



# Predator–prey mass ratios of mid-trophic level fishes in a coastal marine ecosystem vary with taxonomy and body size

Matthew T. Wilson<sup>1</sup> · David G. Kimmel<sup>1</sup>

Received: 11 February 2021 / Accepted: 22 November 2021 / Published online: 13 December 2021  
This is a U.S. government work and not under copyright protection in the U.S.; foreign copyright protection may apply 2021

## Abstract

How predator–prey mass ratios (PPMR) vary across taxa and body sizes has long-standing, unresolved relevance to ecosystem structure, function, and modeling. Mid-level fishes, or forage fishes, convey large amounts of trophic energy in coastal marine ecosystems, but uncertainty in the dependence of their PPMR on predator species and size hampers ecological understanding and model development. Late-summer (September) data (2000, 2001, and 2003) on three major zooplanktivorous forage fishes (capelin *Mallotus catervarius*, eulachon *Thaleichthys pacificus*, and juvenile walleye pollock *Gadus chalcogrammus*) in the western Gulf of Alaska, northeast Pacific Ocean, were used to determine how PPMR varied by species and body size. Differences in species' ability to transition across prey taxa were associated with different allometric relationships in prey size. Transitioning across taxa allowed prey size to increase hyperallometrically resulting in negative size dependence of PPMR for capelin and juvenile walleye pollock, both marine species. In contrast, eulachon, an anadromous species, consumed euphausiids almost exclusively and exhibited positive size dependence of PPMR. Our findings suggest that some predator species differ in transitioning across size-structured taxonomic groups of prey and consequently differ in their size-PPMR relationship. They also suggest that incorporation of taxon-specific PPMR size dependency into multispecies size-based ecosystem models will improve model realism partly because the PPMR is linked theoretically to trophic transfer efficiency.

**Keywords** Trophic ecology · Allometry · Body size · Forage fish · Zooplankton

## Introduction

How and why predator–prey mass ratios (PPMR) vary across taxa and body sizes has long interested trophic and community ecologists and is relevant to the development of ecosystem models. Many aquatic communities are size structured with predator body weight typically greater than prey body weight (Sheldon et al. 1972; Platt and Denman 1977, 1978), which is associated with aquatic predators being gape limited (e.g., Scharf et al. 2000). Long recognized (Lindeman 1942; Hutchinson 1959), this has led to a proliferation of size-based ecosystem models, which assume that body size

is linked to organism functional traits (e.g., metabolism, biomass, growth) and ecosystem functions (e.g., secondary production, trophic transfer efficiency, biogeochemical cycling) (Kremer et al. 2017; Kiørboe et al. 2018). In current models, a predator's selection of particular sized prey is often parameterized with estimates of the PPMR held constant across species (Andersen 2019) or within functional predator groups (Reum et al. 2019). A constant PPMR has practical utility for simplifying trophic interactions in ecosystem models, but assumptions of constancy might reduce model realism because body size and taxonomic effects can be significant (Naisbit et al. 2011; Nakazawa et al. 2011). More information is needed before we can confidently generalize about size and taxonomic effects on PPMR within communities and across systems.

The PPMR is known to vary among broad categories of predators and prey while variation within categories is less resolved. Significant variation in PPMR has been demonstrated among consumer types, habitat and metabolic categories (Brose et al. 2006), and among phyla- and class-level taxonomic groups of predators and prey (Naisbit et al.

Responsible Editor: S. Hamilton.

✉ Matthew T. Wilson  
matt.wilson@noaa.gov

David G. Kimmel  
david.kimmel@noaa.gov

<sup>1</sup> Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA

2011). Increases in PPMR with predator size were observed within a global dataset of mostly marine fish communities (Barnes et al. 2010). This was re-confirmed more recently for pelagic marine fishes whose prey size range increased with predator size (Griffiths 2020). Maximum prey size commonly increases with predator size in association with allometric increases in relevant traits such as mouth gape (e.g., Scharf et al. 2000) that allow easier acquisition of large, energetically rewarding prey within and across taxa (e.g., Brodeur 1998; Mazur et al. 2007). Minimum prey size of pelagic predators, in contrast, changed little as small, readily accessible prey were consumed by all predator sizes to presumably help meet the metabolic demand of active foraging in pelagic habitats (Griffiths 2020). The ready accessibility of small prey reflects the greater abundance (Ursin 1973; Hartvig et al. 2011; Tsai et al. 2016) and easier catchability (e.g., lower handling time) of small organisms relative to larger organisms (Woodward and Warren 2007).

Ideally, for ecosystem modelling, the PPMR is estimated independent of prey availability (Hartvig et al. 2011; Andersen 2019). However, unequal availability across body sizes (i.e., size-structured prey communities), due to the greater abundance of smaller organisms, cause predators to consume more small prey than otherwise dictated by preference. This unequal-abundance bias in PPMR was addressed by Ursin (1973) who simulated equal availability by using biomass instead of count to calculate a weighted mean prey body size. The simulation has been widely used to estimate the PPMR (Horbowy 1982; Dekker 1983; Bundgaard and Sparholt 1992; Lewy and Vinther 2004; Andersen 2019). More recently, Tsai et al. (2016) proposed another method to examine PPMR size dependency free of unequal-abundance bias due to differences in abundance of potential prey sizes. Essentially, they subtract from PPMR a quantity that accounts for differences in abundance across potential prey sizes in the environment. The resulting deviance, they argue, is a proxy for the PPMR of a predator foraging for prey that are equally abundant over all sizes. Importantly, Ursin's method estimates PPMR (hereafter, Ursin's PPMR) while Tsai et al.'s method estimates a PPMR proxy (hereafter, Tsai et al.'s Proxy).

Among marine fishes, prey size and taxonomy are often related. For example, 18 species of marine fishes consumed various sizes of small invertebrate taxa (pandalid shrimp, cancer crabs) and larger vertebrate taxa (fishes) (Scharf et al. 2000), and 3 species of zooplanktivorous fishes consumed small calanoid copepods and larger *Thysanoessa* euphausiids (Brodeur 1998; Wilson et al. 2006, 2009). Here, we investigate variation in prey body weight allometry (i.e., PPMR) among similar, co-occurring neritic midwater fishes that share zooplanktonic resources, but that also exhibit niche partitioning and dietary specialization (Wilson et al. 2006, 2009) potentially affecting specific predator size-PPMR relationship.

Small neritic fishes, often referred to as forage fishes, are important in the transfer of trophic energy within many coastal ecosystems. In the western Gulf of Alaska (GOA), forage fishes commonly consume zooplankton (e.g., copepods, euphausiids) and in turn are consumed by piscivorous fishes, sea birds, and marine mammals (Aydin et al. 2007). Three forage-fish species of particular trophic prominence in the GOA are capelin (*Mallotus catervarius* [= *M. villosus*, see Mecklenburg et al. (2018)]), eulachon (*Thaleichthys pacificus*), and juvenile walleye pollock (*Gadus chalcogrammus*). Capelin and eulachon are both osmerid smelts, but eulachon undergo anadromous spawning runs in winter-spring (Gustafson et al. 2012); pollock are a strictly marine gadid that grows to a relatively large size (Mecklenburg et al. et al. 2002). The trophic energy conveyed by these species critically supports the piscivore-dominated GOA ecosystem (Aydin et al. 2007). Aydin et al. (2007) estimate that 11–39% of the consumption by these species contributes to their production and that 80–98% of their total production is lost to mortality by predation, but they note the paucity of empirical information on prey count and weight.

Although little is known about the comparative prey size allometry among capelin, eulachon, and juvenile pollock, observed differences in diet and foraging ecology indicate the potential for differences in PPMR size dependency. These are primarily particulate feeders that acquire zooplankton in the neritic midwater (Wilson et al. 2006, 2009), which is a 3-dimensional environment where PPMR is particularly relevant to feeding success (Giacomini et al. 2013). Over similar predator size ranges, the diets of capelin and juvenile pollock transitioned from small-sized taxa, mostly copepods, to large-sized taxa, mostly euphausiids, but with greater taxonomic diversity exhibited by juvenile pollock in association with a less-streamlined body, implying lower foraging activity, and nocturnal versus crepuscular foraging chronology (Wilson et al. 2006); in contrast, eulachon of all observed sizes fed almost exclusively on euphausiids, the dietary specialization apparently associated with large palatine and vomerine caniniform teeth (Wilson et al. 2009). These predator specific differences in morphology and feeding behavior were associated with differences in the predator-euphausiid body size relationship (Wilson et al. 2009). For particulate foragers, predator behavior and morphology interact with prey conspicuousness and catchability, often associated with taxonomy, to affect predator selectivity of prey size and taxa (Lazzaro 1987).

Our goal was to learn how taxonomy, body size, and quantitative method affect PPMR for 3 prominent forage fishes in the GOA. Our first objective focused on how counts and body weights of prey taxa might differently vary among individual capelin, eulachon, and juvenile walleye pollock. These prey attributes (count, body weight, and taxonomy) are typically combined in the PPMR denominator, but we

wanted to examine them separately to better understand how each contributes to the variation in PPMR with predator size. Our first hypothesis was that predator size-related increases in prey count would be greater for large-sized taxa than for small-sized taxa because for pelagic predators the maximum prey size increases more with predator size than does the minimum prey size (Griffiths 2020). Our second hypothesis was that predator size-related increases in prey body weight would be lower within than across prey taxonomic groups due to a positive predator–prey body weight relationship (Griffiths 2020) and size-structured taxonomic groups of prey (Brodeur 1998; Wilson et al. 2006, 2009). The implication being that the degree to which predators transition across prey taxa could be a mechanism for predator size–PPMR relationship specificity. Our second objective focused on the predator size dependency of PPMR estimated for individual predators using Ursin’s PPMR and Tsai et al.’s Proxy. These methods have not yet been compared; however, both were designed to address the unequal–abundance bias. Therefore, we expect Ursin’s PPMR and Tsai et al.’s Proxy to similarly exhibit differences in the predator size–PPMR relationship among predator species assuming that previously observed differences in diet and foraging ecology of co-occurring individuals reflect differences in prey preference.

## Materials and methods

### EcoFOCI data

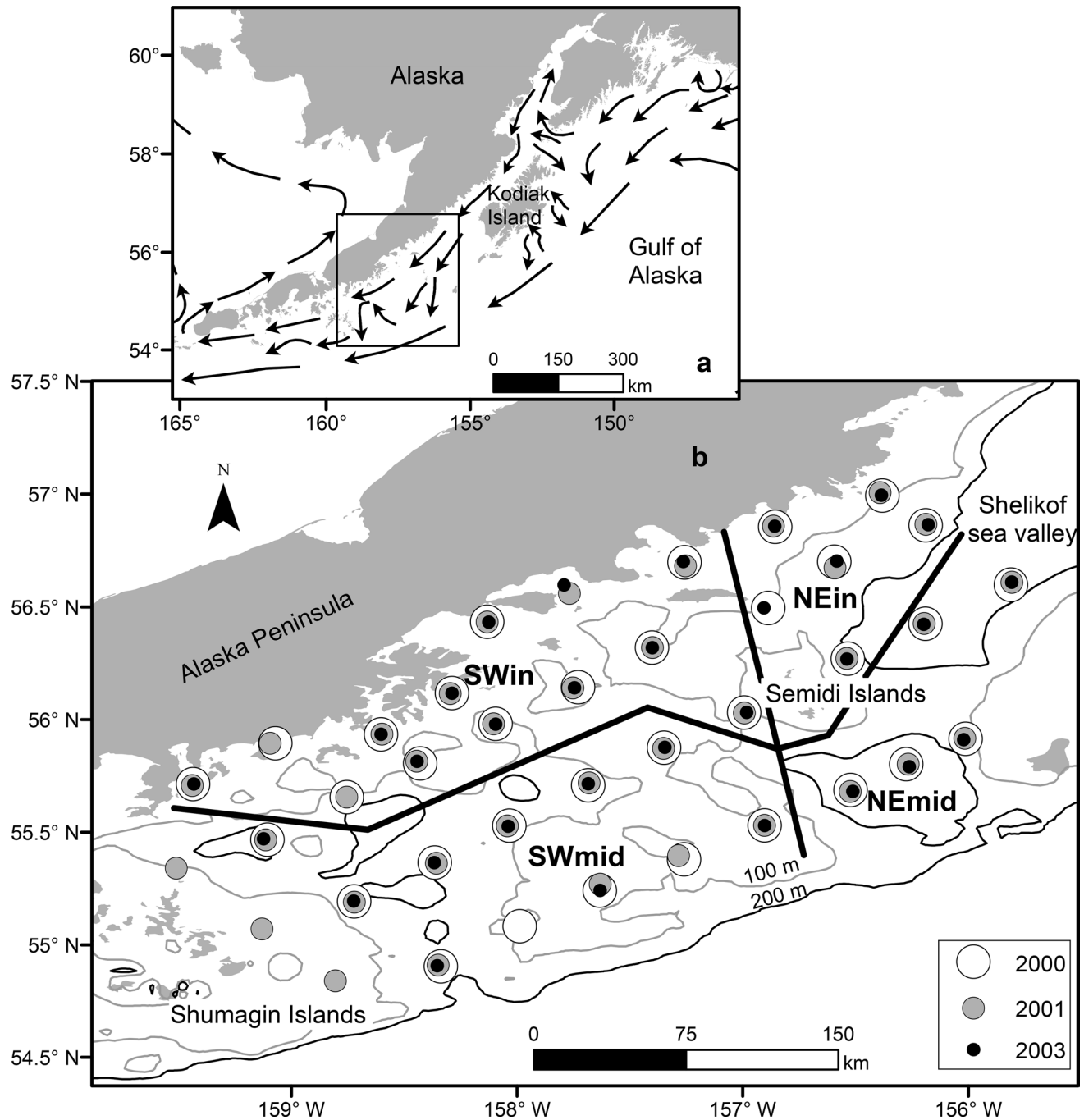
The Ecosystems and Fisheries–Oceanography Coordinated Investigations Program (EcoFOCI) collects data on nektonic forage fishes and zooplankton to study fishery relevant ecosystem processes (Kendall et al. 1996; McClatchie et al. 2014). For this study, we selected data from collection sites situated adjacent to the Alaska Peninsula over the continental shelf southwest of Kodiak Island between the Shelikof sea valley and the Shumagin Islands (Fig. 1, Table 1). Sampling occurred during September 2000, 2001, and 2003 across four hydrographic regions subsequently defined by water temperature, salinity, and model-based estimates of net current velocity (Wilson 2009; Wilson et al. 2009). Specific sampling locations (sites) were predetermined and sited to approximate a grid while allowing for navigational hazards and representation of bathymetry and topographic features (e.g., Semidi Islands, sea valleys, banks). Sites were sampled once or twice by trawling. When sampled twice, one trawl haul (hereafter haul) was conducted during the day (1600–0530 h GMT) and another at night (0600–1500 h GMT) within 24 h. Thus, the sampling design was year crossed with region, and haul nested within site.

Briefly, depth-integrated fish samples were collected using a small-mesh midwater trawl (Table 1). Fish collected in each haul were sorted at sea, enumerated, and samples of select groups were frozen for subsequent analysis of food habits. One species, walleye pollock (hereafter, pollock), exhibited clear delineation of age groups by body size (Brodeur and Wilson 1996) and so was sorted at sea into age 0 ( $\leq 120$  mm standard length, SL) and older (hereafter, age 1) individuals ( $\geq 130$  mm SL) by nonoverlapping body length ranges. Based on the abundance in hauls (Wilson 2009), we selected four groups for analysis: (1) capelin, (2) eulachon, (3) pollock age 0, and (4) pollock age 1.

Predator stomach contents were examined in the laboratory as described by Wilson et al. (2009). Briefly, predators were thawed, blotted dry and weighed individually to the nearest 0.001 g. Body weight ranged from 1.3 to 17 g for capelin, 1.2 to 89 g for eulachon, and 0.4 to 164 g for pollock. Prey from predator stomachs were sorted into ten coarse taxonomic groups by digestion state, a subjective assessment of apparent tissue loss, following Wilson et al. (2009). Lightly digested prey had skeleton intact with low to no soft tissue damage or loss. Highly digested prey had incomplete skeleton with high soft tissue damage and loss. Prey in each taxon-digestion group were collectively blotted dry, counted, and weighed to the nearest 0.01 mg. Mean individual prey body weight was estimated as the collective weight divided by count. We used predator data from hauls that were paired with samples of zooplankton. While the present study does not focus directly on the zooplankton data, it was an important consideration in the methods used to estimate PPMR. Zooplankton samples were collected with a 1-m<sup>2</sup> Tucker trawl as described by Wilson et al. (2009).

### Data analysis

Prey group-specific ratio estimators (Cochran 1977) were applied to highly digested prey body weights to reduce digestion bias. The estimators were calculated by averaging mean individual prey body weight by prey group and digestion category across all predators, and expressed as the ratio of lightly:highly digested prey (Table 2). The ratios were applied if  $> 1$ , assuming digestion reduced mean prey body size, to increase the mean body weight of highly digested items recovered from each predator stomach. Overall, adjusted body weights of 113,044 highly digested prey were combined with 34,817 lightly digested prey to give 147,861 prey recovered from 3414 predator stomachs. The overall dataset was used to estimate prey count and mean body weight for each of the 10 prey taxonomic groups and for each predator. Based on Table 2, we refer to the 10 prey taxonomic groups hereafter either by name or by relative mean individual body weight (e.g., copepods were small-sized prey, euphausiids were large-sized prey). All statistical



**Fig. 1** Map of ocean currents (inset, from Reed and Schumacher (1986)) and 38 sites across 4 hydrographic regions (thick lines) in the Gulf of Alaska where sampling was conducted during September

2000, 2001, and 2003 to collect fish and zooplankton. Regions: northeast inner shelf, NEin; northeast mid-shelf, NEmid; southwest inner shelf, SWin; southwest mid-shelf, SWmid

analyses were conducted in the R computing environment using R version 3.6.1 (R Core Team 2019).

In our analyses, we did not pool the two pollock size groups due to the size gap between them. Our concern was that previously observed differences in dietary transition between them (Wilson et al. 2009) would be obscured if regressions were forced to fit groups separated by a gap

in body size. We acknowledge that by not pooling, the reduced range in predator body size within each group limited statistical detection ability. This was, in our opinion, an acceptable compromise in our attempt to resolve as finely as possible the effect of predator body size on prey count, size, and PPMR.

**Table 1** Number of midwater trawl hauls at collection sites by year and region (Fig. 1) in the western Gulf of Alaska, and the number and body weight (g) of predators in each of the four groups used to examine predator–prey mass ratios

Sampling design				Total no. predators	Predator body weight means (standard error)				
Year	Region	Sites	Hauls		Capelin	Eulachon	Walleye pollock		
								Age-0	Age-1
2000	NEin	6	12	323	4.04 (0.51)	42.75 (5.03)	5.04 (0.16)	50.48 (1.47)	
	NEmid	6	10	275	6.72 (1.75)	23.50 (2.36)	3.52 (0.14)	50.25 (1.54)	
	SWin	12	18	309	3.17 (0.16)	11.32 (5.17)	2.73 (0.08)	–	
	SWmid	10	18	370	2.95 (0.52)	9.64 (2.15)	1.99 (0.05)	43.18 (2.02)	
2001	NEin	5	10	344	4.84 (0.43)	41.46 (2.21)	5.61 (0.16)	67.72 (2.76)	
	NEmid	6	9	164	–	23.19 (2.01)	4.93 (0.25)	93.96 (3.71)	
	SWin	13	20	378	3.86 (0.26)	20.61 (4.49)	3.66 (0.10)	71.25 (4.10)	
2003	SWmid	12	19	374	4.90 (0.31)	21.17 (2.39)	2.59 (0.07)	51.56 (5.15)	
	NEin	6	11	297	4.48 (0.32)	28.00 (3.73)	4.28 (0.12)	68.88 (5.83)	
	NEmid	6	8	107	5.04 (0.52)	20.67 (2.95)	2.73 (0.10)	–	
	SWin	9	16	242	3.81 (0.20)	11.07 (4.96)	3.38 (0.10)	–	
	SWmid	8	12	231	4.40 (0.27)	20.90 (2.34)	2.42 (0.06)	–	

**Table 2** Body weight (mg) ratios and statistics (count, mean, standard deviation) for each of 10 taxonomic prey groups represented in the contents of 3414 predator stomachs

Prey	Lightly digested			Highly digested			Ratio
	Count	Mean	SD	Count	Mean	SD	
Appendicularia	3692	0.080	0.138	24,786	0.069	0.097	1.15
Pteropod	3403	0.213	0.239	8085	0.229	0.357	0.93
Copepod	23,135	0.458	0.747	66,170	0.254	0.323	1.80
Amphipod	455	2.866	4.611	845	1.606	2.571	1.78
Crab	345	5.443	2.320	889	2.805	2.058	1.94
Chaetognath	44	6.507	2.480	702	2.939	3.097	2.21
Mysid	9	9.021	5.351	7	5.120	6.560	1.76
Euphausiid	3682	26.101	26.569	11,341	10.983	11.474	2.38
Shrimp	42	79.245	126.183	46	25.113	41.436	3.16
Fish	10	1059.194	980.780	173	107.993	249.419	9.81

Ratio = lightly:highly digested prey weight means

### Prey count and body weight

For prey count, our expectation was that as predator size increased the count of large-sized taxa (e.g., euphausiids) would increase more than counts of small-sized taxa (e.g., copepods). This was examined separately for each predator and prey group using least-squares linear regression (*lm* function, *stats* package) to estimate the functional relationship between prey count and predator body weight:

$$\ln(c_{qmyd}) = \beta_0 + \beta_1 \ln(m) + \beta_2 year + \beta_3 diel + \beta_4 year : diel + \epsilon_{qmyd},$$

where  $\ln(c_{qmyd})$  denotes the  $\log_e$  count of prey predator<sup>-1</sup> for prey group *q* in predators within the body weight class with midpoint  $\ln m$  that were collected during year *y* and diel period *d*.  $\ln$  body weight class midpoint interval was 0.1. *Year*, *diel* period (day, night), and their interaction, *year:diel*, were included to account for possible effects on

the intercept. We excluded all  $c_{qmyd} = 0$  because the underlying cause might have been insufficient sample size. The model was fitted separately to each predator–prey group combination. Regression residuals appeared normally distributed after  $\ln$  transformation. Terms in the models were evaluated using Type III sum of squares (*Anova* function, *car* package) and sum-to-zero contrasts (Fox and Weisberg 2019).

For prey body weight, our expectation was that predator size-related increases in prey body weight would be lower within groups than across prey groups. This was addressed by comparing predator–prey body weight relationships within each predator and prey group to the relationship for each predator group across all prey groups. Slopes were expected to be lower within groups than for all groups combined. We used linear mixed-effects models to estimate the functional relationship between predator and prey body size (*lmer* function, *lmerTest* package):

$$\ln(w_{qish}) = \beta_0 + \beta_1 \ln(m_i) + \beta_2 year_i + b_{1ish} + b_{2is} + \epsilon_{ish},$$

where  $\ln(w_{qish})$  denotes  $\ln$  mean body weight of prey group  $q$  in predator  $i$  with  $\ln$  body weight  $m_i$ . *Year* was included to account for possible interannual differences in the intercept. Data groups were defined by the random effects of *sample nested within site* ( $b_{1ish}$ ) and of *site* ( $b_{2is}$ ). The model was fitted using reduced maximum likelihood estimation. Residual plots were visually inspected to evaluate homoscedasticity and normality.

For groups combined, we used a linear mixed-effects model to examine the predator–prey body weight relationship while accounting for sampling design (*lmer* function, *lmerTest* package). The relationship was allowed to vary among predator groups, but not among sampling-design levels due to a paucity of within-level observations:

$$\begin{aligned} \ln(w_{ish}) = & \beta_0 + \beta_1 \ln(m_i) + \beta_2 predGrp_i \\ & + \beta_3 \ln(m_i) : predGrp_i \\ & + \beta_4 year_i + \beta_5 region_i \\ & + \beta_6 year_i : region_i + b_{1ish} + b_{2is} + \epsilon_{ish} \end{aligned}$$

The response variable,  $\ln(w_{ish})$ , denotes  $\ln$  mean body weight (i.e., prey weight / prey count) of prey in predator  $i$  with  $\ln$  body weight  $m_i$ . The terms  $\ln(m_i)$  and *predGrp* denote the  $\ln$  body weight and group (capelin, eulachon, age-0 and age-1 walleye pollock), respectively, of predator  $i$ . The interaction term,  $\ln(m_i):predGrp$ , allowed size dependency to vary among predator groups. To account for the sampling design (Table 1), *year* and *region* were crossed and included as fixed effects to allow greater precision in estimating the variance of effects with few levels; data groups were defined by the random effects of haul nested within site ( $b_{1ish}$ ) and site ( $b_{2is}$ ). Accounting for sample grouping is similar to the site-by-site analysis of Nakazawa et al. (2011) except that here it is incorporated into the statistical model. The model was fitted using reduced maximum likelihood estimation. Residual plots were visually inspected to evaluate assumptions of homoscedasticity and normality. Model terms were evaluated statistically using Type III analysis of variance with Satterthwaite’s method (*anova* function, *stats* package). Predictor estimate significance ( $p < 0.05$ ) was computed using the Kenward-Roger degrees of freedom approximation and conditional F tests (*tab\_model* function, *sjPlot* package). Hereafter, we refer to this as the taxon-integrated model.

### Predator–prey mass ratio (PPMR)

We used Ursin’s PPMR and Tsai et al.’s Proxy to test our hypotheses that PPMR would differ among predator groups. Ursin’s PPMR (Ursin 1973) simulates equal availability by

using prey biomass as a weight when averaging  $\ln$ -transformed PPMR across predators and prey size classes. The assumption is that prey is equally available in terms of biomass within communities where organism biomass does not change across body weight classes. We found support for the assumption from an examination of the abundance–body weight relationship using estimates of zooplankton and predator abundance from the Tucker and midwater-trawl samples, respectively, and body weight estimates from the predator diet data (Online Resource 1). We therefore applied Ursin’s method of using a biomass-weighted PPMR to estimate PPMR for each predator:

$$\ln(PPMR_i) = \frac{\sum^Q (\ln(\frac{m_i}{w_{qi}}) W_{qi})}{\sum^Q W_{qi}},$$

where  $m_i$  is body weight of the  $i$ th predator, and  $w_{qi}$  and  $W_{qi}$  are the mean individual body weight and total weight, respectively, of the  $q$ th of  $Q$  possible prey groups (i.e., ten) in predator  $i$ .

The second method, from Tsai et al. (2016), was developed to examine size dependency of the PPMR among predators. They define the environmental PPMR (PPMR<sub>e</sub>) for predator  $i$ :

$$PPMR_e = \sum \frac{m_i}{w_q} e_{qi},$$

where  $m_i$  is the body weight of predator  $i$ ,  $w_q$  is the mean individual body weight of prey group  $q$ , and  $e_{qi}$  is the proportional abundance of prey group  $q$  in the environment during the year when predator  $i$  was collected. They propose that the size dependency of PPMR is equivalent to the size dependency of the difference between  $\log_{10}(PPMR_e)$  and  $\log_{10}(PPMR)$ , their equations:

$$PPMR_i = \log_{10} PPMR_i - \log_{10} PPMR_e$$

$$PPMR_i = \log_{10} \left( \sum \frac{m_i}{w_q} p_{qi} \right) - \log_{10} \left( \sum \frac{m_i}{w_q} e_{qi} \right),$$

where  $p_{qi}$  is proportional abundance of prey group  $q$  in predator  $i$ . Importantly, predator body weight,  $m_i$ , can be removed by simplification:

$$PPMR_i = \log_{10} \left( \sum \frac{p_{qi}}{w_q} \right) - \log_{10} \left( \sum \frac{e_{qi}}{w_q} \right).$$

For predators with equal access to the same prey field, such as those collected together in the same haul, we can assume a common PPMR<sub>e</sub>. Thus, testing for PPMR size dependency among predators collected in the same haul

( $h$ ) is equivalent to testing the null hypothesis  $\beta_1 = 0$  in the relationship

$$\log_{10} \left( \sum^Q \frac{p_{qih}}{w_{qih}} \right) = \beta_0 + \beta_1 \log_{10}(m_{ih}),$$

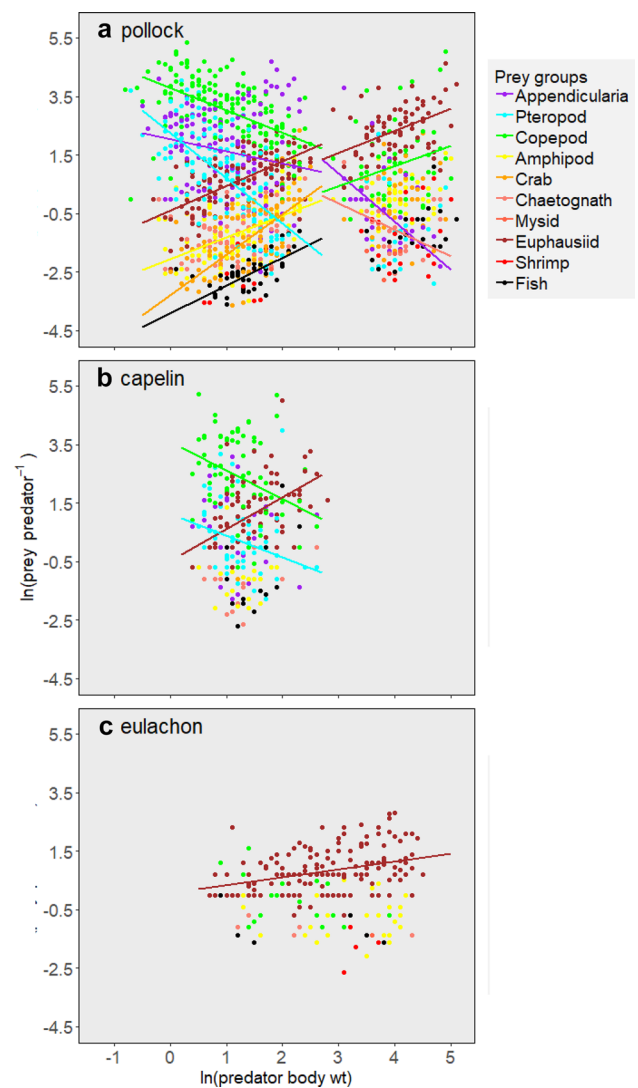
where  $p_{qih}$  and  $w_{qih}$  are proportional abundance and mean individual body weight, respectively, of prey group  $q$  in predator  $i$  from haul  $h$ , and  $m_{ih}$  is the body weight of predator  $i$  from haul  $h$ . For a more direct comparison with Ursin's method, we used base  $e$  rather than base 10 logarithm. Our assumption that all predators from haul  $h$  had equal access to the same prey field was compatible with the need for our statistical model to account for grouping effects imposed by the sampling design.

The taxon-integrated model described above was used to test for predator group and body size effects on Ursin's PPMR and then on Tsai et al.'s Proxy, which were the dependent variables. For Ursin's PPMR, each  $i$ th observation was weighted by the total weight of prey from predator  $i$ . The full model was compared to subsets first without the predator group-body weight interaction and then also without predator body weight using Akaike Information Criterion (AIC) (*AIC* function, *stats* package) and analysis of variance (*anova* function, *stats* package) to select the best model. Models were fitted using maximum likelihood estimation. Residual plots were visually inspected to assess assumptions of homoscedasticity and normality. The best model was then fitted using reduced maximum likelihood. Model terms were evaluated using Type III analysis of variance with Satterthwaite's method (*anova* function, *stats* package). Predictor estimate significance ( $p < 0.05$ ) was computed using the Kenward–Roger degrees of freedom approximation and conditional F tests (*tab\_model* function, *sjPlot* package). If the interaction term,  $\ln(m_i):predGrp$ , was significant ( $p < 0.05$ ), differences among predator groups were evaluated using post hoc Tukey's tests (*emmeans* function, *emmeans* package).

## Results

### Prey count and body weight

As predator body weight increased, prey count predator<sup>-1</sup> tended to decrease for prey groups with small mean body size and increase for prey taxa with larger body sizes (Table 2, Fig. 2). The relationship between prey count and predator size was significant (ANOVA,  $P < 0.05$ ) for 15 predator–prey group combinations (Online Resource 2). Among these relationships, the prey groups that decreased in count as predator size increased were appendicularians, pteropods, and copepods, all relatively small prey (Table 2,



**Fig. 2** Prey count by predator body weight class and prey group for walleye pollock (a), capelin (b), and eulachon (c). Lines represent significant functional relationships (see Online Resource 2 for analysis of variance and regression parameters). Symbol color (purple to black) indicates low-to-high rank order of mean prey body weight (Table 2)

and chaetognaths. Prey groups that increased in count with predator size were amphipods, crabs, euphausiids, and fish, all relatively mid-size or larger prey (Table 2), and copepods consumed by age-1 pollock. For capelin and juvenile pollock, the decrease in small-sized prey counts was commensurate with larger-sized prey counts with no apparent increase in total prey count with predator size (Fig. 2). Among eulachon, euphausiids was the only prey group where counts related to predator body size.

Taxon-specific prey body weight increased with predator body weight for ten predator–prey group combinations based on 8085 total combinations (Fig. 3). All significant relationships had positive slopes (Online Resource 3). Most

relationships involved pteropods, copepods, or euphausiids. Among eulachon, euphausiids was the only prey group where prey body size related to predator body size.

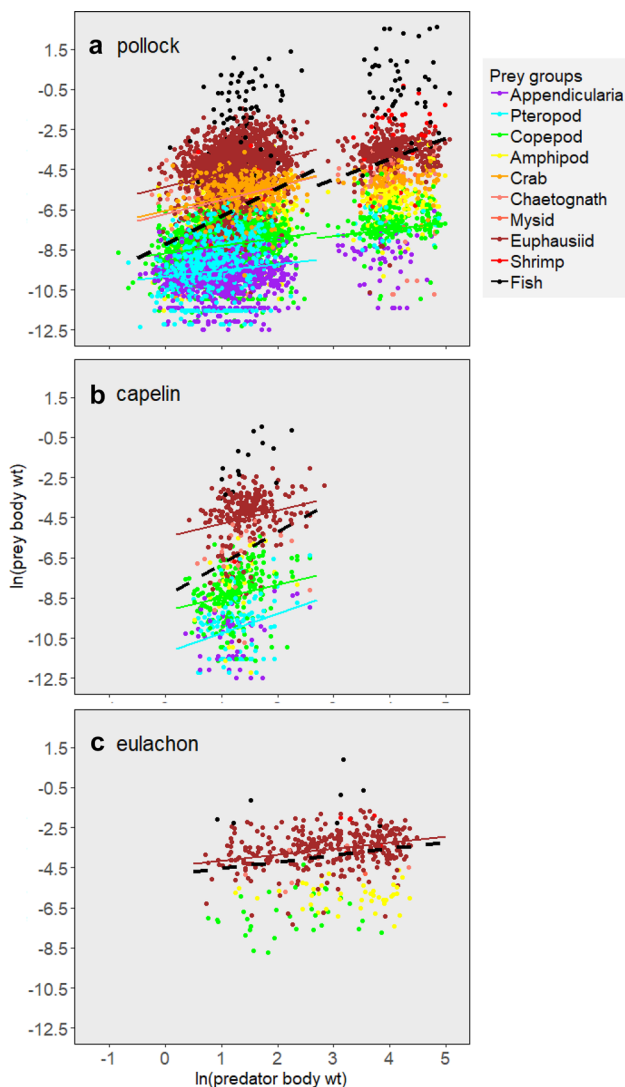
Given the above taxon-specific patterns, it was not surprising that taxon-integrated prey body weights increased with predator body weight (Fig. 4). The predator–prey body weight relationship significantly varied among predator groups as indicated by significance of the interaction term,  $\ln(m_i):predGrp$  (ANOVA,  $P < 0.001$ , Table 3). The model explained 56% (conditional  $R^2$ ) of the variation in prey body weight after accounting for the random effects of

$haul:site$  and  $site$  (Table 4). Residuals were reasonably well distributed (Fig. 4). The predator group effect on regression slope differed significantly from zero for all but age-1 pollock. Eulachon had the flattest slope ( $1.089 - 0.759 = 0.33$ , Table 4), which was similar to the euphausiid-only slope due to the relative paucity of other prey groups. For all predator groups, prey body weight increased more steeply with predator size when prey groups were integrated rather than separated due to the complementary effect of transitioning across prey taxa (Fig. 3); however, this was least pronounced for eulachon because they consumed relatively few prey groups.

### Predator–prey mass ratio

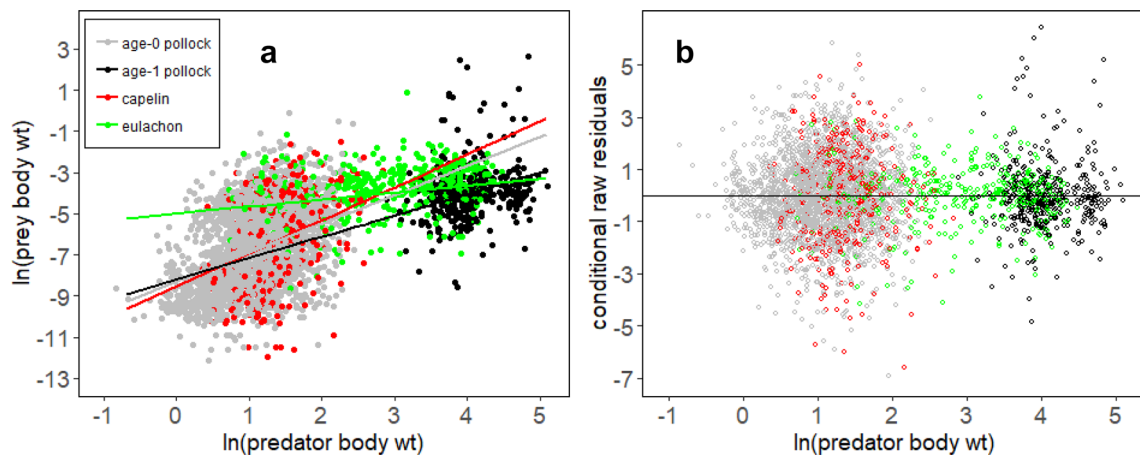
Size dependency varied by predator group for Ursin's PPMR and for Tsai et al.'s Proxy. For each method, the full model was deemed best because elimination of either the covariate,  $\ln(m_i)$ , its interaction with predator group,  $\ln(m_i):predGrp_i$ , or both significantly increased AIC (ANOVA,  $P < 0.001$ ). For Ursin's PPMR, size dependency varied by predator group (Table 3). The greatest disparity in size dependence was between eulachon and the other predator groups as indicated by predictor estimates and confidence intervals (Table 5). Size dependency was strongly positive for eulachon, negative for capelin and age-0 pollock, and absent (i.e., slope not significantly different from 0, Table 5) for age-1 pollock, respectively (Fig. 5). The absence of size dependency is equivalent to isometric changes in prey size. The residual bubble plot shows that the prey weights used to weight each observation were highest for the largest predators and the lowest PPMR (Fig. 5). Note that the largest prey weights were indicative of increased piscivory among larger age-1 pollock. The grouping structure of the population (random effects) explained 86% of the variance indicating high similarity among individuals within hauls (intraclass correlation:  $haul:site = 0.67$ ,  $site = 0.19$ ); thus, the conditional  $R^2 = 0.89$  was much greater than the marginal  $R^2 = 0.23$  (Table 5). Post hoc tests detected significant pairwise differences (Tukey,  $P < 0.002$ ) between all pairwise combinations except capelin and age-1 pollock (Tukey,  $t = -1.92$ ,  $df = 341.5$ ,  $P = 0.22$ ). Estimated marginal means at  $\ln(w_i) = 1.65$  were  $4.1 \pm 0.25$  standard error,  $df = 31$ ;  $5.2 \pm 0.18$ ,  $df = 31$ ;  $5.7 \pm 0.20$ ,  $df = 42$ ; and  $6.2 \pm 0.31$ ,  $df = 246$ , respectively, for eulachon, age-0 pollock, capelin, and age-1 pollock.

The size dependency of Tsai et al.'s Proxy also varied by predator group; however, the Proxy did not increase with body weight for any predator group. All predictor estimates except for age-1 pollock were significant (Table 5) and all slopes were negative (Fig. 5). The grouping structure of the population explained only 23% of the variance indicating low similarity among individuals within hauls (intraclass correlation:  $haul:site = 0.15$ ,  $site = 0.08$ ); thus,



**Fig. 3** Body weight of prey and predator by prey group for walleye pollock (a), capelin (b), and eulachon (c) from the Gulf of Alaska during September 2000, 2001, and 2003. Thin solid lines represent significant functional relationships (see Online Resource 3 for analysis of variance and regression parameters). Symbol color (purple to black) indicates low-to-high rank order of prey body weight (Table 2). Thick dashed line represents the taxon-integrated model of mean prey body weight (Table 4)





**Fig. 4** The relationship between taxon-integrated body weight of prey and the body weight of predators by group (age-0 pollock, age-1 pollock, capelin, and eulachon) from the linear mixed-effects model (a lines represent regression parameters by group and extend across the

full data range to aid visibility) and conditional raw residuals (b). Predators were collected in the western Gulf of Alaska, September 2000, 2001, and 2003

**Table 3** Analysis of variance of taxon-integrated prey body weight, ln(Prey body weight), ln(Ursin’s predator–prey mass ratio, PPMR), and Tsai et al.’s Proxy in relation to predator body weight, ln( $m_i$ ), among four groups of predators (predGrp: capelin, eulachon, age-0 pollock, and age-1 pollock) collected in the western Gulf of Alaska during September 2000, 2001, and 2003

	Sum Sq	Mean Sq	Degrees of Freedom		F	P
			Num	Den		
ln(Prey body weight)						
ln( $m_i$ )	436.44	436.44	1	3379.7	195.91	<0.001
predGrp	316.37	105.46	3	3373.2	47.34	<0.001
ln( $m_i$ ):predGrp	221.65	73.88	3	3369.1	33.17	<0.001
year	6.22	3.11	2	115.9	1.40	0.252
region	0.48	0.16	3	29.7	0.07	0.974
year:region	88.43	14.74	6	112.3	6.62	<0.001
ln(Ursin’s PPMR)						
ln( $m_i$ )	0.63	0.63	1	3375.5	1.86	0.172
predGrp	39.19	13.06	3	3353.2	38.41	<0.001
ln( $m_i$ ):predGrp	59.39	19.80	3	3365.5	58.21	<0.001
year	3.14	1.57	2	96.6	4.61	0.012
region	0.13	0.04	3	19.1	0.13	0.942
year:region	6.16	1.03	6	95.7	3.02	0.010
Tsai et al.’s Proxy						
ln( $m_i$ )	318.86	318.86	1	3390.6	127.14	<0.001
predGrp	394.06	131.35	3	3384.2	52.37	<0.001
ln( $m_i$ ):predGrp	88.56	29.52	3	3381.5	11.77	<0.001
year	1.79	0.89	2	120.8	0.36	0.701
region	2.55	0.85	3	29.3	0.34	0.797
year:region	114.43	19.07	6	116.1	7.60	<0.001

the conditional  $R^2=0.53$  and the marginal  $R^2=0.38$  were similar (Table 5). Post hoc tests detected significant pairwise differences (Tukey,  $P<0.004$ ) between all predator groups except age 0 and age 1 pollock (Tukey,  $t=-1.17$ ,  $df=3374$ ,  $P=0.64$ ).

### Discussion

These findings largely support our hypotheses on predator size-related changes in diet and PPMR. First, dietary transition with increasing predator size was due to greater increase in counts of large-sized prey (e.g., euphausiids)

**Table 4** Regression estimates, including 95% confidence interval (CI) and *P* value, and random effects variance from the fitted, taxon-integrated model of prey body weight and body weight ( $\ln[m_i]$ ) of four groups of predators (capelin, age-0 pollock, age-1 pollock, and eulachon) collected in the western Gulf of Alaska during September 2000, 2001, and 2003

Predictors	$\ln(\text{Prey body weight})$		
	Estimate	CI	<i>P</i>
intercept	-7.403	-7.927 to -6.879	<0.001
$\ln(m_i)$	1.089	0.937–1.242	<0.001
capelin	-1.019	-1.618 to -0.420	0.001
pollock age-0	-0.794	-1.259 to -0.329	0.001
pollock age-1	-0.697	-1.945–0.551	0.273
eulachon	2.510	1.923–3.098	<0.001
$\ln(m_i)$ :capelin	0.506	0.201–0.812	0.001
$\ln(m_i)$ :pollock age-0	0.310	0.132–0.487	0.001
$\ln(m_i)$ :pollock age-1	-0.057	-0.380–0.265	0.727
$\ln(m_i)$ :eulachon	-0.759	-0.950 to -0.567	<0.001
Random effects (variance)			
$\sigma^2$	2.228		
$\tau_{00}$ haul:site	0.548		
$\tau_{00}$ site	0.369		
Intraclass correlation			
haul:site	0.175		
site	0.118		
Marginal $R^2$	0.377		
Conditional $R^2$	0.558		

For brevity, statistics for year and region predictors are omitted. Number of observations was 3414 grouped into 163 haul:sites and 38 sites

than small-sized prey, which decreased with predator size for some taxa (e.g., copepods). Second, prey size increased with predator size more for prey taxa combined than separated indicating that the degree to which predators transition across prey taxa is relevant to the PPMR. Third, Ursin's PPMR and Tsai et al.'s Proxy exhibited similar relative differences in size dependency among predator groups with eulachon having the most-positive and least-negative slope, respectively; however, in contrast to Ursin's PPMR, all slopes for Tsai et al.'s Proxy were negative. Eulachon, regardless of size, fed primarily on euphausiids and therefore did not exhibit the size-related increase in relative prey size exhibited by other predators that transitioned across taxa. Overall, our findings caution against using PPMR as a community-level parameter and we also note that the method used to assess PPMR size dependency warrants careful consideration.

### Prey count and body weight

We attribute the observed count-based diet transitions and changes in prey body weight to predator selectivity

of prey sizes because large-sized prey counts increased commensurate with decreasing counts of small-sized prey. Dietary transitions can relate to size-related changes in behavior, feeding apparatus, and morphology (McCormick 1998; Winkler et al. 2017). For age-0 walleye pollock, the transition to a more euphausiid-dominated diet appears to coincide approximately with behavioral transition from diurnal to nocturnal feeding (Merati and Brodeur 1996; Brodeur 1998; Wilson et al. 2006). Euphausiids may be more available at night when they ascend from near the seafloor to higher in the water column (Merati and Brodeur 1996; Brodeur 1998). Increases in age-0 mouth gape width appear to be hyperallometric (Sogard and Olla 1994), which could motivate larger pollock to search for and reside in areas where large, energy-rich euphausiids are abundant (Wilson 2009; Wilson et al. 2009), subsequent maintenance of isometric changes in prey size likely require greater proportional consumption of euphausiids and fish. This was supported by the increased incidence of piscivory among the largest age-1 pollock. In fact, larger pollock in the GOA consume increasing amounts of fishes and shrimps, which could support an isometric increase in prey size; however, euphausiids continue to be a major dietary item (Aydin et al. 2007; Urban 2012), which might result in hypoallometric increase in prey size.

The observed difference in prey count and body size between eulachon and capelin or pollock can be explained in part by differences in the evolutionary constraint on diet diversity. Eulachon diets were more dominated by a single prey taxon (euphausiids) than were those of capelin or pollock (Wilson et al. 2009). This was most apparent at small predator sizes by the relative dominance of euphausiids in small eulachon diets, which reflects their effectiveness in capturing large euphausiids and may be competitively advantageous by allowing earlier access to the resource than potential competitors. Early access might be facilitated mechanically by a large mouth (Willson et al. 2006) equipped with large palatine and vomerine caniniform teeth (Mecklenburg et al. 2002). Acquisition of large, energy-rich euphausiids (Mazur et al. 2007) during seasonal declines in availability may be critical in provisioning for spawning migrations into coastal streams (Gustafson et al. 2012). The euphausiid-centric diet of eulachon can explain their spatial affiliation with euphausiid abundance (Wilson 2009). Interestingly, hypoallometric changes in prey size were also reported for cod (*Gadus morhua*) (Floeter and Temming 2003), whiting (*Merlangius merlangus*), and gray gurnard (*Eutrigla gurnadus*) (Floeter and Temming 2005); however, these results might reflect exclusion of all prey groups except fish. Similarly, body size within prey groups was hypoallometric for capelin and pollock; however, when integrated across prey groups the relationship was hyperallometric due to dietary transition across prey groups.

**Table 5** Regression estimates, including 95% confidence intervals (CI) and *P* values, and random effects variance from the fitted, taxon-integrated model of Ursin's (1973) PPMR or Tsai et al.'s Proxy for four groups of predators (capelin, age-0 pollock, age-1 pollock, and eulachon) with predator body weight,  $\ln(m_i)$ , as the covariate

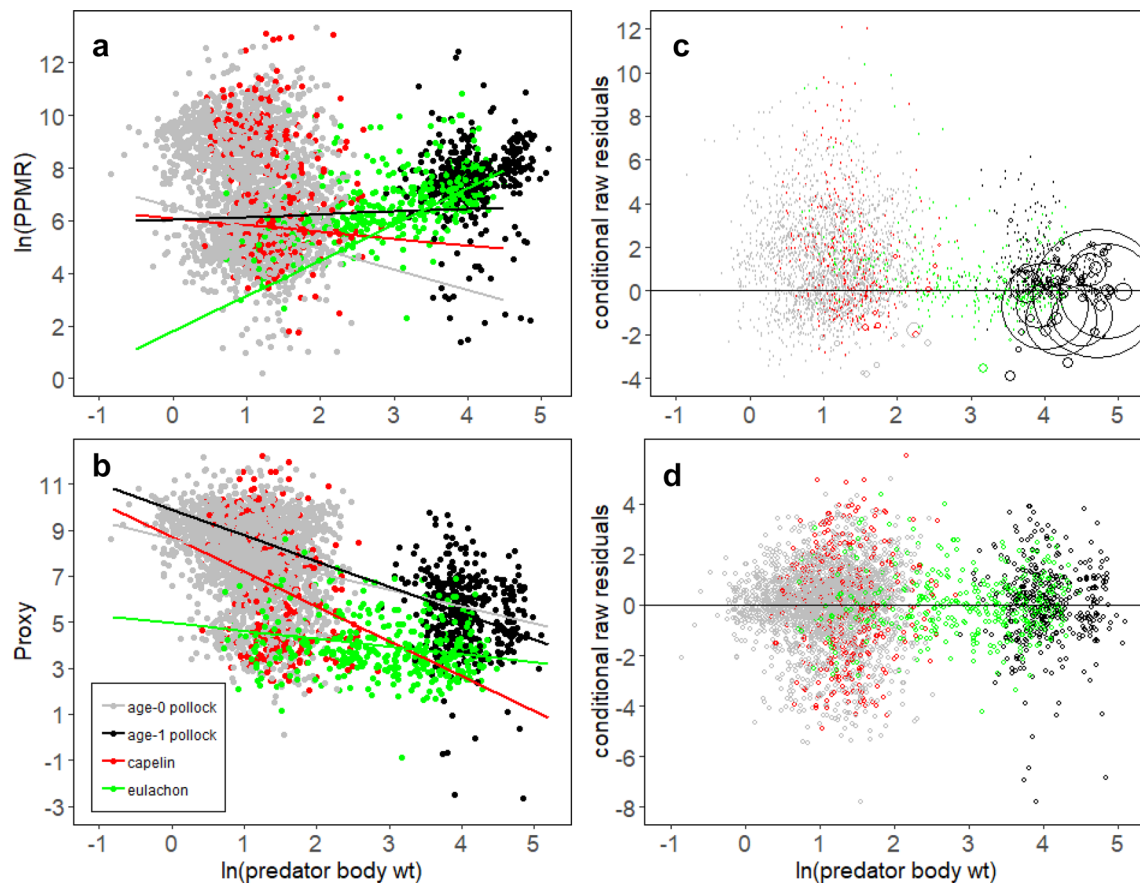
Predictors	ln(Ursin's PPMR)			ln(Tsai et al.'s Proxy)		
	Estimate	CI	<i>P</i>	Estimate	CI	<i>P</i>
intercept	5.136	4.656–5.615	<0.001	8.220	7.686–8.754	<0.001
$\ln(m_i)$	0.104	−0.042–0.250	0.156	−0.928	−1.089 to −0.766	<0.001
capelin	0.983	0.357–1.609	0.004	0.661	0.028–1.293	0.041
pollock age-0	1.400	1.006–1.794	<0.001	0.580	0.088–1.072	0.021
pollock age-1	0.941	0.260–1.622	0.007	1.845	0.525–3.166	0.006
eulachon	−3.324	−3.953 to −2.695	<0.001	−3.086	−3.709 to −2.464	<0.001
$\ln(m_i)$ :capelin	−0.361	−0.703 to −0.019	0.039	−0.586	−0.909 to −0.264	<0.001
$\ln(m_i)$ :pollock age-0	−0.890	−1.091 to −0.688	<0.001	0.192	0.004–0.380	0.045
$\ln(m_i)$ :pollock age-1	−0.006	−0.206–0.194	0.954	−0.196	−0.537–0.145	0.260
$\ln(m_i)$ :eulachon	1.257	1.045–1.468	<0.001	0.590	0.387–0.793	<0.001
Random effects (variance)						
$\sigma^2$	0.340			2.508		
$\tau_{00}$ haul:site	1.649			0.477		
$\tau_{00}$ site	0.484			0.266		
Intraclass correlation						
haul:site	0.668			0.147		
site	0.194			0.082		
Marginal $R^2$	0.228			0.367		
Conditional $R^2$	0.894			0.531		

For brevity, statistics for year and region predictors are omitted. Data were from 3414 predators collected in 163 trawl hauls at 38 sites located on the western Gulf of Alaska and sampled during September 2000, 2001, and 2003

Field-based stomach-content data are influenced by prey traits other than size and abundance, and by environmental effects on the prey field. Prey crypsis, behavior, and shape (e.g., spines) affect defense against predation hence availability to predators (Brodie and Brodie 1999). Once consumed, differences in digestibility among prey types can affect duration and detection in stomach remains. Digestion-related bias in prey taxon-specific size and count is difficult to correct. We attempted to reduce the digestion-related bias in prey body weight by applying an empirically derived correction factor. Encouragingly, the corrected size estimates for euphausiids, the main prey of these predators (Wilson et al. 2009), were similar to the size of euphausiids collected directly from the GOA during late summer (Mazur et al. 2007; Pinchuk and Hopcroft 2007). Finally, environmental effects on prey availability can arise from spatial and temporal heterogeneity in physical and chemical conditions (Wilson 2009) and motivate behaviorally adaptive movement by predators (Nathan et al. 2008). Clearly, data collected from hauls and predator stomachs integrate over space and time, but additional environmental influence was constrained by our use of mixed-effects models to account for the spatial and temporal structure within the data.

## Predator–prey mass ratio

Our results were consistent with previous body size and taxonomic effects on the PPMR and provide additional detail on how specific differences arise among closely associated vertebrate ectotherms foraging in marine habitats. For marine vertebrate ectotherms, Brose et al. (2006) estimated a geometric mean PPMR of 372 ( $10^{2.57}$ ). This was encompassed by our estimates of the geometric mean of Ursin's PPMR (back-transformed marginal means) for eulachon ( $e^{4.06} = 58$ ), age-0 pollock (189), capelin (296), and age-1 pollock (513). In absolute terms, prey size commonly increases with predator size (Barnes et al. 2010; Naisbit et al. 2011; Nakazawa et al. 2011). However, in relative terms, Brose et al. (2006) reported that the proportional increase in body size among prey was generally lower than among predators. A lower proportional increase in prey body size (slope < 1, hypoallometric) results in a positive PPMR–body size relationship (slope > 0); mathematically, 1 minus the slope of the PPMR–body size relationship estimates the allometric coefficient for prey size (i.e., the slope of the log–log predator–prey body weight relationship), and vice versa. Thus, the positive PPMR–body size relationship reported by Barnes et al. (2010) is consistent with an overall hypoallometric



**Fig. 5** Predator–prey mass ratio (PPMR) size dependency (**a**, **b**) and residuals (**c**, **d**) from models fitted to Ursin's PPMR (**a**, **c**) and Tsai et al.'s Proxy (**b**, **d**) with lines representing fitted parameter estimates (Table 5) by predator group: age-0 and age-1 walleye pollock,

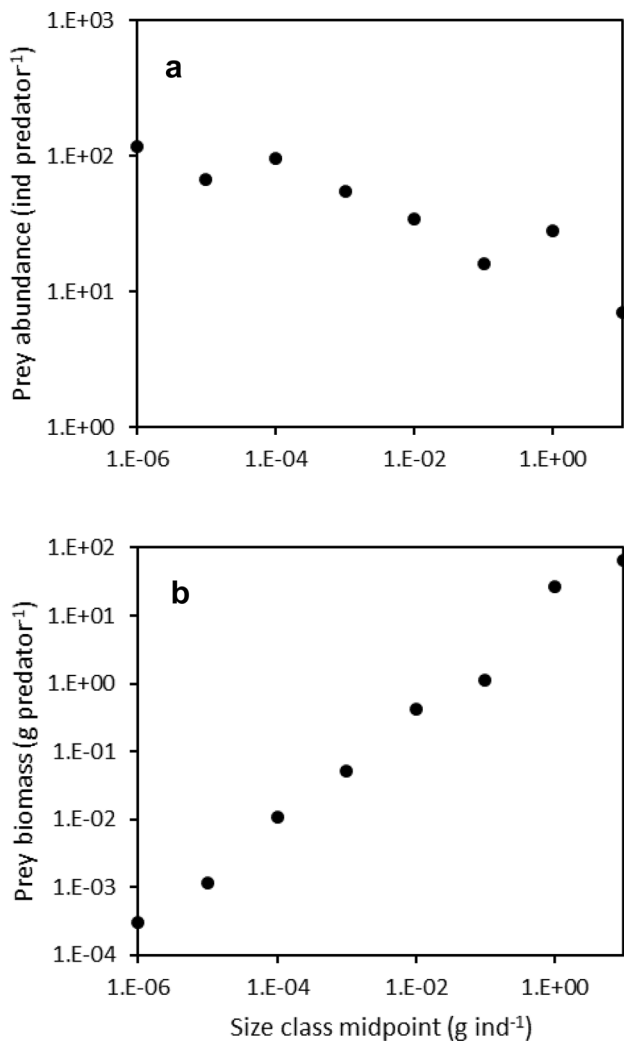
capelin, and eulachon. Predators were collected in the western Gulf of Alaska during September 2000, 2001, and 2003. Symbol size of Ursin's PPMR residuals is scaled to prey weight

change in prey size. However, significant variation in prey size allometry has been associated with taxonomic (Naisbit et al. 2011), habitat (Griffiths 2020), and metabolic categories (Brose et al. 2006). Here, we demonstrated significant variation among closely associated fishes that can at least partly be attributed to differences in functional morphology relevant to prey acquisition.

Field-based estimates of PPMR from stomach-content data are affected by unequal abundance of potential prey. Ursin (1973) addressed unequal abundance by assuming constant prey biomass across prey size classes. This assumption might not have been appropriate over the size range of prey that we examined. From our predator stomach content data, prey abundance decreased across body size classes whereas prey biomass increased (Fig. 6). This could reflect secondary doming structure within size spectra (Rossberg et al. 2019) and size-related changes in zooplankton biomass (Rodríguez and Mullin 1986). Error in the underlying assumption of prey availability might be more concerning for absolute estimates of PPMR than for relative

estimates among predators that share a common resource. If the underlying assumption of availability was incorrect, it was equally incorrect for all predators. That could explain why we observed the same specific differences in prey size allometry for abundance-weighted and for biomass-weighted mean prey size (e.g., the hypoallometric size of eulachon prey). We therefore suggest that while our estimates of the absolute PPMR might be biased, the relative differences among predators were not an artefact of the prey availability assumption.

Two technical aspects of Ursin's method warrant noting. First, Ursin (1973) pooled diet data across different size predators and acknowledged that pooling can cause variance to be overestimated due to size-related differences in predator diets. We chose to apply the method to individuals to enable examination of differences among predators. Weighting each observation by prey weight approximated the estimates based on pooled data. Secondly, we note that Ursin's biomass-weighted PPMR will always be less than the corresponding abundance-weighted PPMR because of



**Fig. 6** Total prey abundance (**a**, ind predator<sup>-1</sup>) and biomass (**b**, g predator<sup>-1</sup>) across size classes of prey body size (g ind<sup>-1</sup>) in stomachs of predators (capelin, pollock, and eulachon) collected in the western Gulf of Alaska during September 2000–2003

the inherent relationship between biomass and abundance (biomass = abundance \* body weight) and for the same simple mathematical reason that an arithmetic mean is always greater than the corresponding harmonic mean.

In contrast to Ursin's PPMR, Tsai et al. (2016) addressed the problem of unequal prey abundance by accounting for an environmental PPMR in the calculation of a PPMR proxy. Their approach differs fundamentally from Ursin's (1973) approach and the two metrics are not well related linearly (Online resource 4). We demonstrated that the negative size dependency of Tsai et al.'s Proxy can be explained by the common pattern for prey body weight to increase with predator body weight rather than any size dependency of the PPMR. In fact, mathematically, Tsai's Proxy varies with prey size only and not predator size implying erroneously that different size predators with equivalent prey size

distributions have equivalent PPMR. Thus, the negative size dependency reported here, and by Tsai et al. (2016) for a goby (*Gymnogobius isaza*), reflects the simple fact that absolute prey size increased with predator size.

Despite similarities among capelin, pollock, and eulachon, our findings add to the evidence of trophic differences within the forage fish community that might affect the realism of ecosystem models. These species are important mid-level trophic components in the GOA ecosystem (Aydin et al. 2007). They are similar as small, silvery, schooling fishes that co-occur in the neritic zone where they feed on seasonally dwindling stocks of zooplankton during late summer (Wilson et al. 2009). Many are juveniles so that within the late-summer time frame, they undergo body size-related transition in diet from small (e.g., copepods) to larger (e.g., euphausiids) prey. There is little evidence of prey limitation (Wilson et al. 2009). However, subtle differences in diet and feeding chronology (Wilson et al. 2006), and prey size preferences (this study) hint at competitive interaction. The species undergo large, apparently unrelated fluctuations in population size that change the composition of the forage fish community (Anderson and Piatt 1999). Our estimates of PPMR ranged from 58 to 513, on average, encompassing the value (100) currently advocated for use in ecosystem modelling (Hartvig et al. 2011; Andersen et al. 2016; Andersen 2019), but our results also indicate that choosing fixed PPMR excludes detail that may be important for improving model realism. Reum et al. (2019) demonstrate the benefit of including realistic detail. The addition of predator species- and size-specific preference for prey taxa significantly improved the realism of their multi-species size spectrum model of the eastern Bering Sea by focusing predation on fish ~ 1–10 g in size, lengthening food chains, and allowing greater feeding specialization, which underscored the importance of species composition and size structure as drivers of ecosystem-level trophic metrics. However, they used a fixed PPMR schedule including PPMR = 1000 for forage fishes. It is less clear what effect the use of fixed PPMR had on model realism. This is relevant because changes in PPMR theoretically relate to inverse changes in trophic transfer efficiency (Barnes et al. 2010) and to the top-down per capita impact predators have on prey populations (Emmerson and Raffaelli 2004).

In summary, forage fish PPMR varied with predator species and body size due to predator species-specific differences in transitioning across size-structured prey taxa. This suggests that innate differences among predator species in transitioning across size-structured taxonomic groups of prey is a determinant of specific prey size allometry. We encourage the incorporation of our findings into multispecies, size-based ecosystem models to explore how changes in zooplankton and forage-fish community composition might affect ecosystem-level processes; however, this should

include careful consideration of current methods to estimate the PPMR.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-04000-z>.

**Acknowledgements** We are grateful for input provided early on by S. Jennings and C. Barnes. Comments by J. Reum were helpful in improving our general understanding of PPMR and sharpening the focus of this work. Comments by K. Andersen were helpful in critically evaluating assumptions on prey availability. K. Mier provided statistical advice. K. Wilson assisted with R. Additional comments by AFSC Publications Unit personnel, K. Wilson, and L. Rogers improved the manuscript. We thank the anonymous reviewers and editors for their helpful comments and suggestions on improving the manuscript. This research is contribution EcoFOCI-0942 to NOAA's Ecosystems and Fisheries–Oceanography Coordinated Investigations (EcoFOCI).

**Authors' contributions** MW conceived the ideas, designed methodology, supervised and assisted data collection, analyzed the data, and led writing the manuscript. DK provided ideas and contributed substantially in revising the manuscript.

**Funding** The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interests** The authors have no relevant financial or non-financial interests to disclose.

**Ethics approval** All sampling was completed under Scientific Research permits granted by the United States Department of Commerce, National Ocean Atmospheric Administration, National Marine Fisheries Service, Alaska Region Administrator.

**Consent to participate** Not applicable.

**Consent to publish** Not applicable.

## References

- Andersen KH (2019) Fish ecology, evolution, and exploitation: a new theoretical synthesis. Princeton University Press, Princeton
- Andersen KH, Jacobsen NS, Farnsworth KD (2016) The theoretical foundations for size spectrum models of fish communities. *Can J Fish Aquat Sci* 73:575–588
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123. <https://doi.org/10.3354/meps189117>
- Aydin K, Giachas S, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. NOAA Technical Memo NMFS-AFSC-178
- Barnes C, Maxwell D, Reuman DC, Jennings S (2010) Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* 91:222–232
- Brodeur RD (1998) Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. *Environ Biol Fishes* 51:175–186. <https://doi.org/10.1023/a:1007455619363>
- Brodeur RD, Wilson MT (1996) A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fish Oceanogr* 5(s1):148–166
- Brodie ED, Brodie ED (1999) Predator–prey arms races. *Bioscience* 49:557–568
- Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier L-F, Blanchard JL, Brey T, Carpenter SR, Blandenier M-FC, Cushing L, Dawah HA, Dell T, Edwards F, Harper-Smith S, Jacob U, Ledger ME, Martinez ND, Memmott J, Mintenbeck K, Pinnegar JK, Rall BC, Rayner TS, Reuman DC, Ruess L, Ulrich W, Williams RJ, Woodward G, Cohen JE (2006) Consumer–resource body–size relationships in natural food webs. *Ecology* 87:2411–2417
- Bundgaard I, Sparholt H (1992) Length-based multi-species model for estimation of predation mortalities of herring and sprat in the Baltic. ICES Committee Meetings: Document D:16
- Cochran WG (1977) Sampling techniques. Wiley, New York, USA
- Dekker W (1983) An Application of the Andersen consumption model in estimating prey size preference of North Sea cod. ICES Committee Meetings: Document G:63
- Emmerson MC, Raffaelli D (2004) Predator–prey body size, interaction strength and the stability of a real food web. *J Anim Ecol* 73:399–409
- Floeter J, Temming A (2003) Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preferences vs. prey availability. *Can J Fish Aquat Sci* 60:140–150
- Floeter J, Temming A (2005) Analysis of prey size preference of North Sea whiting, saithe, and grey gurnard. *ICES J Mar Sci* 62:897–907
- Fox J, Weisberg S (2019) An R companion to applied regression. Sage Publications, Thousand Oaks
- Giacomini HC, Shuter BJ, Lester NP (2013) Predator bioenergetics and the prey size spectrum: do foraging costs determine fish production? *J Theor Biol* 332:249–260
- Griffiths D (2020) Foraging habitat determines predator–prey size relationships in marine fishes. *J Fish Biol* 97:964–973. <https://doi.org/10.1111/jfb.14451>
- Gustafson RG, Ford MJ, Adams PB, Drake JS, Emmett RL, Fresh KL, Rowse M, Spangler EAK, Spangler RE, Teel DJ, Wilson MT (2012) Conservation status of eulachon in the California Current. *Fish Fish* 13:121–138. <https://doi.org/10.1111/j.1467-2979.2011.00418.x>
- Hartvig M, Andersen KH, Beyer JE (2011) Food web framework for size-structured populations. *J Theor Biol* 272:113–122
- Horbowy J (1982) The estimation of parameters of predator–prey preference function for Baltic cod. ICES Committee Meetings: Document J:28
- Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *Am Nat* 93:145–159
- Kendall AW, Schumacher JD, Kim S (1996) Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. *Fish Oceanogr* 5:4–18. <https://doi.org/10.1111/j.1365-2419.1996.tb00079.x>
- Kjørboe T, Visser A, Andersen KH (2018) A trait-based approach to ocean ecology. *ICES J Mar Sci*. <https://doi.org/10.1093/icesjms/fsy090>
- Kremer CT, Williams AK, Finiguerra M, Fong AA, Kellerman A, Paver SF, Tolar BB, Toscano BJ (2017) Realizing the potential of trait-based aquatic ecology: new tools and collaborative approaches. *Limnol Oceanogr* 62:253–271. <https://doi.org/10.1002/lno.10392>
- Lazzaro X (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146:97–167

- Lewy P, Vinther M (2004) A stochastic age-length structured multispecies model applied to North Sea stocks. ICES Committee Meetings: Document FF:20
- Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399–418
- Mazur MM, Wilson MT, Dougherty AB, Buchheister A, Beauchamp DA (2007) Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. *J Fish Biol* 70:816–836. <https://doi.org/10.1111/j.1095-8649.2007.01344.x>
- McClatchie S, Duffy-Anderson J, Field JC, Goericke R, Griffith D, Hanisko DS, Hare JA, Lyczkowski-Shultz J, Peterson WT, Watson W, Weber ED, Zapfe G (2014) Long time series in US fisheries oceanography. *Oceanography* 27:48–67. <https://doi.org/10.5670/oceanog.2014.86>
- McCormick MI (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar Biol* 132:9–20
- Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society, Bethesda
- Mecklenburg CW, Lynghammer A, Johansen E, Byrkjedal I, Dolgov AV, Kaamushko OV, Mecklenburg TA, Møller PR, Steinke D, Wienerroither RM, Christiansen JS (2018) Marine Fishes of the Arctic Region Volume 1, Akureyri, Iceland
- Merati N (1996) Brodeur RD (1996) Feeding habits and daily ration of juvenile walleye pollock in the western Gulf of Alaska. NOAA Tech Rep NMFS. 126:65–79
- Naisbit RE, Kehrli P, Rohr RP, Bersier L-F (2011) Phylogenetic signal in predator–prey body–size relationships. *Ecology* 92:2183–2189
- Nakazawa T, Ushio M, Kondoh M (2011) Scale dependence of predator–prey mass ratio. *Adv Ecol Res* 45:269–302. <https://doi.org/10.1016/b978-0-12-386475-8.00007-1>
- Napp JM, Incze LS, Ortner PB, Siefert DLW, Britt L (1996) The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fish Oceanogr* 5:19–38. <https://doi.org/10.1111/j.1365-2419.1996.tb00080.x>
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse P (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci* 105:19052–19059
- Pearre S (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Mar Ecol Prog Ser* 27:299–314
- Pinchuk AI, Hopcroft RR (2007) Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T-spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska. *Mar Biol* 151:257–269. <https://doi.org/10.1007/s00227-006-0483-1>
- Platt T, Denman K (1977) Organization in the pelagic ecosystem. *Helgol Wiss Meeres* 30:575–581
- Platt T, Denman K (1978) The structure of pelagic marine ecosystems. *Rapp Proc-Verb Reun Cons Int Explor Mer* 173:60–65
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reed RK, Schumacher JD (1986) Physical oceanography. In: Hood DW, Zimmerman ST (eds) *The Gulf of Alaska: Physical Environment and Biological Resources*. US Department of Commerce, US Department of the Interior, Anchorage, Alaska, pp 57–75
- Reum JCP, Blanchard JL, Holsman KK, Aydin K, Punt AE (2019) Species-specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. *Oikos* 128:1051–1064. <https://doi.org/10.1111/oik.05630>
- Rodriguez J, Mullin MM (1986) Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol Oceanogr* 31:361–370
- Rossberg AG, Gaedke U, Kratina P (2019) Dome patterns in pelagic size spectra reveal strong trophic cascades. *Nat Commun* 10:4396. <https://doi.org/10.1038/s41467-019-12289-0>
- Scharf F, Juanes F, Rountree R (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Sheldon RW, Prakash A, Sutcliffe WH (1972) The size distribution of particles in the ocean. *Limnol Oceanogr* 17:327–340
- Sogard SM, Olla BL (1994) The potential for intracohort cannibalism in age-0 walleye pollock, *Theragra chalcogramma*, as determined under laboratory conditions. *Environ Biol Fishes* 39:183–190
- Tsai C-H, Hsieh C-h, Nakazawa T (2016) Predator–prey mass ratio revisited: does preference of relative prey body size depend on individual predator size? *Funct Ecol* 30:1979–1987. <https://doi.org/10.1111/1365-2435.12680>
- Urban D (2012) Food habits of Pacific cod and walleye pollock in the northern Gulf of Alaska. *Mar Ecol Prog Ser* 469:215–222. <https://doi.org/10.3354/meps10135>
- Ursin E (1973) On the prey size preferences of cod and dab. *Medd Dan Fisk-Havunders* 7:85–98
- Willson MF, Armstrong RH, Hermans MC, Koski K (2006) Eulachon: a review of biology and an annotated bibliography
- Wilson MT (2009) Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. *Mar Ecol Prog Ser* 392:223–237. <https://doi.org/10.3354/meps08160>
- Wilson MT, Jump CM, Duffy-Anderson JT (2006) Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. *Mar Ecol Prog Ser* 317:245–258
- Wilson MT, Jump CM, Buchheister A (2009) Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to krill standing stock and the physical environment. *Mar Ecol Prog Ser* 392:239–251. <https://doi.org/10.3354/meps08237>
- Winkler NS, Paz-Goicoechea M, Lamb RW, Perez-Matus A (2017) Diet reveals links between morphology and foraging in a cryptic temperate reef fish. *Ecol Evol* 7:11124–11134. <https://doi.org/10.1002/ece3.3604>
- Woodward G, Warren P (2007) Body size and predatory interactions in freshwaters: scaling from individuals to communities. In: Hildrew AG, Raffaelli DG, Edmonds-Brown R (eds) *Body size: the structure and function of aquatic ecosystems*. Cambridge University Press, Cambridge, pp 98–117

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.