Group size affects predation risk and foraging success in Pacific salmon at sea

Anne Y. Polyakov

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Committee:

Andrew M. Berdahl

Thomas P. Quinn

Gordon W. Holtgrieve

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Abstract

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Anne Y. Polyakov

Chair of the Supervisory Committee

Andrew M. Berdahl

Quantitative Ecology and Resource Management Program

Grouping (schooling, flocking, herding) is broadly distributed across taxa and environments, and is particularly common in marine fishes. A rich body of theory outlines ways in which grouping can enhance individual fitness, especially by improved predator avoidance and foraging efficiency. However, such theories are difficult to test in the wild, especially in marine environments where observing individuals is challenging, and quantifying predation risk or foraging success is often impossible. To overcome these difficulties, I analyzed a multi-decadal data set from sampling of Pacific salmon (*Oncorhynchus spp.*) in the ocean. Across all species, individuals in larger groups had lower risk of predator attack, inferred from wounds on surviving fish. Within groups, outliers (smaller and larger fish) were disproportionately attacked by predators, suggesting that collective predator avoidance resulted from a confusion effect. For slower growing species, individuals in larger groups had lower foraging success, indicating that schooling presented a trade-off between predator avoidance and resource consumption. In contrast, for faster growing species, individuals in larger groups had higher foraging success, indicating that this trade off may not exist and individuals in larger groups may even benefit from collective foraging. These results support long-standing theories on the benefits of group living that have rarely been tested in wild populations, and challenge earlier assertions that adult salmon do not school in the marine environment. Ultimately, these results indicate that survival and growth are group-size dependent and thus understanding the relationship between group-size distributions and population size may be critical to unraveling ecology and population dynamics for these and other marine fishes.

Introduction

Grouping is a well-established evolutionary strategy across taxa and environments that confers a wide range of ecological benefits to members, such as predator avoidance, foraging success, locomotion efficiency, and social and genetic advantages (Ioannou 2017). One key benefit of grouping is the increased ability of individuals to avoid predators, or reduced predation risk (Lima and Dill 1990, Wrona and Dixon 1991, Cresswell 1994, Lima et al. 1999, Cresswell and Quinn 2011, Creel et al. 2014, Creel and Christianson 2014). Several mechanisms have been proposed to explain why grouping decreases predation risk. One mechanism is the "encounter dilution effect," where the probability that any single individual is selected for attack decreases with larger groups (Foster and Treherne 1981, Ioannou 2017). In this scenario, an individual has an advantage in a larger group as long as the probability of detection and the probability of attack do not increase with group size (Turner and Pitcher 1986). A second mechanism is the "predator confusion effect," where a predator will experience more difficulty picking out individual prey in a group of moving targets due to visual sensory overload and associated cognitive constraints (Milinski and Heller 1978, Landeau and Terborgh 1986, Krakauer 1995, Schradin 2019). A third mechanism is the "many eyes effect," which theorizes that the probability of spotting an incoming predator is increased when the task of scanning the environment is spread out over many individuals in the group (Lima 1995, Olson et al. 2015, Ward et al. 2011). This group vigilance also allows more time for individuals to feed, because one individual in the group may forage while others watch for predators. The many eyes effect is applied in a similar manner to explain the benefits of grouping for foraging success: the collective task of searching for food is spread out over many individuals, minimizing individual energy expenditure (Partridge et al. 1983, Pitcher et al. 1982). In fact, grouping is an important strategy utilized by some animals to maximize foraging success (Krause and Ruxton 2002). Group hunting can increase foraging success by helping predators capture large prey that would be difficult for an individual to capture alone (Creel and Creel 1995, Courchamp and Macdonald 2001). Grouping can also allow individuals to use social information to make faster and more accurate decisions about locating and selecting food resources through collective foraging (Torney et al. 2011). Grouping can increase individual locomotion efficiency when traveling together (e.g., birds: Biro et al. 2006, fish 1995, Hemelrijk et al. 2015), and provide social and genetic benefits by allowing increased access to mates (Partridge et al. 1980).

However, grouping can also incur associated costs. One major cost of grouping is increased resource competition between group members, which can lead a reduction in per capita consumption as resources are distributed among more members (Eggers 1976, Chapman and Valenta 2015, Ford and Swearer 2013, Vijayan et al. 2012). In this scenario, an individual may be more likely to find food as part of a group but be less likely to consume that food (Moody and Ruxton 1996, Beauchamp 1998). Grouping can elevate predation risk by increasing the probability of detection by predators, due to larger groups being more conspicuous because of their increased size (Ioannou 2017). Grouping can also lead to lower individual reproductive and development rates due to resource competition (Borries et al. 2008).

The costs and benefits of grouping are dynamic and can be affected by a number of environmental and biological variables. Habitat can provide a refuge from predators and thus reduce the risk of predation (Bugert et al. 1991, Ruiz et al. 1993, Sih 1997, Beauchamp 2007), allowing for more time spent foraging (DeCesare et al. 2014). Group size and competition within a refuge site can also affect the foraging success of individuals (Orrock et al. 2013, Creel et al. 2014). Costs and benefits of grouping, especially those affecting foraging success, can also change with age, species, ontogeny, among other life history traits. Larger fish could experience lower predation risk from gape-limited predators (Urban 2007) and variations in the strength of competition (Werner and Anholt 1993, Cameron et al. 2007). For some species, the benefits of grouping could become negligible with age (Hintz et al. 2018). Ontogenetic-related changes in predation and competition may strongly affect the costs and benefits of grouping and the relationship between grouping and foraging success or predation risk.

The interplay between the costs and benefits of grouping on a single trait, such as foraging success, can be summarized into four general hypotheses (Beauchamp 1998, Beauchamp 2013; Figure 1). Increasing group size might not affect a trait such as foraging success, the null hypothesis (Figure 1A). Larger group sizes might increase foraging success, potentially due to the many-eyes effect (Figure 1B). Increasing group size might decrease foraging success because of competition (Figure 1C). However, typically, there will be costs that balance out the benefits of grouping at some group size, so the most commonly observed relationship is Figure 1D. Figure 1D illustrates a group-mediated interplay between the costs and benefits of grouping, where larger groups increase foraging success up to a certain group size threshold, after which competition outweighs collaboration (costs outweigh benefits) and foraging success decreases for larger group sizes (Figure 1D). The same concepts can be applied to the costs and benefits of grouping on predation risk, where the costs of grouping (such as increased predation risk due to increased detection) can balance the benefits of grouping (such as decreased predation risk due to the confusion effect) at a certain group size threshold. There could also be tradeoffs between the costs and benefits of grouping across traits. For example, if grouping increases an individual’s ability to avoid predators but decreases its foraging success due to competition, the tradeoff could affect whether the individual continues to group at some group size threshold, which would in turn affect predation risk and foraging success of other individuals.

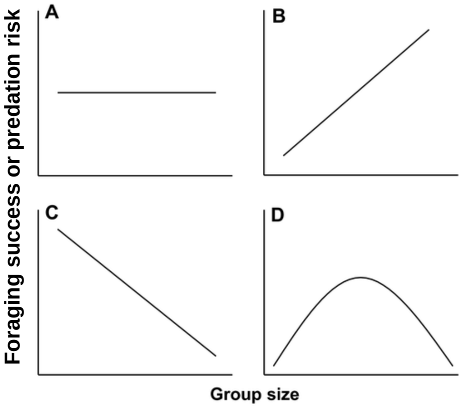

Figure 1. Four general hypotheses for the effect of group size on a single ecological trait, such as foraging success or predation risk.

Although the development of theoretical concepts associated with grouping has made considerable progress, we still do not have a full understanding of the factors that regulate foraging success and predator avoidance in wild animal populations that exhibit grouping. Much of the research on this topic consists of experimental studies, which tend to use a few individuals and thus may not represent the natural variation in group sizes that exist in the wild for many species (Hintz and Lonzarich 2018). There are few observational studies of the effects of grouping on predation risk and foraging success in wild animal populations (Handegard et al. 2012, Hintz and Lonzarich 2018, Rieucau et al. 2015), especially studies incorporating a variety of life stages (Persson and Stenberg 2006). Large, empirical studies are important to test, validate, and refine theoretical predictions. This challenge is especially pertinent in open marine environments, where grouping (schooling) is extremely common but quantifying behaviors and outcomes is notoriously difficult (Hilborn 2002).

Although schooling tendencies of juvenile salmon migrating to sea have long been known (e.g., experimental: Hoar 1958; field: Johnson and Groot 1963), the literature provides some contradictory conclusions about the schooling behavior of salmon in the ocean. Quinn (2018) described salmon schooling as facultative rather than obligate; aggregations of salmon occur more frequently than actual traveling groups of fish in a polarized formation. Consistent with this conclusion, analysis of low frequency acoustic imaging indicated that most salmon were alone or in groups of two to four individuals (Nero and Huster 1996), and analyses of catches in high-seas gillnets and of echogram images (Takagi et al. 1981) suggested that shoals tended to be composed of a few tens of individuals and, most often, of pairs of fish. Other studies suggest that particular stocks of salmon have no tendency to school as a group in the ocean (Royce et al. 1968). Yet other sources cite that schooling behavior follows a gradient, with schooling behavior becoming less pronounced throughout the pelagic marine stage of the salmon life cycle, and an increase in schooling behavior as maturing fish approach coastal waters for spawning migrations (Groot and Margolis 1991, Ch. 2). Groot and Margolis (1991, Ch. 2) also mention that schooling of specifically pink salmon is less structured and more loosely organized in open ocean waters than in coastal waters or rivers. Other sources mention outright that pink salmon do not school in the ocean, because they are active visual feeders with individual (not schooling) behavior (Beamish 2018, Ch. 1). Beamish (2018, Ch. 2) also states that chum salmon do not employ obligate schooling, or even loose schools that break up when it is advantageous to do so, and that there was no evidence of particular stocks of coho salmon schooling together (Beamish 2018, Ch. 4). However, more recent analytical approaches to large purse seine data sets from the North Pacific Ocean have shown that salmon are not distributed randomly and were aggregated in time and space across the ocean (Berdahl et al. 2016a). The three species showing strongest aggregation tendencies (pink, chum, and sockeye) are also the most abundance species of Pacific salmon, and those with the strongest schooling tendencies and least aggressive behavior as juveniles (Hoar 1958b, Hutchinson and Iwata 1997). For this analysis, I assumed that salmon were grouping in the ocean, with some species sorting within groups.

I analyzed the benefits and costs of schooling on foraging success and predation risk using catch records from a multi-decadal program of scientific sampling of Pacific salmon. I estimated foraging success using the fraction of fish in each set with some level of stomach fullness. For this measure, I assumed that stomach fullness was a direct result of foraging success. Using stomach fullness as an empirical measure of foraging success is a typical procedure (Hammock et al. 2019, James et al. 2020). I estimated predation risk using the fraction of fish in each set with predator wounds to define the probability of predator injury for an individual fish. Predation risk is generally defined as an individual’s propensity to be predated upon by another organism (Pettorelli et al. 2015). However, predation risk is notoriously challenging to measure in natural environments and is typically inferred using indirect measures such as changes in habitat use or changes in prey foraging behavior (Schmitz et al. 1997, Heithaus and Dill 2002, Valeix et al. 2009), rather than empirical measures of predation risk such as predator attack rate or direct mortality (Brodie 1993, Marini et al. 1995, Stuart-Fox et al. 2003). Direct, empirical measures of predation risk in the field are thus important to support conclusions from such assumptions. This study provided an empirical measure of predation risk by recording the number of individual fish with observable predator injuries and thus, the number of fish that had been attacked unsuccessfully and injured by predators. Overall predator attack rate can be separated into three possible scenarios. A predator can attack a prey but the prey escapes without injury. A predator can attack a prey but the prey escapes with an injury. A predator can attack and kill a prey, leading to direct mortality. I assumed that the probability of these three scenarios were positively correlated. More specifically, I assumed that the probability of direct mortality by a predator increased with the probability of injury by a predator (in other words, there was an increasing relationship between the number of fish wounded and the number of fish killed in an attack). However, even unsuccessful predator attacks that lead to injury are costly and can lead to decreases in individual fitness through decreased mobility, ability to acquire food, and increased risk of subsequent attack by predators, which often target injured prey (Crook et al. 2014). Thus, I also assumed that increasing number of fish with predator injuries directly correlated with increased mortality of those individuals. In other words, injured fish had a higher probability of mortality.

I hypothesize that across all species, grouping will at least initially increase foraging success due to mechanisms such as collective foraging. I hypothesize that the costs of grouping will outweigh the benefits of grouping for successful foraging after a particular group size threshold, and individual foraging success of group members will decrease in larger groups due to increased competition (Figure 1D). I hypothesize that, across all species, grouping will decrease predation risk (Figure 1C) due to established mechanisms such as the confusion effect and the many-eyes effect. I expect that the costs of grouping will not outweigh the benefits of grouping for predation risk with increasing group size, because increased probability of detection by predators for larger groups will be unlikely in the large expanse of the open ocean. If there is a group size threshold where grouping costs outweigh grouping benefits for predation risk, I expect to find it at very large group sizes (if those exist). Finally, I hypothesize that the effects of grouping on predation risk and foraging success will be muted or substantially reduced for older and larger fish individuals.

Methods

Site and Data Description

I used Pacific salmon catch and specimen data collected during salmon tagging research by the University of Washington’s Fisheries Research Institute (FRI) in 1956-1978, 1980, and 1982 and during cooperative US-USSR (KamchatNIRO, Petropavlovsk-Kamchatsky; TINRO, Vladivostok) salmon tagging research in 1983-1991. These efforts followed the same protocols and thus are fully comparable. Data were collected across the Subarctic North Pacific Ocean, including the Gulf of Alaska, Bering Sea, and Aleutian Islands. Sampling also occurred in the northeastern North Pacific (south of the Gulf of Alaska; i.e., south of 50°N latitude) and in the central and western subarctic North Pacific south of 50°N latitude. To capture salmon for tagging, research vessels deployed primarily purse seines (n = 4330 sets) (but also gillnets (n = 24), longlines (n = 401) and rope trawls (n =10), mostly from 1965-1991 and between April and September, with no sampling in November and December. Total catch size (number of fish) for each of six salmon species - sockeye (*O. nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), chinook (*O. tshawytscha*, and steelhead (*O. mykiss*) was recorded, among other variables. Approximately 50% of all catches were subsampled for biological data and individual fish measurements, including species, length, weight, age, sex, maturity, stomach fullness, and presence of wounds inflicted by predators. Age was determined from annual growth patterns on scales. I limited analysis to data from purse seines because those nets surround and capture a discrete volume of seawater (Hartt 1975), such that catch size is a reliable measure of local density and a reasonable proxy for group size, unlike other gear such as gillnets or longlines that are deployed over much larger distances and longer periods (Berdahl et al. 2016a). After initial data cleaning, I selected only purse seine sets rated after net retrieval as “excellent haul effectiveness," which removed purse seines with net tears and other issues that reduced effectiveness. Selecting those purse seines with excellent haul effectiveness and sub-sampling of individual fish resulted in a total sample size of 2407 sets that caught 69,422 fish. For the stomach fullness analysis, I selected only data for which stomach volume categories (empty, trace, medium, full, distended) were recorded (461 purse seines of 3,913 fish). For the predator injury analysis, I selected data for which predator injury (injury or no injury) was recorded (1303 purse seines and 46,588 total fish). I analyzed data for the four most common salmon species in the catch records: pink, sockeye, coho, and chum. I used the species-specific catch per set of the net as the measure of local density or group size but obtained similar results using total rather than species-specific catches. These data, collected over decades and on multiple species, providing a rare opportunity to investigate the way in which group size mediates predation risk and foraging success in a pelagic environment. Importantly, all data were collected blind with respect to the current purposes and so observer bias is highly unlikely.

A wide variety of potential predators caught in purse seines alongside salmon, including soupfin shark (*Galeorhinus galeus*), longnose lancetfish (*Alepisaurus ferox*), blue shark (*Prionace glauca*), Arctic char (*Salvelinus alpinus*), salmon shark (*Lamna ditropis*), Dolly Varden (*Salvelinus malma*), daggertooth (genus *Anotopterus*), and spiny dogfish (*Squalus acanthias*), among others. Marine mammal predators were also observed near many of the purse seines, including whales, seals, and porpoises. Data showed that 57% of purse seines that recorded bycatch data contained potential salmon predators within catches and/or recorded marine mammals observed nearby.

Statistical Analyses

Predator Injury

I used a logistic regression model to predict the probability of observing a predator wound (binary response variable) for varying species and total catch size (continuous predictor variable), varying relative size (size/mean size per catch), and raw body size values (independent of the mean size of others in the group) for each salmon species. Predator wounds were predatory-specific injuries, as distinguished in the data from fishing-related injuries. I included covariates of sex, length, distance of catch to the nearest shore (km), and a random effect of purse seine and year. I used an information-theoretic approach for model selection as a measure of model parsimony with Akaike's information criterion (AIC). For the relative size models, I ran a piece-wise logistic regression model. I plotted the probability of observing a predator injury as a function of group size and relative size alongside appropriately binned empirical data, and I plotted the probability of observing a predator injury as a function of group size for different lengths. I binned empirical data by dividing the full range of group sizes into evenly spaced bins. For each bin, I calculated the average proportion injured (sum of predator injuries/number of fish), the average group size that those fish were in, and the standard deviation of the data using $\sqrt{\frac{p(1-p)}{n}}$, where p is the average proportion injured. I assumed species catch size was a proxy (reliable indicator) for group size or local density. I ran these models for both species catch size and total catch size. For species catch size, I ran these models for all group sizes but because many larger groups had no predator injuries, I presented truncated figures for each species focusing on smaller group sizes. Due to low sample size, chinook (631 fish; only 2 with predator injuries) and steelhead (25 fish; none with predator injuries) were excluded from the analysis.

Stomach Fullness

I ran three sets of models to understand the effect of group size on stomach fullness for each salmon species. Stomach volume categories were not quantitatively measured or qualitatively standardized among the agencies conducting the shipboard examinations over the 40-year study period. Therefore, the only fully reliable variable was the “empty” stomach fullness category, whereas all other levels (“trace”, “medium”, “full”, and “distended”) were visually estimated. To best utilize the data, I ran three sets of predictive general linear mixed models to quantify the effect of group size on stomach fullness for each species. I included covariates of length, sex, age, distance to shore, and time of day in the models, as well as random effects of seine and year for each species and used AIC as a measure of model parsimony.

For the first set of models, I re-categorized the stomach fullness response variable into two binary categories – empty and non-empty. I then used a logistic regression model to predict the probability of observing a non-empty stomach for varying total species catch size for each salmon species. This model accounted for the lack of standardization in the stomach fullness categories during the study by re-grouping the data into categories that were more certain to be accurate (identifying an empty stomach versus a non-empty stomach). I plotted empirical data alongside the model fit by using appropriately selected bins for the data. I also plotted model predictions for varying lengths (a proxy for size) for each species. I ran these models for total group size in addition to species group size. I fit models for each species using the stats package in R (version 3.5.0).

In the second set of models, I used a generalized ordinal logistic regression, or partial proportional odds (PPO) model, to predict the probability of observing a particular level of stomach fullness (ordinal response variable) for species catch size and total group size for each of the four species. I fitted this model for each species using the VGAM package in R (Yee 2015). The PPO model is similar to the more commonly known ordinal logistic regression, or proportional odds (PO) model. The PO model is used to estimate the cumulative probability of being at or below a particular level of a response variable, $p_k = P(Y \leq k)$ for $k = 1,2, \ldots, K$, where K is the number of distinct response categories in the ordinal response variable Y. We predict and model the log odds ratio, or logit(), and the model is written as:

$$log\left(\frac{p_k}{1-p_k}\right) = \alpha_k + \beta_k X \text{ for } j = 1, \ldots, K-1$$

The predicted probability of observing a particular level or less is:

$$p_k = P(Y \leq k) = \frac{1}{1 + exp\ (-\alpha_k - \beta X)}$$

The predicted probability of observing a particular level individually is:

$$p_k = P(Y \leq k) = \frac{1}{1 + exp(-\alpha_k - \beta X)} - \frac{1}{1 + exp\ (-\alpha_{k-1} - \beta X)}$$

A frequently violated assumption of this model is the proportional odds assumption, which states that the effect of each predictor variable is the same across all the categories of the ordinal response variable. In other words, the effect on the odds of being at or below any category is the same for each predictor variable within the model. This criterion can also be observed in each logit (log odds ratio) equation, where each logit has its own intercept α_k, but the same slope coefficient β. The PPO model relaxes this assumption and allows the effect of each predictor variable that violates the PO assumption to vary across each level of the ordinal response variable, thus adding a unique slope coefficient β_k for each logit equation:

$$log\left(\frac{p_k}{1-p_k}\right) = \alpha_k + \beta_k X \text{ for } j = 1, \ldots, K-1$$

I used the Brant test (Brant 1990) to confirm that the model violated the proportional odds assumption. I included sex and age as fixed effects in the PPO model. Unfortunately, the VGAM package currently only implements fixed-effects models, so I was unable to include purse seine and year as random effects in the model. Predicted probabilities were fit with 95% confidence intervals. With this model, I generated predictions for the probability of observing each stomach fullness category.

Because these results were difficult to interpret in terms of understanding the effects of grouping on overall foraging success, I created a stomach fullness metric consisting of the weighted sum of the probabilities for each stomach fullness category for the third set of models. I weighed each stomach fullness category equally, with weights of 0, 0.25, 0.50, 0.75, and 1.0 assigned to the stomach fullness categories empty, trace, medium, full, and distended, respectively. I then used a linear regression model to predict the probability of observing stomach volume for varying species catch size for each salmon species. I plotted stomach fullness as a function of group size alongside appropriately binned empirical data.

Results

Predation risk

Grouping reduced the individual risk of predation (Figure 2, Figure 3). For each of the four salmon species studied, as local density increased, the proportion of fish with predator wounds decreased (logistic regression: $p_{sockeye} = 0.0004$, $p_{chum} = 0.009$, $p_{pink} = 0.0003$, $p_{coho} = 0.004$). I was unable to fit logistic regression models for Chinook and steelhead salmon due to small sample sizes (630 and 25 observations, respectively). Predation risk decreased to zero for group sizes much smaller than the maximum group size for all species (Figure 2, Figure 3).

The odds ratio is calculated by exponentiating the regression coefficient for group size and tells us the expected change in the probability of predator injury for each unit of group size. Taking pink salmon as an example (OR 0.985), for each individual added to a group, the probability of observing a predator injury decreased by 1.5%. Thus, if the group size increased by 50 members, the risk of predation was cut approximately in half (0.985^50 = 0.47). Similar results were observed for the effect of total group size on predation risk ($p_{sockeye} = 0.002$, $p_{chum} = 0.0005$, $p_{pink} = 0.009$, $p_{coho} = 0.02$; Figure 2). Body size and age (which were highly correlated for all species, $r = 0.914$, $p < 0.00001$) did not affect the direction or strength of the relationship between grouping and predation risk. However, younger and smaller fish were less often observed with injuries (Figure 4).

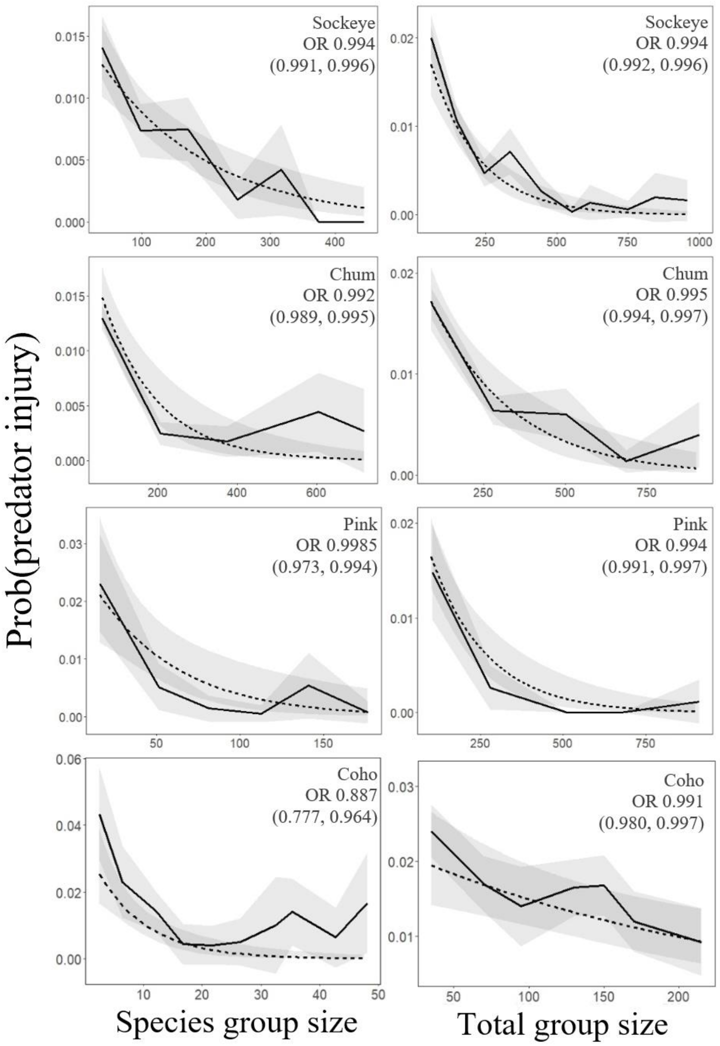

Figure 2. Predation risk. The probability of predator injury decreases as a function of group size (number of fish) for all Pacific salmon species considered (sockeye, chum, pink, and coho). This ‘safety-in-numbers’ is present for both species-specific group size (left column) and total group size (right column), both inferred from purse seine net catches. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals. OR stands for odds ratio, which is the expected change in the probability of predator injury for each unit of group size, with associated 95% confidence intervals.

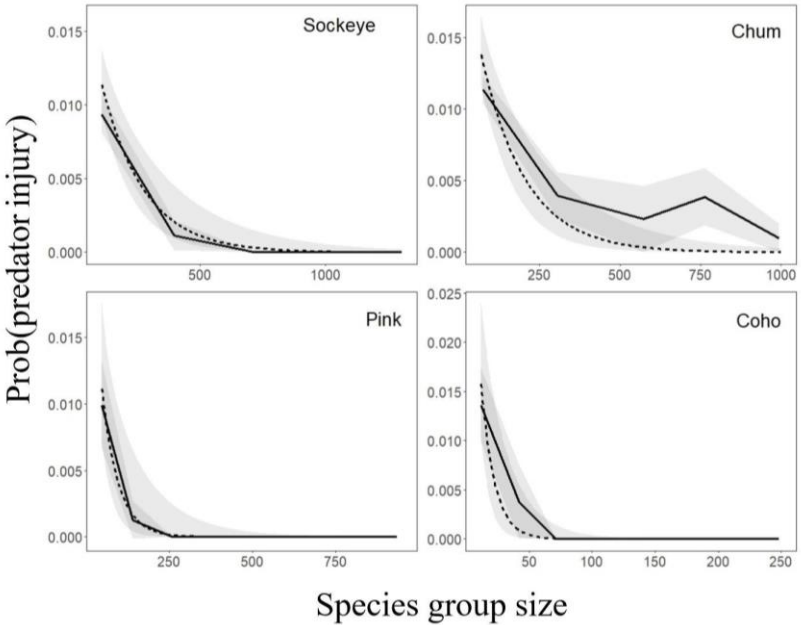

Figure 3. The probability (Prob) of predator injury as a function of species group size (catch per set), inferred from purse seine catch data, for four Pacific salmon species. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95%

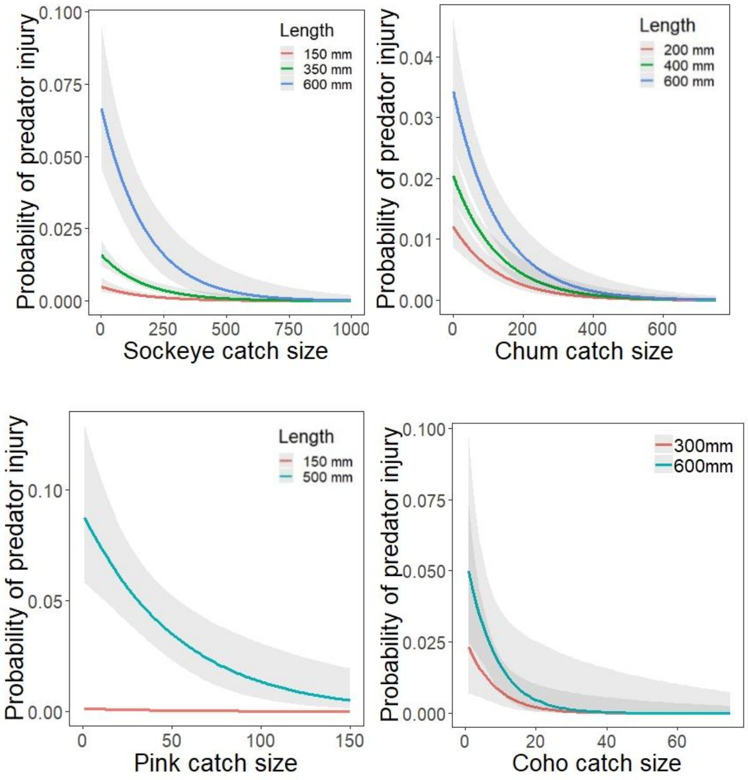

Figure 4. The probability of predator injury as a function of species group size (catch per set) for varying fish lengths of four Pacific salmon species. Solid lines represent model fit ± 95% confidence intervals.

There were sufficient data only for two species (sockeye: 17,116 and chum: 14,993) for this analysis. For both species, predation risk increased for outlier (larger and smaller) fish, whereas fish whose length was similar to the group mean were less likely to be wounded (Figure 5; piecewise logistic regression: β_{sockeye} = -4.38, 5.84, p_{sockeye} = 0.005, breakpoint = 0.947; β_{chum} = -3.66, 2.35, p_{chum} = 0.0004, breakpoint = 1.049).

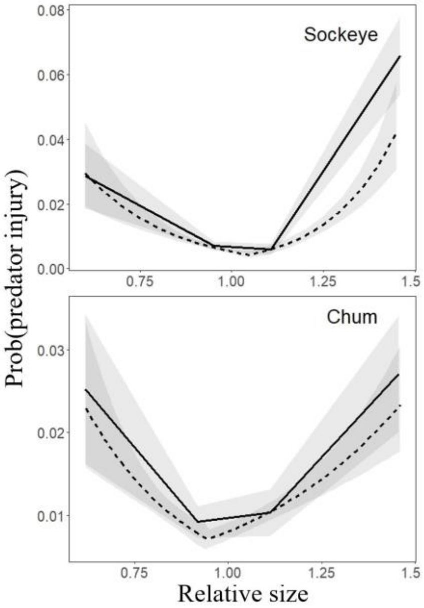

Figure 5. Oddity effect. The probability that an individual salmon had a predator-inflicted injury increased for outlier (smaller and larger) fish. Relative size is an individual's length relative to the mean length of conspecifics in the same purse seine catch. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals.

The probability of observing a predator injury as a function of raw body size was higher for intermediate-sized fish (~400-500 mm), and lower for smaller and larger fish (Figure 6).

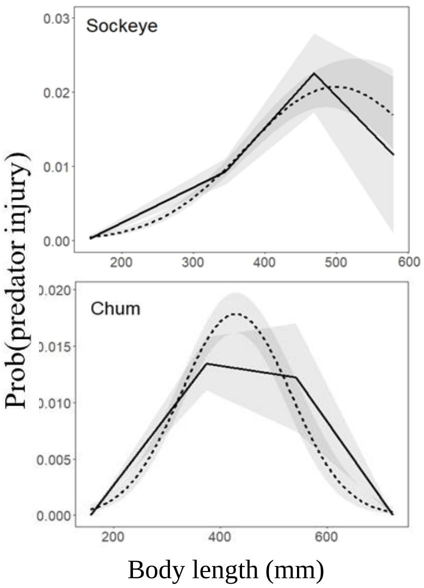

Figure 6. The probability that an individual salmon has a predator-inflicted injury as a function of raw body size. Sufficient data was only present for sockeye and chum. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals.

A group size heterogeneity trait, defined as the coefficient of variation of individual fish lengths for each group, was a significant predictor of predation risk alongside group size for both sockeye and chum ($\beta = 3.5$, $p = 7.33 * 10^{-6}$; $\beta = 2.3$, $p = 0.001$, respectively; Figure 7).

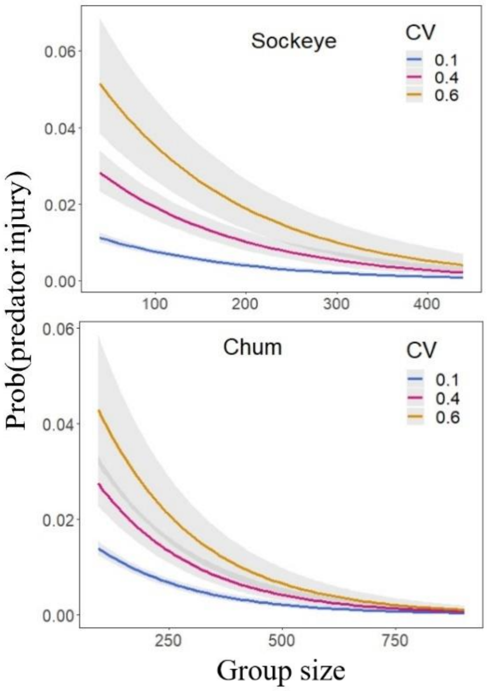

Figure 7. Model estimates ± 95% confidence intervals for the probability of observing a predator injury as a function of group size for a varying group size heterogeneity trait (CV). Increasing size heterogeneity indicates greater variation in body size within a group.

Foraging success

I estimated the foraging success of a group via three metrics: i) the proportion of the group having a non-empty stomach (Figure 8, Figure 9), ii) the average value of a `stomach fullness' scale ('empty'=0.0; 'trace'=0.25; 'medium'=0.5; 'full'=0.75; 'distended'=1.0) (Figure 10), and iii) the proportion of the group having a stomach fullness in each of those categories (Figure 11). I found qualitatively similar results for each measure. For two of the four species (sockeye and chum), foraging success decreased in larger groups (Figure 8, Figure 9; binary logistic regression: species group size $p_{sockeye} = 0.02$, $p_{chum} < 0.001$, total group size $p_{sockeye} = 0.0004$, $p_{chum} < 0.001$; Figure 10, Figure 11), although both species show an initial upward trend in foraging success in small groups (Figure 8, Figure 9, Figure 10), and the best fitting model for chum was a piecewise linear regression model with an initial increase (Figure 8, Figure 9; piecewise logistic regression: $p = 0.006$, breakpoint = 191). For pink salmon, foraging success increased for individuals in larger groups (Figure 8, Figure 9; binomial logistic regression: species group size $p_{pink} = 0.01$, total group size $p_{pink} = 0.009$; Figure 10, Figure 11). For coho salmon, results were less clear. Coho salmon foraging success was unaffected by species-specific group size but significantly declined for total group size (Figure 8, Figure 9; binomial logistic regression: species group size $p_{coho} = 0.4$, total group size $p_{coho} < 0.001$). For the linear regression models with averaged stomach fullness values, coho salmon foraging success increased with species-specific group size and decreased with total group size (Figure 10). The generalized ordinal logistic regression in Figure 11 shows that this increase in coho foraging success with increasing coho group size was driven exclusively by an increase in the extended stomach fullness category for this species.

The top logistic regression model for all three approaches and for all four species included an additive effect of length. For all species, the group-size effect on foraging became more pronounced for larger and older fish (Figure 8, second and fourth column). For pink salmon, the positive increase in foraging success with group size was only significant for larger fish. For sockeye and chum salmon, the decline in foraging success with group size became stronger for larger fish. In sockeye salmon, there was no effect of group size on foraging success for smaller fish, and the effect was only significantly negative for larger fish (logistic regression interactive effect, $p = 0.01$).

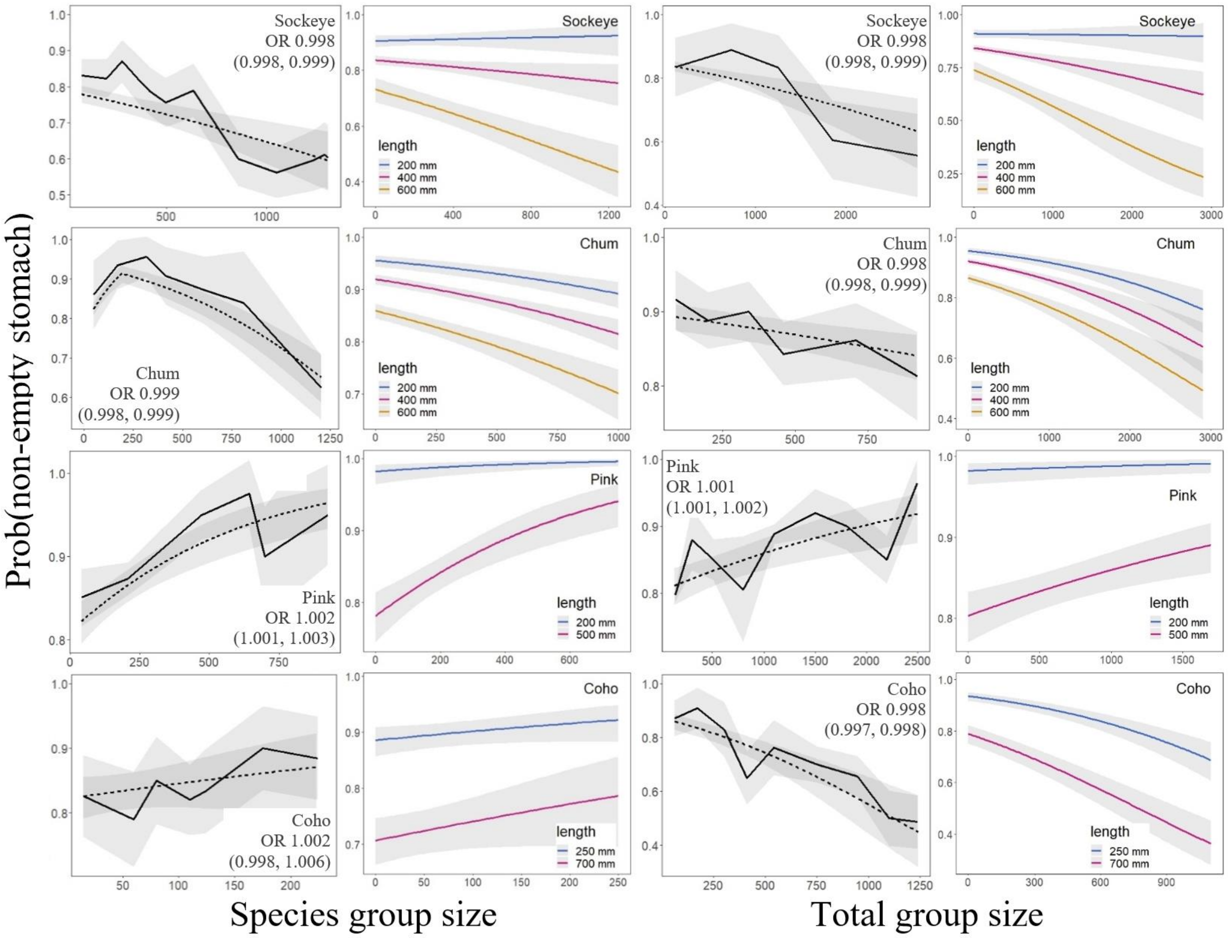

Figure 8: Foraging success. The trend in the probability of a salmon having a non-empty stomach as a function of its group size varied with species and body length. The first and third columns show data aggregated for each species. The second and fourth columns include the effect of body size. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals. OR (the odds ratio) is the expected change in the probability of predator injury for each unit of group size, with associated 95% confidence intervals.

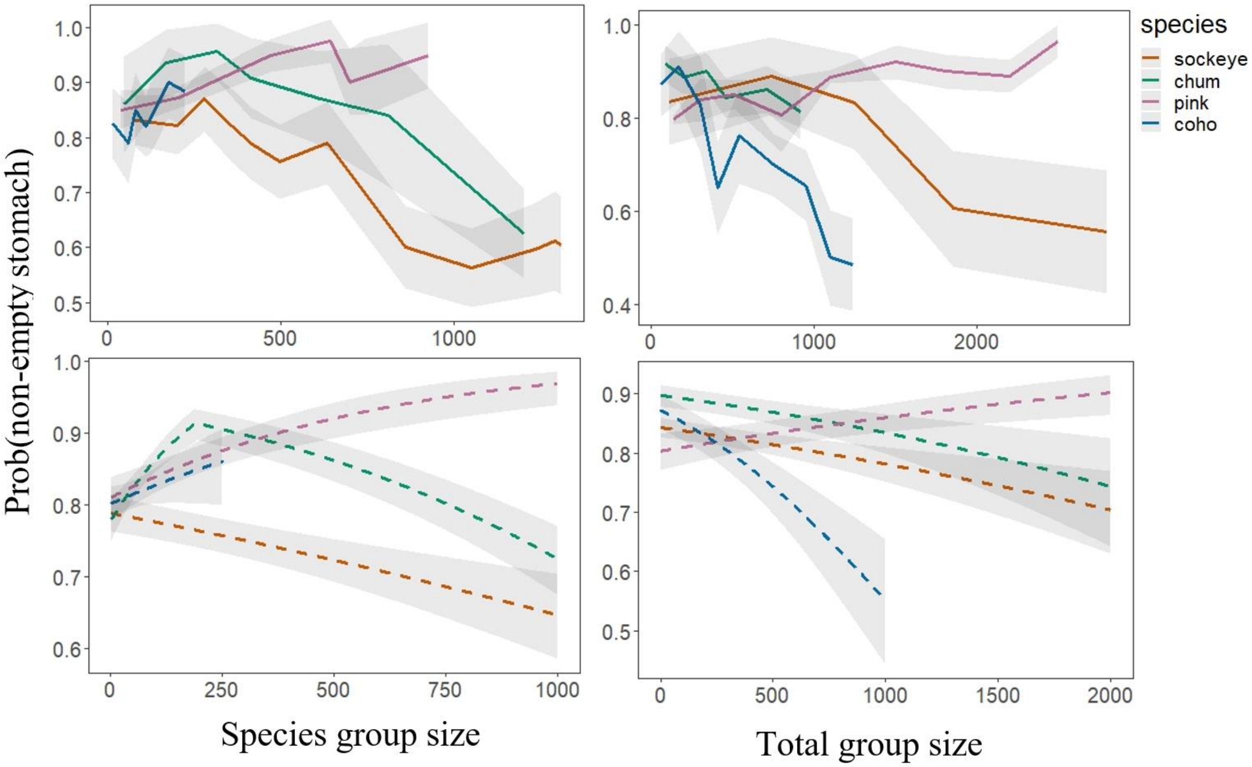

Figure 9: Foraging success. The trend in the probability of a salmon having a non-empty stomach as a function of its group size varied with species. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals.

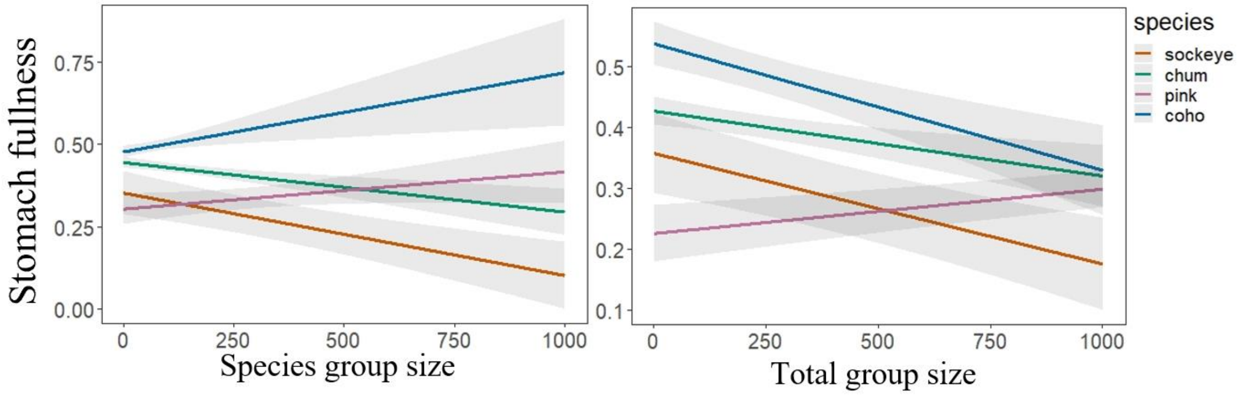

Figure 10: The effect of species (sockeye, chum, pink, and coho salmon) group size and total group size on weighted stomach fullness. Stomach fullness category (assigned weight): empty (0.00), trace (0.25), medium (0.50), full (0.75), and distended (1.00). Solid lines represent model fit ± 95% confidence intervals.

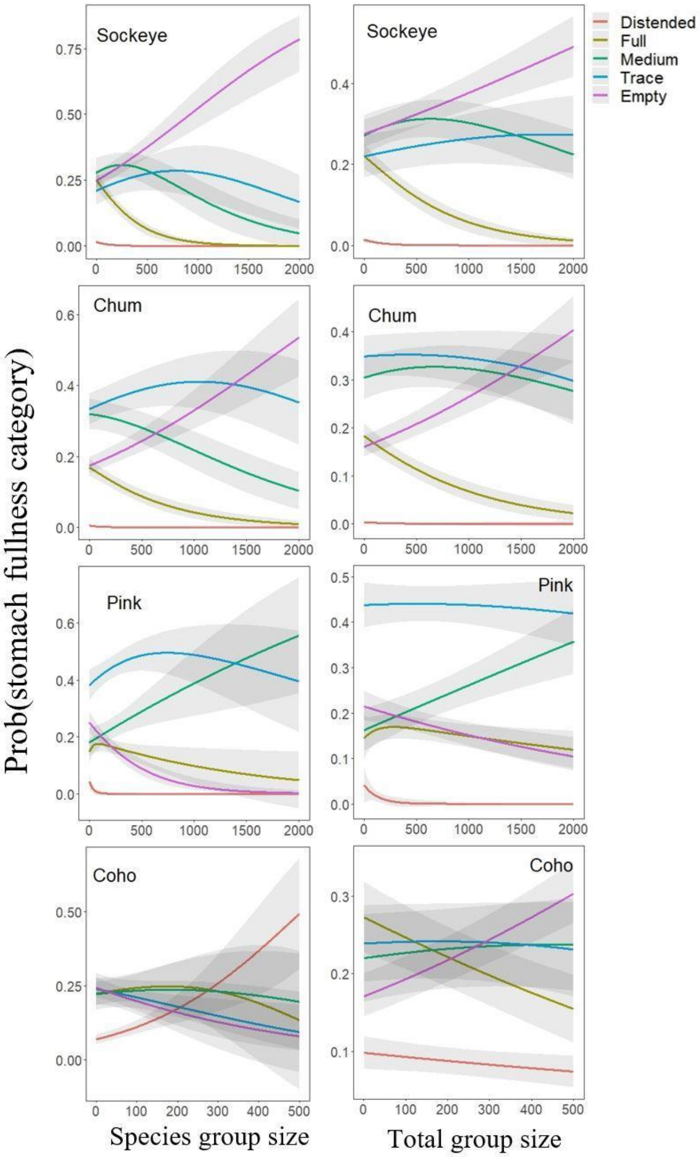

Figure 11: Model estimates ± 95% confidence intervals for the effect of species group size and total group size on the probability of observing a particular category of stomach fullness (empty, trace, medium, full, and distended stomach fullness).

Body size and group size

I considered group size through the life of a fish at sea for each of the four salmon species, by examining the effect of individual fish length (mm) on the size of the group within which the fish was observed (Figure 12). Across all species, larger and older fish tended to form smaller groups (exponential regression, $p_{sockeye} < 0.001$, $p_{chum} < 0.001$, $p_{pink} < 0.001$, $p_{coho} < 0.001$).

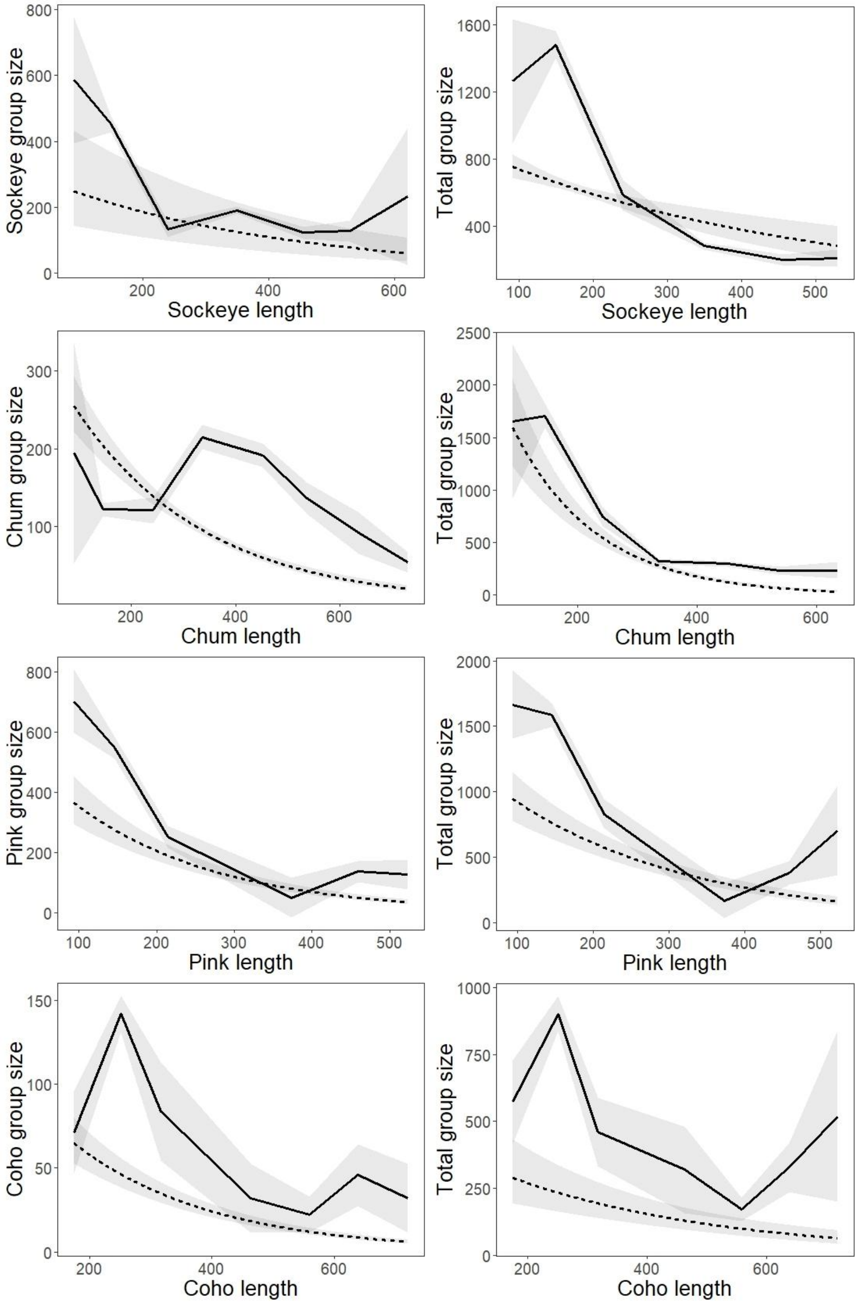

Figure 12: The effect of species length (mm) on species group size for sockeye, chum, pink, and coho species. Solid lines represent raw data ± standard deviation, and dotted lines represent model fit ± 95% confidence intervals.

Discussion

Predator Injury

Grouping dramatically reduced the individual risk of predation for all four species of Pacific salmon. These results were consistent for both species-specific and total group size (Figure 2, Figure 3). In principle, these larger groups could attract more predators (Ioannou 2017), thus the decrease in predation risk for larger groups observed here may be a lower bound for the effect size, given that a school has been detected. These results were consistent with my hypothesis for the effects of grouping on predation risk (Figure 1C). The strength of this relationship varied among species, with close to zero predator injuries observed in groups of coho with ≥ 70 individuals, followed by pink, sockeye, and finally chum (close to zero predator injuries observed in groups of chum with 900 individuals or more; Figure 2, Figure 3). These results demonstrate that grouping significantly reduced individual predation risk and provides empirical support for this theory in wild populations.

This study also provides an empirical measure of predation risk - predator injuries of individual fish - that was directly related to predator encounters. This is important because predation risk is difficult to measure in natural environments and is typically inferred using indirect measures. In cases when the prey is consumed, there may be no evidence, and so distinguishing the absence of predation from successful predation and complete consumption can be difficult. In the case of salmon in the open ocean, there are possible size-biases, as small fish might be completely consumed, and very large fish might escape, leaving fish of intermediate sizes showing wounds (Figure 6). To link predator injury to predator-induced mortality, I assumed that the probability of direct mortality by a predator increased with the probability of injury by a predator. Importantly, this size bias did not affect the strong negative relationship between predation risk and increasing group size.

To examine the mechanism driving this reduced predation risk with larger groups, I explored the probability of observing a predator wound as a function of the relative size of an individual (an individual's length divided by the mean length of all individuals of its species in the set) and found that predation risk increased for outlier (larger and smaller) fish, whereas fish whose length was similar to the group mean were less likely to be wounded. The "V"-shaped response curve observed in Figure 5 shows that predators preferentially target phenotypically distinct, or odd, individuals within a group, commonly known as the oddity effect (Ioannou 2017, Penry-Williams 2018, Murali et al. 2019). The oddity effect is an expected signature of the confusion effect – predators target distinct individuals because it avoids the cognitive constraints associated with the confusion effect (Landeau and Terborgh 1986, Krakauer 1995, Ward and Webster 2016, Giraldeau and Caraco 2018). The likelihood of predation risk as a function of the raw body size did not show a "V"-shaped relationship between the probability of predator injury and body size, suggesting that predation risk does not occur independently of the size of other individuals in the group. In other words, predators were not simply selecting smaller and larger fish, but were targeting odd individuals within a group, providing additional evidence for the oddity effect (Figure 6).

Finally, a group-level size heterogeneity trait, defined as the coefficient of variation of individual fish lengths for each group, was a significant predictor of predation risk alongside group size for both sockeye and chum (Figure 7), and showed that groups with greater phenotypic variation had higher predation risk than groups with less phenotypic variation. This further strengthens the case for the oddity effect, as the oddity effect is observed not only within groups, but also across groups - predators are targeting groups with more “odd” individuals to avoid experiencing the confusion effect. I therefore hypothesize that the confusion effect is driving, or at least contributing to, the decline in predation risk with increasing group size in Pacific salmon. There could be alternative or additional causes for decreased predation risk with larger group size. Larger groups could dilute the individual risk of predation and increase the level of prey vigilance for predators through the many eyes effect. In addition, I am assuming that the presence of individual predator injury is a proxy for individual predation risk. It is possible that since injured fish are already weakened, they are more likely to be outcompeted in larger groups and thus lead to the observation that larger groups contain fewer injured fish.

Across all species, larger fish tended to be in smaller groups (Figure 12). This is consistent with the hypothesis that larger fish have fewer predators (Hintz and Lonzarich 2018), and thus experience less pressure to school to avoid predation. In addition, larger immature and adult salmon are distributed farther offshore where predators are less abundant, compared to juvenile salmon that are nearer to shore (Groot and Margolis 1991, Ch. 2). Larger fish might also experience higher competition which could place more strain on bigger groups of large fish. In addition, maturing fish might be separating out into smaller population-specific groups that migrate directly to their home streams from locations across the geographic extent of their ocean distribution.

The wide variety of potential predators caught in purse seines alongside salmon, and the fact that 57% of purse seines that recorded bycatch data contained potential predators within catches and/or recorded marine mammals observed nearby, demonstrates a very high occurrence of predators. In addition, salmon survival at sea is extremely low, with estimates ranging from 3% for pink salmon to 13% for sockeye salmon, and predation is by far likely to be the greatest contributor to this mortality (Quinn 2018). This suggests that predation risk is very common in the marine environment and likely shapes the evolution of behavioral traits. Predator avoidance is thus likely to be a strong driver of behavior for salmon at sea, even at the expense of food intake.

Foraging success

In addition to reducing predation, grouping may alter an individual's food intake. Theory on foraging success and group size is mixed, and there may be multiple, potentially conflicting mechanisms at play. On one hand, larger groups often mean increased competition for food (Chapman and Valenta 2015, Ford and Swearer 2013, Vijayan et al. 2012), but on the other hand, collective foraging may increase an individual's consumption rate through information transfer or group hunting (Ioannou 2017, Rieucau et al. 2015, Ward and Webster 2016, Giraldeau and Caraco 2018, Partridge et al. 1983, Pitcher et al. 1982). The resulting fitness of an individual depends on the interplay between these positive and negative aspects of grouping (Fryxell & Berdahl, 2018). The three foraging metrics (proportion of the group having a non-empty stomachs, the average value of a `stomach fullness' scale, and the proportion of the group having a stomach fullness in each of those stomach fullness categories) yielded qualitatively similar results. There was evidence for both competition and collective foraging in Pacific salmon, depending on the species.

For two of the four species (sockeye and chum), foraging success decreased in larger groups, indicating that grouping came at a cost of competition for food. It is important to emphasize that, beyond evidence for competition, this result demonstrates that the grouping observed through this data set is not facultative – these are not fish independently converging around a common food resource (Kai et al. 2009), as has been suggested for salmon in the literature (Groot and Margolis 1991, Ch. 2). If these fish were indeed gathering in rich feeding areas, we would not expect their stomach fullness to decline with group size. Both species showed an initial upward trend in foraging success in small groups. For chum salmon, the best fitting model was a piecewise linear regression, with an initial increase up to a breakpoint at 191 chum salmon. This might indicate that sockeye and chum benefit from collective foraging, but that effect is dominated by competition at larger group sizes (Figure 9). This suggests the presence of a trade-off in the costs and benefits of grouping on foraging success (Figure 1D), with a group size threshold around 500 group members for sockeye, and 300 for chum salmon.

For pink salmon, foraging success increased for individuals in larger groups, suggesting that competition for food did not limit group size for this species. Coho salmon foraging success was unaffected by species-specific group size for the logistic regression model (Figure 8, Figure 9) but increased with group size in the linear regression model with averaged stomach fullness values (Figure 10). This increase was largely due to the increase in the distended stomach fullness category (Figure 11), which might suggest aggregation for large feeding events. However, coho salmon foraging success significantly declined with total group size, suggesting that coho salmon may suffer from interspecific competition. The discrepancy between results for species-specific and total catch size in coho is likely due to coho being the least abundant salmon species in this data set and the least likely to school with conspecifics (Figure S4). All other species tended to associate with conspecifics, and their group size-foraging relationship was consistent between species and total group size.

The observed differences between sockeye and chum vs. pink and coho salmon could be due to notable variations in life history traits. Sockeye salmon typically spend two to three years in the ocean and migrate large distances offshore within the Gulf of Alaska, and chum salmon typically spend two to four years there (Quinn 2018). Pink and coho salmon, on the other hand, generally only spend one full year at sea, and often are closer to their natal rivers than are chum and sockeye salmon (Quinn 2018). Catch data from this analysis confirmed that sockeye and chum salmon tend to migrate further offshore, grow more slowly and stay longer in the ocean, whereas pink and coho salmon tend to stay closer to shore, grow faster and spend less time in the ocean (Figure S1, Figure S2).

Species	Years at sea	Migratory patterns
Sockeye	2-4 years	migrate large distances within Gulf of Alaska
Chum	2-3 years	migrate some distances within Gulf of Alaska
Pink	1 year	stay closer to rivers of origin
Coho	1 year	least migratory, remain close to home streams throughout their lives

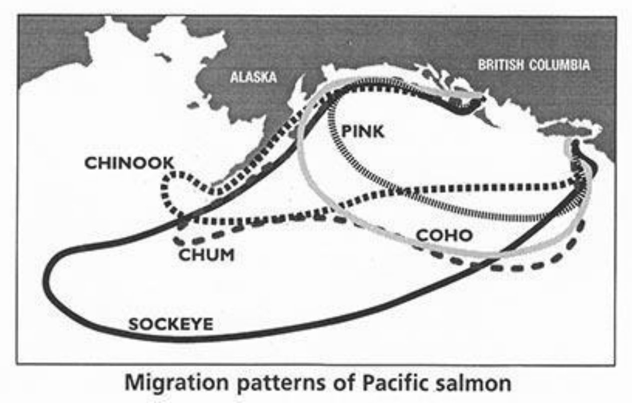

Figure 13. Life history traits (Groot and Margolis 1991, Ch.1-3, 5) and migration patterns of Pacific salmon at sea (BC Salmon 2020).

It is possible that the differences in the foraging success-group size relationship are driven by differences in distributions of food in these environments and differences in food-seeking behaviors related to growth rates. Open ocean environments typically have lower food availability and food sources are more patchily distributed compared to neritic environments (Quinn 2018). For slower growing species such as sockeye salmon and chum salmon, this could lead to increased competition between group members when foraging farther offshore and for longer periods of time. On the other hand, near-shore environments typically have higher food availability, thus muting the need for resource competition for species such as pink or coho salmon that stay closer to shore and spend less time in the ocean. In addition, because pink and coho salmon only spend one year at sea, these species must grow fast and feed quickly in order to mature within a year. Therefore, feeding and growth is likely a strong driver of behavior for these species at sea, and limited competition could allow for groups to benefit from collective foraging.

I further hypothesize the possibility that sockeye and chum salmon not only experience a trade-off between the effects of grouping costs and benefits on foraging success (as described above), but also a trade-off between the effects of grouping costs and benefits across traits. It is possible that sockeye and chum salmon experience a trade-off between the effects of grouping costs on foraging success (reduced food intake due to competition for resources), and the effects of grouping benefits on predation risk (decreased predation risk), and that these species prioritize predator avoidance at the expense of food gain. Environmental conditions might determine the existence of this safety for food trade-off between the costs and benefits of grouping for these species, due to patchier food sources in offshore marine environments, which leads to higher levels of competition between group members. It is important to consider why these offshore species choose to group, if grouping comes at the cost of reduced food intake but reduces predation risk. This suggests that, by grouping, these species are prioritizing safety over food, a trade-off that to our knowledge has not been documented in wild populations of Pacific Ocean salmon. In larger groups, these salmon may have less to eat due to competition, but they themselves will be eaten less. Predator avoidance is an important consideration because of its influence on lifetime fitness. An individual has more than one chance to find food, but only has one chance to be predated on, and being killed decreases future fitness more than hunger (Lima and Dill 1990). It has been shown that animals have the ability to assess and behaviorally influence their risk of being preyed on in ecological time, which strongly influences decision making in feeding animals (Lima and Dill 1990). These results suggest that predator avoidance is the primary driver of grouping for sockeye and chum salmon at sea, and that sockeye and chum salmon actively group in order to avoid predation, at the cost of reduced food intake.

For all species, the group-size effect on foraging became more pronounced for larger and older fish (Figure 8, second and fourth column). For pink salmon, the positive increase in foraging success with group size was only significant for larger fish. For sockeye and chum salmon, the decline in foraging success with group size became stronger for larger fish. In sockeye salmon, there was no effect of group size on foraging success for smaller fish, and the effect was only significantly negative for larger fish. For sockeye and chum salmon, the negative effects of group size on foraging success could be intensified with age or size due to life history traits. Sockeye and chum salmon spend more time in the ocean and travel farther out in the ocean (Figure S1, Figure S2, Figure 13), which could increase competition for food at later ocean life stages as these salmon gradually move offshore after out-migration. Pink and coho stay closer to shore and spent less time in the ocean, which could decrease competition and even suggest that collective foraging behavior was occurring in line with species life history traits for faster growth and shorter life cycles (Figure S1, Figure S2, Figure 13).

These results further challenge the common, albeit still controversial, assertion that salmon do not school in marine environments. Although there is some evidence for strong schooling tendencies in juvenile salmon (especially during inward and outward migrations), little is known about schooling of salmon in the open ocean. The distribution of Pacific salmon in the ocean is poorly understood (Quinn 2018), and literature within this subject area provides some contradictory assertions about marine salmon schooling behavior. Some studies suggest that salmon are not found in groups in the ocean (Nero and Huster 1996, Royce et al. 1968, Takagi et al. 1981). Yet other sources cite that schooling behavior follows a gradient, with schooling becoming less pronounced throughout the pelagic marine stage of the salmon life cycle, and an increase in schooling behavior as maturing fish approach coastal waters for spawning migrations (Groot and Margolis 1991, Ch. 2). Other studies state that certain species such as pink or chum salmon do not group in the ocean at all (Beamish 2018, Ch. 1, 2, 4). Quinn (2018) suggests salmon schooling in the ocean is potentially facultative rather than obligate, and aggregations of salmon occur more frequently than actual traveling groups. Recent analytical approaches have shown that salmon are not distributed randomly and are aggregated in time and space across the ocean (Berdahl et al. 2016a). These results support the conclusions of Berdahl et al. (2016a) and demonstrate the important role that grouping plays in foraging success and predator evasion. These results also provide evidence that salmon are actively schooling in the open ocean, and not simply aggregating around areas such as food sources. If these salmon were gathering in rich feeding areas, stomach fullness would not decrease with group size as it does for sockeye and chum salmon. Finally, these results also show that there is some species sorting within groups (Figure S3).

Mounting evidence suggests that grouping may play an important role in other aspects of salmon life history. Social interactions shape the timing of sockeye salmon final spawning migration (Berdahl et al 2017). Chinook salmon find passage through hydroelectric dams more rapidly when at high densities (Okasaki et al 2020). Such collective navigation during homeward migrations can lead to density-dependent straying rates (Berdahl et al. 2016a). Density-dependent straying could in turn introduce positive feedback and non-linearity into the dynamics of population size and genetic makeup (Berdahl et al 2016b, Yeakel et al 2018).

Increased understanding of how social dynamics affect growth and survival may provide key insights for management (Westley et al. 2018). Specifically, if a species' local density modifies its predation and foraging rates (and therefore its survival and growth), as is the case in this example, quantifying those relationships and incorporating them into stock assessment models could yield better forecasts used for management and conservation. However, to make this feasible, we would also need to know the relationship between the distribution of local densities and the global density (Berdahl et al. 2018). That is, does a reduction in population size result in smaller groups or in fewer of the same-sized groups? Filling this gap in the literature is a critical step to connecting ubiquitous social behavior to population dynamics and more general ecosystem functioning.

Assumptions and caveats

The data examined here presented both strengths and challenges. On the positive side, these unique data provided a large volume of information, collected blind to the hypotheses tested here. However, working with the data necessitated several key assumptions. I assumed that the catch size was a reliable indicator of local density (group size) and to increase confidence in this assumption, I restricted analysis to only purse seine catches (which capture a relatively small but consistent volume of water). I also assumed that groups were stable enough that the foraging success of an individual was related to the size of the group in which it was captured. The use of the proportion of fish with predator wounds within a group as a proxy for predation risk relies on the assumption that there is an increasing relationship between the number of fish wounded and the number of fish killed in an attack.

I assumed that differences in group sizes drive the trends in predation risk and foraging, but briefly want to consider the potential for the reverse causal relationship. Could wounded fish tend to form smaller groups? First, perhaps wounded fish are weaker and get left behind by larger groups because they are outcompeted when foraging or physically fall behind the group due to being weaker. Second, groups having recently encountered a predator attack could be both smaller (due to fish having been eaten, or groups being split apart) and would also have more wounded fish. However, these explanations seem less plausible. If the first were true, I would not expect sockeye and chum to have greater foraging success in smaller (weaker) groups. If the second were true, I would not expect to see any relationship between group size and foraging success, unless predators were preferentially targeting groups with higher or lower foraging success.

Conclusion

This study provided a unique test of the canonical ‘safety-in-numbers’ hypothesis (Cresswell and Quinn 2011, Creel et al. 2014, Ioannou 2017, Schradin 2019), and revealed that Pacific salmon reduced their vulnerability to predation by schooling to confuse predators. This strong drive to avoid predators is likely due to the high predation risk faced by salmon out in the open ocean. For some species (sockeye and chum salmon), schooling to avoid predators comes at the cost of foraging success. For other species (pink and coho salmon), foraging success increased in larger groups, indicating that this trade-off may not exist and individuals in larger groups might even benefit from collective foraging. These results test and validate long-standing theories on the benefits and costs of group living that have rarely been tested in wild populations. In addition, these results show that these trends hold at large spatial and temporal scales, emphasizing the strength of these relationships. Understanding the trade-offs between the costs and benefits of grouping will allow for prediction of optimal group sizes, a more nuanced treatment of density dependence, and elucidation of the ecological role of schooling. Beyond representing a test of doctrinal ecological theory, these results suggest that salmon actively group in the open ocean. This contrasts with the prevailing view that, other than as juveniles migrating to sea, and adults in the final phases of their return migration, salmon are generally isolated from one another in the open ocean and only come together facultatively to feed on common resources (Quinn 2018).

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Supplementary Information

Life history traits

I examined life history traits of four species of Pacific salmon, specifically growth patterns, distance from shore, and mean ocean age. The data were consistent with reference sources (e.g., Quinn 2018) on life history traits for these species (Figure 12, Figure 13). Sockeye and chum salmon tend to grow slower and spend multiple years at sea, whereas pink and coho salmon grow faster and spend one year (or winter) at sea.

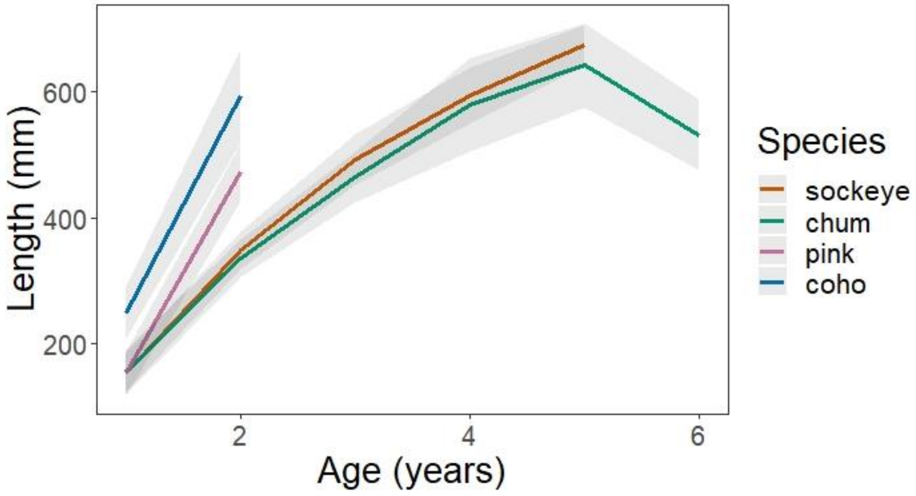

Figure S1: Mean length ± SD (mm) by ocean age (years) for sockeye, chum, pink, and coho salmon.

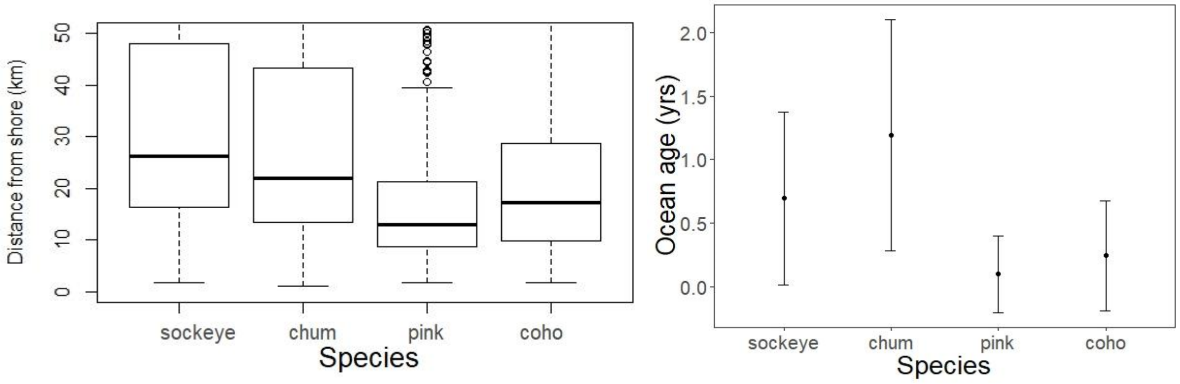

Figure S2: (A) Distance from shore for four species of salmon sampled at sea. The middle line is equal to the median distance from shore (km), boxes indicate interquartile range, the whiskers extend to 1.5 times the interquartile range, and values beyond this are indicated by (o). (B) Mean ocean age (mean ± SD) for four species of salmon.

Species sorting

I examined the possibility of species sorting or multi-species sorting within the catch data set. To do so, I calculated the entropy of each group as $-\sum_i p_i log(p_i)$, where p_i is the proportion of fish in a group that are species i. I then ran a simulation that randomly drew fish from a pool of 306,255 fish (the total number of fish caught in the study). I randomly sampled group sizes ranging from 2-1000 (increasing in multiples of 5), sampled each group size 1000 times, and calculated entropy for each sample. I repeated the simulation using an exponential instead of uniform distribution of group sizes, which better matched the distribution of catch sizes (more smaller and fewer larger catch sizes). Finally, to account for spatial effects, I repeated the simulation using a random draw of fish by grid cell (13.7 x 43.5 km). To do so, I divided the area within which data were collected into 10,000 grid cells of 13.7 km high by 43.5 km long. For each grid cell, I randomly pulled fish from a pool of fish where the total number of fish was equal to the amount actually caught within that grid cell. I then randomly sampled group sizes ranging from 2-1000 (increasing in multiples of 5) and sampled each group size 1000 times, and calculated entropy for each sample.

Random draws from uniform and exponential group size distributions were similar, but different from the distribution of entropies calculated from the data (Figure 14). Distribution of entropies calculated from random draw by grid cell also differed from the entropy distribution calculated from the data. Lower values indicate less mixed groups, while higher values indicate more mixed groups. This suggests that some sorting by species or multi-species groups was occurring because the entropy distribution from the data showed less mixing than if fish were randomly sorted.

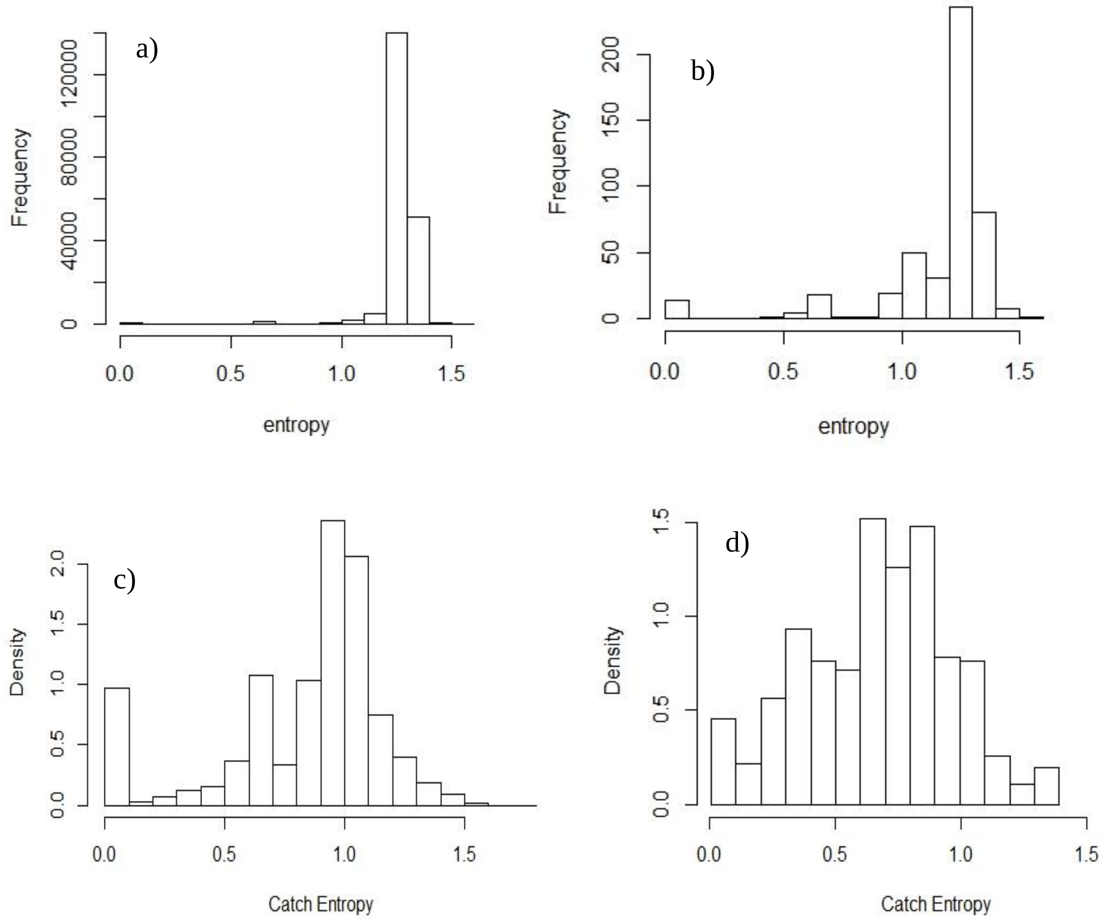

Figure S3. Distribution of entropies for a) random draws of fish from a uniform distribution; b) random draws of fish from an exponential distribution; c) random draws of fish by grid cell; and d) the dataset.

Since many of the catches were mixed species, I plotted the probability of observing specific species fractions of each group weighted by the total number of individuals of that species, for each of the four species (Figure 15). These results indicate that sockeye, chum, and pink salmon tend to be found with individuals of their own species. In contrast, coho were less associated with their own species.

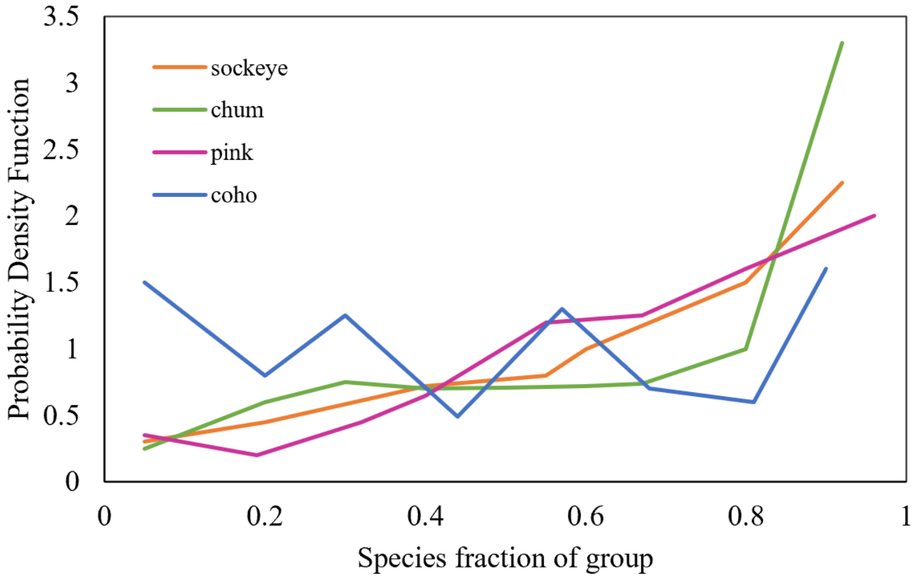

Figure S4. The probability density function (PDF) for the fraction of a catch represented by each species (sockeye, chum, pink, and coho salmon), weighted by the number of individuals of that species in that catch.