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Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon

Strahan Tucker,[1,3] J. Mark Hipfner,[2] and Marc Trudel[1]

[1]*Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7, Canada*
[2]*Wildlife Research Division, Environment Canada, R.R. # 1 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada*

Abstract. Selection of prey that are small and in poor body condition is a widespread phenomenon in terrestrial predator–prey systems and may benefit prey populations by removing substandard individuals. Similar selection is widely assumed to operate in aquatic systems. Indeed, size-selective predation is a longstanding and central tenet of aquatic food web theory. However, it is not known if aquatic predators select prey based on their condition or state, compared to their size. Surprisingly, no comparable information is available for marine systems because it is exceedingly difficult to make direct observations in this realm. Thus the role of body condition in regulating susceptibility to predation remains a black box in the marine environment. Here we have exploited an ideal model system to evaluate selective predation on pelagic marine fish: comparing characteristics (fork length, mass corrected for fork length) of fresh, whole, intact juvenile Pacific salmon delivered by a seabird to its single nestling with salmon collected concurrently in coastal trawl surveys. Three species of juvenile salmon (*Oncorhynchus* spp.) are consumed by provisioning Rhinoceros Auklets (*Cerorhinca monocerata*); an abundant, colonial, pursuit-diving seabird. Samples were collected from multiple colonies and fisheries surveys in coastal British Columbia in two years. As predicted, Auklets preyed on small individuals in poor condition and consistently selected them at levels higher than their relative availability. This is the first study to provide direct evidence for both size- *and* condition-selective predation on marine fish in the wild. We anticipate that our results will be a starting point in evaluating how selective predation may structure or influence marine fish populations and bridges a fundamental incongruity between ecological theory and application; although "bigger is better" is considered a fundamental tenet of marine food webs, marine predators are often assumed to consume indiscriminately.

Key words: chum salmon; condition-selective predation; marine food webs; pink salmon; predator–prey; Rhinoceros Auklet; size-selective predation; sockeye salmon.

Introduction

Selection of prey of small size, or in poor body condition, is a widespread phenomenon in terrestrial ecosystems (Murray 2002, Penteriani et al. 2008, Genovart et al. 2010). Often, young, old, or infirm animals are taken out of proportion to their abundance, especially by predators that pursue rather than ambush prey (Husseman et al. 2003). This selection can occur because more vulnerable individuals have difficulty escaping, or attempt to compensate for poor condition and are more exposed to predators as a consequence (e.g., Fitzgibbon and Fansha 1989, Husseman et al. 2003). For the prey species, the selection by predators of substandard individuals can have important positive effects at the population level, either by reducing competition so that the remaining individuals experience increased survival and reproduction (Estes et al. 2011, Ripple et al. 2014) or by curbing the spread of disease (Packer et al. 2003, Ostfeld and Holt 2004, Levi et al. 2012).

Patterns of substandard prey selection analogous to terrestrial systems are often assumed to operate in aquatic systems (Burke et al. 2013). Body size is one component of the concept. Indeed, size-selective predation is a longstanding and central tenet of aquatic food web theory; a component of the "bigger is better," trait-based hypothesis (Sogard 1997). In essence, larger members of a cohort are thought to gain a survival advantage over smaller conspecifics through decreased vulnerability to predators. The hypothesis also encompasses enhanced tolerance to environmental extremes and buffering against starvation. Supporting evidence for enhanced predation rates on smaller individuals has accumulated for a wide range of organisms across multiple systems and at trophic levels ranging from zooplankton to larval and juvenile fish (Brooks and Dodson 1965, Gagliano and McCormick 2007, Duffy and Beauchamp 2008). However, given the difficulty of making direct observations in the aquatic realm, most studies have used indirect methods to evaluate size-selective predation, such as reconstructions of fish lengths and growth from scales and otoliths from surviving fish (Moss et al. 2005, Tomaro et al. 2012)

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[3]E-mail: strahan.tucker@dfo-mpo.gc.ca

or recovered in the stomachs or feces of predators (Duplisea 2005). Those indirect methods are contingent on several key assumptions that are hard to validate (Campana 1990). Few studies have used direct methods, in which characteristics of survivors and non-survivors are compared simultaneously. Moreover, indirect approaches cannot capture variation in body condition and the current state of the prey.

Although demonstrating size selectivity has been challenging in aquatic ecosystems, especially in vertebrates like fish, even less is known on how aquatic predators select prey based on their condition or state, compared to their size. Poor body condition has been linked to a reduction in the capacity of fish to evade predators under controlled conditions (Mesa et al. 1994); yet surprisingly little field data has been collected to evaluate this effect. In the Columbia River, the pattern of recovery of tags inserted into out-migrating steelhead trout (*Oncorhynchus mykiss*) smolts showed that two species of avian predators, disproportionately preyed upon smaller smolts, and upon smolts that displayed qualitative signs of poor condition: body injuries, descaling, external indicators of disease, fin damage, and ectoparasite infestations (Hostetter et al. 2012). No comparable information is available for marine systems, where the role of body condition in regulating susceptibility to predation remains a black box given the difficulty of studying fish in such a vast, dynamic environment with an array of potential predators, each with their own specific hunting behavior. Although the underlying assumption is that larger, healthier fish will survive and contribute disproportionately to reproduction (presumptively by avoiding predation), there is often an incongruity in studies estimating the impact of marine predators on fish stocks; they are assumed to consume indiscriminately at least with respect to condition (Trzcinski et al. 2006).

Pacific salmon (*Oncorhynchus* spp.) have an anadromous life cycle, spending a few months to two years in freshwater, followed by one to four years at sea where they are significant secondary and tertiary consumers, and prey in turn for a variety of fish, mammals, and birds (Groot and Margolis 1991). Mortality rates during the marine phase of the life cycle of Pacific salmon generally exceed 90%, and it is widely believed that most mortality is due to predation in the first few weeks to months following ocean entry (Beamish and Mahnken 2001). Elevated rates of predation on small, poor-condition fish are widely posited to explain why larger, high condition smolts are more likely to survive to return to spawn (Beamish et al. 2004).

Using predation by a colonial seabird as a model system, we test the hypothesis that juvenile salmon smolts experience size- and condition-dependent predation. On their northerly seaward migration, the vast majority of pink salmon (*O. gorbuscha*), chum salmon (*O. keta*) and sockeye salmon (*O. nerka*) smolts from stocks in southern and central British Columbia funnel past aggregations of hundreds of thousands of Rhinoceros Auklets (*Cerorhinca monocerata*) breeding on colonies scattered along the province's Central and North coasts. The Auklets are wing-propelled, pursuit-diving seabirds that forage mainly in the top 5–10 m of the water column (Kato et al. 2003) and within ~100 km of their breeding colonies (McFarlane-Tranquilla et al. 2005). The smolts' migration occurs in June and July (Groot and Margolis 1991), coinciding with the period when Rhinoceros Auklets are delivering whole and intact fish, including salmon smolts, to their nestlings (Thayer et al. 2008). These three species of juvenile salmon tend to be caught together in trawls and predominantly reside in the upper 15 m of the water column (Beamish et al. 2007, Tucker et al. 2012). Sampling of salmon destined for chicks at several large Auklet colonies coincided with coastal trawl surveys specifically targeting juvenile salmon, enabling us to directly compare characteristics of Auklet-predated smolts against control, trawl-caught smolts. Given their diving behavior, Auklets might select substandard prey as pursuit costs would be reduced if these prey are more easily captured. We did not expect Auklets to have a preference for any of the three salmon species given their similar distributions. Through this complementary and concurrent sampling, we have achieved insight, albeit an opening, into the elusive question of whether predation is size and condition-dependent in pelagic marine systems. Here we demonstrate that Auklets, with few exceptions, consistently preyed on both small and poor-condition juvenile salmon.

METHODS

Auklet food load collection

We collected salmon smolts from adult Rhinoceros Auklets on Triangle Island (50°52′ N, 129°05′ W), Pine Island (50°58′ N, 127°41′ W), and Lucy Island (54°18′ N, 130°37′ W), British Columbia, Canada during the chick provisioning period of summer 2012, and on those three colonies plus Moore Island (52°40′ N, 129°26′ W) in 2013 (Fig. 1). In 2012, Triangle Island was sampled on 24-29 June, Pine Island on 6–11 July, and Lucy Island on 14–18 July; in 2013, Triangle Island was sampled on 24–29 June (although no samples were obtained), Pine Island on 5–9 July, Lucy Island on 12–16 July, and Moore Island on 26–28 July, inclusive (Tables 1 and 2). Adult Auklets arrive back at the colony just after dusk to provision chicks carrying whole fish crosswise in their bills (a "load"). Returning adults were spotlighted with a headlamp as they landed and captured by hand or with a long-handled fish net, then banded and released; others were simply startled till they dropped their loads. Ten to 15 loads were collected each sampling night and immediately placed in plastic **twist-tie** bags for processing, which typically occurred within 1 h. Fish were clearly fresh when

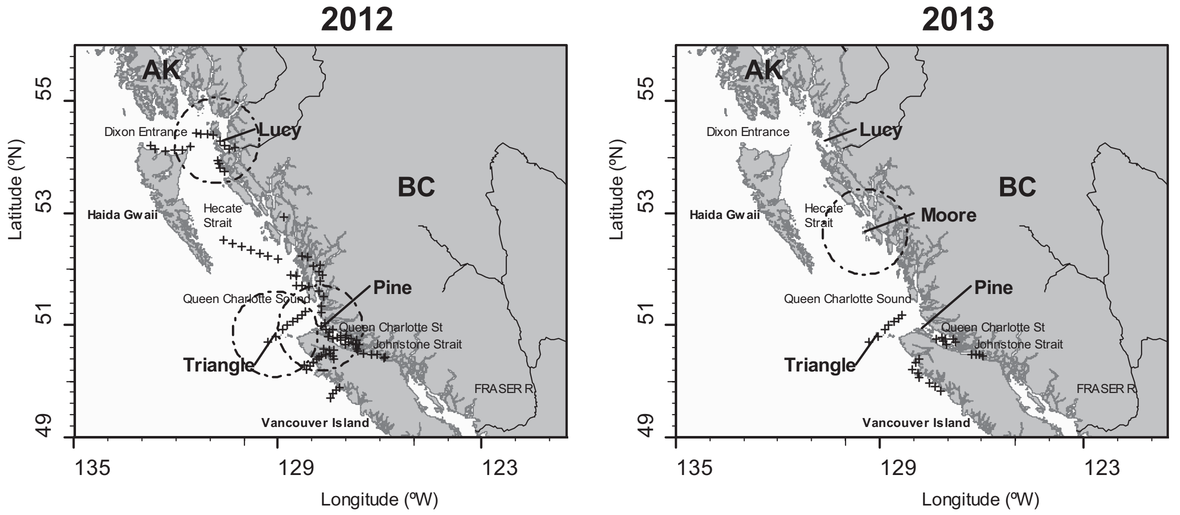

FIG. 1. Rhinoceros Auklet colony locations (Triangle, Pine, Moores, and Lucy islands) and trawl fishing locations (+) in 2012 and 2013 in British Columbia (BC), Canada. Circles denote inferred foraging range from colonies (McFarlane-Tranquilla et al. 2005).

collected, the odd one still twitching in fact. Fork length (mm) and mass (g) were measured for all whole salmon.

Trawl surveys

Our trawl survey followed a similar track between 2008 and 2012 over a 10–23 d period (mean 13 d) beginning in the south off the west coast of Vancouver Island, past Triangle Island, continuing northward up Hecate Strait past Moores and Lucy Islands, then coming down the west side of Haida Gwaii, and back across Queen Charlotte Sound towards Pine Island and finishing in Queen Charlotte Strait (Fig. 1). Specifically, our trawl survey in 2012 involved both repeated cross-shelf transects and opportunistic sampling from southern British Columbia to the border of southeast Alaska (Fig. 1). In 2013, we only fished in Queen Charlotte Sound, Queen Charlotte Strait, and Johnstone Strait due to budget constraints; our sampling was more restricted but effort was still concentrated around two major Auklet colonies where a large portion of predated salmon have been recovered (Pine Island and Triangle Island). A hexagonal-mesh, mid-water?? rope trawl (approximately 90 m long × 30 m wide × 18 m deep; cod-end mesh 0.6 cm; Cantrawl Pacific, Richmond, British Columbia, Canada) was towed in the top 20 m for 30 min at 5 knots (9.3 km/hr) using a chartered fishing vessel, the *Viking Storm*, between 17 June and 3 July 2012. The same gear was used to fish from the Canadian Coast Guard Ship *W. E. Ricker* between 12 July and 15 July 2012, and between 15 July and 20 July 2013. Sampling was conducted between 06:00 and 20:00 (Pacific Time). Trawl catches were sorted by species. A maximum of 15 juvenile pink salmon and chum salmon and 30 sockeye salmon were randomly selected from each net tow, and fork length (mm) and mass (g) were measured onboard the research vessel.

Table 1. Sampling dates for food load collections at four Rhinoceros Auklet colonies in 2012 and 2013 and dates of trawl survey in adjacent waters as defined by a ~100 km radius of Auklet foraging.

Year and colony	Food load collections	Trawl survey
2012		
Triangle	24–29 June	23–24 June, 1 July
Pine	6–11 July	24June, 3, 12–15 July
Lucy	14–18 July	27–29 June
2013		
Triangle	24–29 June†	15–17 July
Pine	5–9 July	17–20 July
Moore	26–28 July	–
Lucy	12–16 July	–

†Denotes no samples obtained.

Salmon condition

There are many different indices of fish condition (Trudel et al. 2005), which provide insight into how

Table 2. Number of pink, chum, and sockeye salmon recovered from Auklet food loads at British Columbia colonies in 2012 and 2013.

Year and species	Pine	Triangle	Moore	Lucy
2012				
Chum	21	5	–	2
Pink	15	10	–	22
Sockeye	47	43	–	2
2013				
Chum	63	0	1	9
Pink	5	0	7	28
Sockeye	7	0	1	2

rotund an individual is relative to its size. However these indices can be subject to bias, as they assume isometry when this is rarely met for salmon (Trudel et al. 2005). Therefore we used the residuals from species-specific relationships between length and mass as an index of body condition (Miller et al. 2013), hereafter referred to as "condition." Fish masses and lengths were ln-transformed to achieve a normal distribution and linear relationship. Positive residuals indicated fish that were heavier than predicted and in good condition, while those with negative residuals weighed less than predicted and were in poor condition.

Analysis

Given the opportunistic nature of our study, there are spatial and temporal mismatches of up to 2 weeks between the trawl and bird colony sampling (Table 1) prompting concern about how representative trawl samples are for comparison with predated fish. This concern is more acute in 2013, when trawling occurred only in the southern half of the study area. We therefore undertook a retrospective analysis to evaluate the consistency of temporal and spatial effects on the size and condition distributions of salmon taken between 2008 and 2012 (Appendix S1).

Predated vs. trawl caught salmon.—We tested whether predated fish were significantly smaller, and in poorer condition, than trawl-caught salmon, and further tested for species and annual effects using an R-based (R version 3.1.2; R Development Core Team 2014) multivariate permutation procedure (PMANOVA, adonis function, Vegan Community Ecology Package Version 1.17–8; Oksanen et al. 2011). PMANOVA is a nonparametric version of MANOVA except that it uses distance matrices to partition sums-of-squares and permutations to develop pseudo-*F* ratios to determine the significances of those partitions (Stevens and Okasanen 2012). This simultaneously evaluates the bivariate distance between central tendencies for predictors. Distance matrices were constructed using pairwise Euclidean distances; we used 10 000 permutations. In so far as it partitions the sums of squares of a multivariate data set, adonis is directly analogous to MANOVA (McArdle and Anderson 2001) and is a robust alternative to both parametric MANOVA and to ordination methods for describing how variation is attributed to different predictors or covariates. The function adonis can handle both continuous and factor predictors.

Because the trawl sampling did not entirely overlap with colony sampling, we used the same multivariate procedure to evaluate the consistency of body size characteristics for predated fish testing for colony and year effects. Because colonies were sampled weeks apart, we attempted to control for any potential growth by introducing sampling date as a dependent variable. If salmon taken between colonies were consistent (and of course within the range of trawl caught fish), we deemed that sampling was sufficiently representative to evaluate selectivity.

Electivity.—We calculated the Electivity Index (ε; Chesson 1983) to provide a measure of prey selection relative to availability. This index is applied in diet selection studies as it allows not only for the consideration of the availability (i.e., percentage) of a particular prey but also for the different numbers of available prey because it weighs the preference for one prey relative to the average preference for the alternative prey (Chesson 1983). First, all fish (trawl and predated) were classified into four categories based on fork length and condition. Fish were either small or large relative to the pooled mean fork length of 122 mm and in good or poor condition depending on a positive or negative mass residual, respectively. The proportion of fish in each category for each species and year was calculated for trawl-caught and predated fish separately. Note that the trawl proportions were adjusted by the total catches (all fish were counted) given the selective sampling of these species (with respect to the maximum number of individuals measured aboard the research vessel). For each prey category, Electivity Index ε contrasts the diet proportions to the relative abundance as indexed by the trawl survey

$$\epsilon_i = \frac{\mathrm{m}\alpha_i - 1}{(\mathrm{m}-2)\,\alpha_i + 1}$$

where m is the number of potential dietary types (in this case 12: 3 species × 2 size classes [small or large] × 2 condition levels [good or poor]) and α_i is Manly's Selection Index for prey type i

$$\alpha_i = \frac{r_i}{n_i}\frac{1}{\sum_{j=1}^{m}(r_j/n_j)}$$

where r_i,r_j are proportions of prey types i and j in the diet (i and j = 1, 2, 3,…, m); n_i, n_j are proportions of prey types i and j available in coastal waters. Values of ε vary from −1 (strong avoidance) to +1 (strong preference).

As an alternative to account for any temporal mismatches between our survey and colony sampling and the potential for growth, we also recalculated the electivity indices (Appendix S2) by standardizing all fish lengths to 1 July by assuming an average growth rate of 1 mm/d (Groot and Margolis 1991).

RESULTS

Total abundances and species composition of salmon caught in the trawl varied substantially between the two years of the predation study (Fig. 2). A total of 18 747 salmon smolts were caught in 2012; 25% sockeye salmon, 48% pink salmon, and 27% chum salmon (Table 3). Only 1533 were caught in 2013; 3% sockeye salmon, 10% pink salmon, and 87% chum salmon (Table 3). Across all colonies, we recovered a total

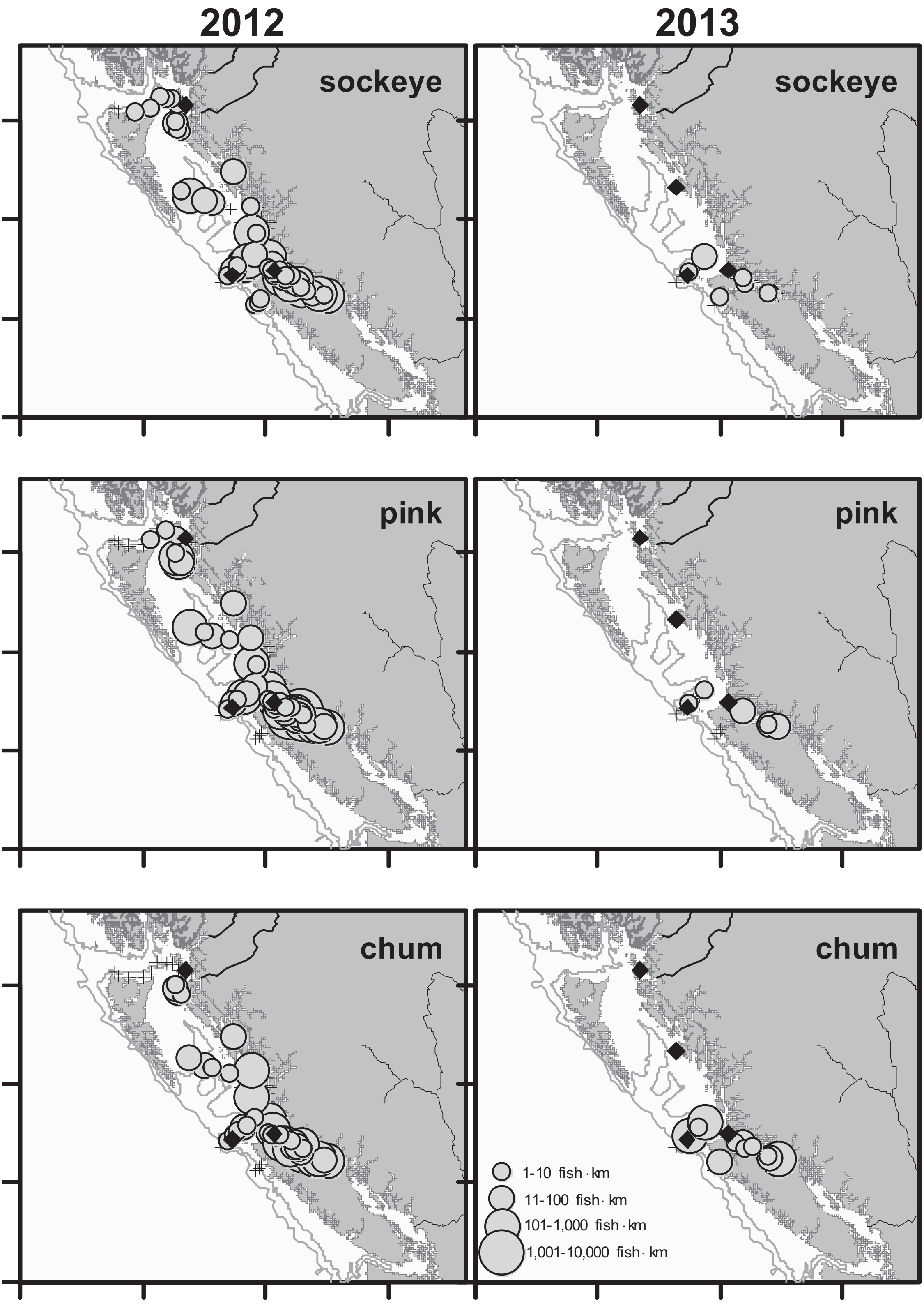

FIG. 2. Fishing locations, abundance, and distribution of catches in June–July 2012 and 2013. Fishing locations are denoted by +. Abundances (gray circles) are expressed as catch per unit effort (CPUE) where CPUE = [(no. salmon)/(tow duration, h)/(tow speed, nautical miles/h)] × 1.5 nautical miles (2.8 km). Locations of Rhinoceros Auklet colonies where salmon samples were obtained are indicated by the black diamonds.

of 179 salmon smolts from provisioning Rhinoceros Auklets in 2012: 55% sockeye salmon, 28% pink salmon, and 17% chum salmon. In 2013, 139 salmon were recovered from Auklets: 8% sockeye salmon, 33% pink salmon, and 59% chum salmon.

There were significant differences in size (fork length) and condition (mass residuals) of predated vs. trawl-caught salmon (factor denoted as "sampling type"; $P < 0.001$): as predicted, predated fish tended to be smaller and to have negative mass residuals (Fig. 3). Both size and condition also varied by species ($P < 0.001$) and year ($P < 0.001$), although the interactions between these two factors and sampling type were nonsignificant ($P = 0.34$ and $P = 0.80$, respectively). That latter result suggests that differences in the size and condition of predated vs. trawl-caught salmon were consistent among species and years. For predated fish, size characteristics were not significantly different among colonies ($P = 0.789$). Cumulatively, 85.5% of predated salmon were smaller than the mean (across species) size of 122 mm and 76.2% were below average in terms of mass (i.e., poor condition); 64% were both small and in poor condition in contrast to 26.5% for the trawl survey salmon at large.

The proportion of fish in each prey category (species x size x condition) varied between years in the trawl sample (Table 3). In 2012, individuals were distributed fairly evenly across all 12 categories (range 5–16%). In contrast, 2013 was dominated by the two large chum salmon categories (total of 73%) with much lower proportions (<9%) in the other 10 categories. The proportion of fish in each prey category also varied between years for the predated fish (Table 3). In 2012, the predated sample was dominated by small and poor-condition sockeye salmon (42%) and pink salmon (22%), while in 2013 the predated sample was dominated by small and poor-condition chum salmon (35%). Auklets disproportionately took sockeye salmon over pink salmon and chum salmon, relative to their respective abundances. In 2012, small, poor-condition pink salmon were 2.3 times more abundant in the trawls than small, poor-condition sockeye salmon, yet their representation in the diet was half that of sockeye salmon; while in 2013, small, poor-condition chum salmon were 50 times more abundant in trawls than equivalent sockeye salmon, but only 7 times as common in the diet.

Table 3. Proportion of trawl caught and predated salmon (2012–2013) in different prey categories.

	2012		2013	
Category	Trawl	Predated	Trawl	Predated
SE large +	0.06	0.00	0.01	0.00
SE large −	0.05	0.02	0.01	0.01
SE small +	0.07	0.11	0.01	0.02
SE small −	0.07	0.42	0.00	0.05
PK large +	0.09	0.00	0.01	0.02
PK large −	0.09	0.01	0.01	0.05
PK small +	0.13	0.06	0.04	0.11
PK small −	0.16	0.22	0.03	0.14
CM large +	0.09	0.00	0.34	0.02
CM large −	0.08	0.05	0.39	0.13
CM small +	0.05	0.04	0.05	0.09
CM small −	0.06	0.08	0.09	0.35

Note: SE, sockeye salmon; PK, pink salmon; CM, chum salmon, large >122 mm, small <122; + is a positive mass residual (good condition), and - is a negative mass residual (poor condition).

Prey selectivity (ε) was similar between years when prey proportions and availability in the trawl were combined within a year (Fig. 4). In both years, the electivity index was in all cases higher for small salmon of either good or poor condition, with the exception of large pink salmon in poor condition in 2013. Within a size category, fish in poor condition consistently had the higher electivity index. In particular, small sockeye salmon in poor condition were strongly selected in both years relative to all other prey classes (0.82 in 2012 and 0.84 in 2013). Large positive sockeye salmon and chum salmon were very strongly avoided in both years (~−1), while large positive pink salmon were strongly avoided (−1) in 2012 and moderately avoided in 2013 (−0.5). In 2012, small positive sockeye salmon were moderately selected along with small negative pink salmon and chum salmon (Fig. 4). In 2013, large and small negative pink salmon were also selected.

DISCUSSION

Selection for prey in poor condition is common in terrestrial ecosystems (Murray 2002, Husseman et al. 2003, Penteriani et al. 2008), but poorly documented in aquatic ecosystems and most especially in the marine environment. As predicted, we found that individual sockeye salmon, pink salmon and chum salmon smolts that were predated by Rhinoceros Auklets tended to match the small and poor-condition fish found in the trawl surveys. That is, from the pool of available smolts in the population, the Auklets consistently selected small fish and individuals in poor condition for any size class at levels higher than their relative availability. This pattern of selection held in two years that varied markedly in terms of the proportion of fish in different size and condition categories and in the abundance of smolts of all three Pacific salmon species in coastal waters off British Columbia, exceptionally high in 2012 and exceptionally low in 2013, which largely reflects variation in parental spawning abundances for these cohorts (DFO 2014, Irvine et al. 2014). This is, to the best of our knowledge, the first study to provide direct evidence for both size-selective and condition-based predation susceptibility for marine fish in the wild.

Given the active hunting strategy of the pursuit-diving Auklets, selection for small and poor-condition salmon might have occurred due to their inability to escape, as swim performance and escape behavior can be compromised by small size or in weakened or stressed fish

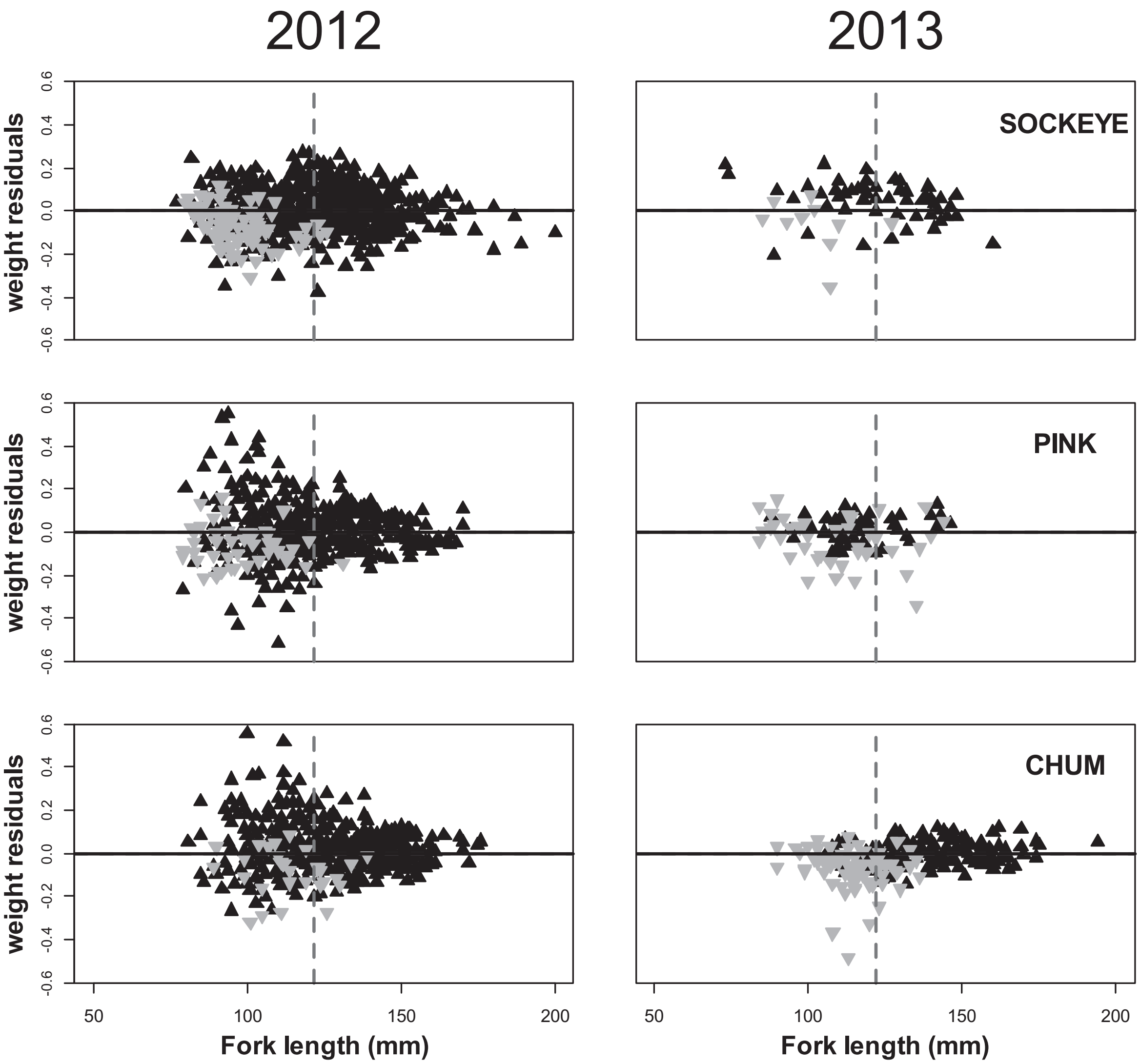

FIG. 3. Fork length and species specific mass residuals for trawl (black triangles) and predated (inverted gray triangles) salmon sampled in 2012 and 2013. The dashed gray vertical line indicates the mean length of 122 mm; black line divides negative (poor condition) and positive (good condition) fish.

(Mesa et al. 1994, Hostetter et al. 2012). In addition, these fish could have potentially undertaken compensatory, risk-prone behavior precipitated by their poor condition. Other putative factors include the distribution of poor-condition fish in the water column facilitating easy access to birds, or the impact of disease. While these species of juvenile salmon are concentrated in surface waters (Beamish et al. 2007), our trawl net is fairly large, sweeping a depth of ~20 m making it impossible to know if there is smaller scale, condition-dependent distribution of fish. Disease is yet one way that fish may become weakened. A small case study on sockeye salmon from this same sample demonstrated that predated smolts had higher microbe loads than smolts taken in trawls (Miller et al. 2014). However, there was no relationship between size/condition and microbe loads. This suggests that microbe infection may play an important role in susceptibility to predation (either independently or additively) although it is important to note that we have not yet established that these fish were in fact manifesting "disease" per se or were simply carriers of disease agents.

These salmon smolts were destined to provision Auklet nestlings, for which the most important prey is young of the year Pacific sand lance (*Ammodytes hexapterus*) up to ~100 mm fork length (Bertram and Kaiser 1993, Borstad et al. 2011). However, much larger fish also figure prominently in nestling diets at colonies in British Columbia (Thayer et al. 2008), including adult sand lance, Pacific herring (*Clupea pallasii*), and Pacific saury (*Cololabis saira*), some of which exceed 200 mm fork length (J. M. Hipfner, *unpublished data*), larger than even the largest salmon smolts caught in the trawls. Therefore, Auklets are likely not selecting small salmon

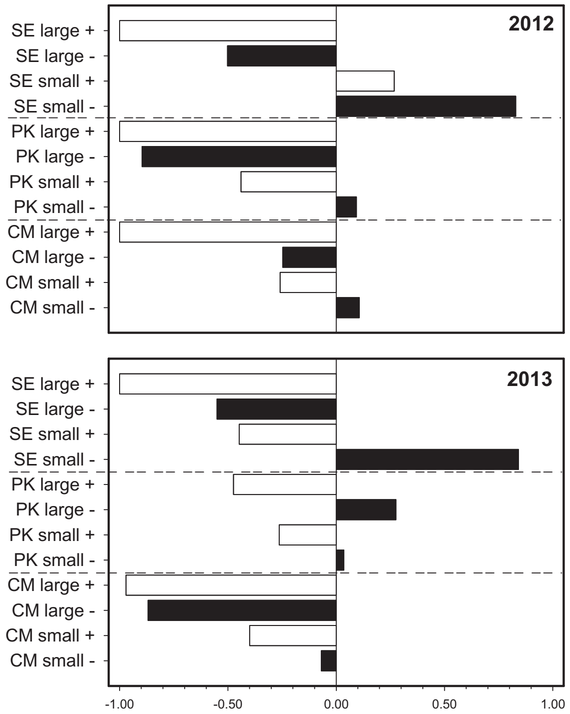

FIG. 4. Electivity index for different salmon prey classes lengths where SE is sockeye salmon, PK is pink salmon, and CM is chum salmon; large >122 mm, small<122, + (white bars) is a positive mass residual and - (black bars) is a negative mass residual.

due to gape-feeding limitations of the chicks; the chicks regularly consume larger fish.

Selection also occurred at another level, in that in both years, Rhinoceros Auklets disproportionately took sockeye salmon over pink salmon and chum salmon, relative to their respective abundances. It is not clear why sockeye salmon would be taken preferentially. Abundances in trawls were higher for pink salmon and chum salmon in both years, although relative catches of these three species tend to be concordant (Tucker et al. 2012). Again, given the size and height of the net, what is not clear from our trawl data is the fine-scale spatial and temporal distribution of the different species within surface waters (i.e., within the top 20 m) that may make them more vulnerable to Auklets feeding at dusk. The vast majority of individuals of these species are found within the top 15–20 m (Beamish et al. 2007). Although sample sizes are small, the distinction in vertical distribution is thought to be relatively minor among these species. Of the three, chum salmon tend to occur slightly deeper in the water column (Beamish et al. 2007), with no clear consensus among studies whether sockeye salmon or pink salmon have the shallowest distribution. However, all three species move close to the surface at night and move vertically during the day (Groot and Margolis 1991, Beamish et al. 2007). Moreover, there is no clear evidence that juvenile sockeye salmon are better quality prey particularly since these are poor-condition fish. Clearly, many different aspects of predation susceptibility remain to be clarified from risk behavior, distribution, and other potential factors such as disease and how prey species might differ in these elements.

Our study was opportunistic in nature. Therefore, there is the potential for bias given spatial and temporal mismatches in colony and trawl sampling, especially in 2013 when our trawl surveys were restricted to the southern portion of the study area. However, results of the comprehensive trawl sampling conducted between 2008 and 2012 lead us to believe that the size and condition of salmon taken in trawl surveys in our two study years were representative of the traits of fish available to Auklets across the region during the time period when they provisioned nestlings (Appendix S1). In those five years, trawl-caught fish varied inter-annually in size and condition, but with no effect of sampling date. Moreover, there was general overlap in the size ranges between colony groupings for trawl sampled fish, while only sockeye salmon displayed a somewhat consistent spatial trend in size, with larger fish found to the north. This has been documented previously (Tucker et al. 2009, Beacham et al. 2014) and is thought to be related to the phenology of migration; larger sockeye salmon tend to migrate earlier and faster (Freshwater et al., in press). However, very few sockeye salmon (n = 5) were taken by Auklets at the two northern colonies and southern sections were well represented in trawl surveys curbing the concern over mismatched sampling for this species. Condition indices also tended to be invariant in all three salmon species. In 2013, the majority of pink salmon (28 of 40) were taken by birds in the north, on Lucy (where we did not fish), while the vast majority of chum salmon (63 of 73) and sockeye salmon (7 of 10) were taken in the south, at Pine (where we did fish). So our survey is likely representative for those fish but there is still a potential time mismatch for Pine samples given the trawl survey was one week later.

The time span of our study is likely too short for any demonstrable change in body size and condition. These fish are thought to be growing at ~1 mm/d (Groot and Margolis 1991) and therefore could only change by ~10% or less over the course a 2-week interval. Salmon are also transiting rapidly (typically on the order of 15 km/d) from south to north in the study area (Tucker et al. 2009, Welch et al. 2011). On the scale and scope of juvenile salmon migrations (with mixed and continually emerging stocks and complex phonologies), 2-week and 400-km mismatches are likely masked by large variation in individual size and condition. Moreover, predated fish were not significantly different between colonies and these fell within the ranges for trawl-sampled salmon, despite more constrained sampling in 2013. Therefore, it is highly unlikely that birds are encountering entirely different size classes of salmon.

The proportion and availability of salmon in the different size and condition categories did vary between years. Yet interestingly, selectivity was similar although not entirely consistent for the different prey categories. Small and poor-condition fish were selected preferentially. The only exception to large fish being avoided was 2013 pink salmon, although these were also in poor condition; the only exception to good-condition fish being selected where sockeye salmon in 2012, but these were small individuals. As an alternative means of controlling for sampling mismatches, we standardized fish size to account for any growth and recalculated electivity indices (Appendix S2). While specific values differed, there were no large changes in selectivity and the overall interpretation of our results remain robust. Ultimately, however, we would advocate for dedicated and concurrent sampling of prey communities and predator diets to test predator selectivity and fish susceptibility in the future.

Several factors could contribute to small size and poor condition in juvenile salmon, thus elevated susceptibility to predation, including competition (Ruggerone and Nielsen 2004), prey type, and quality (Peterson and Schwing 2003, Burke et al. 2013) and poor environmental conditions (Burke et al. 2013). Physical ocean conditions and events can drive the productivity and composition of plankton communities with effects on fish abundance, growth, and survival (Peterson and Schwing 2003). For example, in the northeast Pacific, the most critical time of the seasonal plankton production cycle is when the ocean transitions from a winter downwelling state to a summer upwelling state; the spring transition and can occur at any time between March and June (Bograd et al. 2009). Generally, the earlier in the year that upwelling is initiated, the greater ecosystem productivity will be in that year. This timing could affect condition by determining the productivity regime that the juvenile fish encounter. Over the 15 yrs of our trawl survey program, the proportion of juvenile pink salmon, chum salmon, and sockeye salmon that were small and in poor condition (as defined here), increases with delayed timing of the spring transition in coastal British Columbia waters ($r^2 = 0.65$; S. Tucker, *unpublished data*), suggesting a link between physical oceanographic conditions and salmon size and condition, likely through productivity at the base of the food chain. Coincidentally, Rhinoceros Auklets breed less successfully when the spring transition and the resulting spring phytoplankton bloom occurs later in the spring (Borstad et al. 2011). Of course, these factors might drive poor growth and condition but does not explain why some individuals fare better than others. Individual performance remains unclear and a major gap in ecological knowledge.

Whatever the cause, factors or conditions that lessen the quality and availability of food can decrease growth rates resulting in poor physical condition (Duffy and Beauchamp 2011, Tomaro et al. 2012). Poor physical condition can reduce salmon health and survival directly through immune suppression and susceptibility to pathogens (Arkoosh et al. 2006, Hostetter et al. 2011) and may act in a synergistic manner making individuals more susceptible to predation. Alternatively, the very risk of predation can lead to stress, altered foraging behavior, and persistent changes in physiological state or differential gene expression in prey, which, in turn, can contribute to increased vulnerability to disease and loss of mass (Sheriff et al. 2010, Clinchy et al. 2013). Given the small size and poor condition of these predated fish, it is unclear whether or not these individuals were destined to meet this fate by some other means. That being said, the culling of substandard individuals may very well be beneficial to the survival and health of stocks over all. In terrestrial systems, the selection of individual prey in poor or diseased condition can have important positive effects at the prey population level; prey populations can benefit by increased survival and reproduction for the remaining individuals through reduced competition or by curbed spread of disease (Packer et al. 2003, Ostfeld and Holt 2004; Levi et al. 2012).

Our study has potential implications for how predation might structure marine pelagic fish populations. Salmon are simply the model in this case, as it is the group for which we have the most information; however, even this is not equivalent across salmon species. There are more significant species in the provisioning diets of Auklets whose abundances seemed linked to prevailing environmental conditions (such as sand lance; Borstad et al. 2011) but the specific contribution of Auklets in structuring prey fish populations remains unclear. Our program focuses on juvenile salmon. As such, our trawl survey, gear specificity, and sampling are not designed to sufficiently sample populations of other species in a representative manner. Therefore, we presently lack the ability to evaluate selectivity for other pelagic fishes, even though these fishes are important and critical forage for Auklets (Bertram and Kaiser 1993, Borstad et al. 2011). We would strongly advocate for more comprehensive sampling in the future. Predators are increasingly recognized as pivotal in shaping the structure and functioning of terrestrial ecosystems (Beschta and Ripple 2009*,* Ritchie and Johnson 2009). Despite the recognition that predation is a key ecological and even an evolutionary process (Krebs et al. 2001, Estes et al. 2011), our understanding of the ways in which any marine predator influences population dynamics of its prey is generally lacking due to our inability to observe both highly mobile predators and prey, though much more is known about predation effects on more observable prey and cascading effects though ecosystems (i.e., otter–sea-urchin–kelp forests; Estes et al. 2011, Ripple et al. 2014). Although we have not dealt with an analysis of the diet here (we have only considered one component, namely salmon), perhaps condition of all prey should be an element of prey type categorization when considering diet selectivity. Prey condition may indeed be an important component we are missing when attempting to estimate the impact or role that predators might play in shaping prey communities. Although this may be ideal, it might admittedly be untenable or at least difficult to achieve; how we get there is unclear. In this case, we exploited a distinctive situation and ideal model where intact predated individuals were easily observed. This was complemented by targeted sampling of the prey (salmon) population at large.

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Literature Cited

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223–231.

Beacham, T. D., R. J. Beamish, J. R. Candy, C. Wallace, S. Tucker, J. H. Moss, and M. Trudel. 2014. Stock-specific size of juvenile sockeye salmon in British Columbia Waters and the Gulf of Alaska. Transactions of the American Fisheries Society 143:876–889.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho salmon. Transactions of the American Fisheries Society 133:26–33.

Beamish, R. J., M. Trudel, and R. Sweeting. 2007. Canadian coastal and high seas juvenile Pacific salmon studies. North Pacific Anadromous Fish Commission Technical Report 7:1–4. North Pacific Anadromous Fish Commission, Vancouver, BC, Canada.

Bertram, D. F., and G. W. Kaiser. 1993. Rhinoceros auklet (*Cerorhinca monocerata*) nestling diet may gauge Pacific sand lance (*Ammodytes hexapterus*) recruitment. Canadian Journal of Fisheries and Aquatic Sciences 50:1908–1915.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophysical Research Letters 36:L01602. doi:10.1029/2008GL035933.

Borstad, G., W. Crawford, J. M. Hipfner, R. Thomson, and K. Hyatt. 2011. Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. Marine Ecology Progress Series 424:285–302.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science 150:28.

Burke, B. J., W. T. Peterson, B. R. Beckman, C. Morgan, E. A. Daly and M. Litz. 2013. Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1):e54134. doi: 10.1371/journal.pone.0054134

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47:2219–2227.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.

Clinchy, M., M. J. Sheriff, and L. Y. Zanette. 2013. Predator-induced stress and the ecology of fear. Functional Ecology 27:56–65.

DFO. 2014. Pre-season run size forecasts for Fraser River Sockeye (*Oncorhynchus nerka*) salmon in 2014. DFO Canadian Science Advisory Secretariat Science Response 2014/040, 46pp. Nanaimo, BC, Canada.

Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal piscivory by coastal cutthroat trout (*Oncorhynchus clarki clarki*) in Puget Sound: implications for juvenile salmon. Transactions of the American Fisheries Society 137:165–181.

Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 68:232–240.

Duplisea, D. E. 2005. Running the gauntlet: the predation environment of small fish in the northern Gulf of St Lawrence, Canada. Ices Journal of Marine Science 62:412–416.

Estes, J. A., et al. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Fitzgibbon, C. D., and J. H. Fansha. 1989. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. Journal of Zoology London 218:99–107.

Freshwater, C., M. Trudel, T. D. Beacham, C.-E. Neville, S. Tucker, and F. Juanes. Disentangling individual- and population-scale processes within a latitudinal size-gradient in Sockeye Salmon. *In Press* Can. J. Fish. Aquat. Sci.

Gagliano, M., and M. I. McCormick. 2007. Compensating in the wild: is flexible growth the key to early juvenile survival? Oikos 116:111–120.

Genovart, M., N. Negre, G. Tavecchia, A. Bistuer, L. Parpal and D. Oro. 2010. The young, the weak and the sick: evidence of natural selection by predation. PLoS ONE 5:e9774. doi:10.1371/journal.pone.0009774

Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Hertz, E., M. Trudel, M. K. Cox and A. Mazumder. 2015. Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. Ecology and Evolution 5: 4829–4839.

Hostetter, N. J., A. F. Evans, D. D. Roby, K. Collis, M. Hawbecker, B. P. Sandford, D. E. Thompson, and F. J. Loge. 2011. Relationship of external fish condition to pathogen prevalence and out-migration survival in juvenile steelhead. Transactions of the American Fisheries Society 140:1158–1171.

Hostetter, N. J., A. F. Evans, D. D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. Transactions of the American Fisheries Society 141:1586–1599.

Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591–601.

Irvine, J. R., C. J. G. Michielsens, M. O'Brien, B. A. White, and M. Folkes. 2014. Increasing dominance of odd-year returning pink salmon. Transactions of the American Fisheries Society 143:939–956.

Kato, A., Y. Watanuki, and Y. Naito. 2003. Foraging behaviour of chick-rearing rhinoceros auklets *Cerorhinca monocerata* at Teuri Island, Japan, determined by acceleration-depth recording micro data loggers. Journal of Avian Biology 34:282–287.

Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? BioScience 51:25–35.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences USA 109:10942–10947.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297.

McFarlane-Tranquilla, L., J. R. Ryder, W. S. Boyd, S. G. Shisko, K. Amey, D. F. Bertram and J. M. Hipfner. 2005. Diurnal marine distributions of radio-tagged Cassin's Auklets and Rhinoceros Auklets breeding at Triangle Island, British Columbia. Canadian Wildlife Service Technical Report Series 423. 77 p. Environment Canada, Ottawa

Mesa, M. G., T. P. Poe, D. M. Gadomski, and J. H. Petersen. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81–96.

Miller, J. A., D. J. Teel, A. Baptista, and C. A. Morgan. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 70:617–629.

Miller, K. M., et al. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evolutionary Applications 7:812–855.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley, J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134:1313–1322.

Murray, D. L. 2002. Differential body condition and vulnerability to predation in snowshoe hares. Journal of Animal Ecology 71:614–625.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens and H. Wagner. 2011. Vegan: Community Ecology Package. R package version 1.17-8. http://vegan.r-forge.r-project.org/

Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and the Environment 2:13–20.

Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecology Letters 6:797–802.

Penteriani, V., M. D. M. Delgado, P. Bartolommei, C. Maggio, C. Alonso-Alvarez, and G. J. Holloway. 2008. Owls and rabbits: predation against substandard individuals of an easy prey. Journal of Avian Biology 39:215–221.

Peterson, W. T. and F. B. Schwing. 2003. A new climate regime in northeast pacific ecosystems. Geophysical Research Letters 30:1896. doi:10.1029/2003GL017528, 17.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ripple, W. J., et al. 2014. Status and ecological effects of the World's largest carnivores. Science 343:1241484. DOI: 10.1126/science.1241484

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Ruggerone, G. T., and J. L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Reviews in Fish Biology and Fisheries 14:371–390.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2010. The ghosts of predators past: population cycles and the role of maternal programming under fluctuating predation risk. Ecology 91:2983–2994.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129–1157.

Stevens, M. H. H. and J. Okasanen. 2012. Permutation multivariate analysis of variance. adonis{vegan}. http://cc.oulu.fi/*jarioksa/softhelp/vegan/html/adonis.html

Thayer, J. A., D. F. Bertram, S. A. Hatch, M. J. Hipfner, L. Slater, W. J. Sydeman, and Y. Watanuki. 2008. Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. Canadian Journal of Fisheries and Aquatic Sciences 65:1610–1622.

Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Marine Ecology Progress Series 452:237–252.

Trudel, M., S. Tucker, J. F. T. Morris, D. A. Higgs, and D. W. Welch. 2005. Indicators of energetic status in juvenile coho salmon and Chinook salmon. North American Journal of Fisheries Management 25:374–390.

Trzcinski, M. K., R. Mohn, and W. D. Bowen. 2006. Continued decline of an Atlantic cod population: how important is gray seal predation? Ecological Applications 16:2276–2292.

Tucker, S., et al. 2009. Seasonal stock-specific migrations of juvenile sockeye salmon along the West Coast of North America: implications for growth. Transactions of the American Fisheries Society 138:1458–1480.

Tucker, S., M. E. Thiess, J. F. T. Morris, A. Mazumder and M. Trudel. 2012. Concordant distribution, abundance, growth of juvenile pink, chum and sockeye salmon in Eastern Pacific coastal waters. North Pacific Anadromous Fish Commission Document 1404:13 pp. Fisheries and Oceans Canada, Science Branch, Pacific Region, Pacific Biological Station. Department of Biology, University of Victoria. (Available at http://www.npafc.org/new/pub_documents_2012.html).

Welch, D. W., M. C. Melnychuk, J. C. Payne, E. L. Rechisky, A. D. Porter, G. D. Jackson, B. R. Ward, S. P. Vincent, C. C. Wood, and J. Semmens. 2011. *In situ* measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences USA 108:8708–8713.

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