

Body condition of phocid seals during a period of rapid environmental change in the Bering Sea and Aleutian Islands, Alaska

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ABSTRACT

A warming climate has driven rapid physical changes in the Arctic environment, particularly in the Bering Sea. Biological changes are also increasingly evident in the Bering Sea and adjacent waters. The ecological results have been profound and relatively well documented for fishes and lower trophic levels. Upper trophic predators such as marine mammals, however, have been underrepresented in ecosystem surveys, models, and efforts to practice ecosystem-based fisheries management. We used multiple linear regression to model body condition (mass/length) as a function of species, age class, sex and year for ribbon and spotted seals in the Bering Sea, and harbor seals in the Aleutian Islands, from 2007 to 2018, for evidence of recent trends that might reflect trophic or bottom-up changes in the ecosystem. Model-averaged coefficients (in kg cm^{-1} , relative to the overall mean) indicated that body condition was lower for subadults (-0.063 ; 95% CI: $-0.074 - -0.051$) and pups (-0.120 ; 95% CI: $-0.129 - -0.112$) than for adults (0.183 , the negative sum of the subadults and pups coefficients). Body condition for males (0.010 ; 95% CI: $0.002-0.019$) was higher than for females (-0.010). Overall, body condition declined annually (-0.014 per year; 95% CI: $-0.025 - -0.004$), and there was an additive annual decline in body condition of seal pups across all species and sexes (-0.020 ; 95% CI: $-0.030 - -0.011$). An additive annual increase in body condition of spotted seals across all sexes and age classes (0.013 ; 95% CI: $0.004-0.022$) mitigated the annual declines for this species. Model-averaged fitted values therefore indicated annual declines in body condition for ribbon and harbor seals of all sex and age classes, and for spotted seal pups. We relate these declines to the trend in Bering Sea ice extent and to recent, rapid changes brought on by the significant Northeast Pacific marine heat wave of 2014–2016 and its lingering effects through 2018 and 2019. The results indicate that these typically resilient, long-lived, generalist predators can be impacted by bottom-up forcing.

1. Introduction

The Arctic is changing, driven largely by a warming climate in which temperatures have risen 2° to 3°C since 1880 and 0.75°C in just the past decade (Post et al., 2019). In the past five years, environmental change has been extremely rapid in the Arctic, particularly in the Bering Sea, where short-term variability superimposed on the long-term warming trend reflects ‘teleconnections’ from tropical and temperate Pacific waters in the form of marine heat waves (Di Lorenzo and Mantua, 2016). Globally, marine heat waves are becoming more frequent and intense (Frölicher et al., 2018). The annual extent of seasonal sea ice in the Bering Sea has fluctuated dramatically, with record highs and lows for the satellite era occurring in the past decade (Fetterer et al., 2017, updated daily). Biological changes are also increasingly evident in the

Bering Sea and adjacent waters, including changes in species distributions (Dunmall et al., 2013; Grebmeier, 2012; Mueter and Litzow, 2008; Stafford, 2019; Stevenson and Lauth, 2019), individual condition and health (VanWormer et al., 2019), or vital rates of mortality and reproduction (Piatt et al., 2020). Cumulatively, recent changes in the region have risen to a level that has been characterized as ‘ecosystem transformation’ (Huntington et al., 2020).

The ramifications of environmental and biological change for ecosystem structure, dynamics and function are complex; identifying and understanding them likely will require broad examination across trophic levels. Lower- and mid-trophic species are relatively well-monitored, especially in association with fisheries oceanography studies in the southeastern Bering Sea. Many upper trophic species, however, are comparatively rare and difficult to observe or monitor, and

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challenging to include in integrated ecosystem surveys (e.g. Duffy-Anderson et al., 2019; Van Pelt et al., 2016), models (e.g. Punt et al., 2016), and fisheries management schemes (e.g. Siddon and Zador, 2019). Upper trophic species, especially long-lived generalist predators, may be relatively resilient to 'bottom-up' variability, in some cases making them insensitive as sentinel indicators of ecosystem shifts. When changes in body condition or growth rates do appear in generalist top predators, however, the changes are likely to reflect broad underlying ecological shifts in multiple prey species. Since 2007, we have studied three species of phocid seals that are abundant upper trophic predators in the Bering Sea and Aleutian Islands, for evidence of recent trends that might reflect trophic or bottom-up changes in the ecosystem.

Ribbon seals (*Histiophoca fasciata*) and spotted seals (*Phoca largha*) are ice-associated species with their main breeding distributions in the seasonally ice-covered waters near the continental shelf breaks of the Bering Sea and Sea of Okhotsk (Burns, 1981; Lowry, 1985b). These species depend on the sea ice during key life history events, including pupping, breeding, and molting. In summer, ribbon seals disperse to a variety of offshore foraging habitats in the Gulf of Alaska, North Pacific Ocean, Bering Sea, and Chukchi Sea, while spotted seals divide their time between coastal haul-out sites and foraging zones off the shores of Alaska and Russia. Both species' main prey, at least during the spring and summer when most samples have been collected, consists of fish, squid, and crustaceans (Boveng et al., 2009, 2013; Dehn et al., 2007; Quakenbush et al., 2009), and there is little evidence for substantial niche separation between the two species (Wang et al., 2016).

Harbor seals (*Phoca vitulina richardii*) have a broad range in temperate and sub-Arctic waters of the northeast Pacific Ocean and are found in all coastal Alaska waters north to at least Bristol Bay and the

Pribilof Islands (Muto et al., 2018). Harbor seals forage mostly near shore, and their diet is also mainly fish, squid, and crustaceans, but they do not depend on sea ice for life history events, like ribbon and spotted seals, and therefore may respond differently than those species to ecological change. The primary objective of this study was to assess trends in body condition of ribbon and spotted seals in the Bering Sea and harbor seals in the Aleutian Islands during a period of rapid ecological change.

2. Methods

We captured, sampled, and released ribbon and spotted seals during April to early June of 2007, 2009, 2010, 2014, 2016, and 2018 at the edge of the pack ice in the Bering Sea. Harbor seals were captured, sampled, and released in the Aleutian Islands during September in 2014–2016 (Fig. 1). We used long-handled fish-landing nets to catch ribbon and spotted seals in the Bering Sea, the same nets to catch harbor seals on beaches or exposed reefs in the Aleutian Islands, and tangle nets deployed from small boats to catch harbor seals in nearshore waters of the Aleutians (Jeffries et al., 1993).

Seals were transferred from capture nets to hoop nets and physically restrained or sedated with an intravenous injection of diazepam (2010; 0.1 mg per kg body mass) or midazolam (2014–2018; 0.1–0.2 mg per kg body mass). We occasionally used an intramuscular injection of midazolam depending on the seal's behavior and temperament during capture and initial handling. Prior to releasing sedated seals, the effects of sedation were reversed with an intramuscular injection of flumazenil (0.01 mg per kg of body mass; West-Ward Pharmaceuticals, NJ, USA) if the attending veterinarian determined it was needed.

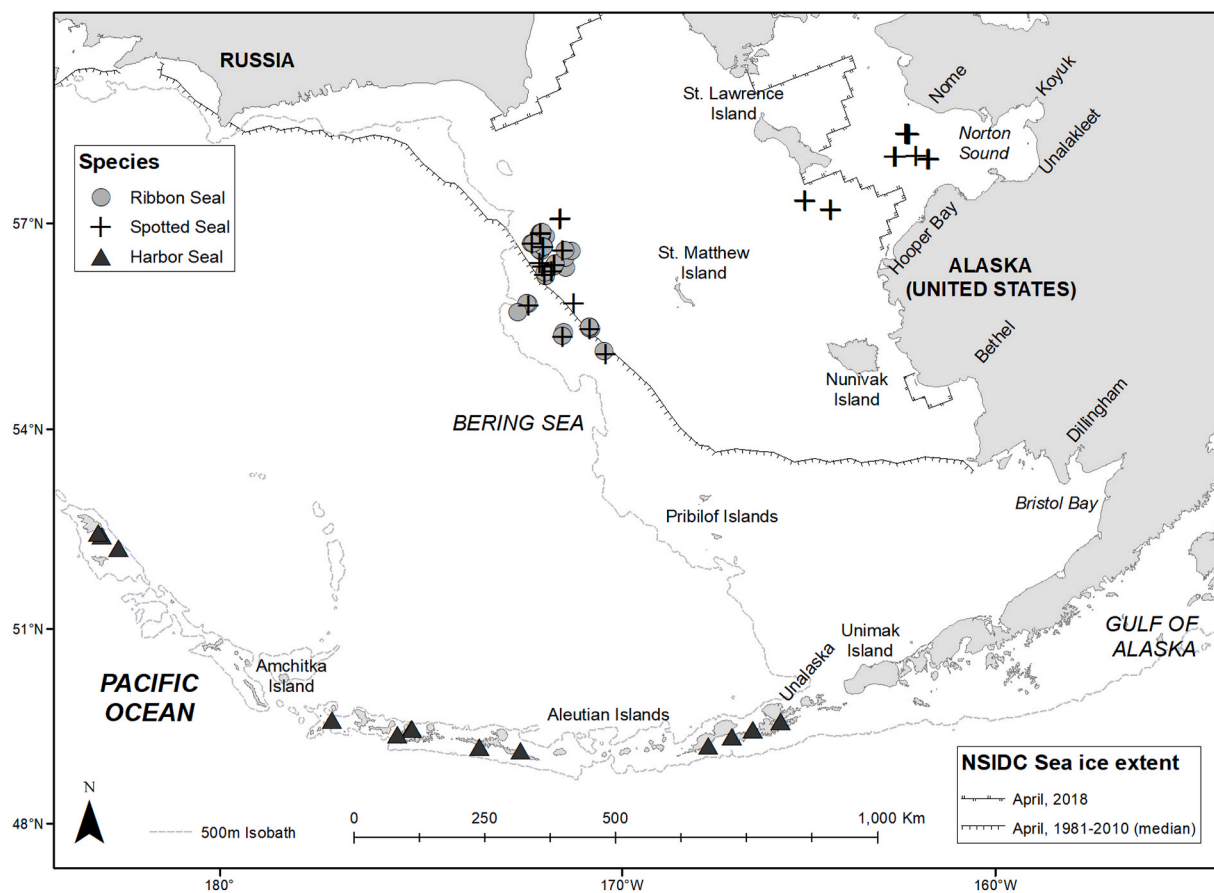


Fig. 1. Locations where spotted, ribbon, and harbor seals were weighed and measured in 2007–2018. The 500 m isobath is shown as a reference for the continental shelf break. Sea-ice extent from the National Snow and Ice Data Center (NSIDC) is shown as the average for the month of April, 2018, and as the median from April, 1981–2010, for comparison (Fetterer et al., 2017, updated daily).

We weighed seals in a sling suspended from a bipod and hanging scale (Dynamlink, 250 kg) on ice floes in the Bering Sea or with a crane and hanging scale on a ship in the Aleutians. All seals were weighed (to the nearest 0.1 kg) and measured (length of prone seal in a straight line from nose to tip of tail, axillary girth, maximum girth, hip girth; to the nearest 0.5 cm), and age class and sex were determined. We classified individuals into four age classes: pup (<1 y, not weaned), young-of-the-year (<1 y, weaned), subadult (1–4 y), and adult (>4 y) (Burns, 1981; Pitcher and Calkins, 1979). We used morphological characteristics (e.g. size, color and, for ribbon seals, distinctness of ribbons) to distinguish between subadults and adults (Burns, 1969, 1981; Naito and Oshima, 1976; Quakenbush et al., 2009; Tikhomirov, 1968).

We used a portable ultrasound scanner to measure blubber depth at four different sites on the seals sampled in 2014–2018. Owing to the relatively short period of ultrasound sampling, we did not use blubber depth for our evaluation of trends in body condition. However, we report linear regression results on the relationships between blubber depth, body condition, and girths in the Supplemental Materials, because they may be useful in future analyses for evaluating relative changes in fat mass versus lean body mass in response to ecological change.

We used multiple linear regression to model our index of body condition, mass per standard length (in kg cm⁻¹), as a function of species, age class ('age_class'), sex, year, and a linear or quadratic trend for day of year ('Day' and 'Day2' respectively). Year was modeled as fully time-dependent ('year'), a linear trend ('Year'), or a quadratic trend ('Year2'). Having found little support for 'year', 'Day2', 'Day:Year', or higher-order annual trend effects in preliminary analyses, we included all possible combinations of main effects and two-way interactions of species, age class, sex, Day, Year, and Year2 (except 'Day:Year') in our candidate model set. To help with numerical stability and to facilitate interpretation of estimated coefficients across models, all categorical covariates were centered at zero, 'Day' was standardized, and the annual trend covariates ('Year' and 'Year2') were orthogonalized. The bias-corrected Akaike's Information Criterion (AICc; Burnham and Anderson, 2002) was used to calculate model weights. Using AICc model weights, standardized estimated coefficients were model-averaged based on Lukacs et al. (2009) and Cade (2015). Model-averaged estimates for body condition were calculated from the predictions for each individual model, based on AICc weights. All analyses were performed with MuMIn package version 1.43.15 (Bartoni, 2019) in R 3.6.3 (R Core Team, 2019). The R code and data are available in Boveng et al., (2020).

3. Results

We weighed and measured 98 ribbon seals and 94 spotted seals at the pack ice edge in the Bering Sea between 2007 and 2018, and 80 harbor seals in the Aleutian Islands between 2014 and 2016 (Table 1). We

Table 1
Numbers of ribbon, spotted, and harbor seals, by age class and sex, sampled for body condition in 2007–2018.

Species	Sex	Adult	Subadult	Pup	Total
Ribbon	Female	29	11	8	48
	Male	24	13	13	50
	Total	53	24	21	98
Spotted	Female	14	5	29	48
	Male	5	10	31	46
	Total	19	15	60	94
Harbor	Female	23	14	7	44
	Male	17	13	6	36
	Total	40	27	13	80
Grand total		112	66	94	272

combined weaned pups and maternally-dependent pups into the single age class 'pup' for analysis.

The most general model, including all two-way interactions, explained much of the variation in body condition (multiple R² = 0.891), but it was not well supported by AICc (Delta AICc = 65.5). There was considerable model selection uncertainty among the more parsimonious models, with the minimum AICc model only receiving 7% of the model weight (Supplemental Material Table S1). Although AICc weights can in some cases be a poor indicator of the relative importance of predictors (Cade 2015), the sums of AICc weights across all models that included a particular variable were largest for 'age_class' (100% of AICc weight), 'Day' (100%), 'species' (100%), 'Year' (100%), 'sex' (99.8%), 'age_class:Year' (98.6%), 'species:Year' (96.9%), 'Day:species' (96.2%), 'Year2' (92.0%), and 'age_class:Day' (83.9%).

Model-averaged coefficient estimates indicated several significant effects on body condition based on species, age class, sex, day, year, or two-way interactions (Table 2; note that all the predictors were centered at zero, making the coefficients relative to the mean body condition across species, age class, sex, day, and year, and—because only n–1 coefficients can be independently estimated for a categorical predictor with n levels—the remaining coefficient is simply the negative sum of the n–1 estimated values). Body condition evaluated across all species was lower for subadults (–0.063 kg cm⁻¹; 95% CI: –0.074 – –0.051) and pups (–0.120 kg cm⁻¹; 95% CI: –0.129 – –0.112), than for adults (0.183 kg cm⁻¹). Males were found to have higher body condition (0.010 kg cm⁻¹; 95% CI: 0.002–0.019) than females (–0.010 kg cm⁻¹). There was a negative 'Year' effect on body condition across all species,

Table 2

Model-averaged predictors for seal body condition (mass per standard length) of ribbon, spotted, and harbor seals sampled between 2007 and 2018 in the Bering Sea and Aleutian Islands, Alaska. For each predictor with >0.5 proportion of AICc model weights ('Weight'), model-averaged estimates ('Estimate'), 95% confidence intervals (Lower, Upper), and p-value codes are provided, where '****' indicates p < .001, '***' indicates p < .01, '**' indicates p < .05, and '.' indicates p < .1. For predictors that are factors, results are provided for each factor level ('Factor'). For a categorical (factor) regression predictor with n levels, only n-1 coefficients and their confidence limits can be estimated. The factor levels we estimated for 'age_class' are subadult and pup, levels for 'species' are spotted and harbor seals, and the level for 'sex' is male. Because all covariates were centered at zero, the estimated coefficients are relative to the mean body condition across species, age class, sex, day, and year. The coefficient for the remaining factor level is therefore the negative sum of the other coefficients. For example, the 'age_class' coefficient for adults is the negative sum of the other age classes (0.063 + 0.120 = 0.183).

Predictor	Weight	Factor	Estimate	Lower	Upper	p-value
age_class	1.000	subadult	-0.063	-0.074	-0.051	***
		pup	-0.120	-0.129	-0.112	***
Day	1.000		-0.012	-0.022	-0.003	**
species	1.000	spotted	0.008	-0.003	0.019	
		harbor	0.008	-0.003	0.018	
Year	1.000		-0.014	-0.025	-0.004	**
sex	0.998	male	0.010	0.002	0.019	*
		female	-0.010	-0.019	-0.001	
age_class:Year	0.986	subadult	0.002	-0.006	0.010	
		pup	-0.020	-0.030	-0.011	***
species:Year	0.969	spotted	0.013	0.004	0.022	**
		harbor	-0.004	-0.013	0.005	
day:species	0.962	spotted	0.010	0.002	0.019	*
		harbor	0.012	0.004	0.020	*
Year2	0.920		0.006	-0.003	0.015	
age_class:Day	0.839	subadult	-0.002	-0.010	0.006	
		pup	0.012	0.004	0.023	.
sex:Year	0.796	male	0.006	-0.004	0.018	
		female	-0.006	-0.014	0.002	
age_class:sex	0.704	subadult:male	-0.004	-0.014	0.002	
		pup:female	-0.007	-0.019	-0.002	
sex:species	0.677	male:spotted	0.006	0.000	0.017	
		male:harbor	0.003	-0.009	0.016	
age_class:Year2	0.612	subadult	0.000	-0.008	0.008	
		pup	-0.006	-0.018	-0.001	
sex:Year2	0.541	male	-0.005	-0.017	0.000	

sexes, and age classes ($-0.014 \text{ kg cm}^{-1}$ per year; 95% CI: $-0.025 - -0.004$). There was an additional negative ‘age_class:Year’ effect on body condition for the pup age class (-0.020 ; 95% CI: $-0.030 - -0.011$) and a positive ‘species:Year’ effect on body condition for spotted seals (0.013 ; 95% CI: $0.004-0.022$). There were several effects related to ‘Day’ that differed between species and age class (Table 2).

Model-averaged predictions (i.e. fitted values) for body condition demonstrate the additive and interaction effects of the covariates, depicted by year (Fig. 2) and day (Fig. 3) for each species, age class, and

sex. For example, the predicted decline in spotted seal pup body condition (Fig. 2) reflects the net effect of the ‘age_class:Year’ term for pups (Table 2; $-0.020 \text{ kg cm}^{-1}$ per year), mitigated by annual increases in body condition for this species as a whole (0.013 kg cm^{-1} per year), plus the contributions of the main ‘Year’ effect and other covariates. With no such mitigation for the other species, the fitted values indicate an annual decline in body condition of ribbon and harbor seals for all sex and age classes. The model also predicts significant daily decreases in body condition for ribbon seals of all age classes during April and May, weak

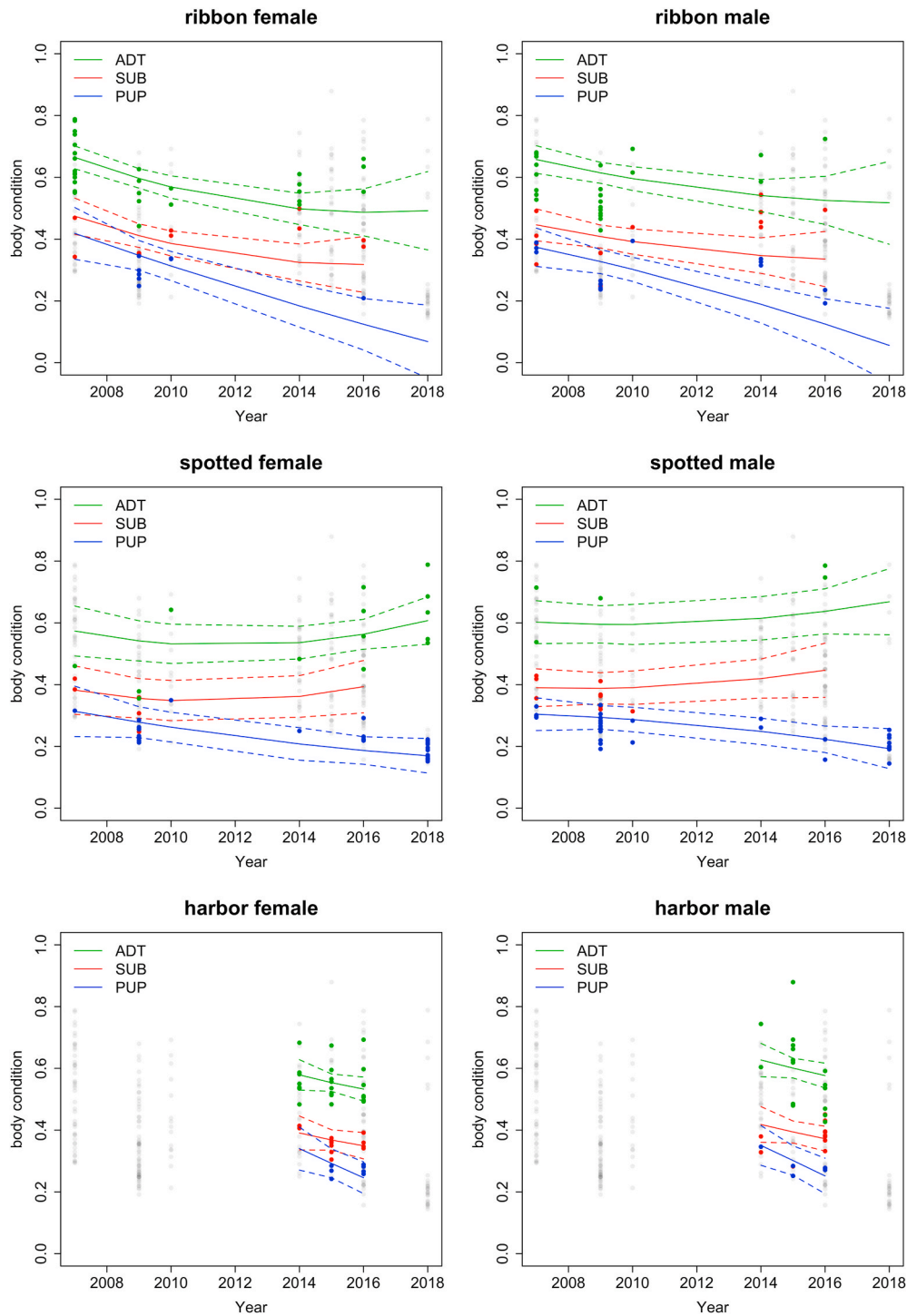


Fig. 2. Model-averaged estimates for body condition by year for each species, age class, and sex of ribbon seals, spotted seals, and harbor seals. For each species and sex, colored symbols depict the data for each age class, superimposed on the light gray symbols for the entire data set. Predictions are based on the mean value for ‘Day’ for each species.

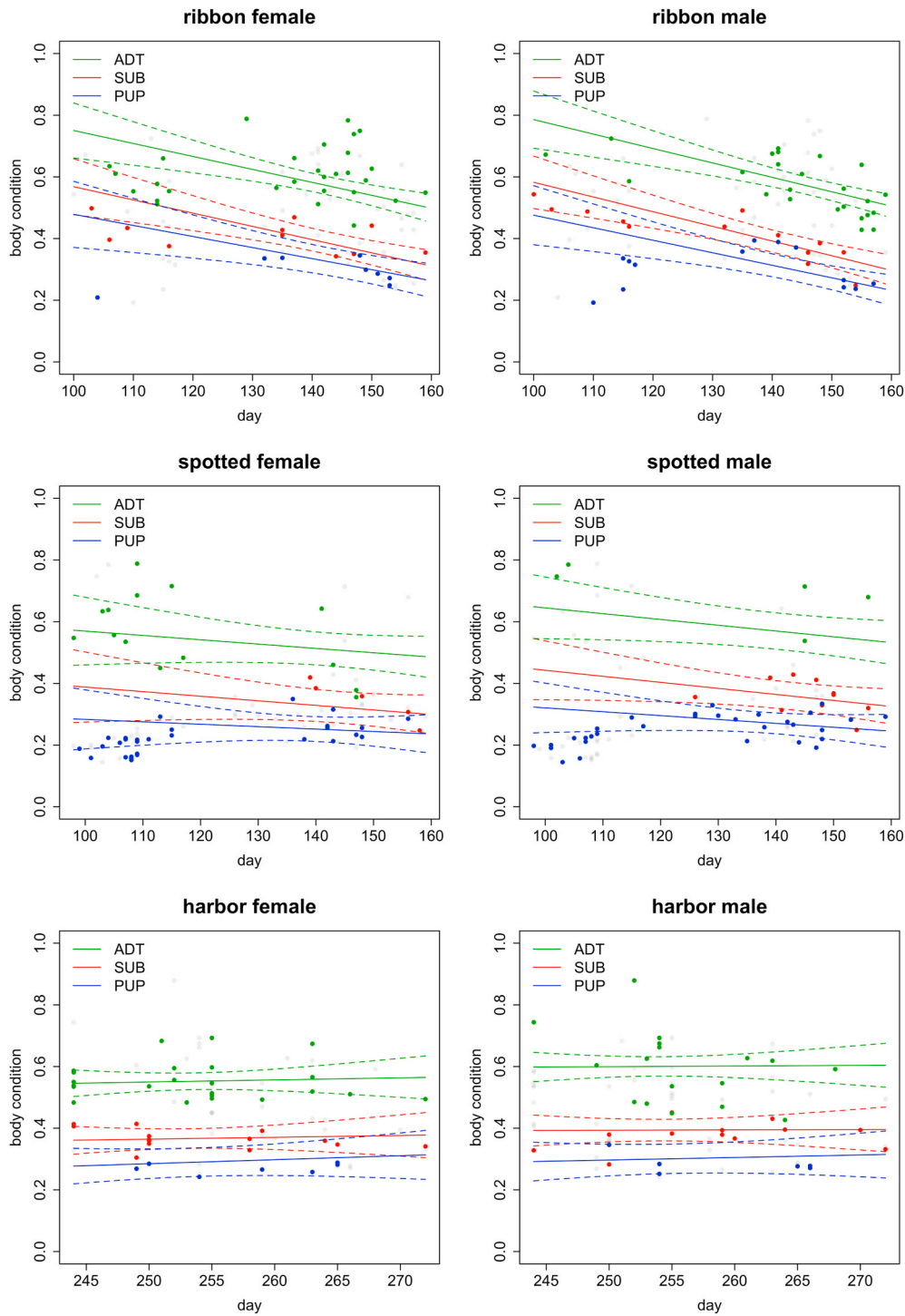


Fig. 3. Model-averaged estimates for body condition by day of year for each species, age class, and sex of ribbon seals, spotted seals, and harbor seals. For each species and sex, colored symbols depict the data for each age class, superimposed on the light gray symbols for the entire data set. Predictions are based on the median value for ‘Year’ for each species.

evidence of daily decreases for spotted seals during April and May, and weak evidence of daily increases for harbor seals during September (Fig. 3).

4. Discussion

4.1. Daily changes in body condition

Despite our modest sample of weights and measurements across

years, we detected notable temporal trends in body condition. Although these differed by species and age class, our models produced sensible predictions of daily changes in body condition. The ribbon and spotted seals were sampled from early April until early June, the period in which births, nursing, mating, and molting take place. These critical life-history events are energy intensive and, at times, they restrict or preclude foraging, requiring most non-pups to rely upon stored reserves compared to other times of the year (Ochoa-Acuna et al., 2009). Thus, most phocid seal non-pups lose mass and body condition during this

period. Pups, on the other hand, are expected to gain mass while nursing, followed by a period of relatively stable or declining mass after weaning (Naito and Nishiwaki, 1972; Tikhomirov, 1968), while gaining foraging proficiency. The negative slopes for non-pup ribbon and spotted seals (Fig. 3) indicate that on average those groups declined daily in body condition over the within-year sampling periods. For pups of both species, particularly ribbon seal pups, the trend lines also indicate a daily net loss of condition. Our relatively small sample did not support higher-order daily effects, and a linear effect is incapable of expressing the initial daily increase and later decrease expected for pups, but there is a hint of that pattern in the distribution of the pups' data points.

The harbor seals in our study were sampled over the month of September, a short period well after harbor seals' birth-nursing-mating period and after most individuals have completed their molt. Harbor seals of all age classes would be expected to be slowly gaining mass during this period, but because the samples were all collected within a 30-day range of dates, our data would have little power to detect this trend. Indeed, the predicted daily body conditions for harbor seals (Fig. 3) are flat or only slightly increasing, consistent with this expectation. Therefore, we note that despite having relatively small samples within species, sex, and age class categories, our body condition data reproduced the expected within-year patterns for all three species.

4.2. Interannual changes in body condition

The interannual declines in body condition of ribbon and spotted seal pups may indicate that nutrition was limiting during the perinatal and maternal provisioning period. Poor foraging conditions for mothers during the winter could also have impacted pup condition, particularly for ribbon seals, in which adult body condition appeared to decline over the course of our study. These are periods when both species are typically concentrated near the southern sea-ice edge in the Bering Sea. Historically, that sea-ice edge has occurred near the continental shelf break, a productive region where upwelling and spring sea-ice melt combine to generate favorable conditions (Mizobata et al., 2006; Springer et al., 1996) for these upper-trophic predators when energetic demands, particularly on pregnant or lactating females, are very high. Both ribbon and spotted seal mothers are believed to continue at least some foraging during lactation (Burns, 1981; Quakenbush, 1988). Although few details of their foraging ecology at that time of year have been documented, ribbon seals are more adapted for deep diving and foraging off the shelf than spotted seals. This difference led Boveng et al. (2013) to predict that ribbon seal reproductive success in the Bering Sea would be sensitive to future declines in ice extent because a northward retraction of the ice edge, away from deeper water over the shelf slope, would displace mother-pup pairs from preferred foraging habitat. Spotted seals, however, were anticipated to be more resilient due to foraging habits more suited to the waters and epibenthic communities on the shelf, where the receding ice edge would occur for the foreseeable future (Boveng et al., 2009). During our study in 2007–2018, sea-ice extent in the Bering Sea fluctuated considerably, with a record high of 1,036,921 km² in 2012, a record low of 137,096 km² in 2018, and an average decline of about 47,000 km² y⁻¹ (Fetterer et al., 2017, updated daily). Over the period 2007–2018, ribbon seal adult body condition in our samples declined, while spotted seal adult condition remained relatively stable or increased slightly (Fig. 2). These patterns seem consistent with the predictions that the reproductive success of ribbon seals would be more sensitive than that of spotted seals to declining sea ice extent and northward retraction of the spring ice edge, away from the Bering Sea shelf break (Boveng et al., 2009, 2013).

Since 2000, conditions have alternated between relatively cold and warm periods that have been termed 'stanzas' (Stabeno et al., 2012). Warm and cold stanzas have been associated with different Bering Sea trophic conditions, posed as the oscillating control hypothesis (OCH), in which alternating cold and warm stanzas are associated with oscillating

bottom-up and top-down control of southeastern Bering Sea pelagic ecosystem function (Hunt et al., 2002) and pollock recruitment (Hunt et al., 2011). After the extreme warm year in 2018, similar trophic implications of cold and warm conditions have been examined in the northern Bering Sea, as well (Duffy-Anderson et al., 2019). The typical pattern in warm periods is an early sea-ice retreat that delays stratification needed to initiate the spring phytoplankton bloom; the phytoplankton, and the zooplankton species that graze on them, tend to be smaller and less lipid rich than the species prevalent in cold years with later ice retreat. More production is expected to accrue to the pelagic system than the benthos during the warm years. Cascading impacts on the quality and abundance of young pollock, other forage fish, and their predators in warm years tend to be negative but complex (Duffy-Anderson et al., 2019; Hunt et al., 2011; Piatt et al., 2020). Hunt et al. (2002) predicted from the OCH that piscivorous pinnipeds (i.e. seals) would prosper in cold years, from reduced competition with large fish for cold-water forage fish, and during the transitions from cold to warm stanzas, nourished by abundant young of large predatory fish species. Our samples in 2007–2010 were collected during a cold stanza, and in 2014–2018, during a warm stanza, with no sampling in the transition years. A simple explanation of the net declines in seal pup body condition we observed could be built on an appeal to the OCH, but without a better understanding of the actual diets of ribbon and spotted seals during the contrasting stanzas—particularly the degree of dependence on forage fish versus large predatory fish—it will remain difficult to do more than speculate about the trophic mechanisms that might underlie declines in seal body condition.

Among the potential relationships between declining sea-ice extent and seal body condition that merit further study is the degree to which ribbon and spotted seals derive energy from sympagic (ice-associated) versus pelagic (water column) primary productivity during the critical gestation, birthing, and nursing periods. Wang et al. (2016) found that a majority of carbon in fatty acids of bearded (*Erignathus barbatus*) and spotted seals' blubber was derived from sympagic production during the relatively cold, high-ice years 2007–2012, and the contribution from sympagic production in bearded seal blubber was significantly greater during those cold years than during warmer years of 2002–2005. Ribbon seals in that study were only sampled in the warmer years, but the data suggested that their blubber fatty acids were derived from sympagic production in high proportions similar to those in spotted seals. Without the contrast from ribbon seal samples in the colder years, it is not possible to assess whether ribbon seals—which seem to have a preference for foraging at the shelf break or in deeper waters—are more dependent than spotted seals on pelagic than on sympagic production. Wang et al. (2016) noted that unless there are differences in prey quality or quantity stemming from sympagic and pelagic carbon sources, shifts between them may not have substantial effects on seals' growth or vital rates. Studies to investigate whether such differences occur in quality or quantity of key forage fish as a result of variability in sea-ice extent could be highly valuable to understanding upper predators' responses in the northern Bering Sea ecosystem.

The edge of the pack ice in mid-April 2018 was hundreds of kilometers farther north than in any other year that we sampled (Fig. 1). In 1967, prior to satellite observations that began in 1979, spring conditions were in many ways similar to those in 2018 and 2019, resulting in distributions of ice-associated pinnipeds far north of where they usually had occurred (Burns, 1968, 1970). Ribbon seals were abundant throughout the northeastern Bering Sea by April 20, 1967. Even the oldest hunters in the region did not recall seeing as many ribbon seals in previous years (Burns, 1968), and the harvest of ribbon seals was the highest ever recorded in Alaska (Lowry, 1985a). In contrast, during the third week of April in 2018, while working at the ice edge in the northeastern Bering Sea, we encountered very few ribbon seals and captured none for sampling, unlike previous years when the pack ice was farther south and we typically captured more ribbon than spotted seals. It is unclear whether or where ribbon seals were successful at

producing and rearing pups in 2018, and the same questions are relevant to 2019, when ice extent was similarly low but we had no seal observations or samples.

A long-term program has been conducted by the Alaska Department of Fish and Game (ADF&G) to monitor health and condition—among many other aspects—of bearded, ringed (*Pusa hispida*), spotted, and ribbon seals (Crawford et al., 2015; Quakenbush and Citta, 2008; Quakenbush et al., 2009). The program samples relatively large numbers of seals in collaboration with Alaska Native subsistence hunters, and has potential for greater statistical power to detect trends than our samples from live-caught seals. Spotted and ribbon seal results from the harvest samples have not yet been published for the years overlapping with our study period. For ringed seals, they found that several indices of condition were lower during a period of greater ice concentration (1975–1984) than during a more recent period (2003–2012) with less ice (Crawford et al., 2015). Correlations of the ringed seal indices with May sea-ice area of $\geq 50\%$ concentration across the years of the two periods were mostly negative, though only two of five indices were significant. For bearded seals, comparisons between these two periods were mixed, and correlations with sea ice were non-significant. Thus, detecting climate-driven change in ice-associated seals appears to be complex, perhaps a reflection of the resilience of these generalist, high-trophic level predators to the typical interannual variability of the Arctic. However, ambiguities in the ADF&G results obtained through 2012 may reflect a lack of changes as profound as those observed in the Pacific Arctic during 2018 and 2019 (this issue).

During the period of our study, NOAA declared two unusual mortality events (UMEs) for seals in Alaska. The first UME (Burk-Huntington et al., 2012; NOAA, 2020), which occurred from May 2011 to December 2016, involved all four species of ice seals in Alaska (ribbon, spotted, bearded, and ringed). The primary symptoms in that UME were hair loss, delayed molting, skin ulcers, lethargy, and labored breathing, but after extensive testing, a definitive cause for the UME was not determined. The second UME, for bearded, ringed, and spotted seals, was declared in September 2019, after large numbers of dead and stranded seals were found in the Bering and Chukchi seas beginning in June 2018 (NOAA, 2020). Ribbon seals seemed to be rare or absent from the reported strandings, though many of the carcasses were decomposed and not conclusively identified. Ribbon seals are also less coastal in their distribution at sea and may simply be underrepresented in the strandings. The investigation of this UME has just begun, but it appears to be different from the first, and more likely food related; most of the stranded seals have been young and/or emaciated. Although no clear link to climate-related changes has been established for the first UME, the co-occurrence of the second UME with record low sea-ice extent and absence of ice from vast portions of the birthing and nursing areas for all four species of ice-associated seals in the Bering Sea is strongly suggestive of a major climate-related impact to the seal populations.

Our harbor seal data comprise just three annual sampling events in September, 2014–2016, near the end of the longer data set for spotted and ribbon seals, a limited perspective for evaluating trends. Still, the apparent rate of decline in harbor seal body condition was striking. A simple linear model including only ‘species*Year’ effects indicated an annual decline in body condition of 45 g body mass per centimeter of body length. Harbor seals are among several ecosystem components that have undergone long-term declines in the Aleutian Islands. They declined precipitously between about 1980 and 1999, particularly in the western Aleutians, where counts dropped by 86% (Small et al., 2008) and have not shown an indication of substantial recovery (Muto et al., 2019). The timing and regional pattern of greatest declines and failure to recover in the western Aleutian Islands mirror those observed in Steller sea lions (Small et al., 2008), plausibly suggestive of a low-frequency ‘ecosystemic’ common cause, but we are aware of no consensus view on what that cause may be. We suspect, though, that the recent declines we estimated in harbor seals’ body condition could be more of an acute response to short-term environmental variation than a continued

chronic response to whatever may have caused the western Aleutian harbor seal numbers to decline.

The sampling period for harbor seals coincided with a very strong marine heat wave in the Northeast Pacific Ocean that had strong effects on most marine ecosystem components being monitored in the region (e.g., Siddon and Zador, 2019). Piatt et al. (2020) offered a plausible synthesis of physical and biological oceanographic indicators, forming an explanation for the mass die-off of common murrens (*Uria aalge*) that occurred in the northeast Pacific during 2015–2016: In simple terms, the warm waters of the marine heatwave reduced phytoplankton and zooplankton productivity, thereby reducing prey availability to forage fish. At the same time, prey requirements of forage fish increased due to the metabolic effect of warmer temperatures, leading to poorer condition and nutritional content. The metabolic effect also increased the needs of larger predatory fish that compete with murrens for their forage-fish prey. The murrens, with high endothermic metabolic demands of their own, were effectively squeezed between the jaws of an ‘ectothermic vise’ because of their heavy reliance on forage fish (Piatt et al., 2020). Harbor seals are generalist predators with diets that vary seasonally and throughout their range. Their diet is poorly characterized for the Aleutian Islands, based on stomach contents from 18 harbor seals taken on Amchitka Island in the months of January, March, and April (Kenyon, 1965; Wilke, 1957). Prey items found were primarily Atka mackerel (*Pleurogrammus monopterygius*) and octopus (*Octopus rubescens*; and *Octopus* sp.). Fringed greenling (*Hexagrammos lagocephalus*), Alaska pollock (*Gadus chalcogrammus*), and unidentified fish and crab were also found in single stomachs or trace amounts. Forage fish, such as sand lance, herring, smelt, and capelin weren’t noted in the Aleutian harbor seal samples but are staples commonly occurring in the few studies that have been conducted on harbor seal diet in the Gulf of Alaska and Bering Sea (Jemison, 2001; Pitcher, 1980a, 1980b). Because of the opportunistic nature of harbor seal prey selection, a broader mechanism than forage fish being caught in an ectothermic vise will be required to understand whether and how the marine heatwave of 2014–2016 impacted body condition of harbor seals in the Aleutians.

As an integrated understanding of the Bering Sea and Aleutian Islands ecosystem dynamics continues to develop, we will attempt to link our observations of species- and age-specific trends in ribbon, spotted, and harbor seal body condition with documented changes in their prey species and their prey’s neighbors in the food web. With high metabolic rates and populations numbering in the hundreds of thousands to low millions in the Pacific Arctic, these seals are significant consumers that have the potential to shape the trophic web. As long-lived generalist predators, they are often thought to be relatively resilient or insensitive to bottom-up variability. In normal or average conditions, their ability to switch among a diverse suite of prey allows them to smooth over variability in one or a few food species, but when they do exhibit a decline in body condition, the trend is likely to reflect strong or broad underlying ecological changes such as those that now seem to be occurring with unprecedented frequency. That studies such as Crawford et al. (2015) and Wang et al. (2016) have found some, but sometimes conflicting, evidence of climate-induced signals in seals may reflect that the ecological variability experienced in the past two decades is just beginning to exceed the long-term bounds to which these species are adapted. If conditions like those recorded in 2018 and 2019 become more frequent as predicted (Oliver et al., 2018), impacts from loss of sea ice on the condition and vital rates of phocid seals are likely to become clearer.

Credit author statement

Peter Boveng: Conceptualization, Investigation, Writing – Original Draft, Writing – Review & Editing, Supervision, Project administration, Funding acquisition. **Heather Ziel:** Methodology, Validation, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing. **Brett McClintock:** Software, Formal analysis, Investigation,

Writing – Original Draft, Writing – Review & Editing. **Michael Cameron:** Investigation, Writing – Review & Editing, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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