224). Thus, in most years, the juvenile sockeye salmon in late summer and fall were virtually all from the Harrison River. When the percent of Harrison River juveniles was lower in 2010, we speculate that it was a result of generally poor survival for the earlier ocean-entering juvenile sockeye salmon, resulting in more lake-type fish remaining longer in the strait.

Escapements

The percent of Harrison River sockeye salmon in the total return of all Fraser River sockeye salmon and escapements were low until 2005 and then increased (Fig. 2A, B, C). The CPUE of juvenile sockeye from 1998 to 2010 showed no relationship with escapement (Fig. 12A). Beam-
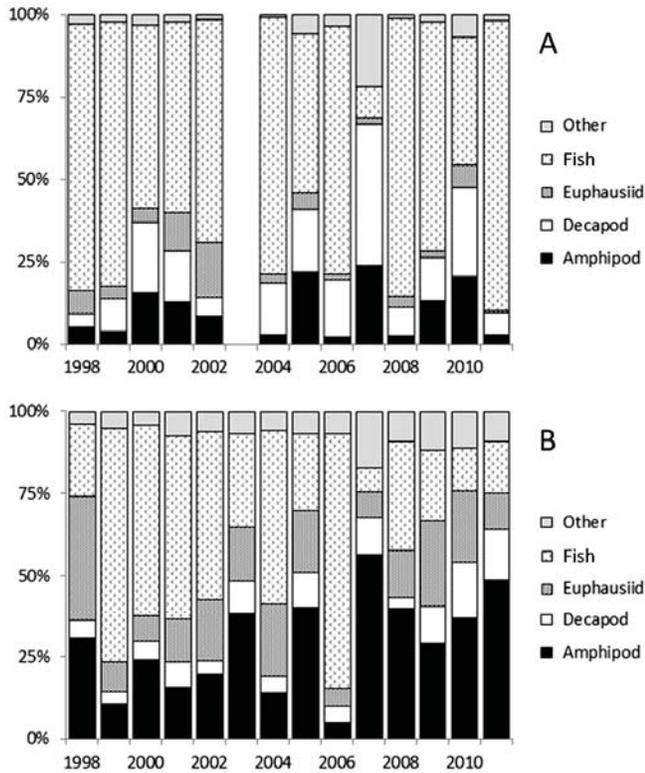
DISCUSSION

Fig. 8. Stomach contents of juvenile Chinook salmon captured in the Strait of Georgia in the July (A) and September (B) surveys from 1998 to 2011.

ish et al. (2016) detected a very weak relationship between escapement and total return (Fig. 12B), but a very strong relationship between CPUE in our September surveys and total return (Fig. 12C). This strong, positive relationship was influenced by the large juvenile abundances in 2007 and 2008, but indicates that conditions within the Strait of Georgia were related to the recent increase in the percentage of the sea-type life-history fish in the total return of all sockeye salmon to the Fraser River.

Diets

From 1998 to 2010, there were 2,208 juvenile sockeye salmon examined for stomach contents in the September surveys (Fig. 13). Amphipods were the preferred prey representing 60.5% of the volume and virtually all were hyperiid amphipods (99.9%). The dominant species of hyperiid amphipod in the diet was *Primno abyssalis* averaging about 75% of the volume of amphipods. Mackas et al. (2013) reviewed the information available for the annual abundances of the various species of zooplankton in the Strait of Georgia and concluded that amphipods represented about 8.2% of the zooplankton biomass in the strait. Thus, there appears to be selection for amphipods, and hyperiid amphipods, in particular.

In 2007 we were first able to use the results of DNA stock identification to determine that most of the juvenile Chinook salmon in the Strait of Georgia in September were from the aggregate of the populations from the South Thompson River. It was one year later, in 2008, that we first used DNA to discover that the sea-type juvenile sockeye salmon from the Harrison River were also abundant in the Strait of Georgia in the fall.

We documented the late ocean-entry timing of the South Thompson River Chinook salmon smolts using DNA analysis of the Chinook smolts in the rotary screw trap catches and DNA analysis of catches of juveniles in the July and September surveys. The trapping in the Fraser River clearly showed that the South Thompson Chinook salmon smolts migrated out of the Fraser River after the smolts from the other populations. The DNA analysis of the catches also showed a large increase in the percentage of the juvenile South Thompson fish in September. The high percentage in July 2007 probably occurred because the July 2007 survey was conducted later and because there was an exceptionally large mortality of the early-entering Chinook salmon juveniles (Beamish et al. 2012). In September, the late ocean-entering juveniles dominated the population of juvenile Chinook salmon from 2007–2011, representing an average of 68.8% of all juvenile salmon. Thus, there is good evidence that the populations of Chinook salmon from the South Thompson River that have an increasing trend in escapement, also have a life history of late ocean-entry that differs from the other populations of Chinook salmon that are experiencing poor survival.

We showed that the South Thompson juveniles were much smaller in July and September than the earlier ocean-entering juveniles. The small size of the fish in July and the apparent higher marine survival indicates that more than just fish size influences mortality of the earlier-entering juvenile Chinook salmon that co-occur in the catches in
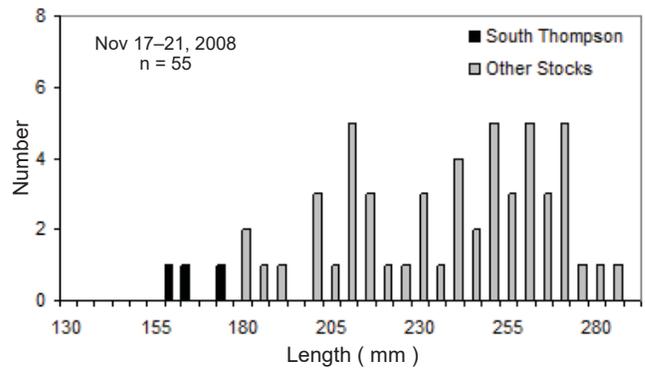

Fig. 9. Lengths of South Thompson Chinook salmon and other populations of Chinook salmon captured in the Strait of Georgia during the November 17–21, 2008 survey, as identified by the DNA analysis.
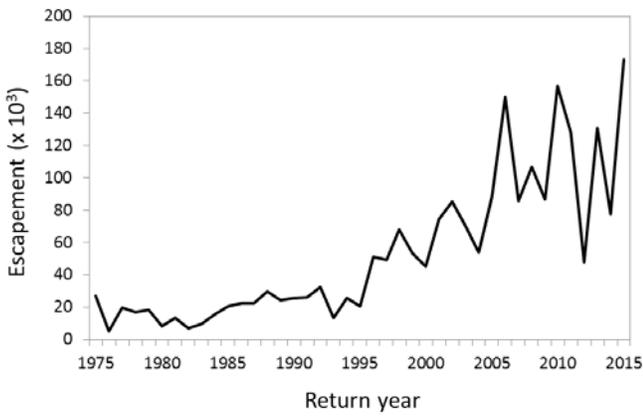
Fig. 10. Escapements of South Thompson River stocks within the Fraser River watershed from 1975 to 2015. Data for 2015 are preliminary.

Fig. 11. CPUE and escapement relationships for juvenile and adult South Thompson River Chinook salmon. (A) CPUE from 1998 to 2010 and the subsequent adult return for these fish in three years, 2001 to 2013. (B) CPUE and the previous year escapement that produced the fish in the CPUE for escapement years 1997 to 2013 and CPUE from 1998 to 2014. (C) South Thompson Chinook salmon escapements from 1998 to 2011 and the subsequent return of adults in four years from 2002 to 2015.

July and September. An acoustic tagging study (Neville et al. 2015) showed that juvenile mortality of the non-South Thompson fish remains high throughout the summer indicating that the source of this mortality, at least partially, may selectively avoid the South Thompson fish or that the South Thompson fish are better able to avoid the mortality (or both) even though they are smaller and distributed throughout the water column. This acoustic tagging study also showed that the tagged South Thompson River juveniles left through Juan de Fuca Strait (Fig. 1) from October 1 to November 24, although the sample size was small (three fish). The dates that the acoustically tagged fish left the Strait of Georgia were consistent with the apparent disappearance of juvenile South Thompson River fish by mid-November as indicated by the very small catch in the trawl survey in November 2008.

An important difference between late ocean-entering and early-entering juvenile Chinook salmon was diet. Late ocean-entering juveniles consumed more amphipods and fewer fish than the early-entering individuals. Virtually all the amphipods in both the July and September samples were hyperiid amphipods which were not the dominant species of amphipod in the zooplankton as reported by Mackas et al. (2013). However, our diet studies do not compare the feeding of the early and late ocean-entering life-history types during the same ocean stages. The early-entering populations were feeding on hyperiid amphipods in July, but it is their diet in the first few weeks after their ocean entry in May that needs to be compared. We speculate that if this comparison were available, the prey quantity and quality in mid-May would be less favourable than that available in mid-July. It is speculation, but we propose that the increased production of the South Thompson Chinook salmon and the Harrison River sockeye salmon resulted from an increased production of hyperiid amphipods in recent years that matched their late ocean-entry time.
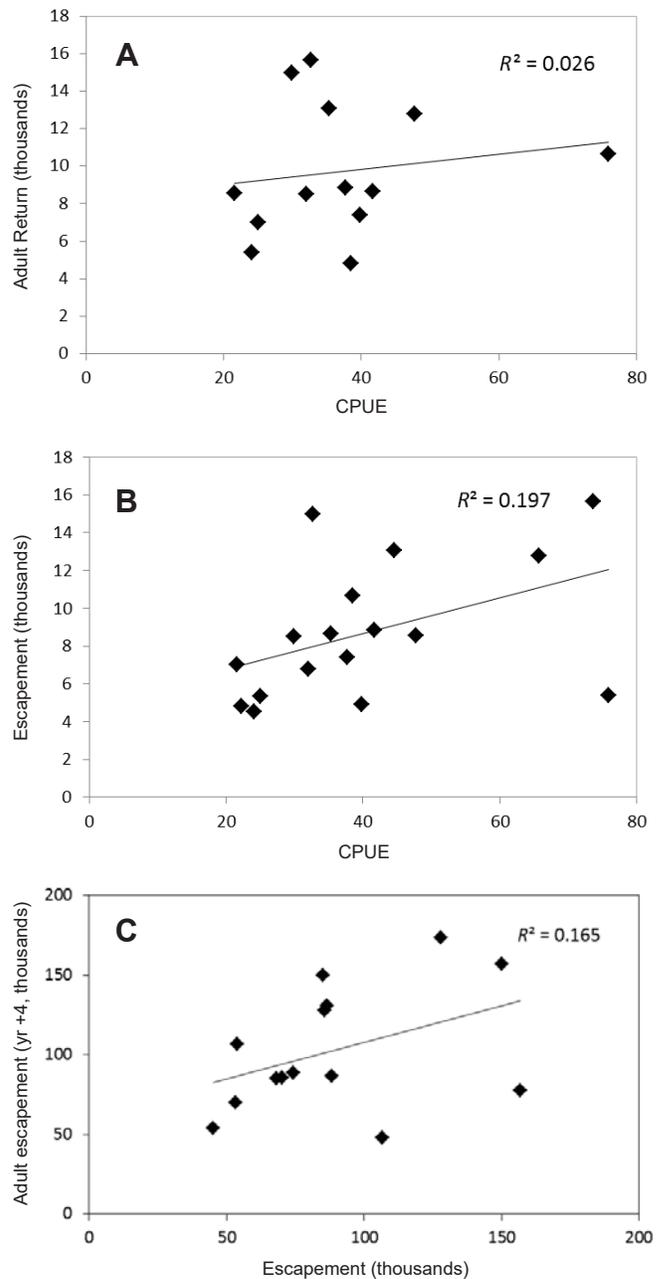
There was a weak relationship between CPUE of juvenile Chinook salmon in September and the escapement in the previous year, possibly indicating that the number of juveniles in the September surveys was only weakly related to production in fresh water. There also was a weak relationship between CPUE and the subsequent return of adults for a

particular brood year. The relationship between escapement and the adult return in four years from this escapement was also very weak during the study years. We considered that the escapement estimates were a general indication of total production because it was unlikely that fishing mortality was progressively less selective for the South Thompson River Chinook salmon. Duffy and Beauchamp (2011) showed that the condition of juvenile Chinook salmon in the first months in Puget Sound was a good predictor of brood year survival. We speculate that a similar relationship exists for the South Thompson River Chinook salmon but is obscured because the CPUE in September includes an average of 31.2% of other populations with a range from 2007 to 2011 of 58% to 77%. Also, the use of escapement numbers does not represent total production. Thus, we propose that if we could relate the specific South Thompson River Chinook salmon CPUE to their total production, there would be a relationship between CPUE and total return similar to that we observed for Harrison River sockeye salmon.

The similarities in the biology of the South Thompson River Chinook salmon and the Harrison River sockeye salmon are (1) a late ocean entry into the Strait of Georgia, (2) late exit time from the Strait of Georgia, (3) small size at ocean entry and (4) a preference for hyperiid amphipods in their diet. There is good evidence that climate influences on plankton production can affect fish production, including Pacific salmon (Farley et al. 2009; Brown et al. 2011; Hunt et al. 2011; Sigler et al. 2011). Thus, it is likely that there were climate-related changes in the plankton in the Strait of Georgia that initiated the trend in improved production. Specifically, it appears that hyperiid amphipods became more accessible and more abundant. We speculate that the improved survival occurred because the juveniles found preferred prey easily and grew faster, quicker. This interpretation is consistent with the critical size-critical period hypothesis proposed by Beamish and Mahnken (2001), except that the hypothesis needs to be adjusted to include the late ocean-entry mechanism.

The critical size-critical period hypothesis proposed that an individual that grew to a critical size by a particular date would begin to store more lipids and be better able to survive the first ocean winter. The principle is that juvenile Pacific salmon would be genetically more sensitive to body condition at a particular time in the early marine period. There would be an external stimulus such as day length or temperature or both that stimulated the hormonal sensitivity. The summer solstice and the fall (autumnal) equinox could be changes that stimulate hormonal activity. According to the hypothesis, a rapid rate of growth early in the marine period would result in body condition that exceeded a genetically controlled threshold and signaled a change in the metabolism of the individual. The energy used for rapid growth would be related to factors that affect food supply, food quality, and food access. Consequently, temperature, temperature change, density of individuals, and competitors could be related to achieving the condition
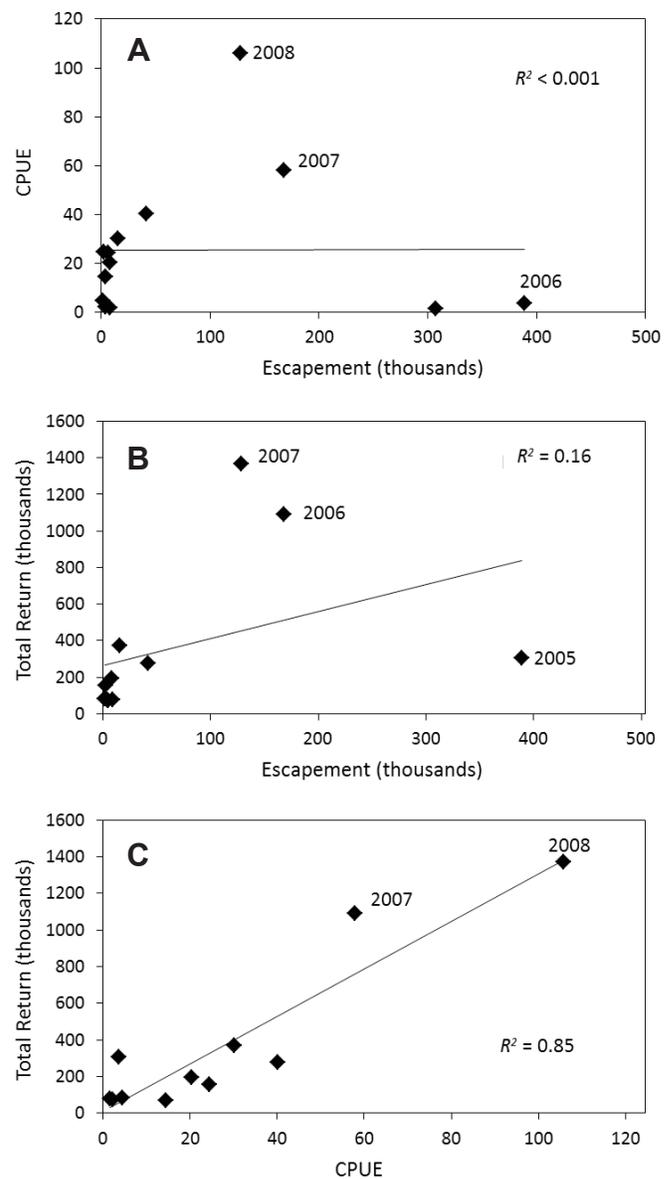

Fig. 12. Relationships between adult returns, escapement, and CPUE of Harrison River sockeye salmon: (A) escapement (number of fish returning to the river in a single year) and juvenile CPUE during September trawl surveys conducted in the next year (1998-2010; ocean-entry years are shown); (B) escapement in 1997-2007 and total brood year return of age-3 and age-4 individuals produced by that escapement (escapement years are shown); (C) CPUE and the total return of the brood year that produced the CPUE (1998-2008; ocean-entry years are shown). For example, juveniles captured via trawling in 2007 were from the 2006 brood year and would return as adults in 2009 and 2010 (age 3 and 4).

threshold. According to the hypothesis, fish not exceeding the condition threshold would continue with their existing metabolism. These individuals would use more lipids to continue to grow and by fall may be the same size as the fish that stored more lipids. The fish with less stored en-
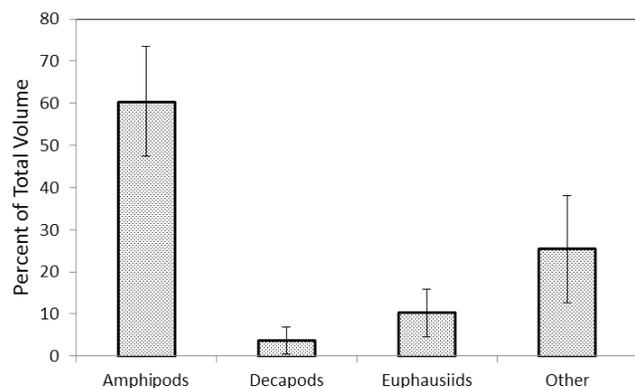
Fig. 13. Average diet composition (% of total volume) based on analysis of stomach contents from 2,208 juvenile sockeye salmon sampled in the Strait of Georgia during September of 1998–2010. Ranges in the annual percent of total volume from 1998–2010 are shown.

ergy would be less likely to survive the first ocean winter and could be considered as "dead fish swimming". Individual size is important but may not be the best term for the hypothesis as it is body condition that is the determinant at the critical period. Thus, in the hypothesis of Beamish and Mahnken (2001), the word "size" could be interpreted as "condition". Size is relevant as it can be an indicator of energy available for growth, but it is the condition of the individual prior to the first ocean winter that is the key to survival. The critical period was initially thought to be around the summer solstice, however, for the Harrison River sockeye salmon and the South Thompson River Chinook salmon, the critical period would be later in the year, possibly around the fall equinox.

The purpose of this paper was to propose that an understanding of the mechanisms that result in the success of a small number of populations of Chinook salmon and the late ocean-entering Harrison River sockeye salmon may facilitate an understanding of the mechanisms that regulate the early marine survival of Pacific salmon. Lindstedt and Nishikawa (2015) used Krogh's wisdom to show that "extremes in nature are rarely the result of novel mechanisms, but rather employ existing solutions in novel ways". Thus, the current difficulty in understanding the mechanisms affecting marine survival of Pacific salmon would result from the numerous ways populations adapt to a broad range of environments throughout their ocean life. However, the fundamental processes that regulate their survival would be similar and a research focus on populations that are anomalously successful may be the fastest way of discovering these processes. We are not suggesting the abandonment of existing research; we are suggesting that a focus on a few exceptional populations may explain the fundamental mechanisms that regulate the production of the aggregate of populations, with insights possibly for other species of Pacific salmon.

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