



Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific

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ABSTRACT: I examined ~2700 food samples collected from adult and nestling black-legged kittiwakes *Rissa tridactyla* from 1978 through 2011 on Middleton Island in the Gulf of Alaska. The kittiwake diet was composed chiefly of fish, but invertebrates were taken in appreciable quantities in April and May. Upon spring arrival at the colony, adult kittiwakes foraged regularly at night on vertically migrating mesopelagic prey—lanternfishes (Myctophidae), squids, crustaceans, and polychaetes—a behavior they largely discontinued by egg-laying. During incubation and chick-rearing, food samples contained mostly (~85% by weight) Pacific sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus*, Pacific herring *Clupea pallasii*, sablefish *Anoplopoma fimbria*, krill (Euphausiidae), and juvenile salmon *Onchorynchus gorboscha* and *O. keta*. A salient finding over the longitudinal study was the emergence, twice, of capelin as a dominant forage species—once in 2000 to 2003, and again in 2008 through 2011. Kittiwakes responded to capelin availability by producing markedly higher numbers of fledged young. The 2000 to 2003 event corresponded to a previously documented shift to cooler conditions in the NE Pacific, which apparently was relatively limited in magnitude or duration. The more recent transition appears stronger and may be more lasting. I submit that 2008 was an important turning point, marking a substantive reversal of warm conditions that began with the well-documented regime shift of 1977. That interpretation is consistent with the existence of a ~60 yr cycle in ocean and atmospheric conditions in the North Pacific. All else being equal, it predicts the next 20 to 30 yr will be favorable for species such as kittiwakes and Steller sea lions, which seemed to respond negatively to the 1977 to 2007 warm phase of the Pacific Decadal Oscillation.

KEY WORDS: Black-legged kittiwake · Steller sea lion · Forage fish · Capelin · Climate change · 60-year cycle · Pacific Decadal Oscillation · Prey relative occurrence

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INTRODUCTION

Since recognition about 20 yr ago that a large-scale climatic change occurred in the North Pacific around 1977, the concept of periodic regime shifts has become an important organizing principle in marine ecology (Miller et al. 1994, Francis et al. 1998, McGowan et al. 1998, Jiao 2009). In simplified terms, a regime shift is a persistent change from warm to cool conditions, or the reverse, with biological responses that propagate through an ecosystem from

plankton (Mackas et al. 1998, 2007, Batten & Welch 2004) to fish (Beamish & Bouillon 1993, Mantua et al. 1997, Mueter et al. 2007), birds (Piatt & Anderson 1996, Irons et al. 2008, Gaston et al. 2009, Sydeman et al. 2009), and mammals (Alverson 1992, Pitcher 1990, Trites & Donnelly 2003). Sensitized to the prospect and significance of regime shifts, marine scientists have scrutinized historical records for evidence of shifts prior to 1977 (Ware 1995, Mantua et al. 1997, Francis et al. 1998) and are ever on the lookout for contemporary shifts in physical and biological

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conditions. In the North Pacific, there is evidence that substantive shifts toward cooler conditions occurred in both 1989 (Ware 1995, Hare & Mantua 2000, McFarlane et al. 2000) and 1999 (Greene 2002, Peterson & Schwing 2003, Batten & Welch 2004), but arguably no full-blown reversal (cold counterpart) of the warm phase established in 1977 has yet been detected.

Two upper trophic-level species that are widely monitored and that seemed to show strong responses to the 1977 regime shift are Steller sea lions *Eumetopias jubatus* and black-legged kittiwakes *Rissa tridactyla*. Over 2 decades from the late 1970s to late 1990s, the western stock of Steller sea lions (Gulf of Alaska through the Aleutian Islands and Bering Sea) declined about 70%, and the species is currently listed as endangered in the region (www.adfg.alaska.gov/static/species/specialstatus/pdfs/stellersealion_recovery.pdf). Likewise, the breeding productivity of Alaska kittiwakes declined after 1977 (Hatch et al. 1993, 2009), and numbers decreased sharply in some colonies (Fig. 1). Changes in both sea lions and kittiwakes are thought to be food related (Hatch et al. 1993, Merrick et al. 1997, Trites & Donnelly 2003), and may in fact be closely linked. Both species likely depend as adults and/or during development on forage fish such as capelin, sand lance, and herring (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m477p271_supp.pdf for scientific names of most fish and invertebrates mentioned in text). Major changes in fish stocks after 1977—declines in forage species and increases in demersal fish (e.g. pollock, halibut *Hippoglossus stenolepis*), salmon, and other species of lesser importance to birds and pinnipeds—are documented (Anderson et al. 1997, Anderson & Piatt 1999).

Kittiwakes are ubiquitous breeders in cold regions of the northern hemisphere and are undoubtedly the most widely monitored seabird species with respect to numbers and productivity (Frederiksen et al. 2005, 2007a, Hatch et al. 2009). Their confinement to surface foraging makes them highly sensitive to factors affecting the vertical distribution of prey. As open cliff-nesters, kittiwakes are easily studied in many respects, but diet information is less available because sampling entails lethal collection of birds or handling chicks and adults frequently to obtain regurgitated food items. Data on the summer diets of Alaska kittiwakes (Hatch et al. 2009) give the general impression of taxonomically stable food bases locally, with clear geographical differences. Birds in the Gulf of Alaska rely heavily on sand lance, capelin, and (especially in Prince William Sound)

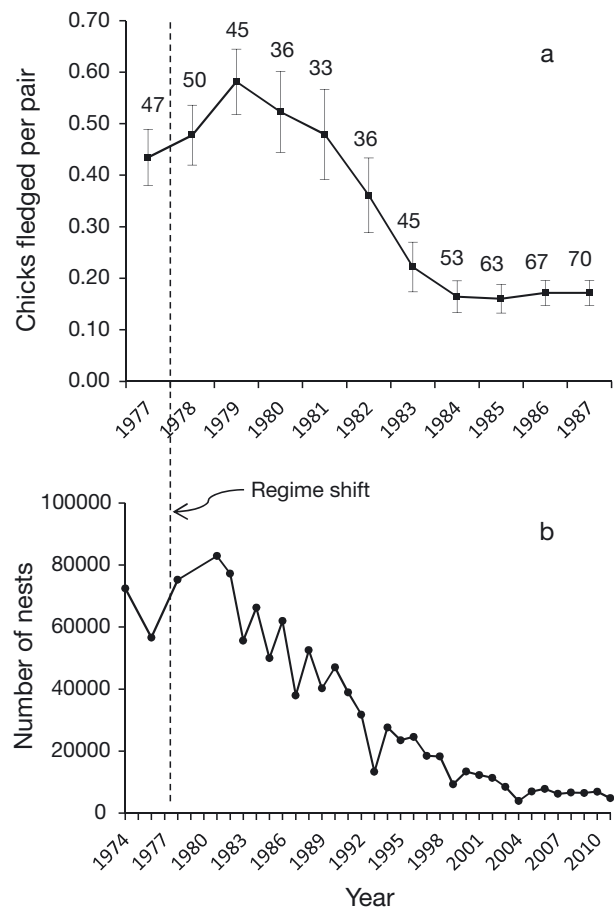


Fig. 1. *Rissa tridactyla*. Declines in kittiwake productivity and numbers following a 1977 regime shift in the North Pacific: (a) 5 yr running means (\pm SE) of annual chick production in kittiwake colonies Alaska-wide (calculated from data in Hatch et al. 1993). Values above error bars are the numbers of measurements (colony-years) included in the means. (b) Population history of kittiwakes on Middleton Island, North-Central Gulf of Alaska

herring, whereas gadids (Arctic cod *Boreogadus saida* and juvenile walleye pollock) are prevalent at some colonies in the Bering and Chukchi seas. Most sampling reported to date is confined to the chick-rearing period, and few published studies document kittiwake diets in more than a few years at any colony (but for the Pribilof Islands, Bering Sea, see Sinclair et al. 2008, Renner et al. 2012).

The aim of this paper is to report on long-running time series of diet samples and chick production in black-legged kittiwakes at an Alaskan colony and to highlight a clear transition that occurred in both parameters around 2008. I will argue that 2008 was an important threshold year, quite possibly marking a substantive reversal of the 1977 regime shift.

MATERIALS AND METHODS

Study area

Middleton Island (59.4°N, 146.3°W) is situated near the edge of the continental shelf in the northern Gulf of Alaska (Fig. 2). It lies squarely in the path of the Alaska Stream (Stabeno et al. 2004), and because of its distance from the mainland is probably influenced little by land morphology, freshwater runoff, and other factors operating locally nearer the coast (Mundy et al. 2010). Given its proximity to the shelf break, kittiwakes *Rissa tridactyla* breeding on Middleton have access to 2 distinct foraging habitats—a shallow (~100 m) neritic zone, extending broadly to the east, west, and north of the island, and deep oceanic waters (200 to 4000 m) over the continental slope and beyond. This situation is unusual for Gulf of Alaska colonies, but also exists at some breeding sites in the Aleutian Islands and Bering Sea. Middleton Island was an important haul-out and irregular breeding site for Steller sea lions until 1989, when an aggregation that numbered ~1000 to 3000 animals abruptly abandoned all use of the island. From 1990 through 2011 (summer seasons), sea lions have not returned in any appreciable numbers (NMFS Steller Sea Lion Count Database: www.afsc.noaa.gov/nmml/alaska/sslhome/databases/adult.php; S. A. Hatch pers. obs.).

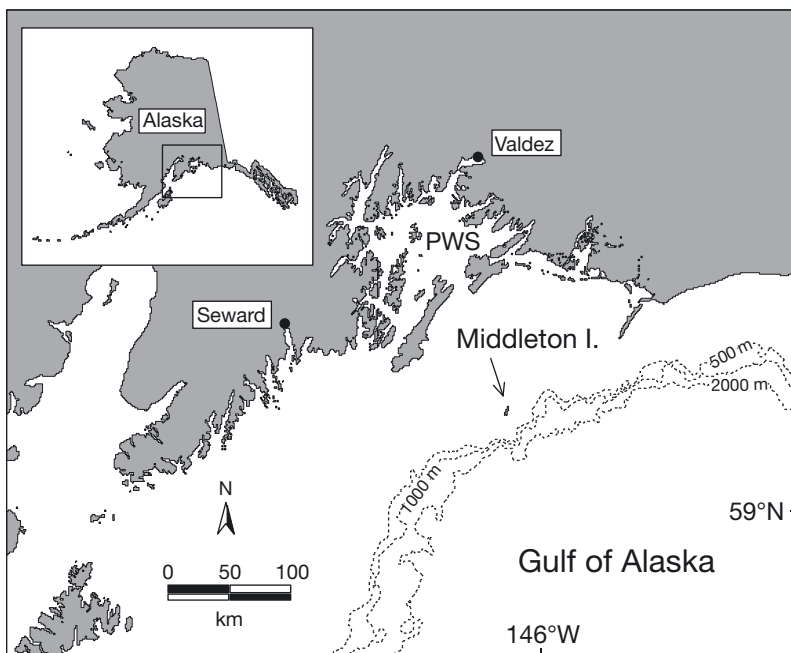


Fig. 2. Location of Middleton Island and its proximity to the continental shelf edge in the northern Gulf of Alaska. PWS: Prince William Sound

Field collections

Diet sampling of kittiwakes on Middleton spanned the period from 1978 to 2011, with large gaps in the early years but continuous observations since 1996. Chick production was measured in 1978 and annually since 1981. Food collections totaled 2703 samples, including 927 samples from adult kittiwakes and 1776 samples from chicks (Table 1). Apart from 75 adults collected offshore by shotgun in 1989 to 1990, all food samples were obtained as regurgitations from birds captured for measurements and banding at the colony. Regurgitated food samples consisted of slightly to moderately digested masses of recently ingested prey, i.e. kittiwakes do not cast pellets of fish bones, otoliths, and other indigestible prey parts, in contrast to some *Larus* gulls and cormorants (Phalacrocoracidae). Samples from the earlier years (through 1992) were preserved in alcohol or formaldehyde solution, whereas later collections were frozen for later sorting and identification in the laboratory.

The mean date of first egg-laying by kittiwakes on Middleton (\pm SE) was 1 June (\pm 2.3 d, $n = 8$ yr between 1993 and 2000; S. A. Hatch unpubl. data), and casual observations by island residents (D. Baxter pers. comm.) indicate the birds typically reoccupy their nest sites in late March or early April. Therefore, samples collected in April and May correspond approximately to the prelaying period, while material from June through August corresponds to incubation and chick-rearing. To highlight changes that occur in spring, I further subdivided the samples into early prelaying (April) and late prelaying (May).

Laboratory analysis and data summary

In the laboratory, prey were identified to the lowest taxon possible, mostly under contract with K. Turco (Alaska's Spirit Speaks: Sound & Science) in the years from 1994 through 2000. Material from 1978 and 2001 to 2011 was processed by me, whereas samples from 1989 to 1992 were analyzed by B. S. Fadely. In learning to distinguish and accurately identify prey types in kittiwake regurgitations, I was aided by having large numbers

Table 1. *Rissa tridactyla*. Temporal distribution of diet samples from black-legged kittiwakes on Middleton Island, 1978 to 2011

Year	Apr Adults	May Adults	Adults	Jun Chicks	Total	Adults	Jul Chicks	Total	Adults	Aug Chicks	Total	Total
1978							38	38		2	2	40
1989	2	2				5		5			0	9
1990	17	7	18		18	21	9	30			0	72
1992		1			0			0	3		3	4
1994	3				0			0			0	3
1996		19			0		37	37		17	17	73
1997		4	4	3	7	3	107	110	1	35	36	157
1998		32	11	16	27	13	130	143	7	64	71	273
1999		11	11		11	9	51	60	2	45	47	129
2000	41	7	13	1	14	4	87	91		29	29	182
2001	10	19	7	23	30	10	321	331		31	31	421
2002	26	14	2	22	24	1	193	194		22	22	280
2003	4	22	24	3	27	22	15	37	5	2	7	97
2004	9	8		1	1	11	7	18			0	36
2005	4	12	3		3	5	10	15	1	2	3	37
2006		6	6	8	14		100	100		19	19	139
2007	1	21	4		4	13	3	16	1	3	4	46
2008	44	10	4	2	6	2	40	42	2	13	15	117
2009	36	21	16	2	18	22	27	49	2	7	9	133
2010	39	51	39	34	73	27	128	155	4	36	40	358
2011	32	14	3		3	9	18	27	8	13	21	97
Total	268	281	165	115	280	177	1321	1498	36	340	376	2703

of prey samples from rhinoceros auklets *Cerorhinca monocerata* and tufted puffins *Fratercula cirrhata* collected on Middleton over the same span of years as the kittiwake studies (S. A. Hatch unpubl. data). The latter samples were whole (un-ingested) fish collected as bill-loads from chick-rearing auklets and puffins—ideal specimens from which to obtain diagnostic materials such as otoliths, parasphenoid bones and other skeletal elements, skin and scale samples, and other prey parts useful for species identification. Auklets and puffins reliably and exhaustively sampled the same forage fish community around Middleton as was used by foraging black-legged kittiwakes.

Thawed samples were weighed and sorted by prey types, each of which was further weighed and quantified by numbers of individual prey items. The latter I obtained by direct count (approximated in many cases) or, for the smallest invertebrate prey (krill and copepods), by extrapolation from prey mass using the average mass of individuals (0.1 g for krill, 0.01 g for copepods). In 2 of the common fish prey (Pacific sand lance and Pacific herring), it was possible to distinguish young-of-the year (age-0) fish from older individuals readily by size.

Ideally, one would express diet composition in terms of percent biomass at the time of ingestion. That is not feasible for regurgitated food samples because it is difficult to separate fleshy material pre-

cisely and also because of variable residence times and differential digestion in the gut (Duffy & Jackson 1986, Barrett et al. 2007). The main comparative measure I used was the frequency of occurrence (i.e. presence–absence data) of each prey type, where the denominator was the sum of all prey type identifications in a given collection of samples. I call the measure ‘relative occurrence’ to distinguish it from a frequency of occurrence where the number of samples examined is used as the denominator. The difference between the 2 methods and the preference for relative occurrence over other possible measures of diet composition is addressed in Supplement 2 at www.int-res.com/articles/suppl/m477p271_supp.pdf. In calculating means across years, I used a ‘mean of (annual) proportions,’ as opposed to a ‘pooled sample proportion’ (see Supplement 2).

To test for age-related differences in diet (adult kittiwakes versus chicks), I applied Pearson chi-squared tests to cross-tabulations of prey types and kittiwake age groups. Analyses were limited to months with chicks present (June to August) in years ($n = 16$) when both age groups were sampled. An expected cell frequency >1 was required for inclusion in the chi-squared statistic. Because sample sizes for chicks and adults differed substantially among years, as did diet composition, I separated tests for years, then did a combined probabilities test

(Sokal & Rohlf 1995, p. 794–797) of the null hypothesis of no difference between chicks and adults.

Most food samples were taken from birds nesting on a tower at Middleton (Gill & Hatch 2002), which has been used for in-depth studies of breeding seabirds since 1995. The tower was also the primary site for observations on chick production, as pairs could be monitored unobtrusively from inside the building through panes of 1-way mirror glass. Away from the tower, productivity was assessed by tallying nests built on a series of index plots in natural habitat (June) and counting the number of chicks surviving in the same plots late in the season (August).

Kittiwakes nesting on the tower were split into treatment groups—some were given supplemental food ad libitum throughout the breeding season, while the rest served as unfed controls (Gill & Hatch 2002, S. A. Hatch unpubl. data). For present purposes, I considered only the productivity of unfed kittiwakes. Most food samples (91%) included in the analysis were also obtained from unfed tower birds. Since 1998, the material used for supplemental feeding has been adult Atlantic capelin obtained from commercial fisheries in Newfoundland, Canada, and/or Iceland. I found that in all cases there was no difficulty distinguishing local capelin from Atlantic capelin, as the latter had distinctly larger bodies. I disqualified any sample containing supplemental Atlantic capelin.

To place the kittiwake diet analysis in the context of ocean regimes, I used graphical data for the Pacific Decadal Oscillation (PDO), which is openly available on the Internet but derives originally from the dataset supplied by N. Mantua (<http://jisao.washington.edu/pdo/PDO.latest>). I also considered a related index (Atmospheric Circulation Index, ACI) published by Klyash-torin (1997, 2001).

RESULTS

At least 40 species of fish and invertebrates occurred in kittiwake *Rissa tridactyla* regurgitations (Supplement 1). A comparison of analysis methods (Supplement 2) revealed that frequency of occurrence per prey type (relative occurrence) was the best-performing method of characterizing the diet, and that is primarily what is reported below.

Although chick samples outnumbered adults nearly 2:1 (Table 1), there was ample material from both groups and scant evidence that they should be treated separately. One of 16 chi-squared tests was significant (1998, $p = 0.03$), 1 test yielded $p = 0.064$, while 14 tests produced p -values between 0.126 and 0.816. Given the number of tests performed, the 1998 result was quite possibly a Type II error (expected in 1 test among 20). The combined probability for 16 independent tests of the null hypothesis (no difference between chicks and adults) was $p = 0.415$. I therefore pooled the samples from adults and chicks in all analyses to follow.

Fish dominated the diet overall, and 5 taxa—sand lance, capelin, herring, myctophids (lanternfish), and sablefish—made up the bulk of the fish prey (Fig. 3). There was, however, a marked seasonal transition. For several weeks following spring arrival, adult kittiwakes preyed heavily on myctophids and invertebrates, the latter consisting mainly of squid, 2 or more species of euphausiids (krill), the amphipod *Paracallisoma alberti*, and large (~9 to 12 cm) pelagic polychaetes. The use of myctophids and invertebrates declined through May, and by the main part of the breeding period (June to August) myctophids decreased to trace levels in the diet.

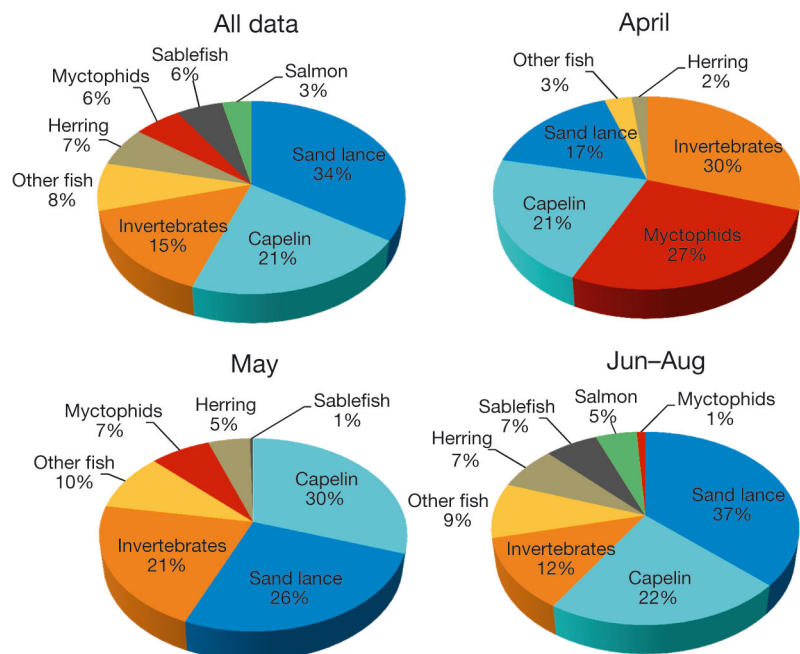


Fig. 3. *Rissa tridactyla*. Overall composition of kittiwake diet and composition during 3 stages of breeding on Middleton Island from 1978 to 2011. Sample sizes as listed in Table 1

Interannual variability and trends

Over the course of the study, sand lance was the single most important prey species, followed by capelin. Capelin were scarce or absent in early years, but were prominent in 2 multi-year intervals after 1999, namely 2000 to 2003 and 2008 to 2011 (Fig. 4). In the latter interval, capelin dominated the diet even early in the season, when formerly either myctophids (April) or sand lance (May) had been the principal

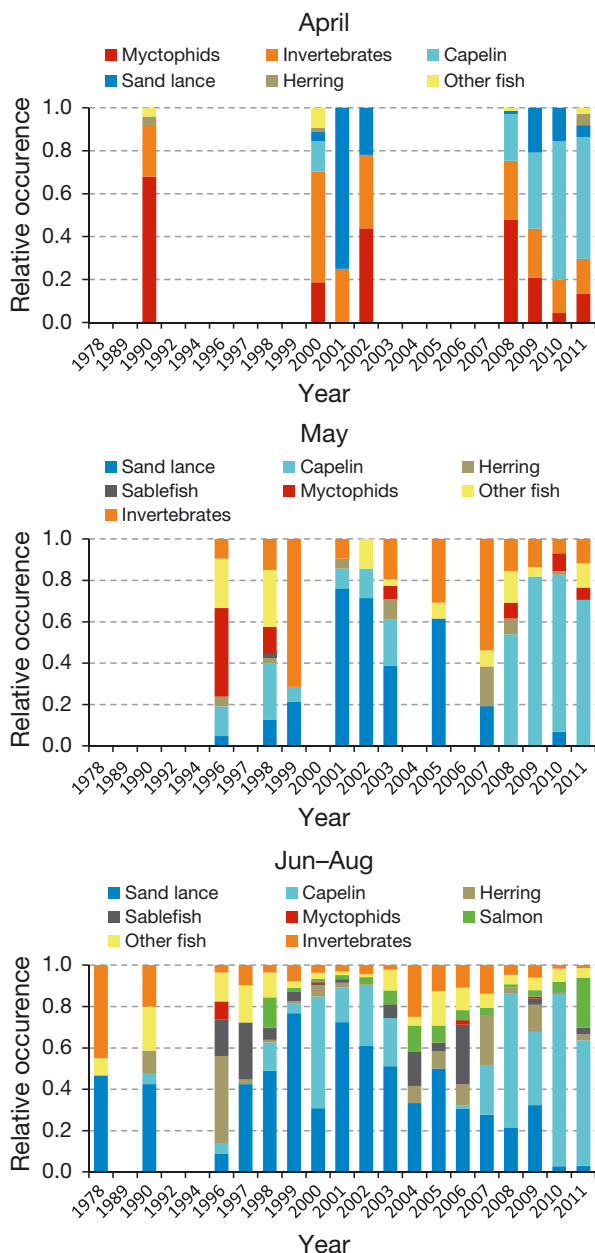


Fig. 4. *Rissa tridactyla*. Interannual variation in kittiwake diet composition at 3 stages of breeding on Middleton Island, 1978 to 2011. Sample sizes as listed in Table 1

fish prey. Charted individually, the complementary (i.e. roughly inverse) relation between relative occurrence of sand lance and capelin is evident ($r = -0.54$, $p = 0.021$; Fig. 5). Other fish prey were important in the diet sporadically, e.g. herring in 1996 and 2007 and sablefish in 1996 to 1997 and 2006 (Fig. 4). Invertebrates (mainly euphausiids) contributed substantially to the chick diet in some years (e.g. 1978, 2004; Fig. 4).

Prey age classes and reproductive status

Among the sand lance and herring consumed, about 40 and 25%, respectively, were first-year individuals, whether quantified by relative occurrence or percentage of biomass (Table 2). Juvenile herring appeared only during July and August, whereas age-0 sand lance occurred in all months, increasing from around 10% of all sand lance in April to around 70% by August. The relative occurrence of first-year sand lance was variable among years (Fig. 6), and a pattern of strong age-0 classes followed by 1 or 2 yr dominated by older fish may have reflected the maturation and continued use by kittiwakes of strong year classes of sand lance produced, for example, in 2004, 2006, and 2009. The appearance occasionally of early post-larval sand lance (~30 to 40 mm; posi-

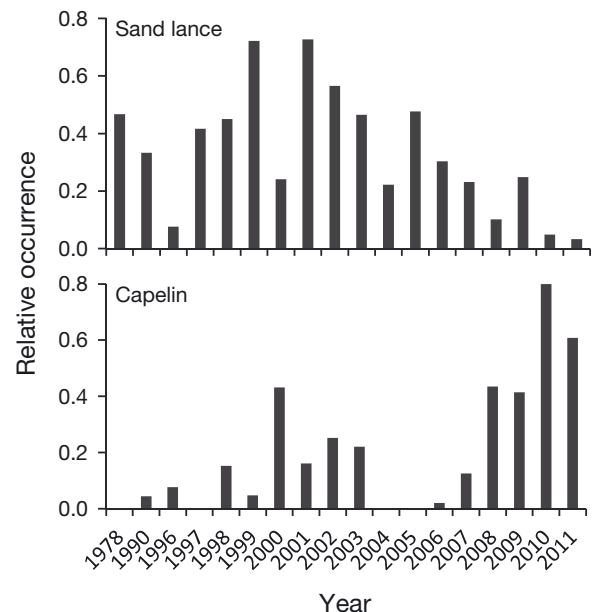


Fig. 5. Inverse relation between relative occurrences of Pacific sand lance and capelin in the summer diet of kittiwakes *Rissa tridactyla* on Middleton Island, 1978 to 2011. Data from all months combined; Pearson's r (sand lance versus capelin relative occurrences) = -0.54 , $p = 0.021$

Table 2. First-year (age-0) sand lance and herring as percentages of each species' occurrence in the kittiwake *Rissa tridactyla* diet on Middleton Island

Month	Sand lance		Herring	
	Relative occurrence	Biomass (%)	Relative occurrence	Biomass (%)
Apr	9.8	6.9	0.0	0.0
May	10.0	11.2	0.0	0.0
Jun	23.5	12.1	0.0	0.0
Jul	45.0	45.0	29.8	24.4
Aug	67.1	70.5	61.9	63.5
All	42.4	44.2	27.8	23.8

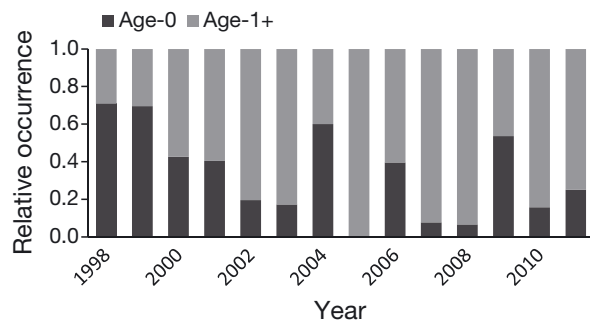


Fig. 6. Year-to-year changes in age composition of Pacific sand lance in the diet of black-legged kittiwakes *Rissa tridactyla* on Middleton Island, 1998 to 2011

tively identified by parasphenoid bones) in June and July suggested the likelihood of late winter spawning in the vicinity of Middleton Island.

Although beach spawning sites of capelin were not discovered on Middleton, the occurrence of gravid females in kittiwake diets and larval capelin in chick meals of rhinoceros auklets *Cerorhinca monocerata*

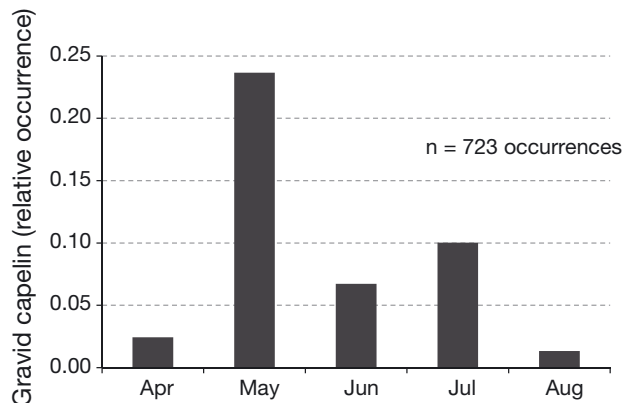


Fig. 7. Seasonal occurrence of gravid female capelin in kittiwake *Rissa tridactyla* diet samples from Middleton Island, 1978 to 2011

(S. A. Hatch unpubl. data) suggested the likelihood of local reproduction, apparently in deeper, offshore sites. The timing of egg-bearing females implies a peak of capelin spawning activity during May (Fig. 7). Years with the greatest numbers of gravid female capelin were 2000 (~30%) and 2009 (~26%).

Sablefish and salmon (including both pink and chum salmon) are species that rapidly outgrow the size range in which they are accessible to seabirds, and thus they occurred strictly as first-year fish in the kittiwake diet. Both species were taken seasonally during July and August, with a peak in sablefish occurrence preceding peak salmon occurrence by about a week (Fig. 8).

Covariation of ocean temperature, capelin, and kittiwake chick production

In the NE Pacific, the period from 1978 through 2007 was characterized by generally warm ocean conditions during summer, as indicated by the positive PDO index averaged over June, July, and August (Fig. 9). Within that period, a temporary shift to cooler conditions occurred from about 1999 to 2002, at which time capelin first appeared in appreciable quantities in the kittiwake diet at Middleton. Kittiwakes responded with markedly higher productivity in 2000 to 2002 (about 1 chick per breeding pair versus 0.2 chicks per pair on average in 20 prior years). From 2003 through 2007, sea surface temper-

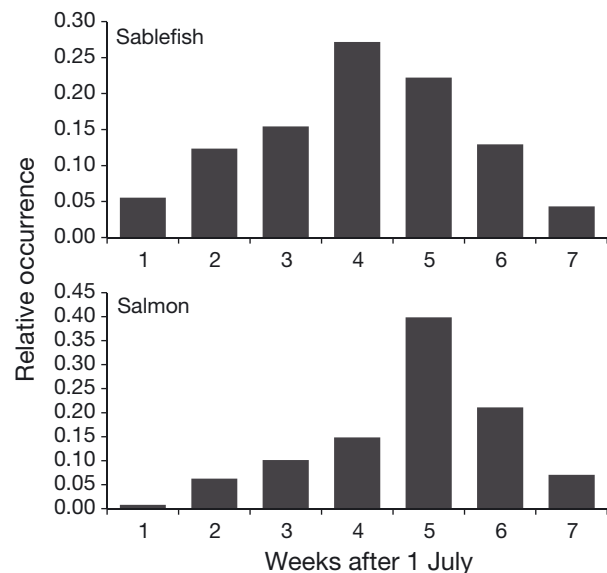


Fig. 8. Seasonality of sablefish and salmon in the diet of black-legged kittiwakes *Rissa tridactyla* on Middleton Island, 1978 to 2011

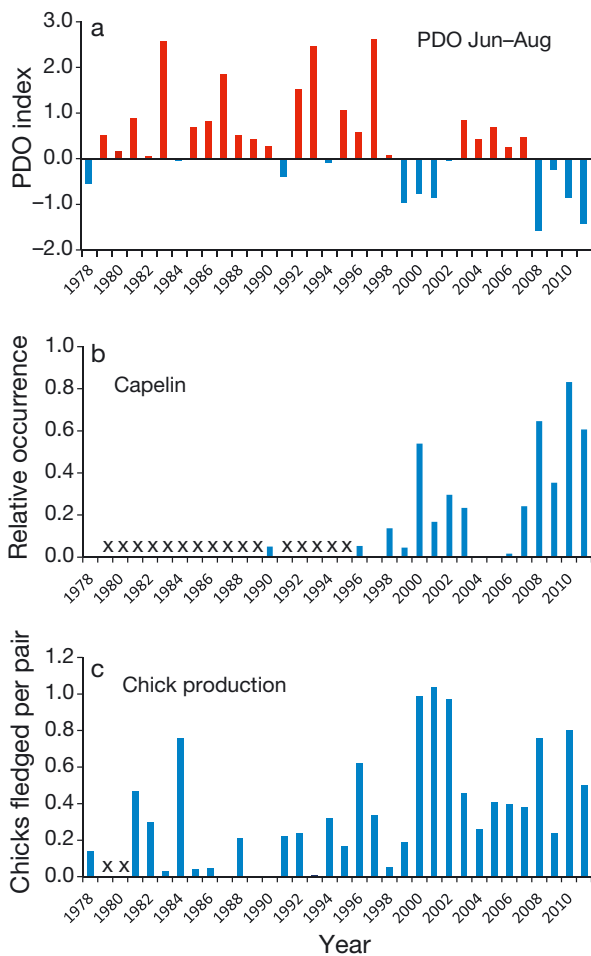


Fig. 9. (a) Relations among the Pacific Decadal Oscillation (PDO) index (June to August), (b) the relative occurrence of dietary capelin, and (c) annual chick production by kittiwakes *Rissa tridactyla* on Middleton Island, 1978 to 2011. Observations of chick production prior to 1991 were made away from the Middleton tower; subsequent data reflect the breeding performance of unfed birds at the tower. X: missing data

ature reverted to a warm state, capelin were scarce or absent in the kittiwake diet, and chick production declined to pre-2000 levels. Finally, 2008 marked the beginning of a second reversal of conditions—cool water, a resurgence of capelin, and improved breeding success among unfed kittiwakes on the Middleton tower. Simple correlation analysis confirmed the statistical significance and moderate explanatory power of the PDO–capelin–kittiwake relations (r^2 values from 0.304 to 0.367; Table 3).

Kittiwakes using natural cliffs as nesting habitat on Middleton are subject to greater harassment and predation by bald eagles *Haliaeetus leucocephalus* and glaucous-winged gulls *Larus glaucescens* than tower birds, and their breeding success was at or

Table 3. Pearson correlations among the Pacific Decadal Oscillation (PDO) index (June to August), relative occurrence of dietary capelin, and kittiwake *Rissa tridactyla* chick production on Middleton Island over 32 yr, between 1978 and 2011

Variable	Statistic	Variable	
		Chick production	Capelin in diet
Capelin in diet	Pearson's r	0.551	–
	p (2-tailed)	0.018	–
	n (yr)	18	–
PDO (Jun–Aug)	Pearson's r	–0.505	–0.606
	p (2-tailed)	0.003	0.008
	n (yr)	32	18

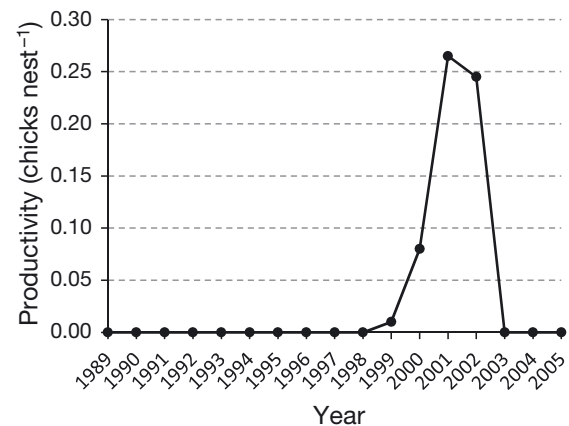


Fig. 10. *Rissa tridactyla*. Productivity of kittiwakes breeding in natural cliff habitat on Middleton Island, 1989 to 2005. A positive response to cooling surface water and dietary capelin was evident in 2000 to 2002

near zero in the decade from 1989 to 1999. Against that background, the birds' response to the cooling episode and capelin abundance in 2000 to 2002 was conspicuous (Fig. 10). The syndrome of abject failure returned subsequently, however, and in recent years the few birds remaining on natural cliffs have effectively ceased to function as a viable colony (i.e. no chick production from 2006 to 2011).

DISCUSSION

Far from being a fixed aspect of the local environment, the forage fish community around Middleton Island, as displayed in kittiwake *Rissa tridactyla* diet composition, changed markedly in the years from 1978 through 2011. Some of the local diversity of fish prey reflects the island's location on the outermost shelf, where myctophids and other mesopelagic prey

are available to kittiwakes foraging at night. Middleton's proximity to the demersal spawning grounds of sablefish (>300 m on the continental slope; Sigler et al. 2001) accounts for that species' appearance in appreciable numbers during some years—juvenile sablefish are epipelagic, moving inshore and growing rapidly there during their first year of life (Kendall & Matarese 1987). Likewise, the outmigration and early development of juvenile pink and chum salmon from spawning streams and hatcheries in SE Alaska and Prince William Sound matches well the chick-rearing period of kittiwakes on Middleton (Willette et al. 2001). Neither salmon species is commonly reported in Alaskan seabird diets.

Studies that examine concurrently the foods of adult and nestling seabirds often find dietary differences between the 2 (Barrett et al. 2007). While that was not the case here, no firm conclusion was possible as most of the regurgitations obtained from adults during chick-rearing probably represented food intended for chicks. The use of pelagic prey (myctophids, squids, polychaetes, crustaceans) by adult kittiwakes in spring did not extend into the chick-rearing period, presumably because forage fish became available closer to the island later in the season.

The most salient finding was that the kittiwake diet shifted conspicuously to capelin when surrounding waters turned relatively cold. The apparent timing of capelin availability has advanced in recent years, with kittiwakes now feeding heavily on capelin upon their arrival at the colony in April, foregoing to a large extent the pelagic foraging they practiced in earlier years. Ecologically, capelin are considered to be a 'cold water' species whose distribution is sensitive to small changes in ocean temperature (Rose 2005, Hollowed et al. 2007). Large movements of capelin among offshore areas in the NW Atlantic have coincided with anomalous cold-water events (Frank et al. 1996); thus, the availability and use of capelin by seabirds in the region is strongly coupled with oceanographic conditions (Carscadden et al. 2002, Davoren et al. 2012). In Alaska, a signature change in fish and shellfish communities following the 1977 regime shift was the virtual disappearance of shrimp and capelin in nearshore trawl surveys (Anderson et al. 1997, Anderson & Piatt 1999). Whether the change in capelin stocks was manifested primarily in overall abundance, distributional shifts, or both is poorly understood (Brown 2002, Doyle et al. 2002, Arimitsu et al. 2008). Certainly, pockets of local capelin abundance (as reflected in seabird diets) persisted in the 1980s (Hatch & Sanger 1992), but limited information on diets prior to 1977

suggests greater use of capelin during the preceding cold period in Alaska (Piatt & Anderson 1996).

At many locations in Alaska, Pacific sand lance has been the primary forage species of kittiwakes and other seabirds in the last 30 yr (Hatch & Sanger 1992, Willson et al. 1999, Hatch et al. 2009). It remains to be seen whether a shift from sand lance to capelin-dominated summer diets, as documented here for Middleton Island, has already transpired or will occur at many of the same locations. Without independent knowledge of species' abundances in the water column, it is not possible to say whether the emergence of capelin as the dominant forage species at Middleton reflects a decline of sand lance, a superabundance of capelin, or both. The dynamics of sand lance and capelin in Alaska may be analogous to the regular fluctuations of sardines *Sardinops sagax*, anchovies *Engraulis* spp., and herrings *Clupea* spp. in other ocean regions, with sand lance (sardines) dominating in warm conditions and capelin (anchovies or herring) holding sway in times of cooler climate (Baumgartner et al. 1992, Kawasaki 1992, Chavez et al. 2003).

Following the well-studied and widely acknowledged regime shift of the late 1970s, analysis of physical and biological time series led some researchers to conclude that substantive shifts (warm to cold) occurred in both 1989 (Ware 1995, Hare & Mantua 2000) and 1998 to 1999 (Minobe 2002, Chavez et al. 2003, Peterson & Schwing 2003, Batten & Welch 2004). The 'reality' or importance of both of those purported change points has been debated (McFarlane et al. 2000, Greene 2002, Bond et al. 2003), and depending on one's temporal frame of interest and criteria for regime change, there will inevitably be 'false positives' identified with sufficient hindsight (Schwing & Moore 2000, Rodionov & Overland 2005). The 1989 and 1999 events, for example, were probably driven to some degree by the La Niña conditions that prevailed in 1988 to 1989 and 1998 to 2001, respectively (National Weather Service, www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). It is possible the proposed 2008 regime change will also prove to be ephemeral—strong La Niña conditions prevailed during many months in 2007 to 2011 (National Weather Service, loc. cit.), and as yet there is little in the kittiwake responses on Middleton Island to distinguish between 2000 to 2003 and 2008 to 2011 (Fig. 9). However, for reasons depicted graphically (Fig. 11) and discussed below, it seems likely that the latest shift to cold water, capelin abundance, and improved kittiwake performance will be a more

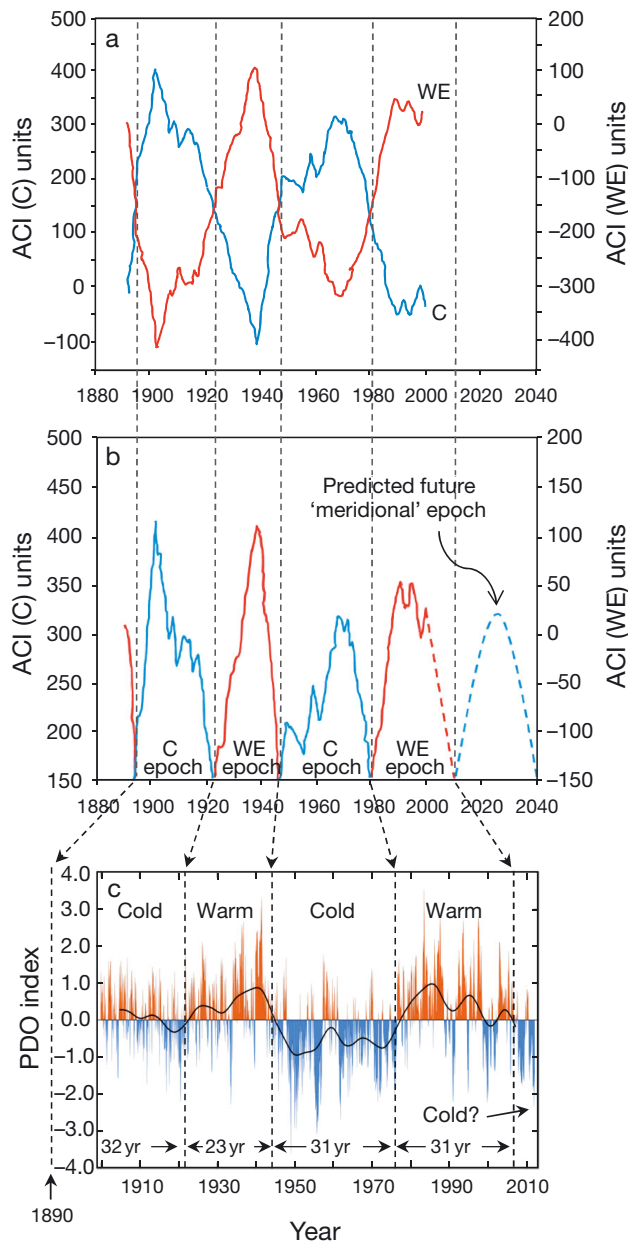


Fig. 11. (a,b) Measured atmospheric circulation index (ACI) and model of air movements over the North Atlantic and Europe (redrawn from Klyashtorin 2001) suggests a close connection between phases of ocean warming and cooling and synoptic patterns of air circulation in the northern hemisphere (see 'Discussion') with 2 competing modes of circulation—meridional (C) and latitudinal (combined west and east, denoted WE). (c) Pacific Decadal Oscillation (PDO) indices 1900 to present (http://en.wikipedia.org/wiki/Pacific_decadal_oscillation, based on data from N. Mantua: <http://jisao.washington.edu/pdo/PDO.latest>), showing 3 previously identified shifts in the PDO (~1921, 1945, and 1977), a prior regime shift (~1890) documented by Minobe (1997), and a presumptive shift from warm to cold conditions in the northeast Pacific around 2008 (curve: multi-year smoothed curve of PDO index). Dashed arrows highlight the close correspondence between change points identified in the ACI and PDO models

robust and lasting change to the ecosystem than that which occurred in either 1989 or 2000. Specifically, there is a basis for viewing the 2008 change point as a true counterpart—a reversal—of the warm phase begun in 1977.

In the literature pertaining to climate fluctuations and associated patterns of species' abundances, there are many references to what is commonly called a (or 'the') '60-year cycle' (e.g. Baumgartner et al. 1992, Klyashtorin 1997, Zhen-Shan & Xian 2007). While 60 yr is a convenient period to use for modeling purposes (Loehle & Scafetta 2011, Zwolinski & Demer 2012), examination of empirical data of various types and durations leads different authors to speak of a '50-year cycle' (Chavez et al. 2003), a 'quasi 60-year cycle' (Mazzarella & Scafetta 2011), a '50–70 year cycle' (Minobe 1997, 1999, Mantua & Hare 2002, Klyashtorin et al. 2009), a '50–79 year cycle' (Humlum et al. 2011), or a '50–75 year cycle' (Ware 1995). Given decidedly noisy signals, long periodicities relative to human lives and datasets, possible lag times, and limited or no understanding of mechanisms, it remains to be shown to what extent such reports are describing either the same or multiple, unconnected phenomena. Without question, the amount and quality of relevant data have increased dramatically in recent decades, and the pace of discovery will continue to accelerate. In the PDO time series (Fig. 11), a mid-1940s change point and the late-1970s change point seem well-defined, giving a bounded cold period of ~31 yr. In the ensuing warm phase, we saw the previously noted jumps to negative PDO values (~1989 and 1999 to 2002), but neither condition persisted. A more lasting transition to cold conditions in 2008 would close a ~31 yr warm phase and complete a full cycle (cold–warm–cold) that began around 1944. Under that scenario, a regime shift in ~2008 was predicted. Time will tell whether the model of a ~60 yr cycle holds up in this instance.

Klyashtorin (1997, 2001) and Klyashtorin et al. (2009) find strong correlations between global commercial fish production and climate indices, including a global temperature anomaly computed for instrumental data collected since ~1850 and another synoptic indicator called the ACI. The ACI summarizes annual patterns of atmospheric pressure and air mass transfer over the Atlantic–Eurasian region. Three basic types of circulation—meridional (denoted C), western (W), and eastern (E)—are recognized, and the index further categorizes circulation into 2 competing modes: meridional (C) and latitudinal (combined W and E, denoted WE or 'zonal'). The 2 modes are strictly complementary (inversely related)

because their measures are obtained in such a way that they sum to zero (Fig. 11a). The points in time at which one mode or the other becomes dominant define so-called 'epochs' of air mass circulation (denoted C and WE epochs, respectively) the durations of which have averaged about 30 yr over the past 120 yr (Fig. 11b). The change points between epochs correspond closely to change points recognized in the PDO index (Mantua & Hare 2002, Minobe 1997; Fig. 11b,c). The ACI model anticipated a phase change to occur in ~2008 and predicts a cold (WE) epoch to persist for ~30 yr thereafter (Fig. 11b). Russian and Australian geophysicists (Sidorenkov & Wilson 2009, Sidorenkov et al. 2010) find close correspondence, with lag times, between global temperature anomalies since 1900, the ACI, and cyclic gravitational characteristics of the solar system. The Russian models deserve careful consideration and further testing, because they offer predictive capability relevant to wildlife conservation and fisheries management and suggest physical mechanisms related to 60 yr cycles.

If 2008 proves to be a definitive change point in a ~60 yr cycle, then the next couple of decades should be good ones for sea lions and kittiwakes in Alaska. We should see kittiwakes on Middleton Island continue to have improved breeding success, and their numbers should increase (subject to availability of suitable nesting habitat, which is declining due to post-earthquake successional change). We should expect to find sea lions rebuilding their numbers, including a recolonization of Middleton Island as a breeding and/or haul-out site. While the change may not be good for Alaskan salmon, stocks in the Pacific Northwest should respond favorably—there is evidence (Francis et al. 1998) that salmon production is inversely affected by warm and cold phases in the California Current and Alaska Current systems.

The concept of natural climate cycles—including, besides the mentioned 60 yr periodicity, purported cycles of ~20 yr (Minobe 1999, Mantua & Hare 2002, Loehle & Scafetta 2011), other relatively high-frequency harmonics (Ware 1995, Zhen-Shan & Xian 2007, Scafetta 2012), and even centenarian and millennial scale oscillations (Humlum et al. 2011)—is controversial, because it impinges on the debate about greenhouse gas effects and anthropogenic global warming. One school of thought (IPCC 2007) maintains that warming since ~1970 is primarily attributable to human activity, while another (Zhen-Shan & Xian 2007, Klyashtorin et al. 2009, Scafetta 2010, 2012, Humlum et al. 2011, Loehle & Scafetta 2011) argues that natural cycles of climate variation

are equally or more important. A third point of view is that the worst effects of human-caused warming are still to come as methane release from melting permafrost and other amplifying feedbacks cause runaway increases in global temperature and sea level (Lawrence & Slater 2005, Hansen & Sato 2012). Fortunately, these competing views make specific and opposing predictions for global temperature measurements in coming decades, and the crux of the issue should be settled within 10 to 20 yr.

The traction that long-term datasets have given us toward understanding ocean dynamics is a strong affirmation of the historical-descriptive approach advocated by Francis & Hare (1994). Going forward, it will be important to systematically monitor as many components of ecosystems as is feasible, and especially to maintain the continuity of extended time series already established for indicators such as sea lions, kittiwakes, Pacific salmon, and sardines. It is safe to say that commercially important species such as salmon and sardines will be monitored *de facto*, as will charismatic and legally supported species such as Steller sea lions. The contribution that seabird monitoring can make during this crucial time of hypothesis-testing and decision-making is at present limited by access to original data that should be synthesized. Useful approaches will include statistical methods that combine and extract information from multiple, concurrent datasets (e.g. Sydeman et al. 2001, Frederiksen et al. 2007b, Wells et al. 2008). Thus, I would emphasize the need for world seabird professionals to distill and capture all past and future results from seabird monitoring in shared databases designed for the purpose and served on the Internet (e.g. World Seabird Trophic Studies Database, Pacific [World] Seabird Monitoring Database; <http://seabirds.net>).

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