

Journal of Fish Biology (2015) **86**, 276–287 doi:10.1111/jfb.12596, available online at wileyonlinelibrary.com

Thermal regime, predation danger and the early marine exit of sockeye salmon *Oncorhynchus nerka*

P. J. KATINIC*[†], D. A. PATTERSON[‡] AND R. C. YDENBERG§

*Fisheries and Oceans Canada, Fisheries and Aquaculture Management, P. O. Box 99, Queen Charlotte, BC, VOT 1Y0, Canada, ‡Fisheries and Oceans Canada, Science Branch, Pacific Region, Co-operative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada and \$Department of Biological Science, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada

(Received 13 February 2014, Accepted 8 October 2014)

Marine exit timing of sockeye salmon *Oncorhynchus nerka* populations on the Haida Gwaii Archipelago, British Columbia, Canada, is described, with specific focus on Copper Creek. Marine exit in Copper Creek occurs > 130 days prior to spawning, one of the longest adult freshwater residence periods recorded for any *O. nerka* population. Copper Creek presents an easy upstream migration, with mild water temperatures (7 to 14° C), short distance (13·1 km) and low elevation gain (41 m) to the lake where fish hold prior to spawning. An energetic model estimates that <1% of the initial energy reserve is required for upstream migration, compared with 62% for lake holding and 38% for reproductive development. Historical records suggest that it is unlikely that water temperature in any of the *O.nerka* streams in Haida Gwaii has ever exceeded the presumed temperature threshold (19° C) for early marine exit. Although it is not impossible that the thermal tolerance of Copper Creek *O.nerka* is very low, the data presented here appear inconsistent with thermal avoidance as an explanation for the early marine exit timing in Copper Creek and in three other populations on the archipelago with early marine exit.

© 2014 The Fisheries Society of the British Isles

Key words: Copper Creek; Haida Gwaii; life-history strategy; river entry; timing of migration.

INTRODUCTION

Anadromous fishes are spawned in freshwater streams, lakes or rivers, migrate to the sea, and after a period of growth return to fresh water to spawn. This life history evolves when the fitness benefits of the growth attainable at sea outweigh the fitness costs of increased mortality there, and the time, energy and risk attendant on migration (Bernatchez & Dodson, 1987; Gross, 1987). Among Pacific salmon species, sockeye salmon *Oncorhynchus nerka* (Walbaum, 1792) show a diverse range of anadromous life histories, with many different combinations of freshwater and marine residence periods known both within and especially between populations (Healey, 1987). This paper focuses on marine exit, the point at which fish terminate the growth phase and depart the marine environment.

†Author to whom correspondence should be addressed. Tel.: +1 250 559 8330; email: Peter. Katinic@dfo-mpo.gc.ca

The timing of marine exit, upriver migration and spawning are population-specific adaptations to in-stream environmental conditions (Groot & Margolis, 1991; Taylor, 1991) that affect the probability of successful spawning (Young *et al.*, 2006) and emergence of offspring the following spring (Brannon, 1987; Webb & McLay, 1996; Quinn, 2005). Hodgson & Quinn (2002) proposed that differences in marine exit timing among populations are related to the thermal regimes encountered during upriver migration and incubation. Temperature is thought to be central because the incubation period of eggs is temperature dependent, and the metabolic rate of salmonids rises steeply with temperature, raising the energy expenditure required to swim upstream, hence reducing the energy reserves available for gonad development and spawning. Physiological and behavioural studies (Farrell *et al.*, 2008; Martins *et al.*, 2011) show that *O. nerka* migratory performance and survival decline above a temperature optimum.

Hodgson & Quinn (2002) explain the extensive variation in marine exit timing among O. nerka populations as follows: (1) If the thermal regime during incubation is cold, dictating early spawning, then fish exit the sea early (before summer migration temperatures peak) and spawn with little delay. This strategy applies to interior O.nerka populations with long and energetically costly migrations and cold winters during egg incubation. (2) If the thermal regime during incubation is mild, dictating late spawning, then fish may return late in the season, after migration temperatures peak, and spawn with little delay. This strategy applies to coastal O. nerka populations with short, easy migrations (<100 km) and mild winters during egg incubation. (3) If the thermal regime during incubation is mild, dictating late spawning, but the river migration thermal regime prior to spawning is warm, populations may migrate to fresh water early (before temperatures peak) and experience a long delay in the lake before spawning. This strategy is proposed for coastal O. nerka populations with short, easy migrations (<100 km) that also experience high river temperatures (e.g. at the southern end of the range). Hodgson & Quinn (2002) proposed 19° C as the stream temperature threshold above which salmonid populations strategically avoid mid-summer migrations (strategy 3 above). They proposed this division based on a statistical separation between streams with early and late exit.

In Haida Gwaii, an archipelago in British Columbia, Canada, the seven known *O.nerka* populations all spawn at similar times over a relatively short duration, but exhibit divergent marine exit timing within and among populations (Fig. 1), separable into groups with early (spring) and late (summer) marine exit. Phylogenetic comparisons show that early marine exit has evolved independently several times (Beacham *et al.*, 2006), with at least two origins on Haida Gwaii alone. Populations with early marine exit leave the marine environment just as primary production and zooplankton in the North Pacific Ocean peak (Brodeur *et al.*, 1996; Rand, 2002; see Fig. 1), suggesting that early marine exit has an opportunity cost in the form of foregone feeding potential.

This paper describes the early marine exit behaviour of *O.nerka* in Copper Creek, Haida Gwaii, and measures the thermal regime in the creek and in the holding environment, Skidegate Lake. Statistical models are developed to describe the relationship between air temperature and Copper Creek temperatures, and applied to reconstruct weekly summer water temperatures in Copper Creek and other *O. Nerka* streams in Haida Gwaii from historic time series of air temperatures. Energetic modelling is used to estimate the costs of migration, maintenance and gonad development in relation to the thermal regime. The purpose is to determine if marine exit strategy 3, proposed



FIG. 1. Oncorhynchus nerka populations on Haida Gwaii (locations denoted by numbers). Marine exit (I) and spawn (I) timings are depicted for each population. Timing and spawning information are based on information from the Haida Fisheries Programme (Katinic, 2009). The curve represents mean zooplankton density (right axis) in the Alaskan Gyre of the open Pacific Ocean as reported by Brodeur *et al.* (1996). Zooplankton density is used as a surrogate for prey availability. Locations of air temperature monitoring stations are: Masset (M), Sewal (S), Port Clements (P), Tlell (T) and Sandspit (Sa).

by Hodgson & Quinn (2002) can adequately explain the early marine exit of Copper Creek *O. nerka* specifically, and Haida Gwaii populations in general.

MATERIALS AND METHODS

Copper Creek is located on Moresby Island in the Haida Gwaii Archipelago (Fig. 1). The mainstem has a length of 13·1 km and gains 41 m in elevation from the estuary at Copper Bay (53° 9' 29·98" N; 131° 47' 59·89" W) to Skidegate Lake. *Oncorhynchus nerka* entering Copper Creek have been counted since 1983 to assist the management of the Haida aboriginal food, social and ceremonial (FSC) fishery. The mean exploitation rate of this stock by the FSC fishery is 18%, and escapement averages 11 084 (range 3664–22 061; Katinic, 2009). Fish were enumerated either from a tower located 2 km upstream from the mouth as they swam over a river-wide aluminium plate under illumination (1983–1993), or in a weir at the mouth of the creek (1994 to present). Historical data consist of a combination of complete and partial counts to estimate total escapement, along with the reported catch from the Haida FSC fishery at Copper Bay.

To obtain the detailed data presented in this study, the weir was operated from 25 April to 1 July 2005, and 23 April to 29 June 2006. Weather observations, stream and air temperature and stream height from a permanent staff gauge were recorded daily. Stream temperature was recoded on a StowAway TidbiT Temperature Logger (model TBI32; www.onsetcomp.com/products/data-loggers/tbi32-0537) at the base of the fish weir. Temperature loggers were also installed in the deepest section (depth 19 m) of Skidegate Lake, suspended at depths of 6, 9, 12 and 15 m on a line tied to a float and anchored in place.

Temperatures were logged at 6 h intervals from the summer of 2005 until the autumn of 2008. Average daily temperatures are reported.

To estimate the length of the freshwater residence period, *O.nerka* were captured at the weir, marked and re-sighted during spawning. In 2005, 317 fish were marked with uniquely numbered Petersen discs blocked into three colour groups identifying the early, mid and late marine exit periods. In 2006, 441 *O.nerka* were marked with two-numbered Floy T-Bar anchor tags (FS-94, http://shop.floytag.ihostsites.net/productinfo.aspx?productid=FD-94), blocked into 12 groups of five-day increments identified by tag colours.

Spawning takes places in three tributaries at the western end of Skidegate Lake. *Oncorhynchus nerka* spawning in Shale, Parsons and Keats Creeks (spawning beds 2100, 1300 and 1100 m in length) were enumerated between 14 September and 15 October 2005, and 19 September and 20 October 2006 during visits at range 4–11 day intervals. The location and identity of all tagged fish were recorded. Often only the colour of the tag (corresponding to one of three periods in 2005 and 12 periods in 2006) was identifiable. The interval between the date of marking and date observed on the spawning grounds was calculated for each marked fish observed. If only the colour code could be observed, that observation was assigned the mean marking date for its colour. Statistical analyses were performed using JMP 7.0.2 (SAS Institute Inc.; www.sas.com).

Oncorhynchus nerka cease feeding prior to marine exit (Burgner, 1991), and hence rely on stored body reserves. The energy is required by Copper River O. nerka for migration, gonad development, basic metabolism during the holding period in Skidegate Lake and for spawning. Copper River O. nerka are estimated to be small (mean \pm s.D. of 192 fish measured in 2005–2006 was 1637 ± 291 g, with males slightly larger), and the estimates reported here were made for an average-sized female of 1.5 kg, based when necessary on regressions of body size on the relevant trait. Body composition and ovary mass estimates at entry and at spawning are based on fish collected at the weir (*i.e.* at marine exit), and on the spawning grounds (P. J. Katinic, unpubl. data). The energy requirement for the 13.1 km upstream migration is based on energy expenditures for O. nerka swum continuously under moderate flows $(1.0-0.3 \text{ ms}^{-1})$ from Clark et al. (2010). The energy required for reproductive development is based on the increase in ovary mass over the freshwater residence period, multiplied by energy density of ovaries (Patterson et al., 2004). Resting metabolism is temperature dependent, so energy consumption was modelled over the whole range of temperatures $(8-19^{\circ} \text{ C})$ in Skidegate Lake, for long (marine exit on 5 May), medium (marine exit 22 May) and short (marine exit 15 June) holding periods. The relationship between metabolic rate and temperature is based on Eliason et al. (2011; converted to kj following Brett, 1995). The energy required for spawning is based on Crossin et al. (2004). The spawning date was assumed to be 4 October (median-observed date). It was assumed that a minimum body energy density of 4 MJ kg⁻¹ is required for survival, and hence temperature and holding duration combinations that dropped below this threshold prior to the median spawn date of 4 October were deemed unable to spawn. Longevity was estimated from the energy reserve remaining (above the minimum) after allocating all of the above requirements.

The methods of Caissie *et al.* (2001) were used to reconstruct mean weekly water temperatures in Copper Creek over the past 50 years. Hydrological regimes of the streams on Haida Gwaii are dominated by precipitation, and hence water and air temperatures should be closely related. Temperature records at Sandspit and four other sites in Haida Gwaii (see Fig. 1) are archived by Meteorological Services Canada (www.climate.weatheroffice.gc.ca/Welcome_e.html). Statistical models were developed relating water temperature in Copper Creek and air temperature at nearby Sandspit. The simplest possible model was used, which regressed weekly mean air temperature on weekly water temperature. More complex models with added seasonal and non-seasonal components, residuals from air temperature anomalies on water temperatures (Caissie *et al.*, 2001) did not improve model fit. Inferences regarding the maximum weekly water temperatures at the other six spawning streams were made using temperature data from four other locations on the archipelago (Tlell, Port Clements, Masset and Sewall) with long-term records (>20 years). Maximum weekly average temperatures are currently used in British Columbia to assess temperature sensitive streams (Nelitz *et al.*, 2007).

Hydrological data are not available for Copper Creek, but Pallant Creek, in an adjacent catchment with a similar area, and a lake-headed stream with similar physical characteristics provides a long-term record (archived in Environment Canada's Hydrometric Data, www.wateroffice.ec.gc.ca/index_e.html).

P. J. KATINIC



FIG. 2. Mean ± s.D. (from 1983 to 2008) per cent of the total migratory of run of *Oncorhynchus nerka* by week in Copper Creek.

RESULTS

Over all years (1983–2008), the mean \pm s.D. date by which 50% of the O. nerka run had exited the sea and entered Copper Creek was 22 May ± 4.5 days. In the years for which detailed records exist the median exit dates were 26 May (2005) and 22 May (2006). In both years the first and last marine exiting individuals were separated by 75 days, and c. 90% of the population entered Copper Creek between 5 May and 15 June, with peak migration during the third week of May (Fig. 2). The interval between peak marine exit and peak spawning date was 134 and 133 days in 2005 and 2006, and the residence times of individually marked fish ranged from 83 to 163 days. There was no relationship between the marine exit date and the spawning date (*i.e.* fish migrating earlier did not spawn earlier), but there was a strong and significant correlation between marine exit date and freshwater residence period in both 2005 (r = 0.94, n = 16, P < 0.001) and 2006 (r = 0.84, n = 40, P < 0.001) such that early-exit individuals had longer freshwater residence. Because tag identity was not always certain, the possibility that error has crept into these estimates cannot be entirely excluded. The intervals between counts, the records of fish position (to eliminate double enumeration on the same visit) and the fact that all the results agree closely in 2005 (only three marking periods) and 2006 (12 marking periods), however, suggest that the error is small.

Water temperature records for Copper Creek show (Fig. 3) that stream temperature closely tracks the air temperature measured at nearby Sandspit, with buffering from daily extremes. Mean weekly air temperature explained 92% of the variation in mean weekly water temperature. The daily mean water temperature of Copper Creek during the *O. nerka* migration period ranged from 7 to 14° C, with means of 12·3, 11·2 and



FIG. 3. Annual pattern of air temperature at Sandspit (____) and water temperature in Copper Creek (____) between 2005 and 2008. Periods of marine exit (____) and spawning (____) of *Oncorhynchus nerka* in Copper Creek are denoted.

11.1° C in 2006, 2007 and 2008. This was somewhat cooler than the maximum air temperature experienced during each summer, which was 16.7, 16.1 and 14.8° C (weekly mean) and 17.6, 17.4 and 16.3° C (daily mean) for the successive years (Fig. 3).

The regression of Sandspit air temperature on Copper Creek water temperature was used to reconstruct the history of water temperatures in Copper Creek, based on the far longer (1960–2009) air temperature record at Sandspit. The regression equation is $T_{\text{water}} = 0.9548 T_{\text{air}} + 0.7211 (r^2 = 0.92)$. The reconstructed weekly mean water temperature series is summarized in Fig. 4. The estimated mean \pm s.D. weekly water temperature over the past 50 years during the warmest week in August was $15.4 \pm 1.3^{\circ}$ C, just slightly below the mean warmest weeks observed from 2006–2008. Neither the maximum weekly air temperature nor the reconstructed water temperatures during the 50 year period ever exceeded 19° C. Air temperatures are similar across the entire archipelago during summer, with mean air temperatures at Sandspit, Tlell, Port Clements, Masset and Sewall of (July) 14.2, 13.9, 14, 13.8 and 14.4° C, and (August) 14.9, 14.4, 14, 14.5 and 15.2° C.

Skidegate Lake becomes thermally stratified during April, as the lake warms in spring (Fig. 5). Thermal stratification is maintained until October. Water temperatures during the summer are highest at the surface (typically $17-20^{\circ}$ C), and cooler in deeper water. At 15 m depth the mid-summer temperature is $8-10^{\circ}$ C.

Estimates for the energetic requirements of 1.5 kg females exiting on 5 May, 22 May and 15 June are 2986, 2915 and 2812 kJ for ovary development; and 5382, 4805 and 4000 kJ for maintenance metabolism. The energy requirement for the upstream migration to the lake is 54 kJ, and is independent of exit date. The total requirement (8422,



FIG. 4. Weekly mean air temperature (T_{air}) at Sandspit was regressed against weekly mean water temperature (T_{water}) of Copper Creek, 2005–2008. The resulting regression equation was $T_{water} = 0.9548 T_{air} + 0.7211$ $(r^2 = 0.92)$. Using this regression equation, weekly mean ± s.D. water temperature in Copper Creek was reconstructed based on air temperatures at Sandspit, 1960–2009. *, maximum weekly values.

7774 and 6866 kJ) depends strongly on the marine exit date (earlier fish require more energy for maintenance) and on holding temperature (more energy required at warmer temperatures). The modelling exercise calculates that a holding temperature of 10° C or cooler is required in order for fish to survive until spawning.

The hydrological record for Pallant Creek shows that discharge has strong seasonal variation (Fig. 6). In particular, the flow is reliably low in late summer. The hydrological regime on Haida Gwaii is dominated by precipitation (Hogan & Schwab, 1990), and as expected, the mean daily discharge by day of the year measured at Pallant Creek between 1985 and 2005 varies directly with the mean daily precipitation of preceding 5 days ($r^2 = 0.90$, P < 0.001; based on data from Environment Canada's National Climate Data and Information Archive and Archived Hydrometric Data). Pallant Creek drains a catchment adjacent to Copper Creek that has a similar area and a lake-headed stream with similar physical characteristics to Copper Creek. Hence, it is reasonable to assume that the discharge pattern of Copper Creek is similar.

DISCUSSION

The period between peak marine exit and peak spawning date (133 - 134 days) measured in the Copper River, Haida Gwaii, is one of the longest recorded for any *O. nerka* population (Hodgson & Quinn, 2002). The temperature of Copper Creek is driven by



FIG. 5. Average daily temperature at various depths within Skidegate Lake (_____, 6 m;, 9 m; ____->, 12 m;, 15 m). Note that the data logger at 6 m depth failed in June 2007.

precipitation that falls through cool maritime air. Even during midsummer, the weekly mean water temperature is a moderate 15° C and is buffered from extremes, so it is unlikely that the historic weekly mean water temperature has ever exceeded 19° C, the temperature purported to pose a risk to migrating *O. nerka* survival (Hodgson & Quinn, 2002; Farrell *et al.*, 2008). The 13·1 km distance to the comparative safety and cool waters of Skidegate Lake can be covered quickly, given that migrating *O. nerka* can swim 40 km per 24 h (English *et al.*, 2005).

Hodgson & Quinn's (2002) thermal-avoidance hypothesis is based on the fact that metabolic costs rise steeply with temperature and could consume a large portion of the energy reserve used to power the upstream migration and subsequent spawning of *O. nerka* (Rand & Hinch, 1998; Rand *et al.*, 2006; Crossin *et al.*, 2009). This is a significant consideration in large rivers like the Fraser, in which salmonids must migrate long distances, often against high flows. But the energetic costs of migration are small in Copper Creek. The energy model for a representative Copper River *O. nerka* (1.5 kg) exiting the sea on 22 May and surviving to spawn on 4 October (equal to the mean freshwater residence period), estimates that 38% of energy reserves are partitioned to direct ovary development and 61% are expended on maintenance and spawning, the great majority of which is used during the long residence in Skidegate Lake. Migration energy represents < 1% of the initial energy reserves on migration, 13% on gonads and only 19% on maintenance (Gilhousen, 1980; Crossin *et al.*, 2004; Patterson *et al.*, 2004).

The present data do not support thermal avoidance as an explanation for the early marine exit timing of the *O. nerka* population in Copper Creek, or in other streams





FIG. 6. Mean ± s.D. weekly river discharge at Pallant Creek (1985–2005). Periods of marine exit (____) and spawning (____) of Oncorhynchus nerka in Copper Creek are denoted.

on Haida Gwaii. All are short (range 2–45 km), have low elevation gain (30-107 m), and flow (and hence water temperature) is precipitation-driven. Air temperatures are similar across the archipelago, and hence these streams all probably show seasonal temperature patterns similar to that in Copper Creek. Nevertheless, the thermal avoidance hypothesis cannot yet be completely ruled out. Although Brett (1971) determined a thermal optimum of 15° C for adult *O. nerka*, Farrell *et al.* (2008) found significant variation among streams in the thermal optimum of *O. nerka* (including streams with optima higher than 15° C). It remains possible, though probably unlikely, that the *O. nerka* population of Copper Creek has a low thermal optimum, and hence avoids the moderate temperatures of summer, even though the migration is short and easy.

Summer temperatures in the holding lake, in contrast, without question play an important role in the overall energy budget. The energy model shows that Copper Creek *O. nerka* require cool lake temperatures in order to keep the metabolic rate low enough to survive the lengthy holding period. *Oncorhynchus nerka* in Lake Washington (Newell & Quinn, 2005) and in the Fraser River (Mathes *et al.*, 2010) thermoregulate behaviourally by choosing lake strata with temperatures that optimize metabolic efficiency, and it appears likely that early-exit *O. nerka* on Haida Gwaii are also able do so, as they all reside in lakes with cool water refugia. Nevertheless, the energy requirement probably constrains the earliest possible marine exit date, or at least places a strong trade-off on the allocation of energy reserves to the gonads.

An alternative hypothesis to explain the early marine exit of Copper Creek O. nerka is that the fish return early to avoid the predation danger attendant on the low flows of midsummer. The data presented here show that if Copper Creek O. nerka exited the marine environment in August (*i.e.* weeks rather than months prior to spawning) they would be in the stream during the period that discharge is lowest. Salmonids can suffer substantial mortality from predators in small streams (Quinn & Buck, 2001; Quinn et al., 2001). On Haida Gwaii, Reimchen (2000) observed that black bears Ursus americanus captured and ate 74% of the O. keta entering Bag Harbour Creek (range among years 58–92%) although many of these were partially or completely spawned-out at the time of capture. Oncorhynchus nerka in Haida Gwaii streams also face bald eagles Haliaetus leucocephalus, river otters Lontra canadensis and of course humans. It is hypothesized that the collective danger from these predators during upriver migration would be highest in small, clear, shallow streams with few deep pools and little large woody debris, which are important features for avoiding predation (Quinn et al., 2001). In Copper Creek at least, marine exit timing is exclusively nocturnal (Katinic, 2009), which suggests that predation danger is a significant factor (Reebs, 2002). Selection has for this reason favoured earlier marine exit, when stream water levels are predictably higher. Note that the hypothesis does not state that mortality because predation is high for O. nerka returning to Copper Creek, but that mortality would be higher if fish migrated upriver later. This hypothesis can be considered an exact analogue of Hodgson & Quinn's (2002) thermal avoidance hypothesis, replacing 'high temperature' with 'high predation danger'.

This hypothesis also provides a potential explanation for the characteristic differences in marine-exit timing between streams on Haida Gwaii (see Fig. 1). Although early and late-exit populations may inhabit streams immediately adjacent to each other [*e.g.* the Ain (late-exit) and Awun, Yakoun (early-exit) Rivers all drain into Masset Inlet within a few kilometres of each other; see Fig. 1], the streams vary in depth, structure, seasonal variation in flow, degree of tannin staining, catchment size and the size of the lake heading the river. The reliably low precipitation of late summer reduces flows in some streams sufficiently that fish would be rendered highly vulnerable, while in others there is safety in the form of deep and wide channels, higher flows from large heading lakes, tannin staining which reduces predator vision, and in-stream features such as deep pools and large woody debris. The hypothesis is that natural selection has advanced the timing of marine exit in some streams from low to higher-flow periods to increase safety, with the exact balance of selective forces on marine exit timing peculiar to each stream.

This work was financially supported by the Haida Fisheries Programme, Fisheries and Ocean Canada's Environmental Watch Programme, Garfield Weston Graduate School Fellowship, Abbot Fretwell Graduate School Fellowship, Coastal Zone Graduate School Fellowship and the Centre for Wildlife Ecology at Simon Fraser University.

References

- Beacham, T. D., McIntosh, B., MacConnachie, C., Miller, K. M. & Withler, R. E. (2006). Pacific rim population structure of Sockeye salmon as determined from microsatellite analysis. *Transactions of the American Fisheries Society* 135, 174–187.
- Bernatchez, L. & Dodson, J. J. (1987). Relationship between bioenergetics and behaviour in anadromous fish migrations. *Canadian Journal of Fisheries and Aquatic Sciences* 44, 399–407.

- Brannon, E. L. (1987). Mechanisms stabilizing salmonid fry emergence timing. *Canadian Special Publication of Fisheries and Aquatic Sciences* **96**, 120–124.
- Brett, R. (1971). Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* **11**, 99–113.
- Brett, R. (1995). Energetics. In *Physiological Ecology of Pacific Salmon* (Groot, C., Margolis, L. & Clarke, W. C., eds), pp. 11–68. Vancouver, BC: University of British Columbia Press.
- Brodeur, R. D., Frost, B. W., Hare, S. R., Francis, R. C. & Ingraham, W. J. (1996). Interannual variations in zooplankton biomass in the Gulf of Alaska, and covariation with California current zooplankton biomass. *California Cooperative Oceanic Fisheries Investigations Reports* 37, 80–99.
- Burgner, R. L. (1991). Life histories of sockeye salmon (Oncorhynchus nerka). In Pacific Salmon Life Histories (Groot, C. & Margolis, L., eds), pp. 3–117. Vancouver, BC: UBC Press.
- Caissie, D., Hassir, E. & Satish, M. G. (2001). Modelling of maximum daily water temperatures in a small stream using air temperatures. *Journal of Hydrology* **251**, 14–28.
- Clark, T. D., Sandblom, E., Hinch, S. G., Patterson, D. A., Frappell, P. B. & Farrell, A. P. (2010). Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*). Journal of Comparative Physiology B 180, 684.
- Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D. & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* 65, 788–810.
- Crossin, G. T., Hinch, S. G., Cooke, S. J., Cooperman, M. S., Patterson, D. A., Welch, D. W., Hanson, K. C., Olsson, I., English, K. K. & Farrell, A. P. (2009). Mechanisms influencing the timing and success of reproductive migration in a capital breeding, semelparous fish species: the sockeye salmon. *Physiological and Biochemical Zoology* 82, 635–652.
- Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G. & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science* 332, 109–112.
- English, K. K., Koski, W. R., Sliwinski, C., Blakley, A., Cass, A. & Woodey, J. C. (2005). Migration timing and river survival of late-run Fraser River sockeye salmon estimated using radiotelemetry techniques. *Transactions of the American Fisheries Society* 134, 1342–1365.
- Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M. & Mathes, M. T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology* 81, 697–708.
- Gilhousen, P. (1980). Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. *International North Pacific Fisheries Commission Bulletin* 22.
- Groot, C. & Margolis, L. (Eds) (1991). Pacific Salmon Life Histories. Vancouver, BC: University of British Columbia Press.
- Gross, M. R. (1987). Evolution of diadromy in fishes. *American Fisheries Society Symposium* 1, 14–25.
- Healey, M. C. (1987). The adaptive significance of age and size at maturity in female sockeye salmon (Oncorhynchus nerka). In Sockeye salmon (Oncorhynchus nerka) Population Biology and Future Management (Smith, H. D., Margolis, L. & Wood, C. C., eds), pp. 110–117. Canadian Special Publication in Fisheries and Aquatic Sciences 96.
- Hodgson, S. & Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. *Canadian Journal of Zoology* 80, 542–555.
- Hogan, D. L. & Schwab, J. W. (1990). Precipitation and runoff characteristics, Queen Charlotte Islands. Land Management Report 60, 14–18. Victoria, BC: BC Ministry of Forests.
- Katinic, P. J. (2009). A life history approach to understanding marine exit timing of a sockeye salmon population from Haida Gwaii. MS thesis, Simon Fraser University, Burnaby, BC, Canada. http://summit.sfu.ca/system/files/iritems1/9761/ETD4828.pdf/
- Martins, E. G., Hinch, S. G., Patterson, D. A., Hague, M. J., Cooke, S. J., Miller, K. M., Lapointe, M. F., English, K. K. & Farrell, A. P. (2011). Effects of river temperature

and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). *Global Change Biology* **17**, 99–114.

- Mathes, M. T., Hinch, S. G., Cooke, S. J., Crossin, G. T., Patterson, D. A., Lotto, A. G. & Farrell, A. P. (2010). Effect of water temperature, timing, physiological condition, and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 67, 70–84.
- Nelitz, M., MacIsaac, E. & Peterman, R. M. (2007). A science-based approach for identifying temperature-sensitive streams for rainbow trout. North American Journal of Fisheries Management 27, 405–424.
- Newell, J. C. & Quinn, T. P. (2005). Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. *Canadian Journal of Zoology* **83**, 1232–1239.
- Patterson, D. A., Macdonald, J. S., Hinch, S. G., Healey, M. C. & Farrell, A. P. (2004). The effect of exercise and captivity on energy partitioning, reproductive maturation and fertilization success in adult sockeye salmon. *Journal of Fish Biology* 64, 1039–1059.
- Quinn, T. P. (2005). *The Behavior and Ecology of Pacific Salmon and Trout*. Seattle, WA: University of Washington Press.
- Quinn, T. P. & Buck, G. B. (2001). Size- and sex-selective mortality of adult sockeye salmon: Bears, gulls, and fish out of water. *Transactions of the American Fisheries Society* 130, 995–1005.
- Quinn, T. P., Wetzel, L., Bishop, S., Overberg, K. & Rogers, D. E. (2001). Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Zoology* **79**, 1782–1793.
- Rand, P. S. (2002). Modeling feeding and growth in Gulf of Alaska sockeye salmon: implications for high-seas distribution and migration. *Marine Ecology Progress Series* 234, 265–280.
- Rand, P. S. & Hinch, S. G. (1998). Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1832–1841.
- Rand, P. S., Hinch, S. G., Morrison, J., Foreman, M. G. G., MacNutt, M. J., Macdonald, J. S., Healey, M. C., Farrell, A. P. & Higgs, D. A. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Transactions of the American Fisheries Society* 135, 655–667.
- Reebs, S. G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries* 12, 349–371.
- Reimchen, T. E. (2000). Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Canadian Journal of Zoology* **78**, 448–458.
- Taylor, E. B. (1991). A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98, 185–207.
- Webb, J. H. & McLay, H. A. (1996). Variation in the time of spawning of Atlantic salmon (Salmo salar) and its relationship to temperature in the Aberdeenshire Dee, Scotland. Canadian Journal of Fisheries and Aquatic Sciences 53, 2739–2744.
- Young, J. L., Hinch, S. G., Cooke, S. J., Crossin, G. T., Patterson, D. A., Farrell, A. P., Van der Kraak, G., Lotto, A. G., Lister, A., Healey, M. C. & English, K. K. (2006). Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 1067–1077.