ECOLOGY

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

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Grouping is ubiquitous across animal taxa and environments. Safety in numbers is perhaps the most cited reason for grouping, yet this fundamental tenet of ecological theory has rarely been tested in wild populations. We analyzed a multidecadal dataset of Pacific salmon at sea and found that individuals in larger groups had lower predation risk; within groups of fish, size outliers (relatively small and large fish) had increased predation risk. For some species, grouping decreased foraging success, whereas for other species, grouping increased foraging success, indicating that safety competition trade-offs differed among species. These results indicate that survival and growth depend on group size; understanding the relationship between group size distributions and population size may be critical to unraveling ecology and population dynamics for marine fishes.

INTRODUCTION

Living in groups is thought to confer many benefits, with protection from predators being especially important (*1*, *2*). Theory and laboratory experiments indicate that grouping dilutes individual risk (*3*, *4*), increases the probability that prey detect predators (*5*–*7*), and confuses predators (*8*–*10*). However, group living can also bring costs such as increased resource competition between group members (*11*–*13*) and increased probability of detection by predators (*4*). 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 roles of grouping.

An outstanding challenge is finding evidence for the costs and benefits of grouping in wild populations (*14*–*18*). Although the development of theoretical concepts associated with grouping has made considerable progress, our understanding of the factors that regulate foraging success and predator avoidance in wild animal populations that exhibit grouping remains limited. Much of the research on this topic consists of experimental studies, which tend to use a small number of individuals and thus may not represent the natural variation in group sizes that exists for many species (*15*). There are few observational studies of the effects of grouping on predation risk and foraging success in wild animal populations, especially studies incorporating a variety of life stages (*19*). Large, empirical studies are important to test, validate, and refine theoretical predictions. This challenge is particularly pertinent in open marine environments, where grouping (schooling) is extremely common, but quantifying behaviors and outcomes is notoriously difficult (*20*). Field studies are typically opportunistic, rather than systematic, and limited to small spatial scales near shore (*21*).

Here, we assessed the benefits and costs of schooling using catch records from a multidecadal (1956–1991) program of scientific sampling of Pacific salmon (*Oncorhynchus* spp.) in epipelagic (neritic and oceanic) habitats across a large area of the subarctic North Pacific Ocean (Fig. 1A). We examined data from purse seine nets that surround and sample a discrete volume of seawater (Fig. 1B). Consequently, catch size is a reliable measure of local density and a reasonable proxy for group size (*22*), unlike other gear such as gillnets or longlines that are deployed over much larger distances and longer periods (*23*). For 1309 purse seine sets, researchers recorded the species, length, age (from examination of scales), stomach fullness, and presence of wounds inflicted by predators on a subset of individual fish (15,977 fish in total; Fig. 1E). We analyzed data for the four most common salmon species in the catch records: pink (*Oncorhynchus gorbuscha*), sockeye (*Oncorhynchus nerka*), coho (*Oncorhynchus kisutch*), and chum (*Oncorhynchus keta*). We used the species-specific catch per set of the net as our measure of local density or group size but obtained similar results using total rather than species-specific catches. We estimated predation risk using the fraction of fish in each set with predator wounds (*24*, *25*) and foraging success using stomach fullness. These data, collected over decades and on multiple species, give us a rare opportunity to investigate group size effects on predation risk and foraging success in a pelagic environment. All data were collected blindly with respect to the current purposes; thus, so observer bias is highly unlikely.

RESULTS

Does school size affect risk of predation?

Grouping markedly reduced the individual risk of predation. For each of the four salmon species studied, as local density increased, the proportion of fish with predator wounds decreased (logistic regression: $p_{\text{sockeye}} = 0.0004$, $p_{\text{chum}} = 0.009$, $p_{\text{pink}} = 0.0003$, and $p_{\text{coho}} = 0.004$; Fig. 2, A to D). The odds ratio (OR; exponential of the regression coefficient) reveals the strength of these trends by quantifying the expected change in the probability of predator injury for each unit of group size. Taking sockeye salmon as an example (OR, 0.994), for each individual added to a group, the probability of observing a predator injury decreased by 0.6%. Thus, if the group size increased by 100 members, then the risk of predation was cut approximately in half ($0.994^{100} = 0.55$). We observed similar results for the effect of total group size on predation risk for all four species (logistic regression: $p_{\text{sockeye}} = 0.002$, $p_{\text{chum}} = 0.0005$, $p_{\text{pink}} = 0.009$, and $p_{\text{coho}} = 0.02$; Fig. 2, E to H). In principle, these larger groups could attract more predators (*4*); thus, the decrease in predation risk for larger groups observed here may be a lower bound for the effect size, given a school that has been detected. Body size and age (which were highly correlated for all species; $r = 0.914$, $P < 0.00001$)

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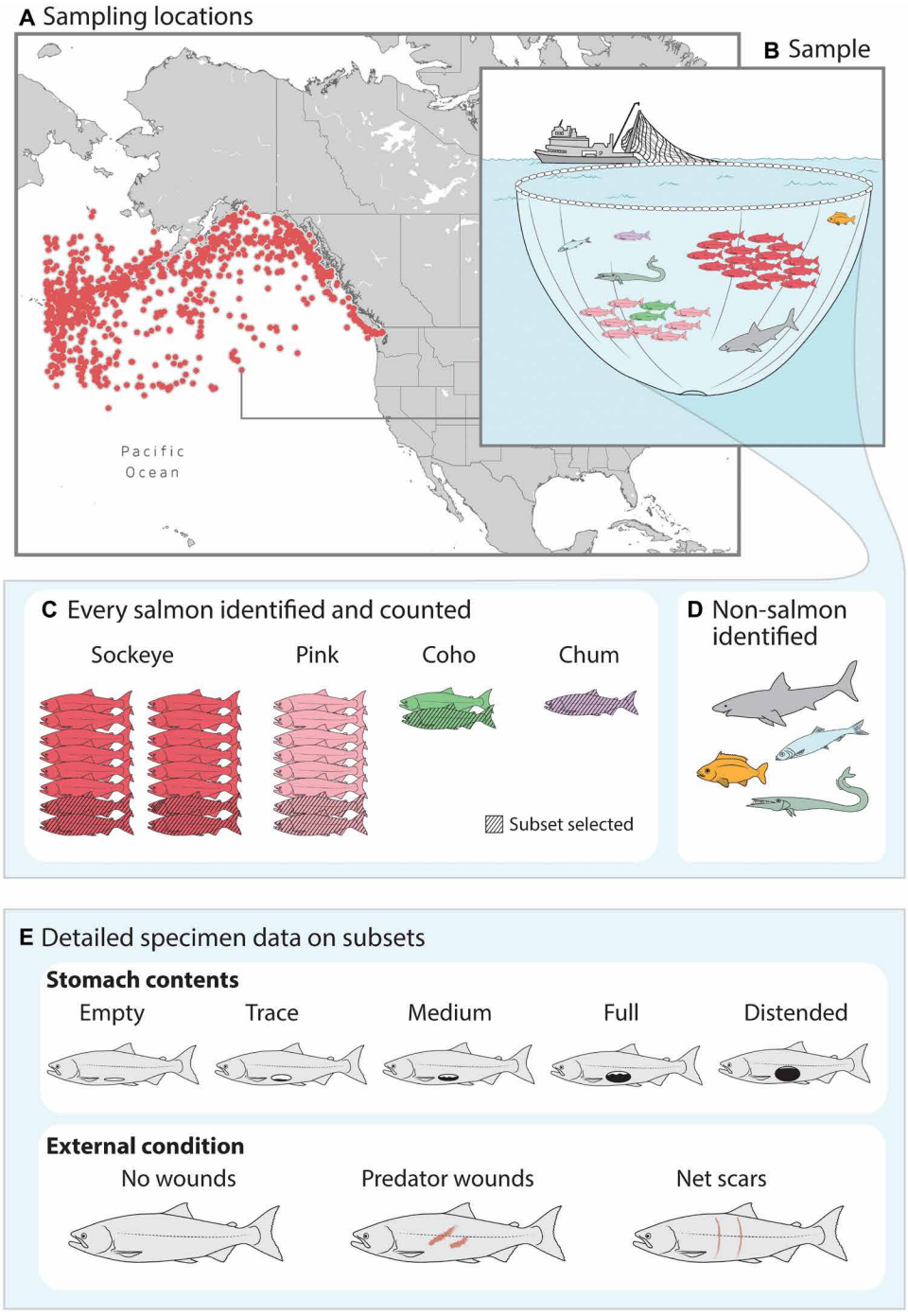

Fig. 1. Overview of dataset. (**A**) Red dots show the location of sampling events, distributed across the North Pacific Ocean. (**B**) At each sampling location, a purse seine was deployed. This style of net captures all of the fish in a discrete volume of water. (**C**) Within each net haul, every salmon was identified to the species and counted. (**D**) Non-salmon species were identified and recorded but not counted. (**E**) Detailed measurements, including length, stomach fullness, and presence of predator wounds, were collected on a subset of salmon from each purse seine sample. Sampling was conducted by the University of Washington's Fisheries Research Institute (FRI) and cooperative United States–Union of Soviet Socialist Republics (US-USSR; KamchatNIRO, Petropavlovsk-Kamchatsky and TINRO, Vladivostok) research from 1956 to 1991.

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 (fig. S2), and larger fish tended to form smaller groups (exponential regression: $p_{\text{sockeye}} < 0.001$, $p_{\text{chum}} < 0.001$, $p_{\text{pink}} < 0.001$, and $p_{\text{coho}} < 0.001$; fig. S10).

How does schooling decrease risk of predation?

To probe the mechanism driving this observed safety in numbers, we explored the probability of having a predator wound as a function of the relative size of an individual (i.e., an individual's length divided by the mean length of all individuals of its species in the set).

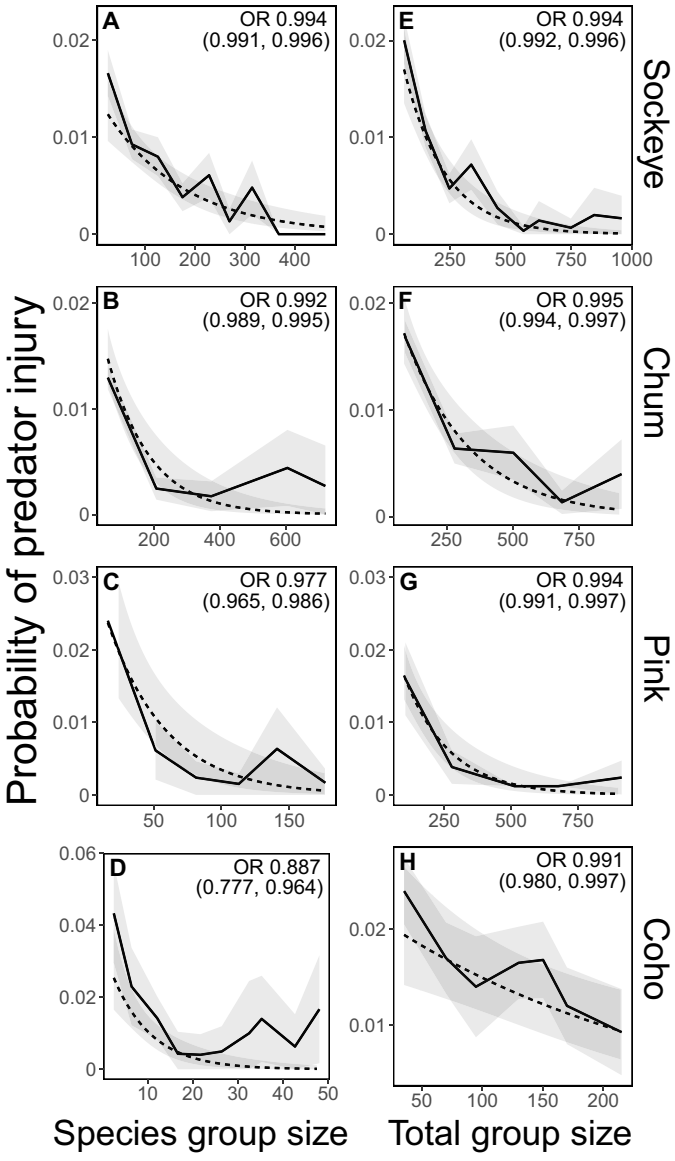

Fig. 2. Effect of group size on predation risk. The probability of predator injury decreased as a function of group size (number of fish caught in purse seine nets) for all Pacific salmon species considered (sockeye, chum, pink, and coho). This safety in numbers was evident for both species-specific group size (left column) and total group size (right column). Solid lines represent raw data ± SD, and dotted lines represent model fit ± 95% confidence intervals. OR stands for odds ratio: the expected change in the probability of predator injury for each unit of group size, with associated 95% confidence intervals. Note that the *y* axis varies between panels, to best illustrate trends in each species.

We had sufficient data for only two species (sockeye: 121; chum: 147 wounded fish) for this analysis and did not analyze data for pink and coho (39 and 14 wounded fish, respectively), following Peduzzi *et al*. (*26*). For both sockeye and chum, predation risk increased for outlier (larger and smaller) fish, whereas fish whose length was similar to the group mean were less often wounded (piecewise logistic regression: $\beta_{sockeye} = -4.38$ and 5.84, $p_{sockeye} = 0.005$, breakpoint = 0.947; $\beta_{chum} = -3.66$ and 2.35, $p_{chum} = 0.0004$, breakpoint = 1.049; Fig. 3). The "V"-shaped response curve observed in Fig. 3 suggests that predators preferentially target morphologically distinct (smaller and larger) individuals within a group, commonly known as the oddity effect (*4*, *27*–*29*). The oddity effect is an expected signature of the confusion effect (*4*)—when predators target distinct and thus conspicuous, individuals—because it avoids the cognitive constraints associated with the confusion effect (*8*, *9*, *30*, *31*). The likelihood of predation as a function of the raw body size did not show a V-shaped relationship between the probability of predator injury and body size (fig. S6), suggesting that predation risk depended on the size of other individuals in the group. Predators were thus not simply selecting smaller and larger fish but were targeting odd individuals within a group, providing additional evidence for the oddity effect. We 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, as shown in Fig. 2. Other potential mechanisms, such as group vigilance or predator handling time limiting the number of prey eaten, may also reduce predation risk (*4*, *32*); however, these mechanisms would not explain the observed oddity effect (Fig. 3).

Further strengthening the case for the confusion effect for sockeye and chum salmon, in addition to targeting odd individuals within a group, predators appeared to target more heterogeneous groups. Body size heterogeneity, 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 ($\beta = 3.5$, $P = 7.33 \times 10^{-6}$ and $\beta = 2.3$, $P = 0.001$, respectively; Fig. 4). Groups with greater variation in body size had higher predation risk than groups with less variation in body size. Thus, we detected evidence of the confusion oddity effect within and across groups of sockeye and chum salmon. We note that, for pink salmon, we observed the opposite effect—groups with higher variation in body size had lower predation risk—and there was no effect of size heterogeneity within groups for coho salmon. However, as discussed above, the small numbers of wounded pink and coho salmon made them unsuitable for this analysis (*26*).

Does school size affect 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 (*33*). On one hand, larger groups often mean increased competition

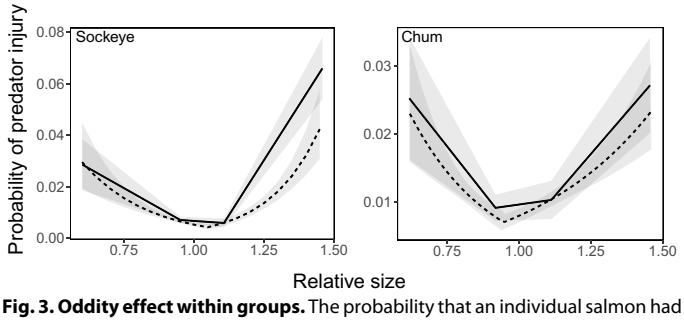

Fig. 3. Oddity effect within groups. The probability that an individual salmon had a predator-inflicted injury increased for outlier (smaller and larger) fish. Relative size was an individual's length relative to the mean length of conspecifics in the same purse seine catch. Sufficient data were only present for sockeye and chum. Solid lines represent raw data ± SD, and dotted lines represent model fit ± 95% confidence intervals. Note that the *y* axis varies between panels, to best illustrate trends in each species.

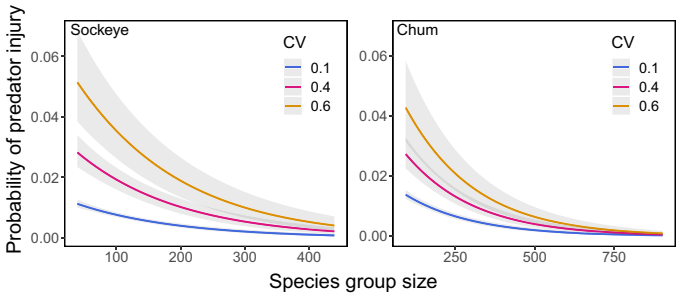

Fig. 4. Size heterogeneity within groups. The effect of a size heterogeneity trait [CV (coefficient of variation)] on the probability of predation risk for sockeye and chum salmon. Increasing size heterogeneity indicates greater variation in body size within a group. Curves represent model fit with shading to indicate ±95% confidence intervals.

for food (*11*–*13*), but on the other hand, collective foraging may increase an individual's consumption rate through information transfer or group hunting (*4*, *14*, *16*, *31*, *34*–*37*).

Sockeye and chum salmon suffer foraging competition

For two of the four species, foraging success decreased in larger groups. The probability of observing a stomach containing prey decreased as a function of group size for sockeye and chum (binary logistic regression: species group size, $p_{sockeye} = 0.02$ and $p_{chum} < 0.001$; total group size, $p_{sockeye} = 0.0004$ and $p_{chum} < 0.001$; Fig. 5, A, B, I, and J; and fig. S3). Both species showed an initial upward trend in foraging success in small groups (Fig. 5 and fig. S3). The best fitting model for chum was a piecewise linear regression model with an initial increase (piecewise logistic regression: $P = 0.006$, breakpoint = 191; Fig. 5B and fig. S3). This initial increase followed by decline in foraging success might indicate that sockeye and chum salmon benefit from collective foraging, but that effect is dominated by competition at larger group sizes. We repeated this analysis using the average value of a "stomach fullness" scale ("empty" = 0.0, "trace" = 0.25, "medium" = 0.5, "full" = 0.75, and "distended" = 1.0) rather than probability of some prey in the stomachs and obtained qualitatively similar results (linear regression: species group size, $p_{sockeye} = 0.01$ and $p_{chum} < 0.001$; total group size, $p_{sockeye} = 0.02$ and $p_{chum} < 0.01$; fig. S4). In this complementary analysis, the initial increase in foraging at small group sizes was visually more pronounced (fig. S4). We also predicted the probability of each particular stomach fullness category separately. This allowed a more detailed analysis of how each recorded category changed with group size and produced qualitatively similar results (fig. S5).

Pink and coho salmon foraging was not limited by conspecific competition

Foraging success of pink salmon increased for individuals in larger groups. The probability of observing prey in the stomach increased as a function of group size (binomial logistic regression: species group size, $p_{pink} = 0.01$; total group size, $p_{pink} = 0.009$; Fig. 5, C and K, and fig. S3). We obtained similar results using our complementary quantification of foraging success, the average value of a stomach fullness scale (species group size, $p_{pink} = 0.04$; total group size, $p_{pink} = 0.04$; fig. S4). These results are consistent with pink salmon benefiting from collective foraging and at least suggest that grouping did not increase competition for food for this species.

Foraging results for coho salmon were mixed. The probability of observing prey in the stomach did not vary significantly with species-specific group size but decreased with total group size (binomial logistic regression: species group size, $p_{coho} = 0.4$; total group size, $p_{coho} < 0.001$; Fig. 5, D and L, and fig. S3). Average stomach fullness increased as a function of species-specific group size but decreased with total group size (species group size, $p_{coho} = 0.01$; total group size, $p_{coho} < 0.001$; fig. S4). Consistent across these measures was decreased foraging as a function of total (species mixed) 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, because coho were the least abundant salmon species in our dataset and the least likely to occur with conspecifics (fig. S7). All other species tended to associate with conspecifics, and their group size–foraging relationships were consistent between species and total group size.

In all species, group size trends were stronger for older fish

For all species, the group size effect on foraging became more pronounced for larger and older fish (Fig. 5, E to H and M to P, and fig. S3). 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: $P = 0.01$; Fig. 5, E and M). For pink salmon, the increase in foraging success with group size was only significant for larger fish (Fig. 5, G and O).

DISCUSSION

Here, we provide a unique test of the canonical "safety-in-numbers" hypothesis (*1*, *2*, *4*, *10*) and demonstrate that Pacific salmon reduced their vulnerability to predation by schooling, likely by confusing predators. Depending on the species, schooling may or may not compromise foraging success due to competition. Our results support long-standing theories, widely accepted but rarely tested in wild populations, on the benefits and costs of group living. Much of the evidence for these benefits comes from elegant but highly artificial studies in small, controlled settings, whose applicability to wild populations in unconfined environments needs to be validated (*7*, *8*, *12*). The data that we used, collected over decades and on multiple species, provide a rare opportunity to investigate how group size mediates predation risk and foraging success in a pelagic environment. Our results show that these trends hold true at large spatiotemporal scales—40 years of sampling across the Northern Pacific Ocean, spanning the late 1970s climate regime shift and expansion of hatchery production, with associated changes in salmon abundance (*38*–*40*). Furthermore, the strength of the trends that we observed, especially for predation risk, emphasizes the power of these relationships; they are unlikely to be artifacts of other processes.

Beyond representing a test of doctrinal ecological theory, our results suggest that at least sockeye and chum salmon actively group in the open ocean. For these species, foraging success dropped precipitously for larger groups, indicating that grouping came at the cost of competition for food. We stress that, beyond evidence for competition, this result demonstrates that the grouping documented in this dataset was not facultative—these fish were not independently converging around a common food resource (*41*), as has been suggested for salmon in the literature (*27*). If so, then we would not expect their stomach fullness to decline with density. This contrasts with the prevailing view that, other than as juveniles entering the ocean and adults aggregating near river mouths as they return (*27*), salmon are generally isolated from one another at sea and only come

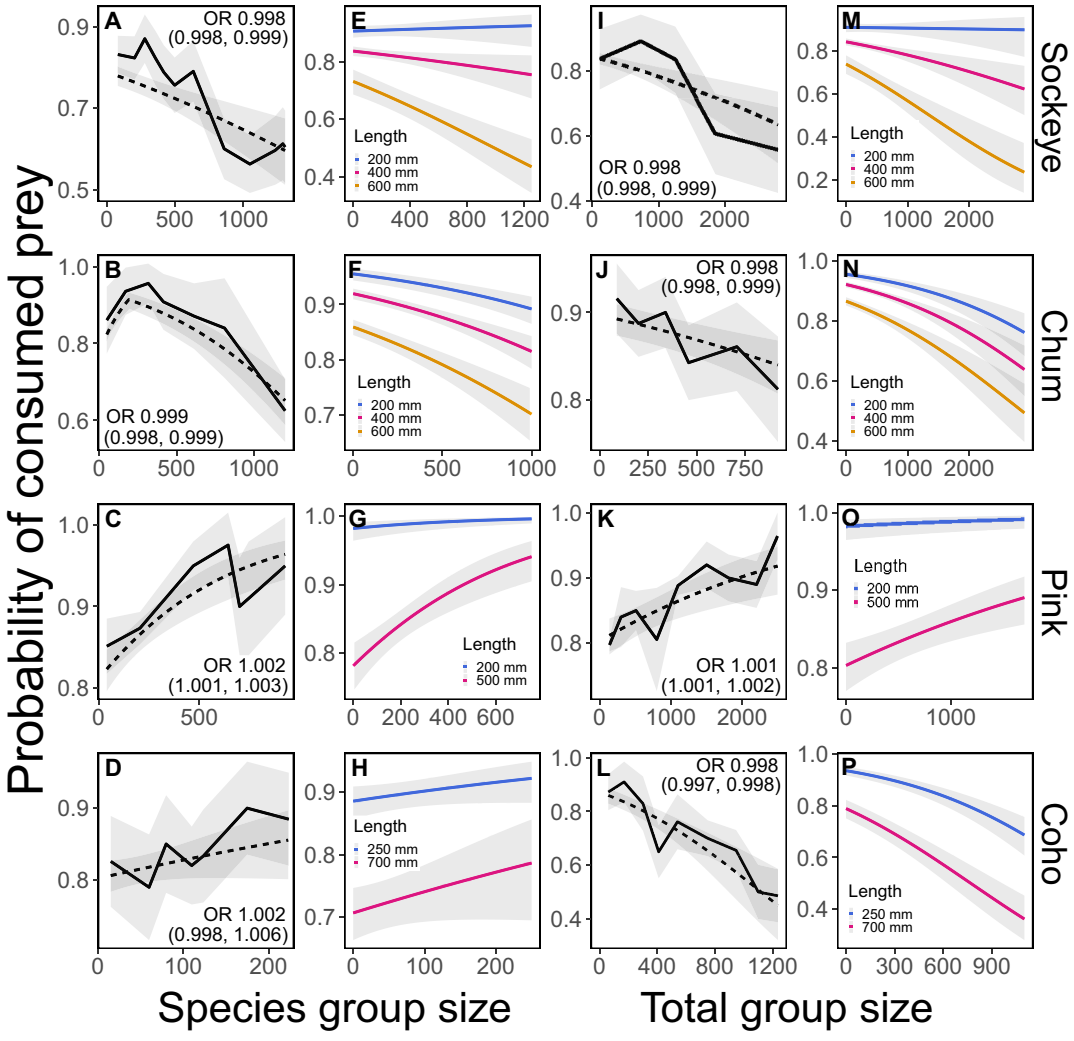

Fig. 5. Effect of group size on foraging success. The trend in the probability of a salmon having consumed prey as a function of its group size varied with species and body length. The first and third columns (**A** to **D** and **I** to **L**) show data aggregated for each species. The second and fourth columns (**E** to **H** and **M** to **P**) include the effect of body size. Consistent results were obtained using a nonbinary stomach fullness measure (see the Supplementary Materials). Solid lines represent raw data ± SD, and dotted lines represent model fit (logistic or piecewise logistic) ± 95% confidence intervals. OR is the expected change in the probability of predator injury for each unit of group size, with associated 95% confidence intervals. Note that the *y* axis varies between panels, to best illustrate trends in each species. Note also that the same data are plotted together for interspecific comparison in fig. S3.

together facultatively to feed on common resources (*40*). Foraging success increased with group size for pink salmon, so they may have been independently aggregating on rich feeding areas; however, the observed increase in foraging success in larger groups is also consistent with them schooling and benefiting from searching, foraging, or hunting collectively.

The observed differences between sockeye and chum versus pink and coho salmon could arise from their life history traits. Sockeye salmon typically spend 2 or 3 years in the ocean and migrate large distances offshore within the Gulf of Alaska, and chum salmon typically spend 2 to 4 years there (*40*). Pink and coho salmon, on the other hand, generally only spend one full year at sea, grow faster, and often are closer to their natal rivers than are chum and sockeye salmon (*40*). Catch data from this analysis confirmed these general patterns; sockeye and chum salmon tended to be farther offshore, grew more slowly, and stayed longer at sea than pink and coho salmon (figs. S8 and S9). 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 (*40*). For slower growing species such as sockeye 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 resource competition for species such as pink or coho salmon that stay closer to shore and spend less time in the ocean. Variations in diet might also contribute to the observed differences in the effects of group size on foraging success between salmon species. Diet differences have been reported for these species in, for example, the tendency to consume fishes, squid, crustaceans, and gelatinous zooplankton

(*39*, *40*). However, these are more matters of degree than absolute differences among species, and diets also vary considerably with fish size and among years. Without detailed information on the prey available to salmon at sea for comparison with their diets and their depth distributions and diel activity patterns, it is difficult to determine how schooling might affect feeding differently among salmon species.

Changes in observed patterns as fish aged/grew were consistent with salmon life history traits. The strength of the effect of group size on foraging success increased with age and size for all species, regardless of the sign of the effect. For sockeye and chum salmon, the negative effect of group size on foraging success increased with age and size, suggesting that these species experienced greater competition as they aged. Sockeye and chum salmon have more diverse age structures, spend more time in the ocean, and travel farther out in the ocean than pink or coho salmon (figs. S8 and S9), which could increase competition for food at later ocean life stages as these salmon move offshore. As the fish grow, they may switch to a more exclusive prey type and will require more food (*40*), so competition may increase. For pink and coho salmon, the positive effect of group size on foraging success generally increased with age and size, suggesting that the potential benefits of collective foraging were primarily experienced by older and larger fish or that older and larger fish tend to feed on more aggregated prey. For all species, while size and age did not affect the relationship between predation risk and group size, larger fish tended to occur in smaller groups. This is consistent with larger fish, which tend to have fewer predators (*15*), experiencing 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 (*27*). Larger fish might also experience higher competition, which could place more strain on bigger groups of large fish. Moreover, 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.

While all species benefited from grouping by reducing predation, for sockeye, chum, and perhaps coho salmon (considering the total rather than species-specific group size), this protection came at the cost of reduced foraging success. 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 oceanic salmon. In larger groups, these salmon may have less to eat due to competition but be less likely to be eaten. Predator avoidance is an important consideration because of its influence on lifetime fitness—a single encounter with a predator may result in death, which is far costlier than depressing even multiple foraging opportunities (*5*). Our results suggest that predator avoidance is the primary driver of grouping at sea for at least sockeye and chum salmon.

In support of predator avoidance as the primary driver of grouping in oceanic salmon, a wide range of predators were commonly caught in, or observed near, the purse seines (Fig. 1D). Soupfin shark (*Galeorhinus galeus*), longnose lancetfish (*Alepisaurus ferox*), blue shark (*Prionace glauca*), Arctic char (*Salvelinus alpinus*), salmon shark (*Lamna ditropis*), Dolly Varden (*Salvelinus malma*), dagger-tooth (genus *Anotopterus*), and spiny dogfish (*Squalus acanthias*) and other potential predators were caught in the purse seines. Marine mammal predators were also observed near many of the purse seines, including whales, seals, and porpoises. We found that 57% of purse seine sets that recorded bycatch data contained potential predators within the net and/or marine mammals nearby. In addition, salmon survival at sea is 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 (*40*). This wide variety and high occurrence of predators suggests that predation risk is very common in the open marine environment. Consequently, predator avoidance is likely to strongly affect the evolution of salmon behavior at sea, even at the expense of food intake.

The data that we examined presented both strengths and challenges. On the positive side, these unique data provided a large volume of information, collected blindly to the hypotheses tested here. However, working with the data necessitated several key assumptions. We assumed that the catch size was a reliable indicator of local density (group size). To increase our confidence in this assumption, we restricted our analysis to only purse seine catches (which capture a relatively small but consistent volume of water), excluding data from other forms of sampling gear. Secchi disk readings (mean = 20 m, SD = 16 m, n = 2817 records) indicated clear water, which would facilitate long-range visual interactions. To give the reader a sense of scale, roughly 370 salmon could fit into the net without seeing one another (assuming nonoverlapping spheres, each with a "sensing radius" of 10 m) (*42*). We note, however, that this estimate assumes salmon actively and perfectly avoid one another, so it is a liberal estimate of the upper bound. The social tendencies of salmon in other contexts suggest that they would be in behaviorally interacting groups at much lower catch sizes. Catches in our data may contain multiple smaller groups; however, given the scale of the net compared to the range of these species across the Pacific, catch size is at least a measure of local density, and our results suggest that this local density is ecologically relevant for predation and foraging. We 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. Our 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 (*24*, *25*). However, fish escaping a predator unscathed, or those that were consumed, would not be included in the proportion exposed to predation.

We assumed that differences in group sizes drive the trends in predation risk and foraging but briefly 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 cannot stay with the group because of diminished swimming performance. 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, then we would not expect sockeye and chum to have greater foraging success in smaller (weaker) groups. If the second were true, then we 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.

Salmon abundance, along with the abundance of their prey and predators, changed notably in the North Pacific in the late 1970s, due to a notable climatic shift and increases in hatchery production (*38*–*40*). To consider the potential role of this regime shift on the observed patterns, we explored disaggregated temporal data (pre- and post-1977). The relationships between predation risk, foraging success,

and group size were consistent before and after this regime shift. However, limitations of the data (inconsistent sampling effort and locations before and after the regime change) did not allow us to explore rigorously the effects of differing densities of salmon, their prey, and predators on the relationships we explored here.

Our results, highlighting the ecological role of grouping in salmon, add to a growing body of evidence that grouping plays an important role in several aspects of salmon life history. Juvenile Pacific salmon form schools, especially while feeding in lakes, during downstream migration, and at sea (*43*–*46*). More recent work shows that social interactions shape the timing of adult sockeye salmon on their final spawning migration (*47*), and adult Chinook salmon find passage through hydroelectric dams more rapidly when at high densities (*48*, *49*). Such collective navigation during homeward migrations can lead to increased straying rates at low population densities (*22*), which could, in turn, introduce positive feedback and nonlinearity into the dynamics of population size and genetic makeup (*50*, *51*). Less numerous species, such as Chinook salmon and steelhead, may be more susceptible to such collapses. For instance, Chinook and coho salmon have similar group sizes (*22*), yet their smaller population size may subject Chinook salmon to strong positive feedback and thus difficulty recovering stocks, consistent with their currently depressed population sizes (*39*, *52*). On the other hand, relatively low perennial population densities, especially in steelhead, could have reduced opportunities for grouping and lead to more solitary strategies, making their population dynamics less mediated by social processes.

Grouping is a ubiquitous and fundamental aspect of the life history of many marine fishes, and increased understanding of how social dynamics affect growth and survival of these species may provide key insights for management (*17*, *53*). Specifically, if a species' local density modifies its predation and foraging rates (and therefore its survival and growth), as is the case in our example, then 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 (*49*). 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.

MATERIALS AND METHODS

Materials

Site and data description

We 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 United States–Union of Soviet Socialist Republics (US-USSR) (KamchatNIRO, Petropavlovsk-Kamchatsky and 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 not only primarily purse seines (n = 4330 sets) but also gillnets (n = 24), longlines (n = 401), and rope trawls (n = 10), mostly from 1965 to 1991 and between April and September, with no sampling in November and December. The most commonly used purse seine net throughout the study period measured 46 m deep with a circumference of 704 m (*54*), which gives an approximate ellipsoid volume of 1,209,490 m^3. There was some variation among years and vessels in net size, and some were on the order of 10 to 20% greater in circumference, making this a conservative estimate. Secchi disk readings were taken at the time of net sampling, and the Secchi disk mean was 20 m with an SD of 16 m (n = 2817). The sample includes all purse seine stations with Secchi disk readings during the FRI tagging research (1956–1982, excluding 1979 and 1981 when there was no ocean research by FRI). There were no Secchi disk data for US-USSR cruises (1983–1991). 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 (*Oncorhynchus tshawytscha*), and steelhead (*Oncorhynchus 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. We limited analysis to data from purse seines because those nets surround and capture a discrete volume of seawater (*21*), 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 (*20*). After initial data cleaning, we 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 subsampling of individual fish resulted in a total sample size of 2407 sets that caught 69,422 fish. For the stomach fullness analysis, we selected only data for which stomach volume categories (empty, trace, medium, full, and distended) were recorded (461 purse seines of 3913 fish). For the predator injury analysis, we selected data for which predator injury (injury or no injury) was recorded (1303 purse seines and 46,588 total fish). We analyzed data for the four most common salmon species in the catch records: pink, sockeye, coho, and chum. We 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, provide a rare opportunity to investigate the way in which group size mediates predation risk and foraging success in a pelagic environment. All data were collected blindly with respect to the current purposes, and so observer bias is highly unlikely.

Methods

Predator injury

We 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 specific injuries, distinguished in the data from fishing-related injuries reported separately. We included covariates of sex, length, distance of the catch to the nearest shore (kilometers), and a random effect of purse seine and year. Distance from shore was measured by calculating the distance in kilometers from the site of the catch to the nearest shore. We 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, we ran a piecewise logistic regression model (Fig. 3). We plotted the probability of observing a predator injury as a function of group size and relative size alongside appropriately binned empirical data, and we plotted the probability of observing a predator injury as a function of group size for different lengths (Figs. 2 and 3). We binned empirical data by dividing the full range of group sizes into evenly spaced bins. For each bin, we calculated the average proportion injured (sum of predator injuries/number of fish), the average group size that those fish were in, and the SD of the data using $\sqrt{\frac{p(1-p)}{n}}$, where p is the average proportion injured. We assumed that species catch size was a proxy (reliable indicator) for group size or local density. We ran these models for both species catch size and total catch size (Fig. 2). For species catch size, we ran these models for all group sizes (fig. S1), but because many larger groups had no predator injuries, we presented truncated figures for each species focusing on smaller group sizes (Fig. 2). Because of low sample size, Chinook (631 fish; two individuals with observed predator injury) and steelhead (25 fish; zero individuals with observed predator injury) were excluded from our analysis.

Stomach fullness

We 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 use the data and collection methods, we ran three sets of predictive general linear mixed models to quantify the effect of group size on stomach fullness for each species. We 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, we recategorized the stomach fullness response variable into two binary categories—empty and containing prey. We then used a logistic regression model (including piecewise logistic regression) to predict the probability of observing prey in the 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 regrouping the data into categories that were more certain to be accurate (identifying an empty stomach versus one with prey). We plotted binned empirical data alongside the model fit for each species separately (Fig. 5) and also for all species together to facilitate interspecies comparison (fig. S3). We ran these models for total group size in addition to species group size (Fig. 5 and fig. S3). We also plotted model predictions for varying lengths (a proxy for size) for each species (Fig. 5). We fit models for each species using the stats package in R (version 3.5.0).

In our second set of models, we 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 (fig. S5). We fitted this model for each species using the VGAM (vector generalized linear and additive models) package in R (*55*). 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 OR or logit(), and the model is written as $\log\left(\frac{p_k}{1-p_k}\right) = \alpha_k + \beta_k X$ 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 PO 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 OR) 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: $\log\left(\frac{p_k}{1-p_k}\right) = \alpha_k + \beta_k X$ for $j = 1, \ldots, K-1$. We used the Brant test (*56*) to confirm that our model violated the PO assumption. We included sex and age as fixed effects in our PPO model. Unfortunately, the VGAM package currently only implements fixed-effects models, so we were unable to include purse seine and year as random effects in our model. Predicted probabilities were fit with 95% confidence intervals. With this model, we 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, we created a stomach fullness metric consisting of the weighted sum of the probabilities for each stomach fullness category for our third set of models. We assigned weights of 0, 0.25, 0.50, 0.75, and 1.0 to the stomach fullness categories empty, trace, medium, full, and distended, respectively. We then used a linear regression model (including piecewise linear regression) to predict the probability of observing stomach volume for varying species catch size for each salmon species. We plotted stomach fullness as a function of group size alongside appropriately binned empirical data (fig. S4A). To allow for interspecies comparison, we plotted model fit and raw data for all species in separate panels (fig. S4B).

SUPPLEMENTARY MATERIALS

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