

Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*)

T.P. Quinn, S.M. Gende, G.T. Ruggerone, and D.E. Rogers

Abstract: The number of sockeye salmon (*Oncorhynchus nerka*) killed by brown bears (*Ursus arctos*) in 13 streams over more than a decade in southwestern Alaska was best explained by an asymptotic increase to about 3000 salmon killed per stream per year as salmon density increased to 10 000 fish-ha⁻¹ of stream. Divergence from this pattern at some streams probably reflected variation in the number of bears using the stream (which we did not determine) and variation in salmon biomass consumed per fish killed. Daily surveys at one creek over 11 years revealed about 100–130 salmon killed per day, ranging from a few to over 600. Higher proportions of the available salmon were killed early and late in the season, when densities were low. Thus the number of salmon killed within and among years increased with salmon abundance but at a declining rate, and the proportion killed generally decreased. Our previous work indicated that the average proportion of salmon killed among streams was controlled mostly by stream size, affecting the ability of bears to catch salmon. These findings are important for understanding the effects of bears on salmon population dynamics and their role in the transport of nutrients from salmon carcasses.

Résumé : Le nombre de saumons rouges (*Oncorhynchus nerka*) tués par les grizzlis (*Ursus arctos*) dans 13 cours d'eau du sud-ouest de l'Alaska, pendant plus d'une décennie, se décrit le mieux comme une augmentation asymptotique atteignant 3000 saumons tués par cours d'eau par année, alors que la densité des saumons croissait pour atteindre 10 000 poissons-ha⁻¹ de cours d'eau. Les écarts de ce modèle dans quelques cours d'eau s'expliquent probablement par des variations du nombre d'ours qui utilisent le cours d'eau (ce que nous n'avons pas déterminé) et de la biomasse consommée par poisson. Des inventaires quotidiens dans un cours d'eau pendant 11 ans révèle que 100–130 saumons sont tués chaque jour, avec un écart allant de 0 à plus de 600. Une proportion plus élevée des saumons présents est tuée tôt et tard dans la saison, lorsque les densités sont faibles. Ainsi, le nombre de saumons tués au cours d'une année et d'une année à l'autre augmente avec l'abondance des saumons, mais à un taux décroissant et la proportion des saumons tués diminue généralement. Nos travaux antérieurs indiquent que la variation de la proportion moyenne de saumons tués d'un ruisseau à l'autre est régie principalement par la taille du cours d'eau qui affecte la capacité des ours de capturer les saumons. Ces résultats sont importants si l'on veut comprendre les effets des ours sur la dynamique de population des saumons et leur rôle dans le transport des nutriments à partir des carcasses de saumons.

[Traduit par la Rédaction]

Introduction

Predation is among the most fundamental ecological interactions between species, and the number and proportion of prey killed often depends on their density. This density dependence is a product of the numeric (changes in number of predators; Solomon 1949; Ricker 1952) and functional responses (changes in kill rate; Holling 1965). The nature of these relationships help to understand the basic ecology of the species involved and also to assess whether low prey density might lead to rebound (persistence) or local extinction (e.g., Seitz et al. 2001). Migratory animals and those with seasonal breeding in discrete areas are especially sub-

ject to density dependence because they are concentrated in time and space, so their availability to predators is constrained but highly predictable. This can result in "predator swamping" if the prey overwhelm the numerical or functional responses of the predators, or cycles of abundance or even local extinction if predators take increasingly high proportions of a population that has declined for other reasons.

Pacific salmon (*Oncorhynchus* spp.) present particularly good opportunities to study such density dependence because they are readily counted, have discrete life-history stages with opportunities for different predators to operate, and vary in density among populations and among years as a result of biotic and abiotic factors. Density-dependent preda-

Received 26 June 2002. Accepted 21 February 2003. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 11 June 2003.
J16963

T.P. Quinn,¹ S.M. Gende,² G.T. Ruggerone, and D.E. Rogers. Fisheries Research Institute, School of Aquatic and Fishery Sciences, P.O. Box 355020, University of Washington, Seattle, WA 98195, U.S.A.

¹Corresponding author (e-mail: tquinn@u.washington.edu).

²Present address: National Park Service, Glacier Field Station, 3100 National Park Road, Juneau, AK 99801, U.S.A.

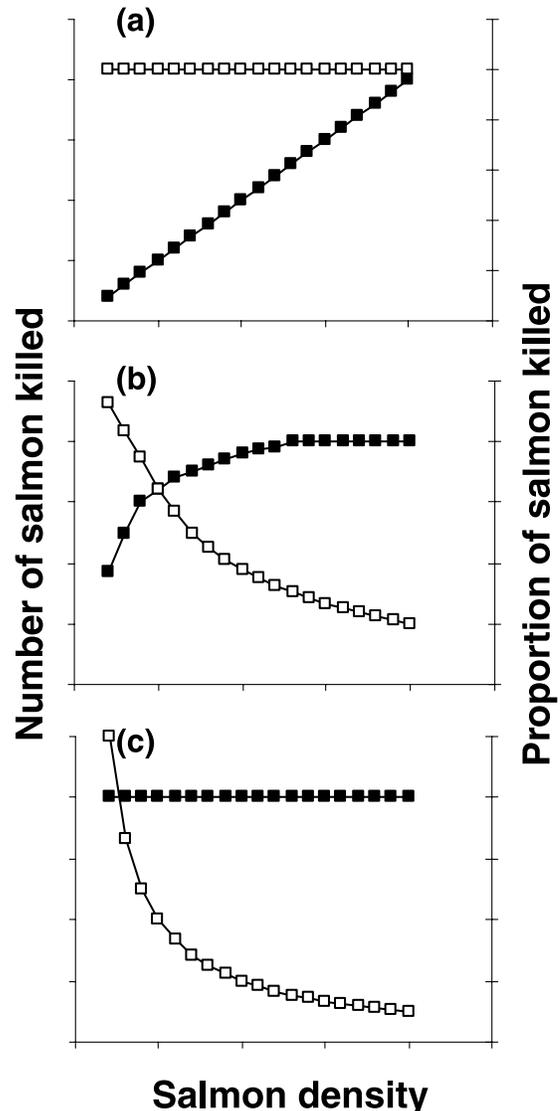
tion has been reported for sculpins, *Cottus* spp., eating salmon eggs (Foote and Brown 1998) and fry (Fresh and Schroder 1987), and common mergansers, *Mergus merganser* (Wood 1987) and Arctic char, *Salvelinus alpinus* (Ruggerone and Rogers 1984), eating seaward-migrating salmon smolts. Few studies have quantified predation pressure on adult salmon, but natural mortality is generally thought to be low on adults at sea (Ricker 1976) and their dispersed distribution may minimize density-dependent effects. However, adult salmon that spawn in small streams around the Pacific Rim can be subjected to intense predation by brown and black bears (*Ursus arctos* and *Ursus americanus*). Predation by bears on salmon has long been recognized (e.g., Shuman 1950; Frame 1974), and Clark (1959, p. 337) noted that "One can walk along almost any Alaska salmon stream in bear country during the summer spawning season and see jaws, heads, and other parts of salmon left by bears".

The relationship between salmon density and predation rates provides insight into the effects of salmon on bears, bears on salmon, and the broader ecological ramifications of this relationship. Bears move to streams to take advantage of the predictable arrival of salmon (e.g., Barnes 1989; Sellers and Aumiller 1994), and body size, litter size, and population densities of bears are correlated with salmon availability (Hilderbrand et al. 1999a). From the salmon perspective, size-selective predation by bears may affect the evolution of salmon populations (Quinn and Kinnison 1999; Ruggerone et al. 2000; Quinn and Buck 2001), as well as numerical effects on the populations. Finally, bears transport salmon carcasses from the stream, facilitating the transfer of marine-derived nutrients into the riparian zone (Ben-David et al. 1998; Helfield and Naiman 2001).

The relationship between density of salmon and the number and proportion killed by bears might take different forms. First, a constant proportion of the salmon might be killed, resulting in a linear increase in the number killed with density (Fig. 1a) if bears aggregated on a stream in direct proportion to salmon abundance, shifting from alternative dietary items as salmon become more abundant. Obviously, the number of bears is finite, but over an observed range of salmon densities, this pattern might occur. Second, the number of salmon killed might increase with density but at a declining rate (i.e., an asymptotic relationship; Fig. 1b) if the bear population was constant and predation was constrained by their handling time or satiation. Finally, all available salmon might be killed at low densities, shifting to a constant number of salmon killed at high densities (Fig. 1c).

Previous studies of bear predation have not been detailed and protracted enough to quantify the density-dependent patterns. Our purpose was to determine the relationship between predation by bears and salmon density at two temporal scales: (i) among spawning seasons at 13 streams and (ii) among days within years at one of these sites over 11 spawning seasons. We did not determine the number of bears using the streams, as it was not our goal to determine the numerical response of bears to salmon density, nor did we estimate components of the functional response relationship such as capture efficiency and handling time. Rather, we sought to determine the overall predatory response of bears to salmon densities. It is this response that is important to the salmon population and also to the forest where the bears may de-

Fig. 1. Hypothetical relationships between the number (■) and proportion (□) of Pacific salmon (*Oncorhynchus* spp.) killed and salmon density: (a) the patterns if bears killed a constant proportion of the available number of salmon, (b) an asymptotic relationship, and (c) the patterns if all available salmon were killed at low densities, shifting to a constant number killed at high densities.



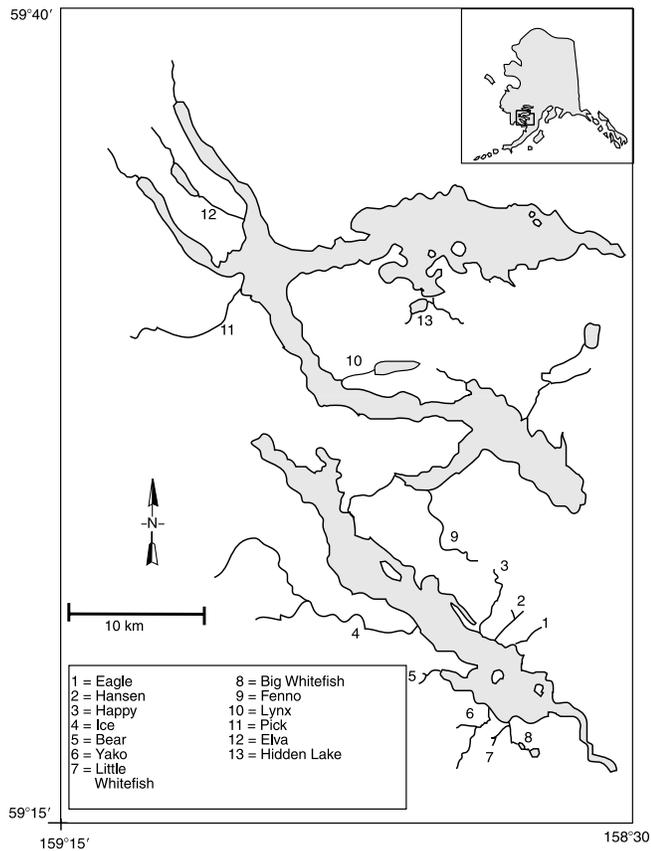
posit nutrients from salmon via carcass deposition and excretion.

Material and methods

Survey methods

We conducted annual surveys of 13 streams in the Wood River system, southwestern Alaska (Fig. 2), encompassing a wide range of physical characteristics that influence salmon density and accessibility to bears (Quinn et al. 2001a). All streams have clear water and pristine habitat, and range in average width from 1.7 m (Little Whitefish Creek) to 15.7 m (Ice Creek; Marriott 1964). The crew (typically three people) walked upstream, counting the live and dead salmon either over the entire usable length (i.e., to a barrier to mi-

Fig. 2. Map of the Wood River system (and insert with its location in Alaska, U.S.A.) showing the locations of the sites that were surveyed for sockeye salmon (*Oncorhynchus nerka*) abundance and brown bear (*Ursus arctos*) predation.



gration or a region with unsuitable habitat and perennial absence of salmon) or over a standard reach of the creek defined from maps and descriptions specific to each creek. The counts included all carcasses readily visible in the stream channel and riparian zone. Beginning in 1986 and regularly since 1990, these surveys have categorized all salmon by mode of death: “senescent” and “bear kill”. Senescent salmon had died after spending 1–3 weeks in the stream (Quinn et al. 2001b) and were easily distinguished by emaciation, dried and scarred skin, and fungus on the body. Bear-killed fish were distinguished by the holes from canine teeth, typically in the dorsal area, and varying amounts of tissue removed (Gende et al. 2001). Some carcasses (about 10–20%; Quinn and Buck 2000) are scavenged by bears after death and left in the stream. Such postmortem bites would inflate the predation rate but would be offset to some extent by fish that were killed but undetected because they were carried from the stream by bears or consumed almost entirely (about 20–30%; Quinn et al. 2001b). There is also scavenging by gulls and, to a lesser extent, other birds, but these wounds are readily distinguishable from wounds inflicted by bears. The mode of death was ambiguous in some severely deteriorated carcasses, but we limited the category “bear killed” to carcasses where this was the obvious cause of death.

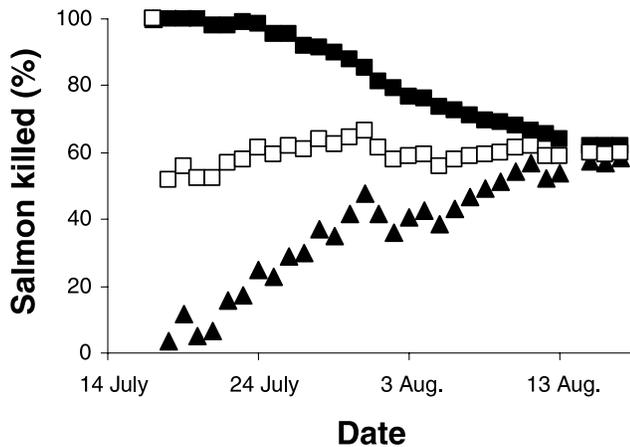
The surveys were conducted when there were still live salmon in the creek in most years, but after virtually all salmon had arrived. This intermediate timing of surveys is

appropriate because at the very end of the run the carcasses are in such an advanced state of decomposition or desiccation that we often cannot reliably determine the cause of death. We therefore developed an index of predation based on these once-a-year surveys to estimate the total number of salmon that would have been killed and validated it (see Quinn et al. 2001a for more details) with daily surveys on Hansen Creek. This creek averages 10 cm deep and 4 m wide (Marriott 1964) and flows 2 km from a beaver pond to Lake Aleknagik. The water is very clear and flow fluctuations are negligible, facilitating accurate surveys for live and dead salmon. Crews walked the entire length of this creek daily from the first day when salmon were seen entering until the run was almost finished in mid- to late August during 1986 and 1990–2001, counting all live and dead salmon and removing fresh carcasses to prevent double counting. If we express predation as the number of bear kills relative to the total number of dead fish (bearkilled + senescent dead), then surveys early in the spawning season overestimate predation because there are few senescent fish and most of the dead have been killed. Towards the end of the season, this number converges on the final proportion of salmon killed, as progressively fewer live fish remain (e.g., 1997; Fig. 3, top line). On the other hand, if we express predation as the number of bear kills relative to the total number of salmon (live + bear-killed + senescent dead), then surveys early in the season underestimate predation because some live fish will eventually be killed (Fig. 3, bottom line). This estimate also converges on the correct proportion at the end of the season when no live fish remain. Examination of daily survey data has repeatedly shown that the average of these two calculated predation levels is nearly constant over all but the first few days of the spawning season (Fig. 3, middle line), and this was our index of predation.

Although the index was a valid estimate of predation throughout much of the run, the total number of salmon seen on the survey near the midpoint of the run used for estimating density was lower than the total run because some fish entered the creeks after the survey and some carcasses were moved into the forest. For example, had the Hansen Creek surveys been conducted on 6 August (the typical date before intensive surveys), we would have estimated the run sizes at, on average, 74.6% of the total, though the run size estimates on 6 August and at the end of the season were highly correlated ($r^2 = 0.98$). We used the 6 August estimates for Hansen Creek when analyses compared Hansen Creek data with those from other creeks (e.g., comparisons of density among sites) but used the slightly more accurate end of season estimates for analyses restricted to Hansen Creek data. The 6 August and final Hansen Creek predation estimates were also highly correlated ($r^2 = 0.84$) and unbiased, having a slope near 1 (regression line $y = 1.056x - 5.791$; 95% confidence interval around slope: 1.17 to 0.94).

The Hansen Creek surveys provided daily estimates of the density and number of salmon killed. On any given survey day, the freshly dead salmon would have been alive on the previous day, so they were included as available for the bears to kill on the day preceding the survey. The most complete surveys were from 1991 to 2001, but there were eight instances when a day passed without a survey during the run: once each in 1997 and 2000, twice in 1991, and four

Fig. 3. Sockeye salmon (*Oncorhynchus nerka*) killed on a given day, plotted as a percent of that day's dead salmon (■), as a percent of that day's live + dead salmon (▲), and the average of those two values (□), for Hansen Creek in 1997 as an example.



times in 1992. In those cases, we estimated the live count on the missing day as the average of the previous and following days and allocated the dead fish evenly between the two dates. This was necessary, because the dead from two days otherwise would be analyzed with the live count on a single day. In some years, our surveys ended before all fish had died. On average, the live count on the last survey date was only 4% of the total number of salmon that entered the stream (live plus cumulative dead to that date), but in some years there were as many as 17% live. Some of these fish would have eventually been killed, so the number of observed kills was expanded in proportion to that year's predation level, estimated from the data through the last survey.

Data analysis

To examine predation across all sites and years, we initially combined the predation indices from all creeks and all surveys, plotting salmon density (live + dead per hectare of wetted stream area) against number killed. We constructed three models (hypotheses) to describe density-related predation rates and used maximum likelihood estimates to determine the model most consistent with the data (Hilborn and Mangel 1997). Each stream was then considered separately to examine patterns of density and predation among creeks. Our first model was that the number of salmon killed (k_i) increased linearly with the density of salmon, which is equivalent to a constant proportion of fish killed (Fig. 1a).

$$(1) \quad k_i = p_i N_i$$

where p_i is the proportion of the population killed each year and N_i is the number of fish in the stream on year i .

Second, we fit an asymptotic curve to the data; the number killed increased with density but at a decreasing rate of increase (Fig. 1b).

$$(2) \quad k_i = \alpha e^{-\beta x}$$

Asymptotic relationships are similar in form to Holling's type II functional response curve. However, we did not fit a type II curve to the data because the parameters of this equation represent the number of prey killed per predator over varying prey densities (e.g., O'Donoghue et al. 1998; Sundell

et al. 2000). We did not know the number of bears using the streams, so our data represent the total response of bears to changes in salmon density: the product of the functional (changes in capture and handling efficiencies) and numerical responses (aggregation of bears at sites).

Our third model was that bears killed a constant number of fish regardless of density once some minimal level was reached (Fig. 1c).

$$(3) \quad k_i = \min(N_i, C_i)$$

where C_i is the constant number eaten. On an annual basis, the model output was either the (predicted) constant number killed or the total number of fish in the stream, whichever was smaller (min), so the model would not predict more fish killed than were present when few fish were available.

We also explored the density-dependent hypotheses on a daily basis at Hansen Creek, where we had about 30 daily estimates of predation for each of 11 years (1991–2001; 325 total daily estimates). Models were fit to the data using similar procedures except that each estimate was on a daily rather than an annual basis. The three models were fit to the observed number of fish killed per year (for each creek) or day (for Hansen Creek) and collectively (when all streams or days were pooled). For each day or year, k_i was the observed number of fish killed, and \hat{k}_i was the predicted number of fish killed for each day or year i for each model. Each model was fit assuming a log-normal error distribution where the deviation (D_i) is the log of observed – log of predicted number of fish killed (Hilborn and Mangel 1997, p. 148).

$$(4) \quad D_i = \ln(k_i) - \ln(\hat{k}_i)$$

We used maximum likelihood estimates to examine which model best fit the data by minimizing the sum of the negative log likelihoods

$$(5) \quad L_i = -\ln \left(\frac{1}{\sqrt{2\pi\sigma^2}} \exp \left(-\frac{(D_i)^2}{2\sigma^2} \right) \right)$$

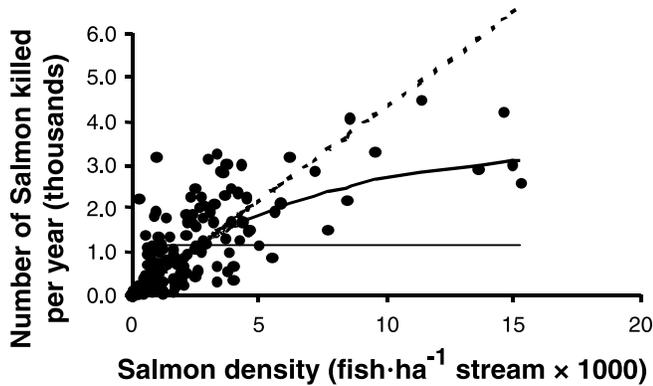
where L is the likelihood of the data for each year or day and σ is the square root of the average of deviations across all i . The performance of each model was evaluated using Akaike's information criterion (AIC; Akaike 1973), which essentially tests for parsimony of models whereby predictive ability is maximized but complexity (number of parameters in the model, P) is penalized. Smaller AIC values indicate more parsimonious models.

$$(6) \quad AIC_i = L(Y|M_j) + 2P$$

where L is the sum of the negative log likelihoods for each model (M_j) given the data (Y).

Analyses of the annual and daily predation rates were all conducted from the perspective of the salmon population, posing forms of the question, "How does salmon density affect the number of salmon killed?" However, the perspective of salmon may also be expressed by the question, "How does the density of salmon affect the probability of an individual being killed?" This perspective is reflected in the secondary y axes in the panels of Fig. 1. Such analyses are typically done by plotting percent killed against abundance, but this produces spurious correlations and is statistically invalid (Berges 1997). Nevertheless, it is still useful to con-

Fig. 4. Predation by brown bears (*Ursus arctos*) as a function of annual density of adult sockeye salmon (*Oncorhynchus nerka*; fish·ha⁻¹ stream) for 13 streams in southwestern Alaska surveyed in at least 8 years between 1986 and 2002. The relationship was best described by an asymptotic curve (heavy line: $r^2 = 0.60$; salmon killed per year = $3784e^{-0.000132x}$). The broken line indicates that pattern that would be expected if bears killed a constant proportion of the available number of salmon, and the thin line shows the pattern that would be expected if all available salmon were killed at low densities, shifting to a constant number killed at high densities.



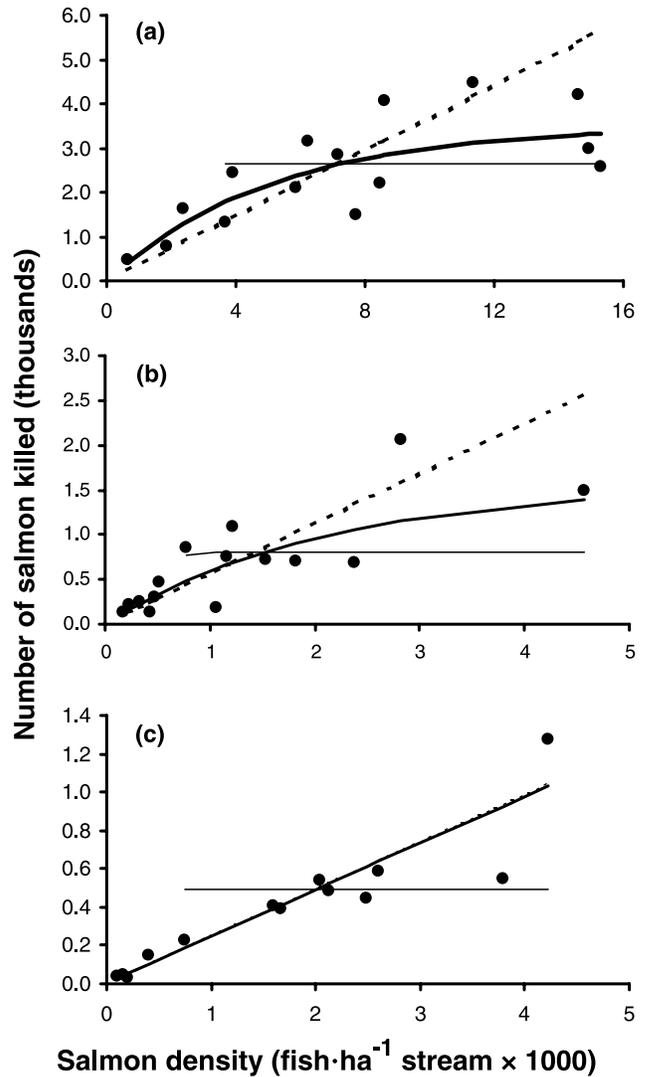
sider this perspective (e.g., Seitz et al. 2001), so we discuss some of the data in this manner.

Results

Responses among streams

There were 168 annual estimates of predation over the 1986–2002 period from 13 streams, providing data on predation and fish abundance. When all sites and years were pooled, the fit of the asymptotic model ($r^2 = 0.60$) was superior to those of the constant model ($\chi_{1,0.05} = 41.39$, $p < 0.001$, $r^2 = 0.27$) and the linearly increasing (proportional) model ($\chi_{1,0.05} = 4.41$, $p < 0.05$, $r^2 = 0.54$; Fig. 4). Such data pooling, however, masks variation among sites, and examination of each creek separately revealed considerable variation in the average number and proportion of the salmon population killed per year (Table 1). At no site did the proportional model clearly explain more of the variation than the asymptotic model, though at about half of them (Bear, Eagle, Fenno, Happy, Little Whitefish, and Yako), the models performed equally well. At most of the other sites, the relationship was better explained by the asymptotic model ($\bar{x} r^2 = 0.46$ for asymptotic relationships among sites; Table 2) with predation leveling off at about 20–33% of the salmon population. However, at some sites, essentially linear relationships between density and number killed were seen (Bear, Fenno, Little Whitefish, and Yako). Hansen, Hidden Lake, and Eagle creeks provide good examples of the spectrum of the relationships (Fig. 5). We were often unable to statistically differentiate between proportional (linearly increasing) and asymptotic predation because there were few data points at the highest densities. The only site at which the asymptotic relationship was significantly different than that of the proportional model was at Hansen Creek, which varied greatly in the density of spawning salmon (range 630 – 15 318 salmon·ha⁻¹ of stream area).

Fig. 5. Predation by brown bears (*Ursus arctos*) over a range of annual densities of spawning sockeye salmon (*Oncorhynchus nerka*; fish·ha⁻¹ stream) in (a) Hansen Creek, (b) Hidden Lake Creek, and (c) Eagle Creek. The lines indicate the models of proportional (broken line), asymptotic (heavy line), and constant (thin line) predation. Note the differences in scale of the x axes for the three creeks. For Eagle Creek, the proportion and asymptotic lines are virtually identical.



Daily responses

Considering all of the 325 daily surveys over an 11-year period, predation at Hansen Creek averaged between 100 and 200 salmon killed per day over a very wide range of densities (Fig. 6). The asymptotic model (AIC = 441) provided a significantly better fit to the data than either the proportional model ($\chi_{1,0.05} = 117.1$, $p < 0.001$, $r^2 = 0.07$) or the constant model ($\chi_{1,0.05} = 89.02$, $p < 0.001$, $r^2 = 0.09$). However, there was great variation, from over 600 fish killed (at intermediate densities) to very few killed, even at some very high densities. On over 50% of the days, fewer than 100 salmon were killed, and density explained only a small amount of the variation in number killed, even for the best-fitting asymptotic model ($r^2 = 0.14$). No model consistently

Table 1. The number of years of data (N), average sockeye salmon abundance (\pm standard error, SE) and density (fish·ha⁻¹ \pm SE), and average predation level (number killed \pm SE and % of the salmon population killed \pm SE) for 13 streams in southwestern Alaska.

| Creek | N | Abundance | Density | No. killed | % killed |
|------------------|-----|-----------|-----------|------------|----------|
| Bear | 13 | 3907±440 | 2488±280 | 1183±117 | 32±3 |
| Big Whitefish | 9 | 786±200 | 1002±254 | 342±101 | 48±6 |
| Eagle | 13 | 818±181 | 1704±378 | 399±93 | 53±4 |
| Elva | 11 | 90±19 | 41±9 | 27±7 | 33±6 |
| Fenno | 14 | 5228±1066 | 1332±272 | 666±201 | 12±3 |
| Hansen | 15 | 6229±1026 | 7509±1236 | 2450±312 | 49±6 |
| Happy | 14 | 9537±1628 | 4859±829 | 1957±249 | 24±3 |
| Hidden Lake | 15 | 2010±491 | 1365±333 | 671±141 | 43±5 |
| Ice | 15 | 9032±2044 | 893±202 | 1299±236 | 19±4 |
| Little Whitefish | 8 | 173±43 | 838±209 | 93±25 | 58±8 |
| Lynx | 15 | 2651±587 | 1545±342 | 547±126 | 24±4 |
| Pick | 14 | 5837±413 | 3170±224 | 1949±243 | 35±4 |
| Yako | 12 | 2862±434 | 1190±181 | 867±189 | 30±4 |

Table 2. Akaike's information criterion (AIC) and r^2 values for three hypothesized models of density-related predation rates (predation is proportional, asymptotic, or constant) in 13 different creeks.

| Site | Proportional | | Asymptotic | | Constant | |
|------------------|--------------|-------|------------|-------|----------|-------|
| | AIC | r^2 | AIC | r^2 | AIC | r^2 |
| Bear | 6.86a | 0.30 | 8.63a | 0.28 | 7.47a | 0.01 |
| Big Whitefish | 7.79ab | 0.48 | 4.89a | 0.58 | 9.20b | 0.05 |
| Eagle | 4.55a | 0.82 | 4.47a | 0.83 | 17.83b | 0.43 |
| Elva | 15.55a | 0.21 | 13.29a | 0.28 | 15.94a | 0.13 |
| Fenno | 23.12ab | 0.54 | 22.13a | 0.54 | 25.95b | 0.26 |
| Hansen | 11.08b | 0.51 | 4.63a | 0.62 | 10.23b | 0.36 |
| Happy | 14.59a | 0.28 | 13.56a | 0.33 | 14.61a | 0.19 |
| Hidden Lake | 13.60a | 0.53 | 12.39a | 0.59 | 15.19a | 0.40 |
| Ice | 20.60a | 0.25 | 20.38a | 0.24 | 21.06a | 0.24 |
| Little Whitefish | 8.02a | 0.51 | 7.60ab | 0.54 | 11.80b | 0.01 |
| Lynx | 16.23a | 0.33 | 15.17a | 0.39 | 17.49a | 0.01 |
| Pick | 16.78a | 0.01 | 15.51a | 0.09 | 15.46a | 0.09 |
| Yako | 15.11a | 0.68 | 15.11a | 0.68 | 16.81a | 0.05 |
| Average | 13.45 | 0.42 | 12.67 | 0.46 | 15.31 | 0.17 |

Note: Smaller, more parsimonious models are indicated by smaller AIC values. Different letters following values indicate significant differences among models at $\alpha = 0.05$.

gave the best fit to the data on daily rates of predation across years at Hansen Creek (Table 3). Furthermore, there was no apparent relationship between the density of salmon and the best-fitting model. That is, a given model did not fit the data best at high, low, or intermediate densities. The years 1998 and 2000 provide good examples of the daily variability in predation relative to salmon density (Fig. 7). In 1998, when salmon densities were high (>13 000 total fish or >1 fish·m⁻² on some days), the number of salmon killed rose almost linearly with salmon densities until the density of salmon exceeded about 4000, when the number of fish killed reached a plateau at about 300 per day. In 2000, the total run was fewer than 4000 salmon and the number killed increased steadily, but the plateau was poorly defined because there were few observations at high densities. In both years, however, there was considerable variation in the number of fish killed per day, and there were many days when salmon were very abundant but few were killed.

The daily surveys provided some evidence as to why the responses varied among years. On average, the abundance of salmon showed a normal distribution, rising sharply to a distinct peak and ending about 4 weeks after they first entered the stream. The proportion of salmon killed was typically high at the beginning, declined rapidly as salmon became more abundant, and then increased slightly at the end. However, there were days, especially near the beginning of the run in some years, when very few fish were killed. The year 1992 exemplified the average pattern. The fish that arrived first experienced high predation rates (over 40% killed per day for the first 3 days and over 10% for the 2 days thereafter), but the abundance of salmon increased and the percentage killed declined quickly until it increased again at the end of the run when few salmon were available (Fig. 8a). In contrast, the first 4 days of 1993 (except for 2 days when only 2–3 fish were present and percent predation would not be meaningful) had low levels of predation, followed by 40–

Fig. 6. Predation by brown bears (*Ursus arctos*) as a function of daily density of adult sockeye salmon (*Oncorhynchus nerka*; fish·ha⁻¹ stream) for 11 years (1991–2001) at Hansen Creek in southwestern Alaska. Solid circles are the observed number of salmon killed per day. The lines indicate the models of proportional (broken line), asymptotic (heavy line), and constant (fine line) predation. Relationship was best described by an asymptotic curve ($r^2 = 0.14$; salmon killed per day = $99e^{-0.0032x}$).

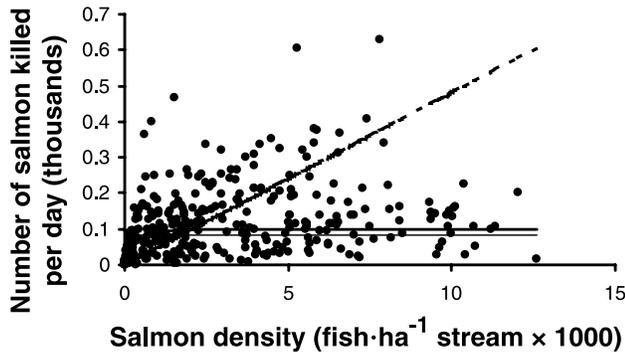


Table 3. Total number of sockeye salmon spawning in Hansen Creek (1991–2000), Akaike’s information criterion (AIC) values, and r^2 values for three hypothesized models of density-related predation rates (predation is proportional, asymptotic, or constant).

| Year | Run size | Proportional | | Asymptotic | | Constant | |
|---------|----------|--------------|-------|------------|-------|----------|-------|
| | | AIC | r^2 | AIC | r^2 | AIC | r^2 |
| 1991 | 16 296 | 43.1a | 0.01 | 41.5a | 0.07 | 40.5a | 0.01 |
| 1992 | 7 292 | 62.0b | 0.01 | 39.2a | 0.03 | 39.6a | 0.01 |
| 1993 | 4 212 | 51.5b | 0.18 | 40.7a | 0.18 | 39.7a | 0.13 |
| 1994 | 7 413 | 15.3a | 0.72 | 17.3a | 0.72 | 40.6b | 0.15 |
| 1995 | 17 435 | 50.4c | 0.02 | 39.7a | 0.10 | 44.4b | 0.08 |
| 1996 | 9 326 | 51.3a | 0.11 | 50.6a | 0.09 | 53.1a | 0.04 |
| 1997 | 8 451 | 36.9a | 0.52 | 38.3a | 0.56 | 48.7b | 0.14 |
| 1998 | 13 646 | 34.3a | 0.62 | 33.1a | 0.63 | 46.9b | 0.07 |
| 1999 | 19 504 | 49.0b | 0.09 | 25.4a | 0.18 | 24.7a | 0.14 |
| 2000 | 3 460 | 19.2a | 0.56 | 17.5a | 0.60 | 24.4b | 0.18 |
| 2001 | 1 966 | 13.9b | 0.61 | 10.1a | 0.70 | 23.1c | 0.29 |
| Average | | 38.8 | 0.31 | 32.1 | 0.35 | 38.7 | 0.11 |

Note: Different letters following values indicate significant differences among models at $\alpha = 0.05$.

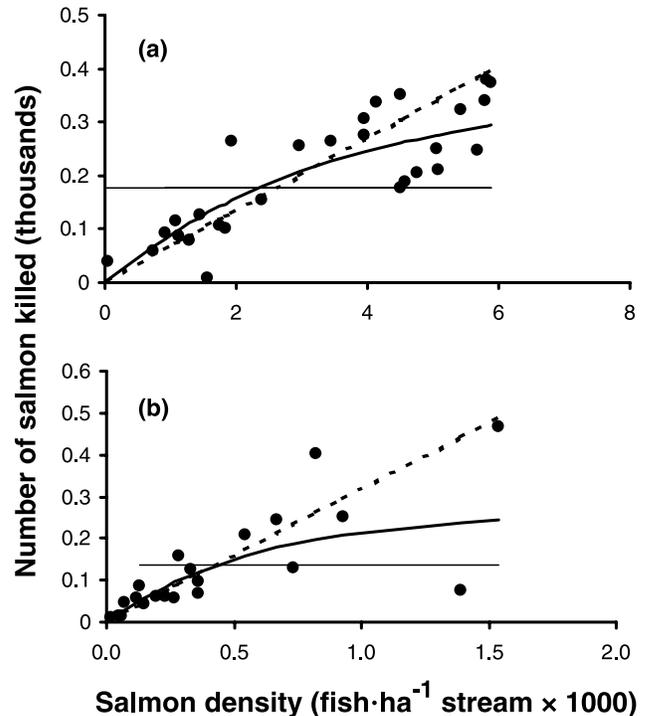
60% predation per day for 2 days before abundance overwhelmed the ability of the bears to kill a high percentage of the run (Fig. 8b).

Discussion

Responses among streams

Bears killed an increasing number of salmon as fish density increased on an annual basis, but the rate of increase tended to decline at high densities so that the total number killed approached an asymptote, though at several sites the data were equally indicative of a linear increase in predation. We do not know the number or status of bears using each stream, and that information would help explain some of the variation among and within creeks. The overall inability of bears to kill a linearly increasing number of salmon proba-

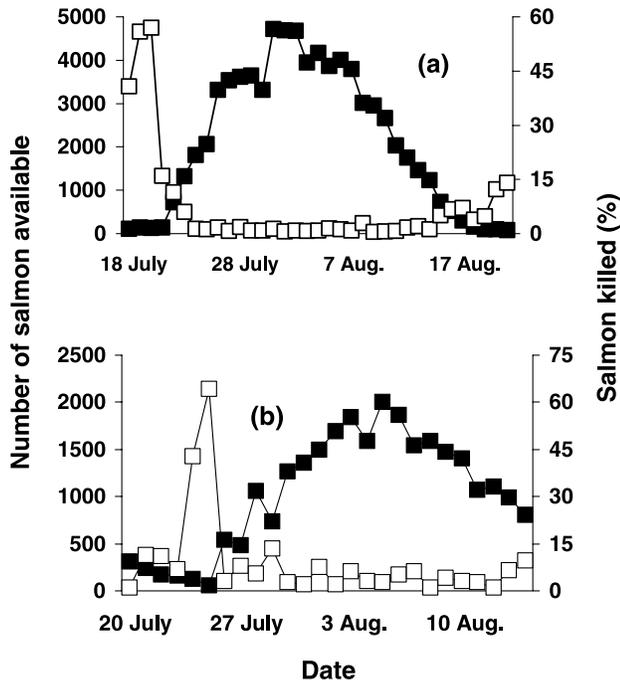
Fig. 7. Variation among years in the predation response of brown bears (*Ursus arctos*) to daily differences in density of spawning sockeye salmon (*Oncorhynchus nerka*; fish·ha⁻¹ stream). Each line represents a different model (hypothesis) including a proportional (linear) model (broken line), asymptotic (heavy line), and constant (thin line) predation. Note the difference in scale of the x axes for (a) 1998 and (b) 2000.



bly reflects both the finite number of bears in the area and social interactions among bears limiting time spent foraging on salmon. The bear’s decision to utilize a salmon stream will presumably be a function of the trade-offs between costs and benefits (Stephens and Krebs 1986). The energy density in salmon is higher than in other dietary items such as berries (Welch et al. 1997), and fitness related variables (e.g., body size and number of cubs) have been linked with access to spawning salmon (Hilderbrand et al. 1999a). However, utilization of clumped food resources often results in agonistic interactions (e.g., Chi 1999), and bears can seriously injure or kill each other (e.g., McClellan 1994). Social interactions among bears can limit predation at high salmon densities. Socially dominant bears spent more time on streams and killed more salmon than subordinate bears; the latter visited the streams less often, spent less time fishing per visit, and spent more time in vigilance behavior when near the stream (Gende 2002). Interference among predators is a common component of predator–prey systems (Ens and Goss-Custard 1984; Abrams and Ginzburg 2000), so at some point bears may simply avoid the streams, limiting the number fishing there.

Although the number of bears using a stream is probably limited by social constraints, lack of clear asymptotes in the models also reflects “adaptive” foraging behavior (Abrams 1990) by bears to changes in salmon density. The biomass consumed per captured salmon was inversely related to salmon density (Gende et al. 2001). Bears selectively consumed body

Fig. 8. Daily predation rate (percent of available fish killed per day, \square) and abundance (■) of salmon during (a) 1992 and (b) 1993 sockeye salmon (*Oncorhynchus nerka*) spawning seasons in Hansen Creek.



parts highest in energy when salmon density was high, thus killing more fish than would otherwise be predicted. Towards the end of the spawning season, many salmon (typically those near death and so nearly devoid of fat; Gende 2002) were bitten by bears but no tissue was eaten. We classified such fish as killed, but they would provide almost no nutrition to the bears and would have died soon anyway.

It is not obvious why a few of the creeks displayed little relationship between salmon density and the number killed. The average proportion of salmon killed among creeks is generally a function of the width of the stream (Quinn et al. 2001a). Pick and Fenno creeks had weak relationships between density and predation, but they are neither the largest nor the smallest creeks and are neither unique nor extreme with respect to structural complexity, gradient, or other features. The variation in overall predation among years at these sites may be related to the number of bears or alternative feeding opportunities but we have no data to evaluate these hypotheses. At the low end of the range of salmon densities, there was no apparent level below which the bears made no effort to catch salmon at all. For example, Elva Creek is comparatively steep with larger substrate than would be considered ideal for sockeye salmon spawning (Marriott 1964). It has had very low densities (average = 90 salmon in the creek or 41 fish·ha⁻¹ of stream area) but there was still an average predation level of 33%, even though this was only 27 salmon per year. Perhaps social dynamics constrained some bears to forage on this creek rather than to move to more profitable sites elsewhere.

Daily responses

Processes that affected the number of bears using streams from year to year probably also operated at Hansen Creek

from day to day, and the patterns of predation there varied among years. In most years, the predation was intense at the beginning of the run, but in some years, few fish were killed for several days, as though the bears were feeding primarily on other resources. On a daily basis, the number of bears using a stream will be related to their movements, and both social status and the degree of satiation influence the number of fish killed per bear each day. For example, it was not uncommon to walk Hansen Creek and find 200 bear-killed fish on one day but far fewer on the next, despite similar densities of salmon and presumably similar numbers of bears in the vicinity. In southeastern Alaska, Gende (2002) observed an individual bear kill up to 25 salmon during a foraging bout but kill only a few during the next visit to the stream (about 4 h later). Interaction between degree of satiation, number of visits to the stream per day, the total number of bears using a stream, and selective consumption all contribute to the daily variation in the number of fish killed.

Implications for salmon populations

Examination of the data from the fish's perspective (i.e., the proportion killed) revealed different patterns than those from the predator's perspective. There was little relationship between the average proportion killed and either average salmon density or overall abundance among creeks, nor was there a relationship between density and proportion killed using all surveys together. Examination of individual creeks revealed a few significant relationships between density and predation. In many cases, the relationships were strongly suggestive but the statistical power was limited ($n = 8-15$) and a single apparent outlier weakened the relationship. The best predictor (52% of the variation) of proportional predation among the creeks was the size of the creek, especially width (Quinn et al. 2001a). The wider the creek, the lower the chance that an individual fish will be killed. This is readily explainable by the escape opportunities afforded by larger habitats and is consistent with our observations elsewhere (Quinn and Kinnison 1999). Nevertheless, the number (as opposed to proportion) of fish killed by bears increases where the fish are more abundant and more dense.

The consequences of predation for the dynamics and evolution of the salmon populations will depend on whether they were killed before or after they spawned. Bears tend to kill newly arrived (i.e., ripe) salmon if possible, but in larger creeks, most of the salmon spawn before they are killed (Quinn et al. 2001b; Gende 2002). However, there can be effects of extreme predation at very low salmon densities. From 1995 through 2002, the great majority of sockeye salmon were killed in a series of small, spring-fed ponds and creeks near Pedro Bay on Iliamna Lake (Quinn and Kinnison 1999; T. Quinn, unpublished data). In 1996, 1997, 2000, 2001, and 2002, the salmon were so scarce that almost all were killed prior to spawning, and almost no redds were seen in several ponds that supported hundreds of salmon in other years. It will remain to be seen how these populations respond (e.g., recruitment and colonization) to such intense predation. On a daily basis, the first salmon to arrive may be at great risk of predation when bears are present, and they might be killed prior to spawning. In general, the proportion of salmon killed was higher at the beginning of the run than at the middle, and such predation may select against early arrival in streams with

high predation risk. A higher proportion were also killed at the end than the middle of the run but by then most salmon had spawned so the effect would be less significant.

In conclusion, the number and proportion of salmon killed can be largely explained by fixed, physical features of streams and the variable density of salmon. Further development of these relationships will help assess the role of bears in the evolution, life history, and population dynamics of salmon (Quinn et al. 2001a, 2001b) and the role of bears in the transport of marine-derived nutrients in riparian ecosystems (Ben-David et al. 1998; Willson et al. 1998; Hilderbrand et al. 1999b).

Acknowledgements

We thank the crews who conducted these surveys, the Pacific Seafood Processors Association for financial support, and the National Science Foundation's Long Term Research on Environmental Biology Program. Comments from Daniel Schindler, Jennifer Ruesink, and Ray Hilborn enhanced the manuscript.

References

- Abrams, P.A. 1990. The effects of adaptive behavior on the Type-2 functional response. *Ecology*, **71**: 877–885.
- Abrams, P.A., and Ginzburg, L.R. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* **15**: 337–341.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* Second international symposium on information theory. *Edited by* B.N. Petrov and F. Csaki. Akadémiai Kiadó, Budapest. pp. 267–281.
- Barnes, V.G. 1989. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. *Int. Conf. Bear Res. Manag.* **8**: 305–313.
- Ben-David, M., Hanley, T.A., and Schell, D.M. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos*, **83**: 47–55.
- Berges, J.A. 1997. Ratios, regression statistics, and “spurious” correlations. *Limnol. Oceanogr.* **42**: 1006–1007.
- Chi, D. 1999. The effects of salmon availability, social dynamics, and people on black bear (*Ursus americanus*) fishing behavior on an Alaskan salmon stream. Ph.D. thesis, Utah State University, Logan.
- Clark, W.K. 1959. Kodiak bear – red salmon relationships at Karluk Lake, Alaska. *Trans. N. Am. Wildl. Conf.* **24**: 337–345.
- Ens, B.J., and Goss-Custard, J.D. 1984. Interference among oystercatchers, *Haematopus ostralegus* L., feeding on mussels, *Mytilus edulis* L., on the Exe estuary. *J. Anim. Ecol.* **53**: 217–232.
- Foote, C.J., and Brown, G.S. 1998. Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Can. J. Fish. Aquat. Sci.* **55**: 1524–1533.
- Frame, G.W. 1974. Black bear predation on salmon at Olsen Creek, Alaska. *Z. Tierpsychol.* **35**: 23–38.
- Fresh, K.L., and Schroder, S.L. 1987. Influence of the abundance, size and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Can. J. Fish. Aquat. Sci.* **44**: 236–243.
- Gende, S.M. 2002. Foraging behavior of bears at salmon streams: intake, choice, and the role of salmon life history. Ph.D. thesis, University of Washington, Seattle.
- Gende, S.M., Quinn, T.P., and Willson, M.F. 2001. Consumption choice by bears feeding on salmon. *Oecologia*, **127**: 372–382.
- Helfield, J.M., and Naiman, R.J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology*, **82**: 2403–2409.
- Hilborn, R., and Mangel, M. 1997. The ecological detective. *Monogr. Popul. Biol.* **28**.
- Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M., and Servheen, C. 1999a. Importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* **77**: 132–138.
- Hilderbrand, G.V., Hanley, T.A., Robbins, C.T., and Schwartz, C.C. 1999b. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia*, **121**: 546–550.
- Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **45**: 1–60.
- Marriott, R.A. 1964. Stream catalog of the Wood River lake system, Bristol Bay, Alaska. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 494.
- McClellan, B. 1994. Density-dependent population regulation of brown bears. *Int. Conf. Bear Res. Manag. Monogr. Ser.* **3**: 15–43.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., and Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**: 1193–1208.
- Quinn, T.P., and Buck, G.B. 2000. Scavenging by brown bears, *Ursus arctos*, and glaucous-winged gulls, *Larus glaucescens*, on adult sockeye salmon, *Oncorhynchus nerka*. *Can. Field-Nat.* **114**: 217–223.
- Quinn, T.P., and Buck, G.B. 2001. Size and sex selective mortality on adult Pacific salmon: bears, gulls and fish out of water. *Trans. Am. Fish. Soc.* **130**: 995–1005.
- Quinn, T.P., and Kinnison, M.T. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia*, **121**: 273–282.
- Quinn, T.P., Wetzel, L., Bishop, S., Overberg, K., and Rogers, D.E. 2001a. Influence of breeding habitat on bear predation, and age at maturity and sexual dimorphism of sockeye salmon populations. *Can. J. Zool.* **79**: 1782–1793.
- Quinn, T.P., Hendry, A.P., and Buck, G.B. 2001b. Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. *Evol. Ecol. Res.* **3**: 917–937.
- Ricker, W.E. 1952. Numerical relations between abundance of predators and survival of prey. *Can. Fish. Cult.* **13**: 5–9.
- Ricker, W.E. 1976. Review of the growth rate and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. *J. Fish. Res. Board Can.* **33**: 1483–1524.
- Ruggerone, G.T., and Rogers, D.E. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. *Fish. Bull.* **82**: 401–410.
- Ruggerone G.T., Hanson R., and Rogers D.E. 2000. Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* **78**: 974–981.
- Seitz, R., Lipcius, R.N., Hines, A., and Eggleston, D.B. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology*, **82**: 2435–2451.
- Sellers, R.A., and Aumiller, A.D. 1994. Brown bear population characteristics at McNeil River, Alaska. *Int. Conf. Bear Res. Manag.* **9**: 283–293.
- Shuman, R.F. 1950. Bear depredations on red salmon spawning populations in the Karluk River system, 1947. *J. Wildl. Manag.* **14**: 1–9.

- Solomon, M.E. 1949. The natural control of animal populations. *J. Anim. Ecol.* **18**: 1–35.
- Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, N.J.
- Sundell, J., Norrdahl, K., Korpimäki, E., and Hanski, I. 2000. Functional response of the least weasel, *Mustela nivalis nivalis*. *Oikos*, **90**: 501–508.
- Welch, C.A., Keay, J., Kendall, K.C., and Robbins, C.T. 1997. Constraints on frugivory by bears. *Ecology*, **78**: 1105–1119.
- Willson, M.F., Gende, S.M., and Marston, B.H. 1998. Fishes and the forest. *Bioscience*, **48**: 455–462.
- Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. 1: Predation during the seaward migration. *Can. J. Fish. Aquat. Sci.* **44**: 941–949.