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Recent Advances in Marine Juvenile Pacific Salmon Research in North America

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Pacific salmon sustain 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 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 (Pearcy 1992; Beamish and Manhken 2001). Hence, studies that investigate the processes affecting the survival of Pacific salmon during the juvenile phase of their marine life are critically needed to understand the recruitment variability of Pacific salmon. Here, we provide a brief overview of the progress that has been made in North America on the marine ecology of juvenile Pacific salmon since the "Second NPAFC International Workshop on Factors Affecting Production of Juvenile Salmon" held in Sapporo, Japan, in 2006. We focused our effort on primary publications in peer-reviewed journals as well as NPAFC publications (i.e., Documents, Technical Reports, and Bulletins) and present selected key findings due to the large number of publications that had to be covered as part of this overview (Fig. 1).

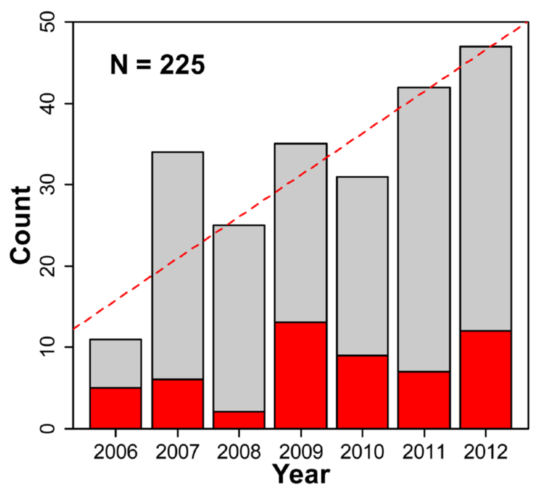

Fig. 1. Number of NPAFC publications (red bars) and peer-reviewed journal articles (grey bars) published between 2006 and 2012 in North America pertaining to marine ecology of juvenile Pacific salmon. The dotted red line represents the trend in the number of publications that are produced each year, excluding seven papers that appeared in a special issue of the American Fisheries Society Symposium Series focusing on juvenile salmon in 2007.

We compiled 225 studies that investigated different aspects of the marine ecology of juvenile Pacific salmon in North America, including survival rates and mechanisms, ocean and climate effects, distribution and migration, bioenergetics and physiology, diet and trophic interactions (Table 1; Fig. 1). Overall, the number of publications has increased steadily by approximately five papers each year since 2006 (Fig. 1). On average, 25% of the papers that have been published during that time period were contributed through NPAFC (Fig. 1). The majority of these studies focused on one (60%) or two (21%) salmon species at a time. Chinook salmon and pink salmon were the two most frequently studied species (Fig. 2).

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Table 1. Focus of juvenile Pacific salmon research conducted in North America (2006-2012).

Topic	N
Distribution & Migration	59
Climate & Physical Oceanography	87
Bioenergetics, Growth & Physiology	41
Diet & Trophic Interactions	58
Ecological Interactions	33
Pathogens & Disease	50
Winter Ecology & Survival	4
Survival Rates & Mechanisms	100

For Chinook salmon, this was possibly because of concerns over their decline over a broad geographic area (Tompkins et al. 2011). In the case of pink salmon, this is probably due to the fact that they are the most abundant species of salmon in North America (Irvine and Fukuwaka 2011). Steelhead was the least studied species, possibly because they rapidly move to offshore waters of the North Pacific Ocean (Hartt and Dell 1986).

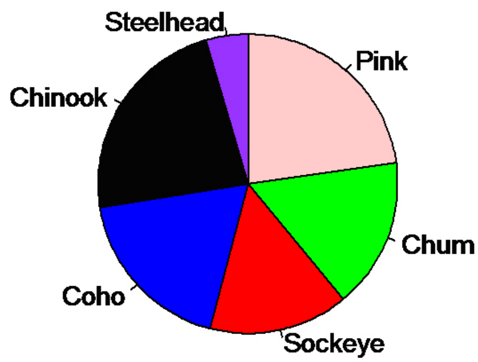

Fig. 2. Proportional representation by species of the number of juvenile Pacific salmon studies investigated in North America (2006-2012).

Survival rates

In North America, considerable effort has been devoted since 2006 to estimate the early marine survival of juvenile salmon (Table 2). However, few of these studies have been performed on juvenile pink and chum salmon compared to other species probably because their small size precludes the utilization of acoustic tags to estimate their survival rate (Table 3). Similarly, few studies have investigated the extent of overwinter mortality in juvenile salmon, probably due to the difficulty of sampling the marine environment during the winter months (Trudel et al. 2007b; Farley et al. 2011). Until acoustic tags became available for relatively small fish, marine survival estimates of salmon also included a freshwater component associated with the downstream migration of smolts and the upstream migration of adults. The application of acoustic tags revealed that significant and variable portion of this "marine mortality" actually occurred in freshwater (Welch et al. 2008; Chittenden et al. 2010a, b; Melnychuk et al. 2012; Moore et al. 2012; Melnychuk et al. 2013). Overall, early marine and winter survival can be quite low (Table 2), though the proximate causes for their low survival remain, for the most part, elusive.

Table 2. Estimates of early marine and first winter marine survival of juvenile Pacific salmon.

Species	Survival	Sources
Pink salmon	--	--
Chum salmon	20-50%	1
Sockeye salmon	20-50%	2-3
Coho salmon	2-20%	4-5
Chinook salmon	2-30%	6-7
Chinook salmon*	10-40%	8
Steelhead salmon	10-80%	9-11

*Winter

Sources: 1. Wertheimer and Thrower (2007); 2. Welch et al. (2009); 3. Wood et al. (2012); 4. Beamish et al. (2010c); 5. Melnychuk et al. (2013); 6. Beamish et al. (2012b); 7. Rechisky et al. (2013); 8. Trudel et al. (2012); 9. Moore et al. (2010b, 2012); 10. Melnychuk et al. (2007); 11. Welch et al. (2004).

Climate effects

The potential effects of climate on salmon production have long been recognized (Beamish 1993; Beamish and Bouillon 1993; Mantua et al. 1997). However, the intermediate steps linking salmon to climate have generally been poorly studied (Baumann 1998). Recent studies conducted in North America suggest that the effects of climate on salmon are largely species, stock, or region-specific (Wells et al. 2008; LaCroix et al. 2009; Malick et al. 2009). In the California Current System and Strait of Georgia, climate effects on salmon survival may be mediated through bottom-up processes that affect juvenile salmon feeding and growth (Beamish et al. 2006b; Wells et al. 2007, 2008; Beamish et al. 2010c; Wells et al. 2012; Daly et al. 2013). Climate may also affect survival in a top-down manner by altering the abundance and distribution of predators and alternative prey (i.e., forage fish) (Emmett et al. 2006; Emmett and Sampson 2007; Emmett and Krutzikowsky 2008), though few salmon have been reported in the stomachs of predators (Emmett et al. 2006; Sturdevant et al. 2009, 2012b). In contrast, no consistent patterns have been observed in Alaska, with both positive and negative effects of temperature on salmon production (Malick et al. 2009; Sharma and Liermann 2010; Sharma et al. 2013). Finally, in addition to large scale climatic effects, local scale processes can also be important and affect salmon survival (Beamish et al. 2010c; Borstad et al. 2011; Sharma et al. 2013).

Table 3. Number of juvenile salmon recovered or tagged to investigate their migration behaviour. HD86: Hartt and Dell (1986); CWT: coded-wire-tags; DNA: genetic stock identification; AT: acoustic tags.

Species	HD86	CWT	DNA	AT
Pink salmon	56	--	--	--
Chum salmon	6	--	1625	--
Sockeye salmon	41	3	8942	1275*
Coho salmon	244	914	2344	417
Chinook salmon	12	2456	8688	3125
Steelhead salmon	1	--	--	1863

*Includes 96 kokanee

Data compiled from Balfry et al. (2011); Beamish et al. (2010a, b, 2012a, b); Chamberlin et al. (2011); Chittenden et al. (2008, 2009, 2010a, b); Farley et al. (2011); Hartt and Dell (1986); Kondzela et al. (2009); McCraney et al. (2010); Melnychuk et al. (2007, 2010, 2013); Moore et al. (2010a, b, 2012); Morris et al. (2007); Murphy et al. (2009); Neville et al. (2010); Preikshot et al. (2012); Quinn et al. (2011); Rechisky et al. (2009, 2012); Rice et al. (2011); Seeb et al. (2011); Thomson et al. (2012); Trudel et al. (2009, 2011); Tucker et al. (2009, 2011, 2012); Van Doornik et al. (2007); Welch et al. (2004, 2009, 2011); Wood et al. (2012).

Distribution and migration

To assess the effects of climate change and ocean conditions on Pacific salmon, we must first determine where they migrate to and how much time they reside in different regions of the ocean (Trudel et al. 2009). Significant progress has been made during the last seven years to understand stock-specific migration behaviour of juvenile Chinook, coho, and sockeye salmon, and steelhead using DNA analyses and tags (Tables 2 and 3). However, little effort has been directed in North America to investigate the migration behaviour of the two most abundant species, pink and chum salmon (Table 2; but see Kondzela et al. 2009). Overall, migration behaviour has been shown to vary among species, stocks, and life-histories, with slow and fast migrants, residents, and southward migrants (Morris et al. 2007; Trudel et al. 2009; Tucker et al. 2009; Beamish et al. 2010a, c). Migration routes may also be genetically programmed (Weitkamp 2010; Sharma and Quinn 2012; Tucker et al. 2012; Burke et al. 2013), but juvenile salmon distribution along their migration trajectory may be affected by size (Tucker et al. 2009; Beacham et al. 2012) and local conditions (Bi et al. 2007, 2008; Farley and Trudel 2009; Bi et al. 2011; Burke et al. 2013). Furthermore, migration behaviour of hatchery and wild fish appear to be different at small scales during the early marine life (Chittenden et al. 2010a; Moore et al. 2012), but similar over larger scales (Tucker et al. 2011). In general, the rapid northward and counterclock-wise migration of juvenile salmon that has been hypothesized by Hartt and Dell (1986) along the continental shelf of the west coast of North America has been supported through the application of coded-wire tags, DNA analyses, and acoustic tags (Morris et al. 2007; Trudel et al. 2009; Tucker et al. 2009, Welch et al. 2009; Tucker et al. 2011, 2012;), though there are some exceptions such as Harrison River sockeye salmon that remain in the Strait of Georgia for an extended period of time before migrating north (Tucker et al. 2009; Beamish et al. 2010a, 2012a).

Growth, bioenergetics, and diet

Although a number of factors may be affecting the survival of juvenile Pacific salmon along their migratory corridor such as prey availability (Tanasichuk and Routledge 2011; Wells et al. 2012) and predator abundance (Emmett and Sampson 2007), it is generally believed that large and fast growing fish have higher survival, either because large fish are less vulnerable to gape-limited predators or can sustain starvation (i.e., winter) for longer periods of time (Beamish and Mahnken 2001). However, it should be noted that while large and fast-growing juvenile salmon have been found to have a survival advantage over small and slow-growing salmon (Beamish et al. 2006a; Duffy and Beauchamp 2011; Farley et al. 2011; Tomaro et al. 2012), size-selective mortality has not always been apparent during summer or winter in juvenile salmon (Welch et al. 2011; Trudel et al. 2012).

Bioenergetics models have been particularly useful for understanding the processes affecting juvenile salmon growth. In particular, they showed that prey quality and quantity may be more important for juvenile salmon growth and survival than temperature itself, and that the effect of temperature on growth is likely indirect and mediated by changes in prey quality and quantity (Beauchamp 2009; Farley and Trudel 2009; Moss et al. 2009). As stomach contents is expected to integrate the variability in prey availability and preferences, diet may also be a key indicator for salmon growth and survival in the marine environment (Armstrong et al. 2008; Kline et al. 2008; Kline 2010; Daly et al. 2013). Recent studies show that juvenile salmon diet is highly variable in space and time, and that diet variability is linked to changes in ocean conditions and climate (Brodeur et al. 2007a, b; Sweeting and Beamish 2009; Daly et al. 2013). In particular, although pink, chum, and sockeye salmon are generally considered planktivorous species, fish may contribute significantly to their diet in the Bering Sea during warm years (Andrews et al. 2009; Farley and Moss 2009; Farley and Trudel 2009). Prey availability may also be influenced by competition with wild and hatchery fish, though competition may be asymmetrical and affect wild and hatchery fish differently (Beamish et al. 2008, 2010d). Competition between hatchery and wild fish is likely more intense in offshore waters as recent studies also indicate that hatchery and wild salmon often feed on different prey in the nearshore environment but on similar prey offshore (Sweeting and Beamish 2009; Daly et al. 2012; Sturdevant et al. 2012a).

Pathogens and disease

Parasites have received the most attention as a mortality agent for salmon, especially in British Columbia, due to a polarized debate over the role of disease transfer from open net pens to juvenile salmon (Brooks and Jones 2008; Krkošek et al. 2008a, b; Riddell et al. 2008). In contrast to other topics, most of this research has focused on pink and chum salmon. The salmon louse (*Lepeophtheirus salmonis*) has been the primary parasite of concern in North America, though other species of lice such as *Caligus clemensi* commonly occur on juvenile salmon and have not always been differentiated from *L. salmonis* during the attached stages in field studies (e.g. Krkošek et al. 2006, 2009). In British Columbia, lice species on farmed and wild salmon varies by location and year: *L. salmonis* and *C. clemensi* are the dominant louse species in the Broughton Archipelago and Discovery Islands, respectively (Jones et al. 2006; Marty et al. 2010; Price et al. 2010, 2011). Laboratory studies have been particularly useful for assessing the susceptibility of different species of salmon to lice infection (Jones et al. 2007, 2008; Sutherland et al. 2011; Braden et al. 2012) and at understanding the lethal and sublethal effects of the salmon louse on juvenile salmon (Webster et al. 2007; Sackville et al. 2011; Tang et al. 2011; Brauner et al. 2012). Field and modeling studies indicate that adult wild salmon can contribute lice to farmed salmon and that farmed salmon can contribute lice to wild juvenile salmon (Krkošek et al. 2006, 2009; Marty et al. 2010), though other fish species contribute lice as well (Jones et al. 2006) and natural infections also occur in areas without salmon farms (Trudel et al. 2007a; Beamish et al. 2009). However, the impacts of disease transmission from aquaculture to wild salmon remain equivocal at this point (Krkošek et al. 2007, Marty et al. 2010; Jones and Beamish 2011; Krkošek and Hilborn 2011; Krkošek et al. 2011).

Future considerations

Despite this recent progress on understanding the marine biology of juvenile salmon, little is known of the causes of mortality of salmon during their marine life. Most of this progress has been achieved by correlating marine survival to one or more factors at a time. It should be kept in mind that correlation does not equal causation (Peters 1991), though correlations are an important step to identify potential mechanisms and generate testable hypotheses in fisheries science (Francis and Hare 1994). Wherever possible, experimental work should be conducted to test these hypotheses. Future effort should aim at quantifying where and when significant mortality occurs in the marine environment, its causes, as well as its contribution to recruitment variability of Pacific salmon.

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