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Contribution to the Theme Section 'Latest advances in research on fish early life stages'

Prey tell: what quillback rockfish early life history traits reveal about their survival in encounters with juvenile coho salmon

H. William Fennie[1,*], Su Sponaugle[1], Elizabeth A. Daly[2], Richard D. Brodeur[3]

[1]Department of Integrative Biology, Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA

[2]Cooperative Institute for Marine Resources Studies, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA

[3]Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2030 SE Marine Science Drive, Newport, OR 97365, USA

ABSTRACT: Predation is a major source of mortality in the early life stages of fishes and a driving force in shaping fish populations. Theoretical, modeling, and laboratory studies have generated hypotheses that larval fish size, age, growth rate, and development rate affect their susceptibility to predation. Empirical data on predator selection in the wild are challenging to obtain, and most selective mortality studies must repeatedly sample populations of survivors to indirectly examine survivorship. While valuable on a population scale, these approaches can obscure selection by particular predators. In May 2018, along the coast of Washington, USA, we simultaneously collected juvenile quillback rockfish *Sebastes maliger* from both the environment and the stomachs of juvenile coho salmon *Oncorhynchus kisutch*. We used otolith microstructure analysis to examine whether juvenile coho salmon were age-, size-, and/or growth-selective predators of juvenile quillback rockfish. Our results indicate that juvenile rockfish consumed by salmon were significantly smaller, slower growing at capture, and younger than surviving (unconsumed) juvenile rockfish, providing direct evidence that juvenile coho salmon are selective predators on juvenile quillback rockfish. These differences in early life history traits between consumed and surviving rockfish are related to timing of parturition and the environmental conditions larval rockfish experienced, suggesting that maternal effects may substantially influence survival at this stage. Our results demonstrate that variability in timing of parturition and sea surface temperature leads to tradeoffs in early life history traits between growth in the larval stage and survival when encountering predators in the pelagic juvenile stage.

KEY WORDS: Selective mortality · Predation · *Oncorhynchus kisutch* · *Sebastes maliger* · Juvenile fish

1. INTRODUCTION

Mortality due to predation on the vulnerable early life stages of marine fish plays a major role in shaping recruitment variability. Because small changes in larval fish mortality rates can lead to large changes in year class strength (Houde 1987, Leggett & DeBlois 1994), much effort has been directed at examining how early life history traits affect vulnerability to predation. The 'growth–mortality hypothesis' (Anderson 1988) suggests that early survival is strongly influenced by the early life history traits of size (Miller et

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*Corresponding author: fennieh@oregonstate.edu

al. 1988), growth rate (Shepherd & Cushing 1980, Hare & Cowen 1997, Takasuka et al. 2003, 2004a, 2007), and development rate (stage duration; Chambers & Leggett 1987, Houde 1987). Trait-based selective mortality is commonly examined within cohorts of larval fish (Miller et al. 1988, Bailey & Houde 1989, Pepin 1993, Takasuka et al. 2003, 2004b, 2007, Robert et al. 2007), with additional predation during the juvenile stage playing a key role in determining the traits beneficial to survival (Sissenwine 1984, Sogard 1997, Searcy & Sponaugle 2001, Grorud-Colvert & Sponaugle 2011).

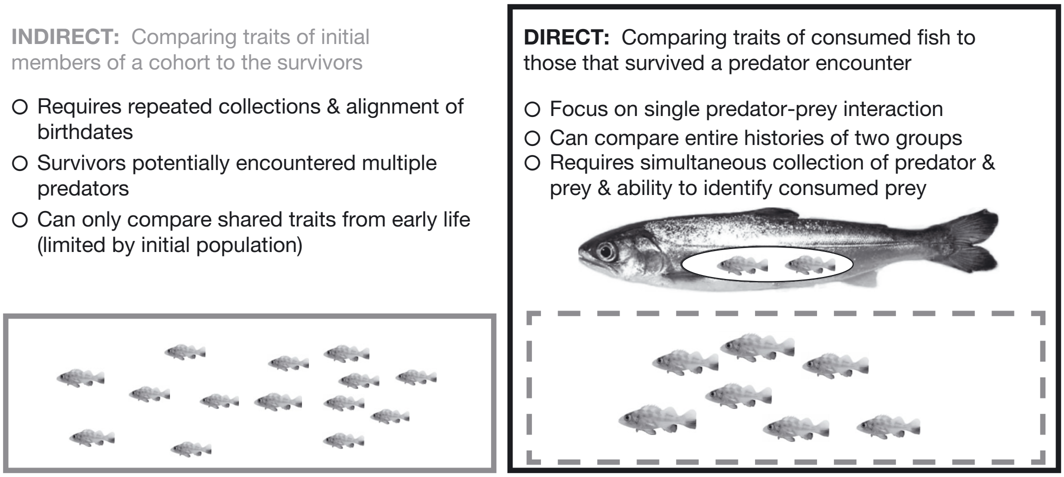
Larval fishes are subject to indiscriminate mortality from a variety of sources, and the importance of early life history traits may not be realized until later life stages (Sogard 1997). Important periods of high mortality and selective predation in fish are often associated with transitions from larval to juvenile stage, and from pelagic to benthic habitat utilization (Hobson et al. 1995, Searcy & Sponaugle 2001, Almany & Webster 2006). Larval traits can 'carry-over' and affect this transition as well as the survival of juvenile stages (Searcy & Sponaugle 2001, Shima & Findlay 2002). The strength of selection for particular traits can vary ontogenetically, among cohorts, and across time and space (Meekan & Fortier 1996, Robert et al. 2007, Grorud-Colvert & Sponaugle 2011, Rankin & Sponaugle 2011). Additionally, the importance of early life history traits appears to be species-specific, with some species, for example, experiencing selective loss of fast-growing individuals during the larval stage (Pepin 1993). For others, larval traits may not convey much success in post-settlement survival compared to the role of juvenile traits (D'Alessandro et al. 2013).

To examine the importance of life history traits on fish survival through early life, most studies utilize indirect methods, such as repeated sampling of particular cohorts coupled with otolith-based examination of traits (e.g. D'Alessandro et al. 2013, Shulzitski et al. 2016). These methods are effective at identifying the traits that survivors possess relative to the initial population of larvae, but can mask the specific roles of multiple predators. Direct studies of predator–prey interactions and the role of natural variability in prey traits are less common but offer valuable insights. For example, direct examination of predation in the wild indicates that Atlantic bluefish *Pomatomus saltatrix* are consistently size-selective across 2 prey fish species (Juanes & Conover 1995), and direct comparisons between surviving and consumed Japanese anchovy *Engraulis japonicus* revealed that different predatory fish have contrasting patterns of selection on larval anchovy (Takasuka et al. 2003, 2004a, 2007). Interannual variability in the strength of selection and recruitment may be influenced by variability in the identity and abundance of predators that fish encounter during their early life. A more nuanced understanding of the selection patterns of specific predators will enable improved predictions of early fish survival and recruitment success.

In the coastal waters of the northeast Pacific Ocean, juvenile rockfishes *Sebastes* spp. and juvenile coho salmon *Oncorhynchus kisutch* overlap during part of their early life histories and allow for direct examination of salmon predation patterns (Fig. 1). Rockfishes are ovoviviparous and their larvae hatch from internally fertilized eggs. Larvae develop within the female, and parturition typically occurs around 5 d post-hatch. Larval rockfish begin forming otolith increments when they are extruded (Laidig & Ralston 1995).

The larvae of quillback rockfish *S. maliger*, an important nearshore species, are extruded in March–June (Love et al. 2002), and pelagic larvae and juveniles spend ~1–2 mo in the upper water column before recruiting to nearshore benthic habitats. In Oregon, USA, quillback rockfish juveniles typically settle from June through August, but can settle as early as May and as late as September and arrive to nearshore habitats at ~15–40 mm standard length (SL; Ottmann et al. 2018). In contrast, juvenile coho salmon from Oregon and Washington spawn in freshwater streams (or in many cases are of hatchery origin) and inhabit freshwater for 1 yr prior to entering the ocean in spring. In coastal waters, juvenile coho salmon primarily inhabit surface waters along the continental shelf where they overlap spatially with juvenile rockfishes (Brodeur et al. 2003, 2004). This transition to a marine existence is accompanied by a dramatic increase in piscivory, and juvenile rockfishes are an important component of juvenile coho salmon diets, comprising up to 25% of their diet by weight (Daly et al. 2009).

In this study, we directly compared the early life history traits of pelagic juvenile quillback rockfish consumed by predatory coho salmon to traits of simultaneously collected free-swimming pelagic juvenile quillback rockfish. Our aim was to determine if juvenile coho salmon are selective predators on juvenile quillback rockfish with particular early life history traits and, if so, to identify which of these traits reduce rockfish vulnerability to predation. We used otolith microstructure analysis to compare the age, size-at-capture, and recent growth between the survivors and consumed rockfish. We compared predator size to the size of prey they consumed. In



INDIRECT: Comparing traits of initial members of a cohort to the survivors

- ○ Requires repeated collections & alignment of birthdates
- ○ Survivors potentially encountered multiple predators
- ○ Can only compare shared traits from early life (limited by initial population)

DIRECT: Comparing traits of consumed fish to those that survived a predator encounter

- ○ Focus on single predator-prey interaction
- ○ Can compare entire histories of two groups
- ○ Requires simultaneous collection of predator & prey & ability to identify consumed prey

Fig. 1. Two different approaches for examining selective mortality in wild fishes. Cohort re-sampling studies examine early life history traits (ELHTs) in an initial population (solid gray box) and compare these to the same cohort at a later time (dashed gray box) to detect how mortality during early life changes the distribution of ELHTs. Direct studies (solid black box) examine differences in ELHTs between free-swimming individuals collected simultaneously with predators (survivors) to the traits of individuals consumed by the predator

addition, we examined daily growth and size-at-age trajectories to compare the growth and size histories of these 2 groups. Finally, we examined the relationship between water temperature and growth during early life to determine how developmental conditions affected the traits of juvenile rockfish and their encounters with juvenile salmon.

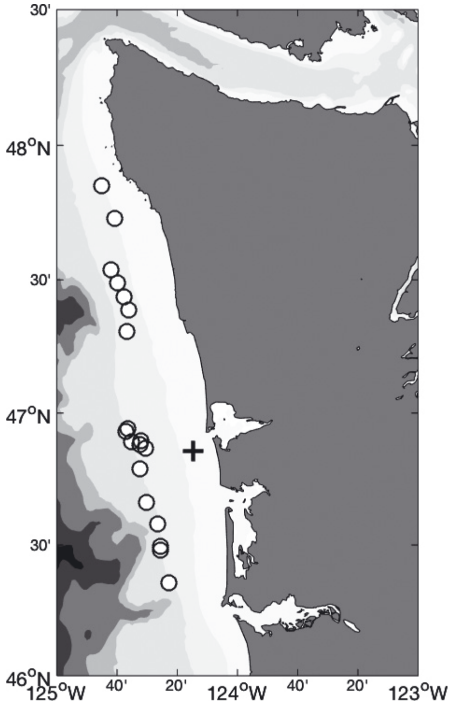


Fig. 2. Sampling locations for juvenile coho salmon and juvenile rockfish along the coast of Washington, USA, from 24–28 May 2018. Stations (circles) were located between the 50 and 100 m isobaths. (+) the buoy used for sea surface temperature data for growth analyses

2. MATERIALS AND METHODS

2.1. Rockfish and salmon collections

To determine if juvenile coho salmon exhibit age-, size-, or growth-selective predation on juvenile rockfishes, we used samples collected during the Juvenile Salmon Ocean Ecology Survey along the coast of Washington, USA, from 24–28 May 2018 (Fig. 2). Juvenile coho salmon and juvenile rockfishes were simultaneously collected using a Nordic 264 pelagic rope trawl towed at the surface with a mouth opening of 30 m wide by 20 m deep and a 3 mm cod-end liner (Litz et al. 2019). This fine mesh lining retains larval fishes as small as 6 mm (Brodeur et al. 2011) and juvenile rockfish in the same size range as those found in the salmon stomachs, suggesting that these nets did not select against the smaller rockfish (Fig. 3). The trawl was towed during daylight hours for 30 min at a ship speed of ~1.7 m s^{-1} between the 50–100 m isobaths. Juvenile salmon were removed from the trawl, identified to species, measured (fork length), and immediately frozen. Juvenile rockfishes sampled by trawl (alive at the time of capture; i.e. 'survivors') were frozen immediately. In the lab, we measured surviving juvenile rockfish to the nearest 0.01 mm (SL) and dissected juvenile rockfishes from

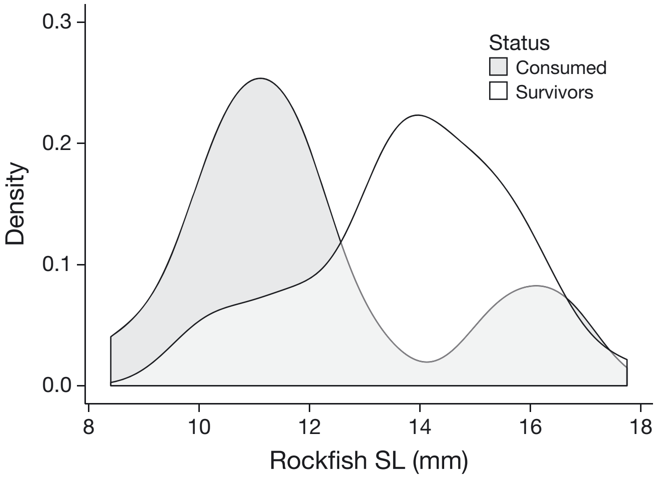


Fig. 3. *Sebastes maliger* size frequency distributions divided into those consumed and those alive at the time of collection (Survivors). Survivor size was based on standard length (SL) measurements while consumed fish size was estimated from the otolith radius to SL ratio of surviving rockfish

the stomachs of the coho salmon ('consumed rockfish'). We used all of the consumed rockfish and all of the surviving rockfish from stations with less than 15 individuals. We took a random subsample of 15 surviving rockfish from stations with >15 individuals in subsequent analyses.

2.2. Molecular identification

Because consumed rockfish were too digested to identify to species morphologically, we modified the protocol in Thompson et al. (2017) and sequenced the cytochrome *b* gene of both consumed and surviving rockfish and compared these to a reference database of rockfish sequences. We extracted DNA from rockfish caudal fin tissue using the cetyl trimethylammonium bromide (CTAB) protocol (Winnepenninckx et al. 1993) followed by ethanol precipitation, and amplified rockfish cytochrome *b* gene sequences using GluRF and CB3RF primers. The PCR had an initial denaturing step of 92°C for 150 s, then consisted of 40 cycles of 94°C for 30 s, 55°C for 90 s, 70°C for 90 s, and a final extension step of 72°C for 5 min. We cleaned the DNA products with shrimp alkaline phosphatase and exonuclease I (GE Healthcare) and sequenced these DNA fragments using the internal primer CBINR3-5′ and BigDye v.3.1 on an ABI 3730XL DNA analyzer (Applied Biosystems). The rockfish haplotype sequences were aligned, edited, and compared to the rockfish reference sequence library developed by Hyde & Vetter (2007) in Sequencher v.4.7 (Gene Codes). We used 100% sequence identity matches of our samples to the reference sequences to determine species identification. Of the positively identified rockfish, *Sebastes maliger* (quillback rockfish) was the dominant rockfish in both the surviving (38/72) and consumed groups (21/22); therefore, our subsequent analyses focused on this species.

2.3. Otolith measurement and analysis

To compare early life history traits and examine patterns of selective mortality among consumed and survivor quillback rockfish, we dissected a total of n = 21 and n = 38 otoliths, respectively. Daily growth increments have been validated for juvenile rockfish (Yoklavich & Boehlert 1987, Laidig & Sakuma 1998), so otolith increment counts can be used to estimate age and widths between successive otolith increments as a proxy for somatic growth (e.g. Miller & Shanks 2004, Wheeler et al. 2017). We embedded sagittal otoliths in Crystalbond thermoplastic resin (Electron Microscopy Science) and used lapping paper to polish otoliths along the sagittal plane. Otoliths were read at 400× using a compound microscope equipped with polarized transmitted light, and increments were interpreted using image analysis software (ImagePro v.9.0). Following standard procedures (Miller & Shanks 2004, Sponaugle 2009), we obtained otolith increment counts and measurements of daily increment widths to estimate the age, daily growth, and size-at-age of each individual. Each otolith was read blind 2 independent times and if the ages differed by >10%, it was read a third time. If no 2 reads were within 10% of one another, the otolith was excluded from further analysis. For reads within 10% of each other, one read was randomly selected for further analysis. There was a significant relationship between the residuals of radius-at-age and size-at-age of surviving rockfish ($F_{1,36}$ = 55.33, $p < 0.0001$, $R^2 = 0.60$), confirming that otolith radius and otolith increment width are proxies for size and growth, respectively.

2.4. Environmental data

To examine the influence of sea surface temperature (SST) on rockfish growth prior to their encounter with salmon, we calculated daily mean SST data from the closest NOAA buoy located off the coast of Grays Harbor, Washington (National Data Buoy Center [NDBC] Stn 46211; Fig. 2). Located inshore of, but in the center of the latitudinal range of the sampling locations, this buoy records water temperature at 1 m depth. This SST is a good proxy for water temperatures experienced by rockfish during their early development because quillback rockfish larvae and juveniles are found in surface waters (Lenarz et al. 1995).

2.5. Data analysis

We used multiple regression analysis to compare the age, size, and recent growth (mean of the last 5 growth increments) between the surviving and consumed rockfish. Latitude was included as a covariate in the analyses to account for the range in latitude over which fish were collected (1.5°). Data were log transformed to meet the assumptions of normality. Additionally, because age is strongly correlated with size and growth, age was included as a covariate in analyses comparing size-at-capture and recent growth between surviving and consumed rockfish.

The relationship between predator size and prey size was examined using linear regression. Quillback rockfish otolith radius and salmon fork length were log transformed to meet assumptions of normality.

Linear mixed effects models (LMM) were used to test whether mean daily growth and mean size-at-age trajectories differed between surviving and consumed rockfish. We used a subset of our data to best examine the patterns of growth and size-at-age across early life history. We limited our analysis to the first 42 d, as this time period was shared by both groups and allowed for a minimum of n = 5 observations d^{-1} $group^{-1}$. The fixed and random effects were selected by fitting models using maximum likelihood and minimizing Akaike's information criterion (AIC; Table 1). Because we repeatedly measured the growth of individual fish, we included fish identity as a random effect in the model and allowed both the intercept and the slope to vary for each fish. To account for the inherent autocorrelation between sequential otolith increments, we incorporated a first order autoregressive correlation structure in the model (Weisberg et al. 2010). The final growth and size-at-age model parameters were estimated using restricted maximum likelihood with the R package 'nlme' (Pinheiro et al. 2019). The full models for testing for differences in growth and size-at-age between consumed and surviving fish had the form:

$$y_{i,s,a} = \alpha_s + \beta_s \text{age} + a_i + b_i \text{age} + \varepsilon_{i,s,a} \qquad (1)$$

where $y_{i,s,a}$ is the growth increment or size of individual i of status s (survivor or consumed) at age a, α_s and β_s are the overall intercept and slope of the growth or size-at-age trajectory, a_i and b_i are the random intercept and slope for individual i, and $\varepsilon_{i,s,a}$ is a residual that is assumed to follow a first-order autoregressive process: $\varepsilon_{i,s,a} = \phi\varepsilon_{i,s,a-1} + \nu_{i,s,a}$, where ϕ is the autoregressive coefficient and $\nu_{i,s,a}$ is a normally distributed residual with mean 0 and variance σ_ν^2. The random effects a_i and b_i are assumed to be normally distributed with zero means, variances σ_a^2 and σ_b^2 and covariance $\sigma_{a,b}$. Note the size-at-age model also included an age^2 term as both a fixed and random effect

Table 1. Model selection for mean daily growth and size-at-age trajectories of *Sebastes maliger*. Fixed effects are listed on the left of the vertical line; random effects to the right. AIC: Akaike's information criterion; ΔAIC: a measure of each model's performance relative to the best model

Model	ΔAIC
Mean daily growth	
Status + age + status × age | random intercept + random slope + autocorrelation	0[a]
Status + age + status × age | random intercept + autocorrelation	25.76
Status + age + status × age | autocorrelation	58.11
Status + age | autocorrelation	79.95
Status | autocorrelation	460.10
Null model	3992.51
Size-at-age	
Status + age + age^2 + status × age | random intercept + random slope + random slope^2 + autocorrelation	0[b]
Status + age + age^2 + status × age | random intercept + autocorrelation	784.53
Status + age + age^2 + status × age | autocorrelation	769.27
Status + age^2 | autocorrelation	818.12
Status + age | autocorrelation	3624.71
Status | autocorrelation	6736.69
Null model	16746.07

[a]Lowest AIC = 5931.85; [b]lowest AIC = 6637.56

to allow for random variation in the linear and quadratic coefficients.

We compared the recent growth of individuals of the same size between surviving and consumed fish using ANCOVA, with size-at-capture (or consumption) as a covariate (see Takasuka et al. 2003). We removed the smallest consumed individual and largest survivor to constrain the data set to the size range shared by both groups.

To examine the relationship between rockfish early growth and SST, growth was averaged over Days 1–25 for all fish born on a given calendar day, and linear regression was used to compare this growth to the mean SST over the same time period. An extra sum of squares *F*-test was used to compare model fits between a simple linear model and a quadratic model, but no support was found for the inclusion of a quadratic term. All analyses were performed using R v.3.6.0 (R Development Core Team 2019), and all figures were created using the R package 'ggplot2' v.2.0.0 (Wickham 2016).

3. RESULTS

Mean age, size-at-capture, and recent growth differed significantly between the surviving and consumed quillback rockfish. After accounting for the effect of latitude, surviving rockfish were significantly older (~7 d on average) than consumed rockfish (Fig. 4A, Table 2). Similarly, after accounting for age and latitude, surviving rockfish otolith radii were significantly larger on average than consumed fish (Fig. 4B, Table 2). The otolith radii of surviving rockfish were linearly related to their SL (SL = 5.599 + 0.0421 × radius, $p < 0.0001$, $R^2 = 0.83$), and conversion of the otolith radius to the length to age relationship of survivors indicated that survivors were ~1.85 mm SL, or 29% larger than consumed fish. Finally, mean recent growth of surviving rockfish was also significantly faster than that of consumed rockfish (Fig. 4C, Table 2).

Salmon size did not affect the size of the rockfish they consumed. There was no significant relationship between salmon fork length and the otolith radii of rockfish consumed ($F_{1,18} = 0.2845$, $p = 0.60$, $R^2 = 0.02$).

Mean daily growth trajectories differed significantly between consumed and surviving rockfish. The best fit model included the fixed effects of status, age, a status × age interaction, the random effects of intercept and slope, and a first order autoregressive process (Table 1). Growth was affected by rockfish status (survivor vs. consumed), age, and the status × age interaction (LMM, $p < 0.0001$; Table 3). Growth was higher for consumed fish during early life and increased with age for both groups. However, the growth of surviving rockfish increased with age more

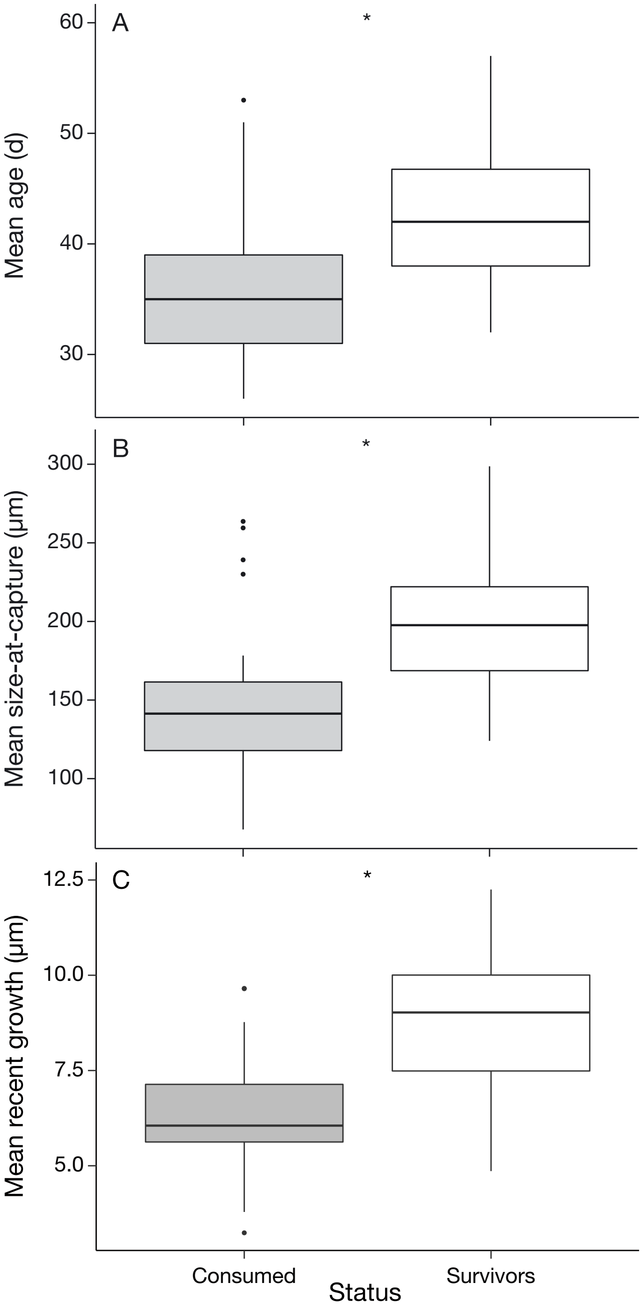


Fig. 4. Differences in otolith-based early life history traits between surviving and consumed juvenile *Sebastes maliger*: (A) age, (B) size-at-capture based on otolith radius, and (C) mean growth over the last 5 d of life. Box plot parameters — thick band: median; bottom and top of box: 25% and 75% quantiles; points: outliers; whiskers: most extreme value less than or equal to 1.5× the inter-quartile range; (*) significant differences ($p < 0.001$)

Table 2. Multiple regression results for age, size, and recent growth of pelagic juvenile *Sebastes maliger* with status (consumed or surviving) and latitude, and status, latitude, and age as covariates, respectively

Dependent variable	Sources of variation	df	*F*	p	Model r^2
Log(age)	Status	1	13.608	<0.001	0.25
	Latitude	1	4.953	0.03	
	Error	56			
Log(radius)	Status	1	45.2	<0.001	0.78
	Latitude	1	16.995	0.001	
	Age	1	137.05	<0.001	
	Error	55			
Log(recent growth)	Status	1	28.35	<0.001	0.51
	Latitude	1	2.632	0.11	
	Age	1	26.817	<0.001	
	Error	55			

rapidly than growth of consumed rockfish, leading to surviving fish exhibiting faster growth than consumed fish prior to their encounter with salmon predators (Fig. 5A).

Quillback rockfish mean size-at-age trajectories differed significantly between those that were consumed and those that survived. The best fit model included the fixed effects of status, age, age^2, and a status × age interaction, as well as a random intercept, a random slope with random variation in both the age and age^2 terms, and a first order autoregressive process (Table 1). Size increased with age, and the relationship between size and age varied between survivors and consumed rockfish. Size-at-age was not affected by status (LMM, $p > 0.05$); however, size was significantly affected by age and age^2 (LMM, $p < 0.001$; Table 3). In addition, there was a significant status × age interaction (LMM, $p = 0.002$). The model indicated that size-at-age was similar for the 2 groups during early growth, that consumed fish were larger-at-age than survivors from Days ~10–35, but size-at-age increased more rapidly for survivors after Day 25, such that by Day ~35 surviving rockfish were the same mean size-at-age as consumed rockfish (Fig. 5B).

There was evidence of growth-selective mortality, as recent growth differed between survivors and consumed fish of similar size. Over the 5 d prior to capture, consumed rockfish grew significantly more slowly than surviving rockfish of the same size ($F_{1,55} = 64.88$, $p < 0.001$; Fig. 6).

As expected, SST increased with day of year ($F_{1,55} = 357.9$, $R^2 = 0.87$, $p < 0.0001$); thus, because consumed rockfish were typically born about 1 wk later than the surviving rockfish, they developed in warmer water. Larval rockfish growth during the first 25 d of life was significantly related to SST, with growth significantly higher for fish born later in the season ($F_{1,25} = 7.19$, $p = 0.013$; Fig. 7).

4. DISCUSSION

Due to the inherent challenges of sampling previously consumed fish, there are few direct studies of the characteristics of these fish that increase their susceptibility to predation mortality. Though the sample size of consumed fish was relatively small, the results of our study provide direct field evidence of selective predation upon and by marine fishes. As predicted by the 'bigger is better' hypothesis, juvenile coho salmon selectively consumed smaller pelagic

Table 3. Mixed effects model results for mean daily growth and size-at-age of pelagic juvenile *Sebastes maliger* with 95 % confidence interval estimates and p-values for each fixed effect, standard deviations (SD) for random effects and residuals, and magnitude of the auto-regressive coefficients (ϕ). **Bold** values are significant ($p < 0.05$)

Parameter	Lower bound	Estimate	Upper bound	p-value	Random effect	SD	ϕ
Mean daily growth model							
Intercept	0.595	0.883	1.172	**<0.001**	Intercept	0.0007	0.564
Status	−0.875	−0.517	−0.16	**0.005**	Slope (age)	0.027	
Age	0.137	0.156	0.174	**<0.001**	Residuals	1.099	
Status × age	0.008	0.030	0.052	**0.007**			
Size-at-age model							
Intercept	12.844	14.300	16.016	**<0.001**	Intercept (age)	0.0003	0.961
Status	−1.614	0.381	2.377	0.704	Slope (age)	0.397	
Age	0.387	0.585	0.800	**<0.001**	Intercept (age^2)	0.009	
Age^2	0.085	0.089	0.093	**<0.001**	Slope (age^2)	0.014	
Status × age	−0.666	−0.405	−0.143	**0.002**	Residuals	3.500	

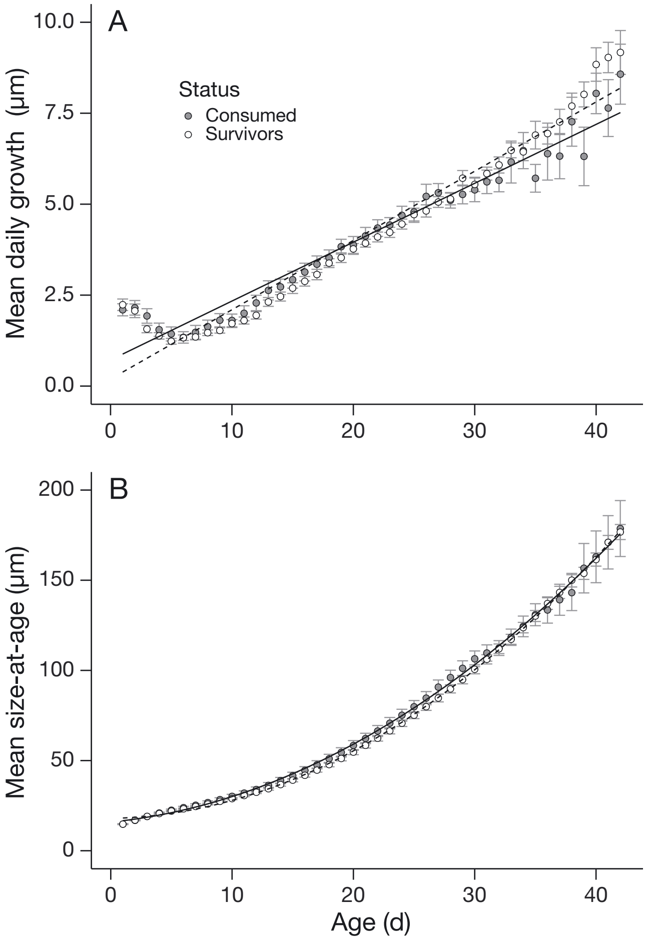


Fig. 5. Mean ± SE (A) daily growth (measured by otolith increment widths) and (B) size-at-age (measured by otolith radius-at-age) for juvenile *Sebastes maliger*. Only ages with n > 5 observations are presented. Fitted lines represent mixed effects models for each trajectory; dashed lines: survivors; solid lines: consumed fish

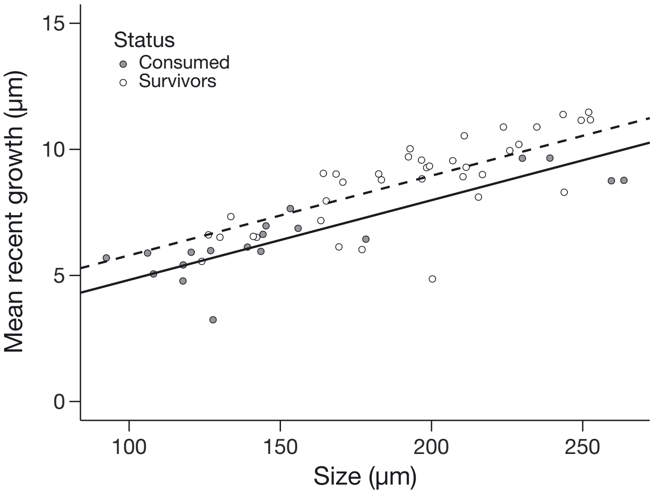


Fig. 6. ANCOVA of mean recent growth and size-at-capture between consumed (solid line) and surviving (dashed line) juvenile *Sebastes maliger*

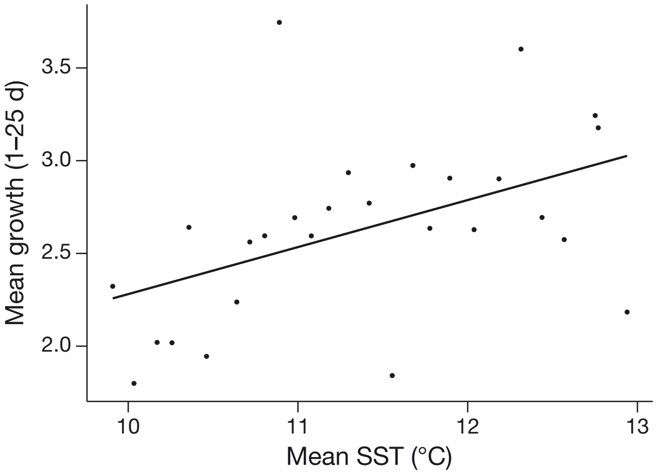


Fig. 7. Mean growth during first 25 d post-extrusion of pelagic juvenile *Sebastes maliger* versus mean sea surface temperature (SST) (Grays Harbor NDBC Buoy Stn 46211). Growth = −0.26 + 0.25 × SST ($r^2 = 0.22$, $p = 0.0013$)

juvenile quillback rockfish. Frequently, size-selective mortality is a function of gape limitation. However, coho salmon are capable of eating prey as large as one-third of their length; previous work has shown that even the smallest coho predator collected (119 mm fork length) has the potential to consume every quillback rockfish encountered in this study (Daly et al. 2009). This pattern of size-selective predation on smaller individuals is consistent with other direct measures of the predatory relationship between marine fishes and their prey. Juvenile Atlantic bluefish *Pomatomus saltatrix* consume relatively smaller juvenile Atlantic silversides *Menidia menidia* and bay anchovies *Anchoa mitchilli* (Juanes & Conover 1995), while larval Japanese anchovy *Engraulis japonicus* experience predator-specific patterns of selective mortality (Takasuka et al. 2003, 2004b, 2007). Also consistent with these studies (Takasuka et al. 2003, 2004b, 2007), our results revealed direct evidence of 'growth-selective predation', with coho salmon selectively consuming juvenile rockfish that were growing more slowly (i.e. with slower recent growth). These findings demonstrate that juvenile coho salmon are selective predators and that large size and rapid recent growth can reduce rockfish vulnerability to predation.

A variety of studies have indirectly tested the 'bigger is better' hypothesis by repeatedly sampling particular cohorts of fish prey and comparing the characteristics of survivors to those of the original population (see Fig. 1). Results of these studies have generally demonstrated the importance of larger sizes-at-age in enhancing survival through larval and juvenile stages (Meekan & Fortier 1996, Hare & Cowen 1997, Robert et al. 2007, D'Alessandro et al. 2013). However, there are also examples of smaller individuals being more likely to survive (Takasuka et al. 2004b, Grorud-Colvert & Sponaugle 2011). Additionally, a study that compared back-calculated size-at-age of juveniles to measured length of larval shortbelly rockfish *Sebastes jordani* found no evidence of size-selective mortality (Laidig et al. 1991). The inconsistency in findings from these indirect studies likely reflects the fact that examined survivors have potentially survived predation by multiple predators, or different predators at different times. Results of our study corroborate the 'bigger is better' hypothesis for a particular predator–prey interaction in the wild.

Laboratory and mesocosm studies of predation in marine fishes provide equivocal evidence of size-selective mortality. While some laboratory/mesocosm studies have identified size-selective predation on smaller size classes of prey fish (e.g. Atlantic bluefish; Juanes & Conover 1994), others provide evidence of selection against larger larvae (e.g. three-spined stickleback *Gasterosteus aculeatus* preying on larval capelin *Mallotus villosus*; Litvak & Leggett 1992). Previous mesocosm predation experiments have demonstrated that coho salmon are selective predators of smaller juvenile pink *Oncorhynchus gorbuscha* (Parker 1971) and chum *O. keta* salmon (Hargreaves & LeBrasseur 1986), findings consistent with our observations of juvenile coho salmon feeding on wild rockfish. The importance of size in reducing predation appears to be predator–prey specific, highlighting the importance of direct studies of particular predator–prey relationships. Our results demonstrate that wild juvenile coho salmon are likely size-selective predators of juvenile quillback rockfish.

Fish that survive their vulnerable early life stages are often those that grow rapidly during their larval stage (Meekan & Fortier 1996, Hare & Cowen 1997, Wilson & Meekan 2002) and/or immediately prior to encountering a predator (Takasuka et al. 2004a). Interestingly, in our study, juvenile coho salmon preferentially preyed upon small quillback rockfish that had rapid early larval growth compared to the survivors, but slower growth at the time of capture. The pattern of consumed fish having slower growth than surviving fish of the same size is consistent with growth-selective predation observed in some larval Japanese anchovy predators (Takasuka et al. 2003, 2004a, 2007). While the salmon may be consuming smaller fish in general and selecting the slower growing individuals when they encounter fish of the same size, the dramatic differences in the growth history of these rockfish suggests vulnerability to coho salmon predation may be determined earlier in life. Fish that were slower growing at the time of encounter with predators actually grew faster earlier in life. It is possible that this faster early growth enhanced their survival at that time, but the reversal to slower growth increased their vulnerability to predation by coho salmon. While it is unclear why the consumed fish grew more slowly prior to capture, because they were born later in the season they encountered warmer water at an earlier age, which likely increased their growth and development. Faster growth and development would have led to their more rapid (younger age and small size) transition to the pelagic juvenile stage, potentially leading to reduced feeding success and reduced growth relative to the older, larger individuals.

These differences in early growth patterns put the fish born later in the season at a disadvantage compared to the individuals born earlier in the season that had slower early larval growth but were growing more rapidly immediately prior to encountering juvenile coho salmon. Thus, traits that might be beneficial early in life (i.e. fast growth) do not always carry over to affect survivorship of later stages in the same way. For young marine fish, there is frequently a tradeoff between growth and stage duration that affects fish size at the time of stage transitions, which can play a critical role in survivorship. For example, fast-growing larval coral reef fish are typically younger and smaller at settlement, which can substantially influence juvenile survivorship (Grorud-Colvert & Sponaugle 2011, Rankin & Sponaugle 2011). Whether or not differences in early larval growth influenced juvenile rockfish survival is unknown, but younger fish that exhibited faster early growth did not grow as quickly as pelagic juveniles, were smaller in size, and were consequently at a disadvantage when they encountered predatory salmon.

Although predation by juvenile salmon upon their rockfish prey largely followed predictions of the 'growth–mortality' hypothesis, rockfish age appears to be the key trait underlying differences in size, growth, development, and ultimately, survival. While mortality generally decreases with fish age, laboratory and mesocosm studies indicate that some predatory fish select older larval fish prey (Fuiman 1989, Litvak & Leggett 1992). Age is fundamentally linked with size and growth rate, but the influence of age is not typically examined in indirect cohort re-sampling studies because age is accounted for when defining cohorts, potentially at the expense of information on how birthdate affects survival (Meekan & Fortier 1996). Aligning re-sampled members of a cohort with those originally sampled is essential in cohort re-sampling studies, as there is strong evidence that differences in developmental conditions affect early life history traits and survival (Hamilton et al. 2008, Grorud-Colvert & Sponaugle 2011, Shulzitski et al. 2016). However, from a predator's perspective, fish of multiple ages and condition can be encountered at the same time, influencing the predator's choice.

Along the coast of Oregon and Washington, rockfish give birth to young once a year with a reproductive season that lasts several months (Love et al. 2002). Larvae produced at different times of the season encounter the highly dynamic California Current System and thus potentially experience very different oceanographic conditions (Checkley & Barth 2009). In our study, the oldest and youngest rockfish were born 31 d apart and encountered SST that varied by 5°C. Differences in the temperature larvae experience can dramatically affect growth and development rates (Green & Fisher 2004) and ultimately determine survival to later life stages (Gagliano et al. 2007, Grorud-Colvert & Sponaugle 2011). Variability in the timing of parturition of quillback rockfish led these fish to develop during substantially different conditions, creating variability in their early growth and development that ultimately affected their survival.

The timing of parturition of rockfish is known to be related to maternal traits (i.e. age and size; Berkeley et al. 2004, Sogard et al. 2008, Rodgveller et al. 2012, Stafford et al. 2014). In many rockfish species, and quillback rockfish in particular, older and larger females produce larvae earlier in the reproductive season (Sogard et al. 2008, Rodgveller et al. 2012). In addition, older females produce higher quality larvae, with higher energy reserves, that are more likely to survive than the offspring of younger mothers (Berkeley et al. 2004, Rodgveller et al. 2012). In our study, these earlier-born fish were more likely to survive predation by juvenile salmon they encountered during their transition to nearshore settlement habitats. Juvenile salmon consumed quillback rockfish that were born later in the spring and that experienced warmer water temperatures. These warmer temperatures led to faster early growth and development, yet slower juvenile growth and smaller juvenile sizes relative to those of the earlier-born rockfish. Juvenile coho salmon encountered juvenile quillback rockfish with variable life history traits and selectively preyed upon the younger, smaller, slower growing individuals. Ultimately, timing of rockfish parturition influences all of their early life history traits and may be the primary factor that best predicts survival of quillback rockfish at the time they encounter predatory salmon in nearshore waters.

5. CONCLUSIONS

Direct examination of predator selectivity improves our understanding of predator–prey relationships and how early life history traits affect survival in specific predator–prey interactions. It remains a challenging goal to fully describe the outcomes of predation in the natural environment with the diversity of predators and variety of prey they encounter, yet these events have important implications for survival and recruitment of prey species. Though we acknowledge the small sample size, our results have shown that a combination of the timing of parturition and SST during the larval stage affect juvenile quillback rockfish early life history traits. We found that large size and rapid recent growth immediately prior to predator encounter improve survival of fish prey, yet these traits may not be consistent throughout the early life of a fish. Depending on which predation events are more intense (predation on early or later stages), detrimental early traits (slower growth, smaller sizes-at-age) may ultimately improve the survival of later stages. Such tradeoffs between early- and late-stage traits may persist in a prey population due to variation in the timing and identity of predator encounter. Young fish face a suite of predators that changes as fish grow and move to different habitats. The role of individual or multiple predators in shaping the traits and recruitment strength of juvenile fishes remains a complex topic, and resolving these processes will require both direct and indirect studies of multiple predator–prey relationships in the wild.

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