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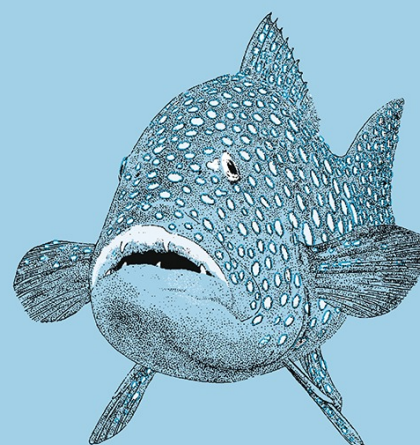
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A critical review of marine adaptability within the anadromous Salmoninae

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Abstract Salmoninae adaptability to the marine environment was evaluated based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. The most-to-least marine adapted genera were *Oncorhynchus*, *Salmo* and *Salvelinus*, agreeing with Rounsefell's anadromy ranking. The lowest and highest thermohaline limits were reached by *O. keta*, *S. salar*, *S. alpinus* and *S. malma*; and *O. kisutch*, *O. keta* and *O. nerka*, respectively. Marine adaptability criteria rearranged Rounsefell's top three species, with *O. keta* and *O. nerka* ranked higher than *O. gorbuscha*, and suggested recently evolved salmonids are adapted to a more marine life history. *Oncorhynchus masou* ranked similar to its sister taxa: *O. mykiss* and *O. clarki*. Lower ranked salmonids usually evolved earlier, adding evidence to a freshwater salmonid ancestor. More research on marine migration is needed

on all Salmoninae, especially the lesser studied trout and charr which demonstrate highly variable life histories compared to salmon.

Keywords Adaptation · Charr · Marine migration · Salmon · Thermohaline limit · Trout

Introduction

In recent years, technology has enabled more detailed studies on anadromous fish marine migration, including behaviour, duration, habitat preferences, routing and survival (Dadswell 2009; Stokesbury et al. 2009; Drenner et al. 2012; Beardsall et al. 2013; McLean et al. 2014). In spite of these advances, there has been relatively little research conducted on the marine migration of some salmonids (Dadswell et al. 2010). For example, amago *Oncorhynchus rhodurus* Jordan and McGregor 1925 and masu *Oncorhynchus masou* (Brevoort 1856) salmon; brook *Salvelinus fontinalis* Mitchill 1814, bull *Salvelinus confluentus* Suckley 1859, cutthroat *Oncorhynchus clarki* (Walbaum 1792) and lake *Salvelinus namaycush* (Walbaum 1792) trout; and Arctic *Salvelinus alpinus* (L. 1758), dolly varden *Salvelinus malma* (Walbaum 1792) and white-spotted *Salvelinus leucomaenis* (Pallas 1814) charr, are poorly represented in the literature. Recent studies, however, have revealed new information on marine migration of the less-studied *Salvelinus* spp. (Goetz et al. 2004; Jensen and Rikardsen 2012; Spares et al. 2012, 2014),

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and on the better studied Atlantic salmon *Salmo salar* L. 1758 (Spares et al. 2007; Dadswell et al. 2010; Chittenden et al. 2013; Lacroix 2013) and steelhead trout *Oncorhynchus mykiss* (Walbaum 1792) (Nielsen et al. 2011).

Salmonid salinity tolerance has been gauged on preparatory physiology/morphology and saltwater acclimation upon marine exposure (McCormick 1994). Recent electronic tracking has recorded temperature and salinity encountered by marine migrating salmonids and results cast doubt on the current salinity tolerance hierarchy (Goetz et al. 2004; Jensen and Rikardsen 2012; Lefèvre et al. 2012; Spares et al. 2012, 2014). Long-distance migratory Salmoninae (*Oncorhynchus* and *Salmo*) have demonstrated salinity tolerance in oceanic environments for months to years (Quinn 2005, Dadswell et al. 2010). Species of the genus *Salvelinus*, however, have been deemed poor osmoregulators in cold water (Saunders et al. 1975; Finstad et al. 1989). Yet *S. alpinus* has been tracked in water with a maximum salinity of 33 and minimum temperature of 0 °C (Jensen and Rikardsen 2008, 2012; Spares et al. 2012) and caught in a salinity of 33 at −1.5 °C (Bystriansky et al. 2007).

With the marine environment being affected by climate change (Grebmeier et al. 2006), it is more likely generalist species may be able to adapt while specialist species may be subject to increasing extinction risk (Townsend et al. 2003; Thomas et al. 2004). With this in mind, the question is posed. Which Salmoninae species are best adapted to the marine environment? This review examines the most recent marine migration research on Salmoninae species to infer relative inter-specific marine adaptability based on horizontal, vertical and thermohaline habitat limits. Species will be dense ranked most (1) to least (14) adaptable to the marine environment. Although *O. rhodurus*, *S. leucomaenis* and *S. namaycush* are known to undertake marine migrations (Dunham et al. 2008; Swanson et al. 2010; Drenner et al. 2012), they were excluded due to lack of information.

Degrees of anadromy

According to Rounsefell (1958), ‘anadromy’ is the degree to which freshwater species establish residency at sea, and suggested the most to least anadromous

Salmoninae genera as *Oncorhynchus*, *Salmo* and *Salvelinus*. Within *Oncorhynchus*, pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792) ranked highest with *O. mykiss* and *O. clarki* ranked lowest. *Oncorhynchus* trout, *Salmo* and *Salvelinus* spp are considered ‘optionally anadromous’ (Table 1; Rounsefell 1958). Based on new information and Rounsefell’s criteria, Quinn and Myers (2004) suggested that chum *Oncorhynchus keta* (Walbaum 1792) and sockeye *Oncorhynchus nerka* (Walbaum 1792) salmon ranked higher than *O. gorbuscha* due to their more extensive range and longer duration at sea. Chinook *Oncorhynchus tshawytscha* (Walbaum 1792) was considered less anadromous than coho *Oncorhynchus kisutch* (Walbaum 1792) salmon due to the existence of mature male parr, and iteroparity under experimental conditions. Upon discovering *O. mykiss* undertook a more extensive open-ocean migration, the species was ranked higher than *O. tshawytscha* (Quinn and Myers 2004). Goetz et al. (2004) suggested *S. malma* would rank slightly higher than *S. alpinus*. *Salvelinus confluentus* and *S. fontinalis* were also ranked lower than *S. malma*, although *S. confluentus* was classified as *S. malma* at the time of Rounsefell’s publication (Goetz et al. 2004). *Oncorhynchus masou*, *O. rhodurus* and *S. leucomaenis* were not included by Rounsefell (Table 1).

Marine adaptability criteria

Rounsefell (1958) based his anadromy hierarchy of Salmoninae on the following criteria: marine migration (1) extent and (2) duration, (3) state of gonad maturation obtained at sea, (4) fresh water or marine spawning, (5) post-spawning mortality, and (6) occurrence of fresh water resident populations. Rounsefell (1958) was assessing anadromy, the ability of Salmoninae species to establish residency at sea, and used freshwater life history characteristics as ‘anadromy’ indicators. Our review aimed to rank Salmoninae marine adaptability, and focuses on marine migration information. For this reason, modifications of Rounsefell’s criteria 1 and 2 were used as marine adaptability criteria. Many species, notably *O. mykiss*, have multiple life history strategies and seasonal runs within a single river whereby some populations enter fresh water with or without fully developed gonads

Table 1 Rounsefell's (1958) rank of anadromous species of Salmoninae with alternative ranking based on more recent studies (Goetz et al. 2004; Quinn and Myers 2004)

Rank	Common name	Genus sp.	Alt rank
<i>Obligatory</i>			
1	pink salmon	<i>Oncorhynchus gorbuscha</i>	3
2	chum salmon	<i>Oncorhynchus keta</i>	1
3	chinook salmon	<i>Oncorhynchus tshawytscha</i>	7
<i>Adaptively</i>			
4	coho salmon	<i>Oncorhynchus kisutch</i>	4
5	sockeye salmon	<i>Oncorhynchus nerka</i>	2
<i>Optionally</i>			
6	Atlantic salmon	<i>Salmo salar</i>	5
7	steelhead trout	<i>Oncorhynchus mykiss</i>	6
8	brown trout	<i>Salmo trutta</i>	8
9	cutthroat trout	<i>Oncorhynchus clarki</i>	9
10	dolly varden charr	<i>Salvelinus malma</i>	10
11	brook trout	<i>Salvelinus fontinalis</i>	11
12	Arctic charr	<i>Salvelinus alpinus</i>	12

(Quinn 2005). Many species are also intermittent spawners undergoing multiple marine migrations between spawning events, thus migrants may not necessarily channel marine energy gained into fecundity (Gulseth and Nilssen 2001). For these reasons, Rounsefell's criterion 3 was not used in our survey. Although a select few *O. gorbuscha*, *O. keta* and *S. trutta* populations spawn in brackish water (Heard 1991; Salo 1991; Landergren and Vallin 1998; Limburg et al. 2001), the vast majority of their populations, like all other salmonids, are freshwater spawners (Rounsefell 1958), thus criterion 4 was not included. Criteria 5 and 6 were excluded, since these criteria did not address salmonid marine adaptability.

For this review, the degree of a species' marine adaptability was inferred based on the following criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced. Migration extent was defined as the maximum straight line distance (SLD) from natal freshwater, where species were ranked highest to lowest in three categories, by traveling $\leq 10,000$, 1000 or 100 km, respectively (Table 2). Duration was defined as the percentage of time in years a migrant spent in salt water during an average lifespan, with the highest to lowest percentages assigned a corresponding rank from 1 to 14 (Table 3). Predominant horizontal and deepest vertical habitats were based on oceanic, neritic and littoral (ranked 1–3, Table 4); and aphotic (maximum depth,

Z_{max} , >400 m), dysphotic (<400 m), euphotic (<150 m) and littoral (<15 m, ranked 1–4, Table 5) zones, respectively (Woodward 2012).

To address thermohaline tolerance, species were evaluated based on how close they approached their lethal limits during marine migration. The thermal and salinity limits were estimated based on preferred minimum and maximum temperature and salinity, expressed as a percentage relative to their lower and upper incipient lethal temperature, respectively, at the global mean salinity of 35 (IOC 2010). Minimum thermohaline limit was calculated using $(T_{min} - S)(T_{low} - 35)^{-1}$; where T_{min} is the minimum preferred marine temperature ($^{\circ}\text{C}$), S is the salinity at T_{min} , and T_{low} is the species' lower incipient lethal temperature ($^{\circ}\text{C}$, Table 6). Maximum thermohaline limit was calculated using $(T_{max} + S)(T_{upp} + 35)^{-1}$; where T_{max} is the maximum preferred marine temperature ($^{\circ}\text{C}$), S is the salinity at T_{max} , and T_{upp} is the species' upper incipient lethal temperature ($^{\circ}\text{C}$, Table 7). Each surveyed species' criteria ranks were summed, with the lowest to highest sums dense ranked 1–14, with rank 1 being the most and rank 14 being the least adapted to the marine environment (Table 8).

Does body size matter?

Salmonids with larger body size tolerate osmoregulatory stress better than smaller bodied ones (Klemetsen

Table 2 Extent of marine migration based on maximum straight line distance (SLD; km) from natal river mouth traveled by surveyed Salmoninae with assigned ranks 1–3 corresponding to distances $\leq 10,000$, 1000 or 100 km, respectively

Common name	Genus sp.	SLD	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>			
pink	<i>O. gorbuscha</i>	2821	1	7, 9
chum	<i>O. keta</i>	5595	1	7, 9
chinook	<i>O. tshawytscha</i>	4557	1	7, 9
coho	<i>O. kisutch</i>	2706	1	7, 9
sockeye	<i>O. nerka</i>	5597	1	7, 9
steelhead	<i>O. mykiss</i>	5370	1	7
cutthroat	<i>O. clarki</i>	133	2	3
masu	<i>O. masou</i>	1700	1	5
Atlantic salmon/trout	<i>Salmo</i>			
Atlantic	<i>S. salar</i>	4422	1	2, 10
brown	<i>S. trutta</i>	600	2	11
charrs	<i>Salvelinus</i>			
dolly varden	<i>S. malma</i>	1690	1	4
brook	<i>S. fontinalis</i>	100	3	6
Arctic	<i>S. alpinus</i>	940	2	1
bull	<i>S. confluentus</i>	250	2	8

1 Jensen and Berg (1977); 2 Gibson and Côté (1982); 3 Trotter (1989); 4 DeCicco (1992); 5 Ohkuma et al. (1999); 6 Lenormand et al. (2004); 7 Quinn and Myers (2004); 8 Brenkman and Corbett (2005); 9 Quinn (2005); 10 Dadswell et al. (2010); 11 Jonsson and Jonsson (2011)

Table 3 Duration of marine migrations of surveyed Salmoninae based on mean saltwater (SW) residency, life span and percentage of SW residency during life span, with assigned ranks (1–14) of highest to lowest % SW residency

Common names	Genus sp.	SW residency (years)	Life span (years)	% SW	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>					
pink	<i>O. gorbuscha</i>	1.6	1.7	95	2	4, 5
chum	<i>O. keta</i>	3.0	3.1	97	1	4, 5
chinook	<i>O. tshawytscha</i>	3.3	3.8	87	3	4, 5
coho	<i>O. kisutch</i>	1.0	2.5	40	6	4, 5
sockeye	<i>O. nerka</i>	3.0	4.5	67	4	4, 5
steelhead	<i>O. mykiss</i>	2.2	5.7	39	8	4, 5
cutthroat	<i>O. clarki</i>	1.1	6.0	18	12	4, 5, 8
masu	<i>O. masou</i>	1.0	2.5	40	6	7
Atlantic salmon/trout	<i>Salmo</i>					
Atlantic	<i>S. salar</i>	3.2	6.3	50	5	4, 13
brown	<i>S. trutta</i>	1.2	3.8	31	9	4, 12, 13
charrs	<i>Salvelinus</i>					
dolly varden ^a	<i>S. malma</i>	5.2	11.0	10	13	1, 6, 11, 15
brook	<i>S. fontinalis</i>	1.2	5.5	21	10	4, 9, 16
Arctic	<i>S. alpinus</i>	1.4	15.0	9	14	1, 3, 4, 6, 10, 14
bull	<i>S. confluentus</i>	1.3	7.0	19	11	4, 8

1 Sprules (1952); 2 Armstrong (1974); 3 Hunter (1976); 4 Randall et al. (1987); 5 Pearcy (1992); 6 Wilson (1997); 7 Tamate and Maekawa (2000); 8 Goetz et al. (2004); 9 Curry et al. (2006); 10 Rikardsen et al. (2007); 11 Stewart et al. (2010); 12 Jonsson and Jonsson (2011); 13 Thorstad et al. (2011); 14 Spares et al. (2012); 15 ADFG (2014); 16 Spares et al. (2014)

^a Estimated to spend <10 % life time at sea feeding (Stewart et al. 2010)

Table 4 Predominant horizontal marine migration habitat occupied by surveyed Salmoninae with assigned ranks (1–3) corresponding to oceanic, neritic and littoral zones, respectively

Common name	Genus sp.	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>		
pink	<i>O. gorbuscha</i>	1	6
chum	<i>O. keta</i>	1	6
chinook	<i>O. tshawytscha</i>	2	6
coho	<i>O. kisutch</i>	2	6
sockeye	<i>O. nerka</i>	1	6
steelhead	<i>O. mykiss</i>	1	6
cutthroat	<i>O. clarki</i>	2	6
masu	<i>O. masou</i>	2	2
Atlantic salmon/trout	<i>Salmo</i>		
Atlantic	<i>S. salar</i>	1	8
brown	<i>S. trutta</i>	3	1
charrs	<i>Salvelinus</i>		
dolly varden	<i>S. malma</i>	3	7
brook	<i>S. fontinalis</i>	3	5
Arctic	<i>S. alpinus</i>	3	3
bull	<i>S. confluentus</i>	3	4

1 Pennell and Barton (1996); 2 Ohkuma et al. (1999); 3 Klemetsen et al. (2003); 4 Goetz et al. (2004); 5 Lenormand et al. (2004); 6 Quinn (2005); 7 COSEWIC (2010); 8 Dadswell et al. (2010)

et al. 2003). Jensen and Rikardsen (2012) suggested that the decreased surface to volume ratio of larger fish, the changing mechanisms for osmoregulation related to increasing fish size, or both were responsible. As ectotherms, a positive correlation exists between ambient water temperature and enzyme activity responsible for salt ion regulation until a maximum threshold saltwater temperature (>20 °C at salinities >30) is reached and enzyme activity decreases. Even small salinity increments near the upper thermal limit often result in osmoregulatory stress or death. For example, *O. kisutch* can tolerate salinities of 28–30 at 18 °C, but experience 80–90 % mortality in salinities of 33–34 at the same temperature (Pennell and Barton 1996). Low temperatures also decrease the salt exchange enzyme activity, which is countered for in cold-acclimated fishes by increasing enzyme concentrations (McCormick et al. 1997). At full-strength saltwater, the minimum lethal temperature is about −0.7 °C for *O. kisutch*, *O. tshawytscha*, *S. salar* and *S. fontinalis* (Balon 1980; Pennell and

Barton 1996), with prolonged exposure to temperatures below 3–4 °C negatively affecting growth and survival (Pennell and Barton 1996; Curry et al. 2006). Some species, such as *O. kisutch*, *O. tshawytscha* and *S. salar*, can tolerate a sustained salinity of 21 within their preferred temperature range at any size (Pennell and Barton 1996). Juvenile *O. gorbuscha* inhabit dilute saltwater of shallow coastal waters during their first few weeks of life, and yet 72-h salinity challenge tests of 0.2 g individuals proved tolerance of 32 and 40 salinities at 11 and 7 °C, respectively (Pennell and Barton 1996; Grant et al. 2010).

Although past studies have gauged Salmoninae marine fitness using salinity tolerance based on minimum size of fish undertaking seaward migration (Finstad et al. 1989; McCormick 1994), success may also improve with increasing fish size due to decreased predation and increased opportunities of larger-sized prey items (Saloniemi et al. 2004). Increasing smolt size may also not consistently confer a survival advantage, as shown by increased survival of larger smolts only when annual marine survival is relatively low (Holtby et al. 1990). Considering these conflicting facts and that body size at saltwater entry is a result of freshwater life history, a criterion based on juvenile size was omitted. It should be noted, however, that migration duration (criterion 2) indirectly considers body size at saltwater entry, as species with juveniles entering the sea earlier increase marine residency percentage of life span, and that in turn causes these species to be ranked higher.

Marine residency

Oncorhynchus keta and *O. gorbuscha* virtually spend their entire lives at sea, 97 and 95 %, respectively (Table 3), as the majority of individuals enter full-strength saltwater soon after emerging from gravel beds (Heard 1991). The percentage marine life history of these two species could even be 100 % as some populations spawn in the intertidal zone (Rounsefell 1958), although the majority spawn in fresh water (Quinn 2005). Although some iteroparous *Salmo salar* are known to spawn up to six times (Ducharme 1969), on average both *Salmo* species spawn twice during their life (Thorstad et al. 2011). *Salvelinus alpinus* was assumed to first spawn at 8 years old (Sprules 1952) and skip marine migrations during spawning years

Table 5 Vertical marine migration habitat of surveyed Salmoninae based on maximum swimming depths (Z_{max} ; m) and assigned ranks (1–4) corresponding to the following verticalzones, respectively: Aphotic ($Z_{max} > 400$ m), dysphotic (<400 m), euphotic (<150 m) and littoral (<15 m)

Common names	Genus sp.	Z_{max}	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>			
pink	<i>O. gorbuscha</i>	74	3	5
chum	<i>O. keta</i>	460	1	5
chinook	<i>O. tshawytscha</i>	482	1	5
coho	<i>O. kisutch</i>	97	3	5
sockeye	<i>O. nerka</i>	240	2	1
steelhead	<i>O. mykiss</i>	89	3	7
cutthroat ^a	<i>O. clarki</i>	1	4	6
masu ^b	<i>O. masou</i>	74	3	2, 5
Atlantic salmon/trout	<i>Salmo</i>			
Atlantic	<i>S. salar</i>	950	1	9
brown	<i>S. trutta</i>	28	3	4
charrs	<i>Salvelinus</i>			
dolly varden	<i>S. malma</i>	11	4	3
brook	<i>S. fontinalis</i>	11	4	10
Arctic	<i>S. alpinus</i>	53	3	8
bull	<i>S. confluentus</i>	25	3	3

1 Ogura and Ishida (1995); 2 Ohkuma et al. (1999); 3 Goetz et al. (2004); 4 Rikardsen et al. (2007); 5 Walker et al. (2007); 6 Haque (2008); 7 Nielsen et al. (2011); 8 Spares et al. (2012); 9 Lacroix (2013); 10 Spares et al. (unpublished data)

^a Mean depth of tracked cutthroat trout

^b Masu captured co-migrating in North Pacific with 6 Pacific salmon spp., therefore Z_{max} was assumed to be the shallowest swimming cohort

(Hunter 1976). *Salvelinus malma* may spend up to 47 % of an average 11 years life span (Wilson 1997) in salt water given a 5 month long marine migration each year (Armstrong 1974). Stewart et al. (2010), however, estimated *S. malma* spend <10 % of their life at sea feeding, and this evidence was used for the marine adaptability review. Although marine residency may reflect an anadromous species' adaptability to the marine environment, residency can be controlled by the period the ocean is inhabitable. As no salmonid possess anti-freeze proteins (Enevoldsen et al. 2003) and salmonid blood plasma freezes between -0.7 and -1.0 °C (Huusko et al. 2007), migrants continuously exposed to temperatures approaching the mean saltwater freezing point of -1.9 °C (DeVries and Cheng 2005) would be forced to move to warmer water (Dempson and Kristofferson 1987). Although anadromy is more prevalent at higher latitudes due to oligotrophic freshwater systems

(Gross et al. 1988; Dunham et al. 2008), Arctic salmonids tend to have less time with favorable marine conditions, resulting in average marine residencies which generally decrease with increasing latitude (L'Abée-Lund et al. 1989).

Horizontal and vertical habitats

Of the surveyed Salmoninae, more than half were reported to travel >1000 km SLD from natal rivers, including *S. salar*, *S. malma* and all *Oncorhynchus* spp. except *O. clarki* (Table 2). *Salvelinus* spp., *S. trutta* and *O. clarki* are predominantly linked to near shore and littoral zones whereas *S. salar* and all other *Oncorhynchus* spp. undertake migration within neritic and oceanic waters (Table 4). *Salvelinus malma* has been tagged in Alaska and recaptured in Russia after traversing the Bering Sea (DeCicco 1992; Quinn and

Table 6 Minimum temperature (T_{min} ; °C) and corresponding salinity (S), lower lethal thermal limit (T_{low} ; °C) and ranked minimum thermohaline limit of marine migrating Salmoninae

Common names	Genus sp.	T_{min}	S	T_{low}	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>					
pink	<i>O. gorbuscha</i>	2.8	34	0.6 ^a	4	1, 8, 14, 16, 20, 25
chum	<i>O. keta</i>	-1.0	34	0.5	1	1, 10, 14, 18
chinook	<i>O. tshawytscha</i>	4.0	34	0.8	6	1, 4, 9
coho	<i>O. kisutch</i>	3.7	34	1.7	4	1, 14
sockeye	<i>O. nerka</i>	3.3	33	1.0	5	2, 14
steelhead	<i>O. mykiss</i>	3.9	34	0.1	7	4, 12, 24
cutthroat	<i>O. clarki</i>	8.0	33	0.6	10	4, 6, 25
masu	<i>O. masou</i>	6.0	33	0.5	9	4, 5, 19
Atlantic salmon/trout	<i>Salmo</i>					
Atlantic	<i>S. salar</i>	0.0	36	-0.8	2	22, 23, 26
brown	<i>S. trutta</i>	1.3	32	-0.8	8	13, 23
charrs	<i>Salvelinus</i>					
dolly varden	<i>S. malma</i>	-1.0	32	-0.4 ^b	3	21
brook	<i>S. fontinalis</i>	-0.5	22	0.1	12	1, 27
Arctic	<i>S. alpinus</i>	-1.5	32	-1.0	3	3, 15, 17, 23
bull	<i>S. confluentus</i>	7.0	28	5.2	11	7, 11

1 Brett (1952); 2 Manzer et al. (1965); 3 Lake and Walker (1973); 4 Favorite et al. (1976); 5 Machidori and Kato (1984); 6 Bell (1991); 7 Staubitz et al. (1997); 8 Babaluk et al. (2000); 9 Nagasawa (2000); 10 Walker et al. (2000); 11 Selong et al. (2001); 12 Currie et al. (2004); 13 Rikardsen (2004); 14 Azumaya et al. (2007); 15 Bystriansky et al. (2007); 16 Rikardsen et al. (2008); 17 Babaluk et al. (2009); 18 Irvine et al. (2009); 19 Kuzishchin et al. (2009); 20 Signorini and McClain (2009); 21 COSEWIC (2010); 22 Dadswell et al. (2010); 23 Elliott and Elliott (2010); 24 Nielsen et al. (2011); 25 NOAA (2012b); 26 Lacroix (2013); 27 Spares et al. (2014)

^a Both *O. gorbuscha* and *O. keta* have Arctic populations (Babaluk et al. 2000) with the later tolerating colder temperatures (Brett 1952), thus the lower lethal thermal limit was estimated at 0.6 °C, slightly higher than *O. keta*

^b Mean of *S. fontinalis* and *S. alpinus*

Myers 2004), yet the majority remain near shore (Kowalchuk et al. 2010). *Salmo salar* kelts were recorded by acoustic and pop-up satellite archival tags diving to a maximum depth of 800–950 m (Jakupstovu 1988, Lacroix 2013). The next two deepest divers: *O. tshawytscha* and *O. keta*, were caught at maximum depths approximately half as deep (Table 5), yet these may underestimate actual maximum dive depths due to the limits of trawling depth (Walker et al. 2007). These three species were within the aphotic mesopelagic zone (Woodward 2012), and therefore assigned the same ranking (Table 5). There is limited data during winter, but vertical distributions may not change substantially from summer in offshore waters because many species migrate so as to remain in their preferred thermal range, even if seasonal vertical shifts occur during coastal and shelf migrations. Continuous year-round data on marine vertical

distribution is needed for all Salmoninae (Walker et al. 2007).

Thermohaline limits

Temperature controls life process of ectothermic organisms, ultimately determining success and survival (McCormick et al. 1997). In anadromous Salmoninae, low temperatures encountered by parr and smolts may not only delay smoltification and emigration to sea, but also decrease movement, growth, organ development and osmoregulation rates at sea, thus increasing both juvenile mortality and marine migration duration. Higher temperatures may trigger earlier spring freshets resulting in earlier coastal plankton blooms which may benefit early sea-run emigration or disadvantage later emigrants

Table 7 Maximum temperature (T_{max} ; °C) and corresponding salinity (S), upper lethal thermal limit (T_{upp} ; °C) and ranked maximum thermohaline limit of marine migrating Salmoninae

Common names	Genus sp.	T_{max}	S	T_{upp}	Rank	References
Pacific salmon/trout	<i>Oncorhynchus</i>					
pink	<i>O. gorbuscha</i>	16.6	34	25.8	6	14, 17
chum	<i>O. keta</i>	15.6	34	23.8	2	1, 14, 18
chinook	<i>O. tshawytscha</i>	13.4	34	26.2	5	12, 14
coho	<i>O. kisutch</i>	15.7	34	23.7	1	9, 14
sockeye	<i>O. nerka</i>	13.3	33	24.5	3	8, 9, 14
steelhead	<i>O. mykiss</i>	13.0	34	26.2	10	9, 19
cutthroat	<i>O. clarki</i>	23.7	29	24.6	4	15, 21
masu	<i>O. masou</i>	15.0	32	25.0 ^a	9	2, 4
Atlantic salmon/trout	<i>Salmo</i>					
Atlantic	<i>S. salar</i>	14.7	34	29.0	11	6, 18
brown	<i>S. trutta</i>	16.7	32	26.8	8	13, 16
charrs	<i>Salvelinus</i>					
dolly varden	<i>S. malma</i>	13.0	32	24.5	12	5, 9, 20
brook	<i>S. fontinalis</i>	19.6	28	28.0	13	3, 22
Arctic	<i>S. alpinus</i>	15.0	20	23.2	14	7, 16
bull	<i>S. confluentus</i>	17.0	28	20.9	7	9, 10, 11

1 Brett (1952); 2 Favorite et al. (1976); 3 Lee and Rinne (1980); 4 Machidori and Kato (1984); 5 Xiong and Royer (1984); 6 Doving et al. (1985); 7 Sutterlin and Stevens (1992); 8 Welch et al. (1998); 9 Selong et al. (2001); 10 Goetz et al. (2003); 11 Goetz et al. (2004); 12 Wurster et al. (2005); 13 Rikardsen et al. (2006); 14 Azumaya et al. (2007); 15 Hamilton et al. (2008); 16 Elliott and Elliott (2010); 17 Fish World (2010); 18 Jonsson and Jonsson (2011); 19 Nielsen et al. (2011); 20 NOAA (2012a); 21 Underwood et al. (2012); 22 Spares et al. (unpublished data)

^a Mean of *Oncorhynchus* spp. surveyed

(Chittenden et al. 2009). At sea, warmer water may enhance feeding and maintenance, but elevated temperatures (>21 °C) may increase respiration and lack of appetite (Straty and Jaenicke 1980), and result in lower energy stores of returning migrants (Chittenden et al. 2009).

Maximum salinity tolerance of migrants may not be accurately defined solely by field observations of the maximum salinity in which fish have been captured (Kefford et al. 2004). Distribution of individuals may be influenced by co-factors, such as food and habitat availability, oxygen concentration, pH and temperature (Bringolf et al. 2005). For example, riverine populations of *S. trutta* and *S. alpinus* with unsuitable freshwater overwintering habitat also use estuarine and marine environments, contradicting previous beliefs that they have low salinity tolerance at low water temperatures, and are restricted to overwintering in fresh water (Jensen and Rikardsen 2012).

Long-term exposure to water <0 °C has not been documented by tracking studies, yet *S. alpinus* has

been captured in salinity of 32 at −1.5 °C (Bystriansky et al. 2007). With decreasing temperatures, body fluid viscosity increases, adding pressure within circulatory systems (DeVries and Cheng 2005). Salmonids adapt physiologically by increasing heart and liver size (Huusko et al. 2007), and lowering their blood viscosity by decreasing plasma salts, increasing glucose (Huusko et al. 2007) and decreasing the number of red blood cells (DeVries and Cheng 2005). Salmonids also often remain inactive in near-freezing temperatures to keep oxygen demand low (DeVries and Cheng 2005). Within cellular membranes, an increase of essential fatty acids (i.e. Omega-3 s) enhances flexibility (Metusalach and Shahidi 1995), facilitating enzyme function (i.e. Na⁺/K⁺-ATPase) and decreasing ion leakage (Wu and Fletcher 2000). *Salvelinus alpinus* further reduces leakage by decreasing activity or density of ion channels (Schwarzbaum et al. 1991, 1992).

Anthropogenic impacts such as riverine acidification has been suggested to increase marine mortality of

Table 8 Rank scores for anadromous Salmoninae based on marine adaptability criteria: (1) extent, and (2) duration of migration; (3) horizontal and (4) vertical habitats; and (5) minimum and (6) maximum thermohaline limits experienced

Common names	Genus sp.	1	2	3	4	5	6	Rank	RA	RV
Pacific salmon/trout	<i>Oncorhynchus</i>							1	1	1
pink	<i>O. gorbuscha</i>	1	2	1	3	4	6	3	1	3
chum	<i>O. keta</i>	1	1	1	1	1	2	1	2	1
chinook	<i>O. tshawytscha</i>	1	3	2	1	6	5	4	3	7
coho	<i>O. kisutch</i>	1	6	2	3	4	1	3	4	4
sockeye	<i>O. nerka</i>	1	4	1	2	5	3	2	5	2
steelhead	<i>O. mykiss</i>	1	8	1	3	7	10	6	7	6
cutthroat	<i>O. clarki</i>	2	12	2	4	10	4	8	9	9
masu	<i>O. masou</i>	1	6	2	3	9	9	6	nr	nr
Atlantic salmon/trout	<i>Salmo</i>							2	2	2
Atlantic	<i>S. salar</i>	1	5	1	1	2	11	5	6	5
brown	<i>S. trutta</i>	2	9	3	3	8	8	7	8	8
charrs	<i>Salvelinus</i>							3	3	3
dolly varden	<i>S. malma</i>	1	13	3	4	3	12	9	10	10
brook	<i>S. fontinalis</i>	3	10	3	4	12	13	12	11	11
Arctic	<i>S. alpinus</i>	2	14	3	3	3	14	11	12	12
bull	<i>S. confluentus</i>	2	11	3	3	11	7	10	nr	nr

RA Rounsefell's anadromy rank, RV Quinn and Myers 2004 revised anadromy rank, nr not reviewed

S. salar post-smolts due to osmotic stress and the resulting increase in estuarine residency for saltwater acclimatization, which may expose post-smolts to higher predation (Halfyard et al. 2012, 2013). Salinity is not just an environmental factor to be tolerated by fishes, it may also be critical in navigation of estuaries on route to river mouths or the open ocean (Straty 1974; Quinn 2005; Bos and Thiel 2006; Dadswell et al. 2010; Thorstad et al. 2011; Lefèvre et al. 2012; Spares et al. 2012). With increased melting of the polar ice caps resulting in localized dilution, rising sea levels and altered seasonal cycles (Magnuson et al. 2000; Livingstone 2001; Robertson et al. 2001; Magnuson 2002; Morris et al. 2002), salinity gradients may be altered. Salinity tolerance of Salmoninae should be considered on population- or region-specific basis depending on environmental conditions. It may be unwise to generalize by salmonid genera or species as salinity tolerance varies considerably (Rounsefell 1958).

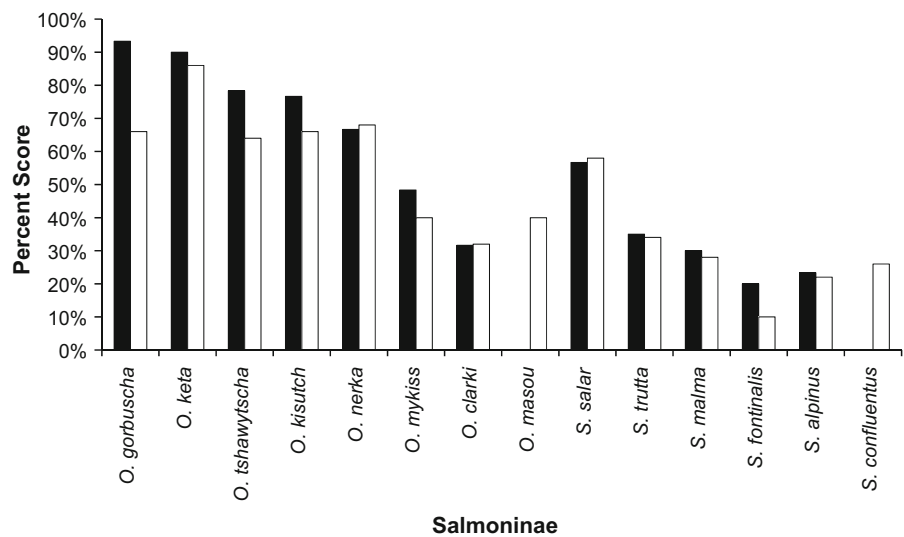
The Salmoninae migrants which ventured closest to their lowest thermohaline limits were *O. keta*, *S. salar*, *S. alpinus* and *S. malma*, as all encountered full saltwater with temperatures ranging from 0 to -1.5 °C

(Table 6). The highest temperatures at the highest salinities were tolerated by *O. kisutch*, *O. keta* and *O. nerka*, even though the highest temperatures at lower salinities were experienced by *O. clarki* (23.7 °C; Table 7) and *S. fontinalis* (20.1 °C; Spares et al. 2014). Ambient salinity measurements were obtained from conductivity-temperature-depth profiles conducted during tracking, or temporally and spatially similar oceanographic studies; thus cited salinities may not accurately represent actual conditions experienced by migrants. To further research in fish migration relative to environmental conditions or bioprobe oceanography (Cooke et al. 2011), development of conductivity/salinity sensor acoustic transmitters or archival tags are necessary to obtain in situ data.

Marine adaptability hierarchy

Surveyed species were scored as a percentage of the most 'anadromous' or 'marine adaptable' total score possible for Rounsefell's (1958) or our survey, respectively. Comparison of percentage scores

Fig. 1 Percentage score of anadromous Salmoninae species surveyed in Rounsefell's (1958) anadromy (solid bar) and this review's marine adaptability (open bar) critique



revealed a similar relative rank for Salmoninae genera and species (Fig. 1) in spite of our survey's solely marine migration focus, broader scoring categories and additional criteria. This may suggest Rounsefell accurately inferred a degree of 'marine adaptability', even with inclusion of freshwater-based criteria. The major difference between the two surveys was our higher ranking of *O. keta* and *O. nerka* relative to Rounsefell's (1958) top ranked *O. gorbuscha*, with our results agreeing with Quinn and Myers' (2004) revised anadromy ranking. Within Rounsefell's (1958) lower anadromy ranks, our results switched rank positions of *S. alpinus* and *S. fontinalis*, with the latter ranked the least adaptable to the marine environment (Fig. 1). Although these species demonstrated a marine migration strategy of remaining near shore and fresh water inputs (Curry et al. 2006; Morinville and Rasmussen 2006; Rikardsen et al. 2007; Spares et al. 2012, 2014), the circumpolar *S. alpinus*'s versus temperate *S. fontinalis*'s distribution ranked the former higher due to extreme thermohaline adaptations (Jensen and Rikardsen 2012; Spares et al. 2012).

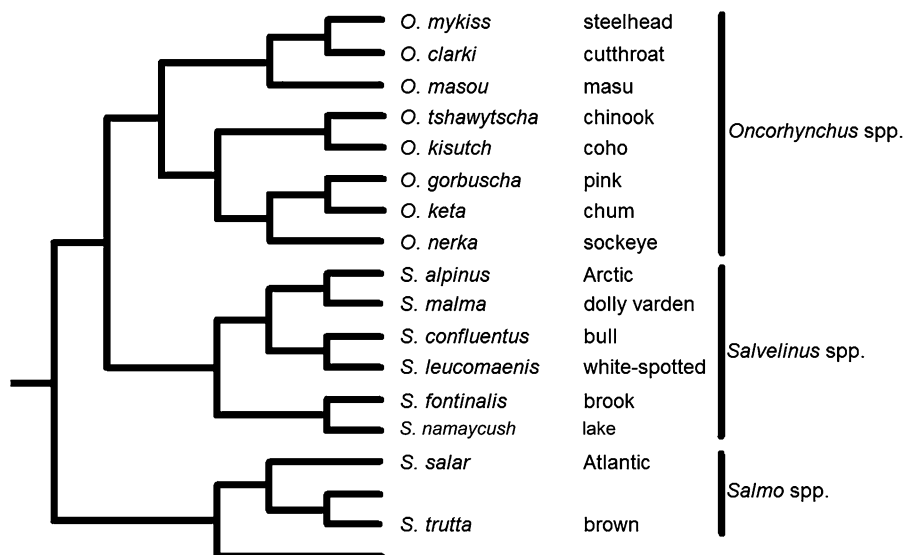
An evolutionary possibility

Based on sequence divergence of mitochondria DNA, separation of the major Salmoninae groups occurred during early to mid-Pleistocene (~2.58–0.126 Ma), yet colonization of today's zoogeographic limits began within the late Pleistocene during the retreat

of ice sheets ~10,000–20,000 years ago. Nuclear microsatellite DNA variation has suggested continuing evolution within salmonid groups (Brunner et al. 2001). Members of the genus *Salmo* originated earliest with *S. salar* evolving before *S. trutta*. *Salvelinus* spp. appeared next with *S. fontinalis* evolving earlier than *S. alpinus*, *S. confluentus* and *S. malma* (Fig. 2). *Oncorhynchus* spp. are the most recently evolved Salmoninae (Crespi and Fulton 2003). *Oncorhynchus masou*, *O. mykiss* and *O. clarki* evolved earliest as a sister group (Crespi and Fulton 2003), which may account for their similar scoring and lower ranking relative to the other *Oncorhynchus* species. *Oncorhynchus gorbuscha*, *O. keta* and *O. nerka* are the most recent species (Crespi and Fulton 2003) and ranked in the top three for this review, suggesting greater adaptability for a marine life history.

Salmo salar may have evolved a longer marine life history due to lack of interspecific salmonid competition or niche availability in the North Atlantic Ocean although in recent years, introduced *O. gorbuscha* and native *S. salar* have been captured in the Greenland and Barents seas, suggesting the genera can co-exist on marine feeding grounds (Rikardsen et al. 2008). With the possibility of a link between Atlantic and Pacific Oceans via the Northwest Passage due to climate change (Cressey 2007), there is still a question of whether or not *Oncorhynchus* spp. might outcompete *S. salar* on marine feeding grounds. For example, adult *S. salar* are known to migrate predominately within the top 40 m of the water column in the open

Fig. 2 Combined nuclear DNA Bayesian analysis phylogeny for anadromous Salmoninae showing species, common names and genera (Crespi and Fulton 2003). Phylogeny of *O. rhodurus* not included by Crespi and Fulton (2003)



ocean (Dadswell et al. 2010), as do *Oncorhynchus* spp. (Walker et al. 2007). Whether or not *S. salar*'s ability to undertake deeper dives (Jakupsstovu 1988; Lacroix 2013) offers a foraging advantage compared to *Oncorhynchus* spp. remains to be seen. On the other hand, repeated introductions of *O. gorbuscha* and *O. kisutch* during the past 100 years into watersheds on the east coast of North America from New England to Newfoundland have failed to establish sustainable populations, the reason for which is unknown (Scott and Scott 1988). This may possibly relate to geomagnetic orienteering which is genetically-linked versus juvenile imprinting upon entering the ocean (Bracis and Anderson 2012), whereas west coast Pacific salmons may orient towards the eastern instead of western Atlantic upon directed homeward migration.

Earlier evolved Salmoninae, such as the lowest ranked *S. fontinalis*, may largely retain fresh water traits, and possess minimal transitional traits associated with adapting from fresh to salt water (Dodson et al. 2009). For example, populations of *S. fontinalis* south of the Gulf of Maine resort to solely freshwater residency (Castric and Bernatchez 2003), which may be due to higher freshwater productivity (Gross 1987) or the species' inability to adapt to warmer marine environmental conditions (i.e. osmoregulation at higher temperatures; Pennell and Barton 1996). Year-round acoustic tracking of *S. fontinalis* in the southern Gulf of St. Lawrence found individuals foraged within the estuarine environment from autumn to spring with body temperatures ranging from -0.5 to 20.1 °C and

returned to fresh water during summer (Spares et al. 2014) where the majority of individuals tracked occupied cool, spring-fed pools (unpublished data Spares et al.). This behaviour suggests high estuarine temperatures during summer (mean \pm SD, 18.7 ± 3.4 °C, $n = 231$, maximum = 25.8 °C; unpublished data Spares et al.) were the main influence for individuals to return to fresh water as marine primary productivity was highest during this period (personal observation). Lower body condition upon estuarine re-entry during the autumn also suggested fasting or poor feeding opportunities within fresh water during summer months (Spares et al. 2014), again lending support to temperature shaping anadromous behaviour.

Once considered the same species, *S. confluentus* and *S. malma* (Goetz et al. 2004) were similarly ranked, which may relate to genetic similarity (Dodson et al. 2009) with *S. malma*'s slightly higher rank explained by longer SLD excursions (DeCicco 1992). Although *S. leucomaenis* and *S. namaycush* were excluded in this survey due to lack of marine migration information, both may rank similarly to their sister species, *S. confluentus* and *S. fontinalis*, respectively (Fig. 2; Crespi and Fulton 2003).

Conclusions

Anthropogenic climate change in marine water acidity, levels, salinity and temperature could alter entire ecosystems and the organisms inhabiting them

(Grebmeier et al. 2006; Chittenden et al. 2009), thus knowledge of niche dimensions and resiliency of marine migrating salmonids is critical. The lowest thermohaline limits were reached by *O. keta*, *S. salar*, *S. alpinus* and *S. malma*, and highest by *O. kisutch*, *O. keta* and *O. nerka*, suggesting these species would cope best to extreme marine temperatures. Based on this review, the most to least marine adaptable genera overall were *Oncorhynchus*, *Salmo* and *Salvelinus*, respectively, agreeing with Rounsefell's (1958) anadromy ranking. Our survey rearranged Rounsefell's top three 'anadromy' species as (1) *O. keta*, (2) *O. nerka* and (3) *O. gorbuscha*, agreeing with the alternative ranking proposed by Quinn and Myers (2004). These top three species are also the most recently evolved Salmoninae, suggesting an evolutionary history of the group for marine adaptation. *Salmo salar* ranked lower than *Oncorhynchus* open ocean migrants, suggesting the possibility of interspecific competition among the species if a connection between Pacific and Atlantic Oceans occurs via the Northwest Passage. Previously unexamined species, *O. masou* and *S. confluentus* ranked similarly to genetically related species, *O. mykiss* and *O. clarki*, and *S. malma*, respectively (Crespi and Fulton 2003; Goetz et al. 2004; Dodson et al. 2009). The lower ranking of *Salvelinus* ssp. suggests earlier evolutionary events, which agrees with genetic findings and adds further evidence for a fresh water ancestry of Salmoninae (Dodson et al. 2009).

As the marine climate has changed (Grebmeier et al. 2006), migratory behaviours of some Salmoninae populations have changed in step; yet there are still many unknowns regarding how environmental factors and ecosystem dynamics will influence marine survival and migratory behaviours (Chittenden et al. 2009). This review summarized recent scientific findings and suggests some broader ecological-evolutionary context predictions. Further marine migration research is needed on all Salmoninae, especially the lesser studied trout and charr species, which have highly variable life histories compared to the salmon (Quinn and Myers 2004; Brenkman et al. 2007).

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