



# Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea

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**ABSTRACT:** The Bering Sea has experienced dramatic warming in this century that has altered elements of the ecosystem, including the structure and productivity of the zooplankton community on the continental shelf, and the extent to which waters and associated plankton of oceanic origin have intruded onto the shelf. We documented temporal and spatial scales of these changes by monitoring diets of least auklets *Aethia pusilla* on the Pribilof Islands—least auklets are planktivores that specialize on the large calanoid copepods *Neocalanus* spp. from the basin and *Calanus marshallae* from the shelf. Diets were estimated in the summers of 1996 to 2006 by enumerating prey in regurgitated meals brought to chicks by adults, and by fatty acid analyses of live biopsy samples of adipose tissue from adult birds in 2003 and 2004, which provided additional insight. In the unusually warm 2000s, *Neocalanus* spp. apparently were excluded from regions of the outer shelf, where they typically occur in cooler years, and, concurrently, *C. marshallae* was depressed over a large region of the shelf because of chronic failures of spring cohorts to survive. Both changes were associated with anomalously high water temperatures over the middle shelf. The information provided by least auklets greatly improves our understanding of the consequences of environmental change and supplies clues about how communities and ecosystem processes respond to physical forcing. Continued warming of the magnitude seen in recent years could become a cause for concern for auklets and other planktivores in the eastern Bering Sea if it alters prey availability in ways detrimental to their populations.

**KEY WORDS:** Bering Sea · Climate change · Seabird · Auklet · Diet · Copepod · Oceanography

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## INTRODUCTION

Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level....Anthropogenic warming and sea level rise would continue for centuries due to the timescales associated with climate processes and feedbacks, even if greenhouse gas concentrations were to be stabilized.

IPCC (2007)

Climate change in the past 3 decades in the North Pacific is thought to have had major effects on marine ecosystems, from physical oceanography to population dynamics of a variety of species (e.g. Ebbesmeyer et al. 1991, Francis & Hare 1994, Anderson & Piatt 1999, Hare & Mantua 2000). The eastern Bering Sea in

particular has undergone dramatic warming in this century, as predicted by global climate models, that has apparently had significant effects on pelagic and benthic community structure and biomass yield (Grebmeier et al. 2006, Coyle et al. 2008, IPCC 2007, Stabeno et al. 2007). Yet, despite intense interest, the mechanisms linking meteorological and oceanographic variability to marine biology and productivity are poorly known, owing largely to the high costs of extensive ship-based oceanographic studies designed specifically to document change and to discover its cause.

Insights into relationships among marine communities, food webs, and oceanographic features can often be found by examining characteristics of species at

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higher trophic levels because they integrate processes at multiple lower trophic levels. Diet studies of predators can be especially informative because forage species and food webs are commonly affected by physical processes and variability. In the Bering Sea, least auklets *Aethia pusilla* have been shown to be especially useful in elucidating ecosystem properties that have much broader implications than simply for the birds and their prey (e.g. Springer & Roseneau 1985).

Least auklets are one of the most numerous and widely distributed species of seabirds in the Bering Sea—they number in the millions and nest at island colonies from the Aleutian Islands to Bering Strait (Jones 1993). They are planktivores that specialize on the large calanoid copepods *Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri*, and *Calanus marshallae* in summer, and supplement them with other taxa of zooplankton, such as hyperiid amphipods, euphausiids, crab, shrimp, and fish larvae, and other miscellaneous organisms (Bedard 1969, Hunt et al. 1981, Bradstreet 1985, Springer & Roseneau 1985, Roby & Brink 1986, Hunt & Harrison 1990, Flint & Golovkin 2002). The composition of the copepod portion of their diets is determined by the relative abundances of the various species, which are in turn influenced by physical processes that structure the Bering Sea into hydrographic and biotic domains with distinct species assemblages (Iverson et al. 1979, Cooney 1981, Coachman 1986, Springer et al. 1996). Interannual variation in physical conditions and primary production can also affect copepod population abundances (Smith & Vidal 1984, 1986). Furthermore, in regions where all 4 species of copepods are available within the foraging range of least auklets, selectivity for one or another species appears to be determined not by differences in nutritional/energetic content, which are small, but by the ability of birds nesting in distinct colonies to find profitable solutions for dietary proclivities (Springer & Roseneau 1985, Flint & Golovkin 2002).

Oceanographic conditions in the southeastern Bering Sea in late July to August 2004, documented by traditional shipboard methodologies, sharply partitioned continental shelf and oceanic domains and created an abrupt and extremely narrow ecotone between them (Coyle et al. 2008). That is, waters of oceanic origin were confined to the very outer part of the continental shelf, with little or no excursion onto the shelf or mixing with waters of the middle shelf domain. Least auklet diets from the Pribilof Islands during summer 2004, which we present here, were indicative of this unusual hydrographic structure. Therefore, we examined our auklet diet data from the Pribilof Is. for 1996 to 2006, and reviewed data from earlier years (St. George I.—1977, 1984, 1985; St. Paul I.—1976, 1977, 1984, 1992), to see if there was evidence that such conditions had

occurred at other times in the past 3 decades. This is among the few data sets that can be used to document the temporal and spatial scale of conditions important to the structure of the pelagic community of continental shelf waters, to the food web supporting least auklets and other planktivorous species at the Pribilof Is., and thus to our view of how climate change may alter characteristics of the marine ecosystem of the Bering Sea. The Pribilof Is. are well situated for such studies: central-place foragers like least auklets on St. George I. are closer to deep basin waters and the associated oceanic plankton community than auklets on St. Paul I., which is somewhat higher on the continental shelf, and thus, birds from the 2 islands sample the region differently and provide contrasting and complementary views of the larger ecosystem.

## MATERIALS AND METHODS

Samples for estimating least auklet diets were obtained during the nesting season (June through early August) from 1996 to 2006, from adults trapped at colonies on St. George I. and St. Paul I. (Fig. 1, Table 1), largely as part of a long-term seabird monitoring program conducted by the Alaska Maritime National Wildlife Refuge (e.g. Dragoo et al. 2006). Contents of sublingual pouches, consisting of fresh zooplankton destined for chicks, were collected when the birds were regurgitated upon being trapped. In 2003 and 2004 on St. Paul I., adipose tissue samples for fatty acid signature analysis were also taken by live biopsy from the

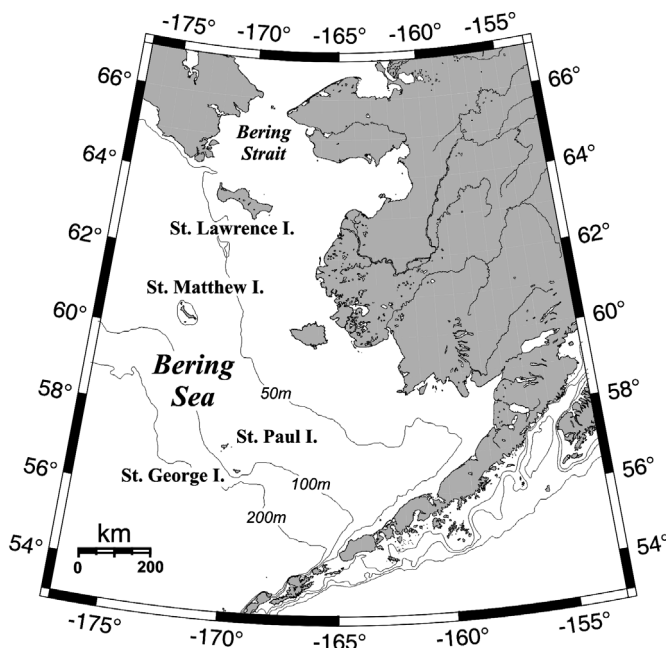


Fig. 1. Pribilof Islands and other locations discussed in the text

Table 1. *Aethia pusilla*. Sample sizes and dates when diet samples were collected at the Pribilof Islands. Asterisks denote samples for fatty acids; all others are regurgitations

	June		Early July		Mid-July		Late July		Early August	
	Date/Interval	n	Date/Interval	n	Date/Interval	n	Date/Interval	n	Date/Interval	n
<b>St. George I.</b>										
1996					Jul 21	20				
1997					Jul 21	21	Jul 31	14		
1998					Jul 19	4	Jul 30	12		
1999									Aug 2	14
2000							Jul 25	15	Aug 6–7	20
2001							Jul 24–30	15		
2002					Jul 17	13	Jul 27–28	18		
2003			Jun 29–Jul 3	14	Jul 11	11	Jul 29–Aug 1	22		
2004			Jun 30–Jul 6	11			Jul 25–27	8		
2005			Jul 1–4	20	Jul 12–23	15	Jul 23–Aug 1	17		
2006					Jul 6–22	19				
<b>St. Paul I.</b>										
1996					~Jul 14	15				
1997					Jul 18–21	10	Jul 22–31	7		
1998					Jul 18–24	7	Jul 27–29	8		
1999										
2000					Jul 17–22	43	Jul 24–30	52	Aug 1–10	26
2001							Jul 24–31	12	Aug 1–9	15
2002									Aug 2	7
2003			Jul 7	12	Jul 12–19	13	Jul 24–31	12		
2003*	Jun 2–12	10			Jul 12–15	16				
2004			Jun 30–Jul 13	67	Jul 19–23	38	Jul 25–31	10		
2004*	Jun 1–11	25			Jul 25–29	17				
2005			Jul 5–7	3	Jul 21	2				
2006					Jul 12–17	13				

synsacral region of the birds (Iverson et al. 2007, this volume). All birds were released after sampling. Regurgitation samples were preserved in 70% ethanol in the field and enumerated at the University of Alaska Fairbanks using methods described by Springer & Roseneau (1985). Prey species were identified to the lowest taxonomic level practical, which precluded separating the closely related copepod species *Neocalanus plumchrus* and *N. flemingeri*. Adipose tissues were placed in chloroform buffered with BHT (an antioxidant) and frozen until analyzed using methods described by Iverson et al. (2007).

## RESULTS

### Diets at St. George I.—adult regurgitations of chick meals

Diets of least auklets during our study at St. George I. were in most respects typical of those reported in earlier years—that is, large calanoid copepods dominated diets in nearly all intervals in all years, with other taxa present in varying, lesser proportions (Fig. 2a, Table 2). Among the copepods, *Neocalanus cristatus* and *N. plumchrus/flemingeri* were generally, but not

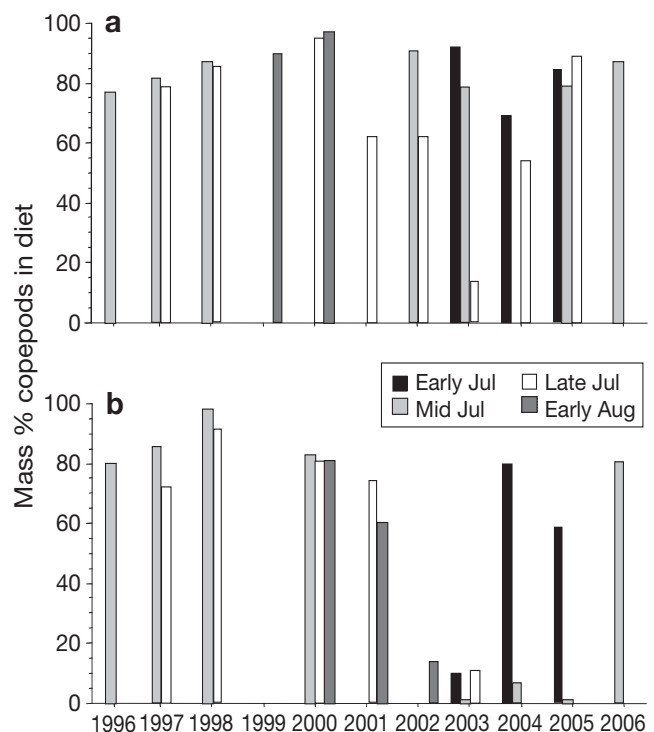


Fig. 2. *Aethia pusilla*. Least auklet diets at the Pribilof Islands—(a) St. George I. and (b) St. Paul I., from 1996 to 2006

Table 2. *Aethia pusilla*. Composition of least auklet diets at the Pribilof Islands from 1996 to 2006. Values are composition of regurgitations as a percentage of total mass of prey

Year	Interval	<i>Neocalanus cristatus</i>		<i>N. plumchrus/flemingeri</i>		<i>Calanus marshallae</i>		Hyperiid amphipods		Euphausiids		Juvenile crabs		Juvenile shrimp		Other invertebrates		Larval fish			
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<b>St. George I.</b>																					
1996	Mid-July	41	5.7	36	4.7	0		0.32	0.25	13	3.1	0.6	0.4	6.9	1.9	0.07	0.03	2.4	2.4		
1997	Mid-July	0.68	0.31	71	4.9	10	3.3	0.08	0.08	12	2.7	4.1	2.2	2.4	0.52	0.07	0.04	0	0		
	Late July	1.1	0.62	42	6	35	6.3	0		17	4.8	0.77	0.42	0.87	0.53	0.33	0.13	0.2	0.11		
1998	Mid-July	0		87	7.5	0		1.8	1.1	1.4	1.4	3.6	3.1	1.3	1.3	0.8	0.8	4	4		
	Late July	2.5	0.94	84	3.2	0.3	0.19	0		3.6	2.1	3.5	1.8	6.2	2.7	0.42	0.1	0	0		
1999	Early August	1.5	1.2	47	4.7	41	3.3	0.92	0.92	8.0	6.1	0.83	0.31	0		0.17	0.1	0	0		
2000	Late July	93	1.3	0.72	0.2	0.49	0.31	0.26	0.17	4.7	1.1	0.51	0.24	0.3	0.3	0		0	0		
	Early August	90	2.9	1.5	0.53	5.5	2.4	0.22	0.09	1.3	0.36	0.19	0.13	0.91	0.43	0.03	0.02	0	0		
2001	Late July	3.4	1.5	2.9	1.7	57	8.3	0.92	0.64	24	8.7	0.04	0.04	8	3.9	4.1	2	0	0		
2002	Mid-July	21	5.2	71	7.3	0		4.0	2.8	2.2	0.78	1.4	0.72	1.3	0.57	0.26	0.26	0	0		
	Late July	14	6.3	41	6.9	7.1	1.9	11	3.6	14	6.8	7.8	2.1	3.7	1.2	1.1	1.1	2.8	2.8		
2003	Early July	17	5.8	75	8.7	0		2.1	1.1	2.6	1.1	1.9	0.84	1.9	0.92	0		0	0		
	Mid-July	33	7.2	46	8.1	0		5.8	3.0	11	8.6	1.2	0.53	3	1.5	0		0	0		
	Late July	4.0	2.0	6.8	4.2	3.4	1.4	6.4	2.3	66	6	13	3.9	0.26	0.26	0.59	0.55	0	0		
2004	Early July	0		69	6.3	0		0		31	6.3	0.02	0.01	0		0		0	0		
	Late July	54	14	0		0		0.9	0.80	45	13	0.32	0.2	0		0		2.9	2.9		
2005	Early July	9.6	3.7	75	4.3	0.34	0.18	0.27	0.20	12	3.2	1.4	0.39	1.3	0.69	0.05	0.03	0	0		
	Mid-July	36	7.4	43	8.0	0		2.4	1.6	19	5.3	0.61	0.35	0.48	0.48	0.04	0.02	0	0		
	Late July	30	5.3	58	5.7	0		0.92	0.45	5.4	2.4	0.45	0.31	3.7	1.6	0.2	0.01	0	0		
2006	Mid-July	44	8.2	43	8.7	0		0		6.7	4.7	1.8	0.95	3	1.7	0.1	0.1	1.2	1.2		
<b>St. Paul I.</b>																					
1996	Mid-July	19	10	61	10	0.29	0.23	0		17	7	1.7	1.2	0.82	0.82	0		0	0		
1997	Mid-July	2.7	1.3	57	14	26	10	0.03	0.03	9.1	4.3	1.5	0.71	3.5	3	0.56	0.37	0.04	0.02		
	Late July	0		3.5	2	68	12	0		26	14	2.5	1.5	0		0.02	0.02	0	0		
1998	Mid-July	1.6	0.99	93	2.8	3.1	1.4	0		0		0.91	0.72	1.1	0.71	0.06	0.04	0.58	0.42		
	Late July	2.2	0.97	88	2.8	1.4	0.77	0.13	0.10	0.31	0.28	1.3	0.44	3.8	2.1	0.09	0.06	2.6	1.9		
2000	Mid-July	12	3.2	13	3.5	58	4.9	0.27	0.10	11	2.6	3.4	0.83	1.6	0.47	0.28	0.25	0	0		
	Late July	15	2.9	26	4.5	40	4.5	1.2	1.2	11	2.5	3.4	0.7	2.4	0.52	0.01	0.01	0	0		
	Early August	11	3.8	34	6.7	36	6.1	4.9	1.6	8.8	3.4	4.2	1.2	1.9	0.78	0.001	0.001	0	0		
2001	Late July	0.20	0.20	0.51	0.34	74	6.1	1.9	0.99	17	6.2	5.7	3.2	0.8	0.46	0		0	0		
	Early August	0		0		60	6.0	5.4	3.6	31	6.1	1.9	0.92	1.4	0.93	0		0	0		
2002	Early August	14	14	0		0		20	7.2	61	13	4.4	3.8	0		0		0	0		
2003	Early July	6.1	4.6	0.69	0.69	3.8	3.8	50	9.1	2.7	1.4	19	7.6	14	6	0		2.8	2.2		
	Mid-July	0.29	0.29	0		0.19	0.19	26	7.7	44	11	22	7.4	2.1	2.1	0.3	0.3	4.4	3.6		
	Late July	11	7.1	0		0.24	0.21	12	3.4	10	2.8	68	7.8	0.24	2.4	0		0.42	0.42		
2004	Early July	1.7	0.43	78	2.8	0		0.13	0.08	6.4	1.4	8.6	2	5.6	1.5	0.22	0.05	0	0		
	Mid-July	0.03	0.03	5.7	2.9	1.5	1.1	5.3	3.2	48	6.5	30	5.9	2.1	1.2	0.28	0.23	5.2	2.2		
	Late July	0		0		0		0.68	0.68	27	12	70	12	0.11	0.11	0.03	0.03	2.9	2.9		
2005	Early July	0		0		0		1.2	0.17	28	14	9.9	3.1	1.7	0.17	0.7	0.6	0	0		
	Mid-July	0		0		0.62	0.62	0		99	0.6	0		0		0		0	0		
2006	Mid-July	54	9.9	27	10	2.6	1.2	0.15	0.15	0		15	4.9	0		0.66	0.42	0	0		

always, more important than *Calanus marshallae*. Only in late July 2003 did copepods contribute relatively little to auklet diets.

#### Diets at St. Paul I.—adult regurgitations of chick meals

In contrast to St. George I., copepods were frequently (7 of 9 intervals) rare or absent from auklet diets at St. Paul I. from 2002 to 2005 (Fig. 2b, Table 2). This was remarkably dissimilar to diets there from 1996 to 2001 and to those previously reported from the Pribilof Is. or elsewhere. Copepods were hardly encountered in any of the 3 intervals sampled in 2003; and in 2004 and 2005 they were plentiful in early July, but declined abruptly and precipitously later in those summers. Furthermore, copepods were not abundant in late July 2002, the only interval sampled that summer. By 2006, copepods were again abundant in mid-July, a time by which, in the previous 2 yr at least, they had already essentially disappeared. At times when copepods were not plentiful, least auklets ate primarily hyperiid amphipods, euphausiids, and juvenile crabs (Table 2).

*Calanus marshallae* was absent in diets, or nearly so, in all intervals we sampled from 2002 to 2004, and in mid-July 2006, when *Neocalanus* spp. were present (Table 2). *C. marshallae* was plentiful in early July 2005, when *Neocalanus* were absent, but disappeared from diets by the middle of the month.

#### Diets at St. Paul I.—adult fatty acids

Calanoid copepod fatty acids are distinguished from fatty acids of all other marine species by the extremely large proportions of long-chain mono-unsaturated fatty acids and fatty alcohols (especially the isomers 20:1n-11, 20:1n-9, 22:1n-11, and 22:1n-9) arising from *de novo* biosynthesis (reviewed in Dalsgaard et al. 2003); this is consistent with our own data on the fatty acid composition of both *Neocalanus* spp. and *Calanus marshallae* (S. J. Iverson unpubl. data). These fatty acid biomarkers of copepods in least auklet adipose tissue were found at very high levels on St. Paul I. in early June in both 2003 and 2004 (Fig. 3), indicating that copepods had been available to them approximately 2 to 4 wk (the approximate integration period of dietary fatty acids) before the first chick meals were collected in early July. By July 2004, these fatty acid isomers had declined, but not to as low levels as by July 2003, which is consistent with the later decline of copepods in 2004 that was evident from chick meals.

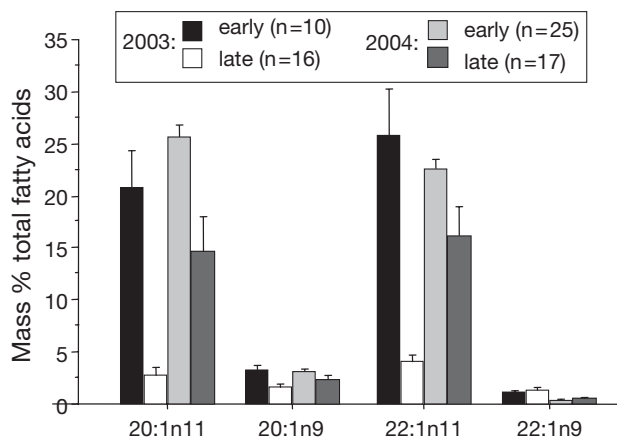


Fig. 3. *Aethia pusilla*. Characteristic copepod fatty acid biomarkers (mean  $\pm$  SE) measured in adipose tissue biopsies obtained from adult least auklets in June (early) and July (late) of 2003 and 2004 on St. Paul I.

## DISCUSSION

### Interannual and inter-island variability

The diets of least auklets *Aethia pusilla* at St. George I. that we observed from 1996 to 2006 were similar to those reported for the chick periods in 1977, 1984, and 1985 (Hunt et al. 1978, Bradstreet 1985, Roby & Brink 1986). Copepods predominated in all sampling periods except late July 2003. Among all copepods, *Neocalanus* spp. predominated in all but 1 collection, when they were replaced by *Calanus marshallae*.

St. George I. lies near the oceanic domain, the habitat of *Neocalanus* spp., which are endemic to oceanic waters of the North Pacific and Bering Sea and are supplied to the outer continental shelf by advection. *Calanus marshallae* replaces *Neocalanus* on the shelf, where it is the only large calanoid species (Cooney 1981). *Neocalanus* are larger than *C. marshallae* and might have been selected preferentially over *C. marshallae* by auklets if both were equally available (i.e. *Neocalanus* might be more profitable in an energetic sense). Lack of *C. marshallae* in diets, therefore, would not necessarily indicate a lack of *C. marshallae* in the environment. Thus, *Neocalanus* spp. were apparently much less abundant/profitable than *C. marshallae* in late July 2001, the only interval (of 20 intervals in 11 yr in our study) when *C. marshallae* was dominant at St. George I., although it was of about equal importance as *Neocalanus* at times in 1997 and 1999. *C. marshallae* was apparently much more profitable than *Neocalanus* within the foraging range of auklets at St. Paul I. at times in 1997, 2000, 2001 and 2005. In the same vein, the switch from *N. plumchrus/flemingeri* in early July to *N. cristatus* in late July 2004 at St. George I.

likely reflected a change in the profitability of these species: all samples were collected from the Ulakaia Hill colony, minimizing the possibility that dietary specialization by birds at individual colonies might have accounted for the difference (Springer & Roseneau 1985, Flint & Golovkin 2002).

A much different picture emerged at St. Paul I., where copepods predominated in diets from 1996 to 2001, but thereafter occurred only during early summer. They were nearly gone, at the latest, by early August 2002, by early July 2003, and by mid-July 2004 and 2005. In 2006, *Neocalanus* and *Calanus marshallae* were again abundant in diets in mid-July, a time by which they had essentially disappeared in the previous 2 yr. Diets from 2002 to 2005 contrasted not only with those from 1996 to 2001 and 2006, but also with those in 1976, 1977, 1984, and 1992, when copepods dominated throughout the chick period (Hunt et al. 1978, Bradstreet 1985, Flint & Golovkin 2002).

As noted earlier, St. Paul I. lies higher on the continental shelf than St. George I. and is therefore not as near to the deep basin, and the source of *Neocalanus* spp. Moreover, the location of St. Paul I. places it somewhat more within the realm of *Calanus marshallae*, a shelf species, than St. George I. Although auklets at St. Paul I. commonly have access to copepods in summer, obviously there can be situations when foraging areas influenced by oceanic waters, i.e. where *Neocalanus* would be expected, are apparently beyond the profitability range of these small seabirds. St. Paul I. lies just 75 km north of St. George I., and although the foraging range of least auklets can be as great as 80 to 100 km, depending on prey distributions (Obst et al. 1995, Flint & Golovkin 2002), from 2002 to 2005 *Neocalanus* were out of range of birds from St. Paul I. much of the time. And, not only were *Neocalanus* commonly unavailable to auklets at St. Paul I. from 2002 to 2005, there were few *C. marshallae* either.

### Causes of copepod anomalies

The unusual paucity of *Calanus marshallae* in continental shelf waters and the sharp demarcation between shelf and oceanic zooplankton communities from 2002 to 2005 were documented by traditional sampling with plankton nets in a single cruise in late July through September 2004 (Coyle et al. 2008). Depleted *Neocalanus* abundances around St. Paul I. at that time were apparently caused by a very sharp boundary between oceanic and shelf water masses (the Middle Front) that restricted the oceanic zooplankton community to the deeper offshore region beyond the reach of foraging least auklets from St. Paul I. The presence of *Neocalanus* spp. in diets at St.

George I. clearly demonstrated that the problem was one of copepod distribution rather than copepod production. In contrast, the lack of *C. marshallae* reflected chronic failures of spring cohorts to persist through summer across a broad region of the shelf in recent years (Coyle et al. 2008).

Transport of shelf water into the vicinity of the Pribilof Is. in summer freshens the upper 50 m of the water column and enhances the strength of the Middle Front (Stabeno et al. 2008) that lies in the vicinity of the 100 m isobath and runs just south of the Pribilof Is. (Coachman & Charnell 1979). Stabeno et al. (2008) proposed one scenario for July to August 2004, in which middle shelf waters expanded southward and westward, dominating the region around the Pribilofs. This kept oceanic water and its zooplankton community away from the Pribilofs (Coyle et al. 2008), sufficiently far that *Neocalanus* spp. were beyond the foraging range of least auklets from St. Paul I. Auklet diets revealed that such a condition apparently occurred many times in the 2000s, and in 2003 it was so strong that auklets at St. George I. also had limited access to oceanic copepods by late July.

Unusually high atmospheric temperatures over the Bering Sea in the 2000s have had a dramatic effect on warming of the upper layer of the water column over the middle shelf (Stabeno et al. 2007), which has apparently had major consequences to the structure of the zooplankton community there. In 2004, a warm year in a series of warm years, the shelf community was dominated by smaller species of copepods and other taxa of zooplankton compared to 1999, a cooler year in a series of cool years (Coyle et al. 2008). Coyle et al. (2008) have proposed that the hot and deep upper layer effectively capped the water column, and in the absence of extreme storms that might have broken down the strong stratification, essential post-bloom primary production was so depressed that spring cohorts of *Calanus marshallae* starved later in summer. Post-bloom new (nitrate) primary production over the middle shelf during summer can augment total annual production by as much as 10 to 50%, depending on the frequency and intensity of storms that break down stratification and mix nutrient-laden water sequestered beneath the pycnocline into the euphotic zone (Sambrotto et al. 1986). But, in 2004 for example, the stratification coefficient had a mean value of  $90 \text{ J m}^{-3}$ , or 2 to 3 times greater than that believed to be optimal for summer primary productivity, and thus, zooplankton productivity (Coyle et al. 2008). As a consequence, a floral community of phytoflagellates and other small taxa likely developed and persisted in 2004 and in other recent years with similar conditions, which fostered the shift from larger species of zooplankton to smaller ones.

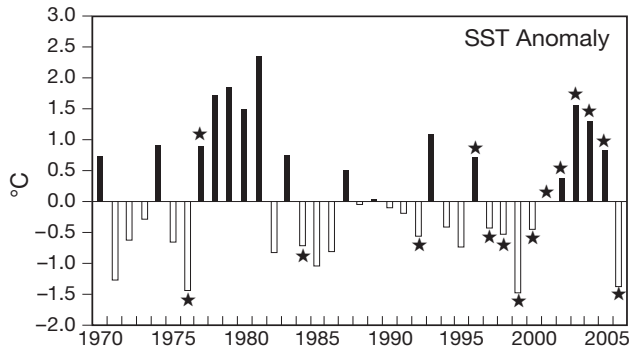


Fig. 4. May sea surface temperature (SST) anomalies in the southeastern Bering Sea (mean temp. = 2.38°C). ★: diet samples obtained at St. Paul I. SST data available at: <http://www.beringclimate.noaa.gov/data/index.php>

There is a notable relationship between one index of environmental conditions in the southeastern Bering Sea, May sea surface temperature (SST), and the presence of copepods in auklet diets at St. Paul I. (Fig. 4). In 8 yr of average or cool May SST, *Neocalanus* spp. and/or *Calanus marshallae* were available to auklets at St. Paul I. However, warm years for which we have diet data were divided into 2 groups: those prior to 2000 (1977 and 1996), when copepods were available despite positive SST anomalies in May, and those after 2000 (2002 to 2005), when copepods were variably scarce. The difference was not simply a consequence of sampling dates—that is, in 1977 and 1996, copepods were available at times in summer when they were scarce in the 2000s. The difference appears to involve the degree of warming that occurred after May in these 2 eras. For example, in 1996, despite early warming of the surface layer, the temperature of the upper layer above the thermocline did not rise to the levels seen from 2002 to 2005, and the total integrated heat content of the water column was correspondingly lower (Stabeno et al. 2008). Similar data from 1979 to 1981 (Sambrotto et al. 1986) suggest that this situation likely prevailed in 1977 as well. These relationships identify a process-oriented conceptual model that could be used to generate hypotheses for future research.

### Consequences of copepod anomalies

For least auklets, the low abundance of their principal copepod prey also had adverse physiological effects, as revealed by elevated levels of corticosterone, an adrenal hormone indicative of nutritional stress (Benowitz-Fredericks et al. 2008). Corticosterone levels of auklets at St. Paul I. were high in June and July 2003, corresponding to the early decline in copepods that year. In 2004, levels were comparatively

low in June and early July, but rose rapidly by late July after copepod abundance collapsed. Field data on aspects of least auklet nesting success or the fitness of chicks at St. Paul I. are not available to evaluate the direct effects of shifts in diets. However, at St. Matthew I. in the central Bering Sea, least auklet chicks grew significantly faster when copepods (*Calanus marshallae*) were abundant in meals brought by adults (Springer et al. 1986); there are strong relationships between least auklet demographic parameters and the amount of copepods in chick diets in the Aleutian Islands (Jones & Williams 2007); and at St. Lawrence I. in the northern Bering Sea, the daily survival rate of least auklet chicks was proportional to the amount of copepods in their diets (Gall et al. 2006). Work on other species of seabirds has found strong negative correlations between stress and various demographic parameters (Kitaysky et al. 2007). Thus, it is reasonable to suspect that the feeding environment for least auklets at St. Paul I. from 2002 to 2005 was detrimental to the health of the population.

In an important respect, the very low abundance of *Calanus marshallae* around the Pribilof Is. in recent years has been just one symptom of the much larger, expansive change in the structure of the pelagic community of the continental shelf of the eastern Bering Sea. Coyle et al. (2008) reported a shift in the size spectrum of zooplankton over the shelf from larger (e.g. *C. marshallae*) to smaller taxa, and suggested that if the condition persisted it would be expected to have numerous repercussions in the pelagic food web for various consumer species of commercial, aesthetic, and ecological importance. Effects of such a shift would be exacerbated around the Pribilof Is., and elsewhere along the outer shelf, by the early expansion of middle shelf waters seaward in summer and the associated offshore displacement of the community of larger oceanic plankton, including notably *Neocalanus* spp.

### CONCLUSIONS

Least auklets at St. Paul I., and probably other planktivores in the region of the Pribilof Is., were subjected to prey (copepod) shortage from 2002 to 2005, apparently brought on by unusually high water temperatures over the continental shelf. A single oceanographic research cruise in summer 2004 documented characteristics of the physical environment and plankton communities that were anomalous compared to previous observations in cooler years. By studying diets of least auklets at the Pribilofs, we extended the temporal and spatial scales of our knowledge of these conditions, and this gave us a much improved under-

standing of responses of the ocean ecosystem to climate warming. There is no evidence that such conditions occurred between the mid-1970s and 2002.

Least auklets sample their environment very efficiently and effectively—despite a limitation on the depth to which they can dive (about 15 m), they are able to forage over considerable distances (up to at least 80 km from their colonies)—and they provide a valuable index of abundance of ecologically important species of zooplankton. The information contained in their diets is large and the cost of acquiring it is small. They should therefore be included and emphasized in any plan to monitor environmental variability in the Bering Sea.

The stories that scientists have to tell about expectations for future impacts of global warming on ecosystems are enriched with integrated observations that link changes in oceanographic conditions with predator and prey data. Collections and analyses of diet data from least auklets in the Bering Sea provide a wealth of information from which we can better understand the ecosystem-scale consequences of climate change. This story tells us that if warming trends continue (e.g. Overland & Wang 2007), there may be serious repercussions to auklets and other planktivorous species in the eastern Bering Sea. Communities and ecosystems are not static, but change over time, yet changes such as those reported here and by others, apparently in response to unusual warming of the Bering Sea in this century, appear to be altering in fundamental ways the structural and functional elements of the ecosystem. We do not know how or if these changes might alter food webs crucial to this highly productive sea over the long term, but they should be a cause for concern to people who depend upon its vast resources and to those charged with their management.

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