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4   Seabird reproductive responses to changing climate and prey communities

5   are mediated by prey packaging

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17

18   **Abstract** Climatic factors drives changes in forage fish communities and may

19   influence the productivity of piscivorous predators, but specific mechanisms of

20   response remain poorly known. We studied the seabird, Rhinoceros Auklet *Cerorhinca*

21   *monocerata*, breeding at Teuri Island, Japan, in the western North Pacific between

22   1984 and 2020. We tested the hypothesis that climate-mediated prey-switching affects

23   "food packaging" (i.e. the way energy is brought to dependent offspring) and breeding

24   success by quantifying relationships between climate, prey energy density, amount of

25   food delivered, and the growth and survival of chicks. Prey composition switched four

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 size of 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 this warm phases.This study shows that climate affects reproduction of seabirds 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, switch of prey

1. INTRODUCTION

2 Climate forcing of marine environments chages "bottom-up" trophic effects that may

3 influence the reproduction and population dynamics of top predators through the

4 changes of forage fish communities (Aebischer et al.1990, Barbraud & Weimerskirch

5 2001, Boyd & Murray 2001, Sydeman et al. 2015). In responding to changes in forage

6 fish communities, "central-place" foraging top predators that feed at sea but provide

7 food for offspring on land may alter their prey use to match prey availability, with

8 potential effects on how food is delivered (i.e. "food packaging") and reproductive

9 success (Piatt et al. 2007, Furness 2007, Cury et al. 2011). They change prey species

10 when forage community structure shifts (Montevecchi et al. 1988, Crawford & Dyer

11 1995, Furness & Tasker 2000). But the responses to the shifts in forage communities

12 are not simple as different prey species have different sizes and energetic values, and

13 may be more or less difficult to procure (Anderson & Piatt 1999).

14 Rhinoceros Auklets *Cerorhinca monocerata* are piscivorous diving seabirds of the

15 North Pacific, and despite the name are actually in the puffin tribe of the Alcidae

16 (Gaston & Jones 1998). They dive down to 65 m depth, and bring a variety of prey,

17 such as sardine *Sardinops* spp., anchovy *Engraulis* spp., sandlance *Ammodytes* spp.,

18 capelin *Mallotus* sp., and squid to colonies to provision chicks in nest burrows (Burger

19 1991, Gaston and Jones 1998, Kuroki et al. 2003, Thayer et al. 2008, Sydeman et al.

20 2017, Cunningham et al. 2018). They switch prey use in relation to interannual

21 changes of forage fish communities, and these shifts result in large variation in chick

22 growth and fledging success (Takahashi et al. 2001, Hedd et al. 2006, Thayer &

23 Sydeman 2007, Borstad et al. 2011). Rhinoceros Auklet parents bring fish in their bills

24 (meal-loads or "food package") usually during evening hours of darkness once per day

1 (Takahashi et al. 1999). Between-year variation in the energetic value (energy density

2 multiplied by the mass) of meal-loads is thought to be a main factor determining chick

3 growth and production (Watanuki et al. 2009), but this idea has not been thoroughly

4 investigated. Like other puffins, Rhinoceros Auklets bring multiple prey in each

5 meal-load. Therefore, they can compensate for potentially small (large) prey size by

6 bringing more (less) fish (see Fig. 1 a,b), and may therefore have the ability to mitigate

7 the effects of change in prey energy density by increasing mass of meal-load.

8   In the North Pacific, warm and cold phases of the Pacific Decadal

9 Oscillation (PDO) cycle at decadal temporal scales (Mantua et al. 1997, Minobe 1997).

10 The PDO index is the first principal component of sea surface temperature north of

11 20 °N latitude after de-trending and is associated with variability of the Aleutian low

12 and El Nino-Southern Oscillation (ENSO) (Schneider & Cornuelle 2005). Positive

13 PDO in NE Pacific means warmer water, but it means colder water in NW Pacific

14 (Mantua & Hare 2002), so biological effects are expected to be quite different between

15 NW and NE Pacific. Populations of some forage fish track these phase shifts of PDO,

16 SST and other factors in NW and NE Pacific (e.g., cycle of sardines *Sardinops* spp.

17 and anchovies *Engraulis* spp., Chavez et al. 2003, Takasuka et al. 2008). Responses of

18 piscivorous predators to changes of PDO, ENSO and SST have been studied in NE

19 Pacific (Hedd et all 2006, Lee et al. 2007, Bertram et al. 2009, Hipfner et al. 2020),

20 while little studies have been carried out in NW Pacific.

21   In northern Japan Sea, NW Pacific, changes in forage fish community have

22 been associated with climatic shifts. A shift from a cold to warm phase was observed in

23 1988/1989; correspondingly, there was collapse of Japanese sardine *S. melanostictus*

24 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 sardine, sand lance *Ammodytes* spp. and Pacific saury *Cololabis saira* to 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 years (1984 --2020) of data from Teuri Island, we investigated how ocean climate drive prey use by Rhinoceros Auklets, and how prey switching affects energy acquisition and chick production.

Specifically, we test the hypothesis that both energy density and 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, northern Japan Sea. First, we applied principal component analyses to diet composition to characterize the use of different forage community members use. We also explored whether timing in the change of prey use co-occurred with recent quasi-decadal scale climate shifts indicated by PDO index and seawater temperature. Second, we examined how between-year variation in chick growth and fledging success depended on the energy density (KJ/g) 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 first in a seabird species that bring multiple fish in a meal-load.

2. STUDY AREA & METHODS

2.1. Seabird data

Field work was carried out at Teuri Island (44°25'N, 141°19'E), 28 km off mainland of

Hokkaido, Japan, during the chick rearing periods of mid-May to early-August, 1984 to 2020 (excluding 1986, and 1988-1991 due to logistic constraints). Parents landing with fish in their bills, as 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 and for about 2 hrs along the road near Akaiwa light house (Fig. S1 in Supplement 1). Meal-loads were collected and placed in individual plastic bags. Samples were brought back to the laboratory where prey was identified. Prey size was measured as 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 12±6.4 (1 – 34) nights every year, mostly once per week throughout the chick rearing period, giving 8±8.1 (1 -- 73) meal-loads each night, 96±30.5 (53 -- 226) each year, and 3,067 in total during the study. The 3,067 meal-loads contained 15,486 individual fish.

We measured chick growth and fledging success (the number of fledglings per nests with chicks) at two monitoring sites. We monitored nests in site A > 50 m distant from the site used for meal-load sampling prior to 2013, and set site B (Fig. S1 in Supplement 1) in 2014 and monitored nests in A and B sites, 200 m apart, since 2014. Although differences in chick growth and fledging success were found between site A and B in 2016 and 2018 respectively, trends were similar in other years (Fig. S2 in Supplement 1). So data of two sites were combined after 2014 for analyzing between year variations. When we found the first sign of hatching (i.e parents carrying meal-loads in the evening or meal-loads on the breeding ground in the morning) by daily observation since early May, we started nest monitoring. We sampled 37±15.3 (10 – 84,

1 n=32 years) nests where eggs hatched every year. We checked nest contents of all nests

2 on the same day and every 5 days but we sometimes changed the schedule of monitoring

3 depending on the weather condition. For years with detailed records of each nest (2001 –

4 2020), average interval of nest monitoring was 4.9±0.8 days (3 – 9 days, n=260

5 intervals) and we found chicks at the first day of monitoring for 19% of 838 nests and

6 age of these chicks were estimated using wing length (Takahashi et al. 2001) and hatch

7 date was back calculated. For others, we assumed that chicks had hatched on the middle

8 day between the nest checks when we saw eggs last time and when we saw chicks first

9 time. All chicks were weighed (± 5g) using a Pesola spring balance at each day of nest

10 check. The slope of the linear regression of the mass on age (g/ 5 days) between 5- and

11 20-day-age for those giving r > 0.9 was defined as the growth rate of chicks (including

12 ones that may have died). This would exclude the non-linear growth periods after

13 hatching and during weight loss before fledging. We tested if mass or energy density of

14 meal-loads affect annual average of the slopes (chick growth rate) using regression

15 analyses. We assumed that the chicks fledged when they disappeared from nests after

16 40 days age (Takahashi et al. 2001) and defined the mass of the last day before

17 disappearance as the mass of fledgling.

18

19 **2.2. Forage community use and energetic value**

20 Sand lance was separated into age-0 ($\leqq$110 mm in fork-length, Bertram & Kaiser

21 1993) and age- >1 ($>$110 mm) classes since the energy content of these age classes

22 were quite different (Table S1 in Supplement 2). All Japan Sea Greenling

23 *Pleurogrammus azonus* were age-0 class since the fork-length were smaller than 180

24 mm (Nagasawa & Torisawa 1991). All salmon *Onchorhynchus* sp., except one

1   *Onchorhynchus masou*, were smaller than 109 mm and categorized as juvenile.

2   The mass composition of each of 9 major prey species/types (Table 1) in each

3   year was calculated, excluding other prey species and prey which were not identified to

4   species. To index forage fish prey composition each year, we applied principal

5   component analyses on mass composition of these major prey species/types, and used

6   the first (PC1) and second (PC2) principal components as indices of forage community

7   use. The energy value of average meal-load in each year was estimated using median

8   values of energy densities for each prey species acquired from the literature (Table S1

9   in Supplement 2), average mass of meal-load and the mass composition of nine major

10   prey species/types in each year.

11

12   **2.3. Climate change and stock size**

13   To assess climate fluctuations, we used winter (December to February), spring (March

14   to May), summer (June to August), and autumn (September to November) Pacific

15   Decadal Oscillation (PDO) indices averaged over 3 month periods (Mantua et al. 1997,

16   Minobe 1997) (https://www.ncdc.noaa.gov/teleconnections/pdo/ 2020.9.25). The PDO

17   is related to changes in the phenology, community structure and abundance of

18   phytoplankton, zooplankton, and forage fish in the NW Pacific (Ohshimo et al. 2009,

19   Chiba et al. 2006, 2012, Kuwae et al. 2017, Nakayama et al. 2018).

20   The maximum foraging range of Rhinoceros Auklets from Teuri Island is

21   estimated to be 164 km (Kato et al. 2003). Variability of interannual and seasonal

22   expansions of Tsushima Current stocks of sardine and anchovy (Muko et al. 2018,

23   Watanabe & Takahashi 2007) possibly make these stocks available to Rhinoceros

24   Auklets breeding at Teuri Island. Stock of age-0 greenling in the northern Japan Sea

1   off Hokkaido are well within auklet foraging range. Stock sizes of sardine and anchovy

2   in the Tsushima warm current and that of age-0 greenling in the northern Japan Sea off

3   Hokkaido were obtained from stock assessment databases

4   (http://abchan.fra.go.jp/digests2019/index.html 2019.9.25. see Hayashi et al. 2018,

5   Morita et al. 2018, Yasuda et al. 2018 also). The stock sizes are assessed by cohort

6   analysis (VPA) and available between 1985 and 2018 for age-0 greenling and between

7   1984 and 2018 for sardine and anchovy.

8

2.4. Statistics

10   To detect decadal-scale shifts in the diet composition and PDO, "sequential t-test

11   analysis of regime shifts" (STARS, Rodionov 2004）was applied to the data from 1980

12   (four years before the study period) through 2020. To minimize the possibility of the

13   Type II error, 10% was chosen as significance level. To find any potential shifts of

14   PDO index primary value of cut off length（L）was 10 years for examining

15   quasi-decadal shifts and 5-year cut off was used for examining short-term shifts. We

16   did not have time series data before 1992 for the diet composition, mass of meal-loads

17   and productivity (chick growth rate, number of fledglings per nest, fledgling mass) of

18   Rhinoceros Auklets. So shifts of these variables were examined using STARS where

19   5-year cut off only was used.　Huber's weight parameter（H）to detect outlier was set

20   to 1. VBA procedure from the NOAA website

21   (https://www.beringclimate.noaa/gov/regimes/ 2017.12.1.）was operated on the macro

22   of Excel 2010 (Microsoft co.).

23   Linear regression analyses were carried out to examine the effects of 1) annual

24   average meal energy density (calculated) and 2) mass of meal-loads on productivity

1 (chick growth, number of fledgling, mass of fledgling). Linear and parabolic effects of

2 prey composition as indexed by PC1 and PC2 on the annual average meal-load mass

3 were also tested. Difference in the mass of meal-loads between prey species was

4 examined using the linear model with Bonferonni-test excluding unknown and minor

5 species/type but including mixture of age-0/>1 sand lance types and other multiple

6 species. To understand the mechanism determining the mass of meal-loads in

7 Rhinoceros Auklet that brings multiple number of prey in a meal-load, we examined

8 the relationships between the number and size of fish and the mass of each meal-load

9 using linear and parabolic regression analyses for each species/type (using SPSS ver.

10 22). To evaluate the appropriateness of either linear or parabolic models in the above

11 regression analyses we used the model selection procedure in addition of value of

12 coefficient of determination (r^2). Candidate Linear Mixed Models (LMM) or Linear

13 Model (LM) were constructed using library lme4 in R ver 3.2.1, (R Development Core

14 Team 2015) and using *glmer* and the model selection was based on corrected Akaike

15 Information Criteria (AICc) using library MuMIn.

16

17 <center>3. RESULTS</center>

18 **3.1. Prey switching**

19 The primary prey used by Rhinoceros Auklets were sardine, anchovy*,* herring *Clupea*

20 *pallasii*, age-0 and age->1 sand lance, Pacific saury, age-0 Japan Sea Greenling

21 *Pleurogrammus azonus*, juvenile salmon *Onchorhynchus* sp., and squid (Table 1).

22 These 9 species/type comprised 76 - 100% of the composition (by mass) of meal-loads

23 each year and were defined as major prey species/type (Table 1). Most (87%)

24 meal-loads were comprised of a single species/type (Table 1). The thirty-four

percentage of meal loads contained a single prey per meal-load, while 66% contained multiple numbers of prey per meal-load. We attribute PC1 (with 38.1% of explained variance) to a community characterized by the presence of sardine and age->1 sand lance, and absence of anchovy and PC2 (24.1% explained variance) to a community characterized by the presence of squid and age-0 greenling, and absence of Pacific saury (Table 2).

Forage fish communities exploited by auklets apparently varied among years (Fig. 2a, see Table S2 in Supplement 2 also). During 1984 – 1987 PC1 was positive and PC2 was negative (Fig. 2b). After 1992, the sequential analyses of 5-year cut off showed that PC1 shifted to negative in 1997/1998, then shifted to positive in 2013/2014, and to greater degree in 2019/2020 (Fig. 2b). PC2 was shifted to positive in 2013/2014, then diminished to lower values in 2017/2018. Thus, PCA revealed five different forage communities used by auklets over the study period (Fig. 2b). Prey communities shifted in species composition between 1) sardine, age->1sand 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->1sand lance in 2018 – 2020 (Fig. 2a,b).

3.2 Climate and stock size

Sequential analyses of 10-year cut off 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 did in 2014/2015 (Fig. 2c). Using a 5-year cut off winter PDO shifted from positive to negative in 1988/1989,

1　summer and autumn PDO did in 1997/1998 and spring PDO did in 1998/1999, and all

2　shifted in 2013/2014 to positive. Last, spring and summer PDO shifted to negative in

3　2019/2020. In summary, we had shifts in 1) late 1988 -- early 1989, 2) late 1997 --

4　early 1999, and then maybe shifts in 3) 2007 -- 2008, something short term in 4) 2013

5　-- 2014, and maybe in 5) 2019/2020.

6　　　　The Tsushima stock of sardine decreased dramatically from1987 to 1992 and

7　remained low thereafter with a slight increase in the late 2010s (Fig. 3a, b). The

8　Tsushima stock of anchovy was relatively high in 1992 – 2008 (Fig. 3b). Stock size of

9　age-0 greenling in northern Hokkaido decreased since 2008 (Fig. 3c). Between-year

10　changes of PDO in all seasons did not linearly explain the stock size of sardine,

11　anchovy and age-0 greenling (r^2=0.001 – 0.009, P>0.05).

12

13　**3.3. Prey use and fish stock**

14　The choice of prey used by auklets appeared to be partly related to the change of stock

15　size. The between-year variation of the mass proportion of each prey species in the

16　meal-loads was explained by its stock size for sardine (r^2=0.668, $F_{(1,28)}$=56.259,

17　P<0.001, Fig. 4a) and anchovy (r^2=0.148, $F_{(1,28)}$=4.853, P=0.036, Fig. 4b), but not for

18　age-0 greenling (r^2=0.016, $F_{(1,27)}$=0.432, P=0.516, Fig. 4c), and in fact, greenling

19　consumption was highest during the years of lowest greenling abundance. The

20　proportion of anchovy in diet inversely correlated with sardine stock size (r^2=0.253,

21　$F_{(1,28)}$=9.469, P=0.005). The use of age-0 greenling did not change with either sardine

22　(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,

23　P=0.283) but it seems to have peaked after 2013 when both sardine and anchovy were

24　lowest level

1

2   **3.4. Meal-load and productivity**

3   The sequential analyses of 5-year cut off after 1992 showed that the mass of meal-load

4   (Fig. 5a) and chick growth rate (Fig. 5b) shifted to lower levels in 2013/2014. The

5   number of fledglings produced also shifted to lower levels in 2012/2013, but recovered

6   to pre-shift levels in 2017/2018 (Fig. 5c). In years of high chick growth rate, the number

7   of fledgling was greater (r^2=0.370, P<0.001, n=32) and fledgling mass was heavier

8   (r^2=0.525, P<0.001, n=29).

9   Between-year variation of productivity (chick growth rate, number of fledglings

10   and the mass of fledglings) related linearly and positively with the mass of meal-loads

11   (Fig. 6a,b,c). The linear relationships were significant (Table 3). Coefficient of

12   determinants (r^2) were greater for the effects of the mass of meal-loads than for the

13   energy density of meal-loads (Table 3). Models including the mass or the mass and

14   energy density were more appropriate than those including the energy density only

15   (Table 3, see Table S3 in Supplement 2 also). Thus we focused on the effects of food

16   packaging on the mass of meal-loads.

17

18   **3.5. Food packaging**

19   PC1 score as an index of forage community use was related to the annual average mass

20   of meal-load in parabolic rather than linear manner (Table S4 in Supplement 3);

21   indicating that Rhinoceros Auklets brought heavier meal-loads on average in years

22   when the forage community was dominated by sardine and age->1sand lance or by

23   anchovy (Fig. 7a). PC2 score also showed a parabolic rather than linear effect (Fig. 7b,

24   see Table S4 in Supplement 3 also); indicating that they brought smaller meal-loads in

years when the forage community was dominated by age-0 greenling and squid or by Pacific saury.

This was because the mass of meal-loads varied between the types ($F_{(10,3015)}$=78.589, P<0.001, n=3,026, Table 1). The meal-loads comprised of 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 comprised of squid, age-0 sand lance or juvenile salmon, which were smallest (Table 1, Bonferonnii Post-hoc, P<0.05, see Fig. S3 in Supplement 3 also,). Those with mixture of age-0 and age->1sand lance laid between sardine and those with multiple species and the latter was between sardine, anchovy or age->1sand lance and juvenile salmon or age-0 sand lance (Fig. S3 in Supplement 3).

This species difference of the mass of meal-load can be explained by the trade-off between 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/type of fish with intact bodies (2,203 meal-loads), relationships between the number and the mean fork-length of fish and the total mass of meal-loads were analyzed. When Rhinoceros Auklets brought back larger numbers of fish, average fish size in a meal-load was smaller for all species/types (Table S5, Fig. S4 in Supplement 3 also). Further, in meal-loads comprised 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. 8 a, b, c, Table 4, see Table S6 in Supplement 3 also). Using these parabolic equations (Table 3), the specific number of fish was expected to give the maximum meal-load mass for anchovy (3.3 fish, 45.4g, Fig. 8a), age-0 greenling (6.2 fish, 34.3g, Fig. 8b), and age-0 sand lance (23.0 fish, 22.6g, Fig. 8 c). When the

14

1   number of fish was greater, the mass of meal-loads were greater for age->1sand lance

2   but smaller for Pcific saury (Fig. 8 e, f, Table 4, see Table S6 in Supplement 3 also).

3   Reversal parabolic relationship was found for herring (Fig. 8 d) while no clear

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

5

6   4. DISCUSSION

7   Our long-term study showed that 1) prey switching coincided with the timing of

8   oceanic climate shifts demarcated by changes in water temperature associated with the

9   Pacific Decadal Oscillation, and, 2) prey switching resulted in "food packaging" that

10   affected various aspects of Teuri auklet's breeding productivity

11

12   **4.1. Climate change and prey switching**.

13   A shift in the PDO from cold to warm phase occurred in late1988 to early1989 (Fig.

14   2c) and again more dramatically in late 1997- early 1999. These shifts of PDO

15   roughly coincided with the timing when the seawater temperature in winter and spring

16   at 50 m depth of western Japan Sea shifted to warmer levels (1986 – 1989, Tian et al.

17   2006, 2008) and that in the summer and autumn further shifted warmer (1996 – 1998

18   or in 1999, Yasunaka & Hanawa 2005, Tameishi et al. 2005, Tian et al. 2006, 2008),

19   respectively. Note that the relationship between PDO and water temperatures is

20   opposite that observed in the NE Pacific, where negative PDO values are associated

21   with warmer water temperatures (Newman et al. 2016). Thus, the prey switching by

22   Rhinoceros Auklets coincided with 1986 – 1989 and 1996 – 1999 shifts of PDO/sea

23   water temperature and can be explained by the change of forage fish community.

24   Japanese sardine and Japanese anchovy are alternately abundant in the cold

1 and warm phases, respectively, in the Japan Sea (Tian et al. 2008). The same relations

2 are observed on the Pacific side of Japan where the range of suitable water

3 temperatures for spawning and larval survival were lower for Japanese sardine than

4 Japanese anchovy (Takasuka et al. 2008). Thus climate-induced shift in the forage fish

5 community (*regime-shifts*) rather than linear effects of climate index and SST affected

6 the prey switching and diet of the seabirds (e.g., Anderson & Piatt 1999). The stock

7 size of sardine and anchovy explained the importance by mass of these prey species in

8 the diet. This is presumably because with the increase in stock size the distribution of

9 these species expands into the foraging range of the birds, making prey more

10 accessible. Expansion of sardine to the north with the increase of the Tsushima stock in

11 1980's (Muko et al. 2018) made this species available to Rhinoceros Auklets at Teuri

12 Island during the cold phase of the PDO. Similarly, anchovy reached the foraging

13 range of Rhinoceros Auklets at Teuri Island with its expansion during warm phase in

14 the 1990's (Watanabe & Takahashi 2007).

15   Relation between climate and the third and fourth prey switch after 2013 are

16 unclear. Age-0 greenling distributes in waters of relatively low SST (8 – 13 C) in our

17 region (Ishigaki & Nakamichi 1958). The prey switch from anchovy to age-0 greenling

18 in 2013/2014 coincided with the shift of PDO in 2013/2014 (Fig. 2b, c). This negative

19 to positive PDO shift, that is also suggested in Kuroda et al (2020), implies the start of

20 cold phase, but we have no evidence of the decrease of SST in 2013/2014 (Fig. S5).

21 After 2014 the stock size of anchovy was small and that of sardine was negligible (Fig.

22 3a, b). Considering the ecology of anchovy, which expands and contracts in

23 distribution according to the stock size (Watanabe & Takahashi 2007, Hayashi et al.

24 2019), anchovy might not extend its distribution to the foraging range of Rhinoceros

1 Auklets at Teuri Island during the recent low stock size period. Therefore age-0

2 greenling might be only available forage fish even if its stock size was smaller than

3 before (Fig. 3c). In the most recent few years, Rhinoceros Auklets switched prey to

4 age-0/>1 sand lance (Fig. 2 a, b) in 2017/2018. Although the shifts of PDO, either 5- or

5 10-year scale, were not detected by STARS in this period, PDO started to decrease and

6 might shift in 2019/2020 (Fig. 2c). Catch of age-0 sand lance in our study region was

7 around 100 – 1200 t before 1995 but no substantial catch occurred there after

8 (Watanuki & Ito 2012). However, warmer waters may have enhanced sand lance

9 recruitment and population stock size (Sydeman et al. 2017).

10   To conclude this section, climate variability in the 1980's and 1990's induced

11 change in the availability of sardine and anchovy and hence the use of these species by

12 Rhinoceros Auklets. Thus Rhinoceros Auklets can be reliable and effective samplers of

13 the marine environment as other puffin species (Hatch & Sanger 1992, Bertram &

14 Kaiser 1993, Sydeman et al. 2017).   During the 2000's and 2010's, when availability of

15 both sardine and anchovy were decreased, age-0 greenling and age-0/>1 sand lance

16 dominated in diets, but environmental factors affecting availability of the latter two

17 prey species were unclear. This may be related to conclusions of a recent review study

18 that "some major marine fisheries resources around Japan showed decadal increases or

19 decreases beginning in the mid-2000s, and appeared to respond to the unconventional

20 SST changes in their early life stages (Kuroda et al. 2020)". Anomalously high SST in

21 NE Pacific (heat wave) was associated with El Nino and high PDO index in 2013 -- 2016

22 (Leising et al. 2015, Tseng et al. 2017) and impacted seabirds (Piatt et al. 2020). In the

23 same period (2013 – 2016) Rhinoceros Auklets were impacted (Fig. 5) but SST of

24 northern Japan Sea did not show apparent increase or decrease (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) the most of the meal-loads were comprised of a single species, and 2) the mass of meal-loads varied with prey species taken and low for multi-species loads, and 3) the mass of meal-loads was the key determinant of chick productivity between climate phases.

Between-year difference in the energy density of prey species explains 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) than sardine, anchovy and age->1 sand lance (5-10 KJ/g, Table S1 in Supplement 2). Thus energy density of prey was higher on average in either cold or warm phases 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 the mass more important to productivity than the energy density. Presumably, this is because the variation of the energy density of average meal-loads between years observed in this study (4.29 – 6.60 KJ/g or 154%) was smaller than that in the average mass (16.6 – 35.9 g or 216%) (Table S2 in Supplement 2). Same is true for Tufted Puffins *Fratercula cirrhata*, where prey species ranges from lean juvenile walleye pollock *Theragra chalcogramma* to fatty capelin *Mallotus villosus* and myctophids, but they do just fine raising chicks on walleye pollock by bringing larger packages (Schoen et al. 2018).

Rhinoceros Auklets brought back heavier meal-loads in years when they fed

mainly on sardine or anchovy than years when their diet was more diverse and

included age-0 greenling, squids and age-0 sand lance (Fig. 4 a,b). In Great Crested

Terns *Thalasseus bergii*, the size of anchovy in meal-loads was smaller when the

parents brought multiple number of anchovy (Gaglio et al. 2018). We found similar

relationships in Rhinoceros Auklets, but with large species difference (Table S5, Fig.

S4 in Supplement 3). With these species-specific size-number relationships, we

expected that the maximum mass of meal-load would vary between species. The

expected maximum mass of three major prey species (Fig. 5 a,b,c) 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 trade-offs is unclear.

Other species of seabirds show different food packaging. Murres *Uria* spp,

guillemots *Cheppus* spp. and terns are obligatory bringing single prey for chicks so the

size and energy density of individually-selected fish is always a direct effect on

production as shown for the North Sea and Baltic Sea (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 species of seabirds, including penguins,

albatrosses, shearwaters, petrels, cormorants and gulls bring food in their stomachs so

may show different responses. We suggest that food packaging is one of factors

influencing the reproductive responses of central-place foraging seabirds to the change

of 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). So, they feed chicks once per night at

1 maximum (Takahashi et al. 1999). Therefore, the mass of meal-loads is the key. In our

2 study, chick growth rate was greater in years with heavier meal-load, and the number

3 of fledgling was greater and fledgling mass was heavier in years with higher chick

4 growth rate as reported in the previous study of this species on the same island

5 (Deguchi et al. 2004b). In an experimental study, Rhinoceros Auklet chicks that

6 received heavier meals per day grew faster, fledged younger and heavier with more fat

7 (Takenaka et al. 2005). In Manx Shearwaters *Puffinus puffinus* and Tufted Puffins

8 *Fratercula cirrhata*, post-fledgling survival is greater and age at first return to the

9 colony is shorter for fledglings having greater body mass (Perrins et al. 1973, Morrison

10 et al. 2009). Therefore the decadal scale changes of fledging success and fledging mass

11 associated with the change of forage fish community we found in this study may

12 influence the population of Rhinoceros Auklets.

13

4.3. Conclusion

15 Teuri Island Rhinoceros Auklets switched prey species in accordance with changes in

16 forage fish communities that were partly affected by ocean climate. They showed

17 highest productivity when the birds used anchovy as prey. Species-specific trade-offs

18 between the composition, size and number of prey in meal-loads, i.e. "food packaging"

19 explained the linkage between food resources in the environment and their breeding

20 productivity. The manner in which food is packaged for offspring could be a new

21 response to climate change impacts on marine ecosystems and effects on central-place

22 foraging predators.

23

13

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15

FIGURE LEGENDS

Fig. 1. Rhinoceros auklets bring back variable number of fish as a meal-load. A parent

bring back eight of age-0 greenlings (a) and one anchovy (b). Photo by M.I.

Fig. 2. Between-year changes in the mass proportion of prey species/type in meal-load

(a), the scores of the first (PC1, red closed circle) and second (PC2, black closed circle)

principal component of the mass composition of prey species with dominant prey

species (b), and PDO index (thin lines) in winter (Dec to Feb, PDOW), spring (Mar to

May, PDUSp), summer (June to Aug, PDOSu) and autumn (Sep to Nov, PDOA) (c).

The weighted average values during each phase between the shifts determined by

sequential t test analysis (STARS) using 5-year cut off for PC1 (PCA-V5, red broken

line) and PC2 (PCA-V5, black broken line) are shown in (b) and those using 10-year

cut off (broken thick line, 10AV) and 5-year cut off (broken thin line, 5AV) for PDO

index are in (c). The shifts determined by STARS and that assumed by the change of

PC1 and PC2 are shown by closed and open triangles, respectively in (b) and (c). The

two shifts in 50 m depth water temperature and PDO reported in the previous studies

(Tian et al. 2006, 2008, Yasunaka and Hanawa 2005, Tameishi et al. 2005) are shown

by thin broken lines.

Fig. 3. Between year changes in Tsushima Warm Current stock size of sardine (a),

Tsushima Warm Current stock size of anchovy (b), and the stock size of age-0 Japan

Sea greenling in northern Japan Sea off Hokkaido (c). Shifts of PDO using 10-year and

5-year cut off are shown by thin broken lines (see Fig. 2 c).

1   Fig. 4. Relationships between stock sizes of sardine (a) and anchovy (b) in the

2   Tsushima warm current and that of age-0 greenling in the northern Japan Sea off

3   Hokkaido (c) and the mass proportion of each prey species in diet. Linear regression

4   line and 95% confidence interval are shown for (a) and (b) where the relationships are

5   significant.

6

7   Fig. 5. Between year changes in average ± SD of the mass of meal-loads (a), the

8   growth rate of chicks (b), and the number of fledglings per nests with chicks (c).

9   Weighted average values given by STARS with 5-year cut off are shown by broken

10 lines. Shifts of PDO using 10-year and 5-year cut off are shown by thin broken line

11 (see Fig. 2 c).

12

13 Fig. 6. Linear relationships between the annual averages of the mass of meal-load and

14 the growth rate of chicks (a), the number of fledglings per nest with chicks (b) and the

15 mass of fledglings (c). Linear regression lines with 95% confidence interval are show.

16 Sample size is 32 years but 29 years for the mass of fledglings since no chicks fledged

17 in 2014 – 2016. Crosses, open circles, closed circles, open squares and closed squares

18 refer to 1) sardine, age->1 sand lance, and Pacific saury period in 1984 – 1987, 2)

19 anchovy and age-0 greenling period in 1992 – 1997, 3) mostly anchovy period in 1998

20 – 2013, 4) age-0 greenling and squid period in 2014 – 2017, and 5) age-0 and age->1

21 sand lance period in 2018 – 2020, respectively (Fig. 2 a, b). See Table 4 for regression

22 equation and statistics.

23

24 Fig. 7. Parabolic relationships between the mass of meal-loads and the diet

composition indexed by the score of the first axis of principal component (PC1) of the

mass composition of prey species (a) and that of the second axis (PC2) (b). Parabolic

regression lines with 95% confidence intervals are show. Annual average values of

each year are used (n=32 years). Prey species with positive and negative PC loadings

are shown (See Table 2). See explanation of Fig. 6a for symbols.

Fig. 8. Parabolic or linear relationships between the number of prey and the mass of

food-loads in anchovy (a), age-0 greenling (b), age-0 sand lance (c), herring (d),

Pacific saury (e), age->1 sand lance (f), juvenile salmon (g), sardine (h) and squids (i).

Significant regression lines and 95% confidence interval are shown. No significant

effects were observed in juvenile salmon, sardine and squids. See Table 4 for

regression equation and statistics.

Table 1. The mass (average±SD) of meal-loads and the number of fish in those comprized of a single major or minor species of fish. We categorized the species as major and minor if the number of meal-loads including these fish species was greater than 14 meal-loads and if the number was smaller than 13 meal-loads, respectively. The meal-loads comprized of mixture of age-0 and age->1 sand lance and those including multiple species were categorized as multiple types.

Species/age classe	Mass of meal-load (g)	No. of fish per meal-load	No. of meal-load
Major species			
Sardine (*Sardinops melanostictus*)	40.3±9.3	1~5	71
Anchovy (*Engraulis japonicus*)	32.9±11.6	1~15	1,395
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 sandlance (*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 sandlance	29.9±10.0	2~21	38
Multiple species	23.2±12.7	2~38	354
Total	27.9±12.8		3,067

1

Table 2 Loadings of each species/type along Principle Component 1 (PC1) and 2 (PC2) given by principal component analysis of the proportional mass composition of 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

1

2

Table 3. Linear effects of annual average of the mass (BLM, g) and the energy density (EDN, KJ/g) of meal-loads on the chick growth rate (CG, g/5 days), the number of fledglings per nests with chicks (NF, n/nest), and the mass of fledglings (FLM, g). Coefficients of determination (r^2) and significance level (P) are shown. No apparent curvilinear effects are observed (Figure 6). Sample size is 32 years for the chick growth rate and the number of ledglings but 29 years for the mass of fledglings as no chicks fledged in the study plots in 3 years. To see importance of factors, model selection is performed basing on AICc (Table S3). Better models with smaller AICc in those incuding either BLM or EDN as an explanatory factor are in bold. Linear effect of the energy value of meal-load (EVU, KJ) is examined separately as EVU is calculated as BLM x END in this study.

	r^2	F-value	P	AICc
Chick gorwth rate (CG)				
CG=-17.775+2.029BLM	**0.665**	**62.475**	**<0.001**	**225.2**
CG=-40.193+13.831EDN	0.396	21.3	<0.001	244.1
CG=-3.517+0.263EVU	0.677	65.917	<0.001	
Number of fledglings				
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=-37.074+12.383BLM	**0.62**	**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	

1

Table 4. Linear and parabolic regressions of the number of fish in meal-loads (N) on the mass of meal-loads (M). Meal-loads including only fish with intact body are used. Model selection is performed using AICc (see Table S6). Better models giving smaller AICc in the linear or parabolic equations and that giving significant coefficient of determination (r^2) are in bold.

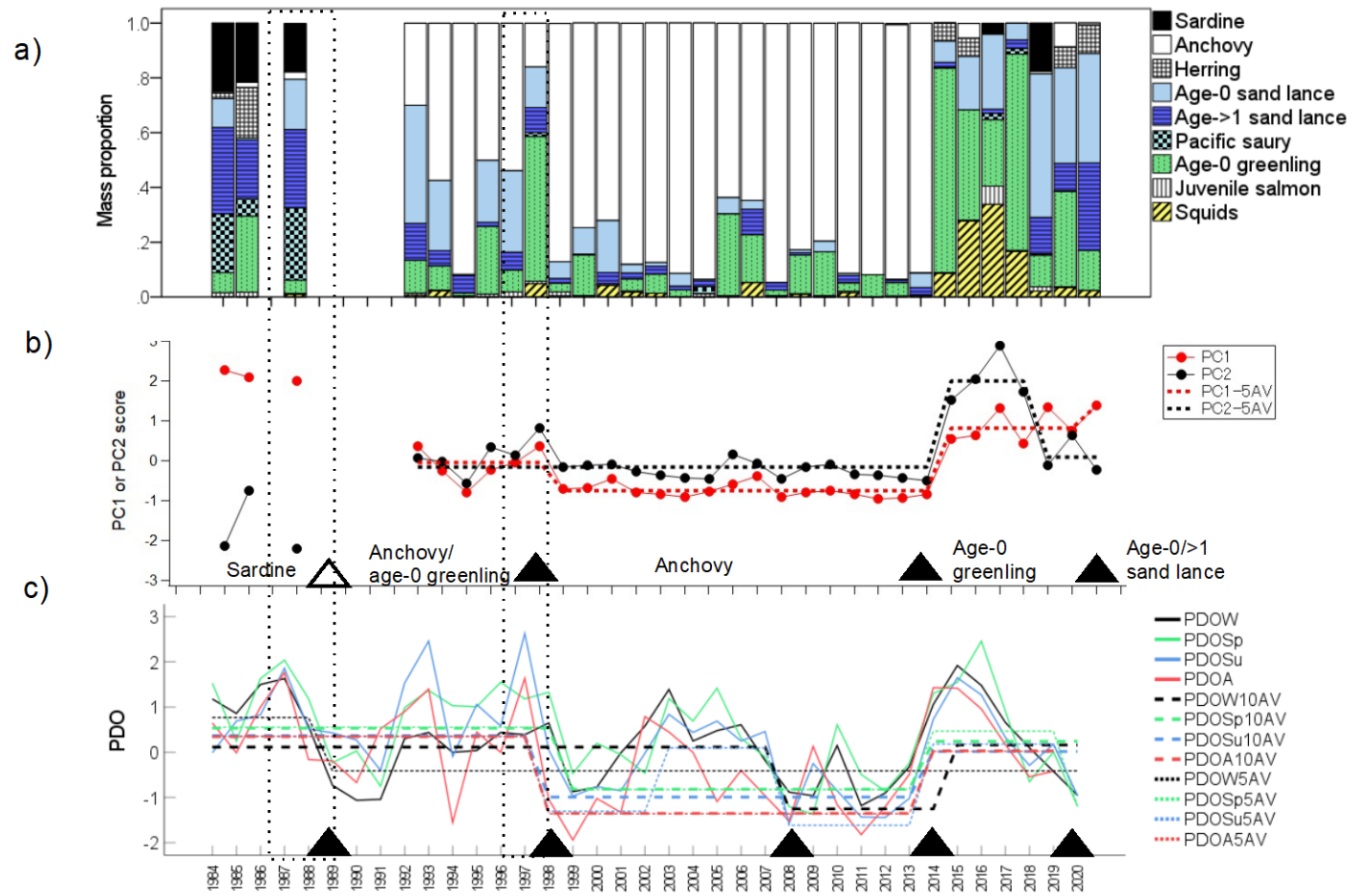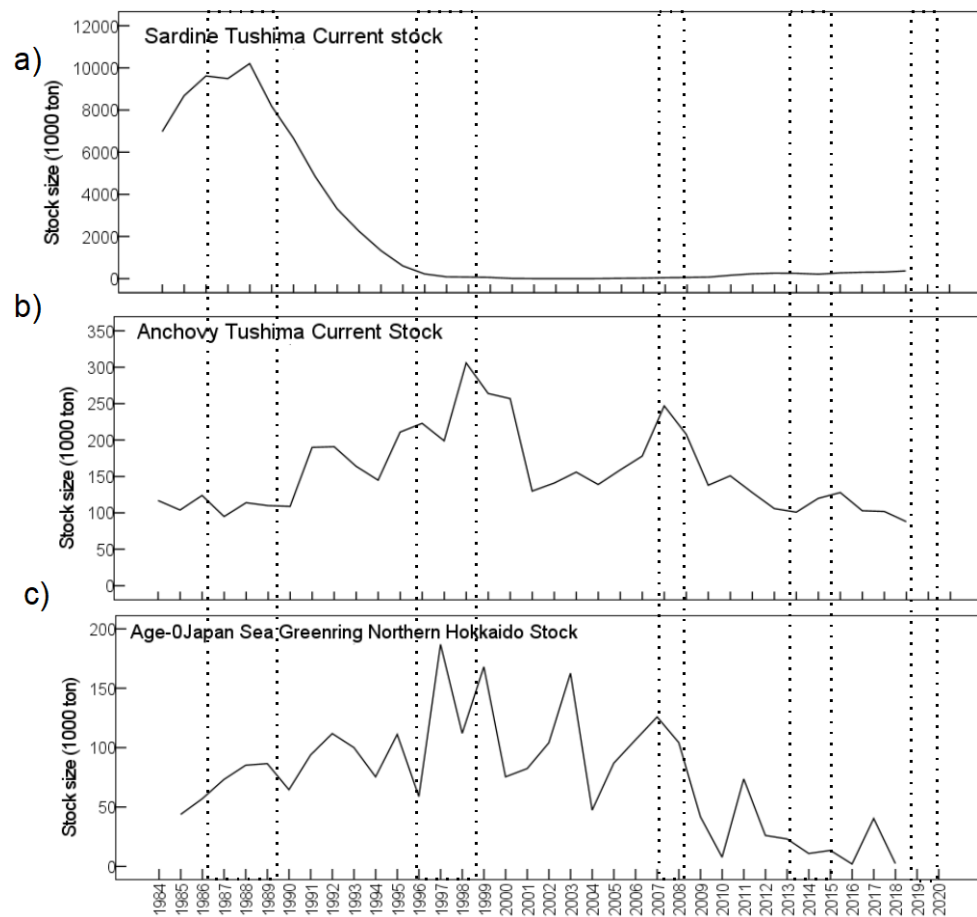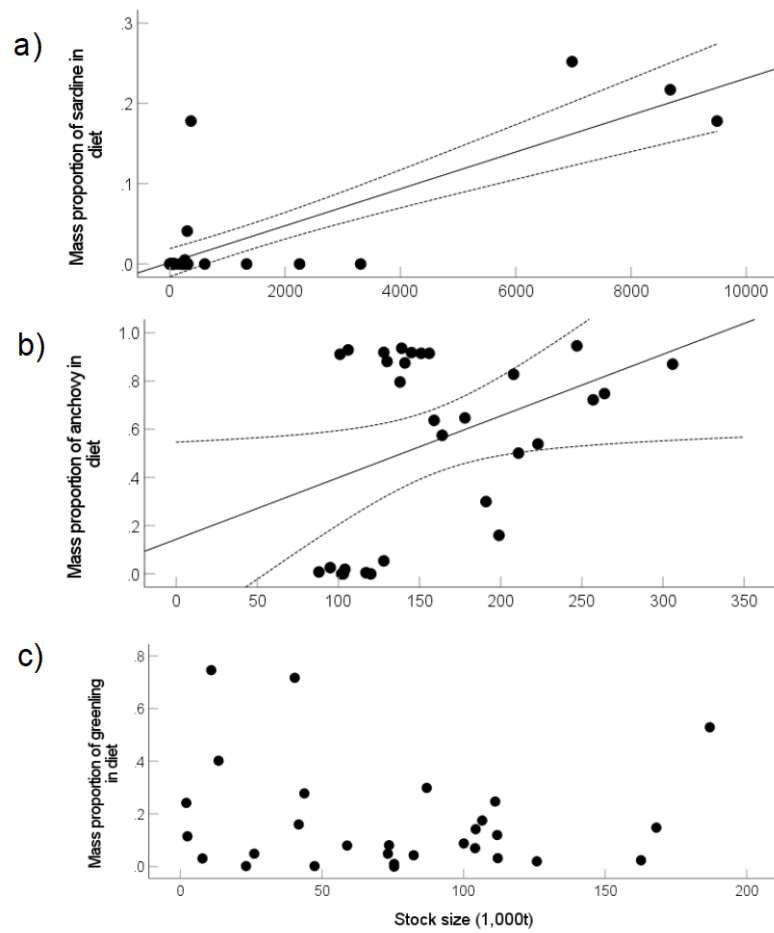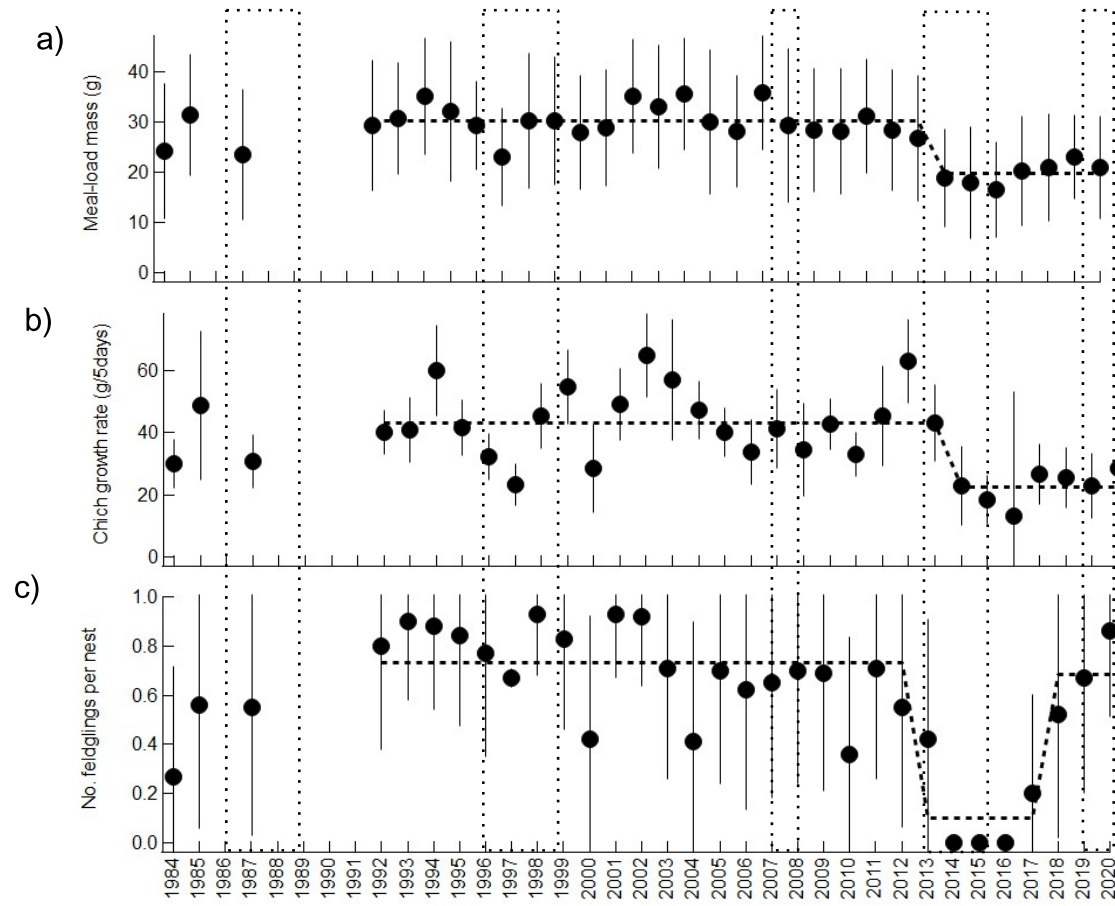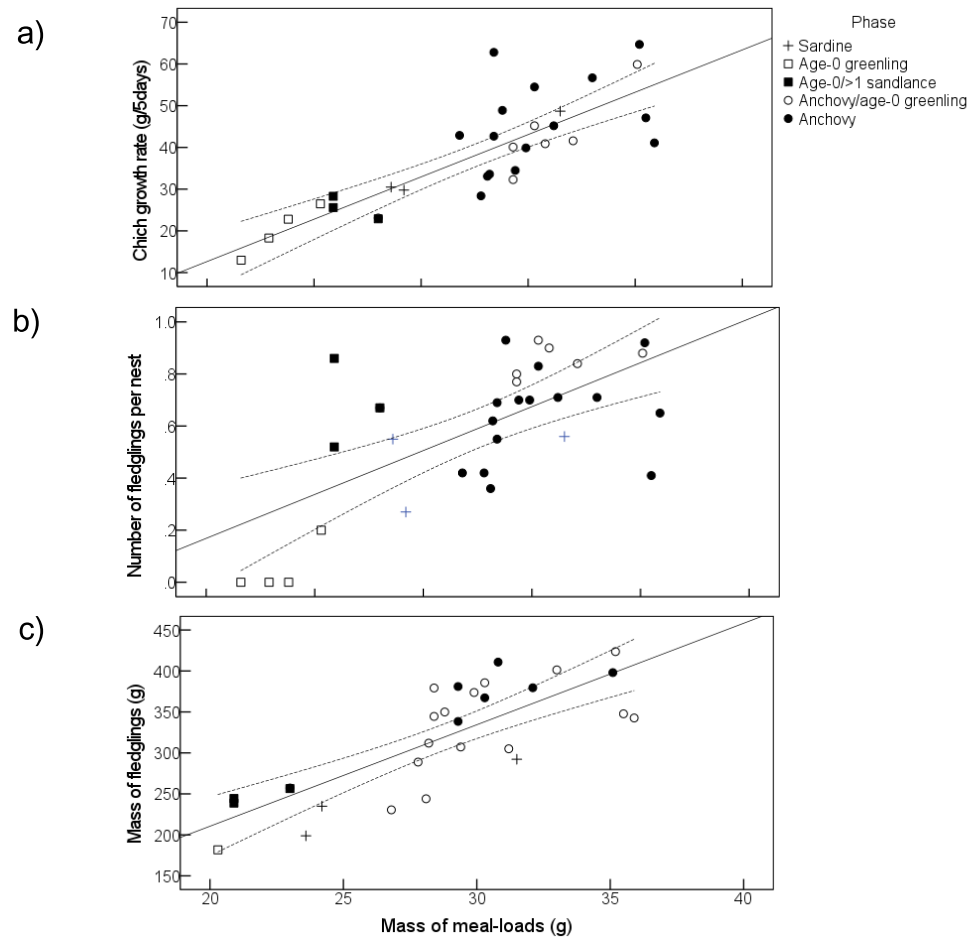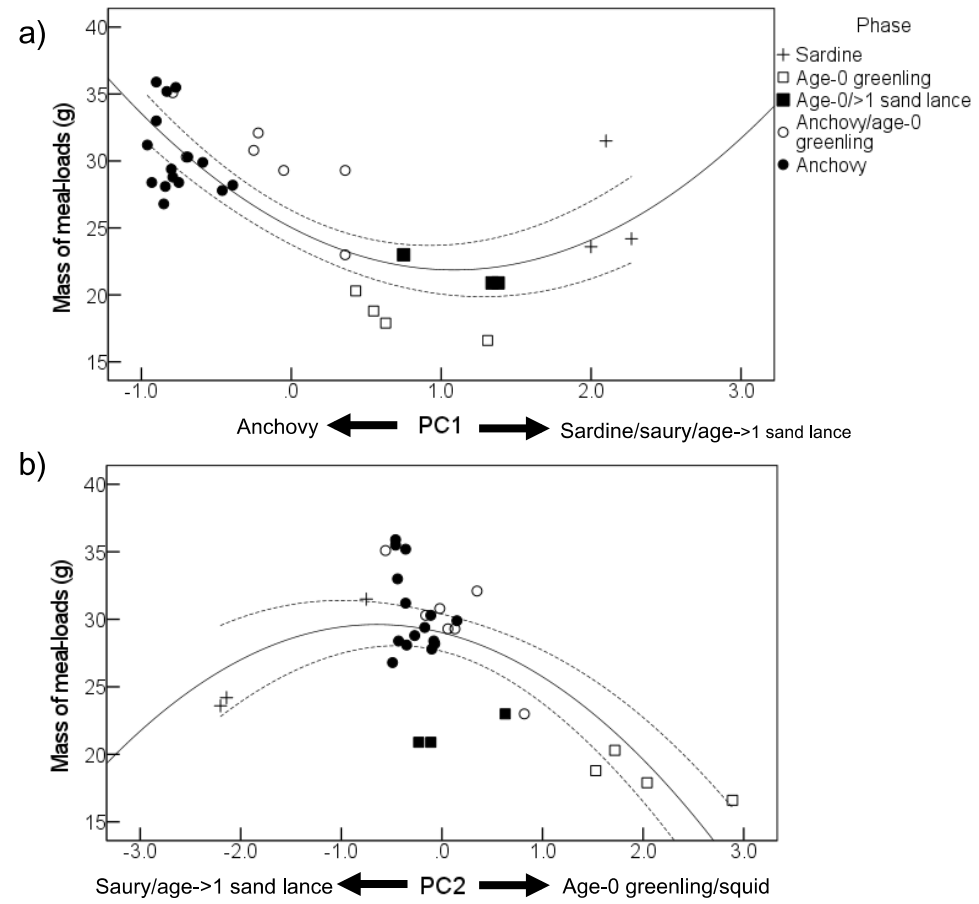| Species (sample size)	Effects	Equations	r^2	P	AICc
Anchovy (1,230)	**Parabolic**	**$M=3.455+26.488N-3.875N^2$**	**0.503**	**<0.001**	**8643**
	Linear	$M=17.140+10.560N$	0.39	<0.001	8897.2
Age-0 greenling (284)	**Parabolic**	**$M=14.247+6.462N-0.521N^2$**	**0.188**	**<0.001**	**2138.1**
	Linear	$M=21.811+1.718N$	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	$M=14.392+0.276N$	0.06	<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**	**$M=48.506-14.416N+1.098N^2$**	**0.21**	**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
Squid (52)	Linear	$M=16.589+2.470N$	0.029	0.23	401
	Parabolic	$M=13.801+5.797N-0.784N^2$	0.032	0.455	403.2

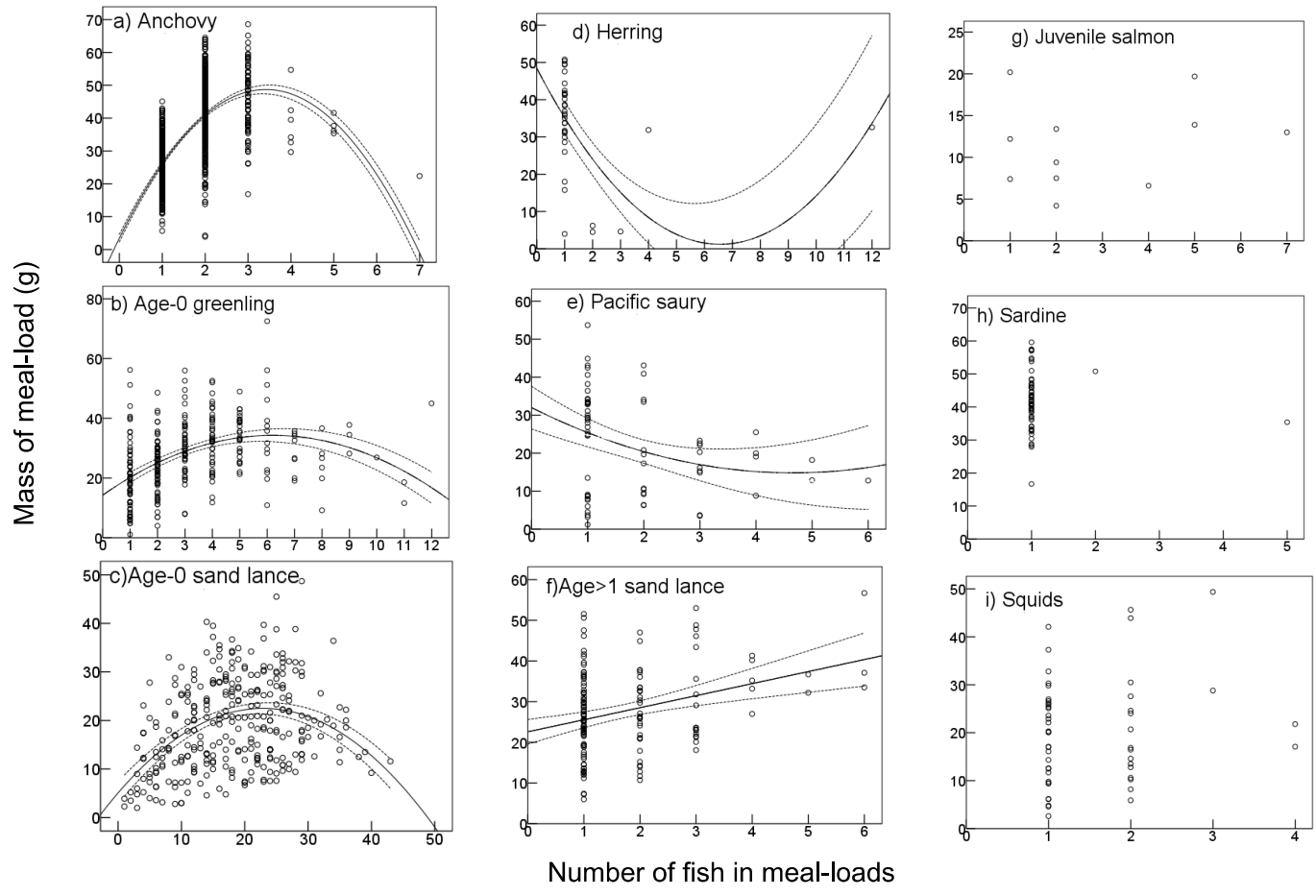1

a)

b)

Fig. 1.

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2

Fig. 2.

Fig. 3.

Fig. 4.

1
2

Fig. 5

1
2

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Fig. 6.

Fig. 7.

Fig. 8.