Vol. 683: 179–194, 2022
https://doi.org/10.3354/meps13943

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 3

Seabird reproductive responses to changing climate and prey communities are mediated by prey packaging

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ABSTRACT: Climatic factors drive changes in forage fish communities and may influence the productivity of piscivorous predators, but specific mechanisms of response remain poorly known. Between 1984 and 2020, we studied the rhinoceros auklet *Cerorhinca monocerata*, a seabird breeding in the western North Pacific at Teuri Island, Japan. We tested the hypothesis that climate-mediated prey-switching affects 'food packaging' (i.e. the way energy is brought to dependent offspring) and breeding success by quantifying relationships between climate, prey energy density, amount of food delivered, and the growth and survival of chicks. Prey composition switched 4 times: 1988–1992, 1997–1998, 2013–2014, and 2017–2018. All but the last of these switches were associated with (lagged) shifts in seawater temperature/Pacific Decadal Oscillation. Rhinoceros auklets brought multiple fish in each meal-load to chicks, and numbers were inversely correlated with the size of the fish. These relationships varied between fish species. The heaviest meal-loads were achieved when diets were dominated by anchovy *Engraulis japonicas*, which occurred during warm phases (1992–2013). Chick production, growth rates, and mass at fledgling were also highest during the warm phases. This study shows that climate affects seabird reproduction by shifting the manner in which food is selected relative to changes in forage fish community structure and abundance.

KEY WORDS: North Pacific · Rhinoceros auklets · Forage fish · Meal-loads · Prey-switching

1. INTRODUCTION

Climate forcing of marine environments changes 'bottom-up' trophic effects that may influence the reproduction and population dynamics of top predators through changes in forage fish communities (Aebischer et al. 1990, Barbraud & Weimerskirch 2001, Boyd & Murray 2001, Sydeman et al. 2015). In responding to changes in forage fish communities, central-place foraging top predators that feed at sea but provide food for offspring on land may alter their prey use to match prey availability, changing prey species when the forage community structure shifts (Montevecchi et al. 1988, Crawford & Dyer 1995, Furness & Tasker 2000), with potential effects on how food is delivered (i.e. 'food packaging') and reproductive success (Piatt et al. 2007, Furness 2007, Cury et al. 2011). But the responses to shifts in forage communities are not simple, as different prey species have different sizes and energetic values, and may be more or less difficult to procure (Anderson & Piatt 1999).

Rhinoceros auklets *Cerorhinca monocerata* are piscivorous diving seabirds of the North Pacific which,

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despite their name, belong to the puffin tribe of the Alcidae (Gaston & Jones 1998). They dive to 65 m depth and prey on a variety of species, such as sardine *Sardinops* spp., anchovy *Engraulis* spp., sand lance *Ammodytes* spp., capelin *Mallotus* sp., and squid, which they bring back to their colonies to provision chicks in nest burrows (Burger 1991, Gaston & Jones 1998, Kuroki et al. 2003, Thayer et al. 2008, Sydeman et al. 2017, Cunningham et al. 2018). They switch prey use with interannual changes in forage fish communities, and these shifts result in large variations in chick growth and fledging success (Takahashi et al. 2001, Hedd et al. 2006, Thayer & Sydeman 2007, Borstad et al. 2011). Rhinoceros auklet parents bring fish in their bills (meal-loads or food packages) once per day, usually at night, when it is dark (Takahashi et al. 1999). Between-year variations in the energetic value (energy density multiplied by the mass) of the meal-loads is thought to be the main factor determining chick growth and production (Watanuki et al. 2009), but this idea has not been thoroughly investigated. Like other puffins, rhinoceros auklets bring multiple prey items in each meal-load. Therefore, they can compensate for potentially small (large) prey size by bringing more (less) fish (see Fig. 1), and may therefore have the ability to mitigate the effects of changes in prey energy density by increasing the mass of the meal-load.

In the North Pacific, warm and cold phases of the Pacific Decadal Oscillation (PDO) cycle at decadal temporal scales (Mantua et al. 1997, Minobe 1997). The PDO index is the first principal component of sea surface temperature (SST) north of 20° N latitude after de-trending and is associated with variability of the Aleutian Low and El Niño–Southern Oscillation (ENSO) (Schneider & Cornuelle 2005). The positive phase of the PDO brings warmer water to the NE Pacific and colder water to the NW Pacific (Mantua & Hare 2002), so biological effects are expected to be quite different between the NW and NE Pacific. Populations of some forage fish track these phase shifts of the PDO, SST, and other factors in the NW and NE Pacific (e.g. cycle of sardines *Sardinops* spp. and anchovies *Engraulis* spp.; Chavez et al. 2003, Takasuka et al. 2008). Responses of piscivorous predators to changes in the PDO, ENSO, and SST have been studied in the NE Pacific (Hedd et all 2006, Lee et al. 2007, Bertram et al. 2009, Hipfner et al. 2020), but little research has been carried out in NW Pacific.

In the northern Japan Sea in the NW Pacific, changes in the forage fish community have been associated with climatic shifts. A shift from a cold to warm phase was observed in 1988–1989; correspondingly, there was a collapse of Japanese sardine *S. melanostictus* and an increase in Japanese anchovy *E. japonicus* stocks (Tian et al. 2008, Takasuka et al. 2008). Consequently, rhinoceros auklets in this region switched prey from cold-water related species such as sardine, sand lance *Ammodytes* spp., and Pacific saury *Cololabis saira* to the warm-water related anchovy (Deguchi et al. 2004a). Shifts in climate, forage fish stocks, and auklet diet since the early 1990s have not been re-examined.

In this study, using 32 yr (1984–2020) of data from Teuri Island in the northern Japan Sea, we investigated how ocean climate drives prey use by rhinoceros auklets, and how prey switching affects energy acquisition and chick production. Specifically, we tested the hypothesis that both energy density and

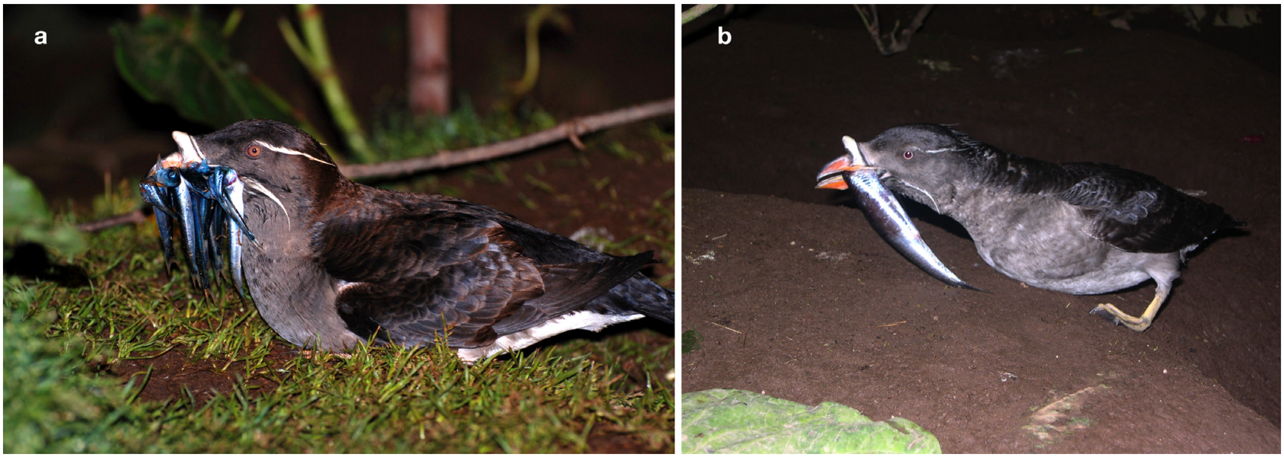

Fig. 1. Rhinoceros auklets on Teuri Island, Japan, bring back variable numbers of fish in each meal-load. A parent brings back (a) 8 age-0 greenlings and (b) one anchovy. Photo by M. Ito

the amount of prey delivered as a food package affects reproductive success, measured by chick growth, fledging success, and fledgling mass in rhinoceros auklets breeding at Teuri Island. First, we applied principal component analyses to the auklet's diet composition to characterize the use of different forage community members. We also explored whether the timing of the change in prey use co-occurred with recent quasi-decadal scale climate shifts indicated by the PDO index and seawater temperatures. Second, we examined how between-year variations in chick growth and fledging success depended on the energy density (kJ g^{-1}) and amount of prey (g) delivered in meal-loads. Third, we explored how the relationships between the number and size of fish affect the amount of prey delivered. In our discussion, we provide explanations for the reproductive consequences of decadal-scale prey switching in a seabird species that brings multiple fish in a meal-load.

2. MATERIALS AND METHODS

2.1. Seabird data

Field work was carried out at Teuri Island (44° 25′ N, 141° 19′ E), 28 km off mainland Hokkaido, Japan, during the chick-rearing periods of mid-May–early-August, 1984–2020 (excluding 1986 and 1988–1991 due to logistic constraints). Parents landing with fish in their bills (i.e. with meal-loads) after sunset were captured by hand or in hand nets in the diet sampling plot (~100 m in length) from 30 min after sunset for about 2 h along the road near the Akaiwa lighthouse (Text S1 & Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m683p179_supp.pdf; for all supplements). Meal-loads were collected and placed in individual plastic bags. Samples were brought back to the laboratory where prey items were identified. Prey size was measured as the fork length of each prey item (to 1 mm), and each prey item was weighed (to 0.1 g). When multiple numbers of small (<0.1 g) fish (such as age-0 sand lance) were found together, we weighed these as a group but measured the fork length separately. Prey-use sampling was carried out on (mean ± SD [range]) 12 ± 6.4 (1–34) nights per year, mostly once per week throughout the chick-rearing period, resulting in 8 ± 8.1 (1–73) meal-loads each night, 96 ± 30.5 (53–226) each year, and 3067 in total during the study. The 3067 meal-loads contained 15 486 individual fish.

We measured chick growth and fledging success (the number of fledglings per nest with chicks) at 2 monitoring sites. Site A was established >50 m distant from the site used for meal-load sampling prior to 2013. Site B (200 m from Site A; Fig. S1) was added in 2014. Nests in Sites A and B were monitored since 2014. Although differences in chick growth and fledging success were found between sites in 2016 and 2018 respectively, trends were similar in other years (Fig. S2 in Supplement 1); therefore, data from the 2 sites were combined after 2014 to analyze between-year variations. At the first sign of hatching (i.e. parents carrying meal-loads in the evening) in early May, we started nest monitoring. We sampled 37 ± 15.3 (10–84, n = 32 yr) nests where eggs hatched every year. We checked nest contents of all nests on the same day and every 5 d but occasionally changed the monitoring schedule depending on weather conditions. For years with detailed records of each nest (2001–2020), the average interval of nest monitoring was 4.9 ± 0.8 d (3–9 d, n = 260 intervals). We found chicks on the first day of monitoring for 19% of 838 nests; the ages of these chicks were estimated using wing length (Takahashi et al. 2001), and hatch dates were back-calculated. For others, we assumed that chicks had hatched on the day between nest checks when we saw eggs in one visit and chicks in the next visit. All chicks were weighed (±5 g) using a Pesola spring balance at each nest check. The slope of the linear regression of the mass on age (g per 5 d) between 5 and 20 d of age for those giving $r > 0.9$ was defined as the growth rate of chicks (including ones that may have died). This excluded the non-linear growth periods after hatching and during weight loss before fledging. We tested if the mass or energy density of the meal-loads affected the annual average of the slopes (chick growth rate) using regression analyses. We assumed that the chicks fledged when they disappeared from nests after 40 d of age (Takahashi et al. 2001) and defined the mass of the last day before disappearance as the mass at fledging.

2.2. Forage community use and energetic value

Sand lance individuals were separated into age-0 (≤110 mm fork length; Bertram & Kaiser 1993) and age->1 (>110 mm) classes since the energy content of these age classes differed (Text S2 & Table S1 in Supplement 2). All Japan Sea greenling *Pleurogrammus azonus* were age-0, since the fork lengths were smaller than 180 mm (Nagasawa & Torisawa 1991). All salmon *Onchorhynchus* sp. were smaller than 109 mm (except one *O. masou*) and were categorized as juveniles.

The mass of each of 9 major prey species/types (see Table 1) in each year was calculated, excluding other prey species and prey which were not identified to species level. To index forage fish prey composition each year, we applied principal component analyses on the mass of these major prey species/types and used the first (PC1) and second (PC2) principal components as indices of forage community use. The energy value of an average meal-load in each year was estimated using median values of energy densities for each prey species acquired from the literature (Table S1), the average mass of the meal-load, and the mass composition of 9 major prey species/types in each year.

2.3. Climate change and stock size

To assess climate fluctuations, we used winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) PDO indices averaged over 3 mo periods (Mantua et al. 1997, Minobe 1997, https://www.ncdc.noaa.gov/teleconnections/pdo/). The PDO is associated with changes in the phenology, community structure, and abundance of phytoplankton, zooplankton, and forage fish in the NW Pacific (Chiba et al. 2006, 2012, Ohshimo et al. 2009, Kuwae et al. 2017, Nakayama et al. 2018).

The maximum foraging range of rhinoceros auklets from Teuri Island is estimated to be 164 km (Kato et al. 2003). Variability in the interannual and seasonal expansions of Tsushima Current stocks of sardine and anchovy (Watanabe & Takahashi 2007, Muko et al. 2018) may make these stocks available to rhinoceros auklets breeding at Teuri Island. Stocks of age-0 greenling in the northern Japan Sea off Hokkaido are well within the auklets' foraging range. Stock sizes of sardine and anchovy in the Tsushima Warm Current and that of age-0 greenling in the northern Japan Sea off Hokkaido were obtained from stock assessment databases (http://abchan.fra.go.jp/digests2019/index.html, accessed 25 September 2019; see Hayashi et al. 2018, Morita et al. 2018, Yasuda et al. 2018). The stock sizes are assessed by cohort analysis and are available between 1985 and 2018 for age-0 greenling and between 1984 and 2018 for sardine and anchovy.

2.4. Statistics

To detect decadal-scale shifts in the auklets' diet composition and the PDO, a sequential *t*-test analysis of regime shifts (STARS; Rodionov 2004) was applied to data from 1980 (4 yr before the study period) through 2020. To minimize the possibility of a Type II error, a significance level of 10% was chosen. To determine any potential shifts in the PDO index, a primary value of cutoff length of 10 yr was established for examining quasi-decadal shifts, and a 5 yr cutoff was used for examining short-term shifts. We did not have time-series data before 1992 for the diet composition, mass of meal-loads, and productivity (chick growth rate, number of fledglings per nest, fledgling mass) of rhinoceros auklets; therefore, shifts in these variables were examined using STARS where only the 5 yr cutoff was used. We used Huber's weight parameter (H; set at $H = 1$) to detect outliers. A Visual Basic for Applications procedure from the NOAA website (https://www.beringclimate.noaa.gov/regimes/, accessed 1 December 2017) was operated with a macro in Excel 2010 (Microsoft).

Linear regression analyses were carried out to examine the effects of (1) annual average meal energy density (calculated) and (2) mass of meal-loads on auklet productivity (chick growth, number of fledglings, mass of fledgling). Linear and parabolic effects of prey composition as indexed by PC1 and PC2 on the annual average meal-load mass were also tested. Differences in the mass of meal-loads between prey species were examined using the linear model with a Bonferroni test, excluding unknown and minor species/types but including a mixture of age-0 and >1 sand lance types and other multiple species. To understand the mechanism determining the mass of meal-loads with multiple numbers of prey, we examined the relationships between the number and size of fish and the mass of each meal-load using linear and parabolic regression analyses for each species/type (using SPSS v.22). To evaluate the appropriateness of either linear or parabolic models in the above regression analyses, we used a model selection procedure in addition to the value of the coefficient of determination (r^2). Candidate linear mixed models or linear models were constructed using the 'lme4' library in R v.3.2.1 (R Development Core Team 2015) and 'glmer'; model selection was based on corrected Akaike information criteria (AICc) using the 'MuMIn' library.

3. RESULTS

3.1. Prey switching

The primary prey of rhinoceros auklets were sardines, anchovies, herring *Clupea pallasii*, age-0 and

Table 1. Average (±SD) mass of rhinoceros auklet meal-loads, the number of fish comprising a single major or minor species of fish and the number of meal-loads. We categorized the species as major if the number of meal-loads including these species was >14 and minor if <13. The meal-loads contained a mixture of age-0 and age->1 sand lance; those including multiple species were categorized as multiple types

Species/age class	Mass of meal-load (g)	Fish per meal-load	Meal-loads
Major species			
Sardine *Sardinops melanostictus*	40.3 ± 9.3	1–5	71
Anchovy *Engraulis japonicus*	32.9 ± 11.6	1–15	1395
Herring *Clupea pallasii*	27.8 ± 14.1	1–23	53
Age-0 sand lance *Ammodytes* spp.	18.5 ± 9.4	1–59	401
Age->1 sand lance *Ammodytes* spp.	27.6 ± 10.7	1–6	159
Age-0 Japan Sea greenling *Pleurogrammus azonus*	25.5 ± 11.4	1–20	414
Pacific saury *Cololabis saira*	22.1 ± 12.8	1–6	70
Juvenile salmon *Onchorhynchus* sp.	11.0 ± 4.9	1–7	14
Squid	20.0 ± 10.9	1–6	57
Minor species			
Capeline *Mallotus villosus*	31.2	5	1
Smelt *Hypomesus* sp.	26.6 ± 15.9	1–5	4
Walleye pollock *Gadus chalcogrammus*	14.5 ± 4.5	5–18	7
Naked sand lance *Hypoptychus dybowskii*	0.9	5	1
Spottybelly greenling *Hexagrammos agrammus*	14.2 ± 8.9	1–15	13
White-edged rockfish *Sebastes taczanowskii*	0.6	3	1
Ocalled blenny *Opisthocentrus ocellatus*	6.1	1	1
Purple puffers *Takifugu porphyreus*	16.0	1	1
Puffers *Takifugu* sp.	34.4 ± 3.0	1	3
Snailfish *Liparis* sp.	16.2	1–4	2
Three spined stickle back *Gasterosteus aculeatus*	3.1 ± 1.0	1	3
Masu salmon *Oncorhynchus masou*	33.0	1	1
Unidentified pelagic fish	14.8	6	1
Unknow	5.6	1–2	2
Multiple types			
Age-0/age->1 sand lance	29.9 ± 10.0	2–21	38
Multiple species	23.2 ± 12.7	2–38	354
Total	27.9 ± 12.8		3067

age->1 sand lance, Pacific saury, age-0 Japan Sea greenling, juvenile salmon *Onchorhynchus* sp., and squid (Table 1). These 9 species/types comprised 76–100% of the composition (by mass) of meal-loads each year and were defined as major prey species/types (Table 1). Most (87%) meal-loads contained a single species/type (Table 1); 34% of meal loads contained a single prey item per meal-load, while 66% contained multiple prey items per meal-load. We attribute PC1 (with 38.1% of variance explained) to a community characterized by the presence of sardine and age->1 sand lance and the absence of anchovy and PC2 (24.1% explained variance) to a community characterized by the presence of squid and age-0 greenling and the absence of Pacific saury (Table 2).

Forage fish communities exploited by auklets varied among years (Fig. 2a, also see Table S2 in Supplement 2). During 1984–1987, PC1 was positive and PC2 was negative (Fig. 2b). After 1992, sequential analyses of the 5 yr cutoff showed that PC1 shifted to negative in 1997–1998, then shifted to positive in 2013–2014, and to a greater degree in 2019–2020 (Fig. 2b). PC2 shifted to positive in 2013–2014, then

Table 2. Loadings of each species/type along principal component 1 (PC1) and 2 (PC2) given by principal component analysis of the proportional mass composition of rhinoceros auklet prey species in the meal-loads in each year

Species/type	PC1	PC2
Sardine	0.769	−0.460
Anchovy	−0.921	−0.317
Herring	0.562	0.064
Age-0 sand lance	0.521	0.222
Age->1 sand lance	0.795	−0.490
Pacific saury	0.643	−0.534
Age-0 greenling	0.334	0.660
Juvenile salmon	0.391	0.437
Squid	0.312	0.805

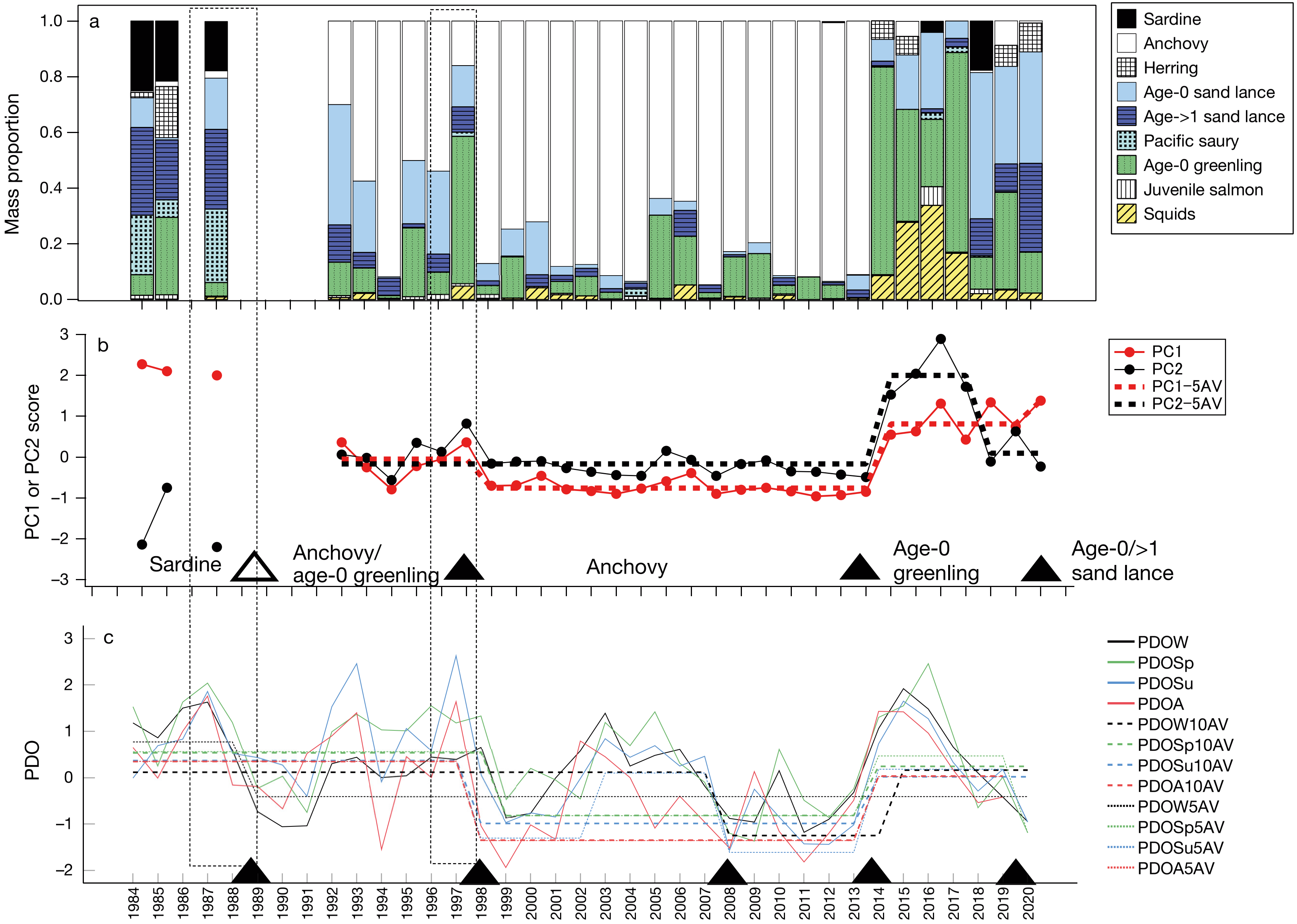

Fig. 2. Between-year changes in the (a) mass proportion of rhinoceros auklet prey species/type in a meal-load, (b) the scores of the first (PC1) and second (PC2) principal component of the mass composition of prey species with dominant prey species, and (c) Pacific Decadal Oscillation (PDO) index in winter (Dec–Feb; PDOW), spring (Mar–May; PDUSp), summer (Jun–Aug; PDOSu), and autumn (Sep–Nov; PDOA). The weighted average values during each phase between the shifts determined by sequential *t*-test analysis (STARS) using 5 yr cutoff (5AV) for PC1 and PC2 are shown in (b) and those using 10 yr cutoff (10AV) and 5 yr cutoff (5AV) for the PDO index are in (c). The shifts determined by STARS and that assumed by the change in PC1 and PC2 are shown by closed and open triangles, respectively in (b) and (c). The 2 shifts in 50 m depth water temperature reported in the previous studies (Tian et al. 2006, 2008, Yasunaka and Hanawa 2005, Tameishi et al. 2005) are shown by thin vertical broken lines

diminished to lower values in 2017–2018. Thus, PCA revealed 5 different forage communities used by auklets over the study period (Fig. 2b). Prey communities shifted in species composition between (1) sardine, age->1 sand lance, and Pacific saury in 1984–1987, (2) anchovy and age-0 greenling in 1992–1997, (3) mostly anchovy in 1998–2013, (4) age-0 greenling and squid in 2014–2017, and (5) age-0 and age->1 sand lance in 2018–2020 (Fig. 2a,b).

3.2. Climate and stock size

Sequential analyses of the 10 yr cutoff showed that summer and autumn PDO shifted from positive (cold) to negative (warm) in 1997–1998, spring PDO shifted in 1998–1999, and winter PDO shifted in 2007–2008, and then spring to autumn PDO shifted from negative to positive in 2013–2014 and winter PDO in 2014–2015 (Fig. 2c). Using a 5 yr cutoff, winter PDO shifted from positive to negative in 1988/1989, summer and autumn PDO in 1997/1998 and spring PDO in 1998/1999, and all shifted in 2013/2014 to positive. Last, spring and summer PDO shifted to negative in 2019/2020. In summary, shifts occurred in (1) late 1988–early 1989, (2) late 1997–early 1999, and then possibly (3) 2007–2008, along with a short-term shift in (4) 2013–2014, and possibly again in (5) 2019–2020.

The Tsushima stock of sardine decreased dramatically from 1987–1992 and remained low thereafter with a slight increase in the late 2010s (Fig. 3a,b), whereas anchovy populations remained relatively high from 1992–2008 (Fig. 3b). The stock size of age-0 greenling in northern Hokkaido has decreased since 2008 (Fig. 3c). Between-year changes in the PDO over all seasons could not linearly explain the stock size of sardine, anchovy, or age-0 greenling ($r^2 = 0.001–0.009$, $p > 0.05$).

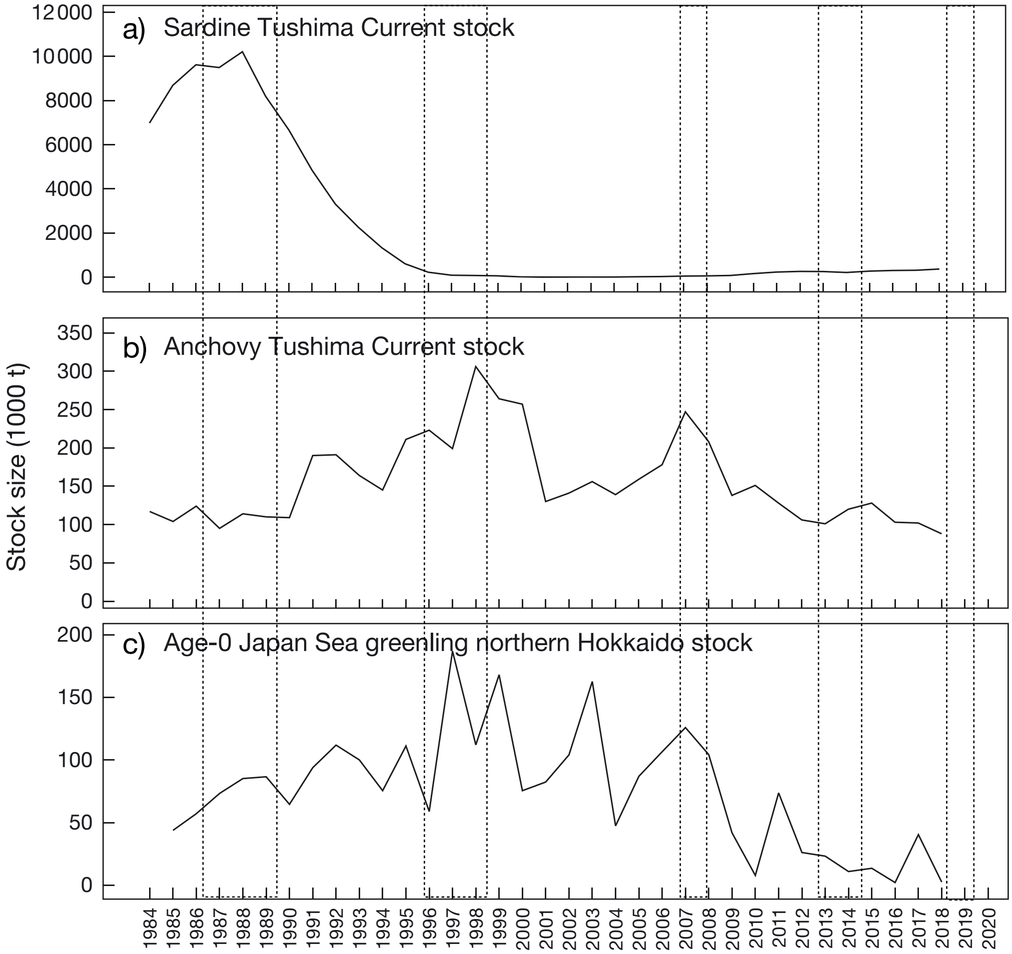

Fig. 3. Between-year changes in stock size of (a) Tsushima Warm Current sardine, (b) Tsushima Warm Current anchovy, and (c) age-0 Japan Sea greenling in the northern Japan Sea off Hokkaido from the stock assessment database of Japan Fisheries Agency (http://abchan.fra.go.jp). Shifts of the PDO using 10 yr or 5 yr cutoffs (closed triangles in Fig. 2c) and shifts in 50 m depth water temperature (thin vertical broken lines in Fig. 2) are shown by thin vertical broken lines

3.3. Prey use and fish stock

The choice of prey by auklets appeared to be partly related to changes in prey stock sizes. Between-year variations in the proportional mass of each prey species in the meal-loads was explained by stock size for sardine ($r^2 = 0.668$, $F_{1,28} = 56.259$, $p < 0.001$; Fig. 4a) and anchovy ($r^2 = 0.148$, $F_{1,28} = 4.853$, $p = 0.036$; Fig. 4b), but not for age-0 greenling ($r^2 = 0.016$, $F_{1,27} = 0.432$, $p = 0.516$; Fig. 4c); indeed, greenling consumption by auklets was highest during the years of lowest greenling abundance. The proportion of anchovy in the auklet diet was inversely correlated with sardine stock size ($r^2 = 0.253$, $F_{1,28} = 9.469$, $p = 0.005$). The use of age-0 greenling did not change with either sardine ($r^2 = 0.005$, $F_{1,28} = 0.135$, $p = 0.716$) or anchovy stock size ($r^2 = 0.041$, $F_{1,28} = 1.196$, $p = 0.283$), but appears to have peaked after 2013, when both sardine and anchovy stocks were at their lowest levels.

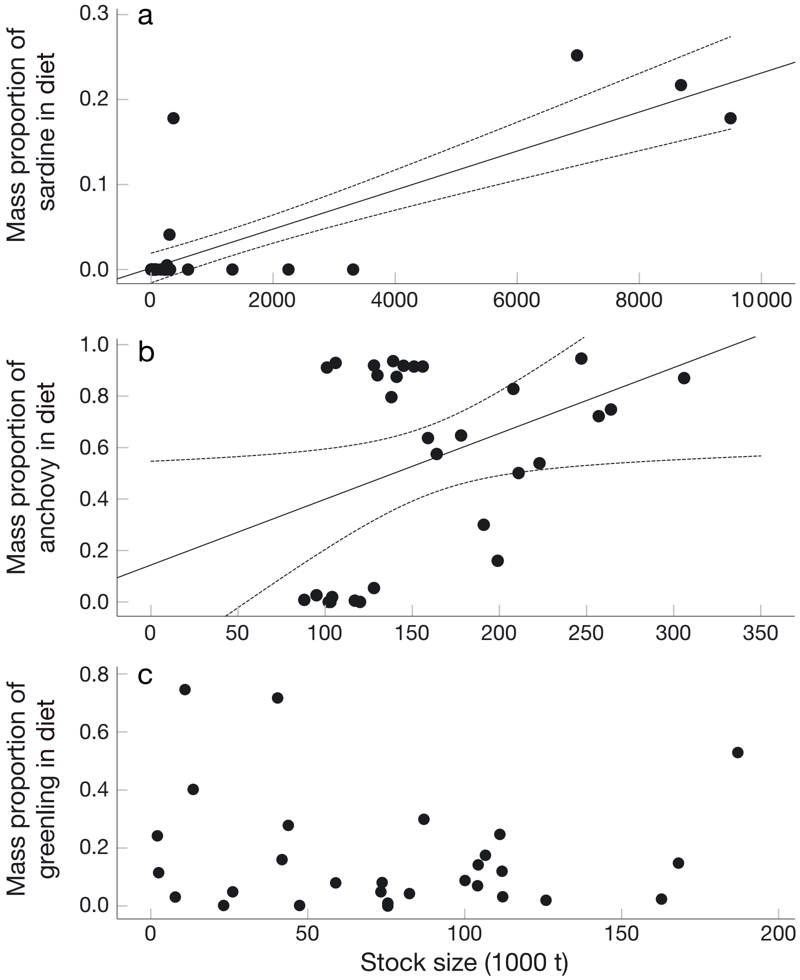

Fig. 4. Relationships between stock sizes of (a) sardine and (b) anchovy in the Tsushima Warm Current and that of (c) age-0 greenling in the northern Japan Sea off Hokkaido and the mass proportion of each prey species in the diet of the rhinoceros auklet. Linear regression line and 95% confidence interval are shown for (a) and (b) where the relationships are significant

3.4. Meal-loads and productivity

Sequential analyses of the 5 yr cutoff after 1992 showed that the mass of meal-loads (Fig. 5a) and chick growth rates (Fig. 5b) shifted to lower levels in 2013–2014. The number of fledglings produced was also lower in 2012–2013, but recovered to pre-shift levels in 2017–2018 (Fig. 5c). In years of high chick growth rates, the number of fledglings produced was greater ($r^2 = 0.370$, $p < 0.001$, $n = 32$), and fledgling mass was heavier ($r^2 = 0.525$, $p < 0.001$, $n = 29$).

Between-year variation in productivity (chick growth rate, number of fledglings, and fledgling mass) related linearly and positively with the mass of meal-loads (Fig. 6). The linear relationships were significant (Table 3). Coefficient of determinants (r^2) were greater for the effects of the mass of meal-loads than for the energy density of meal-loads (Table 3). Models including the mass or the mass and energy density were more appropriate than those incorporating energy density alone (Table 3, see also Table S3 in Supplement 2). Thus, we focused on the effects of food packaging on the mass of meal-loads.

3.5. Food packaging

The PC1 score, as an index of forage community use, was related to the annual average mass of the meal-load in a parabolic rather than linear manner (Text S3 & Table S4 in Supplement 3), indicating that rhinoceros auklets brought heavier meal-loads on average in years when the forage community was dominated by sardine and age->1 sand lance or anchovy (Fig. 7a). PC2 scores also showed a parabolic rather than linear effect (Fig. 7b, Table S4), indicating that they brought smaller meal-loads in years when the forage community was dominated by age-0 greenling and squid or Pacific saury.

This difference was because the mass of meal-loads varied between the

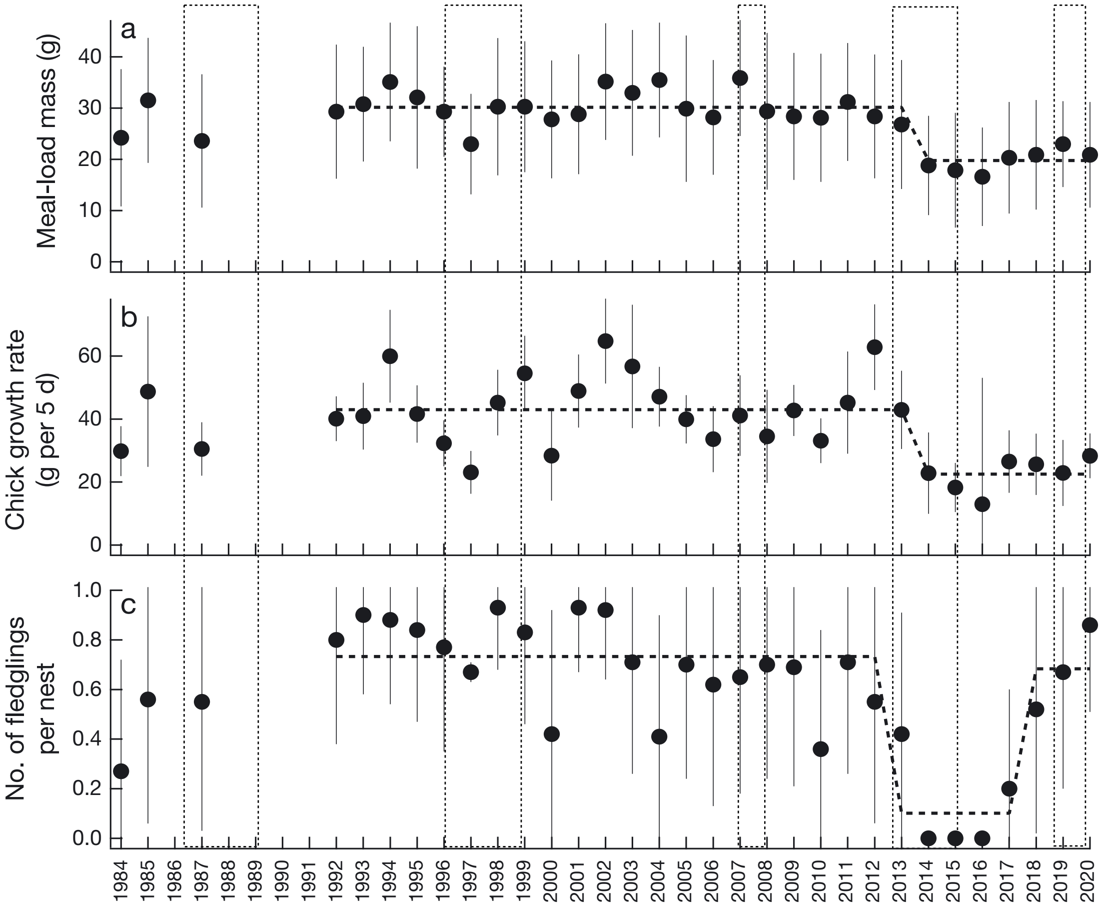

Fig. 5. Between-year changes in average (±SD) (a) mass of meal-loads, (b) growth rate of rhinoceros auklet chicks, and (c) number of fledglings per nests with chicks. Weighted average values given by STARS with 5 yr cutoff are shown by broken lines. Shifts of the PDO using 10 yr or 5 yr cutoff (closed triangles in Fig. 2c) and shifts in 50 m depth water temperature (thin vertical broken lines in Fig. 2) are shown by thin vertical broken lines

meal-loads of 9 major species and 2 multiple types ($F_{10,3015} = 78.589$, $p < 0.001$, n = 3026; Table 1). Meal-loads comprising sardine were heaviest, followed by those containing anchovy or herring, then by age->1 sand lance, age-0 greenling or Pacific saury, and finally, by those of squid, age-0 sand lance or juvenile salmon, which were smallest (Table 1, Bonferroni post hoc, $p < 0.05$; see Fig. S3 in Supplement 3). Those with a mixture of age-0 and age->1 sand lance were positioned between sardine and multiple-species meal-loads, and the latter was positioned between sardine, anchovy or age->1 sand lance, and juvenile salmon or age-0 sand lance (Fig. S3).

The difference in the mass of a meal-load by species can be explained by the trade-off between the number and size of fish. The number of fish in a meal-load varied between 1 and 59 (Table 1). Using meal-loads containing single species/types of fish with intact bodies (2203 meal-loads), relationships between the number and mean fork length of fish and the total mass of meal-loads were analyzed. When rhinoceros auklets brought back larger numbers of fish, the average fish size in a meal-load was smaller for all species/types (Table S5, Fig. S4 in Supplement 3). Further, in meal-loads composed of either anchovy, age-0 greenling, or age-0 sand lance (84 % of single-species meal-loads; Table 1), the number of fish showed a parabolic relationship with mass (Fig. 8a,b,c, Tables 4 & S6 in Supplement 3). Using these parabolic equations (Table 3), a specific number of fish was expected to give the maximum meal-load mass for anchovy (3.3 fish, 45.4 g; Fig. 8a), age-0 greenling (6.2 fish, 34.3 g; Fig. 8b), and age-0 sand lance (23.0 fish, 22.6 g; Fig. 8c). When the number of fish was greater, the mass of meal-loads was greater for age->1 sand lance but smaller for Pacific saury (Fig. 8e,f, Tables 4 & S6). A reversed parabolic relationship was found for herring (Fig. 8d), while no

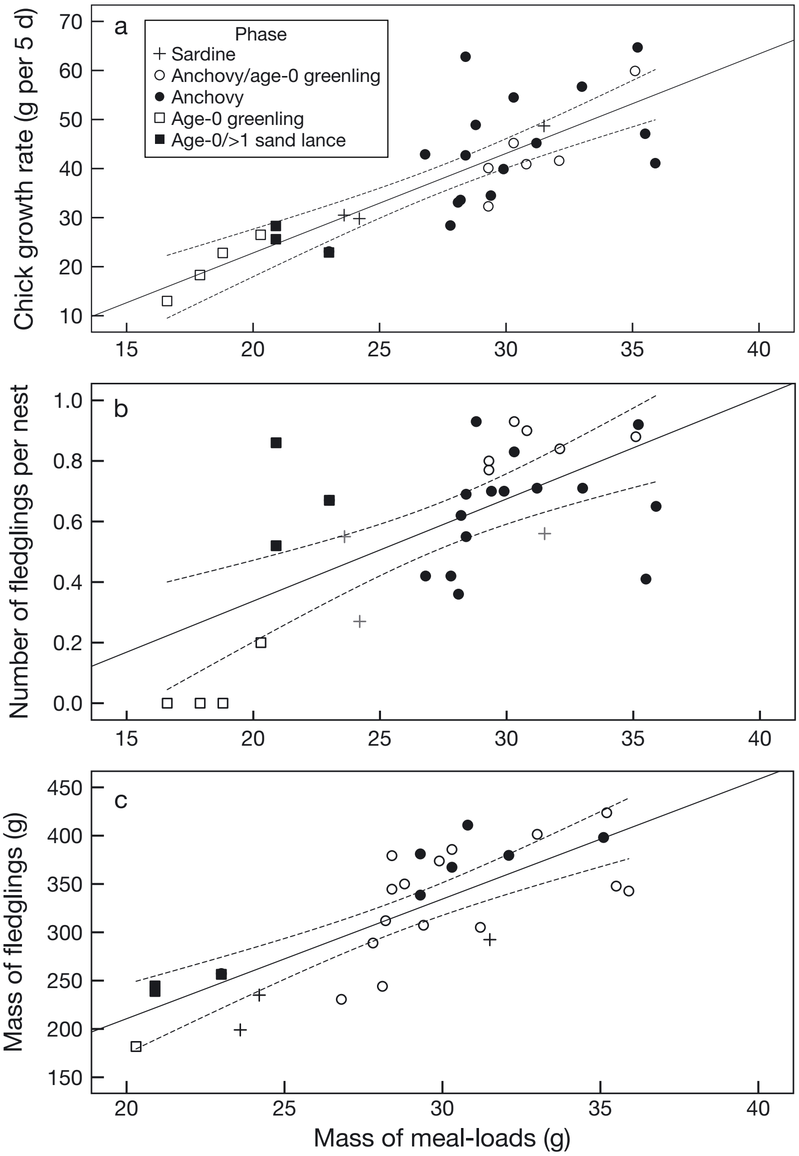

Fig. 6. Linear relationships between the annual averages of the (a) mass of rhinoceros auklet meal-loads and the growth rate of chicks, (b) number of fledglings per nest with chicks, and (c) mass of fledglings. Linear regression lines with 95% confidence intervals are shown. Sample size is 32 yr (29 yr for mass of fledglings since no chicks fledged in 2014–2016). Crosses: sardine period in 1984–1987; open circles: anchovy and age-0 greenling period in 1992–1997; closed circles: mostly anchovy period in 1998–2013; open squares: age-0 greenling and squid period in 2014–2017; closed squares: age-0 and age->1 sand lance period in 2018–2020 (Fig. 2a,b). See Table 4 for regression equation and statistics

clear relationships were found for juvenile salmon, sardine, and squids (Fig. 8g,h,i).

4. DISCUSSION

Our long-term study showed that (1) prey switching coincided with the timing of oceanic climate shifts demarcated by changes in water temperature associated with the PDO and (2) prey switching resulted in food packaging that affected various aspects of the Teuri Island rhinoceros auklet's breeding productivity

4.1. Climate change and prey switching

A shift in the PDO from cold to warm phase occurred in late 1988 to early 1989 (Fig. 2c) and again more dramatically in late 1997 to early 1999. These shifts roughly coincided with the seawater temperature in winter and spring at 50 m depth off western Japan Sea shifting to warmer levels (1986–1989; Tian et al. 2006, 2008) and further warming in the summer and autumn (1996–1998 or 1999; Yasunaka & Hanawa 2005, Tameishi et al. 2005, Tian et al. 2006, 2008), respectively. Note that this relationship between PDO and water temperatures is opposite that observed in the NE Pacific, where negative PDO values are associated with warmer water temperatures (Newman et al. 2016). Thus, prey switching by rhinoceros auklets coinciding with 1986–1989 and 1996–1999 shifts of PDO/seawater temperature and can be explained by the change in the forage fish community.

Japanese sardine and Japanese anchovy are alternately abundant in the cold and warm phases, respectively, in the Japan Sea (Tian et al. 2008). The same relationships are observed on the Pacific side of Japan, where the range of suitable water temperatures for spawning and larval survival is lower for Japanese sardine than Japanese anchovy (Takasuka et al. 2008). Thus, climate-induced shifts in the forage fish community (i.e. regime shifts) rather than linear effects of climate indices and SST affected the prey switching and diet of the seabirds (e.g. Anderson & Piatt 1999). The stock size of sardine and anchovy explained the importance by mass of these prey species in the diet. This is presumably because, with an increase in stock size, the distribution of these spe-

Table 3. Linear effects of the annual average of the mass (BLM; g) and energy density (EDN; kJ g^{-1}) of meal-loads on rhinoceros auklet chick growth rate (g per 5 d), number of fledglings per nest with chicks (no. $nest^{-1}$), and mass of fledglings (g). Coefficients of determination (r^2) and significance level (p) are shown. No apparent curvilinear effects were observed (Fig. 6). Sample size: 32 yr for chick growth rate and number of fledglings; 29 yr for mass of fledglings, as no chicks fledged in the study plots in 3 yr. To determine importance of factors, model selection was performed based on Akaike's information criterion adjusted for small sample size (AICc) (Table S3). Better models with smaller values of AICc and those including either BLM or EDN as an explanatory factor are in **bold**. Linear effects of the energy value of a meal-load (EVU; kJ) was examined separately, as EVU was calculated as BLM × END in this study

	r^2	*F*	p	AICc
Chick growth rate (CG)				
CG = −17.775 + 2.029BLM	**0.665**	**62.475**	**<0.001**	**225.2**
CG = −40.193 + 13.831EDN	0.396	21.30	<0.001	244.1
CG = −3.517 + 0.263EVU	0.677	65.917	<0.001	
Number of fledglings (NF)				
NF = −0.337 + 0.034BLM	**0.408**	**22.394**	**<0.001**	**−4.1**
NF = −0.408 + 0.177EDN	0.127	5.503	0.026	8.3
NF = −0.021 + 0.04EVU	0.319	15.531	<0.001	
Mass of fledglings (FLM)				
FLM = −37.074 + 12.383BLM	**0.620**	**46.754**	**<0.001**	**304.4**
FLM = 159.594 + 24.894EDN	0.007	1.207	0.282	331.1
FLM = 96.330 + 1.327EVU	0.416	20.943	<0.001	

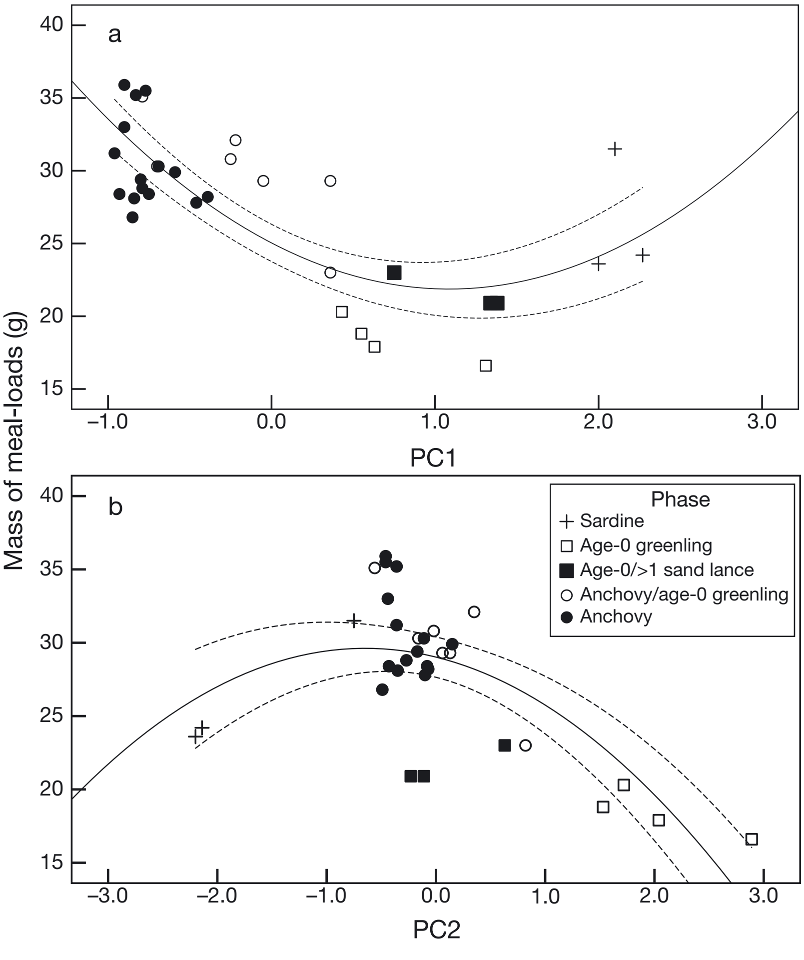

Fig. 7. Parabolic relationships between the mass of rhinoceros auklet meal-loads and the diet composition indexed by the score of the (a) first axis of principal component (PC1) of the mass composition of prey species and (b) that of the second axis (PC2). Parabolic regression lines with 95% confidence intervals are shown. Annual average values of each year are used (n = 32 yr). Prey species with positive and negative PC loadings are shown (see Table 2). See Fig. 6 for symbols

cies expands into the foraging range of the birds, making them more accessible as prey. Expansion of sardine to the north with the increase of the Tsushima stock in the 1980s (Muko et al. 2018) made this species available to rhinoceros auklets at Teuri Island during the cold phase of the PDO. Similarly, anchovy reached the foraging range of rhinoceros auklets at Teuri Island with the species' expansion during the warm phase in the 1990s (Watanabe & Takahashi 2007).

Relationships between climate and the third and fourth prey switch after 2013 are unclear. Age-0 greenling are found in relatively low SSTs (8–13°C) in our region (Ishigaki & Nakamichi 1958). The prey switch from anchovy to age-0 greenling in 2013–2014 coincided with the PDO shift in 2013–2014 (Fig. 2b,c). This negative to positive PDO shift, which is also suggested in Kuroda et al. (2020), implies the start of a cold phase, but we have no evidence of a decrease in SSTs in 2013–2014 (Fig. S5). After 2014, populations of anchovy were small and sardines were negligible (Fig. 3a,b). Considering the ecology of anchovy, which expands and contracts in distribution according to stock size (Watanabe & Takahashi 2007, Hayashi et al. 2019), the distribution of this species might not have extended into the foraging range of rhinoceros auklets at Teuri Island during the recent low stock size period. Therefore, age-0 greenling might have been the only available forage fish even if its stock size was smaller than before (Fig. 3c). In the

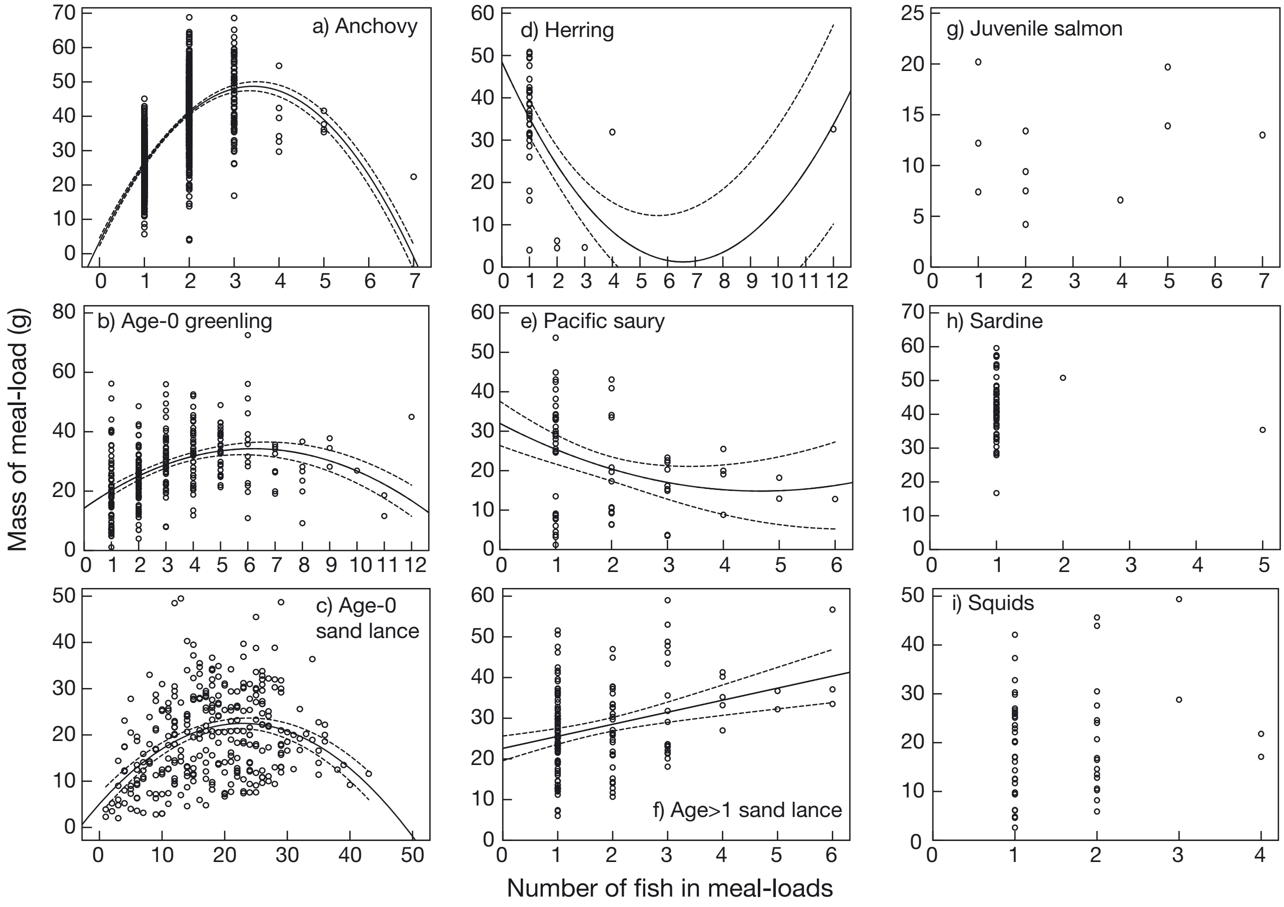

Fig. 8. Parabolic or linear relationships between the number of prey and the mass of rhinoceros auklet meal-loads consisting of (a) anchovy, (b) age-0 greenling, (c) age-0 sand lance, (d) herring, (e) Pacific saury, (f) age->1 sand lance, (g) juvenile salmon, (h) sardine and (i) squids. Significant regression lines and 95% confidence intervals are shown. No significant effects were observed for juvenile salmon, sardine, and squids. See Table 4 for regression equation and statistics

Table 4. Linear and parabolic regressions of the number of fish provided by rhinoceros auklets in meal-loads (N) on the mass of meal-loads (M). Meal-loads including only fish with intact bodies were used. Model selection was performed using AIC (see Table S6). Better models giving smaller values of AICc in the linear or parabolic equations and those giving significant ($p < 0.05$) coefficients of determination (r^2) are in **bold**

Species (sample size)	Effects	Equations	r^2	p	AICc
Anchovy (1230)	**Parabolic**	**$M = 3.455 + 26.488N - 3.875N^2$**	**0.503**	**<0.001**	**8643.0**
	Linear	$M = 17.140 + 10.560N$	0.390	<0.001	8897.2
Age-0 greenling (284)	**Parabolic**	**$M = 14.247 + 6.462N - 0.521N^2$**	**0.188**	**<0.001**	**2138.1**
	Linear	$M = 21.811 + 1.718N$	0.099	<0.001	2165.7
Age-0 sand lance (315)	**Parabolic**	**$M = 5.079 + 1.522N - 0.033N^2$**	**0.152**	**<0.001**	**2265.6**
	Linear	$M = 14.392 + 0.276N$	0.060	<0.001	2296.1
Age->1 sand lance (148)	**Linear**	**$M = 22.592 + 2.960N$**	**0.097**	**<0.001**	**1107.9**
	Parabolic	$M = 23.899 + 1.602N + 0.247N^2$	0.099	0.001	1109.7
Sardine (62)	Linear	$M = 43.118 - 1.054N$	0.004	0.61	443.7
	Parabolic	$M = 26.088 + 19.352N - 3.498N^2$	0.029	0.423	444.5
Pacific saury (66)	**Linear**	**$M = 27.874 - 3.064N$**	**0.083**	**0.019**	**523.8**
	Parabolic	$M = 31.998 - 7.369N + 0.791N^2$	0.094	0.045	525.3
Herring (34)	**Parabolic**	**$M = 48.506 - 14.416N + 1.098N^2$**	**0.210**	**0.026**	**272.7**
	Linear	$M = 34.587 - 0.963N$	0.02	0.423	277.5
Juvenile salmon (11)	Linear	$M = 9.935 + 0.569N$	0.049	0.512	75.1
	Parabolic	$M = 12.924 - 1.803N + 0.321N^2$	0.091	0.682	80.0
Squid (52)	Linear	$M = 16.589 + 2.470N$	0.029	0.23	401.0
	Parabolic	$M = 13.801 + 5.797N - 0.784N^2$	0.032	0.455	403.2

most recent few years (2017–2018), rhinoceros auklets switched prey to age-0/>1 sand lance (Fig. 2a,b). Although the 5 or 10 yr scale shifts in the PDO were not detected by STARS in this period, the PDO started to decrease and may have shifted in 2019–2020 (Fig. 2c). Catch of age-0 sand lance in our study region was around 100–1200 t before 1995 but no substantial catch occurred thereafter (Watanuki & Ito 2012). However, warmer waters may have enhanced sand lance recruitment and population size (Sydeman et al. 2017).

In summary, climate variability in the 1980s and 1990s induced a change in the availability of sardine and anchovy and hence the use of these species by rhinoceros auklets. Thus, rhinoceros auklets, as with other puffin species, can be reliable and effective indicators of the marine environment (Hatch & Sanger 1992, Bertram & Kaiser 1993, Sydeman et al. 2017). During the 2000s and 2010s, when availability of both sardine and anchovy decreased, age-0 greenling and age-0/>1 sand lance dominated the auklets' diets, but the environmental factors affecting the availability of the latter 2 prey species are unclear. This may be related to the conclusions of a recent review study, that 'some major marine fisheries resources around Japan showed decadal increases or decreases beginning in the mid-2000s, and appeared to respond to the unconventional SST changes in their early life stages' (Kuroda et al. 2020, p. 1). Anomalously high SST in the NE Pacific (heat wave) was associated with El Niño and a high PDO index in 2013–2016 (Leising et al. 2015, Tseng et al. 2017), and these conditions impacted seabirds (Piatt et al. 2020). In the same period (2013–2016), rhinoceros auklets were impacted (Fig. 5) but the SST in the northern Japan Sea did not show any apparent increase or decrease (Text S4 & Fig. S5 in Supplement 4).

4.2. Prey size-number trade-off

Shifts in the prey community available to rhinoceros auklets affected their productivity because (1) most of the meal-loads were composed of a single species, (2) the mass of meal-loads varied with prey species and was low for multi-species loads, and (3) the mass of meal-loads was the key determinant of chick productivity between climate phases.

Between-year differences in the energy density of prey species has been demonstrated to explain reproductive success in other seabirds (Litzow et al. 2002, Wanless et al. 2005, Grémillet et al. 2008). Energy density is lower in juvenile salmon, squids, age-0 sand lance, and age-0 greenling (3–5 kJ g^{-1}) than in sardine, anchovy, and age->1 sand lance (5–10 kJ g^{-1}; Table S1). Thus, the energy density of the prey was higher on average in either the cold or warm phases of the PDO, when rhinoceros auklets fed on dominant sardine and anchovy, than later when they fed on age-0 greenling and age-0 sand lance. However, in this study, we found that mass was more important to productivity than energy density. Presumably, this is because the variation in energy density of average meal-loads between years observed in this study (4.29–6.60 kJ g^{-1} or 154 %) was smaller than that of the average mass (16.6–35.9 g or 216 %) (Table S2). The same is true for tufted puffins *Fratercula cirrhata*, where prey species range from lean juvenile walleye pollock *Theragra chalcogramma* to fatty capelin *Mallotus villosus* and myctophids; the puffins can successfully raise their chicks when providing them walleye pollock because they bring larger packages (Schoen et al. 2018).

Rhinoceros auklets brought back heavier meal-loads in years when they fed mainly sardine or anchovy than in years when their diet was more diverse and included age-0 greenling, squids, and age-0 sand lance (Fig. 4a,b). In great crested terns *Thalasseus bergii*, the size of anchovy in meal-loads was smaller when the parents brought multiple individuals (Gaglio et al. 2018). We found similar relationships in rhinoceros auklets but with large species differences (Table S5, Fig. S4 in Supplement 3). With these species-specific size–number relationships, we expected that the maximum mass of a meal-load would vary between species. The expected maximum mass of 3 major prey species (Fig. 5) was anchovy > age-0 greenling > age-0 sand lance. This order was the same as found in the average mass of meal-loads (Table 1). Parents may change the number of fish brought back depending on species to achieve maximum delivery mass. The mechanisms of this species-specific size–number tradeoff is unclear.

Other species of seabirds show different food packaging behaviors. Murres *Uria* spp., guillemots *Cepphus* spp., and terns bring single prey items for their chicks, so the size and energy density of individually selected fish always has a direct effect on production, as shown in the North and Baltic seas (Wanless et al. 2005, Österblom et al. 2006). Parents of murres *U. aalge* can compensate for smaller fish by increasing feeding rates (Kadin et al. 2016). Many seabirds, including penguins, albatrosses, shearwaters, petrels, cormorants, and gulls, bring food in their stomachs, so these species may show different responses. We suggest that food packaging is one of the factors influencing the reproductive responses of central-place foraging seabirds to changes in the fish community.

Parents of rhinoceros auklets bring meal-loads in the evening and do not forage at sea during the night (Kuroki et al. 2003). Because of this behavior, they are only able to feed chicks a maximum of once per night (Takahashi et al. 1999). Therefore, the mass of the meal-loads is key to their chicks' growth and survival. In our study, chick growth rates were greater in years when the adults brought heavier meal-loads, and the number and mass of fledglings was greater in years with higher chick growth rates, as reported in the previous study of this species on the same island (Deguchi et al. 2004b). In an experimental study, rhinoceros auklet chicks that received heavier meals grew faster and fledged younger and heavier with more fat (Takenaka et al. 2005). In Manx shearwaters *Puffinus puffinus* and tufted puffins *Fratercula cirrhata*, post-fledgling survival is greater and age at first return to the colony is younger for fledglings having greater body mass (Perrins et al. 1973, Morrison et al. 2009). Therefore, the decadal-scale changes in fledging success and fledgling mass associated with the change in the forage fish community we found in this study may ultimately influence the population of rhinoceros auklets.

4.3. Conclusions

Teuri Island rhinoceros auklets switched prey species following changes in forage fish communities that were partly affected by ocean climate. The birds exhibited highest productivity when they provided anchovy to their chicks. Species-specific tradeoffs between the composition, size, and number of prey items in meal-loads (i.e. 'food packaging') explained the linkage between food resources in the environment and the auklets' breeding productivity. The manner in which food is packaged for offspring could be a new response to climate change impacts on marine ecosystems and effects on central-place foraging predators.

Acknowledgements. We thank A. Kato, M. Kuroki, Y. Niizuma, A. Takahashi, K. Iseki, M. Takenaka, T. Kagami, T. Deguchi, K. Matsumoto, D. Ochi, Y. Manabe, H. Nomura, Y. Tanaka, M. Shikata, T. Tanaka, A. Kubo, N. Sato, A. Umeyama, S. Hashimoto, U. Shimabukuro, T. Kitagawa, N. Nagatani, R. Sato, and E. Iida for their field assistance, and M. Aotsuka, R. Yorozuya, and Y. Kusakabe for their hospitality on Teuri Island. A. Takahashi gave invaluable comments on a draft of the manuscript. The fieldwork was carried out under permits from the Agency for Cultural Affairs and the Ministry of the Environment. This study was supported by JSPS Grants-in-Aid for Scientific Research (#16108002 to M. Kishi, #17370007 to Y.W.), by the 21st Century Centers of Excellence (COE) program 'Neo-Science of Natural History', led by H. Okada, and 2017 Summer Institute Program, Hokkaido University (to W.S.). Two anonymous reviewers and J. Piatt gave useful and helpful comments on the manuscript.

LITERATURE CITED

Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels. Nature 347:753–755

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. Nature 411:183–186

Bertram DF, Kaiser GW (1993) Rhinoceros auklets (*Cerorhinca monocerata*) nestling diet may gauge Pacific sand lance (*Ammodytes hexapterus*) recruitment. Can J Fish Aquat Sci 74:1906–1915

Bertram DF, Harfenist A, Hedd A (2009) Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations. Mar Ecol Prog Ser 393:199–210

Borstad G, Crawford W, Hipfner JM, Thomson R, Hyatt K (2011) Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. Mar Ecol Prog Ser 424:285–302

Boyd IL, Murray AWA (2001) Monitoring a marine ecosystem using responses of upper trophic level predators. J Anim Ecol 70:747–760

Burger AE (1991) Maximum dive depths and underwater foraging in alcids and penguins. Can Wildl Serv Occas Pap 68:9–15

Chavez FP, Ryan J, Lluch-Cota SE, Niquen MC (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217–221

Chiba S, Tadokoro K, Sugisaki H, Saino T (2006) Effects of decadal climate change on zooplankton over the last 50 years in the western subarctic North Pacific. Glob Change Biol 12:907–920

Chiba S, Batten S, Sasaoka K, Sasai Y, Sugisaki H (2012) Influence of the Pacific Decadal Oscillation on phytoplankton phenology and community structure in the western North Pacific. Geophys Res Lett 39:L15603

Crawford RJM, Dyer BM (1995) Responses by four seabird species to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. Ibis 137: 329–339

Cunningham JT, Elliott KH, Cottenie K, Hatch SA, Jacobs SR (2018) Individual foraging location, but not dietary, specialization: implications for rhinoceros auklets as samplers of forage fish. Mar Ecol Prog Ser 605:225–240

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T and others (2011) Global seabird response to forage fish depletion? One-third for the birds. Science 334:1703–1706

Deguchi T, Watanuki Y, Niizuma Y, Nakata A (2004a) Interannual variations of the occurrence of epipelagic fish in the diets of the seabirds breeding on Teuri Island, northern Hokkaido, Japan. Prog Oceanogr 61:267–275

Deguchi T, Takahashi A, Watanuki Y (2004b) Proximate factors determining fledging age and mass in rhinoceros auklets: a study of within- and inter-year variations. Auk 121:452–462

Furness RW (2007) Responses of seabirds to depletion of food fish stocks. J Ornithol 148:S247–S252

Furness RW, Tasker ML (2000) Seabird–fishery interactions: quantifying the sensitivity of seabirds to reduction in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202:253–264

Gaglio D, Cook TR, Sherley RB, Ryan PG (2018) How many can you catch? Factors influencing the occurrence of multi-prey loading in provisioning greater crested terns. Ostrich 89:145–149

Gaston AJ, Jones IL (1998) The auks. Oxford University Press, Oxford

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan P (2008) A junk-food hypothesis for gannets feeding on fishery waste. Proc R Soc B 275: 1149–1156

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1–14

Hayashi A, Yasuda T, Kuroda H, Takahashi M (2018) Stock assessment and evaluation for Japanese anchovy Tsushima Warm Current subpopulation (fiscal year 2017). In: Fisheries Agency, Fisheries Research and Education Agency of Japan (eds) Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2017/2018), p 884–912. http://abchan.fra.go.jp/ (accessed 9 May 2019) (in Japanese)

Hayashi A, Goto T, Takahashi M, Watanabe Y (2019) How Japanese anchovy spawn in northern waters: start with surface warming and end with day length shortening. Ichthyol Res 66:79–87

Hedd A, Bertram DF, Ryder JL, Jones IL (2006) Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey. Mar Ecol Prog Ser 309:263–278

Hipfner JM, Galbraith M, Bertram DF, Green DJ (2020) Basin-scale oceanographic processes, zooplankton community structure, and diet and reproduction of a sentinel North Pacific seabird over a 22-year period. Prog Oceanogr 182:102290

Ishigaki T, Nakamichi Y (1958) A study of Japan Sea greenling (IV), behaviour, diet and habitat. Hokusuishi-Geppou 15:4–13 (in Japanese)

Kadin M, Olsson O, Hentani-Sundberg J, Ehrning EW, Blenckner T (2016) Common guillemot *Uria aalge* parents adjust provisioning rates to compensate for low food quality. Ibis 158:167–178

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

Kuroda H, Saito T, Kaga T, Takasuka A, Kamimura Y, Furuichi S, Nakanowatari T (2020) Unconventional sea surface temperature regime around Japan in the 2000s–2010s: potential influences on major fisheries resources. Front Mar Sci 7:574904

Kuroki M, Kato A, Watanuki Y, Niizuma Y, Takahashi A, Naito Y (2003) Diving behavior of an epipelagically-feeding alcid, the rhinoceros auklets (*Cerorhinca monocerata*). Can J Zool 81:1249–1256

Kuwae M, Yamamoto M, Sagawa T, Ikehara K and others (2017) Multidecadal, centennial, and millennial variability in sardine and anchovy abundances in the western North Pacific and climate–fish linkages during the late Holocene. Prog Oceanogr 159:86–98

Lee DE, Nur N, Sydeman WJ (2007) Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. J Anim Ecol 76:337–347

Leising AW, Schroeder ID, Bograd SJ, Abell J and others (2015) State of the California Current 2014–15: impacts of the warm-water 'blob'. CCOFI Rep 56:31–68

Litzow MA, Piatt JF, Prichard AK, Robby D (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286–295

Mantua NJ, Hare SR (2002) The Pacific Decadal Oscillation. J Oceanogr 58:35–44

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78: 1069–1079

Minobe S (1997) A 50–70 year climatic oscillation over the North Pacific and North America. Geophys Res Lett 24: 683–686

Montevecchi WA, Birt VL, Cairns DK (1988) Dietary changes of seabirds associated with local fisheries failures. Biol Oceanogr 5:153–161

Morita S, Yamashita Y, Hamatsu T, Yamashita N (2018) Stock assessment and evaluation for arabesque greenling Northern Japan Sea subpopulation (fiscal year 2017). In: Fisheries Agency, Fisheries Research and Education Agency of Japan (eds) Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2017/2018), p 884–912. http://abchan.fra.go.jp/ (accessed 9 May 2019) (in Japanese)

Morrison KW, Hipfner JM, Gjerdrum C, Green DJ (2009) Wing length and mass at fledging predict local juvenile survival and age at first return in tufted puffins. Condor 111:433–441

Muko S, Ohshimo S, Kurota H, Yasuda T, Fukuwaka MA (2018) Long-term change in the distribution of Japanese sardine in the Sea of Japan during population fluctuations. Mar Ecol Prog Ser 593:141–154

Nagasawa K, Torisawa M (1991) Fish and marine invertebrates of Hokkaido: biology and fisheries. Kita-nihon Kaiyo Center, Sapporo (In Japanese)

Nakayama S, Takasuka A, Ichinokawa M, Okamura H (2018) Climate change and interspecific interactions drive species alternations between anchovy and sardine in the western North Pacific: detection of causality by convergent cross mapping. Fish Oceanogr 27:312–322

Newman M, Alexander MA, Ault TR, Cobb KN and others (2016) The Pacific Decadal Oscillation, revisited. J Clim 29:4399–4427

Ohshimo S, Tanaka H, Hiyama Y (2009) Long-term stock assessment and growth changes of the Japanese sardine (*Sardinops melanostictus*) in the Sea of Japan and East China Sea from 1953 to 2006. Fish Oceanogr 18:346–358

Österblom H, Casini M, Olsson O, Bignert A (2006) Fish, seabird and trophic cascades in the Baltic Sea. Mar Ecol Prog Ser 323:233–238

Perrins CM, Harris MP, Britton CK (1973) Survival of Manx shearwaters *Puffinus puffinus.* Ibis 115:535–548

Piatt JF, Harding AMA, Shultz M, Speckman SG, van Pelt TI, Drew GS, Kettle AB (2007) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234

Piatt JF, Parrish JK, Renner HM, Schoen SK and others (2020) Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave 2014–2016. PLOS ONE 15:e0226087

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. Geophys Res Lett 31:L09204

Schneider N, Cornuelle BD (2005) The forcing of the Pacific Decadal Oscillation. J Clim 18:4355–4373

Schoen SK, Piatt JF, Arimitsu ML, Heflin BM and others (2018) Avian predator buffers against variability in marine habitats with flexible foraging behavior. Mar Biol 165:47

Sydeman WJ, Poloczanska E, Reed TE, Thompson SA (2015) Climate change and marine vertebrates. Science 350: 772–777

Sydeman WJ, Piatt JF, Thompson SA, Garcia-Reyes M and others (2017) Puffins reveal contrasting relationships between forage fish and ocean climate in the North Pacific. Fish Oceanogr 26:379–395

Takahashi A, Kuroki M, Niizuma Y, Watanuki Y (1999) Parental food provisioning is unrelated to manipulated offspring food demand in a nocturnal single-provisioning alcid, the rhinoceros auklet. J Avian Biol 30: 486–490

Takahashi A, Kuroki A, Niizuma Y, Kato A, Saitoh S, Watanuki Y (2001) Importance of the Japanese anchovy (*Engraulis japonicus*) to breeding rhinoceros auklets (*Cerorhinca monocerata*) on Teuri Island, Sea of Japan. Mar Biol 139:361–371

Takasuka A, Oozeki Y, Kubota H, Lluch-Cota SE (2008) Contrasting spawning temperature optima: Why are anchovy and sardine regime shifts synchronous across the North Pacific? Prog Oceanogr 77:225–232

Takenaka M, Niizuma Y, Watanuki Y (2005) Resource allocation in fledglings of the rhinoceros auklet under different feeding conditions: an experiment manipulating meal size and frequency. Can J Zool 83:1476–1485

Tameishi H, Fujii S, Maebayashi A (2005) Relationship between regime-shifts of SST and fisheries condition (Spanish mackerel and yellowtail) in Japan Sea. Bull Coast Oceanogr 42:125–131 (in Japanese)

Thayer JA, Sydeman WJ (2007) Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. Mar Ecol Prog Ser 329:253–265

Thayer JA, Bertram DF, Hatch SA, Hipfner MJ, Slater L, Sydeman WJ, Watanuki Y (2008) Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. Can J Fish Aquat Sci 65:1610–1622

Tian Y, Kidokoro H, Watanabe T (2006) Long-term changes in the fish community structure from the Tsushima warm current region of the Japan/East Sea with an emphasis on the impacts of fishing and climate regime shift over the last four decades. Prog Oceanogr 68:217–237

Tian Y, Kidokoro H, Watanabe T, Iguchi N (2008) The late 1980s regime shift in the ecosystem of Tsushima warm current in the Japan/East Sea: evidence from historical data and possible mechanisms. Prog Oceanogr 77: 127–145

Tseng YH, Ding R, Huang Xm (2017) The warm Blob in the northeast Pacific — the bridge leading to the 2015/16 El Niño. Environ Res Lett 12:054019

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 294:1–8

Watanabe Y, Takahashi M (2007) Ecology of sardine/anchovy and regime shift. In: Kawasaki T, Hanawa K, Taniguchi A, Nihira A (eds) Regime shift: climate change and management of biological resources. Seizando Shoten, Tokyo, p 141–155 (in Japanese)

Watanuki Y, Ito M (2012) Climatic effects on breeding seabirds of the northern Japan Sea. Mar Ecol Prog Ser 454: 183–196

Watanuki Y, Ito M, Deguchi T, Minobe S (2009) Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. Mar Ecol Prog Ser 393:259–271

Yasuda T, Kuroda H, Hayashi A, Yoda M, Suzuki K, Takahashi M (2018) Stock assessment and evaluation for Japanese sardine Tsushima Warm Current subpopulation (fiscal year 2017). In: Fisheries Agency, Fisheries Research and Education Agency of Japan (eds) Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2017/2018), p 57–95. http://abchan.fra.go.jp/ (accessed 9 May 2019) (in Japanese)

Yasunaka S, Hanawa K (2005) Regime shift in the global sea-surface temperatures: its relation to El Niño–Southern Oscillation events and dominant variation modes. Int J Climatol 25:913–930

Editorial responsibility: Kyle Elliott,
Sainte-Anne-de-Bellevue, Québec, Canada
Reviewed by: 2 anonymous referees

Submitted: June 6, 2021
Accepted: October 21, 2021
Proofs received from author(s): January 25, 2022