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Aggregative response in white-tailed eagles- an initial study of the terrestrial implications of invasive Pacific pink salmons *(Oncorhynchus gorbuscha)* in northern Norway.

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“Today’s special”

Cover photo by the author.

A lone white-tailed eagle and five common ravens, all foraging on Pacific pink salmons at Skallelv August 26th in 2021.

Acknowledgment

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Bror Bonde

Tromsø, May 15th in 2023

Abstract

The spawning population of invasive Pacific pink salmon (*Oncorhynchus gorbuscha*) has only continued to increase in the river systems on the Varanger peninsula in Norway, causing concerns across institutional boundaries and management communities. So far, the Norwegian research efforts on Pacific pink salmon have been centred on consequential effects in marine- and freshwater ecosystems, while terrestrial ecosystems have received less attention from both the scientific- and management community. The trophic linkage of riverine- and terrestrial ecosystems is likely to be the key determinant of transfers of marine-derived resources through Pacific pink salmon. This thesis shed light on how marine-derived resources became available to the wider scavenger community through white-tailed eagles (*Haliaeetus albicilla*). Data materials were collected at Skallelv on the Varanger peninsula in Norway from July 1st to September 5th in 2021 and 2022. I find that the relative abundance of white-tailed eagles was indeed much higher when Pacific pink salmon spawned in Skallelv in 2021 than in 2022, when no spawning occurred. The spatiotemporal synchrony of white-tailed eagles and Pacific pink salmon was observed at several scales, suggesting an aggregational response on part of the highly mobile white-tailed eagle. The aggregation of white-tailed eagles corresponded to the time that an increasing number of Pacific pink salmon had entered the post-spawning stage.

This study has identified the white-tailed eagle as a key driver in the cross-boundary transfer of marine-derived resources from invasive Pacific pink salmon spawning in river systems on the Varanger peninsula in Norway. The white-tailed eagle temporary extended the food supply for the wider community of scavenger, also after post-spawners were naturally contributing to the carcass pool as most were submerged and remained unavailable to terrestrial scavengers. A main aspect of my observations is the suggested importance of white-tailed eagle. This is presented in a model for the cross-boundary transfers of marine-derived energy, nutrients, and organic matter from the Pacific pink salmon that spawns in our northern river systems.

Keywords: Terrestrial, riparian, riverine, trophic linkages, cross-ecosystem boundary transfers, carcass-derived resources, scavenger community, Varanger, Norway, white-tailed eagle, Pacific pink salmon.

Contents

Introduction

Terrestrial arctic ecosystems are low-productive systems with simple trophic structures, where food webs also depend on resource exchanges from across arctic ecosystem boundaries (Gauthier et al., 2011; Giroux et al., 2012; Killengreen et al., 2011). As such, resource subsidies have been recognized to affect the ecosystem structure, function, and regulation in terrestrial arctic ecosystems (Gauthier et al., 2011; Killengreen et al., 2012). The movement of resources through seasonal migrations to Arctic regions, is a key process in linking terrestrial arctic food webs to more productive ecosystems (Giroux et al., 2012). Spawning migrations of anadromous salmonids can transport and distribute marine-derived resources to riparian-, and terrestrial ecosystems through trophic interactions and nutrient dynamics (Helfield & Naiman, 2006). The spawning migrations by anadromous salmonids such as Atlantic salmon (*Salmo salar*) have, unlike Pacific salmons (*Oncorhynchus spp.*), only moderate influence on the terrestrial ecosystem in northern Fennoscandia (Jonsson & Jonsson, 2003). However, the recent invasions by the Pacific pink salmon (*Oncorhynchus gorbuscha*) that spawn in river systems on the Varanger peninsula in Norway, may add additional resources to the terrestrial community of scavengers (Dunlop et al., 2020).

The spawning population of Pacific pink salmon has increased in northern Norway in recent years (Sandlund et al., 2019), with particular increases in 2017, 2019, and 2021 (Berntsen et al., 2018; Berntsen et al., 2020; Berntsen et al., 2022). The spawning migrations of Pacific salmons have, unlike resident salmonids, a large potential to affect terrestrial communities through resource exchanges (Jonsson & Jonsson, 2003). The increasingly larger spawning runs and the rapid expansion of Pacific pink salmon is causing concerns across institutional boundaries and management communities (Hindar et al., 2020), whereof recent research has found no sign of the spawning population having peaked yet (Diaz Pauli et al., 2023). So far, the Norwegian research efforts on Pacific pink salmon has been centred on consequential effects in marine- and freshwater ecosystems, while terrestrial ecosystems have received less attention from both the scientific- and management community (Hindar et al., 2020). Only one study has been published with respect to potential effects in terrestrial ecosystems in Norway (Dunlop et al., 2020). Dunlop et al., (2020) monitored Pacific pink salmon carcasses along a river on the Varanger peninsula in Norway in 2019, whereof the common raven

(*Corvus corax*), hooded crow (*Corvus cornix*), and red fox (*Vulpes vulpes*) were recorded to scavenge on the available carcasses.

From a cross-boundary perspective, the carcasses in Dunlop et al., (2020) were made available to the scavengers by design, as these carcasses were moved from the river and onto elevated riverbanks. The study design had thereby undertaken an ecological function, whereby carcass-derived resources were made available to the wider scavenger community. Such cross-boundary transfers are a central topic within this study, and perhaps most associated with large carnivores foraging on salmonids in riparian ecosystems e.g., in Alaska (Helfield & Naiman, 2006). For other than Dunlop et al., (2020), no additional studies have been published on the terrestrial aspects of Pacific pink salmon in Scandinavia, and our current knowledge offers only limited information on terrestrial implications going forward. There is currently no empirical evidence on potential predators on the Pacific pink salmon that spawn in Norwegian rivers.

An essential step in evaluating the potential for a trophic linkage of the riverine- and terrestrial ecosystem is to assess terrestrial species that may traverse the limnic habitat boundary to forage on spawning Pacific pink salmons within the riverine ecosystem. This could underpin the potential for the terrestrial consumption of carcass-derived resources seen in Dunlop et al., (2020). One such link could be through the white-tailed eagle (*Haliaeetus albicilla*), as they have been recognized to be efficient foragers in both marine- and riverine ecosystems (Myklebust, 2020). Although white-tailed eagles were suggested to be avian scavengers in Dunlop et al., (2020), there is currently no empirical evidence for whether white-tailed eagles may prey or scavenge on Pacific pink salmon in Norwegian river systems. The white-tailed eagle is highly mobile (Duvall, 2022), which make them interesting with respect to a possible functional response on Pacific pink salmon, seeing that high mobility was found to be a key functional trait for an aggregational response to areas with an abundant food source (Gutiérrez-Cánovas et al., 2020).

The main objective of this thesis has been to evaluate the potential for cross-boundary transfers of marine-derived resources from spawning Pacific pink salmon, and with special interest in the white-tailed eagle. In Norway, the biannual occurrence of large spawning runs of Pacific pink salmon (Sandlund et al., 2019), is key in evaluating the response of white-tailed eagles. The shift in prey density may act on the functional trait of white-tailed eagles, which make them good subjects for survey techniques used to derive relative measures of bird abundance over time (Duvall, 2022). During the biannual spawning run the terrestrial community could be assessed in 2021, and then reassessed in 2022 with the absence of spawning Pacific pink salmons. Whereby, the relative abundance of white-tailed eagle could be recorded to make an initial empirical evaluation of their response to the presence of spawning Pacific pink salmons in the river.

In this study I used the biannual presence of spawning runs as a natural case-control design to assess the responses by the terrestrial community to the presence-absence of spawning Pacific pink salmon. Observational data is collected through two consecutive years from the river and adjacent terrestrial ecosystem in Skallelv, a river on the Varanger peninsula in northern Norway. Specifically, I evaluate whether the abundance of white-tailed eagles differ between the two study years, and whether changes in white-tailed eagle abundance is associated with demographic shifts in the spawning population of Pacific pink salmon. Furthermore, I report observations of the wider scavenger community along the river and suggest a model for how nutrients from Pacific pink salmon enter and spread in the terrestrial ecosystem.

Materials and method

Study area and species

The study was conducted along Skallelv, a sub-arctic river system on the east coast of the Varanger Peninsula in Norway (Fig. 1). The study area has a rich topography of glacial- and marine landforms, mostly characterized by kame terraces *(berms of sediments deposited along valley walls)*, eskers *(ridges of stratified sediments deposited throughout the valley)*, and marine terraces *(brims of sediments deposited at former shorelines)*. These features have an influence on river characteristics of the upper, middle, and lower sections of Skallelv. The upper section(s) is mostly characterized by highly braided riffles *(high-velocity, high-turbulence, and shallow streams that frequently diverge and converge)*, with mid-channel banks *(elevated ridges of sediment with flow on both sides)*, irregular backwater *(deeper pools formed by obstructions, such as large boulders)*, and the confluence of smaller tributaries. The middle section is mostly characterized by meandered channels *(series of curved bens with alternating flows of deeper water)*, with point bars *(elevated banks of sediments deposited at the convex bank of meander bends)*, attached bars *(elevated banks of sediments deposited along riverbanks)*, and widen channels of shallow, low-velocity, and low-turbulent water. The lower section is mostly characterized by deeper channels with large pools of slow and low-turbulent water, and with sections of breaks *(riffles of shallow, high-velocity, and high-turbulence waterflows)*. The vegetative structure offers few obstructions for visibility within the study area. Most of the study area is dominated by sub-arctic tundra, although the riparian vegetation has patchy formations of willows (*Salix herbacea*, *Salix phylicifolia*, and *Salix polaris*) along the lower sections of the main river channel and larger tributaries.

The study area has a set of avian, terrestrial, and semi-aquatic species that may prey or scavenge on Pacific pink salmons, whereof the species suggested by Dunlop et al., (2020): (i) the avian species were the white-tailed eagle, common raven, and hooded crow, (ii) the terrestrial species was the red fox, and (iii) the semi-aquatic species were the American mink (*Neovison vison*) and Eurasian otter (*Lutra lutra*). Among these, there is no consensus on whether the white-tailed eagle, American mink, and Eurasian otter prey or scavenge on the Pacific pink salmon in Norwegian river systems.

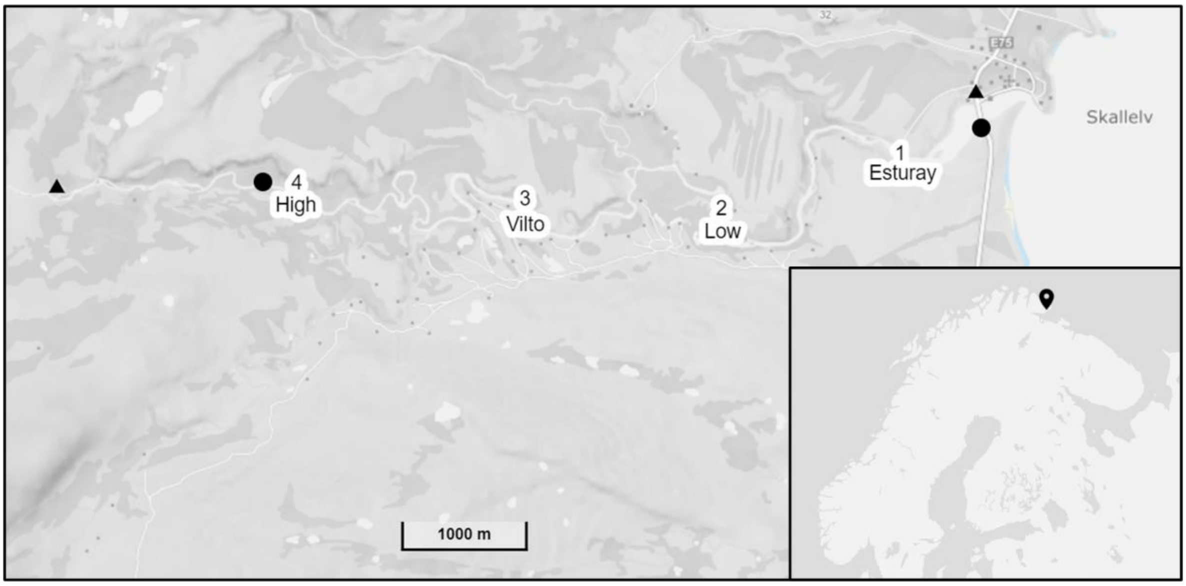

Figure 1. Overview of the study area and the geographical location of Skallelv, a sub-arctic river system on the Eastern coast of the Varanger Peninsula in Norway. The mapped reference points are as follows: The line transect for white-tailed eagles is delineated by triangular reference points, while the expected local range of Pacific pink salmon is delineated by the circular reference points. The numbered site references refer to the river sections used to survey the demographic stages of the spawning run in 2021 (Kartverket, 2023).

Study design

Data materials were collected by two consecutive seasons of line transects, drift counts, and observational surveys made at Skallelv from July 1st to September 5th in 2021 and 2022, whereof spawning Pacific pink salmons were only present in 2021. During the biannual spawning run, the terrestrial community could be assessed in 2021 and then reassessed with the absence of spawning Pacific pink salmons in 2022. The study was designed to detect differences in the terrestrial predator/scavenger community to make an initial empirical evaluation of potential cross-boundary transfers of marine-derived resources through the invasive Pacific pink salmon.

Line transects

These surveys were centred on white-tailed eagle's response to the large spawning runs of Pacific pink salmon in 2021, and used a defined line transect to record the relative abundance of white-tailed eagles from July 1st to September 5th in 2021 and 2022. In these surveys, all observations were made by line transects from an upper point at N70.1967° - E30.1368° (Fig. 1, upper triangle) to the bridge that crosses the estuary at N70.1862° - E30.3284° (Fig. 1, lower triangle). The upper boundary was based on previous drift counts made at Skallelv, and the highest recorded spawning run of Pacific pink salmon in 2019, hence the local range of Pacific pink salmons. The footpath that follows the riverbank of Skallelv was used as the fixed line from which to count the number of white-tailed eagles along the main river channel. Here, the objective was to include each eagle individually and summarize this count as the number of observed white-tailed eagles per day. All transects were traversed forenoon and the same methodology and criteria were used in 2021 and 2022. Certain criteria had to be met before encountered white-tailed eagles were included in the count. Valid observations of white-tailed eagles were recognized as the observed: (i) predation events, (ii) other foraging behavior, (iii) scavenging behavior, (iv) active presence, by posting on bank formations or resting near the main channel, and (v) low flight along the main river channel. The observations outside of these criteria were precluded: (i) the eagles observed further up the valley from the upper triangle, and (ii) high-altitude transit flights that crossed the coastal headland where the study site was located.

Data were collected along the eagle transect 63 days out of 67 from July 1st to September 5th in 2021 and 2022. The rare occasions when the eagle transects were not completed was due to days with personal issues (i.e., July 27th – July 28th, August 13th – August 14th).

Drift counts

The method of drift counts has become a standard method for estimating the abundance of salmonids in streams (Orell & Erkinaro 2007; Orell et al., 2011). In Skallelv, drift counts were used to record abundance, distribution, and demography of Pacific pink salmon from July 1st to September 5th in 2021 and 2022. All drift counts were made by the author, who also had drift counted at the study site for years prior to these surveys and who had experience using the same methodology as that which was used in 2021 and 2022.

In these surveys, all observations in the river were made by drift counts within a stretch that ranged from an upper point at N70.1937° - E30.1792° (Fig. 1, upper circle) to the bridge that crosses the estuary at N70.1862° - E30.3284° (Fig. 1, lower circle). The upper boundary was based on the local range of Pacific pink salmons in 2019. All drift counts were made in environmental conditions that optimized the observer efficiency, and were timed to concur with tidal shifts, as most runs occurred at high tide (Heard, 1991). In 2021, the total drift length varied as the large mass of Pacific pink salmons moved upstream over the season. In July, all drift counts ran through Vilto, whereof most drifts were centred on the high-density areas from below the Low reference point and downstream (Fig. 1). All drift counts also ran through Vilto in August, whereof most drifts were centred on spawning sites from the High reference point and downstream (Fig. 1). In September, all drifts ran the total drift length as Pacific pink salmon had spread to the whole drift range and were also found beyond the upper point of the drift counts (Fig. 1). In 2022, all drift count ran through Vilto, whereof most started from the upper boundary (Fig. 1). A total of 37 drift counts were completed over the course of the study period in 2021, while 20 drifts were made over the course of the study period in 2022.

In 2021 the main objectives of the drift counts were to count the number of Pacific pink salmons in Skallelv and record seasonal change in the spatial and demographic distribution of the population. The successional spawning stages were visually identified by physical characteristics and behavioral changes over the course of the study period in 2021. The pre-spawners were classified by being in the morphological transition phase, where males had not yet developed a pronounced dorsal hump or the curved jaw (see appendix Fig. A1, A), while females had no dig marks on their tail-, anal-, or pelvic fins. Spawners had developed these traits and by the behavioral changes that left marks on both sexes. The male spawners had developed large dorsal humps, covered in bite marks, and the curved jaw with sharp-elongated teeth (see appendix Fig. A1, B). The female spawners had developed an enlarged abdomen, covered in dig marks, with both the tail-, anal-, and pelvic fins being worn. The spawning activity was also audible to the submerged observer, as the female spawners dug nests, called redd. Post-spawners were severely marked by spawning activities and physical deterioration. Both male and female post-spawners were physically reduced and did no longer respond when approached during drift counts. Most males had open wounds, blurred eyes, and pronounced deterioration on areas marked by spawning activities, parts of dorsal fins and entire tail-, anal-, and pelvic fins could be gone (see appendix Fig. A1, E). Most females also had open wounds, blurred eyes, and pronounced deterioration on areas marked by spawning activities, and entire tail-, anal-, and pelvic fins could be gone. The physical state of post-spawners made both males and females drift or roll downstream and made the carcasses challenging to distinguished from late post-spawners. An no adult Pacific pink salmons were observed in 2022.

Observational surveys

On completion of white-tailed eagle counts, the transect line was also used to recognize the bird and mammalian species that may prey or scavenge on Pacific pink salmon in sub-arctic river systems (Dunlop et al., 2020), including spoor signs such as tracks, faeces, and pellets. From mid-August, there were specific sites along the transect line with high activity and spoor signs. These locations were selected to for point observations by binoculars (Swarovski CL 10x25) on the return trip once the daily line transect had been completed. Scavengers were recognized when they were observed: (i) foraging on naturally occurred carcasses of post-spawners, (ii) scavenging on sites with white-tailed eagles, (iii) active presence, by posting on bank formations or on levees near the main channel, (v) when pellets or faeces contained fish shells and bones were found (see appendix Fig. A2, A, B, C). In addition, 51 entrances at 13 separate red fox den sites, within the study area, were monitored for signs of activity.

The valid observations of American minks were recognized as the observed: (i) foraging on naturally occurred carcasses, (ii) scavenging behavior on sites with white-tailed eagles, (iii) active presence, or by spoor signs on bank formations, and (iv) transport of carcasses. Here, a total of 10 attached banks were selected to be monitored for spoor sings on the return trip once the daily line transects had been completed. The Eurasian otter was also suggested by Dunlop et al., (2021). However, signs of Eurasian otter were only sighted once over the course of the study period in 2021.

These surveys were intended to be supplementary for the data acquired through deployment of 10 camera traps planned to revolve across 40 preselected plots at Skallelv, each with a submerged Pacific pink salmon carcass (see appendix Fig. A3). However, cameras were not deployed due to high shifts in water level. The elevated water level impeded the physical mounting of the cameras, and also tracking of terrestrial and semi-aquatic scavengers as most banks-formations became temporary submerged. Hence, for other than the white-tailed eagle, resulting in an observational and non-quantitative approach.

Statistical analysis

Data material from line transects

All statistics and graphics were computed using the open-source software R-studio, R version 4.0.3. (Rstudio, 2020). Count data of white-tailed eagles from the line transects were structured by the dates within each season. The seasonal subsets were then plotted to visually inspect the distribution and spread of the counts of white-tailed eagles within each season, and across years with the presence and absence of Pacific pink salmon. To account for the pattern seen in the initial plot, I chose to analyze seasonal variation in the relative abundance of white-tailed eagles using generalized additive model. In the model assumed Poisson error distribution for the counts, a log link function, and regulated smoothing spline function to capture nonlinear seasonal changes in average counts, using the mgcv package (v1.8-34; Wood, 2011). Here, the counts were first analysed with year and date within the seasons as predictor variables. Year was modelled as a factor (year), while the dates within seasons were modelled as continuous variable (sample day). Using the R package mgcv, the most simple model we fitted included an additive effect of year and sample day, where sample day was modelled using a spline (*gam(count ~ year + s(sampleday, k = 7), family=poisson)*). The more complex model we adopted allowed the non-linear pattern in White-tailed eagle counts to differ between years. (*gam(count ~ year + s(sampleday, by = year, k = 7), family=poisson)*). The models were compared using analysis of deviance and assumptions evaluated using residual plots.

To evaluate whether the seasonal variation in the relative abundance of white-tailed eagles was related to the demography of Pacific pink salmons at Skallelv, I coded the presence and absence of spawning stages at survey dates as binary factors, to relay when each spawning stage were present in the river. We then fitted a generalised linear model to the counts white-tailed eagles in 2021 and used the four factorial spawning stage variables as predictor variables. The best fit model using spawning stages as predictors was compared with a generalised additive model with sample day fitted as a smoothing spline, to evaluate whether the seasonal variation in the relative abundance of white-tailed eagles could be explained by the presence of these spawning stages.

Results

The data materials from line transects made in 2021 and 2022 were used to visualize seasonal variation in the relative abundance of white-tailed eagles at Skallelv (Fig. 2). Here, the predicted regression lines relay the estimated average number of white-tailed eagles observed by day along the transect line (Fig. 2). The relative abundance of white-tailed eagles differed substantially across years with the presence and absence of Pacific pink salmons ($\chi 2 = 8.4$, df = 1.06, $P < 0.01$). Here, the white-tailed eagle had a significant seasonal change in abundance in 2021 ($P < 0.01$), while there was no evidence of a seasonal change in abundance in 2022 ($P = 0.28$) (Fig. 2). In 2021, the initially low abundance of white-tailed eagles in July (mean = 0.38, 95% CI = [0.20, 0.65]) increased over the course of August. August 1st (mean = 0.50, 95% CI = [0.27, 0.95]) to August 20th (mean = 11.27, 95% CI = [9.28, 13.69]) had the largest shift in relative abundance, and remained high to September 5th (mean = 9.09, 95% CI = [6.20, 13.32]) when the study period ended (Fig. 2).

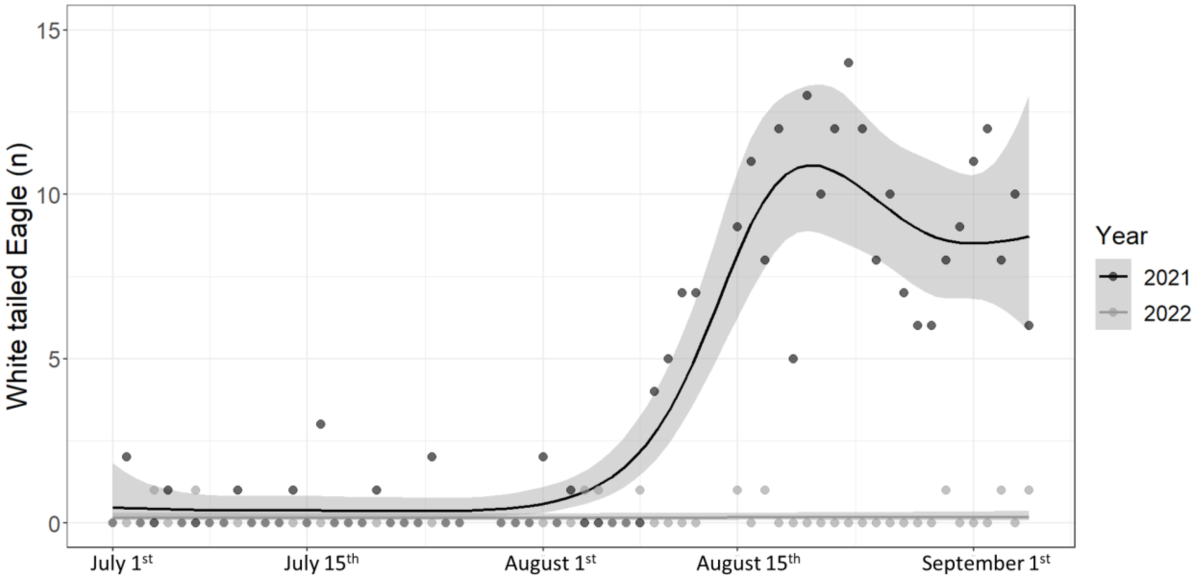

Figure 2. Seasonal variation in the number of observed white-tailed eagles at Skallelv in 2021 and 2022. The number of observed white-tailed eagles is assigned to the y-axis (n), while the temporal scale of study periods was assigned to the x-axis (July 1st – September 5th). The dark grey points represent daily observations in 2021, whereas the lighter grey points represent daily observations in 2022. The lines display the predicted regression lines respectively.

Pacific pink salmons were already present by the time that the first drift count was made on July 1st, and late spawning stages were also present beyond September 5th when the study period ended (Fig. 3). Only the initial and latest drift counts obtain valid counts of Pacific pink salmons, whereby extreme densities of Pacific pink salmons became the main limitation for the accuracy of drift counts (see appendix Fig. A1, C). All drift counts made after July 10th encountered areas with extreme densities of Pacific pink salmons from about 500 meter above the referenced Estuary point and till past the bridge (Fig. 1). Whereas drift counts made after July 20th encountered the extreme densities from about 500 meters below the Low reference and downstream to the Estuary reference point (Fig. 1). The drift counts made between July 22nd and August 1st had all encountered extreme densities from the Low reference point, from where the large masses of Pacific pink salmons started to disperse further upstream on August 2nd (Fig. 1). An approximate count of the spawning population was, however, made when the mass of Pacific pink salmons had moved further upstream and dispersed across separate spawning grounds (August 7th). This count suggests that an approximately 1000 Pacific pink salmons managed to spawn at Skallelv in 2021.

Pre-spawners of Pacific pink salmon were first sighted in mid-July (July 15th), and r spawners were first sighted at the end of July (July 30th) (Fig. 3). The first post-spawners were sighted in early August (August 8th), and the first carcasses were sighted in mid-August (August 15th) (Fig. 3). The abundance of eagles stayed low until the post-spawners started to appear in the river and peaked when post-spawners and carcasses were available (Fig. 3). However, the variation in the entrance dates of pre-spawners and smaller runs that occurred after August 7th, caused substantial overlap in the presence of spawning stages throughout the season (Fig. 3).

Table 1. Model estimates from a generalized linear model assuming poisson error and a log link function for the relationship between observed numbers of white-tailed eagles and with the presence and absence of different Pacific pink salmon spawning stages fitted as binary factors.

Parameter	**Estimate**	**Std. Error**	**p- value**
Pre-spawners	-0.28	0.32	0.39
Spawners	0.22	0.33	0.48
Post-spawners	1.58	0.56	0.0045
Carcasses	1.16	0.49	0.017

The observed number of white-tailed eagles was relatively uncorrelated to the presence of pre-spawners and spawners in the river (Table 1, Fig. 3). However, the number of observed eagles was strongly associated with the presence of post-spawners and carcasses (Table 1, Fig. 3). A model for eagle counts was then fitted with the predictor variable sample day fitted as a smoothing spline, and the factors describing the presence of post-spawners and carcasses fitted in the same model. Compared to a model including only the presence of post-spawners and carcasses as predictors suggested that the presence of post-spawners and carcasses explained all the seasonal variation in eagle counts, and the estimated smooth term for sample day explained little additional variation ($P>0.05$).

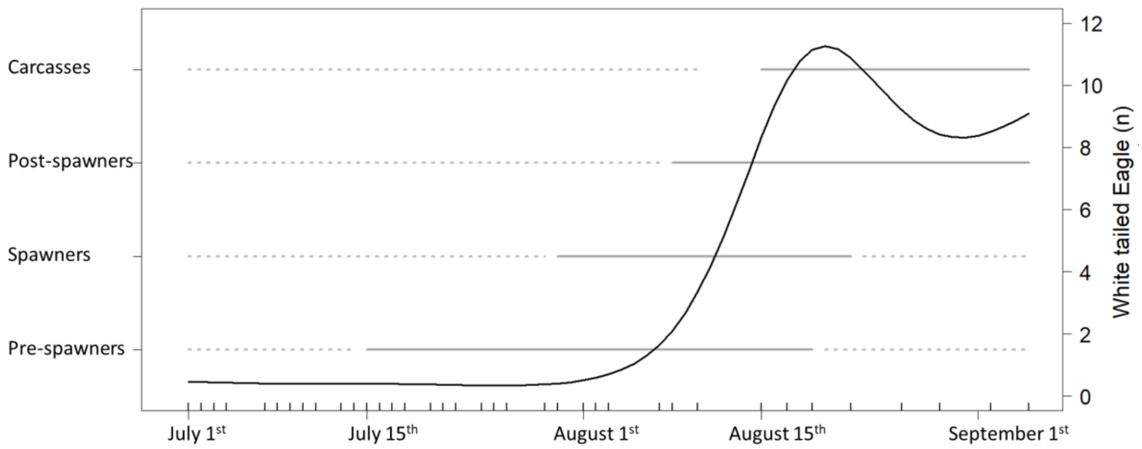

Figure 3. The estimated average abundance of white-tailed eagles plotted together with the time periods the Pacific pink salmon spawning stages were observed at Skallelv in 2021. The predicted regression line for the abundance of white-tailed eagles is displayed as the solid black line, and with its scale assigned to the right y-axis (n). The time periods with observations of the spawning stages of Pacific pink salmon are displayed by grey lines, whereof solid lines reflect presence, and the dotted lines reflect absence of the stage. The temporal scale of the study period is on the x-axis (July 1st – September 5th) The dates of the 37 drift counts done are shown as inverted marks on the x-axis.

During the transect surveys, a total of 254 separate observations of white-tailed eagles were made, whereof 244 were made in 2021. Adult Pacific pink salmons were recognized as a prey item for the white-tailed eagles at Skallelv. The white-tailed eagles were regularly observed to prey on spawners and post-spawners from August 8th and to September 5th when the study period ended (Fig. 4, A). The eagles were observed to wade with their kill ashore, and no eagle were sighted to transport these kills far outside the riparian zone. Over the course of the study period in 2021, most white-tailed eagle observations tended to be clustered on either bank-formations or natural levees near the main river channel (Fig. 4, A, B, C) and these sites tended to be used as foraging and resting sites (Fig. 4, D, E, F). The first foraging sites were recognized during the first two weeks of August, and most were located from the High reference point and downstream to about 300 meters above Vilto (Fig. 1). Additional foraging sites were recognized during the three last weeks of August, most of these were located from the Vilto reference point and downstream to about 150 meter above the Low reference point (Fig. 1). These sites were also located at sections with specific topographic features and waterflow conditions. The repeatedly used foraging sites had either mid-channel banks (Fig. 4, B), point- or attached banks (Fig. 4, E) that were situated in sections of wider river channels with shallow, low-velocity, and low-turbulent waterflows. There were no carcasses found at the repeatedly used resting sites (Fig. 4, C, F, I), while such remains were abundant at the repeatedly used foraging sites from mid-August to September 5th (Fig. 4, D, E, G, H).

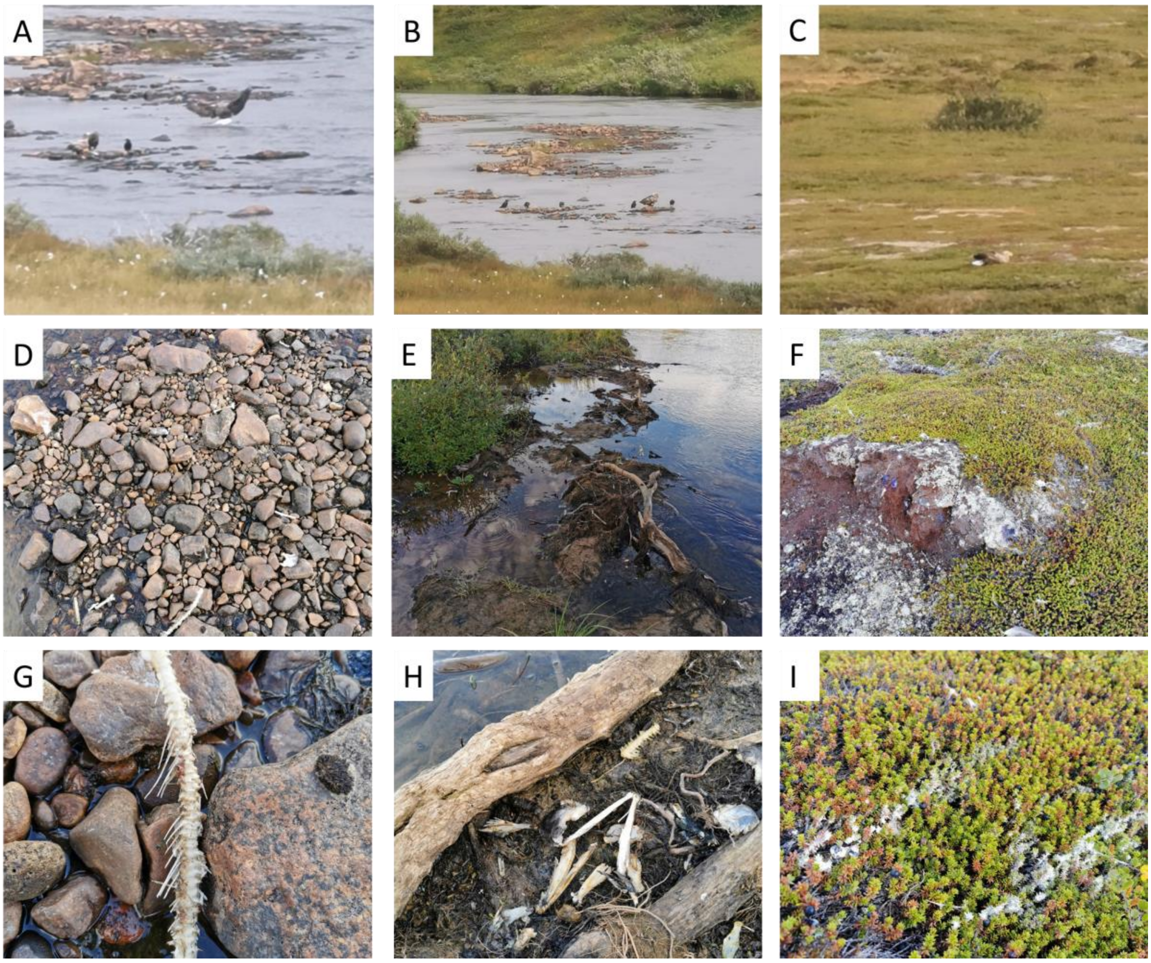

Figure 4. Photo series of valid observations. Picture **A** shows a predation event as one of the three white-tailed eagles strikes a Pacific pink salmon (August 24th); **B** shows a lone white-tailed eagle with five scavenging common ravens (August 26th); **C** shows a white-tailed eagle resting (August 24th); **D** shows a repeatedly used foraging site (mid-channel bank), where carcasses were regularly deposited; **E** shows a repeatedly used foraging site (point-bank), where carcasses were regularly deposited; **F** shows frequently used resting site (natural levee); **G** shows disregarded bones at the repeatedly used mid-channel bank; **H** shows disregarded bones at the repeatedly used point-bank; **I** shows excrements of white-tailed eagle at the repeatedly used natural levee.

Five species, including the white-tailed eagle, were observed to actively scavenge on available Pacific pink salmon carcasses from August 8th and to September 5th when the study period ended. Most sightings were made at the repeatedly used foraging sites where white-tailed eagles had produced carcasses of spawners and post-spawners. These scavengers included, (i) common ravens, (ii), hooded crows, (iii) red fox, and (iv) American mink. Among these, common ravens were perceived to be the most abundant and frequently sighted scavenger. Common ravens were regularly observed to transport smaller pieces (e.g., partial heads, gill lids, jaws, spines) from bank-formations in the river and out of the riparian ecosystem (Fig. 5, A). The observed pattern was that ravens flew longer when chased by others, and then further inland (Fig. 5, B). The red foxes were observed to transport considerably larger pieces (e.g., either single- or multiple whole carcasses at once) from bank-formations in the river and out of the riparian ecosystem. From August 15th, red foxes were regularly observed to cache carcasses at previously unoccupied den sites that was near the main river channel (Fig. 5, C). These den sites then became a secondary source for avian scavengers from August 17th, when both the common raven and hooded crows were observed to aggregate at recently occupied den sites. The American minks were observed to search at repeatedly used foraging sites, and spoors were regularly observed. Although predation by American mink was not directly observed, spoors were found along drag-marks leading to post-spawners that had no sign of predation by white-tailed eagles. In contrast to American minks, the Eurasian otter was only observed once over the course of the study period in 2021 on September 2nd.

Figure 5. Photo series of valid observation; Picture **A** shows the jaw of a male Pacific pink salmon transported out of the riparian ecosystem by avian scavengers, such as the common raven; **B** shows one of the numerous small pieces dispersed onto the sub-Arctic tundra by avian scavengers, such as the hooded crow; **C** shows the entrance of a previously unoccupied red fox den (August 15th).

There were no adult Pacific pink salmons observed in 2022. However, shoals of Pacific pink salmons fry (see appendix Fig. A1, F) were encountered on all drift counts made between July 1st – July 26th. Most observations were made from about 400 meter above Vilto and downstream past the Estuary reference point (Fig. 1). The number of shoals appeared to decrease over the course of July, with only a few shoals sighted on late drift counts in 2022.

The observations of Pacific pink salmon fry in July 2022 came as a surprise. It was therefore no pre-planned methodology for monitoring the impact of these on the food web. However, it was my impression that the abundance of Arctic terns (*Sterna paradisaea*) was higher along the river in 2022 than in previous years, and also Arctic terns seemed to forage higher upstream than in previous years. Although predation by American mink was not directly observed in 2022, they were observed to actively hunt on smaller prey that could be Pacific pink salmon fry.

Discussion

This study has identified the white-tailed eagle as a key driver in the cross-boundary transfer of marine-derived energy, nutrients, and organic matter from invasive Pacific pink salmon spawning in Skallelv on the Varanger peninsula in Norway. The results suggest that the relative abundance of white-tailed eagles was indeed much higher when Pacific pink salmon spawned in Skallelv in 2021 than in 2022, when no spawning occurred (Fig. 2). The elevated abundance of white-tailed eagles was positively linked to the presence of Pacific pink salmon in late spawning stages (Fig.3). Furthermore, the white-tailed eagles seemed to be the only trophic linkage between the riverine- and terrestrial ecosystem, whereby carcass-derived resources from spawning salmonids became available to the wider scavenger community (Fig. 4, A, B). White-tailed eagles also temporary extended the food supply for scavengers, through sustained carcass availability at their repeatedly used foraging sites (Fig. 4, E, D). From here, scavengers, such as common raven and red fox, transported the available carcass-derived resources out of the riparian zone and into the terrestrial sub-arctic ecosystem (Fig. 5, A, B, C).

Although the occurrence of large spawning runs of Pacific pink salmon is relatively new in the sub-arctic river systems in Norway (Berntsen et al., 2018, Berntsen et al., 2020, Berntsen et al., 2022), the white-tailed eagles clearly recognized the spawning run as a new food source. Spawners and post-spawners seemed to be the principal prey items for white-tailed eagles, but also carcasses were consumed. Admittedly, the data supporting a food web link between white-tailed eagles and Pacific pink salmon is based on acquired data from only one river and two years of observations, i.e., no replication. However, the spatiotemporal synchrony of white-tailed eagles and Pacific pink salmon was observed at several scales, suggesting that observed patterns were due to food web interactions between the two species and were not a spurious correlation. The two species co-occurred at the between year level, with high abundance of both species in 2021 and absence or low abundance in 2022. Within 2021, they also co-occurred at the seasonal scale with eagles aggregating when the Pacific pink salmon entered the post-spawning stage in August, when the salmon is easy to catch. The two species also co-occurred at local spatial scales; white-tailed eagles aggregated along the stretches of river with Pacific pink salmon spawning aggregations, typically stretches with shallow water and low current speed. In these areas the white-tailed eagles were observed to kill Pacific pink salmon and wade with their kill ashore. However, it may imply that their foraging was also restricted by the physical characteristics of the stream (e.g., Huxel & Polis, 2013).

The elevated aggregation of white-tailed eagles along the river coincided in time with the presence of post-spawning salmon. This may suggest that the presence of post-spawners was the main attractant for white-tailed eagles, although both spawners and post-spawners were observed killed by eagles. Post-spawners are easy to detect due to white areas of skin, and are probably also easy to catch due to slow responses to disturbance. Spawners may have been bycatch for eagles attracted to post-spawners. Alternatively, the eagles may have shown a slow aggregative response to spawners as well as post-spawners, the main clue being the presence of Pacific pink salmon on the shallow spawning grounds, i.e., the temporal association with post-spawners was the result of a delayed response to spawners. A third factor that may have affected the timing of white-tailed eagle aggregation is that the recreational fishing season for resident salmonoids closed on August 8th in 2021. It resulted in a reduced human-presence along the river in the latter half of August and could impede our perspective on what caused the swift shift in the abundance of white-tailed eagles in 2021. However, it is good reason to suggest that the aggregation could be a result of spawners and post-spawners being more available to predation by the white-tailed eagle. They stayed at the spawning sites in widen channels of shallow, low-velocity, and low-turbulent water flow, while the pre-spawners occupied reaches of high-velocity and high-turbulence water flows (Heard, 1991).

An approximate and qualitative knowledge of feeding links is the required information to construct an initial connectivity food web, herein using observed predation events, scavenging, and co-occurrence as proxies for ecological interactions (Huxel & Polis, 2013). My results suggest that white-tailed eagles were able to capitalize on the pulsed resource of the biannual spawning run through an aggregative behavioural response to adult Pacific pink salmon in August. Furthermore, the white-tailed eagle appeared to be the key component in the transfer of salmon-derived resources from the freshwater into the terrestrial sub-arctic ecosystem, the white-tailed eagles provided the trophic link between the riverine- and terrestrial ecosystem (Fig. 6, P^1, E^1). As such, the white-tailed eagle extended the food supply for the other scavengers (Fig. 6, R^1, S^1). The salmon carcasses brought ashore by white-tailed eagles were dispersed further inland by the other scavengers, particularly, the common raven and red fox (Fig. 6, E^2). Natural carcasses also became available along the riverbanks, but as most natural carcasses remained submerged, they remained unavailable to the terrestrial scavengers (Fig. 6, R^2, S^2, E^3).

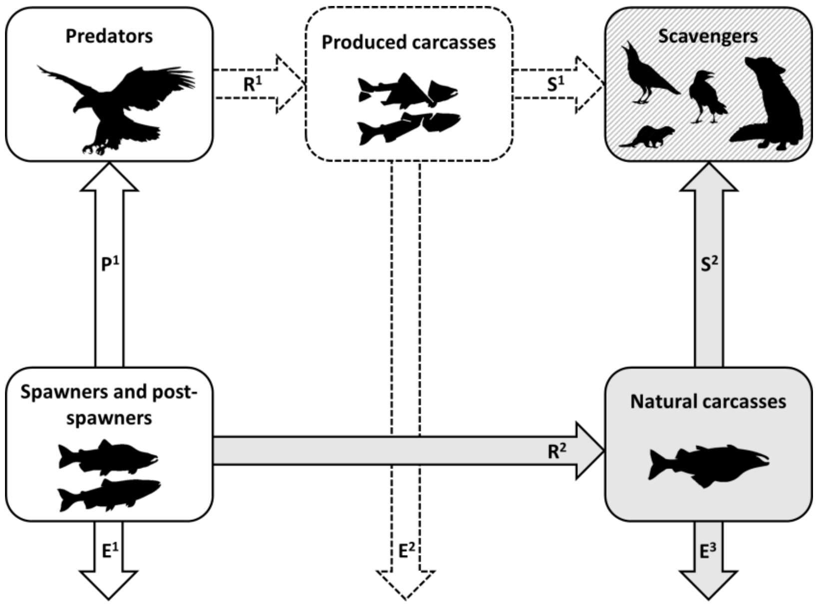

Figure 6. Suggested model for the cross-boundary transfers of marine-derived energy, nutrients, and organic matter from Pacific pink salmon spawning in rivers in northern Norway. The natural conversion of marine-derived resources are represented by solid arrows, while carcass-derived resources made available by white-tailed eagles have dotted arrows; $\mathbf{P^1}$ is predation on spawners and post-spawners by white-tailed eagles; $\mathbf{R^1}$ is the production of carcasses by predators; $\mathbf{S^1}$ is scavenging on produced carcasses by common raven, hooded crows, red fox, and American mink; $\mathbf{R^2}$ are the natural carcasses production by spawned adults; $\mathbf{S^2}$ is scavenging on naturally occurred carcasses by red fox, common raven, and crows; while $\mathbf{E^1}$, $\mathbf{E^2}$ and $\mathbf{E^3}$ are the ephemeral resources of remaining biomass.

From a cross-boundary perspective, the carcasses in Dunlop et al., (2020) were made available to the scavengers by design, as these carcasses were moved from the river and onto elevated riverbanks. In this study, white-tailed eagles had assumed an ecological function, whereby carcass-derived resources became available to the wider scavenger community. Naturally, the scavenger species recorded in Dunlop et al., (2020) were the same species using the carcasses made available by white-tailed eagles (Fig. 4, D, E). The comparability of our results may form a clear rational to argue that these scavengers seemed highly dependent on resources being moved across a restrictive habitat boundary, that appeared to be the land-water interface for most scavengers observed at Skallelv (e.g., Huxel & Polis, 2013). The facilitatory dependence by scavengers further reinforces the perception of white-tailed eagle as a key driver in the cross-boundary transfers of Pacific pink salmon.

The white-tailed eagles generated patches with carcass-derived resources at the repeatedly used foraging sites along the stream, much like the patches generated by Alaskan grizzly bears (*Ursus arctos horribilis*) forging in salmonids systems (Gende et al., 2004). The foraging behaviour of white-tailed eagles created localized abundance of carcass-derived resources, as prey-remains were frequently deposited onto elevated riverbanks along the main river channel at Skallelv. These patches attracted avian- and terrestrial scavengers that frequently visited these sites to scavenge, whereof the common raven and hooded crows usually attended foraging sites in groups (Fig. 4, B). The facilitatory role of white-tailed eagles appeared to temporary extend the food supply for the wider community of scavenger, much like the Alaskan grizzly bears, and may cause similar localized effects (Johnson-Bice et al., 2022). The specific foraging sites may experience both direct- and indirect effects including degradation of the riparian vegetation and accumulation of biochemicals (Fig. 4, E, H, Fig. 6, E^1). Interestingly, the white-tailed eagles and the wider functional group of scavengers had contrasting functional traits that may lead to spatially separated indirect effects through their distinctive movement of resources. The white-tailed eagles generated patches of prey carcasses at foraging sites along the main river channel, and no white-tailed eagles were sighted to transport these kills far outside the riparian zone (see appendix Fig. A1, D). In contrast, smaller carcass-pieces were scattered inland by common raven and hooded crow, while larger pieces were cached by red foxes at den sites near the main river channel (Fig. 5, A, B, C, Fig. 6, E^2). Avian scavengers were regularly sighted to aggregate at such den sites in Skallelv, possibly searching for available remains of Pacific pink salmon carcasses that were cached at den sites (Gharajehdaghipour & Roth 2018) and utilizing these sites as a secondary foraging site (Zhao et al., 2021).

The detection of shoals of Pacific pink salmon fry throughout July 2022, was unexpected. The established knowledge has been that Pacific pink salmon fry leave the river in early spring (Heard, 1991). One reason for this discrepancy could be linked to the behaviour of the Pacific pink salmon fry. The diel downstream migration pattern of Pacific pink salmon fry has been found to be highly influenced by a setting sun, whereof the downstream migration occur as a series of successional stages shortly after sunset (Yamada et al., 2022). In the study area in northern Norway there is midnight sun from May 15^{th} – July 27^{th} i.e., there is no sunset before the end of July. Whether this absence of sunsets influenced the diel downstream migration pattern of Pacific pink salmon fry at Skallelv is beyond this study. However, Arctic terns and possibly the American mink preyed on the Pacific pink salmon fry present at Skallelv in July 2022. Of these, only the American mink has the potential to be subsidized by the Pacific pink salmon every year, as it could forage on both spawning adults and fry (see appendix Fig. A4)

The spawning population is projected to increase further (Diaz Pauli et al., 2023). This makes the terrestrial implications through Pacific pink salmon increasingly relevant, also considering the projected impact of climate change in Norwegian terrestrial arctic ecosystems and on endemic species (Pedersen, 2021). The Pacific pink salmon is subject to predation by white-tailed eagle and represent a new subsidy to the terrestrial ecosystem in northern Norway. For other than Dunlop et al., (2020), no additional studies have been published on the terrestrial aspects of Pacific pink salmon in Scandinavia, and the contribution by this study offers no measure on ecological effects. Instead, it suggests that the Pacific pink salmon subsidies that enter terrestrial ecosystem are likely to have a positive impact on primarily boreal generalist predator/scavenger species, while negative impacts are likely to cause indirect effect on the regional biodiversity. The white-tailed eagle is for instance known to impact nearby sea bird colonies (Anker-Nilssen et al., 2023). The timing of these inputs may also act on the overall outcome, as autumnal subsidies may improve the winter survival of the red fox and could affect their reproduction if carcasses reappear in spring (Killengreen et al., 2011). Red fox is known to have negative impacts on the resident Arctic foxes (*Vulpes lagopus*) (Elmhagen et al., 2017), that are already under increasing pressure by the impacts of climate change (Pedersen, 2021).

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Scandinavian breagle (Ursus haliaeetus)

Appendix

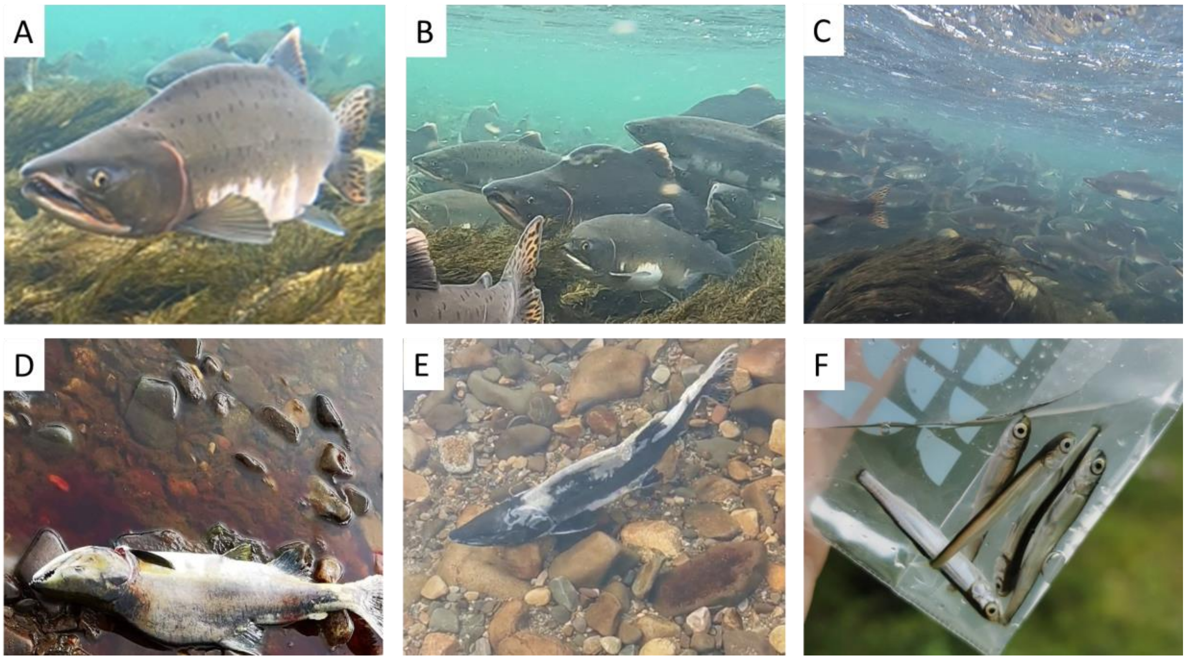

Figure A1. Photo series of valid observation; Picture **A** shows a male pre-spawner that has not yet developed the pronounced hump and curved jaw; **B** shows a male spawner that had a bleeding bite mark on his large hump and where the curved jaw with sharp-elongated teeth was pronounced; **C** illustrates the extreme density of late pre-spawners encountered on drift counts at Skallelv in July in 2021. illustrates the extreme densities observed in 2021; **D** shows a carcass on a mid-channel bank in Vilto; **E** shows a male post-spawner with open wounds, blurred eyes, and pronounced deterioration on areas marked by spawning activities, with partial tail fins and dorsal fins being gone; **F** shows five Pacific pink salmon fry's caught at Skallelv in July. Note their counter-shaded coloration.

Figure A2. Photo series of valid observation; Picture **A** shows a pellet deposited by common raven on a mid-channel bank; **B** shows a pellet deposited by common raven on top of a natural levee; **C** shows a pellet deposited by common raven on a repeatedly used resting site.

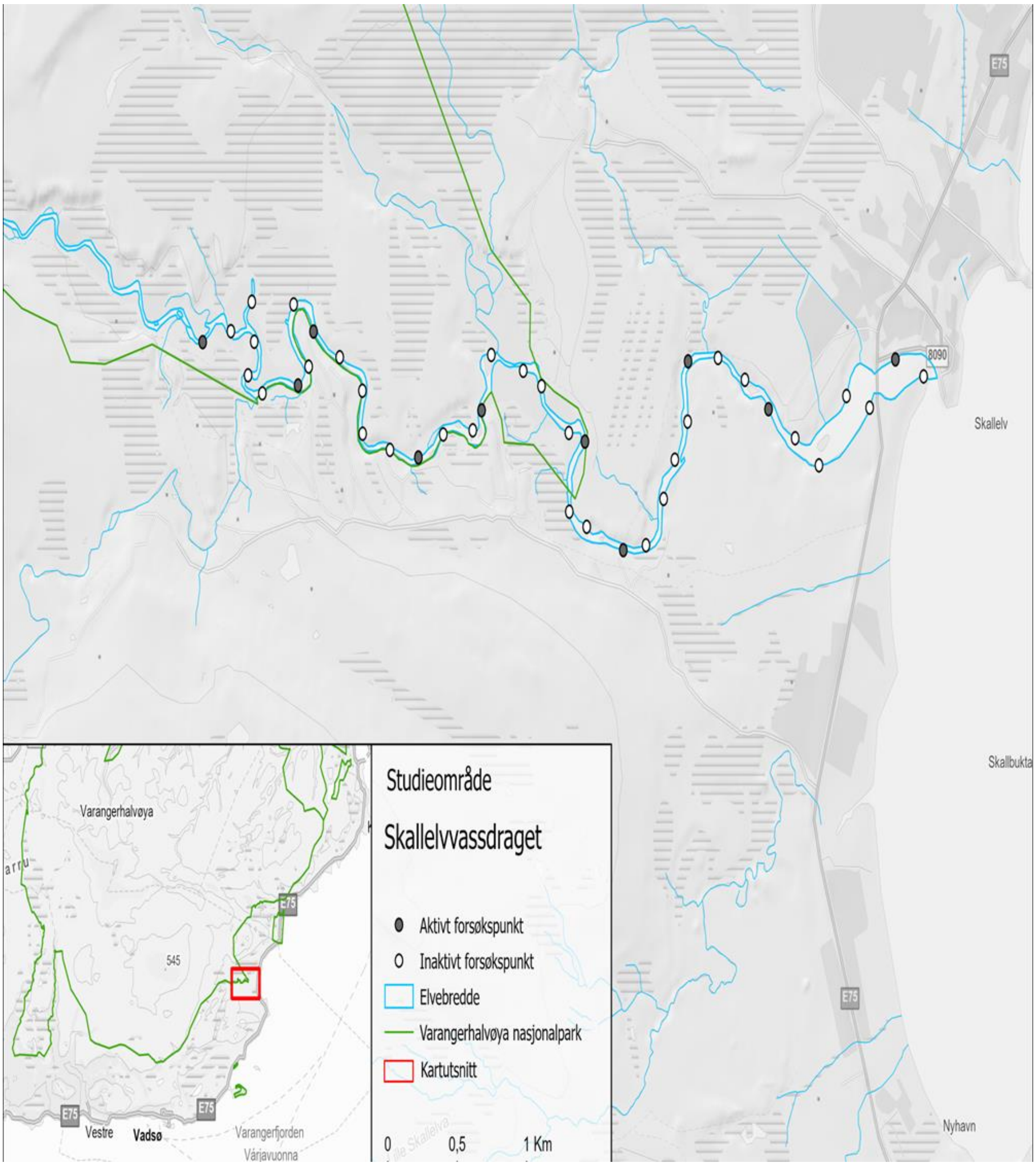

Figure A3. The mapped plots for the deployment of 10 camera traps to systematically revolve across 40 preselected plots at Skallelv, each with a submerged Pacific pink salmon carcass, Whereof the black points mark a set of active sites, while the white point mark the three sets of inactive sites. The permits for this setup were approved by the Varanger national park board in spring of 2021 (Arkivsaksnr: 2021/5234-4).

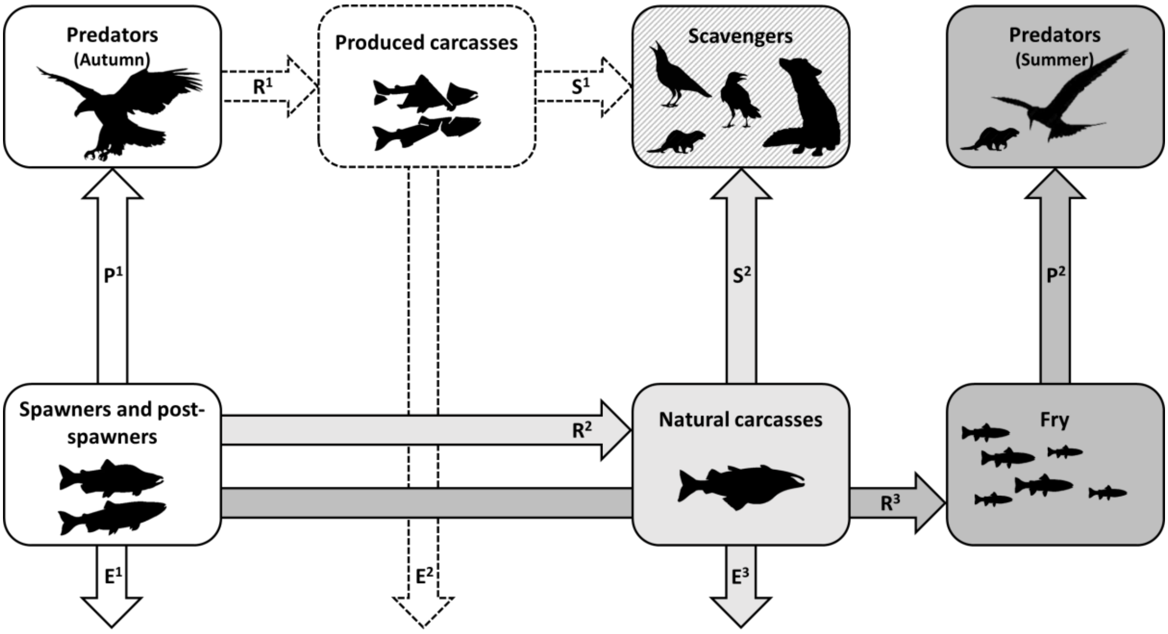

Figure A4. An initial suggestion for the cross-boundary transfers of marine-derived energy, nutrients, and organic matter from invasive Pacific pink salmon on the Varanger peninsula in Norway in 2021 and 2022. The natural conversion of marine-derived resources are represented by solid arrows, while carcass-derived resources made available by white-tailed eagles have dotted arrows; $\mathbf{P^1}$ is predation on spawners and post-spawners by autumn predators (white-tailed eagles); $\mathbf{R^1}$ is the production of carcasses by autumn predators; $\mathbf{S^1}$ is facultative scavenging on produced carcasses by scavengers (common raven, hooded crows, red fox, and American mink); $\mathbf{R^2}$ are the naturally occurring carcasses of spawned adults; $\mathbf{S^2}$ is obligate scavenging on naturally occurred carcasses (red fox, common raven, and crows); $\mathbf{R^3}$ is the production of fry; $\mathbf{P^2}$ is predation on fry by summer predators (Arctic tern and possibly American mink); while $\mathbf{E^1}$, $\mathbf{E^2}$ and $\mathbf{E^3}$ are the ephemeral resources of remaining biomass.