NRC Research Press

ARTICLE

Pacific Great Blue Herons (*Ardea herodias fannini*) consume thousands of juvenile salmon (*Oncorhynchus* spp.)

Z.T. Sherker, K. Pellett, J. Atkinson, J. Damborg, and A.W. Trites

Abstract: An array of predators that consume juvenile salmon (genus *Oncorhynchus* Suckley, 1861) may account for the poor returns of adult salmon to the Salish Sea. However, the Pacific Great Blue Heron (*Ardea herodias fannini* Chapman, 1901) is rarely listed among the known salmon predators, despite being regularly seen near salmon streams. Investigating heron predation by scanning nesting sites within 35 km of three British Columbia (Canada) rivers for fecal remains containing passive integrated transponder (PIT) tags implanted in >100 000 juvenile salmon from 2008 to 2018 yielded 1205 tags, representing a minimum annual predation rate of 0.3%–1.3% of all juvenile salmon. Most of this predation (99%) was caused by ~420 adult Pacific Great Blue Herons from three heronries. Correcting for tags defecated outside of the heronry raised the predation rates to 0.7%–3.2%, and was as high as 6% during a year of low river flow. Predation occurs during chick-rearing in late spring and accounts for 4.1%–8.4% of the Pacific Great Blue Heron chick diet. Smaller salmon smolts were significantly more susceptible to Pacific Great Blue Heron predation than larger conspecifics. The proximity of heronries relative to salmon-bearing rivers is likely a good predictor of Pacific Great Blue Heron predation on local salmon runs, and can be monitored to assess coast-wide effects of Pacific Great Blue Herons on salmon recovery.

Key words: predation, salmon, *Oncorhynchus* spp., smolts, Pacific Great Blue Heron, *Ardea herodias fannini*, chicks, diet, mortality.

Résumé : Un éventail de prédateurs consommant des saumons (genre *Oncorhynchus* Suckley, 1861) juvéniles pourrait expliquer les faibles retours de saumons adultes vers la mer des Salish. Le grand héron du Pacifique (*Ardea herodias fannini* Chapman, 1901) ne figure toutefois que rarement dans les listes de prédateurs connus des saumons, bien qu'il soit régulièrement observé à proximité de cours d'eau à saumons. Le balayage de sites de nidification dans un rayon de 35 km de trois rivières britanno-colombiennes (Canada) dans le but de retrouver des restes fécaux contenant des étiquettes à transpondeur passif intégré implantées dans plus de 100 000 saumons juvéniles de 2008 à 2018 pour étudier la prédation par les grands hérons du Pacifique a produit 1205 étiquettes, ce qui représente un taux de prédation annuel minimum de 0,3 % – 1,3 % de tous les saumons juvéniles. La majeure partie de cette prédation (99 %) est le fait de ~420 adultes des grands hérons du Pacifique provenant de trois héronnières. Après correction pour les étiquettes déféquées à l'extérieur de la héronnière, ce taux passe à 0,7 % – 3,2 %, atteignant même 6 % durant une année de faible débit des rivières. La prédation se produit durant l'élevage des héronneaux à la fin du printemps et représente de 4,1 % à 8,4 % du régime alimentaire des héronneaux. Les petits saumoneaux sont significativement plus vulnérables à la prédation des grands hérons du Pacifique que leurs conspécifiques plus gros. La proximité de héronnières à des rivières à saumons est probablement un bon prédicteur de la prédation par les grands hérons du Pacifique de saumons dans les montaisons locales et peut être surveillée pour évaluer les effets à l'échelle de la côte des grands hérons du Pacifique sur le rétablissement des saumons. [Traduit par la Rédaction]

Mots-clés : prédation, saumon, *Oncorhynchus* spp., saumoneaux, grand héron du Pacifique, *Ardea herodias fannini*, héronneaux, régime alimentaire, mortalité.

Introduction

Many salmon (genus *Oncorhynchus* Suckley, 1861) populations in the Pacific Northwest have declined in recent decades (Slaney et al. 1996; Coronado and Hilborn 1998; Gustafson et al. 2007; Scott and Gill 2008; Labelle 2009; Irvine and Akenhead 2013). One possible explanation for the declines is that high numbers of young salmon (smolts) may be dying during outmigration from natal streams (Holtby et al. 1990; Michel 2019; Henderson et al. 2019). Salmon tracking studies suggest that >50% of mortality incurred by juvenile salmon that initiate outmigration occurs prior to ocean entry (Buchanan et al. 2013; Michel et al. 2015; Clark et al. 2016; Michel 2019; Henderson et al. 2019), with predation suspected as being the main source of death (Heggenes and Borgstrøm 1988; Healey 1991; Cavallo et al. 2013).

Salmon smolts attract an array of predators during freshwater outmigration. These include Common Mergansers (*Mergus merganser* Linnaeus, 1758), North American river otters (*Lontra canadensis* (Schreber, 1777)), American minks (*Neovison vison* (Schreber, 1777)),

Received 22 August 2020. Accepted 20 December 2020.

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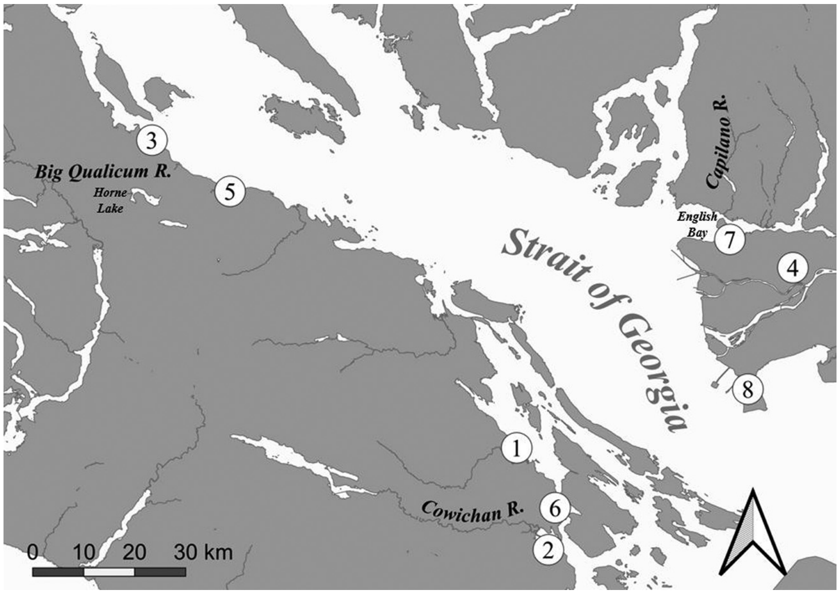
Fig. 1. Map of the study system showing the Cowichan, Capilano, and Big Qualicum rivers, British Columbia, Canada, and the neighboring heronries (1, Chemainus; 2, Cowichan Bay; 3, Deep Bay; 4, Deer Lake Park; 5, Little Qualicum Estuary; 6, Maple Bay; 7, Stanley Park; 8, Tsawwassen). Map was created in QGIS version 3.10 (available from https://qgis.org/en/site/).



Caspian Terns (*Hydroprogne caspia* (Pallas, 1770)), Double-crested Cormorants (*Phalacrocorax auritus* (Lesson, 1831)), and Pacific harbour seals (*Phoca vitulina richardii* (Gray, 1864)) (Melquist and Hornocker 1983; Wood 1986; Heggenes and Borgstrøm 1988; Greenstreet et al. 1993; Ben-David et al. 1997; Collis et al. 2001, 2002; Ryan et al. 2001, 2003; Roby et al. 2002, 2003; Antolos et al. 2005; Schreck et al. 2006; Hostetter et al. 2012; Evans et al. 2012). The avian piscivores on this list of predators are known to cause significant mortality of outmigrating salmon smolts (Wood 1986; Collis et al. 2001, 2002; Roby et al. 2002, 2003; Antolos et al. 2005; Schreck et al. 2006; Hostetter et al. 2012; Evans et al. 2012; Osterback et al. 2013). However, the impacts of another avian piscivore — the Pacific Great Blue Heron (*Ardea herodias fannini* Chapman, 1901) (or simply Heron) — that feeds along the riverbanks and estuaries of smolt-bearing rivers is unknown.

The Pacific Great Blue Heron is a non-migratory bird that nests along the coast of Washington (USA), British Columbia (Canada), and Alaska (USA) (COSEWIC 2008). These birds feed primarily on small fish in freshwater streams and estuarine marshes during their breeding season (March–June) when energy demand to support reproduction is the highest (Butler 1993, 1997; Hodgens et al. 2004). Observational studies suggest that herons (genus *Ardea* Linnaeus, 1758) consume fish ranging from 10 to 30 cm in length (Glahn et al. 1999; Hodgens et al. 2004), though small fish (<15 cm), such as salmon smolts, may be underrepresented in these studies (Cook 1978). One study found juvenile rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) made up as much as 67% of the daily energy requirements of one breeding population of Great Blue Herons (*Ardea herodias* Linnaeus, 1758) (Hodgens et al. 2004), while another study found a significant number of radio tags from juvenile Atlantic salmon (*Salmo salar* Linnaeus, 1758) under the nests of Grey Herons (*Ardea cinerea* Linnaeus, 1758) (Koed et al. 2002). It is thus conceivable that salmon smolts are nutritionally important for Pacific Great Blue Herons in British Columbia, but difficulty in quantifying Heron diets has precluded recognizing them as a significant predator of salmon smolts.

Our study aimed to assess Pacific Great Blue Heron predation on salmon smolts based on recovering passive integrated transponder (PIT) tags from the remains of fish defecated at local heronries. We assumed that all tags recovered were defecated and not regurgitated based on their small size (12 mm × 2.1 mm) and ability to pass through the digestive tract (R. Butler, personal communication), as well as their presence in fresh guano under Heron nests. PIT tags were implanted in both wild and hatchery-reared salmon smolts prior to outmigration from select rivers in British Columbia. We used the recovered tags to calculate a minimum predation estimate and to determine the proportion of the Heron diet consisting of salmon smolts during the breeding season. Finally, we investigated the influence of smolt size and river flow during outmigration on the susceptibility of smolts to Heron predation. The size of heronries and their proximity to salmon-bearing rivers may be a good predictor of coast-wide Heron predation on salmon populations, as well as the importance of smolt consumption in the breeding Heron diet. Identifying major sources of mortality and the factors that influence survival is an important step in developing an effective recovery plan to mitigate the decline of Pacific salmon populations.

Materials and methods

Study sites

Our study focused on the Cowichan River, the Big Qualicum River, and the Capilano River (Fig. 1). The Cowichan River flows 47 km east from Lake Cowichan to Cowichan Bay in the Salish Sea at the southeast end of Vancouver Island, British Columbia. The Cowichan River is home to a key indicator stock of Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)) used by Fisheries and Oceans Canada (DFO) to monitor the health and recovery of salmon populations in the Salish Sea. The Big Qualicum River is situated on the east coast of Vancouver Island running 11 km northeast from Horne Lake to the Strait of Georgia,

Table 1. Local heronries where PIT tags from juvenile salmon (*Oncorhynchus* spp.) were detected, as well as the river system where the tags originated, the number of active nests in the heronries, the distance to their respective rivers (km), the number of PIT tags recovered, and the percentage of all river-released tags these recoveries represent.

Heronry	River system	No. of active nests	Distance to river (km)	No. of tags recovered	Percentage of river-released tags (%)
Chemainus	Cowichan	30	20	1	<0.001
Cowichan Bay	Cowichan	100	<1	456	1.21
Deep Bay	Big Qualicum	20	10	126	0.32
Deer Lake Park	Capilano	30	15	3	0.01
Little Qualicum	Big Qualicum	10	10	10	0.02
Maple Bay	Cowichan	7	10	1	<0.001
Stanley Park	Capilano	90	<1	605	1.30
Tsawwassen	Capilano	350	35	3	0.01

while the Capilano River flows 6 km south from Capilano Lake into Burrard Inlet on the mainland of British Columbia. Extensive hatchery programs operate on all three of these river systems.

Local heronries

There were an estimated 4000–5000 Pacific Great Blue Herons nesting in British Columbia in 2008 (COSEWIC 2008). Of these, 29%–38% used heronries that bordered the three river systems of our study where juvenile salmon were tagged (5%–7% Cowichan Bay, 1%–2% Qualicum Estuary, 5%–6% English Bay, and 18%–23% Fraser Estuary) (Table 1).

The Cowichan Bay heronry is the closest nesting site to the Cowichan River and Bay (located within 1 km of the river mouth). It was established in 2004 and has increased in size from 2 to 100 active nests since that time (J. Cragg, personal communication). Since 2017, the number of active nests in the Cowichan Bay heronry has remained stable at ~100 (J. Cragg, personal communication). The next closest heronries to the Cowichan River are at Maple Bay (10 km north of Cowichan River, 7 active nests) and Chemainus (20 km north of Cowichan River, 30 active nests).

Local heronries surrounding the Qualicum Estuary include the Deep Bay heronry (10 km north of Big Qualicum River, 20 nests) and the Little Qualicum Estuary heronry (10 km south of Big Qualicum River, 10 nests).

English Bay is the primary feeding area for birds nesting in the Stanley Park heronry. This heronry has 90 nests and is less than 1 km from the Capilano River. Herons started nesting here in 1921 and have relocated several times to different locations within the park since then, settling at its current location in 2001. Another local heronry within feeding range of English Bay is the Deer Lake Park heronry (15 km southeast of the Capilano River, 30 nests). It has grown considerably since forming in 2005. Capilano River salmon likely transit through English Bay to the Fraser River Estuary during their seaward migration, taking them within close proximity of the Tsawwassen heronry (35 km south of Capilano River, 350–450 nests), which is the largest in British Columbia.

PIT-tag releases

PIT tags were released in salmon smolts from three river systems. This included wild and hatchery-reared Chinook smolts in the Cowichan River, hatchery-reared coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)) smolts in the Capilano River, and hatchery-reared coho smolts in the Big Qualicum River. Details of the tagging methodologies for each river system are as follows.

From 2014 to 2018, a mean of 2588 PIT tags (SD = 2195 PIT tags; 12 mm × 2.1 mm) were inserted annually into wild Chinook salmon in the Cowichan River, and a mean of 4399 PIT tags (SD = 1423 PIT tags) were implanted in hatchery-reared Chinook salmon smolts released into the Cowichan River (PSF 2016) (Supplementary Tables S1 and S2).[1] Tags were inserted directly into the stomach cavity of the fish using a PIT-tag applicator that created a small incision (<1 mm) in the abdomen, through which the tag entered the fish (PSF 2016). Fork lengths were recorded for all tagged fish. Tagging was conducted by members of the British Columbia Conservation Foundation and employees at the Cowichan Fish Hatchery.

Hatchery-reared smolts were measured and tagged at the Cowichan Fish Hatchery in early May of each year, and they were allowed to recover from the effects of tagging in holding tanks for a minimum of 14 days prior to being released into the river. Most PIT-tagged hatchery fish (>66%) were released with ~600 000 untagged hatchery smolts in each year. This release took place ~25 km upstream of Cowichan Bay. The remaining PIT-tagged hatchery smolts were released in five smaller groups (100–500 smolts per group) at five sites along the Cowichan River (sites ranging from 5 to 40 km upstream of Cowichan Bay). All releases took place on 22 May of each year.

Wild Chinook smolts were opportunistically caught and PIT-tagged along the Cowichan River using a single beach seine from May until the end of the smolts' freshwater residency in late June in all years except 2017. Tagging of wild smolts occurred over 7–14 days in the field and resulted in ~10 000 smolts being captured and tagged over the course of this study. Following smolt entry into the ocean (late May – July), beach and purse seining was conducted in Cowichan Bay to deploy ~5000 additional PIT tags annually in wild and hatchery-reared fish (PSF 2016). Hatchery smolts captured in the estuary were identified by adipose fin clips given prior to release.

In 2015, 40 000 hatchery-reared coho smolts were measured and PIT tagged, and released with ~380 000 untagged smolts from the Big Qualicum Fish Hatchery, located 1 km upstream of the Strait of Georgia (PSF 2016) (Supplementary Table S3).[1] In the Capilano River, a mean of 4227 (SD = 4209) PIT tags were deployed annually from 2008 to 2018 in hatchery-reared coho smolts from the Capilano Fish Hatchery (Braun et al. 2016) (Supplementary Table S4).[1] These fish were measured and tagged prior to being released with ~600 000 untagged hatchery smolts downstream of the Cleveland Dam on the Capilano River, with all tagged fish being released on the same day in each year (Braun et al. 2016).

[1]Supplementary tables are available with the article at https://doi.org/10.1139/cjz-2020-0189.

Scanning heronries

Forest floors in heronries were scanned using a custom-designed mobile PIT antenna consisting of a Biomark IS1001 reader board and three conduit, 12-gauge cable-wire looped at the end of a 4-foot pole housed in PCV tubing. The array was powered by a 24 volt, 7 Ah lead acid battery and equipped with a beeper to notify the operators when a tag was detected. The battery and reader board were carried in a 150 L backpack. Two people systematically scanned each heronry by dividing the heronry into sections based on natural borders (e.g., standing or fallen trees) and scanning along transects within sections. Areas that appeared to have high tag densities were scanned multiple times along different transects to minimize the effect of PIT-tag signal collisions on the array's detection efficiency. A similar methodology for PIT-tag recovery in nesting sites has successfully been used to assess avian predation on salmon smolts in the Columbia River (Collis et al. 2001; Ryan et al. 2001, 2003; Roby et al. 2002; Antolos et al. 2005; Hostetter et al. 2012; Sebring et al. 2013; Hostetter et al. 2015; Evans et al. 2016). All heronry scanning was conducted from 2017 to 2018. However, the long life of PIT tags that accumulated under the nests allowed us to assess predation from all years that tagging was conducted in our study systems (2008–2018).

Predation rates

Annual minimum predation rates for each river system equaled the number of PIT tags recovered in local heronries divided by the total number of tags deployed in the river. The tags recovered under the nests reflect the minimum proportion of tagged smolts that Pacific Great Blue Herons consumed. However, this is a conservative rate of predation because it does not account for tags that Herons consumed and defecated away from their heronries. It also does not account for broken or otherwise undetectable tags deposited in the heronry.

Unfortunately, there were no Heron data to estimate the proportion of tags defecated outside of heronries. We therefore used data from a Double-crested Cormorant study that fed known numbers of tagged fish to a colony of birds, and counted the numbers of tags deposited at the rookery (Hostetter et al. 2015). This study yielded a probability distribution (mean and standard deviation) for the likelihood of recovering tags at a Cormorant rookery. In the absence of a similar study for Great Blue Herons, we assumed that the probability of recovering a tag at a heronry was similar to the probability of recovering a tag at a Double-crested Cormorant rookery.

We used a Monte Carlo simulation procedure to randomly select deposition rates from the probability distribution of recovering a fish tag at a Double-crested Cormorant rookery (n = 6 trials). We also randomly selected the proportion of salmon tags recovered under heronries from the probability distribution of tags recovered from each site and all years (n = 5-year hatchery-reared Cowichan Chinook; n = 4-year wild Cowichan Chinook; and n = 11-year hatchery-reared Capilano coho). Each simulation selected one value for each site from the Heron tag recovery distributions, and one value from the Double-crested Cormorant tag recovery distribution, to estimate the corrected annual predation rate as

$$P_c = \frac{T_{\text{herons}}}{T_{\text{cormorants}}}$$

where P_c is the corrected annual predation rate by Herons, T_{herons} is the proportion of salmon tags recovered at a given heronry, and $T_{\text{cormorants}}$ is the proportion of tags consumed by Double-breasted Cormorants that were deposited in Cormorant colonies.

We ran the simulation with 10 000 trials for each site and tagged population to produce mean-corrected annual rates of predation (with standard deviations) inflicted on salmon smolts by Herons for each heronry and cohort of fish (i.e., hatchery or wild). Confidence limits were calculated based on the mean and standard deviation of the 10 000 trials.

We logit-transformed the parameters that described the probability distributions prior to running the Monte Carlo simulations to assure that no negative values could be randomly selected in the trials. Logit transformations are commonly used when working with proportional values to avoid misinterpreting datasets ranging from 0 to 1. Logit transformations were completed using the logit transformation formula:

$$\text{logit}(p) = \log\left(\frac{p}{1-p}\right)$$

where p is the proportional value being transformed. We back-transformed the Monte Carlo selected values prior to applying them in the corrected predation rate formula using the inverse-logit transformation formula, also known as the logistic transformation formula:

$$\text{logistic}(\alpha) = \frac{1}{1+\exp(-\alpha)}$$

where α is any value selected by our Monte Carlo simulations.

We ran simulations for the hatchery-reared Cowichan Chinook (n = 5 years of annual tag recovery rates), wild Cowichan Chinook (n = 4 years of annual tag recovery rates), and hatchery-reared Capilano coho (n = 11 years of annual tag recovery rates). We also directly applied the mean and standard deviations from the on-colony Cormorant tag deposition trials to the Big Qualicum annual heronry tag recovery rate to calculate corrected predation estimates and confidence limits for this site. Big Qualicum data were not corrected using Monte Carlo simulations because there was only 1 year of annual tag recovery data available for this river system.

Heron observations

We opportunistically observed Pacific Great Blue Herons from the Cowichan Bay heronry during low-tide foraging events in May and June of 2018. Observational counts were conducted from the southwestern shore of Cowichan Bay near the confluence zone of the south arm of the Cowichan River. Seven low-tide foraging events were included in these observations, and total counts were averaged to estimate a mean flock size with a 90% confidence interval.

River flow and annual predation

Mean flow during smolt outmigration in the Cowichan was calculated using hourly hydrometric measurements taken by a Government of Canada water station located approximately 7 km upstream of Cowichan Bay (station code 08HA011). Similar data were provided by Metro Vancouver that consisted of hourly flow measurements taken downstream of the Cleveland Dam, where hatchery smolts from the Capilano River were released in all years of our study. The influence of flow on heron smolt predation was assessed using correlations between mean flow during outmigration and annual tag recoveries in local heronries.

Smolt size and predation

Fork lengths were collected for both wild and hatchery-reared smolts tagged in the Cowichan and Capilano rivers just prior to release into the freshwater environment. We used these values to evaluate the influence of smolt size on susceptibility to Heron predation. The fork lengths of river-released smolts detected under the nests at local heronries and those whose tags were not detected were compared using a general logistic regression model, with the independent variable of fork length upon release tested against heronry detection as a binomial response variable.

Smolts from the 2016 Cowichan River release were excluded from this analysis due to high levels of predation resulting from low-flow conditions in that year, which rendered all smolts increasingly vulnerable to Heron predation, regardless of size.

Timing of predation

Daily scans were conducted under the nests at the Cowichan Bay heronry during smolt migration in 2018 to determine at what point in the Heron breeding season predation occurred. Extreme care was used when scanning under nests to avoid startling birds in the heronry, and bird behaviours were monitored at all times to ensure no disturbance was caused during scanning surveys. A total of 18 full scans of the heronry were completed from 22 May to 22 June 2018, covering the entire Cowichan Chinook hatchery release and the bulk of the outmigration run of both hatchery-reared and wild Chinook smolts. Two scans were subsequently completed every 2 weeks thereafter to document any further predation of late migrants, with the final scan taking place on 23 July 2018. A discovery curve was constructed from the cumulative detections of 2018 smolt tags from each scan of the Cowichan Bay heronry.

Tag distribution within heronries

Sectioned scans were conducted in the heronries with the highest rates of tag recoveries (Cowichan Bay and Stanley Park) to explore tag distributions relative to nest positioning. This allowed us to deduce whether most Herons were taking part in the smolt predation or if there were just a few smolt specialists. Heronry sections contained 15–30 nests and were separated by flagging tape to assure there was no overlap between sections during scanning. The total number of tags detected in each section was divided by the number of nests present to obtain the mean number of tags per nest in each section of the heronry. The resulting tags per nest ratios were then compared using ANOVA, with individual sections serving as the independent variable and tags per nest ratios as the response.

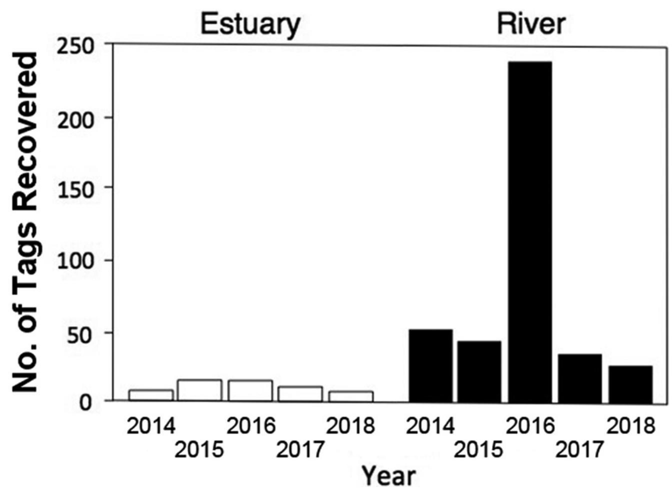
Heron dietary analysis

Daily heronry scans throughout smolt outmigration in the Cowichan indicated that predation occurred during chick rearing, when chicks had emerged from eggs and remained in the nests to be fed by both parents. Published Heron adult and chick energetic requirements from this period were used to determine what proportion of the diet was made up of hatchery salmon smolts. Whole nest energetic requirements were calculated for two adult Herons and two chicks, which is the mean number of chicks per active nesting attempt in North America (reviewed by Butler 1997).

Hatchery-reared and wild Cowichan Chinook energy densities (kJ/g wet weight) and weights were obtained from in-river and estuary sampling of Chinook smolts conducted by DFO throughout late May and June in all years that our study was conducted. For Capilano River hatchery-reared coho smolts, published energy densities (kJ/g wet weight) were applied to the mean wet weight collected from smolts tagged in our study and released in the Capilano from 2008 to 2018.

Estimates of overall annual hatchery smolt consumption were derived from the total number of smolts released into the rivers in each year multiplied by the proportion of smolt tags recovered at local heronries. This total consumption was then multiplied by the mean wet weight of in-river smolts to obtain a total weight of consumed smolts. This weight was used, in conjunction with the energy density of Cowichan Chinook, to determine overall energy input of hatchery-reared Chinook to the Heron diet in each year. Dividing this number by the total dietary requirements of Herons and chicks in major heronries during the smolt run produced the proportion of Heron diets consisting of hatchery-reared smolts.

Fig. 2. Annual number of tags recovered in the Cowichan Bay heronry from estuary- and river-released Chinook (*Oncorhynchus tshawytscha*) smolts from the Cowichan River (2014–2018). Approximately 5000 tagged fish were released in both the estuary and the river each year.



Results

Heron predation on outmigrating salmon smolts

We detected 1205 PIT tags in heronries near the three river systems where salmon smolt tagging had been conducted. Some of the tags had been lying under the Heron nests for as long as 11 years and tags from every smolt release group were recovered in heronries, suggesting that Pacific Great Blue Herons are a consistent predator of outmigrating salmon smolts. These detections included 458 tags from the Cowichan River, 136 tags from the Big Qualicum River, and 611 tags from the Capilano River. Few tags were recovered from estuary-tagged fish, and thus, reported predation rates are derived from river-tagged fish only.

Preliminary analysis comparing Heron predation rates among groups of hatchery-reared juvenile salmon released at different locations along the Cowichan River (using a general logistic regression model that set release location, measured as river distance from the location to the estuary, as the independent variable and heronry detection as the binomial response variable) revealed that release location did not significantly affect the likelihood of a tag being detected in the local heronry ($p > 0.10$). Grouping river-released hatchery smolts from the Cowichan system (independent of where along the river they were released) thus showed a mean of 1.24% (SD = 1.14%; 2014–2018) of the tags implanted in hatchery-reared Chinook smolts released in the Cowichan River ended up in the heronry (Supplementary Table S1).[1] Similarly, we recovered a mean of 1.15% (SD = 0.34%) of the tags from wild Chinook smolts released in the Cowichan River during the same period (Supplementary Table S2).[1] In contrast, 0.34% of coho hatchery-reared smolt tags released into the Big Qualicum River were recovered at its nearby heronry in 2015 (Supplementary Table S3)[1] compared with the finding of 1.3% (SD = 0.62%; 2008–2018) of the coho hatchery-reared smolt tags released in the Capilano River under the heronry in Stanley Park (Fig. 1, Supplementary Table S4[1]).

As Herons do not defecate exclusively in the heronry, and not all defecated tags are detectable due to damage or deposition in

Fig. 3. Distributions of fork lengths of wild and hatchery-reared PIT-tagged salmon (*Oncorhynchus* spp.) smolts (solid bars) compared with those of fish detected in local heronries (open bars) from Chinook salmon (*Oncorhynchus tshawytscha*) released in the Cowichan River (2014–2018) and coho salmon (*Oncorhynchus kisutch*) released in the Capilano River (2008–2018). Pacific Great Blue Heron (*Ardea herodias fannini*) predation was significantly higher on smaller hatchery smolts in both river systems (as indicated by *p* values).

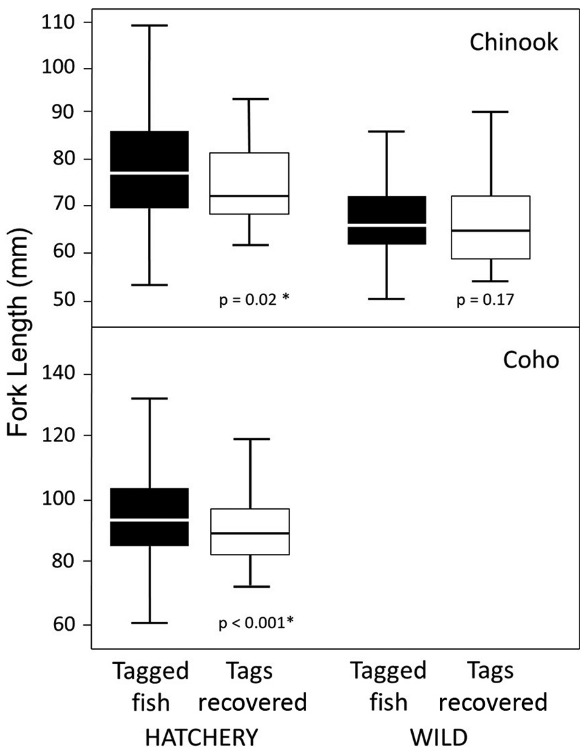
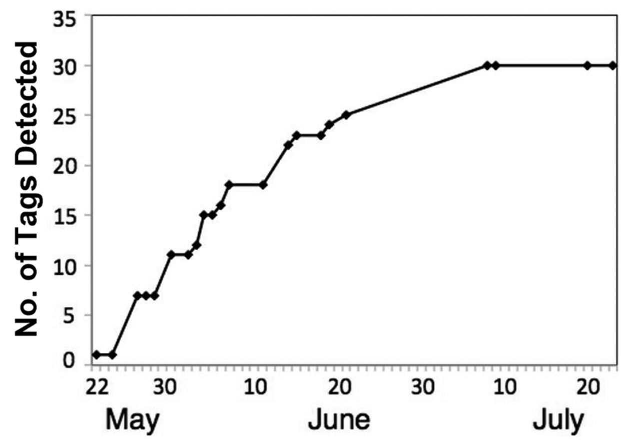


Fig. 4. Discovery curve showing cumulative number of PIT tags from Chinook salmon (*Oncorhynchus tshawytscha*) smolts released in the Cowichan River in 2018 detected per scan at the Cowichan Bay heronry during outmigration (22 May – 23 July 2018). Cowichan hatchery release occurred on 22 May.



inaccessible areas within the heronry (e.g., tree branches, nests), these tag recoveries represent a minimum predation estimate, and actual predation rates may be considerably higher. Correcting for tags that had been consumed, but not recovered, yielded predation estimates of 3.24% (SD = 1.14%) for hatchery-reared Cowichan River Chinook, 2.17% (SD = 0.34%) for wild Cowichan River Chinook, 0.67% for hatchery-reared Big Qualicum coho, and 2.90% (SD = 0.62%) for hatchery-reared Capilano coho.

River vs. estuary predation

From 2014 to 2018, a similar number of PIT tags were implanted in Chinook salmon smolts released in the river and the estuary in the Cowichan system. However, only 10% of the tags recovered in local heronries were from estuary-released fish, while 90% of the tags recovered in the local heronries were from river-released fish (Fig. 2). This finding indicates that Herons in the Cowichan fed on smolts primarily in the freshwater segment of their migration, upon entry into the estuary, or during early bay residency when smolts inhabit shallow nearshore habitats.

Heron observations

Most Herons observed in the southwestern reach of Cowichan Bay from May to June during the 2018 smolt migration were seen wading in the confluence between the river and the estuary along the tide line near the outlet of the south arm of the Cowichan River. A mean of 55 Herons (90% CI = 16–94) were observed actively foraging during the low-tide events monitored at this time.

River flow and annual predation rates

Mean river flow in the Cowichan during outmigration was negatively correlated with annual Heron predation rates throughout all tag release years ($R = -0.67$, $p = 0.23$), and a majority of the tags detected in local heronries (52.4%) were from fish released in 2016, a critically low water flow year (Fig. 2). Mean river flow during outmigration in 2016 (4.31 m/s^2) was comparable with that of 2015 (6.23 m/s^2), a year with only moderate levels of Heron predation (0.66% of tags recovered at heronry; Fig. 1). The point of entry of smolts into the estuary was not assessed during the years that our study was conducted in the Cowichan River system. Mean flow during outmigration was not correlated with annual Heron predation rates in the Capilano River ($R = -0.02$, $p = 0.95$).

Smolt size

Smaller salmon smolts were more susceptible to Pacific Great Blue Heron predation in our study (Fig. 3). Tags recovered at heronries were from fish with significantly smaller fork lengths (FL) than those of undetected smolts tagged and released in the river for hatchery-reared Chinook smolts from the Cowichan River in all years except a critically low-flow year in 2016 ($p = 0.016$; recovered smolt FL = 74.0 mm, SD = 8.8 mm; tagged smolt FL = 76.8 mm, SD = 9.2 mm) and hatchery-reared coho smolts from the Capilano River ($p < 0.0001$; recovered smolt FL = 90.4 mm, SD = 12.3 mm, tagged smolt FL = 94.4 mm, SD = 14.4 mm). Heronry-detected smolts were also smaller than river-released smolts for wild Chinook tagged in the Cowichan River, though the difference in fork lengths was not significant ($p = 0.174$; recovered smolt FL = 65.7 mm, SD = 7.8 mm; tagged smolt FL = 66.6 mm, SD = 7.1 mm). Smolt fork lengths were not measured for hatchery-reared coho smolts tagged and released in the Big Qualicum River.

Timing of predation

PIT tags from Chinook smolts released in late May 2018 were detected within 48 h at the Cowichan Bay heronry. Most of the 2018 tags (>80%) were deposited in the heronry within the first month following smolt release, and 100% of the 2018 tags were detected by 8 July, 47 days after hatchery tag releases (Fig. 4). Tag deposition averaged approximately one new tag per day throughout the freshwater portion of smolt migration in the Cowichan in 2018, a year of relatively low Heron predation.

Tag distribution in heronries

Sectioned scans of the heronries at Stanley Park and Cowichan Bay indicated that PIT tags were evenly distributed under the Heron nests. Tags were detected in all heronry sections scanned in our study, with a mean of 3.7 tags per nest (SD = 0.8 tags per nest) at the Cowichan Bay heronry and 6 tags per nest (SD = 2.3 tags per nest) at the Stanley Park heronry near the Capilano River. A sectioned scan was not conducted at the Deep Bay heronry, where most of the PIT tags from Big Qualicum River smolts (93%) were detected.

Predation as a factor of heronry distance

Full PIT-tag scans conducted at heronries within 35 km of the study rivers revealed that most Herons feeding on smolts came from relatively large heronries (30–100 nests) within 15 km of the lower river. In the Cowichan River, 456 of the 458 salmon smolt tags detected in heronries occurred under the nests at the Cowichan Bay heronry (100 active nests, <1 km from the mouth of the Cowichan River), while 1 tag was detected at the Maple Bay heronry (7 nests, 10 km from river mouth) and 1 tag was detected at the Chemainus heronry (30 nests, 25 km from river mouth) (Fig. 1). For the Capilano River, 605 tags were detected at the Stanley Park heronry (100 nests, 5 km from the mouth of the Capilano River) and 3 tags were detected at both the Deer Lake Park heronry (15 nests, 15 km from river mouth) and the Tsawwassen heronry (300 nests, 30 km from river mouth) (Fig. 1). A total of 126 tags from the Big Qualicum release in 2015 were detected at the Deep Bay heronry (30 nests, 10 km north of the Big Qualicum River) and 10 tags were detected at the Little Qualicum Estuary heronry (10 nests, 10 km south of the Big Qualicum River) (Fig. 1).

Heron energetics

Using the documented energy requirements of adult herons (1860 kJ/day) and heron chicks during peak energy demand (2027 kJ/day) (Bennett et al. 1995), the total energy demand of breeding herons is 7774 kJ/day per nest and 4054 kJ/day per set of chicks. The mean energy densities of hatchery smolts caught exiting the Cowichan River in our study years averaged 57.1 kJ/fish, and the published mean energy density of coho smolts (5.7 kJ/g: Trudel et al. 2005) and wet weight of fish tagged in our study resulted in energy density estimates of 61.2 kJ/fish.

Annual estimates of hatchery-reared smolt predation rates at major heronries along the Cowichan, Capilano, and Big Qualicum rivers corrected for off-colony tag deposition indicated that a mean of 5.6% (95% CI = 4.1%–8.4%) of chick energy requirements could be provided by hatchery-reared smolt predation alone. This represents annual consumption rates of 116 hatchery-reared smolts per nest (95% CI = 85–175 hatchery-reared smolts per nest) over all years and heronries.

Throughout our study, hatchery-reared Chinook smolts from the Cowichan River accounted for 7.5% (95% CI = 5.5%–11.3%) of the annual dietary requirements of chicks nesting in the Cowichan Bay heronry in the month following tag releases. Hatchery-reared coho smolts supplied 5.0% (95% CI = 3.6%–7.4%) of the annual energy requirements of chicks reared in the Stanley Park heronry and 4.3% (95% CI = 3.1%–6.4%) for chicks nesting in the Deep Bay heronry.

Discussion

The many PIT tags recovered under the nests of Pacific Great Blue Herons from the remains of wild and hatchery-reared juvenile salmon show that the Pacific Great Blue Heron is a prevalent predator of salmon smolts. The recovered tags provide information about the rates of predation, sizes of fish targeted, the influence of water flow on predation rates, and the locations where Herons are effective at catching smolts. This information helps to place Herons among the list of other predators of salmon smolts. It also reveals where and why smolts are vulnerable to Heron predation and provides a method to assess the contribution that smolts make to the growth and development of Heron chicks. Ultimately, the information gained from the tagged fish fills in a previously unknown piece of the salmon life history and shows one more way in which salmon contribute to sustaining populations of marine and freshwater predators.

Heron smolt predation

Pacific Great Blue Heron preyed on outmigrating salmon smolts in all river systems and years that tagging was conducted. Approximately 1% of the PIT tags released in wild and hatchery-reared Chinook and coho salmon smolts were subsequently recovered under the nests at Pacific Great Blue Heron rookeries. However, these tag recovery rates represent minimum predation estimates since not all Heron-consumed tags were deposited within the heronry, nor were all heronry-deposited tags detectable (e.g., some tags were likely deposited in nests or branches, or may have been broken). For example, only 51% (95% CI = 34%–70%) of the tags consumed by Double-crested Cormorants were subsequently detected in their rookery (Hostetter et al. 2012). As Double-crested Cormorants and Pacific Great Blue Herons exhibit similar nest attendance during the breeding season (Vennesland and Butler 2011; Dorr et al. 2014), it is plausible that this detection probability is applicable to tags consumed by Pacific Great Blue Herons.

When corrected for undetected tags consumed by Herons during our study, estimated annual predation rates were about 1%–3%, though predation was as high as 6% in a particularly low river-flow year in the Cowichan River. The lowest annual predation rate occurred in the Big Qualicum River, where the hatchery is located very close to the estuary, allowing for a rapid smolt migration through the system that potentially limited Heron abilities to cue into the feeding event. Low predation in this system may also have been due to a high number of tags being synchronously released within a large hatchery-reared smolt population (PSF 2016), resulting in a "predator swamping" effect that limited Heron predation (Furey et al. 2016). Sectioned scans in the two largest heronries further revealed an even distribution of deposited tags under all nests, suggesting that most Herons took part in the documented smolt predation as opposed to there being just a few smolt-consuming specialists.

Pacific Great Blue Herons spend the majority of their on-heronry time at their nests incubating eggs and tending to their chicks during the breeding season (Vennesland and Butler 2011). As a result, tag recovery locations are likely a good indicator of which birds are involved in the documented smolt predation.

Over 99% of the tags that we detected under Heron nests were in the heronries closest to the rivers where tagged fish were released, alluding to a potential partitioning of foraging habitats between Heron colonies. It has been noted that a 5% reduction in early life mortality could reverse the declining trends of some Pacific salmon populations (Kareiva et al. 2000). As such, predation by Herons could impact salmon population dynamics and could affect the recovery of some salmon populations.

Historically, Pacific Great Blue Heron predation on juvenile salmonids has not been thoroughly investigated, though breeding Herons are known to forage extensively in the freshwater and estuarine habitats used by salmonid smolts during their seaward migration (Butler 1997). Juvenile salmonids were not reported as part of Great Blue Heron diets in rivers and estuaries (Owen 1955; Quinney 1982; Butler 1993, 1997; Adams and Mitchell 1995; COSEWIC 2008), although some herons have been known to take juvenile fish at salmonid-rearing facilities (Glahn et al. 1999; Hodgens et al. 2004). More recently, however, Great Blue Herons nesting along the

Columbia River were found to have consumed salmon smolts (based on recovered smolt PIT tags in heronries; Myrvold and Kennedy 2018), which are similar to our findings.

How herons rank among other smolt predators

Smolt predation by Great Blue Herons and other known predators during outmigration might explain some of the high mortality associated with this stage of the salmon life history (Buchanan et al. 2013; Melnychuk et al. 2014; Michel et al. 2015; Clark et al. 2016; Michel 2019). In the Cowichan River, as many as 50% of juvenile salmon die throughout the downstream migration, with variability between years (K. Pellett, personal communication). In-stream detections imply that tagged fish were removed from the system by land-based predators. However, mobile PIT-tag scans that we conducted at river otter latrines, mink dens, Common Mergansers roosts, and along raccoon (*Procyon lotor* (Linnaeus, 1758)) trails in the Cowichan system during this study failed to detect even a single juvenile salmon tag. Instead we found >450 tags in the nearby Pacific Great Blue Heron nesting site.

The predation by Pacific Great Blue Herons that we documented accounts for only a small part of the overall mortality incurred by juvenile salmon while outmigrating. Nevertheless, its occurrence near the end of the freshwater migration may impose a heavy toll on the fish that make it past the preceding freshwater gauntlet. Where the other fish disappeared to remains a mystery.

It is not possible to know the full influence that Pacific Great Blue Herons have on smolt survival because unknown numbers of tags were excreted outside of heronries. However, it is possible to gauge the potential impact that a Heron population could theoretically have on salmon if they acquired all their dietary needs from juvenile salmon alone during freshwater outmigration. Using the Cowichan system as an example, birds from the nearby heronry would have to consume as many as ∼410 000 juvenile salmon during outmigration to meet all adult and chick energy demands through smolt consumption alone. To put this into perspective, this represents more than 100% of the hatchery-reared smolts that entered the Cowichan Bay in any given year of our study. The similarity in rates of predation between wild and hatchery-reared juvenile salmon further indicates that Herons could have a substantial influence on both wild and hatchery-reared salmon populations.

Avian predation on salmon smolts is being increasingly well documented with technological improvements. In the Columbia River, large-scale telemetry studies have investigated salmon smolt survival during outmigration and subsequent tag recoveries at local bird colonies have identified avian predators as a major source of mortality for salmonid populations (Ruggerone 1986; Collis et al. 2001, 2002; Ryan et al. 2001, 2003; Glabek et al. 2003; Roby et al. 2003; Antolos et al. 2005; Hostetter et al. 2012; Evans et al. 2012, 2016; Sebring et al. 2013). Aside from avian piscivores, there are a host of other predators that forage opportunistically on cohorts of outmigrating salmon smolts.

Seals are also known to prey on salmon smolts during their estuary residence prior to continuing out to the open ocean. Scanning efforts at seal haul-outs in Cowichan Bay yielded 18 PIT tags from Chinook smolts tagged in our study, though potentially poor tag retention at tidally inundated haul-outs and unknown seal defecation rates in other areas away from the haul-outs render this an inadequate method for quantifying seal predation rates. Other studies have shown that some Pacific harbour seals congregate in river mouths during smolt outmigration and consume significant numbers of juvenile salmon in the estuary (Greenstreet et al. 1993; Thomas et al. 2017; Allegue et al. 2020), and the number of seals present during estuary residence was negatively correlated to Chinook production in most of the river systems assessed in one study conducted in the Pacific Northwest (Nelson et al. 2019). The large numbers of Pacific harbour seal populations in this area is estimated to adversely affect the survival of salmon smolts (Chasco et al. 2017). While seals consume smolts in estuaries, avian predators may be intercepting smolts earlier in the migration run.

Where predation by herons occurs

Unlike other avian predators that prey on salmon smolts higher in the river system (e.g., mergansers, kingfishers) or lower in the estuarine system (e.g., Double-crested Cormorants, Caspian Terns, Common Murres (*Uria aalge* (Pontoppidan, 1763)), various Gull species (genus *Larus* Linnaeus, 1758)) (Wood 1987; Feltham 1990, 1995*a*, 1995*b*; Wilson et al. 2003; Penaluna et al. 2016; Collis et al. 2002; Antolos et al. 2005; Phillips et al. 2017; Wells et al. 2017), Great Blue Herons primarily consumed juvenile salmon in the lower river or early upon estuary residency prior to the young fish migrating away from the nearshore habitat into the deeper waters of the bay. And unlike these other birds that plunge or dive in pursuit of smolts in the deeper waters of the mid-river and upper estuary, Great Blue Herons are restricted to wading and feeding in shallow waters along the lower river and estuary. There is thus considerable partitioning among the avian predators in terms of where and how they catch salmon smolts.

Efforts to put PIT tags into salmon smolts in the Cowichan River were divided equally between the river migration and the estuary residency phase of the smolt run. However, 90% of the tags recovered in the Cowichan Bay heronry were from river-tagged fish. Chinook salmon smolts in the Cowichan system generally spend a few weeks to 2 months in the estuary following outmigration from the river, moving from shallow nearshore habitats to deeper waters in the middle of the estuary as they grow before completing their migration to sea (K. Pellett, personal communication). During estuary residence, salmon smolts may be vulnerable to heron predation in nearshore habitats, with predation risk decreasing as they move into deeper waters of the bay.

The Pacific Great Blue Heron observations that we made during smolt outmigration indicated that predation most likely occurs in the lower river or upper estuary in the Cowichan system. Daily heronry scans conducted throughout the smolt run in 2018 indicated that tags were still being deposited after smolts exited the river, suggesting that Heron predation also occurred early in estuary residency when smolts inhabited the shallow nearshore environment. PIT-tagging efforts focused on smolts during their estuary residence in Cowichan Bay were conducted by purse seine in deeper waters near the centre of the bay. These estuary-tagged smolts had likely moved away from the nearshore environment where Herons feed, potentially explaining the small number of bay-released tags subsequently detected in heronries. A number of abiotic conditions associated with the lower river and nearshore estuary designate these areas ideal smolt foraging habitat for Herons.

The lower river and upper estuary are shallower and slower moving than upstream and downstream environments, providing prime feeding habitat for Pacific Great Blue Herons, whose foraging success is limited by depth (Power 1987; Ntiamoa-Baidu et al. 2008). Wading birds that prey on fish are more successful when foraging in shallow water (Hodgens et al. 2004; Gawlik and Crozier 2007) and Herons exhibit higher capture rates when fishing in shallow habitats compared with deep pools in the freshwater environment (Power 1987; Harvey and Stewart 1991). Reduced water flow in tidally influenced portions of the lower river may also reduce smolt migration rates and increase exposure to predation (Anderson et al. 2005; Buchanan et al. 2013), while salinity shock upon entry into the bay can render smolts increasingly susceptible to Heron predation. Annual variability in abiotic conditions may also play a role in the intensity of Heron smolt consumption.

Influence of tags and water flow on predation rates

Tags have the potential to influence the survival, swimming, and buoyancy of tagged fish. However, tags under 8%–10% of the fish weight should have minimal to no effects on survival and swimming (Brown et al. 2006; Collins et al. 2013; Clark et al. 2016; Furey et al. 2016). This implies that the tags used in our study (0.1 g, <1% of smolt weight) did not influence downstream survival and migration. In terms of buoyancy, Atlantic salmon smolts tagged with 5.6 g PIT tags have been shown to recover neutral buoyancy within 6 h if they can gulp air at the surface and expand their swim bladders to counteract the weight of the tags (Fried et al. 1976). All hatchery-reared smolts used in our study should therefore have recovered neutral buoyancy by the time they began downstream migration because they were held for a minimum of 14 days with access to air before being released. Similarly, wild smolts would have had days to weeks to recover after being tagged before encountering Herons downstream. Thus, PIT tags likely did not significantly influence a smolt's susceptibility to being preyed upon, although we recognize that tag weight cannot be completely ruled out as contributing factor.

Another factor that may influence rates of predation by Pacific Great Blue Herons on salmon smolts is water depth and flow rate. In 2016, water flow rates were critically low in the Cowichan River and predation levels were the highest recorded. River flows were so low in 2016 that the primary migration corridor for outmigrating salmon smolts through the north arm of the Cowichan River dried up, potentially stranding a large number of juvenile salmon. Combining data from other years showed that river flow was negatively correlated with annual predation rates in the Cowichan River. River flow has also been identified in other river systems as the most important environmental factor influencing the downstream survival of outmigrating salmon smolts (Smith et al. 2003; Gauld et al. 2013; Zeug et al. 2014; Michel et al. 2015; Michel 2019; Henderson et al. 2019; Antolos et al. 2005; Hostetter et al. 2012). Flow rates correlate positively with migration speed and survival.

Herons likely have increased access to foraging habitat under low-flow conditions (Master et al. 2005; Gawlik and Crozier 2007). Low flow means slower smolt migration rates (Cavallo et al. 2013; Boavida et al. 2017) and increased exposure to Heron predation (Høgåsen 1998; Cavallo et al. 2013) due to reduced volumetric space to evade predation (Buchanan et al. 2013), higher smolt densities increasing Heron predation success (Draulans 1987), and limited access to cover (Power 1987; Harvey and Stewart 1991; Reinhardt and Healey 1997; Sommer et al. 2001; Hakala and Hartman 2004; Penaluna et al. 2016). Shallow waters with low flow may also translate into higher foraging success for visual predators due to reduced turbidity and higher water clarity (Gregory and Levings 1998; Antolos et al. 2005; Hostetter et al. 2012; Ferrari et al. 2014). Salmon smolts may also experience greater salinity shock when entering the bay if the low flow results in less mixing of fresh and salt waters in the confluence zone. Herons may play a role in the poor survival of salmon smolts in low-flow conditions that has been documented in other research (Smith et al. 2003; Gauld et al. 2013; Zeug et al. 2014; Michel et al. 2015; Henderson et al. 2019; Michel 2019). These findings may inform efforts to mitigate poor smolt survival to sea through coordinated flow releases by dam operators to ensure adequate river conditions for seaward migrations.

Unlike the Cowichan River, water flow did not influence predation rates in the Capilano River. Flow may have a lesser impact on Heron predation in this system because birds nesting in the Stanley Park heronry, where nearly all recovered Capilano-released tags were detected, do not congregate primarily at the mouth of the river as is in the case for birds at the Cowichan Bay heronry. Rather, Herons from this heronry forage for fish along the tide lines of the comparably larger estuary system of the Burrard Inlet and English Bay near Stanley Park, Spanish Banks, and along the West Vancouver waterfront (R. Butler, personal communication). The spread of these Heron foraging efforts suggest that Stanley Park Herons are consuming smolts in the nearshore environment of the estuary, after the fish have exited the Capilano River. All tagged smolts released in the Big Qualicum River were released in 1 week in 2015, so no river flow data was analyzed for this system.

Size-selective predation

Physical characteristics of salmon smolts appear to have predisposed some individuals to Pacific Great Blue Heron predation given that predation rates were higher on smaller smolts than larger smolts tagged and released in the river. This was true for hatchery smolts released in all years in the Capilano River, hatchery smolts from all years, save a low-flow year, in the Cowichan River, and was nearly significant for wild smolts from all years in the Cowichan River. The observed reduction in size-selective predation for hatchery smolts during the low-flow year on the Cowichan was likely due to heightened susceptibility to predation for all smolts, regardless of size, in years of low-flow conditions, which is consistent with findings that size-selective mortality in juvenile salmonids weakens with reduced flows (Good et al. 2001). Laboratory studies indicate that smaller fish are disproportionately preyed upon by predators in the aquatic environment (Mesa et al. 1994). Field studies investigating avian predation on salmon smolts also support this theory (Hostetter et al. 2012; Tucker et al. 2016). Tucker et al. (2016) found that 85.5% of juvenile salmonids preyed on by Rhinoceros Auklets (*Cerorhinca monocerata* (Pallas, 1811)) in the coastal marine environment were undersized. Smaller juvenile salmonids were also preyed upon more heavily by Belted Kingfishers (*Megaceryle alcyon* (Linnaeus, 1758)) in a riverine environment (Penaluna et al. 2016), though this may reflect a size refuge for larger conspecifics from the gape-limited predator (Salyer and Lagler 1949).

Other studies have suggested that piscivorous birds target larger smolt species because they are more visible than smaller ones (Britton and Moser 1982; Eriksson 1985; Magnhagen 1988; Trexler et al. 1994) or intermediate-sized smolts within a population for capture efficiency (Hostetter et al. 2012; Osterback et al. 2014). Caspian Terns, for example, have a disproportionately higher predation impact on larger species of salmon smolts (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012), while Caspian Terns and Double-crested Cormorants selectively prey on intermediate-sized individuals within a the larger species population of smolts (Hostetter et al. 2012; Osterback et al. 2014).

It seems unlikely that Pacific Great Blue Herons selectively chose small smolts over larger individuals based on visual size-based cues given there was relatively little difference in the size of smolts released in each year of our study. A more likely explanation is that smaller smolts were more susceptible to predation because of their reduced ability to evade predators (Taylor and McPhail 1985; Mesa et al. 1994; Healey and Reinhardt 1995), slower migration speeds (Giorgi et al. 1997), and riskier behaviour (Grant and Noakes 1987; Reinhardt and Healey 1997; Reinhardt 1999; Naman et al. 2019). Smaller smolts are also found in shallower habitats that are more effectively foraged by herons, and can be excluded from predator refuge habitat by larger smolts (Jenkins 1969; Heggenes 1990; Harvey and Stewart 1991; Bremset and Berg 1997; Reinhardt and Healey 1997; Reinhardt 1999; Vehanen et al. 1999; Bardonnet and Baglinière 2000). Relative tag burden may also have contributed to smaller smolts being more susceptible to heron predation (Brown et al. 2006; Collins et al. 2013).

Another possibility is that herons may have selected shallower foraging habitats during chick emergence to target smaller fish that were appropriately sized for their brood (Moser 2008). This is consistent with the tendency for Great Blue Herons to feed their young small prey items early in the hatchling phase, providing their chicks with increasingly larger items as they grow to match the gape limitations of chicks and avoid choking hazards (Quinney 1982).

Although predation often carries negative connotations, higher rates of predation by Pacific Great Blue Herons on smaller juvenile salmon may be beneficial to salmon populations. Smaller salmon smolts often exhibit poorer survival to adulthood than larger conspecifics (Parker 1971; West and Larkin 1987; Henderson and Cass 1991; Beamish et al. 2004). Heron predation may therefore work in favor of salmon by weaning out smolts that were unlikely to survive to adulthood, potentially reducing competition for limited food sources in the early marine stage of the salmon life history. Predation by Herons on juvenile salmonids may also be compensatory as recently shown for Double-crested Cormorants and Caspian Terns in the Columbia River system (Haeseker et al. 2020). Thus, predation by Herons might ultimately have a null effect on overall salmon survival if the juveniles are later consumed by another predator.

Why consume smolts?

Daily scans conducted at the Cowichan Bay heronry throughout the smolt migration in 2018 indicated that predation occurred primarily during the month following tag releases (22 May – 23 June), with a mean of one new tag deposited per day under the nests. This window of time overlaps with the period of peak energy demand from recently hatched chicks (Bennett et al. 1995). Since Great Blue Herons are known to feed their chicks relatively small prey items during this time (Quinney 1982), and the smolts tagged in our study were considerably smaller than other prey fish commonly targeted by adult herons (Glahn et al. 1999; Hodgens et al. 2004), it is likely that salmon smolts serve as a valuable food source for heron chicks during the critical stage of chick growth and development. Smolt predation by adult Pacific Great Blue Herons in our study systems may have provided a sizeable portion of the energy requirements of rearing chicks in the nearest heronries.

Energetic analyses of Pacific Great Blue Herons nesting in the largest heronries on the Cowichan, Capilano, and Big Qualicum rivers suggest that hatchery-reared salmon smolts could provide 5.4% (95% CI = 3.9%–8.1%) of the daily energy requirements of Heron chicks in the month following hatchery releases. Due to a lack of information regarding the size of wild smolt populations in our study systems, we were unable to include the input of wild smolt consumption in these energetics analyses. However, historic evidence suggests that there were considerably more wild smolts of 2–3 million in our study rivers during the 1960s and 1970s, compared with the current hatchery releases of 400 000 – 600 000 (DFO 1962; Lister et al. 1971). Given that we observed similar predation rates on wild and hatchery-reared smolts from the Cowichan River, it is possible that wild salmon smolt consumption provides a substantially larger share of the energy demands of Heron chicks in local heronries than that documented for hatchery-reared smolts. Nonetheless, the hatchery-reared Cowichan Chinook consumption in our study could have provided 4.3% (95% CI = 3.1%–6.4%) of the total energy demands of both adult and juvenile herons in the Cowichan Bay heronry, while hatchery-reared coho smolts likely accounted for 2.4% (95% CI = 1.7%–3.5%) of the requirements of adults and chicks in the Stanley Park heronry and 2.2% (95% CI = 1.6%–3.3%) for birds in the Deep Bay heronry.

Conclusion

Salmon are a bridge from land to sea that serve as a significant source of energy and nutrients to the host of species that they encounter throughout their life cycle. Recovering tags from marked fish in heronries revealed that small smolts are an important food source for Pacific Great Blue Herons and their chicks during a time of peak energy demand. The recovered tags also allowed the quantification of the numbers of smolts consumed by Pacific Great Blue Herons, as well as the identification of an overlooked predator responsible for a portion of high mortality occurring during seaward migrations of juvenile salmon. These findings contribute to the growing body of knowledge about the wide range of predators that juvenile salmon encounter throughout their migration from natal streams, as well as the factors that influence the ability of salmon to survive the early stages of their life history.

Acknowledgements

This research was funded by the Pacific Salmon Foundation with support of a Mitacs Accelerate grant. We thank all the members of the British Columbia Conservation Foundation and Cowichan Tribes that assisted in data collection and provided support and guidance throughout this project, as well as Metro Vancouver for running all salmon tagging operations in the Capilano River and allowing us access to their data. We thank C. Costain, T. Kulchyski, P. Rosenbaum, R. Togunov, S. Naman, J. Craig, and R. Storlund for their invaluable logistical, field, and statistical support. R. Butler, C. Walters, and V. Christensen provided edits and comments that greatly improved earlier drafts of the manuscript. We are particularly grateful for the constructive comments made by the reviewers that further improved the manuscript. All parts of this research were reviewed and approved by The University of British Columbia Animal Ethics Committee under Animal Care Permit No. A17-0091.

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