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Integrating seabird dietary and groundfish stock assessment data: Can puffins predict pollock spawning stock biomass in the North Pacific?

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Abstract

Information on the annual variability in abundance and growth of juvenile groundfish can be useful for predicting fisheries stocks, but is often poorly known owing to difficulties in sampling fish in their first year of life. In the Western Gulf of Alaska (WGoA) and Eastern Bering Sea (EBS) ecosystems, three species of puffin (tufted and horned puffin, *Fratercula cirrhata*, *Fratercula corniculata*, and rhinoceros auklet, *Cerorhinca monocerata*, Alcidae), regularly prey upon (i.e., "sample") age-0 groundfish, including walleye pollock (*Gadus chalcogramma*, Gadidae) and Pacific cod (*Gadus microcephalus*, Gadidae). Here, we test the hypothesis that integrating puffin dietary data with walleye pollock stock assessment data provides information useful for fisheries management, including indices of interannual variation in age-0 abundance and growth. To test this hypothesis, we conducted cross-correlation and regression analyses of puffin-based indices and spawning stock biomass (SSB) for the WGoA and EBS walleye pollock stocks. For the WGoA, SSB leads the abundance of age-0 fish in the puffin diet, indicating that puffins sample the downstream production of the WGoA spawning stock. By contrast, the abundance and growth of age-0 fish sampled by puffins lead SSB for the EBS stock by 1–3 years, indicating that the puffin diet proxies incoming year class strength for this stock. Our study indicates connectivity between the WGoA and EBS walleye pollock stocks. Integration of non-traditional data sources, such as seabird diet data, with stock assessment data appears useful to inform information gaps important for managing US fisheries in the North Pacific.

KEYWORDS
leading indicators, marine bird food habits, Northeast Pacific, puffins, spawning stock biomass, verification

1 | INTRODUCTION

The Gulf of Alaska (GoA) and adjacent Eastern Bering Sea (EBS) ecosystems support vast fisheries targeting a diverse array of demersal fish, including key fisheries for walleye pollock (*Gadus chalcogramma*, Gadidae) and Pacific cod (*Gadus microcephalus*, Gadidae). Fisheries management of these resources relies upon annual stock assessments designed to understand and predict stock status and trends. In turn, predictions are used in conjunction with physical and biological "ecosystem considerations" to implement harvest guidelines under policies outlined in species-specific Fisheries Management Plans (Dorn & Zador, 2020). Stock assessment models generally use a variety of data streams including fishery landings, historical estimates of population biomass, growth estimates and age/size-frequency distributions to model future biomass (Methot & Wetzel, 2013). Predicting variation in gadid and other demersal fish biomass is challenging, owing in large part to uncertainty about the production and survival of juvenile age classes, and their recruitment (Barbeaux et al., 2018; Dorn et al., 2018; Hilborn & Walters, 1992). Traditionally, much of the information used in stock assessment models is obtained from fisheries-dependent surveys (Hilborn & Walters, 1992; Methot, 1989), but the use of fisheries-independent survey data and other non-conventional sources of information is growing in the USA and elsewhere in the world as new policies requiring holistic, ecosystem-based approaches to fisheries management are implemented (Link, 2010; Pikitch et al., 2004).

Predator-based sampling of juvenile age classes (particularly age-0 fish) is complementary to direct, survey-based sampling with catch per unit effort (CPUE) that may proxy abundance, and is one method proposed to fill information gaps in the population biology of commercially valuable fish (Hatch & Sanger, 1992; Link, 2004; Mills et al., 2007; Scopel et al., 2018; Velarde et al., 2015). The relative proportion of a fish species represented in the predator diet is commonly used and has been correlated with abundance of age-0 fish in local environments (e.g., Mills et al., 2007; Piatt et al., 2018), but this relationship varies with degree of diet specialization and spatio-temporal overlap between predator and prey. Recognizing the potential significance of sampling of age-0 fish early on, Cairns (1992) suggested in a unique paper that several seabird-based dietary parameters could be used as leading indicators of potential recruitment and year class strength, as well as direct inputs needed for models of variable natural mortality (e.g., Hill et al., 2020; Saraux et al., 2021). Notably, Cairns assumed that relationships between seabird diet and year class strength would be non-linear.

The use of seabird dietary data as a leading indicator of groundfish recruitment and biomass remains largely untested, but there are a few examples to present. Using data from Alaska (1985–1987), Hatch and Sanger (1992) found an association between modelled recruitment to age-1 and the abundance of age-0 walleye pollock in puffin diet, but this relationship was not statistically significant owing to the small sample of years ($n = 3$). More recently, Lorentsen et al. (2018) showed that the relative abundance of age-1 fish in the diet of European shags (*Phalacrocorax aristotelis*, Phalacrocoracidae) predicts ($r^2 = .67$)

recruitment of age-2 plaice (*Pleuronectes platessa*, Pleuronectidae). The only US stock assessment to use seabird dietary data quantitatively is that of the shortbelly rockfish (*Sebastes jordani*, Sebastidae) in the southern California Current ecosystem (Field et al., 2007). Shortbelly rockfish are a dominant species in the diet of some seabirds in the region (Ainley et al., 1996; Sydeman et al., 2001), and the proportion of age-0 *Sebastes* spp. in the diet of one of the most abundant seabirds in the region, the common murre (*Uria aalge*, Alcidae), is well correlated with the abundance of age-0 *Sebastes* spp. in the environment based on mid-water trawls (Mills et al., 2007; linear relationship, $r^2 = .81$). For the shortbelly rockfish stock assessment, Field et al. (2007) used the proportion of juvenile shortbelly in common murre diet as an index of age-0 abundance and showed that interannual variability in this index verified modelled recruitment to age 1.

In the Alaskan North Pacific, piscivorous seabirds foraging on the continental shelf often target juvenile (mostly age-0 fish) gadids and other groundfish (e.g., hexagrammids) to provision developing offspring at breeding colonies during the summer (Cunningham et al., 2018; Drummond, 2016; Hatch, 2013; Hatch & Sanger, 1992; Renner et al., 2012; Thayer et al., 2008). Age-0 fish brought to colonies may be collected for measurement, and in this manner, the seabirds "sample" gadid age classes that are not routinely sampled by other means. Puffins appear to take age-0 walleye pollock proportionately to what is available in the environment (Piatt et al., 2018). Indeed, apparent distribution patterns of capelin and sand
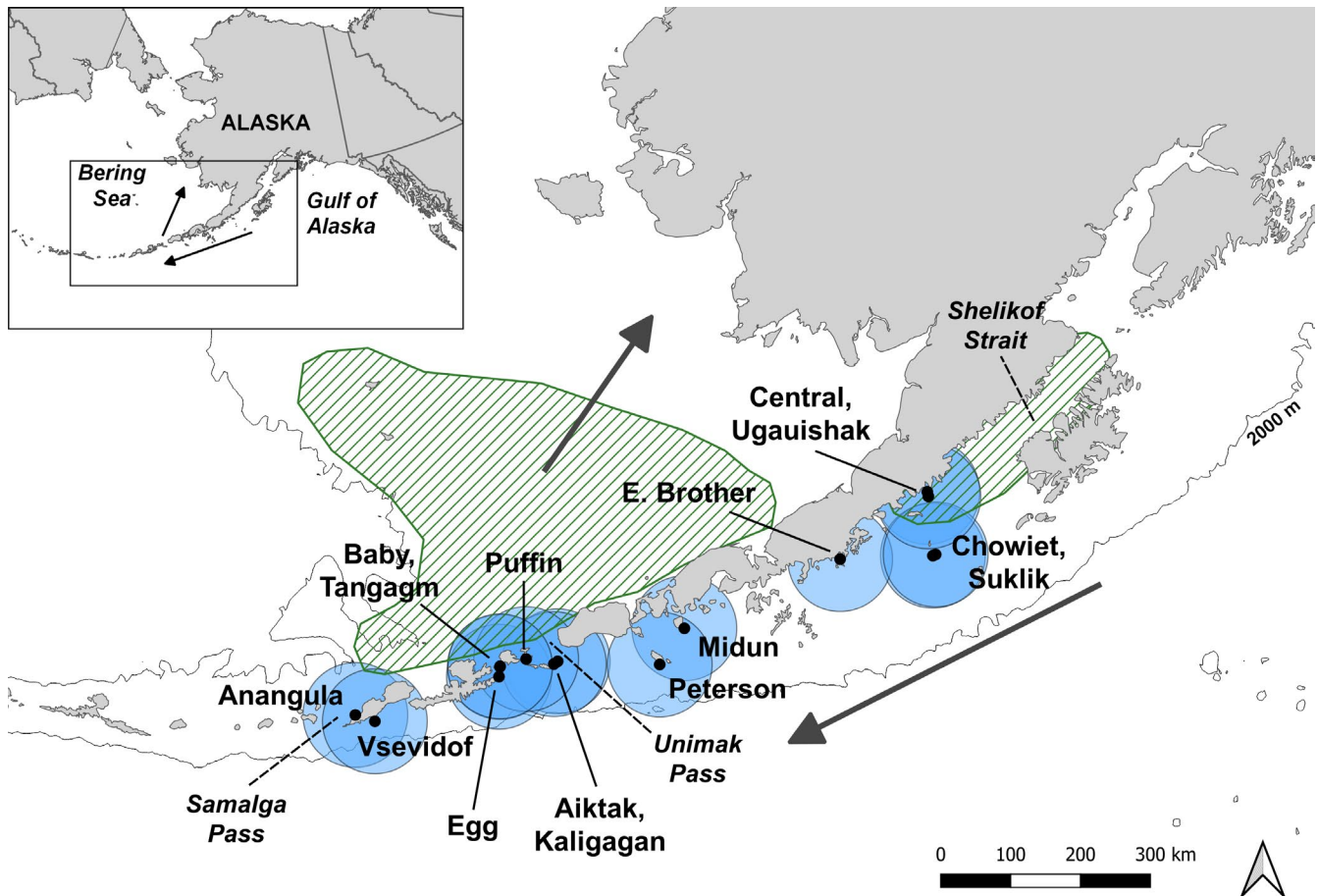
FIGURE 1 Map showing 15 sites in the Western Gulf of Alaska where age-0 gadids were sampled by puffins over 31 years, 1985–2015. A 75-km foraging/sampling radius for the birds is shown for each site. Approximate walleye pollock spawning regions in the Shelikof Strait area and Eastern Bering Sea are shown as green hatched areas (based on Bacheler et al. 2009, 2010; Hinckley et al., 2016). Larval pollock produced in/near Shelikof Strait are advected along the Alaska Peninsula and through Unimak Pass (Hinckley, 1987; Parada et al., 2016) where Aiktak Island is located. The 2000-m isobath is shown for context

lance in the GoA and Aleutian Islands differed most between trawl net and puffin samplers, while prevalence in puffin diets was much better spatially correlated with groundfish diets than with trawl net CPUE (Piatt et al., 2018). We investigate in this paper the hypothesis that seabird-based indices of age-0 walleye pollock abundance and growth can be used as predictors of year class strength and thus help inform aspects of stock assessments. To test this hypothesis, we extracted information from multi-decadal studies of the diet of the puffin community (tufted puffin (*Fratercula cirrhata*, Alcidae), horned puffin (*Fratercula corniculata*, Alcidae) and rhinoceros auklet (*Cerorhinca monocerata*, Alcidae)) from sites in the Western Gulf of Alaska (WGoA) (Figure 1). The vast majority of the diet data came from tufted puffins (>97% of the individual fish used in analyses were sampled by this species), and data on rhinoceros auklets and horned puffins are spatially and temporally constrained to the Semidi Islands, which were sampled primarily in the early 1990s (Figure S1). The foraging ranges of puffins from the WGoA colonies overlap with walleye pollock spawning areas and the overall region where larval and age-0 walleye pollock are transported by wind-driven currents along the Alaska Peninsula (Hinckley et al., 2016;

Wilson & Laman, 2021) and into the EBS (Parada et al., 2016). The diving depths of tufted puffin have not been studied directly, but a power function of diving depths in alcids relative to body mass indicates that these puffins could forage to ~140 m with typical foraging depths in the range of 30–75 m (based on Piatt & Nettleship, 1985). Similarly, foraging radii of tufted puffin are not well known, but the limited evidence suggests a regular maximum range of about 100 km and that 10–50 km from breeding colonies is typical (Piatt et al., 2018). For this study, we assumed that 75-km radii from breeding colonies represent the average areal extent of puffin sampling of age-0 gadids in the study region (Figure 1).

We analysed the puffin diet data with respect to estimates of female spawning stock biomass (SSB) available from recent walleye pollock stock assessments in the GoA (primary assessed area was WGoA) and EBS (Dorn et al., 2018; Ianelli et al., 2018). Walleye pollock are considered mature at age 3 (Dorn et al., 2018; Ianelli et al., 2018); thus, if our hypothesis is supported, we will expect that significant relationships between age-0 abundance based on puffin diet and SSB will appear with a lag of 2–3 years. For comparative purposes, we examined similar relationships for another commercially targeted gadid in the GoA, Pacific cod (provided in the SM).

2 | METHODS

Since the mid-1970s, seabird ecologists mainly from the US Fish and Wildlife Service/Alaska Maritime National Wildlife Refuge and US Geological Survey have studied seabird diets each summer at colonies across the GoA, Aleutian Islands, and into the EBS (Drummond, 2016; Piatt et al., 2018; Renner et al., 2012). Sampling methods for puffins are detailed by Hatch and Sanger (1992) and Drummond (2016). Briefly, researchers intercepted fish caught by adult puffins and carried back to colonies to feed developing offspring. Puffins dropped their fish at temporarily blocked nesting burrows, and the fish were then collected, identified and measured in the field, or frozen or preserved with formalin and ethanol for later identification and measurement in the laboratory. There were no mitigation actions taken to replace fish lost to sampling, but sampling was occasional (roughly once per week at the most heavily sampled sites) and dispersed across densely packed colonies; no one bird or pair was subjected to intense daily sampling. Breeding success and chick condition is not impacted by this kind of sampling (Schoen et al., 2018), in part because puffins have a protracted chick-rearing period (60+ days), a life history strategy that makes them resilient to short periods of food shortage (Piatt & Kitaysky, 2002). Data for these samples have been used in a series of recent papers (Piatt et al., 2018; Sydeman et al., 2017; Thompson et al., 2019); this database is currently available upon request from Farallon Institute and/or Alaska Maritime National Wildlife Refuge.

For this study, we collated data on fish caught by puffins from 15 of the 42 sites available, using data over 31 years, 1985–2015 (Figure 1). These sites were chosen because walleye pollock are known to spawn in this WGoA region, particularly in the Kodiak Island/Shelikof Strait area (Bailey et al., 1999; Parada et al., 2016; Sheffield Guy et al., 2014), and are subsequently dispersed by currents along the Alaska Peninsula and eastern Aleutian Archipelago (Hinckley et al., 2016; Wilson & Laman, 2021). In the EBS, larvae are advected from offshore spawning areas onto the shelf which takes them away from the Aleutian Islands puffin colonies (Ianelli et al., 2018). The age-0 fish sampled by puffins in the WGoA almost certainly come from the regional stock there. According to Hatch and Sanger (1992), there are hundreds of puffin colonies in the WGoA region, encompassing over two million birds, with the largest concentrations along the Alaska Peninsula and into the eastern Aleutian Islands. One site in the eastern Aleutians, Aiktak Island, has been consistently sampled since 1986, with only two missing years (Figure S1; Drummond, 2016; Hatch & Sanger, 1992). The forage fish community used by puffins in this region is dominated by age-0 walleye pollock, age-0 Pacific cod and Pacific sand lance (*Ammodytes personatus*, Ammodytidae, a non-commercially targeted forage fish) (Sydeman et al., 2017). This composition led Piatt et al. (2018) to describe the forage community as "transient" as it is based largely upon the transport of age-0 gadids, specifically walleye pollock, along the Alaska Peninsula (Hinckley et al., 2016; Wilson & Laman, 2021).

Based on the puffin sampling, we derived two puffin-based indices for the WGoA region: (a) an index of annual relative abundance, calculated as the proportion by number of the puffin diet composed of walleye pollock each year, and (b) a seasonal growth index based on the rate of change in length measurements obtained for each sampling date within each year.

The primary walleye pollock spawning grounds in the GoA are in Shelikof Strait, which in recent years have represented upwards of 90% of the pre-spawning biomass in winter acoustic surveys (Dorn et al., 2019). The spawning season is relatively compressed, extending from early April to early May, with peak spawning on April 19 (Rogers & Dougherty, 2018). During the spring, a cloud of larval pollock is transported slowly to the south-west along the Alaska Peninsula by the Alaska Coastal Current to retention areas in the WGoA (Brodeur & Wilson, 1996). Puffin foraging around breeding colonies in WGoA during summer should encounter a mostly static population of age-0 pollock, although the possibility of continuing alongshore transport cannot be entirely excluded. Still, we would expect that this would be a second-order effect on growth measurements, particularly since the year-to-year differences in growth, not the absolute values, are our main interest.

For the relative abundance index, we used only those fish and squid prey identified to species; all other invertebrates, such as euphausiids, and unidentified fish were excluded. As we were focusing on gadid species, all unidentified gadids were also excluded from our calculations of the abundance index ($n = 2,444$ specimens of 30,125 (8%) obtained from the 15 sampling sites across all years). For the WGoA, we pooled samples across islands for each year (equal weighting) because the number of samples within each year was too few to estimate within site variability, except at Aiktak Island. We then examined the Aiktak Island samples alone due to the richness of the dataset there, and to investigate if sampling on the western edge of the apparent age-0 walleye pollock distribution in the GoA would correlate with biomass upstream in the GoA and downstream in the EBS. Due to its location at the entrance of Unimak Pass, we thought Aiktak Island samples might be particularly important for understanding potential relationships between the GoA and EBS walleye pollock stocks, which are currently considered individual stocks and are assessed separately (Dorn et al., 2018; Ianelli et al., 2018). Another site, Suklik Island, provided a large sample size of puffin-caught age-0 fish (Figure S1), but most of the fish there were collected in the late 1980s/early 1990s, whereas Aiktak Island was sampled consistently across the period of interest. Moreover, most of the fish collected by puffins at Suklik (and indeed more generally in the eastern sites) were Pacific sand lance, suggesting that Aiktak may be a more appropriate focal site for providing walleye pollock fisheries-relevant data.

We calculated a seasonal growth index for walleye pollock based on length measurements (Table 1). First, we converted fork length measurements to total length using a regression established from fish samples where both measurements were taken (total length = 2.605 + (1.046*fork length), $R^2 = .99$). Second, an annual growth rate index was calculated from a linear regression of length and sample date within each year for all sites pooled (WGoA) as well as Aiktak individually. The regression coefficient

TABLE 1 Summary of length (mm) measurements for walleye pollock and Pacific cod across (A) all sites and years and (B) all sites by year, 1985–2015

Species	# Sites	# Years	N	Mean (SD)	Skewness	Kurtosis
(A)						
Walleye pollock	15	23	13,129	56.65 (14.62)	1.16	12.05
Pacific cod	14	18	1,277	59.95 (12.68)	0.93	5.92

	Walleye pollock			Pacific cod		
Year	N	Mean	SD	N	Mean	SD
(B)						
1985	400	61.00	9.22			
1986	845	65.22	8.63	11	60.00	6.00
1987	594	74.90	10.00			
- -						
1990	11	37.45	6.64			
1991	465	70.60	22.93	10	80.40	13.10
1992	2421	57.05	12.17	267	62.19	12.50
1993	1511	54.32	15.27	185	66.18	10.60
1994	3053	48.81	14.70	277	61.10	13.21
1995	808	51.93	11.44	170	56.86	12.02
1996	64	70.03	13.08	26	68.27	15.34
1997	103	64.83	10.68	16	64.06	9.70
1998	69	70.35	9.76	4	71.00	12.36
1999	2	46.00	4.24			
- -						
2006	41	60.90	11.50	9	65.33	6.54
2007	3	46.33	1.15			
2008	1	52.00		13	57.15	7.34
2009	13	43.54	6.06	7	51.57	10.18
2010	2	54.50	10.61	5	53.00	11.90
2011	25	42.68	4.61	13	59.38	12.35
2012	2240	56.75	8.87	104	52.90	9.08
2013	184	52.81	11.76	133	50.77	9.77
2014	246	65.78	12.73	27	59.30	6.09
2015	28	66.01	22.45	3	55.00	10.58

No data were available for 1988–1989 and 2000–2005. Length data were used in the growth index calculations (see Methods).

for date represents the amount of change in length (mm) by day each year. To limit this analysis to age-0 fish only, we excluded from regressions any fish where length ≥ 100 mm ($n = 39$). Additionally, at each site, we only used data from summers in which there were at least three sampling days over a minimum 14-day period.

The relative abundance index for Aiktak Island has been used each year for the past decade in the Aleutian Island Ecosystem Status Report (Zador & Ortiz, 2018), but has yet to be formally compared with stock assessment data. We related our derived relative abundance and growth indices to SSB time series obtained from 2018 NOAA stock assessments for the WGoA (Dorn et al., 2018, table 1.22) and EBS (Ianelli et al., 2018 table 30). We used female

SSB as this variable is assumed to be proportional to annual productivity each year for these stocks.

For analyses, SSB data were log_{10}-transformed (since they were not normally distributed) and the relative abundance index (proportion of age-0 fish in the puffin diet) was arcsin-transformed to approximate normality. SSB data were autocorrelated (Table S1). The age-0 abundance data were also autocorrelated, but not as strongly (Table S1). Relationships between the puffin data (relative age-0 abundance and growth) and stock assessment data were first examined using Spearman rank cross-correlations of -3 (diet/growth leading biomass) to +3 (diet/growth lagging biomass) years to examine how the puffin data compared to SSB temporally. We considered correlations with nominal $p < .10$ to be worthy of further

investigation using linear regression models. Age-0 abundance for the lags with nominally significant rank correlations was a predictor variable in these models. As SSB is assumed to be an indicator of stock egg production, we expected that a correlation at lag 0 would reflect a mechanistic relationship between SSB and age-0 abundance in the puffin diets. In support of this assumption, we also tested the puffin age-0 abundance index against larval walleye pollock CPUE in the WGoA (Rogers et al., 2020) and found a non-significant positive correlation ($\rho = 0.29$, $p = .16$, $n = 24$ years). We focused on SSB rather than age-1 recruitment estimates from the stock assessments because the latter modelled values are known to reflect many uncertainties. In support of this decision, we found no relationships between the puffin-based age-0 abundance indices and modelled age-1 abundance estimates for either the WGoA or EBS stocks (Spearman rank correlation; $\rho = 0.11$, $p = .58$, $n = 27$; $\rho = 0.14$, $p = .47$, $n = 27$, respectively).

3 | RESULTS

3.1 | Puffins as samplers of age-0 gadids

Sample sizes and proportion of walleye pollock in puffin diet (with Pacific cod and Pacific sand lance for context) for each site from 1985–2015 are shown in Figure S1. For sites with >900 fish samples

($n = 9$), about half had diets consisting of ~50% age-0 walleye pollock. The take (proportion in diet) of age-0 walleye pollock and cod within years but across sites was weakly positively correlated ($\rho = 0.384$, $p = .044$, $n = 28$). The take of age-0 walleye pollock and cod combined was strongly negatively correlated with the take of Pacific sand lance across sites ($\rho = -0.663$, $p = .0001$). The relative abundance of age-0 walleye pollock and cod also varied substantially between years (Figure S2). Lengths of more than 14,000 fish were measured, primarily during two periods: 1992–1995 and 2012–2014 (Table 1, Figure 2, Figure S1). Walleye pollock lengths demonstrated unimodal, approximately normal distributions, with the peak distribution at ~60 mm (Figure 2). The length-frequency distribution of age-0 fish from Aiktak was similar to all sites in the region, with non-significant variation towards slightly smaller fish.

3.2 | Trends in age-0 abundance and biomass

Walleye pollock age-0 abundance based on puffin diet showed generally higher values in the 1990s followed by a period of lower abundance in the 2000s (Figure 3). In the WGoA, walleye pollock SSB decreased in the late 1990s and through the 2000s, increasing some thereafter (Figure 3a). In the EBS, SSB was relatively constant for about 20 years, from the mid-1980s through the mid-2000s, decreasing substantially in the late 2000s, and has increased since
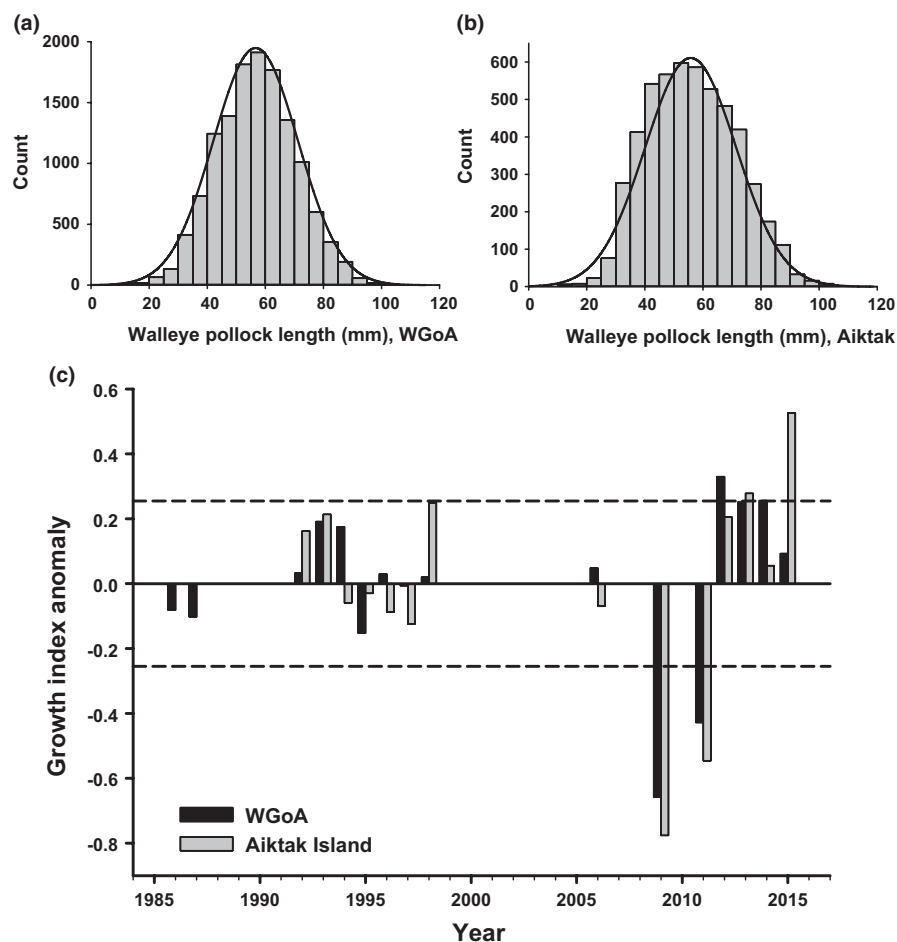

FIGURE 2 (a) Length-frequency distribution with normal distribution curve across all years for walleye pollock 0–120 mm in length at WGoA sites; 23 fish longer than 120 mm are not shown. (b) Length-frequency distribution with normal distribution curve across all years at Aiktak Island for fish 0–120 mm in length; 4 fish longer than 120 mm are not shown. (c) Growth index anomalies for walleye pollock over 16 years based on a linear regression of length by date within each year for all sites in the WGoA and Aiktak Island alone. Dashed lines show ± 1 SD for the WGoA data. Years without bars reflect no data

FIGURE 3 Pollock spawning stock biomass (bars) and age-0 abundance index at Aiktak Island (points) through time, with Loess smoothing lines (black, biomass; blue, age-0 abundance). (a) WGoA SSB and (b) EBS SSB
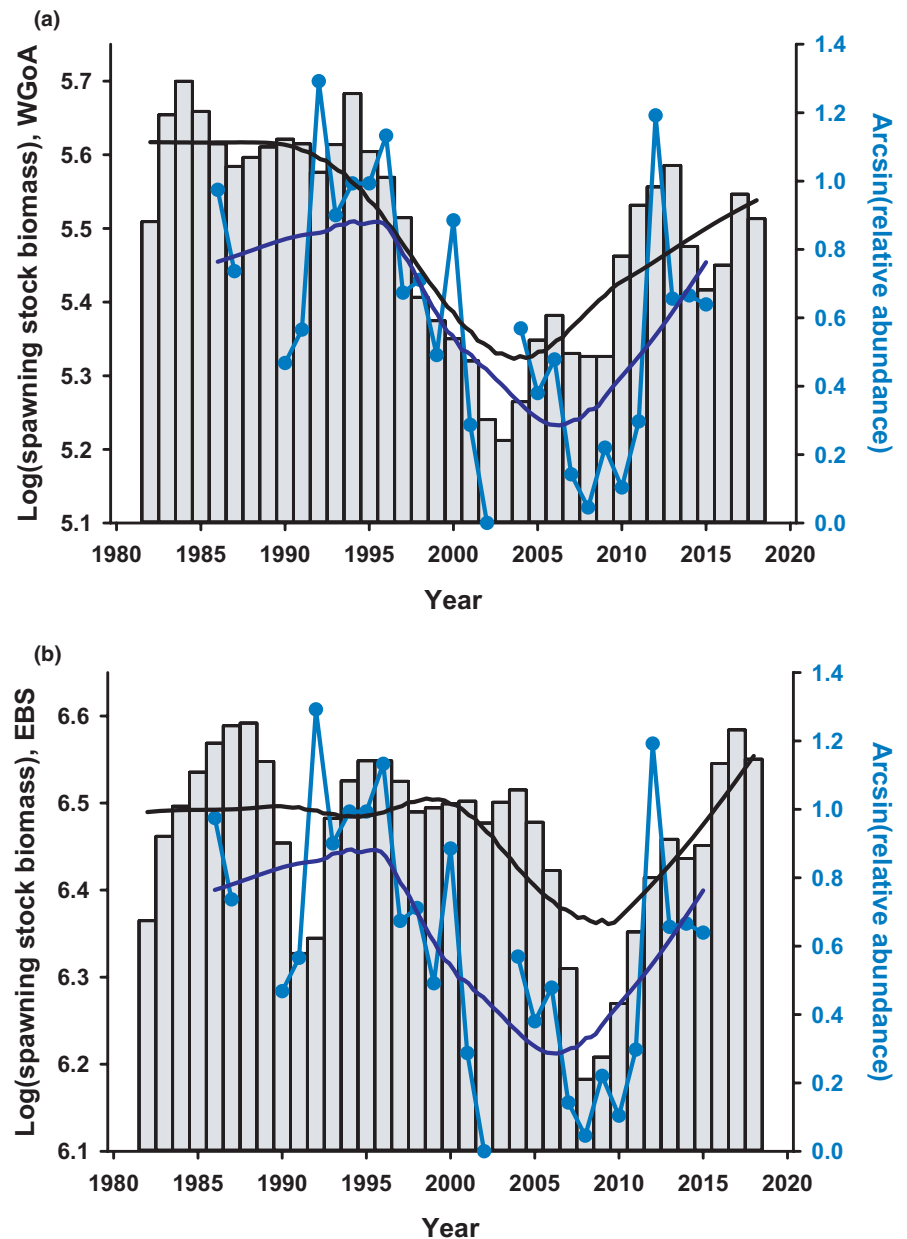
2008 (Figure 3b). Loess smoothing curves indicate that changes in the age-0 abundance index from Aiktak Island generally lagged changes in WGoA SSB. The reverse was indicated for the EBS where changes in age-0 abundance at Aiktak appeared to lead changes in SSB (Figure 3).

3.3 | Cross-correlations of age-0 abundance and SSB

WGoA SSB was positively correlated with age-0 abundance in puffin diets from WGoA colonies and Aiktak Island alone at no lag/lead and leads of 1–3 years (Figure 4a). That age-0 walleye pollock abundance in puffin diets was positively correlated with WGoA SSB in the same year provides support that the presumed egg production of WGoA pollock is reflected in age-0 abundance

as sampled by puffins. Notably, no significant correlations were found for EBS SSB leading the puffin-based age-0 abundance indices (Figure 4c). However, age-0 abundance in puffin diets was positively correlated with EBS SSB at leads of 1–3 years (Figure 4c), supporting our hypothesis that age-0 fish in puffin diets may inform SSB 2–3 years later, but this is applicable to the EBS only. The strongest correlation was at a lead of 1 year for Aiktak ($\rho = 0.66$; Figure 4c).

The relationship between WGoA SSB in non-log space and the age-0 abundance index in the same year indicates a linear relationship (Figure 5a, Aiktak sampling only; see also Table S2) that explained 43% of the variance in the puffin-based age-0 abundance index (Table 2). Age-0 abundance-biomass deviations were greatest in 4 years: 1992, 1996, 2000, and 2012 (Figure 5b), which correspond to strong year classes in the EBS (Ianelli et al., 2018). All other relationships were best fit by log-linear functions
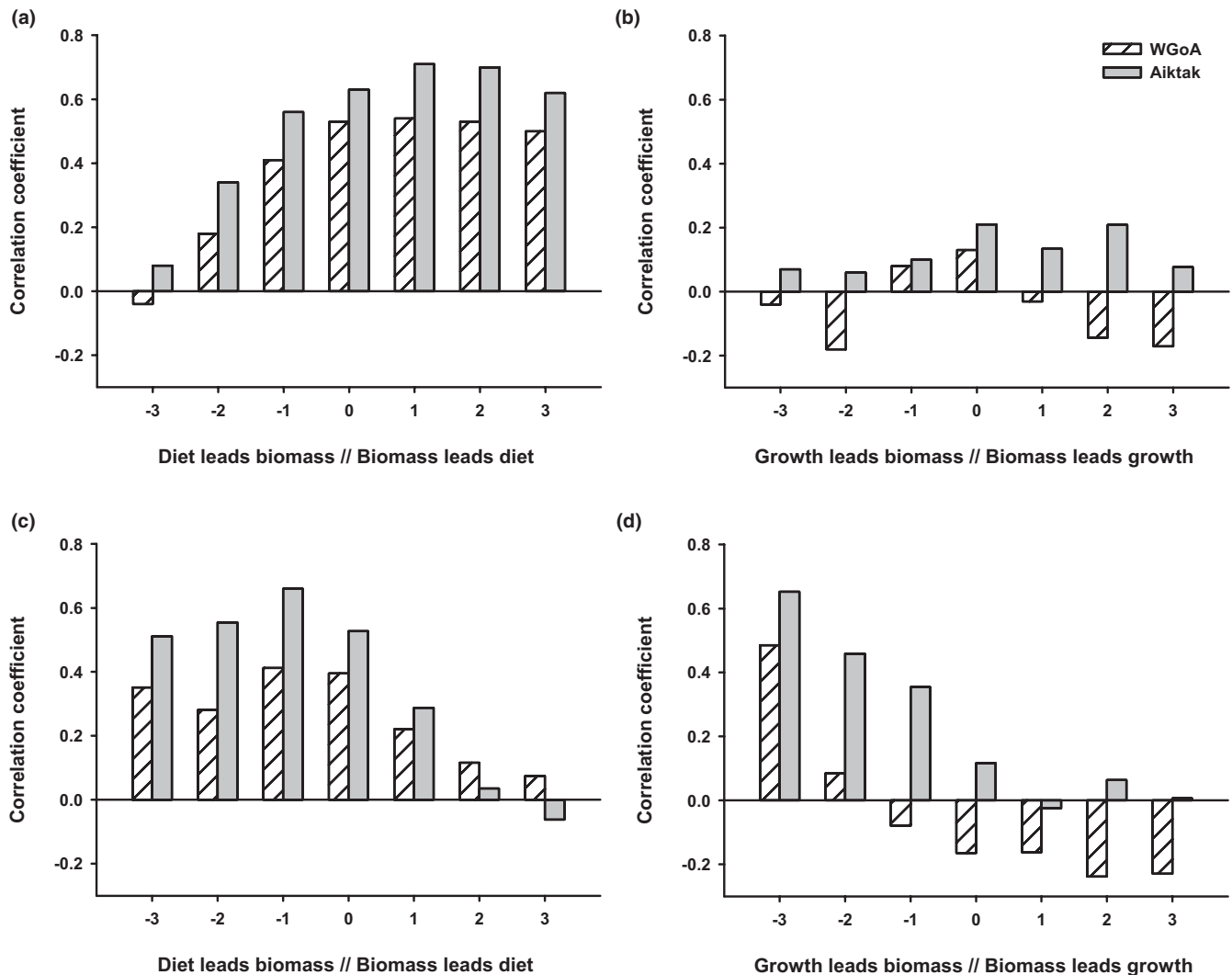
FIGURE 4 Spearman rank cross-correlations between SSB and age-0 abundance or growth from all WGoA sites or Aiktak Island alone. (a) WGoA SSB vs. age-0 abundance, (b) WGoA SSB and growth, (c) EBS SSB and age-0 abundance, and (d) EBS SSB and growth. Spearman ρ is shown on the y-axis, and lags/leads of up to 3 years are shown on the x-axis. Negative lags indicate age-0 abundance or growth leading SSB, while positive values indicate SSB leading age-0 abundance or growth. WGoA correlations are hatched bars, while Aiktak correlations are grey bars. Significance (p-value) of the correlations is shown by asterisks: *≤.1, **≤.01, and ***≤.001. Regressions of key selected key relationships are shown in Table 2, with corresponding scatter-plots of relationships in Figure 5

with age-0 abundance leading EBS SSB by 1–3 years (Table 2, Figure 5c–e; quadratic regression results with R^2 and AIC are reported in Table S2).

3.4 | Age-0 growth indices and spawning stock biomass

The puffin-based age-0 growth index varied interannually (Figure 2c). The years 2009 and 2011 were years of exceptionally low growth, while 2012–2013 were high. There was also very high growth rate in 2015, though only for Aiktak Island, not the WGoA sites together. There were no significant correlations between age-0 growth and SSB in the WGoA at any lag (Figure 4b). Age-0 growth at Aiktak, however, correlated with EBS SSB 2–3 years

later, providing support that age-0 growth indices may inform EBS SSB (Figure 4d), similar to the pattern found in the age-0 abundance index (Figure 4c). The relationship between walleye pollock growth at Aiktak Island and biomass in the EBS three years later has an outlier due to low biomass in the EBS in 2009 (Figure 5f). Regressions run on the full data set produced no significant results, but a linear relationship was evident when 2009 was removed from the analysis (Table 2; also see the linear relationship plotted without 2009 in Figure 5f).

4 | DISCUSSION

Seabirds are data-rich members of the GoA and EBS groundfish fisheries ecosystems. To date, seabird data have been formally incorporated
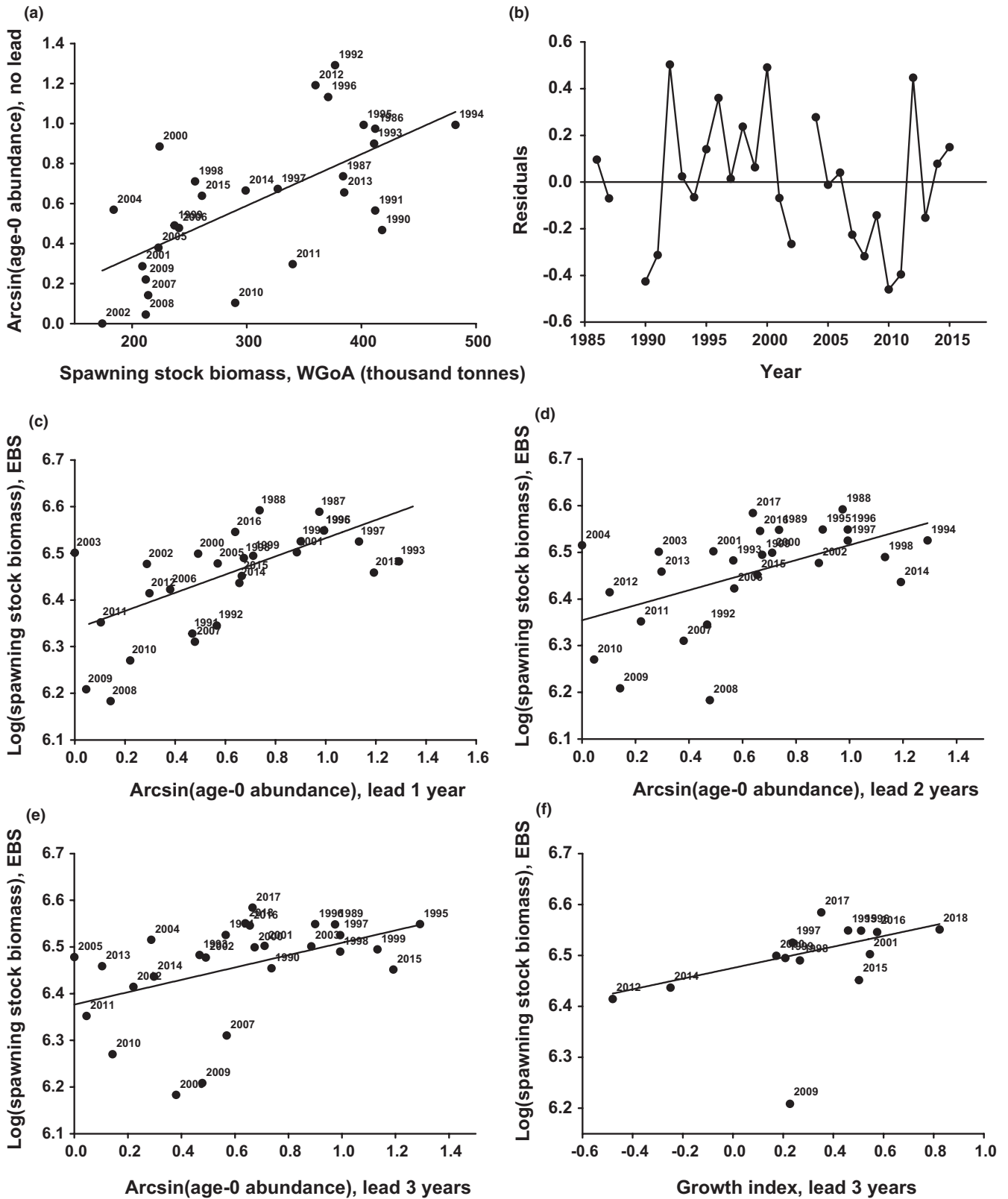
FIGURE 5 Relationships between Aiktak Island age-0 abundance or growth and SSB. Age-0 abundance data were arcsin-transformed, and SSB data were log-transformed in (c–f). (a) Age-0 abundance and WGoA SSB (KMT), no lag. (b) Residuals for the linear relationship shown in (a). Age-0 abundance leading EBS SSB by (c) 1 year, (d) 2 years, and (e) 3 years. (f) Growth leading EBS SSB by 3 years; the regression line does not include 2009. See Table 2 for statistics

into federal fisheries management processes in Alaska to provide contextual advice on ecosystem productivity (Zador et al., 2017). Examples include a multivariate indicator of seabird breeding success in the EBS (Siddon & Zador, 2018) and abundance indicators for age-0 gadids, hexagrammids, sand lance, and capelin (*Mallotus villosus*, Osmeridae) from diets in both the Aleutian Islands (Zador & Ortiz, 2018) and GoA reports (Zador & Yasumiishi, 2018). Some contextual information also appears in the recent Pacific cod stock assessment (Barbeaux et al., 2018) and walleye pollock stock assessment and associated Ecosystem and Socioeconomic Profile (Dorn et al., 2019; Shotwell et al., 2019). Here, we demonstrate that beyond providing contextual information, seabird data have potential to be quantitatively integrated with traditional data used in stock assessment models to enhance information about fisheries population dynamics in the region.

A caveat to our study is that SSB is strongly temporally autocorrelated (Table S1). Therefore, since puffin diet is linked to pollock SSB, it is also autocorrelated, although to a lesser extent. Autocorrelation in puffin diet also could be driven by some other unrelated process. The concern with autocorrelation in these time series is that p-values in statistical tests assume independence of annual values, and autocorrelation will bias p-values too low. As such, the p-values we report in Tables 2 and Table S2 should be considered nominal. Since our study is largely exploratory relative to the possible uses of seabird data in groundfish stock assessment, we are not overly concerned about the precise accuracy of p-values in these lagged correlations. Indeed, the fact that puffin diet leads EBS SSB by a series of years is perhaps one of the most noteworthy results of this study, despite the autocorrelation in these time series.

4.1 | Selectivity of puffins as samplers

One of the central issues to consider for any fisheries data is selectivity, or the disproportionate take of particular species or size classes by the sampling devices. This issue certainly applies to the use of seabirds

as samplers (Cairns, 1992; Mills et al., 2007; but see Reid & Brierley, 2001). In this study, potential selectivity in the age-0 abundance indices is particularly evident spatially (Figure S1B), with puffins at sampling sites nearest to the Shelikof Strait spawning grounds, where age-0 pollock may be more accessible, showing lesser take of walleye pollock than at sampling sites further downstream. Temporally, walleye pollock was clearly most prevalent in the puffin diets in the mid-1990s and in 2012, whereas other species, notably Pacific sand lance and capelin, were utilized more frequently in the other groups of years (Hunt et al., 2002; Sydeman et al., 2017; Figure S2). Importantly, some species such as age-0 Pacific cod may settle before summer and are therefore not available to surface trawls or seabirds, so fundamental differences in fish life histories may affect how well puffins serve as sampling devices of different species. In theory, if a sampling device collects a random sample of what is available in the environment, selectivity will be 1 and the sampling device will be considered to be perfect. We do not expect puffins to be perfect samplers any more than we expect fishing nets to be, but puffins appear to take age-0 walleye pollock proportionately to what is available in the environment (Piatt et al., 2018). Indeed, apparent distribution patterns of capelin and sand lance in the Gulf of Alaska and Aleutian Islands differed most between trawl net and puffin samplers, while prevalence in puffin diets was much better spatially correlated with groundfish diets than with trawl net CPUE (Piatt et al., 2018). The inference taken from this is that biological samplers may not be unreasonably selective (Piatt et al., 2018).

Length composition data also can indicate selectivity and may be useful to establishing the degree of selectivity by comparison of seabird- and net-caught individuals (Reid & Brierley, 2001). Notably, length data and modelled selectivity curves can be used as inputs to stock assessment models to ensure that all size classes are represented, and in this manner the puffin data may contribute in various ways to the stock assessment process. In this study, we found length-frequency distributions that approximated normal distributions (Figure 2) which suggests that the length composition of age-0 fish obtained by the birds (with

TABLE 2 Linear regressions for Aiktak Island age-0 abundance or growth against WGoA or EBS SSB

Model description	N	F	p > F	R²	Coefficient	t	p > |t|
Can SSB predict age-0 abundance?							
WGoA SSB and age-0 abundance, no lead/lag	27	18.61	.000	.43	0.2377	4.31	<.001
WGoA SSB leads age-0 abundance by 1 year	27	23.48	.001	.48	1.8100	4.85	<.001
Can age-0 abundance predict SSB?							
Age-0 abundance leads EBS SSB by 1 year	27	17.03	.000	.41	0.1949	4.13	<.001
Age-0 abundance leads EBS SSB by 2 years	27	9.67	.005	.28	0.1611	3.11	.005
Age-0 abundance leads EBS SSB by 3 years	27	6.36	.018	.20	0.1324	2.52	.018
Can growth predict SSB?							
Growth leads EBS SSB by 3 years (all years)	14	2.67	.128	.18	0.1184	1.63	.128
Growth leads EBS SSB by 3 years (2009 outlier removed)	13	12.30	.005	.53	0.1046	3.51	.005

Note: Shading indicates nominal significance of $p < .05$.

maximum length ~100 mm) corresponded with size availability in the environment and selectivity for size may also have been close to 1.

4.2 | Puffin-derived age-0 abundance and growth portend year class strength

On an interannual basis, the puffin-based age-0 abundance index from Aiktak Island explained 41%, 28%, and 20% of the variation in EBS SSB at lags of 1, 2, and 3 year(s), respectively (Table 2). Growth, which may reflect quality of age-0 fish, was also a leading indicator of EBS SSB with an appropriate 3-year lag (Table 2, Figure 5e,f). These relationships indicate that the abundance and quality of age-0 fish in Aleutian Island puffin diets may provide an index to upcoming year class strength for the EBS walleye pollock stock. These relationships may relate to recruitment processes, but so far results do not support any conclusions on this possibility. In support of this idea, however, the particularly high relative abundance of age-0 pollock in the puffin diet in 2012 (Figure 5b) was associated with high age-1 recruitment in the WGoA in 2013 (Dorn et al., 2018, figure 1.35, page 102) as well as EBS in 2013 (Ianelli et al., 2018, figure 47, page 126). Years of low abundance showed a similar pattern, with low relative abundance values in 2002 and 2009 preceding low age-1 recruitment in 2003 and 2010. That these relationships between puffin diet and age-1 recruitment are apparent only when there is an extreme recruitment anomaly (both high and low) may reflect the marginal location of sampling relative to the centre of pollock distribution in the WGoA. In addition, pollock year-class strength is thought to be established during the first year of life (Bailey et al., 2005), so the puffin diet of age-0 pollock may show a mixed signal with characteristics of both the spawning biomass that produced the age-0 fish and the eventual recruitment of pollock at age 1. However, our tests between age-0 abundance and modelled recruitment found no significant correlations, so we remain unclear on the actual mechanisms and processes that support the strong correlations between age-0 abundance in puffin diet and SSB in the EBS.

Another complication is that the "best" leading relationship between age-0 abundance and EBS biomass was for a 1-year lead, whereas SSB represents female fish aged 3+ years (Dorn et al., 2018; Ianelli et al., 2018); we expected that lagged relationships of 2–3 years would be strongest. Any leading relationship, however, lends credence to the idea that these correlations are mechanistically related to population fluctuations. It is plausible that autocorrelation in the puffin-based age-0 index and/or SSB estimates could explain these patterns. Indeed, Pearson autocorrelation coefficients in the puffin-based age-0 time series were 0.48 with a lag of 1 year and 0.29 with a lag of 2 years. We therefore interpret the puffin-derived age-0 abundance as a generalized index to potential year class strength in the fishable stock rather than a precise index to recruitment of age-1 fish.

Our integration of puffin dietary data with walleye pollock biomass estimates from recent stock assessments in both the WGoA and EBS was compelling, but few robust relationships were established for

Pacific cod using the same approach (SM). Undoubtedly, this is related to the fact that age-0 Pacific cod are not preyed upon as much as age-0 walleye pollock (Figure S1B), and this lack of take limits the utility of puffin diet composition as a quantitative indicator of abundance.

4.3 | Walleye pollock larval transport and connectivity between stocks

Leading relationships for both WGoA and EBS stocks were best modelled by the puffin diet sampled at Aiktak Island alone, and not by integrating seabird samples obtained over the wider WGoA region. This is probably related to more complete temporal sampling at Aiktak in comparison with the other sites. Indeed, when we integrated the data over all years and all sites, this resulted in some years including data from many sites, and some years including data only from Aiktak, which could introduce some temporal biases in the combined dataset. Thus, the Aiktak dataset is the most consistent in space and time, and this alone may explain why data from this location are best related to SSB. Aiktak Island is also located at the western edge of the walleye pollock range in the GoA (Dorn et al., 2018; Hinckley et al., 2016) and at the entrance to Unimak Pass where age-0 fish may be transported from the WGoA into the EBS (Parada et al., 2016). The consistency of the Aiktak Island data appears to make it a key location for indexing age-0 abundance, especially as it pertains to the potential connectivity to the EBS stock, but this could be changed if sampling was more consistent elsewhere, e.g., at the Semidi islands. However, countering this idea is the fact that puffins at sampling sites located further downstream from the primary Shelikof Strait spawning grounds in the WGoA showed greater use of walleye pollock, and this is probably not related to the inconsistency in sampling between sites (Figure S1, see also Hatch & Sanger, 1992; Piatt et al., 2018). The greater use of age-0 pollock further downstream may be explained by the slow but active transport of walleye pollock larvae along the Alaska Peninsula by the Alaska Coastal Current (Hinckley et al., 2016; Parada et al., 2016; Wilson & Laman, 2021). Piatt et al. (2018) referred to the forage fish community used by puffins in this region as "transient", meaning that its composition varied in structure relative to transport mechanisms. This idea matches modelled results of Hinckley et al. (2016) suggesting that as larvae are swept downstream from Shelikof Strait to the eastern Aleutian Islands they grow to sufficient size and are targeted by puffins as prey when they reach ~30–50 mm (Figure 2). Indeed, Hatch and Sanger (1992) noted that the largest puffin populations in Alaska overlap with this transport process and the substantial abundance of larger age-0 fish in the eastern Aleutian region. Finally, it should be noted that the pollock stock in the EBS is approximately an order of magnitude larger than the WGoA stock, so the supply of age-0 pollock to the EBS is likely to be much lower than in situ production in the EBS. Nevertheless, it is possible that advection from the WGoA may seed age-0 pollock into habitat that cannot be reached with spawning in the EBS due to unfavourable drift. Another possibility, albeit somewhat remote, is that the conditions favourable

for transport into the EBS are also conditions that support in situ production in the EBS. This could help explain why correlations between puffin diet and EBS spawning biomass are not strongest at the age of maturation.

Holistically, our study supports the hypothesis that WGoA-produced age-0 fish are advected westward towards puffin colonies where they are sampled by the birds. It seems less likely that Aiktak puffins sample EBS-derived age-0 fish as they are advected north-easterly, and thus shouldn't be within the foraging range of those puffins. The fact that WGoA SSB leads Aiktak age-0 abundance by 0–2 years indicates that autocorrelation in the WGoA stock may be playing a role in determining these lagged relationships. Lastly, our study supports the hypothesis of connectivity between the WGoA and EBS stocks through advection of WGoA age-0 fish into the EBS (Parada et al., 2016). Given no leading relationships between EBS SSB and Aiktak age-0 pollock, however, this connectivity appears uni-directional from WGoA to EBS, and no corresponding relationship from the EBS stock to the WGoA stock. This directional larval drift has also been identified for other groundfish (Sadorus et al., 2021). In summary, Aiktak Island appears to be the prime location for sampling age-0 walleye pollock since sampling there indicates the pro-portion of the age-0 population advected to the edge of the WGoA range and also the WGoA production that may determine EBS SSB 1–3 years later. To be able to assess aspects of the WGoA and EBS walleye pollock stocks simultaneously is a unique and valuable con-tribution that perhaps only sampling of Aiktak puffins can provide.

4.4 | Importance of stock assessment data to seabird diets

Stock assessments for walleye pollock are completed annually by NOAA Alaska Fisheries Science Center, with biomass estimates typically available in the fall of each year (e.g., Dorn et al., 2018, 2019). Walleye pollock SSB in the WGoA was strongly correlated with our puffin-based age-0 abundance index at no lag (Figure 4). This relationship is probably reflective of SSB leading egg production, which manifests as age-0 abundance in the diet of the puffins each year. Walleye pollock WGoA SSB also was strongly correlated with the age-0 abundance index at a lag of 1–3 years, with the strongest correlation at 1 year at Aiktak Island (Table 2, Figure 4a). These lagged relationships could indicate that the puffins are somewhat resilient to changes in walleye pollock SSB and productivity. From a fisheries perspective, this resiliency could indicate that the seabird data may reflect a "hy-perstability bias" (sensu Hilborn & Walters, 1992) in that changes in age-0 abundance lag changes in biomass. Alternatively, the relation-ship between SSB and the take of age-0 fish by the puffins could be described by a non-linear threshold relationship, where the take of age-0 pollock only changes when biomass drops/exceeds a certain value, but we did not see this clearly in the relationship between wall-eye pollock SSB and age-0 pollock in the puffin diet (Figure 5a). More study and additional years of data are needed to evaluate if there is a threshold in this relationship, but to date it appears linear.

4.5 | Next steps

We have taken the basic ideas put forth by Cairns (1992) and ap-plied them to key groundfish fisheries of the Alaskan North Pacific. Cairns' original paper was conceptual, not focused on any particu-lar fishery or region, and was published in an ornithological journal where it has remained obscure to many in the fisheries science com-munity. Integration of seabird dietary and Alaskan groundfish stock assessment data provides "proof-of-concept" that integrating these disparate sources of information is valuable and that lessons learned in Alaska can be applied to other regions with fewer sources of fisher-ies and fisheries-independent survey data. To implement this approach more fully in Alaska and elsewhere, a collaborative network of seabird ecologists and fisheries scientists is needed to both educate parties on the availability and utility of data from both disciplines, as well as plan and implement appropriate analyses. Building upon the tradi-tional stock assessment and ecosystem status reports, other new ap-proaches are being explored, including holistic multi-species Fisheries Ecosystem Plans and Ecological-Socioeconomic Profiles (ESP) for spe-cific fisheries (Shotwell, 2018). Both FEP and ESP are next steps in a process designed to enhance the ecosystem approach to fisheries management in the USA by using conventional and non-traditional in-formation, such as seabird data, in the fisheries stock assessment and management process.

5 | CONCLUSION

Seabird-derived observational data on fish stocks and modelled stock assessment data are complementary. We have shown impor-tant relationships in both directions, with examples of the seabird data leading or verifying the stock assessment data, as well as the assessment data leading or verifying the seabird data. Notably, both data sources provide indirect estimates of biological processes that are not well known, including determinants of the reproductive suc-cess of groundfish and the effects of variation in fish abundance on seabird food habits. The seabird data can be used to fill some gaps in information on age-0 walleye pollock in the WGoA and EBS. Advantages of using seabirds as age-0 samplers include cost, repli-cation, sampling during inclement weather, and data management and processing time. Disadvantages of using seabirds include spa-tial resolution and sample size. Prey-switching and some resiliency to biomass change could also be impediments to using seabirds as samplers and leading indicators, but for walleye pollock, puffin data provide indicators of year class strength that can be used to help understand variability in the populations of these economically and ecologically important stocks.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Puffin diet data are available upon request from Farallon Institute (www.faralloninstitute.org) and/or Alaska Maritime National Wildlife Refuge. Contributed USGS data are available at https://doi.org/10.5066/F7TQ60GV. Fisheries stock assessment data are publicly available in the annual stock assessment reports published by NOAA Fisheries (www.fisheries.noaa.gov).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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